

**First revision of the family *Metarbelidae* Strand, 1909  
(*Lepidoptera*, *Cossoidea* Leach, 1815) and a phylogeny based  
on adult morphology of 60 genera from the  
Afrotropical and Oriental Region**

**Dissertation**

zur Erlangung der Doktorwürde (Dr. rer. nat.) der  
Mathematisch-Naturwissenschaftlichen Fakultät der  
Rheinischen Friedrich-Wilhelms-Universität Bonn

vorgelegt von  
**Ingo Lehmann**  
aus  
Hamburg

Bonn, im März 2019

Angefertigt mit der Genehmigung der  
Mathematisch-Naturwissenschaftlichen Fakultät der  
Rheinischen Friedrich-Wilhelms-Universität Bonn.  
Die Arbeiten wurden in Hamburg sowie am  
Zoologischen Forschungsmuseum Alexander Koenig  
Leibniz Institute for Animal Biodiversity, Bonn,  
durchgeführt.

Erstgutachter: Univ.-Prof. Dr. Johann-Wolfgang Wägele, Bonn

Zweitgutachter: Univ.-Prof. Dr. Eberhard Fischer, Koblenz-Landau

Tag der Mündlichen Doktorprüfung: 19. Juni 2019 in Bonn  
Erscheinungsjahr: 2019

*Gigasiphon macrosiphon* (Harms) Brenan



*To the memory of my grandfather*

**Willi Eduard Haberland** (1922–1982) to whose companionship on many excursions to make observations and collections on Lepidoptera in my childhood I owe so much

*As well as to*

my son **Shimoni** (May 2003 – ) and **all collectors** (1882 – 2017) of the specimens I studied

*my thesis is affectionately and gratefully dedicated*



<b>TABLE OF CONTENTS</b>	<b>Page</b>
<b>1. INTRODUCTION</b>	<b>12</b>
1.1. The Metarbelidae Strand, 1909	
1.2. Present distribution	
1.3. Present distribution ranges and diversity	
<b>2. MATERIAL AND METHODS</b>	<b>15</b>
2.1. Sampling	
2.2. Photographing and genitalia analysis	
2.3. Character polarity and phylogenetic character analysis	
2.4. Phylogenetic analyses for tree construction and ancestral areas	
2.5. Terms and Definitions	
2.5.1. Geographical and geological regions	
2.5.2. Altitude	
2.5.3. Endemism	
2.5.4. Flora	
<b>3. RESULTS IN SYSTEMATICS</b>	<b>23</b>
3.1. Introduction: Notes on the taxonomy of Metarbelidae species, the genus <i>Stenagra</i> , apomorphies of Ratardidae, synapomorphies shared with Dudgeoneidae and plesiomorphies of Metarbelidae	
3.2. Phylogenetic systematics	
3.2.1. Topology, parsimony-informative characters and ancestral areas	
3.2.1.1. Basal Taxa (Two genera: “Basal Group”)	
3.2.1.2. The Afromontane archipelago-like regional centre of endemism and its significance for the evolution of Metarbelidae (24 genera: “Afromontane Group”)	
3.2.1.3. The Somalia-Masai regional centre of endemism and the coastal Lowlands of Eastern and Southern Africa as a link to the Arabian Peninsula (Two genera: “ <i>Salagena</i> -Arabia Group”)	
3.2.1.4. The transition zones and the Somalia-Masai regional centre of endemism: their link to the West Malagasy	

regional centre of endemism (14 genera: “Mali-Zambezia-Somalia-Malagasy Group”)

3.2.1.5. The Afromontane Region, the Guineo-Congolian Region and its transition zones with Metarbelidae evolution via the Arabian Peninsula and Nepal to the Sunda shelf (14 genera: “West Africa-Sunda Group”)

3.2.1.6. Lower Guinea: its link to the Sunda shelf (Two genera: “Lower Guinea-Sunda Group”)

3.2.1.7. Autapomorphies based only on females (Two genera)

#### **4. TAXONOMY**

**44**

The genera – their autapomorphies, description and distribution

- 4.1 *Teragra* Walker, 1855
- 4.2 Gen. Nov.A
- 4.3 *Paralebedella* Strand, 1923
- 4.4 *Haberlandia* Lehmann, 2011
- 4.5 Gen.Nov.B
- 4.6 Gen.Nov.C
- 4.7 Gen.Nov.D
- 4.8 *Lebedodes* Holland, 1893
- 4.9 Gen.Nov.E
- 4.10 Gen.Nov.F
- 4.11 *Kroonia* Lehmann, 2010
- 4.12 Gen.Nov.G
- 4.13 *Saalmulleria* Mabilie, 1891
- 4.14 Gen.Nov.H
- 4.15 Gen.Nov.I
- 4.16 Gen.Nov.J
- 4.17 Gen.Nov.K
- 4.18 Gen.Nov.L
- 4.19 *Salagena* Walker, 1865
- 4.20 Gen.Nov.M
- 4.21 Gen.Nov.O
- 4.22 Gen.Nov.P
- 4.23 Gen.Nov.N
- 4.24 Gen.Nov.Q

- 4.25 Gen.Nov.R
- 4.26 Gen.Nov.S
- 4.27 Gen.Nov.T
- 4.28 Gen.Nov.V
- 4.29 Gen.Nov.U
- 4.30 Gen.Nov.W
- 4.31 Gen.Nov.X
- 4.32 Gen.Nov.Y
- 4.33 Gen.Nov.Z
- 4.34 Gen.Nov.ZA
- 4.35 *Squamura* Heylaerts, 1890
- 4.36 Gen.Nov.ZB
- 4.37 *Shimonia* Lehmann & Rajaei, 2013
- 4.38 *Metarbelodes* Strand, 1909 (subgroup G<sub>2</sub>)
- 4.39 *Mountelgonia* Lehmann, 2013
- 4.40 *Moyencharia* Lehmann, 2013
- 4.41 *Metarbelodes* Strand, 1909 (subgroup G<sub>1</sub> & G<sub>3</sub>)
- 4.42 *Arbelodes* Karsch, 1896
- 4.43 *Bjoernstadia* Lehmann, 2012
- 4.44 Gen.Nov.ZC
- 4.45 *Ortharbela* Aurivillius, 1910
- 4.46 Gen.Nov.ZD
- 4.47 Gen.Nov.ZE
- 4.48 Gen.Nov.ZF
- 4.49 Gen.Nov.ZG
- 4.50 Gen.Nov.ZH
- 4.51 Gen.Nov.ZI
- 4.52 Gen.Nov.ZJ
- 4.53 *Janegoodallia* Lehmann, 2014
- 4.54 *Marshalliana* Aurivillius, 1901
- 4.55 *Metarbela* Holland, 1893
- 4.56 Gen.Nov.ZK
- 4.57 *Dianfosseya* Lehmann, 2014
- 4.58 *Aethiopina* Gaede, 1929
- 4.59 Gen.Nov.ZL
- 4.60 Gen.Nov.ZM

<b>5. ENDEMISM</b>	<b>319</b>
Examples of genera that comprise only endemic species and their distribution	
<b>6. SPECIES OF THE ORIENTAL REGION</b>	<b>322</b>
A present overview of apomorphies, plesiomorphies, symplesiomorphies and one synapomorphy shared with species of the Afrotropical Region	
<b>7. DISCUSSION</b>	<b>324</b>
<b>7.1 The Afrotropical Region</b> Dispersal, the link to geology/geomorphology and vegetation types	
7.1.1 Metarbelidae – sedentary and slow dispersers?	
7.1.1.1 The role of young and ancient coastal forest sites in Kenya	
7.1.1.2 How did Metarbelidae arrive on Madagascar?	
7.1.1.3 The driftwood scenario and the age of Metarbelidae on Madagascar under this scenario	
7.1.1.4 High rates of local extinctions on Madagascar support late arrivers	
7.1.1.5 The wind scenario in regard to Madagascar and in general	
7.1.1.6 How did Metarbelidae arrive on the Comoros Archipelago – a missing link to southeast Laurasia?	
7.1.2 Basal taxa – highest diversities in habitats under long stable geomorphological conditions?	
7.1.2.1 Development of the Southern African Plateau – a major area for species of the “Basal Group” and early lineages of the “Afromontane Group”	
7.1.2.2 Why did Metarbelidae evolve in the Afromontane Region?	
7.1.2.3 The Afromontane Region – the major area for old lineages that occurred in habitats dominated by gymnosperms	

- 7.1.2.4 The Eastern Arc Mountains and their adjacent Lowlands – species of early lineages of the “Afromontane Group” and Guineo-Congolian Region have not yet been found
- 7.1.2.5 Development of the East African Rift System (EARS) – an area of high species diversity
- 7.1.2.6 The “Western Branch” and “Southwestern Branch” of the EARS
- 7.1.2.7 The “Eastern Branch” of the EARS
- 7.1.3 The association of Metarbelidae with legume-dominated lowland tropical forests or woodlands or other legume-dominated tropical woody vegetation types

## **7.2 The Oriental Region**

- 7.2.1 Dispersal patterns, the possible age of the local Metarbelidae fauna and reasons for their low diversity
  - 7.2.1.1 Dispersal of *Squamura* and Gen.Nov.ZB
  - 7.2.1.2 Dispersal of species of genera U, V, X and the possible age of their stem lineage representatives
- 7.2.2 Reasons for a low diversity of Metarbelidae on the Sunda shelf

<b>8. CONSERVATION</b>	<b>349</b>
<b>9. ACKNOWLEDGEMENTS</b>	<b>352</b>
<b>10. REFERENCES</b>	<b>357</b>
<b>11a. SUMMARY</b>	<b>373</b>
<b>11b. ZUSAMMENFASSUNG</b>	<b>375</b>
<b>12a. APPENDIX 12.1</b>	<b>378</b>

*APOMORPHIES OF THE METARBELIDAE IN 60 GENERA COMPRISING 442 SPECIES FROM THE AFROTROPICAL AND ORIENTAL REGION*

<b>12b. APPENDIX 12.2</b>	<b>391</b>
---------------------------	------------

- ❖ *CURRICULUM VITAE*
- ❖ *FIELDWORK IN KENYA FOR PhD STUDIES BASED ON RESEARCH PERMITS (2015-2018)*
- ❖ *RESEARCH VISITS TO NATURAL HISTORY MUSEUMS (2009-2016)*
- ❖ *DESCRIBED AND PUBLISHED NEW GENERA AND NEW SPECIES FROM THE AFROTROPICAL REGION (2010-2014)*
- ❖ *PEER-REVIEWED INTERNATIONAL PUBLICATIONS (2012-2014)*
- ❖ *OTHER PUBLICATIONS FOR THE PhD THESIS (2010-2018)*

“ ... To my taste there is nothing so fascinating as spending a night out in an African forest, or plantation; but I beg you to note I do not advice any one to follow the practice. Nor indeed do I recommend African forest life to any one. Unless you are interested in it and fall under its charm, it is the most awful life in death imaginable. It is like being shut up in a library whose books you cannot read, all the while tormented, terrified, and bored. And if you do fall under its spell, it takes all the colour out of other kinds of living. ...”

Mary Henrietta Kingsley (1897, 102)

# 1. INTRODUCTION

## 1.1 The *Metarbelidae* Strand, 1909

Worldwide 237 species of *Metarbelidae* occur that belong to 27 genera at present. No less than 218 species belonging to 24 genera are recorded from the Afrotropics (De Prins & De Prins 2018; Mey 2018), where this group has only recently received some systematized attention. Lehmann (1997, 2007, 2008, 2009, 2010a, b, 2011, 2012, 2013, 2014; Lehmann & Rajaei 2013, Lehmann *et al.* 2018) discussed the diversity of the family in the Afrotropical Region *sensu* Crosskey & White (1977) and revised nine genera (*cf.* Appendix 12.2) with descriptions of 97 species including 81 species new to science from mainland Africa. Additionally, two manuscripts were recently completed with revisions of the Afrotropical genus *Metarbelodes* Strand, 1909 (Lehmann & Husemann *in prep.*) and on two new genera from Nepal and Indonesia (Oriental Region) (Lehmann *in prep.*). In regard to the Oriental Region *sensu* Wallace (1876), 19 species occur and belong exclusively to the Oriental genera *Squamura* Heylaerts, 1890, *Squamicapilla* Schultze, 1908 and *Indarbela* Fletcher, T.B., 1922.

Wahlberg *et al.* (2013) suggest using molecular methods, based on the Ditrysian phylogeny by Mutanen *et al.* (2010) that *Metarbelidae* originated *ca.* 90 to 100 Ma (= 100 million years ago). In all recent works utilizing either solely wide-scale molecular, or combined molecular and morphological analyses, *Metarbelidae* is placed among *Cossoidea* Leach, 1815 (Regier *et al.* 2009; Mutanen *et al.* 2010; van Nieukerken *et al.* 2011; Heikkilä *et al.* 2015). The most recent classification of Lepidoptera includes seven families in the superfamily *Cossoidea*, namely the *Brachodidae* Agenjo, 1966; *Cossidae* Leach, 1815; *Dudgeoneidae* Berger, 1957 [Berger proposed the new family name *Dudgeonidae*]; *Metarbelidae* Strand, 1909; *Ratardidae* Hampson, 1898 [*cf.* also Dudgeon *et al.* 1901]; *Castniidae* Boisduval, 1828a and *Sesiidae* Boisduval, 1828b (van Nieukerken *et al.* 2011). Within the *Cossoidea* the *Metarbelidae* share several important morphological characters with the phylogenetically older *Cossidae* (Wahlberg *et al.* 2013) as well as with *Ratardidae*, *e.g.* one strong anal vein on the forewing and the deep, 8-shaped ovipositor lobes (*cf.* Holloway 1986; Kobes & Ronkay 1990; Edwards *et al.* 1999; Jeremy Holloway pers. comm. 2013). Heikkilä *et al.* (2015), with the largest morphological data presented to date, and combined with extensive molecular evidence suggest that *Metarbelidae* might be a sister group of *Dudgeoneidae* s. l., and, *e.g.*, *Mehariinae* the closest, more basally arising group thus forming the sister of the clade in which *Dudgeoneidae* + *Metarbelidae* (+ *Ratardidae*) belong. This view is supported here based on two synapomorphies shared between *Metarbelidae* and *Dudgeoneidae* (*cf.* chapter 3.1). Both results are in contrast with Schoorl (1990) who suggested “...The shape of the parapatagia is perhaps a synapomorphy of the *Metarbelidae* and *Cossidae*...”

The adult *Metarbelidae* are night active moths. Males were rarely found by the author hiding among dead litter or wood on the ground during day-time. The forewing

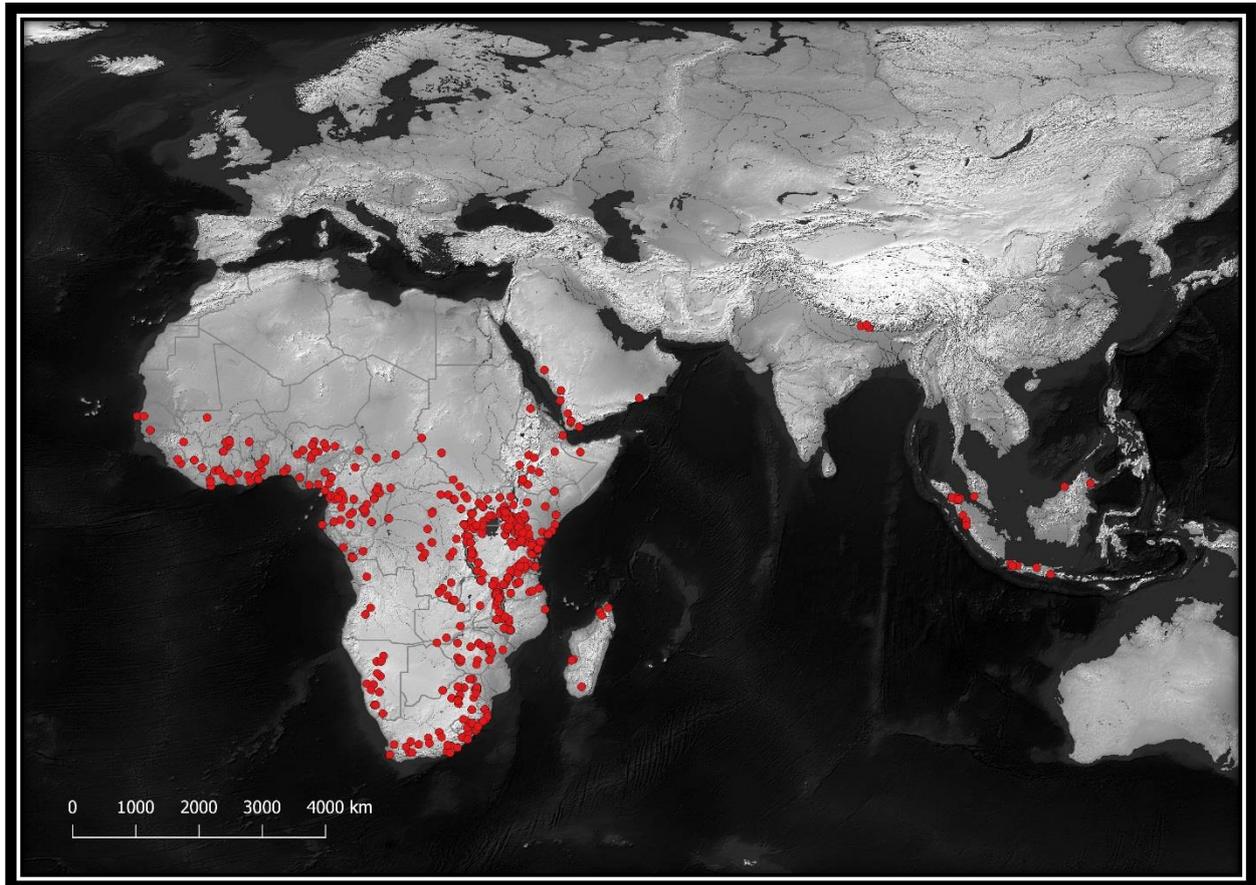
length ranges from 6.1 mm to 33.5 mm; females are often larger than males. However, the females are unknown for many genera. Both sexes can be described in general as follows: Head rugulose, not retracted under the prothorax, rarely very small; antennae bipectinate, unipectinate or filiform in males as well as females. Thorax: forewings usually broad, very rarely narrow; the size of forewing and hindwing rarely of almost equal size, butterfly-like; hindwings usually rounded, rarely triangular in shape; wings usually without a geometric design, a pattern is weak or absent, often reticulate or transversely striated on a pale brown, grey or cream ground-colour; various shades of pink, orange, red, yellow or green are present but rare; transparent parts on wings occur very rarely with or without scales; vein CuA<sub>2</sub> often distinctly coloured pure white or cream on forewing; frenulum and retinaculum occur rarely; chaetosemata and tympanal organs are always absent; epiphysis present or absent; hindleg not dilated, with one or two pairs of spurs; basal stem of vein M in discal cell of both wings very rarely forked; vein CuP in forewing only known at present in basal taxa; one strong anal vein in forewing always present (fused veins 1A+2A), its base rarely very long forked. Abdomen: male genitalia with a variable uncus that might be very broad or very narrow, strongly sclerotized or thinly membranous; gnathos absent or present, relicts of a gnathos sometimes present; valvae large or small, strongly sclerotized or extremely thinly membranous with or without various appendages; sacculus present, reduced or absent; transtilla rarely present, semi-transtilla usually present, sometimes absent. Female genitalia often simple with thinly membranous ductus bursae and corpus bursae, the latter is sometimes very large, usually pear-shaped or oval-shaped, rarely is the ductus bursae sclerotized, very rarely is the base of corpus bursae sclerotized, both are always without any structures; ovipositor 8-shaped in posterior view with few exceptions (*cf.* Gen. Nov. ZD, chapter 4.46), distal lobes are very large or extremely small, usually in vertical position, rarely in horizontal position (viewed laterally) (*cf.* also Lehmann & Rajaei 2013).

Little is known about the immature stages of Metarbelidae. The existing information on eggs, larvae and pupae was summarized by Lehmann (2008). Additional detailed field observations were presented for one species by Jenoh *et al.* (2016). All published observations mention that the larvae are feeding first on and/or under the bark of living trees before boring into the wood of their branches.

## **1.2 Present distribution**

The Metarbelidae occur from mainland Africa (only south of the Sahara), the Comoros Archipelago (Viette 1981) and Madagascar across the southwestern and southern Arabian Peninsula (Afrotropical Region) to the Oriental Region, via Sri Lanka (Matthew Cock & Wade Jenner pers. comm. 2014), India, Bangladesh, Nepal, southern Myanmar, northern Vietnam, southeastern China, Taiwan (Lehmann, *in prep.*), Thailand, Malaysia, Sumatra, Nias, Borneo, Java and the Philippines (Holloway 1986; Lehmann 2009, 2013; De Prins & De Prins 2018). East of Borneo only a single endemic

species occurs on Sulawesi (Holloway 1986). Sulawesi is located east of the Wallace Line (Wallace 1860) and hence, in Wallacea. Since the Metarbelidae occur just east as well as west of the Wallace Line the family extends into the transition zone between Indomalaya and Australasia (*cf.* Figure 1). Several alleged New World *Indarbela* Fletcher (1922) species belong to the Hypoptinae (Edwards *et al.* 1999). The Metarbelidae are absent from South America.



**FIGURE 1:** Distribution of 442 species of studied Metarbelidae in 60 genera (red dots). Metarbelidae that occur in India were not studied; species from Sri Lanka were studied but are not included here. Only few Metarbelidae that occur from southeast China via Thailand to northern Malaysia were studied but are not included here since the research is not yet completed on those species.

### 1.3 Present distribution ranges and diversity

General trends suggest that (i) Metarbelidae are diverse on the African mainland with *ca.* 570 species, many more yet to be discovered (Lehmann, personal observation). (ii) Metarbelidae represent a typical element of the fauna of the Afrotropical Region, but are less diverse on Madagascar, possibly due to large-scale forest destruction (*cf.* Dufils 2003). (iii) Only a minority of Metarbelidae have a large distribution range; a large distribution range is defined as a range that exceeds 50.000 km<sup>2</sup>. Instead, it was found that many areas have endemic or near-endemic, often sedentary, Metarbelidae

species (*cf.* Lehmann *et al.* 2018; Figure 2; Table 1 herein). (iv) The diversity in the Oriental Region is low, and does probably not exceed 50–100 species in less than ten genera. At present, 36 species (including 17 undescribed species) in seven genera (including four undescribed genera; *cf.* descriptions herein) are known.



**FIGURE 2.** The picture shows a riparian forest with leafless trees, *Faidherbia albida* (Delile) A Chev. (Mimosaceae), possibly not older than 60 years. Such stands of *Faidherbia* are cohorts established on alluvium deposited by an exceptional flood, and are confined to the immediate vicinity of significant rivers (Mike Bingham, Lusaka, Zambia, pers. comm. 2016). The size of the African savanna elephant, *Loxodonta africana* (Blumenbach, 1797), shows that this tree species is fast growing since the huge stems are of a relatively young age. Although large leguminous trees occur, the site is most probably not diverse in endemic Metarbelidae due to the young age of the habitat that was once flooded by the Zambezi River *ca.* six decades ago. Mana Pools National Park (Zimbabwe), October 2010, picture by Jürgen Lenz (Leipzig).

## 2. MATERIAL AND METHODS

This thesis provides morphological diagnoses of 60 genera of Metarbelidae, including 20 already published genera. Seven published genera are not included here due to the following reasons:

- (a) *Stenagra* Hampson, 1920 is excluded from the Metarbelidae (*cf.* chapter 3.1).
- (b) The six genera *Melisomimas* Jordan, 1907; *Squamicapilla* Schultze, 1908; *Indarbela* Fletcher, T.B., 1922; *Pecticossus* Gaede, 1929b; *Subarchaeopacha* Dufrane,

1945 and *Dukearbela* Mey, 2018 were not studied since their type species were not found at the time when the author has been working in various museums.

In this context it has to be noted that *Indarbela* is a replacement name for *Arbela* Moore, 1879. Its type species *Arbela tetraonis* occurs only in the Oriental Region. Hence, the Afrotropical species *Arbela tegula* (Distant, 1897), that is usually treated as an Afrotropical representative of *Indarbela*, has been transferred here into a new genus based on its autapomorphy and distribution (*cf.* Gen. Nov. P, chapter 4.22).

## 2.1 Sampling

The 60 genera are based on the author's studies of 442 species of Metarbelidae since 1994 that are a representative sample from the Afrotropical Region as well as from the Oriental Region (with species from Nepal, Sri Lanka, Malaysia, Thailand and the Sunda shelf). The not yet completed work includes a total of *ca.* 570 species in additional 24–30 new genera. Some were not included here to avoid the description of too many monotypic genera and oversplitting, others were not included since the studies are not yet completed.

The examined material is housed in the following collections:

The Natural History Museum, London, U.K. (BMNH); the Natural History Museum, Paris, France (MNHN); Museum Witt, Munich, Germany (MWM); the Natural History Museum, University of Oslo, Norway (NHMO); the National Museums of Kenya, Nairobi, Kenya (NMK); the Natural History Museum of Zimbabwe, Bulawayo (NMZB); the Swedish Natural History Museum, Stockholm, Sweden (NRM); the Royal Museum for Central Africa, Tervuren, Belgium (RMCA); the Naturalis Biodiversity Center, Leiden, The Netherlands (RMNH); the Senckenberg Natural History Museum, Frankfurt am Main, Germany (SMNF); the State Museum of Natural History Stuttgart, Germany (SMNS); the Ditsong (Transvaal) National Museum of Natural History, Pretoria, Republic of South Africa (TMP, formerly TMSA); the Zoological Research Museum Alexander Koenig, Bonn, Germany (ZFMK); the Zoological Museum of the University of Hamburg, Hamburg, Germany (ZMH); the Natural History Museum and Leibniz Institute for Evolution and Biodiversity Research, Berlin (ZMHU, formerly ZMHB); the Zoological Museum of the University of Copenhagen, Copenhagen, Denmark (ZMUC) and the Zoological State Collection, Munich, Germany (ZSM).

Additionally, the following colleagues made available remarkable private Metarbelidae collections: Anders Bjørnstad (Skien, Norway) with species from western Tanzania; Rhett Butler (Harare, Zimbabwe) with species from central Zimbabwe; Matthew Cock (CABI, Egham, Surrey, U.K.), Wade Jenner (CABI, Delémont, Switzerland) presented a species from Sri Lanka; Steve Collins (ABRI) with species from Karen (Nairobi); the late Professor Dr. Lutz Kobes (Göttingen, Germany) gave unique species from Sumatra; Jürgen Lenz (Leipzig, Germany) contributed records from eastern Zambia and Zimbabwe; Raymond James Murphy (Nkhorongo, Mzuzu, Malawi) sent a comprehensive collection from northern, central and southern Malawi;

Raymond John Revell (Cambridge, U.K.) gave species from Namibia; Mike Roberts (Ole Naishu Ranch) presented species from the Lolldaiga Hills and Nairobi; Dirk Stadie (Lutherstadt Eisleben), Ralf Fiebig (Roßleben) sent noteworthy records from Djibouti, Swaziland and the Republic of South Africa; Dr. John E. Rawlins (Carnegie Museum of Natural History, Pittsburgh, U.S.A., CMNH) provided important pictures of types.

The author's collection includes species recorded and/or collected during long-term field research in Kenya (based on various research permits since 1994) around Lodwar, Kitale, Londiani, Embu, Machakos, Kitui and Malindi (1989–1995); on the Athi River-Kapiti Plains (1989–2002); in the Chyulu Hills (1996–1997); in five coastal forests of Kwale District (Kaya Muhaka, Kaya Kinondo, Kaya Diani, Gogoni Forest Reserve, Shimoni Forest) as well as near Mombasa and Ukunda (1994–2008); in Karura Forest, Ololua Forest, at the NMK and at the house of the late Karen Blixen, Nairobi (2015–2017); at Punda Milias Camp, Nakuru (2016); on the Laikipia Plateau at Mpala Research Center (2016–2017); at Naro Moru, Gatuamba and on Mount Kenya (1992–2018) as well as on the Lolldaiga Hills Ranch (2016–2018) (cf. Figure 3).

Localities and depository numbers are given in the following taxonomic chapters.



**FIGURE 3.** “Single-dominant Afromontane forest” sensu White (1983) dominated by the gymnosperm *Juniperus procera* Hochst. (Cupressaceae; height 29–32 m, dbh 108–112 cm, age 270–300 years) and *Olea europaea* L. (Oleaceae, dbh 59 cm with broken stem at 5.6 m, right) on “Kambi ya Simba” at 2.165 m (Lolldaiga Hills Ranch, Kenya). The age of trees suggests that the site is continuously forested for 300 years or more. Two new species of *Metarbelodes* and *Mountelgonia* and two undescribed species of two undescribed genera were recorded in March 2016. This is one of the highest diversities of Metarbelidae for Kenya on 625 m<sup>2</sup>; in contrast, on this site only three woody species occur. No species was recorded in May 2017. This indicates that Metarbelidae are locally seasonal. Metarbelidae diversity was much lower in younger gymnosperm forests nearby. Picture by Ingo Lehmann (Hamburg), March 2016.

## 2.2 Photographing and genitalia analyses

The specimens were photographed and then compared with all available types of described and published Metarbelidae.

The maceration of the abdomen was done as follows: first, it was detached and macerated for one day in a glass tube containing a cold 10% solution of potassium hydroxide. Secondly, the genitalia were removed from the abdomen and drawn (in a lateral view) on a piece of paper, then transferred to distilled water for cleaning and spreading. The preparation of the genitalia was flooded with isopropyl alcohol and remained as such for 30 minutes before being mounted in Euparal. The genitalia slides were photographed using a digital stereo-microscope (ZEISS-SteREO: Discovery.V20); in addition specimens of several taxa examined were studied with a Scanning Electron Microscope (SEM, Hitachi S-2460N), both at ZFMK (Bonn). Pictures of CuP folds on the forewing were taken with a microscope with a fixed camera (Leica M 205 C) at SMNS (Stuttgart). For each species that was studied at least one detailed pencil painting of its venation and genitalia was done for male and/or female as well as a detailed description of the whole studied specimen. The terminology for external characters is based on Janse (1925), Scoble (1995), Edwards *et al.* (1999) and for internal features on Sibatani *et al.* (1954) and Klots (1970). The biogeographical names follow White (1983) and Burgess *et al.* (2004).

## 2.3 Character polarity and phylogenetic character analysis

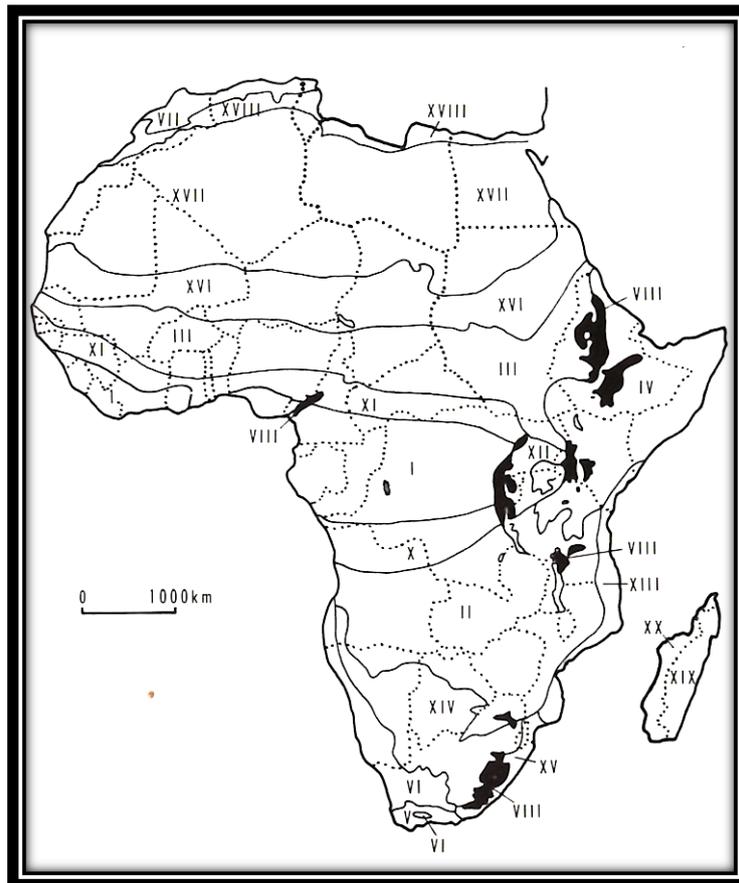
A phylogenetic character analysis was performed with outgroup (Dudgeoneidae) comparison and the ground pattern was reconstructed for every genus to delimit monophyla using the steps described by Wägele (2005). A high probability of homology of a character was estimated when characters are complex based on the “criterion of position”, “criterion on specific quality” and “criterion of continuity”. Variable characters were omitted from the further analysis, if the variations were found to be significant within the same species. The established ground pattern of each genus comprises autapomorphies (evolutionary novelties only present in the ground pattern of one genus) and apomorphies (evolutionary novelties). Each apomorphic character was described in detail. For the cladistic analyses a coding of apomorphic characters was performed to create a binary data matrix in the form of an absence/presence character matrix. The homoplasies that were found were omitted from this data matrix, but are nevertheless mentioned for the family (*cf.* appendix 12.1). Synapomorphies (homologous evolutionary novelties that evolved in the last common stem species of sister taxa) were detected to name the sister taxon for each monophylum (*cf.* description of genera).

## 2.4 Phylogenetic analyses for tree construction and ancestral areas

In order to code data and construct nexus files as input for Paup and MrBayes the NDE version 0.5.0 (Page 2001) was used, a total of 161 binary traits were scored for 60 ingroup taxa at the generic level. Additionally, three species of Dudgeoneidae were used as outgroup. The final dataset was used as input for Paup v.4.ob10 (Swofford 2002) to perform phylogenetic reconstruction using Maximum Parsimony at ZMH (Hamburg). All traits were equally weighted. Branch support was obtained by calculating 1000 bootstrap replicates. Further, MrBayes v. 3.2 (Ronquist *et al.* 2012) was used to generate a second phylogenetic hypothesis using Bayesian Inference. The standard discrete model of evolution was used and ran the analysis for 10 million generations sampling every 1000 generations for a total of 10 000 trees. Convergence was checked using standard split frequencies, as well as effective sample sizes assessed with Tracer v. 1.5 (Rambaut & Drummond 2009). A burn-in of 25 % of sampled trees was discarded before generating a consensus tree. The tree was visualized using FigTree v.1.4.2 (<http://tree.bio.ed.ac.uk/software/figtree/>). To reconstruct trait evolution the 'describe trees' function in Paup was used.

Further, to infer ancestral areas the sDIVA algorithm implemented in RASP (Yu *et al.* 2015) was used. The 10 000 trees from MrBayes were used as input. In a first step a consensus tree was constructed. Then the sDIVA algorithm was used allowing a maximum of two areas per node. The areas were defined mainly *sensu* White (1983, *cf.* Figure 4), for the Sunda shelf and Sahul shelf *sensu* Whitmore (1984) and for Nepal *sensu* Corlett (2014) as follows: A – The Guineo-Congolian regional centre of endemism; B – The Zambezan regional centre of endemism; C – The Sudanian regional centre of endemism; D – The Somalia-Masai regional centre of endemism; E – The Cape regional centre of endemism; F – The Karoo-Namib regional centre of endemism; G – The Afromontane archipelago-like regional centre of endemism; H – The Guinea-Congolia/Zambezia regional transition zone, the Guinea-Congolia/Sudania regional transition zone, the Lake Victoria regional mosaic; I – The Zanzibar-Inhambane regional mosaic and the Tongaland-Pondoland regional mosaic; J – The Kalahari-Highveld regional transition zone; K – The East Malagasy regional centre of endemism, the West Malagasy regional centre of endemism; L – The Arabian Peninsula Afromontane Region; M – the Sunda shelf, Oriental Region, and Sulawesi, Wallacea; N – Australia, the Sahul shelf, Australasian Region; O – Nepal below 4.000 m altitude, Oriental Region.

White (1983) represented a total of 18 phytochoria for the African mainland and two phytochoria for Madagascar (*cf.* Figure 4). Of these 20 phytochoria, 16 phytochoria are represented herein where Metarbelidae occur. The Metarbelidae are, at present, absent from the following four phytochoria: The Sahel regional transition zone (Metarbelidae might occur here); the Sahara regional transition zone; The Mediterranean/Sahara regional transition zone, the Mediterranean regional centre of endemism.



**FIGURE 4:** Main phytochoria of Africa and Madagascar for designations, see text.

I, Guineo-Congolian regional centre of endemism; II, Zambezan regional centre of endemism; III, Sudanian regional centre of endemism; IV, Somalia-Masai regional centre of endemism; V, Cape regional centre of endemism; VI, Karoo-Namib regional centre of endemism; VII, Mediterranean regional centre of endemism; VIII, Afromontane archipelago-like regional centre of endemism, including IX, Afroalpine archipelago-like region of extreme floristic impoverishment (not shown separately); X, Guinea-Congolia/Zambezia regional transition zone; XI, Guinea-Congolia/Sudania regional transition zone; XII, Lake Victoria regional mosaic, XIII, Zanzibar-Inhambane regional mosaic; XIV, Kalahari-Highveld regional transition zone; XV, Tongaland-Pondoland regional mosaic; XVI, Sahel regional transition zone; XVII, Sahara regional transition zone; XVIII, Mediterranean/Sahara regional transition zone; XIX, East Malagasy regional centre of endemism; XX, West Malagasy regional centre of endemism (Source: White 1983).

White's (1983) phytochoria (cf. Figure 4) were choosed to delimit the distribution of Metarbelidae species since his phytochoria are also based on distribution patterns of plants at the species level. His regional mosaics "XIII" and "XV" were put by the author into one area 'I' for the designations of ancestral areas (cf. Figure 6d). The new classification of Clarke (1998) for the "*Swahilian region sensu lato*" and the adjacent "*Swahilian/Maputaland regional transition zone*" to the South, that enlarge, divide and

rename White's (1983) Zanzibar-Inhambane regional mosaic "XIII" was not considered herein to avoid too many terms.

## **2.5 Terms and Definitions**

### **2.5.1 Geographical and geological regions**

"Eastern Africa" as treated here includes the entire areas of Sudan, Ethiopia, Djibouti, Somalia, Kenya and Tanzania based on Sayer *et al.* (1992); Uganda and Eritrea were added by the author.

"Southern Africa" comprises the areas south of the ninth parallel of southern latitude and most of Angola, southeastern Democratic Republic of the Congo, Zambia, Malawi, Mozambique, Namibia, Botswana, Zimbabwe, the Republic of South Africa, Lesotho and Swaziland (Werger 1978).

"West Africa" includes nine countries that are aligned to the coast of the Atlantic Ocean, namely Senegal, The Gambia, Guinea Bissau, Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana and Togo (Poorter *et al.* 2004). The rain forests of this region are separated from Central Africa by the "Dahomey interval".

The Guineo-Congolian Region of West and Central Africa was first recognized as "Région guinéenne" by Lebrun (1947). Monod (1957) renamed Lebrun's area as the "Région guinéo-congolaise", and White (1965) anglicized the term to the "Guineo-Congolian Region". White (1979) presented three "subdivisions": "Upper Guinea" lies in West Africa from Guinea Republic to south-central Ghana ( $14^{\circ}$ - $0^{\circ}$ W;  $11^{\circ}$ - $5^{\circ}$ N), while the other two subdivisions are located in Central Africa, namely "Lower Guinea" from southern Benin to Cabinda and eastwards to the Congo River ( $2^{\circ}$ - $17^{\circ}30'$ E,  $8^{\circ}$ N- $6^{\circ}50'$ S), and "Congolia" from the Congo River in the West to the Kivu centre and the western shore of Lake Victoria in the East ( $17^{\circ}50'$ - $32^{\circ}$ E,  $3^{\circ}$ N- $6^{\circ}$ S). These subdivisions are separated by two areas with few endemic forest species. The first two subdivisions are separated by the savannas of the "Dahomey interval" ( $0^{\circ}3'$ W- $2^{\circ}5'$ E) and the latter two by the "Sangha River interval" ( $14^{\circ}$ - $18^{\circ}$ E) that includes large swamps with areas of swamp forest.

"Geological/geomorphologically stable" is used here for regions where no rifting, uplift or volcanism occurred since *ca.* 65 Ma (= 65 million years ago) based on the cited literature in this thesis.

### **2.5.2 Altitude**

Regarding the altitude of Africa and Madagascar the "Lowlands" are treated here as areas below 600 m based on White (1983). "Montane" areas were defined by Keay (1959) as regions "above 1,300 m" for tropical Africa. All areas between 600-1,300 m are treated here as "submontane" and the same terms are adapted for areas of the western/southern Arabian Peninsula that are part of the Afrotropical Region as figured by Burgess *et al.* (2004). In regard to the Sunda shelf the "Lowlands" comprise areas

below 1.200 m, “submontane” regions are located between 1.200–1.500 m and “montane” areas are above 1.500 m based on Whitmore (1984).

### **2.5.3 Endemism**

If possible, the distinctiveness between genera in regard to the restriction of their species to certain phytochoria and ecoregions was measured by using the terms “strict endemic” and “near-endemic”. Strict endemic species are confined to only one ecoregion as defined by Burgess *et al.* (2004). If all studied species of one genus occur within one ecoregion, and not at the edge of this ecoregion, the genus is treated here as strict endemic. The term “near-endemic” was defined by BirdLife International (Bibby *et al.* 1992) as well as by Burgess *et al.* (2004) as follows: more than 75% of the species’ global range is found only in one ecoregion, or a species has a restricted global range of less than 50.000 km<sup>2</sup> but is found in more than one ecoregion. If all studied species of one genus have ranges smaller than 50.000 km<sup>2</sup> and if the same species of the same genus occur in several ecoregions but only in one of the 18 phytochoria (for Madagascar in both phytochoria) then this genus is treated here as near-endemic in regard to the ecoregions and the phytochorion that is mentioned (*cf.* Table 1).

### **2.5.4 Flora**

A Regional Centre of Endemism as a phytochorion means that more than 50% of its species are confined to it and a total of more than 1000 endemic species occur in it. Such regional centres are always separated by transition zones. They have less than 50% endemic species. A Regional Mosaic forms a complex mosaic of different physiognomic types with different floristic relationships (White 1983, *cf.* Figure 4).

The Leguminosae family assemblage, from the author’s point of view one of the most important links of tropical lowland Metarbelidae to the flora, is divided here into three families, the Papilionaceae, Caesalpiaceae and Mimosaceae following Beentje (1994) (*cf.* Figures 2, 198a, 198b, 200).

### 3. RESULTS IN SYSTEMATICS

**3.1 Introduction** – Notes on taxonomy of Metarbelidae species, the genus *Stenagra*, apomorphies of the family Ratardidae, synapomorphies shared with the family Dudgeoneidae and plesiomorphies of Metarbelidae

The first comprehensive systematic approach on the generic level for the family Metarbelidae with the systematization of 60 genera, the description of their phenotypical diversity and their distribution is presented herein based on the present data. In consequence, the systematics on the species level will change in the future for *ca.* 120 already published species from the African mainland, Madagascar, the Comoros Archipelago and the Arabian Peninsula. A list of those species that have to be transferred into undescribed genera will be presented in future publications (Lehmann *in prep.*). The majority of them were published incorrectly as species of the genera *Teragra* Walker, 1855; *Salagena* Walker, 1865; *Lebedodes* Holland, 1893; *Metarbela* Holland, 1893 and *Aethiopina* Gaede, 1929. One reason for these mistakes was the lack of knowledge based on an incomplete description of the morphology for many species as genitalia structures were often not studied in the past. Additionally, there was no revision on any genus available for the last 81 years until the author began to publish the first two revisions in the year 2010 in the frame of this PhD project. Of these *ca.* 120 species eleven are described herein as type species for an undescribed genus, *e.g.* *diagonalis* (Hampson, 1910); *eustrigata* (Hampson, 1916); *violascens* (Gaede, 1929); *fraterna* (Gaede, 1929) and *willihaberlandi* (Lehmann, 2008). Additionally, some described species not chosen as the type species for a new genus are figured, *e.g.* *simillima* (Hampson, 1910); several of those already published species are figured herein for the first time, including type specimens.

Based on studies of one female of *Stenagra multipunctata* Hampson, 1920 the genus *Stenagra* Hampson is excluded here from the Metarbelidae since it has various characters that are absent in Metarbelidae, *e.g.* head: the short thick branches of the antennae look like a whole sea anemone with long setae (its tentacles) on top; thorax: unusually long legs and two rudimentary anal veins that are stalked in hindwing; abdomen: a very large membrane (almost twice as large as segment 8) with a very small papillae anales occurs. The studied female is from the type region: Northern Nigeria [no locality mentioned], E.C.T. Clouston, 17.February.1915, G.W. [leg.?], B.M. 1921–77, genitalia slide number 05/082007 I. Lehmann, depository in BMNH.

Two species of the extremely rare Ratardidae, one from Sumatra (*Sumatratarda diehli* Kobes & Ronkay, 1990, paratype, male) and one from Thailand (*Ratarda tertia* Strand, 1917, male) were studied for the present analysis. Apomorphies found in both species, like the complete loss of CuP in forewing, the absence of an areole in the forewing, the two-segmented labial palpi and one pair of spurs on the hindleg suggest

that Ratardidae are most probably phylogenetically younger than basal Metarbelidae and also younger than Dudgeoneidae. Ratardidae appear to be more closely related to the Metarbelidae of the Oriental Region as the apomorphies mentioned above suggest (*cf.* chapter 6).

The author's studies of the morphology of three new species of the rare Dudgeoneidae from Kenya, Tanzania and the Republic of South Africa revealed two synapomorphies that are shared with the Metarbelidae: "*CuP absent in forewing of male; (11)*" and "*Two gnathal arms are sclerotized, fused or connected by a more or less long, narrow band ventrally, basally connected to the base of uncus; (18)*"; (*cf.* Appendix 1).

No synapomorphy has been found with the Cossidae based on studies of ten undescribed species from the Ivory Coast, Kenya, Tanzania and Malawi (*cf.* Schoorl 1990).

Based on these morphological results the Metarbelidae are treated here as the sister group of the Dudgeoneidae (*cf.* chapter 1.1 and statements on plesiomorphies below).

The phylogenetic analysis (*cf.* chapter 3.2) is important to understand the dispersal of species groups. The following seven putative plesiomorphic characters (*cf.* below a–g) of Metarbelidae are presented as a basis for the delimitation of clades using apomorphic characters. An apomorphic character is an evolutionary novelty which originated as result of mutations or gene transfer in populations of the stem lineage of a monophylum (a new detail homology), or originated as an evolutionary novelty in a frame-homology (Wägele 2005). The 211 apomorphic characters listed in Appendix 1 do not occur in basal taxa of Metarbelidae. They all originated in populations of the stem lineage.

The state of a frame-homology in the period before an evolutionary novelty occurred is "plesiomorphic". The approach concerning statements whether a character state is more derived or primitive (= plesiomorphic character states) is based on three characters that were described by Holloway (1986) for the older Cossidae (Wahlberg *et al.* 2013), in particular from species of Cossidae of the Oriental Region. These three character states were confirmed for the Cossidae by Roman V. Yakovlev (Altai State University, Russia, pers. comm. 2017). The most ancient or basal Metarbelidae species are those species in which all three plesiomorphic characters (*cf.* below a–c) were found. Those species of Metarbelidae, none of which occur outside the Afrotropical Region (at present not further than 90 km north of the Zambezi River), nor in Madagascar, have always additional four plesiomorphic character states (*cf.* below d–g).

- a) The presence of an areole in the forewing that is small or large (= large is an areole in Metarbelidae when it has at least *ca.* 20% of the size of the upper half of discal cell in the forewing). This is present in many, yet not in all

Metarbelidae. An areole is absent in the studied specimens of Ratardidae, but it is present in all studied Dudgeoneidae and Cossidae.

- b) The presence of a fully developed CuP vein in the forewing. Present in few Metarbelidae but in many, yet not in all Cossidae. The CuP is absent in the studied specimens of Dudgeoneidae (*cf.* statements on the CuP below) and Ratardidae.
- c) The presence of a broader base of the uncus in the male genitalia. The entire uncus is rather broad in all Cossidae while in all Metarbelidae only the base of the uncus is broader. The broader base of the uncus is present in all Cossidae, Metarbelidae, Dudgeoneidae and Ratardidae.

In the present analysis it has been found that only those Metarbelidae species that have all plesiomorphic characters a–c also have additionally always four plesiomorphic character states:

- d) Three-segmented labial palp. These are present in some, yet not in all Cossidae; but absent from the studied specimens of Dudgeoneidae and Ratardidae.
- e) The entire antenna in male is bipectinated. This is present in some, yet not in all Cossidae, absent in the studied Dudgeoneidae, but present in Ratardidae.
- f) Two pairs of spurs on hindleg. These are present in some, yet not in all Cossidae, present in Dudgeoneidae, but absent in Ratardidae.
- g) The whole male genitalia is very simple (= *e.g.*, no structures on the valvae with no tiny setae; no appendices on aedeagus or on juxta; transtilla absent; semi-transtilla reduced) and thinly membranous (including the uncus, tegumen and vinculum) in combination with a small, narrow and thinly membranous gnathos. Only known at present from basal Metarbelidae. It is unknown to the author if this combination of character states might occur in the Cossidae, Dudgeoneidae or Ratardidae. In all male genitalia that were studied or seen by the author character g) was absent in Cossidae, Dudgeoneidae and Ratardidae.

The presence of CuP in the forewing is plastic within the Metarbelidae, yet all species with a fully developed CuP vein occur only close to the Zambezi River (*ca.* 90 km or less to the North) or to the South of the Zambezi River (*cf.* Figure 5) mainly on the Southern African Plateau. They belong to the genus *Teragra* Walker, 1855 and to at least one undescribed genus (*cf.* description of both genera in chapter 4).

As the Dudgeoneidae are treated herein as the sister group of the Metarbelidae based on two synapomorphies (*cf.* chapters 1.1 and 3.1 above) it has to be stated that a continuous, strong tubular-like fold, partly sclerotized, of the CuP vein in the forewing was found, *e.g.* looking similar in *Metarbelodes* species of G<sub>1</sub> and G<sub>2</sub> (*cf.* description of genera). This is an apomorphic character state since it is transitional before a complete loss of the CuP in the forewing is seen. However, the prevailing state of the CuP in Metarbelidae is that a portion of the basal part is present as fold and distal part as fold, rarely are both parts tubular.



**FIGURE 5.** “Escarpment woodland” (Mike Bingham, Lusaka, Zambia, pers. comm. 2016) occurs just north of Mana Pools National Park (Zambia). The tree in the foreground is *Uapaca kirkiana* Müll. Arg. (Euphorbiaceae); a typical species of the local miombo. In the far distant is the Zambezi River (the light line in the centre of the picture). It is one of the two oldest drainage systems on earth and originated *ca.* 280 Ma (Key *et al.* 2015). South and close to the Zambezi River occurs a very rare plesiomorphic character state of the Metarbelidae, namely a fully developed CuP vein in the forewing that is absent elsewhere in the Afrotropical and Oriental Region. Picture by Jürgen Lenz (Leipzig), October 2010.

### 3.2 Phylogenetic systematics

Two hypotheses are presented: the first one on the phylogenetic relationships of 60 groups of species that reflect the natural processes of repeated splitting of populations through irreversible genetic divergence, based on morphological apomorphies and autapomorphies. The dendrogram in Figure 6a represents the rooted topology for these 60 genera as terminal taxa. Rooting was done by adding the outgroup.

The second hypothesis represents the ancestral areas reconstructed with RASP for these terminal taxa, their unknown stem lineage representatives and their ancestors in Figure 6d.

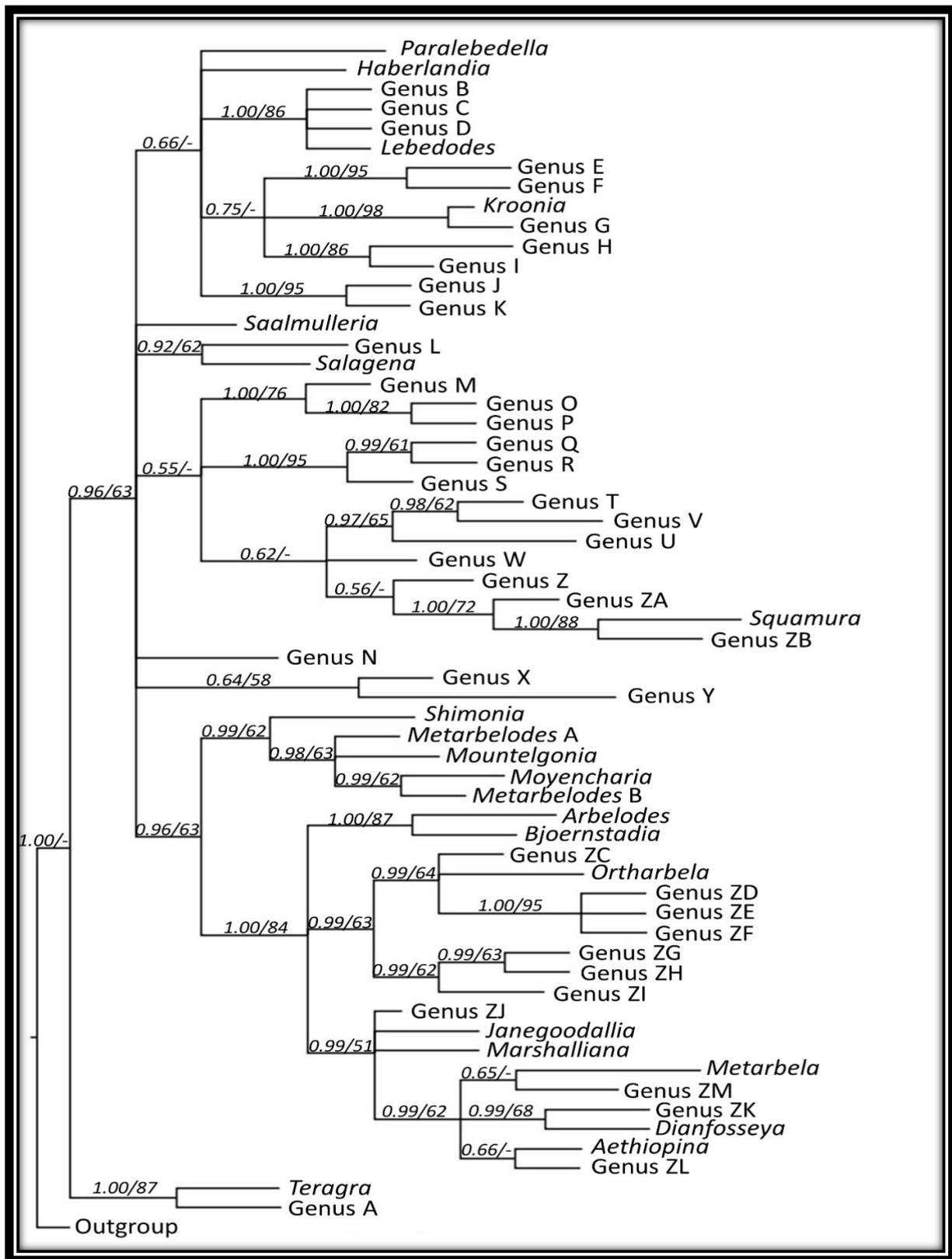
The dataset consisted of 161 apomorphic characters. These characters include 101 variable, but not parsimony-informative characters, and 60 parsimony-informative characters (*cf.* Appendix 1). These 60 characters (all are mentioned in chapter 3.2.1) occur with at least two states per character and each state occurs in more than one terminal taxon. Only such characters produce a splitting, and hence, are informative. The number of 60 parsimony-informative characters means that usually one character exists for each splitting that occurred among the 60 genera and that the probability of a chance similarity (analogy) between species of two genera is rather low (*cf.* Figure 6c).

Phylogenetic reconstruction using Maximum Parsimony (MP) and Bayesian Inference yielded largely consistent results. The MP analysis had relatively low support for most branches although the CI-value: 0.8154 (CI = consistency index), RI-value: 0.8318 (RI = retention index) and HI-value: 0.1846 (HI = homoplasy index) showed relatively high consistency of the data.

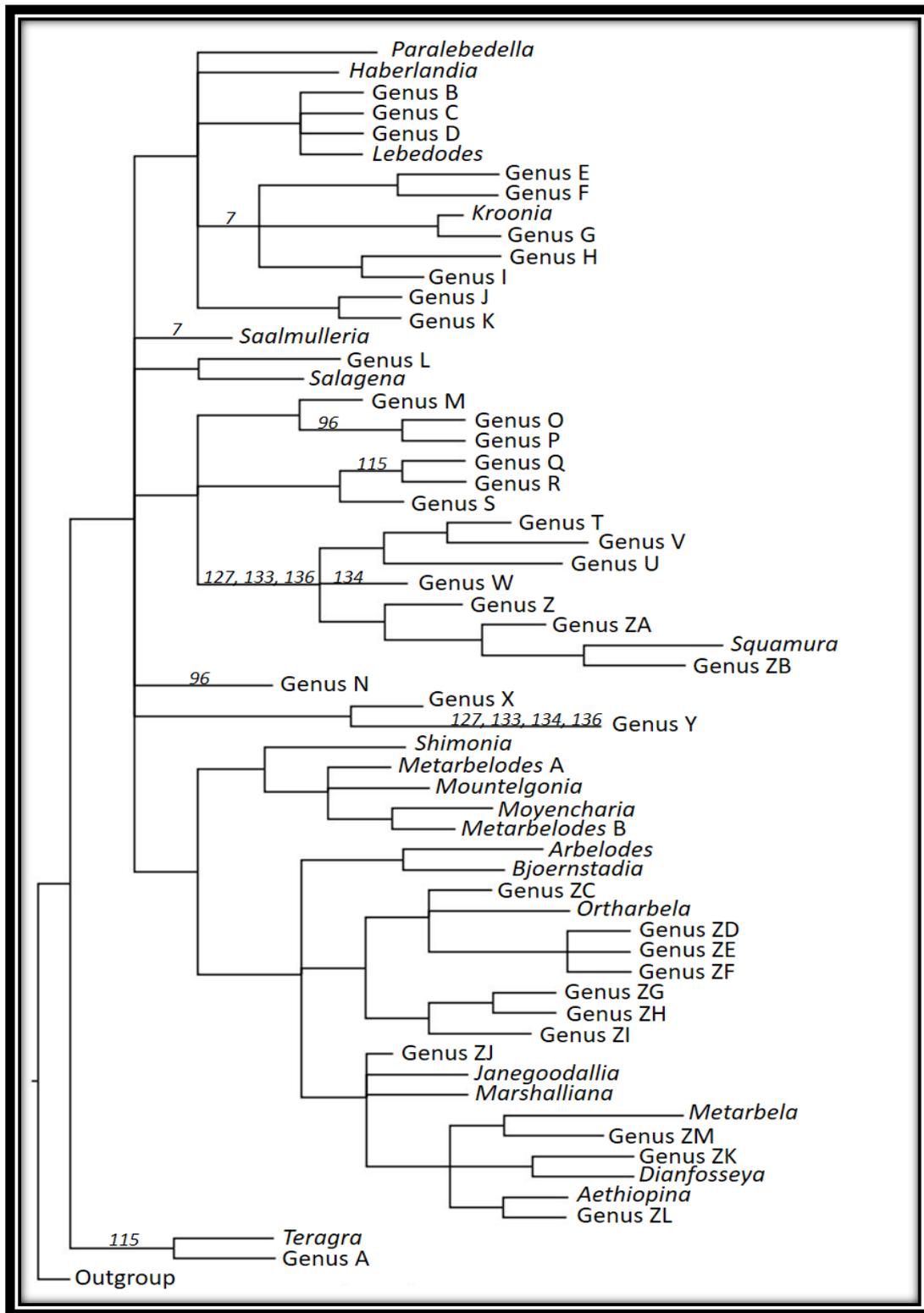
One reason why the MP method found for most branches low support (*cf.* Figure 6a) are homoplasies that occurred in the dataset. Homoplasies are incompatible characters that are distributed in a dendrogram as analogies or convergences (*cf.* Figure 6b). The homoplasy index (HI) is complementary to the consistency index (CI) and is taken to be a measure for the noise present in data caused by homoplasies (Wägele 2005). The HI-value is low herein which is the result of few homoplasies in the dataset found by the Bayesian Inference and MP analysis (*cf.* Figure 6b). These figured homoplasies are not marked as such in Appendix 1 that represents all 211 apomorphies including additionally 50 homoplasies (marked as such in Appendix 1) that were found by the author. The marked homoplasies were excluded from the dataset.

A second reason is the result of the methodological bases of bootstrapping. In this method of branch support pseudosamples (in this case 1000) are taken from the original dataset. As in the present dataset 161 characters are coded (*cf.* Appendix 1) and many of these are (aut-)apomorphic for single lineages, the deletion and replication of bootstrapping will automatically lead to the deletion of apomorphic traits of lineages which then will not be detected in the pseudosample. Therefore, it is not surprising that bootstrap values are much lower than “posterior probabilities (pp)” from Bayesian analyses. By contrast, the phylogeny showed high support for monophyletic Metarbelidae in the Bayesian analysis (pp: 1.00; Bootstrap: no support in MP). The reason is that this analysis injects information already contained in the data based on the observation of how the data behaves when constructing a topology with the aim to improve the previous state of knowledge in the data.

However, every topology represents always a hypothesis (*cf.* Figure 6a).



**FIGURE 6a.** Phylogeny of 60 genera of Metarbelidae using Maximum Parsimony (MP) and Bayesian Inference based on 161 apomorphies (excluding 50 homoplasies identified by the author, *cf.* Appendix 1). The first number for each splitting, *e.g.* 1.00, represents the support in Bayesian analysis, the second number, *e.g.* 87, represents the bootstrapping value for the MP analysis (*cf.* *Teragra*-Genus A).



**FIGURE 6b.** Homoplasies predicted by PAUP found in the dataset of 161 morphological characters examined mapped on the phylogeny described in Figure 6a. The characters which are incompatible with this topology are represented by their character number (*cf.* Appendix 1); *e.g.* character 115 is incompatible since it has been detected for the splitting of *Teragra*-Genus A as well as for the splitting of Genus Q-Genus R.

### 3.2.1 The topology, parsimony-informative characters, ancestral areas

In the following chapters 3.2.1.1–2.2.1.6 the 60 parsimony-informative characters are presented and explained. Each of these 60 apomorphic characters has a number. All 211 apomorphies (including 57 homoplasies, *cf.* Figures 6a, 6b, 6c) are listed with their numbers in Appendix 1.

#### 3.2.1.1 Basal taxa (Two genera: “Basal Group”)

The first split separates *Teragra* and Gen. Nov. A (“Basal Group”) from all other ingroup taxa with highest support in the Bayesian analysis (pp: 1.00; Bootstrap: no support in MP). This clade occurred in an unknown ancestral area and is supported by two parsimony-informative characters: “*Soft, thinly membranous valva without any structures but few tiny setae, all edges are softer and with no setae, the whole valva breaks easily during preparation (123)*” and “*gnathos only thinly membranous and appears soft, not well sclerotized, ventrally fused, (124)*”. Since the rooting of the dendrogram implies a determination of character polarity it can be assumed that these two characters represent earliest evolutionary novelties among the basal Metarbelidae. In general, apomorphic characters result in an increasing number of tiny setae on the valvae and in a stronger sclerotization of the whole male genitalia.

The second split (pp: 0.96; Bootstrap: 63 in MP) creates three large groups of genera with 24, 14 and 14 genera. Two sister-groups comprising four genera; Gen. Nov. N and *Saalmulleria* remain as single genera. These clades occurred in an unknown ancestral area. The split is supported with one parsimony-informative character: “*CuP absent in forewing of male and/or female (11)*”. This result backs the author’s view that a complete loss of the CuP vein in the forewing occurred as an early apomorphy among Metarbelidae since a CuP is absent from all studied species that occur 90 km further to the North from the Zambezi River, including species on Madagascar, the Arabian Peninsula and in the Oriental Region.

In summary, the first and the second split are supported by three parsimony-informative characters (numbers 123, 124, 11).

#### 3.2.1.2 The Afromontane archipelago-like regional centre of endemism and its significance for evolution of Metarbelidae (24 genera: “Afromontane Group”)

This chapter presents those parsimony-informative characters in bold that first originated in species of the Afromontane Region. The remaining parsimony-informative characters that are not in bold originated in species of the Afromontane Region and/or in one other phytochorion, or their area of origin is unknown (*cf.* text; Figure 6d).

A third split with high support for monophyly in the Bayesian analysis (pp: 0.96; Bootstrap: 63 in MP) separates the “Afromontane Group” from the remaining genera and occurred for this clade in the Afromontane archipelago-like regional centre of endemism. This split is supported with one parsimony-informative character: “**More or less large weakly sclerotized, skin-like, transparent projection along the costa and inner distal edge of valva (39)**”. As this character first originated in the Afromontane Region it is linked to the earliest montane Metarbelidae species.

The fourth split in the “Afromontane Group” (pp: 0.99; Bootstrap: 62 in MP) separates the “*Shimonia* Group” (*Shimonia*/*Metarbelodes*G<sub>2</sub>/*Mountelgonia*/*Moyencharia*/*Metarbelodes*G<sub>1</sub>G<sub>3</sub>) from all other 19 genera. This split is supported with the parsimony-informative character: “**The end of each gnathal arm looks like a hand with tiny thorn-like appendices; (41)**”. As the gnathal arms are ventrally fused in basal taxa (cf. number 124 in chapter 3.2.1.1) it is likely that species of *Shimonia* are the oldest in the “*Shimonia* Group” since in the other four genera the gnathal arms are ventrally not fused (cf. number 21 below). Hence, species of *Shimonia* might have been first originated in this group and are possibly linked to ancient plateau areas of the Rwenzori Mountains, the geomorphologically oldest of their present montane distribution ranges (cf. 7.1.2.6). The next split in the “*Shimonia* Group” (pp: 0.98; Bootstrap: 63 in MP) confirms the author’s opinion and separates *Mountelgonia*/*Metarbelodes*G<sub>2</sub> (= *Metarbelodes* A in the dendrogram) and *Moyencharia*/*Metarbelodes*G<sub>1</sub>G<sub>3</sub> (= *Metarbelodes* B in the dendrogram) from *Shimonia*, supported by one parsimony-informative character: “*Gnathal arms not connected ventrally; (21)*”. The ancestral area for this clade could not be reconstructed. The next split in the *Shimonia* Group (pp: 0.99; Bootstrap: 62 in MP) separates *Moyencharia* and *Metarbelodes* B, supported by the parsimony-informative character: “*Well sclerotized thorn-like process(-es) at the posterior margin of valva are hollow inside; (54)*”. The ancestral area for this clade could not be reconstructed but it might be linked to the reconstructed and predicted ancestral areas for the latter two genera (cf. chapter 4) that are the Guinea-Congolia/Zambezia regional transition zone and the Guinea-Congolia/Sudania regional transition zone.

The next split in the “Afromontane Group” separates 19 genera into three groups, namely *Arbelodes*–*Bjoernstadia* (“*Arbelodes* Group”); Gen.Nov.ZC–Gen.Nov.ZI (“*Ortharbela* Group”) and Gen.Nov.ZJ–Gen.Nov.ZL (“Afro-Arabian montane/lowland rain forest Group”). The clade occurred in the Afromontane archipelago-like regional centre of endemism and has very high support for monophyly in the Bayesian analysis as well as in the MP method (pp: 1.00; Bootstrap: 84 in MP) and is backed by two parsimony-informative characters: “**Two tips of uncus stronger sclerotized than remaining uncus, both tips small or strongly reduced but bifurcated and acuminate; (58)**” and “**Gnathos absent; (105)**”. The latter character is often found in species of various genera that occur in lowland areas today but it did first originate in clades of the Afromontane Region.

A further split separates *Arbelodes* and *Bjoernstadia* in an unknown ancestral area with very high support for monophyly (pp: 1.00; Bootstrap: 87 in MP) backed by two parsimony-informative characters: “*Valva consists of two long narrow lobes, sometimes with a small third one between both lobes; (56)*” and “*Discal cell open towards termen in male; (57)*”. Both characters for this clade possibly originated first in the Afromontane archipelago-like regional centre of endemism that is the reconstructed and predicted ancestral area for the “*Arbelodes Group*” (cf. chapter 4).

The next split (pp: 0.99; Bootstrap: 63 in MP) separates the “*Ortharbela Group*” in the Afromontane archipelago-like regional centre of endemism into two groups of five genera (Gen.Nov.ZC–Gen.Nov.ZF, “*Dimbelenge Group*”) and three genera (Gen.Nov.ZG–Gen.Nov.ZI, “*coastal forest Group*”) and is supported by two parsimony-informative characters: “***Valva connected ventrally by a very broad band (as broad as half of width of valva) that is thin and sclerotized; (121)***” and “***Triangular-shaped and narrow bifurcated uncus with acuminate tips; (103)***”. Here appears for the first time the apomorphy that the valvae are connected ventrally, and hence, the valvae are not separated. This band is still thinly sclerotized in contrast to various species of genera that occur in lowland rain forest. It is very likely that this apomorphy originated first in montane areas and later became more developed with a stronger sclerotized band in species of the lowland rain forest.

The next split (pp: 0.99; Bootstrap: 64 in MP) separates the “*Dimbelenge Group*” into the two groups Gen.Nov.ZC/*Ortharbela* and Gen.Nov. ZD/ZE/ZF supported by one parsimony-informative character: “*Valvae not separated, but connected by a broad strongly sclerotized band ventrally; (71)*”. This character appears to be among the earliest apomorphies in species of genera that occur in rain forests of the Guineo-Congolian Region where it is still present in species of various genera. The clade occurred first in the rain forests of Guineo-Congolian regional centre of endemism as well as in the Afromontane archipelago-like regional centre of endemism.

The further splitting of the genera Gen.Nov.ZD/ZE/ZF has very high support for monophyly (pp: 1.00; Bootstrap: 95 in MP) and is supported by three parsimony-informative characters: “*A spoon-like, strongly sclerotized appendice (without a keel line ventrally) is attached to the upper part of a thinly membranous valva; (74)*”; “*Large, hollow, sclerotized rounded appendice on ventral distal side of valva (not an extension of the sacculus, or an extension of the sacculus) is connected to the plate that links both valva; (85)*”; “*Two pairs of spurs to the hindleg but very unequal in length; (88)*”. The ancestral area of this clade could not be reconstructed. Since the reconstructed and predicted ancestral areas for all three genera are the Guineo-Congolian regional centre of endemism, the Guinea-Congolia/Sudania regional transition zone and the Guinea-Congolia/Zambezia regional transition zone it is likely that these apomorphies originated first in species that occurred in the rain forest block and/or in its transition zones, that means mainly in lowland areas and submontane regions.

The next split (pp: 0.99; Bootstrap: 62 in MP) separates the “*coastal forest Group*” into Gen.Nov.ZI and Gen.Nov.ZG/ZH. This clade occurred in the Afromontane

archipelago-like regional centre of endemism, and additionally, in the Zanzibar-Inhambane regional mosaic as well as Tongaland-Pondoland regional mosaic. The split is backed by one parsimony-informative character: “*Valvae not separated, but connected by a narrow strongly sclerotized band ventrally; (70)*”. It is likely that this character occurred first in species inhabiting forests of the Eastern Arc Mountains and/or of the coastal plains of Somalia, Kenya, Tanzania and Mozambique since all present species of these three genera still occur in such forests and because the reconstructed and predicted ancestral areas are the Zanzibar-Inhambane regional mosaic and the Tongaland-Pondoland regional mosaic for the genera ZG/ZH. The next split (pp: 0.99; Bootstrap: 63 in MP) separates the “coastal forest Group” into the genera Gen.Nov.ZG and Gen.Nov.ZH and is supported by one parsimony-informative character: “*The uncus has a large hole dorsally that is larger than 60% of the dorsal surface and is located near the centre of the uncus; (100)*”.

The next split separates nine genera in the “Afro-Arabian montane/lowland rain forest Group” (pp: 0.99; Bootstrap: 51 in MP) into two groups, namely into Gen.Nov.ZJ/*Janegoodallia*/*Marshalliana* (“*Marshalliana Group*”) and *Metarbela*/Gen.Nov.ZM/ZK/*Dianfosseyia*/*Aethiopina*/Gen.Nov.ZL (“*Metarbela-Arabian Group*”). This split is supported by two parsimony-informative characters: “***Areole in forewing long, narrow elongated and M<sub>1</sub>, R<sub>5</sub>, R<sub>3</sub> and R<sub>2</sub> initiating from areole in male; (118)***”; “***Strongly rounded edges of valva; (119)***”. The ancestral area for this clade is the Afromontane archipelago-like regional centre of endemism. Further splitting occurred in the “*Metarbela-Arabian Group*” (pp: 0.99; Bootstrap: 62 in MP) with the result of three pairs of genera: *Metarbela*/Gen.Nov.ZM, Gen.Nov.ZK/*Dianfosseyia* and *Aethiopina*/Gen.Nov.ZL. This split is supported by three parsimony-informative characters: “*Valvae not separated, but almost entirely connected by a broad sclerotized band ventrally; (80)*”; “*Uncus has a tiny hole (< 10%) of its dorsal surface near the centre of uncus; (99)*”; “*Large uncus triangular-shaped and almost as large as valva (ventral view); (177)*”. The ancestral areas for this clade are the Guineo-Congolian regional centre of endemism and the Afromontane archipelago-like regional centre of endemism. Among the further splittings in the “*Metarbela-Arabian Group*” only the split between *Dianfosseyia* and Gen.Nov.ZK has support for monophyly (pp: 0.99; Bootstrap: 68 in MP) and is backed by one parsimony-informative character: “*An oval-shaped projection is present ventral distally that looks like a piece of fur with short setae on a straight surface; (106)*”. The ancestral area of this clade is the Afromontane Region or the Guineo-Congolian Region. As this apomorphic character is more primitive in Gen.Nov.ZK that occurs in montane areas of Djibouti close to the Arabian Peninsula (Afrotropical Region) it is more likely that the clade originated in the Afromontane archipelago-like regional centre of endemism.

Finally, the described splittings among the “Afromontane Group” are supported by 22 different parsimony-informative characters of which eight (in bold) first occur in clades of the Afromontane Region. Among those eight apomorphies, two are noteworthy: the absence of the gnathos and the basal fusion of the valvae. Since both

characters are common in many lowland species, including those of the rain forest block, this might indicate the importance of the Afromontane Region for the early evolution of Metarbelidae from montane via submontane into lowland areas since it is visible that groups of descendants diverged irreversibly from their ancestors along a time axis in physically isolated montane regions and spread into submontane and lowland areas, *e.g.* species of *Shimonia*; Gen.Nov.ZC and *Ortharbela*.

### **3.2.1.3 The Somalia-Masai regional centre of endemism and the coastal Lowlands of Eastern and Southern Africa as a link to the Arabian Peninsula (Two genera: “*Salagena*-Arabia Group”)**

A split with high support for monophyly (pp: 0.92; Bootstrap: 62 in MP) separates the sister-group of Gen.Nov.L and *Salagena* from the remaining 34 genera. This clade occurred in an unknown ancestral area. It is likely that the ancestral area of the “*Salagena*-Arabia Group” is the reconstructed and predicted ancestral area for both genera that are the Somalia-Masai regional centre of endemism, Zanzibar-Inhambane regional mosaic and Tongaland-Pondoland regional mosaic. The split is supported by one parsimony-informative character: “*Uncus strongly elongated, always narrow, only thinly sclerotized, never bifid at tip; (87)*”. In contrast to the large, often heavy sclerotized uncus of many species of Metarbelidae of various genera that occur today mainly in wetter areas, *e.g.* in the rain forests of the Guineo-Congolian Region and/or in its transition zones, or in the Madagascar Dry Deciduous Forests, it becomes obvious that the uncus as described with number 87 originated in species, possibly occurring in drier areas of lowland and submontane areas of Eastern and/or Southern Africa outside of the rain forest block. Both genera are at present rich in species (Gen.Nov.L: 15; *Salagena*: 29) and together, have one of the largest distribution ranges among Metarbelidae on the African mainland outside of Congolia, and including the Aftrotropical Region of the Arabian Peninsula (*cf.* description of genera). Hence, character 87 is still a visible synapomorphy of the African Metarbelidae of both genera to species of Gen.Nov.L of Saudi Arabia, the Republic of Yemen and Oman.

### **3.2.1.4 The transition zones and the Somalia-Masai regional centre of endemism: their link to the West Malagasy regional centre of endemism (14 genera: “Mali-Zambezia-Somalia-Malagsy Group”)**

This chapter presents those parsimony-informative characters in bold that first originated in species of the Guinea-Congolia/Zambezia regional transition zone, the Guinea-Congolia/Sudania regional transition zone and Lake Victoria regional mosaic (for explanation of “transition zone” and “regional mosaic” *cf.* chapter 2.5.4). The remaining parsimony-informative characters that are not in bold originated in species of these transition zones and/or in species of one other phytochorion, or their area of origin is unknown (*cf.* text).

A split with high support for monophyly (pp: 0.96; Bootstrap: 63 in MP) separates a “Mali-Zambezia-Somalia-Malagasy Group” (*Paralebedella*-Gen.Nov.K) from all remaining genera (cf. chapter 3.2.1.1 for character 11). A further split with low support for monophyly (pp: 0.66; Bootstrap: no support in MP) separates these genera into various groups supported by one parsimony-informative character: “***Uncus has a heavy appearance, it is strongly sclerotized with a more or less flat dorsal surface; (44)***”. The group of four genera (Gen.Nov.B-*Lebedodes*, “*Lebedodes* Group”) has high support for monophyly (pp: 1.00; Bootstrap: 86 in MP) but no monophyly was found for the group of *Paralebedella* and *Haberlandia*. The ancestral areas for this clade are the Guinea-Congolia/Zambezia regional transition zone, the Guinea-Congolia/Sudania regional transition zone and the Lake Victoria regional mosaic. The split for the “*Lebedodes* Group” is supported by two parsimony-informative characters: “***R<sub>1</sub>+R<sub>2</sub> on a short stalk (stalk has the length of 30% of R<sub>3</sub>) in male; (8)***”; “***Narrow vinculum (one-third or less of width of aedeagus), no saccus, and very broad tegumen (at least 4 x broader than vinculum); (31)***”. Of particular interest is the last parsimony-informative character as well as the stalked condition of R<sub>1</sub>+R<sub>2</sub> that occur also in further clades, although the stalk has a different length and the uncus a different lateral and ventral shape (cf. in Appendix 1, e.g. characters 6, 7, 8; 190, 191). The evolution of the stalked condition of R<sub>1</sub>+R<sub>2</sub> as well as an heavy uncus (character 44) have most probably first evolved in species of the drier transition zones on the African mainland. A further split has low support for monophyly (pp: 0.75; Bootstrap: no support in MP) and created four groups of sister-taxa with two genera for each sister-group. The ancestral area for this clade is the Somalia-Masai regional centre of endemism. Each sister-group has very high support for monophyly. The first sister-group Gen.Nov.E/Gen.Nov.F (“West Africa-Somalia Group”) has very high support for monophyly (pp: 1.00; Bootstrap: 95 in MP) and is backed by two parsimony-informative characters: “***Gnathal arms well developed and connected by a small, broad and short plate-like (rectangular) structure, namely by a small bulla, ventrally; (19)***”; “***Gnathos large, 40% or 50% of the size of valva, elongated, looking like a wing of a penguin, its rounded end is well above or below the costa of valva; (91)***”; . Of interest is a very large wing-like gnathos that possibly originated in the Somalia-Masai regional centre of endemism. It becomes larger in the second sister-group *Kroonia*/Gen.Nov.G (“Zambezia Group”) that occurs outside of the rain forest block. This supports the author’s view that a very large wing-like gnathos originated not in the rain forest but in drier areas. The “Zambezia Group” has highest support for monophyly (pp: 1.00; Bootstrap: 98 in MP) and is supported by four parsimony-informative characters: “***Gnathal arms extremely long, almost touching upper part of juxta; (22)***”; “***Valva narrow, only twice or less as broad as gnathal arm in lateral view; (28)***”; “***Valva long, almost as long as tegumen+vinculum, tip suddenly very narrow and elongated, tip might be as long as uncus in lateral view, end of tip slightly pointed; (29)***”; “***Posterior apophyses extend as crescent-shaped flap onto the papillae anales; (32)***”.

The third sister-group Gen.Nov.H/Gen.Nov.I (“African east coast-Madagascar Group”) has high support for monophyly (pp: 1.00; Bootstrap: 86 in MP) and is backed by two parsimony-informative characters: “*Gnathal arm represents a strongly sclerotized thorn with a broader base and an acuminate tip and is connected by a band to the base of uncus; the gnathal arms are connected by a narrow band ventrally and end well above the costa of valva; (156)*”; “*Transtillia is very broad (ca. 30% of width of valva); (158)*”. The “African east coast-Madagascar Group” is of interest because species of Gen.Nov.H occur only in Madagascar Dry Deciduous Forests and their sister species in an area on the African mainland where the West Malagasy regional centre of endemism was once attached. For the “African east coast-Madagascar Group” the reconstructed and predicted ancestral areas are the Somalia-Masai regional centre of endemism, the West Malagasy regional centre of endemism and the East Malagasy regional centre of endemism. Characters 156 and 158 occur only in species of both genera and hence, represent the only two synapomorphies that were found in the present analysis shared between species on Madagascar and the African mainland: (cf. *Saalmulleria* where no sister-taxon has been found).

The fourth sister-group Gen.Nov.J/Gen.Nov.K (“Mali-African east coast Group”) has high support for monophyly (pp: 1.00; Bootstrap: 95 in MP) and is supported by three parsimony-informative characters: “*R<sub>1</sub>+R<sub>2</sub> on a very long stalk (stalk has the length of 60-70% of R<sub>3</sub>) in male; (6)*”; “*The whole gnathal arms are not thorn-like but each arm comprises a small thorn-like appendice that is ca. 10% in size of each gnathal arm; (24)*”; “*Uncus strongly thickened ventrally, looking like a strongly sclerotized lunule in lateral view; (25)*”.

Finally, the described splittings in the “Mali-Zambezia-Somalia-Malagasy Group” are supported by 14 different parsimony-informative characters of which three first originated in species of the transition zones, 11 in species of the Somalia-Masai regional centre of endemism, including two characters that occur in species of the eastern African coast and in the West Malagasy regional centre of endemism. This indicates an importance of the Somalia-Masai regional centre of endemism for the evolution of Metarbelidae on Madagascar since it is visible that one group of descendants diverged on Madagascar irreversibly from their ancestors of unknown stem lineage representatives on the African mainland that occurred somewhere in the Somalia-Masai regional centre of endemism, perhaps close to the Tana River.

The importance of the transition zones is that the stalked condition of R<sub>1</sub>+R<sub>2</sub> as well as character number 44 have originated for the first time in species of these zones. It appears that both characters became more pronounced (longer stalk; larger, more strongly sclerotized uncus with heavy appearance) in species that spread into the lowland rain forests, into the Somalia-Masai Region and further east to Madagascar.

No evidence has been found for all 14 parsimony-informative characters that any similar structures evolved in species occurring on the Arabian Peninsula or in the Oriental Region.

### **3.2.1.5 The Afromontane Region, the Guineo-Congolian Region and its transition zones with Metarbelidae evolution via the Arabian Peninsula and Nepal to the Sunda shelf (14 genera: “West Africa-Sunda Group”)**

This chapter presents those parsimony-informative characters in bold that first originated in species that had somehow a contact to species of the Sunda shelf via the Arabian Peninsula/Eritrea or Madagascar/the Comoros Archipelago, respectively. The parsimony-informative characters that are not in bold originated in species of the Afromontane Region and/or Guineo-Congolian Region and/or in species of one other phytochorion, or their area of origin is unknown (*cf.* text).

A split with low support of monophyly (pp: 0.55; Bootstrap: no support in MP) separates a group of six genera into two groups of three genera each (Gen.Nov.M–Gen.Nov.P and Gen.Nov.Q–Gen.Nov.S) and is backed by one parsimony-informative character: “*Uncus strongly elongated, narrow or broad, but only thinly sclerotized, bifid at tip; (86)*”. The ancestral area for this clade is the Afromontane archipelago-like regional centre of endemism and the Guineo-Congolian regional centre of endemism.

The clade of the first three genera (“Nigeria-Zimbabwe Group”) has high support for monophyly (pp: 1.00; Bootstrap: 76 in MP) and is based on two parsimony-informative characters: “*Valva rectangular, 1.5 x taller than its width; (95)*”; “*Gnathos only thinly membranous and appears soft, not well sclerotized, ventrally fused, is very long (ending at half width of valva) and broader at base; (155)*”. The next split in the “Nigeria-Zimbabwe Group” separates Gen.Nov.M from Gen.Nov.O/Gen. Nov.P and is supported by one parsimony-informative character with high support for monophyly from both methods (pp: 1.00; Bootstrap: 82 in MP): “*The valva is rectangular, 1.5 x taller than its width, and has a small sclerotized appendice that looks like a lunule ventral distally;(137)*”. The next split separated Gen.Nov.S from Gen.Nov.Q/Gen.Nov.R (“Southern Africa-Eritrea-Arabian Peninsula Group”). The ancestral areas for this clade are the Afromontane archipelago-like regional centre of endemism and the Guineo-Congolian regional centre of endemism. The clade is backed by three parsimony-informative characters with high support for monophyly from both methods (pp: 1.00; Bootstrap: 95 in MP): “*Whole gnathos thinly membranous, only half width of sacculus, long and stick-like, ventrally connected by a thin membrane that breaks up easily; (97)*”; “*Valvae thinly membranous, basally not connected, with a tiny thorn-like appendice on the ventral side distally; (98)*”; “*Valva rectangular, 1.5 x broader than tall, only thinly membranous; (113)*”. The next split separates the “Eritrea-Arabian Peninsula Group” (Gen.Nov.Q from Gen.Nov.R) and is backed by one parsimony-informative character with high support for monophyly (pp: 0.99; Bootstrap: 61 in MP): “*Male antenna with short, thinly membranous, broad rectangular branches that are not fused at base towards tip; (115a)*”. The latter character of Gen.Nov.Q (species occurs in Eritrea) and Gen.Nov.R (species occurs on the Arabian Peninsula) represents a possible link to the

antennae of the “Basal Group”. Also the thinly membranous structures of the male genitalia might suggest a very ancient contact within the Afromontane Region to basal species of montanous parts of the northeastern Republic of South Africa or southern Malawi, respectively.

The split with low support of monophyly (pp: 0.55; Bootstrap: no support in MP), as mentioned above, that is supported by the parsimony-informative character “*Uncus strongly elongated, narrow or broad, but only thinly sclerotized, bifid at tip; (86)*”, separates also a group of eight genera into two groups, one with three genera (Gen.Nov.T–Gen.Nov.U, “West Africa-Nepal-Sunda Group”) and another one with five genera (Gen.Nov.W–Gen.Nov.ZB, “Ghana-Comoros-Sunda Group”). The ancestral area for the clade of both groups is the Guineo-Congolian regional centre of endemism with low support of monophyly (pp: 0.62; Bootstrap: no support in MP). The split is backed by one parsimony-informative character: “*Two large, hollow, rectangular-shaped appendices on ventral part of valva that are basally connected, are as large as ca. 30–40% of the soft outer surface of one valva; (129)*”. However, the split of the first three genera that separates Gen.Nov.U from Gen.Nov.T/Gen.Nov.V has higher support for monophyly (pp: 0.97; Bootstrap: 65 in MP) and is backed by one parsimony-informative character: “*Entire narrow uncus is longer or equal to basal width of valva and has a tip that represents a broad “V”; (151)*”. A further split in the “West Africa-Nepal-Sunda Group” separates Gen.Nov.T and Gen.Nov.V and has high support of monophyly (pp: 0.98; Bootstrap: 62 in MP). The clade is backed by one parsimony-informative character: “***Uncus and tegumen very long, namely ca. 2.3 x longer than basal width of valva; (183)***”. The latter character connects species from the African mainland with one species from the Sunda shelf. As the clade has the ancestral area in the Guineo-Congolian Region it indicates that the ancestors of the species on the Sunda shelf that belong to the “West Africa-Nepal-Sunda Group” originated first in rain forest of West and/or Central Africa.

The split that separates the “Ghana-Comoros-Sunda Group” separates Gen. Nov.W from the remaining four genera with low support of monophyly (pp: 0.62; Bootstrap: no support in MP) and is backed by the same parsimony-informative character as mentioned above (character 129). The next split that separates Gen.Nov.Z from Gen.Nov.ZA/*Squamura*/Gen.Nov.ZB has low support for monophyly (pp: 0.56; Bootstrap: no support in MP) and is backed by one parsimony-informative character: “*Two large, hollow, triangular-shaped appendices on ventral part of valva, that are basally connected, are as large as ca. 35% of the soft outer surface of one valva; (130)*”. The split of Gen.Nov.ZA from *Squamura*/Gen.Nov.ZB has high support for monophyly (pp: 1.00; Bootstrap: 72 in MP). It is backed by one parsimony-informative character: “***Large, ear-shaped valva with many soft and very long straight setae (not bent) on inner surface of valva and one patch of strongly sclerotized long straight setae near the base where usually a small relict of semi-transtilla occurs but the latter is entirely absent; (149)***”. This split separates species in Gen.Nov.ZA that occur on the African mainland and on the Comoros Archipelago from species that occur on

the Sunda shelf. The reconstructed and predicted ancestral areas for Gen.Nov.ZA are the Guinea-Congolia/Zambezia regional transition zone, the Guinea-Congolia/Sudania regional transition zone and the Sunda shelf/Sulawesi. As the ancestral area of the clade is the Guineo-Congolian regional centre of endemism it is likely that the ancestors of species of the genera *Squamura*/Gen.Nov.ZB occurred in rain forests of the Guineo-Congolian Region and/or in rain forest patches of its transition zones. The final split in the “Ghana-Comoros-Sunda Group” separates *Squamura* from Gen.Nov.ZB with high support of monophyly (pp: 1.00; Bootstrap: 0.88 in MP) and is backed by one parsimony-informative character: “*Both, ductus bursae and corpus bursae strongly reduced and small; (141)*”.

Finally, the splittings in the “West Africa-Sunda Group” are supported by 14 different parsimony-informative characters that evolved in the Afromontane Region and/or Guineo-Congolian Region and/or in its transition zones. The parsimony-informative characters (183, 149), that occur in species of the “West Africa-Nepal-Sunda Group” and in species of the “Ghana-Comoros-Sunda Group” represent a possible ancient link from the Sunda shelf to species of the rain forests and/or its transition zones of West and Central Africa since the reconstructed and predicted ancestral areas are the Guinea-Congolia/Sudania regional transition zone, the Guinea-Congolia/Zambezia regional transition zone and the Sunda shelf/Sulawesi. From the author’s point of view show these results that the ancestors of the “West Africa-Nepal-Sunda Group” and “Ghana-Comoros-Sunda Group” originated somewhere in the rain forests and/or in its transition zones in West and/or Central Africa while their ancestors originated somewhere in the Afromontane Region and/or Guineo-Congolian Region as one parsimony-informative character suggest (86).

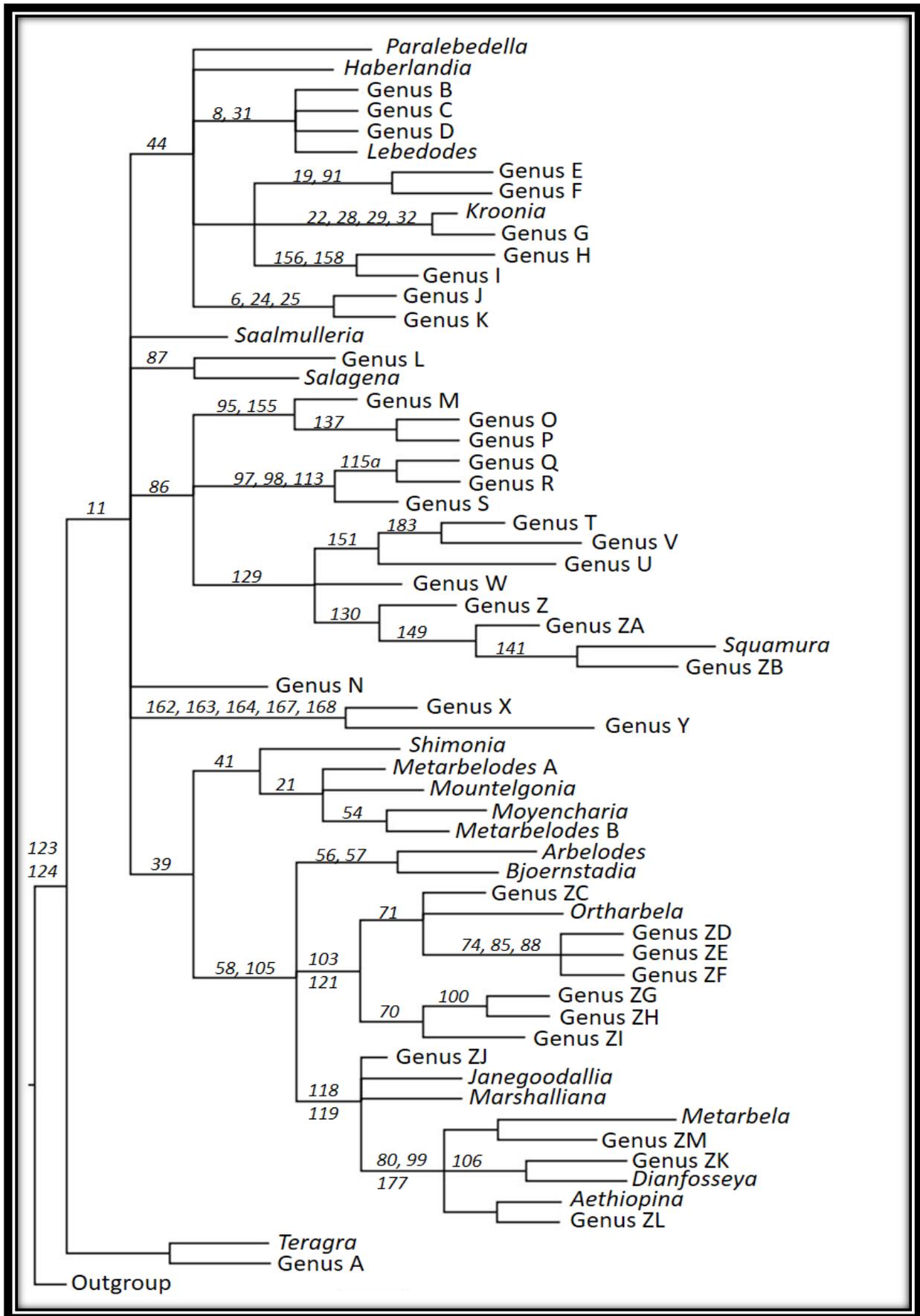
### **3.2.1.6 Lower Guinea: its link to the Sunda shelf (Two genera: “Lower Guinea-Sunda Group”)**

A split with medium high support for monophyly (pp: 0.64; Bootstrap: 58 in MP) separates Gen.Nov.X and Gen.Nov.Y. Both genera were formed because their species have very different autapomorphies. The ancestral area for the clade is unknown. The split is backed by five parsimony-informative characters: “*Very long, pure white, hair-like scales, not or only slightly curled, have an upright position on upperside of forewing well above the normal scale-layer; (162)*”; “*Very rare forewing pattern in both sexes where a broad grey band extends from termen into the discal cell in between  $M_2$  and  $M_1$  or  $M_2$  and  $R_5$  as well as a broad white or light cream band extends from  $R_5$  to costal margin and to  $R_i$ ;  $CuA_2$  is not distinctly marked in this pattern; (163)*”; “*Corpus bursae not sclerotized, small, only one-third the size of segment 8; (164)*”; “*Posterior apophyses at base V-shaped, but “V” strongly unequal in length and with thorn-like end, somehow fork-like; (167)*”; “*Anterior apophyses narrow and short, length less than width of segment 8 (including the ventral plate), near base very broad with a small rounded hole at centre; (168)*”. First, of particular interest is character 164 since it occurs in two species of Gen.Nov.X on the Sunda shelf while in all other studied species from the

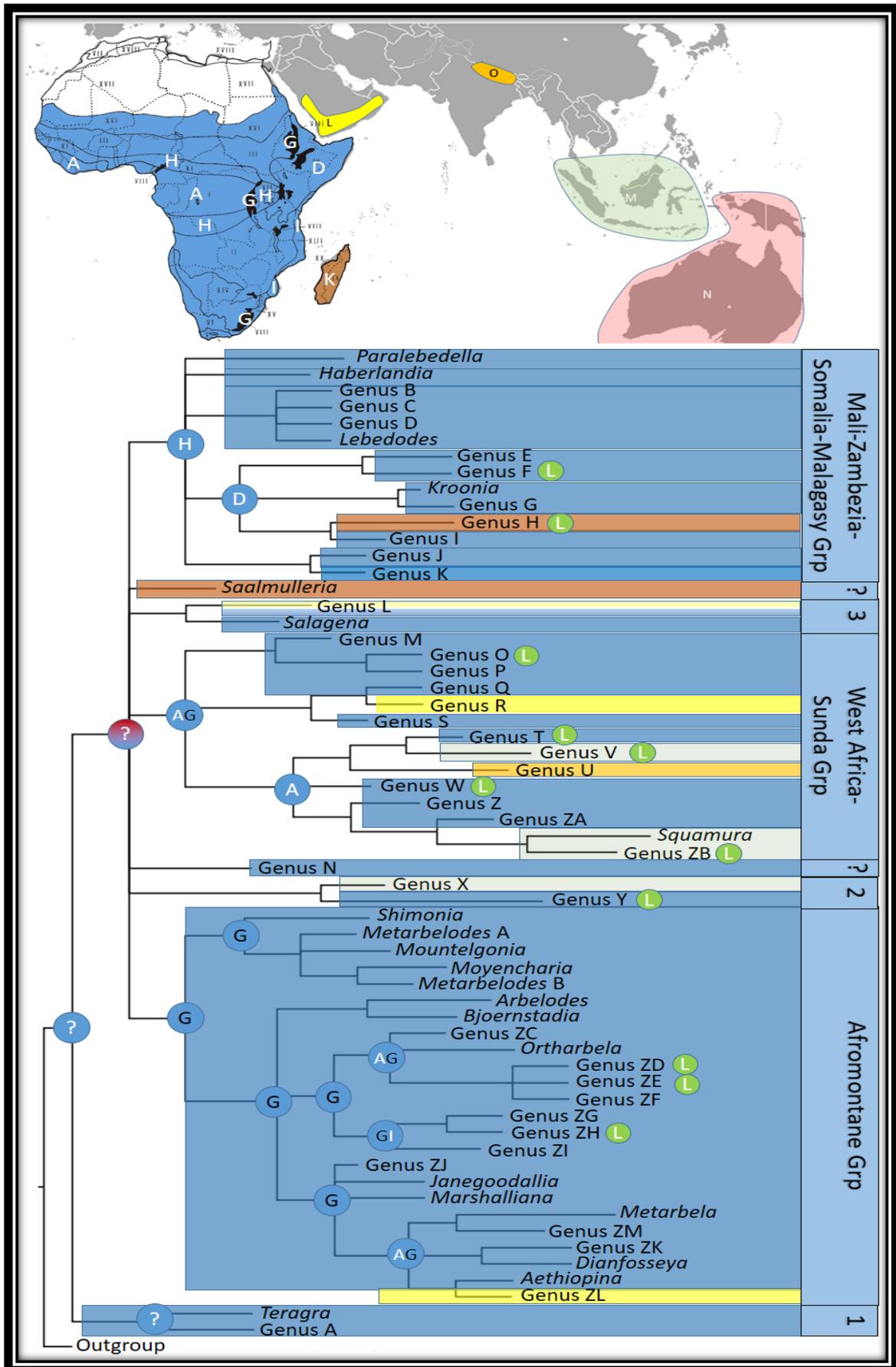
Oriental Region the corpus bursae is sclerotized or in part sclerotized. This is evidence that ancestors of Gen.Nov.X occurred on the African mainland. Characters 162 and 163 are known from no other species and represent a unique link between species of Lower Guinea to species of the Sunda shelf.

### **3.2.1.7 Autapomorphies based only on females (Two genera)**

The phylogeny for species of *Saalmulleria* and Gen.Nov.N remains unresolved. One reason for this problem is that autapomorphies of both genera are exclusively based on females with unique postabdominal structures unknown in other species, combined with the fact, that females are not known for many genera described herein. The author's observation on museum specimens is that among many genera the females are extremely rare or unknown. This observation is supported through long-term field experience: For example, many males of one species of Gen.Nov.ZG were found during 14 years of research with hundreds of light-trappings (using two different lamps) and bait-trappings (using different baits) during different months but a female of this group was never seen in five coastal forests (*cf.* Lehmann & Kioko 2005).



**FIGURE 6c.** Parsimony-informative characters (N=60) mapped on the phylogeny of Metarbelidae (Figure 6a).



**FIGURE 6d.** Ancestral areas of Metarbelidae using the sDIVA algorithm implemented in RASP. Geographic distribution areas are colour-coded (cf. text below for explanations).

**Figure 6d** shows the five ancestral areas A, D, H, I and G (**Lavender Blue**) that are all located on the African mainland (*cf.* phytochoria in Figure 4). In the dendrogram below the map ancestral areas are shown with the same colour and letter coded at the terminals and nodes (*e.g.* “Mali-Zambezia-Somalia-Malagasy Grp” (‘Grp’ = Group) (*cf.* chapter 3.2.1.4), “West Africa-Sunda Group” (*cf.* chapter 3.2.1.5) as well as in the “Afromontane Group” (*cf.* chapter 3.2.1.2). Nodes with question marks represent unknown ancestral distributions. In this context the “Basal Group” is marked with number “1”; the “Lower Guinea-Sunda Group” with number “2” and the “*Salagena*-Arabia Group” with number “3” (*cf.* chapters 3.2.1.1; 3.2.1.3; 3.2.1.6). Since the two genera *Saalmulleria* and Genus N do not belong to any group they have a black question mark (*cf.* chapter 3.2.1.7).

The reconstructed ancestral areas comprise: **A=I**, the Guineo-Congolian regional centre of endemism; **D=IV**, the Somalia-Masai regional centre of endemism; **H=X**, the Guinea-Congolia/Zambezia regional transition zone, **XI**, the Guinea-Congolia/Sudania regional transition zone, **XII**, the Lake Victoria regional mosaic; **I=XIII**, the Zanzibar-Inhambane regional mosaic, **XV**, the Tongaland-Pondoland regional mosaic.

**Black** areas in the map represent **G = VIII**, the Afromontane archipelago-like regional centre of endemism. All areas where Metarbelidae occur on the African mainland are coloured in the map in **Lavender Blue**, including the Sahel regional transition zone, where they might be recorded in the future. Further color coding: Madagascar (**Walnut Brown**) is marked with **K** that comprises **XIX**, The East Malagasy regional centre of endemism, and **XX**, The West Malagasy regional centre of endemism. The Arabian Peninsula (**Lemon Yellow**) is marked with **L** and comprises montane, submontane and lowland areas of the Afrotropical Region. Nepal (**Apricot Yellow**) is marked with **O** and includes areas below an altitude of 4.000 m in the Oriental Region. The Sunda shelf and Sulawesi (Wallacea) are marked with **M** (**Water Green**). Areas marked with **N** (**Pale Persian Lilac**) represent regions where no Metarbelidae occur, but comprise additional areas of the distribution range of species in the outgroup that occur also in Australia as well as on the Sahul shelf that runs north of Australia, around New Guinea and the offshore islands.

The **Apple Green** oval-shaped spot with an **L** inside and at the end of some genera in the dendrogram indicates those genera that comprise only species occurring in lowland areas (*cf.* definitions).

## 4. TAXONOMY

The genera – their autapomorphies, description and distribution

### 4.1 *Teragra* Walker, 1855

The genus is defined by the following autapomorphies:

- Gnathos only thinly membranous and appears soft, not well sclerotized, ventrally fused, it is short (ending well above costa of valva) and broad (40–50% of width of valva); (125).

Additionally diagnostic characters of the genus are:

- CuP present in forewing of male [most probably also in female];
- Male antenna with short, thinly membranous, broad rectangular branches (115), and these branches are fused at base for one-third of the branch length for the last *ca.* 25% of the antenna length (hence, the antenna becomes more and more unipectinated towards tip); (115b), [115b is preliminary and was not included in dataset since more males have been studied];
- Soft, thinly membranous valva without any structures but few tiny and longer setae, all edges are softer and with no setae, the whole valva breaks easily during preparation; (123);
- Gnathos only thinly membranous and appears soft, not well sclerotized, ventrally fused; (124).

Type species of genus: *Teragra conspersa* Walker, 1855

Type locality: [Republic of] South Africa, Port Natal [Durban, KwaZulu-Natal].

Studied specimens (*cf.* Figures 8, 9): S. Afr. [Republic of South Africa], E. Tvl. [East Transvaal] Blyde River Canyon, 26.–27.11.1991, [Dr.] M. Krüger leg., ex TMSA, male, genitalia slide number 21/102017 I. Lehmann; depository in TMSA; [Republic of] South Africa, KwaZulu-Natal, Umlalazi Nature Reserve, Munzini Forest, 20 m, 01.–03.11.2015, Fiebig, Schellhorn & Stadie leg., ex coll. D. Stadie, male, genitalia slide number 03/092017 I. Lehmann; depository in ZSM.

Number of species in genus at present: 02

All localities of studied species per country: Republic of South Africa.

Distribution of genus at present (*cf.* Figure 7): lowland, submontane and montane areas in the eastern Republic of South Africa.

The ancestral area could not be reconstructed with RASP.

Phylogenetic position: Basal taxon. The sister genus could not be reconstructed unambiguously.

Description: *Head:* Rough-scaled; medium long hair-like scales of vinaceous grey on fronto-clypeus; a pair of small pits present on lower fronto-clypeus, but a pair of small conical projections absent on lower fronto-clypeus in male; pits behind the labial palpi

very small and oval-shaped; the labial palpi long, almost as long as eye diameter, very rarely longer than eye diameter, and consist of three segments, the central segment is slightly longer than basal segment and broadest at base, the segment at tip is the shortest and has half times the length of the basal segment; male antennae bipectinated, with short, thinly membranous, broad rectangular branches that are fused at base for one-third of the branch length for the last *ca.* 25% of the antenna length (hence, the antenna becomes more and more unipectinated towards tip); dorsal and lateral side of branches not scaled but covered with tiny setae; flagellum scaled grey.

*Thorax:* Densely covered with broader, not hair-like scales, and with a pale brown collar ring; tegulae somehow pronounced; with a short crest on metathorax. Epiphyses are absent. Hindlegs with two pairs of narrow tibial spurs of almost equal length (the inner spur is only slightly shorter); pretarsus with a pair of pulvilli.

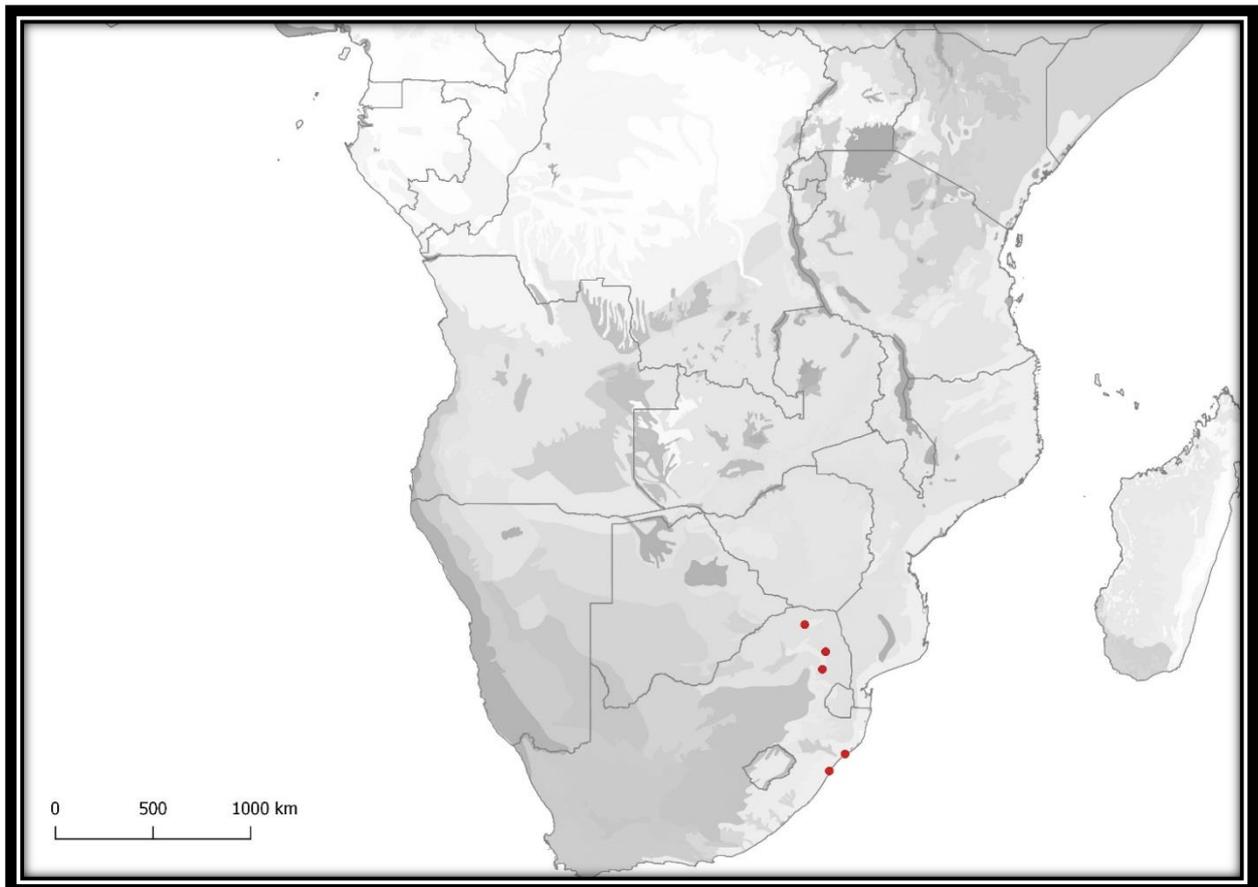
Forewing upperside without a geometric design as well as without any simple pattern, except of brown striae towards termen; a glint shine is present. Fringe hair-like and short (ciliae shorter than 0.8 mm). Wing venation: in forewing 1A+2A long forked at base, sometimes very long forked; CuP present from base of wing to the dorsum in male (most probably also in female) – an extremely rare character state among the Metarbelidae; CuA<sub>2</sub> originating from hind margin of posterior cell; CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> separated and initiating from apical angle of posterior cell; M<sub>1</sub> initiating from distal margin of median cell; R<sub>1</sub> initiating from anterior margin of median cell; R<sub>2</sub> initiating from anterior angle of a small areole (areole sometimes strongly reduced); R<sub>3</sub>+R<sub>4</sub>+R<sub>5</sub> long stalked and initiating from or close to posterior angle of areole; Sc more or less parallel to R<sub>1</sub>. In hindwing 3A present; 1A+2A long forked at base, sometimes obsolete towards termen; CuP present; CuA<sub>2</sub> initiating from hind margin of posterior cell; CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> initiating from apical angle of posterior cell, separated; M<sub>1</sub> and R<sub>s</sub> initiating from apical angle of anterior cell, widely separated; without a bar from R<sub>s</sub> to Sc+R<sub>1</sub>; with a small vein in discocellular cell on both forewing and hindwing, sometimes forked in forewing near hind margin of cell. Retinaculum and frenulum absent.

*Abdomen:* With dense hair-like scales and short abdominal tuft, never longer than one-fourth of abdomen length.

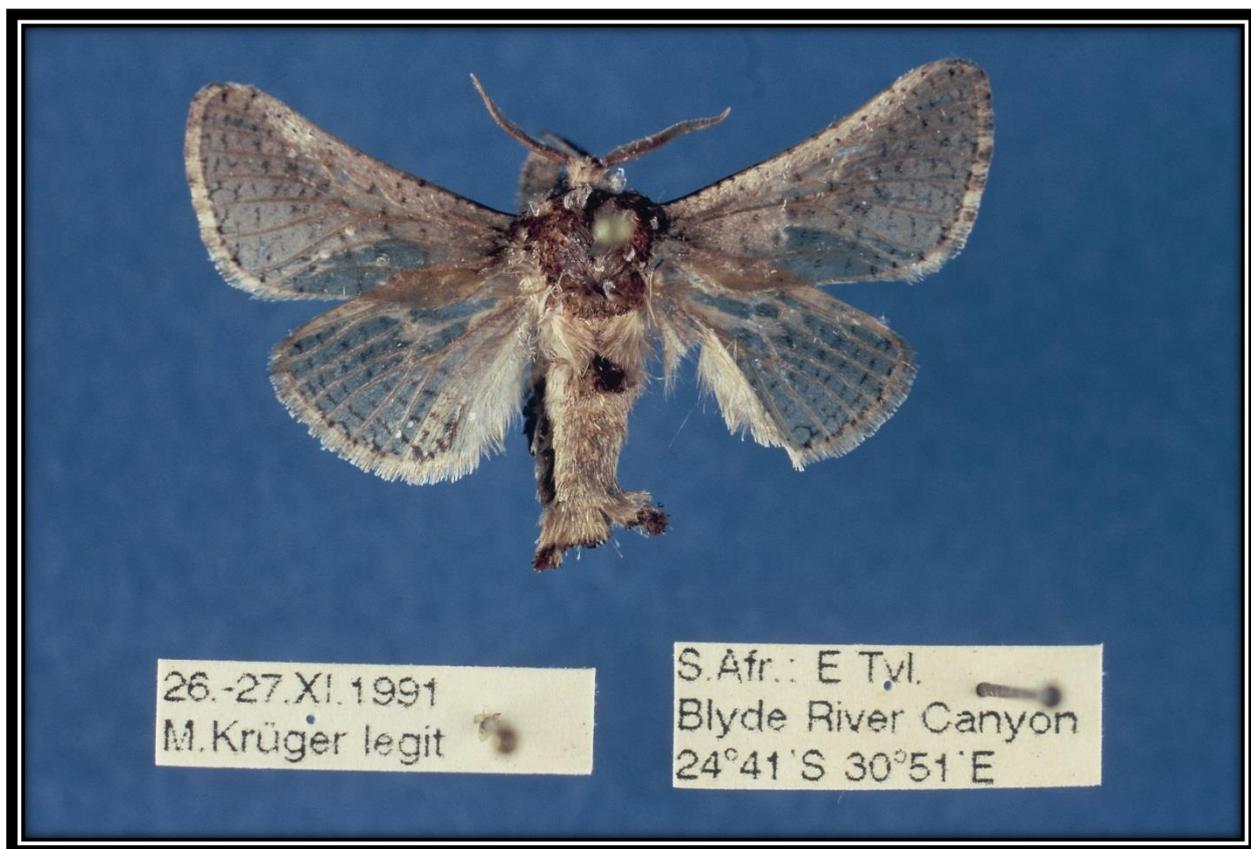
*Male genitalia.* Saccus short but broad triangular, smaller than juxta, acuminate at tip; the vinculum and tegumen are fused, forming a firm and narrow ring, lower half of vinculum not broader; uncus rather short and narrow, not bifurcated at tip and bent near base in lateral view. Valva soft, thinly membranous and without any structures but have few short and long setae near centre of valva distally, all edges are softer and with no setae, the whole valva breaks easily during preparation; a broad and short semi-transtilla (attached to the costa of valva and opposite of the vinculum) is present, it has no setae but a longer narrow structure. Sacculus pronounced but only present on 40% of length of valva near its base. Gnathos only thinly membranous and appears soft, not well sclerotized, ventrally fused, it is short (ending well above costa of valva)

and broad (40–50% of width of valva). Juxta broad and simple, band-like, larger than sacculus without any processes. Phallus simple, tube-like, short and broad (in length only slightly longer than length of valva), straight; vesica without cornuti.

*Female postabdominal structure and genitalia.* Unknown.



**FIGURE 7.** Distribution of the basal taxon genus *Teragra* (red dots).



**FIGURE 8.** Basal taxon, *Teragra conspersa*, S. Afr. [Republic of South Africa], E. Tvl. [East Transvaal], Blyde River Canyon, 26.-27.11.1991, [Dr.] M. Krüger leg., ex TMSA, male, genitalia slide number 21/102017 I. Lehmann. Wingspan 32.5 mm



**FIGURE 9.** Basal taxon, *Teragra conspersa*, [Republic of] South Africa, Umlalazi Nature Reserve, Munzini Forest, 01.-03.11.2015, Fiebig, Schellhorn & Stadie leg., ex coll. D. Stadie, male, genitalia slide number 03/092017 I. Lehmann. Wingspan 33.0 mm

## 4.2 Gen.Nov.A

The genus is defined by the following autapomorphies:

- Male antenna with short, thick (well sclerotized), broad rectangular branches that are not fused at base towards tip; (114);
- Gnathos only thinly membranous and appears soft, not well sclerotized, ventrally fused, it is long (ending below costa of valva) and narrow (20% of width of valva) on its whole length; (126).

Additionally one diagnostic character of the genus is:

- CuP present in forewing of both sexes.

Type species of genus (cf. Figure 11): Gen.Nov. A + sp. nov. a

Type locality: [Republic of] South Africa, Mpumalanga, Blyde River Canyon, 2.2 km west of forest station Mariep's Kop, 1.000 m, 24°35'S 30°50'E, 26.11.2008, D. Bartsch leg., ex SMNS Lep. 2008-05, male, genitalia slide number 27/082017 I. Lehmann; depository in SMNS.

Number of species in genus at present: 04

All localities of studied species per country: Malawi; Republic of South Africa.

Distribution of genus at present (cf. Figure 10): disjunct, submontane and montane areas in the eastern Republic of South Africa and on the plateau area of Mount Mulanje (at present only known from the Lichenya Plateau) in southern Malawi ca. 90 km north of the Zambezi River.

The ancestral area could not be reconstructed with RASP.

Phylogenetic position: Basal taxon. The sister genus could not be reconstructed unambiguously.

Description: *Head:* Rough-scaled; medium long hair-like scales of white and black on fronto-clypeus; a pair of very small pits present on lower fronto-clypeus, a pair of small conical projections present on lower fronto-clypeus in both sexes; pits behind the labial palpi very small and oval-shaped; the labial palpi long, almost as long as eye diameter and consist of three segments, the segments are of almost equal length (the third segment on top strongly reduced in female); male antennae bipectinated with short (2× width of shaft), thick (well sclerotized), broad rectangular branches of equal width from base to tip; female antennae unipectinated, branches shorter than in male; dorsal and lateral side of branches not scaled but covered with tiny setae in both sexes; flagellum scaled cream in both sexes.

*Thorax:* Densely covered with broader, not hair-like scales, mainly white and sepia or black with a reduced dark grey collar ring, glossy; tegulae somehow pronounced; with a short crest on metathorax. Epiphyses are absent. Hindlegs with

two pairs of narrow tibial spurs of almost equal length (the inner spur is only slightly shorter) with a thorn-like tip; pretarsus with a pair of pulvilli.

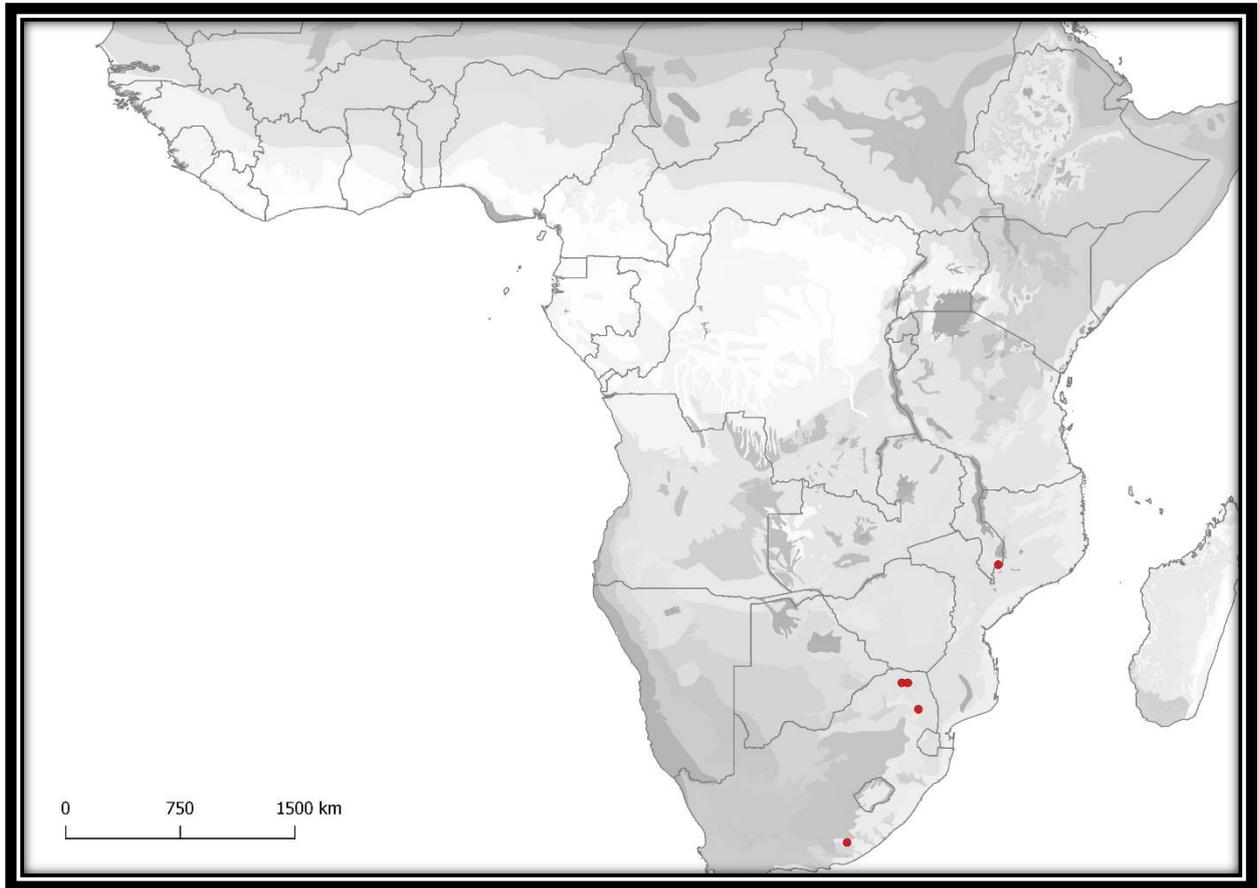
Forewing upperside without a geometric design but with a simple pattern comprising a broad sepia distal band from near costal margin to dorsum with a horizontal patch in the centre of this band in male (in female this band is strongly reduced); a glint shine of the white ground-colour is present in both sexes; a dark chestnut brown patch below  $CuA_2$  and above  $1A+2A$  in male. Fringe hair-like and short in both sexes (ciliae shorter than 1.1 mm). Wing venation: in forewing  $1A+2A$  long forked at base in both sexes, sometimes very long forked;  $CuP$  present from base of wing to the dorsum in both sexes – an extremely rare character state among the *Metarbelidae*;  $CuA_2$  originating from hind margin of posterior cell;  $CuA_1$ ,  $M_3$  and  $M_2$  separated and initiating from apical angle of posterior cell;  $M_1$  initiating from distal margin of median cell;  $R_1$  initiating from anterior margin of median cell;  $R_2$  initiating from anterior angle of an areole (areole well developed);  $R_3+R_4$  stalked and initiating from or close to posterior angle of areole in both sexes;  $R_5$  initiating from below posterior angle of areole in both sexes;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  forked at base, sometimes obsolete towards termen;  $CuP$  present in both sexes;  $CuA_2$  initiating from hind margin of posterior cell;  $CuA_1$ ,  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1$  and  $Rs$  initiating from apical angle of anterior cell, widely separated; without a bar from  $Rs$  to  $Sc+R_1$ ; with a small vein in discocellular cell on both forewing and hindwing in both sexes, forked in forewing towards hind margin of cell in female, but forked in hindwing towards hind margin of cell in both sexes. Retinaculum and frenulum are absent in both sexes.

*Abdomen:* With dense hair-like scales and short abdominal tuft, never longer than one-fourth of abdomen length.

*Male genitalia.* Saccus short but narrow triangular with long acuminate tip, larger than juxta; the vinculum and tegumen are fused, forming a firm and narrow ring, lower half of vinculum very narrow; uncus rather short and narrow, not bifurcated at tip, tip rectangular, uncus with graben-like structure ventrally, and bent near base in lateral view. Valva soft, thinly membranous and without any structures but have few short and long setae near centre of valva distally, all edges are softer and with no setae, the whole valva breaks easily during preparation; a narrow and short semi-transtilla of triangular shape (attached to the costa of valva and opposite of the vinculum) is present, it has no setae. Sacculus pronounced but only present on 40% of length of valva near its base. Gnathos only thinly membranous and appears soft, not well sclerotized, ventrally fused, it is long (ending below costa of valva) and narrow (20% of width of valva) on its whole length. Juxta broad and simple, band-like, smaller than sacculus without any processes. Phallus simple, tube-like, short and broad (in length shorter than length of valva), straight; vesica without cornuti.

*Female postabdominal structure and genitalia.* Papillae anales broad, dorsal part obliquely 8-shaped or elliptic in posterior view, covered with short setae; segment 8 narrow, setose along its posterior margin, not emarginated dorso-anteriorly. Ductus

bursae and corpus bursae broad, thinly membranous, ductus bursae short, *ca.* 15% of length of corpus bursae, corpus bursae narrowly oval-shaped, larger than segment 8 in lateral view, without any processes or other distinct characters.



**FIGURE 10.** Distribution of the basal taxon Gen. Nov. A (red dots).



**FIGURE 11.** Basal taxon, Gen. Nov. A, sp. nov. a, [Republic of] South Africa, Mpumalanga, Blyde River Canyon, 2.2 km west of forest station Mariep's Kop, 26.11.2008, D. Bartsch leg., ex SMNS Lep. 2008-05, male, genitalia slide number 27/082017 I. Lehmann. Wingspan 34.0 mm



**FIGURE 12.** Basal taxon, Gen. Nov. A, sp. nov. a1, [Republic of South Africa], Katberg pass, "south side forest", 11.12.2002, A. Legrain leg., ex RMCA, female, genitalia slide number 06/052017 I. Lehmann. Wingspan 46.0 mm

### 4.3 *Paralebedella* Strand, 1923

The genus is defined by the following autapomorphies:

- Huge, strongly sclerotized elongated uncus (larger than valva), in lateral view almost as broad as basal width of valva with a deep graben-like structure ventrally; (191);
- In forewing, very narrow, elongated and small upper discal and lower discal cell, both ends are strongly acuminate and deeply bifurcated in both sexes; (192);
- In hindwing, RS from mid-point of a long vein that connects the upper half of discal cell with Sc+R<sub>1</sub> in both sexes; (193);
- Anterior apophyses in female extremely S-shaped; (194).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing in both sexes; (11).

Type species of genus (cf. Figure 14): *Paralebedella carnescens* (Hampson, 1910)

Type locality: [ex Type collection Clark], [Co-Type?], [Republic of South Africa], “Durban”, [no date], “ex coll. Clark, A.J.T. Janse”, ex TMSA, male, genitalia slide number 23/092017 I. Lehmann; depository in TMSA.

Number of species in genus at present: 10

All localities of studied species per country: Nigeria; Gabon; Democratic Republic of the Congo; Uganda; Kenya; Tanzania; Republic of South Africa.

Distribution of genus at present (cf. Figure 13): lowland and submontane areas from southern Nigeria eastwards via Gabon, through the Congo Basin eastwards through Uganda to western, central and coastal Kenya, probably southwards along the coast of Tanzania, extending ca. 150 km inland from the Indian Ocean coast, to the eastern part of the Republic of South Africa.

The reconstructed and predicted ancestral area is the Guinea-Congolia/Sudania regional transition zone and the Guinea-Congolia/Zambezia regional transition zone.

The following biogeographic events were reconstructed: First, dispersal from the Guinea-Congolia/Sudania regional transition zone and the Guinea-Congolia/Zambezia regional transition zone into the Guineo-Congolian regional centre of endemism, the Lake Victoria regional mosaic, the Afromontane archipelago-like regional centre of endemism, the Zanzibar-Inhambane regional mosaic and the Tongaland-Pondoland regional mosaic. Secondly, vicariance between the Guineo-Congolian regional centre of endemism, the Guinea-Congolia/Sudania regional transition zone, the Guinea-Congolia/Zambezia regional transition zone and all other phytochoria as mentioned above.

Phylogenetic position: The sister genus could not be reconstructed unambiguously.

Description: *Head*: Rough-scaled; medium long scales on fronto-clypeus; a pair of pits absent on lower fronto-clypeus, a pair of conical projections absent on lower fronto-clypeus in both sexes; pits behind labial palpi very small, narrow, elongated, slit-like; the labial palpi medium long, less than eye diameter and consist of three segments, the segments are narrow, central segment is the longest (2× length of basal segment), the third segment on top the shortest; antennae bipectinated in both sexes, branches shorter in female (2× width of shaft), narrow in both sexes (well sclerotized), branches of equal width from base to tip; dorsal and lateral side of branches not scaled but covered with tiny setae in both sexes; flagellum scaled in both sexes.

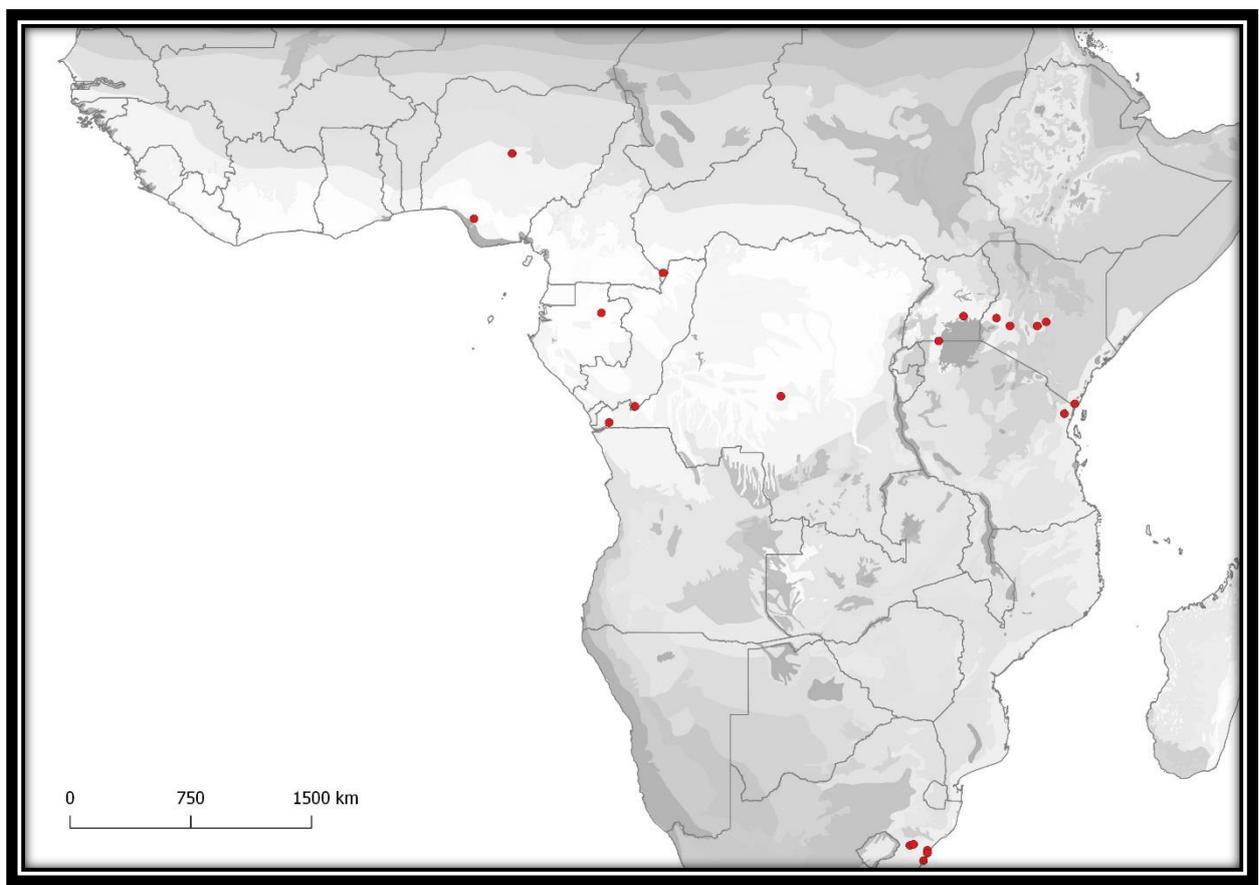
*Thorax*: Densely covered with hair-like scales, mainly brown, glossy; tegulae not pronounced; with a crest on metathorax. Epiphyses are present in both sexes, narrow and long. Hindlegs with two pairs of tibial spurs in both sexes, of almost equal length (the inner spur is slightly shorter) with lower pair slightly thicker, both with a thorn-like tip; pretarsus with a pair of pulvilli.

Forewing upperside without a geometric design as well as without a simple pattern, but with a transparent appearance towards termen in both sexes; a glint shine of pink and vinaceous is present on the whole upperside in both sexes; small sepia patches and sometimes a white patch occur below CuA<sub>2</sub> and above 1A+2A mainly in male. Fringe hair-like and short in both sexes on forewing and hindwing (ciliae shorter than 1.2 mm). The whole upperside of hindwing usually pink or light pink (a very rare colour among Metarbelidae), sometimes cream, with a slightly transparent appearance. Wing venation: In forewing, very narrow, elongated and small upper discal cell and lower discal cell, both ends are strongly acuminate, deeply bifurcated in between in both sexes; 1A+2A forked at base in both sexes; CuP absent in both sexes; CuA<sub>2</sub> originating from near hind margin of posterior cell; CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> separated and M<sub>3</sub> and M<sub>2</sub> initiating from an acuminate tip of apical angle of posterior cell; M<sub>1</sub> initiating from or near an acuminate tip of anterior angle of median cell; R<sub>1</sub> initiating from anterior margin of median cell; R<sub>2</sub> initiating from an acuminate tip of anterior angle of median cell and is long stalked with R<sub>3</sub>+R<sub>4</sub>+R<sub>5</sub> in both sexes; Sc more or less parallel to R<sub>1</sub>. In hindwing 3A present; 1A+2A obsolete; CuP absent in both sexes; CuA<sub>2</sub> initiating from hind margin of posterior cell; CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> initiating from apical angle of posterior cell, separated; M<sub>1</sub> initiating from a base of a very long bar that connects the upper half of a small discal cell with Sc+R<sub>1</sub>, widely separated to R<sub>s</sub>, the latter initiates from mid-point of this long bar in both sexes; with a small vein in discocellular cell on both forewing and hindwing in both sexes, never forked. Retinaculum and frenulum absent in both sexes.

*Abdomen*: With dense hair-like scales, sometimes mixed with pink and short abdominal tuft, never longer than one-third of abdomen length.

*Male genitalia.* Saccus short, sometimes strongly reduced, narrow, finger-like, smaller than juxta; the vinculum and tegumen are fused, forming a firm ring, lower half of vinculum narrow; the uncus has a heavy appearance, it is strongly sclerotized with a more or less flat dorsal surface, huge and elongated (larger than valva), in lateral view almost as broad as basal width of valva with a deep graben-like structure ventrally. Valva soft, narrow and elongated, sclerotized along costa, without any structures but with short and long setae near centre of valva distally; a broad and long semi-transtilla of rectangular shape is present (attached to the costa of valva and opposite of the vinculum). Sacculus narrow, only present on 60% of length of valva. Gnathos membranous, sclerotized, gnathal arms ventrally fused with a narrow sclerotized bulla, entire gnathos broad and of triangular in shape (lateral view), ending above costa of valva. Juxta broad and simple V-shaped, without any processes. Phallus simple, tube-like, short and broad (in length shorter than length of valva), straight; vesica without cornuti.

*Female postabdominal structure.* Papillae anales broad but small, dorsal part obliquely 8-shaped or elliptic in posterior view covered with scattered short setae and with a prominent sclerotized structure at centre; segment 8 rather broad, only with groups of scattered setae on its surface, not setose along its posterior margin, not emarginated dorso-anteriorly.



**FIGURE 13.** Distribution of the genus *Paralebedella* (red dots).



**FIGURE 14.** *Paralebedella carnescens*, [Republic of South Africa], Durban, ex coll. Clark [Co-Type?], Janse, ex TMSA, male, genitalia slide number 23/092017 I. Lehmann. Wingspan 41.0 mm



**FIGURE 15.** *Paralebedella* sp. nov.2, Kenya, Kakamega Forest, Nov. 1964, R.H. Carcasson leg., ex NMK, male, genitalia slide number 26/082007 I. Lehmann. Wingspan 38.5 mm



**FIGURE 16.** *Paralebedella shimonii* Lehmann 2009, Holotype, Kenya, Coast, Marenji Forest, 05.01.1996, Dr. H. Politzar leg., ex ZSM, female, genitalia slide number 20/o62008 I. Lehmann. Wingspan 31.0 mm

#### 4.4 *Haberlandia* Lehmann, 2011

The genus is defined by the following autapomorphies:

- Gnathos large (at least 50% the size of valva in lateral view) and heavy in appearance, well sclerotized, tabular in shape dorsally; (45);
- Segment 8 in female with narrow gap-like shape dorsally, extending to 50% of its dorsal length; (46);
- the tarsi have a peculiar colour of a glossy rust (xanthine orange) in both sexes; (47).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing in both sexes; (11).

Type species of genus (cf. Figures 18, 19): *Haberlandia odzalaensis* Lehmann, 2011

Type locality: Republic of the Congo, Odzala National Park, 29.01.–03.03.1997, V. Siniaev & S. Murzin leg., genitalia slide number 02/082009 I. Lehmann, ex MWM; depository in ZSM;

Number of species in genus at present: 26

All localities of studied species per country: Sierra Leone; Ivory Coast; Ghana; Togo; Cameroon; Gabon; Republic of the Congo; Central African Republic; Democratic Republic of the Congo; Uganda; Tanzania.

Distribution of genus at present (cf. Figure 17): lowland and lower submontane areas within the boundaries of the tropical rain forest from southern Sierra Leone eastwards via Cameroon, through the whole Congo Basin further northwards to the Central African Republic with few disjunct records in south-central Uganda (Entebbe) and around Ndolage (northwest Tanzania).

The reconstructed and predicted ancestral area is the Guinea-Congolia/Sudania regional transition zone and the Guinea-Congolia/Zambezia regional transition zone.

The following biogeographic events were reconstructed: First, dispersal from the Guinea-Congolia/Sudania regional transition zone and the Guinea-Congolia/Zambezia regional transition zone into the Guineo-Congolian regional centre of endemism and the Lake Victoria regional mosaic. Secondly, vicariance between the Guineo-Congolian regional centre of endemism, the Guinea-Congolia/Sudania regional transition zone, the Guinea-Congolia/Zambezia regional transition zone with the Lake Victoria regional mosaic.

Phylogenetic position: The sister genus could not be reconstructed unambiguously.

Description: *Head:* Rough-scaled; medium long scales on fronto-clypeus; a pair of large rounded pits present on lower fronto-clypeus, a pair of conical projections absent on

lower fronto-clypeus in both sexes; pits behind the labial palpi deep and oval-shaped; the labial palpi medium long, less than eye diameter and consist of two segments, the segments are rather narrow, upper segment is the longest (2× length of basal segment); antennae bipectinated in both sexes, branches shorter in female only at base (2× width of shaft, in male 3× width of shaft), narrow in both sexes (well sclerotized), branches of equal width from base to tip; dorsal and lateral side of branches not scaled but covered with tiny setae in both sexes; flagellum scaled in both sexes.

*Thorax:* Densely covered with hair-like scales, mainly brown, glossy; tegulae pronounced with a peculiar glossy colour in both sexes, often Hay's russet or xanthine orange (= a kind of rust colour); with a short crest on metathorax. Epiphyses are present in both sexes, rather narrow. Hindlegs with one pair of tibial spurs, but usually two pairs of tibial spurs are present in both sexes, spurs longer in female, both with a thorn-like tip; pretarsus with a pair of pulvilli.

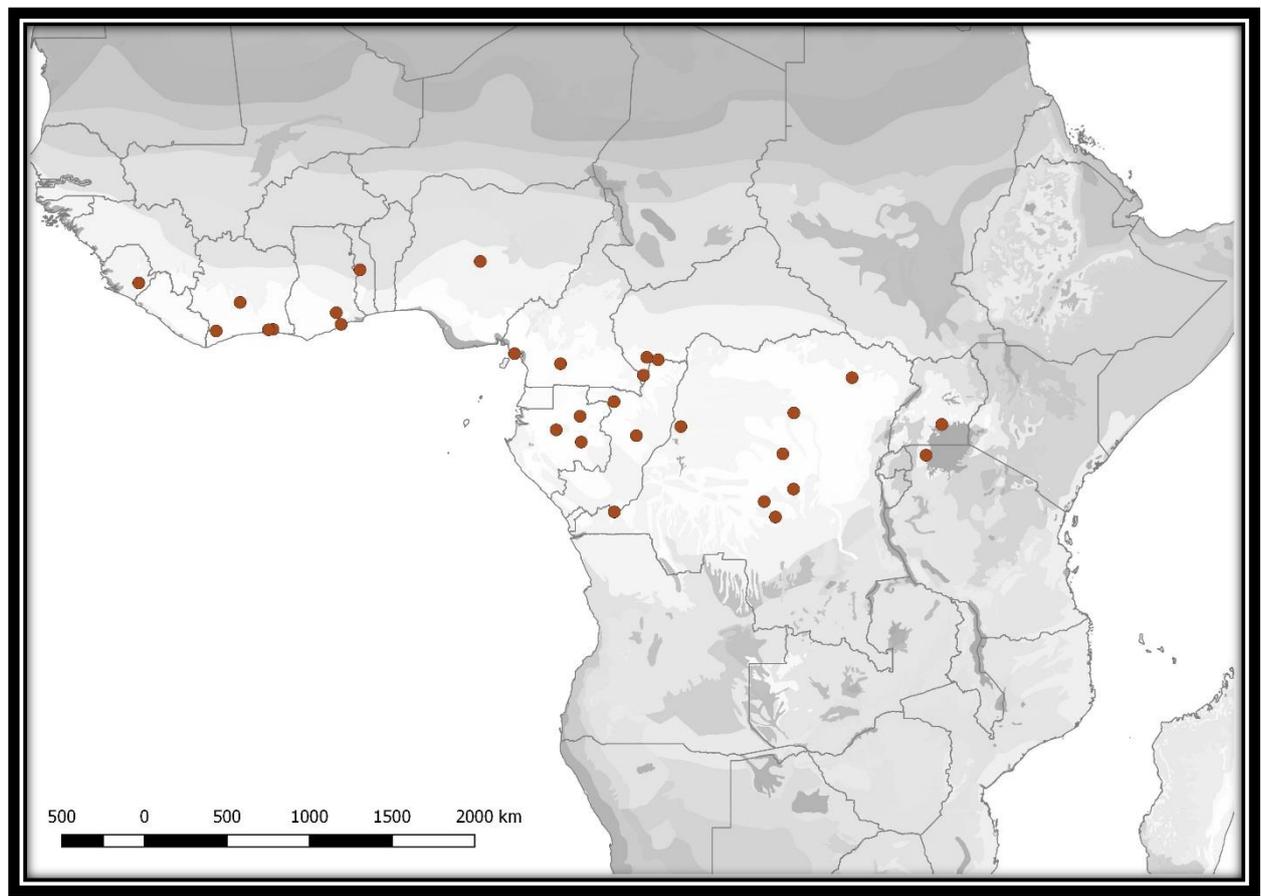
Forewing upperside and hindwing upperside are brown with a geometric design of a usually short-stalked "V" in both sexes; a glint shine of vinaceous is sometimes present on the whole upperside in both sexes; a narrow patch of sepia occurs near the base of forewing and below 1A+2A to half of inner margin; CuA<sub>2</sub> sometimes distinctly marked by a thin dark brown line in both sexes. Fringe is hair-like, short in both sexes on forewing and hindwing (ciliae shorter than 1.3 mm). Wing venation: In forewing, 1A+2A forked at base in both sexes; CuP absent in both sexes; CuA<sub>2</sub> originating from near hind margin of posterior cell; CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> separated and initiating from apical angle of posterior cell; R<sub>1</sub> initiating from anterior margin of median cell; R<sub>2</sub> is absent; R<sub>3</sub>+R<sub>4</sub>+R<sub>5</sub> long stalked in both sexes; Sc more or less parallel to R<sub>1</sub>. In hindwing 3A present; 1A+2A present, sometimes obsolete; CuP absent in both sexes; CuA<sub>2</sub> initiating from hind margin of posterior cell; CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> initiating from apical angle of posterior cell, separated; M<sub>1</sub> and Rs initiating from apical angle of anterior cell, widely separated; Sc+R<sub>1</sub> usually without a bar to the median cell in both sexes; with a small vein in discocellular cell on both forewing and hindwing in both sexes, never forked. Retinaculum and frenulum absent in both sexes.

*Abdomen:* With dense hair-like scales and short abdominal tuft, never longer than one-fourth of abdomen length.

*Male genitalia.* Saccus broad, tip rounded, slightly smaller than juxta; the vinculum and tegumen are fused, forming a firm ring, lower half of vinculum narrow, tegumen might consist of two or three overlapping plates; the uncus has a heavy appearance, it is strongly sclerotized with a more or less flat dorsal surface and a straight lateral surface, never bifid, in lateral view almost as broad as basal width of valva. Valva soft, almost rectangular in shape, sclerotized along costa, without any structures (except at the inner edge a tiny slightly sclerotized thorn occurs), but with short and long setae near centre of valva distally; a broad, short, rather ear-shaped semi-transtilla is present (attached to the costa of valva and opposite of the vinculum). Sacculus broad, sclerotized, present up to 90% of length of valva. Gnathos strongly sclerotized, gnathal arms ventrally not fused, dorsal surface of a tabular shape, outer

edges more or less foliaceous and resulting sometimes in thorn-like structures, the ventral end of the gnathos is above costa of valva but its ventral base is below the costa (lateral view). Juxta is broad with two rather ear-shaped lobes without any processes. Phallus simple, tube-like, broad, long (in length longer than length from saccus to end of valva) with a spoon-like distal end; vesica without cornuti.

*Female postabdominal structure.* Papillae anales broad, dorsal part obliquely 8-shaped or elliptic in posterior view covered with scattered short and long setae; segment 8 broad, sometimes with a wave-like dorsal surface that is always divided by a prominent narrow gap (viewed dorsally), posterior edge of segment 8 with very long setae ventrally that often extend beyond the papillae anales; the lateral surface of segment 8 sometimes with prominent slits.



**FIGURE 17.** Distribution of the genus *Haberlandia* (red dots).



**FIGURE 18.** *Haberlandia odzalaensis*, Holotype, Republic of the Congo, Odzala National Park, 29.01.–03.03.1997, V. Siniaev & S. Murzin leg., ex MWM, male, genitalia slide number 02/082009 I. Lehmann. Wingspan 51.5 mm



**FIGURE 19.** *Haberlandia odzalaensis*, Paratype, Republic of the Congo, Odzala National Park, 29.01.–03.03.1997, V. Siniaev & S. Murzin leg., ex MWM, female, genitalia slide number 09/082009 I. Lehmann. Wingspan 53.5 mm

#### 4.5 Gen. Nov. B

The genus is defined by the following autapomorhy:

- Uncus longer than width of valva, narrow elongated and deeply bifurcated (*ca.* at least one-third of uncus length); (27).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing in both sexes; (11).

Type species of genus (cf. Figure 21): Gen. Nov. B + sp. nov. b

Type locality: Uganda, Ankole, Kalinzu Forest, 11.1961, R.H. Carcasson leg., male, genitalia slide number 22/032009 I. Lehmann, ex NMK; depository in NMK.

Number of species in genus at present: 10

All localities of studied species per country: Nigeria; Cameroon; Democratic Republic of the Congo; Ethiopia; Uganda; Kenya; Tanzania; Malawi.

Distribution of genus at present (cf. Figure 20): disjunct; lowland, submontane and montane areas in central Nigeria eastwards to Cameroon and from southwest Ethiopia, southwest Uganda, south-central Tanzania to the southeastern Congo Basin and to southern Malawi.

The reconstructed and predicted ancestral area is the Afromontane archipelago-like regional centre of endemism.

The reconstructed biogeographic events comprise: First, the dispersal from the Afromontane archipelago-like regional centre of endemism into the Guineo-Congolian regional centre of endemism, the Guinea-Congolia/Sudania regional transition zone, the Guinea-Congolia/Zambezia regional transition zone and the Lake Victoria regional mosaic. Secondly, the vicariance between the Afromontane archipelago-like regional centre of endemism and the Lake Victoria regional mosaic with the Guineo-Congolian regional centre of endemism, the Guinea-Congolia/Sudania regional transition zone and the Guinea-Congolia/Zambezia regional transition zone.

Phylogenetic position: The sister genus could not be reconstructed unambiguously. The genus belongs to a monophylum together with *Lebedodes*, and the new genera B, C, D.

The synapomorphies shared with Gen. Nov. C, Gen. Nov. D and *Lebedodes* comprise:

- R<sub>1</sub>+R<sub>2</sub> on a short stalk (stalk has the length of 30% of R<sub>3</sub>) in male; (8);
- Narrow vinculum (one-third or less of width of aedeagus), no saccus, and very broad tegumen (at least 4 x broader than vinculum); (31);
- Uncus has a heavy appearance, it is strongly sclerotized with a more or less flat dorsal surface; (44).

Description: *Head:* Rough-scaled; medium long hair-like scales of usually dark olive-buff on fronto-clypeus; a pair of pits absent on lower fronto-clypeus, a pair of small conical projections present on lower fronto-clypeus in both sexes, but more pronounced in females; pits behind the labial palpi small and oval-shaped; the labial palpi medium long, less than eye diameter and consist of three segments, the central segment is the longest (2× as long as basal segment, third segment on top short, conical); antennae bipectinated in both sexes, branches shorter in females (2× width of shaft), narrow (well sclerotized) and of equal width from base to tip; dorsal and lateral side of branches not scaled but covered with long setae in both sexes; flagellum scaled cream in both sexes.

*Thorax:* Densely covered with broader and hair-like scales, mainly dark olive-buff, slightly glossy; tegulae not pronounced; with a short crest on metathorax. Epiphyses are present in both sexes. Hindlegs with two pairs of narrow tibial spurs, inner spur shorter, with a thorn-like tip in both sexes; pretarsus with a pair of pulvilli.

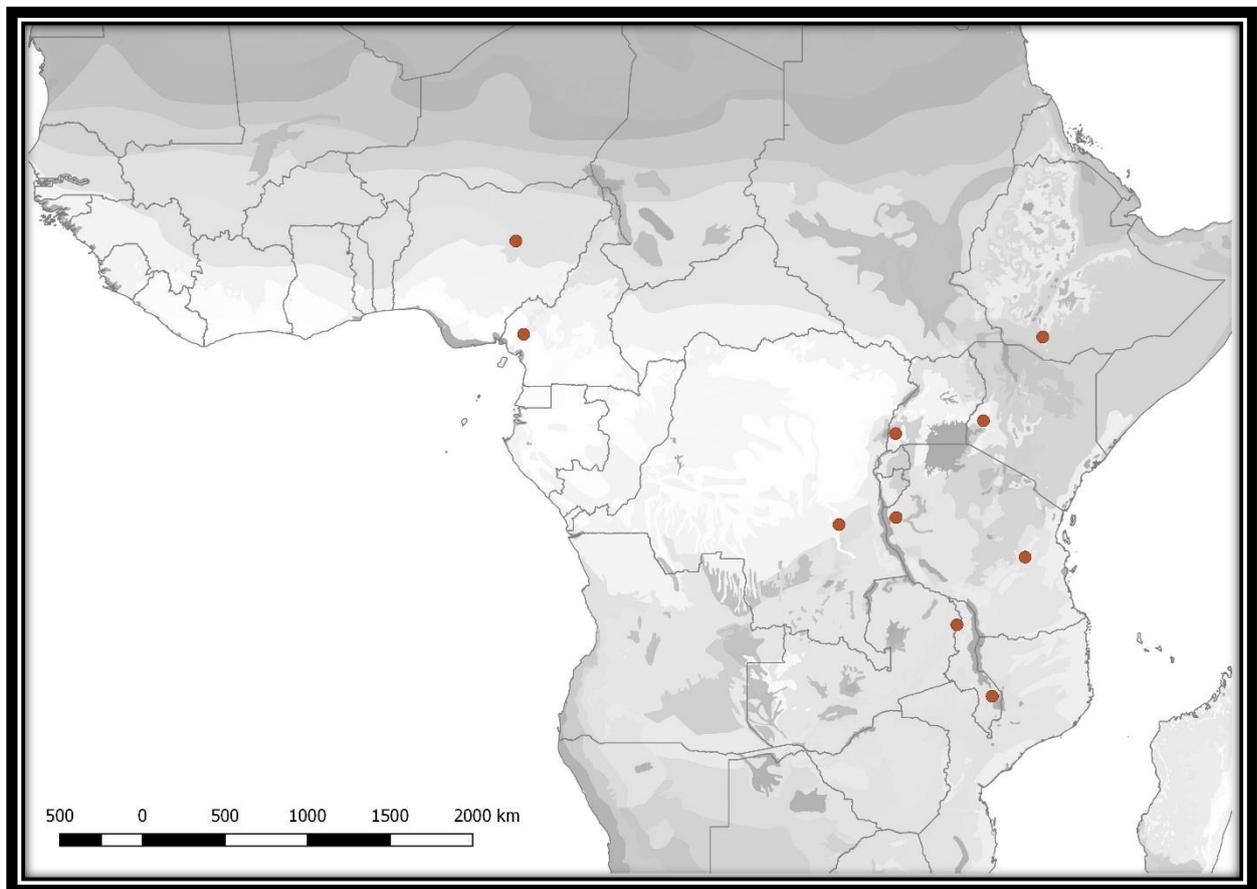
Forewing upperside without a geometric design but with a simple pattern comprising narrow and broader lines and bands of light olive from near costal margin to dorsum with light olive on all veins, a dark olive rounded spot near median cell; a glint shine of light vinaceous is present towards termen in both sexes. Fringe hair-like and short in both sexes (ciliae shorter than 0.8 mm). Wing venation: in forewing  $1A+2A$  forked at base in both sexes; CuP absent;  $CuA_2$  originating from hind margin of posterior cell;  $CuA_1$ ,  $M_3$  and  $M_2$  separated and initiating from apical angle of posterior cell;  $M_1$  initiating from distal margin of median cell;  $R_1+R_2$  on a short stalk (stalk has the length of 30% of  $R_3$ ) and initiating from anterior margin of median cell;  $R_3+R_4+R_5$  stalked and initiating from anterior angle of median cell in both sexes; Sc more or less parallel to  $R_1+R_2$ . In hindwing  $3A$  present;  $1A+2A$  present; CuP absent in both sexes;  $CuA_2$  initiating from hind margin of posterior cell;  $CuA_1$ ,  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1$  and  $R_s$  initiating from apical angle of anterior cell, widely separated; without a bar from  $R_s$  to  $Sc+R_1$ ; with a small vein in discocellular cell on both forewing and hindwing in both sexes, never forked. Retinaculum and frenulum absent in both sexes.

*Abdomen:* With dense hair-like scales and short abdominal tuft, never longer than one-fourth of abdomen length.

*Male genitalia.* Saccus absent; the vinculum and tegumen are fused, forming a firm and narrow ring, lower half of vinculum extremely narrow; uncus very long, narrow, bent downwards (in lateral view) and deeply bifurcated for at least one-third of uncus length, both tips slightly rounded. Valva soft, thinly membranous and without any structures, very elongated and very narrow towards tip that is rectangular, many short setae on inner side of valva, all edges are soft, the whole valva breaks easily during preparation; a very broad (half the width of valva), thinly membranous transtilla is present, it has no setae. Sacculus narrow, only present on 30% of length of valva near its base. Gnathos large, membranous, slightly sclerotized, ventrally fused with a narrow bulla, gnathos looks like half of a shoe (in lateral view) its broad edge

becomes a broad stronger sclerotized “V” in ventral view; the gnathos is long (ending below costa of valva) and very broad (at least 90% of width of valva). Juxta is small (less than 30% the size of the transtilla), broadly V-shaped and without any processes. Phallus simple, tube-like, short and narrow (in length 60% the length of valva), straight; vesica without cornuti.

*Female postabdominal structure.* Papillae anales broad, dorsal part obliquely 8-shaped or elliptic in posterior view, covered with short as well as very long setae; segment 8 narrow ventrally, setose along its posterior margin only on lower half, not emarginated dorso-anteriorly, with a narrow band below base of anterior apophysis to ventral edge of segment 8.



**FIGURE 20.** Distribution of Gen. Nov. B (red dots).



**FIGURE 21.** Gen. Nov. B, sp. nov. b, Uganda, Ankole, Kalinzu Forest, 11.1961, R.H. Carcasson leg., ex NMK, male, genitalia slide number 22/032009 I. Lehmann. Wingspan 39.5 mm



**FIGURE 22.** Gen. Nov. B, sp. nov. b1, Malawi, Vwaza Marsh Game Reserve, Zaro Camp, 25.-27.02.2006, R.J. Murphy leg., ex own coll., female, genitalia slide number 21/122008 I. Lehmann. Wingspan 41.5 mm

#### 4.6 Gen. Nov. C

The genus is defined by the following autapomorhy:

- Gnathal arms well developed, almost triangular at lower half of their length with many deep folds distally and connected by a large, broad and short rectangular bulla ventrally; (20).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male [possibly also in female]; (11).

Type species of genus (cf. Figures 24, 25): Gen. Nov. C + *violascens* (Gaede, 1929)

Type locality: Ost-Afrika [East Africa], südl. [south of] Uhehe, [Tanzania], Jringa [= Iringa?], Mgololo, 03.99 [1899], S. Goetze leg., male, genitalia slide number 04/102008 I. Lehmann, ex ZMHU; depository in ZMHU.

Number of species in genus at present: 04

All localities of studied species per country: Kenya; Tanzania.

Distribution of genus at present (cf. Figure 23): submontane and montane areas from north-central Kenya to south-central Tanzania.

The reconstructed and predicted ancestral area is the Afromontane archipelago-like regional centre of endemism and the Kalahari-Highveld regional transition zone.

The reconstructed biogeographic events comprise: First, dispersal from the Afromontane archipelago-like regional centre of endemism and the Kalahari-Highveld regional transition zone into the Somalia-Masai regional centre of endemism. Secondly, vicariance between the Afromontane archipelago-like regional centre of endemism, the Kalahari-Highveld regional transition zone and the Somalia-Masai regional centre of endemism.

Phylogenetic position: The sister genus could not be reconstructed unambiguously. The genus belongs to a monophylum together with *Lebedodes*, and the new genera B, C, D.

The synapomorphies shared with Gen. Nov. B, Gen. Nov. D and *Lebedodes* comprise:

- R<sub>1</sub>+R<sub>2</sub> on a short stalk (stalk has the length of 30% of R<sub>3</sub>) in male; (8);
- Narrow vinculum (one-third or less of width of aedeagus), no saccus, and very broad tegumen (at least 4 x broader than vinculum); (31);
- Uncus has a heavy appearance, it is strongly sclerotized with a more or less flat dorsal surface; (44).

Description: *Head:* Rough-scaled; medium long hair-like scales of usually light greyish-olive on fronto-clypeus; a pair of pits absent on lower fronto-clypeus, a pair of small

conical projections absent on lower fronto-clypeus in male; pits behind the labial palpi very tiny slits or absent; the labial palpi medium long, less than eye diameter and consist of three segments, the central segment is the longest (2.5× as long as basal segment), third segment on top short, conical; antennae bipectinated, narrow, well sclerotized and of equal width from base to tip; dorsal and lateral side of branches not scaled but covered with long setae; flagellum scaled cream.

*Thorax:* Densely covered with broader and hair-like scales, mainly light greyish-olive, slightly glossy; tegulae pronounced, chestnut coloured; with a short crest on metathorax. Epiphyses are present in male, long, broad and flat. Hindlegs with two pairs of tibial spurs, inner spur shorter, with a thorn-like tip, lower pair more narrow and longer (up to 1.2 mm) than upper pair; pretarsus with a pair of pulvilli.

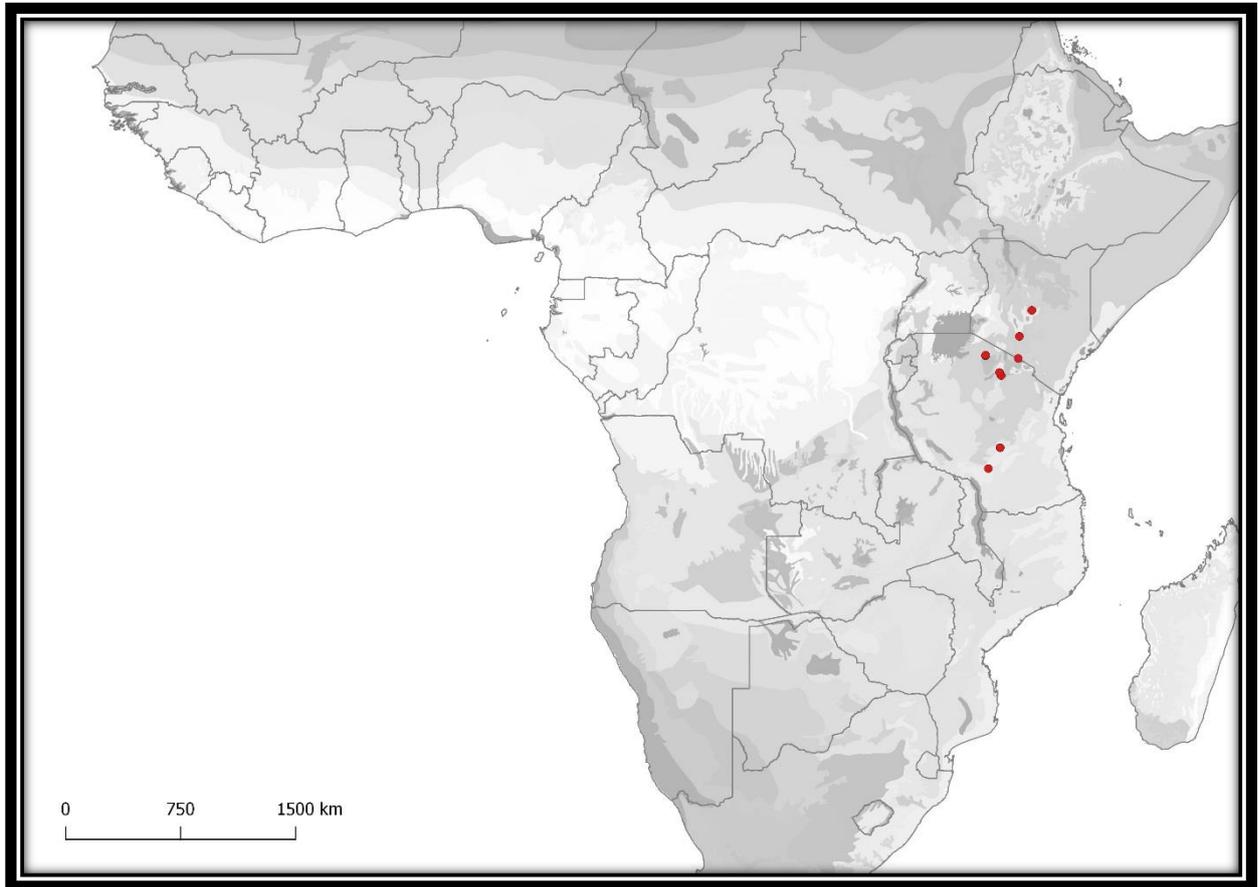
Forewing upperside without any geometric design but with a simple narrow net-like pattern of deep greyish-olive comprising a narrow sepia patch below first half of  $1A+2A$  and a broader, larger, grey oval-shaped patch, always rather faded, between at least  $R_5$  and  $M_1$ ; a glint shine is present towards termen. Hindwing upperside is cream and glossy. Fringe hair-like and long on both wings (ciliae at least 1.3 mm). Wing venation: in forewing  $1A+2A$  forked at base; CuP absent;  $CuA_2$  originating from hind margin of posterior cell;  $CuA_1$ ,  $M_3$  and  $M_2$  separated and initiating from apical angle of posterior cell;  $M_1$  initiating from distal margin of median cell;  $R_1+R_2$  on a short stalk (stalk has the length of 30% of  $R_3$ ) and initiating from anterior margin of median cell;  $R_3+R_4+R_5$  stalked and initiating from anterior angle of median cell; Sc more or less parallel to  $R_1+R_2$ . In hindwing  $3A$  present;  $1A+2A$  present; CuP absent;  $CuA_2$  initiating from hind margin of posterior cell;  $CuA_1$ ,  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1$  and  $R_s$  initiating from apical angle of anterior cell, widely separated; a short bar present from near base of  $R_s$  to  $Sc+R_1$ ; with a small vein in discocellular cell on both forewing and hindwing, never forked. Retinaculum and frenulum absent.

*Abdomen:* With dense hair-like scales and short abdominal tuft, never longer than one-fourth of abdomen length.

*Male genitalia.* Saccus absent; the vinculum and tegumen are fused, forming a firm and narrow ring, lower half of vinculum extremely narrow; uncus with heavy appearance but short (only 40% of length of gnathos), narrow, strongly bent downwards (in lateral view – looking like a hook) and not bifurcated at tip. Valva soft, thinly membranous and without any structures, short but elongated, narrow towards tip that is rounded, many short setae on inner side of valva, all edges are soft, the whole valva breaks easily during preparation; a very long (70% of length of valva) and medium broad (one-third the width of valva), sclerotized semi-transtillia is present, it has no setae. Sacculus narrow, only present on 20% of length of valva near its base. Gnathal arms medium large, slightly sclerotized, with deep folds distally (resulting in a distal edge looking like many teeth), arms are connected by a large, broad and short rectangular bulla ventrally; the gnathos is short (ending well above costa of valva) and broad (50% of width of valva). Juxta is small (less than 15% the size of the semi-

transtilla), V-shaped and without any processes. Phallus simple, tube-like, long (in length 90% the length of tegumen + valva in lateral view), slightly bent; vesica without cornuti.

*Female postabdominal structure and genitalia.* Unknown.



**FIGURE 23.** Distribution of Gen. Nov. C (red dots).



**FIGURE 24.** Gen. Nov. *C. violascens*, Type, Ost-Afrika [East Africa], südl. [south of] Uhehe, [Tanzania], Jringa [= Iringa?], Mgololo, 03.99 [1899], S. Goetze leg., ex ZMHU, male, genitalia slide number 04/102008 I. Lehmann. Wingspan 39.0 mm



**FIGURE 25.** Gen. Nov. *C. violascens*, Tanzania, Iringa Region, Iyayi, 04.04.2006, Ph. Darge leg., ex MWM, male, genitalia slide number 04/092009 I. Lehmann. Wingspan 37.5 mm



**FIGURE 26.** Gen. Nov. C, sp. nov. c1, Kenya Colony [Kenya], Isiolo, April–May 1951, Mrs. [Joy] Adamson leg., ex BMNH, male, genitalia slide number 11/062009 I. Lehmann. Wingspan 35.0 mm

#### 4.7 Gen. Nov. D

The genus is defined by the following autapomorphy:

- The whole gnathal arms are not thorn-like but each arm comprises a prominent thorn-like appendice that is *ca.* 60% in size of each gnathal arm; (23).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing in both sexes; (11).

Type species of genus (cf. Figure 28): Gen. Nov. D + sp. nov. d

Type locality: Br. [British] Somaliland [Somalia], Burau [today Burao], 3,000 feet, September–October 1929, C.L. Collenette leg., male, genitalia slide number 09/022009 I. Lehmann, ex BMNH, B.M. 1930–212; depository in BMNH.

Number of species in genus at present: 11;

all localities of studied species per country: Central African Republic; Uganda; Somalia, Kenya; Tanzania; Malawi; Zimbabwe; Republic of South Africa; Swaziland.

Distribution of genus at present (cf. Figure 27): disjunct; lowland, submontane and montane areas from northern Somalia southwestwards into southwestern Uganda, eastern Kenya and eastern Tanzania, further southwards through Malawi to southern Zimbabwe, Swaziland and the eastern Republic of South Africa with a disjunct distribution in the southern Central African Republic.

The reconstructed and predicted ancestral area is the Afromontane archipelago-like regional centre of endemism and the Kalahari-Highveld regional transition zone.

The reconstructed biogeographic events comprise: First, dispersal from the Afromontane archipelago-like regional centre of endemism and the Kalahari-Highveld regional transition zone into the Somalia-Masai regional centre of endemism, the Zanzibar-Inhambane regional mosaic and the Tongaland-Pondoland regional mosaic. Secondly, vicariance between the Afromontane archipelago-like regional centre of endemism and all other phytochoria mentioned above.

Phylogenetic position: The sister genus could not be reconstructed unambiguously. The genus belongs to a monophylum together with *Lebedodes*, and the new genera B, C, D.

The synapomorphies shared with Gen. Nov. B, Gen. Nov. C and *Lebedodes* comprise:

- Narrow vinculum (one-third or less of width of aedeagus), no saccus, and very broad tegumen (at least 4 x broader than vinculum); (31);
- Uncus has a heavy appearance, it is strongly sclerotized with a more or less flat dorsal surface; (44).

Description: *Head:* Rough-scaled; medium long hair-like scales of usually dark ocher on fronto-clypeus; a pair of pits absent on lower fronto-clypeus, a pair of small conical projections present on lower fronto-clypeus in male and female; pits behind labial palpi very tiny slits or absent; the labial palpi medium long, less than eye diameter and consist of three segments, the central segment is the longest (2.5× as long as basal segment), third segment on top very short, conical in both sexes; antennae bipectinated in both sexes; branches narrow, well sclerotized and of equal width from base to tip; dorsal and lateral side of branches not scaled but covered with long setae; flagellum scaled cream.

*Thorax:* Densely covered with broader and hair-like scales, mainly light chestnut or dark chestnut, glossy; tegulae pronounced, chestnut coloured; with a short crest on metathorax. Epiphyses are present in both sexes, medium long, rather broad and flat. Hindlegs with two pairs of tibial spurs, inner spur shorter, with a thorn-like tip, lower pair thick and shorter (up to 1.0 mm), upper pair more narrow and longer (up to 1.6 mm); pretarsus with a pair of pulvilli.

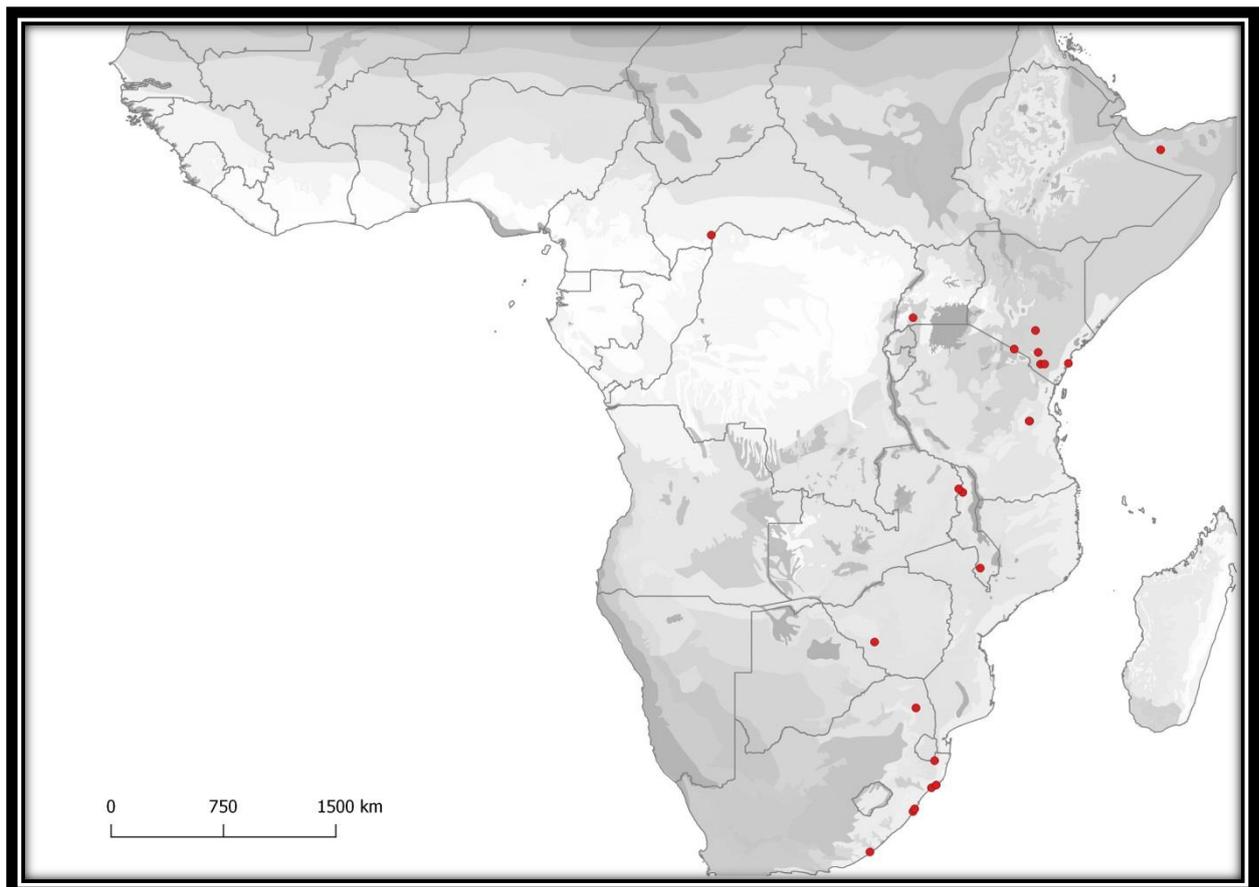
Forewing upperside without any geometric design but with a simple net-like pattern of narrow brownish-olive lines from costa to dorsum and with partly light brownish-olive veins and a small sepia patch below first half of  $1A+2A$ ; often a dark brown and elongated narrow patch on or close to lower half of discal cell extending to below base of  $M_2$ ; a glint shine is present towards termen. Hindwing upperside is dark cream or light cream and glossy. Fringe hair-like and long on both wings (ciliae at least 1.0 mm). Wing venation: in forewing  $1A+2A$  forked at base;  $CuP$  absent;  $CuA_2$  originating from hind margin of posterior cell;  $CuA_1$ ,  $M_3$  and  $M_2$  separated and initiating from apical angle of posterior cell;  $M_1$  initiating from distal margin of median cell;  $R_2$  absent;  $R_3+R_4+R_5$  stalked and initiating from anterior angle of median cell;  $Sc$  more or less parallel to  $R_1$ ; the latter initiating from anterior margin of median cell. In hindwing  $3A$  present;  $1A+2A$  present, often with a small fork at base;  $CuP$  absent;  $CuA_2$  initiating from hind margin of posterior cell;  $CuA_1$ ,  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1$  and  $Rs$  initiating from apical angle of anterior cell, widely separated; a bar absent from  $Rs$  to  $Sc+R_1$ ; with a small vein in discocellular cell on both forewing and hindwing, never forked, always weak or obsolete. Retinaculum and frenulum absent.

*Abdomen:* With dense hair-like scales and short abdominal tuft, often with a chestnut tip, never longer than one-fourth of abdomen length.

*Male genitalia.* Saccus absent; the vinculum and tegumen are fused, forming a firm and narrow ring, lower half of vinculum narrow; uncus with heavy appearance but short (only 40% or 50% of length of gnathos), broad, with flat lateral sides, slightly bent downwards (in lateral view) and slightly bifurcated at tip. Valva soft, thinly membranous and without any structures, elongated and narrow towards tip that is rounded, many long setae on inner side of valva, all setae appear often dark grey in colour, edges are soft, the whole valva breaks easily during preparation; a broad (50% of width of valva), rectangular, slightly sclerotized semi-transtilla is present, it has no

setae. Sacculus narrow, only present on 60% of length of valva. Gnathal arms large and attached to lower uncus, a strongly sclerotized prominent thorn-like appendice is present (it is hollow inside), *ca.* 60% or slightly more in size of each gnathal arm, arms without deep folds distally and are connected by a very narrow, band-like bulla ventrally; the gnathal arms are short (ending well above costa of valva) and broad (40% of width of valva). Juxta is rather large (almost as large as one semi-transtilla), broadly V-shaped and without any processes. Phallus simple tube-like, rather short (in length 60% the length of tegumen + valva in lateral view), slightly bent; vesica without cornuti.

*Female postabdominal structure.* Papillae anales broad, dorsal part obliquely 8-shaped or elliptic in posterior view, covered with short as well as long setae; segment 8 rather triangular in shape (lateral view), very narrow ventrally, setose along its entire posterior margin with a second row of long setae running parallel, not emarginated dorso-anteriorly; a narrow band is attached to below each base of anterior apophysis running to below ventral edge of segment 8.



**FIGURE 27.** Distribution of Gen. Nov. D (red dots).



**FIGURE 28.** Gen. Nov. D, sp. nov. d, [Somalia], Burau [Burao], Sept.-Oct. 1929, C.L. Collette leg., ex BMNH, male, genitalia slide number 09/022009 I. Lehmann. Wingspan 23.5 mm



**FIGURE 29.** Gen. Nov. D, sp. nov. d1, [Kenya], Yatta, Kitui, April 1960, R.H. Carcasson leg., ex NMK, female, genitalia slide number 12/092009 I. Lehmann. Wingspan 24.5 mm

#### 4.8 *Lebedodes* Holland, 1893

The genus is defined by the following autapomorphy:

- Gnathal arms broad, rectangular (*ca.* 40% of size of valva) and connected basally with a narrow band that is acuminate at middle (hook-like); (241).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing in male; [possibly also in female] (11).

Type species of genus: *Lebedodes cossula* Holland, 1893

Type locality: French Congo [Gabon], Kangwé [a little south of Cap Lopez], leg. A. C. Good., depository in CMNH.

Note: *Lebedodes clathratus* Grünberg, 1911 (*cf.* Figure 31) is treated as a synonym of *L. cossula* by Gaede (1929), but might be a valid species (treated herein as a species different to *cossula*) once the genitalia of *cossula* has been seen. Type locality: S. Kamerun [South Cameroon], Ngoko-Station, 03.03.1902, S. Hösemann leg., male, genitalia slide number 28/032009 I. Lehmann, ex ZMHU; depository in ZMHU.

Number of species in genus at present: 11;

all localities of studied species per country: Burkina Faso; Ivory Coast; Ghana; Cameroon; Chad; Ethiopia; Uganda; Burundi; Tanzania; Kenya.

Distribution of genus at present (*cf.* Figure 30): disjunct; lowland, submontane and montane areas from southwestern Burkina Faso via Ivory Coast and southern Ghana (Dahomey interval) to southwestern Chad, southern Cameroon and coastal Gabon; and from central and southwestern Ethiopia to western and east-central Uganda, western Kenya, southwestwards to Burundi and southwestern Tanzania.

The reconstructed and predicted ancestral area is the Afromontane archipelago-like regional centre of endemism, the Guinea-Congolia/Sudania regional transition zone and the Guinea-Congolia/Zambezia regional transition zone.

The reconstructed biogeographic events comprise: First, dispersal from the Afromontane archipelago-like regional centre of endemism, the Guinea-Congolia/Sudania regional transition zone and the Guinea-Congolia/Zambezia regional transition zone. Secondly, vicariance between the Afromontane archipelago-like regional centre of endemism and both other phytochoria mentioned above.

Phylogenetic position: The sister genus could not be reconstructed unambiguously. The genus belongs to a monophylum together with *Lebedodes*, and the new genera B, C, D.

The synapomorphies shared with Gen. Nov. B, Gen. Nov. C and Gen. Nov. D comprise:

- Narrow vinculum (one-third or less of width of aedeagus), no saccus, and very broad tegumen (at least 4 x broader than vinculum); (31);
- Uncus has a heavy appearance, it is strongly sclerotized with a more or less flat dorsal surface; (44).

Description: *Head:* Rough-scaled; medium long hair-like scales of usually dark brown mixed with dark olive, glossy; a pair of pits absent on lower fronto-clypeus, a pair of small conical projections present on lower fronto-clypeus in male; pits behind the labial palpi very tiny slits or absent; the labial palpi medium long, less than eye diameter and consist of three segments, the central segment is the longest (1.8× as long as basal segment), third segment on top very short, conical; antennae bipectinated in male, branches narrow (well sclerotized) and of almost equal width from base to tip; dorsal and lateral side of branches not scaled but covered with long setae; flagellum scaled cream.

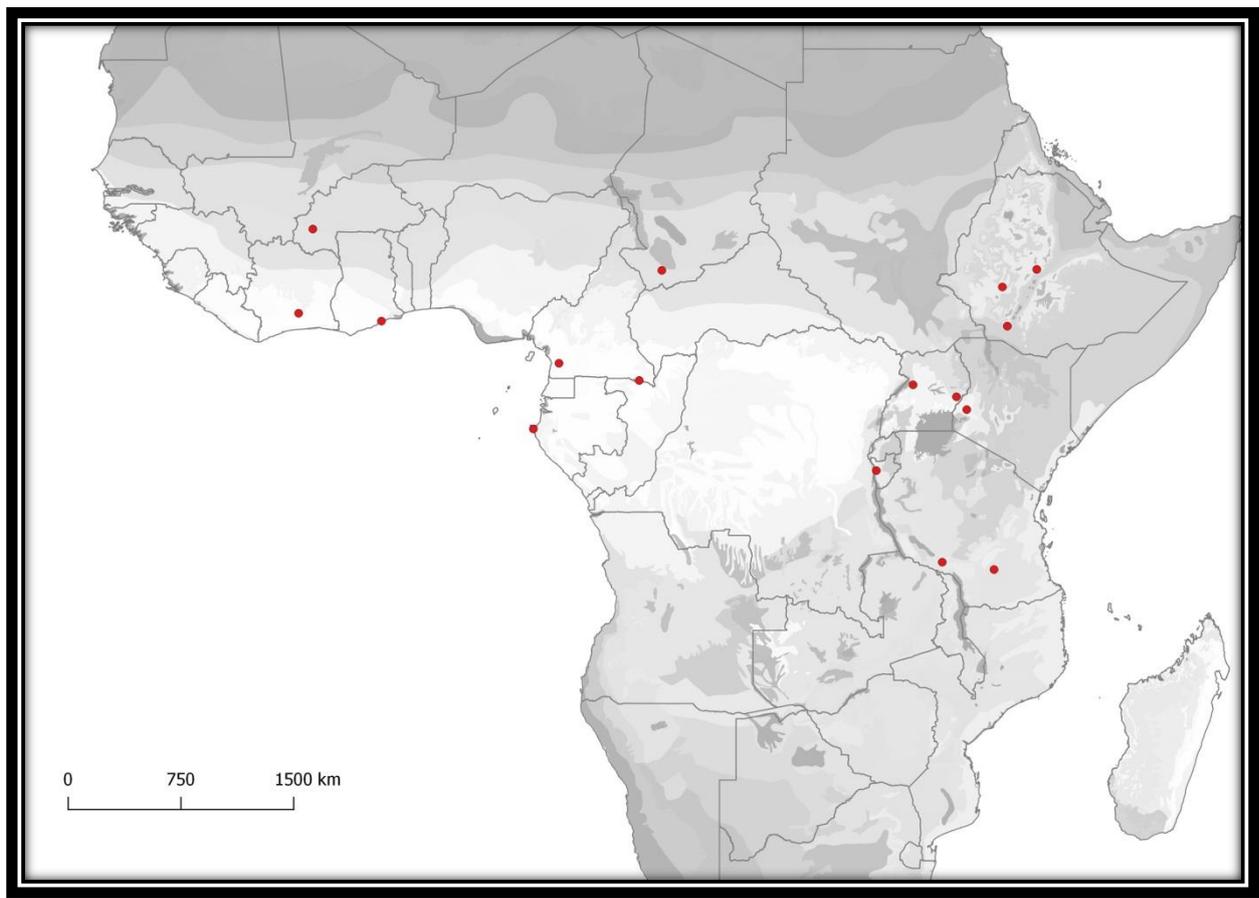
*Thorax:* Densely covered with broader and hair-like scales, mainly dark olive on patagia, glossy; tegulae pronounced, dark chestnut or sepia coloured; with a short crest on metathorax. Epiphyses are present in male, medium long, rather broad and flat. Hindlegs with two pairs of tibial spurs, inner spur shorter, with a thorn-like tip, lower pair thick and longer (up to 1.1 mm), upper pair more narrow and shorter (up to 1.0 mm), inner spur very short (up to 0.5 mm); pretarsus with a pair of pulvilli.

Forewing upperside without any geometric design but with a simple net-like pattern of narrow dark brownish-olive lines from costa to dorsum and with partly brownish-olive veins and a sepia patch below first half of 1A+2A; an oblique sub-terminal line from apex to CuA<sub>1</sub> and an oblique post-medial line from costa to dorsum forming both a “V”; a vinaceous glint is present towards termen; CuA<sub>2</sub> sepia. Hindwing upperside is dark olive and glossy, often with faded lines of dark olive-brown, but never forming a pronounced “V” as in forewing. Fringe hair-like and short on both wings (ciliae less than 1.0 mm). Wing venation: in forewing 1A+2A forked at base; CuP absent; CuA<sub>2</sub> originating from near hind margin of posterior cell; CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> separated (separation of CuA<sub>1</sub> and M<sub>3</sub> very wide), and initiating from apical angle of posterior cell; M<sub>1</sub> initiating from distal margin of median cell; R<sub>2</sub> absent; R<sub>3</sub>+R<sub>4</sub>+R<sub>5</sub> long stalked and initiating from anterior angle of median cell; Sc more or less parallel to R<sub>1</sub>; the latter initiating from anterior margin of median cell. In hindwing 3A present; 1A+2A present, often with a small fork at base; CuP absent or obsolete; CuA<sub>2</sub> initiating from near hind margin of posterior cell; CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> initiating from apical angle of posterior cell, separated; M<sub>1</sub> and Rs initiating from apical angle of anterior cell, widely separated; a bar absent from Rs to Sc+R<sub>1</sub>; with a small vein in discocellular cell on both forewing and hindwing, never forked. Retinaculum and frenulum absent.

*Abdomen:* With dense hair-like scales and short abdominal tuft, never longer than one-fourth of abdomen length; end of abdomen often dark chestnut ventrally.

*Male genitalia.* Saccus absent; the vinculum and tegumen are fused, forming a firm ring, very broad tegumen (at least 4 x broader than vinculum), lower half of vinculum narrow; uncus with heavy appearance but short (only 30% of length of gnathos), broad, with flat lateral sides, bent downwards (in lateral view), never bifurcated at tip. Valva soft, thinly membranous and without any structures, broadly elongated and at tip broadly rounded, many short setae on inner side of valva, edges are soft, the whole valva breaks easily during preparation; a broad (50% of width of valva), rectangular, slightly sclerotized semi-transtilla is present, it might be sometimes narrowly connected and forms a transtilla; it has no setae. Sacculus broad and present on 70% of length of valva. Gnathal arms large (as large as tegumen), mainly attached to upper part of tegumen, arms with many deep folds distally and are connected by a narrow, band-like bulla ventrally that is acuminate, hook-like and well sclerotized at middle; the gnathal arms are short (ending well above costa of valva) and broad (30% of width of valva). Juxta is rather large (almost as large as one semi-transtilla), broadly V-shaped and without any processes. Phallus simple, tube-like, very long (in length slightly longer than the length of tegumen + valva in lateral view), slightly bent; vesica without cornuti.

*Female postabdominal structure and genitalia.* Unknown.



**FIGURE 30.** Distribution of the genus *Lebedodes* (red dots).



**FIGURE 31.** *Lebedodes clathratus*, Type, [Cameroon], Ngoko-Station, 03.03.1902, S. Höse-mann leg., ex ZMHU, male, genitalia slide number 28/032009 I. Lehmann. Wingspan 48.0 mm



**FIGURE 32.** *Lebedodes* sp. nov.7, Uganda, Budongo Forest, Oct.–Nov. 1970, B. Watulege leg., ex NMK, male, genitalia slide number 05/072009 I. Lehmann. Wingspan 43.5

#### 4.9 Gen. Nov. E

The genus is defined by the following autapomorphy:

- Large, sclerotized and broad gnathos, in lateral view two-thirds of the size of valva, extending to basal costa of valva; (17).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes; (11).

Type species of genus (cf. Figure 34): Gen. Nov. E + *fraterna* (Gaede, 1929)

Type locality: [Cameroon], Bipindi, [no date, no collector], male, genitalia slide number 08/112008 I. Lehmann, ex ZMHU; depository in ZMHU.

Number of species in genus at present: 07;

all localities of studied species per country: Burkina Faso; Ivory Coast; Nigeria; Cameroon; Uganda.

Distribution of genus at present (cf. Figure 33): disjunct; lowland and submontane areas from southwestern Burkina Faso via northern Ivory Coast and central Nigeria to west and southwestern Cameroon; a disjunct distribution in central and east-central Uganda.

The reconstructed and predicted ancestral area is the Somalia-Masai regional centre of endemism.

The reconstructed biogeographic events comprise: First, dispersal in the Somalia-Masai regional centre of endemism, the Guinea-Congolia/Sudania regional transition zone, the Guinea-Congolia/Zambezia regional transition zone and the Guineo-Congolian regional centre of endemism. Secondly, vicariance between the Somalia-Masai regional centre of endemism and all other phytochoria mentioned above.

Phylogenetic position: The sister genus is Gen. Nov. F.

The synapomorphies shared with Gen. Nov. F comprise:

- R<sub>1</sub>+R<sub>2</sub> on a long stalk (stalk has the length of 50% of R<sub>3</sub>) in male and female; (7);
- Gnathal arms well developed and connected by a small, broad and short plate-like (rectangular) bulla ventrally; (19);
- Uncus has a heavy appearance, it is strongly sclerotized with a more or less flat dorsal surface; (44);
- Gnathos large, 40% or 50% of the size of valva, elongated, looking like a wing of a penguin, its rounded end is well above or below the costa of valva; (91).

Description: *Head:* Rough-scaled; medium long hair-like scales of usually brown mixed with olive, glossy; a pair of pits absent on lower fronto-clypeus, a pair of conical projections absent on lower fronto-clypeus in both sexes; pits behind the labial palpi are tiny slits or absent; the labial palpi medium long, less than eye diameter and consist of two segments, the upper segment is the longest (2.5× as long as basal segment); antennae bipectinated in both sexes, branches narrow (well sclerotized) and of almost equal width from base to tip; dorsal and lateral side of branches not scaled but covered with long setae; flagellum scaled cream.

*Thorax:* Densely covered with broader and hair-like scales, mainly olive on patagia, glossy; tegulae not pronounced, olive or dark cream coloured, glossy; with a short crest on metathorax. Epiphyses are absent in both sexes. Hindlegs with two pairs of short, thick tibial spurs with a thorn-like tip, inner spur shorter, sometimes tiny, lower pair longer (up to 0.7 mm), upper pair shorter (up to 0.5 mm); pretarsus with a pair of pulvilli.

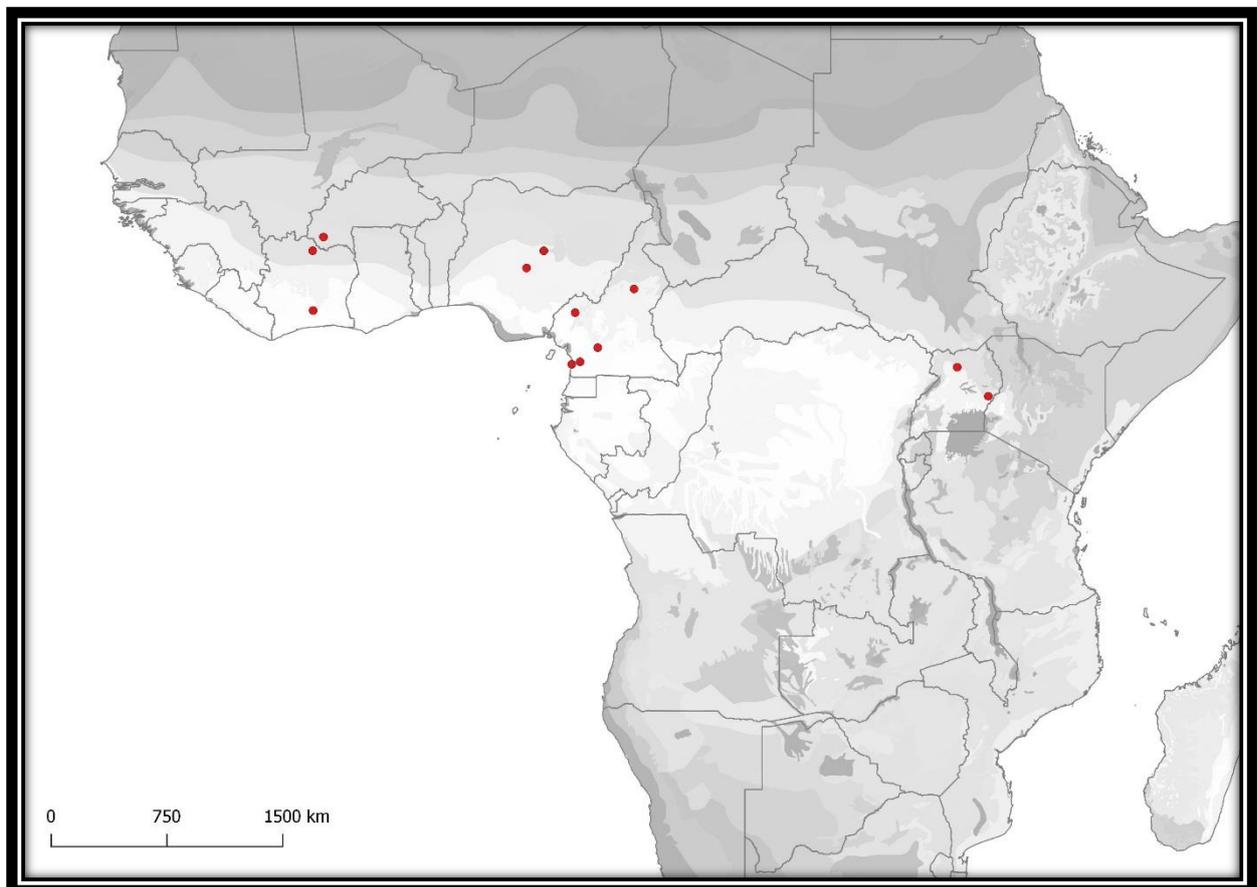
Forewing upperside without any geometric design but with a simple and reduced net-like pattern of narrow dark brownish-olive short lines from costa to dorsum; a sub-terminal line from apex to end of CuA<sub>2</sub> is always present in both sexes but varies in width (it might be a narrow band or just a line), usually cream or dark olive; CuA<sub>2</sub> dark olive and cream below. Hindwing upperside is light olive and glossy. Fringe hair-like and short on both wings (ciliae less than 1.0 mm). Wing venation: in forewing 1A+2A long forked at base; CuP absent; CuA<sub>2</sub> originating from near hind margin of posterior cell; CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> separated (separation of CuA<sub>1</sub> and M<sub>3</sub> greater) and initiating from apical angle of posterior cell; M<sub>1</sub> initiating from distal margin of median cell; R<sub>1</sub>+R<sub>2</sub> on a long stalk (stalk has the length of 50% of R<sub>3</sub>) and initiating from near anterior angle of median cell in male and female; R<sub>3</sub>+R<sub>4</sub>+R<sub>5</sub> long stalked and initiating from anterior angle of median cell; Sc more or less parallel to R<sub>1</sub>. In hindwing 3A present; 1A+2A present, often with a small fork at base; CuP reduced to a fold, sometimes sclerotized near base; CuA<sub>2</sub> initiating from near hind margin of posterior cell; CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> initiating from apical angle of posterior cell, separated; M<sub>1</sub> and Rs initiating from apical angle of anterior cell, widely separated; a long bar is present from base of Rs to Sc+R<sub>1</sub>, the latter is sometimes slightly S-shaped at its centre; with a small vein in discocellular cell on both forewing and hindwing, sometimes with a tiny fork at distal margin in forewing. Retinaculum and frenulum absent.

*Abdomen:* With dense hair-like scales and short abdominal tuft, never longer than one-fourth of abdomen length.

*Male genitalia.* Saccus short, broadly rounded at tip; the vinculum and tegumen are fused, forming a firm ring, tegumen 2 x broader than vinculum; uncus with heavy appearance and medium long (50% length of gnathos), broad, hollow inside, flat dorsally, slightly bent downwards (in lateral view), not bifurcated at tip. Valva soft, thinly membranous and without any structures, broadly elongated, distal edge strongly oblique, at tip broadly rounded, short setae on inner side, edges are soft, the whole valva breaks easily during preparation; a broad (50% of width of valva) sclerotized

transtilla is present; it has no setae. Sacculus is narrow and present on 40% of length of valva. Gnathal arms large (one arm as large as 80% of valva in ventral view), mainly attached to upper part of tegumen, arms with many short folds distally and are connected by a narrow, very short band-like bulla ventrally; the gnathal arms are short (ending close to costa of valva) and broad (50% of width of valva). Juxta is large (as large as 40% of transtilla), broadly V-shaped and without any processes. Phallus is simple and tube-like, narrow, very long (in length slightly longer than the length of tegumen + valva in lateral view), not bent; vesica without cornuti.

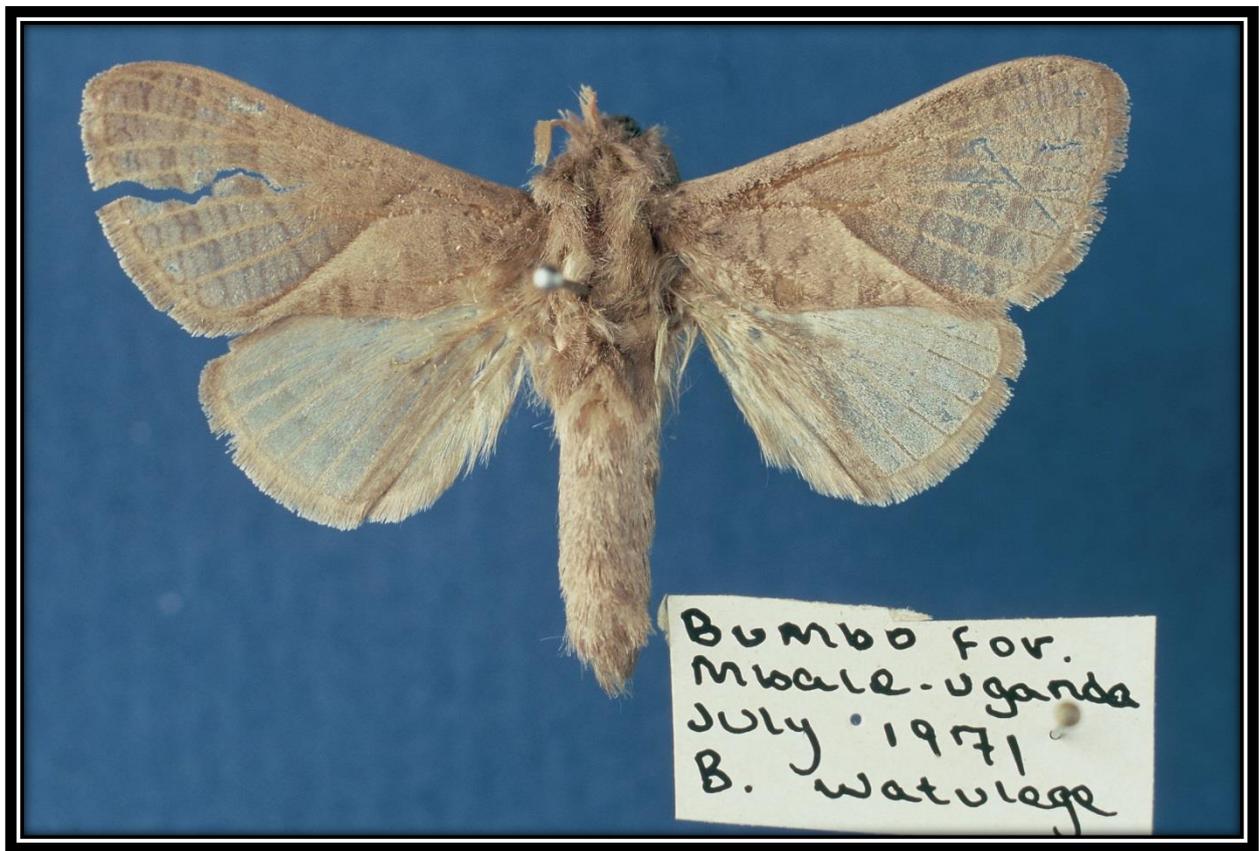
*Female postabdominal structure.* Papillae anales broad, dorsal part obliquely 8-shaped or elliptic in posterior view, covered with short setae; segment 8 rather triangular in shape (lateral view) with a flat dorsal side, narrow ventrally, setose only along its entire posterior margin, not emarginated dorso-anteriorly; a narrow band is attached to below each base of anterior apophysis running to below ventral edge of segment 8; posterior apophyses with a large broad and rectangular-shaped base.



**FIGURE 33.** Distribution of Gen. Nov. E (red dots).



**FIGURE 34.** Gen. Nov. E, *fraterna*, Type, [Cameroon] Bipindi [on third label] [no date, no collector], ex ZMHU, male, genitalia slide number 08/112008 I. Lehmann. Wingspan 37.5 mm



**FIGURE 35.** Gen. Nov. E, sp. nov. 1, Uganda, Mbale, Bumbo Forest, July 1971, B. Watulege leg., ex NMK, male, genitalia slide number 21/012008 I. Lehmann. Wingspan 40.0 mm



**FIGURE 36.** Gen. Nov. E, sp. nov.2, Uganda, Gulu, Abera Forest, August 1971, B. Watulege leg., ex NMK, female, genitalia slide number 23/012008 I. Lehmann. Wingspan 44.0 mm

#### 4.10 Gen. Nov. F

The genus is defined by the following autapomorphies:

- Extremely long (at least 3 x as long as width of segment 8) and extremely narrow anterior apophyses with a very small broad base; (33);
- Gnathos large, 50% of the size of valva, elongated with many strong folds on its whole length, its rounded end is below basal costa of valva but well above juxta; (94).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes; (11).

Type species of genus (cf. Figures 38, 39): Gen. Nov. F + sp. nov. f

Type locality: Somalia, Deshek Wamu [misspelling of Deshek Wama], 26.04.1989, Dr. H. Politzar leg., male, genitalia slide number 12/082009 I. Lehmann, ex ZSM; depository in ZSM.

Number of species in genus at present: 05;

all localities of studied species per country: Somalia; Kenya.

Distribution of genus at present (cf. Figure 37): lowland areas of the Somalia-Masai regional centre of endemism, at present from the Laag Dheere River (around Afmadow) and Caamnoole River in southern Somalia, northwestwards to Mandera (Kenya) and westwards to Wajir, Kacheliba, Lokori and Lodwar (west of Lake Turkana) in northwestern Kenya.

The reconstructed and predicted ancestral area is the Somalia-Masai regional centre of endemism.

The reconstructed biogeographic events comprise: First, dispersal in the Somalia-Masai regional centre of endemism, the Guinea-Congolia/Sudania regional transition zone, the Guinea-Congolia/Zambezia regional transition zone and the Guineo-Congolian regional centre of endemism. Secondly, vicariance between the Somalia-Masai regional centre of endemism and all other phytochoria mentioned above.

Phylogenetic position: The sister genus is Gen. Nov. E.

The synapomorphies shared with Gen. Nov. E comprise:

- R<sub>1</sub>+R<sub>2</sub> on a long stalk (stalk has the length of 50% of R<sub>3</sub>) in male and female; (7);
- Uncus has a heavy appearance, it is strongly sclerotized with a more or less flat dorsal surface; (44);

- Gnathos large, 40% or 50% of the size of valva, elongated, looking like a wing of a penguin, its rounded end is well above or below the costa of valva; (91).

Description:

*Head:* Rough-scaled; medium long hair-like scales of usually light grey mixed with sepia, glossy; a pair of small pits present on lower fronto-clypeus in both sexes, a pair of conical projections absent on lower fronto-clypeus in both sexes; pits behind the labial palpi are tiny slits or absent; the labial palpi medium long, less than eye diameter and consist of two segments, the upper segment is the longest (2.0× as long as basal segment), shape unusual for Metarbelidae since it is thick and oval; a strongly reduced tiny third segment on top is present or absent; antennae bipectinated in both sexes (female with unusual long branches of 3.5× width of shaft and slightly longer than in male), narrow branches (well sclerotized) and of almost equal width from base to tip; dorsal and lateral side of branches not scaled but covered with long setae; flagellum scaled cream.

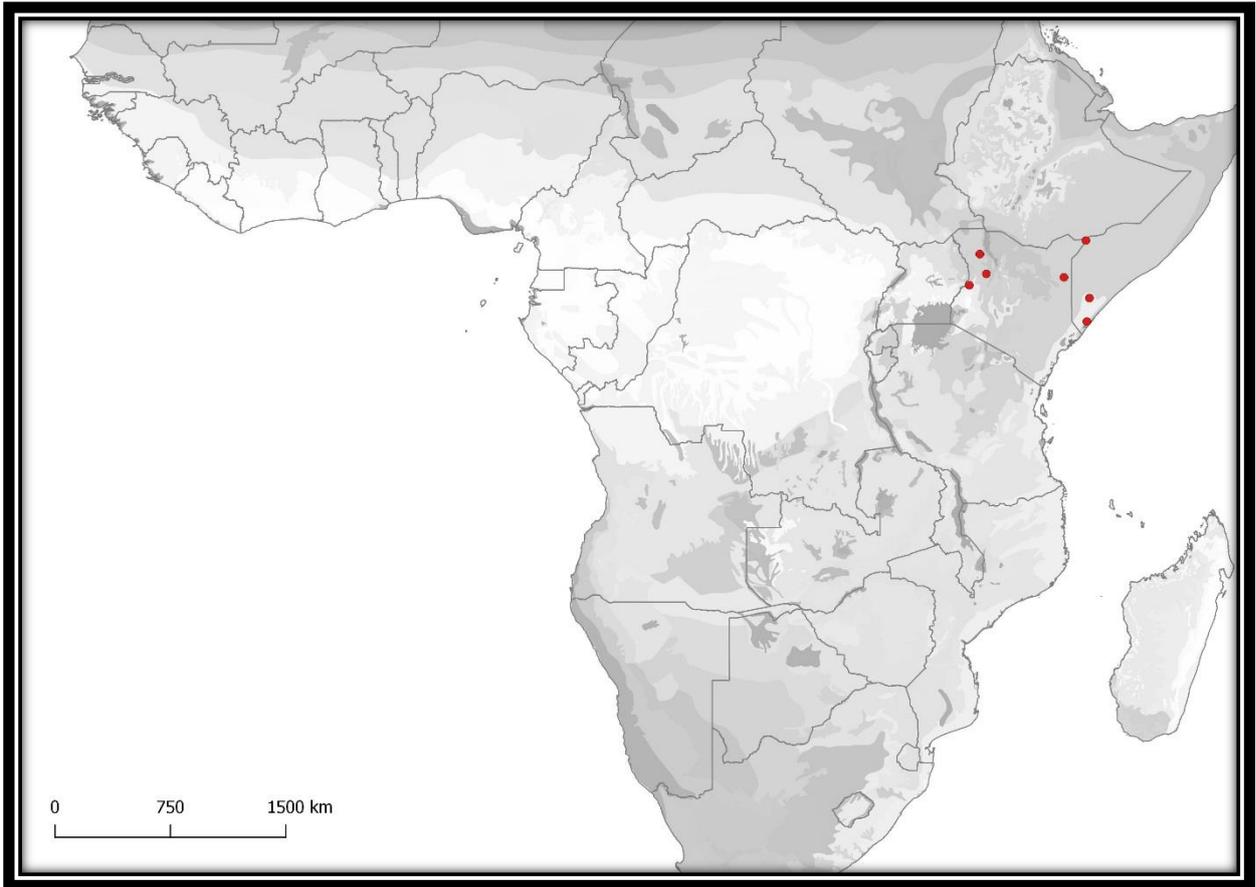
*Thorax:* Densely covered with broader and hair-like scales, mainly light grey or light ocher on patagia, glossy; tegulae not pronounced light grey or chestnut coloured mixed with some sepia scales, glossy; with a short crest on metathorax. Epiphyses are present in both sexes and long (1.9 mm). Hindlegs with two pairs of long, very narrow tibial spurs with a thorn-like tip, inner spur shorter, upper pair longer (up to 1.3 mm), lower pair shorter (up to 1.0 mm); pretarsus with a pair of pulvilli.

Forewing of both sexes narrow with a rounded apex; forewing upperside without any geometric design but with a simple and reduced net-like pattern of narrow dark brownish-olive lines from costa to dorsum on a light ocher or light grey ground-colour; below base of 1A+2A a short patch of sepia; CuA<sub>2</sub> not distinctly marked. Hindwing upperside is light grey or light cream and glossy. Fringe hair-like and rather long on both wings (ciliae less than 1.3 mm). Wing venation: in forewing 1A+2A forked at base; CuP absent; CuA<sub>2</sub> originating from near hind margin of posterior cell; CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> separated (separation of CuA<sub>1</sub> and M<sub>3</sub> greater) and initiating from apical angle of posterior cell; M<sub>1</sub> initiating from distal margin of median cell; R<sub>1</sub>+R<sub>2</sub> on a long stalk (stalk has the length of 50% of R<sub>3</sub>) and initiating from near anterior angle of median cell in male and female; R<sub>3</sub>+R<sub>4</sub>+R<sub>5</sub> long stalked and initiating from anterior angle of median cell; Sc more or less parallel to R<sub>1</sub>. In hindwing 3A present; 1A+2A present, sometimes with a small fork at base; CuP reduced to a fold; CuA<sub>2</sub> initiating from near hind margin of posterior cell; CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> initiating from apical angle of posterior cell, separated; M<sub>1</sub> and R<sub>s</sub> initiating from apical angle of anterior cell, separated; no bar is present from base of R<sub>s</sub> to Sc+R<sub>1</sub>; with a small vein in discocellular cell on both forewing and hindwing. Retinaculum and frenulum absent.

*Abdomen:* With dense hair-like scales and short abdominal tuft, never longer than one-fourth of abdomen length.

*Male genitalia.* Saccus short, broadly rounded at tip; the vinculum and tegumen are fused, forming a firm ring, tegumen 3 x broader than vinculum; uncus with heavy appearance but short (25% length of gnathos), narrow, hollow inside, flat dorsally, slightly bent downwards (in lateral view), not bifurcated at tip, tip rounded. Valva soft, thinly membranous and without any structures, narrowly elongated, at tip rounded, short setae on inner side, edges are soft, the whole valva breaks easily during preparation; a very broad (60% of width of valva) thinly membranous transtilla is present (breaks easily during preparation in the middle); it has no setae. Sacculus is narrow and present on 40% of length of valva. Gnathal arms large (one arm as large as 50% or 60% of valva in ventral view), mainly attached to upper part of tegumen, arms with many long, deep folds that cover almost the whole gnathos; gnathal arms are broadly connected by a bulla (as broad as 35% of gnathos = one of the broadest among Metarbelidae) that is ventrally with no folds only distally; the gnathal arms are long (ending a little below costa of valva) and broad (30% of width of valva). Juxta is large (as large as 40% of transtilla), broadly V-shaped, tips acuminate, and without any processes. Phallus is simple and tube-like, narrow, long (in length longer than the length of valva in lateral view), not bent; vesica without cornuti.

*Female postabdominal structure.* Papillae anales broad, dorsal part obliquely 8-shaped or elliptic in posterior view, covered with short setae; segment 8 rectangular in shape (lateral view) with a flat dorsal side, narrow ventrally, setose only along its entire posterior margin with very long setae, not emarginated dorso-anteriorly; a narrow band is attached to below each base of anterior apophysis running to below ventral edge of segment 8; extremely long (at least 3 x as long as width of segment 8) and extremely narrow anterior apophyses with a very small broad base.



**FIGURE 37.** Distribution of Gen. Nov. F (red dots).



**FIGURE 38.** Gen. Nov. F, sp. nov. f, Somalia, Deshek Wamu [Wama], 26.04.1989, Dr. Politzar leg., ex ZSM, male, genitalia slide number 12/082009 I. Lehmann. Wingspan 24.0 mm



**FIGURE 39.** Gen. Nov. F, sp. nov. f, Somalia, Deshek Wamu [Wama], 12.05.1989, Dr. Politzar leg., ex ZSM, female, genitalia slide number 21/082009 I. Lehmann. Wingspan 26.5 mm

#### 4.11 *Kroonia* Lehmann, 2010a

The genus is defined by the following autapomorphy:

- Posterior apophyses extend as crescent-shaped flap onto the papillae anales; (32).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes; (11).

Type species of genus (cf. Figures 41, 42): *Kroonia murphyi* Lehmann, 2010a

Type locality: Malawi, Mount Mulanje, Ruo Gorge, 07. -10.02.2004, L. Aarvik leg., male, genitalia slide number 28/092008 I. Lehmann, ex NHMO; depository in NHMO.

Number of species in genus at present: 14;

all localities of studied species per country: Senegal; Cameroon; Democratic Republic of the Congo; Kenya; Tanzania; Malawi; Zimbabwe; Republic of South Africa; Namibia.

Distribution of genus at present (cf. Figure 40): at present disjunct in West Africa; outside of the Guineo-Congolian rain forest in lowland, submontane and montane areas from southwestern Senegal probably to northern Cameroon; from western and southern Kenya as well as eastern Tanzania southwestwards to Katanga and via Malawi and Zimbabwe southwards to the Republic of South Africa and westwards to north-central Namibia.

The reconstructed and predicted ancestral area is the Zambesian regional centre of endemism.

The reconstructed biogeographic events comprise: First, dispersal in the Zambesian regional centre of endemism, from there dispersal into the Somalia-Masai regional centre of endemism, the Karoo-Namib regional centre of endemism, the Zanzibar-Inhambane regional mosaic and the Tongaland-Pondoland regional mosaic. Secondly, vicariance between the Zambesian regional centre of endemism and all other phytochoria mentioned above.

Phylogenetic position: The sister genus is Gen. Nov. G.

The synapomorphies shared with Gen. Nov. G comprise:

- R<sub>1</sub>+R<sub>2</sub> on a long stalk (stalk has the length of 50% of R<sub>3</sub>) in male and female; (7);
- Gnathal arms extremely long, almost touching upper part of juxta; (22);
- Valva narrow, only twice or less as broad as gnathal arm in lateral view; (28);
- Valva long, almost as long as tegumen + vinculum, tip very narrow and long elongated, tip as long as uncus in lateral view, end of tip slightly pointed; (29);

- Uncus has a heavy appearance, it is strongly sclerotized with a more or less flat dorsal surface; (44).

Description: *Head:* Rough-scaled; medium long hair-like scales of usually cream or light brown mixed with sepia, glossy, on fronto-clypeus; a pair of small rather reduced pits present on lower fronto-clypeus in both sexes, a pair of conical projections absent on lower fronto-clypeus in both sexes; pits behind the labial palpi are tiny and oval shaped; the labial palpi rather short, less than eye diameter and consist of two segments, the upper segment is the longest (1.5× as long as basal segment); a strongly reduced tiny third segment on top is sometimes present; antennae bipectinated in both sexes (female with branches of 3.0× width of shaft and slightly shorter than in male), branches narrow (well sclerotized) and of almost equal width from base to tip; dorsal and lateral side of branches not scaled but covered with long setae; flagellum scaled cream.

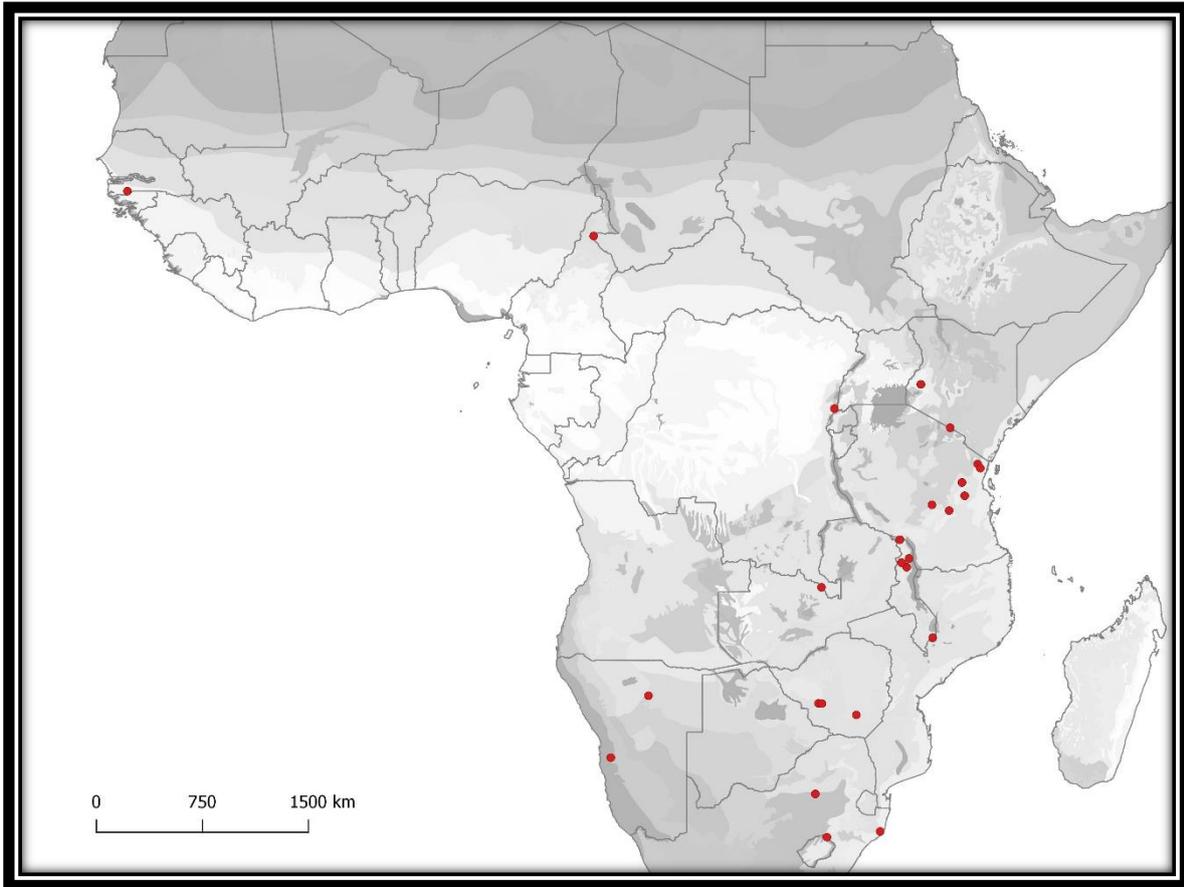
*Thorax:* Densely covered with broader and hair-like scales, mainly light brown, light olive or light ocher on tegulae that are not pronounced; patagia often sepia or chestnut, glossy; with a short crest on metathorax. In fresh specimens three rounded dark chestnut spots are present, one on each lower part of tegulae and the third one on the crest of metathorax. Epiphyses are present in both sexes and narrow, long (up to 2.0 mm). Hindlegs with two pairs of tibial spurs with a thorn-like tip, inner spur shorter, upper pair narrow and longer (up to 1.3 mm), lower pair thick and shorter (up to 0.8 mm); pretarsus with a pair of pulvilli.

Forewing of both sexes broad with a rounded apex; forewing upperside without any geometric design but with a simple net-like pattern of narrow and short dark brownish-olive lines from costa to dorsum on a light ocher or brown ground-colour; a sepia or chestnut coloured long streak is usually prominent and occurs on the lower median extending well onto the base of CuA<sub>2</sub>, CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> in both sexes; CuA<sub>2</sub> not distinctly marked. Hindwing upperside is light grey or cream, with some fine brown striae, glossy. Fringe hair-like and rather short on both wings (ciliae less than 1.0 mm). Wing venation: in forewing 1A+2A forked at base; CuP absent; CuA<sub>2</sub> originating from near hind margin of posterior cell; CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> separated and initiating from apical angle of posterior cell; M<sub>1</sub> initiating from distal margin of median cell; R<sub>1</sub>+R<sub>2</sub> on a long stalk (stalk has the length of 50% of R<sub>3</sub>) and initiating from near anterior angle of median cell in male and female; R<sub>3</sub>+R<sub>4</sub>+R<sub>5</sub> long stalked and initiating from anterior angle of median cell; Sc more or less parallel to R<sub>1</sub>. In hindwing 3A present; 1A+2A present, sometimes with a small fork at base; CuP present in both sexes; CuA<sub>2</sub> initiating from near hind margin of posterior cell; CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> initiating from apical angle of posterior cell, separated; M<sub>1</sub> and Rs initiating from apical angle of anterior cell, separated; a bar is usually absent from Rs to Sc+R<sub>1</sub>; with a small vein in discocellular cell on both forewing and hindwing. Retinaculum and frenulum absent.

*Abdomen:* With dense hair-like scales and short abdominal tuft, never longer than one-fourth of abdomen length.

*Male genitalia.* Saccus long or very long, sometimes 30% of length of valva, broadly rounded at tip; the vinculum and tegumen are fused, forming a firm ring, tegumen 3 x broader than vinculum; uncus with heavy appearance but short (up to 30% length of gnathos), narrow, flat dorsally, not bifurcated at tip, tip rounded. Valva soft, thinly membranous and without any structures, narrowly elongated, at very narrow elongated tip rounded, short setae on inner side, edges are soft; a narrow (ca. 15% of width of valva) and very thinly membranous structure is present (not easy to see), possibly a transtilla that is not well developed, it has no setae. Sacculus is narrow and present on 40% of length of valva. Gnathal arms very large (one arm as large as 80% or 90% of valva in ventral view), attached to upper part or central part of uncus, arms with medium long and fine folds that cover the lower outer part of gnathos; gnathal arms are only distally connected by a narrow sclerotized band-like bulla (as broad as 20% of width of valva) near the ventral end; the gnathal arms are often very long (ending near juxta) and broader than basal width of valva. Juxta is broadly V-shaped, tips rounded, without any processes. Phallus is simple and tube-like, narrow, arrow-shaped distally, very long (longer than length of valva), not bent; vesica without cornuti.

*Female postabdominal structure.* Papillae anales broad, dorsal part obliquely 8-shaped or elliptic in posterior view, covered with long and short setae; segment 8 rectangular in shape, more narrow ventrally (lateral view), with a wave-like dorsal surface, setose along its entire posterior margin with very long setae; a broad band is attached to below each base of anterior apophysis running to below ventral edge of segment 8; posterior apophyses extend as crescent-shaped flap onto the papillae anales.



**FIGURE 40.** Distribution of the genus *Kroonia* (red dots).



**FIGURE 41.** *Kroonia murphyi*, Holotype, Malawi, Mount Mulanje, 07.-10.02.2004, L. Aarvik leg., ex NHMO, male, genitalia slide number 28/092008 I. Lehmann. Wingspan 33.5 mm



**FIGURE 42.** *Kroonia murphyi*, Paratype, Malawi, Misuku Hills, Mugesse Forest Reserve, 13.01.2009, R.J. Murphy leg., ex NHMO, female, genitalia slide number 14/062009 I. Lehmann. Wingspan 40.5 mm

#### 4.12 Gen. Nov. G

The genus is defined by the following autapomorhy:

- A band-like transtilla is present, connected by a narrow thin membrane, but a well sclerotized dorsal edge is tube-like with a hook-like appendice and is not connected to the membrane; (92).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes; (11).

Type species of genus (cf. Figure 44): Gen. Nov. G + *willihaberlandi* (Lehmann, 2008)

Type locality: Tanzania, Mufindi, 1955, P. Burton leg., ex. coll. Townsend 14936, male, genitalia slide number 01/112006 I. Lehmann, ex NMK; depository in NMK.

Note: the locality for both sexes is Gen. Nov. G + sp. nov. g, Malawi, Lilongwe District, Dzalanyama Forest, 1.300 m, 21.-25.04.2006, R.J. Murphy leg., male, genitalia slide number 16/022008 I. Lehmann, author's collection; depository in ZFMK.

Number of species in genus at present: 05;

all localities of studied species per country: Zambia; Tanzania; Malawi.

Distribution of genus at present (cf. Figure 43): disjunct, submontane and montane areas of the Udzungwa Mountains (including Sao Hill west of Mufindi) in eastern Tanzania, the extreme northeast Zambia (Mbala) and various isolated habitats in northern, central and southern Malawi.

The reconstructed and predicted ancestral area is the Zambeesian regional centre of endemism.

The reconstructed biogeographic events comprise: First, dispersal in the Zambeesian regional centre of endemism, from there dispersal into the Somalia-Masai regional centre of endemism, the Karoo-Namib regional centre of endemism, the Zanzibar-Inhambane regional mosaic and the Tongaland-Pondoland regional mosaic. Secondly, vicariance between the Zambeesian regional centre of endemism and all other phytochoria mentioned above.

Phylogenetic position: The sister genus is *Kroonia*.

The synapomorphies shared with *Kroonia* comprise:

- R<sub>1</sub>+R<sub>2</sub> on a long stalk (stalk has the length of 50% of R<sub>3</sub>) in male and female; (7);
- Gnathal arms extremely long, almost touching upper part of juxta; (22);
- Valva narrow, only twice or less as broad as gnathal arm in lateral view; (28);

- Valva long, almost as long as tegumen + vinculum, tip suddenly very narrow and long elongated, tip might be as long as uncus in lateral view, end of tip slightly pointed; (29);
- Uncus has a heavy appearance, it is strongly sclerotized with a more or less flat dorsal surface; (44).

Description: *Head:* Rough-scaled; medium long hair-like scales of usually light grey mixed with grey, glossy; a pair of small rather reduced pits present on lower fronto-clypeus in both sexes, a pair of conical projections absent on lower fronto-clypeus in both sexes; pits behind the labial palpi are tiny and oval shaped; the labial palpi rather short, less than eye diameter and consist of three segments, upper segment rather short (half of length of central segment, but sometimes reduced), the basal segment is 1.5× shorter than central segment; antennae bipectinated and with short branches in both sexes (female and male with branches of 1.5× width of shaft), narrow (well sclerotized) and of almost equal width from base to tip; dorsal and lateral side of branches not scaled but covered with long setae; flagellum scaled cream.

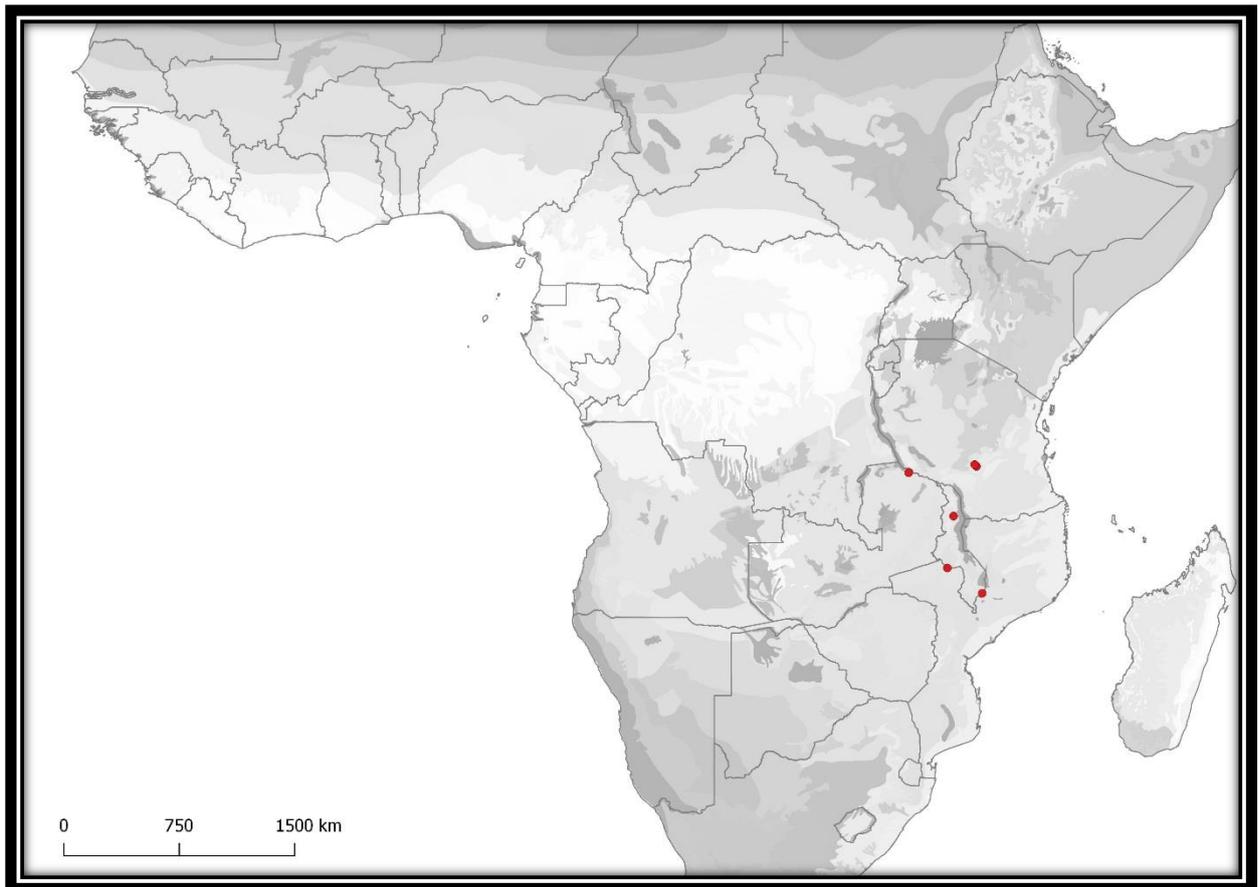
*Thorax:* Densely covered with broader and hair-like scales, mainly light grey with a strong silvery shine on tegulae and patagia; with a short crest on metathorax. Epiphyses are present in both sexes and narrow, long (up to 1.9 mm). Hindlegs with two pairs of tibial spurs with a thorn-like tip, inner spur shorter, upper pair narrow and longer (up to 1.1 mm), lower pair thick and shorter (up to 0.8 mm); pretarsus with a pair of pulvilli.

Forewing of both sexes rather narrow with a rounded apex; forewing upperside without any geometric design but with a simple pattern on a light grey or grey-olive ground-colour with a strong silvery shine in both sexes; the pattern comprises small patches of dark brownish-olive that occur in the sub-terminal and post-medial area from costa to dorsum with a dark grey patch from base of CuA<sub>2</sub> to base of M<sub>3</sub>; CuA<sub>2</sub> not distinctly marked. Hindwing upperside is light grey or cream, glossy. Fringe hair-like and rather short on both wings (ciliae less than 1.0 mm). Wing venation: in forewing 1A+2A forked at base; CuP absent; CuA<sub>2</sub> originating from near hind margin of posterior cell; CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> separated and initiating from apical angle of posterior cell; M<sub>1</sub> initiating from distal margin of median cell; R<sub>1</sub>+R<sub>2</sub> on a long stalk (stalk has the length of 50% of R<sub>3</sub>) that is sometimes hard to see but is initiating from near anterior angle of median cell in male and female; R<sub>3</sub>+R<sub>4</sub>+R<sub>5</sub> long stalked and initiating from anterior angle of median cell; Sc more or less parallel to R<sub>1</sub>. In hindwing 3A present; 1A+2A present, sometimes with a small fork at base; CuP present in both sexes; CuA<sub>2</sub> initiating from near hind margin of posterior cell; CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> initiating from apical angle of posterior cell, separated; M<sub>1</sub> and Rs initiating from apical angle of anterior cell, separated; a bar is usually absent from Rs to Sc+R<sub>1</sub> or it is very short; with a small vein (weak in male) in discocellular cell on both forewing and hindwing; sometimes forked in female. Retinaculum and frenulum absent.

*Abdomen:* With dense hair-like scales and short abdominal tuft, never longer than one-fourth of abdomen length.

*Male genitalia.* Saccus absent or strongly reduced, sometimes small rectangular, broadly rounded at tip; the vinculum and tegumen are fused, forming a firm ring, tegumen 3-4 x broader than vinculum, that is very narrow; uncus bent downwards with heavy appearance but short (up to 30% length of gnathos), narrow, flat dorsally, not bifurcated at tip, tip rounded. Valva soft, strongly bent upwards in lateral view, thinly membranous and without any structures, narrowly elongated, a more narrow elongated tip is rather rectangular or rounded, short setae on inner side, but dorsal side of valva with very long setae that touch the edge of gnathos, edges of valva are soft; a band-like transtilla is present, connected by a narrow thin membrane but a well sclerotized dorsal edge is tube-like with an hook-like appendice and is not connected; transtilla without setae. Sacculus is narrow and present on 30% to 40% of length of valva. Gnathal arms large (one arm as large as 50% of valva in ventral view), attached to base of uncus, arms with medium long and fine folds that cover the outer part and two deep folds extending on the whole width of gnathos; gnathal arms are only distally connected by a narrow sclerotized band-like bulla (as broad as 10% of width of valva) near the ventral end; the gnathal arms are often long (ending a little bit above juxta) but only 50% as broad as basal width of valva. Juxta is broadly V-shaped, tips rounded, without any processes. Phallus is simple and tube-like, broad, slightly arrow-shaped distally, short (not longer than 40% of length of valva), not bent; vesica without cornuti.

*Female postabdominal structure.* Papillae anales broad, dorsal part obliquely 8-shaped or elliptic in posterior view, covered with short setae; segment 8 rectangular in shape, more narrow ventrally but with a broad rounded end (lateral view), with an open dorsal surface on *ca.* 90% of dorsal side, setose along its posterior margin with short setae, long setae only on ventral half; a broad band (broadest part at its centre) is attached to below each base of anterior apophysis and extends close to the ventral edge of segment 8; anterior apophyses are broad on *ca.* 50% of their length.



**FIGURE 43.** Distribution of Gen. Nov. G (red dots).



**FIGURE 44.** Gen. Nov. G, *willihaberlandi*, Paratype, Tanzania, Udzungwa Mountains, Sao Hill [west of Mufindi], 19.-20.03.1993, L. Aarvik leg., ex NHMO, male, genitalia slide number 25/022008 I. Lehmann. Wingspan 27.5 mm



**FIGURE 45.** Gen. Nov. G, sp. nov. g, Malawi, Dzalanyama Forest, 21.-25.04.2006, R.J. Murphy leg., ex own coll., male, genitalia slide number 16/022008 I. Lehmann. Wingspan 31.5 mm



**FIGURE 46.** Gen. Nov. G, sp. nov. g, Malawi, Lilongwe District, Dzalanyama Forest, 11.-13.04.2008, R.J. Murphy leg., ex own coll., female, genitalia slide number 112008 I. Lehmann. Wingspan 40.5 mm

#### 4.13 *Saalmulleria* Mabilie, 1891

The genus is defined by the following autapomorphy:

- Very large, two pear-shaped papillae anales in horizontal position; (181).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of female; [possibly also in male absent] (11).

Type species of genus (cf. Figure 48): *Saalmulleria stumpffi* (Saalmüller, 1884)

Type locality: Madag. [Madagascar], Loucoubè, 82 [or] 83, [on tiny second label: x.II.82 = 10.02.1882], Stumpff [leg.], [on third label: “Saalmülleria stumpffi”], female, genitalia slide number 20/122008 I. Lehmann, ex SNMF; depository in SNMF.

Number of species in genus at present: 03

all localities of studied species per country: Madagascar.

Distribution of genus at present (cf. Figure 47): lowland and submontane areas of Madagascar, at present known from the northern and southern part.

The reconstructed and predicted ancestral areas are the Guinea-Congolia/Zambezia regional transition zone and the Guinea-Congolia/Sudania regional transition zone.

The reconstructed biogeographic events comprise: First, dispersal from the Guinea-Congolia/Zambezia regional transition zone, the Guinea-Congolia/Sudania regional transition zone into the East Malagasy regional centre of endemism and West Malagasy regional centre of endemism. Secondly, vicariance between the East Malagasy regional centre of endemism, West Malagasy regional centre of endemism and all other phytochoria mentioned above.

Phylogenetic position: The genus is part of an unresolved polytomy (cf. Figure 6a).

Description: *Head:* Unusually small (up to 3.0 mm in diameter only), rough-scaled; medium long hair-like scales of brown with a vinaceous glint on fronto-clypeus; a pair of pits absent on lower fronto-clypeus in female, a pair of conical projections absent on lower fronto-clypeus; pits behind the labial palpi are absent; labial palpi very short, less than half of eye diameter and consist of three segments, all segments are of almost equal length, the basal segment is 1.5× broader than the two other segments; antennae bipectinated in female with long branches (3.5× width of shaft), narrow (well sclerotized) and of almost equal width from base to tip; dorsal and lateral side of branches not scaled but covered with long setae; flagellum scaled dark cream.

*Thorax:* Densely covered with broader and hair-like scales, mainly brown with a vinaceous shine on tegulae and patagia; with a chestnut coloured crest on metathorax. Epiphyses are present in female and medium broad, flat, long (up to 2.5 mm). Hindlegs with two pairs of tibial spurs with a thorn-like tip, inner spur shorter, upper pair

narrow and longer (up to 2.1 mm), lower pair thick and shorter (up to 1.4 mm); pretarsus with a pair of pulvilli.

Forewing with a length of up to 33.5 mm (representing the largest *Metarbelidae* worldwide) very broad with a rounded apex; forewing upperside without any geometric design but with a simple pattern of a large dark brownish-olive lunule-like patch (sometimes absent or reduced), in its centre with a vitreous appearance, from near base of  $CuA_1$  to base of  $M_2$  and various dark olive terminal, sub-terminal and post-medial patches and bands, sometimes broadly V-shaped, from near costa to  $CuA_2$  on a grey-olive or light brown-olive ground-colour;  $CuA_2$  not distinctly marked; below base of  $1A+2A$  a dark chestnut patch. Hindwing with a pointed apex, upperside is grey-olive or light brown-olive, glossy, sometimes with a large dark brownish-olive lunule-like patch from near base of  $CuA_1$  to base of  $M_2$ . Fringe hair-like and short on both wings (ciliae less than 1.1 mm). Wing venation: in forewing  $1A+2A$  forked at base;  $CuP$  represented by a fold on two-thirds of its original length;  $CuA_2$  originating from near hind margin of posterior cell;  $CuA_1$ ,  $M_3$  and  $M_2$  separated and initiating from apical angle of posterior cell;  $M_1$  initiating from distal margin of median cell;  $R_1+R_2$  on a long stalk (stalk has the length of 50% of  $R_3$ ) and initiating from near anterior angle of median cell in female;  $R_3+R_4+R_5$  long stalked and initiating from anterior angle of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  present with a fork at base;  $CuP$  present;  $CuA_2$  initiating from near hind margin of posterior cell;  $CuA_1$ ,  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1$  and  $Rs$  initiating from apical angle of anterior cell, separated; a bar is absent from  $Rs$  to  $Sc+R_1$ ; with a vein in discocellular cell on both forewing and hindwing, vein long forked in forewing of female. The discocellular cell of the hindwing has an unusual shape since it looks like a fish-tail. Retinaculum and frenulum absent.

*Abdomen:* With dense hair-like scales and short abdominal tuft, never longer than one-fifth of abdomen length. Noteworthy, is a kind of leather-like and strong skin-like structure after all scales have been removed.

*Male genitalia.* Unknown.

*Female postabdominal structure and genitalia.* Papillae anales very large, comprising two pear-shaped lobes in horizontal position with many short setae (mainly ventrally) that are sclerotized; segment 8 represents a medium broad rectangular band, more narrow ventrally but with a narrow rounded end (lateral view), setose near its posterior margin with long setae; a very narrow band (broadest part at its base) is weakly attached at its base with a rectangular plate-like structure (sometimes hard to see) to the base of anterior apophysis and extends close to the ventral edge of segment 8; anterior apophyses are narrow, broader and slightly knee-like close to their base. Ductus bursae and corpus bursae are strongly membranous, but not sclerotized, and without any structures. Corpus bursae is oval; ductus bursae broad and short.



**FIGURE 47.** Distribution of the genus *Saalmulleria* (red dots).



**FIGURE 48.** *Saalmulleria stumpffi*, Type, Madag. [Madagascar], Loucoubè, 82 [on tiny third label: 10.02.1882], Stumpff leg., ex SNMF, female, genitalia slide number 20/122008 I. Lehmann. Wingspan 70.5 mm

#### 4.14 Gen. Nov. H

The genus is defined by the following autapomorphies:

- Triangular-shaped forewings and triangular-shaped hindwings with straight termen in male; (157);
- Small thorn-like gnathal arm (25% the size of valva) and connected to the base of uncus by a long broad band; (159);
- Male antenna has suddenly very short branches (at *ca.* half of antenna); (161).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; [possibly also in female absent] (11).

Type species of genus (cf. Figure 50): Gen. Nov. H + sp. nov. h

Type locality: Madagascar, N. [North] de Morondava, forêt de [forest] Marofandilia, 15 m, 12.1969, P. Griveaud leg., male, genitalia slide number 08/102009 I. Lehmann, ex MNHN; depository in MNHN.

Number of species in genus at present: 01

all localities of studied species per country: Madagascar.

Distribution of genus at present (cf. Figure 49): lowland areas of Madagascar, at present known from near Marofandilia and Morondava in southwest Madagascar.

The reconstructed and predicted ancestral areas are the Somalia-Masai regional centre of endemism, the West Malagasy regional centre of endemism and the East Malagasy regional centre of endemism.

The reconstructed biogeographic events comprise: First, dispersal in the Somalia-Masai regional centre of endemism, the West Malagasy regional centre of endemism and the East Malagasy regional centre of endemism. Secondly, dispersal into the Afromontane archipelago-like regional centre of endemism, the Zanzibar-Inhambane regional mosaic and the Tongaland-Pondoland regional mosaic. Thirdly, vicariance between the West Malagasy regional centre of endemism, the East Malagasy regional centre of endemism and all other phytochoria mentioned above.

Phylogenetic position: The sister genus is Gen. Nov. I.

The synapomorphies shared with the sister genus comprise:

- R<sub>1</sub>+R<sub>2</sub> on a long stalk (stalk has the length of 40–50% of R<sub>3</sub>) in male and/or female; (7).
- Uncus has a heavy appearance, it is strongly sclerotized with a more or less flat dorsal surface; (44);

- Gnathal arm represents a strongly sclerotized thorn with a broader base and an acuminate tip and is connected by a band to the base of uncus; the gnathal arms are connected by a narrow band ventrally and end well above the costa of valva; (156);
- Transtilla is very broad (ca. 30% of width of valva); (158).

Description: *Head:* rough-scaled; medium long hair-like scales of brown with an olive glint on fronto-clypeus; a pair of pits absent on lower fronto-clypeus in male, a pair of conical projections absent on lower fronto-clypeus; pits behind the labial palpi are absent; labial palpi very short, less than half of eye diameter and consist of two segments, the basal segment is very short; antennae bipectinated in male with very long, narrow branches (7.0x width of shaft) at lower half, at ca. half of antenna the branches become suddenly very short (3.0x or less than width of shaft), branches are almost equal in width from base to tip; dorsal and lateral side of branches not scaled but covered with long setae; flagellum scaled brown.

*Thorax:* Densely covered with rather short broader and hair-like scales, mainly brown-olive with a vinaceous shine on tegulae and patagia; with a chestnut coloured crest on metathorax. Epiphyses are present in male, medium broad, flat, long (up to 2.1 mm). Hindlegs with two pairs of narrow tibial spurs with a thorn-like tip, inner spur shorter, upper pair shorter (up to 1.0 mm), lower pair longer (up to 1.2 mm); pretarsus with a pair of pulvilli.

Forewing triangular in shape with a rounded apex and short scales, not densely scaled; forewing upperside without any geometric design and without any simple pattern, except of a small sepia patch near base of  $M_3$  and very fine short dark brown lines, rather scattered or faded from near costa to dorsum, on a light brown ground-colour;  $CuA_2$  not distinctly marked; below base of  $1A+2A$  a dark chestnut patch. Hindwing triangular with a pointed apex, darker in ground-colour than forewing, upperside is mainly sepia with the outer half slightly transparent, glossy. Fringe hair-like and extremely short on both wings (ciliae less than 0.3 mm). Wing venation: in forewing  $1A+2A$  slightly forked at base;  $CuP$  represented by a fold on two-thirds of its original length;  $CuA_2$  originating from near hind margin of posterior cell;  $CuA_1$ ,  $M_3$  and  $M_2$  separated and initiating from apical angle of posterior cell;  $M_1$  initiating from near anterior angle of median cell;  $R_1+R_2$  on a long stalk (stalk has the length of 40 % of  $R_3$ ) and initiating from near anterior angle of median cell;  $R_3+R_4+R_5$  very long stalked and initiating from anterior angle of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  present with a fork at base;  $CuP$  represented by a fold on two-thirds of its original length;  $CuA_2$  initiating from near hind margin of posterior cell;  $CuA_1$ ,  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1$  and  $Rs$  initiating from apical angle of anterior cell, separated; a short bar is present from near base of  $Rs$  to  $Sc+R_1$ ; a vein in discocellular cell on both forewing and hindwing is weak or absent. The discocellular cell of the hindwing has an unusual shape since it looks almost like a fish-tail. Retinaculum and frenulum absent.

*Abdomen:* With hair-like scales and very short abdominal tuft.

*Male genitalia.* Saccus strongly reduced, broadly rounded at tip; the vinculum and tegumen are fused, forming a firm ring, tegumen 2-3 x broader than vinculum, that is very narrow; uncus bent downwards with heavy appearance but short (up to 30% length of gnathos), narrow, flat dorsally, not bifurcated at tip, tip rounded. Valva soft, strongly bent upwards in lateral view, thinly membranous and without any structures, elongated, short and long setae on inner side, edges of valva are soft; a band-like broad transtilla is present (ca. 30% of basal width of valva), well sclerotized and without setae. Sacculus is narrow and present on 40% of length of valva. Gnathal arms medium large (one arm as large as 30% of valva in ventral view), attached with a long broad band (as long as 80% of basal width of valva) to base of uncus, arms comprise a sclerotized thorn-like structure (in length 50% of basal width of valva) that is hollow and has fine folds; thorn-like gnathal arms are connected ventrally by a sclerotized band (as broad as 30% of width of transtilla); the gnathal arms are short (ending above costa of valva). Juxta is broadly V-shaped, tips rounded, without any processes. Phallus is unusually large, simple tube-like, broad, strongly bent and looks like a banana (longer than length of valva); vesica without cornuti.

*Female postabdominal structure and genitalia.* Unknown.



**FIGURE 49.** Distribution of Gen. Nov. H (red dots).



**FIGURE 50.** Gen. Nov. H, sp. nov. h, Madagascar, N. [North] de Morondava, forêt de [forest] Marofandilia, 12.1969, P. Griveaud leg., ex MNHN, male, genitalia slide number 08/102009 I. Lehmann. Wingspan 49.5 mm

#### 4.15 Gen. Nov. I

The genus is defined by the following autapomorphy:

- The thorn-like gnathal arm is large (35% the size of valva) and connected to the base of uncus by a long and very narrow band; (160).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes; (11).

Type species of genus (cf. Figure 53): Gen. Nov. I + sp. nov. i

Type locality: Kenya, Shimba Hills, 04.1964, R.H. Carcasson leg., male, genitalia slide number 16/012009 I. Lehmann, ex NMK; depository in NMK.

Number of species in genus at present: 09

all localities of studied species per country: Nigeria [?]; Kenya; Tanzania; Republic of South Africa.

Distribution of genus at present (cf. Figure 51): lowland, submontane and montane areas from coastal Kenya (Tana River) southwards via coastal Tanzania to coastal areas of the eastern Republic of South Africa; extending locally up to *ca.* 400 km inland from the coast of the Indian Ocean. A disjunct distribution was found in Nigeria for one species (locality unknown; wrong label on specimen?).

The reconstructed and predicted ancestral areas are the Somalia-Masai regional centre of endemism, the West Malagasy regional centre of endemism and the East Malagasy regional centre of endemism.

The reconstructed biogeographic events comprise: First, dispersal in the Somalia-Masai regional centre of endemism, the West Malagasy regional centre of endemism and the East Malagasy regional centre of endemism. Secondly, dispersal into the Afromontane archipelago-like regional centre of endemism, the Zanzibar-Inhambane regional mosaic and the Tongaland-Pondoland regional mosaic. Thirdly, vicariance between the West Malagasy regional centre of endemism, the East Malagasy regional centre of endemism and all other phytochoria mentioned above.

Phylogenetic position: The sister genus is Gen. Nov. H.

The synapomorphies shared with the sister genus comprise:

- R<sub>1</sub>+R<sub>2</sub> on a long stalk (stalk has the length of 40–50% of R<sub>3</sub>) in male and/or female; (7).
- Uncus has a heavy appearance, it is strongly sclerotized with a more or less flat dorsal surface; (44);
- Gnathal arm represents a strongly sclerotized thorn with a broader base and an acuminate tip and is connected by a band to the base of uncus; the

gnathal arms are connected by a narrow band ventrally and end well above the costa of valva; (156);

- Transtilla is very broad (ca. 30% of width of valva); (158).

Description: *Head:* rough-scaled; medium long hair-like scales of grey-olive on fronto-clypeus; a pair of pits absent on lower fronto-clypeus, a pair of conical projections absent on lower fronto-clypeus in both sexes; pits behind the labial palpi are tiny slits or absent; labial palpi short, less than half of eye diameter and consist of two segments, the basal segment is short, segment on top narrow elongated (3.0x length of basal segment), a third tiny segment is sometimes present on top but it is strongly reduced or absent; antennae bipectinated in both sexes with long, narrow branches (4.0x width of shaft), branches are almost equal in width from base to tip; dorsal and lateral side of branches not scaled but covered with long setae; flagellum scaled brown.

*Thorax:* Densely covered with broader and hair-like scales, mainly grey-olive on patagia and dark chestnut with a vinaceous shine on tegulae; with a light olive coloured crest on metathorax. Epiphyses are present in both sexes, broad, flat, long (up to 2.0 mm). Hindlegs with two pairs of thick tibial spurs with a thorn-like tip, inner spur longer, upper pair longer (up to 1.6 mm), lower pair shorter (up to 1.2 mm); pretarsus with a pair of pulvilli.

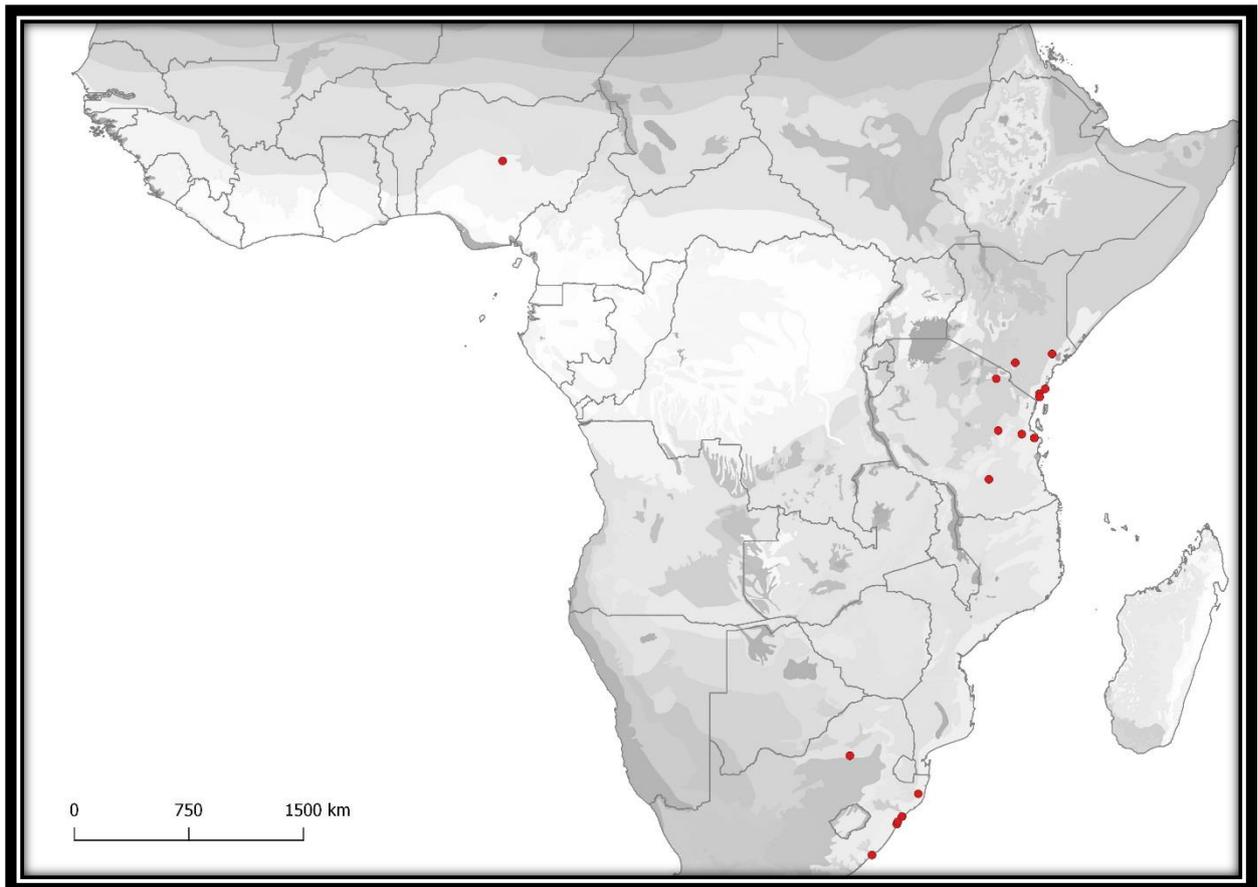
Forewing broad with a rounded apex, female more densely scaled; forewing upperside without any geometric design and with a simple pattern, comprising a broadly V-shaped dark grey or brown coloured marking from near centre of CuA<sub>2</sub> to R<sub>5</sub> and very fine sepia lines, sometimes representing a faded reticulated pattern, from near costa to dorsum, on a light grey or grey-olive ground-colour with a strong glint; CuA<sub>2</sub> not distinctly marked, sometimes it represents a fine sepia line; below base of 1A+2A a dark chestnut patch. Hindwing cream mixed with a light grey reticulated pattern on ground-colour, glossy. Fringe hair-like and short on both wings (ciliae less than 1.0 mm). Wing venation: in forewing 1A+2A slightly forked at base; CuP absent; CuA<sub>2</sub> originating from near hind margin of posterior cell; CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> separated and initiating from apical angle of posterior cell; M<sub>1</sub> initiating from near anterior angle of median cell; R<sub>1</sub>+R<sub>2</sub> on a long stalk (stalk has the length of 50 % of R<sub>3</sub>) and initiating from near anterior angle of median cell; R<sub>3</sub>+R<sub>4</sub>+R<sub>5</sub> long stalked and initiating from anterior angle of median cell; Sc more or less parallel to R<sub>1</sub>. In hindwing 3A present; 1A+2A present without a fork at base; CuP represented by a fold; CuA<sub>2</sub> initiating from near hind margin of posterior cell; CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> initiating from apical angle of posterior cell, separated; M<sub>1</sub> and Rs initiating from apical angle of anterior cell, separated; a bar is absent from Rs to Sc+R<sub>1</sub>; a vein in discocellular cell on both forewing and hindwing is present and never forked. Retinaculum and frenulum absent.

*Abdomen:* With hair-like scales and short abdominal tuft of 25% of abdomen length.

*Male genitalia.* Saccus strongly reduced or absent, broadly rounded at tip; the vinculum and tegumen are fused, forming a firm ring, tegumen 3 x broader than

vinculum, that is narrow; uncus not bent downwards and with heavy appearance, short (up to 40% length of gnathos), narrow, flat dorsally, not bifurcated at tip, tip rounded. Valva soft, thinly membranous and without any structures, broad, short, tip broadly rounded, few short setae on inner side, edges of valva are soft; a band-like broad transtilla is present (ca. 40% of basal width of valva), well sclerotized and without setae. Sacculus is narrow and present on 40% of length of valva. Gnathal arms medium large (one arm as large as 20% of valva in ventral view), attached with a medium long broad band (as long as 25% of basal width of valva) to base of uncus, arms comprise a sclerotized thorn-like structure (in length 40% of basal width of valva) that is not hollow and has short thorns along its edge instead of folds; thorn-like gnathal arms are connected ventrally by a weakly sclerotized band (as broad as 30% of width of transtilla); the gnathal arms are short (ending above costa of valva). Juxta is broadly ear-shaped, tips rounded, without any processes. Phallus is unusually large, simple tube-like, broad, bent and is longer than length of valva; vesica without cornuti.

*Female postabdominal structure.* Papillae anales medium large with many short setae; segment 8 represents a medium broad rectangular band, more narrow ventrally but with a narrow rounded end (lateral view), setose near its posterior margin with long setae; a very narrow band is attached at its base with the base of anterior apophysis and extends close to the ventral edge of segment 8; anterior apophyses are narrow, broader and slightly knee-like close to their base. The posterior apophyses have a broad tip.



**FIGURE 51.** Distribution of Gen. Nov. I (red dots)



**FIGURE 52.** Gen. Nov. I, sp. nov. i5, Tanzania, Usa River, 06.02.1992, L. Aarvik leg., ex NHMO, female, genitalia slide number 27/062009 I. Lehmann. Wingspan 51.0 mm



**FIGURE 53.** Gen. Nov. I, sp. nov. i, Kenya, Shimba Hills, 04.1964, R.H. Carcasson leg., ex NMK, male, genitalia slide number 16/012009 I. Lehmann. Wingspan 50.0 mm



**FIGURE 54.** Gen. Nov. I, sp. nov. ii, Republic of South Africa, Port St. Johns, 09.01.1973, D.M. Kroon leg., ex BMNH, male, genitalia slide number 07/022009 I. Lehmann. Wingspan 48.5 mm

#### 4.16 Gen. Nov. J

The genus is defined by the following autapomorphy:

- Valva becomes suddenly narrow (decreasing by two-thirds of its width) at half of its length towards tip; (93).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes; (11).

Type species of genus (cf. Figure 56): Gen. Nov. J + sp. nov. j

Type locality: Mali, Mourdiah, 18.09.1985, Marcus Matthews leg., male, genitalia slide number 01/122008 I. Lehmann, ex BMNH, B.M. 1985-396; depository in BMNH.

Number of species in genus at present: 08

all localities of studied species per country: Mali; Burkina Faso; Chad; Togo; Nigeria; Democratic Republic of the Congo; Uganda.

Distribution of genus at present (cf. Figure 55): lowland and submontane areas from southwestern Mali southwards via Burkina Faso to west-central Togo and eastwards to northern Nigeria and southern Chad further eastwards through the northern Democratic Republic of the Congo to southwestern Uganda.

The reconstructed and predicted ancestral areas are the Zambebian regional centre of endemism, Guinea-Congolia/Sudania regional transition zone and Guinea-Congolia/Zambesia regional transition zone.

The reconstructed biogeographic events comprise: First, dispersal from the Zambebian regional centre of endemism, Guinea-Congolia/Zambesia regional transition zone and Guinea-Congolia/Sudania regional transition zone into the Guineo-Congolian regional centre of endemism. Secondly, vicariance between the Guinea-Congolia/Zambesia regional transition zone, Guinea-Congolia/Sudania regional transition zone, Guineo-Congolian regional centre of endemism and the Zambebian regional centre of endemism.

Phylogenetic position: The sister genus is Gen. Nov. K.

The synapomorphies shared with the sister genus comprise:

- R<sub>1</sub>+R<sub>2</sub> on a very long stalk (stalk has the length of 60-70% of R<sub>3</sub>) in male; (6);
- the whole gnathal arms are not thorn-like but each arm comprises a small thorn-like appendice that is ca. 10% in size of each gnathal arm; (24);
- Uncus strongly thickened ventrally, looking like a strongly sclerotized lunule in lateral view; (25);

- Uncus has a heavy appearance, it is strongly sclerotized with a more or less flat dorsal surface; (44).

Description: *Head:* rough-scaled; medium long hair-like scales of light grey-olive on fronto-clypeus; a pair of small pits present on lower fronto-clypeus, a pair of conical projections absent on lower fronto-clypeus in both sexes; pits behind the labial palpi are small and oval shaped; labial palpi short, less than half of eye diameter and consist of two segments, the basal segment is short and slightly broader, segment on top narrow elongated, triangular with rounded tip (2.0× length of basal segment), a third tiny segment is absent in both sexes; antennae bipectinated in both sexes, in male with long, narrow branches (2.0× width of shaft), in female with shorter branches (1.0× width of shaft), branches are almost equal in width from base to tip; dorsal and lateral side of branches not scaled but covered with long setae in both sexes; flagellum scaled cream.

*Thorax:* Densely covered with hair-like scales, mainly light grey-olive on patagia and tegulae with a golden shine; with a light grey-olive coloured crest on metathorax. Epiphyses are present in both sexes, short (up to 1.8 mm), flat. Hindlegs with two pairs of tibial spurs with a thorn-like tip, upper pair slightly longer (up to 1.2 mm); pretarsus with a pair of pulvilli.

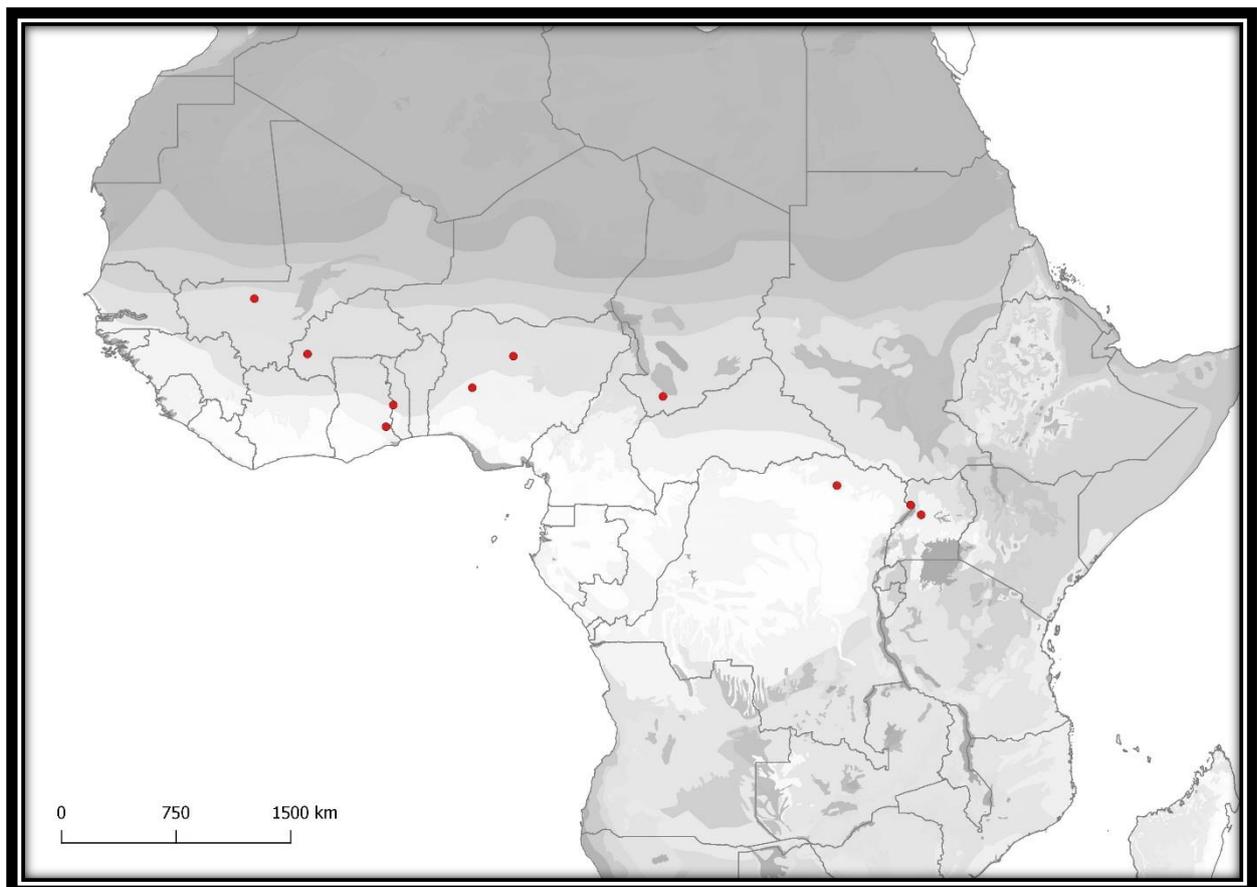
Forewing upperside light grey-olive, glossy, without any geometric design and with a simple pattern, comprising several short narrow brown lines, two of them from near costa to dorsum; CuA<sub>2</sub> not distinctly marked; below half of 1A+2A a dark narrow brown patch in both sexes. Hindwing light grey-olive, glossy. Fringe hair-like and short on both wings (ciliae less than 1.2 mm). Wing venation: in forewing 1A+2A forked at base; CuP absent; CuA<sub>2</sub> originating from near hind margin of posterior cell; CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> separated and initiating from apical angle of posterior cell; M<sub>1</sub> initiating from near anterior angle of median cell; R<sub>1</sub>+R<sub>2</sub> on a long stalk (stalk has the length of 60 % of R<sub>3</sub>) and initiating from near anterior angle of median cell; R<sub>3</sub>+R<sub>4</sub>+R<sub>5</sub> long stalked and initiating from anterior angle of median cell; Sc more or less parallel to R<sub>1</sub>. In hindwing 3A present; 1A+2A present with a fork at base; CuP represented by a fold or absent; CuA<sub>2</sub> initiating from near hind margin of posterior cell; CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> initiating from apical angle of posterior cell, separated; M<sub>1</sub> and Rs initiating from apical angle of anterior cell, separated; a bar is absent from Rs to Sc+R<sub>1</sub>; a vein in discocellular cell on both forewing and hindwing is absent or weak. Retinaculum and frenulum absent.

*Abdomen:* With hair-like scales and short abdominal tuft of 20% of abdomen length.

*Male genitalia.* Saccus short, broadly rounded at tip; the vinculum and tegumen are fused, forming a firm ring, tegumen 2-3 x broader than vinculum, that is narrow; uncus bent downwards at middle, hollow, with heavy appearance, long (up to 90% length of gnathos), narrow, flat dorsally, slightly bifurcated at tip. Valva soft, thinly membranous and without any structures, broad at base, very narrow at outer half with rounded tip, many short setae on inner side, edges of valva are soft; a band-like

broad semi-transtilla is present (ca. 30% of basal width of valva), sclerotized and without setae. Sacculus is narrow, broadest at middle, present on 80% of length of valva. Gnathal arms medium large (one arm as large as 25% of valva in ventral view), attached with a medium long broad band (as long as 20% of basal width of valva) to base of uncus, arms comprise a sclerotized fish fin-shaped structure with a small thorn-like appendice that is ca. 10% in size of each gnathal arm; gnathal arms are connected ventrally by a weakly sclerotized narrow band (as broad as 10% of width of semi-transtilla); the gnathal arms are short (ending above costa of valva). Juxta is large (as large as 60% of one gnathal arm), broadly V-shaped, tips rounded, without any processes. Phallus is large, simple tube-like, broad, not bent and is slightly longer than length of valva; vesica without cornuti.

*Female postabdominal structure.* Papillae anales medium large with many short setae; segment 8 represents a medium broad rectangular band, more narrow ventrally but with a narrow rounded end (lateral view), setose near its posterior margin with long setae; a very narrow band is attached at the base of anterior apophysis and extends close to the ventral edge of segment 8; anterior apophyses are narrow, but very broad, oval-shaped, at first one-third of length. The posterior apophyses are narrow with a broad base.



**FIGURE 55.** Distribution of Gen. Nov. J (red dots).



**FIGURE 56.** Gen. Nov. J, sp. nov. j, Mali, Mourdiah, 18.09.1985, Marcus Matthews leg., ex BMNH, B.M. 1985-396, male, genitalia slide number 01/122008 I. Lehmann. Wingspan 26.0 mm



**FIGURE 57.** Gen. Nov. J, sp. nov. j4, Obervolta[Burkina Faso], Bobo Dioulasso, 06.10.1981, Dr. Politzar leg., ex ZSM, female, genitalia slide number 30/082009 I. Lehmann. Wingspan 31.5 mm

#### 4.17 Gen. Nov. K

The genus is defined by the following autapomorphy:

- Gnathal arm very large and almost as large as valva; (208).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes (11).

Type species of genus (cf. Figure 59): Gen. Nov. K + sp. nov. k

Type locality: Tanzania, Morogoro, Kihonda, 500 m, 05.04.1992, L. Aarvik leg., male, genitalia slide number 19/102008 I. Lehmann, ex NHMO; depository in NHMO.

Number of species in genus at present: 06

all localities of studied species per country: Kenya; Tanzania; Republic of South Africa.

Distribution of genus at present (cf. Figure 58): disjunct; lowland, submontane and montane areas from central Kenya southwards to northwest and eastern Tanzania; possibly through coastal Mozambique to the eastern Republic of South Africa.

The reconstructed and predicted ancestral areas are the Guinea-Congolia/Sudania regional transition zone, Guinea-Congolia/Zambesia regional transition zone, the Lake Victoria regional mosaic and the Zambezian regional centre of endemism.

The reconstructed biogeographic events comprise: First, dispersal from the Zambezian regional centre of endemism, Guinea-Congolia/Zambesia regional transition zone and Guinea-Congolia/Sudania regional transition zone into the Guineo-Congolian regional centre of endemism. Secondly, vicariance between the Guinea-Congolia/Zambesia regional transition zone, Guinea-Congolia/Sudania regional transition zone, Guineo-Congolian regional centre of endemism and the Zambezian regional centre of endemism.

Phylogenetic position: The sister genus is Gen. Nov. J.

The synapomorphies shared with the sister genus comprise:

- R<sub>1</sub>+R<sub>2</sub> on a very long stalk (stalk has the length of 60–70% of R<sub>3</sub>) in male; (6);
- the whole gnathal arms are not thorn-like but each arm comprises a small thorn-like appendice that is ca. 10% in size of each gnathal arm; (24);
- Uncus strongly thickened ventrally, looking like a strongly sclerotized lunule in lateral view; (25);
- Uncus has a heavy appearance, it is strongly sclerotized with a more or less flat dorsal surface; (44).

Description: *Head:* rough-scaled; medium long hair-like scales of light grey-olive on fronto-clypeus; a pair of small pits absent on lower fronto-clypeus, a pair of conical projections present on lower fronto-clypeus in male; pits behind the labial palpi are tiny elongated slits; labial palpi short, less than half of eye diameter and consist of two segments, the basal segment is short and slightly broader, segment on top narrow elongated (1.5× length of basal segment); antennae bipectinated in male with long, narrow branches (3.5× width of shaft), branches are almost equal in width from base to tip; dorsal and lateral side of branches not scaled but covered with long setae; flagellum scaled light cream.

*Thorax:* Densely covered with hair-like scales, mainly light grey-olive on patagia and tegulae; with a light grey-olive coloured crest on metathorax. Epiphyses are present in male, long (up to 1.4 mm) broad. Hindlegs with two pairs of narrow tibial spurs, upper pair longer (up to 1.1 mm) lower pair is shorter; pretarsus with a pair of pulvilli.

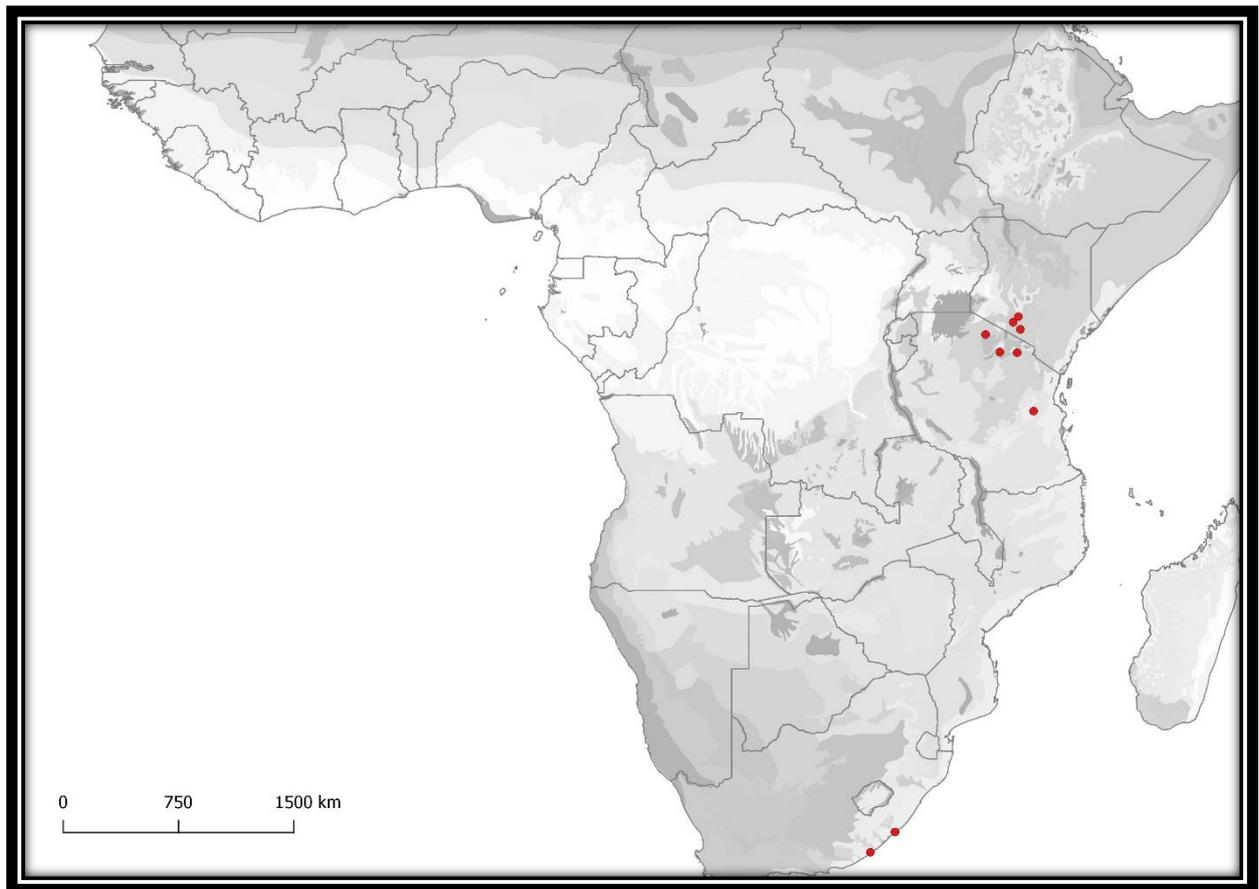
Forewing upperside with a grey-olive or light olive ground-colour, glossy, without any geometric design and with a simple pattern, comprising one oblique sub-terminal band that is always lighter in colour than the ground-colour; CuA<sub>2</sub> not distinctly marked. Hindwing grey, or light olive, glossy. Fringe hair-like and short on both wings (ciliae less than 1.2 mm). Wing venation: in forewing 1A+2A forked at base; CuP absent; CuA<sub>2</sub> originating from near hind margin of posterior cell; CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> separated (M<sub>3</sub> and M<sub>2</sub> sometimes originate from almost the same point), initiating from apical angle of posterior cell; M<sub>1</sub> initiating from near anterior angle of median cell; R<sub>1</sub>+R<sub>2</sub> on a long stalk (stalk has the length of 60 % of R<sub>3</sub>) and initiating from near anterior angle of median cell; R<sub>3</sub>+R<sub>4</sub>+R<sub>5</sub> long stalked and initiating from anterior angle of median cell; Sc more or less parallel to R<sub>1</sub>. In hindwing 3A present; 1A+2A present as a fold; CuP absent; CuA<sub>2</sub> initiating from near hind margin of posterior cell; CuA<sub>1</sub>, M<sub>3</sub> and M<sub>2</sub> initiating from apical angle of posterior cell, separated; M<sub>1</sub> and Rs initiating from apical angle of anterior cell, separated; a bar is absent from Rs to Sc+R<sub>1</sub>; a vein in discocellular cell on both forewing and hindwing is weak. Retinaculum and frenulum absent.

*Abdomen:* With hair-like scales and short abdominal tuft of 20% of abdomen length.

*Male genitalia.* Saccus short, finger-shaped or slightly triangular with finger-like tip; the vinculum and tegumen are fused, forming a firm ring, tegumen 3 x broader than vinculum, the latter is narrow; uncus slightly bent downwards, hollow, with heavy appearance, long (at least 90% length of gnathos in ventral view), rather narrow, flat dorsally, bifurcated at tip. Valva soft, thinly membranous and without any structures, very elongated (up to 1.5 x longer than gnathos), slightly broader at base, more narrow at outer half with broadly rounded tip, many short setae on inner side, edges of valva are soft; a broadly rounded, short finger-like semi-transtilla is present (ca. 50% of basal width of valva), sclerotized and without setae. Sacculus is narrow and only present on 20% of length of valva. Gnathal arms large (one arm is up to 85% of valva size),

attached to base of uncus; with a small thorn-like appendice that is *ca.* 10% in size of each gnathal arm; gnathal arms are not connected ventrally and have a few short folds in upper part; the gnathal arms are long (ending just below base of valva). Juxta is small (as large as 20% of one gnathal arm), broadly V-shaped, tips rounded, without any processes. Phallus is short (not longer than basal width of valva), simple tube-like, broad, not bent; vesica without cornuti.

*Female postabdominal structure and genitalia.* Unknown. The abdomen of the only female did break (*cf.* Figure 6o).



**FIGURE 58.** Distribution of Gen. Nov. K (red dots).



**FIGURE 59.** Gen. Nov. K, sp. nov. k, Tanzania, Morogoro, Kihonda, 05.04.1992, L. Aarvik leg., ex NHMO, male, genitalia slide number 19/102008 I. Lehmann. Wingspan 19.5 mm



**FIGURE 60.** Gen. Nov. K, sp. nov. k3, Kenya, Nairobi, Loresho Ridge, January.1976, M. P. Clifton leg., ex NMK, female, genitalia slide number 12/012009 I. Lehmann. Wingspan 24.5 mm



**FIGURE 61.** Gen. Nov. K, sp. nov. k5 or *reticulata* (Gaede, 1929), [Republic of South Africa], Port St. Johns, 10.-22.02.1955, A. J. T. Janse leg., ex TMSA, male, genitalia slide number 02/012009 I. Lehmann. Wingspan 25.0 mm

#### 4.18 Gen. Nov. L

The genus is defined by the following autapomorphies:

- Gnathal arms sclerotized, narrow and only slightly connected ventrally but not fused; (198);
- Juxta comprises mainly two long thorns originating from a common broader base; (199);
- Valva strongly rectangular and twice as broad as tall; (209).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes; (11).

Type species of genus (cf. Figure 63): Gen. Nov. L + *eustrigata* (Hampson, 1916)

Type locality: Co-Type, [Kenya], Mandera, 09.1909, W. Feather leg., male, genitalia slide number 27/102007 I. Lehmann, ex BMNH; depository in BMNH.

Number of species in genus at present: 15

all localities of studied species per country: Oman; Saudi Arabia; Republic of Yemen; Ethiopia; Kenya; Tanzania.

Distribution of genus at present (cf. Figure 62): montane, submontane and lowland areas from northern Tanzania via southern, eastern and central Kenya to central Ethiopia and further northeast to western Saudi Arabia, Republic of Yemen and southern Oman (Arabian Peninsula, Afrotropical Region). The reconstructed and predicted ancestral areas are the Somalia-Masai regional centre of endemism, Zanzibar-Inhambane regional mosaic and Tongaland-Pondoland regional mosaic.

The reconstructed biogeographic events comprise: First, dispersal from the Somalia-Masai regional centre of endemism, Zanzibar-Inhambane regional mosaic and Tongaland-Pondoland regional mosaic to the Guineo-Congolian regional centre of endemism, Zambezian regional centre of endemism, Lake Victoria regional mosaic and Kalahari-Highfeld regional transition zone. Secondly, vicariance between the Somalia-Masai regional centre of endemism and all other phytochoria mentioned above.

Phylogenetic position: The sister genus is *Salagena*.

The synapomorphy shared with the sister genus comprises:

- Uncus strongly elongated, always narrow, only thinly sclerotized, never bifid at tip; (87).

Description: *Head:* rough-scaled; medium long hair-like scales of light grey, often mixed with white and sepia scales, on fronto-clypeus; a pair of pits is absent on lower fronto-clypeus, a pair of conical projections is absent on lower fronto-clypeus in both

sexes; pits behind the labial palpi are tiny elongated slits; labial palpi short, less than half of eye diameter and consist of two segments, the basal segment is slightly shorter, segment on top narrow elongated triangular with sometimes an acuminate tip; antennae bipectinated in both sexes with short, medium broad, sometimes almost club-like branches (3.0x width of shaft), branches are always a little bit narrower at base; dorsal and lateral side of branches not scaled but covered with tiny setae; flagellum scaled cream or white.

*Thorax:* Densely covered with hair-like scales, mainly light grey, often mixed with white and sepia on patagia and tegulae; crest on metathorax pronounced and often light orange-brown or light chestnut. Epiphyses are present in both sexes, rather long (up to 1.6 mm), narrow. Hindlegs with one pair of narrow tibial spurs (up to 1.1 mm); pretarsus with a pair of pulvilli.

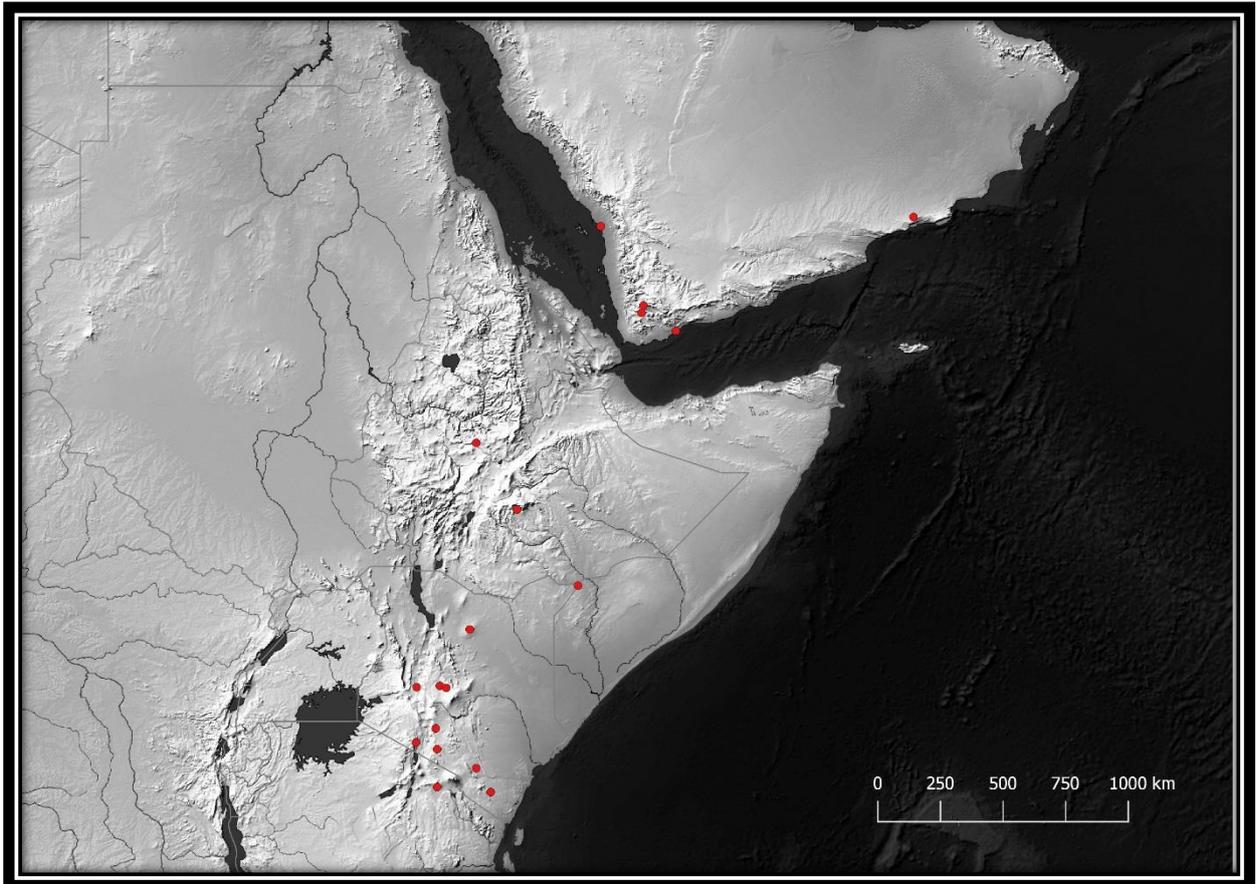
Forewing upperside with a cream or pure white ground-colour, glossy, with fine long transverse striae of light brown and/or sepia on the whole wing; any geometric design is absent, a simple pattern comprises a more or less broad, short band of cream or pure white above the base of  $1A+2A$ , two or three pure white or cream spots with one spot below near middle of  $CuA_2$ , one spot near base of  $M_2$  and a third one (might be reduced or absent) near the end of  $M_2$ ;  $CuA_2$  not distinctly marked. Hindwing is light greyish-olive or pure white, always with a faded (sometimes hard to see in worn specimens), more or less continuous sub-terminal band of cream or light grey, glossy. Fringe hair-like and short on both wings (ciliae less than 1.3 mm). Wing venation: in forewing  $1A+2A$  forked at base (fork sometimes strongly reduced);  $CuP$  absent;  $CuA_2$  originating from two-thirds of posterior cell (hence, far away from hind margin of posterior cell);  $CuA_1$  originates from near hind margin of posterior cell,  $M_3$  and  $M_2$  originate from almost the same basal point from apical angle of posterior cell;  $M_1$  initiating from near anterior angle of median cell, sometimes close to the basal point of  $R_3+R_4+R_5$ ;  $R_1$  and  $R_2$  are separated, initiating from near anterior angle of median cell;  $R_3+R_4+R_5$  long stalked and initiating from anterior angle of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  present as a fold;  $CuP$  absent;  $CuA_2$  initiating from two-thirds of posterior cell;  $CuA_1$  initiates from near hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from almost the same basal point and from apical angle of posterior cell;  $M_1$  and  $Rs$  initiating from apical angle of anterior cell, widely separated; a short bar is present from  $Rs$  to  $Sc+R_1$ , the latter is rather strongly bent on its first one-third of length, sometimes touching the median of anterior cell; a vein in discocellular cell on both forewing and hindwing is absent or strongly reduced. Retinaculum and frenulum absent.

*Abdomen:* With hair-like white or grey scales; abdominal tuft 25% of abdomen length.

*Male genitalia.* Saccus absent; the vinculum and tegumen are fused, forming a firm ring, tegumen 3 x broader than vinculum but with a very large hole (ca. 40% the size of tegumen), vinculum medium broad; uncus very narrow, usually pointing upwards but is sometimes slightly bent downwards (in lateral view), hollow, long

(slightly longer than length of gnathos in ventral view), never bifurcated at tip, the latter is always rounded. Valva strongly rectangular, soft, thinly membranous, always with some long, sclerotized setae that appear usually grey in colour near the upper end of valva dorso-distally, with a small sclerotized finger-like or thorn-like structure at the end of sacculus medio-distally, edges of valva are soft, the whole valva breaks easily during preparation; transtilla and semi-transtilla are absent, but a band-like structure occurs that links somehow both valva above the aedeagus, the band is possibly originating from near upper base of valva, is thinly membranous or slightly sclerotized, with few short setae at base and more thinly membranous at middle (sometimes separated at middle). Sacculus is very broad and present on 50% of length of valva. Gnathal arms simple, band-like, thinly sclerotized, very narrow (one arm is less than 10% of valva width), attached to upper part of tegumen; gnathal arms are not connected ventrally or connected by a thin membrane that breaks easily; the gnathal arms are medium long (ending just at upper base of valva). Juxta is large (slightly smaller than sacculus), comprising two long thorns (looking like two elephant tusks) that originate from a common broader base, without any processes. Phallus is very short (not longer than sacculus), simple tube-like, broad, not bent, with a sclerotized small thorn at the distal end.

*Female postabdominal structure.* Papillae anales large (2 x broader than segment 8) with short and long setae; segment 8 is a narrow rectangular band, more narrow ventrally, setose near its posterior margin with long setae, particularly near dorsal and ventral end; a narrow band is attached to base of anterior apophysis, extending to ventral edge of segment 8; anterior apophyses narrow, knee-like at one-third of length. The posterior apophyses narrow, straight, slightly less than half length of anterior apophyses, with broader base.



**FIGURE 62.** Distribution of Gen. Nov. L (red dots).



**FIGURE 63.** Gen. Nov. L, *eustrigata*, Co-Type, [Kenya], Mandera, 09.1909, W. Feather leg., ex BMNH, male, genitalia slide number 27/102007 I. Lehmann. Wingspan 22.5 mm



**FIGURE 64.** Gen. Nov. L, sp. nov. 13, Kenya, Lolldaiga Hills Ranch, close to General Manager's house, 03.2016, M. Roberts leg., ex own coll., male, genitalia slide number 27/102018 I. Lehmann. Wingspan 23.0 mm



**FIGURE 65.** Gen. Nov. L, sp. nov. 15, [Kenya], Marsabit, 02.1956, J. G. Williams leg., ex NMK, female, genitalia slide number 11/052008 I. Lehmann. Wingspan 25.0 mm

#### 4.19 *Salagena* Walker, 1865

The genus is defined by the following autapomorphies:

- Male antenna filiform, slightly unipectinated at tip; (195);
- Gnathal arms thinly membranous, narrow and fused for at least one-third of their entire length; (196).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes; (11).

Type species of genus: *Salagena transversa* Walker, 1865

Type locality: Sierra Leone – no further data. The studied specimen is close to the type (*cf.* Figure 67): Congo [Republic of the Congo], Kuilu, [no date], Mocqu. [Mocquerys] leg., male, genitalia slide number 29/072008 I. Lehmann, ex ZMHU; depository in ZMHU.

Number of species in genus at present: 29

all localities of studied species per country: Senegal; Sierra Leone; Burkina Faso; Nigeria; Republic of the Congo; Uganda; Chad; Republic of the Sudan; Kenya; Tanzania; Malawi; Zambia; Zimbabwe, Republic of South Africa.

Distribution of genus at present (*cf.* Figure 66): disjunct; lowland, submontane and lower montane areas from Dakar and Bambey (coastal Senegal) possibly along the coast southwards to coastal areas of the Republic of the Congo; from Sierra Leone eastwards via southern Burkina Faso, northern and central Nigeria to southern Chad and West-Darfur in Sudan; a disjunct distribution from south-central Uganda as well as from the Tana River (Kenya) southwards through Kenya to north-central and eastern Tanzania, locally further inland *ca.* 450 km from the Indian Ocean coast, through Malawi to eastern Zambia and southwards to Zimbabwe and the northeastern Republic of South Africa.

The reconstructed and predicted ancestral areas are the Somalia-Masai regional centre of endemism, Zanzibar-Inhambane regional mosaic and Tongaland-Pondoland regional mosaic.

The reconstructed biogeographic events comprise: First, dispersal from the Somalia-Masai regional centre of endemism, Zanzibar-Inhambane regional mosaic and Tongaland-Pondoland regional mosaic to the Guineo-Congolian regional centre of endemism, Zambezi region regional centre of endemism, Lake Victoria regional mosaic and Kalahari-Highveld regional transition zone. Secondly, vicariance between the Somalia-Masai regional centre of endemism and all other phytochoria mentioned above.

Phylogenetic position: The sister genus is Gen. Nov. L.

The synapomorphy shared with the sister genus comprises:

- Uncus strongly elongated, always narrow, only thinly sclerotized, never bifid at tip; (87).

Description: *Head:* rough-scaled; medium long hair-like scales of cream or light orange-brown, often mixed with chestnut and/or dark cream scales on fronto-clypeus; a pair of pits is absent on lower fronto-clypeus, a pair of small conical projections is present on lower fronto-clypeus in both sexes; pits behind the labial palpi are tiny elongated slits or absent; labial palpi short, less than half of eye diameter and consist of three segments, the basal segment is half the length of central segment, central segment narrow elongated, segment on top very short or rudimentary; antennae filiform in both sexes, when strongly bent (artificially) sometimes slightly serrated towards tip, not scaled, covered with many very tiny setae.

*Thorax:* Densely covered with hair-like scales, mainly cream or light orange-brown, often mixed with chestnut and sepia on patagia and tegulae; crest on metathorax pronounced and often light orange-brown or light chestnut. Epiphyses are present in both sexes, but are sometimes strongly reduced, usually short (up to 1.0 mm), narrow. Hindlegs with one pair of narrow tibial spurs (up to 1.0 mm); pretarsus with a pair of pulvilli.

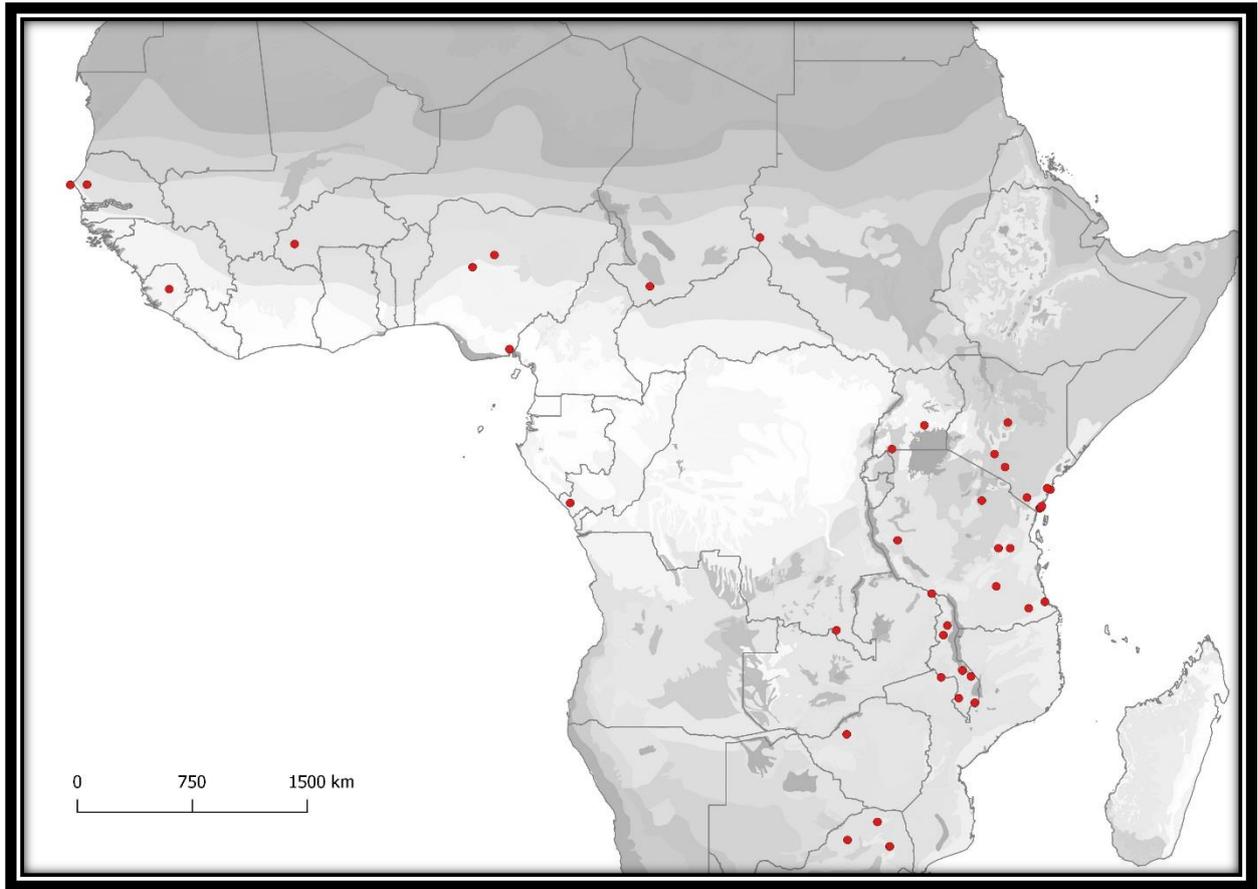
Forewing upperside with a light yellow-cream, chestnut or orange-brown ground-colour with a strong vinaceous and/or light blue and/or lilac glint on the whole wing, more pronounced in male (also on the underside), with fine long transverse striae of light brown and/or sepia and/or black in both sexes or with rounded spots of dark brown in both sexes and on the whole wing; a geometric design is absent; CuA<sub>2</sub> not distinctly marked in both sexes. Hindwing is cream or light greyish-olive or grey or light brown, often with a vinaceous glint in male. Fringe hair-like and short on both wings (ciliae less than 0.9 mm), in male sometimes light yellow. Wing venation: in forewing 1A+2A forked at base (fork sometimes strongly reduced); CuP absent; CuA<sub>2</sub> originating from two-thirds of posterior cell (hence, far away from hind margin of posterior cell); CuA<sub>1</sub> originates from near hind margin of posterior cell, M<sub>3</sub> and M<sub>2</sub> originate from almost the same basal point or from the same basal point from apical angle of posterior cell; M<sub>1</sub> initiating from near anterior angle of median cell, sometimes close to the basal point of R<sub>3</sub>+R<sub>4</sub>+R<sub>5</sub>; R<sub>1</sub> and R<sub>2</sub> are separated, initiating from near anterior angle of median cell; R<sub>3</sub>+R<sub>4</sub>+R<sub>5</sub> long stalked and initiating from anterior angle of median cell; Sc more or less parallel to R<sub>1</sub>, but sometimes touching R<sub>1</sub> at centre in female. In hindwing 3A present; 1A+2A present as a fold; CuP absent; CuA<sub>2</sub> initiating from two-thirds of posterior cell; CuA<sub>1</sub> initiates from near hind margin of posterior cell; M<sub>3</sub> and M<sub>2</sub> initiating from almost the same basal point and from apical angle of posterior cell; M<sub>1</sub> and Rs initiating from apical angle of anterior cell, widely separated; a long bar is always present from Rs to Sc+R<sub>1</sub> in both sexes, the latter is rather strongly bent on its first one-third of length; the discocellular cell is very long in forewing and

covers two-thirds of forewing length in both sexes; a vein in discocellular cell on both forewing and hindwing is weak or absent. Retinaculum and frenulum absent.

*Abdomen:* With hair-like grey, sepia or chestnut scales; abdominal tuft long, 35% of abdomen length.

*Male genitalia.* Saccus absent; the vinculum and tegumen are fused, forming a firm ring, tegumen 3 x broader than vinculum (tegumen always without a hole), vinculum medium broad; uncus very narrow, usually pointing upwards, never downwards (in lateral view), hollow, long, but shorter than length of gnathos in ventral view, never bifurcated at tip, the latter is always rounded. Valva more or less rectangular, soft, thinly membranous, always with some long, but not sclerotized setae near the upper end of valva dorso-distally, with a small sclerotized lunule-like structure (not hollow) at the end of sacculus medio-distally, edges of valva are soft, the whole valva breaks easily during preparation; transtilla and semi-transtilla are absent. Sacculus is very narrow and present on 20% of length of valva. Gnathal arms simple, band-like, thinly sclerotized, narrow (one arm is 15% of valva width), attached to upper part of tegumen; gnathal arms are fused ventrally for at least one-third of their entire length; the gnathal arms are very long (ending at middle of valva width). Juxta is large (at least twice as large as sacculus), rectangular, elongated, slightly emarginated at tip, without any processes. Phallus is very short (not longer than sacculus), simple tube-like, broad, not bent, with a sclerotized small thorn at the distal end.

*Female postabdominal structure and genitalia.* Papillae anales medium large with short and very long setae; segment 8 is a broad rectangular band, more narrow ventrally where many tiny and short setae occur, setose near its posterior margin with long setae, particularly near dorsal and ventral end; a narrow band-like structure is attached to base of anterior apophysis, extending to ventral edge of segment 8, but there is no open space between the band-like structure and segment 8; anterior apophyses and posterior apophyses of almost equal length, not bent. Ductus bursae is thickly membranous (particularly at base) but not sclerotized, not longer than vertical length of segment 8; corpus bursae is small, oval shaped, thinly membranous, almost as large as segment 8 and without any structures.



**FIGURE 66.** Distribution of the genus *Salagena* (red dots).



**FIGURE 67.** *Salagena* sp. nov.9 [close to *transversa*], Congo [Republic of the Congo], Kuilu, [no date], Mocqu. [Mocquerys] leg., ex ZMHU, male, genitalia slide number 29/072008 I. Lehmann. Wingspan 19.5 mm



**FIGURE 68.** *Salagena* sp. nov.6, [Republic of South Africa], Punda Milia, K.N.P. [Kruger National Park] Survey, 09.-11.12.1963, L. Vári leg., ex TMSA, male, genitalia slide number 21/072008 I. Lehmann. Wingspan 18.0 mm



**FIGURE 69.** *Salagena* sp. nov.4, W. [West] Darfur, [Republic of the Sudan], N. [North] Jebel Murra, Kurra, 5.600 feet, 04.07.1932, M. Steele leg., ex BMNH, female, genitalia slide number 31/102018 I. Lehmann. Wingspan 32.5 mm



**FIGURE 70.** *Salagena* sp. nov.10, Malawi, Lake Malawi National Park, 16.12.2010, R.J. Murphy leg., ex own coll., female, genitalia slide number 01/112018 I. Lehmann. Wingspan 29.0 mm

#### 4.20 Gen. Nov. M

The genus is defined by the following autapomorphy:

- The whole forewing upperside is light green coloured mixed with cream; (154).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; [possibly also in female] (11).

Type species of genus (cf. Figure 72): Gen. Nov. M + sp. nov. m

Type locality: S. [South] Rhodesia [Zimbabwe], Umgusa Forest Sawmills, 04.12.1971, E. Pinhey leg., Nat. [National] Museum S. [South] Rhodesia, male, genitalia slide number 09/122015 I. Lehmann, ex NMZB; depository in NMZB.

Number of species in genus at present: 02

all localities of studied species per country: Zimbabwe; Namibia.

Distribution of genus at present (cf. Figure 71): disjunct; a submontane area in west-central Zimbabwe and a montane area in west-central Namibia.

The reconstructed and predicted ancestral areas are the Afromontane archipelago-like regional centre of endemism, Guinea-Congolia/Sudania regional transition zone and Guinea-Congolia/Zambezia regional transition zone.

The reconstructed biogeographic events comprise: First, dispersal from the Afromontane archipelago-like regional centre of endemism, Guinea-Congolia/Sudania regional transition zone and Guinea-Congolia/Zambezia regional transition zone to the Guineo-Congolian regional centre of endemism. Secondly, vicariance between the Afromontane archipelago-like regional centre of endemism and all other phytochoria mentioned above.

Phylogenetic position: The sister genus could not be reconstructed unambiguously. The genus belongs to a monophylum together with the new genera M, O and P.

The synapomorphies shared with Gen.Nov. O and P comprise:

- Uncus strongly elongated, narrow or broad, but only thinly sclerotized, bifid at tip; (86);
- Valva rectangular, 1.5 x taller than its width, well sclerotized; (95);
- Gnathos only thinly membranous and appears soft, not well sclerotized, ventrally fused and is very long (ending at half width of valva) and broader at base; (155).

Description: *Head:* rough-scaled; medium long hair-like scales of light green, often mixed with white and cream on fronto-clypeus; a pair of pits is absent on lower fronto-clypeus, a pair of conical projections is absent on lower fronto-clypeus in male; pits behind the labial palpi are tiny oval-shaped holes; labial palpi short, less than half of eye diameter and consist of three segments, the basal segment is slightly shorter than the central segment, segment on top small conical with rounded tip; antennae long, bipectinated with long, narrow branches (3.5× width of shaft); dorsal and lateral side of branches not scaled but covered with tiny setae; flagellum scaled cream.

*Thorax:* Densely covered with hair-like scales, mainly light green, often mixed with white and cream on patagia and tegulae; crest on metathorax cream and white. Epiphyses are absent in male. Hindlegs with one pair of narrow tibial spurs (up to 1.1 mm); pretarsus with a pair of pulvilli.

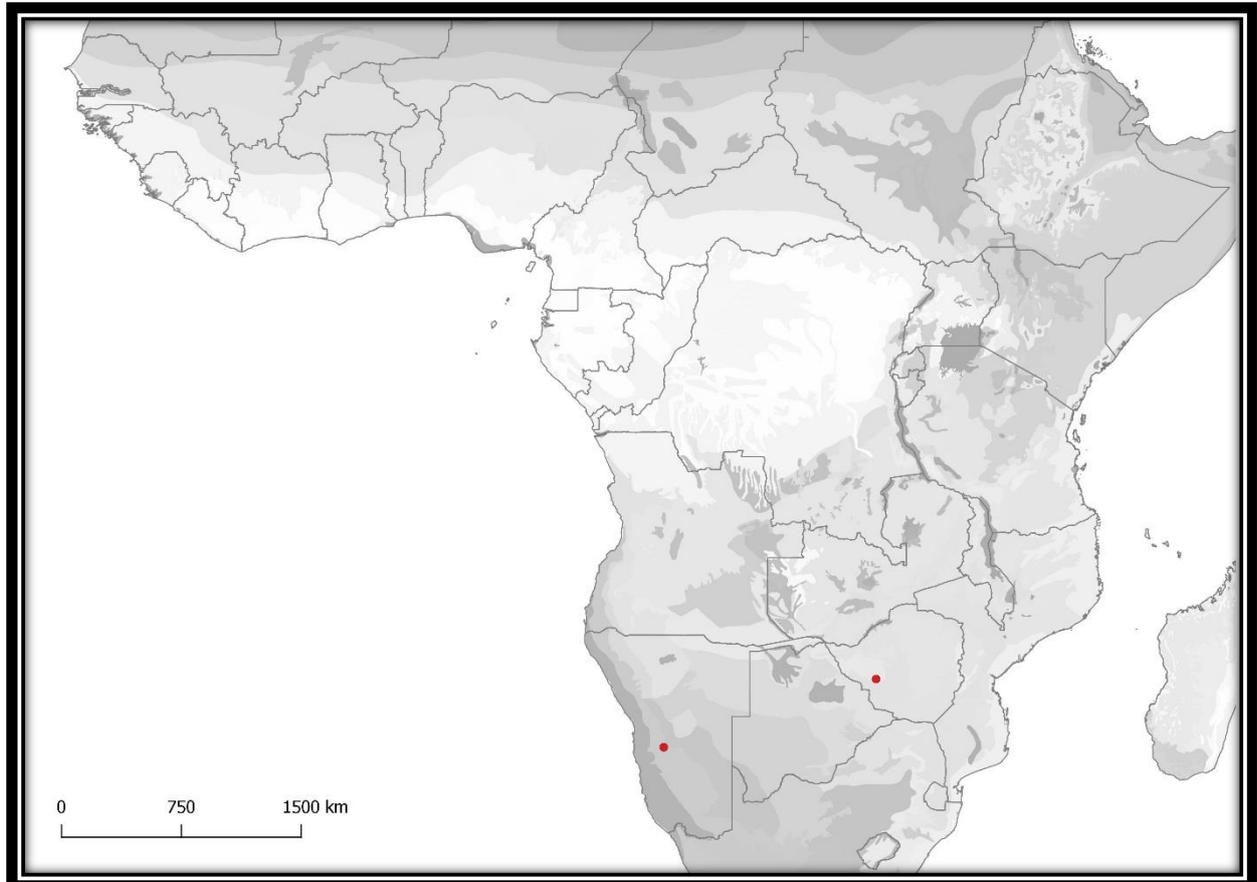
Forewing upperside with a simple pattern of a light cream ground-colour, not glossy, with broad long transverse bands of light green (faded light yellow in older specimen) on the whole wing from costa to dorsum; any geometric design is absent; CuA<sub>2</sub> not distinctly marked. Hindwing is light greyish-olive mixed with pure white, glossy. Fringe hair-like and long on both wings (ciliae 1.5 mm). Wing venation: in forewing 1A+2A long forked at base; CuP is a fold, not sclerotized; CuA<sub>2</sub> originating from two-thirds of posterior cell (hence, far away from hind margin of posterior cell); CuA<sub>1</sub> originates from near hind margin of posterior cell, M<sub>3</sub> and M<sub>2</sub> originate from almost the same basal point from apical angle of posterior cell; M<sub>1</sub> initiating from near anterior angle of median cell and not close to the basal point of R<sub>2</sub>+R<sub>3</sub>+R<sub>4</sub>+R<sub>5</sub>; R<sub>1</sub> initiating from two-thirds of median cell; R<sub>2</sub>+R<sub>3</sub>+R<sub>4</sub>+R<sub>5</sub> long stalked and initiating from anterior angle of median cell; Sc more or less parallel to R<sub>1</sub>. In hindwing 3A present; 1A+2A present as a fold with a small fork at base; CuP present; CuA<sub>2</sub> initiating from two-thirds of posterior cell; CuA<sub>1</sub> initiates from near hind margin of posterior cell; M<sub>3</sub> and M<sub>2</sub> initiating from apical angle of posterior cell, separated; M<sub>1</sub> and Rs initiating from apical angle of anterior cell, widely separated, M<sub>1</sub> slightly arch-shaped; a short bar is present from Rs to Sc+R<sub>1</sub>, the latter is rather strongly bent on its first one-third of length; a vein in discocellular cell on both forewing and hindwing is present, in forewing with a weak fork as a fold. Retinaculum and frenulum absent.

*Abdomen:* With hair-like white, cream and light green scales; abdominal tuft 20% of abdomen length.

*Male genitalia.* Saccus small, broadly rounded; the vinculum and tegumen are fused, forming a firm ring, tegumen 4 x broader than vinculum; vinculum rather narrow; uncus narrow, bent downwards in lateral view, hollow, very long (longer than broad width of valva), bifurcated at tip, the tips are rounded. Valva strongly rectangular, 1.5 x taller than its width, well sclerotized, always with many fine tiny setae, with a small sclerotized lunule-like structure at the end of sacculus medio-distally, edges of valva are soft; transtilla and semi-transtilla are absent. Sacculus is narrow and present on 100% of the narrow length of valva; it ends in a lunule-like sclerotized structure. Gnathal arms simple, thinly membranous, rather broad where

they are attached to the upper part of tegumen but narrow ventrally, the arms are connected ventrally, but a bulla is absent; the gnathal arms are very long (ending at middle of valva). Juxta is small (only 50% larger than the lunule-like structure), comprising a small emargination on top, without any processes. Phallus is long (50% longer than sacculus), simple tube-like, broad at base, not bent, with a sclerotized small thorn at the distal end.

*Female postabdominal structure and genitalia. Unknown.*



**FIGURE 71.** Distribution of Gen. Nov. M (red dots).



**FIGURE 72.** Gen. Nov. M, sp. nov. m, S. [South] Rhodesia [Zimbabwe], Umgusa Forest Sawmills, 04.12.1971, E. Pinhey leg., Nat. [National] Museum S. Rhodesia, ex NMZB, male, genitalia slide number 09/122015 I. Lehmann. Wingspan 33.0 mm



**FIGURE 73.** Gen. Nov. M, sp. nov. m<sub>1</sub>, Namibia, Farm Probeer, Farm-Nr. 398 [Farm number 398], an den Rantbergen [adjacent to the mountains of the Rantberge], 26.12.1996, M. Müller leg., ex ZSM, male, genitalia slide number 14/032013 I. Lehmann. Wingspan 29.0 mm

#### 4.21 Gen. Nov. O

The genus is defined by the following autapomorphy:

- Corpus bursae very small and pyriform; (138).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes; (11).

Type species of genus (cf. Figure 75, female): Gen. Nov. O + sp. nov. o

Type locality: Nigeria, Oyo State, Gambari Forest Reserve, 12.03.1977, J. Riley leg., male [not figured, wingspan 25.0 mm, wing pattern as in female], genitalia slide number 05/032017 I. Lehmann, ex BMNH; depository in BMNH.

Number of species in genus at present: 03

All localities of studied species per country: Ivory Coast; Nigeria.

Distribution of genus at present (cf. Figure 74): lowland areas in southwestern Ivory Coast and southern Nigeria.

The reconstructed and predicted ancestral areas are Guineo-Congolian regional centre of endemism, Guinea-Congolia/Sudania regional transition zone and Guinea-Congolia/Zambezia regional transition zone.

The reconstructed biogeographic events comprise: First, dispersal from the Guineo-Congolian regional centre of endemism, Guinea-Congolia/Sudania regional transition zone and Guinea-Congolia/Zambezia regional transition zone into the Zambezan regional centre of endemism, Zanzibar-Inhambane regional mosaic, Tongaland-Pondoland regional mosaic and Kalahari-Highveld regional transition zone. Secondly, vicariance between the Guineo-Congolian regional centre of endemism and all other phytochoria mentioned above.

Phylogenetic position: The sister genus is Gen. Nov. P.

The synapomorphies shared with the sister genus are:

- The base of a long ductus bursae is sclerotized; (96);
- Valva with a small sclerotized appendice that looks like a lunule ventral distally; (137).

The synapomorphies shared with the new genera M and P comprise:

- Uncus strongly elongated, narrow or broad, but only thinly sclerotized, bifid at tip; (86);
- Valva rectangular, 1.5 x taller than its width, well sclerotized; (95);

- Gnathos only thinly membranous and appears soft, not well sclerotized, ventrally fused and is very long (ending at half width of valva) and broader at base; (155).

*Description: Head:* rough-scaled; medium long hair-like scales of light grey, often mixed with sepia and cream on fronto-clypeus; a pair of pits is absent on lower fronto-clypeus, a pair of conical projections is absent on lower fronto-clypeus in both sexes; pits behind the labial palpi are small oval-shaped holes; labial palpi long, almost as long as eye diameter and consist of three segments, the basal segment has two-thirds the length of central segment, segment on top almost of same length with a rather acuminate tip; antennae short, bipectinated with long, narrow branches (2× width of shaft) in male, shorter in female, slightly club-like in female; dorsal and lateral side of branches not scaled but covered with tiny setae; flagellum scaled cream or white.

*Thorax:* Densely covered with hair-like scales, mainly grey, often mixed with sepia and cream on patagia and tegulae; crest on metathorax pronounced cream and sepia. Epiphyses are absent in both sexes. Hindlegs with two pairs of extremely reduced tiny narrow tibial spurs (only up to 0.2 or 0.3 mm) pretarsus with a pair of pulvilli.

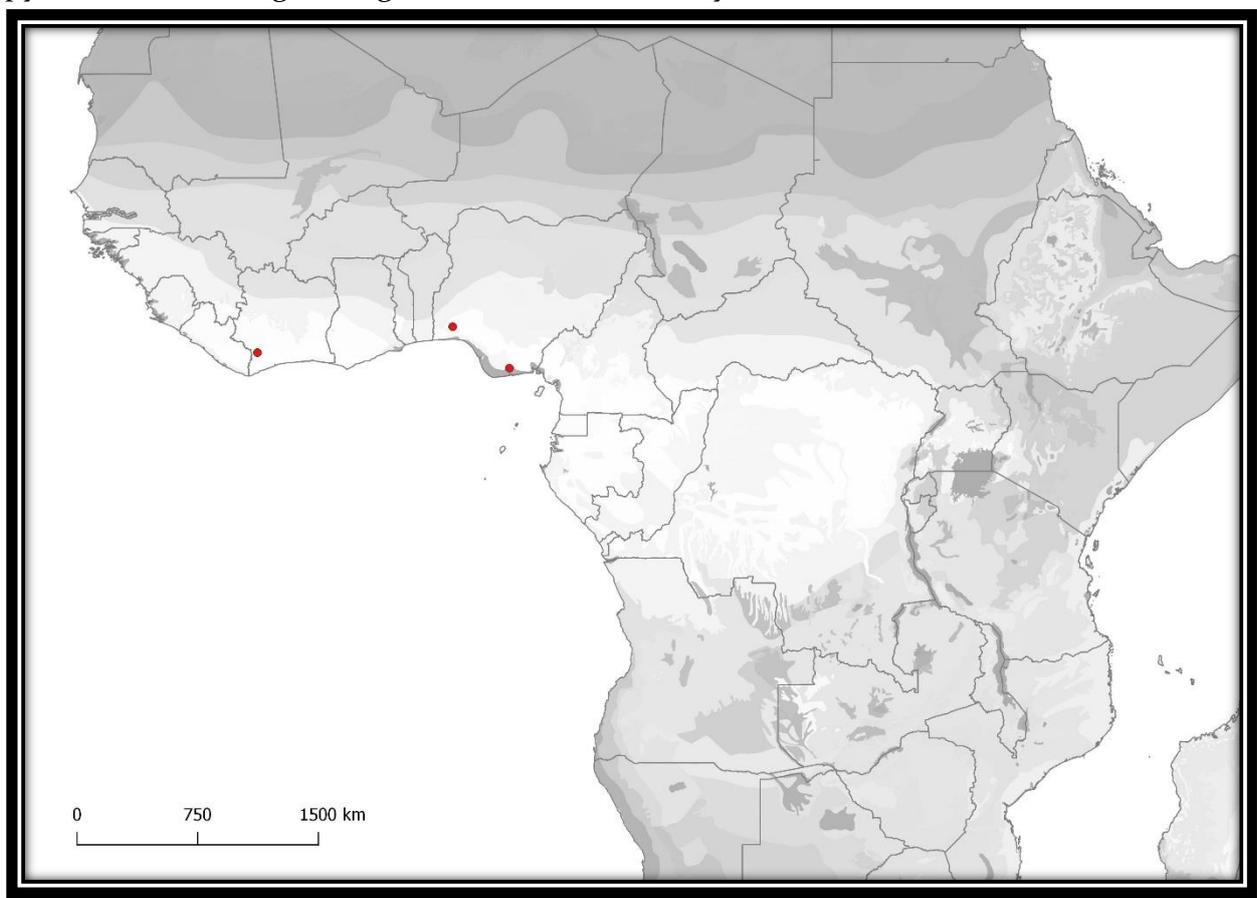
Forewing upperside with a simple pattern of a light ocher ground-colour in male and pure white in female, with a strong silvery gloss and always with a broad white patch close to apex in both sexes, three broad transverse bands of light grey edged sepia with a silvery gloss from costa to dorsum in male (in female are the bands reduced to large patches), base of forewing light ocher or pure white; any geometric design is absent; CuA<sub>2</sub> not distinctly marked. Hindwing is light greyish-olive with a strong glint. Fringe hair-like, glossy and short on both wings (ciliae 0.5 mm). Wing venation: in forewing 1A+2A forked at base; CuP absent; CuA<sub>2</sub> originating from two-thirds of posterior cell (hence, far away from hind margin of posterior cell); CuA<sub>1</sub> originates from hind margin of posterior cell, M<sub>3</sub> and M<sub>2</sub> originate from almost the same basal point from apical angle of posterior cell; M<sub>1</sub> initiating from near anterior angle of median cell or is short stalked with R<sub>3</sub>+R<sub>4</sub>+R<sub>5</sub>; R<sub>2</sub> parallel with R<sub>1</sub> and both are separated and initiating from anterior angle of median cell; Sc more or less parallel to R<sub>1</sub>. In hindwing 3A present; 1A+2A present as a strong fold with a small fork at base; CuP present as strong fold; CuA<sub>2</sub> initiating from two-thirds of posterior cell; CuA<sub>1</sub> initiates from hind margin of posterior cell; M<sub>3</sub> and M<sub>2</sub> initiating from apical angle of posterior cell, separated; M<sub>1</sub> and Rs initiating from almost the same base from apical angle of anterior cell; a bar is present from Rs to Sc+R<sub>1</sub>; a vein in discocellular cell on both forewing and hindwing is present but weak. Retinaculum and frenulum absent.

*Abdomen:* With hair-like white, cream and sepia scales; abdominal tuft 20% of abdomen length.

*Male genitalia.* Saccus small, broadly triangular; the vinculum and tegumen are fused, forming a firm ring, tegumen 2 x broader than vinculum; vinculum rather narrow; uncus narrow, bent downwards in lateral view, hollow, long (shorter than

broad width of valva), bifurcated at tip, the tips are acuminate. Valva strongly rectangular, 1.5 x taller than its width, only the elongated tip dorso-distally is not sclerotized and has many fine setae; a small sclerotized lunule-like or finger-like structure at the end of sacculus medio-distally; semi-transtilla small rectangular with few setae. Sacculus is narrow and present on the narrow ventral width of valva. Gnathal arms simple, thinly membranous, rather broad where they are attached to the upper part of tegumen but narrow ventrally, the arms are connected ventrally and end in a rather broad hook-like structure, but a bulla is absent; the gnathal arms are very long (ending at middle of valva). Juxta is large (50% larger than saccus), oval-shaped and comprising a tiny emargination on top, without any processes. Phallus is short (only 30% longer than juxta), simple tube-like, broad, not bent.

*Female postabdominal structure and genitalia.* Papillae anales medium large with short and very long setae; segment 8 is a broad rectangular band on upper half, more narrow ventrally where many long setae occur, not setose near its posterior margin, but with long setae on dorsal part of segment 8; a broad band-like structure is attached to base of anterior apophysis, extending to ventral edge of segment 8 with a large open space between the band-like structure and segment 8; anterior apophyses and posterior apophyses of almost equal length, the former are strongly bent at middle. Ductus bursae is thickly membranous, at base sclerotized; corpus bursae is small and pyriform, not as large as segment 8 and without any structures.



**FIGURE 74.** Distribution of Gen. Nov. O (red dots).



**FIGURE 75.** Gen. Nov. *O*, sp. nov. *o*, Nigeria, Oyo State, Gambari Forest Reserve, 12.03.1977, J. Riley leg., ex BMNH, female, genitalia slide number 19/022017 I. Lehmann. Wingspan 25.5 mm



**FIGURE 76.** Gen. Nov. *O*, sp. nov. *o1*, Nigeria, Port Harcourt, 03.02.1957 or 1951 [?], B.J. MacNulty leg., ex BMNH: "B.J. MacNulty Bequest 1994-226", male, genitalia slide number 01/122018 I. Lehmann. Wingspan 21.0 mm

#### 4.22 Gen. Nov. P

The genus is defined by the following autapomorphy:

- Frenulum only in male but not in female present; (180).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes; (11).

Type species of genus: Gen. Nov. P + *tegula* (Distant, 1897)

Type locality: [Republic of South Africa], Transvaal, Pretoria, 15.10.1894, W.L. Distant leg.; studied specimen collected closest [45 km north] to type locality (*cf.* Figure 78): [Republic of South Africa], northwest Gauteng, Rust de Winter road, Didimala, 1.200 m, 12.-15.11.2003, A. Legrain leg., male, genitalia slide number 07/032017 I. Lehmann, ex RMCA; depository in RMCA.

Number of species in genus at present: 09

All localities of studied species per country: Republic of South Africa; Malawi; Democratic Republic of the Congo; Tanzania.

Distribution of genus at present (*cf.* Figure 77): disjunct; submontane and montane areas from western and east-central Tanzania southwards to Katanga (Upemba National Park, Democratic Republic of the Congo) and Malawi; possibly via Zimbabwe and Mozambique to the eastern Republic of South Africa.

The reconstructed and predicted ancestral areas are the Guineo-Congolian regional centre of endemism, Guinea-Congolia/Sudania regional transition zone and Guinea-Congolia/Zambezia regional transition zone.

The reconstructed biogeographic events comprise: First, dispersal from the Guineo-Congolian regional centre of endemism, Guinea-Congolia/Sudania regional transition zone and Guinea-Congolia/Zambezia regional transition zone to the Zambezian regional centre of endemism, Zanzibar-Inhambane regional mosaic, Tongaland-Pondoland regional mosaic and Kalahari-Highveld regional transition zone. Secondly, vicariance between the Guineo-Congolian regional centre of endemism and all other phytochoria mentioned above.

Phylogenetic position: The sister genus is Gen. Nov. O.

The synapomorphies shared with the sister genus are:

- The base of a long ductus bursae is sclerotized; (96);
- Valva with a small sclerotized appendice that looks like a lunule ventral distally; (137).

The synapomorphies shared with the new genera M and O comprise:

- Uncus strongly elongated, narrow or broad, but only thinly sclerotized, bifid at tip; (86);
- Valva rectangular, 1.5 x taller than its width, well sclerotized; (95);
- Gnathos only thinly membranous and appears soft, not well sclerotized, ventrally fused and is very long (ending at half width of valva) and broader at base; (155).

Description: *Head:* rough-scaled; medium long hair-like scales of light yellow, often mixed with cream on fronto-clypeus; a pair of pits is absent on lower fronto-clypeus, a pair of conical projections is absent on lower fronto-clypeus in both sexes; pits behind the labial palpi are small oval-shaped holes; labial palpi less than eye diameter and consist in male of two segments, the basal segment has 40% the length of segment on top, but three segments are present in female with the segment on top almost as long as basal segment; antennae bipectinated in both sexes with narrow branches (2x width of shaft) in male, branches shorter in female; dorsal and lateral side of branches not scaled but covered with scattered tiny setae; flagellum scaled cream or light yellow.

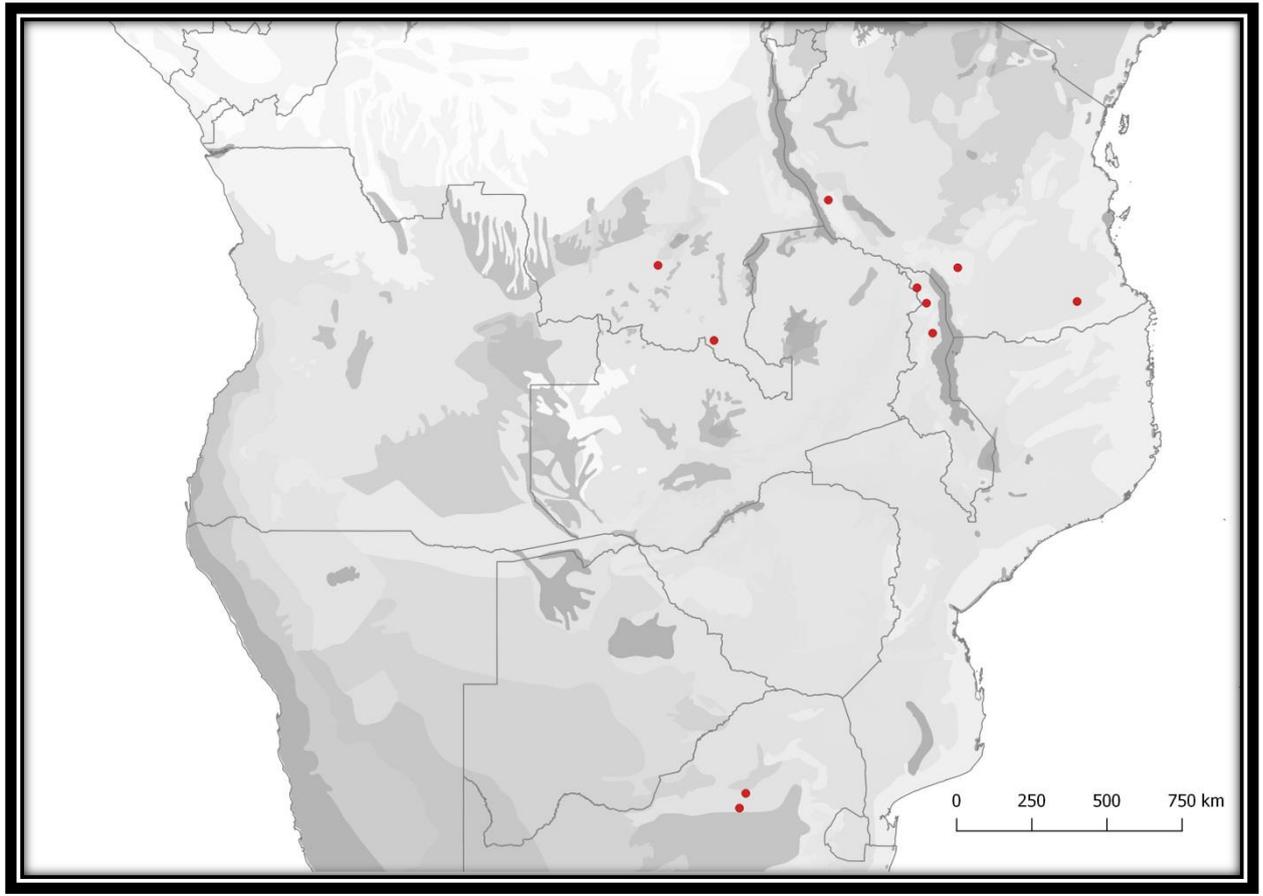
*Thorax:* Densely covered with hair-like scales, mainly yellow, mixed with light chestnut on patagia and tegulae; crest on metathorax light yellow. Epiphyses are absent in both sexes. Hindlegs with one pair of narrow tibial spurs, medium long (up to 0.9 mm); pretarsus with a pair of pulvilli.

Forewing upperside with a yellow ground-colour in both sexes, with a strong gloss and small grey patches along the costa in male, rather broad transverse bands of faded light chestnut or faded light orange from costa to dorsum in both sexes, the bands are always bright light orange between  $1A+2A$  and the lower median; a small light chestnut rounded patch occurs at the end of the discocellular cell;  $CuA_2$  not distinctly marked. Hindwing is light yellow or cream with a strong glint. Fringe hair-like, glossy and long on both wings (ciliae up to 2.0 mm). Wing venation: in forewing  $1A+2A$  forked at base (in females sometimes with a second but reduced fork);  $CuP$  absent (but in few females represented as a continuous not sclerotized fold);  $CuA_2$  originating from near hind margin of posterior cell;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  are separated and originate from apical angle of posterior cell;  $M_1$  initiating from anterior angle of median cell;  $R_2+R_3+R_4+R_5$  are on a long stalk;  $R_1$  initiating from near anterior angle of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  present as a strong fold with a fork at base;  $CuP$  present;  $CuA_2$  initiating from two-thirds of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1$  initiating from apical angle of anterior cell,  $Rs$  initiating from near apical angle of anterior cell and is strongly bent; a bar is present from near base of  $Rs$  to  $Sc+R_1$ ; a vein in discocellular cell on both forewing and hindwing is present. Retinaculum absent in both sexes; a frenulum is always present in male, up to 3.2 mm long.

*Abdomen:* With hair-like light yellow scales; abdominal tuft short, 20% of abdomen length.

*Male genitalia.* Saccus absent or very small, broadly rounded with a tiny emargination; the vinculum and tegumen are fused, forming a firm ring, tegumen and vinculum broad and of almost same width, vinculum more narrow (lateral view); uncus narrow elongated, not bent downwards in lateral view, hollow, very long (1.5 x longer than width of valva), bifurcated at tip, the tips are acuminate, with a graben-like structure at base. Valva is strongly rectangular, 1.5 x taller than its width, sclerotized with many tiny, fine and soft setae, longer along costal margin; a small sclerotized lunule-like or finger-like structure at the end of sacculus medio-distally; transtilla or semi-transtilla absent. Sacculus is narrow and present on the ventral width of valva. Gnathal arms simple, thinly membranous, rather broad where they are attached to the upper half of tegumen but narrow ventrally, the arms are connected ventrally and end in a rather tiny hook-like structure, but a bulla is absent; the gnathal arms are very long (ending at middle of valva). Juxta is large (50% the length of phallus), narrowly oval-shaped and comprising a tiny emargination on top, without any processes. Phallus is slightly longer than basal width of valva, simple tube-like, very broad, not bent, with a medium long thorn-like structure distally.

*Female postabdominal structure and genitalia.* Papillae anales large with short and very long setae and two ear-shaped structures dorsally; segment 8 is a broad rather triangular band, more narrow ventrally where many long setae occur, setose near its posterior margin; a narrow band-like structure is attached to base of anterior apophysis, extending to ventral edge of segment 8, with a large open space between the band-like structure and segment 8; anterior apophyses have a small rounded hole in the broader base, posterior apophyses much shorter. A large and elongated strongly sclerotized ventral plate is present. Ductus bursae very narrow, sclerotized at base; corpus bursae is elongated and pear-shaped with a broad rounded end, thinly membranous, without any structures.



**FIGURE 77.** Distribution of Gen. Nov. P (red dots).



**FIGURE 78.** Gen. Nov. P, *tegula* or sp. nov. p1 [close to *tegula*], [Republic of South Africa], northwest Gauteng, Rust de Winter road, Didimala, 12.-15.11.2003, A. Legrain leg., ex RMCA, male, genitalia slide number 07/032017 I. Lehmann. Wingspan 26.5 mm



**FIGURE 79.** Gen. Nov. P, sp. nov. p6, T.T. [Tanganyika Territory = Tanzania], Masasi, Farm Nachingwea, 11.1951, Dr. A.C. Evans leg., ex NMK, male, genitalia slide number 06/092017 I. Lehmann. Wingspan 27.0 mm



**FIGURE 80.** Gen. Nov. P, sp. nov. p8, [Democratic Republic of the Congo], Luena, 25.09.1983, Th. Bouyer leg., ex RMCA, female, genitalia slide number 18/102015 I. Lehmann. Wingspan 42.5 mm

#### 4.23 Gen. Nov. N

The genus is defined by the following autapomorphies:

- Anterior apophyses in broader base with one oval-shaped, elongated, large hole; (142);
- Segment 8 very large (4–5 times as large as papillae anales), strongly sclerotized, extending broadly above anterior apophyses and covering half of them dorsally; (143).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of female; [possibly also in male absent] (11).

Type species of genus (cf. Figure 82): Gen. Nov. N + sp. nov. n

Type locality: Obervolta [Burkina Faso], Bobo Dioulasso, 26.07.1976, Dr. H. Politzar leg., female, genitalia slide number 06/032017 I. Lehmann, ex MWM; depository in ZSM.

Number of species in genus at present: 07

All localities of studied species per country: Burkina Faso; Ivory Coast; Gabon; Republic of the Congo; Democratic Republic of the Congo; Angola; Malawi.

Distribution of genus at present (cf. Figure 81): lowland, submontane and montane areas from Burkina Faso and Ivory Coast further southeastwards to the Republic of the Congo and Gabon, from northwest Angola via the southern Democratic Republic of the Congo to extreme northwest Malawi (close to Ifisa Hill). The reconstructed and predicted ancestral areas are the Afromontane archipelago-like regional centre of endemism, Guinea-Congolia/Sudania regional transition zone and Guinea-Congolia/Zambezia regional transition zone.

The reconstructed biogeographic events comprise: First, dispersal from the Afromontane archipelago-like regional centre of endemism, Guinea-Congolia/Sudania regional transition zone and Guinea-Congolia/Zambezia regional transition zone to the Sudanian regional centre of endemism. Secondly, vicariance between the Guinea-Congolia/Sudania regional transition zone, Guinea-Congolia/Zambezia regional transition zone, Sudanian regional centre of endemism and the Afromontane archipelago-like regional centre of endemism.

Phylogenetic position: The sister genus could not be reconstructed unambiguously. The genus is part of an unresolved polytomy (cf. Figure 6a).

Description: *Head:* rough-scaled; medium long hair-like scales of light brown mixed with dark brown on fronto-clypeus; a pair of pits is absent on lower fronto-clypeus, a pair of conical projections is absent on lower fronto-clypeus in female; pits behind the

labial palpi are small rounded or oval-shaped holes; labial palpi less than eye diameter and consist in female of two segments (sometimes a tiny third strongly reduced segment is present on top), the basal segment is broadest and has 40% the length of second segment; antennae bipectinated in female with narrow branches ( $1.5 \times$  width of shaft); dorsal and lateral side of branches not scaled but covered with tiny setae; flagellum scaled cream and brown.

*Thorax:* Densely covered with long hair-like and broad scales, mainly light brown and dark brown mixed with pure white or cream on patagia and tegulae, usually long pure white hair-like scales at the end of tegulae (in fresh specimens); crest on metathorax pronounced and chestnut brown. Epiphyses are absent in female. Hindlegs with one pair of narrow tibial spurs, medium long (up to 0.9 mm); pretarsus with a pair of pulvilli.

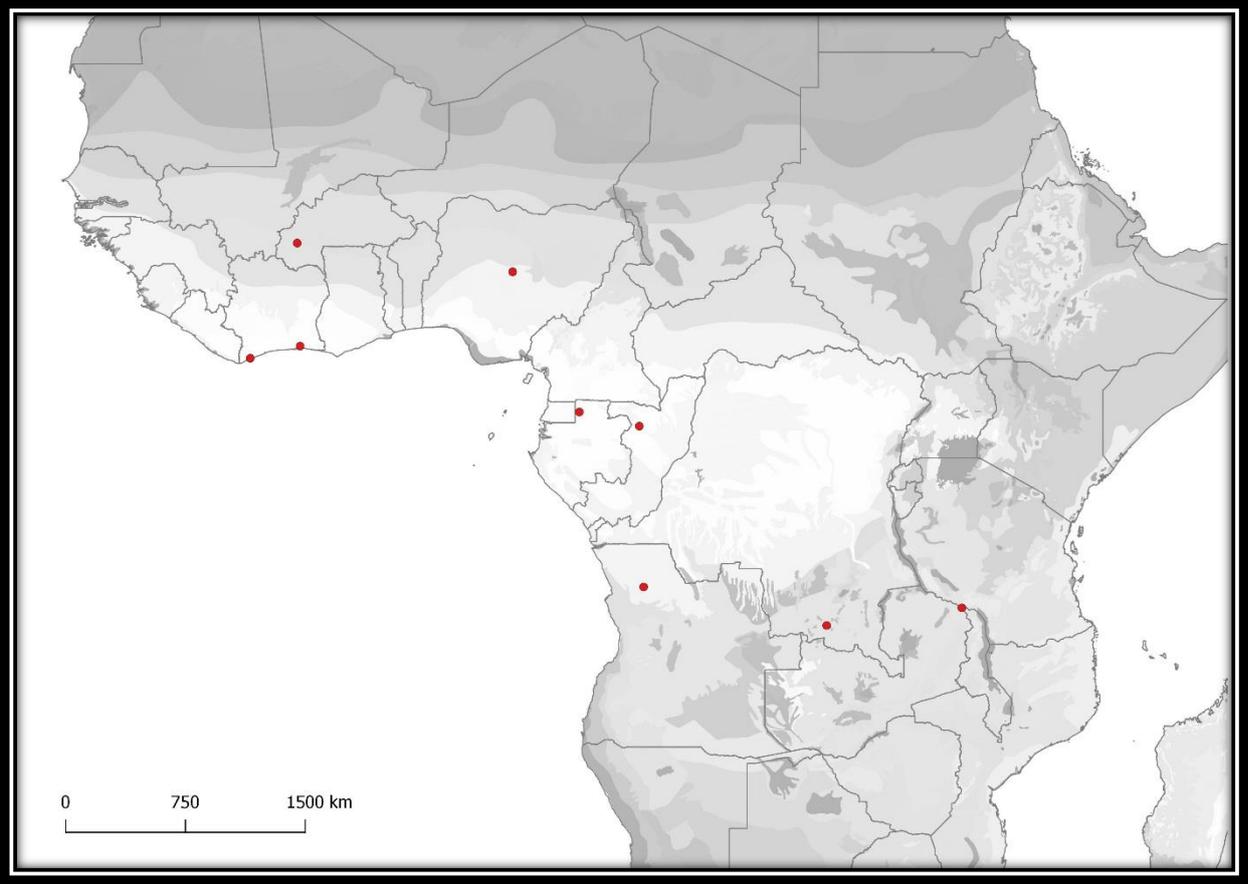
Forewing upperside with a light brown and cream ground-colour in female, with a strong gloss of vinaceous and light-grey, often rectangular patches that are edged sepia, a large white or cream coloured oblique patch below apex; a broad transverse sub-terminal band of light grey, glossy, from costa to dorsum; a rectangular large light grey patch at the end of discocellular cell and below lower median including the base of  $CuA_2$ ;  $CuA_2$  not distinctly marked. Hindwing is light brown-olive or light grey with a strong glint. Fringe is hair-like, alternating brown and grey, glossy and very short on both wings (ciliae up to 0.5 mm). Wing venation: in forewing  $1A+2A$  forked at base;  $CuP$  absent;  $CuA_2$  originating from near hind margin of posterior cell;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from almost the same base from apical angle of posterior cell;  $M_1$  initiating from anterior angle of median cell;  $R_3+R_4+R_5$  are on a long stalk;  $R_2$  and  $R_1$  separated and initiate from near anterior angle of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  present as a more or less strong fold with a fork at base;  $CuP$  present;  $CuA_2$  initiating from near end of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1$  initiating from apical angle of anterior cell close at base with  $R_s$ ; a bar is present from  $R_s$  to  $Sc+R_1$ ; a vein in discocellular cell on both forewing and hindwing is present. Retinaculum and frenulum absent.

*Abdomen:* With hair-like and broad scales of brown and cream; abdominal tuft short, 20% of abdomen length.

*Male genitalia.* Unknown.

*Female postabdominal structure and genitalia.* Papillae anales large with short and very long setae; segment 8 is very large (among the largest in Metarbelidae) representing a broad rectangular band that extends broadly above anterior apophyses and covering half of them dorsally; segment 8 very broad ventrally without long setae, setose near its posterior margin; anterior apophyses have a large elongated hole in the broader base, posterior apophyses much shorter and narrower with an emargination at base. Ductus bursae lunule-like shaped at base, sclerotized at base, becomes thickly

membranous to base of corpus bursae but is not sclerotized; corpus bursae is pear-shaped with a broad rounded end, thinly membranous, without any structures.



**FIGURE 81.** Distribution of Gen. Nov. N (red dots).



**FIGURE 82.** Gen. Nov. N, sp. nov. n, Obervolta [Burkina Faso], Bobo Dioulasso, 26.07.1976, Dr. H. Politzar leg., ex MWM, female, genitalia slide number 06/032017 I. Lehmann. Wingspan 47.0 mm



**FIGURE 83.** Gen. Nov. N, sp. nov. n3, Nordwest [northwest] Angola, Prov. [Province] Nordcuanza, Canzele, 30 km nördl. [30 km north] Ouiculungo, 16.10.1957, Gerd H. Heinrich leg., ex MWM, female, genitalia slide number 06/122018 I. Lehmann. Wingspan 44.0 mm

#### 4.24 Gen. Nov. Q

The genus is defined by the following autapomorphy:

- A narrow uncus is strongly bent downwards in the middle (lateral view); (117).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; [possibly also in female absent] (11).

Type species of genus (cf. Figure 85): Gen. Nov. Q + sp. nov. q

Type locality: [Eritrea], Ostafrika [East Africa] Expedition 1939, Abessinien, Cheren [Keren], 08.02.1939, E. von Saalfeld leg., male, genitalia slide number 19/012015 I. Lehmann, ex MWM; depository in ZSM.

Number of species in genus at present: 01

All localities of studied species per country: Republic of Eritrea.

Distribution of genus at present (cf. Figure 84): montane area in northeast Eritrea (Northeast Africa).

The reconstructed and predicted ancestral areas are the Afromontane archipelago-like regional centre of endemism and the montane regions of the Arabian Peninsula.

The reconstructed biogeographic event comprises: Vicariance between the Afromontane archipelago-like regional centre of endemism (African mainland) and the montane regions of the Arabian Peninsula.

Phylogenetic position: The sister genus is Gen. Nov. R.

The genus belongs to a monophylum together with the new genera S, Q and R.

The synapomorphy shared with Gen. Nov. R is:

- Male antenna with short, thinly membranous, broad rectangular branches that are not fused at base towards tip; (115a).

The synapomorphies shared with Gen. Nov. S and Gen. Nov. R comprise:

- Uncus strongly elongated, narrow or broad, but only thinly sclerotized, bifid at tip; (86);
- Whole gnathos thinly membranous, only half width of sacculus, long and stick-like, ventrally connected by a thin membrane that breaks up easily; (97);
- Valvae thinly membranous, basally not connected, with a tiny thorn-like appendice on the ventral side distally; (98);
- Valva rectangular, 1.5 x broader than tall; (113).

Description: *Head:* rough-scaled; medium long hair-like scales of light cream mixed with white and some scales with sepia coloured tips on fronto-clypeus; a pair of pits is present on lower fronto-clypeus, a pair of conical projections is absent on lower fronto-clypeus in male; pits behind the labial palpi are small oval-shaped holes; labial palpi less than eye diameter and consist in male of two segments, both segments are of almost equal length, second segment with an acuminate tip; antennae bipectinated with unusual shape: if the branches are viewed laterally they are extremely narrow and close together, but, if the branches are viewed anteriorly they are flat, broad rectangular with a broadly rounded tip densely covered with minute setae; branches are  $3.5 \times$  width of shaft and are not fused at base towards tip; dorsal and lateral side of branches not scaled but covered with tiny setae; flagellum scaled cream.

*Thorax:* Densely covered with long hair-like and broad scales, mainly light grey and white on patagia but mixed with pure white or cream scales with brown tips on tegulae, some longer pure white hair-like scales at the end of tegulae; crest on metathorax small and light brown. Epiphyses are present in male, narrow, 1.2 mm long. Hindlegs with one pair of narrow tibial spurs, medium long (0.9 mm outer spur, 0.7 mm inner spur); pretarsus with a pair of pulvilli.

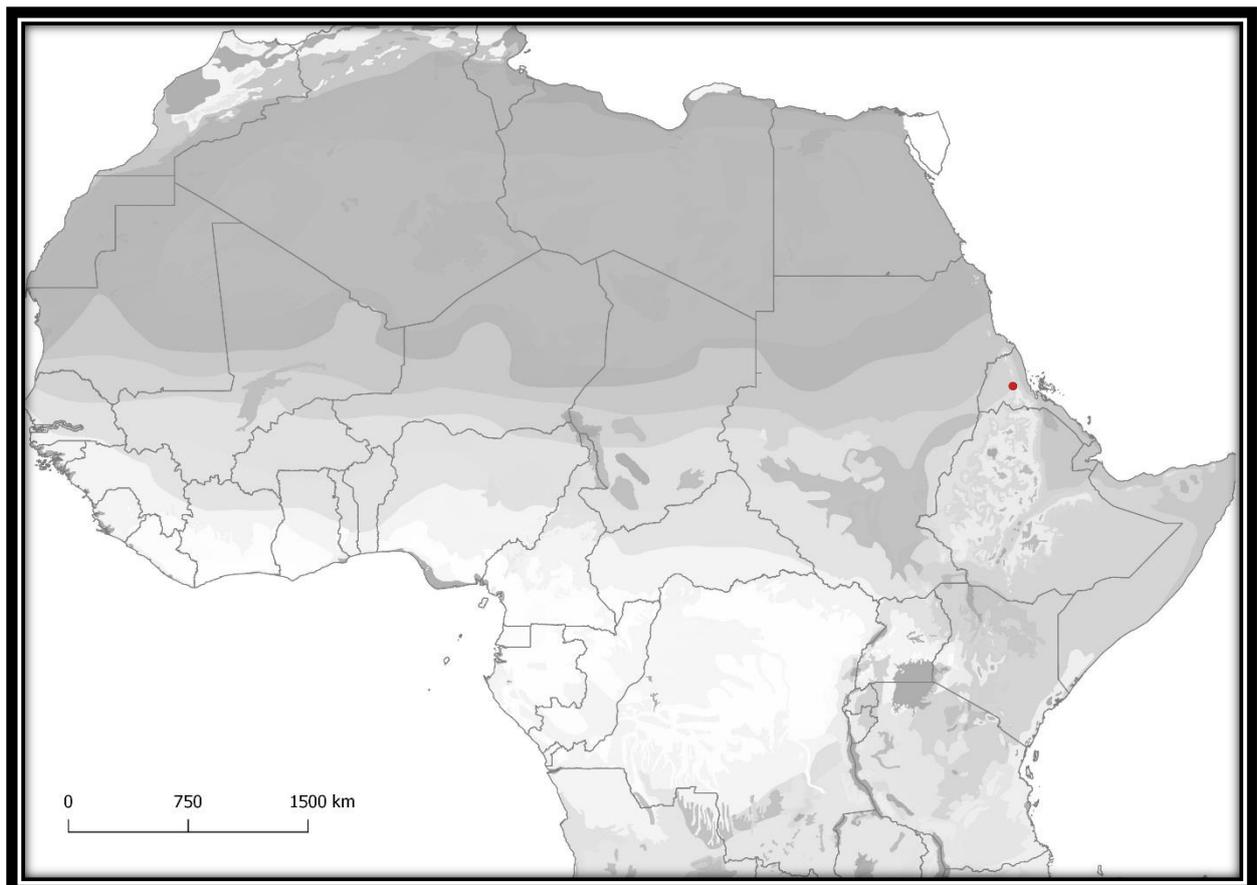
Forewing short, almost as long as hindwing, upper side with a light grey and pure white ground-colour in male, with a little gloss, but without any geometric design or pattern, except that all veins are covered by pure white and light brown scales; large cream coloured lunules, edged partly sepia, occur along the whole costal margin and below  $1A+2A$ ; a brown spot is present at the end of the discocellular cell that is pure white; a white patch below  $CuA_2$ ; small brown lunules along termen and in between white patches;  $CuA_2$  not distinctly marked. Hindwing is pure white with a strong glint. Fringe is not hair-like but with rather broad scales of pure white at base and sepia coloured tips, glossy and long on both wings (ciliae up to 1.3 mm). Wing venation: in forewing  $1A+2A$  broadly forked at base;  $CuP$  absent, but represented by an almost continuous fine fold;  $CuA_2$  originating from half of lower median;  $CuA_1$  far away from the former since it originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from almost the same base from apical angle of posterior cell;  $M_1$  initiating from anterior angle of median cell;  $R_3+R_4+R_5$  are on a long stalk;  $R_2$  and  $R_1$  separated and initiate from near anterior angle of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  represented by a strong fold;  $CuP$  present but very narrow;  $CuA_2$  initiating from near half of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1$  initiating from apical angle of anterior cell; a bar is present from  $R_s$  to  $Sc+R_1$ , the latter is strongly bent towards its base; a vein in discocellular cell on both forewing and hindwing is present but weak. Retinaculum and frenulum absent.

*Abdomen:* With hair-like and broad scales of white, brown and cream; abdominal tuft short, 20% of abdomen length.

*Male genitalia.* Saccus very small and rounded; the vinculum and tegumen are fused, forming a firm ring, tegumen and vinculum broad, tegumen twice as broad as

vinculum with a large hole; uncus very narrow elongated, strongly bent downwards in the middle in lateral view, hollow, long but shorter than width of valva, bifurcated at tip. Valva is rectangular, 1.5 x broader than tall, not well sclerotized with many fine and soft setae dorso-distally; a bunch of sclerotized setae at middle of sacculus; one sclerotized thorn-like structure above the end of sacculus medio-distally; transtilla present but extremely thinly membranous with a few setae, broader at base and very narrow at centre. Sacculus is narrow and present on the ventral width of valva. Gnathal arms simple, thinly membranous, very narrow and attached to the half of tegumen, the arms are connected ventrally and end in a rather tiny thinly membranous hook-like structure; a bulla is absent; the gnathal arms are long (ending near base of costa of valva). Juxta is very large (50% the length of valva width) but narrow with two very long and downwards bent thorn-like structures, without any processes. Phallus is only slightly longer than juxta, simple tube-like, broad, not bent, with a medium long thorn-like structure distally.

*Female postabdominal structure and genitalia. Unknown.*



**FIGURE 84.** Distribution of Gen. Nov. Q (red dot).



**FIGURE 85.** Gen. Nov. Q, sp. nov. q, [Eritrea], Ostafrika [East Africa] Expedition 1939, Abessinien, Cheren [Keren], 08.02.1939, E. von Saalfeld leg., ex MWM, male, genitalia slide number 19/012015 I. Lehmann. Wingspan 29.0 mm

#### 4.25 Gen. Nov. R

The genus is defined by the following autapomorphy:

- Uncus narrow and not bent downwards in the middle (lateral view) in combination with a juxta that is extremely large, almost 50% the size of valva; (179).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; [possibly also in female] (11).

Type species of genus (cf. Figure 87): Gen. Nov. R + sp. nov. r

Type locality: Yemen Arab Republic [Republic of Yemen], Province Sana'a, Makaban, Naqil Manakhah "(West side)", 1.730 m, 21.04.1998, A. Bischof, J. Bittermann, M. Fibi-ger, H. Hacker, H. Peks & H.-P. Schreier leg., male, genitalia slide number 25/012015 I. Lehmann, ex MWM; depository in ZSM.

Number of species in genus at present: 01

All localities of studied species per country: Republic of Yemen.

Distribution of genus at present (cf. Figure 86): southwestern Arabian Peninsula; montane area in western Yemen (Afrotropical Region).

The reconstructed and predicted ancestral areas are the Afromontane archipelago-like regional centre of endemism and the montane regions of the Arabian Peninsula.

The reconstructed biogeographic event comprises: The vicariance between the Afromontane archipelago-like regional centre of endemism (African mainland) and the montane regions of the Arabian Peninsula.

Phylogenetic position: The sister genus is Gen. Nov. Q.

The genus is in a monophylum together with the new genera S, Q and R.

The synapomorphy shared with Gen. Nov. Q is:

- Male antenna with short, thinly membranous, broad rectangular branches that are not fused at base towards tip; (115a).

The synapomorphies shared with Gen. Nov. S and Gen. Nov. Q comprise:

- Uncus strongly elongated, narrow or broad, but only thinly sclerotized, bifid at tip; (86);
- Whole gnathos thinly membranous, only half width of sacculus, long and stick-like, ventrally connected by a thin membrane that breaks up easily; (97);
- Valvae thinly membranous, basally not connected, with a tiny thorn-like appendice on the ventral side distally; (98);

- Valva rectangular, 1.5 x broader than tall; (113).

Description: *Head:* rough-scaled; medium long hair-like scales of pure white mixed with some scales of sepia on fronto-clypeus; a pair of small pits is present on lower fronto-clypeus, a pair of conical projections is absent on lower fronto-clypeus in male; pits behind the labial palpi are small oval-shaped holes; labial palpi less than eye diameter and consist in male of two segments, both segments are of almost equal length, second segment with an acuminate tip; antennae bipectinated with unusual shape: if the branches are viewed laterally they are narrow and close together, but, if the branches are viewed anteriorly they are flat, broad rectangular with a broadly rounded tip densely covered with minute setae; branches are transparent and are 3 × width of shaft and are not fused at base towards tip; dorsal and lateral side of branches not scaled but covered with tiny setae; flagellum scaled cream.

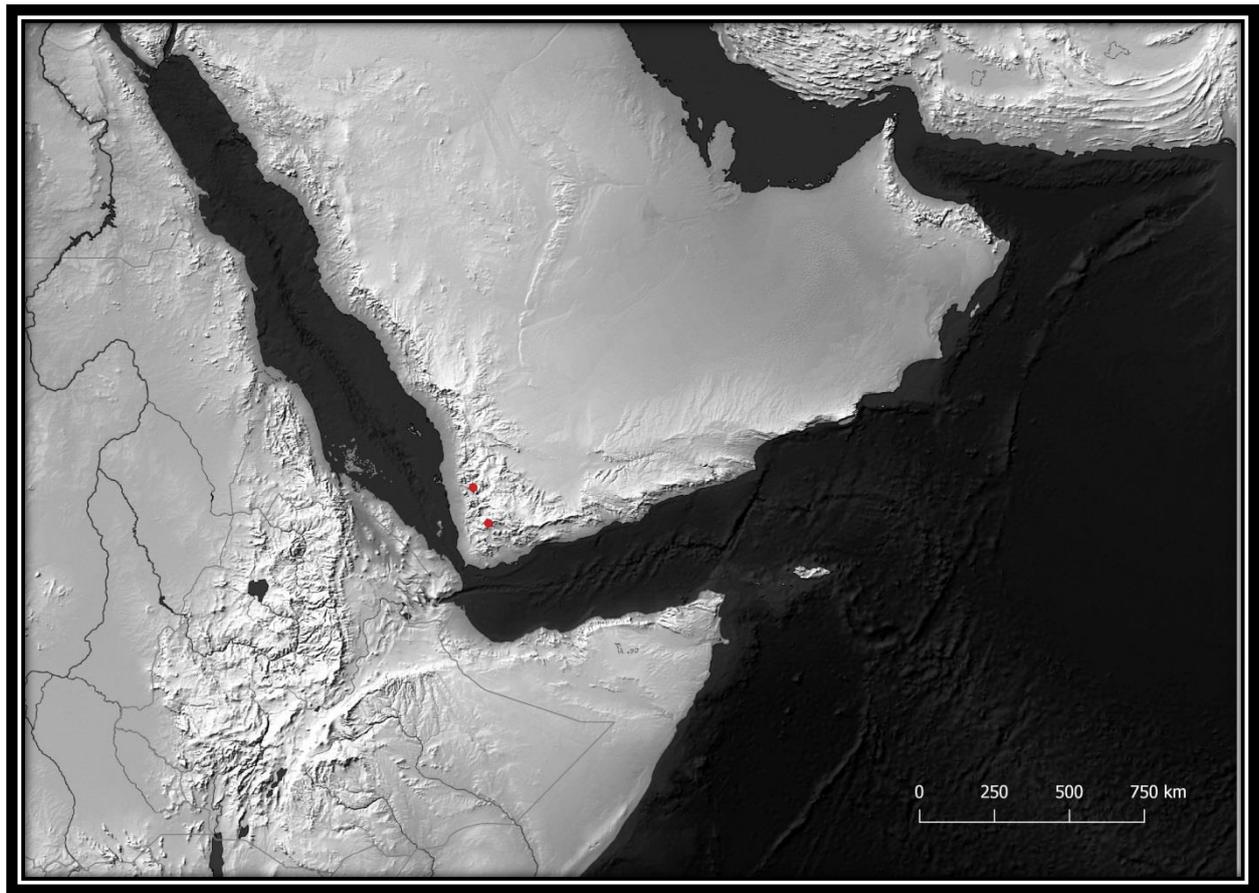
*Thorax:* Densely covered with long hair-like and broad scales, mainly light grey, sepia and white on patagia but pure white scales, some with brown tips, on tegulae, some longer pure white hair-like scales at the end of tegulae; crest on metathorax small and pure white. Epiphyses are very narrow in male, 0.9 mm long. Hindlegs with one pair of narrow tibial spurs, medium long (0.8 mm outer spur, 0.6 mm inner spur); pretarsus with a pair of pulvilli.

Forewing broadly elongated, much longer than hindwing, upperside with pure white ground-colour in male, glossy, without any geometric design or pattern except that all veins are covered by sepia scales; large lunules are absent on the whole wing; a brown spot is present at the end of the discocellular cell that is pure white and light grey; small brown lunules along termen and in between white patches; CuA<sub>2</sub> not distinctly marked. Hindwing is pure white or cream, glossy. Fringe is not hair-like but with rather broad scales of pure white at base and sepia coloured tips, glossy and long on both wings (ciliae up to 1.2 mm). Wing venation: in forewing 1A+2A forked at base; CuP absent, but represented by an almost continuous fine fold; CuA<sub>2</sub> originating from two-thirds (and not from half, *cf.* sister genus) of lower median; CuA<sub>1</sub> is weak and originates from hind margin of posterior cell, M<sub>3</sub> and M<sub>2</sub> originate from almost the same base from apical angle of posterior cell; M<sub>1</sub> initiating from anterior angle of median cell; R<sub>3</sub>+R<sub>4</sub>+R<sub>5</sub> are on a long stalk; R<sub>2</sub> and R<sub>1</sub> separated and initiate from near anterior angle of median cell; Sc more or less parallel to R<sub>1</sub>. In hindwing 3A present; 1A+2A represented by a strong fold; CuP present but very narrow; CuA<sub>2</sub> initiating from two-thirds (and not from near half) of lower median of posterior cell; CuA<sub>1</sub> initiates from hind margin of posterior cell; M<sub>3</sub> and M<sub>2</sub> initiating from apical angle of posterior cell, separated; M<sub>1</sub> initiating from apical angle of anterior cell; a bar is present from Rs to Sc+R<sub>1</sub>; a vein in discocellular cell on both forewing and hindwing is present but weak. Retinaculum and frenulum absent.

*Abdomen:* With hair-like and broad scales of white, brown and cream; abdominal tuft short, 20% of abdomen length.

*Male genitalia.* Saccus absent; the vinculum and tegumen are fused, forming a firm ring, tegumen and vinculum broad, tegumen with a large hole (50% of width of tegumen); uncus very narrow elongated, not bent downwards in the middle in lateral view, hollow, long but shorter than width of valva, slightly bifurcated at tip. Valva is rectangular, 1.5 x broader than tall, strongly rounded dorso-distally, not well sclerotized with many fine and soft setae dorso-distally; a sclerotized thorn-like structure above the end of sacculus medio-distally; transtilla absent, semi-transtilla short rectangular. Sacculus is narrow and present on the ventral width of valva. Gnathal arms simple, thinly membranous, very narrow and attached to the half of tegumen, the arms are not connected ventrally and hence, a membranous hook-like structure is absent (*cf.* sister genus); the gnathal arms are long (ending near base of costa of valva). Juxta is extremely large (it would cover 50% of whole valva surface) comprising a well sclerotized oval-shaped plate (50% of lower half) and two long and bent thorn-like structures (50% of upper half), without any processes. Phallus is shorter than juxta, simple tube-like, broad, not bent, with a medium long thorn-like structure distally.

*Female postabdominal structure and genitalia.* Unknown.



**FIGURE 86.** Distribution of Gen. Nov. R (red dots).



**FIGURE 87.** Gen. Nov. R, sp. nov. r, Yemen Arab Republic [Republic of Yemen], Province Sana'a, Makaban, Naqil Manakhah "(West side)", 21.04.1998, A. Bischof, J. Bittermann, M. Fibi-ger, H. Hacker, H. Peks & H.-P. Schreier leg., male, ex MWM, genitalia slide number 25/012015 I. Lehmann. Wingspan 32.5 mm

#### 4.26 Gen. Nov. S

The genus is defined by the following autapomorphy:

- Aedeagus extremely short (shorter than juxta) and broad (only 2 – 5 x longer than broad) with a well developed and strongly sclerotized thorn-like appendice distally (thorn less than 1/3 of valva length in lateral view); (207).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; [possibly also absent in female] (11).

Type species of genus (cf. Figure 89): Gen. Nov. S + *reticulata* (Janse, 1925)

Type locality and studied type specimen [including genitalia slide]: [Republic of South Africa], Umkomaas, 6.1.14 [06.01.1914], A. J. T. Janse leg., male, Type no. 1122, genitalia slide number 352a A.J.T. Janse, ex TMSA, depository in TMSA.

Number of species in genus at present: 05

All localities of studied species per country: Republic of South Africa; Namibia; Angola.

Distribution of genus at present (cf. Figure 88): lowland, submontane and montane areas from eastern parts of the Republic of South Africa westwards via the Cape and northwards via Namibia to west-central Angola.

The reconstructed and predicted ancestral area is the Afromontane archipelago-like regional centre of endemism.

The reconstructed biogeographic event comprises: First, dispersal in the Afromontane archipelago-like regional centre of endemism. Secondly, dispersal to the Cape regional centre of endemism, Karoo-Namib regional centre of endemism, the Kalahari-Highveld regional transition zone and to the montane regions of the Arabian Peninsula. Thirdly, vicariance between the Afromontane archipelago-like regional centre of endemism and the montane regions of the Arabian Peninsula with all other phytochoria mentioned above.

Phylogenetic position: The sister genus could not be reconstructed unambiguously. The genus is part of a monophylum together with the new genera S, Q and R.

The synapomorphies shared with Gen. Nov. R and Gen. Nov. Q comprise:

- Uncus strongly elongated, narrow or broad, but only thinly sclerotized, bifid at tip; (86);
- Whole gnathos thinly membranous, only half width of sacculus, long and stick-like, ventrally connected by a thin membrane that breaks up easily; (97);
- Valvae thinly membranous, basally not connected, with a tiny thorn-like appendice on the ventral side distally; (98);

- Valva rectangular, 1.5 x broader than tall; (113).

Description: *Head:* rough-scaled; medium long hair-like scales of only pure white or pure white mixed with scales of sepia on fronto-clypeus; a pair of small pits is present on lower fronto-clypeus, a pair of short conical projections is present on lower fronto-clypeus in male; pits behind the labial palpi are small oval-shaped holes; labial palpi less than eye diameter and consist in male of two segments, both segments are of almost equal length, second segment slightly longer than basal segment and with an acuminate tip; antennae bipectinated, if the branches are viewed anteriorly they are broad rectangular with a narrower base and a broadly rounded tip; branches are 3 × width of shaft; dorsal and lateral side of branches not scaled but covered with tiny setae; flagellum scaled cream or pure white.

*Thorax:* Densely covered with long hair-like and mainly narrow scales of pure white on patagia and tegulae or of sepia and light chestnut on patagia and tegulae; crest on metathorax pronounced pure white or light chestnut. Epiphyses are narrow in male, long, 1.3 mm. Hindlegs with one pair of narrow tibial spurs, medium long (1.0 mm outer spur, 0.8 mm inner spur); pretarsus with a pair of pulvilli.

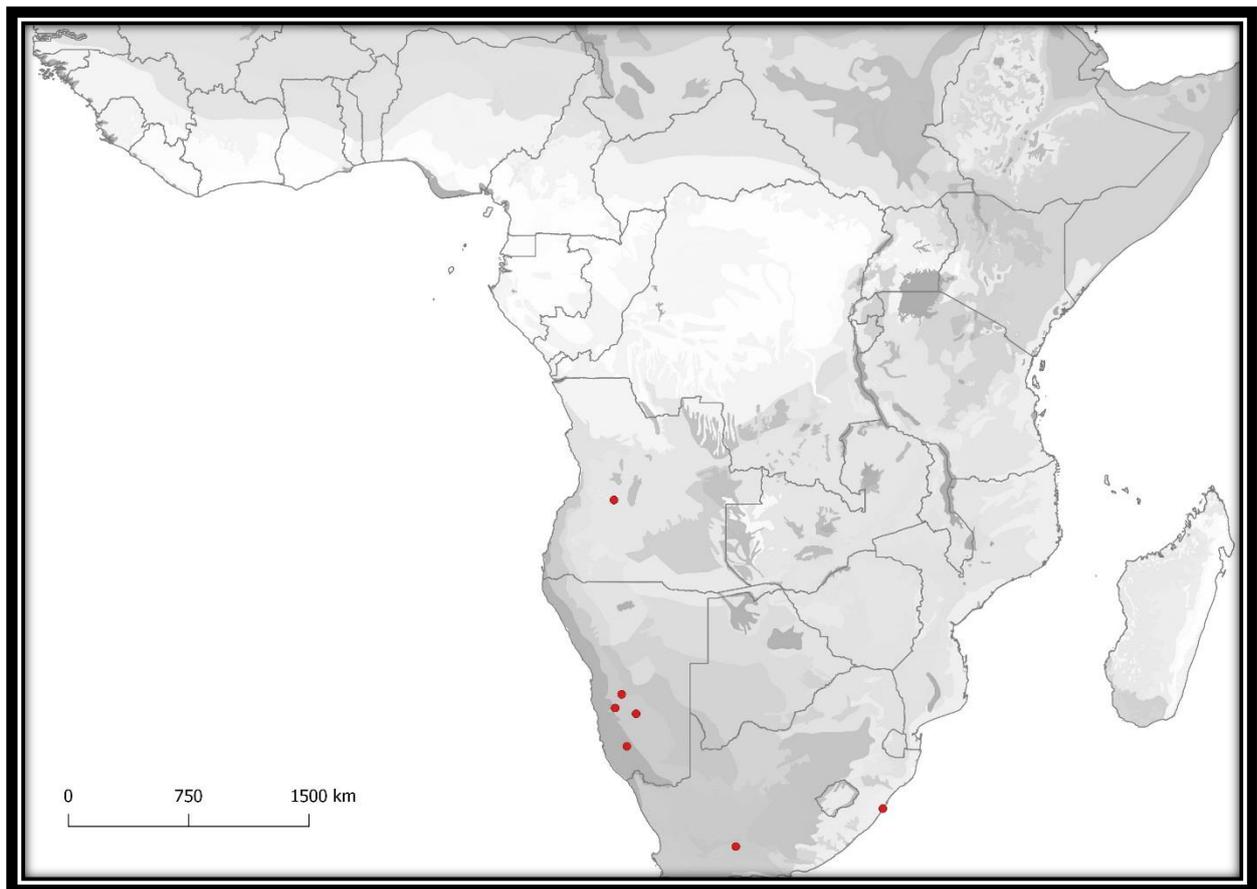
Forewing upperside with pure white ground-colour in male, glossy, without any geometric design; the pattern comprises rectangular patches of light grey or light chestnut on the whole upperside with two pure white patches between  $R_5$  and  $M_1$  and a broad white band below lower median and  $CuA_2$ ; only  $CuA_2$  not distinctly marked. Hindwing is pure white or cream, glossy. Fringe is hair-like and pure white, glossy, short on both wings (ciliae up to 0.6 mm). Wing venation: in forewing  $1A+2A$  forked at base;  $CuP$  absent;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from the same basal point from apical angle of posterior cell;  $M_1$  initiates from the same basal point like  $R_3+R_4+R_5$  (that are on a long stalk) from anterior angle of median cell;  $R_2$  and  $R_1$  separated and initiate from near anterior angle of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  represented by a strong fold without a fork at base;  $CuP$  absent;  $CuA_2$  initiating from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from the same basal point from apical angle of posterior cell;  $M_1$  initiating from apical angle of anterior cell; a bar is present from  $R_s$  to  $Sc+R_1$ ; a vein in discocellular cell on both forewing and hindwing is absent, sometimes represented only by a weak incomplete fold. Retinaculum and frenulum absent.

*Abdomen:* With hair-like and broad scales of pure white or light chestnut brown mixed with cream; abdominal tuft short, 20% of abdomen length.

*Male genitalia.* Saccus absent; the vinculum and tegumen are fused, forming a firm ring, tegumen and vinculum broad, both of almost equal width, tegumen with a large slit (20% of width of tegumen); uncus very narrow elongated, bent upwards at base in lateral view, hollow, long, but ca. 40% shorter than width of valva. Valva is large and rectangular, 1.5 x broader than tall, strongly rounded dorso-distally,

sclerotized with many fine and soft setae dorso-distally; a short sclerotized thorn-like structure with a rounded tip occurs above the end of sacculus medio-distally; transtilla absent, semi-transtilla absent. Sacculus is narrow, tube-like and present on 50% of the ventral width of valva. Gnathal arms simple, thinly membranous, very narrow and attached to half of tegumen, the arms are not connected ventrally and hence, a membranous hook-like structure is absent; the gnathal arms are short (ending just above the base of costa of valva). Juxta is not large but very long (slightly longer than aedeagus) comprising two well sclerotized thorn-like structures that are strongly bent downwards (in lateral view), without any processes. Phallus is shorter than juxta, simple tube-like, broad, not bent, with a medium long thorn-like structure distally.

*Female postabdominal structure and genitalia.* Unknown.



**FIGURE 88.** Distribution of Gen. Nov. S (red dots).



**FIGURE 89.** Gen. Nov. *S. reticulata*, Holotype, [Republic of South Africa], Umkomaas, 06.01.1914, A. J. T. Janse leg., ex TMSA, male, Type no. 1122, genitalia slide number 352a A.J.T. Janse. Wingspan 27.0 mm



**FIGURE 90.** Gen. Nov. *S.* sp. nov. s1, Angola, Nova Lisboa, 05.-07.03.1972, [no collector], ex BMNH: "Southern African Expedition B.M. 1972-1", male, genitalia slide number 12/1996 I. Lehmann. Wingspan 30.5 mm

#### **4.27 Gen. Nov. T**

The genus is defined by the following autapomorphy:

- Large, ear-shaped valvae with many very long straight setae on almost whole inner surface of valva but without one patch of strongly sclerotized long setae near the base of a small relict of a semi-transtilla; (152).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; [possibly also in female] (11).

Type species of genus (cf. Figure 92): Gen. Nov. T + sp. nov. t

Type locality: Nigeria, Oyo State, Gambari Forest Reserve, 12.03.1977, J. Riley leg., male, genitalia slide number 19/032017 I. Lehmann, ex BMNH; depository in BMNH.

Number of species in genus at present: 09

All localities of studied species per country: Republic of Guinea; Burkina Faso; Ivory Coast; Nigeria; Central African Republic.

Distribution of genus at present (cf. Figure 91): lowland areas from south-eastern Republic of Guinea to southwest Burkina Faso and via the southern Ivory Coast and western Nigeria extending eastwards to the southern Central African Republic.

The reconstructed and predicted ancestral areas are the Guinea-Congolia/Sudania regional transition zone, the Guinea-Congolia/Zambezia regional transition zone and the Sunda shelf/Sulawesi.

The reconstructed biogeographic event comprises: First, dispersal from the Guinea-Congolia/Sudania regional transition zone and the Guinea-Congolia/Zambezia regional transition zone into the Guineo-Congolian regional centre of endemism and the Sunda shelf/Sulawesi. Secondly, vicariance between the Sunda shelf/Sulawesi and the Guinea-Congolia/Sudania regional transition zone, Guinea-Congolia/Zambezia regional transition zone, Guineo-Congolian regional centre of endemism.

Phylogenetic position: The sister genus is Gen. Nov. V.

The genus belongs to a monophylum together with the new genera U, V and T.

The synapomorphy shared with Gen. Nov. V is:

- Uncus and tegumen very long, namely *ca.* 2.3 x longer than basal width of valva; (183).

The synapomorphies shared with Gen. Nov. U are:

- Uncus strongly elongated, narrow or broad, but only thinly sclerotized, bifid at tip; (86);

- Relicts of two narrow gnathal arms are attached to the lower part of tegumen (not uncus!); (127);
- Uncus tip represents a broad “V”; (133);
- Large, oval-shaped valva has many very long setae, soft or sclerotized, on the inner surface at least near costa; (136);
- Entire narrow uncus is longer or equal to basal width of valva and has a tip like a broad “V”; (151).

Description: *Head:* underside with short, fine scales of pure white; upperside rough-scaled with medium long hair-like scales mixed with broad scales of pure white and chestnut or pure white mixed with light ocher and sepia on fronto-clypeus; a pair of small pits is present on lower fronto-clypeus, but rather rudimentary, a pair of conical projections is absent on lower fronto-clypeus in male; pits behind the labial palpi are small oval-shaped holes or absent; labial palpi very small, often pure white, much less than half of eye diameter and consist in male of two segments with a tiny rudimentary third segment on top, both segments are of almost equal length, second segment slightly longer than basal segment; antennae bipectinated, branches are 1.5 × width of shaft; dorsal and lateral side of branches not scaled but covered with many tiny setae; flagellum scaled cream.

*Thorax:* Densely covered with long hair-like but mainly broad scales of pure white mixed with chestnut on patagia and tegulae or of sepia and light chestnut with little white on patagia and tegulae, tegulae pronounced; underside of thorax with short fine scales of pure white; crest on metathorax pronounced and light chestnut. Epiphyses are very narrow and short, appear rudimentary in male, only 0.5 mm long. Hindlegs with one pair of narrow tibial spurs, medium long (0.6 mm outer spur, 0.5 mm inner spur); pretarsus with a pair of pulvilli.

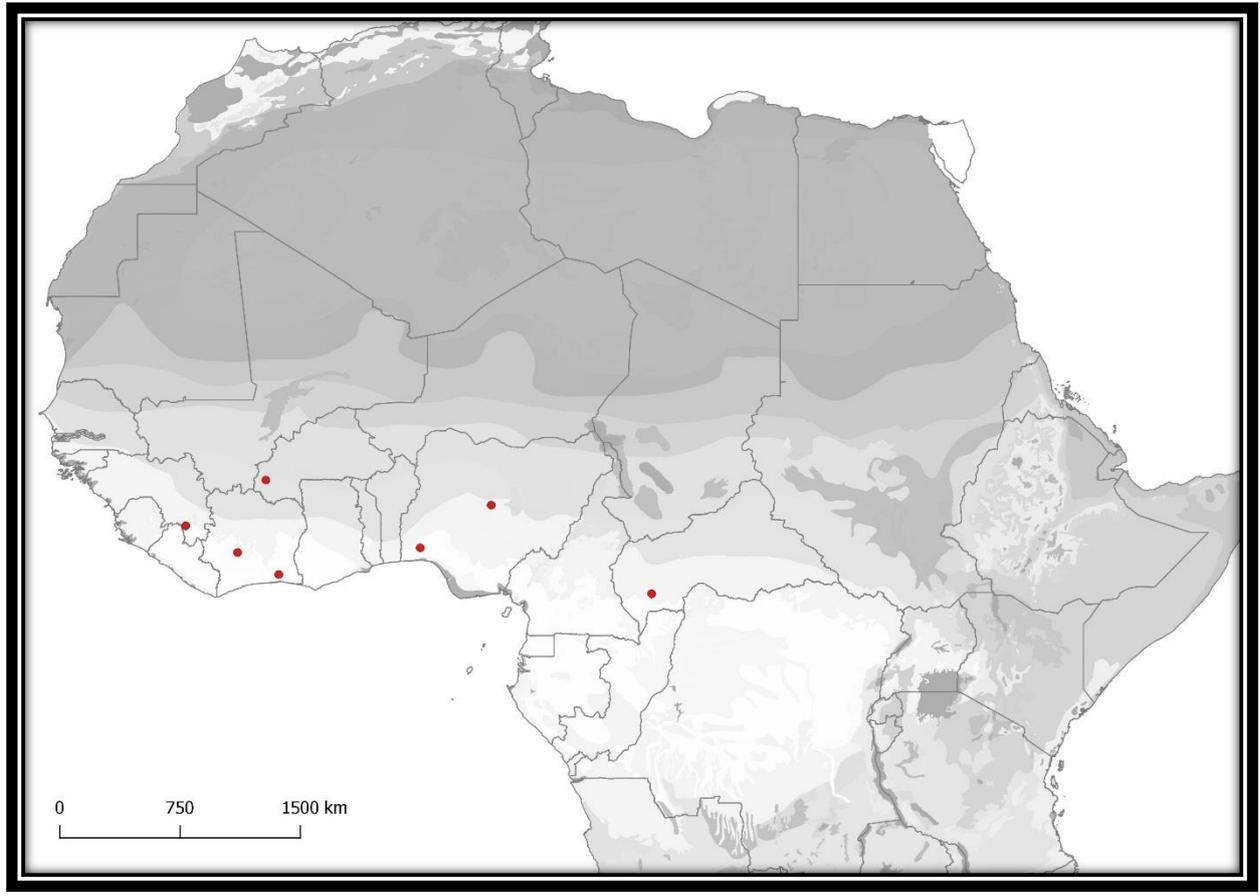
Forewing upperside with a light brown-olive or chestnut-olive ground-colour and a strong glint, without any geometric design; the pattern comprises a short sepia streak between  $M_2$  and  $M_1$  towards termen that is edged narrowly white or cream above; small rectangular patches of white or cream along costa and termen, a larger cream patch below base of  $1A+2A$ ; a more or less rectangular grey patch at end of discocellular cell as well as a more rounded patch of same colour between middle of  $1A+2A$  and lower median; a light brown and broad sub-terminal band is present, more or less pronounced, but only edged sepia towards base of wing;  $CuA_2$  not distinctly marked. Hindwing is light brown or grey-olive with a vinaceous glint. Fringe is hair-like, white or cream, glossy, very short on both wings (ciliae up to 0.3 mm). Wing venation: in forewing  $1A+2A$  forked at base;  $CuP$  absent;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from apical angle of posterior cell, separated;  $M_1$  initiates from anterior angle of median cell;  $R_3+R_4+R_5$  on a long stalk;  $R_2$  and  $R_1$  separated and initiate from near anterior angle of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  represented by a fold without a fork at base;  $CuP$  absent or represented by a

fold; CuA<sub>2</sub> initiating from two-thirds of lower median of posterior cell; CuA<sub>1</sub> initiates from hind margin of posterior cell; M<sub>3</sub> and M<sub>2</sub> initiating from apical angle of posterior cell, separated; M<sub>1</sub> initiating from apical angle of anterior cell; a bar is present from Rs to Sc+R<sub>1</sub>; a vein in discocellular cell on both forewing and hindwing is present; lower cell always smaller and shorter, sometimes only half the size than upper cell. Retinaculum and frenulum absent.

*Abdomen:* With hair-like and short scales of pure white on underside, on upperside light chestnut brown mixed with cream; abdominal tuft long, 30% of abdomen length, pronounced with light chestnut.

*Male genitalia.* Saccus absent; the vinculum and tegumen are fused, each forming a firm broadly triangular-shaped ring, tegumen is very long (longer than basal width of valva); uncus elongated, triangular-shaped, tip looks like a broad "V" sometimes similar to a fish tail. Valva is large, ear-shaped, strongly rounded at tip, upper half weakly sclerotized, lower half strongly sclerotized; very long, sclerotized setae (that appear grey in colour) are present on the weakly sclerotized part of valva; transtilla absent, semi-transtilla absent. Sacculus is prominent, broadly T-shaped at end, hollow and present on 60% of the ventral width of valva. Gnathal arms are a simple band, sclerotized, probably a relict of a gnathos that is attached to lower end of tegumen or upper end of vinculum, the arms are not connected ventrally; above this relict gnathal arms is a prominent hollow and broadly H-shaped structure with rounded tips that have a bunch of long, straight, sclerotized setae; the length of this structure is equal to the length of the gnathal arms. Juxta is large (60% the size of aedeagus) with a rounded emargination but without any processes. Phallus is very short, simple tube-like, broad, not bent, with a long and bent thorn-like structure distally (40% the length of aedeagus).

*Female postabdominal structure and genitalia.* Unknown.



**FIGURE 91.** Distribution of Gen. Nov. T (red dots).



**FIGURE 92.** Gen. Nov. T, sp. nov. t, Nigeria, Oyo State, Gambari Forest Reserve, 12.03.1977, J. Riley leg., ex BMNH, male, genitalia slide number 19/032017 I. Lehmann. Wingspan 35.0 mm



**FIGURE 93.** Gen. Nov. T, sp. nov. t4, Guinee Fse [Guinea], Sérédou, 23.02.1958, R. Pujol leg., ex MNHN, male, genitalia slide number 19/112018 I. Lehmann. Wingspan 32.5 mm

#### 4.28 Gen. Nov. V

The genus is defined by the following autapomorphies:

- Uncus extremely long and bent downwards in lateral view, extending well below the costa of valva; (172);
- Very long, strongly sclerotized and bent setae on almost the whole inner side of valva and densest near the base of a small relict of semi-transtilla; (184);
- Narrow, elongated forewing with rounded apex and almost triangular hindwings in male; (185).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; (11).

Type species of genus (cf. Figure 95): Gen. Nov. V + sp. nov. v

Type locality: [Indonesia], Sumatra, North Sumatra Province, Asahan District, Aek Tarum III, 09.10.1994, ca. 186 m, Dr. Eduard Diehl leg., male, genitalia slide number 06/122016 I. Lehmann, ex coll. Dr. Lutz Kobes; depository in ZSM.

Number of species in genus at present: 01

All localities of studied species per country: Indonesia.

Distribution of genus at present (cf. Figure 94): lowland areas of the Sunda shelf, at present only known from northern Sumatra.

Reconstructed, predicted ancestral areas are the Guinea-Congolia/Sudania regional transition zone and Guinea-Congolia/Zambezia regional transition zone, Sunda shelf/Sulawesi.

The reconstructed biogeographic event comprises: First, dispersal from the Guinea-Congolia/Sudania regional transition zone and the Guinea-Congolia/Zambezia regional transition zone into the Guineo-Congolian regional centre of endemism and the Sunda shelf/Sulawesi. Secondly, vicariance between the Sunda shelf/Sulawesi and the Guinea-Congolia/Sudania regional transition zone, Guinea-Congolia/Zambezia regional transition zone, Guineo-Congolian regional centre of endemism.

Phylogenetic position: The sister genus is Gen. Nov. T.

The genus belongs to a monophylum together with the new genera U, V and T.

The synapomorphy shared with Gen. Nov. T is:

- Uncus + tegumen very long, ca. 2.3 x longer than basal width of valva; (183).

The synapomorphies shared with Gen. Nov. U are:

- Uncus strongly elongated, narrow or broad, but only thinly sclerotized, bifid at tip; (86);
- Relicts of two narrow gnathal arms are attached to the lower part of tegumen (not uncus!); (127);
- Uncus tip represents a broad “V”; (133);
- Large, oval-shaped valva has many very long setae, soft or sclerotized, on the inner surface at least near costa; (136);
- Entire narrow uncus is longer or equal to basal width of valva and has a tip like a broad “V”; (151).

Description: *Head:* rough-scaled with medium long hair-like and broad scales of cream with light brown tips on fronto-clypeus; a pair of pits is absent on lower fronto-clypeus, a pair of conical projections is present on lower fronto-clypeus in male; pits behind labial palpi are small oval-shaped holes; labial palpi short, less than eye diameter and consist in male of two segments, basal segment broader and *ca.* 35% shorter than the second, more narrow segment; antennae bipectinated, branches are 3.0 × width of shaft; dorsal and lateral side of branches not scaled but covered with many tiny setae; flagellum scaled cream only on lateral side, dorsal side of the flagellum in broken antennae appear without scales.

*Thorax:* Densely covered with hair-like scales of cream on patagia and tegulae, glossy, some scales on tegulae have brown tips; crest on metathorax small and mixed with sepia. Epiphyses are narrow and short, 0.9 mm long. Hindlegs with one pair of narrow tibial spurs, medium long (0.8 mm outer spur, 0.7 mm inner spur); pretarsus with a pair of pulvilli.

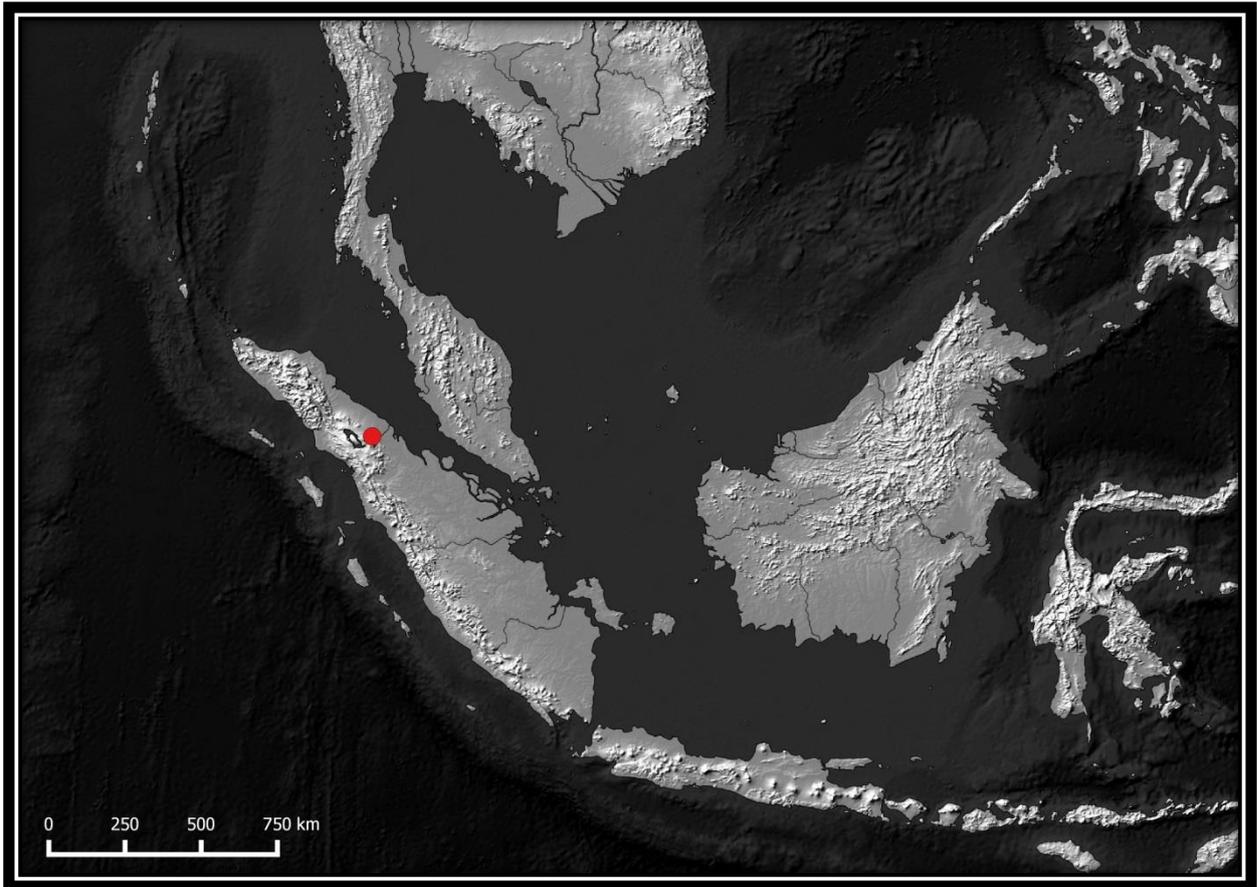
Forewing upperside with a light brown-olive ground-colour without any geometric design; the pattern comprises a large dark brown patch that covers half of the discocellular cell; almost black spots of oval shape between all veins close to termen and a broad dark grey terminal band with a vinaceous glint; CuA<sub>2</sub> not distinctly marked. Hindwing is sepia with a slightly vinaceous glint. Fringe is hair-like, very short on both wings (ciliae up to 0.2 mm only). Wing venation: in forewing 1A+2A is long forked at base; CuP absent; CuA<sub>2</sub> originating from middle of lower median; CuA<sub>1</sub> originates from hind margin of posterior cell, M<sub>3</sub> and M<sub>2</sub> originate from a long stalk from apical angle of posterior cell; M<sub>1</sub> initiates from a long stalk with R<sub>3</sub>+R<sub>4</sub>+R<sub>5</sub> from anterior angle of median cell; R<sub>2</sub> and R<sub>1</sub> separated and initiate from anterior part of median cell; Sc more or less parallel to R<sub>1</sub>. In hindwing 3A present; 1A+2A represented by a fold with a tiny fork at base; CuP represented by a fold; CuA<sub>2</sub> initiating from two-thirds of lower median of posterior cell; CuA<sub>1</sub> initiates from hind margin of posterior cell; M<sub>3</sub> and M<sub>2</sub> initiating from apical angle of posterior cell, separated; M<sub>1</sub>+R<sub>s</sub> long stalked and initiate from apical angle of anterior cell; a very long bar is present from R<sub>s</sub> to Sc+R<sub>1</sub> that extends beyond the apical angle of anterior cell; a discocellular vein on

both forewing and hindwing is present; the anterior margin of the median cell is very short and ends well before base of wing. Retinaculum and frenulum absent.

*Abdomen:* With hair-like and short scales of dark brown mixed with cream; abdominal tuft short, 20% of abdomen length.

*Male genitalia.* Saccus absent; the vinculum and tegumen are fused, forming a firm ring, tegumen is twice as broad as the narrow vinculum; uncus elongated, narrow, very long (one of the longest among *Metarbelidae*), triangular-shaped towards tegumen, deeply bifurcated between two broad tips with a rounded end. Valva is very large, strongly rounded at tip, costal margin extremely arc-shaped; very long, well sclerotized setae are present on inner side of valva particularly below costal margin, the setae are densest around a structure that looks like a relictual transtilla-like process; transtilla absent, semi-transtilla absent. Sacculus is prominent and hollow with an acuminate tip at end; a small rectangular sclerotized projection occurs on the valva above the end of the sacculus and is separated from the latter. Gnathal arms are a simple structure that looks like a "T", it is sclerotized and attached to the lower end of tegumen, the arms are not connected ventrally; between the lowest part of the gnathal arms originates a partly tube-like structure that is not tube-like on its lower half but very thinly membranous, tip of tube-like part not broader and with setae. Juxta is large (35% the size of aedeagus), wide and elongated, without any processes. Phallus is long (longer than basal width of valva), simple tube-like, broader at base, not bent, with a long and bent thorn-like structure distally (25% the length of aedeagus).

*Female postabdominal structure and genitalia.* Unknown.



**FIGURE 94.** Distribution of Gen. Nov.V (red dot).



**FIGURE 95.** Gen. Nov. V, sp. nov. v, [Indonesia], Sumatra, Asahan District, Aek Tarum III, [rain forest habitat destroyed, this species might be extinct] 09.10.1994, Dr. Eduard Diehl leg., ex coll. Dr. Lutz Kobes, male, genitalia slide number 06/122016 I. Lehmann. Wingspan 31.5 mm

#### **4.29 Gen. Nov. U**

The genus is defined by the following autapomorphies:

- Segment 8 strongly reduced and linked to band-like structures of number 153; (144);
- Segment 8 comprises only narrow band-like structures; (153);
- Extension of sacculus is strongly sclerotized and looks like a mountain top at end distally; (171);
- Very large, pot-shaped juxta, almost as broad as width of a broad V-shaped uncus; (186).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes; (11).

Type species of genus (cf. Figure 97): Gen. Nov. U + sp. nov. u

Type locality: Nepal, Kathmandu Valley, Lalitpur District, Godavari, 26.05.1992, ca. 1.500 m, H. Schnitzler leg., male, genitalia slide number 01/022016 I. Lehmann, ex ZFMK; depository in ZFMK.

Number of species in genus at present: 01

All localities of studied species per country: Federal Democratic Republic of Nepal.

Distribution of genus at present (cf. Figure 96): submontane and montane areas of central and eastern Nepal (Oriental Region) [occurs most probably also in the Kingdom of Bhutan).

The reconstructed and predicted ancestral areas are the Guinea-Congolia/Sudania regional transition zone, the Guinea-Congolia/Zambezia regional transition zone and Nepal.

The reconstructed biogeographic event comprises: First, dispersal from the Guinea-Congolia/Sudania regional transition zone and the Guinea-Congolia/Zambezia regional transition zone into Nepal and the Sunda shelf/Sulawesi. Secondly, vicariance between Nepal and the Sunda shelf/Sulawesi, the Guinea-Congolia/Sudania regional transition zone, the Guinea-Congolia/Zambezia regional transition zone.

Phylogenetic position: The sister genus could not be reconstructed unambiguously. The genus belongs to a monophylum together with the new genera U, V and T.

The synapomorphies shared with Gen. Nov. T and Gen. Nov. V are:

- Uncus strongly elongated, narrow or broad, but only thinly sclerotized, bifid at tip; (86);
- Relicts of two narrow gnathal arms are attached to the lower part of tegumen (not uncus!); (127);

- Uncus tip represents a broad “V”; (133);
- Large, oval-shaped valva has many very long setae, soft or sclerotized, on the inner surface at least near costa; (136);
- Entire narrow uncus is longer or equal to basal width of valva and has a tip like a broad “V”; (151).

**Description:** *Head:* rough-scaled with medium long hair-like and broad scales of light grey and cream with light brown tips on fronto-clypeus; a pair of small pits is present on lower fronto-clypeus, a pair of conical projections is absent on lower fronto-clypeus in male; pits behind labial palpi are small oval-shaped slits; labial palpi short, less than eye diameter and consist in male of two segments, basal segment slightly broader and *ca.* 35% shorter than the second, more narrow segment that has a strongly sclerotized acuminate tip; antennae bipectinated, branches are 2.0 × width of shaft, slightly club-like; branches not scaled but covered with many tiny setae; flagellum scaled cream.

*Thorax:* Densely covered with hair-like scales of cream and light grey with brown tips on patagia and tegulae, glossy; crest on metathorax small and brown coloured. Epiphyses are long (1.1 mm), narrow and tube-like, S-shaped. Hindlegs with one pair of narrow tibial spurs, medium long (0.9 mm outer spur, 0.8 mm inner spur); pretarsus with a pair of pulvilli.

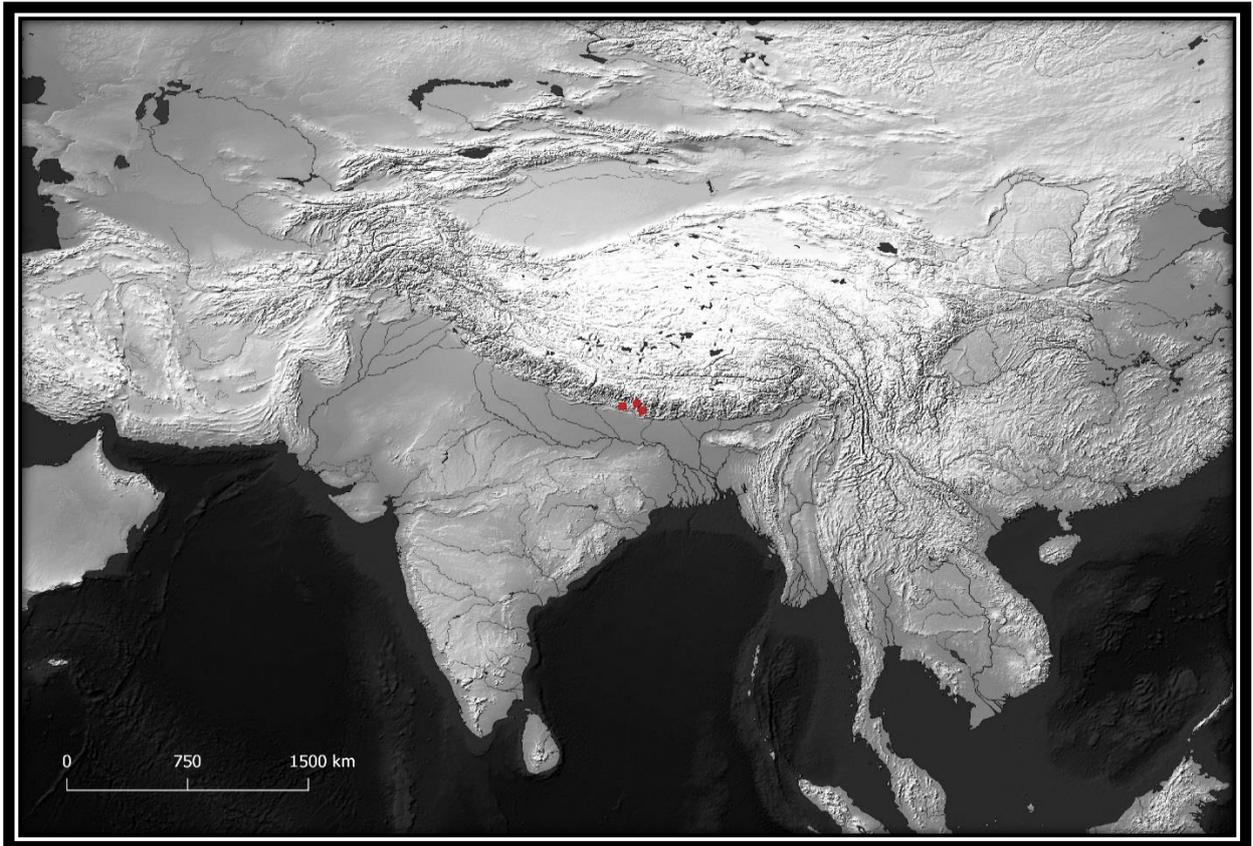
Forewing upperside with a pure white ground-colour, light grey towards termen, not glossy, with some geometric design of brown rounded patches along costa and lunules along termen; the pattern comprises a rectangular brown patch at the end of the discocellular cell and a slightly oblique sub-terminal band of light grey rectangular and rounded patches; some pure white very long scales above 1A+2A and below discocellular cell in a rather horizontal position; CuA<sub>2</sub> not distinctly marked. Hindwing is grey with a slightly vinaceous glint. Fringe is hair-like, short on both wings (ciliae up to 0.8 mm). Wing venation: in forewing 1A+2A is forked at base; CuP absent; CuA<sub>2</sub> originating from two-thirds of lower median; CuA<sub>1</sub> originates from hind margin of posterior cell, M<sub>3</sub> and M<sub>2</sub> originate from almost same basal point from apical angle of posterior cell; M<sub>1</sub> initiates from a short stalk with R<sub>3</sub>+R<sub>4</sub>+R<sub>5</sub> from anterior angle of median cell; R<sub>2</sub> and R<sub>1</sub> are widely separated at base and initiate from anterior part of median cell; Sc more or less parallel to R<sub>1</sub>. In hindwing 3A present; 1A+2A represented by a sclerotized fold with a fork at base; CuP present; CuA<sub>2</sub> initiating from two-thirds of lower median of posterior cell; CuA<sub>1</sub> initiates from hind margin of posterior cell; M<sub>3</sub> and M<sub>2</sub> initiating from apical angle of posterior cell, separated; M<sub>1</sub>+Rs long stalked and initiate from apical angle of anterior cell; a long bar is present from Rs to Sc+R<sub>1</sub> that does not extend beyond the apical angle of anterior cell; a discocellular vein on both forewing and hindwing is present. Retinaculum and frenulum absent.

*Abdomen:* With hair-like and short scales of dark brown mixed with grey; abdominal tuft short, 20% of abdomen length.

*Male genitalia.* Saccus absent; the vinculum and tegumen are fused, forming a firm ring, vinculum is twice as broad as the narrow tegumen; uncus elongated, narrow,

long, slightly broader in the middle with few setae, bifurcated between two broad truncate tips. Valva is large, rectangular in lateral view but more oval when viewed ventrally; very long, but little sclerotized, rather soft setae are present on inner side of valva, brush-like long setae and more sclerotized occur on upper base of valva, the setae are densest around a structure that looks like a relictual transtilla-like process; transtilla absent, semi-transtilla absent. Sacculus is prominent and hollow with a tip at end that looks like a mountain with an acuminate tip onto the valva distal-ventrally, ventral side of sacculus with some long setae. Gnathal arms are a simple structure that looks like a short "T", it is sclerotized and attached to the lower end of tegumen, the arms are not connected ventrally; between the lowest part of the gnathal arms originates a partly tube-like structure that is not tube-like on its lower one-third but very thinly membranous, towards the tip the tube-like part is broader at middle. Juxta is large oval-shaped or pot-like (90% the size of aedeagus), without any processes. Phallus is short (shorter than basal width of valva), simple tube-like, broader at base, not bent, with a long straight thorn-like structure distally (20% the length of aedeagus).

*Female postabdominal structure.* Papillae anales with short and long setae; segment 8 is extremely reduced and represented only by two narrow bands with long setae ventrally. In between both bands occurs a large thin membrane; anterior apophyses have a hole in the broader base; posterior apophyses are small and narrow.



**FIGURE 96.** Distribution of Gen. Nov. U (red dots).



**FIGURE 97.** Gen. Nov. U, sp. nov. u, Nepal, Kathmandu Valley, Lalitpur District, Godavari, 26.05.1992, H. Schnitzler leg., ex ZFMK, male, genitalia slide number 01/022016 I. Lehmann. Wingspan 28.0 mm

#### 4. 30 Gen. Nov. W

The genus is defined by the following autapomorhy:

- Two large, hollow, rectangular-shaped appendices on ventral part of valva, that are basally connected, are as large as *ca.* 30–40% of the soft outer surface of one valva; (129).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; [possibly also in female] (11).

Type species of genus (cf. Figure 99): Gen. Nov. W + sp. nov. w

Type locality: Ivory Coast, Danané, 04.03.1981, *ca.* 360 m, Dr. H. Politzar leg., male, genitalia slide number 09/092017 I. Lehmann, ex MWM; depository in ZSM.

Number of species in genus at present: 04

All localities of studied species per country: Ivory Coast, Nigeria.

Distribution of genus at present (cf. Figure 98): disjunct; lowland areas of northern, western and southern Ivory Coast with a record from eastern Nigeria.

The reconstructed and predicted ancestral area is the Guineo-Congolian regional centre of endemism.

The reconstructed biogeographic event comprises: First, dispersal from the the Guineo-Congolian regional centre of endemism into the Guinea-Congolia/Sudania regional transition zone, the Guinea-Congolia/Zambezia regional transition zone further east to Nepal. Secondly, vicariance between the Guineo-Congolian regional centre of endemism and the Guinea-Congolia/Sudania regional transition zone, the Guinea-Congolia/Zambezia regional transition zone and Nepal.

Phylogenetic position: The sister genus could not be reconstructed unambiguously.

Description: *Head:* rough-scaled with medium long hair-like and broad scales of cream mixed with light brown and/or sepia on fronto-clypeus; a pair of small pits is present (rather rudimentary) on lower fronto-clypeus, a pair of conical projections is absent on lower fronto-clypeus in male; pits behind labial palpi are small oval-shaped holes; labial palpi less than eye diameter and consist in male of two segments, basal segment slightly broader and *ca.* 40% shorter than the second, more narrow segment that has a more or less sclerotized acuminate tip; antennae bipectinated, branches are 3.0 × width of shaft, not scaled but covered with many tiny setae; flagellum scaled cream.

*Thorax:* Densely covered with hair-like and broad scales of cream or pure white mixed with sepia and/or light ocher on patagia and tegulae, glossy, with pure white very long hair-like scales always at the end of tegulae; crest on metathorax small and

sepia or cream coloured mixed with light ocher. Epiphyses are long (1.2 mm), very narrow viewed laterally, but rather broad viewed ventrally. Hindlegs with one pair of narrow tibial spurs, almost equal in length, rather short (only 1.0 mm in largest species; usually 0.6 mm long); pretarsus with a pair of pulvilli.

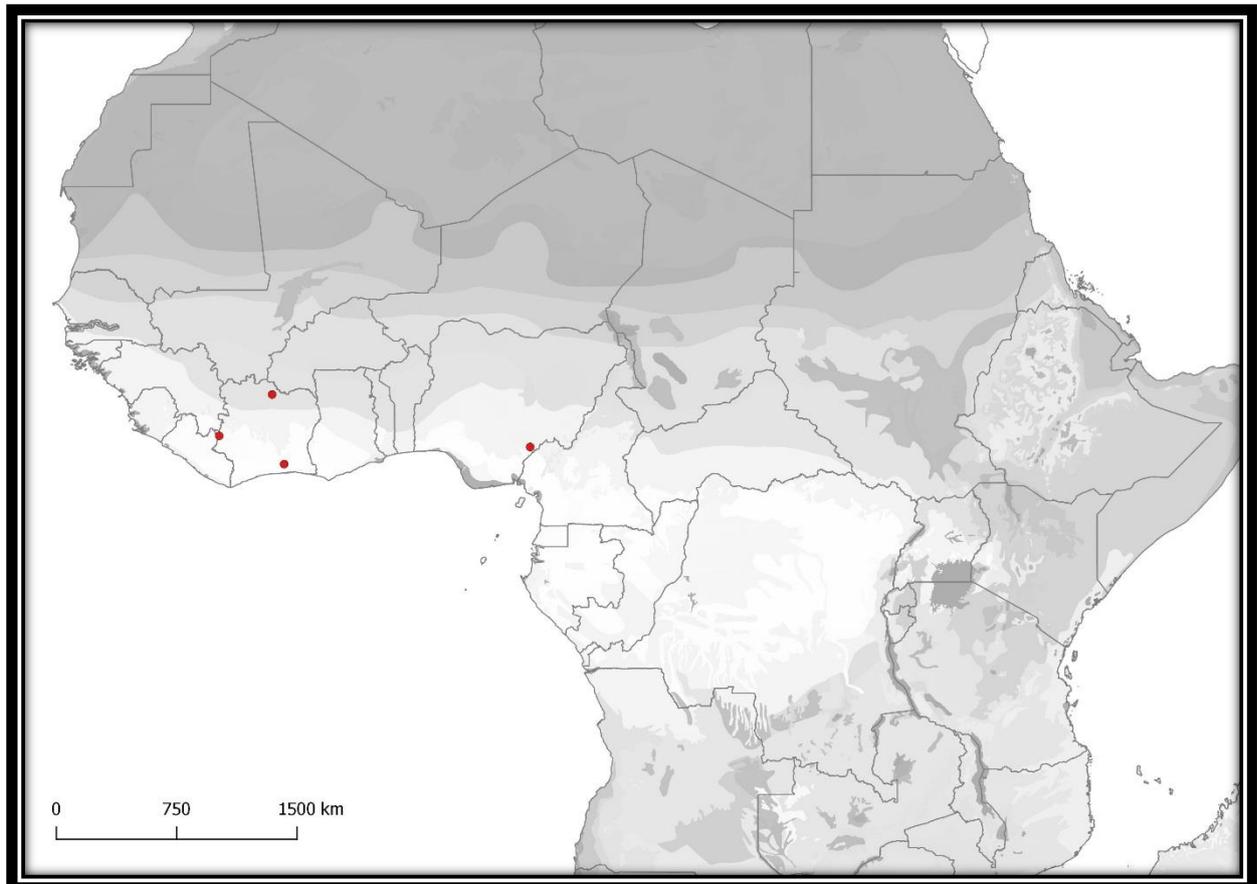
Forewing upperside with pure white or dark cream ground-colour, glossy, a geometric design is absent; the pattern comprises always a pronounced rectangular sepia spot at the end of the discocellular cell and more or less visible slightly oblique sub-terminal and terminal bands of light brown or light grey rectangular and rounded patches, these patches are sometimes very many and give the upperside a mainly light brown appearance; very long scales above  $1A+2A$  and below discocellular cell are absent;  $CuA_2$  not distinctly marked. Hindwing is pure white, glossy or light grey with a slightly vinaceous glint. Fringe is hair-like, short on both wings (ciliae up to 0.6 mm). Wing venation: in forewing  $1A+2A$  is forked at base;  $CuP$  absent, but represented by a more or less continuous fine fold;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from apical angle of posterior cell, separated;  $M_1$  initiates from the same basal point with the long stalk of  $R_3+R_4+R_5$  from anterior angle of median cell;  $R_2$  and  $R_1$  are widely separated at base and initiate from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  represented by a sclerotized fold with a fork at base;  $CuP$  present;  $CuA_2$  initiating from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1+Rs$  initiate from apical angle of anterior cell, separated; a short bar is present from  $Rs$  to  $Sc+R_1$ ; a discocellular vein on both forewing and hindwing is present, discal cell in forewing long (60% of wing length) and narrow (only 25% of width of forewing or less). Retinaculum and frenulum absent.

*Abdomen:* With hair-like and short scales of pure white mixed with light ocher or dark brown mixed with grey and light ocher; abdominal tuft long, 30% of abdomen length.

*Male genitalia.* Saccus absent; the vinculum and tegumen are fused, forming a firm broad ring; uncus elongated with a broad triangular base (viewed ventrally), narrow towards tip, long, bifurcated between two broad truncate tips. Valva is large, broadly oval in lateral view and when viewed ventrally, outer half thinly membranous, inner basal half sclerotized; very long, sclerotized setae (that appear grey in colour) are present on outer inner half of valva and at the rounded tip; transtilla absent, semi-transtilla absent. Sacculus is narrow with a large end that has two rectangular appendices that are basally connected and hollow towards tip, occurring more distal-ventrally; almost the entire ventral side of sacculus has long straight setae in grey colour. Gnathal arms are a simple structure that looks like a narrow stick with a rounded tip, it is sclerotized and attached to the lower end of tegumen, the arms are not connected ventrally; between the lowest part of the gnathal arms originates a broadly V-shaped, large, partly tube-like structure that points downwards (towards the ventral part of valva), it is basally connected, not tube-like on its upper one-third

(=the base of this structure) but very thinly membranous, towards the broadly rounded tips, the tube-like part is hollow and covered with many long, straight sclerotized setae. Juxta is large oval-shaped (90% the size of aedeagus) with an emargination, but without any processes. Phallus is short (shorter than basal width of valva), simple tube-like, broader at base, not bent, with a long straight thorn-like structure distally (20% the length of aedeagus).

*Female postabdominal structure and genitalia. Unknown.*



**FIGURE 98.** Distribution of Gen. Nov. W (red dots).



**FIGURE 99.** Gen. Nov. *W*, sp. nov. w, Ivory Coast, Danané, 04.03.1981, Dr. H. Politzar leg., ex MWM, male, genitalia slide number 09/092017 I. Lehmann. Wingspan 33.0 mm



**FIGURE 100.** Gen. Nov. *W*, sp. nov. w3, Nigeria, Obudu Cattle Ranch, 19.-20.12.1970, Dr. H. Politzar leg., ex MWM, male, genitalia slide number 16/052017 I. Lehmann. Wingspan 40.0 mm

#### 4.31 Gen. Nov. X

The genus is defined by the following autapomorphy:

- Corpus bursae not sclerotized, small, only one-third the size of segment 8; (164).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of female; [possibly also in male] (11).

Type species of genus: Gen. Nov. X + *acutistriata* (Mell, 1923)

Type locality: [Indonesia], Malang [Java], three females; depository in ZMHB; no further data published by Mell (1923).

Closest localities to type locality of studied specimens (*cf.* Figures 102, 103): [Indonesia], North Sumatra, Prapat, HW2A, 1.200 m, 23.11.1997, Dr. E. Diehl leg., female, genitalia slide number 23/012017 I. Lehmann, ex coll. Dr. Lutz Kobes; depository in ZSM; [Indonesia], northeast Sumatra, Dolok Merangir, ca. 180 m, 27.07.1976, Dr. Eduard Diehl leg., female, genitalia slide number 26/092017 I. Lehmann, ex ZFMK, "Museum A. Koenig Eing.Nr. 95/448 ex coll. Dr. R. Bender"; depository in ZFMK.

Number of species in genus at present: 02 (on Sumatra)

All localities of studied species per country: Indonesia and Brunei (in regard to Borneo).

Distribution of genus at present (*cf.* Figure 101): lowland, submontane and montane areas of the Sunda shelf, at present known from the islands of Borneo, Sumatra and Java. The reconstructed and predicted ancestral area is the Guineo-Congolian regional centre of endemism and the Sunda shelf/Sulawesi.

The reconstructed biogeographic event comprises: Vicariance between the Guineo-Congolian regional centre of endemism and the Sunda shelf/Sulawesi.

Phylogenetic position: The sister genus is Gen. Nov. Y.

The synapomorphies shared with Gen. Nov. Y are:

- Very long, pure white, hair-like scales, not or only slightly curled, have an upright position on upperside of forewing well above the normal scale-layer; (162);
- Very rare forewing pattern in both sexes where a broad grey or light brown band extends from termen into the discal cell in between  $M_2$  and  $M_1$  or  $M_2$  and  $R_5$  as well as a broad white or light cream band extends from  $R_5$  to costal margin and to  $R_1$ ;  $CuA_2$  is not distinctly marked in this pattern; (163);
- Posterior apophyses at base V-shaped, but "V" strongly unequal in length and with thorn-like end, somehow fork-like; (167);

- Anterior apophyses narrow and short, length less than width of segment 8 (including the ventral plate), near base very broad with a small rounded hole at centre; (168).

Description: *Head:* rough-scaled with medium long broad scales of cream and white mixed with light brown on fronto-clypeus; a pair of small rudimentary pits is present on lower fronto-clypeus, a pair of conical projections is absent on lower fronto-clypeus in female; pits behind labial palpi are small oval-shaped or rounded holes; labial palpi short, less than half of eye diameter and consist in female of two segments, basal segment broader and *ca.* 50% shorter than the second, more narrow segment that has a more or less sclerotized acuminate tip; antennae short (only 3 mm long), bipectinated, branches are  $2.0 \times$  width of shaft, not scaled but covered with many tiny setae; flagellum scaled cream.

*Thorax:* Densely covered with broad scales of cream and light ocher with light brown tips on patagia and tegulae, not glossy, tegulae pronounced; thorax at centre with pure white scales; crest on metathorax small and cream coloured mixed with light ocher. Epiphyses are small (1.0 mm long), narrow. Hindlegs with one pair of narrow tibial spurs, rather short (0.8 mm long); pretarsus with a pair of pulvilli. All legs have unusually white and very long hair-like scales (above the normal long scales) that occur also on the forewing upperside on the lower median and on  $CuA_2$ .

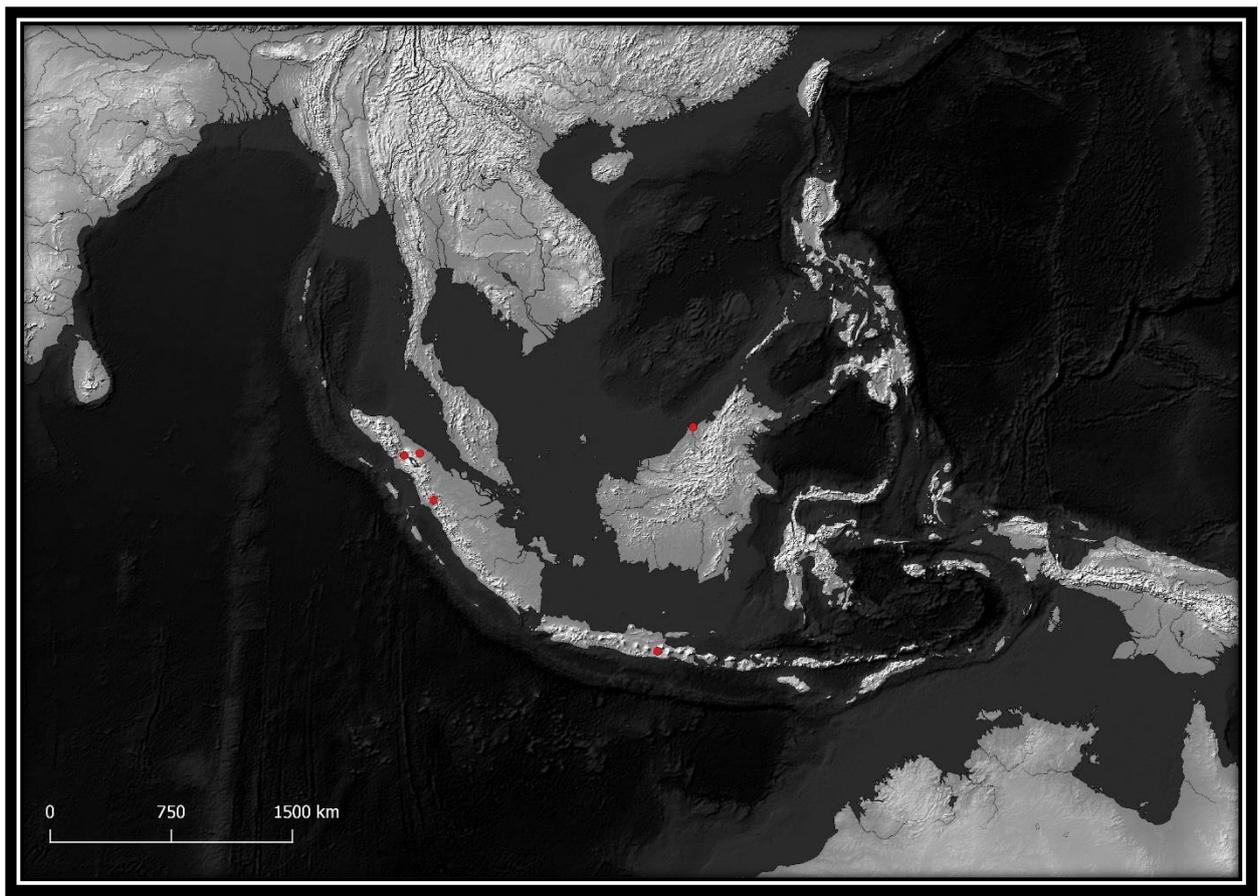
Forewing upperside with cream ground-colour, not glossy, a geometric design is present (unique in the Oriental Region), it comprises always a pronounced broad grey rectangular band that extends from termen into the discocellular cell in between  $M_2$  and  $R_5$  as well as a very broad white or light cream rectangular band that extends from  $R_5$  along the costal margin to  $R_1$ ; a large light cream rectangular patch extends from  $M_2$  or  $M_3$  to  $CuA_2$ ; very long white scales occur densely on the lower median of discocellular cell and on  $CuA_2$ ; these scales are much longer than the normal scale layer and occur also scattered between the lower median and the dorsum;  $CuA_2$  not distinctly marked. Hindwing is light grey, glossy with a vinaceous glint. Fringe is hair-like, short on both wings (ciliae up to 0.6 mm). Wing venation: in forewing  $1A+2A$  is forked at base, sometimes very short forked;  $CuP$  absent;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from the same basal point from apical angle of posterior cell;  $M_1$  initiates from the same basal point with the long stalk of  $R_3+R_4+R_5$  from anterior angle of median cell;  $R_2$  and  $R_1$  are widely separated at base and initiate from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  represented by a fold with a fork at base;  $CuP$  rudimentary towards base;  $CuA_2$  initiating from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1+Rs$  initiate from apical angle of anterior cell, slightly separated at base; a bar is present from  $Rs$  to  $Sc+R_1$ ; a discocellular vein on both forewing and hindwing is rather weak and sometimes absent in forewing; discal cell in forewing with a rather acuminate apical

angle at end of posterior cell and median cell, both have almost the same length. Retinaculum and frenulum absent.

*Abdomen:* With hair-like and broad scales of cream mixed with light ochre and brown; abdominal tuft short, 20% of abdomen length.

*Male genitalia.* Unknown.

*Female postabdominal structure and genitalia.* Papillae anales large with short and very long setae; segment 8 is large and almost rectangular with a sclerotized plate ventrally that is as large as segment 8 and broadly rectangular with an extended rounded end ventrally; segment 8 with long setae ventrally and along its posterior margin; anterior apophyses have a larger base (that extends ventrally) with a small rounded hole; posterior apophyses much shorter (only 30% or less of the length of anterior apophyses) and narrow with a fork-like emargination at base. Ductus bursae very long (at least 2.5 x longer than corpus bursae), thinly membranous, not sclerotized at base; corpus bursae is very small if compared to the large size of segment 8, pear-shaped with a broad base and a rounded end, thinly membranous, without any structures.



**FIGURE 101.** Distribution of Gen. Nov. X (red dots).



**FIGURE 102.** Gen. Nov. X, *acutistriata* or sp. nov. xi, [Indonesia], N. [North] Sumatra, Prapat, HW2A, 23.11.1997, Dr. Eduard Diehl leg., ex coll. Dr. Lutz Kobes, female, genitalia slide number 23/012017 I. Lehmann. Wingspan 33.0 mm



**FIGURE 103.** Gen. Nov. X, *acutistriata* or sp. nov. x2, [Indonesia], NE [Northeast] Sumatra, Dolok Merangir, 27.07.1976, Dr. Eduard Diehl leg., ex ZFMK, female, genitalia slide number 26/092017 I. Lehmann. Wingspan 36.5 mm

#### 4.32 Gen. Nov. Y

The genus is defined by the following autapomorphy:

- Very long, pure white, hair-like scales, not or only slightly curled, occur well above the normal scale layer evenly distributed on the whole upperside of forewing in both sexes; (206).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes; (11).

Type species of genus (cf. Figure 105): Gen. Nov. Y + sp. nov. y

Type locality: Republic of the Congo, Odzala National Park, [1°23'N 14°50'E] on label: 0°23'N 14°50'E [that is a different area and hence, appears to be a mistake?], ca. 530 m, 29.01.-03.03.1997, Siniaev & Murzin leg., male, genitalia slide number 08/112014 I. Lehmann, ex MWM; depository in ZSM.

Number of species in genus at present: 02

All localities of studied species per country: Republic of the Congo.

Distribution of genus at present (cf. Figure 104): rain forests of Lower Guinea, at present known from a lowland area in the northwestern Republic of the Congo. The reconstructed and predicted ancestral area is the Guineo-Congolian regional centre of endemism and the Sunda shelf/Sulawesi.

The reconstructed biogeographic event comprises: Vicariance between the Guineo-Congolian regional centre of endemism and the Sunda shelf/Sulawesi.

Phylogenetic position: The sister genus is Gen. Nov. X.

The synapomorphies shared with Gen. Nov. X are:

- Very long, pure white, hair-like scales, not or only slightly curled, occurring on upperside of forewing well above the normal scale-layer; (162);
- Very rare forewing pattern in both sexes where a broad grey band extends from termen into the discal cell in between  $M_2$  and  $M_1$  or  $M_2$  and  $R_5$  as well as a broad white or light cream band extends from  $R_5$  to costal margin and to  $R_1$ ;  $CuA_2$  is not distinctly marked in this pattern; (163);
- Posterior apophyses at base V-shaped, but “V” strongly unequal in length and with thorn-like end, somehow fork-like; (167);
- Anterior apophyses narrow and short, length less than width of segment 8 (including the ventral plate), near base very broad with a small rounded hole at centre; (168).

Description: *Head:* rough-scaled with long hair-like scales of pure white and orange on fronto-clypeus in both sexes (the orange is more pronounced in male); a pair of pits is absent on lower fronto-clypeus, a pair of conical projections is absent on lower fronto-clypeus in both sexes; pits behind labial palpi are small oval-shaped holes; labial palpi short, less than half of eye diameter and consist of three segments in both sexes, basal segment very broad (1.5 × broader than segment above) and *ca.* 50% shorter than the second, more narrow and longer segment, third segment on top tiny but present, sclerotized with an acuminate tip; antennae short (only 3.5 mm long in male, 3.0 mm in female), bipectinated, branches are 2.0 × width of shaft in male and 1.3 × width of shaft in female, branches not scaled but covered with many tiny setae; flagellum scaled cream in both sexes.

*Thorax:* Densely covered with long hair-like scales of orange and pure white in male, mixed with chestnut in female, on patagia and tegulae, glossy, tegulae pronounced with long orange and much longer pure white hair-like scales particularly in male; thorax at centre mainly orange in male, mixed with chestnut in female; crest on metathorax pronounced in male, long, with broader pure white scales. Epiphyses are short (0.7 mm long in male; 0.5 mm in female), very narrow in male, medium broad in female. Hindlegs with one pair of narrow tibial spurs, short (0.6 mm long in outer spur, 0.5 mm inner spur in both sexes); pretarsus with a pair of pulvilli. All legs have only unusually very long hair-like scales of pure white mixed with light chestnut and light vinaceous in both sexes.

Forewing upperside with a pure white ground-colour in both sexes, not glossy in male but glossy in female; a geometric design is present (unique in shape in the Afrotropical Region) in male and less pronounced in female; this design comprises always a pronounced broad light grey-vinaceous rectangular band that extends from termen into the discocellular cell in between  $M_2$  and  $M_1$ , extending partly to  $R_5$  only in male, as well as a very broad pure white rectangular band that extends from  $R_5$  along the costal margin to the base of wing in both sexes; a large pure white rectangular patch extends from termen into the discocellular cell in between  $M_2$  and  $M_3$  and further along the termen in male; below  $M_3$  to below  $CuA_2$  is a large light grey-vinaceous patch present with an elongated rectangular shape, that ends a little before base of wing; below this patch occurs a large triangular orange patch to the dorsum; along the costal margin occur large rectangular light orange patches in male, increasingly replaced towards base of wing with light chestnut in female; all veins are light orange in male but pure white in female; very long white scales occur evenly distributed on the whole upperside of both sexes; these scales are much longer than the normal scale layer;  $CuA_2$  not distinctly marked in both sexes. Hindwing is light grey-vinaceous in female but pure white in male, glossy in both sexes. Fringe is hair-like mixed with broad scales on both wings, medium long (ciliae up to 1.0 mm). Wing venation: in forewing  $1A+2A$  forked at base in both sexes;  $CuP$  absent;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from almost the same basal point from apical angle of posterior

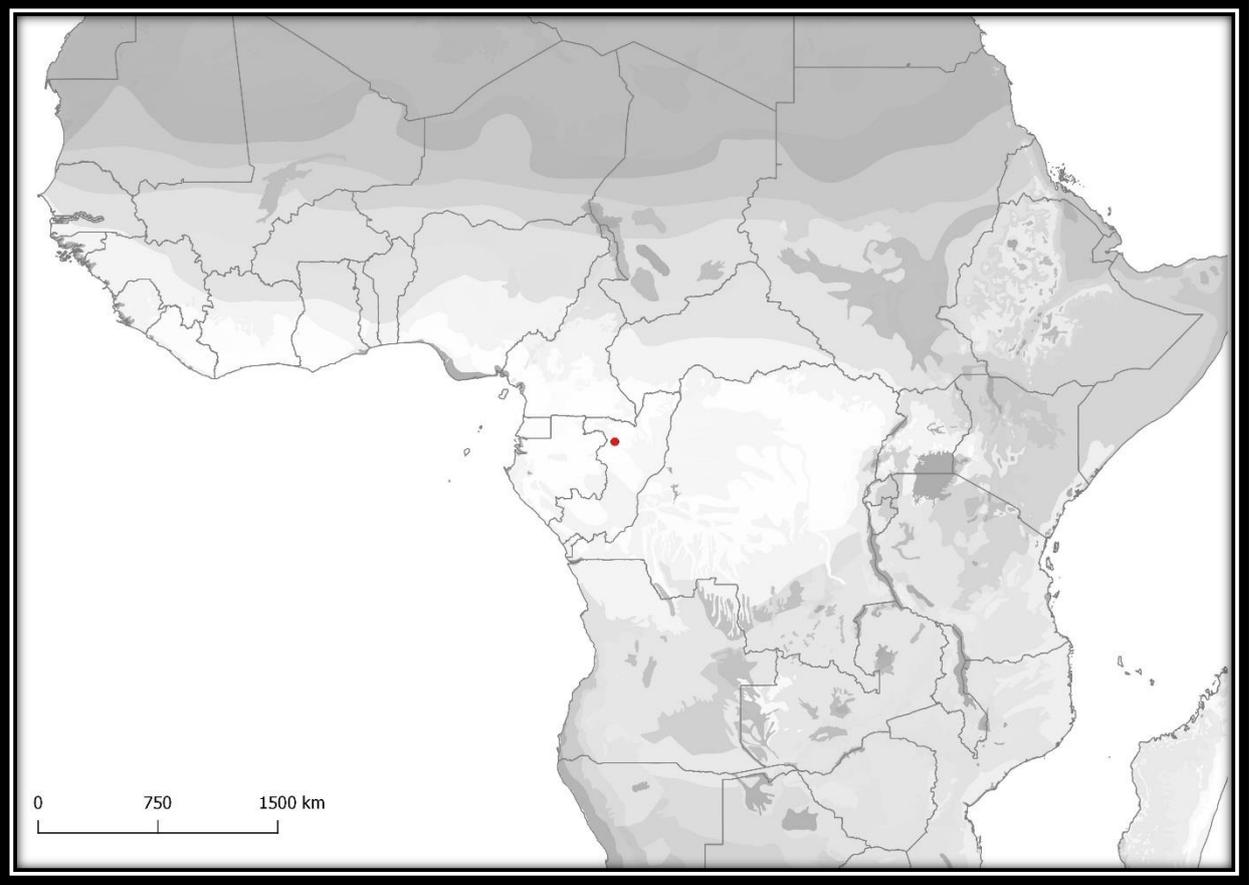
cell, still separated;  $M_1$  initiates from the same basal point with the long stalk of  $R_3+R_4+R_5$  from anterior angle of median cell in male, but is separated in female;  $R_2$  and  $R_1$  are widely separated at base and initiate from anterior part of median cell; Sc more or less parallel to  $R_1$ . In hindwing 3A present;  $1A+2A$  present with a fork at base; CuP present but weak towards base;  $CuA_2$  initiating from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1+Rs$  initiate from apical angle of anterior cell, from same basal point or separated at base; a bar is present from Rs to  $Sc+R_1$ ; a discocellular vein on both forewing and hindwing is rather weak and sometimes absent in forewing; discal cell in forewing with a rather acuminate apical angle at end of posterior cell and median cell, both have almost the same length, in male, less pronounced in female. Retinaculum and frenulum absent.

*Abdomen:* With very long hair-like scales of pure white or light grey; abdominal tuft pronounced in male, long, 35% of abdomen length, with light chestnut.

*Male genitalia.* Saccus rudimentary, broadly rectangular; the vinculum and tegumen are fused, forming a firm broad ring; uncus short with a broad triangular base (viewed ventrally), narrow towards tip, slightly bifurcated between two broad truncate tips, looking like a fish-tail. Valva is small, rectangular, outer half thinly membranous, inner basal half slightly sclerotized; soft, short setae are present on outer inner half of valva and at the rectangular tip; transtilla absent, semi-transtilla absent. Sacculus is extremely short or absent, two broadly rounded appendices that are basally connected and not hollow towards tip, occurring distal-ventrally. Gnathal arms are simple, looking like a narrow stick with a rounded tip, arms are sclerotized and attached to the lower end of tegumen, the arms are not connected ventrally; between the lowest part of the gnathal arms originates a broadly V-shaped, large, partly tube-like sclerotized structure that points upwards (towards the uncus), it is basally connected but not tube-like on its lower one-third (= the base of this structure), towards the broadly rounded tips the tube-like part is hollow and covered with many long, straight sclerotized setae. Juxta is large oval (50% larger than aedeagus) with an emargination, without processes. Phallus is short (slightly longer than juxta), simple tube-like, broader at base, not bent, with a long straight thorn-like structure distally (50% the length of aedeagus).

*Female postabdominal structure and genitalia.* Papillae anales large with short and very long setae; segment 8 is large and almost rectangular with a sclerotized plate ventrally that is as large as segment 8 and broadly rectangular, but only strongly sclerotized along its edge and largely thinly membranous in between this edge, with an extended sclerotized bent acuminate end ventrally; segment 8 with very long setae dorsally, ventrally and along its posterior margin that is more sclerotized; anterior apophyses are shorter than width of segment 8 and have a large oval shape near centre with a small rounded hole; posterior apophyses as long as anterior apophyses and as broad as anterior apophyses with a fork-like emargination at base. Ductus bursae broad and very long (at least 2.5 x longer than corpus bursae), thinly membranous, not sclerotized at base; corpus bursae is small if compared to the large size of segment 8,

oval-shaped with a narrow base and a rounded end, thinly membranous, without any structures.



**FIGURE 104.** Distribution of Gen. Nov. Y (red dot).



**FIGURE 105.** Gen. Nov. Y, sp. nov. y, Republic of the Congo, Odzala National Park, 29.01.–03.03.1997, Siniaev & Murzin leg., ex MWM, male, genitalia slide number 08/112014 I. Lehmann. Wingspan 19.5 mm



**FIGURE 106.** Gen. Nov. Y, sp. nov. y1, Republic of the Congo, Odzala National Park, 29.01.–03.03.1997, Siniaev & Murzin leg., ex MWM, male, genitalia slide number 23a/012016 I. Lehmann. Wingspan 24.5 mm



**FIGURE 107.** Gen. Nov. Y, sp. nov. y1, Republic of the Congo, Odzala National Park, 29.01.–03.03.1997, Siniaev & Murzin leg., ex MWM, female [with worn forewing pattern], genitalia slide number 23b/012016 I. Lehmann. Wingspan 28.0 mm

#### 4.33 Gen. Nov. Z

The genus is defined by the following autapomorphy:

- Two large, hollow, triangular-shaped appendices on ventral part of valva, that are basely connected, are as large as *ca.* 35% of the soft outer surface of one valva; (130).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; [possibly also absent in female] (11).

Type species of genus (cf. Figure 109): Gen. Nov. Z + sp. nov. z

Type locality: Obervolta [Burkina Faso], Sidéradougou, *ca.* 320 m, 27.04.1977, Dr. H. Politzar leg., male, genitalia slide number 26/022017 I. Lehmann, ex MWM; depository in ZSM.

Number of species in genus at present: 03

All localities of studied species per country: Burkina Faso; Ghana; Nigeria.

Distribution of genus at present (cf. Figure 108): lowland and submontane areas from the southwestern part of Burkina Faso eastwards via northern Ghana to north-central Nigeria.

The reconstructed and predicted ancestral areas are the Guinea-Congolia/Zambezia regional transition zone and the Guinea-Congolia/Sudania regional transition zone.

The reconstructed biogeographic event comprises: First, dispersal in the Guinea-Congolia/Zambezia regional transition zone and the Guinea-Congolia/Sudania regional transition zone. Secondly, vicariance occurred between the Guinea-Congolia/Zambezia regional transition zone and the Guinea-Congolia/Sudania regional transition zone. Thirdly, dispersal occurred into the Sudanian regional centre of endemism and the Sunda Shelf/Sulawesi. Fourthly, vicariance between the Guinea-Congolia/Zambezia regional transition zone, the Guinea-Congolia/Sudania regional transition zone, the Sudanian regional centre of endemism and the Sunda shelf/Sulawesi.

Phylogenetic position: The sister genus could not be reconstructed unambiguously.

Description: *Head:* rough-scaled with long hair-like as well as broader scales of pure white and cream sometimes mixed with light brown around the eyes and on fronto-clypeus in male; a pair of pits is absent on lower fronto-clypeus, a pair of conical projections is absent on lower fronto-clypeus in male; pits behind labial palpi are small oval-shaped holes; labial palpi short, less than half of eye diameter and consist of two segments, basal segment slightly broader (1.3 × broader than segment above) and almost as long as the second, more narrow and slightly longer segment; antennae

bipectinated, branches are  $2.5 \times$  width of shaft in male, branches not scaled but covered with many tiny setae; flagellum scaled cream in male.

*Thorax:* Densely covered with broad scales of light brown and often hair-like scales of cream on patagia and tegulae, glossy, tegulae not pronounced with only slightly longer light brown scales particularly in male; crest on metathorax pronounced in male, long, with broad light brown scales. Epiphyses are medium long (1.0 mm long), flat and broad in male. Hindlegs with one pair of narrow tibial spurs, short (0.6 mm long in outer spur, 0.5 mm inner spur); pretarsus with a pair of pulvilli.

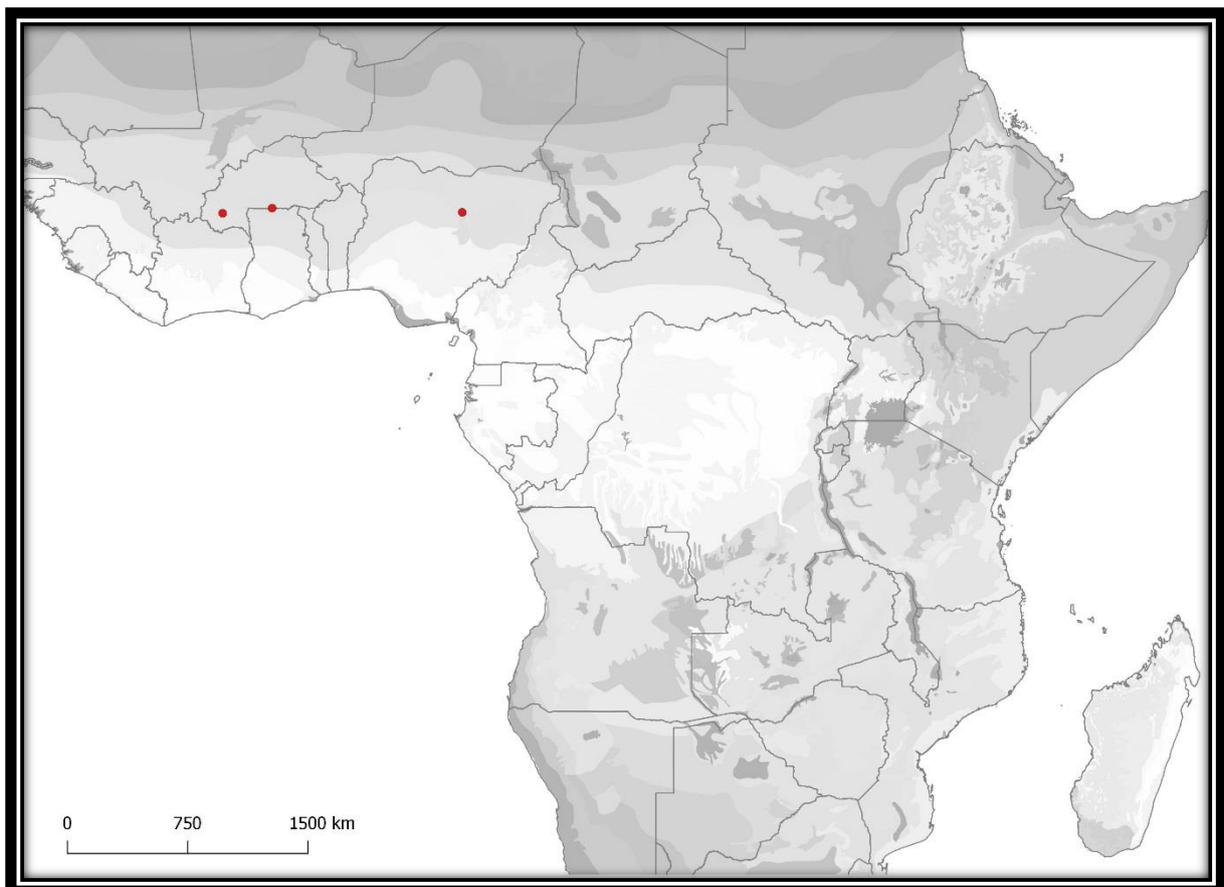
Forewing is thin, it breaks easily during preparation, this character is similar to the wings of *Squamura* that appear like greaseproof paper; upperside with a pure white ground-colour in male with a strong glint; a geometric design is absent; a simple pattern is present and comprises a pronounced rounded sepia coloured patch, with a centre of light grey-vinaceous, that occurs at the end of the discocellular cell, as well as sepia patches of light brown and rectangular shape along the costa and between  $1A+2A$  and the dorsum; a faded oblique sub-terminal band, comprising separated light grey oval shaped patches, occurs from below  $M_2$  to below  $CuA_2$  (more pronounced on the underside); smaller patches of the same colour occur in two rows from below the sepia coloured patch at the end of the discocellular cell to  $1A + 2A$  (also more pronounced on the underside);  $CuA_2$  not distinctly marked in male. Hindwing is pure white with a strong glint, sometimes with a small light brown but faded lunule-like patch between the middle of  $CuA_2$  and  $CuA_1$ . Fringe is hair-like and pure white on both wings, short (ciliae up to 0.5 mm). Wing venation: in forewing  $1A+2A$  forked at base;  $CuP$  absent, sometimes weakly represented for 50% of original length towards dorsum;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from the same base from apical angle of posterior cell;  $M_1$  initiates from almost the same basal point with the long stalk of  $R_3+R_4+R_5$  from anterior angle of median cell;  $R_2$  and  $R_1$  are separated at base and initiate from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  rudimentary with a fork at base;  $CuP$  present but weak towards base;  $CuA_2$  initiating from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1+Rs$  initiate from apical angle of anterior cell, from same basal point or slightly separated at base; a bar is present from  $Rs$  to  $Sc+R_1$ ; a discocellular vein on both forewing and hindwing is present and strong; discal cell in forewing narrow and long (25% of width of wing and 60% of length of wing) with a rather acuminate apical angle at end of posterior cell, less in median cell, both have almost the same length. Retinaculum and frenulum absent.

*Abdomen:* With mainly hair-like scales of pure white with a strong glint; abdominal tuft short, 20% of abdomen length, with light brown.

*Male genitalia.* Saccus rudimentary, broadly oval; the vinculum and tegumen are fused, forming a firm broad ring; uncus short with a broad triangular base (viewed ventrally), narrow towards tip, bifurcated between two broad truncate tips. Valva is

large, oval-shaped, outer half membranous, inner basal half slightly sclerotized; very long, sclerotized setae (grey in colour) are present on the whole valva, more or less evenly distributed, and at the rounded tip; transtilla absent, semi-transtilla absent. Sacculus is not visible, probably entirely absent; two broadly triangular appendices that are basely connected and hollow, occurring distal-ventrally. Gnathal arms are a simple structure that looks like a narrow stick with a rounded tip, it is sclerotized and attached to the lower end of tegumen, the arms are not connected ventrally; between the lowest part of the gnathal arms originates a broadly V-shaped, large, partly tube-like sclerotized structure that points downwards (towards the juxta), it is basely connected but not tube-like on its upper one-third (= the base of this structure) where the two basal ends have one large ear-shaped appendice; towards the broadly rounded tips the tube-like part is hollow and covered with many long, straight sclerotized setae (grey in colour). Juxta is large oval-shaped (30% larger than aedeagus), rather thinly membranous, with an emargination, but without any processes. Phallus is extremely short (only slightly longer than juxta), simple tube-like, broader at base, not bent, with a short small straight thorn-like structure distally (20% the length of aedeagus).

*Female postabdominal structure and genitalia. Unknown.*



**FIGURE 108.** Distribution of Gen. Nov. Z (red dots).



**FIGURE 109.** Gen. Nov. Z, sp.nov.z, Obervolta [Burkina Faso], Sidéradougou, 27.04.1977, Dr. Politzar leg., male, ex MWM, genitalia slide number 26/022017 I. Lehmann. Wingspan 39.0 mm



**FIGURE 110.** Gen. Nov. Z, sp. nov. z3, Gold Coast [Ghana], Navaro, 06.1923, A. W. Cardinall leg., male, ex BMNH, B.M. 1923-391, genitalia slide number 08/092007 I. Lehmann. Wingspan 35.0 mm

#### **4.34 Gen. Nov. ZA**

The genus is defined by the following autapomorphy:

- Two large hollow appendices, the upper one is narrow rectangular with a flat tip, the lower one is triangular with a rounded tip, on ventral part of valva, both appendices are basely connected, and as large as *ca.* 30% of the soft outer surface of one valva; (150).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes; (11).

Type species of genus (cf. Figures 112, 113): Gen. Nov. ZA + sp. nov. za

Type locality: Kenya, Gazi, “old fisherman landing site”, 13.09.2012, Elisha Enoh leg., male, genitalia slide number 28/032013 I. Lehmann, ex NMK; depository in NMK.

Number of species in genus at present: 11

All localities of studied species per country: Ghana; Kenya; Tanzania; Malawi; Republic of South Africa; Namibia.

Distribution of genus at present (cf. Figure 111): disjunct; lowland, submontane and montane areas from Kiunga (Kenya North Coast close to Somalia) southwards via eastern and southern Tanzania, through the whole of Malawi. Disjunct records exist from the Comoros Archipelago (cf. Viette 1981), Mount Elgon (western Kenya), the eastern Republic of South Africa; the Waterberg (northern Namibia) and the former Kete-Krachi (southeast Ghana, cf. Figure 116).

The reconstructed and predicted ancestral areas are the Guinea-Congolia/Zambezia regional transition zone, the Guinea-Congolia/Sudania regional transition zone and the Sunda shelf/Sulawesi.

The reconstructed biogeographic event comprises: First, dispersal from the Guinea-Congolia/Zambezia regional transition zone and the Guinea-Congolia/Sudania regional transition zone into the Guineo-Congolian regional centre of endemism, Somalia-Masai regional centre of endemism, the Karoo-Namib regional centre of endemism, the Afromontane archipelago-like regional centre of endemism, the Kalahari-Highveld regional transition zone, the Zanzibar-Inhambane regional mosaic and the Sunda shelf/Sulawesi. Secondly, vicariance between the Sunda shelf/Sulawesi and all remaining phytochoria mentioned above.

Phylogenetic position: The sister genus could not be reconstructed unambiguously. The genus belongs to a monophylum together with *Squamura* and the new genus ZB.

The synapomorphies shared with *Squamura* and Gen. Nov. ZB are:

- Uncus strongly elongated, narrow or broad, but only thinly sclerotized, bifid at tip; (86);
- Relicts of two narrow gnathal arms are attached to the lower part of tegumen (not uncus!); (127);
- Uncus tip represents a broad “V”; (133);
- Entire broad uncus is longer or equal to basal width of valva and has a tip like in number 133; (135).

Description: *Head:* rough-scaled with long hair-like scales of pure white and black eyes on fronto-clypeus in male, with light cream and brown eyes in female; a pair of pits is present but rather rudimentary on lower fronto-clypeus in both sexes (less visible in female), a pair of conical projections is absent on lower fronto-clypeus in both sexes; pits behind labial palpi are oval-shaped holes in both sexes; labial palpi short, less than half of eye diameter and consist of two segments, basal segment slightly broader ( $1.3 \times$  broader than segment above) and almost as long as the second, more narrow and slightly longer segment in both sexes; antennae bipectinated in both sexes, branches are  $2.5 \times$  width of shaft in male,  $1.2 \times$  width of shaft in female, branches not scaled but covered with many tiny setae; flagellum scaled cream with a strong vinaceous gloss in male.

*Thorax:* Densely covered with broad scales of light chestnut-orange and pure white or dark chestnut and sepia mixed with cream and white in male, more cream and light chestnut in female, with long pure white hair-like scales on patagia and tegulae in both sexes, glossy, tegulae pronounced with slightly longer light chestnut scales particularly in male, centre of torax mainly pure white in both sexes; underside of thorax and forelegs have a rare feature, namely very long only pure white hair-like scales in both sexes; crest on metathorax pronounced in male, long, with broad light chestnut scales. Epiphyses are medium long (up to 1.2 mm), narrow tube-like in both sexes. Hindlegs with one pair of narrow tibial spurs in both sexes; they are short (up to 0.9 mm in male, up to 1.0 mm in female); pretarsus with a pair of pulvilli in both sexes.

Forewing upperside with a light brown-olive or light grey-blue ground-colour and a strong glint shine of light vinaceous with some scales that have a light blue gloss in male, or the upperside has a dark brown ground-colour with mainly scales that have a light blue gloss in male; basal area of forewing sometimes cream or pure white; in the larger female the upperside is pure white mixed with cream with scales that have a strong cream glint shine; a geometric design is absent in both sexes; a simple pattern is present and comprises a pronounced rounded sepia coloured patch, with a centre of light brown-vinaceous, that occurs at the end of the discocellular cell in both sexes; a faded oblique sub-terminal band, comprising separated light brown oval shaped patches, occurs from below  $M_2$  to below  $CuA_2$  (more pronounced in the dark brown male, faded in female); smaller patches of light brown occur in two rows from below the brown patch at the end of the discocellular cell to  $1A + 2A$  (also more pronounced

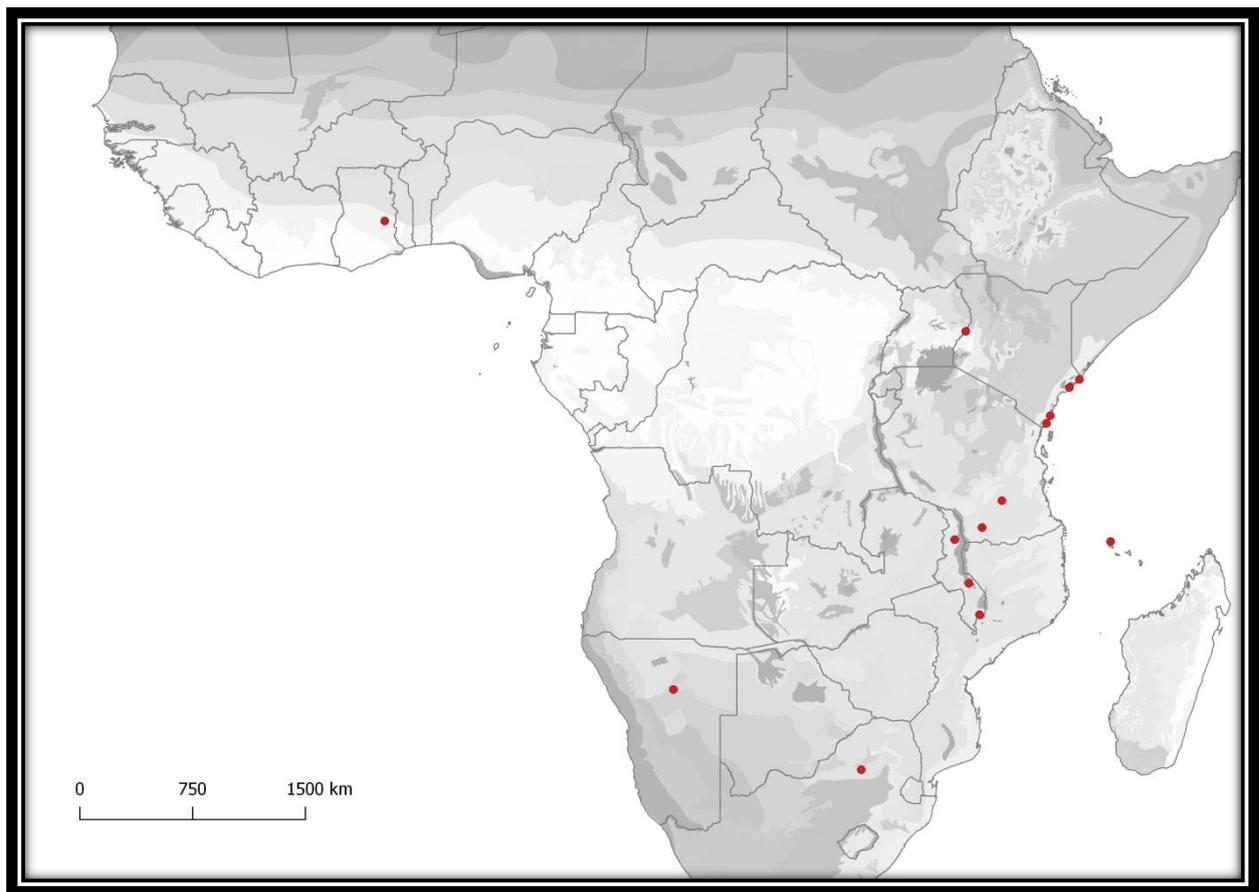
in the dark brown male, faded in female), scales with a strong light blue glint occur in particular around these patches;  $CuA_2$  not distinctly marked in both sexes. Hindwing in male is light brown-olive or light grey-olive, glossy; in female light brown mixed with cream and white. Fringe is hair-like and cream in female, but with broad brown scales in male on both wings, short (ciliae up to 0.6 mm). Wing venation: in forewing  $1A+2A$  forked at base;  $CuP$  absent;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from apical angle of posterior cell, separated;  $M_1$  initiates from the same or almost the same basal point with the very long stalk of  $R_3+R_4+R_5$  from anterior angle of median cell;  $R_2$  and  $R_1$  are separated at base and initiate from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  rudimentary, sometimes with a fork at base;  $CuP$  present but weak;  $CuA_2$  initiating from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1+Rs$  initiate from apical angle of anterior cell, from same basal point or slightly separated at base; a bar is present from  $Rs$  to  $Sc+R_1$  in both sexes; a discocellular vein on both forewing and hindwing is present. Retinaculum and frenulum absent.

*Abdomen:* With mainly long hair-like scales of pure white mixed with light brown with a strong glint on upperside as well as underside; abdominal tuft long in male only, 25% of abdomen length, with light chestnut and sepia.

*Male genitalia.* Saccus absent or rudimentary, broadly oval; the vinculum and tegumen are fused, forming a firm broad ring that is broadest at middle (in lateral view); uncus short with a broad triangular base (viewed ventrally), narrow towards tip, bifurcated between two broad truncate tips. Valva is large, oval-shaped with an extremely S-shaped base ventrally, outer half membranous, inner basal half slightly sclerotized; very long, sclerotized setae (grey in colour) are present on the more soft outer half of valva and near the rounded tip; transtilla absent, semi-transtilla absent. Sacculus is narrow and ends in two sclerotized appendices of different shape that are basally connected, hollow, occurring distal-ventrally. Gnathal arms are a simple structure that looks like a narrow stick with a rounded tip, it is sclerotized and attached to the lower end of tegumen, the arms are not connected ventrally; between the lowest part of the gnathal arms originates a broadly V-shaped, large, partly tube-like sclerotized structure that points downwards (towards the juxta), it is basally connected but on its upper one-third (= the base of this structure) represents a membrane; towards the broadly rounded tips the tube-like part is hollow and covered with many long, straight sclerotized setae (grey in colour). Juxta is large oval-shaped (80% the size of the aedeagus), rather thinly membranous, with an emargination, but without any processes. Phallus is short (only slightly longer than juxta), simple tube-like, broader at base, not bent, with a long and strongly bent thorn-like structure distally (40% the length of aedeagus).

*Female postabdominal structure and genitalia.* Papillae anales with short and long setae; segment 8 is large and almost rectangular with a large open space from near

base of anterior apophyses to the ventral side; segment 8 with few medium long setae near posterior edge dorsally and ventrally; anterior apophyses are slightly shorter than width of segment 8 and have a more or less rounded hole near centre of the base; posterior apophyses are slightly longer and broader than anterior apophyses with a broad base that has a hook-like or thorn-like end. Ductus bursae is broad, short, thinly membranous, not sclerotized at base; corpus bursae is very large, twice as large as segment 8, rather pear-shaped but with a broad base and a broadly rounded end, thinly membranous, without any structures.



**FIGURE 111.** Distribution of Gen. Nov. ZA (red dots).



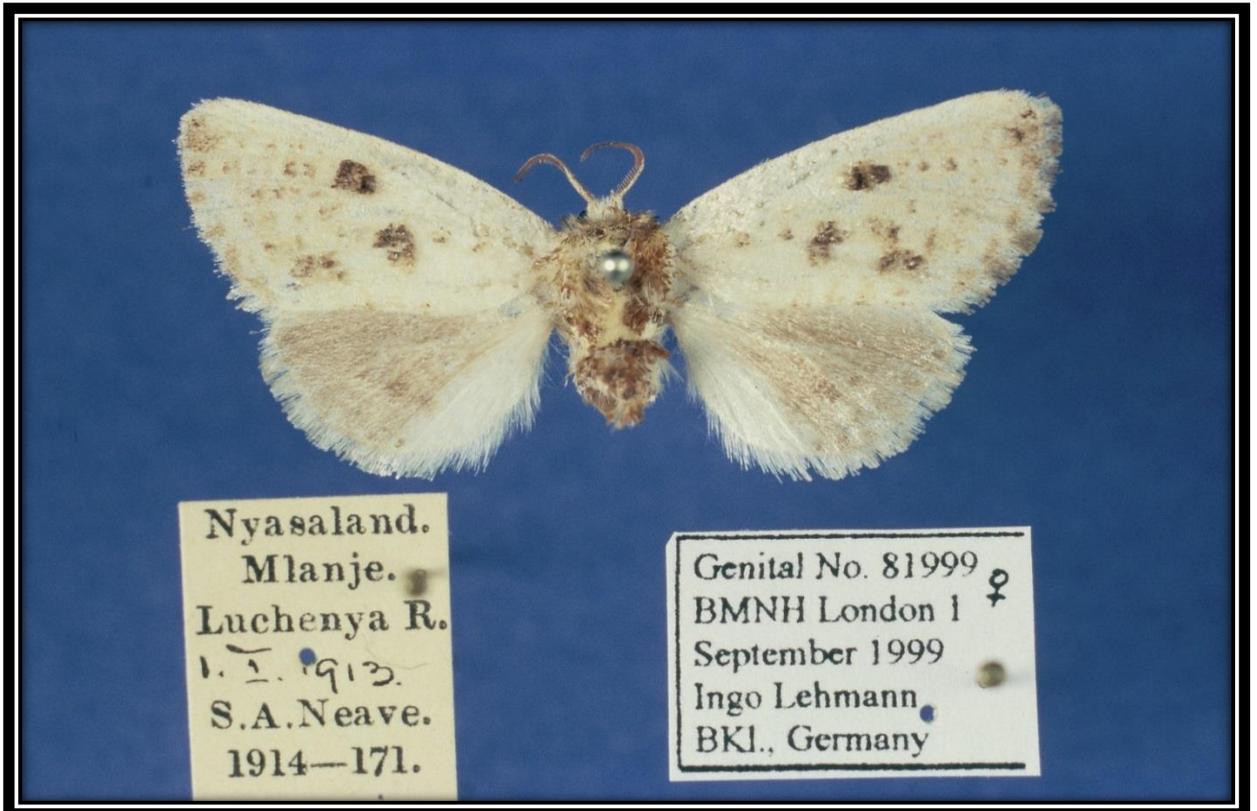
**FIGURE 112.** Gen. Nov. ZA, sp. nov. za, Kenya, Gazi, 13.09.2012, Elisha Mrabu reared, ex NMK, male, genitalia slide number 28/032013 I. Lehmann. Wingspan 30.5 mm



**FIGURE 113.** Gen. Nov. ZA, sp. nov. za, Kenya, Gazi, 07.05.2012, Elisha Mrabu reared, ex NMK, female, genitalia slide number 23/052013 I. Lehmann. Wingspan 42.0 m



**FIGURE 114.** Gen. Nov. ZA, *albicilia* (Hampson, 1920a) or sp. nov. za4, Malawi, Mount Mulanje, Likhubula [Likabula] Forest Reserve, 13.11.2012, R.J. Murphy leg., ex own coll., male, genitalia slide number *albicilia*/032014 I. Lehmann. Wingspan 27.0 mm



**FIGURE 115.** Gen. Nov. ZA, *albicilia* (Hampson, 1920a) or sp. nov. za4, Nyasaland [Malawi], Mlanje [Mount Mulanje], Luchunya R. [Lichenya River, just east of Likabula River], 01.01.1913, S.A. Neave leg., ex BMNH, B.M. 1914-171, female, genitalia slide number *albicilia*/81999 I. Lehmann. Wingspan 39.5 mm



**FIGURE 116.** Gen. Nov. ZA, sp. nov. za9, Gold Coast [Ghana], N. [North] Territories, Kete-Krachi [this locality is under water of Lake Volta since 1966 and this species might be already extinct], [no date], A.W. Cardinall leg., ex BMNH, B.M. 1925-143, male, genitalia slide number 19/062013 I. Lehmann. Wingspan 36.0 mm

#### 4.35 *Squamura* Heylaerts, 1890

The genus is defined by the following autapomorphies:

- Corpus bursae small and 60% sclerotized; (139);
- the base of ductus bursae strongly sclerotized; (140);
- extension of sacculus is strongly sclerotized and looks like a boat at end distally; (169).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes; (11).

Type species of genus: *Squamura maculata* Heylaerts, 1890

Type locality: [Indonesia], Sumatra, Fort de Kock.

Closest localities to type locality of studied specimens (*cf.* Figures 118, 119): [Indonesia], Sumatra, Simalungun, Prapat, HW2, 1.050 m, 21.03.1996, Dr. Eduard Diehl leg., male, genitalia slide number 06/022017 I. Lehmann, ex coll. Dr. Lutz Kobes; depository in ZSM; [Indonesia], N. [North] Sumatra, Huta Padang, 310 m, 24.10.1990, Dr. Eduard Diehl leg., male, genitalia slide number 18/032017 I. Lehmann, ex coll. Dr. Lutz Kobes; depository in ZSM.

Number of species in genus at present: 06

All localities of studied species per country: Indonesia; Malaysia.

Distribution of genus at present (*cf.* Figure 117): Sunda shelf and Sulawesi, at present known from lowland and submontane areas on the islands of Borneo [including Brunei but this specimen was not studied], Sumatra, Nias, Java and Sulawesi [specimen not studied] as well as from the southern peninsula of Malaysia.

The reconstructed and predicted ancestral area is the Sunda shelf/Sulawesi.

The reconstructed biogeographic event comprises: First, dispersal in the Sunda shelf/Sulawesi. Secondly, vicariance in the Sunda shelf/Sulawesi.

Phylogenetic position: The sister genus is Gen. Nov. ZB.

The genus is part of a monophylum with *Squamura* and the new genera ZA, ZB.

The synapomorphies shared with Gen. Nov. ZB comprise:

- Both, ductus bursae and corpus bursae strongly reduced and small; (141);
- Anterior apophysis looks at base like a huge sail that is connected by a thin membrane dorsally; (145).

The synapomorphies shared with Gen. Nov. ZA and Gen. Nov. ZB comprise:

- Uncus strongly elongated, narrow or broad, but only thinly sclerotized, bifid at tip; (86);

- Relicts of two narrow gnathal arms are attached to the lower part of tegumen (not unculus!); (127);
- Uncus tip represents a broad “V”; (133);
- Entire broad unculus is longer or equal to basal width of valva and has a tip like in number 133; (135).

Description: *Head:* rough-scaled with hair-like as well as medium broad scales of light yellow ochre and sepia below the eyes on fronto-clypeus in both sexes; a pair of rudimentary pits is present in male but absent or strongly reduced in female on lower fronto-clypeus, a pair of conical projections is absent on lower fronto-clypeus in both sexes; pits behind labial palpi are oval-shaped holes in both sexes; labial palpi short, half of eye diameter and consist of two segments, basal segment not broader and only of half the length than segment on top, second segment oval-shaped in both sexes; antennae bipectinated in both sexes, branches are  $2.5 \times$  width of shaft in male,  $2.0 \times$  width of shaft in female, branches not scaled but covered with many tiny setae; flagellum scaled light cream.

*Thorax:* Densely covered with broad and hair-like scales of light yellow-ochre and pure white mixed with dark ochre or chestnut on patagia and tegulae in both sexes, with very long pure white hair-like scales at the end of tegulae in male, slightly glossy, tegulae pronounced in male; crest on metathorax small, light ochre. Epiphyses are medium long in male (up to 1.2 mm), shorter in female, narrow tube-like in both sexes. Hindlegs with one pair of narrow tibial spurs in both sexes; they are short (up to 0.6 mm in male, up to 0.7 mm in female); pretarsus with a pair of pulvilli in both sexes.

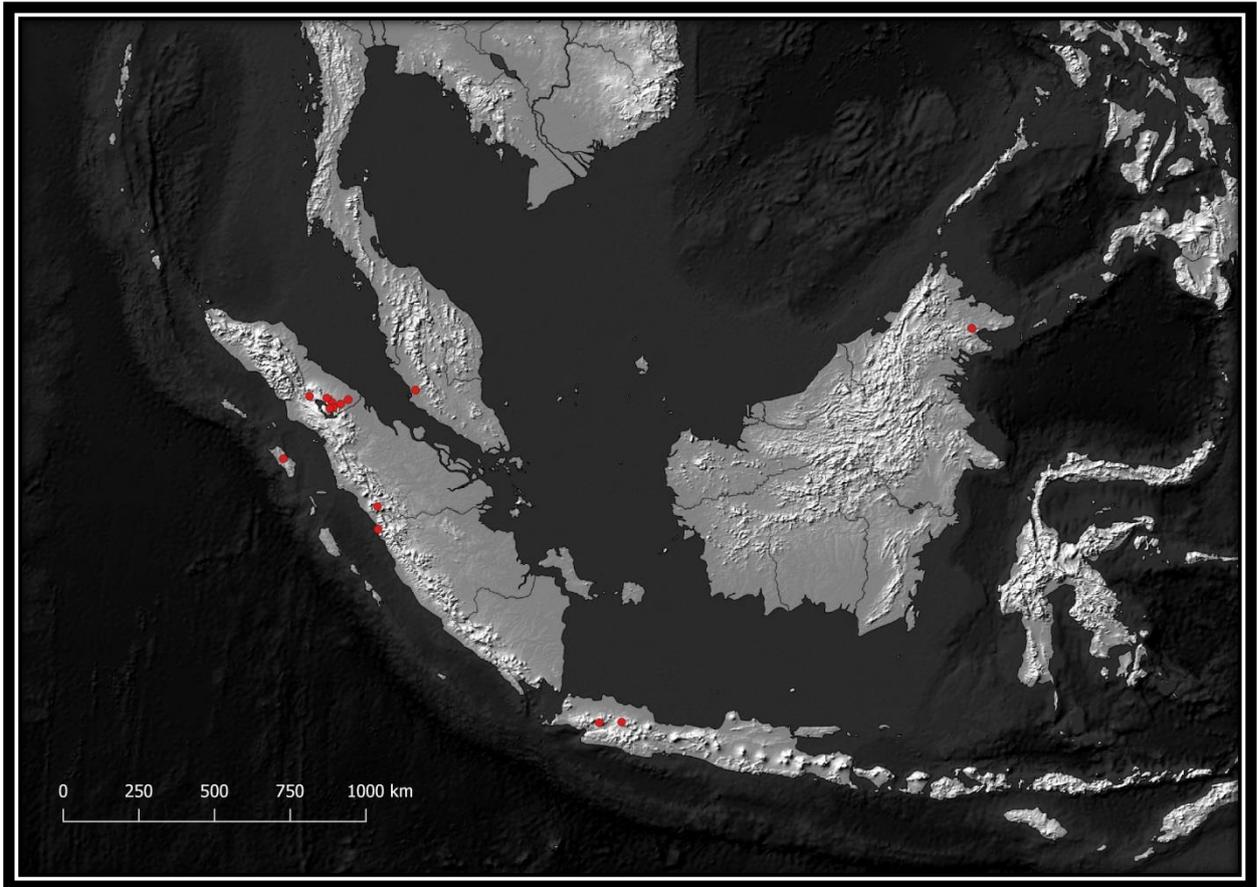
Forewing very thin and like greaseproof paper, it breaks easily during preparation; upperside with a light cream or whitish ground-colour and a strong glint shine in both sexes; a geometric design is absent in both sexes; a simple pattern is present and comprises a pronounced rounded or rectangular chestnut coloured patch that occurs at the end of the discocellular cell in both sexes; some chestnut striae and faded chestnut or light grey patches are always present in both sexes, sometimes represent an oblique faded light greyish sub-terminal band in both sexes;  $CuA_2$  not distinctly marked in both sexes. Hindwing is pure white or light cream, always glossy, in both sexes. Fringe is hair-like, alternating cream with chestnut or grey in both sexes, short (ciliae up to 0.8 mm). Wing venation: in forewing  $1A+2A$  forked at base;  $CuP$  absent or strongly reduced;  $CuA_2$  originating from half of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from apical angle of posterior cell, only slightly separated at base or from the same basal point;  $M_1$  initiates from almost the same basal point or is stalked with the long stalk of  $R_3+R_4+R_5$  from anterior angle of median cell; the distance between the base of  $R_2$  and the base of the stalk of  $R_3+R_4+R_5$  is very great;  $R_2$  and  $R_1$  are often close together but separated at base and initiate from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  rudimentary, sometimes with a fork at base;  $CuP$  present but weak;  $CuA_2$  initiating from near half of lower median of posterior cell;  $CuA_1$

initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, only slightly separated at base;  $M_1+R_s$  initiate from apical angle of anterior cell, from same basal point or slightly separated at base; a bar is present from  $R_s$  to  $Sc+R_1$  in both sexes; a discocellular vein on both forewing and hindwing is present. In the forewing the posterior cell (= lower cell) is always smaller than the upper cell; the apical angle and anterior angle are both nearly acuminate. Retinaculum and frenulum absent.

*Abdomen:* With mainly long hair-like scales of pure white and/or cream with a strong glint on upperside as well as underside; abdominal tuft long in both sexes, 25% of abdomen length, with light chestnut and sepia.

*Male genitalia.* Saccus absent; the vinculum and tegumen are fused, forming a firm medium broad ring; uncus long, narrowly elongated, with a broad triangular base (viewed ventrally), rather deep bifurcated between two narrow tips. Valva is large, broadly rounded with an oblique edge ventrally (ventral view); very long, soft setae, often bent, are present mainly on the upper half of valva; transtilla absent; a relict of semi-transtilla present, it is surrounded with a dense bunch of straight, sclerotized long setae that have a chestnut colour. Sacculus is dominant and narrow with an extension that is strongly sclerotized and looks like a boat at end distally; above its end is one sclerotized appendice of different shape, either lunule-like or stick-like, occurring distal-ventrally and is basally connected to the boat-like structure. Gnathal arms are a simple structure that looks like a narrow T-shaped stick with rounded tips, it is sclerotized and attached to the lower end of tegumen, the arms are not connected ventrally; between the lowest part of the gnathal arms originates a broadly large tube-like, thinly sclerotized, structure that points upwards (towards the uncus), it is basally thinly membranous but on its upper two-thirds it represents a hollow, broad tube that is open towards uncus. Juxta is large, elongated oval-shaped (70% the size of the aedeagus), rather thinly membranous, with an emargination, but without any processes. Phallus is short (only slightly longer than juxta), simple tube-like, broader at base, not bent, with a short thorn-like structure distally (15% the length of aedeagus).

*Female postabdominal structure and genitalia.* Papillae anales large with short and very long setae; segment 8 almost rectangular with large open space dorsally, usually with a very thin membrane, few medium long setae ventrally; anterior apophyses are slightly longer than width of segment 8 and have a large base, looking like a huge sail that is dorsally connected to the thin membrane that covers the open space of segment 8; a hole in the sail-like base is absent; posterior apophyses are shorter than width of segment 8, with a broad fork-like base, broader than anterior apophyses. Corpus bursae and ductus bursae are strongly reduced in length and size, in length not longer than segment 8 and the anterior apophyses; corpus bursae is very small (less than 25% the size of segment 8) and on 60% of its surface it is sclerotized; the base of ductus bursae is strongly sclerotized. Ductus bursae is narrow; corpus bursae is smaller than one sail-like structure, rather pear-shaped but with a broad base and a broadly rounded end, thinly membranous on 40% of its surface, without any structures.



**FIGURE 117.** Distribution of the genus *Squamura* (red dots).



**FIGURE 118.** *Squamura maculata* [based on genitalia Figure 94 in Holloway 1986] or *Squamura* sp. nov. 1, [Indonesia], Sumatra, Huta Padang, 24.10.1990, Dr. Eduard Diehl leg., ex coll. Dr. Lutz Kobes, male, genitalia slide number 18/032017 I. Lehmann. Wingspan 29.0 mm



**FIGURE 119.** *Squamura maculata* or *Squamura* sp. nov. 1, [Indonesia], Sumatra, Dairi, ca. 1.000 m, 28.02.1981, Dr. Eduard Diehl leg., ex coll. Dr. Lutz Kobes, female, genitalia slide number 18/022017 I. Lehmann. Wingspan 30.0 mm



**FIGURE 120.** *Squamura* sp. nov. 2, [Indonesia], Sumatra, Simalungun, Prapat, HW2, 1.050 m, 23.04.1990, Dr. Eduard Diehl leg., ex coll. Dr. Lutz Kobes, male, genitalia slide number 04/022017 I. Lehmann. Wingspan 24.5 mm

#### **4.36 Gen. Nov. ZB**

The genus is defined by the following autapomorphies:

- Very long scales above normal scale layer, pure white, hair-like, not or only slightly curled, occur densely in a mainly horizontal and less upright position only below base of discal cell on upperside of forewing in both sexes; (166);
- Extension of sacculus is strongly sclerotized, looks simple and like half of a boat with a strongly reduced boat tip at end distally; (170).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes; (11).

Type species of genus (cf. Figures 122, 123): Gen. Nov. ZB + sp. nov. zb1

Type locality: [Indonesia], Java, Delona [?], 22.09.1935, L.G.E. Kalshoven leg., number 1473[?], male, genitalia slide number 04/072017 I. Lehmann, ex RMNH; depository in RMNH.

Number of species in genus at present: 02

All localities of studied species per country: Indonesia.

Distribution of genus at present (cf. Figure 121): Sunda shelf, at present known from lowland areas on the island of Java. The reconstructed and predicted ancestral area is the Sunda shelf/Sulawesi.

The reconstructed biogeographic event comprises: First, dispersal in the Sunda shelf/Sulawesi. Secondly, vicariance in the Sunda shelf/Sulawesi.

Phylogenetic position: The sister genus is *Squamura*.

The genus is part of a monophylum with *Squamura* and the new genera ZA, ZB.

The synapomorphies shared with *Squamura* comprise:

- Both, ductus bursae and corpus bursae strongly reduced and small; (141);
- Anterior apophysis looks at base like a huge sail that is connected by a thin membrane dorsally; (145).

The synapomorphies shared with Gen. Nov. ZA and *Squamura* comprise:

- Uncus strongly elongated, narrow or broad, but only thinly sclerotized, bifid at tip; (86);
- Relicts of two narrow gnathal arms are attached to the lower part of tegumen (not uncus!); (127);
- Uncus tip represents a broad “V”; (133);

- Entire broad uncus is longer or equal to basal width of valva and has a tip like in number 133; (135).

Description: *Head:* rough-scaled with hair-like as well as medium broad scales of light ocher and white below the eyes on fronto-clypeus in both sexes; a pair of rudimentary pits is present in both sexes on lower fronto-clypeus, a pair of conical projections is absent on lower fronto-clypeus in both sexes; pits behind labial palpi are oval-shaped holes in both sexes; labial palpi short, half of eye diameter and consist of two segments, basal segment not broader, second segment elongated with an acuminate tip,  $1.2 \times$  as long as basal segment in both sexes; antennae bipectinated in both sexes, branches are  $2.5 \times$  width of shaft in male,  $1.5 \times$  width of shaft in female, branches not scaled but covered with many tiny setae; flagellum scaled light cream.

*Thorax:* Densely covered with broad and hair-like scales of cream or white often with tips of chestnut or sepia on patagia and tegulae in both sexes, slightly glossy, tegulae not pronounced in male; crest on metathorax small, light cream. Epiphyses are medium long (up to 1.0 mm), very narrow and tube-like in both sexes. Hindlegs with one pair of narrow tibial spurs in both sexes; they are short (up to 0.3 mm in male, up to 0.5 mm in female); pretarsus with a pair of pulvilli in both sexes.

Forewing upperside with a light cream ground-colour largely without a glint shine in female, but glossy in male; a geometric design is absent in both sexes; a simple pattern is present and comprises a pronounced almost rectangular chestnut coloured patch that occurs at the end of the discocellular cell in both sexes; smaller rectangular chestnut patches, representing sometimes a band, are present between the veins from  $M_2$  to below  $CuA_2$  in both sexes, but less pronounced in male;  $CuA_2$  not distinctly marked in both sexes. On the almost rectangular chestnut patch between base of  $1A+2A$  and lower median occur very long pure white scales above the normal scale layer, they are hair-like and slightly curled in both sexes, but shorter in male. Hindwing is light brown, glossy, in male, but light brown with dark brown patches towards termen in female, less glossy. Fringe is with broader scales, alternating cream with chestnut in both sexes, short (ciliae up to 0.3 mm in male; 0.6 mm in female). Wing venation: in forewing  $1A+2A$  forked at base;  $CuP$  absent or strongly reduced towards its base;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from apical angle of posterior cell, only slightly separated at base;  $M_1$  initiates from almost the same basal point or is shortly stalked with  $R_3+R_4+R_5$  from anterior angle of median cell; the distance between the base of  $R_2$  and the base of the stalk of  $R_3+R_4+R_5$  is very great;  $R_2$  and  $R_1$  are often close together but separated at base and initiate from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  rudimentary, sometimes with a fork at base;  $CuP$  present but weak;  $CuA_2$  initiating from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, only slightly separated at base;  $M_1+R_s$  initiate from apical angle of anterior cell, from same basal point or slightly separated at

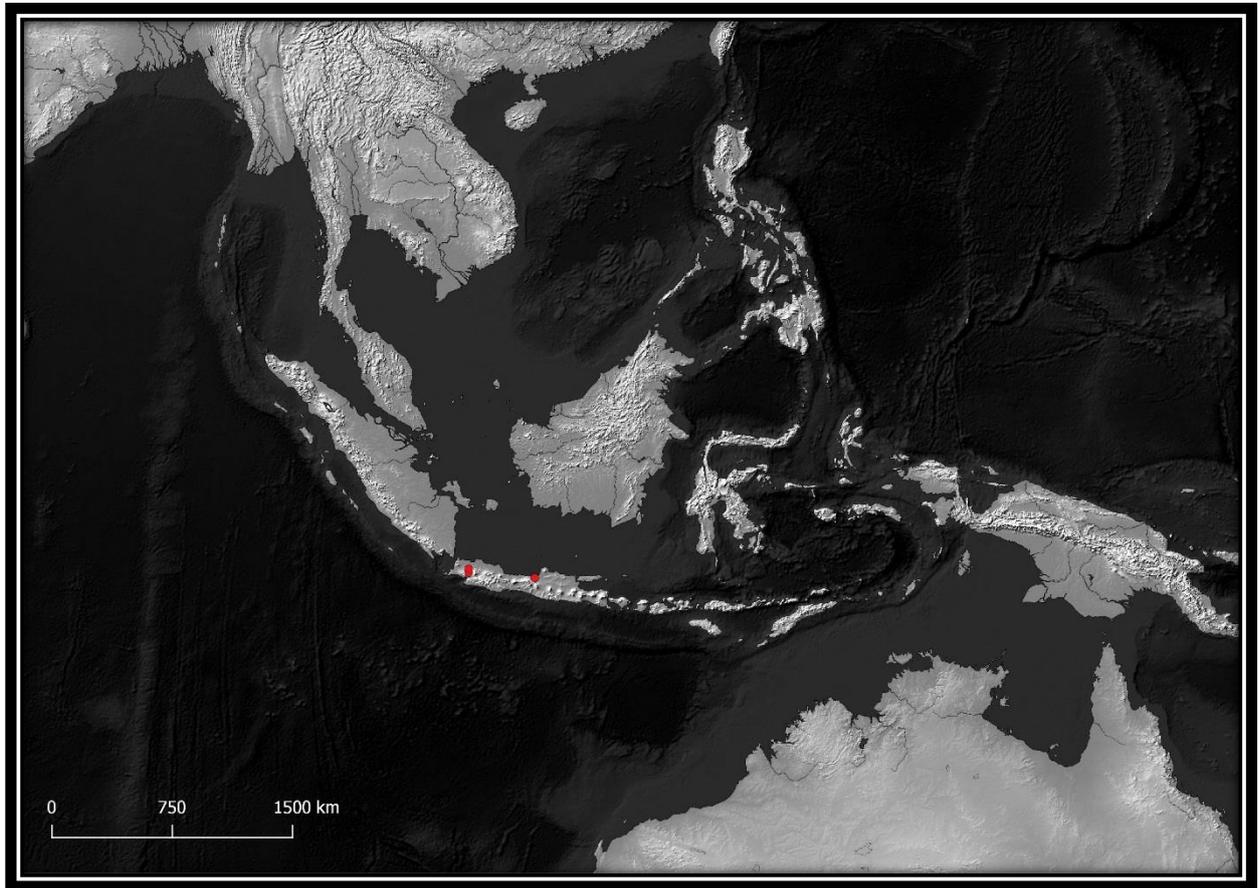
base; a bar is present from  $R_s$  to  $Sc+R_1$  in both sexes, but sometimes weak; a discocellular vein on both forewing and hindwing is present, but weak towards its base. In the forewing the posterior cell (= lower cell) is always smaller than the upper cell; the anterior angle is nearly acuminate. Retinaculum and frenulum absent.

*Abdomen:* With mainly broad scales of cream with sepia tips and a strong glint on upperside as well as underside; abdominal tuft short in both sexes, 20% of abdomen length, with cream and sepia.

*Male genitalia.* Saccus absent; the vinculum and tegumen are fused, forming a firm narrow ring; uncus long, narrowly elongated, with a broad triangular base (viewed ventrally), rather deep bifurcated between two rather broad hollow tips, in each tip with one small thorn-like sclerotized structure. Valva is large, almost rectangular with a slightly arc-shaped costal margin, S-shaped ventrally (ventral view); very long, sclerotized setae, sometimes bent, are present mainly on the upper half of valva along the costa and rounded tip; transtilla absent; a relict of semi-transtilla present, it is only ventrally surrounded with a dense bunch of straight, sclerotized long setae that have a chestnut colour; this semi-transtilla-like structure has a hole in the centre. Sacculus is dominant and narrow with an extension that is sclerotized and looks like a half of a boat at end distally; above its end is one sclerotized appendice of lunule-like shape, occurring distal-ventrally and is basally thinly connected to the half boat-like structure. Gnathal arms are a simple structure that looks like a broad T-shaped stick with rounded tips, it is sclerotized, broader basally and attached to the lower end of tegumen, the arms are connected ventrally via a tube-like structure, this basal connection is relatively broad and thinly sclerotized; it occurs between the lowest part of the gnathal arms and originates as thinly sclerotized structure that points upwards (towards the uncus), it is basally thinly membranous but on its upper two-thirds it represents a hollow, broad tube that is open towards uncus. Juxta is large, oval-shaped (70% the size of the aedeagus), rather thinly membranous, with an emargination, but without any processes. Phallus is short (slightly longer than juxta), simple tube-like, broader at base, not bent, with a short thorn-like structure distally (10% the length of aedeagus).

*Female postabdominal structure and genitalia.* Papillae anales large with short and very long setae; segment 8 is almost rectangular with a large open space dorsally and ventrally, usually covered with a very thin membrane, and with few medium long setae only ventrally; anterior apophyses are longer than width of segment 8 and have a large base, looking like a huge sail (with an acuminate tip dorsally and a rounded tip ventrally) that is dorsally and ventrally connected to the thin membrane that covers the open spaces of segment 8; a large oval and horizontally elongated hole occurs near the centre of the sail-like base; posterior apophyses are shorter than width of segment 8, with a broad fork-like base, and are narrower than anterior apophyses. Corpus bursae and ductus bursae are strongly reduced in length and size, in length slightly longer than segment 8 and the anterior apophyses; corpus bursae is on 90% of its surface not sclerotized; the whole short ductus bursae is sclerotized and connected to a

relatively large strongly sclerotized ventral plate that is linked to a ring-like structure of segment 8. Ductus bursae is narrow; corpus bursae is twice as large as one sail-like structure, elongated oval-shaped with a narrow base and a broadly rounded end, thinly membranous, without any structures.



**FIGURE 121.** Distribution of Gen. Nov. ZB (red dots).



**FIGURE 122.** Gen. Nov. ZB, sp. nov. zb1, [Indonesia], Java, Delona [?], 22.09.1935, L.G.E. Kalshoven leg., number 1473 [?], male, ex RMNH, genitalia slide number 04/072017 I. Lehmann. Wingspan 30.0 mm



**FIGURE 123.** Gen. Nov. ZB, sp. nov. zb1, [Indonesia], West Java, Buikenang or Buibenang [?], no date, 1892 [only the year is mentioned], [no collector mentioned], female, ex RMNH, genitalia slide number 22/092017 I. Lehmann. Wingspan 33.0 mm

#### 4.37 *Shimonia* Lehmann & Rajaei, 2013

The genus is defined by the following autapomorphies:

- Two prominent, long, narrow acuminate, thorn-like appendices on valva arising externally from its base; (51);
- Long setae occur in groups of two or three on segment 8; (52);
- Below segment 8 occur two large and strongly sclerotized oval or rounded plates that are connected by a narrow short band ventrally; (53).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes; (11).

Type species of genus (Figures 125, 126): *Shimonia+timberlakei* Lehmann & Rajaei, 2013

Type locality: Belgian Congo [Democratic Republic of the Congo], Eala, 19.06.1935, J. Ghesquière leg., male, genitalia slide number 31/072010 I. Lehmann, ex RMCA; depository in RMCA.

Number of species in genus at present: 05

All localities of studied species per country: Democratic Republic of the Congo; Uganda; Kenya.

Distribution of genus at present (cf. Figure 124): lowland, submontane and montane areas from the eastern side of the central Congo River southeastwards via the Congo Basin to the Katangan Copper Bow and eastwards via the Rwenzori Mountains to areas just east of Mount Elgon (Kenya).

The reconstructed and predicted ancestral area is the Afromontane archipelago-like regional centre of endemism.

The reconstructed biogeographic event comprises: First, dispersal in the Afromontane archipelago-like regional centre of endemism. Secondly, vicariance in the Afromontane archipelago-like regional centre of endemism and dispersal into the Guineo-Congolian regional centre of endemism. Thirdly, vicariance between the Afromontane archipelago-like regional centre of endemism and the Guineo-Congolian regional centre of endemism.

Phylogenetic position: The sister genus could not be reconstructed unambiguously. The genus is part of a monophylum together with *Mountelgonia*, *Metarbelodes* G<sub>2</sub>, *Moyencharia* and *Metarbelodes* G<sub>1</sub>/G<sub>3</sub>.

The synapomorphy shared with *Mountelgonia*, *Metarbelodes* G<sub>2</sub>, *Moyencharia* and *Metarbelodes* G<sub>1</sub>/G<sub>3</sub> comprises:

- The end of each gnathal arm looks like a hand with tiny thorn-like appendices; (41).

Description: *Head:* rough-scaled with hair-like scales of light ocher below the eyes on fronto-clypeus in both sexes; a pair of pits is absent in both sexes on lower fronto-clypeus, a pair of conical projections is present on lower fronto-clypeus in both sexes; pits behind labial palpi are oval-shaped holes in both sexes; labial palpi very long, 1.5 × longer than eye diameter and consist of three segments (a tiny fourth segment occurs on top or is rudimentary), basal segment not broader, second segment is 2.1 × longer than basal segment and elongated, third segment is as long as basal segment and with an acuminate tip in both sexes; antennae very long, bipectinated in male, unipectinated in female; branches are narrow and strongly bent and 7.5 × width of shaft in male, 1.5 × width of shaft in female, branches are densely scaled cream in both sexes; flagellum scaled cream.

*Thorax:* Densely covered with hair-like scales of light ocher with tips of cream on patagia and tegulae in both sexes, slightly glossy, tegulae not pronounced; crest on metathorax pronounced and large, light ocher. Epiphyses are medium long (up to 2.0 mm) and flat in both sexes. Hindlegs with two pairs of narrow tibial spurs in both sexes; they are unequal in length and long (lower pair: outer spur up to 2.0 mm, inner spur up to 1.0 mm; upper pair: outer spur up to 1.5 mm, inner spur up to 0.7 mm); pretarsus with a pair of small or rudimentary pulvilli in both sexes.

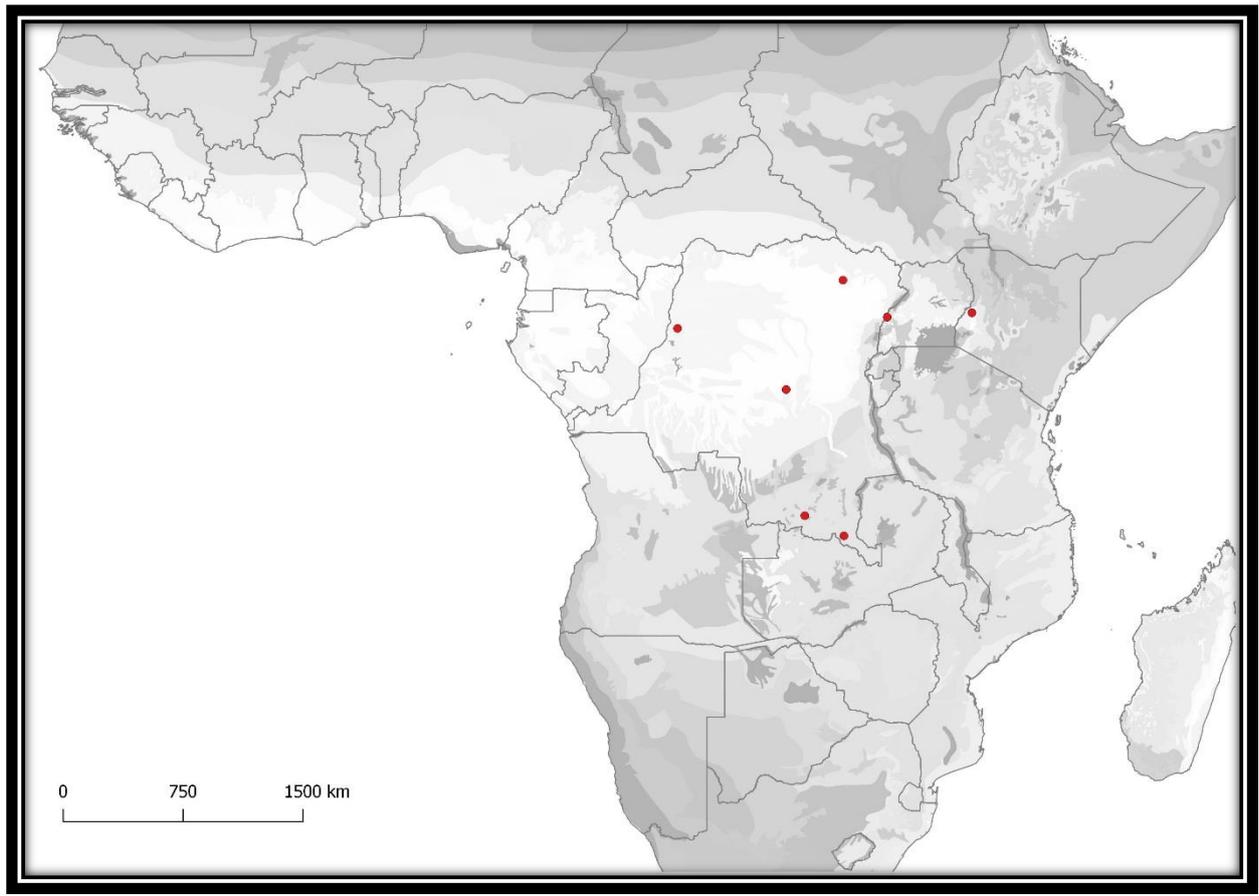
Forewing upperside with a light ocher or light cream ground-colour mixed with dark cream and/or light greenish olive (the greenish olive colour is possibly only visible in fresh specimens), glossy in both sexes; a geometric design is absent in both sexes; a simple pattern is present and comprises light brown striae on the whole upperside (the striae might be faded or absent) and a usually pronounced light brown postmedial band, edged cream towards base of wing, as well as a small sepia spot in the discocellular cell; CuA<sub>2</sub> is distinctly marked in both sexes with light brown edged cream towards base of wing; all colours are only slightly contrasting or contrasting if the ground-colour is light cream. Hindwing is light brownish-olive or dark cream, glossy, in both sexes. Fringe has an unusual appearance resembling somehow the vane of a bird feather, scales with a very long shaft or stalk branching only on tip, light ocher in both sexes, scales very long (ciliae up to 2.1 mm). Wing venation: in forewing 1A+2A long forked at base; CuP represents a more or less continuous fold that is not sclerotized; CuA<sub>2</sub> originating from two-thirds of lower median; CuA<sub>1</sub> originates from hind margin of posterior cell, M<sub>3</sub> and M<sub>2</sub> originate from apical angle of posterior cell, separated; M<sub>1</sub> initiates from anterior angle of median cell; R<sub>5</sub> originates from anterior angle of median cell and at base of a large areole; R<sub>3</sub>+R<sub>4</sub> separated or on a very short stalk and originate from posterior angle of areole; R<sub>2</sub> originates from anterior angle of areole; R<sub>1</sub> initiates from anterior part of median cell; Sc more or less parallel to R<sub>1</sub>. In hindwing 3A present; 1A+2A rudimentary, sometimes with a fork at base; CuP present but weak; CuA<sub>2</sub> initiating from two-thirds of lower median of posterior cell; CuA<sub>1</sub> initiates from hind margin of posterior cell; M<sub>3</sub> and M<sub>2</sub> initiating from apical angle of posterior cell, separated; M<sub>1</sub>+R<sub>s</sub> initiate from apical angle of anterior cell, separated; a bar is present from R<sub>s</sub> to Sc+R<sub>1</sub> in both sexes, but sometimes weak and very short; a

discocellular vein on both forewing and hindwing is present, but weak towards its base. In the forewing the posterior cell (= lower cell) is always longer than the upper cell. Retinaculum and frenulum absent.

*Abdomen:* With mainly hair-like scales of cream with light ocher; abdominal tuft short or medium long in both sexes, up to 20% of abdomen length, cream.

*Male genitalia.* Saccus small, broadly finger-like; the vinculum and tegumen are fused, forming a firm narrow ring; uncus very large, broadly elongated, with a broad rectangular shape and broadly rounded tips of lobes with a small rounded emargination (viewed ventrally). Valva is rather small (not larger than uncus in ventral view), almost rectangular, comprising a larger thinly membranous inner valva and a more sclerotized outer valva; two thorn-like and sclerotized appendices are prominent and arising from the outer valva; both appendices are strongly bent in various directions (viewed laterally); very long, mainly soft setae, sometimes bent, are present on the inner valva; transtilla absent; a semi-transtilla is oval-shaped, large or small. Sacculus is medium broad or narrow, dorsally not closed but open, with many soft setae on entire length, the end is open. Gnathal arms are a simple structure looking similar to a broad short arm with a hand at end, with small thorn-like sclerotized appendices on the hand; the arms are narrowly connected ventrally and thinly sclerotized, they originate from the lower part of tegumen. Juxta is large triangular-shaped (60% the size of the aedeagus), rather thinly membranous, with an emargination at base, a broadly rounded tip and without any processes. Phallus is simple tube-like, slightly longer than width of valva, slightly broader at base, straight or bent, without any structures.

*Female postabdominal structure and genitalia.* Papillae anales is small with short setae; segment 8 is almost rectangular and covered with long setae in groups of two or three as well as long setae occur along its posterior margin; anterior apophyses are narrow and *ca.* 40% longer than width of segment 8; posterior apophyses have a broader elongated base that covers *ca.* 50% of their entire length; below segment 8 occur two large and strongly sclerotized oval or rounded plates that are connected by a narrow short band ventrally. Corpus bursae and ductus bursae are thinly membranous and without any structures.



**FIGURE 124.** Distribution of the genus *Shimonia* (red dots).



**FIGURE 125.** *Shimonia timberlakei*, Holotype, Belgian Congo [Democratic Republic of the Congo], Eala, 19.06.1935, J. Ghesquière leg., male, ex RMCA, genitalia slide number 31/072010 I.Lehmann. Wingspan 38.0 mm



**FIGURE 126.** *Shimonia timberlakei*, Paratype, Belgian Congo [Democratic Republic of the Congo], Eala, 19.06.1935, J. Ghesquière leg., female, ex RMCA, genitalia slide number 12/072010 I. Lehmann. Wingspan 41.0 mm

#### 4.38 *Metarbelodes* Strand, 1909 - subgroup G2

The genus (“true” *Metarbelodes*) is defined by the following autapomorphy:

- Well sclerotized, hollow and long thorn-like process originates at the costal margin and is strongly bent downwards to the ventral edge of valva; (55).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male but it represents a strong tubular-like continuous fold that extends from base of wing to the dorsum; [possibly also in female present] (11).

Type species of genus (cf. Figure 128): *Metarbelodes + umtaliana* (Aurivillius, 1901)

Type locality: Rhodesia [Southern Rhodesia since 1901], Mashonaland [Zimbabwe], Umtali [no date, since “Rhodesia” is mentioned the type was certainly collected before 1901, possibly between 1894 and 1900, Lehmann & Husemann *in prep.*], G.A.K. Marshall leg., male, genitalia slide number 25/122009 I. Lehmann, ex NRM; depository in NRM.

Number of species in genus subgroup G2 at present: 01

All localities of studied species per country: Zimbabwe.

Distribution of genus at present (cf. Figure 127): submontane and/or montane area near Umtali (today Mutare) or near Old Umtali (cf. Chipangura 2013), both are located close to the Bvumba Mountains in eastern Zimbabwe.

The reconstructed and predicted ancestral area is the Afromontane archipelago-like regional centre of endemism, the Guinea-Congolia/Zambezia regional transition zone and the Guinea-Congolia/Sudania regional transition zone.

The reconstructed biogeographic event comprises: First, dispersal in the Afromontane archipelago-like regional centre of endemism, the Guinea-Congolia/Zambezia regional transition zone and the Guinea-Congolia/Sudania regional transition zone. Secondly, vicariance between the Afromontane archipelago-like regional centre of endemism and the Guinea-Congolia/Zambezia regional transition zone as well as the Guinea-Congolia/Sudania regional transition zone.

Phylogenetic position: The sister genus could not be reconstructed unambiguously. The genus is part of a monophylum together with *Mountelgonia*, *Moyencharia* and *Metarbelodes* G1/G3.

The synapomorphy shared with *Mountelgonia*, *Moyencharia* and *Metarbelodes* G1/G3 comprises:

- The gnathal arms are not connected ventrally; (21).

Description: *Head:* rough-scaled with hair-like scales of light ocher below the eyes on fronto-clypeus in male; a pair of pits is absent on lower fronto-clypeus, a pair of conical projections is present on lower fronto-clypeus; pits behind labial palpi are oval-shaped holes; labial palpi long, almost as long as eye diameter and consist of three segments, the central segment is the longest, up to 1.5–2.3× longer than the basal segment, the segment at tip is the shortest and has half times the length of the basal segment; antennae bipectinated in male, branches are narrow and 3.5 × width of shaft, densely scaled cream; flagellum scaled cream.

*Thorax:* Densely covered with hair-like scales of light ocher on patagia and tegulae, slightly glossy, tegulae not pronounced; crest on metathorax small, light ocher. Epiphyses are absent. Hindlegs with one pair of narrow tibial spurs, slightly unequal in length (outer spur 1.4 mm, inner spur 1.3 mm); pretarsus with a pair of pulvilli.

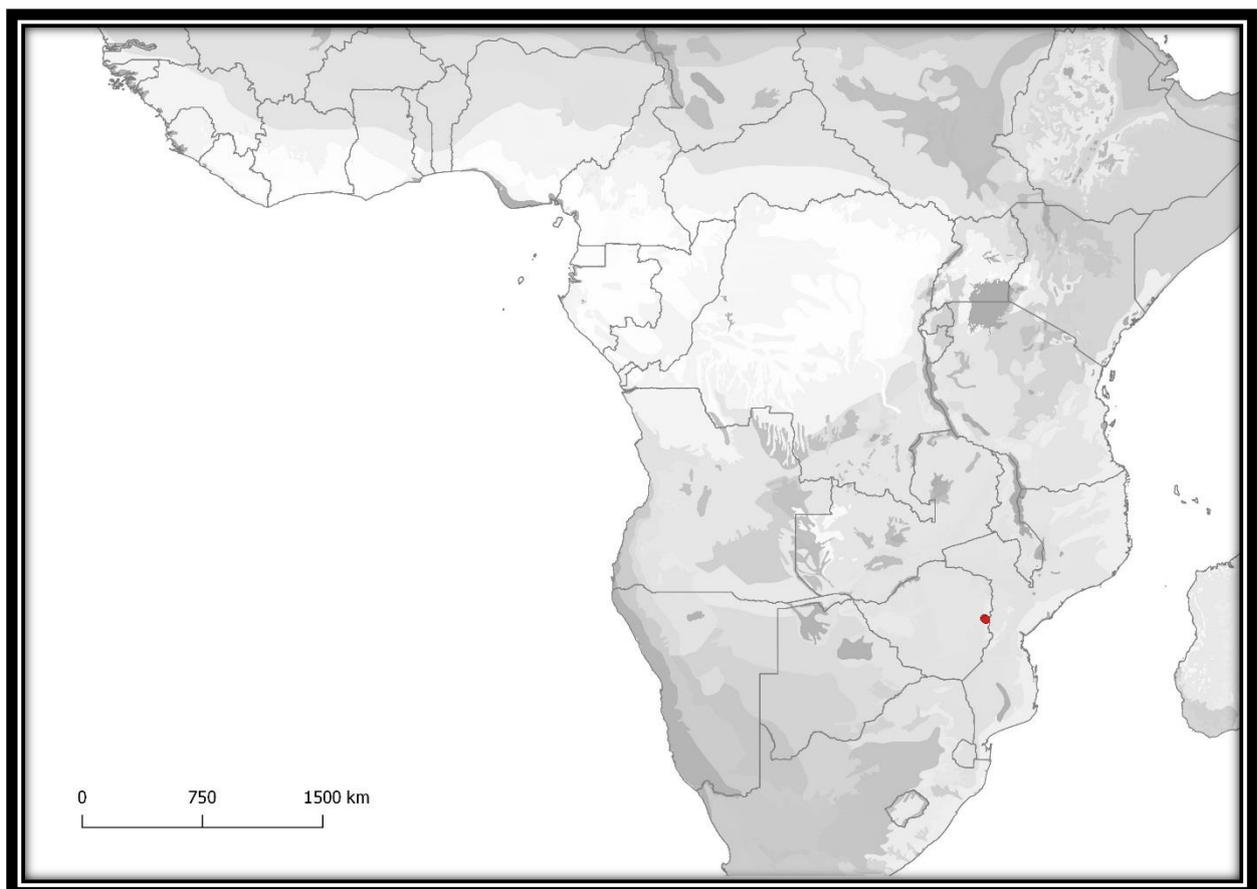
Forewing upperside with a dark ocher ground-colour mixed with cream, not glossy, with striae of sepia along costa and on whole upperside; a geometric design is absent; a simple pattern is present and comprises a straight sepia terminal line, not parallel to termen, from near apex to dorsum, strongly bent towards base of wing at  $M_3$ ;  $1A+2A$  as well as discocellular vein sepia;  $CuA_2$  is distinctly marked cream, rather narrow, edged sepia above. Hindwing is cream, glossy. Fringe is long (ciliae up to 1.5 mm), cream, glossy. Wing venation: in forewing  $1A+2A$  long forked at base;  $CuP$  represents a strong tubular-like continuous fold that is not sclerotized;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from apical angle of posterior cell, separated;  $M_1$  initiates from anterior angle of median cell and close to base of a relatively large areole;  $R_5$  originates from posterior angle of areole;  $R_4+R_3+R_2$  on a long stalk and originate from anterior angle of areole close to base of  $R_5$ ;  $R_1$  initiates from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  rudimentary;  $CuP$  present but weak;  $CuA_2$  initiating from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1+Rs$  initiate from apical angle of anterior cell, long stalked; a short bar is present from  $Rs$  to  $Sc+R_1$ ; a discocellular vein on both forewing and hindwing is present. Retinaculum and frenulum absent.

*Abdomen:* With mainly hair-like scales of cream with light ocher; abdominal tuft short, up to 25% of abdomen length, cream.

*Male genitalia.* Saccus finger-shaped, gently rounded caudally; the vinculum and tegumen are fused, forming a firm ring; vinculum opposite of saccus broad, namely twice as large as the saccus, forming a plate-like structure; uncus large, almost oval with narrowly rounded lobes, short setae ventrally, basal edge of uncus bent like a lunule in the middle. Valva is oval with a broader base, costa without setae, inner side of median sector with few setae; from near base of valva and along costal margin occurs a large, setose and weakly-sclerotized projection that is attached to a thorn-like process; this thorn-like process is prominent and hollow, it has at the end of its base an

open long part dorsally where it is connected by a thin membrane with the weakly-sclerotized projection; the thorn-like process originates from the outer side of valva near the costa and is strongly bent downwards towards the ventral edge of valva. Sacculus strongly reduced to one-third near base of valva. A short emargination (less than 25% of the length of valva) extends in between the weakly-sclerotized projection and the thorn-like process. A transtilla is absent; a semi-transtilla is short, rectangular with a somehow leaf-like shape, attached to the costa of valva and opposite of the vinculum, without setae. Gnathal arms short, well above costa, covered with short teeth-like processes at its distal end, resembling a hand, not connected by a sclerotized band basally. Juxta is almost twice as large as saccus with two acuminate tips and a short process at each tip, between the tips occurs a deep emargination (90% the length of juxta). Phallus is simple, 1.5× longer than basal width of valva, slightly trumpet-like, bilobed with a cleft on both ends.

*Female postabdominal structure and genitalia. Unknown.*



**FIGURE 127.** Distribution of the “true” genus *Metarbelodes* (red dot).



**FIGURE 128.** *Metarbelodes umtaliana* [G2], Type, Rhodesia [on third label], Mashonaland [Zimbabwe], Umtali [Umtali or Old Umtali?], [no date, most probably collected between 1894 and 1900] G.A.K. Marshall leg., male, ex NRM, genitalia slide number 25/122009 I. Lehmann. Wingspan 32.5 mm

#### **4.39 *Mountelgonia* Lehmann, 2013**

The genus is defined by the following autapomorphy:

- Small thorn-like process at ventral posterior end of valva, process soft, only slightly sclerotized, not hollow on entire length; (38).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes; (11).

Type species of genus (cf. Figures 130, 131): *Mountelgonia + percivali* Lehmann, 2013

Type locality: Kenya, Mount Elgon National Park, Chepnyalil Cave, 2.500 m, 24.01.1992, A. Lobmayer leg., male, genitalia slide number 27/022012 I. Lehmann, ex MWM; depository in ZSM.

Number of species in genus at present: 09

All localities of studied species per country: Kenya, Tanzania, Rwanda, Burundi, Zambia.

Distribution of genus at present (cf. Figure 129): submontane and montane areas of the Afromontane archipelago-like regional centre of endemism in Rwanda, Burundi and eastwards via northern Tanzania and Uganda to western, southern and central Kenya. A disjunct record exists from extreme northwest Zambia (Mbala).

The reconstructed and predicted ancestral area is the Afromontane archipelago-like regional centre of endemism.

The reconstructed biogeographic event comprises: First, dispersal in the Afromontane archipelago-like regional centre of endemism. Secondly, dispersal occurred in the Guinea-Congolia/Zambezia regional transition zone and the Guinea-Congolia/Sudania regional transition zone. Thirdly, vicariance occurred between the Afromontane archipelago-like regional centre of endemism and within the Afromontane archipelago-like regional centre of endemism with the Guinea-Congolia/Zambezia regional transition zone as well as the Guinea-Congolia/Sudania regional transition zone.

Phylogenetic position: The sister genus could not be reconstructed unambiguously. The genus is part of a monophylum together with *Metarbelodes* G<sub>2</sub>, *Moyencharia* and *Metarbelodes* G<sub>1</sub>/G<sub>3</sub>.

The synapomorphy shared with *Metarbelodes* G<sub>2</sub>, *Moyencharia* and *Metarbelodes* G<sub>1</sub>/G<sub>3</sub> comprises:

- The gnathal arms are not connected ventrally; (21).

Description: *Head:* rough-scaled with hair-like scales of dark ocher or cream below the eyes on fronto-clypeus in both sexes; a pair of pits is absent on lower fronto-clypeus, a pair of conical projections is present on lower fronto-clypeus in both sexes; pits behind labial palpi are large oval-shaped holes; labial palpi long, almost as long as eye diameter and consist of three segments, the central segment is the longest, at least 3× longer than the basal segment in both sexes; antennae bipectinated in male, branches 5.5 × width of shaft, rather unipectinated in female, branches 1.5 × width of shaft; branches and flagellum densely scaled cream, but branches less scaled in female.

*Thorax:* Densely covered with hair-like scales (very fine scales in female) of dark ocher or cream on patagia and tegulae, slightly glossy, tegulae not pronounced; crest on metathorax small. Epiphyses are absent in both sexes. Hindlegs with one pair of narrow tibial spurs, slightly unequal in length (outer spur at least 0.7 mm, inner spur at least 0.6 mm); pretarsus with a pair of pulvilli.

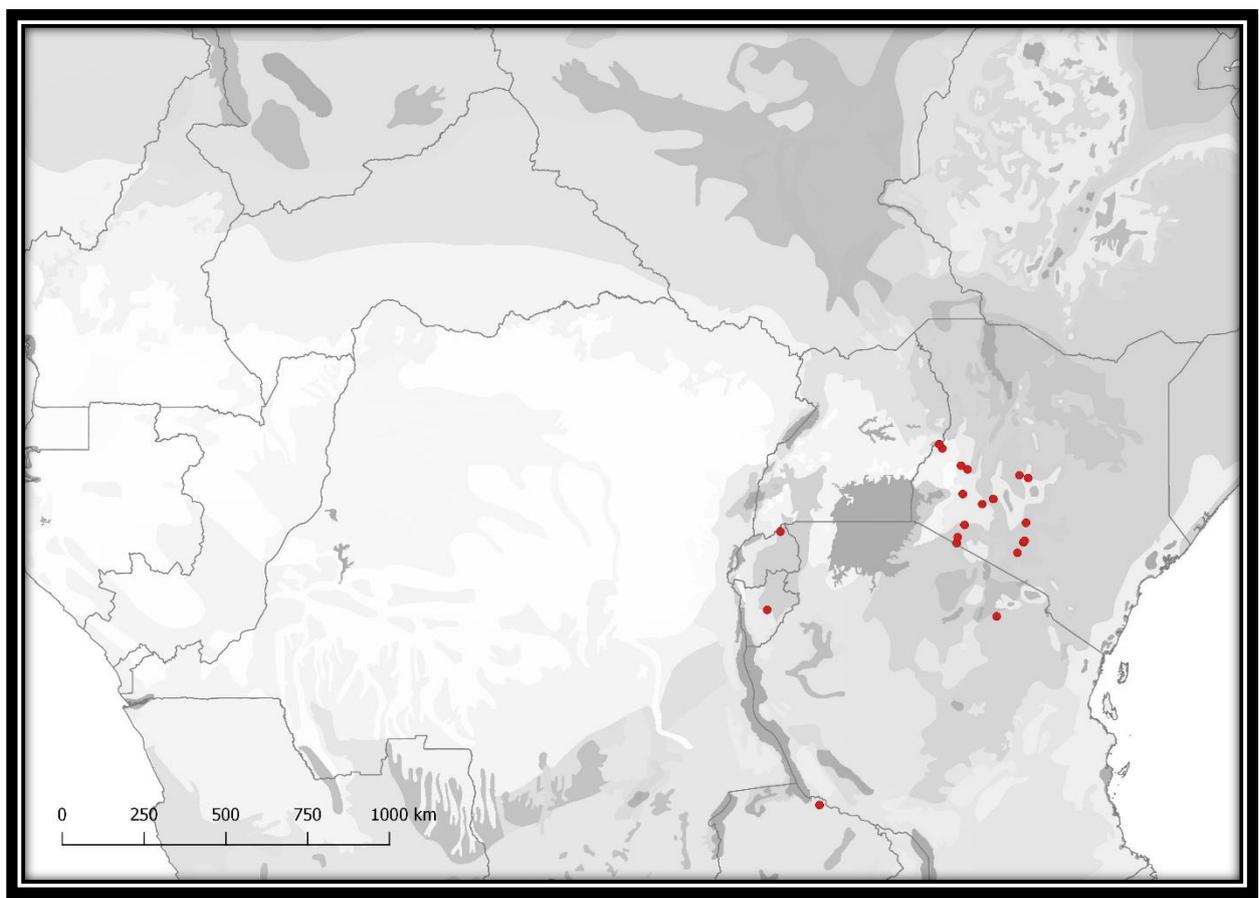
Forewing upperside with a sepia or cream ground-colour mixed with cream, not glossy; a geometric design is absent; a simple pattern is present and comprises the sepia coloured veins except of the lower median and CuA<sub>2</sub> that are distinctly marked light cream, rather broad, edged sepia above in both sexes. Hindwing is cream, glossy, with all veins dark brown in both sexes. Fringe is very long (ciliae up to 2.0 mm in male, shorter in female), cream mixed with sepia, glossy. Wing venation similar in both sexes: in forewing 1A+2A forked at base; CuP absent; CuA<sub>2</sub> originating from two-thirds of lower median; CuA<sub>1</sub> originates from hind margin of posterior cell, M<sub>3</sub> and M<sub>2</sub> originate from apical angle of posterior cell, separated; M<sub>1</sub> initiates from anterior angle of median cell and more or less close to the base of a rather small areole; R<sub>5</sub> originates from posterior angle of areole or is stalked with R<sub>4</sub>+R<sub>3</sub>, R<sub>2</sub> originates from anterior angle of areole; R<sub>1</sub> initiates from anterior part of median cell; Sc more or less parallel to R<sub>1</sub>. In hindwing 3A present; 1A+2A present in male, sometimes rudimentary in female; CuP present but weak in both sexes; CuA<sub>2</sub> initiating from two-thirds of lower median of posterior cell; CuA<sub>1</sub> initiates from hind margin of posterior cell; M<sub>3</sub> and M<sub>2</sub> initiating from apical angle of posterior cell, separated; M<sub>1</sub>+Rs initiate from apical angle of anterior cell, stalked; a short bar is sometimes present from Rs to Sc+R<sub>1</sub>; a discocellular vein on both forewing and hindwing is present. Retinaculum and frenulum absent.

*Abdomen:* With mainly hair-like scales of cream or dark ocher; abdominal tuft short, up to 20% of abdomen length, cream.

*Male genitalia.* Saccus short, broad, usually gently rounded caudally; the vinculum and tegumen are fused, forming a firm but very narrow ring; vinculum opposite of saccus only sometimes slightly broader, but never forming any plate-like structure; uncus large, with elongated rounded lobes, short setae ventrally, basal edge of uncus bent like a lunule in the middle. Valva is oval with a broader base, costa without setae, on inner side the median sector is with few tiny setae; from near base of valva and along costal margin occurs a large, setose and weakly-sclerotized projection; a thorn-like process originates from the ventral side of valva, it is short, not much developed, never extending beyond the weakly sclerotized projection, it is not hollow on its entire

length, but flat, and can be easily folded because it is only weakly sclerotized. Sacculus narrow, broader near base of valva. A short emargination (less than 20% of the length of valva) extends in between the weakly-sclerotized projection and the thorn-like process. A transtilla is absent; a semi-transtilla is short, rectangular in shape, attached to the costa of valva and opposite of the vinculum, without setae. Gnathal arms short, well above costa, covered with short teeth-like processes at its distal end, resembling a hand, not connected by a sclerotized band basally. Juxta is small, not as large as saccus, with two acuminate tips and a short process at each tip, between the tips occurs a deep emargination (95% the length of juxta). Phallus is simple, 2.3× longer than basal width of valva, trumpet-like, bilobed with a cleft on both ends.

*Female postabdominal structure and genitalia.* Papillae anales is broad with long setae; segment 8 is almost rectangular and without setae except along its posterior margin; dorso-anterior margin without emargination; segment 8 with one narrow, latero-ventral sclerotized band with a V-shaped end laterally, the band is not hollow. Anterior apophyses are narrow on the whole length and rarely a little longer than width of segment 8, tips bent; posterior apophyses have usually a broader elongated part near their base. Corpus bursae and ductus bursae are thinly membranous and without any structures.



**FIGURE 129.** Distribution of the genus *Mountelgonia* (red dots).



**FIGURE 130.** *Mountelgonia percivali*, Holotype, Kenya, Mount Elgon National Park, Chepnyalil Cave, 24.01.1992, A. Lobmayer leg., ex MWM, male, genitalia slide number 27/022012 I. Lehmann. Wingspan 22.0 mm



**FIGURE 131.** *Mountelgonia percivali*, Paratype, Kenya, Mount Elgon National Park, Chepnyalil Cave, 24.01.1992, A. Lobmayer leg., ex MWM, female, genitalia slide number 31/032012 I. Lehmann. Wingspan 26.5 mm



**FIGURE 132.** *Mountelgonia* sp. nov.6 [close to *lumbuaensis* Lehmann, 2013], Kenya, Nakuru, Punda Miliyas Camp, 17.03.2016, Ingo & Shimoni Lehmann leg., ex own coll., male [no genitalia dissection done since this is the best specimen from Punda Miliyas]. Wingspan 25.5 mm



**FIGURE 133.** *Mountelgonia* sp. nov.9, Kenya, Lolldaiga Hills Ranch, Three Dams, 02.03.2016, Mike Roberts, Julius Mathiu & Ingo Lehmann leg., ex own coll., male [no genitalia dissection done since this is one of the best specimens from Three Dams]. Wingspan 19.0 mm

#### 4.40 *Moyencharia* Lehmann, 2013

The genus is defined by the following autapomorphies:

- Valva with prominent elongated emargination that is edged by a prominent thorn-like structure below and above the emargination; (42);
- Large, well sclerotized, rectangular plate-like structure close to ventral end of vinculum; (43).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes; (11).

Type species of genus (cf. Figures 135, 136): *Moyencharia + mineti* Lehmann, 2013

Type locality: [Republic of] Chad, Region du Moyen-Chari, Canton de Gondey, Makoga, 04.-12.05.1965, J.M. Fonteneau leg., male, genitalia slide number 22/012012 I. Lehmann, ex MNHN; depository in MNHN.

Number of species in genus at present: 06

All localities of studied species per country: Republic of Guinea; Ghana; Burkina Faso; Nigeria; Republic of Chad; Republic of South Sudan; Democratic Republic of the Congo.

Distribution of genus at present (cf. Figure 134): lowland and submontane areas from the Republic of Guinea via southern Burkina Faso, northern and southeastern Ghana, northern Nigeria eastwards to southern Chad and southeastwards to the southwestern Republic of South Sudan and northeastern Democratic Republic of the Congo.

The reconstructed and predicted ancestral area is the Guinea-Congolia/Sudania regional transition zone and the Guinea-Congolia/Zambezia regional transition zone.

The reconstructed biogeographic event comprises: First, dispersal in the Guinea-Congolia/Zambezia regional transition zone and the Guinea-Congolia/Sudania regional transition zone. Secondly, dispersal from the Guinea-Congolia/Zambezia regional transition zone and the Guinea-Congolia/Sudania regional transition zone into the Sudanian regional centre of endemism, the Afromontane archipelago-like regional centre of endemism and the Kalahari-Highveld regional transition zone. Thirdly, vicariance between the Guinea-Congolia/Zambezia regional transition zone, the Guinea-Congolia/Sudania regional transition zone, the Sudanian regional centre of endemism and all other phytochoria mentioned above.

Phylogenetic position: The sister genus is *Metarbelodes* G<sub>1</sub>/G<sub>3</sub>. The genus is part of a monophylum together with *Metarbelodes* G<sub>2</sub>, *Mountelgonia* and *Metarbelodes* G<sub>1</sub>/G<sub>3</sub>.

The synapomorphy shared with *Metarbelodes* G<sub>1</sub>/G<sub>3</sub> comprises:

- Well sclerotized thorn-like process(-es) at the posterior margin of valva are hollow inside; (54).

The synapomorphy shared with *Metarbelodes* G<sub>2</sub>, *Mountelgonia* and *Metarbelodes* G<sub>1</sub>/G<sub>3</sub> comprises:

- The gnathal arms are not connected ventrally; (21).

Description: *Head:* rough-scaled with hair-like scales of dark ocher, chestnut or yellow-ocher below the eyes on fronto-clypeus in both sexes; a pair of pits as well as a pair of conical projections is absent on lower fronto-clypeus but a large lip-like structure is present on lower fronto-clypeus in both sexes; pits behind labial palpi are small oval-shaped flat holes; labial palpi long, almost as long as eye diameter or slightly longer and consist of three segments, all segments have almost the same length, the central segment is sometimes the longest in both sexes; antennae very long and bipectinated in male, branches up to  $6.0 \times$  width of shaft; in female are the antennae shorter, bipectinated, branches  $1.5 \times$  width of shaft; branches and flagellum densely scaled cream or dark ocher in both sexes.

*Thorax:* Densely covered with hair-like scales of dark ocher, yellow ocher or cream on patagia and tegulae, slightly glossy, a collar ring is usually present in male, tegulae not pronounced; crest on metathorax small. Epiphyses are absent in both sexes. Hindlegs with two pairs of narrow tibial spurs, slightly unequal in length (outer spur at least 0.7 mm, inner spur at least 0.6 mm); pretarsus with a pair of pulvilli.

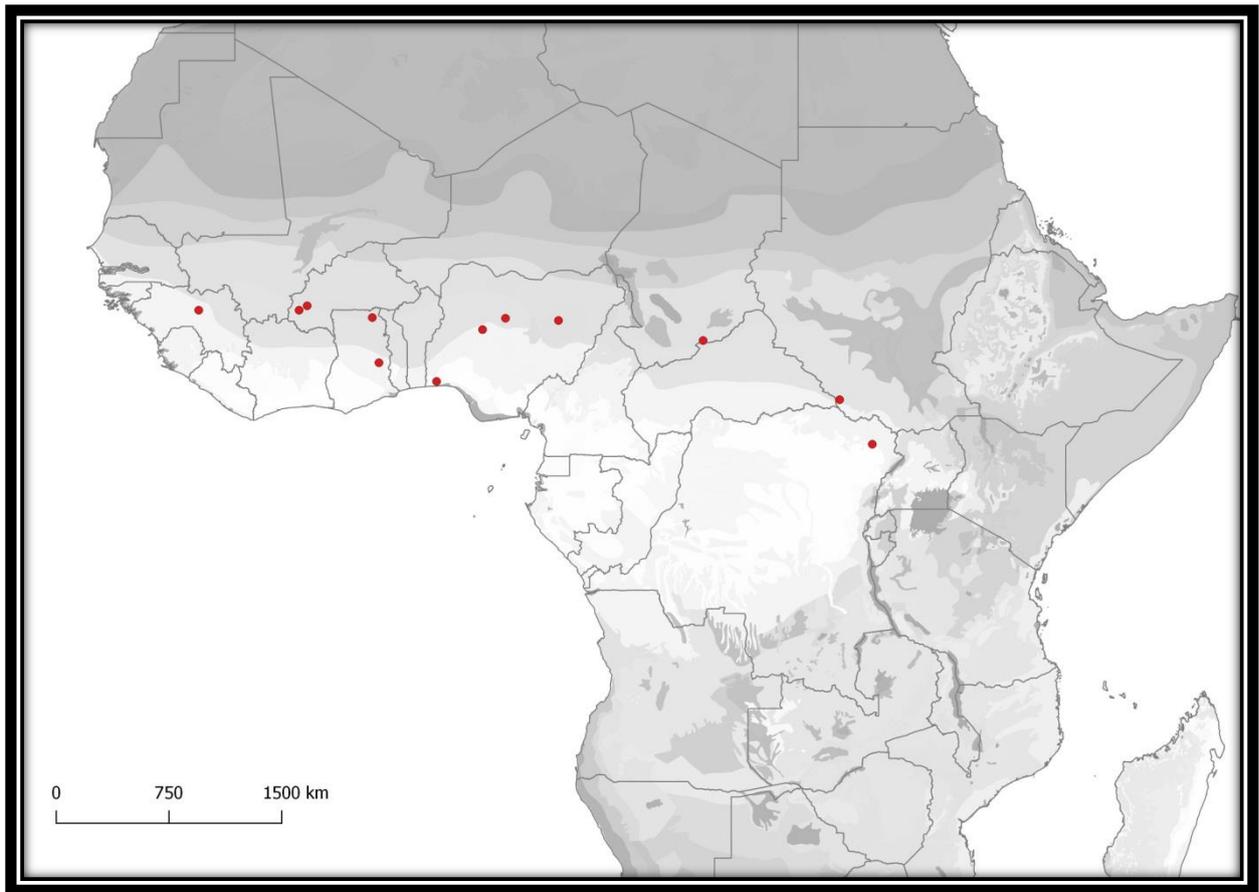
Forewing upperside with a yellow-ocher and/or brown ground-colour mixed with sepia, cream, sometimes black, usually not glossy; a geometric design is absent; a simple pattern is present and comprises a broad band that is usually yellow-ocher along costal margin; a broad yellow-ocher or chestnut and arc-shaped sub-terminal band (not always present) from near apex to dorsum; CuA<sub>2</sub> distinctly marked narrowly yellow-ocher or cream, at end with a white or cream spot and smaller spots of same colour in male, less marked in female. Hindwing is cream, light grey or yellow-ocher mixed with brown, slightly glossy, in both sexes. Fringe is long (ciliae up to 1.1 mm in male, longer in female, up to 1.5 mm), cream or orange-yellow, sometimes mixed with very long pure white scales, glossy. Wing venation similar in both sexes: in forewing 1A+2A forked at base; CuP absent; CuA<sub>2</sub> originating from two-thirds of lower median; CuA<sub>1</sub> originates from hind margin of posterior cell, M<sub>3</sub> and M<sub>2</sub> originate from apical angle of posterior cell, separated; M<sub>1</sub> initiates from anterior angle of median cell and more or less close to the base of a rather small areole; R<sub>5</sub> originates from posterior angle of areole, either from the same basal point with R<sub>4</sub>+R<sub>3</sub> or is stalked with R<sub>4</sub>+R<sub>3</sub>, R<sub>2</sub> originates from anterior angle of areole; R<sub>1</sub> initiates from anterior part of median cell; Sc more or less parallel to R<sub>1</sub>. In hindwing 3A present; 1A+2A present, sometimes rudimentary in both sexes; CuP present but weak or rudimentary in both sexes; CuA<sub>2</sub> initiating from two-thirds of lower median of posterior cell; CuA<sub>1</sub> initiates from hind

margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1+R_s$  initiate from apical angle of anterior cell, stalked; a bar is sometimes present from  $R_s$  to  $Sc+R_1$ ; a discocellular vein on both forewing and hindwing is present. Retinaculum and frenulum absent.

*Abdomen:* With mainly hair-like scales of cream, dark ocher or yellow ocher; abdominal tuft short, up to 25% of abdomen length, cream.

*Male genitalia.* Saccus absent or present, variable in shape, usually broad and gently rounded caudally, or narrow rather finger-shaped; a sclerotized structure extends sometimes from saccus posteriorly towards or below the sacculus, it can be very long, up to half width of valva; the vinculum and tegumen are fused, forming a firm but very narrow ring; upper part of vinculum with a very broad rectangular sclerotized structure; uncus large, with slightly elongated rounded lobes, densely covered with short setae ventrally, basal edge of uncus rarely bent like a lunule in the middle. Valva is rather rectangular with a slightly broader base, on ventral surface of upper half with two thorn-like prominent and bent appendices with acuminate tips; between these appendices occurs a narrow elongated emargination that is almost as long as the width of valva and is covered with a weakly sclerotized skin-like structure; this skin-like structure has many tiny setae and extends from costa to median sector of valva. Sacculus is strongly reduced and very narrow, broader near base of valva. A transtilla is absent; a semi-transtilla is weakly sclerotized and narrow elongated, attached to the costa of valva and opposite of the vinculum, without setae. Gnathal arms short, well above costa, covered with short teeth-like processes at its distal end, resembling a hand, not connected by a sclerotized band basally and strongly bent towards uncus. Juxta is small, larger as saccus, oval, without acuminate tips and without a deep emargination. Phallus is simple, sometimes 1.2× longer than basal width of valva, basally strongly bent or straight, sometimes bilobed with a small cleft on both ends with tiny acuminate appendices.

*Female postabdominal structure and genitalia.* Papillae anales is broad or beak-like with mainly short setae, a few long setae ventrally; segment 8 is almost rectangular and usually without setae except few setae along its posterior margin and longer setae dorsally; dorso-anterior margin without emargination; segment 8 without any latero-ventral sclerotized band. Anterior apophyses are narrow on the whole length and a little longer than width of segment 8, tips not bent, acuminate; posterior apophyses are shorter than anterior apophyses, narrow but with a broader elongated part near their base. Corpus bursae and ductus bursae are thinly membranous and without any structures.



**FIGURE 134.** Distribution of the genus *Moyencharia* (red dots).



**FIGURE 135.** *Moyencharia mineti*, Holotype, [Republic of] Chad, Region du Moyen-Chari, Canton de Gondey, Makoga, 04.-12.05.1965, J.M. Fonteneau leg., male, ex MNHN, genitalia slide number 22/012012 I. Lehmann. Wingspan 20.0 mm



**FIGURE 136.** *Moyencharia mineti*, Paratype, [Republic of ] Chad, Region du Moyen-Chari, Canton de Gondey, Makoga, 04.-12.05.1965, J.M. Fonteneau leg., female, ex MNHN, genitalia slide number 06/012012 I. Lehmann. Wingspan 32.0 mm

#### 4.41 *Metarbelodes* Strand, 1909 - subgroups G1/G3 or two new genera

The genus subgroups G<sub>1</sub>/G<sub>3</sub> are defined by the following autapomorphy:

- Thorn-like process of posterior margin sclerotized, hollow, bent upwards and represents an extension of the sacculus; (176).

Additionally one apomorphic character of the genus subgroup G<sub>1</sub> is:

- CuP absent in forewing of both sexes, but it represents in G<sub>1</sub> in both sexes a strong tubular-like continuous fold that extends from base of wing to the dorsum; (11).

Additionally one apomorphic character of the genus subgroup G<sub>3</sub> is:

- CuP absent in forewing of both sexes (without strong tubular-like continuous fold); (11).

Type species of G<sub>1</sub> (cf. Figure 139): *Metarbelodes* [or new genus Met<sub>1</sub>] + sp. nov. g<sub>1</sub>

Type locality: Botswana, Chobe Rapids, Kasane, 15.09.1974, [no collector mentioned on label], male, genitalia slide number 27/092015 I. Lehmann, ex NMZB; depository in NMZB.

Type species of G<sub>3</sub>: *Metarbelodes* [or new genus Met<sub>2</sub>] + *obliquilinea* (Bethune-Baker, 1909)

Type locality: Kenya, Nairobi, 18.02.1906, F.J. Jackson leg., male, genitalia slide number "Cossid 49 BMNH"; depository in BMNH; [genitalia will be presented by Lehmann & Husemann *in prep.*]. Studied specimen close to type (cf. Figure 140): [Kenya], Nairobi, February 1928, Dr. van Someren leg., genitalia slide number 26/082012 I. Lehmann, ex BMNH: "van Someren collection 1959-468"; depository in BMNH.

Number of species in genus subgroup G<sub>1</sub> at present: 06

All localities of studied species per country: Ethiopia; Zimbabwe; Botswana.

Number of species in genus subgroup G<sub>3</sub> at present: 28

All localities of studied species per country: Ethiopia; Uganda; Kenya; Tanzania; Mozambique; Malawi; Zambia; Democratic Republic of the Congo; Zimbabwe; Botswana; Namibia.

Distribution of genus subgroup G<sub>1</sub> at present (cf. Figure 137): disjunct; submontane and montane areas of the Harar Plateau (northeastern Ethiopia), the Bvumba Mountains (eastern Zimbabwe) and the Southern African Plateau (north-central Zimbabwe, northeastern Botswana).

The reconstructed and predicted ancestral area is the Guinea-Congolia/Zambezia regional transition zone and the Guinea-Congolia/Sudania regional transition zone.

Distribution of genus subgroup G<sub>3</sub> at present (cf. Figure 138): disjunct; submontane and montane areas on mountain ranges, dormant volcanic mountains and highland and/or plateau areas near the northern edges of the Southern African Plateau and/or areas linked to the Eastern Branch and Western Branch of the East African Rift System. The reconstructed and predicted ancestral area is the Guinea-Congolia/Zambezia regional transition zone and the Guinea-Congolia/Sudania regional transition zone.

The reconstructed biogeographic events for subgroups G<sub>1</sub>/G<sub>3</sub> comprise: First, dispersal in the Guinea-Congolia/Zambezia regional transition zone and the Guinea-Congolia/Sudania regional transition zone. Secondly, dispersal from the Guinea-Congolia/Zambezia regional transition zone and the Guinea-Congolia/Sudania regional transition zone into the Sudanian regional centre of endemism, the Afromontane archipelago-like regional centre of endemism, the Kalahari-Highveld regional transition zone and the Karoo-Namib regional centre of endemism. Thirdly, vicariance between the Guinea-Congolia/Zambezia regional transition zone, the Guinea-Congolia/Sudania regional transition zone, the Sudanian regional centre of endemism and all other phytochoria mentioned above.

Phylogenetic position: The sister genus is *Moyencharia*. The two subgroups [or two new genera?] belong to a monophylum together with *Metarbelodes* G<sub>2</sub>, *Mountelgonia*, and *Moyencharia*.

The synapomorphy shared with *Moyencharia* comprises:

- Well sclerotized thorn-like process(-es) at the posterior margin of valva are hollow inside; (54).

The synapomorphy shared with *Mountelgonia*, *Moyencharia* and *Metarbelodes* G<sub>2</sub> comprises:

- The gnathal arms are not connected ventrally; (21).

Description: *Head:* rough-scaled with long hair-like scales of ocher on fronto-clypeus; a pair of pits is absent on lower fronto-clypeus, a pair of small conical projections is present on lower fronto-clypeus in both sexes (more pronounced in females); the two projections are separated although occur closely together; pits behind labial palpi are oval-shaped holes; the labial palpi are long, almost as long as eye diameter, very rarely longer than eye diameter, and consist of three segments, the central segment is the longest, up to 1.5–2.3× longer than the basal segment, the segment at tip is the shortest and has half times the length of the basal segment in both sexes; labial palpi in females sometimes narrower if compared to the males; male antennae bipectinate; female antennae rather unipectinate, sometimes slightly bipectinate towards the tip of antenna; dorsal and lateral side of branches and flagellum scaled in both sexes

(branches appear to be generally less scaled in females); in males tip of branches broader and sometimes slightly spoon-like shaped, always densely scaled, cream.

*Thorax:* Densely covered with hair-like scales (finer scales in females) of light ocher on patagia and tegulae, slightly glossy, tegulae not pronounced; crest on metathorax small, light ocher. Epiphyses are absent in both sexes. Hindlegs with one pair of narrow tibial spurs, slightly unequal in length (outer spur at least 0.6 mm, inner spur at least 0.5 mm), very rarely are two pairs present with the upper pair rudimentary, not longer than 0.3 mm; pretarsus with a pair of pulvilli.

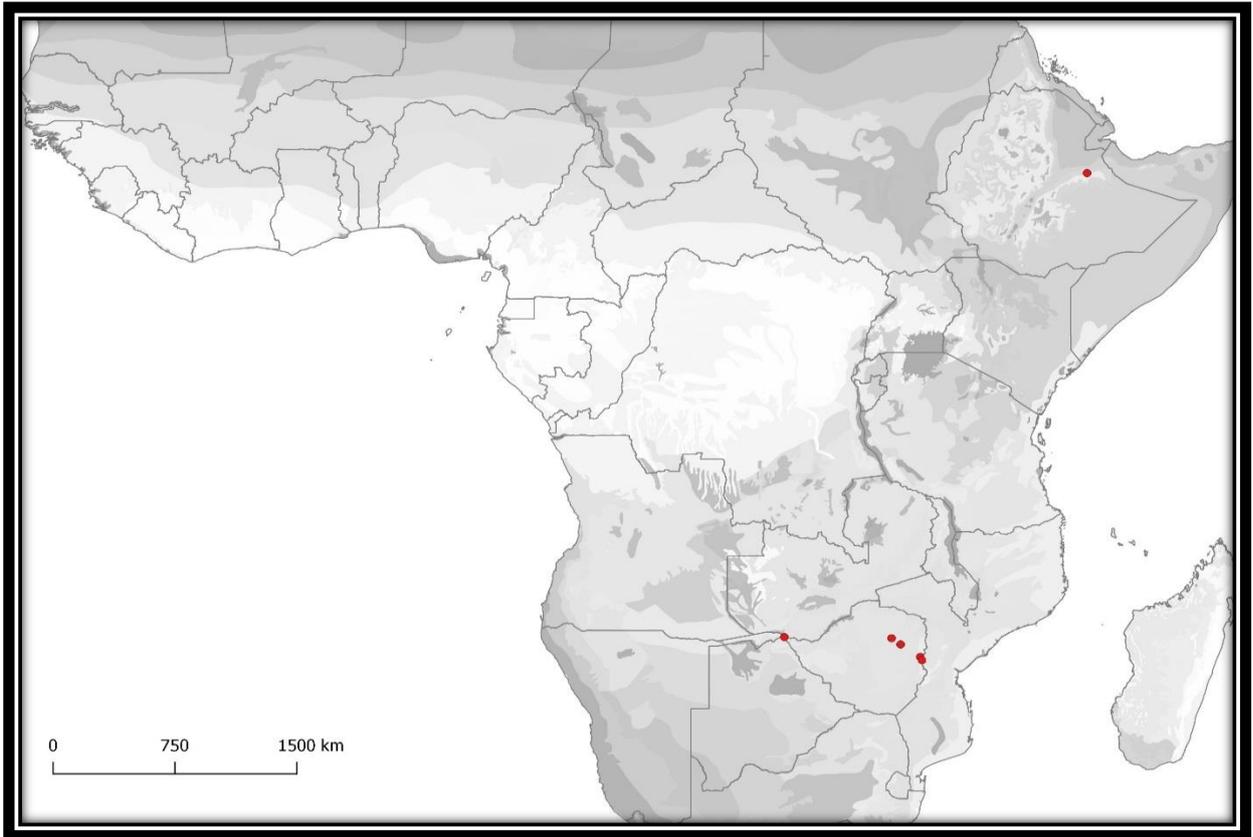
Forewing upperside with a dark ocher or light ocher ground-colour mixed with cream, not glossy, sometimes with short striae of sepia along costa and on whole upperside; a geometric design is absent; a simple pattern is absent; a sepia terminal line, not parallel to termen, is strongly reduced to striae from near apex to dorsum;  $CuA_2$  is always distinctly marked cream, rather broad, edged sepia above in both sexes. Hindwing is cream, light ocher or white, glossy. Fringe is very long (ciliae up to 2.1 mm), cream or light ocher, glossy. Wing venation similar in both sexes: in forewing  $1A+2A$  forked at base, sometimes very long forked in  $G_1$ ;  $CuP$  represents a strong tubular-like continuous fold that is slightly sclerotized in  $G_1$ ,  $CuP$  is absent in  $G_3$ ;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from apical angle of posterior cell, separated;  $M_1$  initiates from anterior angle of median cell and more or less close to the base of a relatively large areole in  $G_1$ , areole smaller in  $G_3$ ;  $R_5$  originates from posterior angle of areole;  $R_4+R_3+R_2$  stalked and originate from anterior angle of areole or base of  $R_2$  shares the same basal point with  $R_4+R_3$ ;  $R_1$  initiates from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  rudimentary;  $CuP$  present, sometimes weak;  $CuA_2$  initiating from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1+Rs$  initiate from apical angle of anterior cell, usually stalked in both sexes; a bar is absent or present from  $Rs$  to  $Sc+R_1$ ; a discocellular vein on both forewing and hindwing is present. Retinaculum and frenulum absent.

*Abdomen:* With dense hair-like scales of cream with light ocher; abdominal tuft short, up to 25% of abdomen length, rarely very long up to 40%, cream.

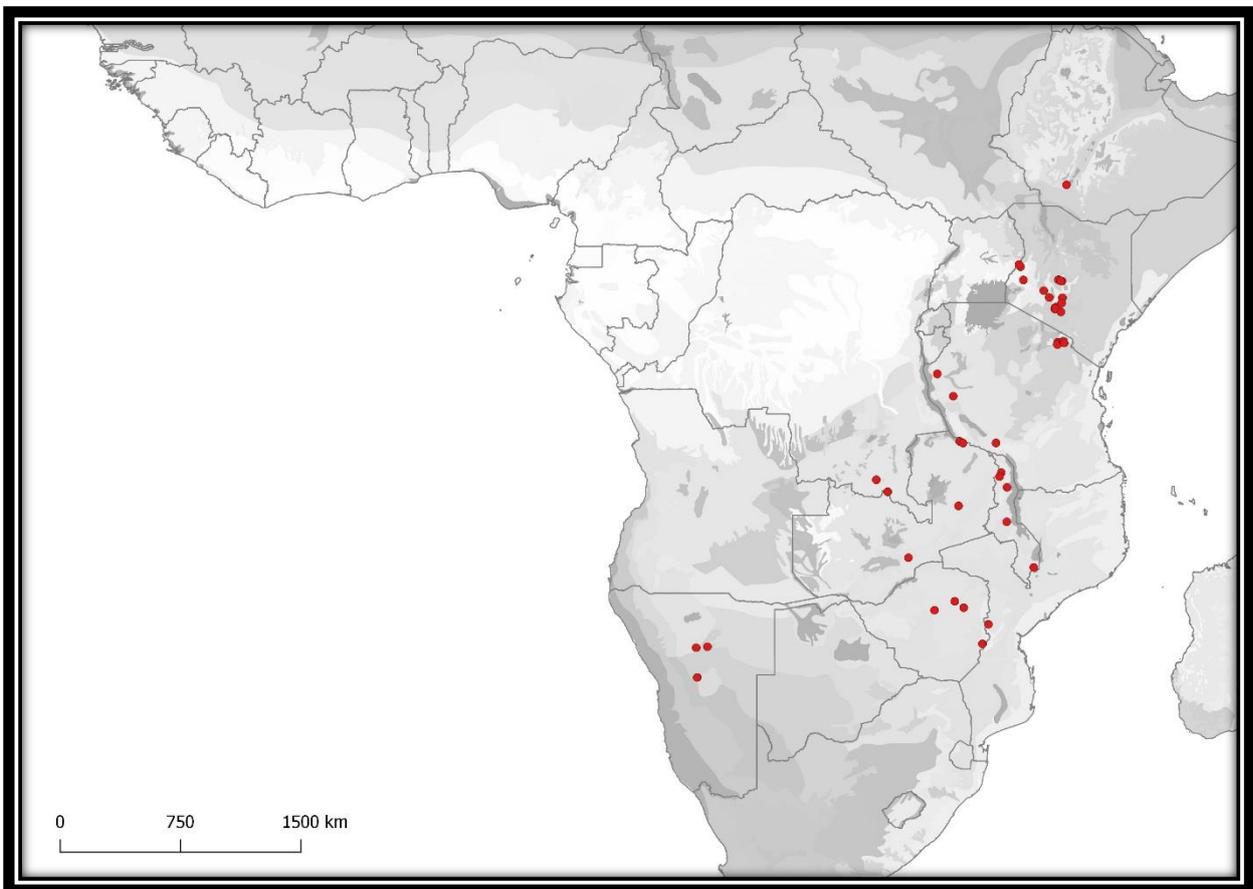
*Male genitalia.* Saccus finger-shaped or narrow triangular; the vinculum and tegumen are fused, forming a very narrow firm ring; vinculum broader on lower half, forming sometimes opposite of saccus a broad plate-like structure; uncus large and broad, short setae ventrally and sometimes dorsally, basal edge of uncus bent like a lunule in the middle or straight. Valva is oval or rather rectangular with a broader base, costa without setae, inner side of median sector with few setae; from near base of valva and along costal margin occurs a large, setose and weakly-sclerotized projection; a thorn-like process is prominent and hollow, it occurs ventral-posteriorly, is strongly sclerotized, usually bent upwards, rarely setose, sometimes reduced (in  $G_1$ ). Sacculus strongly reduced or narrow. A short emargination (less than 30% of the length of valva) extends in between the weakly-sclerotized projection and the thorn-like process.

A transtilla is absent; a semi-transtilla is short, rectangular with a somehow leaf-like shape, attached to the costa of valva and opposite of the vinculum, without setae. Gnathal arms short, well above costa, rarely long, covered with short teeth-like processes at its distal end, resembling a hand, not connected by a sclerotized band basally, sometimes connected with a thinly membranous band. Juxta is broad and elongated, rarely small and narrow, almost twice as large as saccus with two acuminate tips and a short process at each tip, between the tips occurs a deep emargination (95% the length of juxta). Phallus is simple, long, sometimes very long, namely 1.5× longer than basal width of valva, straight or strongly bent at middle, bilobed with a cleft on both ends, vesica without cornuti.

*Female postabdominal structure and genitalia.* Papillae anales broad, dorsal part obliquely 8-shaped or elliptic in posterior view, covered with short and long setae; segment 8 setose along its posterior margin and with long setae on its dorsal as well as anterior part, sometimes with many setae on the whole segment 8 (in G<sub>1</sub>), not emarginated dorso-anteriorly. Latero-ventral surface of segment 8 with two rather large strongly sclerotized plates (probably two sterigma bands) that are either partly separated or sometimes entirely fused along the posterior margin of the plates, always broadest at middle. Ductus bursae and corpus bursae broad, thinly membranous, corpus bursae often pear-like shaped, rarely rounded like a ball, always large or very large (very large = larger than segment 8 in lateral view), always without any processes or other distinct characters.



**FIGURE 137.** Distribution of *Metarbelodes* subgroup G<sub>1</sub> [or new genus *Met1*] (red dots).



**FIGURE 138.** Distribution of *Metarbelodes* subgroup G<sub>3</sub> [or new genus *Met2*] (red dots).



**FIGURE 139.** *Metarbelodes* [or new genus *Met1*] sp. nov. g1, Botswana, Chobe Rapids, Kasane, 15.09.1974, NMZB, male, genitalia slide number 27/092015 I. Lehmann. Wingspan 25.5 mm



**FIGURE 140.** *Metarbelodes* [or new genus *Met2*] *obliquilinea* [subgroup G3], [Kenya], Nairobi, February 1928, Dr. van Someren leg., ex BMNH: “van Someren collection 1959–468”, male, genitalia slide number 26/082012 I. Lehmann. Wingspan 31.0 mm

#### 4.42 *Arbelodes* Karsch, 1896

The genus is defined by the following autapomorphies:

- In hindwing Sc+R<sub>1</sub> crosses the base of upper median of discal cell in both sexes; (59);
- Anterior apophyses very narrow and rudimentary; (61).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes; (11).

Type species (cf. Figure 142): *Arbelodes meridialis* Karsch, 1896

Type locality: [Republic of South Africa], Cape [no locality], [no date], S. Bachmann leg., male, ex ZMHU; depository in ZMHU. Studied specimen (cf. Figure 143): [Republic of South Africa], [Eastern Cape], Steynsburg, 13.-27.03.1965, R.J. Southy leg., male, genitalia slide number 22/022010 I. Lehmann, ex TMSA; depository in TMSA.

Number of species in genus at present: 32

All localities of studied species per country: Namibia; Republic of South Africa; Botswana; Zimbabwe; Malawi; Zambia.

Distribution of genus at present (cf. Figure 141): disjunct; lowland, submontane and montane areas from central and southern Namibia southwards to Cape Town and eastwards through the Cape Floristic Region to the Great Escarpment-Drakensberg extending further eastwards to coastal areas of the Republic of South Africa along the Indian Ocean. Disjunct records are known from eastern Botswana and from few areas north of the Limpopo River in southern and eastern Zimbabwe (e.g., Matopos Hills, ruins of Great Zimbabwe and Bvumba Mountains), from plateau areas of northern Malawi (e.g., Nyika Plateau), the southeastern Democratic Republic of the Congo (Sakania) and southern as well as extreme northeast Zambia (Mbala).

The reconstructed and predicted ancestral area is the Afromontane archipelago-like regional centre of endemism.

The reconstructed biogeographic events comprise: First, dispersal in the Afromontane archipelago-like regional centre of endemism. Secondly, dispersal from the Afromontane archipelago-like regional centre of endemism into the Zambezan regional centre of endemism, the Cape regional centre of endemism, the Karoo-Namib regional centre of endemism, the Kalahari-Highveld regional transition zone, the Tongaland-Pondoland regional mosaic and the Zanzibar-Inhambane regional mosaic. Thirdly, vicariance between the Afromontane archipelago-like regional centre of endemism and all other phytochoria mentioned above.

Phylogenetic position: The sister genus is *Bjoernstidia*.

The synapomorphies shared with *Bjoernstadia* comprise:

- Valva consists of two long narrow lobes, sometimes with a small third one between both lobes; (56);
- Discal cell of forewing open towards termen in male; (57).

Description: *Head:* rough-scaled with long hair-like scales of grey, brown or sepia on fronto-clypeus; a pair of pits is absent or present but always rudimentary on lower fronto-clypeus, a pair of small conical projections is absent on lower fronto-clypeus in both sexes; pits behind labial palpi are relatively large oval-shaped holes; the labial palpi are long, almost as long as eye diameter or longer than eye diameter, and consist of three segments, the central segment is the longest, up to 2.5–3.0x longer than the basal segment, the segment at tip is the shortest and has half times the length of the basal segment in both sexes; labial palpi in females sometimes narrower if compared to the males and with very long hair-like scales ventrally; male antennae bipectinate with very long branches; female antennae unipectinate; dorsal and lateral side of branches and flagellum are densely scaled in both sexes (the short branches of female appear to be generally less scaled), cream or brown.

*Thorax:* Densely covered with hair-like scales (finer scales in females) of light ocher, pure white or brown on patagia and tegulae, slightly glossy, a collar ring is sometimes present; tegulae not pronounced; crest on metathorax small. Epiphyses are absent in both sexes or present in both sexes, if present the epiphyses are extremely narrow (needle-like) and have a rudimentary appearance. Hindlegs with two pairs of narrow tibial spurs in both sexes, slightly unequal in length (outer spur at least 0.9 mm, inner spur at least 0.8 mm); pretarsus with a pair of pulvilli.

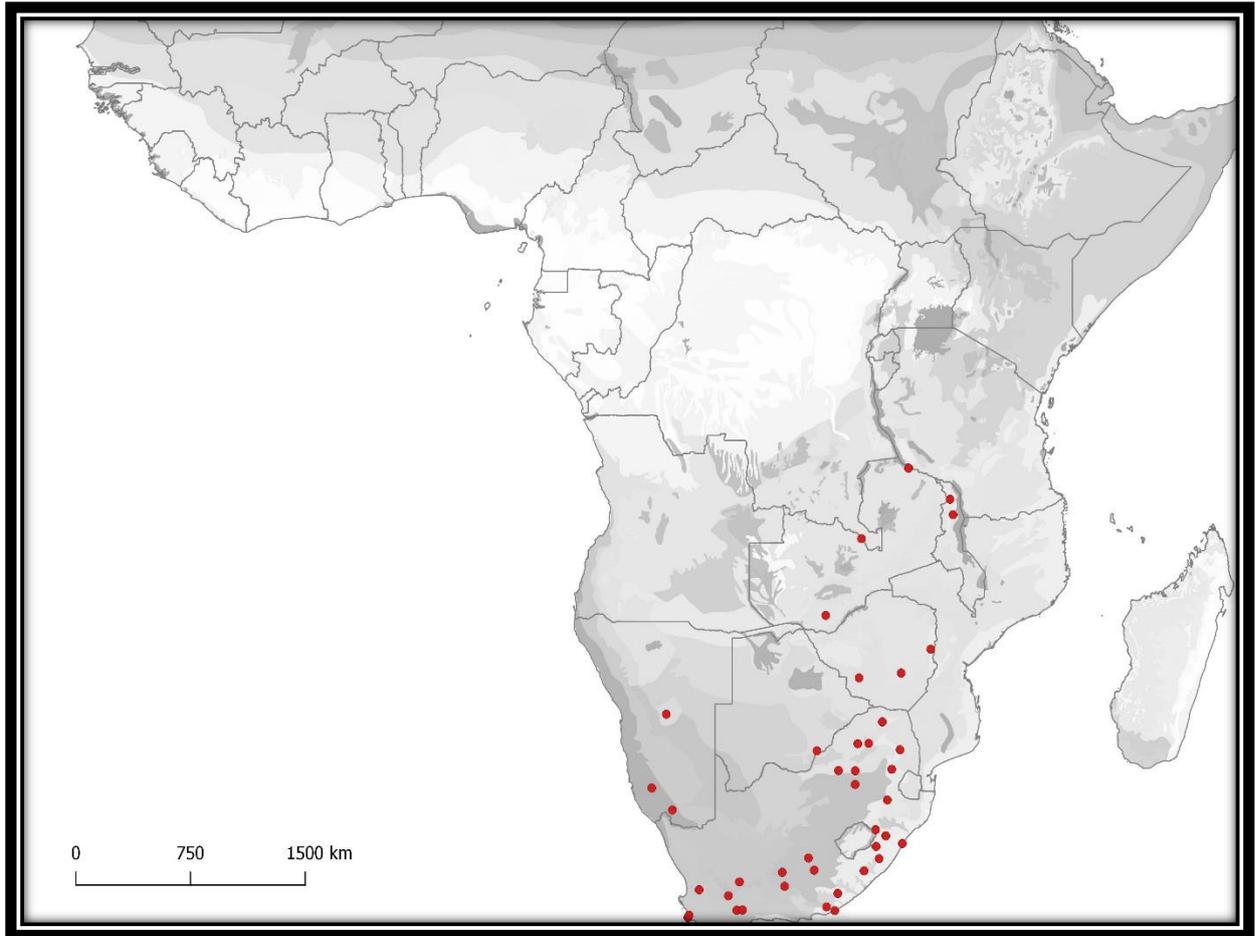
Forewing upperside: with a dark ocher, brown, light grey or pure white ground-colour mixed with cream-olive, sometimes with a strong silvery, pure white or vinaceous gloss; the forewing upperside is unusually variable comprising very different looking species that belong to the same genus (a very rare feature among Metarbelidae): a geometric design is present (*e.g.*, with triangular-like and/or rectangular-like and/or T-like and/or leaf-like design) or absent; a simple pattern is usually present; below CuA<sub>2</sub> and the lower median occur usually several prominent rounded or horseshoe-like patches of black or orange or chestnut or pure white often mixed with cream-olive; a sub-terminal line is sometimes present and originates near the apex or at two-thirds of the costal margin, it might be oblique, broader or narrow; CuA<sub>2</sub> is often distinctly marked cream or white or sepia, rather narrow in both sexes. Hindwing upperside is also unusually variable, often cream-olive, light grey, brown, but also pure yellow with a broad black terminal band, glossy. Fringe is long (ciliae up to 1.2 mm), cream or light ocher or pure white, glossy. Wing venation similar in both sexes: in forewing 1A+2A forked at base; CuP absent; CuA<sub>2</sub> originating from two-thirds of lower median; CuA<sub>1</sub> originates from hind margin of posterior cell, M<sub>3</sub> and M<sub>2</sub> originate from apical angle of posterior cell, separated; M<sub>1</sub> initiates from anterior angle of median cell and more or less close to the base of a small areole; R<sub>5</sub> originates from

posterior angle of areole or  $R_5$  is stalked with  $R_3+R_4$ ;  $R_3+R_4$  are always stalked;  $R_2$  originates from anterior angle of areole;  $R_1$  initiates from anterior part of median cell; Sc more or less parallel to  $R_1$ . In hindwing 3A present; 1A+2A present or weak; CuP present or rudimentary;  $CuA_2$  initiating from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1+Rs$  initiate from apical angle of anterior cell, short or long stalked in both sexes; a bar is absent from Rs to Sc+ $R_1$ ; Sc+ $R_1$  crosses the base of upper median of discal cell in both sexes; a discocellular vein on both forewing and hindwing is present, but often reduced in forewing; median cell, sometimes also posterior cell in forewing is/are open towards termen. Retinaculum and frenulum absent.

*Abdomen:* With dense hair-like scales of cream or pure white or yellow or sepia; abdominal tuft long in male, it looks often like a swallowtail, up to 35% of abdomen length; in female much shorter.

*Male genitalia.* Saccus long, rudimentary or absent, finger-shaped or narrow triangular; the vinculum and tegumen are fused, forming a very broad firm ring; tegumen sometimes narrow on upper half; uncus broad, very long or very short, always triangular-shaped with a broader base, some setae are ventrally and sometimes dorsally present. Valva comprises two or three lobes, of which the dorsal lobe is usually the longest. The lobes are usually strongly bent towards the uncus and have many setae along the edges. In some species occurs a prominent short structure near the base of the dorsal lobe, probably a valval apodeme. Sacculus is absent or strongly reduced, narrow. A transtilla is absent; a semi-transtilla is absent or extremely short, triangular, attached to the costa of valva and opposite of the vinculum. Gnathos is absent. Juxta is elongated with two acuminate tips and an emargination. Phallus is simple, long, sometimes very long, namely 1.9× longer than basal width of valva, straight or strongly bent at middle, broader at base, bilobed with a cleft at least distally, vesica without cornuti.

*Female postabdominal structure.* Papillae anales broad, dorsal part obliquely 8-shaped or elliptic in posterior view, covered with short and long setae; segment 8 setose along its posterior margin, rarely with setae on its dorsal as well as anterior part, not emarginated dorso-anteriorly. Latero-ventral surface of segment 8 with a large or small emargination, usually oval shaped; segment 8 broad rectangular; anterior apophyses very narrow and rudimentary; posterior apophyses very large, very broad, often plate-like.



**FIGURE 141.** Distribution of the genus *Arbelodes* (red dots).



**FIGURE 142.** *Arbelodes meridialis*, Type [Republic of South Africa], Cape [no locality], [no date], S. Bachmann leg., male, ex ZMHU. Wingspan 27.0 mm



**FIGURE 143.** *Arbelodes meridialis*, [Republic of South Africa], [Eastern Cape], Steynsburg, 13.-27.03.1965, R.J. Southy leg., ex TMSA, male, genitalia slide number 22/022010 I. Lehmann. Wingspan 28.5 mm

#### 4.43 *Bjoernstadia* Lehmann, 2012

The genus is defined by the following autapomorphies:

- large sack-like, membranous structure below base of uncus extending to its tip; (63);
- two thorn-like processes below the large sack-like structure; (64).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; [possibly also in female absent] (11).

Type species (cf. Figure 145): *Bjoernstadia kasuluensis* Lehmann, 2012

Type locality: Tanzania, Kigoma Region, Kasulu District, Kasulu, 16.09.1990, A. Bjørnstad leg., male, genitalia slide number 12/022012 I. Lehmann, ex NHMO; depository in NHMO.

Number of species in genus at present: 01

All localities of studied species per country: Tanzania.

Distribution of genus at present (cf. Figure 144): Albertine Rift, at present known from a submontane area in northwestern Tanzania.

The reconstructed and predicted ancestral area is the Afromontane archipelago-like regional centre of endemism.

The reconstructed biogeographic events comprise: First, dispersal in the Afromontane archipelago-like regional centre of endemism. Secondly, dispersal from the Afromontane archipelago-like regional centre of endemism into the Zambezian regional centre of endemism. Thirdly, vicariance between the Afromontane archipelago-like regional centre of endemism and the Zambezian regional centre of endemism.

Phylogenetic position: The sister genus is *Arbelodes*.

The synapomorphies shared with *Arbelodes* comprise:

- Valva consists of two long narrow lobes, sometimes with a small third one between both lobes; (56);
- Discal cell of forewing open towards termen in male; (57).

Description: *Head:* rough-scaled with long hair-like scales of brown, black and ocher on fronto-clypeus; a pair of pits is absent on lower fronto-clypeus, a pair of small conical projections is present on lower fronto-clypeus in male; pits behind labial palpi are oval-shaped holes; the labial palpi are shorter than eye diameter and consist of three segments, the central segment is the longest, the segment at tip is rudimentary; male antennae bipectinate with very long branches; dorsal and lateral side of branches

not scaled but with very long hair-like structures (three times longer than width of branch) ventrally; flagellum is densely scaled cream.

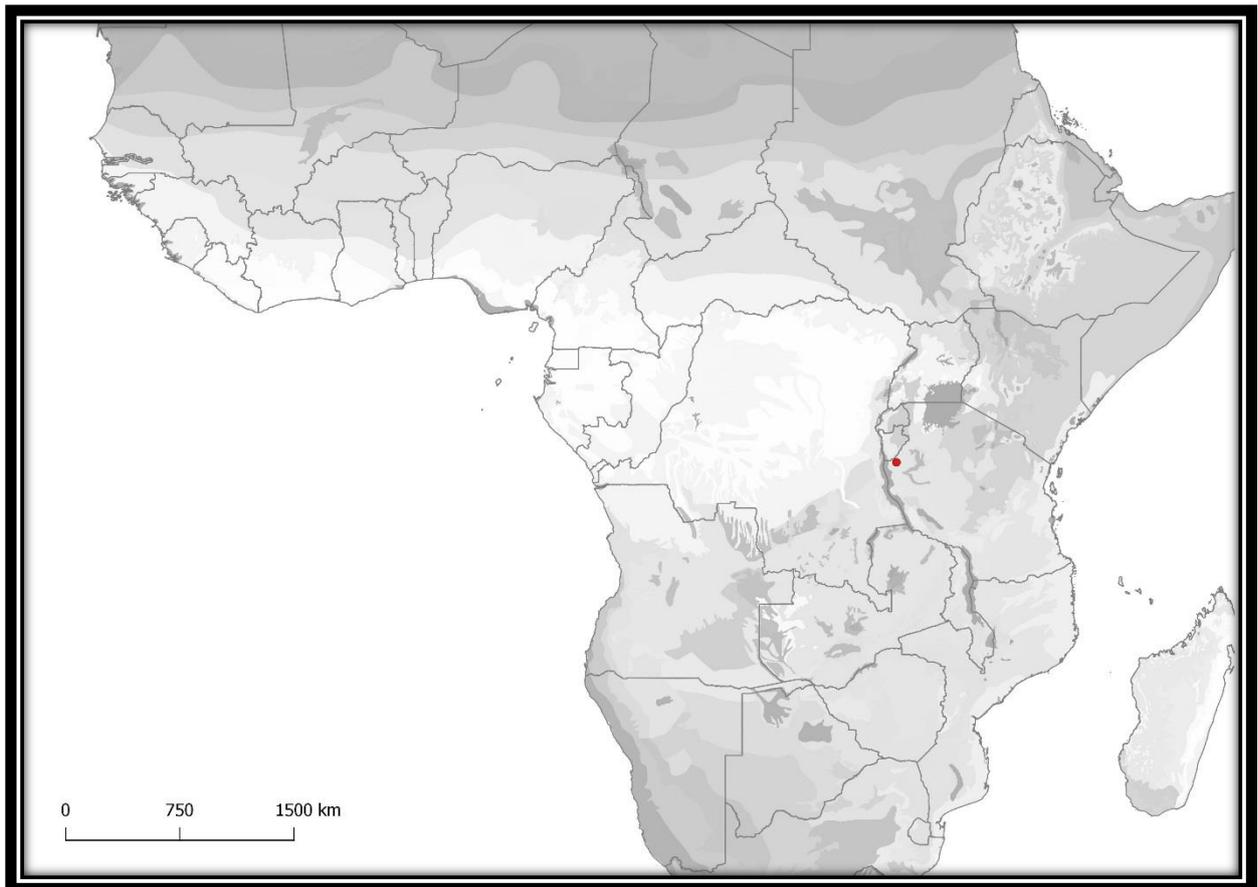
*Thorax:* Densely covered with hair-like scales of grey, mixed with olive-ocher and black on patagia and tegulae, glossy; crest on metathorax small, olive-ocher. Epiphyses are present, unusually long (from base of foretibiae to one-third of first tarsomere) and extremely narrow (needle-like). Hindlegs with one pair of narrow tibial spurs, slightly unequal in length (outer spur 0.5 mm, inner spur 0.4 mm); pretarsus with a pair of pulvilli.

Forewing with the shortest length of any *Metarbelidae* (6.1 mm length) at present (hence, the only species of this genus represents the smallest *Metarbelidae* worldwide), upperside with a dark olive ground-colour; a geometric design is absent; a simple pattern is present and comprises a small rounded olive-ocher spot below the centre of  $CuA_2$ , the latter is a pure white band and hence,  $CuA_2$  is distinctly marked; in the anterior part of the discal cell occurs an olive-ocher spot with a small brown rounded spot distally, forming almost an "8". Hindwing upperside is light olive, glossy. Fringe is very long (ciliae up to 0.9 mm), brown with alternating white, glossy. Wing venation: in forewing  $1A+2A$  forked at base;  $CuP$  absent;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from apical angle of posterior cell, separated;  $M_1$  initiates from anterior angle of median cell and not close to the base of a small areole;  $R_5$  is stalked with  $R_3+R_4$ ;  $R_2$  originates from posterior angle of areole;  $R_1$  initiates from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  present;  $CuP$  absent;  $CuA_2$  initiating from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1+Rs$  initiate from apical angle of anterior cell, short stalked; a bar is present from  $Rs$  to  $Sc+R_1$ ; a discocellular vein on both forewing and hindwing is present, but rudimentary towards base of both wings; posterior cell in forewing is open towards termen. Retinaculum and frenulum absent.

*Abdomen:* With hair-like scales of cream mixed with brown; abdominal tuft short in male, 25% of abdomen length.

*Male genitalia.* Saccus long, broad, rounded; the vinculum and tegumen are fused, forming a broad firm ring; uncus small, broad, bifid with two acuminate tips, a broader base present. Valva comprises two lobes, of which the ventral lobe is the longest. The lobes originate from a broad base of valva, are slightly bent towards the uncus and have many setae along the edges with very long setae ventral-distally. Sacculus is narrow, rather reduced. A transtilla is absent; a semi-transtilla is absent. Gnathos is absent. Juxta is small, triangular. Phallus is simple, long, 1.2× longer than basal width of valva, straight, broader at base, bilobed with a cleft at least distally, vesica without cornuti.

*Female postabdominal structure and genitalia.* Unknown.



**FIGURE 144.** Distribution of the genus *Bjoernstidia* (red dot).



**FIGURE 145.** *Bjoernstidia kasuluensis*, Holotype, Tanzania, Kasulu, 16.09.1990, A. Bjørnstad leg., ex NHMO, male, genitalia slide number 12/022012 I. Lehmann. Wingspan 14.5 mm

#### 4.44 Gen. Nov. ZC

The genus is defined by the following autapomorphy:

- Very long setae on ventral side of uncus, the setae almost touch the costa of valva in lateral view; (69).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; [possibly also absent in female] (11).

Type species of genus (cf. Figure 147): Gen. Nov. ZC + sp. nov. zc

Type locality: [Democratic Republic of the Congo], Station de L'Epulu, January.1975, S.L. Sutton leg., male, genitalia slide number 21/122014 I. Lehmann, B.M. 1975–229, ex BMNH; depository in BMNH. On a second label there is the following note: “Riverside grassy clearing rain forest nearby”.

Number of species in genus at present: 01

All localities of studied species per country: Democratic Republic of the Congo.

Distribution of genus at present (cf. Figure 146): rain forests of Congolia, at present known from a submontane area along the riverside of the Epulu River in the Democratic Republic of the Congo.

The reconstructed and predicted ancestral area is the Guineo-Congolian regional centre of endemism.

The reconstructed biogeographic events comprise: First, dispersal in the Guineo-Congolian regional centre of endemism. Secondly, vicariance occurred in the Guineo-Congolian regional centre of endemism.

Phylogenetic position: The sister genus could not be reconstructed unambiguously. The genus is part of a monophylum together with the new genera ZC, ZD, ZE, ZF and *Ortharbela*.

The synapomorphy shared with Gen. Nov. ZD, Gen. Nov. ZE, Gen. Nov. ZF, *Ortharbela* comprises:

- Valvae not separated, but connected by a broad strongly sclerotized band ventrally; (71).

Description: *Head:* rough-scaled with hair-like scales of sepia and brown with a light violet glint below the eyes on fronto-clypeus; a pair of pits is present in male on lower fronto-clypeus, a pair of conical projections is absent on lower fronto-clypeus; pits behind labial palpi are small rounded holes; labial palpi short, half of eye diameter and consist of three segments, basal segment is the longest and broadest, central segment more narrow and segment on top is well developed but the smallest; antennae

bipectinated, branches are narrow and  $3.5 \times$  width of shaft, not scaled; flagellum scaled light cream.

*Thorax:* Densely covered with hair-like scales of light brown-olive, scales cream towards base on patagia and tegulae, glossy, scales on tegulae pronounced and very long, light brown in male, glossy; crest on metathorax small, light brown-olive. Epiphyses are very long (1.9 mm), narrow and flat. Hindlegs with two pairs of tibial spurs; lower pair is thick (up to 0.8 mm), upper pair narrow and longer (1.0 mm); pretarsus with a pair of pulvilli.

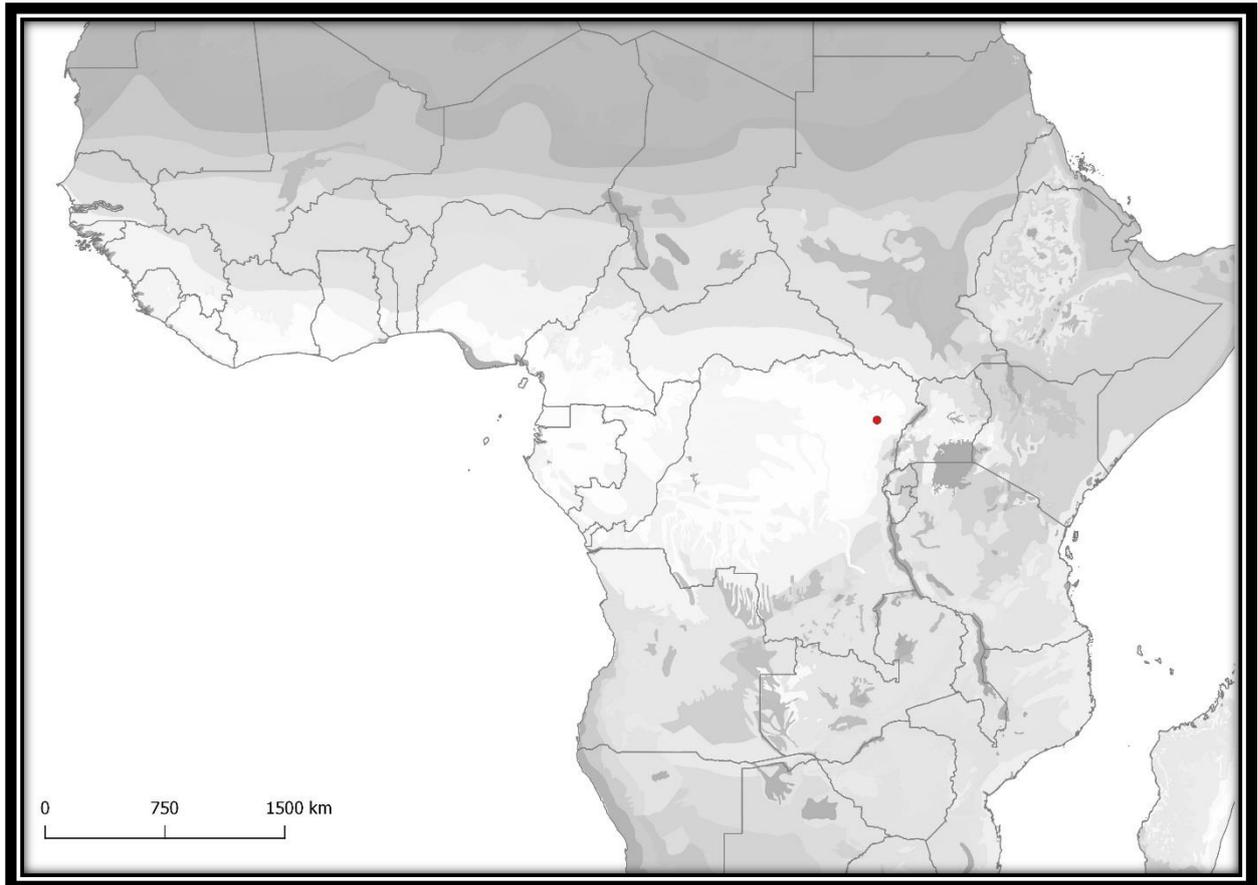
Forewing upperside with a light brown-olive ground-colour without a glint shine; longer but not hair-like scales, these are light brown and glossy, occur between the lower median and  $1A+2A$ . A geometric design is absent; a simple pattern is present and comprises a narrow cream coloured median of the discocellular cell and a cream coloured base of  $1A+2A$ ;  $CuA_2$  is narrowly distinctly marked cream. Hindwing is light grey-olive, glossy. Fringe is with slightly broader scales of light brown-olive, medium long (ciliae up to 0.7 mm). Wing venation: in forewing  $1A+2A$  forked at base;  $CuP$  absent;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from apical angle of posterior cell, separated;  $M_1$  initiates from anterior angle of median cell;  $R_3+R_4+R_5$  stalked and originate from posterior angle of a large areole;  $R_2$  originates from the anterior angle of areole;  $R_1$  initiates from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  rudimentary, with a fork at base but absent towards termen;  $CuP$  present but weak;  $CuA_2$  initiating from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, broadly separated at base;  $M_1+Rs$  initiate from apical angle of anterior cell and are very long stalked; a long bar is present from  $Rs$  to  $Sc+R_1$ , but does not extend beyond the apical angle; a discocellular vein on both forewing and hindwing is present, but weak in hindwing. In the forewing the posterior cell (= lower cell) is twice as large as the anterior cell; the whole discal cell is small and in length less than half of the width of the forewing. Retinaculum and frenulum absent.

*Abdomen:* With scales of light brown mixed with light grey-olive and a strong glint; abdominal tuft short, 20% of abdomen length, with cream and brown.

*Male genitalia.* Saccus very long (two-thirds of the length of uncus) and broad, rounded at tip; the vinculum and tegumen are fused, forming a firm broad ring; uncus prominent: long, narrowly elongated with a broad triangular base (viewed ventrally), bifurcated between two tiny and more sclerotized tips, ventral side of uncus with extremely long setae (up to 1.0 mm in length) that are sclerotized and appear grey in colour; similar but shorter setae also on the whole dorsal surface of uncus. Valva is large, medium broad and rectangular with a rounded end, without any structures but the whole inner surface is covered with short sclerotized setae including the costal margin and sacculus, some setae appear thick, others narrow, all are grey in colour; transtilla absent; a relict of semi-transtilla present, it is small rather triangular with few tiny setae. Sacculus is narrow. Gnathos is absent. The valvae are connected ventrally by

a broad sclerotized band. Juxta is relatively large with a broadly T-shaped ventral part, but upper part with an emargination and two acuminate tips that are bent downwards. Phallus is long (slightly longer than width of valva), simple tube-like, broader at base with a ring-like sclerotized structure, not bent, with an arrow-like shape distally (20% the length of aedeagus).

*Female postabdominal structure and genitalia. Unknown.*



**FIGURE 146.** Distribution of Gen. Nov. ZC (red dot).



**FIGURE 147.** Gen. Nov. ZC, sp. nov. zc, [Democratic Republic of the Congo] Station de L'Epulu, January.1975, S.L. Sutton leg., male, ex BMNH, B.M. 1975-229, genitalia slide number 21/122014 I. Lehmann. Wingspan 31.0 mm

#### 4.45 *Ortharbela Aurivillius, 1910*

The genus is defined by the following autapomorphies:

- Egg-shaped small valva with a rounded tip; (188);
- Very long and narrow aedeagus, at least 2.5 x as long as width of valva, only slightly S-shaped; (189);
- Uncus triangular-shaped, extremely broad and large, twice as large as valva in ventral view, with two claw-like tips; (190).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; [possibly also absent in female] (11).

Type species of genus (cf. Figure 149): *Ortharbela guttata* Aurivillius, 1910

Type locality: type specimen with three labels comprising the following data: [Tanzania], Kilimanjaro, Kibonoto, Kulturz. [= Kulturzone = cultural zone], 1905–1906, Sjöstedt leg., 30. March [1906?]; male, genitalia slide number 26/092017 I. Lehmann, ex NRM; depository in NRM.

Number of species in genus at present: 04

All localities of studied species per country: Tanzania, Kenya.

Distribution of genus at present (cf. Figure 148): disjunct; montane, submontane and (rarely?) lowland areas: on isolated mountains, namely Mount Kilimanjaro, East Usambara Mountains and the Uluguru Mountains in north-central and eastern Tanzania extending northeastwards with a single record from one coastal lowland forest in southeast Kenya (Buda Forest).

The reconstructed and predicted ancestral areas are the Guineo-Congolian regional centre of endemism and the Afromontane archipelago-like regional centre of endemism.

The reconstructed biogeographic events comprise: First, dispersal in the Guineo-Congolian regional centre of endemism and the Afromontane archipelago-like regional centre of endemism. Secondly, vicariance between the Guineo-Congolian regional centre of endemism and the Afromontane archipelago-like regional centre of endemism.

Phylogenetic position: The sister genus could not be reconstructed unambiguously. The genus is part of a monophylum together with the new genera ZC, ZD, ZE and ZF.

The synapomorphy shared with Gen. Nov. ZC, Gen. Nov. ZD, Gen. Nov. ZE and Gen. Nov. ZF comprises:

- Valvae not separated, but connected by a broad strongly sclerotized band ventrally; (71).

Description: *Head:* rough-scaled with hair-like scales of brown below the eyes on fronto-clypeus; a pair of pits is present in male on lower fronto-clypeus, a pair of conical projections is absent on lower fronto-clypeus; pits behind labial palpi are small triangular-shaped holes; labial palpi long, half of eye diameter and consist of three segments, basal and central segment of equal length, segment on top is slightly shorter and pyriform; antennae long, bipectinated, branches are  $6.5 \times$  width of shaft, densely scaled brown and cream; flagellum scaled light cream and brown.

*Thorax:* Densely covered with hair-like scales of brown and cream on patagia and tegulae, not glossy, scales on tegulae slightly pronounced with tips of cream, not glossy; crest on metathorax small, light ocher and brown. Epiphyses are very long (1.7 mm), narrow and flat. Hindlegs with two pairs of thick tibial spurs; spurs unequal in length; lower pair is longer (up to 1.1 mm), upper pair shorter (0.8 mm); pretarsus with a pair of pulvilli.

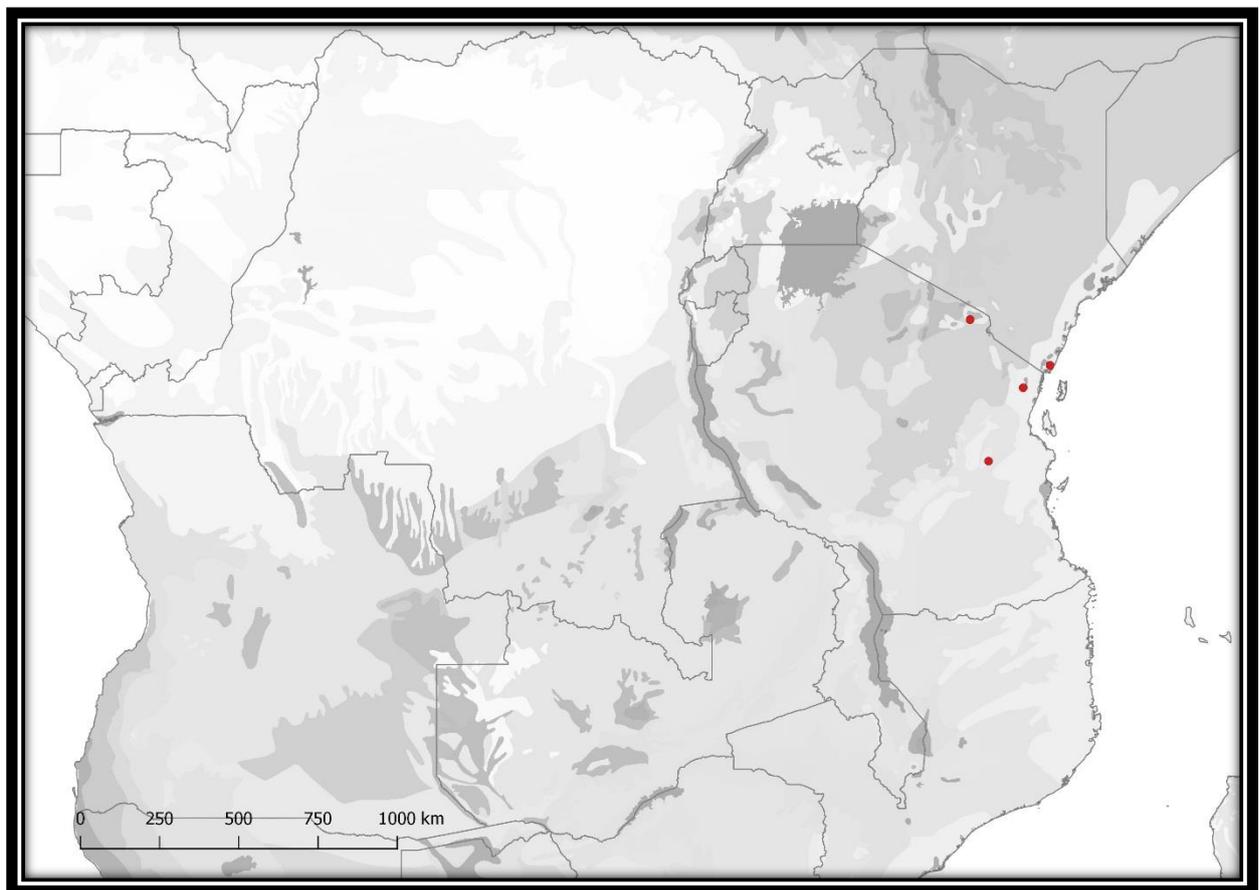
Forewing upperside with a brown ground-colour without a glint shine. A geometric design is absent; a simple pattern is present and comprises several patches of orange-ocher between the lower median and  $1A+2A$ , one patch at the end of the discocellular cell and an elongated patch between  $CuA_1$  and  $R_4$ ;  $CuA_2$  is distinctly marked with five or six small white spots. Hindwing is brown with a vinaceous glint. Fringe is brown, long (ciliae up to 0.9 mm). Wing venation: in forewing  $1A+2A$  forked at base;  $CuP$  absent;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from apical angle of posterior cell, separated;  $M_1$  initiates from anterior angle of median cell;  $R_3+R_4+R_5$  stalked and originate from apical angle of anterior cell;  $R_2$  originates from near apical angle of anterior cell;  $R_1$  initiates from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  rudimentary or absent;  $CuP$  present, sometimes weak;  $CuA_2$  initiating from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, broadly separated at base;  $M_1+R_s$  initiate from apical angle of anterior cell and are long stalked; a bar is present from  $R_s$  to  $Sc+R_1$ ; a discocellular vein on both forewing and hindwing is present, but weak in forewing. In the forewing the posterior cell and the anterior cell are of almost equal size; the whole discal cell is small and in length less than half of the width of the forewing. Retinaculum and frenulum absent.

*Abdomen:* With scales of light brown mixed with light grey-olive and cream; abdominal tuft long, pronounced, swallowtail-like in male, 35% of abdomen length, with ocher, cream and brown.

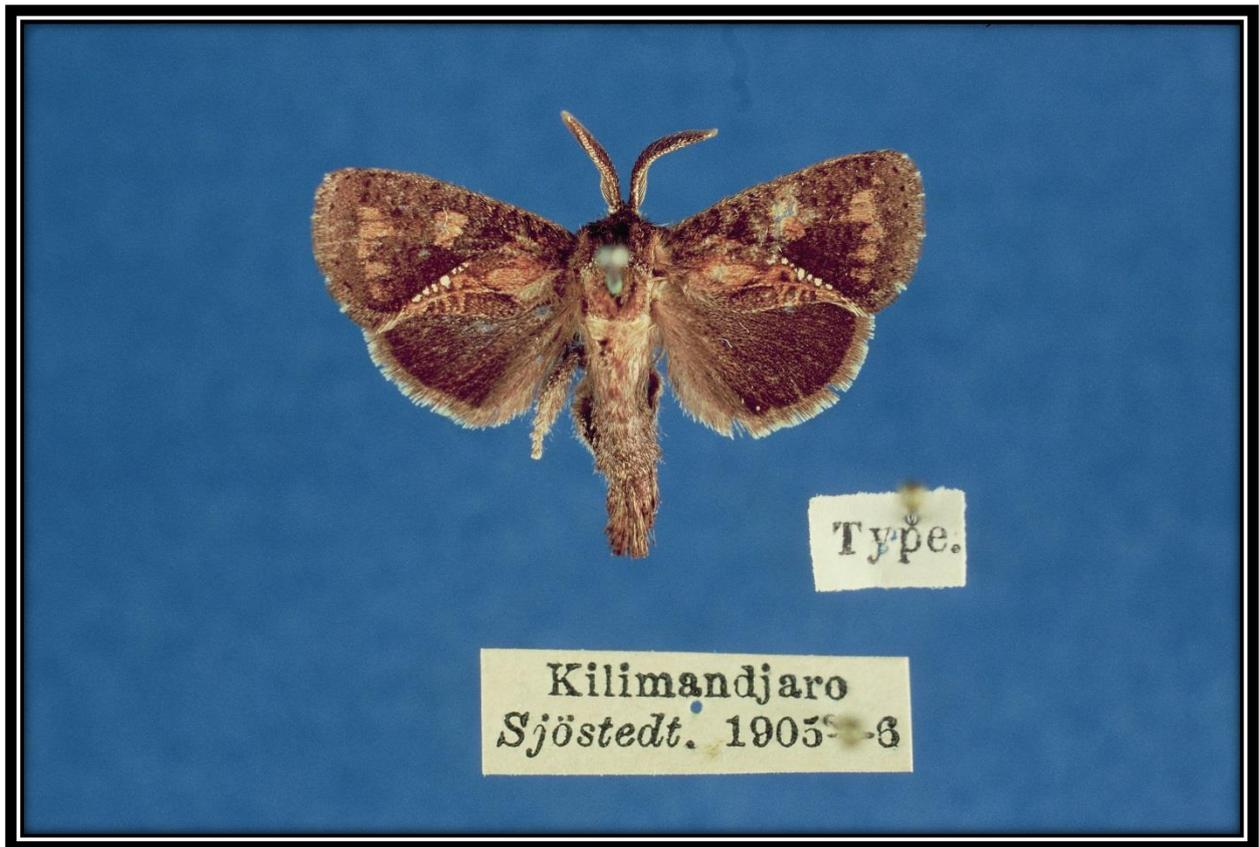
*Male genitalia.* Saccus very long (almost two-thirds of the width of valva) and narrow, rounded at tip; the vinculum and tegumen are fused, forming a firm broad

ring; uncus prominent: very large (twice as large as valva) and triangular shaped, with a very broad triangular base (viewed ventrally), bifurcated between two tiny claw-like tips that are strongly sclerotized, ventral side of uncus without setae. Valva is medium large, egg-shaped with a rounded end that is slightly bifurcated; without any structures but the whole inner surface is covered with short setae including the costal margin; sacculus absent or rudimentary; transtilla absent; semi-transtilla present and large rectangular with a broad sclerotized costal margin and many tiny setae. Gnathos is absent. The valvae are connected ventrally by a broad sclerotized band. Juxta is relatively small, band-like. Phallus is extremely long (at least twice as long as width of valva), simple tube-like, slightly broader at base, not bent, with a short rounded tip distally.

*Female postabdominal structure and genitalia. Unknown.*



**FIGURE 148.** Distribution of the genus *Ortharbela* (red dots).



**FIGURE 149.** *Ortharbela guttata*, Type, [Tanzania], Kilimanjaro, Kibonoto, Kulturz. [= Kulturzone = cultural zone], 30. March [1906?], Sjöstedt leg., male, ex NRM, genitalia slide number 26/092017 I. Lehmann. Wingspan 22.5 mm



**FIGURE 150.** *Ortharbela* sp. nov.4, Tanganjika [Tanzania], Uluguru Berge [Uluguru Mountains], 04.01.1962, Gerd H. Heinrich leg., male, ex ZSM, genitalia slide number 26d/092017 I. Lehmann. Wingspan 21.0 mm

#### **4.46 Gen. Nov. ZD**

The genus is defined by the following autapomorphy:

- Areole tiny (pyriform or elongated), almost not visible in both sexes; (89).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes; (11).

Type species of genus (cf. Figure 152): Gen. Nov. ZD + sp. nov. zd

Type locality: Ivory Coast, Bossematié Forest, ca. 180 m, 05.February.1996, Dr. Ugo Dall'Asta leg., male, genitalia slide number 06/112014 I. Lehmann, ex RMCA; depository in RMCA.

Number of species in genus at present: 06

All localities of studied species per country: Ivory Coast; Ghana; Nigeria; Cameroon; Democratic Republic of the Congo.

Distribution of genus at present (cf. Figure 151): disjunct; lowland areas from the southern parts of the Ivory Coast via southern Ghana and southern Nigeria to southwest Cameroon. A disjunct record is known from a submontane area at Isiro (northeastern Democratic Republic of the Congo).

The reconstructed and predicted ancestral areas are the Guineo-Congolian regional centre of endemism, the Guinea-Congolia/Sudania regional transition zone and the Guinea-Congolia/Zambezia regional transition zone.

The reconstructed biogeographic events comprise: First, dispersal in the Guineo-Congolian regional centre of endemism, the Guinea-Congolia/Sudania regional transition zone and the Guinea-Congolia/Zambezia regional transition zone. Secondly, vicariance between the Guineo-Congolian regional centre of endemism and the other phytochoria.

Phylogenetic position: The sister genus could not be reconstructed unambiguously. The genus is part of a monophylum together with the new genera ZC, ZD, ZE, ZF and *Ortharbela*.

The synapomorphy shared with Gen. Nov. ZC, Gen. Nov. ZE, Gen. Nov. ZF, *Ortharbela* comprises:

- Valvae not separated, but connected by a broad strongly sclerotized band ventrally; (71).

The synapomorphies shared with Gen. Nov. ZE and Gen. Nov. ZF comprise:

- A small spoon-like, strongly sclerotized appendice (without a keel line ventrally) is attached to the upper part of a thinly membranous valva; (74);
- large, hollow, sclerotized rounded appendice on ventral distal side of valva (not an extension of the sacculus) is broadly connected to the plate that links both valva; (85);
- two pairs of spurs to the hindleg but very unequal in length; (88).

Description: *Head:* rough-scaled with broader and only few hair-like scales of sepia and light ocher with a glint below the eyes on fronto-clypeus; a pair of pits is present in male, sometimes rudimentary, on lower fronto-clypeus, a pair of conical projections is absent on lower fronto-clypeus; pits behind labial palpi are absent; labial palpi short, less than half of eye diameter and consist of two segments, both segments are of equal length, sometimes occurs a third but tiny rudimentary segment on top; antennae short, bipectinated, branches are narrow and between 2.5 and 3.5 × width of shaft, densely scaled cream with sepia; flagellum densely scaled cream with sepia.

*Thorax:* Densely covered with hair-like and broader scales of light ocher with a strong glint, scales cream and light ocher on patagia and tegulae, but towards the end of tegulae the scales are sometimes xanthine orange or orange, glossy, scales on tegulae pronounced and long; crest on metathorax small, light ocher mixed with orange or it is pure orange. Epiphyses are long (up to 1.4 mm), narrow and flat. Hindlegs with two pairs of tibial spurs; lower pair is narrow, spurs unequal in length (up to 1.1 mm), upper pair narrow and shorter (up to 0.8 mm), sometimes rudimentary (up to 0.3 mm only); pretarsus with a pair of pulvilli.

Forewing upperside similar in both sexes: with a chestnut-brown ground-colour mixed with orange and without a glint shine. A geometric design is present and comprises a narrow cream band on CuA<sub>2</sub> extending from its upper end like a wave in shape downwards to the middle of 1A+2A and following it to the wing base; a simple pattern is present and comprises a large orange or xanthine orange patch that extends from the costal margin near wing base into the whole discal cell and further to the wave-like cream band; a weak but broad brown-orange subterminal-band usually exists from near apex to dorsum; CuA<sub>2</sub> is narrowly distinctly marked cream. Hindwing is light grey-olive or cream-olive with a light vinaceous glint. Fringe is with broader scales of light grey-olive, medium long (ciliae up to 0.8 mm in male; slightly longer in female up to 1.0 mm). Wing venation similar in both sexes: in forewing 1A+2A not forked at base; CuP absent; CuA<sub>2</sub> originating from two-thirds of lower median; CuA<sub>1</sub> originates from hind margin of posterior cell, M<sub>3</sub> and M<sub>2</sub> originate from apical angle of posterior cell, separated or from the same basal point; M<sub>1</sub> initiates from anterior angle of median cell; R<sub>3</sub>+R<sub>4</sub>+R<sub>5</sub> stalked and originate from posterior angle of a tiny elongated areole or from top of a tiny pyriform areole; R<sub>2</sub> originates from the anterior angle of an

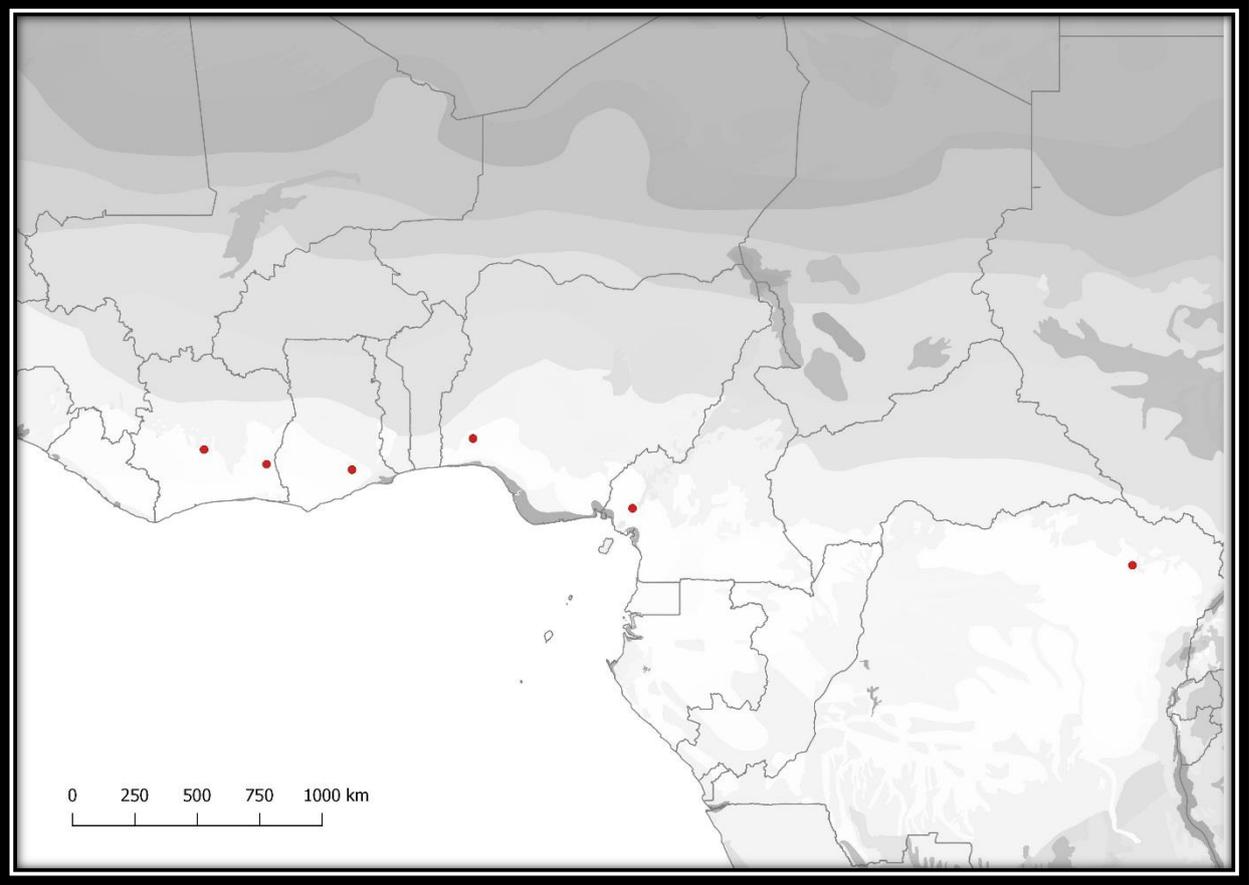
elongated tiny areole or is stalked with  $R_3+R_4+R_5$  if the tiny areole is pyriform; due to the very small size of the areole it is in some specimens present only on one forewing;  $R_1$  initiates from anterior part of median cell; Sc more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  rudimentary, with a fork at base but absent towards termen; CuP present but weak;  $CuA_2$  initiating from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1+Rs$  initiate from apical angle of anterior cell and are very long stalked or short stalked; a bar is present from  $Rs$  to  $Sc+R_1$ , but does not extend beyond the apical angle; a discocellular vein on both forewing and hindwing is present. In forewing the posterior cell has an almost acuminate apical angle and is longer than the anterior cell; the whole discal cell is of medium size and in length longer than half of the width of the forewing. Retinaculum and frenulum absent.

*Abdomen:* With scales of light cream mixed with grey-olive; abdominal tuft short, 25% of abdomen length, with orange or xanthine-orange.

*Male genitalia.* Saccus medium long, broad with more or less rounded at tip; the vinculum and tegumen are fused, forming a firm narrow ring, vinculum with a very large broad base ventrally; uncus long, broadly elongated with a broad triangular base (viewed ventrally), bifurcated between two tiny tips, ventral side of uncus without setae except short and few long setae along its upper edge. Valva is small, thinly sclerotized with a strongly arc-shaped distal margin, inner surface with a prominent strongly sclerotized structure, similar in shape like a spoon, but its upper end rather narrow, its base with many tiny setae; valva dorso-distally with a rounded, elongated, hollow tip that is covered with setae; the whole inner surface of valva is without setae; the valvae are not separated ventrally, but connected by a broad sclerotized band; transtilla absent; semi-transtilla absent. Sacculus is rudimentary or absent. Gnathos is absent. Juxta is absent and somehow replaced by the broad band that connects the valvae ventrally and by a thin membrane on the other side (this membrane looks like a large lunule with few tiny setae and occurs above the saccus in lateral view), between both structures appears the large phallus that is long (longer than width of valva), simple tube-like, broader at base, bent distally, with a rounded end.

*Female postabdominal structure and genitalia.* At present the most complex structure among female Metarbelidae: Papillae anales small and located ventrally where it lies in a strongly sclerotized structure that is open towards the extremely long, very broad posterior apophyses, hence, the dorsal part of the papillae anales is not obliquely 8-shaped or elliptic in posterior view (= This might be an autapomorphy for this genus. However, it was omitted here since no females are known from related taxa.). The papillae anales are covered with short setae; segment 8 not setose, largely open dorso-anteriorly, and it appears like it is comprising two parts: the posterior part is broad and able to move slightly from left to right, the anterior part is also of similar width but fixed and has very short and broad anterior apophyses; both parts are connected by a very narrow sclerotized ring dorsally. Ductus bursae is membranous,

broad, rather long, and looks like several bands are bound together; corpus bursae is oval, broad, thinly membranous, without any processes or other distinct characters.



**FIGURE 151.** Distribution of Gen. Nov. ZD (red dots).



**FIGURE 152.** Gen. Nov. ZD, sp. nov. zd, Ivory Coast, Bossematié Forest, 05.02.1996, Dr.Ugo Dall'Asta leg.,ex RMCA, male, genitalia slide number 06/112014 I. Lehmann. Wingspan 25.0 mm



**FIGURE 153.** Gen. Nov. ZD, sp. nov. zd2, Ivory Coast, Pakodji [?] near Degbézéré [ca. 15 km south of Bouaflé], 06.02.1984, R.T.A. Schouten & J.R.M. Buijsen leg., ex ZMA, male, genitalia slide number 07/122014 I. Lehmann. Wingspan 23.0 mm



**FIGURE 154.** Gen. Nov. ZD, sp. nov. zd5, [Democratic Republic of the Congo], Uele, Paulis [Isiro], 17.05.1958, Dr. M.Fontaine leg., ex RMCA, female, genitalia slide number 03/122014 I. Lehmann. Wingspan 29.0 mm

#### 4.47 Gen. Nov. ZE

The genus is defined by the following autapomorhy:

- Anterior cell (= upper part of discal cell) in forewing unusually small, namely only slightly larger than the elongated areole (76).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; [possibly also in female absent] (11).

Type species of genus (cf. Figure 156): Gen. Nov. ZE + sp. nov. ze

Type locality: Democratic Republic of the Congo, Bas-Congo, Luki-Mayumbe Nature Reserve [= Biosphere Reserve], ca. 320 m, 12. April. 2006, Dr. Jurate De Prins leg., male, genitalia slide number 10/012015 I. Lehmann, ex RMCA; depository in RMCA.

Number of species in genus at present: 02

All localities of studied species per country: Democratic Republic of the Congo; Central African Republic.

Distribution of genus at present (cf. Figure 155): rain forests of Lower Guinea, known from lowland areas in the southwestern Central African Republic and southwestern Democratic Republic of the Congo.

The reconstructed and predicted ancestral area is the Guineo-Congolian regional centre of endemism.

The reconstructed biogeographic events comprise: First, dispersal in the Guineo-Congolian regional centre of endemism. Secondly, vicariance between the Guineo-Congolian regional centre of endemism and the Guinea-Congolia/Sudania regional transition zone as well as the Guinea-Congolia/Zambezia regional transition zone.

Phylogenetic position: The sister genus could not be reconstructed unambiguously. The genus is part of a monophylum together with the new genera ZC, ZD, ZE, ZF and *Ortharbela*.

The synapomorphy shared with Gen. Nov. ZC, Gen. Nov. ZD, Gen. Nov. ZF, *Ortharbela* comprises:

- Valvae not separated, but connected by a broad strongly sclerotized band ventrally; (71).

The synapomorphies shared with Gen. Nov. ZD and Gen. Nov. ZF comprise:

- A small spoon-like, strongly sclerotized appendice (without a keel line ventrally) is attached to the upper part of a thinly membranous valva; (74);

- large, hollow, sclerotized rounded appendice on ventral distal side of valva (not an extension of the sacculus) is broadly connected to the plate that links both valva; (85);
- two pairs of spurs to the hindleg but very unequal in length; (88).

Description: *Head:* rough-scaled with broader and only few hair-like scales of sepia and light ocher without a glint below the eyes on fronto-clypeus; a pair of pits is present in male, sometimes rudimentary, on lower fronto-clypeus, a pair of conical projections is absent or rudimentary on lower fronto-clypeus; pits behind labial palpi are absent or tiny slit-like; labial palpi short, less than half of eye diameter and consist of two segments, both segments are of equal length, sometimes occurs a third but tiny rudimentary segment on top; antennae medium long, bipectinated, branches are broad and between 3.0 and 3.5 × width of shaft, densely scaled cream; flagellum densely scaled cream.

*Thorax:* Densely covered with broader scales that are light cream at top and light brown towards base without a glint, same scales on patagia and tegulae, scales on tegulae only slightly pronounced; crest on metathorax small and with same scales. Epiphyses are long (up to 1.9 mm), narrow and tube-like. Hindlegs with two pairs of tibial spurs; lower pair is narrow, spurs unequal in length (up to 1.2 mm), upper pair narrow and shorter (up to 0.9 mm); pretarsus with a pair of pulvilli.

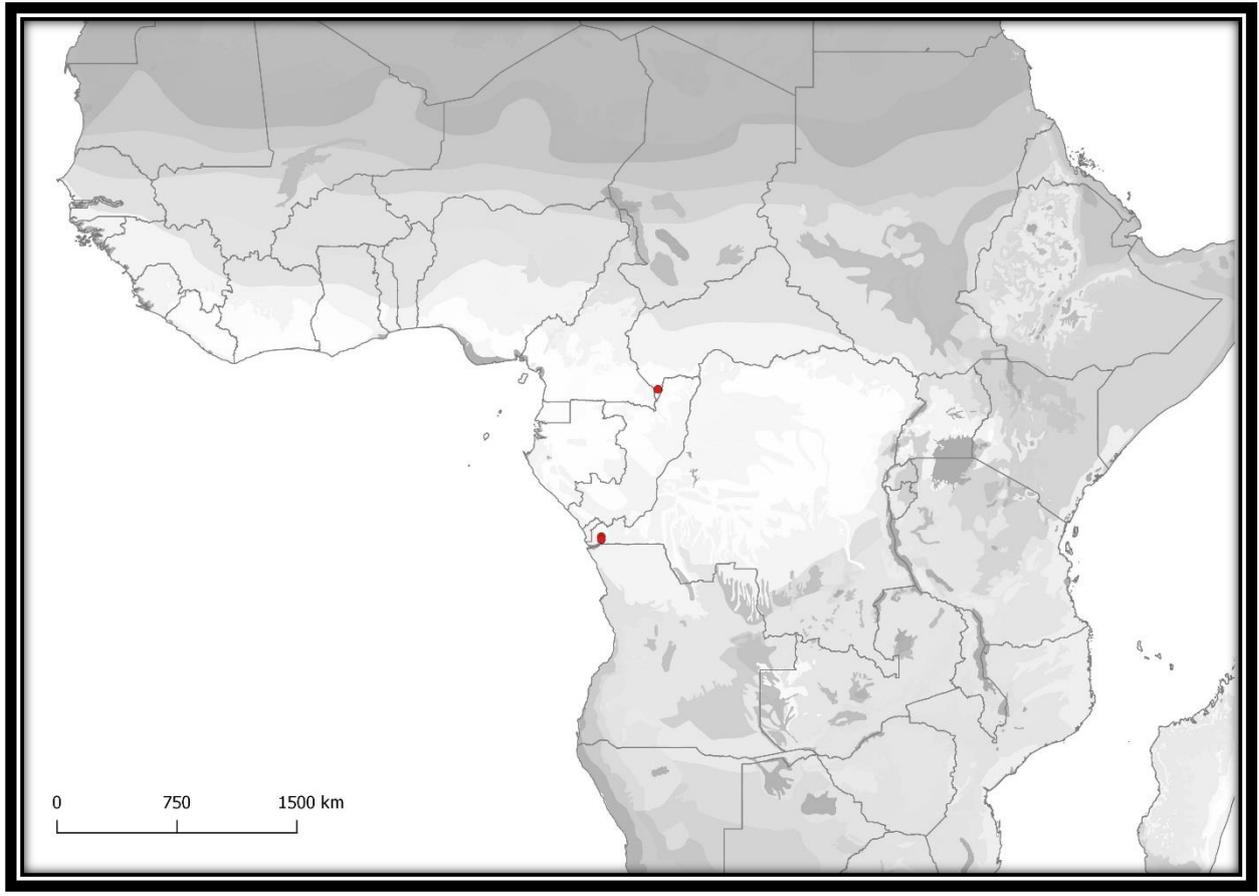
Forewing upperside has a light ocher or light cream ground-colour; without a glint. A geometric design is absent; a simple pattern is absent; sometimes occurs a rudimentary pattern and comprises a narrow wavy and brown coloured sub-terminal line from  $CuA_1$  to  $R_4$ , three or four narrow brown lines below lower median and  $CuA_2$ , a large faded brown patch between half of  $CuA_1$  and  $M_2$  and sepia lunules along the termen;  $CuA_2$  is not distinctly marked. Hindwing is light ocher or cream with a strong glint. Fringe is with broader scales of cream, medium long (ciliae up to 1.0 mm in male). Wing venation: in forewing  $1A+2A$  slightly forked at base or the fork is absent;  $CuP$  absent;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from apical angle of posterior cell, separated or from nearly the same basal point;  $M_1$  initiates from anterior angle of median cell;  $R_3+R_4+R_5$  stalked and originate from posterior angle of an elongated areole or  $R_5$  is slightly separated;  $R_2$  originates from the anterior angle of an elongated areole; the areole is almost as large as anterior cell of median cell;  $R_1$  initiates from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  rudimentary;  $CuP$  present but weak;  $CuA_2$  initiating from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1+R_s$  initiate from apical angle of anterior cell and are long stalked; a bar is present from  $R_s$  to  $Sc+R_1$ , but does not extend beyond the apical angle; a discocellular vein on both forewing and hindwing is present. In forewing the posterior cell has an almost acuminate apical angle and is longer and at least twice as large as anterior cell; the posterior cell is *ca.* 45-55% of

length of forewing in male; the anterior cell is only slightly larger than the areole; the whole discal cell is of medium size. Retinaculum and frenulum absent.

*Abdomen:* With scales of light cream and a strong glint; abdominal tuft long, 35% of abdomen length, with light cream mixed with brown, glossy, often shaped like a swallow-tail.

*Male genitalia.* Saccus medium long, broad with a rounded tip; the vinculum and tegumen are fused, forming a firm narrow ring, vinculum with a very large broad base ventrally; uncus long, broadly elongated with a broad triangular base (viewed ventrally), bifurcated between two tips, ventral side of uncus without setae except short and few long setae along its upper edge, a second membrane occurs on *ca.* half of the uncus ventrally and hence, the uncus is largely hollow on its upper part. Valva is large, mainly thinly sclerotized with a strongly arc-shaped distal margin that has a tiny thorn towards its upper edge, inner surface with a prominent strongly sclerotized structure, similar in shape like a narrow and short spoon, its base with many tiny setae; valva dorso-distally with a rounded, long and elongated hollow tip that is covered with setae; the whole inner surface of valva is without setae; the valvae are not separated ventrally, but connected by a broad sclerotized band; transtilla absent; semi-transtilla absent. Sacculus is rudimentary or absent. Gnathos is absent. Juxta is absent and somehow replaced by the broad band that connects the valvae ventrally and by a thin membrane on the other side (this membrane looks like a very large lunule with tiny setae and occurs above the saccus in lateral view), between both structures appears the large phallus that is long (longer than width of valva), simple tube-like, broader at base, slightly bent distally, with a rounded end; at centre and at its distal end occur many tiny setae.

*Female postabdominal structure and genitalia.* Unknown.



**FIGURE 155.** Distribution of Gen. Nov. ZE (red dots).



**FIGURE 156.** Gen. Nov. ZE, sp. nov. ze, Democratic Republic of the Congo, Bas-Congo, Luki-Mayumbe Nature Reserve [= Biosphere Reserve], 29.March.2006, Dr. J. De Prins leg., ex RMCA, male [no genitalia dissection done since this specimen is the best]. Wingspan 33.0 mm



**FIGURE 157.** Gen. Nov. ZE, sp. nov. ze1, Central African Republic, Bayanga-Kongana, 20.-23.07.2009, T.Bouyer-Vanaerschodt leg., ex RMCA, male, genitalia slide number 10b/012015 I. Lehmann. Wingspan 27.5 mm

#### 4.48 Gen. Nov. ZF

The genus is defined by the following autapomorphy:

- The whole male genitalia have a shape like a penguin in lateral view; (147).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; [possibly also absent in female] (11).

Type species of genus (cf. Figure 159): Gen. Nov. ZF + sp. nov. zf

Type locality: [Democratic Republic of the Congo] Sankuru, Dimbelenge, ca. 620 m, 06. April. 1951, Dr. M. Fontaine leg., male, genitalia slide number 22/112014 I. Lehmann, ex RMCA; depository in RMCA.

Number of species in genus at present: 01

All localities of studied species per country: Democratic Republic of the Congo.

Distribution of genus at present (cf. Figure 158): submontane area in the south-central part of the Democratic Republic of the Congo.

The reconstructed and predicted ancestral areas are the Guineo-Congolian regional centre of endemism, the Guinea-Congolia/Sudania regional transition zone and the Guinea-Congolia/Zambezia regional transition zone.

The reconstructed biogeographic event comprises: First, dispersal in the Guineo-Congolian regional centre of endemism, the Guinea-Congolia/Sudania regional transition zone and the Guinea-Congolia/Zambezia regional transition zone. Secondly, vicariance between the Guineo-Congolian regional centre of endemism and the other phytochoria.

Phylogenetic position: The sister genus could not be reconstructed unambiguously. The genus is part of a monophylum together with the new genera ZC, ZD, ZE, ZF and *Ortharbela*.

The synapomorphy shared with Gen. Nov. ZC, Gen. Nov. ZD, Gen. Nov. ZE, *Ortharbela* comprises:

- Valvae not separated, but connected by a broad strongly sclerotized band ventrally; (71).

The synapomorphies shared with Gen. Nov. ZD and Gen. Nov. ZE comprise:

- A spoon-like, strongly sclerotized appendice (without a keel line ventrally) is attached to the upper part of a thinly membranous valva; (74);
- large, hollow, sclerotized rounded appendice on ventral distal side of valva (not an extension of the sacculus, or an extension of the sacculus) is connected to the plate that links both valva; (85);

- two pairs of spurs to the hindleg but very unequal in length; (88).

Description: *Head:* rough-scaled with broader and only few hair-like scales of light ocher with a glint below the eyes on fronto-clypeus; a pair of pits is present in male on lower fronto-clypeus, a pair of conical projections is present on lower fronto-clypeus; pits behind labial palpi are narrow, elongated slits; labial palpi short, less than half of eye diameter and consist of three segments, both lower segments are of almost equal length, the third segment on top has 20% of the length of the basal segment; antennae short, bipectinated, branches are narrow and  $3.5 \times$  width of shaft, only slightly scaled cream; flagellum scaled cream.

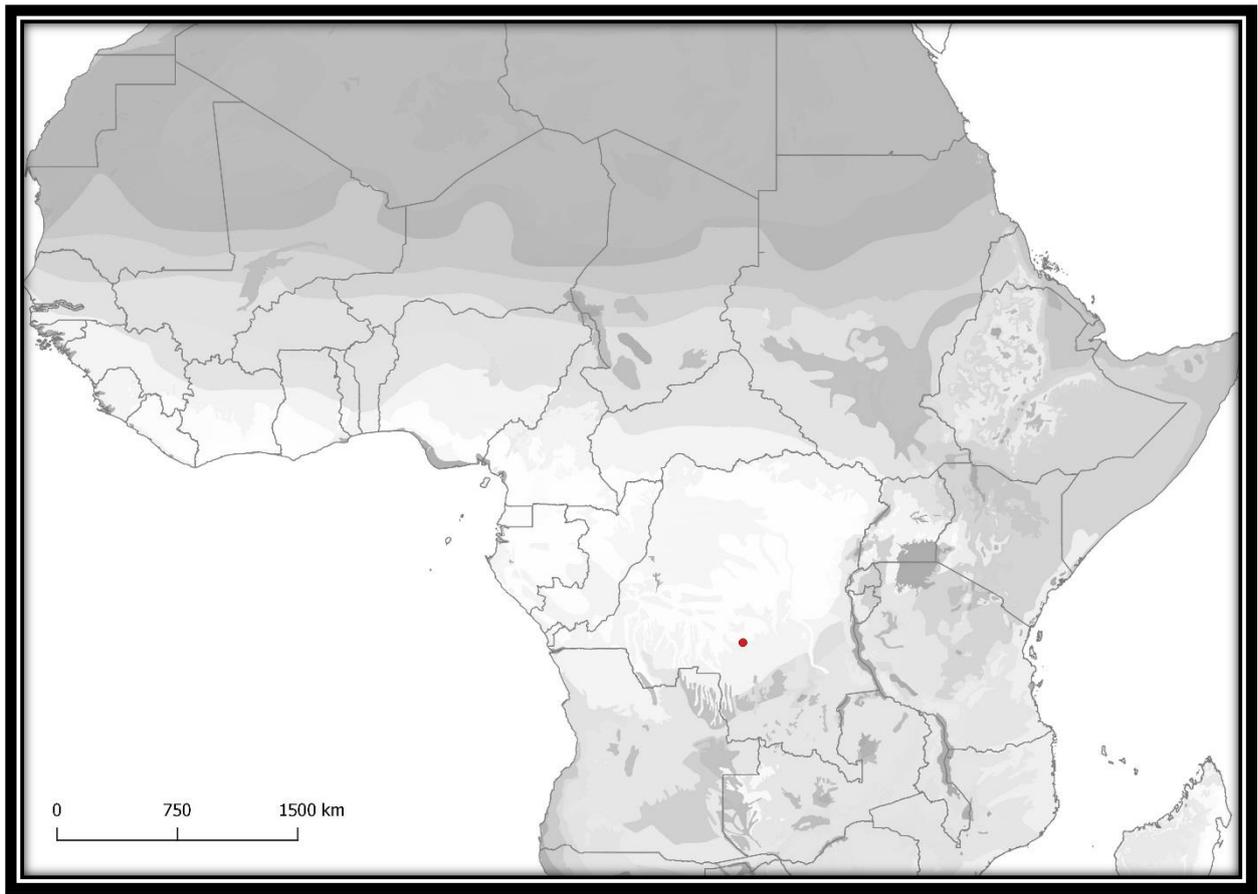
*Thorax:* Densely covered with hair-like and broader scales of light ocher with a strong glint, scales cream and light ocher on patagia and tegulae, but towards the end of tegulae the scales are orange, glossy, scales on tegulae pronounced and long; crest on metathorax small, light ocher mixed with orange. Epiphyses are long (up to 1.2 mm), narrow and tube-like. Hindlegs with two pairs of tibial spurs; lower pair is narrow, spurs unequal in length (up to 0.9 mm), upper pair narrow and longer (up to 1.1 mm); pretarsus with a pair of pulvilli.

Forewing upperside: with a light brown ground-colour mixed with orange and with a glint shine. A geometric design is present and comprises a narrow cream band on  $CuA_2$  extending from its upper end like a wave in shape downwards to the middle of  $1A+2A$  and following it to the wing base; a simple pattern is present and comprises a large orange or xanthine orange patch that extends from the costal margin near wing base into the whole discal cell and further to the wave-like cream band; a faded dark brown narrow subterminal line is present;  $CuA_2$  is narrowly distinctly marked cream. Hindwing is light grey-olive with a light vinaceous glint. Fringe is with broader scales of light grey-olive, short (ciliae up to 0.5 mm in male). Wing venation: in forewing  $1A+2A$  not forked at base;  $CuP$  absent;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from apical angle of posterior cell, separated;  $M_1$  initiates from anterior angle of median cell;  $R_5$  originates from posterior angle of a narrowly elongated, but long, areole;  $R_3+R_4$  are stalked and originate from top of areole;  $R_2$  originates from the anterior angle of the areole;  $R_1$  initiates from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  rudimentary;  $CuP$  present but weak;  $CuA_2$  initiating from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1+R_s$  initiate from apical angle of anterior cell and are long stalked; a long bar is present from  $R_s$  to  $Sc+R_1$ , it does extend beyond the apical angle; a discocellular vein on both forewing and hindwing is present. In forewing the posterior cell has a broad apical angle and is much longer than the anterior cell; the whole discal cell is of medium size and in length longer than half of the width of the forewing. Retinaculum and frenulum absent.

*Abdomen:* With scales of light cream mixed with grey-olive; abdominal tuft short, 20% of abdomen length, with orange.

*Male genitalia.* Saccus medium long, broad with a rounded tip; the vinculum and tegumen are fused, forming a firm broad ring, but the end of the tegumen and the beginning of the vinculum are very narrow, vinculum with a very large broad base ventrally; uncus long, with a broad triangular base, but suddenly towards top more narrow, similar in shape to a tongue with a broader base (viewed ventrally), not bifurcated at tip, but broadly rounded; ventral side of uncus without setae except short setae along its upper edge. Valva is small, thinly sclerotized with a strongly arc-shaped distal margin ventrally, inner surface with a prominent strongly sclerotized structure, similar in shape like a spoon, with its upper end broad, its base with few setae; valva dorso-distally with a rounded, elongated, hollow tip that is covered with few long setae; the whole inner surface of valva is without setae; the valvae are not separated ventrally, but connected by a broad sclerotized band; transtilla absent; semi-transtilla absent. Sacculus is present and narrow. Gnathos is absent. Juxta is present and broadly connected with the broad band that connects the valvae ventrally, distally the juxta is sclerotized and has an emargination between two acuminate tips; the distal part of the juxta is connected to a large elongated thin membrane with many tiny setae, it looks like a large lunule and occurs above the saccus in lateral view; the phallus is large, longer than width of valva, simple tube-like, broader at base, bent distally, with a very long (almost 50% the length of phallus) and narrow tip distally.

*Female postabdominal structure and genitalia.* Unknown.



**FIGURE 158.** Distribution of Gen. Nov. ZF (red dot).



**FIGURE 159.** Gen. Nov. ZF, sp. nov. zf, [Democratic Republic of the Congo] Sankuru, Dimbelenge, 06. April. 1951, Dr. M. Fontaine leg., ex RMCA, male, genitalia slide number 22/112014 I. Lehmann. Wingspan 28.0 mm

#### 4.49 Gen. Nov. ZG

The genus is defined by the following autapomorphy:

- Very long, narrow saccus (in lateral view), almost as long as ventral edge of a broad, rectangular valva; (102).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; [possibly also in female absent] (11).

Type species of genus (cf. Figure 161): Gen. Nov. ZG + sp. nov. zg

Type locality: Kenya, Coast, Kwale District, Gogoni Forest Reserve, ca. 65 m, site 7, 04.February.2006, I. Lehmann, S.A. Chidzinga & M. Abdulrahman leg., male, genitalia slide number 05/022015 I. Lehmann, ex own coll.; depository in NMK.

Number of species in genus at present: 09

All localities of studied species per country: Kenya; Tanzania; Mozambique.

Distribution of genus at present (cf. Figure 160): lowland and submontane areas, namely from the coast of the Indian Ocean inland to ca. 300 km in Kenya (westwards to the Kathita River as well as to Kibwezi and Taveta) and Tanzania (westwards to the East Usambara Mountains, Uluguru Mountains and Rubeho Mountains) and southwards to northern coastal Mozambique.

The reconstructed and predicted ancestral areas are the Zanzibar-Inhambane regional mosaic and the Tongaland-Pondoland regional mosaic.

The reconstructed biogeographic event comprises: First, dispersal in the Zanzibar-Inhambane regional mosaic and the Tongaland-Pondoland regional mosaic. Secondly, vicariance within the Zanzibar-Inhambane regional mosaic and the Tongaland-Pondoland regional mosaic.

Phylogenetic position: The sister genus is Gen. Nov. ZH.

The genus is part of a monophylum together with the new genera ZI, ZG and ZH.

The synapomorphy shared with Gen. Nov. ZH comprises:

- The uncus has a large hole dorsally that is larger than 60% of the dorsal surface and is located near the centre of the uncus; (100).

The synapomorphy shared with Gen. Nov. ZI and Gen. Nov. ZH comprises:

- Valvae not separated, but connected by a narrow strongly sclerotized band ventrally; (70).

Description: *Head:* rough-scaled with mainly hair-like scales of light ocher or cream sometimes mixed with sepia and always with a strong glint below the eyes on fronto-clypeus; a pair of pits is absent in male on lower fronto-clypeus, a pair of small conical

projections is present on lower fronto-clypeus; pits behind labial palpi are small rounded or slightly oval shaped holes; labial palpi short, less than half of eye diameter and consist of three segments, both segments are of almost equal length, central segment sometimes slightly longer than basal segment, the third segment on top is small, it has 10% of the length and 30% of the width of the basal segment and has a conical shape; antennae rather short, bipectinated, branches are narrow and  $3.0 \times$  width of shaft, scaled cream or light ocher; flagellum scaled cream or light ocher.

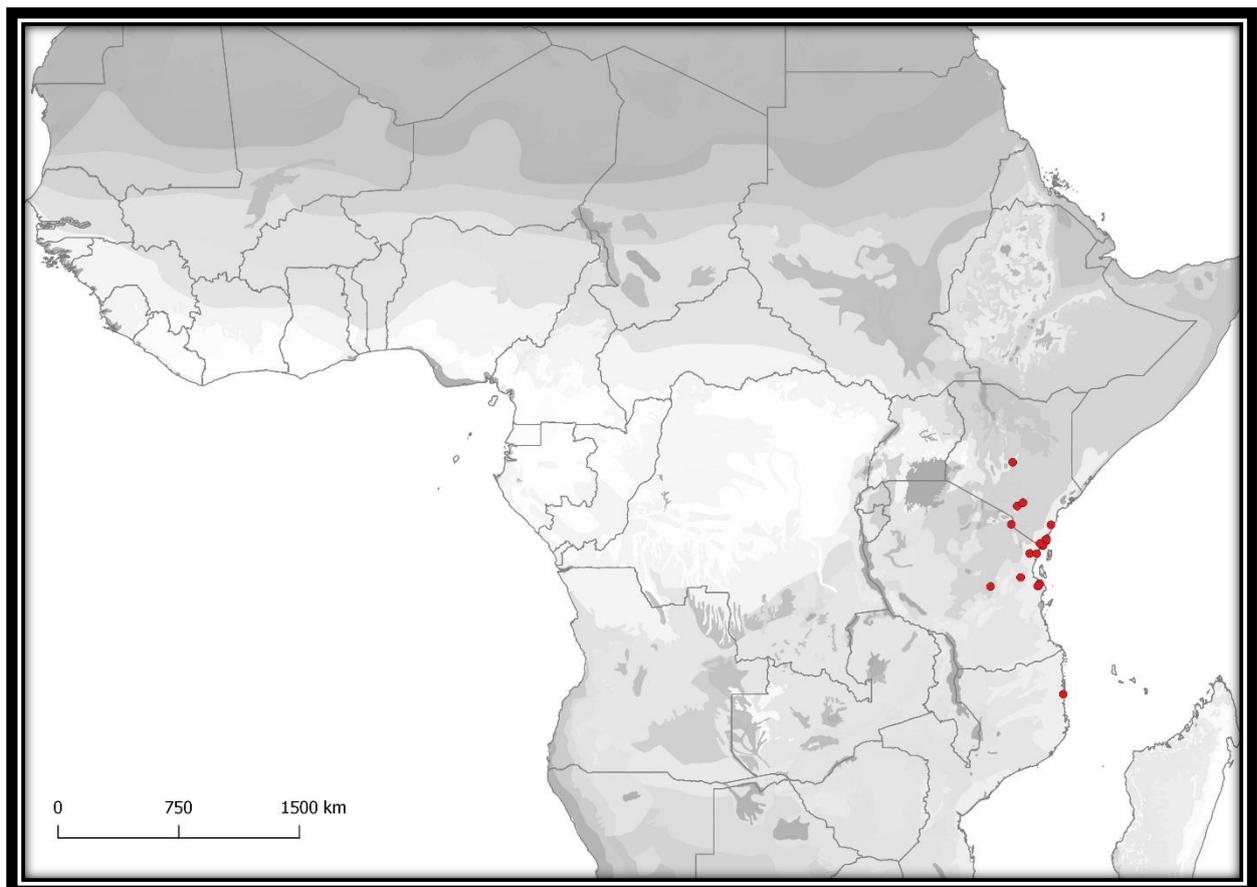
*Thorax:* Densely covered with mainly hair-like and few broader scales of light ocher or cream or light grey with a strong glint, scales dark cream or ocher on patagia and lighter on tegulae, glossy, scales on tegulae pronounced and long; crest on metathorax small, light ocher or light grey with a small patch of sepia. Epiphyses are long (up to 1.4 mm), narrow and tube-like. Hindlegs with two pairs of tibial spurs; lower pair is narrow, spurs slightly unequal in length (up to 1.1 mm), upper pair is narrow and also slightly unequal in length (up to 1.1 mm); pretarsus with a pair of pulvilli.

Forewing upperside: with a light ocher or dark cream ground-colour with a strong light vinaceous or strong light ocher glint. A geometric design is absent; a simple pattern is present and comprises a large dark grey or light brown or faded light grey patch that extends from the middle of  $CuA_2$  to the base of  $M_2$ , a wave-like narrow dark cream band, that is more or less continuous and is strongly bent inwards between  $R_5$  and  $M_2$  extends from near apex to end of  $CuA_2$ ;  $CuA_2$  is not distinctly marked; below  $CuA_2$  and  $1A+2A$  occur usually three brown and oval shaped markings that are more or less reduced; lunules along termen of same colour and also reduced. Hindwing is light grey-olive or dark cream with a strong glint. Fringe is with narrow scales of light cream, long (ciliae up to 1.0 mm in male). Wing venation: in forewing  $1A+2A$  not forked at base or fork strongly reduced;  $CuP$  absent;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from apical angle of posterior cell, separated;  $M_1$  initiates from anterior angle of median cell;  $R_5$  originates from posterior angle of a broadly elongated areole;  $R_3+R_4$  are very long stalked and originate from the top of areole or are stalked with  $R_5$ ;  $R_2$  originates from the anterior angle of the areole;  $R_1$  initiates from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  rudimentary or absent;  $CuP$  present but weak;  $CuA_2$  initiating from two-thirds or near half of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1+R_s$  initiate from apical angle of anterior cell and are short stalked or originate from near the same basal point; a short bar is present from  $R_s$  to  $Sc+R_1$ ; a discocellular vein on both forewing and hindwing is present. In forewing the posterior cell is slightly larger and longer than the anterior cell; the whole discal cell is of medium size and in length not longer than half of the width of the forewing. Retinaculum and frenulum absent.

*Abdomen:* Usually very long and extending well beyond hindwing, with scales of light cream mixed with dark grey; abdominal tuft long, 35% of abdomen length.

*Male genitalia.* Saccus very long, usually narrow, sometimes broad but elongated, with a rounded tip; the vinculum and tegumen are fused, forming a firm ring, tegumen narrow, vinculum at least three times broader with a very large broad base ventrally; uncus rather short, broad triangular, bifurcated at tip, both ribs are slightly more sclerotized; ventral side of uncus with many long and/or short setae. Valva is rather large, broadly rectangular, sclerotized with a slightly arc-shaped distal margin, inner surface with a prominent oblique row of tiny setae; dorso-distally with a small only thinly sclerotized tip that is covered with tiny setae, ventral-distally with a very short, rather conical shaped appendice; the valvae are not separated ventrally, but connected by a relatively narrow sclerotized band; transtilla absent; semi-transtilla present and thorn-like, slightly bent towards the acuminate tip. Sacculus is absent or very narrow. Gnathos is absent. Juxta is present but somehow reduced and connected with the narrow band that connects the valvae ventrally, the juxta is sclerotized and short tube-like with an open part on its entire length; the phallus is narrow on its whole length, very long, at least twice as long as the ventral width of valva, simple tube-like, not bent.

*Female postabdominal structure and genitalia.* Unknown.



**FIGURE 160.** Distribution of Gen. Nov. ZG (red dots).



**FIGURE 161.** Gen. Nov. ZG, sp. nov. zg, Kenya, Coast, Kwale District, Gogoni Forest Reserve, 04.February.2006, I. Lehmann, S.A. Chidzinga & M. Abdulrahman leg., ex own coll., male, genitalia slide number 05/022015 I. Lehmann. Wingspan 23.0 mm



**FIGURE 162.** Gen. Nov. ZG, *simillima* (Hampson, 1910), Kenya, [Makueni County] Kibwezi, 01.-15.05.2001, Dr. H. Politzar leg., ex MWM, male, genitalia slide number *simillima*/072012 I. Lehmann. Wingspan 28.0 mm



**FIGURE 163.** Gen. Nov. ZG, sp. nov. zg3, Kenya, Coast, Kwale District, Shimoni Forest, 19. February. 2007, I. Lehmann & S.A. Chidzinga leg., ex own coll., male, genitalia slide number 05/062007 I. Lehmann. Wingspan 26.5 mm



**FIGURE 164.** Gen. Nov. ZG, sp. nov. zg4, Kenya, [Taita-Taveta County] Kitobo Forest [near Taveta], October. 1974, M.P. Clifton leg., ex NMK, male, genitalia slide number 08/072012 I. Lehmann. Wingspan 26.5 mm

#### 4.50 Gen. Nov. ZH

The genus is defined by the following autapomorphy:

- Vinculum broad with a rectangular broad end below ventral base of valva; the end appears as vertical edge in lateral view; (112).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; [possibly also in female absent] (11).

Type species of genus (cf. Figure 166): Gen. Nov. ZH + sp. nov. zh

Type locality: Kenya, Coast, Lamu District, Manda Island, “mangrove swamp habitat”, July–August 1982, Brathay Expedition, male, genitalia slide number 17/032013 I. Lehmann, ex NMK; depository in NMK.

Number of species in genus at present: 01

All localities of studied species per country: Kenya.

Distribution of genus at present (cf. Figure 165): lowland area on Manda Island (Kenya North Coast).

The reconstructed and predicted ancestral areas are the Zanzibar-Inhambane regional mosaic and the Tongaland-Pondoland regional mosaic.

The reconstructed biogeographic event comprises: First, dispersal in the Zanzibar-Inhambane regional mosaic and the Tongaland-Pondoland regional mosaic. Secondly vicariance within the Zanzibar-Inhambane regional mosaic and the Tongaland-Pondoland regional mosaic.

Phylogenetic position: The sister genus is Gen. Nov. ZG.

The genus is part of a monophylum together with the new genera ZI, ZG and ZH.

The synapomorphy shared with Gen. Nov. ZG comprises:

- The uncus has a large hole dorsally that is larger than 60% of the dorsal surface and is located near the centre of the uncus; (100).

The synapomorphy shared with Gen. Nov. ZI and Gen. Nov. ZG comprises:

- Valvae not separated, but connected by a narrow strongly sclerotized band ventrally; (70).

Description: *Head:* rough-scaled with mainly hair-like scales of cream mixed with sepia and without a strong glint below the eyes on fronto-clypeus; a pair of pits is absent in male on lower fronto-clypeus, a pair of small conical projections is present on lower fronto-clypeus; pits behind labial palpi are oval shaped holes; labial palpi short, less than half of eye diameter and consist of three segments, both segments are of almost equal length, central segment slightly longer than basal segment, the third segment on

top is elongated, it has 40% of the length and 70% of the width of the basal segment and has an oval shape; antennae rather short, bipectinated, branches are narrow and 3.0 × width of shaft, scaled white; flagellum scaled white mixed with light brown.

*Thorax:* Densely covered with mainly hair-like and broader scales of light ocher, sepia and cream without a glint, scales sepia and light ocher on patagia and lighter on tegulae, mainly cream, slightly glossy, scales on tegulae pronounced and long; crest on metathorax small, cream. Epiphyses are long (1.2 mm), broad and tube-like. Hindlegs with one pair of tibial spurs; spurs slightly unequal in length (up to 0.9 mm); pretarsus with a pair of pulvilli.

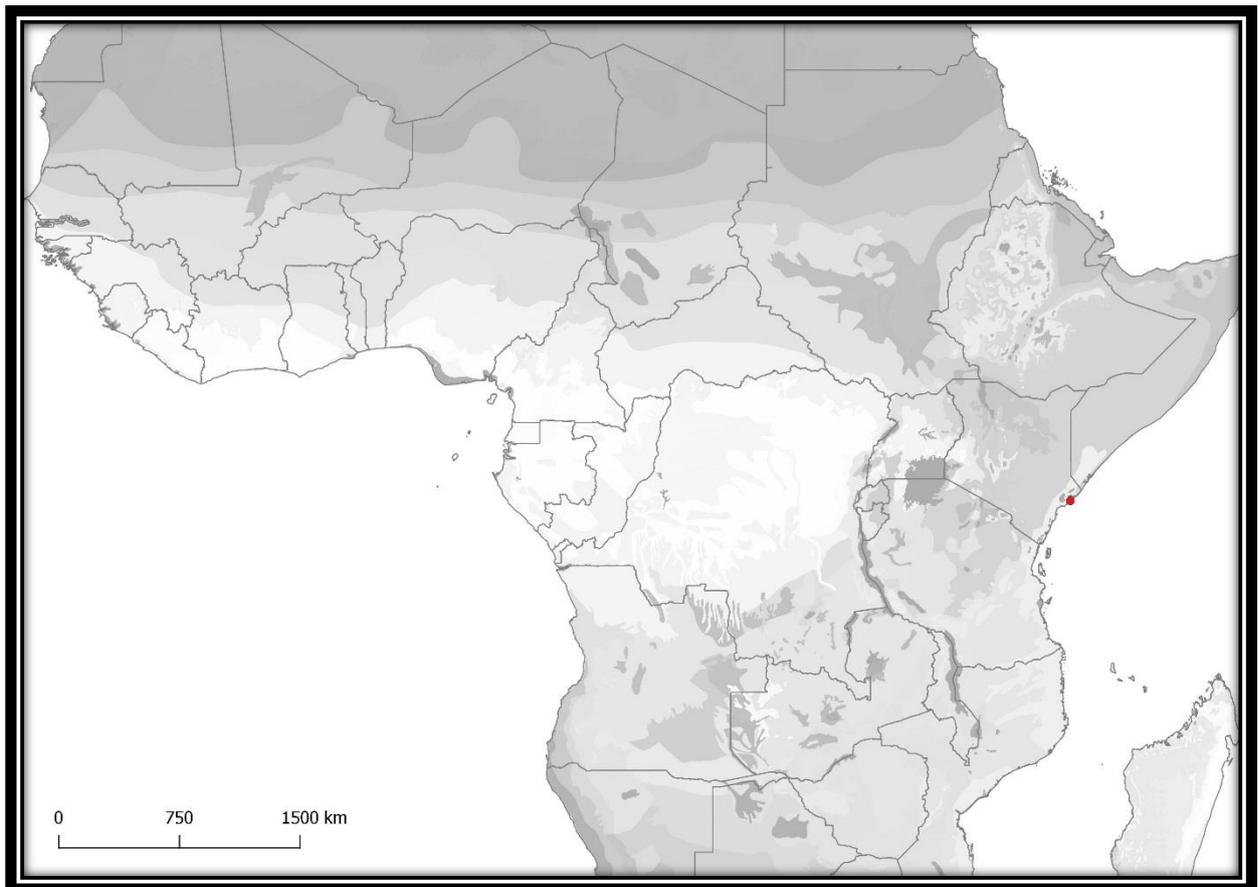
Forewing upperside: with a light cream ground-colour and only slightly glossy towards termen. A geometric design is absent; a simple pattern is present and comprises a large chestnut brown patch that extends from the middle of CuA<sub>2</sub> to the base of M<sub>2</sub>, a wave-like broad sepia band, edged light grey towards termen, is strongly bent inwards between R<sub>5</sub> and M<sub>2</sub> and extends from near apex to below half of CuA<sub>2</sub> and along the dorsum to the base of the forewing; CuA<sub>2</sub> is not distinctly marked; sepia lunules occur along the termen and rounded spots of sepia along the costal margin. Hindwing is light cream with a strong glint. Fringe is with narrow scales of light cream, long (ciliae up to 1.0 mm in male). Wing venation: in forewing 1A+2A not forked at base; CuP absent; CuA<sub>2</sub> originating from two-thirds of lower median; CuA<sub>1</sub> originates from hind margin of posterior cell, M<sub>3</sub> and M<sub>2</sub> originate from apical angle of posterior cell, separated; M<sub>1</sub> initiates from anterior angle of median cell; R<sub>5</sub> originates from posterior angle of a broadly rather triangular areole and is stalked with R<sub>3</sub>+R<sub>4</sub>; R<sub>2</sub> originates from the anterior angle of the areole; R<sub>1</sub> initiates from anterior part of median cell; Sc more or less parallel to R<sub>1</sub>. In hindwing 3A present; 1A+2A absent; CuP absent; CuA<sub>2</sub> initiating from two-thirds of lower median of posterior cell; CuA<sub>1</sub> initiates from hind margin of posterior cell; M<sub>3</sub> and M<sub>2</sub> initiating from apical angle of posterior cell, separated; M<sub>1</sub>+Rs initiate from apical angle of anterior cell and are stalked; a short, weak bar is present from Rs to Sc+R<sub>1</sub>; a discocellular vein on both forewing and hindwing is rudimentary. In forewing the posterior cell is slightly larger and longer than the anterior cell; the whole discal cell is of medium size and in length not longer than half of the width of the forewing. Retinaculum and frenulum absent.

*Abdomen:* long and extending well beyond hindwing, mainly with scales of light cream, glossy; abdominal tuft long, 30% of abdomen length.

*Male genitalia.* Saccus short, broad with an obconic end; the vinculum and tegumen are fused, forming a firm ring, tegumen very narrow, vinculum two times broader with a very large broad base ventrally that has an obconic end (viewed ventrally); uncus very long, broadly elongated, almost twice as long as width of valva, slightly bifurcated at tip; ventral side of uncus with few very long setae that appear grey in colour. Valva is rather large, broadly rectangular, sclerotized with an arc-shaped distal margin, inner surface with a short prominent oblique row of medium long setae that are grey in colour; dorso-distally with a rather large thinly sclerotized tip that is covered with tiny and few long setae, ventral-distally with a very short,

rather conical shaped appendice; the valvae are not separated ventrally, but connected by a relatively narrow sclerotized band; transtilla absent; semi-transtilla present and thorn-like, slightly bent towards the acuminate tip. Sacculus is absent. Gnathos is absent. Juxta is present but somehow reduced and connected with the narrow band that connects the valvae ventrally, the juxta is sclerotized and short tube-like with a very wide open part on its entire length; the phallus is narrow on its whole length, very long, twice as long as the ventral width of valva, simple tube-like, not bent.

*Female postabdominal structure and genitalia. Unknown.*



**FIGURE 165.** Distribution of Gen. Nov. ZH (red dot).



**FIGURE 166.** Gen. Nov. ZH, sp. nov. zh, Kenya, Coast, Lamu District, Manda Island, “mangrove swamp habitat”, July–August 1982, Brathay Expedition, ex NMK, male, genitalia slide number 17/032013 I. Lehmann. Wingspan 19.0 mm

#### 4.51 Gen. Nov. ZI

The genus is defined by the following autapomorphy:

- A wide emargination (looking like a wide “V”) forms the posterior edge of valva; (67).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; [possibly also in female] (11).

Type species of genus (cf. Figure 168): Gen. Nov. ZI + *lornadepewae* (Lehmann, 2009)

Type locality: Tanzania, Udzungwa Mountains, Mufindi District, Mufindi, 1.960 m, 15. January.1993, L. Aarvik leg., male, genitalia slide number 09/072008 I. Lehmann, ex NHMO; depository in NHMO.

Number of species in genus at present: 01

All localities of studied species per country: Tanzania.

Distribution of genus at present (cf. Figure 167): Eastern Arc Mountains, only known from one montane area in the Udzungwa Mountains.

The reconstructed and predicted ancestral areas are the Afromontane archipelago-like regional centre of endemism, the Zanzibar-Inhambane regional mosaic and the Tongaland-Pondoland regional mosaic.

The reconstructed biogeographic events comprise: First, dispersal in the Afromontane archipelago-like regional centre of endemism, the Zanzibar-Inhambane regional mosaic and the Tongaland-Pondoland regional mosaic. Secondly vicariance between the Afromontane archipelago-like regional centre of endemism and the Zanzibar-Inhambane regional mosaic as well as Tongaland-Pondoland regional mosaic.

Phylogenetic position: The sister genus could not be reconstructed unambiguously. The genus is part of a monophylum together with the new genera ZI, ZG and ZH.

The synapomorphy shared with Gen. Nov. ZG and Gen. Nov. ZH comprises:

- Valvae not separated, but connected by a narrow strongly sclerotized band ventrally; (70).

Description: *Head:* rough-scaled with mainly hair-like scales of black mixed with sepia below the eyes on fronto-clypeus; a pair of pits is absent in male on lower fronto-clypeus, a pair of small conical projections is present on lower fronto-clypeus; pits behind labial palpi are oval shaped holes; labial palpi as long as eye diameter and consist of three segments, central segment longer than basal segment, the third segment on top is elongated and has an oval shape; antennae very long, strongly

bipectinated, branches are narrow and  $7.0 \times$  width of shaft, slightly scaled brown; flagellum scaled light brown.

*Thorax:* Densely covered with mainly hair-like and broader scales of black, sometimes with white tips on patagia and on tegulae, glossy, scales on tegulae pronounced and long; crest on metathorax cream. Epiphyses are long (1.2 mm) and tube-like. Hindlegs with two pairs of tibial spurs; spurs slightly unequal in length (up to 1.0 mm); pretarsus with a pair of pulvilli.

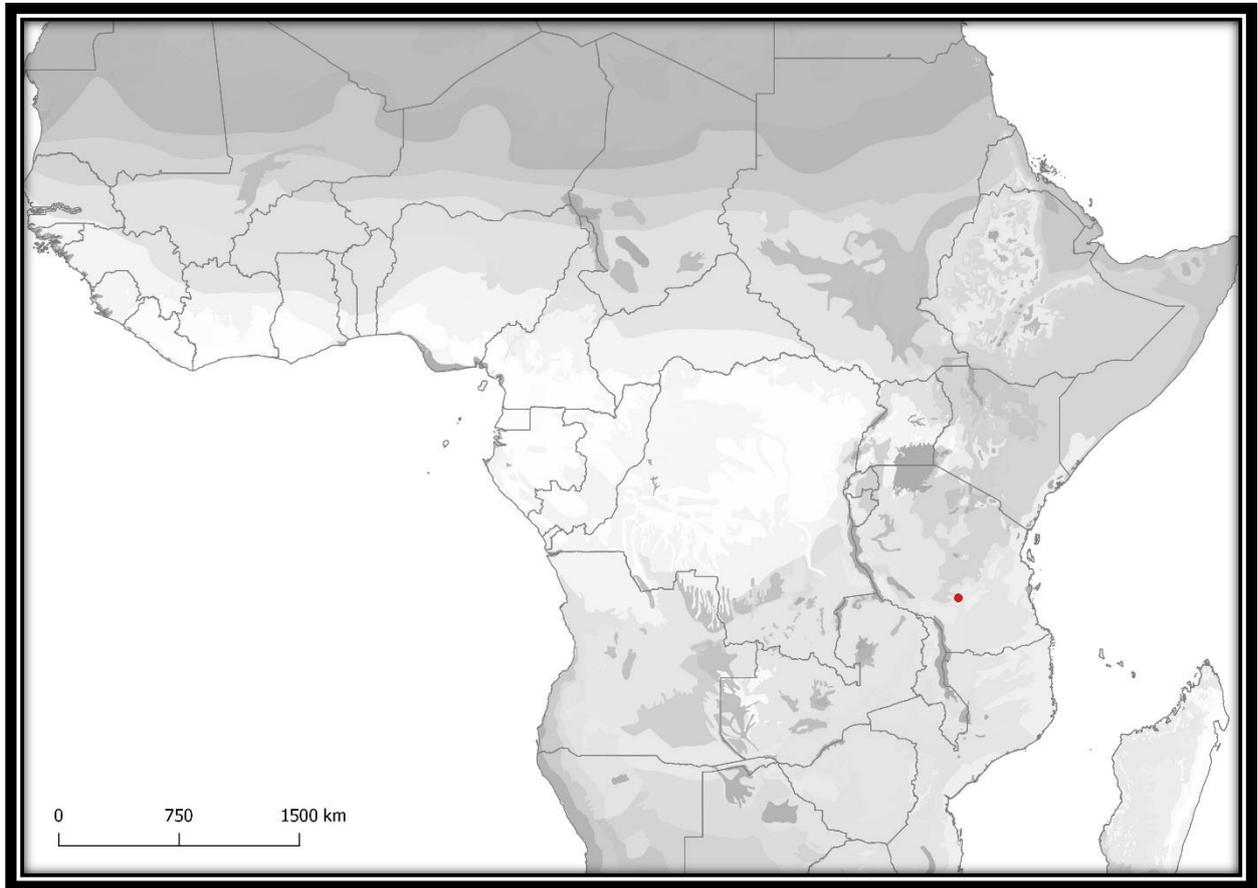
Forewing upperside: with a black ground-colour and only slightly glossy towards termen. A geometric design is absent; a simple pattern is present and comprises three prominent pure white spots at the end of  $1A+2A$  that form almost a triangle and pure white spots along the costal margin. Hindwing is buff-yellow turning brownish-olive towards its margin. Fringe is with scales of brownish-olive alternating with pure white, long (ciliae up to 1.1 mm in male). Wing venation: in forewing  $1A+2A$  not forked at base; CuP absent;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from apical angle of posterior cell, separated;  $M_1$  initiates from anterior angle of median cell;  $R_5$  originates from posterior angle of a broadly elongated areole and close to the base of a very long stalk of  $R_3+R_4$ ;  $R_2$  originates from anterior angle of the areole;  $R_1$  initiates from anterior part of median cell; Sc more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  present; CuP rudimentary;  $CuA_2$  initiating from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1+R_s$  initiate from apical angle of anterior cell and are very long stalked; a bar is absent from  $R_s$  to  $Sc+R_1$ ; a discocellular vein on both forewing and hindwing is weak. In forewing the posterior cell is slightly larger but not longer than the anterior cell; the whole discal cell is of medium size and in length slightly longer than half of the width of the forewing. Retinaculum and frenulum absent.

*Abdomen:* long and extending well beyond hindwing, mainly with buff-yellow scales, glossy; abdominal tuft prominent with broad scales of black, 40% of abdomen length.

*Male genitalia.* Saccus medium long, half of the width of valva, broad, not tapering towards the rounded tip; the vinculum and tegumen are fused, forming a firm ring, tegumen narrow, vinculum two times broader with a large broad base ventrally that has an almost obconic end (viewed ventrally); uncus long, broadly elongated, slightly longer than width of valva, bifurcated at tip with a rounded emargination between the acuminate tips; ventral side of uncus with many long and short setae. Valva is rather large, broadly rectangular, sclerotized with a wide V-shaped distal margin, inner surface with a long prominent oblique row of medium long setae; the valvae are not separated ventrally, but connected by a relatively narrow sclerotized band; transtilla absent; semi-transtilla present and short thorn-like, slightly bent towards the acuminate tip. Sacculus is narrow. Gnathos is absent. Juxta is rather large and connected with the narrow band that connects the valvae ventrally, the juxta is

sclerotized and has two acuminate tips; the phallus is narrow on its whole length, very long, almost twice as long as the ventral width of valva, simple tube-like, not bent; vescica without cornuti.

*Female postabdominal structure and genitalia. Unknown.*



**FIGURE 167.** Distribution of Gen. Nov. ZI (red dot).



**FIGURE 168.** Gen. Nov. ZI, *lornadepewae*, Holotype, Tanzania, Udzungwa Mountains, Mufindi District, Mufindi, 15.January.1993, L. Aarvik leg., ex NHMO, male, genitalia slide number 09/072008 I. Lehmann. Wingspan 23.5 mm

#### **4.52 Gen. Nov. ZJ**

The genus is defined by the following autapomorhy:

- Two long, sclerotized, narrow sinuate processes originate from the same point, a third long narrow sinuate process is close to, and all three processes are attached with a narrow band to the upper part of valva as well as somehow to the vinculum; (204).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes; (11).

Type species of genus (cf. Figures 170, 171): Gen. Nov. ZJ + sp. nov. zj

Type locality: Malawi, Nyika National Park, Kasaramba Forest, 2.340 m, 22.December.2011–05.January.2012, R.J. Murphy leg., male, genitalia slide number 29/052013 I. Lehmann; depository in ZFMK.

Number of species in genus at present: 07

All localities of studied species per country: Burundi; Kenya; Tanzania; Malawi; Zimbabwe.

Distribution of genus at present (cf. Figure 169): disjunct; montane and submontane areas from Gitega in central Burundi southwards to Mkuyu in western Tanzania, with a disjunct record from the Aberdare Range in central Kenya, further south to the Nyika Plateau and Mzuzu (northern Malawi), Mount Mulanje and southwards to the Nyanga National Park in eastern Zimbabwe.

The reconstructed and predicted ancestral area is the Afromontane archipelago-like regional centre of endemism.

The reconstructed biogeographic events comprise: First, dispersal in the Afromontane archipelago-like regional centre of endemism. Secondly, dispersal into the Guineo-Congolian regional centre of endemism, Zambezian regional centre of endemism, Sudanian regional centre of endemism, the Guinea-Congolia/Sudania regional transition zone, the Lake Victoria regional mosaic, the Guinea-Congolia/Zambezia regional transition zone and the Kalahari-Highveld regional transition zone. Thirdly, vicariance between the Afromontane archipelago-like regional centre of endemism and all other phytochoria mentioned above.

Phylogenetic position: The sister genus could not be reconstructed unambiguously.

Description: *Head:* rough-scaled with mainly broad scales of light cream mixed with sepia or orange-ocher mixed with light brown and cream below the eyes on fronto-clypeus; a pair of small pits is present but rudimentary in both sexes on lower fronto-clypeus, a pair of projections is absent in both sexes on lower fronto-clypeus; pits

behind labial palpi are very narrow rudimentary slits or entirely absent; labial palpi long, almost as long as eye diameter and consist of three segments in both sexes, central segment slightly longer or of same length as basal segment, the third segment on top is long, elongated and has an oval shape, it is almost half as long as basal segment; antennae medium long in both sexes; in male strongly bipectinated, branches are narrow and  $3.0 \times$  width of shaft, scaled brown mixed with cream; flagellum scaled light brown and cream; in female unipectinated, branches are narrow,  $1.0 \times$  width of shaft, slightly scaled cream; flagellum more densely scaled cream.

*Thorax:* Densely covered with hair-like and broader scales of cream or dark ocher, sometimes with white tips on tegulae, glossy, scales on tegulae slightly pronounced and longer only in male; crest on metathorax dark ocher. Epiphyses are present in both sexes, but more developed in male, very long (up to 2.0 mm), broad or narrow and tube-like; epiphyses in female strongly reduced, often less than 0.9 mm, very narrow, tube-like. Hindlegs with two pairs of tibial spurs in both sexes; spurs slightly unequal in length, broad or narrow, upper pair up to 1.2 mm long, lower pair up to 1.0 mm; pretarsus with a pair of pulvilli.

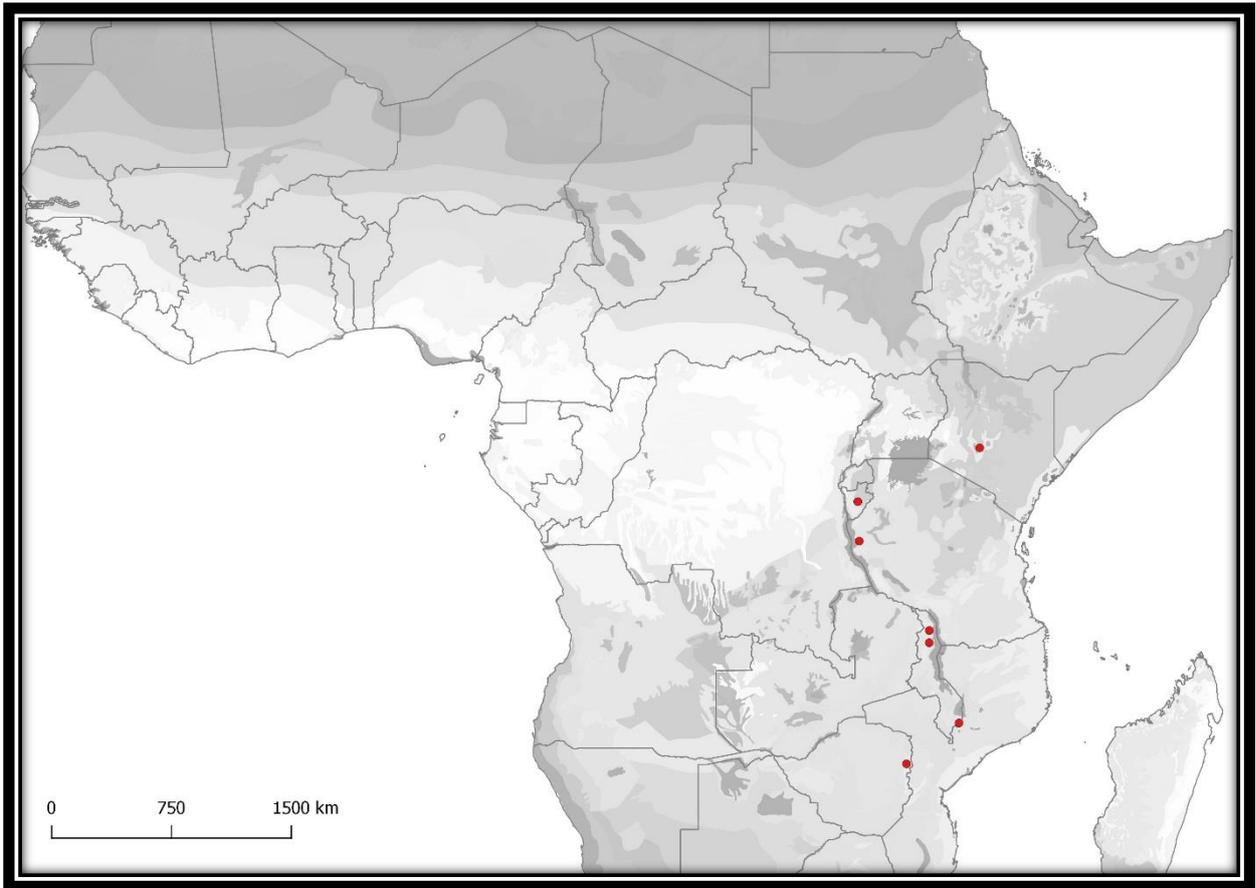
Forewing upperside: with a light cream or light ocher or light orange-ocher ground-colour and slightly glossy towards termen. A geometric design is absent; a rather complex pattern is present in male and comprises a more or less continuous sepia or brown oblique band from near apex via near half of  $CuA_2$  to the dorsum near the base of wing, in female this band is weak or absent; below  $CuA_2$  occur one or several white spots always in male, the spots are sometimes absent in female; along the costal margin occur prominent small sepia spots in male, sometimes absent in female; along termen occur sepia lunules in both sexes; a prominent sepia or dark brown narrow band or line is present from near apex to  $CuA_2$ , it is wavy and nearest to termen from  $M_2$  to  $CuA_2$  in both sexes; this band or line is largely edged white or light cream or light orange-ocher extending into the discal cell as well as towards the base of wing, and only interrupted by few narrow brown lines, in both sexes; below  $CuA_2$  with a dark brown or chestnut brown patch in male. Hindwing is light olive-grey and glossy in both sexes. Fringe is with scales of grey-olive, glossy and rather long (ciliae up to 1.1 mm). Wing venation: variable in forewing since an areole is present or absent in male and/or female of the same species;  $1A+2A$  long forked at base, but fork weak, sometimes the fork is absent in female;  $CuP$  absent;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from apical angle of posterior cell, separated;  $M_1$  initiates from anterior angle of median cell in both sexes;  $R_5+R_4+R_3+R_2$  are stalked and originate from anterior angle of anterior cell or  $R_2$  is separated (in these cases an areole is absent) or, if an areole is present,  $R_5+R_4+R_3$  are stalked and originate from posterior angle of a broad or small areole and  $R_2$  originates from anterior angle of areole;  $R_1$  initiates from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present in both sexes;  $1A+2A$  absent or strongly reduced in both sexes;  $CuP$  present or weak in both sexes;  $CuA_2$  initiating from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind

margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1+R_s$  initiate from apical angle of anterior cell and are stalked, usually long stalked; a bar is present from  $R_s$  to  $Sc+R_1$  in both sexes; a discocellular vein on both forewing and hindwing is present. In forewing the posterior cell is as twice as large as the anterior cell and also longer than the anterior cell; the whole discal cell is of a small size and in length shorter than half of the width of the forewing in both sexes. Retinaculum and frenulum absent.

*Abdomen:* mainly with cream or light grey scales, glossy; abdominal tuft short, 15% of abdomen length in both sexes.

*Male genitalia.* Saccus medium long, half or up to two thirds of the width of valva, broad, tapering towards the rounded tip; the vinculum and tegumen are fused, forming a firm ring, tegumen narrow, vinculum *ca.* two times broader with a large broad and rounded base ventrally (viewed ventrally); uncus rather short, broadly elongated, triangular, longer than width of valva, slightly bifurcated at tip with a large, almost heart-shaped hole that has the size of 30-40% of the size of uncus, ventral side of uncus with many short setae. Valva is rather large, broadly rectangular, sclerotized with a slightly arc-shaped distal margin, inner upper margin of valva with a short prominent row of medium long setae, with an oval-shaped hole-like structure ventral-distally; the valvae are not separated ventrally, but connected by a relatively broad sclerotized band; transtilla absent; semi-transtilla present and very short thorn-like, slightly bent towards the acuminate tip. Two long, sclerotized, sinuate processes, increasingly serrate towards their tip, originate from the same point, a third long sinuate process is close to, all three processes are attached with a narrow band to the upper part of valva as well as somehow to the vinculum. Sacculus is absent. Gnathos is absent. Juxta is absent and probably replaced by a small folded structure that originates from the band that connects the valvae ventrally; the phallus is narrow on its whole length, slightly longer than the ventral width of valva, simple tube-like, not bent; vesica without cornuti.

*Female postabdominal structure and genitalia.* Papillae anales small, dorsal part obliquely 8-shaped or elliptic in posterior view, covered with short setae; segment 8 triangular in shape with the anterior apophyses forming the top of this triangle, rather narrow and small, only slightly setose along its posterior margin with tiny weakly sclerotized setae, not emarginated dorso-anteriorly. The posterior apophyses are very long and narrow, *ca.* three times longer than the anterior apophyses, with a strongly sclerotized T-shaped base. Ductus bursae short and narrow, corpus bursae broad oval, both are thinly membranous; corpus bursae is larger than segment 8 in lateral view and without any processes or other distinct characters.



**FIGURE 169.** Distribution of Gen. Nov. ZJ (red dots).



**FIGURE 170.** Gen. Nov. ZJ, sp. nov. zj, Malawi, Nyika National Park, Kasaramba Forest, 22.December.2011–05.January.2012, R.J. Murphy leg., ex own coll., male, genitalia slide number 29c/052013 I. Lehmann. Wingspan 33.0 mm



**FIGURE 171.** Gen. Nov. ZJ, sp. nov. zj, Malawi, Nyika National Park, Kasaramba Forest, 22.December.2011–05.January.2012, R.J. Murphy leg., ex own coll., female, genitalia slide number 05/032013 Dr. Dieter Stüning. Wingspan 32.5 mm



**FIGURE 172.** Gen. Nov. ZJ, sp. nov. zj4, Burundi, Gitega, 02.10.1968, Dr. M. Fontaine leg., ex RMCA, male, genitalia slide number 05/102014 I. Lehmann. Wingspan 23.0 mm



**FIGURE 173.** Gen. Nov. ZJ, sp. nov. zj5, Kenya, Aberdares Nat. [National] Park, 03.04.2000, [Dr.] Ugo Dall'Asta leg., ex RMCA, female, genitalia slide number 10/102010 I. Lehmann. Wingspan 29.0 mm

#### 4.53 *Janegoodallia* Lehmann, 2014

The genus is defined by the following autapomorphy:

- Largely transparent hindwing and forewing in male, and the transparent parts are covered with tiny scales at least half of them are transparent scales; (120).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; [possibly also absent in female] (11).

Type species of genus (cf. Figure 175): *Janegoodallia + davenporti* Lehmann, 2014

Type locality: Belgian Congo [Democratic Republic of the Congo], Uele-Paulis [Isiro], 09.January.1957, Dr. M. Fontaine leg., male, genitalia slide number 09/102010 I. Lehmann, ex RMCA; depository in RMCA.

Number of species in genus at present: 01

All localities of studied species per country: Democratic Republic of the Congo.

Distribution of genus at present (cf. Figure 174): submontane area at Isiro in the northeastern Democratic Republic of the Congo.

The reconstructed and predicted ancestral area is the Afromontane archipelago-like regional centre of endemism.

The reconstructed biogeographic events comprise: First, dispersal from the Afromontane archipelago-like regional centre of endemism into the Guineo-Congolian regional centre of endemism. Secondly, vicariance between the Afromontane archipelago-like regional centre of endemism and the Guineo-Congolian regional centre of endemism.

Phylogenetic position: The sister genus could not be reconstructed unambiguously.

Description: *Head:* rough-scaled with hair-like as well as broad scales of pale olive-brown below the eyes on fronto-clypeus; a pair of small pits is absent on lower fronto-clypeus, a pair of projections is absent on lower fronto-clypeus; pits behind labial palpi are very narrow slits; labial palpi short, less than eye diameter and consist of three segments, central segment slightly longer than basal segment, the third segment on top is oval and very small; antennae short, bipectinated, branches are narrow and 3.0 × width of shaft, scaled pale olive-brown; flagellum scaled olive-brown.

*Thorax:* Densely covered with hair-like and broader scales of pale olive-brown, glossy, scales on tegulae slightly pronounced with longer scales, some are copper coloured; crest on metathorax cream mixed with light olive. Epiphyses are present, long (1.2 mm), narrow and tube-like. Hindlegs with two pairs of tibial spurs; spurs

slightly unequal in length, narrow, upper pair up to 0.9 mm long, lower pair up to 0.8 mm; pretarsus with a pair of pulvilli.

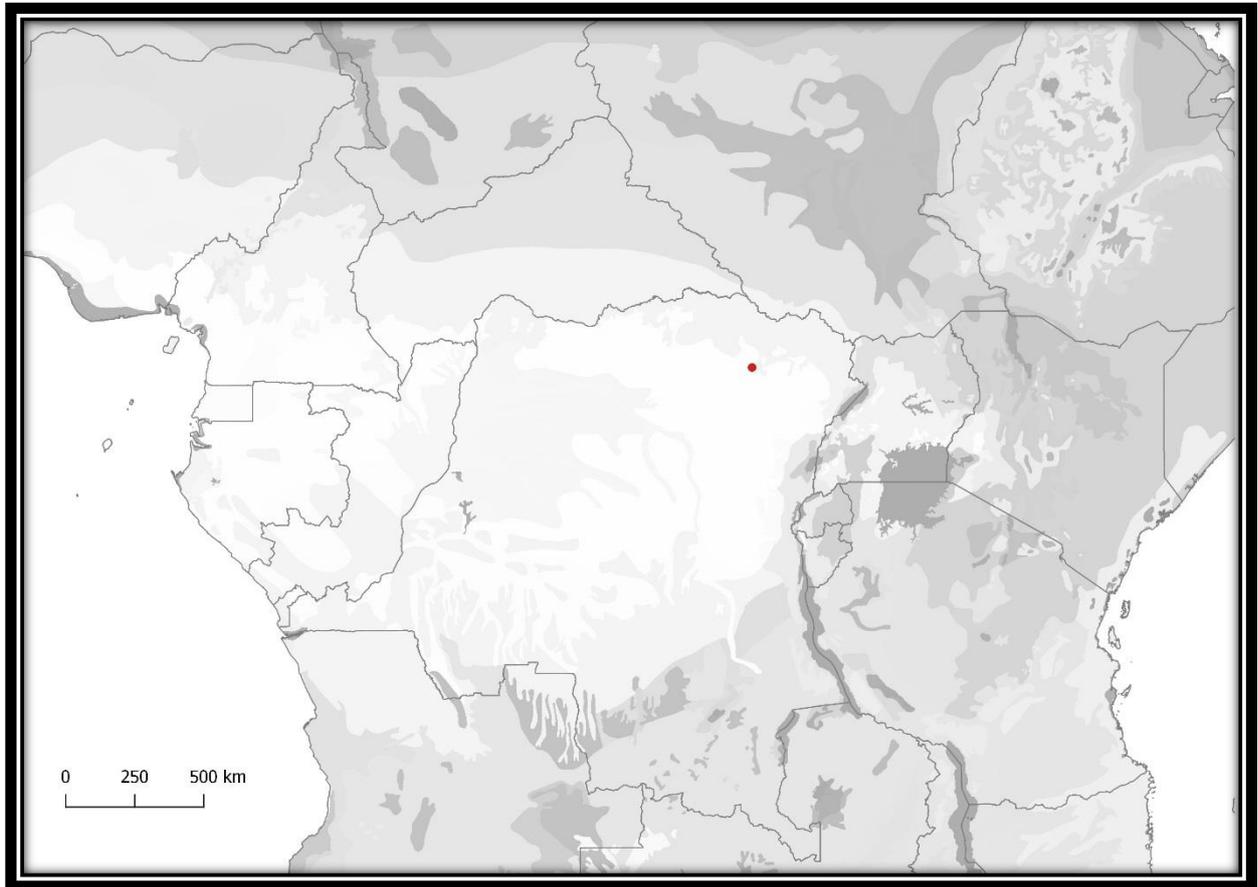
Forewing upperside: largely transparent, the not transparent parts are brown-olive in ground-colour. A geometric design is absent; a simple pattern is present in the central part of forewing and comprises a broad pale brown-olive band from costa to dorsum that is edged black along the transparent parts;  $CuA_2$  is not distinctly marked. Hindwing is largely transparent, along the edges broadly brown-olive. Fringe is very short with scales of olive, glossy (ciliae 0.5 mm long). Wing venation:  $1A+2A$  forked at base, but fork is rudimentary;  $CuP$  absent;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from apical angle of posterior cell, separated;  $M_1$  initiates from posterior vein of areole; areole is narrow rectangular and elongated, relatively large;  $R_5$  originates from posterior angle of areole;  $R_4+R_3$  are stalked and originate also from posterior angle of areole and are slightly separated from base of  $R_5$ ;  $R_2$  originates from anterior angle of areole;  $R_1$  initiates from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  rudimentary without a fork at base;  $CuP$  present but weak;  $CuA_2$  initiating from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1+Rs$  initiate from apical angle of anterior cell and are long stalked; a bar is present from  $Rs$  to  $Sc+R_1$ ; a discocellular vein on forewing is rudimentary but present in hindwing. In forewing the posterior cell is almost of the same size and length like the anterior cell; the whole discal cell is of a small size and in length shorter than half of the width of the forewing. Retinaculum and frenulum absent.

*Abdomen:* mainly with brown-olive scales, slightly glossy; abdominal tuft long and prominent, 30% of abdomen length.

*Male genitalia.* Saccus medium long, half of the width of valva, broad, not tapering towards the rounded tip; the vinculum and tegumen are fused, forming a firm ring, tegumen very narrow, vinculum *ca.* three times broader with a large broad and rounded base ventrally (viewed ventrally); uncus long, broadly elongated, triangular, longer than width of valva, slightly bifurcated at tip with two small oval shaped holes below the tip, ventral side of uncus with few short setae, longer setae along its edge. Valva is large, broadly squarish, sclerotized with an arc-shaped distal margin and a weakly sclerotized skin-like appendage dorso-distally and with a small narrow elongated appendice ventral-distally; the valvae are not completely separated ventrally but narrowly connected to a broad sclerotized band; transtilla absent; semi-transtilla present and very short, rectangular. Two long, sclerotized, sinuate processes (relicts of a gnathos?), a narrow and short one (not serrate) and a three times larger and long one (slightly serrate ventrally), originate from nearly the same point and are attached to a narrow band that is connected to the lower part of the tegumen; this narrow band becomes very broad between the tegumen (viewed ventrally). Sacculus is absent. Gnathos is absent. Juxta is probably absent and appears to be replaced by a large and

wide folded structure that originates from the band that connects narrowly the valvae ventrally; the phallus is narrow basally, broader distally, almost twice as long as the ventral width of valva, simple tube-like, not bent; vescica without cornuti.

*Female postabdominal structure and genitalia. Unknown.*



**FIGURE 174.** Distribution of the genus *Janegoodallia* (red dot).



**FIGURE 175.** *Janegoodallia davenporti*, Holotype, Belgian Congo [Democratic Republic of the Congo], Uele-Paulis [Isiro], 09.January.1957, Dr. M. Fontaine leg., ex RMCA, male, genitalia slide number 09/102010 I. Lehmann. Wingspan 25.0 mm

#### 4.54 *Marshalliana* Aurivillius, 1901

The genus is defined by the following autapomorphy:

- Very small discal cell in forewing (less than 15% of forewing size) with the anterior part of discal cell only half or slightly less than half of the length of antenna in both sexes; (122).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of both sexes; (11).

Type species of genus (cf. Figure 177): *Marshalliana + bivittata* Aurivillius, 1901

Type locality: Type with four labels: first, “Marshallia Typ. bivittata Aur.”, second “Mashuna” [Zimbabwe], third “E. Umtali Mashu.” [Old Umtali or Umtali?, cf. Chipangura 2013], fourth “Marshall” [leg.], [no date, but most probably collected between 1894 and 1900], male, genitalia slide number 03/122017 I. Lehmann, ex NRM; depository in NRM.

Type locality of female, description herein (cf. Figure 178): *Marshalliana + jansei* Gaede, 1929: Type, [Republic of South Africa], Transv. [Transvaal], Johannisb. [Johannisburg], [no date], S. Wichgraf & V. Lück-Gehlen leg., genitalia slide number 21/122009 I. Lehmann, ex ZMHU; depository in ZMHU.

Number of species in genus at present: 49

All localities of studied species per country: Ivory Coast; Cameroon; Central African Republic; Democratic Republic of the Congo; Republic of South Sudan; Ethiopia; Uganda; Kenya; Tanzania; Rwanda; Burundi; Malawi; Mozambique; Zimbabwe; Republic of South Africa; Angola.

Distribution of genus at present (cf. Figure 176): one of the largest, rather continuous distribution ranges among Metarbelidae in montane, submontane and (rarely?) lowland areas from the northern Ivory Coast eastwards via the southern Central African Republic, Republic of South Sudan to south-central Ethiopia; from Cameroon to northwest Angola, from the eastern and southern parts of the Democratic Republic of the Congo, the whole of Uganda, Rwanda, Burundi to western Tanzania (eastwards to the Uluguru and Udzungwa Mountains); from western and central Kenya to Malawi, eastern Zimbabwe and central Mozambique; further south to northeastern parts of the Republic of South Africa.

The reconstructed and predicted ancestral area is the Afromontane archipelago-like regional centre of endemism.

The reconstructed biogeographic events comprise: First, dispersal in the Afromontane archipelago-like regional centre of endemism. Secondly, dispersal from the Afromontane archipelago-like regional centre of endemism into the Guineo-Congolian regional centre of endemism, the Zambezian regional centre of endemism, the

Sudanian regional centre of endemism, the Guinea-Congolia/Sudania regional transition zone, the Guinea-Congolia/Zambezia regional transition zone, the Lake Victoria regional mosaic, the Kalahari regional transition zone. Thirdly, vicariance between the Afromontane archipelago-like regional centre of endemism and all other phytochoria mentioned above.

Phylogenetic position: The sister genus could not be reconstructed unambiguously.

Description: *Head*: rough-scaled with hair-like as well as broad scales of pale olive-brown or ocher or light cream below the eyes on fronto-clypeus; a pair of small pits is absent on lower fronto-clypeus, a pair of projections is absent on lower fronto-clypeus in both sexes; pits behind labial palpi are relatively large holes, oval in shape in both sexes; labial palpi long, as long as eye diameter and consist of three segments, central segment 1.5 × as long as basal segment, the third segment on top is elongated oval and small in both sexes; antennae very long in male, slightly shorter in female, bipectinated in both sexes; branches are narrow and 3.5 × width of shaft in male but only 2.0 × width of shaft in female, scaled cream; flagellum scaled cream.

*Thorax*: Densely covered with mainly hair-like scales, broader scales few, of pale olive-brown or ocher or cream, glossy in both sexes, scales on tegulae slightly pronounced with longer scales; crest on metathorax cream mixed with light olive. Epiphyses are present in both sexes, short (up to 1.0 mm in male, up to 0.9 mm in female), narrow and shorter in female, relatively thick in male, tube-like in both sexes. Hindlegs with two pairs of tibial spurs in both sexes; spurs slightly unequal in length, narrow, upper pair up to 1.2 mm long, lower pair up to 0.9 mm; pretarsus with a pair of pulvilli.

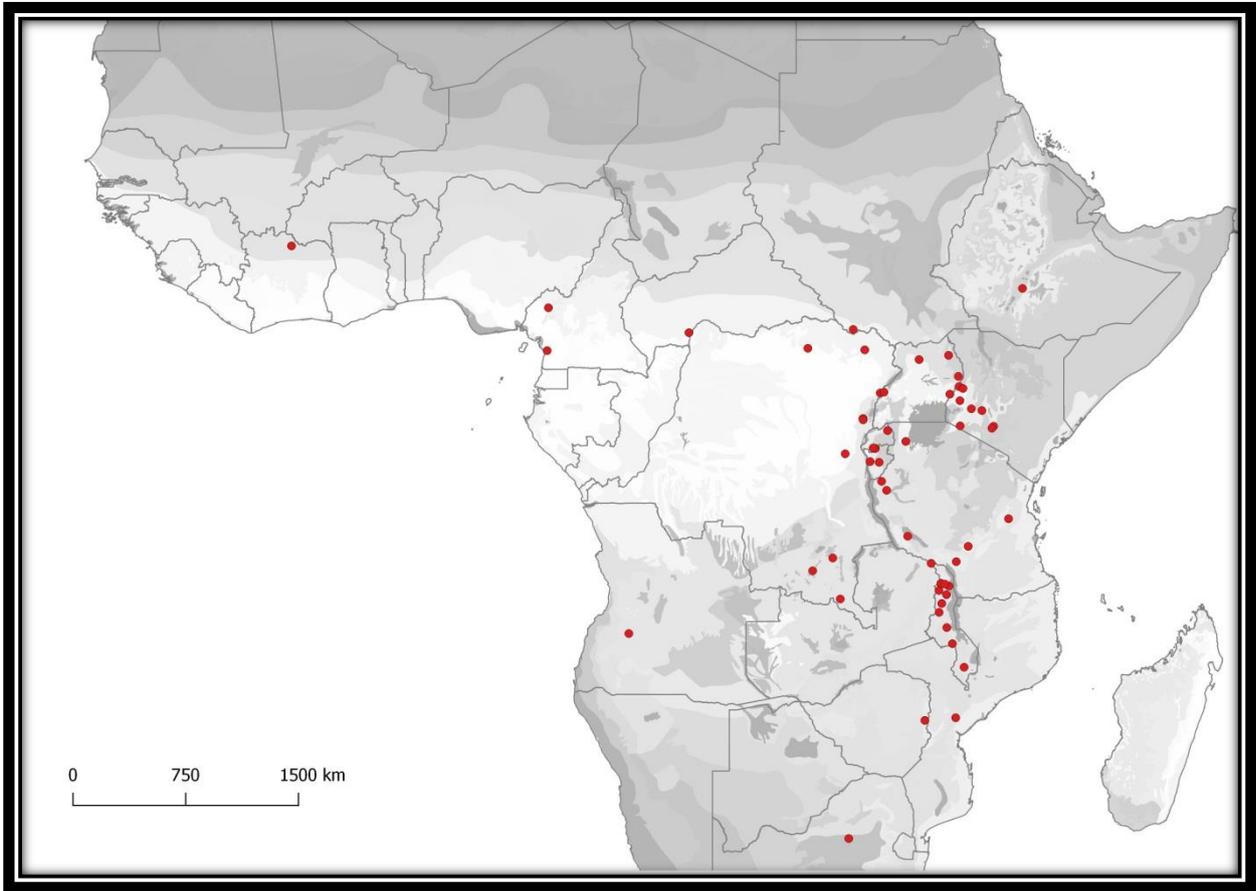
Forewing upperside: light grey or light chestnut-olive mixed with a light brown-olive ground-colour in both sexes, usually glossy. A geometric design is absent; a simple pattern is present but variable and comprises usually dark brown spots along the costal margin, dark brown lunules along the termen and in the majority of studied specimens a large dark brown patch from base of wing to  $CuA_2$  and below discal cell; a narrow pale brown-olive band occurs usually from near apex to the end of  $CuA_2$  that is sharply bent inwards between  $R_5$  and  $M_2$  in both sexes; half of discal cell is sometimes dark brown and/or the posterior part of discal cell is light cream; usually half of lower median and the entire length of  $CuA_2$  are pure white with one or more small pure white spots below  $CuA_2$ , and hence,  $CuA_2$  is distinctly marked. Hindwing is light grey-olive or light brown-olive. Fringe is very long with scales of light grey-olive, glossy (ciliae up to 1.6 mm long). Wing venation:  $1A+2A$  forked at base;  $CuP$  absent;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from apical angle of posterior cell, separated;  $M_1$  initiates from near apical angle of anterior cell;  $R_5+R_4+R_3+R_2$  are stalked and originate from apical angle of anterior cell;  $R_1$  initiates from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  rudimentary or absent;  $CuP$

present but usually weak; CuA<sub>2</sub> initiating from about half of lower median of posterior cell; CuA<sub>1</sub> initiates from hind margin of posterior cell; M<sub>3</sub> and M<sub>2</sub> initiating from apical angle of posterior cell, separated; M<sub>1</sub>+Rs initiate from apical angle of anterior cell and are long or short stalked, rarely M<sub>1</sub>+Rs are not stalked but originate from nearly the same basal point; a bar is present from Rs to Sc+R<sub>1</sub>; a discocellular vein on forewing and hindwing is present. In forewing the whole discal cell is of a very small size and less than 15% of forewing size. Retinaculum and frenulum absent.

*Abdomen:* mainly with light grey-olive or brown-olive scales, glossy; abdominal tuft medium long, 20% of abdomen length.

*Male genitalia.* Saccus long, broad, almost as long as ventral width of valva, not tapering towards the rounded tip; the vinculum and tegumen are fused, forming a firm ring, tegumen slightly narrower than vinculum; uncus long, narrowly elongated, triangular, longer than width of valva, slightly bifurcated at tip, on each side of uncus occurs a long well sclerotized hollow tube-like structure with many short setae, long setae originate from the dorsal edge of uncus. Valva is large with a strongly oblique costal margin (bent downwards) and a short rounded distal margin near the ventral edge of valva (viewed laterally and only visible if the genitalia is not pressed); a weakly sclerotized skin-like structure represents the outer valva with short setae, the inner valva is strongly sclerotized and with long setae ventrally, a large hollow space occurs in between the inner and outer valva; a semi-transtilla is absent but seems to be replaced by a thinly sclerotized band (with short setae at its base) that is attached to the costal margin of the outer valva and somehow to the lower half of vinculum; the inner valvae are not separated ventrally but connected with a medium broad sclerotized band (sometimes rather thinly sclerotized). Transtilla is absent. Sacculus is absent. Gnathos is absent. Juxta appears to be absent and is replaced by a small folded structure that originates from the middle of the band that connects the inner valvae ventrally; the phallus is narrow, twice as long as the ventral width of valva, simple tube-like, not bent; vesica without cornuti.

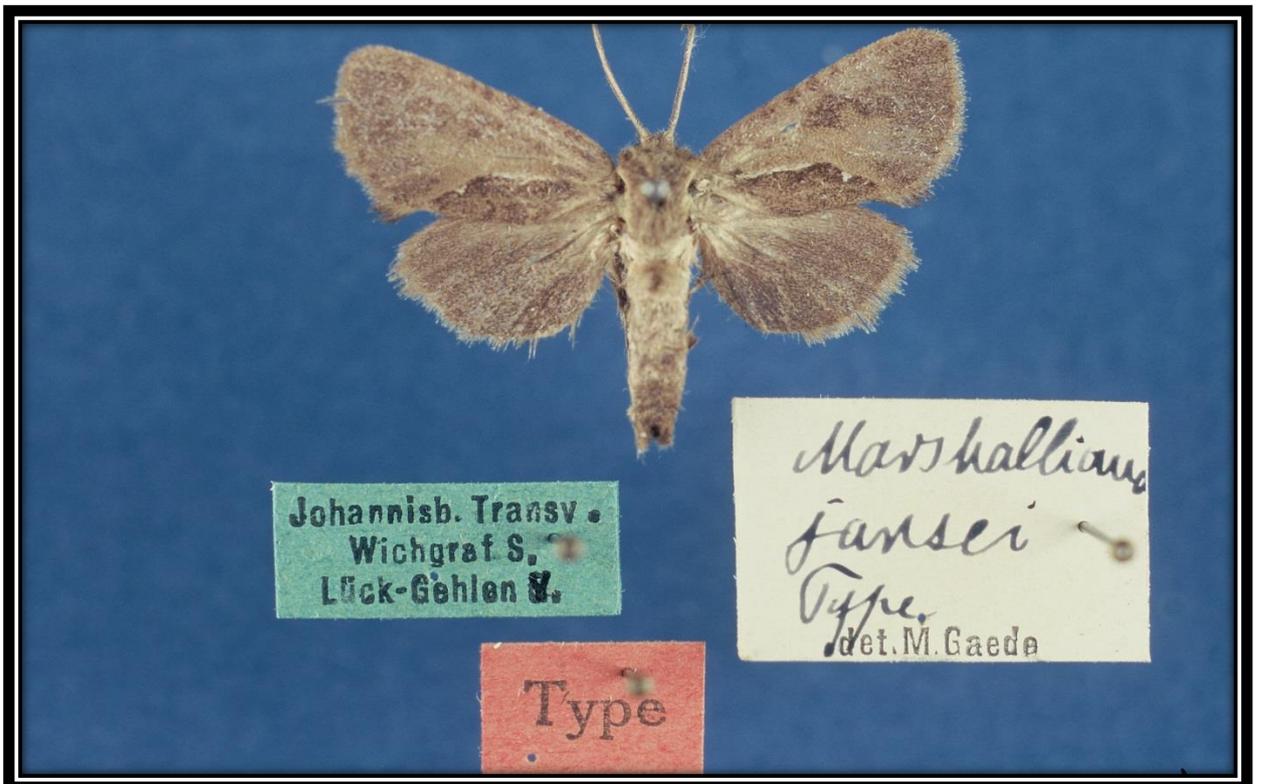
*Female postabdominal structure and genitalia.* Papillae anales rather large, dorsal part obliquely 8-shaped or elliptic in posterior view, covered with many short as well as long setae; segment 8 narrowly band-like in shape, not setose, including the posterior margin, and not emarginated dorso-anteriorly. Sometimes occurs a small patch of tiny setae near the base of the anterior apophyses and a very narrow slit in the centre of segment 8. The posterior apophyses are very long and narrow, almost 2.0 × longer than the narrow anterior apophyses, with a strongly sclerotized and mainly narrow T-shaped base. Ductus bursae long (1.5 × as long as corpus bursae) and narrow; corpus bursae broad and rather round or broadly oval in shape; ductus bursae and corpus bursae are thinly membranous; corpus bursae is 2.5 × larger than segment 8 in lateral view and without any processes or other distinct characters.



**FIGURE 176.** Distribution of the genus *Marshalliana* (red dots).



**FIGURE 177.** *Marshalliana bivittata*, Type, Mashuna [Zimbabwe], E. Umtali [Umtali or Old Umtali?], Marshall [leg.], [no date], ex NRM, male, genitalia slide number 03/122017 I. Lehmann. Wingspan 31.0 mm



**FIGURE 178.** *Marshalliana jansei* Gaede, 1929, Type, [Republic of South Africa], Transv. [Transvaal], Johannisb. [Johannisburg], [no date], S. Wichgraf & V. Lück-Gehlen leg., ex ZMHU, female, genitalia slide number 21/122009 I. Lehmann. Wingspan 27.5 mm



**FIGURE 179.** *Marshalliana* sp. nov.19, Angola, Caconda, 13.10.1930, Romieux [?] leg., ex MNHN, male, genitalia slide number 019/122017 I. Lehmann. Wingspan 37.0 mm



**FIGURE 180.** *Marshalliana* sp. nov.20, [Central African Republic], Oubangui [Bangui?], 26.05.1929, Romieux [?] leg., ex MNHN: "1920 Coll. R. Homberg Muséum Paris", male, genitalia slide number 020/122017 I. Lehmann. Wingspan 26.0 mm

#### 4.55 *Metarbela* Holland, 1893

The genus is defined by the following autapomorphies:

- Valvae are extremely thinly membranous and small but are attached to a strongly sclerotized large spoon-like appendice that has a keel line ventrally; (79);
- large, hollow, strongly sclerotized thorn-like appendice on ventral inner side of valva (not an extension of the sacculus) that is broadly connected to the strongly sclerotized band that links both valva; (83).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; [possibly also absent in female] (11).

Type species of genus: *Metarbela + stivafer* Holland, 1893

Type locality: [Gabon], Valley of the Ogooué River;

Note: no other data available from labels of one holotype male and 12 male paratypes, depository in CMNH; studied specimen collected closest to type locality (*cf.* Figure 182): *Metarbela* sp. nov.1, Republic of the Congo, Odzala National Park, 400–500 m, 29.01.–03.03.1997, S. Murzin & V. Siniaev leg., male, genitalia slide number 30/102014 I. Lehmann, ex MWM; depository in ZSM.

Number of species in genus at present: 07

All localities of studied species per country: Cameroon; Central African Republic; Gabon; Democratic Republic of the Congo; Republic of the Congo.

Distribution of genus at present (*cf.* Figure 181): lowland and lower submontane areas within the present boundaries of the tropical rain forest of the Guineo-Congolian regional centre of endemism, extending from the southern Central African Republic and southern Cameroon southwards through Gabon and the Republic of the Congo to the southwestern and south-central Democratic Republic of the Congo. The most eastern record exists from Isiro (northeastern Democratic Republic of the Congo) and hence, species of *Metarbela* are at present absent from rain forests in Upper Guinea. The reconstructed and predicted ancestral area is the Guineo-Congolian regional centre of endemism.

The reconstructed biogeographic events comprise: First, dispersal in the Guineo-Congolian regional centre of endemism. Secondly, vicariance in the Guineo-Congolian regional centre of endemism.

Phylogenetic position: The sister genus could not be reconstructed unambiguously. The genus is part of a monophylum together with the new genera ZK, ZL, ZM and *Metarbela*, *Dianfosseya* and *Aethiopina*.

Synapomorphies shared with Gen. Nov. ZK, Dianfosseya, Aethiopina, Gen. Nov. ZL and Gen. Nov. ZM:

- Valvae not separated, but almost entirely connected by a broad sclerotized band ventrally; (80);
- Large uncus triangular-shaped and almost as large as valva (ventral view); (177).

Description: *Head:* rough-scaled with hair-like as well as broad scales of pale ocher or light cream mixed with dark brown below the eyes on fronto-clypeus; a pair of small rudimentary pits is present on lower fronto-clypeus, a pair of projections is usually present on lower fronto-clypeus in male; pits behind labial palpi are small narrow slits or absent; labial palpi short, half of eye diameter and consist of two segments, upper segment oval and  $1.2 \times$  as long as basal segment, rarely a tiny rudimentary third segment on top is present; antennae short in male, bipectinated; branches are narrow and  $2.5 \times$  width of shaft in male, densely scaled cream; flagellum densely scaled cream.

*Thorax:* Densely covered with mainly hair-like scales, broader scales few, of light cream or light ocher, glossy in male, scales on patagia usually light grey mixed with light cream, tegulae pronounced with longer scales, upper half is light cream or white, lower half light ocher or light orange-ocher; small crest on metathorax cream or light orange-ocher, glossy. Epiphyses are present and needle-like, long (up to 1.5 mm in male), narrow. Hindlegs with two pairs of tibial spurs; spurs slightly unequal in length, narrow, upper pair up to 1.0 mm long, lower pair up to 1.1 mm; pretarsus with a pair of pulvilli.

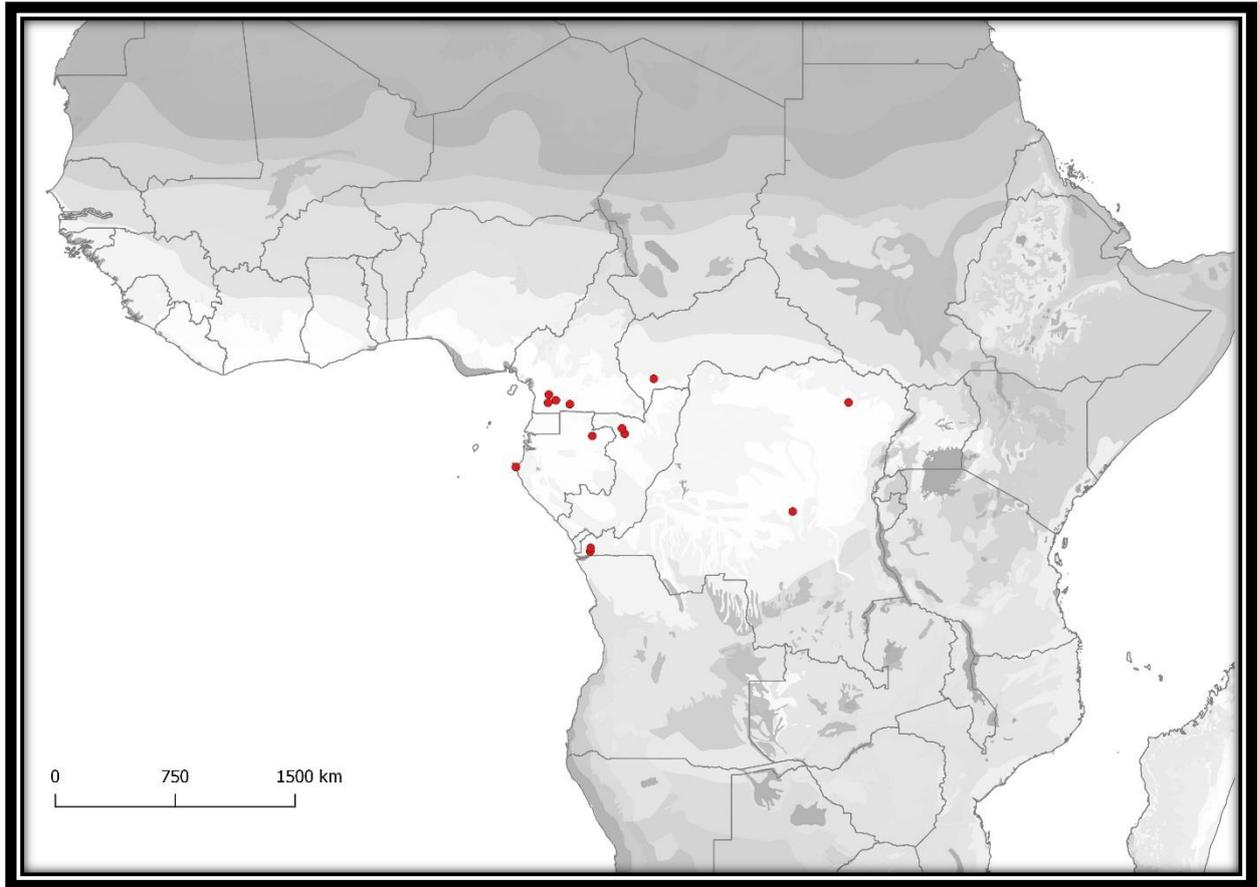
Forewing upperside: light yellow or light orange-ocher mixed with a light grey-olive ground-colour, only glossy towards termen. A simple geometric design is present and comprises a pronounced wave-like pure white band that covers the first half of  $1A+2A$  and then turns upwards to the base of  $CuA_2$  and follows  $CuA_2$  to the dorsum; hence,  $CuA_2$  is always distinctly marked pure white; where this white band meets the base of  $CuA_2$  is a dark brown patch below, usually triangular in shape; a simple pattern is present but more or less faded and comprises a brown subterminal band that is bent inwards between  $M_1$  and  $R_5$  (this band is sometimes entirely absent), light grey-olive patches near the termen and below  $1A+2A$  as well as a white narrow band along termen with a glint shine and without any markings. Hindwing is light grey-olive, glossy. Fringe is short with scales of light ocher, glossy (ciliae up to 0.9 mm long). Wing venation:  $1A+2A$  not forked at base or only weakly forked;  $CuP$  absent;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from the same basal point of apical angle of posterior cell;  $M_1$  initiates from hind margin of anterior cell;  $R_5+R_4+R_3$  are shortly stalked or  $R_5$  originates from the same basal point with  $R_3+R_4$  from posterior angle of areole; the areole is narrow elongated;  $R_2$  initiates from anterior angle of areole;  $R_1$  initiates from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  rudimentary or absent;  $CuP$  present;  $CuA_2$  initiates from two-thirds

of lower median of posterior cell; CuA<sub>1</sub> initiates from hind margin of posterior cell; M<sub>3</sub> and M<sub>2</sub> initiating from apical angle of posterior cell, separated; M<sub>1</sub>+Rs initiate from apical angle of anterior cell and are usually long stalked; a bar is present from Rs to Sc+R<sub>1</sub>; a discocellular vein on forewing and hindwing is present, sometimes weak in forewing. In forewing the whole discal cell is of a medium size and not longer than half of the width of wing; posterior cell with an almost acuminate apical angle and slightly longer and larger than anterior cell. Retinaculum and frenulum absent.

*Abdomen:* mainly with light ocher or ocher scales, glossy; abdominal tuft ocher, long, 30% of abdomen length.

*Male genitalia.* Saccus long, broad, large (up to half the size of the valva), sometimes tapering towards the rounded tip or broadly rounded at tip; the vinculum and tegumen are fused, forming a firm ring, tegumen and vinculum narrow, but vinculum becomes very broad ventrally, along most of the narrow parts of both has the distal margin many tiny setae; uncus short, broad, bifurcated at tip, emargination with rounded base, tips broadly rounded; uncus dorsally with two small hill-like structures (viewed laterally). Valvae are small, rectangular and very thinly membranous, soft in appearance, with few setae distally, distal edge wave-like. Each valva is attached to a strongly sclerotized large spoon-like appendice, that has a keel line ventrally and long setae near its base, it is attached to a strongly sclerotized band; valvae not separated but linked through this strongly sclerotized band ventrally; a large, hollow, strongly sclerotized thorn-like appendice occurs on the inner side of valva ventrally (not an extension of the sacculus) that is broadly connected to the strongly sclerotized band that links both valva. Sacculus is absent. Transtilla is absent. Semi-transtilla is absent. Gnathos is absent. Juxta is a rather thinly sclerotized hollow ring with many short and long setae that occurs above the strongly sclerotized band; the phallus is very large, twice as long as the ventral width of valva, bent in the middle, basal half is thinly sclerotized with many tiny dots and few tiny setae, the distal half is more sclerotized has a rounded tip and is without dots and setae, the central part has a skin-like ring with tiny dots; vesica without cornuti. Above the base of the phallus occurs in lateral view a small thinly membranous, often ear-shaped, structure with tiny dots.

*Female postabdominal structure and genitalia.* Unknown.



**FIGURE 181.** Distribution of the genus *Metarbela* (red dots).



**FIGURE 182.** *Metarbela* sp. nov.1, Republic of the Congo, Odzala National Park, 29.01.–03.03.1997, S. Murzin & V. Siniaev leg., ex MWM, male, genitalia slide number 09/112014 I. Lehmann. Wingspan 27.5 mm



**FIGURE 183.** *Metarbela* sp. nov.5, [Democratic Republic of the Congo] Sankuru, Katakoko-Kombe, 25.08.1952, Dr. M. Fontaine leg., ex RMCA, male, genitalia slide number 24/122014 I. Lehmann. Wingspan 30.0 mm

#### 4.56 Gen. Nov. ZK

The genus is defined by the following autapomorphy:

- A very large and elongated (35% the size of valva) thorn-like semi-transtilla (with an acuminate end) originates from a skin-like, weakly sclerotized costal margin of valva; (148).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; [possibly also absent in female] (11).

Type species of genus (cf. Figure 185): Gen. Nov. ZK + spec. nov. zk

Type locality: Djibouti, Mabla Mountains, 873 m, 13.02.2015, Dirk Stadie leg., male, genitalia slide number 29/082017 I. Lehmann, ex coll. Dirk Stadie; depository in ZSM.

Number of species in genus at present: 01

All localities of studied species per country: Djibouti.

Distribution of genus at present (cf. Figure 184): submontane area in the Mabla Mountains of eastern Djibouti (northeastern Africa).

The reconstructed and predicted ancestral areas are the Guineo-Congolian regional centre of endemism and the Afromontane archipelago-like regional centre of endemism.

The reconstructed biogeographic events comprise: First, dispersal in the Guineo-Congolian regional centre of endemism and the Afromontane archipelago-like regional centre of endemism. Secondly, vicariance between the Guineo-Congolian regional centre of endemism and the Afromontane archipelago-like regional centre of endemism.

Phylogenetic position: The sister genus is *Dianfosseya*.

The genus is part of a monophylum together with the new genera ZL, ZM, ZK and *Metarbela*, *Dianfosseya* and *Aethiopina*.

Synapomorphy shared with *Dianfosseya*:

- An oval-shaped projection is present ventral distally that looks like a piece of fur with short setae on a straight surface; (106).

Synapomorphies shared with *Metarbela*, *Dianfosseya*, *Aethiopina*, Gen. Nov. ZL and Gen. Nov. ZM:

- Valvae not separated, but almost entirely connected by a broad sclerotized band ventrally; (80);
- Large uncus triangular-shaped and almost as large as valva (ventral view); (177).

Description: *Head:* rough-scaled with mainly hair-like as well as broad scales of light grey mixed with cream below the eyes on fronto-clypeus; a pair of small rudimentary pits is present on lower fronto-clypeus, a pair of projections is absent on lower fronto-clypeus in male; pits behind labial palpi are small narrow slits; labial palpi short, half of eye diameter and consist of three segments, central segment almost rectangular and  $1.2 \times$  as long as basal segment, a tiny third segment on top is present and oval shaped; antennae short in male, bipectinated; branches are narrow and  $3.0 \times$  width of shaft in male, densely scaled cream; flagellum densely scaled cream.

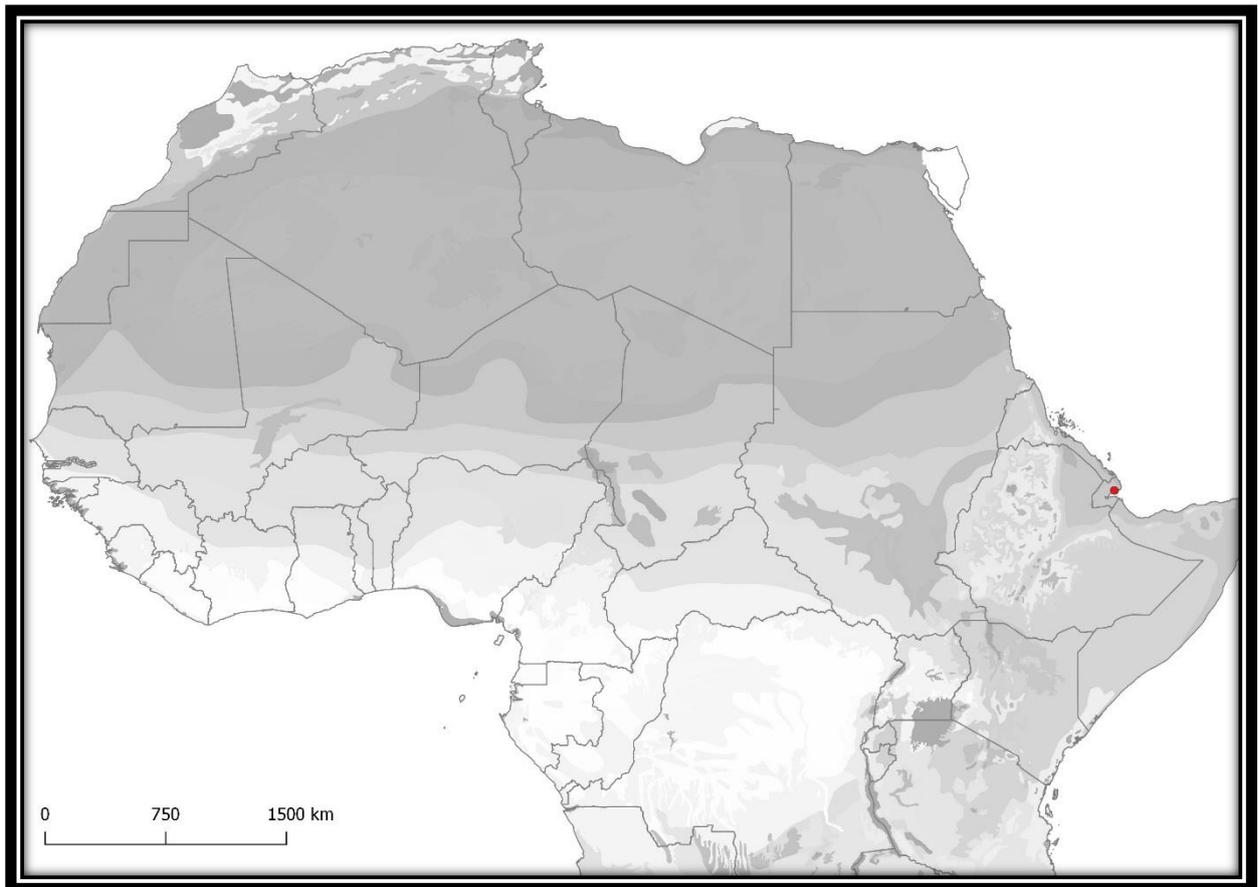
*Thorax:* Densely covered with mainly hair-like scales, broader scales few, of light grey, slightly glossy in male, scales on patagia light grey, tegulae slightly pronounced with longer scales of dark grey with white tips; small crest on metathorax sepia, slightly glossy. Epiphyses are present and very long (up to 1.7 mm in male), narrow, tube-like. Hindlegs with two pairs of tibial spurs; spurs slightly unequal in length, narrow, upper pair up to 0.5 mm long, lower pair up to 0.9 mm; pretarsus with a pair of pulvilli.

Forewing upperside: light grey ground-colour, not glossy with very long hair-like scales above normal scale layer, grey-white, not curled, occur densely in a horizontal position on the whole upperside. A simple geometric design is present and comprises a pronounced wave-like sepia band, representing an almost oblique "S", that originates near the base of wing above the dorsum and then turns upwards close to the base of  $CuA_2$  and ends as a curled line in the basal part of the discal cell;  $CuA_2$  is extremely narrowly marked pure white with a large white patch at its end. A simple pattern is present and comprises a sepia subterminal band that is serrate and is slightly bent inwards between  $M_1$  and  $R_5$ , a grey-olive patch occurs above two-thirds of  $CuA_2$  to the base of  $M_2$  and faded grey lunules are present along the termen. Hindwing is white with light grey-olive veins, glossy. Fringe is long with scales of light grey, glossy (ciliae up to 1.1 mm long). Wing venation:  $1A+2A$  forked at base but the fork is weak;  $CuP$  absent;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate almost from the same basal point of apical angle of posterior cell, slightly separated;  $M_1$  initiates from hind margin of anterior cell;  $R_5$  originates almost from the same basal point with  $R_4+R_3$  that are long stalked originating from posterior angle of areole; the areole is elongated and large, half the size of anterior cell;  $R_2$  initiates from anterior angle of areole;  $R_1$  initiates from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  rudimentary;  $CuP$  present;  $CuA_2$  initiates from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1+R_s$  initiate from apical angle of anterior cell and are long stalked; a bar is present from  $R_s$  to  $Sc+R_1$ ; a discocellular vein on forewing and hindwing is present, weak in forewing. In forewing the whole discal cell is of a medium size and not longer than half of the width of wing; posterior cell as well as anterior cell with an almost acuminate apical angle, the former is slightly longer and larger than anterior cell. Retinaculum and frenulum absent.

*Abdomen:* mainly with light grey mixed with cream scales, glossy; abdominal tuft cream, short, 20% of abdomen length.

*Male genitalia.* Saccus short, broad, small (up to 20% the size of the valva), rounded at tip; the vinculum and tegumen are fused, forming a firm ring, tegumen narrow, vinculum twice as broad as tegumen, becomes broad ventrally; uncus long triangular, narrow, bifurcated at tip, emargination small with rounded base, tips acuminate; along the edge of uncus medium long setae. Valvae are large, oblique rectangular with a broad thinly membranous costal margin, distal edge C-shaped, dorso-ventrally occurs a long row of dots with many tiny setae. Each valva is attached to a sclerotized large band ventrally and hence, the valvae are not separated; the whole valva surface has ventrally and distal ventrally many tiny dots mainly without setae mixed with few short setae (best visible if viewed laterally); a fur-like structure occurs distal ventrally and is not an extension of the sacculus. Sacculus is absent. Transtilla is absent. Semi-transtilla is very large (35% the size of valva) and thorn-like, this results in a very wide basal width of valva (longer than aedeagus). Gnathos is absent. Juxta is a rather thinly sclerotized folded structure that occurs on the sclerotized band; the phallus is large, broad, but shorter in length than basal width of valva, not bent, without dots and setae; vesica without cornuti.

*Female postabdominal structure and genitalia.* Unknown.



**FIGURE 184.** Distribution of Gen. Nov. ZK (red dot).



**FIGURE 185.** Gen. Nov. ZK, sp. nov.zk, Djibouti, Mabla Mountains, 13.02.2015, Dirk Stadie leg., ex coll. Dirk Stadie, male, genitalia slide number 29/082017 I. Lehmann. Wingspan 21.5 mm

#### 4.57 *Dianfosseya* Lehmann, 2014

The genus is defined by the following autapomorphies:

- An oval, large tail-like projection (it has 30% the size of the saccus) is present on valva ventral distally and looks like a piece of fur with short setae; (107);
- A well sclerotized valva with an outer edge (including costal margin and distal margin) that is strongly arc-shaped; (108).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; [possibly also absent in female] (11).

Type species of genus (cf. Figure 187): *Dianfosseya + leakeyi* Lehmann, 2014

Type locality: Belgian Congo [Democratic Republic of the Congo], Uele: Paulis [Isiro], 750 m, 03.04.1957, Dr. M. Fontaine leg., male, genitalia slide number 27/102013 I. Lehmann, ex COLL. MUS. [Collection Museum] CONGO [RMCA]; depository in RMCA.

Number of species in genus at present: 01

All localities of studied species per country: Democratic Republic of the Congo.

Distribution of genus at present (cf. Figure 186): lower submontane area in the northeastern Democratic Republic of the Congo at Isiro.

The reconstructed and predicted ancestral areas are the Guineo-Congolian regional centre of endemism and the Afromontane archipelago-like regional centre of endemism.

The reconstructed biogeographic events comprise: First, dispersal in the Guineo-Congolian regional centre of endemism and the Afromontane archipelago-like regional centre of endemism. Secondly, vicariance between the Guineo-Congolian regional centre of endemism and the Afromontane archipelago-like regional centre of endemism.

Phylogenetic position: The sister genus is Gen. Nov. ZK.

The genus belongs to a monophylum together with the new genera ZK, ZL, ZM and *Metarbela*, *Dianfosseya* and *Aethiopina*.

Synapomorphy shared with Gen. Nov. ZK:

- An oval-shaped projection is present on valva ventral distally that looks like a piece of fur with short setae on a straight surface; (106).

Synapomorphies shared with *Metarbela*, *Aethiopina*, Gen. Nov. ZL, ZK and ZM:

- Valvae not separated, but almost entirely connected by a broad sclerotized band ventrally; (80);
- Large uncus triangular-shaped and almost as large as valva (ventral view); (177).

Description: *Head:* rough-scaled with mainly hair-like as well as broad scales of light brown mixed with chestnut, glossy, below the eyes on fronto-clypeus; a pair of pits is absent on lower fronto-clypeus, a pair of projections is absent on lower fronto-clypeus in male; pits behind labial palpi are small narrow, slightly oval shaped slits; labial palpi short, half of eye diameter and consist of two segments, upper segment oval and  $1.2 \times$  as long as basal segment; antennae short in male, bipectinated; branches are narrow and  $3.0 \times$  width of shaft in male, scaled light brown; flagellum densely scaled light brown.

*Thorax:* Densely covered with mainly hair-like scales, broader scales few, brown, glossy in male, scales on patagia chestnut coloured, tegulae slightly pronounced with longer scales of chestnut and light brown above; small crest on metathorax sepia mixed with light brown, glossy. Epiphyses are present and very long (1.9 mm in male), narrow, tube-like. Hindlegs with two pairs of tibial spurs; spurs unequal in length, narrow, upper pair up to 1.2 mm long, lower pair up to 1.1 mm; pretarsus with a pair of pulvilli.

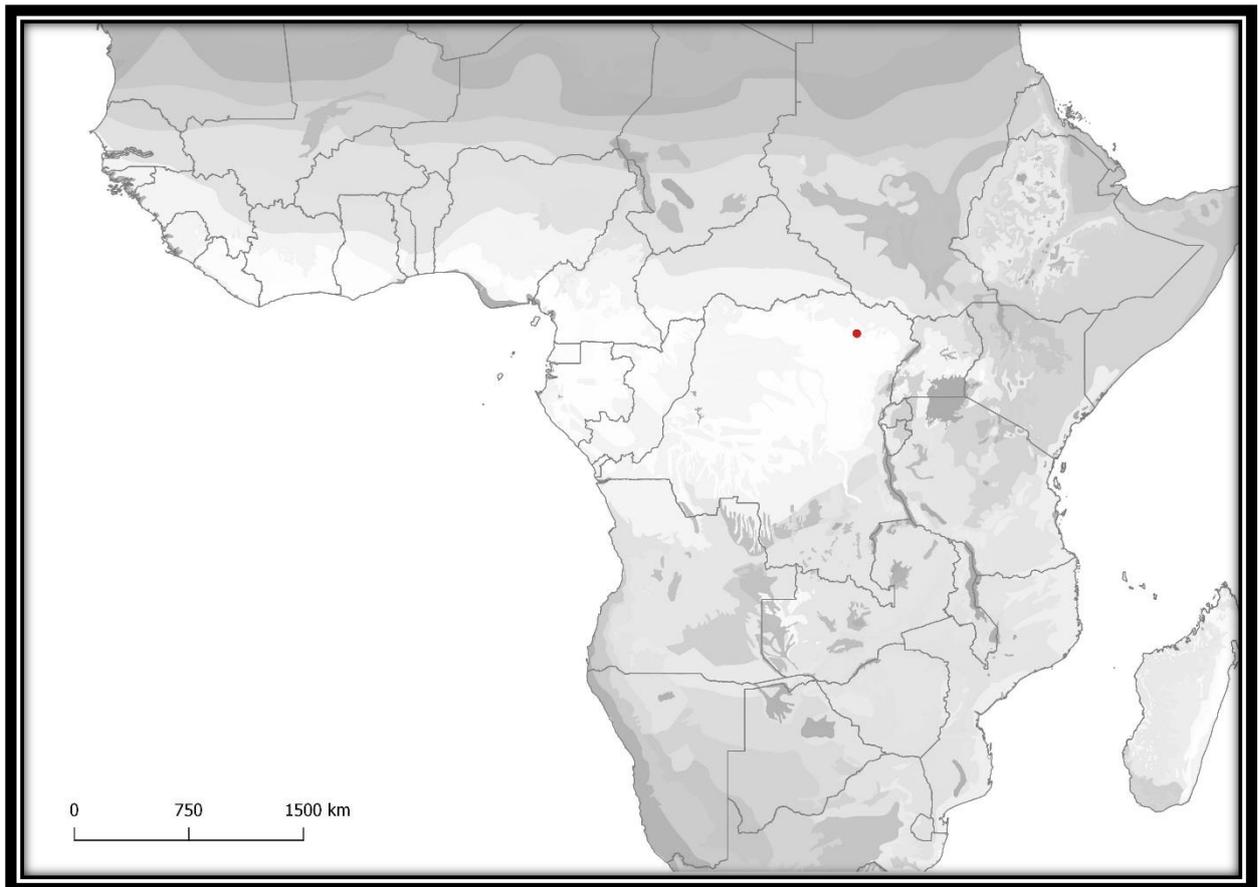
Forewing narrow elongated in shape with an acute apex but a rounded termen and a chestnut ground-colour, not glossy. A simple geometric design is present and comprises a terminal band and five broad oblique bands, all light cinnamon-brown and parallel to each other, running from close to the costal margin to  $CuA_2$  and the lower median vein of discal cell;  $CuA_2$  is extremely narrowly marked with four tiny pure white rounded spots and a larger rounded pure white spot at its beginning close to the posterior cell. A pattern is absent. Hindwing is light brown-olive, glossy. Fringe is short with scales of light brown, glossy (ciliae up to 0.6 mm long). Wing venation:  $1A+2A$  not forked at base;  $CuP$  absent;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from apical angle of posterior cell, separated;  $M_1$  initiates from hind margin of anterior cell;  $R_5$  is shortly stalked with  $R_4+R_3$  originating from posterior angle of areole; the areole is elongated and large, half the size of anterior cell;  $R_2$  initiates from anterior angle of areole; areole of medium size and slightly elongated;  $R_1$  initiates from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  rudimentary, forked at base;  $CuP$  present;  $CuA_2$  initiates from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1+R_s$  initiate from apical angle of anterior cell and are very long stalked; a bar is present from  $R_s$  to  $Sc+R_1$ ; a discocellular vein on forewing and hindwing is present. In forewing the whole discal cell is of a medium size and the

anterior part is slightly longer than half of the width of wing; posterior cell as well as anterior cell with broad apical angle; posterior cell smaller, much shorter than anterior cell. Retinaculum and frenulum absent.

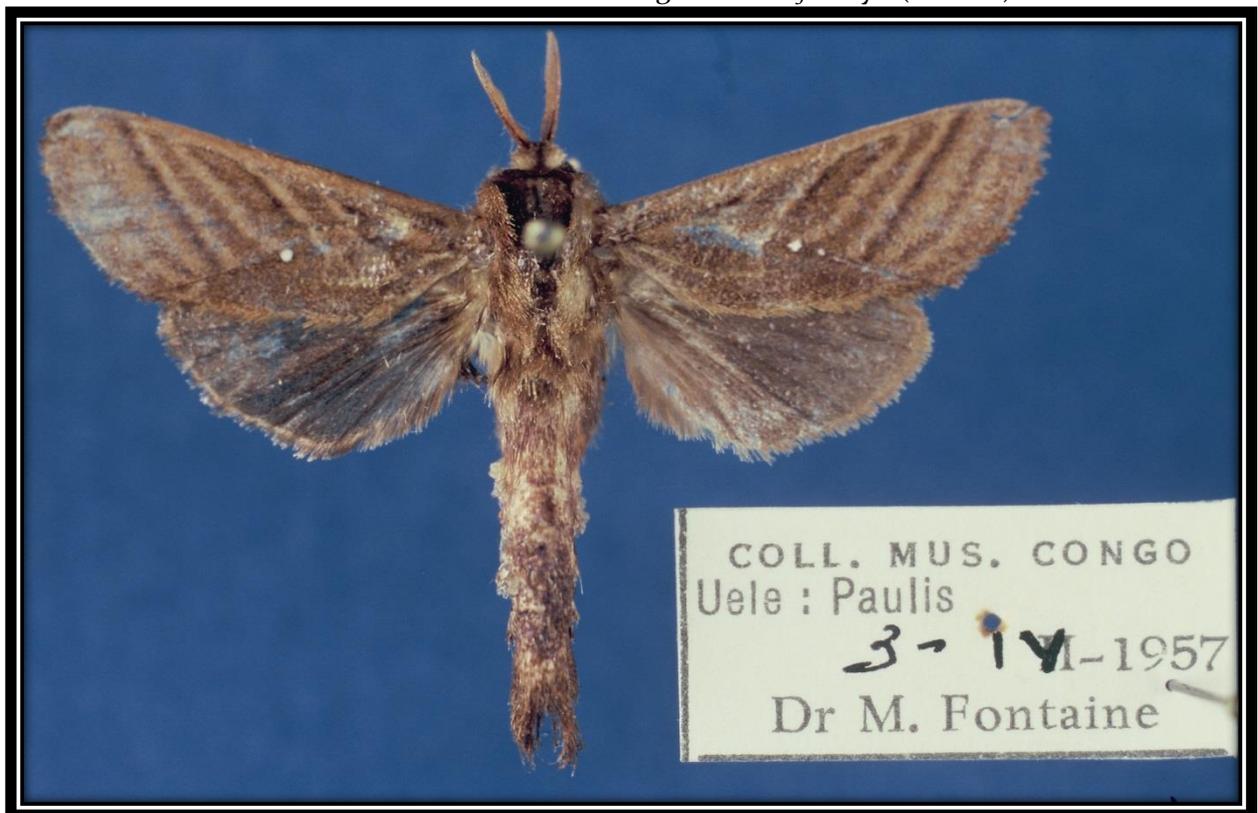
*Abdomen:* mainly with light brown mixed with chestnut scales, glossy; abdominal tuft brown, short, 20% of abdomen length.

*Male genitalia.* Saccus medium long, broad, rounded at tip; the vinculum and tegumen are fused, forming a firm ring, tegumen narrow, vinculum twice as broad as tegumen that becomes very broad and large (60% the size of valva) ventrally; uncus long triangular, narrow, bifurcated at tip, emargination small with rounded base, tips acuminate; along the edge of uncus occur two long slits, the upper one represents a tube-like process, very long and medium long setae are numerous and appear grey in colour along the whole edge of uncus. Valvae are large, broadly squarish with a strongly arc-shaped costal margin as well as distal margin; at half of valva occurs a long horizontal row of dots with tiny setae that is somehow fixed on a thin membrane that originates from the upper half of the basal edge of valva. Each valva is attached to a sclerotized band ventrally and hence, the valvae are not separated; a long fur-like structure occurs distal ventrally and is not an extension of the sacculus. Sacculus is very narrow. Transtilla is absent. Semi-transtilla is large (20% the size of valva) and thorn-like, this results in a wide basal width of valva (slightly shorter than aedeagus). Gnathos is absent but a relict appears to be attached somehow to the semi-transtilla; this relict is sclerotized, broadly C-shaped and its ventral surface has at top 12-14 short teeth-like processes and ventrally a short and a very long thorn-like process. Juxta is a rather thinly sclerotized folded structure that occurs on the sclerotized band; the phallus is large, rather narrow, slightly longer than basal width of valva, not bent, without dots and setae; vesica without cornuti.

*Female postabdominal structure and genitalia.* Unknown.



**FIGURE 186.** Distribution of the genus *Dianfosseya* (red dot).



**FIGURE 187.** *Dianfosseya leakeyi*, Holotype, [Democratic Republic of the Congo], Uele: Paulis [Isiro], 03.04.1957, Dr. M. Fontaine leg., ex COLL. MUS. [Collection Museum] CONGO [RMCA], male, genitalia slide number 27/102013 I. Lehmann. Wingspan 37.0 mm

#### 4.58 *Aethiopina* Gaede, 1929

The genus is defined by the following autapomorhy:

- A unique shape of valvae in ventral view: The whole valvae are vertical elongated with a large and elongated (25% the size of valva) semi-transtilla (with a squarish end) that has a very broad base (50% of costal margin) and that originates from a skin-like, weakly sclerotized, almost vertical costal margin; the distal margin is almost C-shaped; (200).

Additional characteristic character of the genus is:

- CuP absent in forewing of male; (11).

Type species of genus (cf. Figure 189): *Aethiopina + argentifera* Gaede, 1929

Type locality: Brit. O.-Afrika [British East Africa, today Kenya], Kikuyu [adjacent to Nairobi], no date, F. Thomas S. leg., male, genitalia slide number 10/092009 I. Lehmann, ex ZMHU; depository in ZMHU.

Number of species in genus at present: 02

All localities of studied species per country: Kenya.

Distribution of genus at present (cf. Figure 188): only known from two montane areas in central Kenya (Kikuyu and Nyeri).

The reconstructed and predicted ancestral areas are the Afromontane archipelago-like regional centre of endemism and the montane regions of the Arabian Peninsula.

The reconstructed biogeographic events comprise: First, dispersal in the Afromontane archipelago-like regional centre of endemism and the montane regions of the Arabian Peninsula. Secondly, vicariance between the Afromontane archipelago-like regional centre of endemism and the montane regions of the Arabian Peninsula.

Phylogenetic position: The sister genus could not be reconstructed unambiguously. The genus belongs to a monophylum together with *Metarbela*, the new genera ZK, ZL, ZM, *Dianfosseya* and *Aethiopina*.

Synapomorphies shared with *Metarbela*, *Dianfosseya*, Gen. Nov. ZK, ZL and ZM:

- Valvae not separated, but almost entirely connected by a broad sclerotized band ventrally; (80);
- Large uncus triangular-shaped and almost as large as valva (ventral view); (177).

Description: *Head:* rough-scaled with mainly hair-like as well as broad scales of light ocher mixed with sepia below the eyes on fronto-clypeus; a pair of pits is absent on lower fronto-clypeus, a pair of projections is absent on lower fronto-clypeus in male;

pits behind labial palpi are small oval shaped holes; labial palpi short, less than half of eye diameter and consist of two segments, upper segment rather oval and  $1.2 \times$  as long as basal segment; antennae medium long, bipectinated in male; branches are narrow and  $4.5 \times$  width of shaft in male, scaled cream; flagellum densely scaled cream mixed with sepia.

*Thorax:* Densely covered with mainly hair-like scales, broader scales few, of light ocher and dark chestnut, slightly glossy, scales on patagia dark chestnut, tegulae slightly pronounced with longer scales of light chestnut or light ocher with white or cream coloured tips; small crest on metathorax cream with dark brown, slightly glossy. Epiphyses are long (up to 1.1 mm in male), narrow, tube-like. Hindlegs with two pairs of tibial spurs; upper pair is narrow and short, 0.6 mm, lower pair much longer (up to 0.9 mm) and thicker, spurs slightly unequal in length; pretarsus with a pair of pulvilli.

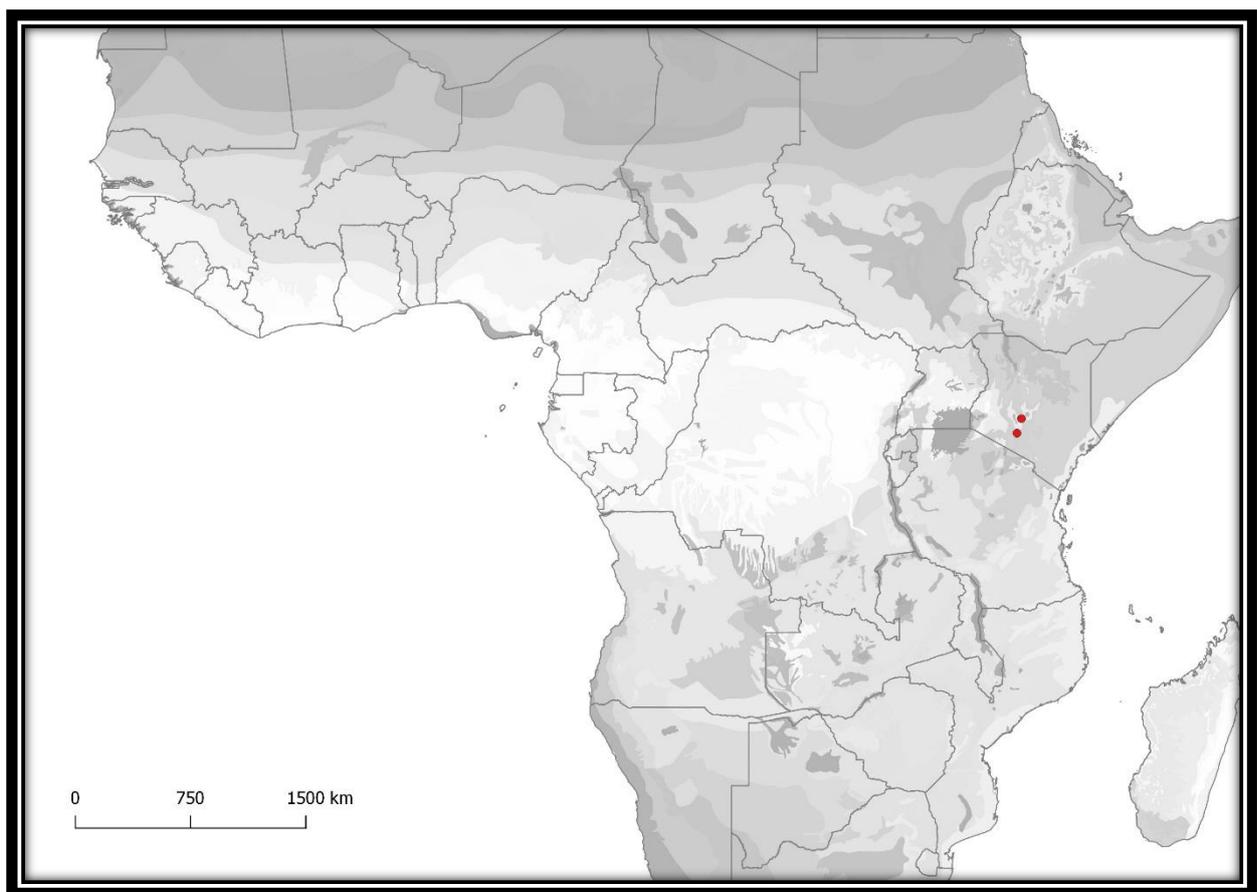
Forewing upperside: dark brown-olive in ground-colour with a slightly vinaceous glint. A geometric design is absent. A simple pattern is present and comprises large patches of light orange-yellow below the base of lower median, below  $1A+2A$  as well as  $CuA_2$  and a small light orange-yellow spot at the end of the anterior cell; a rudimentary subterminal line comprises several small spots of light orange-yellow; three large pure white spots are present along the costal margin, several smaller and one larger pure white patch occur below  $CuA_2$ . Hindwing is brown-olive, slightly glossy. Fringe is long with scales of light brown alternating with pure white in forewing and only pure white in hindwing, glossy (ciliae up to 1.0 mm long). Wing venation:  $1A+2A$  forked at base but the fork is weak;  $CuP$  absent;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from apical angle of posterior cell, separated;  $M_1$  initiates from hind margin of anterior cell; end of discal cell slightly open between  $M_2$  and  $M_1$ ;  $R_5$  is stalked with  $R_4+R_3+R_2$  originating from posterior angle of anterior cell; areole is absent;  $R_1$  initiates from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  rudimentary;  $CuP$  present;  $CuA_2$  initiates from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1+R_s$  initiate from apical angle of anterior cell and are stalked; a bar is present from  $R_s$  to  $Sc+R_1$ ; a discocellular vein on forewing and hindwing is present, weak in forewing. In forewing the whole discal cell is of a medium size and not longer than half of the width of wing; posterior cell as well as anterior cell with a rather rectangular apical angle, the former is slightly longer and larger than anterior cell. Retinaculum and frenulum absent.

*Abdomen:* mainly with light brown mixed with cream scales, slightly glossy; abdominal tuft pronounced and brown-olive, very long, 35% of abdomen length.

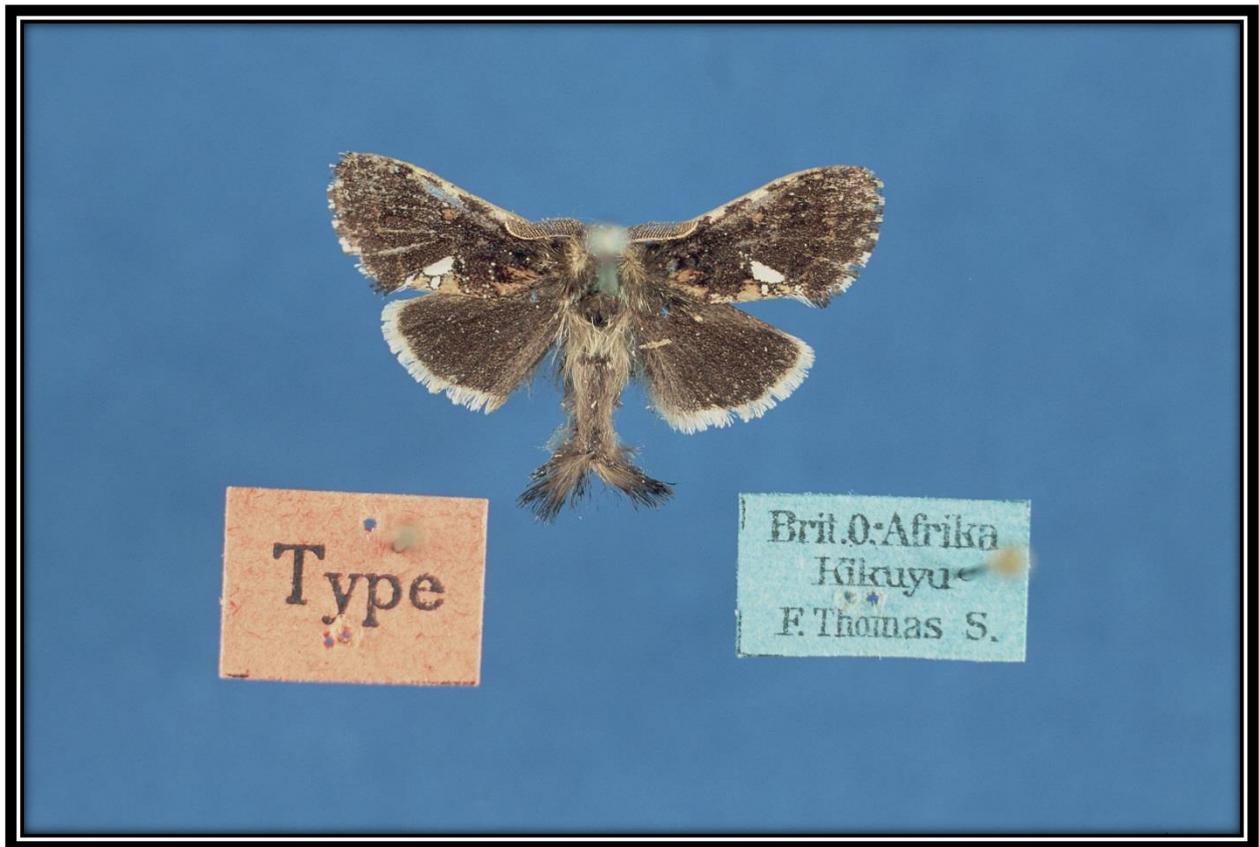
*Male genitalia.* Saccus medium long, broad, finger-shaped (up to 50% the size of the basal width of valva), rounded at tip; the vinculum and tegumen are fused, forming a firm ring, tegumen narrow, vinculum twice as broad as tegumen, becomes broad ventrally; uncus long triangular, narrow, bifurcated at tip, emargination small with rounded base, tips acuminate; a small hole is present in dorsal surface of uncus; along

the edge of uncus mainly short setae occur and are mixed with few long setae. Valvae are large (ca. 80% the size of uncus), vertically strongly elongated, resulting in an almost triangular shape in ventral view (cf. autapomorphy); oblique thinly membranous costal margin, distal edge almost C-shaped, dorso-ventrally elongated but without any structures. Each valva is attached to a sclerotized large band ventrally and hence, the valvae are not separated; the valva surface has only in the basal centre a short oblique row of dots and tiny setae (best visible if viewed ventrally). Sacculus is absent. Transtilla is absent. Semi-transtilla is large (25% the size of valva) and squarish in shape, this results in a very wide basal width of valva (slightly longer than aedeagus); ventral of the semi-transtilla occur two very small and thinly sclerotized plates that are connected by a very thin membrane to the semi-transtilla (both plates can disappear easily during preparation) – both plates might be relicts of a transtilla. Gnathos is absent. Juxta is a rather thinly sclerotized folded structure that occurs on the sclerotized band; the phallus is large, broad, tube-like, only slightly shorter in length than basal width of valva, not bent, without dots and setae, distally with an almost acuminate end; vesica without cornuti.

*Female postabdominal structure and genitalia.* Unknown.



**FIGURE 188.** Distribution of the genus *Aethiopina* (red dots).



**FIGURE 189.** *Aethiopina argentifera*, Type, Brit.O.-Afrika [British East Africa], [Kenya], Kikuyu [adjacent to Nairobi], [no date], F. Thomas S. leg., ex ZMHU, male, genitalia slide number 10/092009 I. Lehmann. Wingspan 23.0 mm



**FIGURE 190.** *Aethiopina* sp. nov.1, [Kenya], Nyeri, [no date], 1952, A. Townsend & C.H. Stöcklen [?] leg., NMK, male, genitalia slide number 05/072006 I. Lehmann. Wingspan 24.0 mm

#### 4.59 Gen. Nov. ZL

The genus is defined by the following autapomorphy:

- A broadly rectangular, thinly-membranous valva has a narrow strongly sclerotized band along the whole basal width and a distal margin that is C-shaped; (111).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; [possibly also absent in female] (11).

Type species of genus (cf. Figure 192): Gen. Nov. ZL + *taifensis* (Wiltshire, 1988)

Type locality: Ta'if. Studied specimen: Paratype, Arabia [Saudi Arabia], Ta'if, 02.08.1934, H. St. J. B. Philby leg., male, genitalia slide number 12/092007 I. Lehmann, ex BMNH, B.M. 1934-536; depository in BMNH.

Number of species in genus at present: 01

All localities of studied species per country: Saudi Arabia.

Distribution of genus at present (cf. Figure 191): Arabian Peninsula, only known from two montane areas in western and southwestern Saudi Arabia (Afrotropical Region).

The reconstructed and predicted ancestral areas are the Afromontane archipelago-like regional centre of endemism and the montane regions of the Arabian Peninsula.

The reconstructed biogeographic events comprise: First, dispersal in the Afromontane archipelago-like regional centre of endemism and the montane regions of the Arabian Peninsula. Secondly, vicariance between the Afromontane archipelago-like regional centre of endemism and the montane regions of the Arabian Peninsula.

Phylogenetic position: The sister genus could not be reconstructed unambiguously. The genus belongs to a monophylum together with the new genera ZK, ZL, ZM and *Metarbela*, *Dianfosseya* and *Aethiopina*.

Synapomorphies shared with *Metarbela*, *Dianfosseya*, *Aethiopina*, Gen. Nov. ZK and ZM:

- Valvae not separated, but almost entirely connected by a broad sclerotized band ventrally; (80);
- Large uncus triangular-shaped and almost as large as valva (ventral view); (177).

Description: *Head:* rough-scaled with mainly hair-like as well as broad scales of light ochre mixed with brown below the eyes on fronto-clypeus; a pair of pits is absent on lower fronto-clypeus, a pair of projections is absent on lower fronto-clypeus in male; pits behind labial palpi are tiny oval shaped holes or absent; labial palpi short, less than

half of eye diameter and consist of two segments, upper segment rather oval and  $1.2 \times$  as long as basal segment; a third tiny segment is sometimes present but strongly reduced; antennae long, bipectinated in male; branches are narrow and  $3.5 \times$  width of shaft, scaled light cream; flagellum densely scaled light cream.

*Thorax:* Densely covered with mainly hair-like scales, broader scales few, of light ocher and light grey, slightly glossy, scales on patagia mainly light ocher or dark cream, tegulae slightly pronounced with longer scales of light grey with white or light cream coloured tips; small crest on metathorax grey mixed with dark cream, slightly glossy. Epiphyses are very long (up to 1.6 mm in male), narrow, tube-like with a rounded tip. Hindlegs with one pair of tibial spurs; spurs rather thick and short, up to 0.9 mm long, spurs slightly unequal in length; pretarsus with a pair of pulvilli.

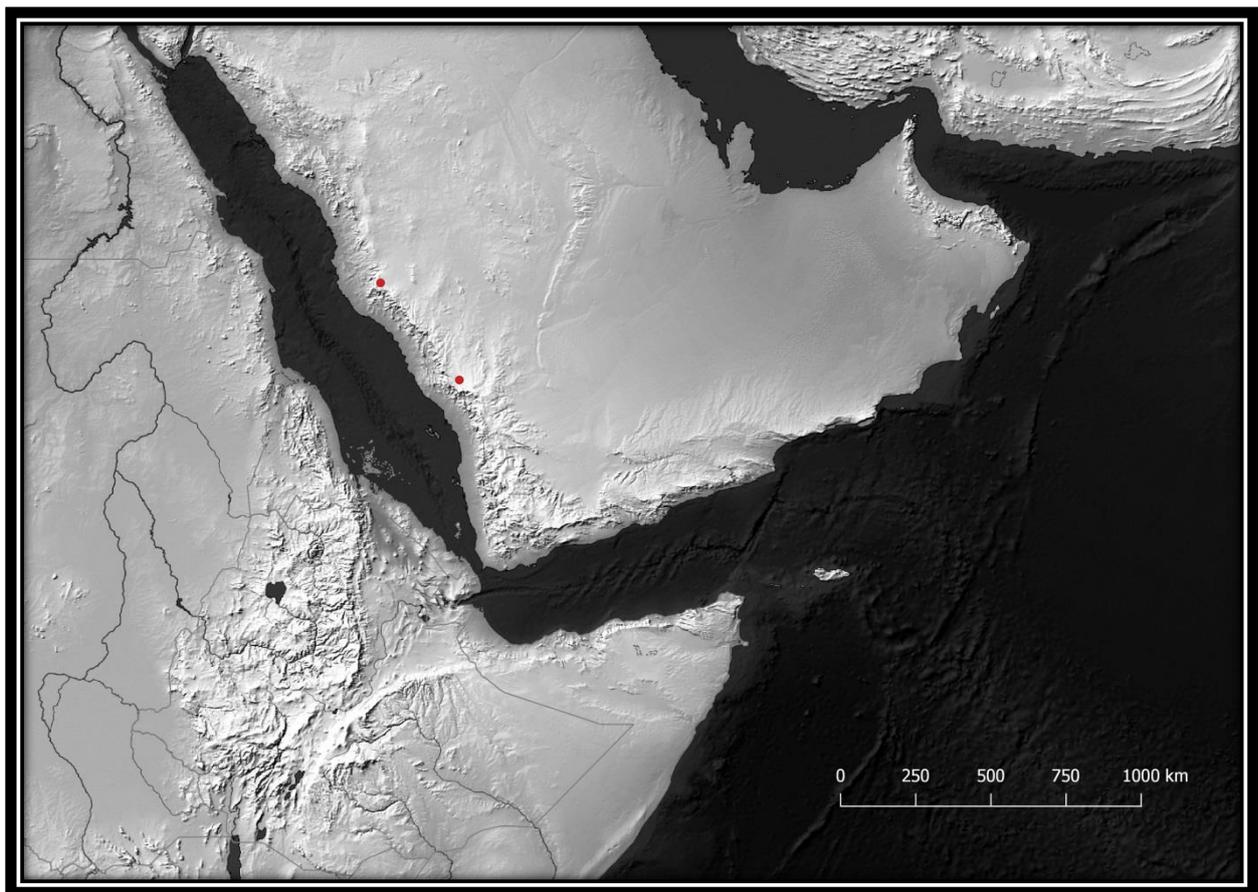
Forewing upperside: light olive-grey or light olive-cream in ground-colour without a glint. A geometric design is absent. A simple pattern is present and comprises dark olive-grey striae from near half the wing from costa towards dorsum with a rather fine more or less reticulated pattern towards the apex; basal part of wing without any pattern and only mixed with scales of light olive-cream and dark olive-grey;  $CuA_2$  is not distinctly marked. Hindwing is light cream and light olive-grey on veins as well as towards the base of wing, slightly glossy. Fringe is long with scales of light olive-grey or light olive-cream, slightly glossy (ciliae up to 1.0 mm long). Wing venation:  $1A+2A$  forked at base but the fork is weak;  $CuP$  absent;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from apical angle of posterior cell, separated;  $M_1$  initiates from hind margin of anterior cell very close to areole or from half of posterior part of areole; areole of medium size;  $R_5$  is stalked with  $R_4+R_3$  originating from posterior angle of areole;  $R_2$  initiates from anterior angle of areole;  $R_1$  initiates from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  rudimentary or absent;  $CuP$  absent;  $CuA_2$  initiates from two-thirds of lower median of posterior cell;  $CuA_1$  initiates from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1+Rs$  initiate from apical angle of anterior cell and are stalked; a bar is present from  $Rs$  to  $Sc+R_1$ ; a discocellular vein on forewing and hindwing is present, sometimes weak in hindwing. In forewing the whole discal cell is of a medium size and not longer than half of the width of wing; posterior cell with a rather rectangular apical angle, more acuminate in anterior cell; the former is slightly longer and larger than anterior cell. Retinaculum and frenulum absent.

*Abdomen:* mainly with light cream mixed with dark olive or grey scales, slightly glossy; abdominal tuft not pronounced, dark cream-olive mixed with grey-olive, short, 20% of abdomen length.

*Male genitalia.* Saccus medium long, broad, finger-shaped (up to 50% the size of the basal width of valva), rounded at tip; the vinculum and tegumen are fused, forming a firm ring, tegumen narrow, vinculum twice as broad as tegumen, becomes broad ventrally; uncus very long and elongated (*ca.*  $1.5 \times$  longer than basal width of valva), triangular, narrow, bifurcated at tip, emargination small with rounded base, tips

acuminate; a small hole is present in dorsal surface of uncus; along the edge and ventral surface of the upper part of uncus occur many short setae and tiny dots dorsally. Valvae are large (one valva is as large as the uncus + upper half of tegumen), broadly rectangular, largely thinly membranous, below the costal margin the valva is extremely thinly membranous; the whole valva is without any structures, only a short row of tiny dots and setae occurs in the upper basal area. Each valva has a strongly sclerotized narrow band along the whole basal width and is attached to a sclerotized large band ventrally. Hence, the valvae are not separated. Sacculus is absent. Transtilla is absent. Semi-transtilla is very small and thorn-like. Gnathos is absent. Juxta is a rather thinly sclerotized folded structure that occurs on the sclerotized band; the phallus is long (slightly longer than basal width of valva), medium broad (not broader than saccus), tube-like, not bent, without dots and setae, distally with an almost acuminate end; vesicula without cornuti.

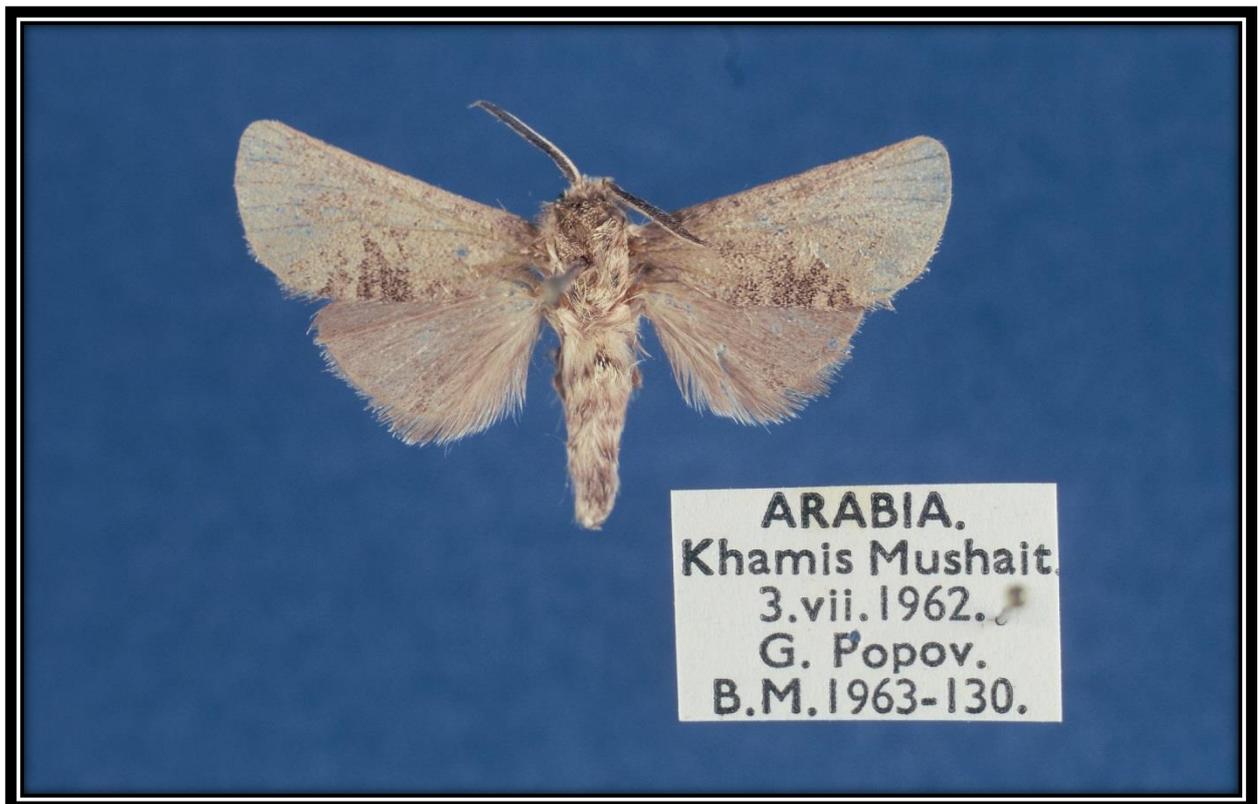
*Female postabdominal structure and genitalia. Unknown.*



**FIGURE 191.** Distribution of Gen. Nov. ZL (red dots).



**FIGURE 192.** Gen. Nov. ZL, *taifensis*, Paratype, Arabia [Saudi Arabia], Ta'if, 02.08.1934, H. St. J. B. Philby leg., ex BMNH, B.M. 1934-536, male, genitalia slide number 12/092007 I. Lehmann. Wingspan 28.0 mm



**FIGURE 193.** Gen. Nov. ZL, *taifensis*, Arabia [Saudi Arabia] Khamis Mushait, 03.07.1962, G. Popov leg., ex BMNH, male, genitalia slide number 03/032017 I. Lehmann. Wingspan 26.5 mm

#### 4.60 Gen. Nov. ZM

The genus is defined by the following autapomorphies:

- Two prominent and long, narrow sinuate, serrate processes, thorn-like, are attached to the upper part of the semi-transtilla; (202);
- A large, broad, more or less V-shaped, thinly sclerotized simple plate (relict of a transtilla?) occurs above the juxta, sometimes extending in between upper basal parts of valvae; (203).

Additionally one apomorphic character of the genus is:

- CuP absent in forewing of male; [possibly also in female] (11).

Type species of genus: Gen. Nov. ZM + *diagonalis* (Hampson, 1910)

Type locality: Gold Coast [Ghana], Obuassi [Obuasi], 150 miles inland, 1902–3, G.E. Bergman leg., depository in BMNH. The studied specimen is close to the type of *diagonalis* (cf. Figure 195): Ghana, Kakum National Park, 19.–21.11.2009, Sáfián, Sz. leg., male, genitalia slide number 11/112014 I. Lehmann, ex RMCA; depository in RMCA.

Number of species in genus at present: 11

All localities of studied species per country: Ivory Coast; Ghana; Central African Republic; Cameroon; Democratic Republic of the Congo; Rwanda; Uganda.

Distribution of genus at present (cf. Figure 194): disjunct; lowland and submontane areas in the southeastern Ivory Coast and in southwestern Ghana; from the southern Central African Republic to southern Cameroon; from the northeastern Democratic Republic of the Congo to the south-central Democratic Republic of the Congo; (rarely?) montane areas in southwestern Rwanda and south-central Uganda.

The reconstructed and predicted ancestral area is the Guineo-Congolian regional centre of endemism.

The reconstructed biogeographic events comprise: First, dispersal in the Guineo-Congolian regional centre of endemism. Secondly, vicariance occurred in the Guineo-Congolian regional centre of endemism.

Phylogenetic position: The sister genus could not be reconstructed unambiguously. The genus belongs to a monophylum together with the new genera ZK, ZL, ZM and *Metarbela*, *Dianfosseya* and *Aethiopina*.

Synapomorphies shared with *Metarbela*, *Dianfosseya*, *Aethiopina*, Gen. Nov. ZK and ZL:

- Valvae not separated, but almost entirely connected by a broad sclerotized band ventrally; (80);

- Large uncus triangular-shaped and almost as large as valva (ventral view); (177).

Description: *Head:* rough-scaled with mainly hair-like as well as broad scales of ocher with often cream coloured tips mixed with chestnut and/or sepia and/or cream coloured scales below the eyes on fronto-clypeus, glossy; a pair of pits is absent or sometimes rudimentary on lower fronto-clypeus, a pair of projections is absent on lower fronto-clypeus in male; pits behind labial palpi are tiny oval shaped slits; labial palpi medium long, longer than half of eye diameter and consist of three segments, central segment oval and  $1.1 \times$  as long as basal segment or of equal length; a third small segment is present on top and oval, half as long as basal segment; antennae short, bipectinated in male; branches are narrow and  $3.0 \times$  width of shaft, densely scaled light ocher mixed with sepia, space between branches unusually narrow; flagellum densely scaled light ocher mixed with sepia.

*Thorax:* Densely covered with mainly hair-like scales, broader scales few, of light vinaceous-ocher or dark chestnut often with light grey tips, with a strong glint, scales on patagia mainly light vinaceous-ocher or dark chestnut, tegulae slightly pronounced with longer scales of light ocher or cream with a strong glint; small crest on metathorax dark chestnut or dark cream, glossy. Epiphyses are very long (up to 1.8 mm in male), narrow, tube-like with a rounded tip. Hindlegs with two pairs of tibial spurs; spurs rather thick and short, up to 0.9 mm long (upper pair), lower pair shorter, up to 0.7 mm or sometimes only 0.5 mm long; spurs of both pairs unequal in length; pretarsus with a pair of pulvilli.

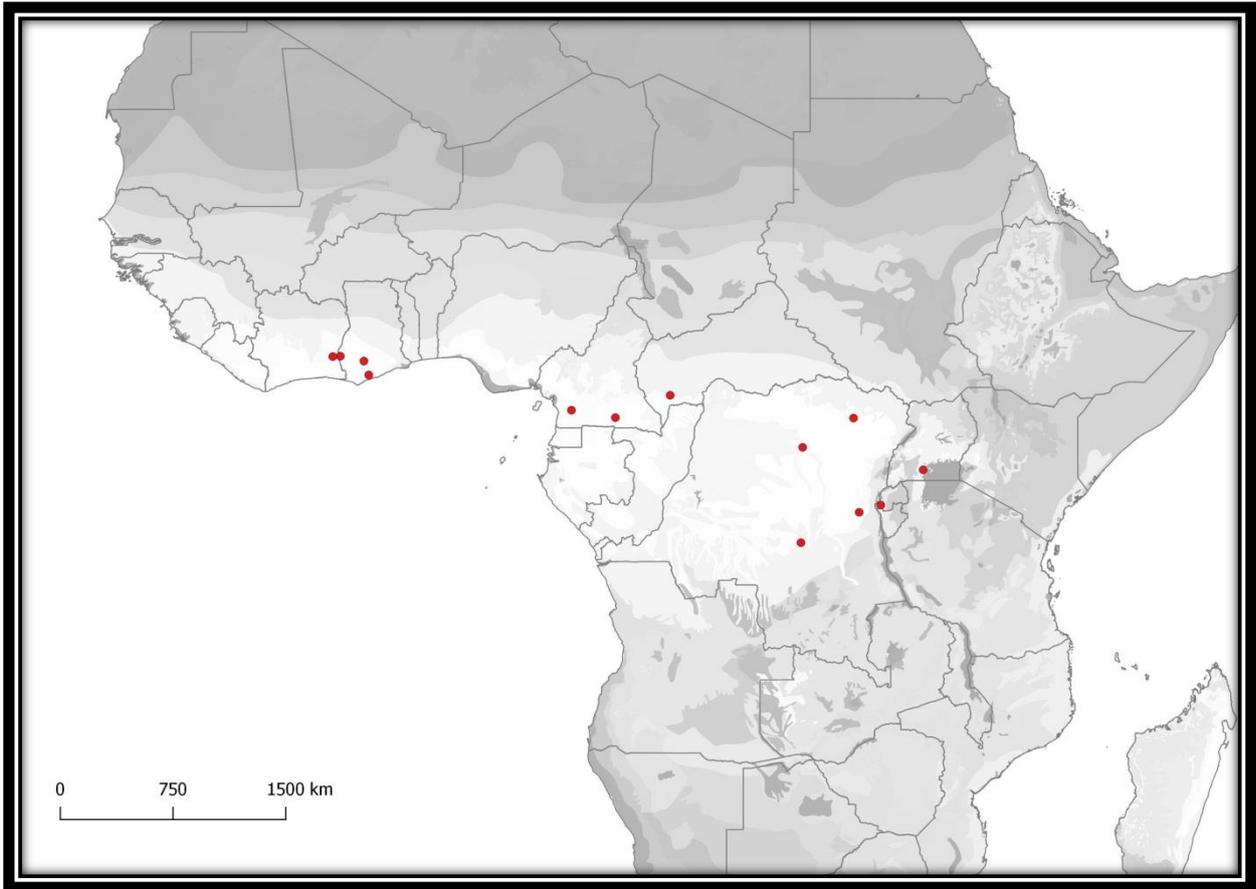
Forewing upperside: ocher mixed with cream or dark ocher in ground-colour with a strong light vinaceous glint along the costal margin as well as termen. A geometric design is absent. A simple pattern is present and comprises a usually prominent (sometimes faded) dark chestnut or sepia coloured narrow oblique line extending from near base of anterior part of median cell to the dorsum on  $CuA_2$ , and hence,  $CuA_2$  is distinctly marked; the remaining pattern is more or less faded, but usually present is a pale brown triangular shaped pattern along the termen as well as a pale brown postmedial line that is strongly bent inwards between  $M_2$  and  $R_5$ . Hindwing is dark cream or light olive-grey or light olive-brown, slightly glossy. Fringe is long with scales of light olive-grey or light olive-cream, glossy (ciliae up to 1.1 mm long). Wing venation:  $1A+2A$  forked at base but the fork is weak;  $CuP$  absent;  $CuA_2$  originating from two-thirds of lower median;  $CuA_1$  originates from hind margin of posterior cell,  $M_3$  and  $M_2$  originate from apical angle of posterior cell, separated;  $M_1$  initiates from hind margin of anterior cell; areole present and of medium size (in one specimen the areole was absent);  $R_5$  is stalked with  $R_4+R_3$  originating from posterior angle of areole;  $R_2$  initiates from anterior angle of areole;  $R_1$  initiates from anterior part of median cell;  $Sc$  more or less parallel to  $R_1$ . In hindwing  $3A$  present;  $1A+2A$  rudimentary with a fork at base or entirely absent;  $CuP$  present but weak, sometimes absent;  $CuA_2$  initiates from two-thirds of lower median of posterior cell;  $CuA_1$  initiates

from hind margin of posterior cell;  $M_3$  and  $M_2$  initiating from apical angle of posterior cell, separated;  $M_1+R_s$  initiate from apical angle of anterior cell and are stalked; a bar is present from  $R_s$  to  $Sc+R_1$ ; a discocellular vein on forewing and hindwing is present, sometimes weak in forewing. In forewing the whole discal cell is of a medium size and not longer than half of the width of wing; posterior cell and anterior cell usually with a rectangular apical angle; the former is slightly longer and larger than the anterior cell. Retinaculum and frenulum absent.

*Abdomen:* mainly cream with dark chestnut mixed with ocher scales, with a light vinaceous glint; abdominal tuft rather pronounced in male, dark chestnut mixed with ocher, long with a strong glint, 30% of abdomen length.

*Male genitalia.* Saccus medium long, broad, finger-shaped (up to 50% the size of the basal width of valva), broadly rounded at tip; the vinculum and tegumen are fused, forming a firm ring, tegumen narrow, vinculum *ca.* 3 × as broad as tegumen, becomes broader ventrally; uncus long and elongated (not longer than basal width of valva), triangular, narrow, bifurcated at tip, emargination small with rounded base, tips acuminate; along the edge and ventral surface of the upper part of uncus occur short setae and tiny dots. Valvae are very large (one valva is *ca.* 1.5 × as large as the uncus), broadly oblique rectangular, rather thinly membranous along the costal margin; an ellipsoid process occurs ventral-distally, it might be a relict of a formerly extension of the sacculus; the sacculus is absent or strongly reduced from the middle of valva ventrally; a broad band of rows of tiny dots and setae occurs in the upper basal area of valva and is connected with a thin membrane to a broad, V-shaped sclerotized plate, that might be a relict of a transtilla. Each valva is attached to a sclerotized large band ventrally. Hence, the valvae are not separated. The semi-transtilla is pronounced: it is long and thorn-like with a thin membrane that is attached to the acuminate end of each “thorn” as well as to the lower part of the tegumen. From this membrane originate close to the semi-transtilla two long, strongly sclerotized narrow serrate and sinuate processes. Gnathos is absent or represented as a relict by these processes. Juxta is reduced to a sclerotized folded structure that occurs on the sclerotized band that connects both valva ventrally. Above the base of the phallus occurs in lateral view a large thinly membranous, often ear-shaped, structure with many tiny dots. The phallus is long (but not longer than basal width of valva), medium broad (not broader than saccus), tube-like, not bent, without dots and setae, distally with an almost acuminate end; vesica without cornuti.

*Female postabdominal structure and genitalia.* Unknown.



**FIGURE 194.** Distribution of Gen. Nov. ZM (red dots).



**FIGURE 195.** Gen. Nov. ZM, sp. nov. zm1 [close to *diagonalis*], Ghana, Kakum National Park, 19.-21.11.2009, Sz. Sáfian leg., ex RMCA, male, genitalia slide number 11/112014 I.Lehmann. Wingspan 32.0 mm



**FIGURE 196.** Gen. Nov. ZM, sp. nov. zm9, [Democratic Republic of the Congo], Sankuru, Lubefu, 19.06.1952, Dr. M. Fontaine leg., ex RMCA, male, genitalia slide number 13/112014 I. Lehmann. Wingspan 29.0 mm.

## 5. ENDEMISM

### Examples of genera that comprise only endemic species and their distribution

Species endemism and the number of endemic species is the most important measure of an ecoregion's distinctiveness (Burgess *et al.* 2004), *e.g.* to set conservation priorities with protected areas.

The majority of Metarbelidae species are confined to one phytochorion, but this is changing on the genus level due to their often larger distribution ranges depending, *e.g.* on the number of species per genus. Table 1 represents 20 genera. Every genus has only strict endemic or near-endemic species. It is visible that all genera with endemic species occur in a "Regional centre of endemism" *sensu* White (1983) where also the highest numbers of endemic plant species have been found. No genus with only endemic species has been found in White's (1983) "Regional transition zones or mosaics" (*cf.* definitions chapter 2.5.4). Hence, endemic genera occur in three regions that have been identified as ancestral areas. This means that an ancestral area is not automatically rich in endemic genera (*cf.* Figure 6d). It is encouraging that all regions where endemic Metarbelidae genera occur show a high degree of agreement with those areas identified by Burgess *et al.* 2004 (*cf.* Figure 4.6) as areas that are "globally outstanding" or "regionally outstanding" in regard to their species richness as well as endemism. These areas comprise in regard to Metarbelidae: Lower Guinea, the Somalia-Masai Region, the Afromontane Region (particularly of Eastern Africa) as well as Madagascar. For Lepidoptera there is generally not much data available for these four regions. Interestingly high numbers of endemic species in the butterfly sub-families Acraeinae and Charaxinae occur in the same four areas with highest numbers in the Afromontane Region of Eastern Africa (*cf.* Figure 4.3b in Burgess *et al.* 2004).

Lower Guinea has a higher importance for endemic lowland Metarbelidae, *e.g.* *Metarbela*, than Upper Guinea where the author did not yet find enough evidence for one endemic genus. There might be two reasons for this pattern: First, there is the highest concentration of African forest refuges during the last maximum arid phase (*ca.* 18.000 years ago) in Lower Guinea. Secondly, the richest sector in regard to endemic taxa and high biodiversity in the African forest comprises the evergreen Biafran forest, largely dominated by gregarious Caesalpinaceae, extending from southern Nigeria's Cross River to southwest Cameroon, western Gabon and the southwestern Democratic Republic of the Congo (Maley 2001). Species of Gen.Nov.F occur in arid and semi-arid areas of Kenya and Somalia (*cf.* Figure 37). This genus is probably only one example that Metarbelidae of arid and semi-arid areas are local endemics (*cf.* Figures 62, 88). No genus or species has been found yet by the author that occurs in the whole "drought corridor" *sensu* Balinsky (1962). This was a broad corridor stretching from the Western Cape/Namibia unbroken northeasterly to the Somali Peninsula during the Tertiary and arid glacial phases, *e.g.* 18.000 years ago.

**TABLE 1.** Twenty genera include only near-endemic or strict endemic species, *ca.* 19% of the total sample. Eight genera comprise twelve strict endemics (in bold, *cf.* definitions).

Genus	Number of Species	Phytochoria White (1983)	Ecoregions Burgess <i>et al.</i> (2004)	Zoogeographic region Whitmore (1984)	Classification Stainton (1972)
Gen. Nov. H	1	West Malagasy regional centre of endemism	Madagascar Dry Deciduous Forests		
<i>Saalmulleria</i>	3	West Malagasy regional centre of endemism; East Malagasy regional centre of endemism	Madagascar Subhumid Forests; Madagascar Dry Deciduous Forests; Madagascar Succulent Woodlands		
<i>Squamura</i>	6			Sunda shelf; Tropical lowland and submontane evergreen rain forest	
Gen. Nov. V	1			Sunda shelf; Tropical lowland evergreen rain forest; Meranti forest	
Gen. Nov. X	2			Sunda shelf; Tropical lowland evergreen rain forest	
Gen. Nov. ZB	2			Sunda shelf; Tropical lowland evergreen rain forest	
Gen. Nov. U	1				Sub-Himalaya: Subtropical broad-leaved evergreen forest and Lower temperate mixed broad-leaved forest (Nepal)
<i>Aethiopina</i>	2	Afromontane archipelago-like regional centre of endemism	East African Montane Forests		
<i>Metarbelodes</i> subgroup G2	1	Afromontane archipelago-like regional centre of endemism	Southern Miombo Woodlands		
Gen. Nov. ZI	1	Afromontane archipelago-like regional centre of endemism	Eastern Arc Forests		
<i>Mountelgonia</i>	9	Afromontane archipelago-like regional centre of endemism	East African Montane Forests; Southern Rift Montane Forest-Grassland Mosaic; Northern and Southern <i>Acacia-Commiphora</i> Bushlands and Thickets		
<i>Ortharbela</i>	4	Afromontane archipelago-like regional centre of endemism	Eastern Arc Forests; East African Montane Forests; Northern Zanzibar-Inhambane Coastal Forest Mosaic		

Gen. Nov. ZJ	7	Afromontane archipelago-like regional centre of endemism	East African Montane Forests; Southern Rift Montane Forest-Grassland Mosaic; South Malawi Montane Forest-Grassland Mosaic; Eastern Zimbabwe Montane Forest-Grassland		
Gen. Nov. F	5	Somalia-Masai regional centre of endemism	Somali <i>Acacia-Commiphora</i> Bushlands and Thickets; Northern <i>Acacia-Commiphora</i> Bushlands and Thickets		
<i>Haberlandia</i>	26	Guineo-Congolian regional centre of endemism	lowland, swamp and coastal forests including Northern and Southern Congolian Forest-Savanna Mosaic, Victoria Basin Forest-Savanna Mosaic		
<i>Metarbela</i>	7	Lower Guinea, Congolia; Guineo-Congolian regional centre of endemism	Atlantic Equatorial Coastal Forests; Northwestern and Northeastern Congolian Lowland Forests; Central Congolian Lowland Forests		
<b>Gen. Nov. Y</b>	2	Lower Guinea; Guineo-Congolian regional centre of endemism	Northwestern Congolian Lowland Forests		
Gen. Nov. ZE	2	Lower Guinea; Guineo-Congolian regional centre of endemism	Northwestern Congolian Lowland Forests; Western Congolian Forest-Savanna Mosaic		
Gen. Nov. R	1		Afromontane Region; Montane areas on SW-Arabian Peninsula		
Gen. Nov. ZL	1		Afromontane Region; Montane areas on SW-Arabian Peninsula		

## 6. SPECIES OF THE ORIENTAL REGION

A present overview of apomorphies, plesiomorphies, symplesiomorphies and one synapomorphy shared with species of the Afrotropical Region

The species of the five “Oriental genera” from Nepal (Gen. Nov. U) and the Sunda shelf (new genera V, X, ZB and *Squamura*) are described in chapter 4 (*cf.* also dendrogram in Figures 6a, 6c). Species from Sri Lanka, Malaysia and Thailand were studied but are not included in chapter 4 due to ongoing research on the Oriental Metarbelidae. All studied Oriental species have five apomorphic characters (see below a, d, e, h, i). The synapomorphy (d) suggests that there was the same stem species from which all Afrotropical species on one hand and all Oriental species on the other hand, originated somewhere on the African mainland (*cf.* Figure 6d). The symplesiomorphies are no evidence for a sistergroup relationship and can also occur in other Lepidoptera.

### 1. Head

- a) The presence of only two-segmented labial palpi that are short (= less than eye diameter). This is an apomorphic state (*cf.* basal taxa). Basal taxa have three-segmented labial palpi; many species of the Afrotropical Region have longer palpi (= equal to eye diameter or longer).
- b) The antennae of males and females are bipectinated. This is a plesiomorphic state (*cf.* basal taxa). Bipectinated antennae occur also in the Afrotropical Region, particularly in males, where additionally filiform and unipectinate antennae occur in males and/or females.
- c) The branches of the antennae are not covered with scales in both sexes. This is a plesiomorphic state (*cf.* basal taxa). This character is interesting since the author found usually in rain forest species of the Afrotropical Region, that the branches are densely covered with scales (*cf.* Gen. Nov. ZD, *Metarbela* – in contrast to rain forest species of the “Oriental genera”). However, there are a few interesting exceptions from West African rain forests as well that are not yet included here.

### 2. Thorax

- d) The absence of a fully developed CuP vein in the forewing. This is an apomorphic state, and a synapomorphy shared with all species from the Afrotropical Region excluding basal taxa. A fully developed CuP vein in the forewing is only known in basal taxa that occur close to or south of the Zambezi River mainly on the Southern African Plateau.
- e) The absence of an areole in the forewing. This is an apomorphic state (*cf.* basal taxa).
- f) The absence of a distinctly marked CuA<sub>2</sub> vein in the forewing. This character is a plesiomorphic state (*cf.* basal taxa).

- g) The retinaculum and frenulum are absent. This character is a plesiomorphic state (*cf.* basal taxa).
- h) On the foreleg an epiphysis is always present (although sometimes very short as in *acutistriata* Mell, 1923). This is an apomorphic state (*cf.* basal taxa).
- i) The occurrence of only one pair of spurs to the hindleg. This is an apomorphic state (*cf.* basal taxa).

### 3. Abdomen

- j) Male genitalia: A broad base of uncus is present. This is a symplesiomorphy with all species of the Afrotropical Region.
- k) Female genitalia: Corpus bursae without any structures. This is a symplesiomorphy with all species of the Afrotropical Region.
- l) An abdominal tuft in both sexes is present. This is a symplesiomorphy with all species of the Afrotropical Region.
- m) A short crest on metathorax is present in both sexes. This is a symplesiomorphy with all species of the Afrotropical Region.

## 7. DISCUSSION

### 7.1 The Afrotropical Region

Dispersal, the link to geology/geomorphology and vegetation types

Three results will be discussed in regard to Metarbelidae, here in summary:

- 7.1.1 Species are slow dispersers or mainly sedentary. Hence, a sedentary species cannot be older than the geological/geomorphological age of the region where this species occurs, *e.g.* any uplifted area, rift or mountain, or lowland area.
- 7.1.2 The highest diversities of basal taxa are linked to areas that are geological /geomorphologically stable and hence, provide habitats under long stable geological conditions. Rifting, uplift and volcanism followed pre-existing structures in the lithosphere, but mainly avoiding stable Archean and Paleoproterozoic mantle lithosphere areas. If rifting, uplift and volcanism are absent for very long periods of time, *e.g.* 65 Ma, the author assumes that the same regions have also a higher climatic stability. Two of these areas are the Kaapvaal craton and the Zimbabwean craton. Regarding South America, a high topography is absent in Brazil and westwards since the Andes (not older than 25 Ma) only attained a higher altitude (> *ca.* 5.000 m) during the Quaternary (Coltorti & Ollier 2000) and hence, any montane/submontane Metarbelidae are absent. If the author's hypothesis is correct that possibly all lowland Metarbelidae species have stem lineage representatives that originated from a last common ancestral montane population (*cf.* Figure 6d) then Metarbelidae must be entirely absent from South America.
- 7.1.3 Lepidoptera are usually linked to certain vegetation types (Van Dyck 2011). A particular association of Metarbelidae to legume-dominated tropical forests or woodlands or other legume-dominated tropical woody vegetation types was substantiated by Lehmann (2008, 2010a) as well as by Lehmann & Kioko (2000, 2005) based on 14 years of field research in southeast coastal Kenya. A link of habitats with the dominance of woody plants of the Leguminosae family assemblage (= Fabaceae) is confirmed for the majority of the species with the exception of those Metarbelidae that occur in Afromontane forests and riparian forests where woody legumes are not or rarely dominant. A low diversity or absence of Metarbelidae was always recorded by the author in degraded vegetation types or in young habitats (*cf.* Figure 2) and hence, Metarbelidae are in general at risk of local extinctions once their habitat has been destroyed or degraded, *e.g.* by humans, or fire.

### 7.1.1 Metarbelidae – sedentary and slow dispersers?

The present results show that Metarbelidae are purely African in origin (cf. Figure 6d). Few other families of Lepidoptera may be also of African origin, like the Brahmaeidae (= Lemoniidae), with *Spiramiopsis* among the most basal taxa within this family, and the Eupterotidae may have a similar origin, although their phylogeny is far from well known (Joël Minet pers. comm. 2018). Based on the result that Metarbelidae are of African origin the following discussions as well as the two hypotheses below are substantiated mainly with examples from the Afrotropical Region.

The first hypothesis is that Metarbelidae are slow dispersers or mainly even sedentary, because: (1) Metarbelidae certainly depend on various types of woody vegetation, mainly forest or woodland, since their larvae feed on bark and/or in wood (Lehmann 2008). (2) There appear to be very few forest or woodland species of Metarbelidae that are able to migrate through distinctly other habitats, e.g. between isolated coastal forest patches, or above desert or water. Only few species might be mobile, e.g. within narrow but continuous habitats such as riparian forests, riparian woodlands and mangrove forests including mangroves along continental coast lines.

The second hypothesis is that the oldest lineages of Metarbelidae remained due to their sedentary behavior (supported by geological/geomorphological stability), e.g. on the Southern African Plateau and on the Chimanimani-Bvumba-Inyanga mountainland. This might also indicate that the majority of Metarbelidae species are stenoecious.

#### 7.1.1.1 The role of young and ancient coastal forest sites in Kenya

The author's field research revealed that even if the distance is only a few kilometers, e.g. in between isolated coastal or montane forest habitats, the majority of species do not occur in forests that are nearby if the forest site is of a significantly younger age, e.g. Kenyan coastal forest sites that are situated on ca. 190.000–60.000 years old fossil coral reefs along the Indian Ocean shoreline (Caswell 1953) have no Metarbelidae or only one species in contrast to older forest sites that have at least six species and are situated on sands of Upper Pliocene age, and in the Shimba Hills, representing remnants of a possible Miocene surface (Caswell 1953) only 6–15 kilometers further inland from the present shoreline (Lehmann & Kioko 2000, 2005; Lehmann 2008; cf. Figures 198a, b; 199). These coastal forests on older as well as younger sites experience a stable climate at least during the last 2.3 Ma (Lovett 1993). Hence, there is an ecological stability in the coastal forests for the last 2.3 Ma. This means that if Metarbelidae would be stenoecious they should occur also in a similar high diversity on younger coastal forest sites. As that was not found it indicates in the author's view that relatively young forest sites (< 190.000 years) do not support a high diversity as well as no high number of coastal forest strict-endemic and/or near-endemic Metarbelidae (a "high number of endemic species per site" was defined by Lehmann

2008, comprising more than five endemic species on 625 m<sup>2</sup>). The author also found that older lineages of Metarbelidae are absent from geological/geomorphologically young sites like basal taxa are absent from young volcanoes (< 2 Ma). One biological reason that supports a sedentary behavior might be that females lay their eggs in the old frass from which they emerged and hence, stay always close to that tree or woody shrub. Although this behavior was observed in only one undescribed species of Gen.Nov.ZA occurring in mangroves along the Kenyan coast (Jenoh *et al.* 2016) it is possible that this behavior is widely distributed among Metarbelidae and could also explain the scarcity of females at light-trappings and in all collections mentioned herein.

#### 7.1.1.2 How did Metarbelidae arrive on Madagascar?

If Metarbelidae are mainly sedentary it might explain why their diversity appears to be low on Madagascar since only four species were found in major collections. Of interest is one of those species (Gen.Nov.H) that has its sister-taxon on the African mainland (Gen.Nov.I). As these two genera represent a sistergroup of the African mainland and Madagascar it has to be discussed how Metarbelidae did arrive on Madagascar: Both genera do not represent basal taxa. Hence, there is no indication that Metarbelidae on Madagascar are a remnant from the time when it was not yet isolated. The same conclusion is confirmed for “*most of the specialized fauna of Madagascar nowadays*” (Rienk de Jong pers. comm. 2016).

The separation of Madagascar from West Gondwana began *ca.* 167–165 Ma (Rabinowitz *et al.* 1983, Reeves 2014). The present western and northwestern part was attached to the eastern end of the Marda Fault and to the present coast of Somalia, extending southwards along the East African Orogenic Belt (including coastal areas of Kenya and Tanzania) and further south to the Selous Basin. The westernmost angle of Madagascar was aligned with the angle occupied today by the Lamu area and Tana River Delta (Reeves 2014). The present northernmost distribution of species of Gen.Nov.I is the Tana River and the species of Gen.Nov.H occurs on Madagascar just to the South of the westernmost angle of Madagascar. Hence, the distribution ranges of both genera still coincide well with those areas in Kenya that were once attached to Madagascar.

Madagascar was completely separated from West Gondwana due to the loss of continent-continent contact across the Davie Fracture Zone between East Gondwana (Madagascar) and West Gondwana (Mozambique mainland) *ca.* 145 Ma and has remained in a more or less fixed position since *ca.* 120 Ma (Reeves 2014). Its isolation was completed when its eastern edge was formed by the separation from India and the Seychelles in between *ca.* 88 and 83 Ma (Wells 2003, Torsvik *et al.* 2012). As the dendrogram (*cf.* Figures 6a, 6d) indicates have all “Oriental genera” that belong to the “West Africa-Sunda Group” and to the “Lower Guinea-Sunda Group”, different ancestral areas than the genera *Saalmulleria* and Gen.Nov.H as well as different stem

lineage representatives. This supports the author's view that all four species arrived on Madagascar from the eastern coast of the African mainland after it was completely isolated and hence, Metarbelidae on Madagascar cannot be older than 83 Ma.

#### **7.1.1.3 The driftwood scenario and the age of Metarbelidae on Madagascar under this scenario**

If various species survive with driftwood the sea water for several weeks (*cf.* Trewick 2000; Coulson *et al.* 2002) it appears very likely that caterpillars and/or pupae of Metarbelidae are able to survive in or attached to driftwood the floating and/or temporary submersion in sea water. Driftwood has to float in open water *ca.* 400–1.000 km (since *ca.* 120 Ma) from the African mainland to the western coast of Madagascar. Federman *et al.* (2015) found that even in the absence of monsoons (that was the case possibly 38–23 Ma), dispersal for a six times longer distance, namely from Sumatra to Madagascar, would be possible at present in less than 30 days for *ca.* 6.200 km. Another condition for the driftwood scenario is that predominant marine currents were eastward or southeastward. There are indications that together with the beginning of the development of the rain forest on Madagascar during the late Eocene and early Oligocene (*ca.* 38–34 Ma) the marine currents became increasingly eastward, a situation that was stable for the whole Oligocene, *ca.* 34–23 Ma (Federman *et al.* 2015). If so, the endemic Metarbelidae on Madagascar would represent species that are younger than 38 Ma. This assumption implies that those rather late arrivers on Madagascar became adapted to wet forest conditions and subsequently diversified successfully because earlier arrivers of Metarbelidae were absent and hence, did not limit the establishment of Late Eocene/Oligocene Metarbelidae. Marine currents between the African mainland and Madagascar were exclusively westward during the Miocene 23–5.3 Ma (Federman *et al.* 2015) and are since then unsuitable for dispersal from Africa to Madagascar (Ali & Huber 2010). Hence, Metarbelidae on Madagascar are probably older than the Miocene which means that the stem lineage representatives of species of both genera are between 23 and 83 million years old.

#### **7.1.1.4 High rates of local extinctions on Madagascar support late arrivers**

Since Malagasy rain forests experience hyper-variable climates, *e.g.* regarding rainfall, temperature and cyclones, high rates of local extinctions among flora and fauna are very likely from time to time. Due to the very high rates of endemic species on Madagascar, *e.g.* among primates and reptiles, such extinctions might occur only locally. The result of local extinctions is a periodic resetting of the ecological stage in forests or woodlands providing the opportunity for late arrivers to become established on the island and radiate. This climatic variability on Madagascar causes also unpredictable patterns in phenology (*cf.* Dewar & Richard 2007), *e.g.* gigantism. The latter might be also supported by other factors such as little competition for resources.

Gigantism is visible among Metarbelidae since species of *Saalmulleria* represent the largest Metarbelidae worldwide and species of Gen.Nov.H belong also to the largest Metarbelidae. The hyper-variable climate might be another reason (together with large-scale forest destruction in recent times by humans) why Metarbelidae diversity is low. It is very likely that late arrivers survived successfully.

#### **7.1.1.5 The wind scenario in regard to Madagascar and in general**

Rota *et al.* (2016) stated that “... the ability to use the atmospheric conditions for long-range dispersal has been documented in all major orders of insects and has evolved multiple times...” and “... Using these fast, high-altitude air currents enables insects to cover distances of hundreds or even thousands of kilometers in just a few days...” (also Chapman *et al.* 2011). The dendrogram does not support this opinion (*cf.* Figure 6a, 6d). All “Oriental genera” belong to the “West Africa-Sunda Group” or “Lower Guinea-Sunda Group” with stem lineage representatives and ancestral areas in the Guineo-Congolian Region and/or Afromontane Region. There is also no indication that species of Gen.Nov.H arrived by wind on Madagascar.

The author’s observations that wind does not play any major role for short-distance as well as long-distance dispersal of Metarbelidae in general is supported by the fact that six species of Metarbelidae are absent from forests close to the Indian Ocean coastline but occur just 6–15 km further inland (Lehmann & Kioko 2000, 2005; Lehmann 2008). These Kenyan coastal areas experience – like other coastal areas of Eastern Africa – a feature unique to the Indian Ocean, namely a complete reversal in wind direction each year. The prevailing trade wind is the Northeast-Monsoon (called *Kaskazi*) during November–March and the Southeast-Monsoon (called *Kusi*) during May/June–September/October. These Indian Ocean monsoon pathways originated the first time *ca.* 9 Ma (Federman *et al.* 2015). This monsoon pattern appears to be stable since at least 2.3 Ma (Lovett 1993). At least 2.3 million years should be enough time for the dispersal of many species from the diverse Metarbelidae fauna of Eastern Africa towards the Arabian Peninsula and/or towards the Oriental Region and/or towards Madagascar. Based on the dendrogram in Figures 6a, 6c and 6d (*cf.* also chapters 3.2.1.5 and 3.2.1.6) there is no indication for a diverse exchange of species between coastal forests (particularly between those close to the shoreline of the Indian Ocean and those a few kilometers further inland) or from Eastern Africa towards the Oriental Region or Madagascar by high-altitude air currents or monsoon winds in short as well as long distances during the last 2.3 Ma.

#### **7.1.1.6 How did Metarbelidae arrive on the Comoros Archipelago – a missing link to southeast Laurasia?**

The Comoros Archipelago is located *ca.* 300–650 km northwest of Madagascar. The westernmost island is located *ca.* 300 km east from the northern coast of Mozambique.

The Comoros Archipelago is midway between the northwestern coast of Madagascar and the eastern coast of the African mainland. All islands are the result of hotspot volcanism and are not continental or oceanic fragments that predate the motion between the African mainland and Madagascar (Coffin & Rabinowitz 1987). The Comoros volcanicity is relatively young and developed during the last *ca.* 7.7 Ma following a SE–NW younging volcanic trend with the three westernmost islands younger than 1 Ma. Since the Miocene the marine currents are westward and they are dominated by the “South Equatorial Current” at present. There is only one Metarbelidae species, published by Viette (1981) as *Salagena ngazidya*, known from the Comoros Archipelago. This species belongs to Gen.Nov.ZA and hence, is not related to the species on Madagascar but to species of *Squamura* and Gen.Nov.ZB from the Sunda shelf (*cf.* dendrogram Figure 6a). Species of the related Gen.Nov.ZA have a large and very strange distribution range on the African mainland with an unusual disjunct, often rather scattered distribution pattern, occurring in coastal areas of Eastern Africa and on isolated mountains, *e.g.* Mount Elgon in West Kenya (*cf.* 7.1.2.7), or on plateau areas in southwest Africa, but without any coastal records in the Republic of South Africa and Namibia, also with one single distant record from Lowlands in West Africa (Ghana, *cf.* Figure 116). Such a “pattern” might represent the relict of an ancient large distribution range of species of Gen.Nov.ZA. An active and more recent distribution is unlikely as there are not more records from West Africa and/or southwestern Africa since these regions are relatively well represented in the author’s sample of species. In the author’s view does this pattern indicate an ancient species group – the reconstructed ancestral area for this group is the rain forest block of the Guineo-Congolian Region (*cf.* Figure 6d). Since the related Oriental taxa *Squamura* and Gen.Nov.ZB are descendants from species of Gen.Nov.ZA (*cf.* dendrogram) there are two possible scenarios for the origin of Metarbelidae on the Comoros Archipelago:

First, an ancient one: the marine currents from the African mainland became increasingly eastwards 38 Ma and it is likely that species of Gen.Nov.ZA dispersed on driftwoods from the African mainland towards the southeast extremity of Laurasia until 23 Ma (the Sunda shelf originated at only *ca.* 15–3 Ma) via Madagascar where Gen.Nov.ZA later became extinct (or species still occur on Madagascar and have not yet been found). However, accepting the driftwood scenario species of Gen.Nov.ZA dispersed from Madagascar during the last 7.7 Ma to the Comoros Archipelago. If so, *ngazidya* (this species belongs to Gen.Nov.ZA) arrived on driftwoods with marine currents that were westward from Madagascar (Federman *et al.* 2015), but in fact represents an ancient link to ancestors of a species group that arrived in southeast Laurasia via Madagascar on driftwoods. The present island habitat of *ngazidya* is younger than one million years. This is enough time for any driftwood scenario from Madagascar, but the present island habitat cannot represent any link to the Sunda shelf and to species of *Squamura* and Gen.Nov.ZB, respectively.

Secondly, a very young scenario: it is likely that *ngazidya* somehow arrived in mangrove poles from the A

African mainland. The author's reason for this scenario is the fact that one undescribed species of Gen.Nov.ZA that is related to *ngazidya*, occurs as a common species in various mangrove forests along the Kenyan coast and is feeding in mangrove wood (Jenoh *et al.* 2016). This also supports the driftwood scenario described above. But it is also likely that *ngazidya* arrived on the Comoros Archipelago more than 1400 years ago with mangrove poles transported by early traders on their ships, *e.g.* prior to the T'ang period (AD 618–907) when mangrove poles and other commodities reached also distant countries like China from various parts of the Indian Ocean (Bradley Martin 1973). As there were no marine currents suitable for dispersal from the African mainland towards the Comoros Archipelago in the last 23 Ma (Federman *et al.* 2015; Ali & Huber 2010), the author assumes, under this scenario, that the species *ngazidya* occurs in fact in forests along the coast of southern Tanzania and/or northern Mozambique and is not a native species on the Comoros Archipelago.

The author excludes dispersal by wind from the African mainland since this requires enough females for a new population on these islands. As the behavior of females is sedentary in the studied related Kenyan species of Gen.Nov.ZA, it is likely that the females of *ngazidya* have a similar behavior. This makes dispersal by wind difficult (*cf.* chapter 7.1.1.1).

### **7.1.2 Basal taxa – highest diversities in habitats under long stable geomorphological conditions?**

The species of the “Basal Group” *Teragra* and Gen.Nov.A (*cf.* dendrogram) occur south of the Zambezi River on the Southern African Plateau and in a disjunct distribution *ca.* 90–100 km north of the Zambezi (only one record on the plateau of Mount Mulanje). Highest diversities of the “Basal Group” occur in areas that are geomorphologically stable (*cf.* chapter 7.1.2.1) and hence, provide habitats under long stable geological conditions. The author assumes that in such areas the climate is also more stable for many millions of years. A stable physical environment and a stable climate are two of the most important factors to prevent extinctions among species of the “Basal Group” (excluding here fires and forest/woodland destruction by humans, *cf.* chapter 8).

#### **7.1.2.1 Development of the Southern African Plateau– a major area for species of the “Basal Group” and early lineages of the “Afromontane Group”**

The “*Southern African Plateau*” *sensu* Nyblade & Sleep (2003) and defined by the elevation model *sensu* Said *et al.* (2015) respectively, is the most dominant geological structure in Southern Africa and represents today an interior plateau of flat relief but on high elevations between 900 and 1,500 m. It spans nearly two-thirds of Southern Africa.

Since the habitats of all species of the “Basal Group” as well as of species representing early lineages in the “Afromontane Group” are located on the Southern African Plateau, the author decided to present herein some aspects of its geology including information on geomorphologically stable areas. Based on the dendrogram (cf. Figures 6a, 6d) represent among the “Afromontane Group”, e.g. species of the genera *Shimonia* and *Metarbelodes* (subgroups G<sub>1</sub> and G<sub>2</sub>) early lineages, comprising in particular the following species: *Shimonia oyiekeae* Lehmann & Rajaei, 2013 that occurs on the northeastern part of the Southern African Plateau; five undescribed species of *Metarbelodes* subgroup G<sub>1</sub> that occur in the central and eastern part of the Southern African Plateau, including the Zimbabwean craton, and *Metarbelodes umtaliana* (Aurivillius, 1901) that occurs on the Bvumba Mountains (Lehmann & Husemann *in prep.*).

Despite of the uncertainty surrounding the uplift history of the Southern African Plateau there appears to be general agreement that a region of broad uplift (>2.500 m) existed across much of present Southern Africa around the time of the initiation of the breakup of West Gondwana and East Gondwana in between ca. 180–167 Ma (Torsvik *et al.* 2012; Reeves 2014). In the past ca. 180 Ma a total thickness of 2 to 7 km of rock was eroded during two punctuated episodes of exhumation that occurred in the Early-Cretaceous and Mid-Cretaceous (e.g. Van Der Beek *et al.* 2002; Tinker *et al.* 2008a, b). The Southern African Plateau was well established 150 Ma (Lawver *et al.* 1998). It appears to be generally clear that the Southern African Plateau had become flat and low-lying over most of its areas at 66 Ma (cf. Said *et al.* 2015). The Cenozoic (65 Ma to present) is treated by various researchers as an era with a lack of any uplift (e.g. Cockburn *et al.* 2000) or as an era representing a principal period of uplift, topographic development and escarpment formation in Southern Africa (e.g. Partridge & Maud 1987, Burke & Gunnell 2008, Said *et al.* 2015).

The Chimanimani–Bvumba–Inyanga mountainland in eastern Zimbabwe (cf. Figure 197) would be considered to be an elevated margin of the Southern African Plateau from the geographic point of view, but from a geological point of view, these highlands accreted onto the Zimbabwean craton around 1 billion years ago (= 1 Ga) and hence, are much older than the Southern African Plateau. They are relics of a major North-South mountain chain of Himalayan proportions. Hence, the author treats both regions as different and considers their geological history: the highland areas in eastern Zimbabwe are cored by sediments dating back to about 1 Ga, which experienced a later metamorphic reworking event at around 500–600 Ma, when Antarctica (part of East Gondwana) collided with Africa (West Gondwana). Thus the ancient Kaapvaal craton (older than 2.5 Ga), covering the interior of Southern Africa, and Zimbabwean craton, formed the core of the southern section of West Gondwana, and the mountainland was added to this core in two major geological events, dated at 1 Ga and ~600 Ma (Andy Moore pers. comm. 2018).

Although until present no species of the “Basal Group” has been found yet on the ancient Chimanimani–Bvumba–Inyanga mountainland it is very unlikely that such

species are absent. The author expects that species of the “Basal Group” will be found in the future since one species of Gen.Nov.A occurs further north on the plateau of Mount Mulanje. The age of the rock formations of both the Southern African Plateau and the mountainland of eastern Zimbabwe are extremely old (150 Ma/500 Ma) which is one issue, but the age of the erosion cycle that has been imprinted on both formations is another aspect and it can be very young. Hence, to consider the Chimanimani–Bvumba–Inyanga mountainland (and the highlands of Lesotho) as relics of Gondwana erosion cycles is probably no longer correct (Andy Moore pers. comm. 2016). In general, the oldest cycle of erosion is considered to be the African cycle initiated in the early Cretaceous and long continued until the late Paleogene. In consequence of this erosion cycle the “*African Surface*” *sensu* Burke & Gunnell (2008) developed and is a result of deep weathering under geomorphologically stable conditions following the break-up of Gondwana. Its development ended abruptly *ca.* 30 Ma when the establishment of the present geological structure of the African continent began. All areas on the Zimbabwean and Kaapvaal cratons that are linked by the Limpopo Mobile Belt, represent geomorphologically stable areas with no volcanism or rifting during the last 70–60 Ma (*cf.* Figure 3 in Moore *et al.* 2008). Hence, habitats of species of the “Basal Group” as well as of *Metarbelodes* subgroups G<sub>1</sub> and G<sub>2</sub> that occur on both cratons experienced probably also a more stable climate for millions of years with ancient sites covered by woodland and/or forest (*cf.* Figure 197).

Species of the “Basal Group” occur at the Soutpansberg, the Blyde River Canyon, the Katberg pass, on the coastal plain east of the Great Escarpment (all areas are located in the northeastern Republic of South Africa) and on the plateau of Mount Mulanje (90 km to the North of the Zambezi River in southern Malawi).

The Soutpansberg is largely situated on the “*African Surface*” above the Limpopo Mobile Belt with Archaean basement rocks. The Blyde River Canyon and Katberg pass developed both on the Great Escarpment which forms a horseshoe-shaped elevated zone almost surrounding the inland plateau and overlooking the coastal plain. The actual zone of break-up is offshore, at the edge of the continental shelf. The classical model for evolution of the coastal plain (the plain on the coastal side of the escarpment) is that it was formed by headward (inland) retreat of the escarpment after break-up of Gondwana. However, this model is very controversial (Andy Moore pers. comm. 2018). Mount Mulanje (3.002 m) is a result of shoulder uplift of the active Malawi Rift (*cf.* 7.1.2.6) and a local topographic anomaly with a relative young age (post-15 Ma) (Burke & Gunnell 2008). The fact that one species of the “Basal Group” occurs only on the plateau of Mount Mulanje, with no additional record in Malawi (Raymond Murphy pers. comm. 2018), suggests that Mount Mulanje could be much older than 15 Ma. The author’s opinion is supported by Woolley (1987). Although he did not mention a specific age for Mount Mulanje, Woolley found (based on his extensive field work) that this mountain is part of the Chilwa Alkaline Igneous Province and that the magmatism is contemporaneous with the Mesozoic igneous activity. An age determination is ranging from 105 to 138 Ma for the Chilwa Province.

One more support for the author's view comes from Andy Moore (pers. comm. 2018) who stated that Mount Mulanje "is a deeply eroded sub-volcanic complex (deep-seated rocks underlying an old volcano), and would almost certainly have been originally located on an extension of the mountainland forming eastern Zimbabwe ... around 125 Ma occurred the opening of the Atlantic Ocean. This was a multi-cyclic erosion event, probably with a period of further accelerated erosion at the end of the Cretaceous. I think that it is reasonable to postulate that this early-end Cretaceous episode of erosion was responsible for isolating volcanic massifs such as Mulanje, Zomba and Gorongozo from the high level Southern African Plateau, which included the highlands of eastern Zimbabwe."

#### **7.1.2.2 Why did Metarbelidae evolve in the Afromontane Region?**

The long lived North–South mountain chain that was formed *ca.* 500 Ma when Antarctica collided with (Southern) Africa as part of the continental amalgamation to form the Gondwana super-continent, and of which the Chimanimani–Bvumba–Inyanga mountainland and the highlands of Lesotho are still existing relicts, separated the (coastal) lowlands to the East (in present Mozambique) from the Southern African Plateau in the interior during the last *ca.* 180 Ma. Geomorphological changes occurred, particularly after the break-up of Gondwana and the opening of the Indian Ocean *ca.* 168–145 Ma (Reeves 2014), and initiated driving forces on the evolution in general. Additionally, the early northwestward course of the ancient Zambezi River was linked to the old headwaters of the Chimanimani–Bvumba–Inyanga mountainland. The modern drainage direction towards the East into the Indian Ocean initiated with the break-up of Gondwana (Key *et al.* 2015).

Since the origin of Metarbelidae was much later and began at *ca.* 100 Ma as suggested by Wahlberg *et al.* (2013; *cf.* introduction) driving forces for their evolution do possibly not include the opening up of the Indian Ocean as well as the initiation of the modern drainage direction of the Zambezi River. The re-constructed biogeographic events that are presented for each genus herein (*cf.* chapter 4) indicate that vicariance in the Afromontane Region certainly is one driving force for speciation. Another driving force in the Afromontane Region might be the climate in relation to the altitude combined with the existence of high altitude moist temperate forest or other woody vegetation refuges that preserved species of the "Basal Group" for further speciation and dispersal into the adjacent Lowlands of the coastal plain to the East of the Great Escarpment. The differing elevation with different climates, the long geomorphological stability coupled with climatic stability and only local climatic changes, *e.g.* during the Pleistocene, created and preserved many different micro-environments for Metarbelidae evolution. Hence, a main driving force was and perhaps still is 'elevation'.

### 7.1.2.3 The Afromontane Region – the major area for old lineages that occurred in habitats dominated by gymnosperms

Drier and wetter Afromontane forests constitute an important habitat for both, species of the “Basal Group” and “Afromontane Group” including strict endemic and/or near-endemic species (*cf.* Table 1; Figure 6d). White (1981) stated that all species of trees and shrubs that occur in the Afromontane Region, and that are not intruders from the lowlands, show disjunctions that are greater than the distance between neighbouring islands and “... *simple historical explanations, involving drastic climate changes ... cannot provide adequate explanation ...*” The author found among all species of those genera that are at least near-endemic to the Afromontane archipelago-like regional centre of endemism, *e.g.* *Aethiopina*, *Metarbelodes* (subgroups G<sub>1</sub>, G<sub>2</sub>, G<sub>3</sub>, Lehmann & Husemann *in prep.*), *Mountelgonia* and *Ortharbela* a disjunct pattern that has five features: (1) Disjunct species did not evolve different wing patterns (*cf.* Figures 128, 139, 140). The wing pattern has a great uniformity in both sexes (*cf.* Figures 130, 131, 132, 133) although the species occur at different altitudes, in different habitats and under a different average annual rainfall. This uniformity in the wing pattern is an example for a stabilizing selection in which morphological traits remain stable as a result of similar selective pressures over a long period of time. At this state of knowledge it is unknown what these selective pressures might be. (2) The disjunctions are visible in male genitalia of genera with more than eight studied species in *Metarbelodes* (all subgroups) and *Mountelgonia*, *e.g.* an absent, partly absent or well developed sacculus as well as a nearly absent, small or long developed thorn-like process on the valva. (3) In species of those two genera the next intermediate character state does not occur in species in the adjacent area. Instead, several hundred or several thousand kilometers separate intermediate states in species (best visible in all three subgroups of *Metarbelodes*). (4) The longest disjunction of *ca.* 3.300 km occurs in species of *Metarbelodes* G<sub>1</sub> with species occurring along the Chobe River/Zambezi River and the closest related species that occurs on the Harar Plateau (*cf.* Figure 137). (5) At present, and based on the morphology, only one species among 35 species of *Metarbelodes* has its sister-species in an adjacent area in northern Tanzania (Mount Kilimanjaro – Mount Meru) while all other species have a sister-species at least more than 1000 km away (a phylogenetic analysis for all subgroups of *Metarbelodes* will be later presented by Lehmann & Husemann). Species from Mount Kilimanjaro and Mount Meru are among the youngest *Metarbelodes* since the age of the two volcanoes is less than 2 Ma.

The Afromontane Region had a temperate climate in contrast to the hothouse conditions that occurred in the adjacent Lowlands, *e.g.* *ca.* 145–65 Ma. This might be the main reason why species of the “Basal Group” and species of early lineages among the “Afromontane Group”, *e.g.* *Metarbelodes* G<sub>1</sub>, G<sub>2</sub>, still occur in geologically long stable montane areas but are absent from lowland areas that are far away from the

Afromontane Region. At the time 65 Ma or earlier, montane habitats were dominated by gymnosperms. This assumption is supported by the facts: (1) Angiosperms did not originate in Southern Africa but migrated from the northern Afro-Arabian continent southwards (Zavada 2004). (2) In tropical Africa (not in the Afromontane phytochorion that was and is temperate-seasonal) the diversification of angiosperms began with an associated reduction in gymnosperms *ca.* 95 Ma (Jacobs 2004). (3) Evidence for a diverse but small herbaceous (none-woody) angiosperm flora that existed *ca.* 95 Ma was found in the Orapa kimberlite pipe (Botswana). Rayner *et al.* (1997) indicate that the whole area of Orapa was forested and had a temperate and seasonal climate. Pollen belonging to woody gymnosperms were found representing, *e.g.* Araucariaceae, Cupressaceae and †*Ephedripites* Bolkhovitina & Potonié. Woody angiosperms were not found. (4) Jacobs (2004) pointed out that angiosperm woods are absent from all fossil records in tropical Africa dated from the Cenomanian *ca.* 100–93 Ma and that they are absent from older deposits. Instead fossil records from the Cenomanian comprise only gymnosperm trees, particularly from xerophilous conifers (Cheirolepidiaceae) that disappeared towards the end of the Cretaceous under an increasingly humid climate. (5) Evidence for the occurrence of woody angiosperms in Southern Africa is not older than *ca.* 86.3 Ma (Burgoyne *et al.* 2005) and was found in the Mzamba Formation (Middle to Late Santonian *ca.* 86.3–83.6 Ma) of the Eastern Cape (Pondoland) with trunks that possibly belong to Euphorbiaceae and Monimiaceae (Laurales).

However, montane habitats dominated by gymnosperms at present can have a remarkable high diversity of *Metarbelidae* if they are continuously dominated by gymnosperms on old forest sites comprising trees that are more than 300 years old (*cf.* Figure 3).

#### **7.1.2.4 The Eastern Arc Mountains and their adjacent Lowlands – species of early lineages of the “Afromontane Group” and Guineo-Congolian Region have not yet been found**

It is remarkable that there is not a single record from the Eastern Arc Mountains and from their adjacent Lowlands of one species representing early lineages among the “Afromontane Group” such as *Metarbelodes*, or of one species that belongs to a genus of the Guineo-Congolian Region.

The Eastern Arc Mountains comprising 13 isolated mountain blocks uplifted *ca.* 30–25 Ma in eastern Tanzania, *e.g.* the East Usambara, Udzungwa, Uluguru, Ukaguru mountains and the Taita Hills in southeast Kenya (Burgess *et al.* 2007). The lowland areas of Eastern Africa, including the Lowlands adjacent to the Eastern Arc Mountains, are of interest since for example, the coastal forests of Somalia, Kenya and Tanzania (possibly also of Mozambique) were once linked with the lowland rain forests of “*Congolia*” during *ca.* 75–25 Ma (Axelrod & Raven 1978) but became increasingly separated due to geological instability linked to the EARS (*cf.* 7.1.2.5) as well as due to a

drier climate that caused significant reductions in lowland rain forest in Central Africa, *e.g.* between 8 and 5 Ma, 2.5 Ma and 800.000 years ago (Maley 2001). Hemp *et al.* (2016) demonstrated for northeast Tanzania and southeast Kenya in regard to Orthoptera that lowland and submontane forest expanded during 2.7–2.5 Ma and 1.9–1.7 Ma while montane forest occurred also on lower elevations 1.1–0.9 Ma favoring the spread of montane species. An example for a favored spread of a montane species among Lepidoptera was found by the author during 14 years of extensive field studies (1994–2008) only in regard to the montane butterfly *Charaxes acuminatus* subsp. *shimbanus* van Someren (1963) in the coastal forests (first record for Kenya below an altitude of 10 m, *cf.* Kroon 2001; Lehmann & Kioko 2005). Only one other example is presented here in regard to the species of the genus *Ortharbela* that occur on Mount Kilimanjaro (*cf.* 7.1.2.7), the East Usambara Mountains and the Uluguru Mountains with an additional record from Buda Forest, representing a lowland coastal forest in southeast Kenya.

At present, there is no visible extension of any Metarbelidae species that belongs to a genus of the Guineo-Congolian Region into areas of the Eastern Arc Mountains although the flora has strong affinities with the Guineo-Congolian Region (Lovett 1993b). As one species of Gen.Nov.I occurs on the relatively dry Ukaguru Mountains it represents one link to species of Gen.Nov.H occurring on Madagascar. Lovett (1993b) stated in regard to the flora of drier Eastern Arc forest types that “... *It may well be that some Eastern Arc species with southerly distributions ... have their origins in Madagascar...*” However, in contrast to some plant species that might have their origin on Madagascar is an origin of species of Gen.Nov.I on Madagascar and a subsequent dispersal to the African mainland and the Eastern Arc Mountains, respectively, not supported by the reconstructed ancestral areas for Metarbelidae (*cf.* Figure 6d and chapter 7.1.1.2). The absence of species of the “Basal Group” and possibly also of species representing early lineages in the “Afromontane Group” (*e.g.* species of *Metarbelodes* subgroups G<sub>1</sub>/G<sub>2</sub>) might be linked to the relatively young age as well as to the long isolation of all 13 mountain blocks. More research on Metarbelidae is necessary in the Eastern Arc Mountains to confirm this hypothesis and to find the still missing link to the Guineo-Congolian Region and to species of *Metarbelodes* subgroup G<sub>3</sub>.

#### **7.1.2.5 Development of the East African Rift System – an area of high species diversity**

The species diversity of Metarbelidae is in general high in the East African Rift System (EARS) *sensu* McConnell (1972). This is also visible in Figure 1 where the red dots are particularly dense in the regions of the EARS.

A total of 127 species, or 29%, occur only in the EARS. These species belong to Gen.Nov.B, Gen.Nov.L, *Mountelgonia*, *Metarbelodes* (subgroups G<sub>1</sub>, G<sub>3</sub>), Gen.Nov.ZJ, *Marshalliana* and *Aethiopina*. The latter five genera belong to the “Afromontane Group” and have their present distribution centre in the Afromontane Region of the

EARS. Early lineages in the “Afromontane Group” comprise three species and their distributions will be discussed below and in the following two chapters: one undescribed species belongs to the genus *Metarbelodes* (subgroup G<sub>1</sub>) and occurs on the Somalian Plateau (cf. Figure 137); *Shimonia splendida* (Fletcher, 1968, cf. Lehmann & Rajaei, 2013) occurs on the Rwenzori Mountains (cf. chapter 7.1.2.6); one undescribed species of *Shimonia* occurs close to Mount Elgon in West Kenya (cf. chapter 7.1.2.7). Species of the “Basal Group” are entirely absent in the EARS.

In the following text the author discusses a scenario explaining the distribution of the undescribed species of *Metarbelodes* G<sub>1</sub> on the Somalian Plateau based on its different geomorphological history if compared to the adjacent EARS.

Much of present Eastern Africa and Arabia represented Lowlands (not exceeding 500 m) between 65–30 Ma (Merla & Minucci 1938; Şengör 2001). The EARS began its development within the Main Ethiopian Rift (MER) (Mohr 1983). Three discontinuities occur along the strike of the rift, separating the northern (NMER), central (CMER) and southern (SMER) rift sectors (Keranen & Klemperer 2008). The northern end of the SMER corresponds to the division of the rift valley into the Chamo Basin and Galana Basin both just east of Gamo-Gidole. The first eruptions of basalts occurred in the SMER with the greatest eruption 31–28 Ma extending over an area of ca. 1.000 km in diameter and reaching up to 2 km thickness. This “*Ethiopian Flood Basalt Province*” *sensu* Mohr (1983) only borders the Harar Plateau (that pertains to the Somalian Plateau) in the West. A species of an older lineage of *Metarbelodes* (subgroup G<sub>1</sub>) has been found further to the East on a mountain chain that extends from the Harar Plateau eastwards into northwest Somalia. Hence, the present habitat of this undescribed species of G<sub>1</sub> is excluded from the “*Ethiopian Flood Basalt Province*” and was not destroyed by flood basalts. Additionally, the volcanic activity continued in the SMER from the pre-rift event ca. 45 Ma until 11 Ma and hence, the Somalian Plateau was not affected by this volcanism. Magmatism in the Kenya Rift further south has occurred in stages roughly coeval with this extensional deformation (Keranen *et al.* 2009). Various fault-escarpments (with often vertical boundaries of > 1.000 m height) separate the MER rift valley from the Ethiopian Plateau in the West and from the Somalian Plateau in the East. Both plateaus rise to elevations of > 2.000 m. The Somalian Plateau includes the Harar Plateau and lies south of the Afar Depression, extends from northwestern Somalia to southeastern Ethiopia. The Somalian Plateau has been not significantly modified by Cenozoic rifting and magmatism in contrast to the Ethiopian Plateau (Keranen & Klemperer 2008). This is possibly one of the main reasons why an old lineage of the “Afromontane Group” survived on the Somalian Plateau but is absent from the Ethiopian Plateau. There appears to be no consensus about the timing of both plateau uplifts, but if there was any uplift of the Somalian Plateau, the strongest plateau uplift occurred ca. 30 Ma (Pik *et al.* 2008). Hence, the Somalian Plateau is geomorphologically older, more stable and a potential refuge area for old lineages of species of the “Afromontane Group”.

A second phase of flood basalt volcanism occurred between 11–10 Ma in the NMER (Wolfenden *et al.* 2005). In the CMER no major tectonic events occurred until 6 Ma (Bonini *et al.* 2005). Since 1.8 Ma volcanism in the MER is largely correlated with the Wonji Fault Belt and slow spreading along the centre of the rift valley has been recorded (Keranen & Klemperer 2008). Hence, all areas in the MER are geomorphologically not stable and, *e.g.* species of the “Basal Group” as well as species representing descendants of older lineages in the “Afromontane Group” are most probably absent.

#### 7.1.2.6 The “Western Branch” and “Southwestern Branch” of the EARS

Both branches are geomorphologically not stable. Nevertheless, they are presented here since *Shimonia splendida* (*cf.* chapter 7.1.2.5) occurs in the northern part of the “Western Branch”. In this context the author discusses a scenario explaining the distribution of the genus *Shimonia* (*cf.* Figure 124) that is considered as an early lineage among the “Afromontane Group” (*cf.* chapter 3.2.1.2 as well as Lehmann & Rajaei, 2013).

The “Western Branch” extends over a distance of *ca.* 2.000 km. Its northernmost extension comprises the Albert Rift Basin that begins *ca.* 30 km north of Lake Albert in northwestern Uganda. The other rift basin sectors towards the South include the Edward Rift, the Kivu Rift, the Tanganyika Rift, the Rukwa Rift and the Malawi Rift. The rift basins of Lake Albert, Lake George and Lake Edward belong together to an area referred to as the Albertine Rift (Wayland 1921) that extends to the southern end of Lake Tanganyika. Plumptre *et al.* (2007) included the adjacent areas that are located to the South from the lake tip and more or less close to or on the edge of the Southern African Plateau in Zambia into the “*Albertine Rift Region*”. This region comprises geomorphologically young areas that were once covered by a large Paleolake (Lake Obveruka) between 8–2.5 Ma (Pickford *et al.* 1993). Lake Obveruka was separated into the present Lake Albert and Lake Edward due to a tectonic event only *ca.* 2.5 Ma (Ebinger 1989; Pickford *et al.* 1993). The “Western Branch” terminates with the Malawi Rift that extends from the “*Rungwe Volcanic Province*” to the Urema and Dombe half-grabens in Mozambique – this sector is assumed to be the youngest, with rifting possibly younger than late Miocene (Ebinger *et al.* 1987). The extent south of the Malawi Rift is unclear (*cf.* Mougnot *et al.* 1986; Hartnady 2006; Fonseca *et al.* 2014). The “Western Branch” is characterized by high seismic activities, deep rift lakes and steep fault scarps rising up several thousand meters adjacent to the graben floor. Various authors argued that the “Western Branch” is considerably younger than the “Eastern Branch” with its development beginning *ca.* 12–7 Ma (*e.g.* Burke 1996; Nyblade & Brazier 2002). More recently it has been found by Roberts *et al.* (2012) that the initiation of rifting begun in the “Western Branch” contemporaneously with the “Eastern Branch” 26–25 Ma.

The “Southwestern Branch” was possibly first recognized by Fairhead & Girdler (1969) and includes a network of rift basins occurring along a ca. 250 km wide corridor from the Northeast (Upemba and Lufira rift basins in southeast DRC) to the Southwest into the Okavango Rift Zone, ORZ (Scholz *et al.* 1976; Kinabo 2007). Rifting in the ORZ began 179 Ma (Le Gall *et al.* 2002) and again ca. 41 ka (= 41 thousand years ago) (Ringrose *et al.* 2005) including the area of the developing half-graben of Linyanti-Chobe.

The habitat of *Shimonia splendida* is located on more ancient plateau areas, *e.g.* like the “Albertine high”, that is located in the “Western Branch” but belongs to the very ancient Rwenzori Mountains rising up to 5.109 m today and in particular to its northern part. Based on thermochronological data (mainly apatite fission-track & (U-Th)/He ages) a prolonged exhumation history for the Rwenzori Mountains was derived by Bauer *et al.* (2012, 2016). Separate blocks can be distinguished that experienced differentiated exhumation through time: the southern part of the Rwenzoris reached upper crustal levels (ca. 2 km below surface) already in the Carboniferous ca. 300 Ma, the northern part was exhumed to upper crustal level much later ca. 130 Ma. Thus a pre-Cenozoic plateau like “Albertine high” of ca. 1.500–2.000 m is conceivable (Bauer *et al.* 2010, 2013). Exhumation along the western flank initiated in the Oligocene ca. 30 Ma. Final surface uplift to current elevations occurred during the Plio-Pleistocene ca. 5 Ma (Bauer *et al.* 2013). The geomorphologically oldest parts of the Rwenzori Mountains are potential ancestral areas of the stem lineage representatives of the genus *Shimonia*. As these montane areas are geomorphologically older than adjacent regions of the “Western Branch” it is likely that ancestors of species of *Shimonia* spread from the ancient plateau areas of the Rwenzori Mountains into the Congo Basin in the West as well as towards Mount Elgon in the East.

#### 7.1.2.7 The “Eastern Branch” of the EARS

Extensive volcanism only occurred in the “Eastern Branch” that was well established ca. 20 Ma and which is – if compared to the “Western Branch” – surrounded by a broad regional plateau (Ring 2014). The “Eastern Branch” extends from the MER through the ca. 50 km wide Kenya Rift and terminates in the “Northern Tanzanian Divergence Zone” (NTDZ) (Dawson 1992) in the South along the Manyara-Balangida axis in the isolated Kwaraha and Hanang eruptive centres that developed ca. 1.5 Ma (Bagdasaryan *et al.* 1973). Volcanism commenced ca. 23 Ma in the Kenya Rift, *e.g.* Mount Elgon, a large off-rift volcano begun to erupt ca. 20 Ma (Burke & Gunnell 2008). Hence, the author assumes that all species of Metarbelidae that occur today in the “Eastern Branch” or in its adjacent areas cannot be older than 23 Ma. Species of Metarbelidae should be younger the closer they occur towards the NTDZ while species of the genus *Aethiopina* that occur only in areas close to the main Kenya Rift should be older since this rift sector has grabens that are distinctly older and more mature with

voluminous volcanics if compared to the NTDZ (*cf.* Ring 2014). Based on the author's hypothesis, it is very unlikely that ancestors of species of the genus *Shimonia* have any ancestral area close to or on Mount Elgon where one undescribed species occurs at present. Almost certainly the ancestors of this species "migrated" from the Rwenzori Mountains towards the East earlier than 20 Ma.

The reason for the absence of any species of *Shimonia* from central Kenya might be the period of intense phonolite volcanism that initiated first in the central Kenya Rift with the development of a halfgraben 14–6 Ma. After the eruption of the Yatta phonolite the rift basin was filled, magma overflowed the margins with a further eastern flank uplift of *ca.* 500 m towards the Yatta Plateau. This period of volcanism extended from Laikipia to the Uasin Gishu Plain and to the Kitale area (near Mount Elgon) as well as towards Tarime (northwest Tanzania) (Shackleton 1978). Such geomorphologically not stable regions cannot provide refuges for old lineages of Metarbelidae. Again voluminous lavas and trachytes evolved in the Kenya Rift 5–2 Ma (Ring 2014). The full graben of the central sector developed 5.5–3.7 Ma (Roessner & Strecker 1997). A stunning feature of that period is Mount Kenya. The reconstruction of Schoorl *et al.* (2014) indicate that an at least 5,600–7,000 m high active Mount Kenya existed in the Pliocene between 5.1 and 2.8 Ma with a first build-up phase *ca.* 5.8 Ma and was one of the highest mountains globally during that period of time. The author assumes that Metarbelidae species occurring on Mount Kenya or nearby are not older than the mountain. This hypothesis is supported by the fact that the last major collapse event around 2.8 Ma coincided with a major change in regional vegetation (Schoorl *et al.* 2014). This suggests that new habitats evolved together with new lineages of Metarbelidae, also in consequence of the truncating of Mount Kenya that may have caused significant changes in the local climate with possible implications for environmental change in the whole central Kenya Rift. Most of the lakes of the central sector are located on a wider inner rift depression that was created *ca.* 2.6 Ma (Bergner *et al.* 2009). Species of Metarbelidae that occur within the NTDZ must be relatively young due to the volcanic activities that began in the Essimngor region (Nonnotte *et al.* 2008) northeast of Lake Manyara with Mount Losimingur 2,179 m 8.1–7.3 Ma. The Ngorongoro–Kilimanjaro Volcanic Belt (NKVB) began to develop 8.1 Ma (*cf.* Evernden & Curtis 1965; Dawson 1992). In the Manyara Rift, volcanism appears to have migrated southwards (Ring 2014) with ages of 4.9–1.5 Ma for its northern part and 1.5–0.7 Ma for its southern part (Bagdasaryan *et al.* 1973). Mount Meru developed during the last 2 Ma; Mount Kilimanjaro developed first *ca.* 2.5 Ma.

Most rift basins with their rivers and lakes in northern Tanzania are younger than 2–1 Ma (also Ring 2014).

The author gave some supporting arguments in the above chapters that Metarbelidae possibly first originated in the Afromontane Region where still species of the "Basal Group" as well as descendants of species of old lineages occur on ancient mountains. In regard to plants, Burgoyne *et al.* (2005) stated that this phytochorion "... may well comprise the largest assemblage of ancient persistent floristic elements on the

*African continent*". White (1981) already pointed out that the history of the present Afromontane Region flora "... goes back to the Cretaceous".

A relict character of the Afromontane Region becomes obvious in the archipelago-like summit mountains with their patchy dispersal of forests comprising mainly strict endemic or near-endemic species of Metarbelidae on each summit mountain (*cf.* Table 1; Figure 197).



**FIGURE 197.** View from the summit of the Bvumba Mountains taken from Castle Beacon (1.911 m, Zimbabwe) in May 1969 by the late botanist Darrel Plowes (Mutare, formerly Umtali). Beyond the flowering *Aloe arborescens* Mill. (Aloaceae) (right) is the Burma Valley below and on the southeast side, the high hill in the middle distance is Leopard Rock, a so called "granite bornhardt" (a type of inselberg). Where the high Bvumba ground drops sharply down into the Burma Valley (730–880 m, both part of the post-African surface developing since 30–25 Ma) in the right centre of the picture, the Witchwood Valley forest (also known as Bungu Forest) begins. The forests seen towards the Burma Valley and Leopard Rock belong to the "Mixed submontane forest" type with the highest tree species diversity recorded for Zimbabwe (Müller 2006). Within a few kilometers a different, much older erosion surface (possibly "African Surface") may be preserved on Castle Beacon (Lister 1987; Andy Moore pers. comm. 2016). The row of hills in the background of the picture forms the border with Mozambique and still belongs geomorphologically to the Bvumba Mountains. The Bvumba Mountains are considered by the author as a potential refuge area for species of the "Basal Group".

### 7.1.3 The association of Metarbelidae with legume-dominated lowland tropical forests or woodlands or other legume-dominated tropical woody vegetation types

The author has not any doubt that lowland tropical Metarbelidae species are strongly associated to woody legumes. Based on long-term field studies in lowland as well as montane forests of Kenya, Lehmann (2008) stated that Metarbelidae of lowland tropical areas “*are closely associated with legume-dominated forests, woodlands or other legume-dominated woody vegetation types*”. This opinion is supported by the following facts:

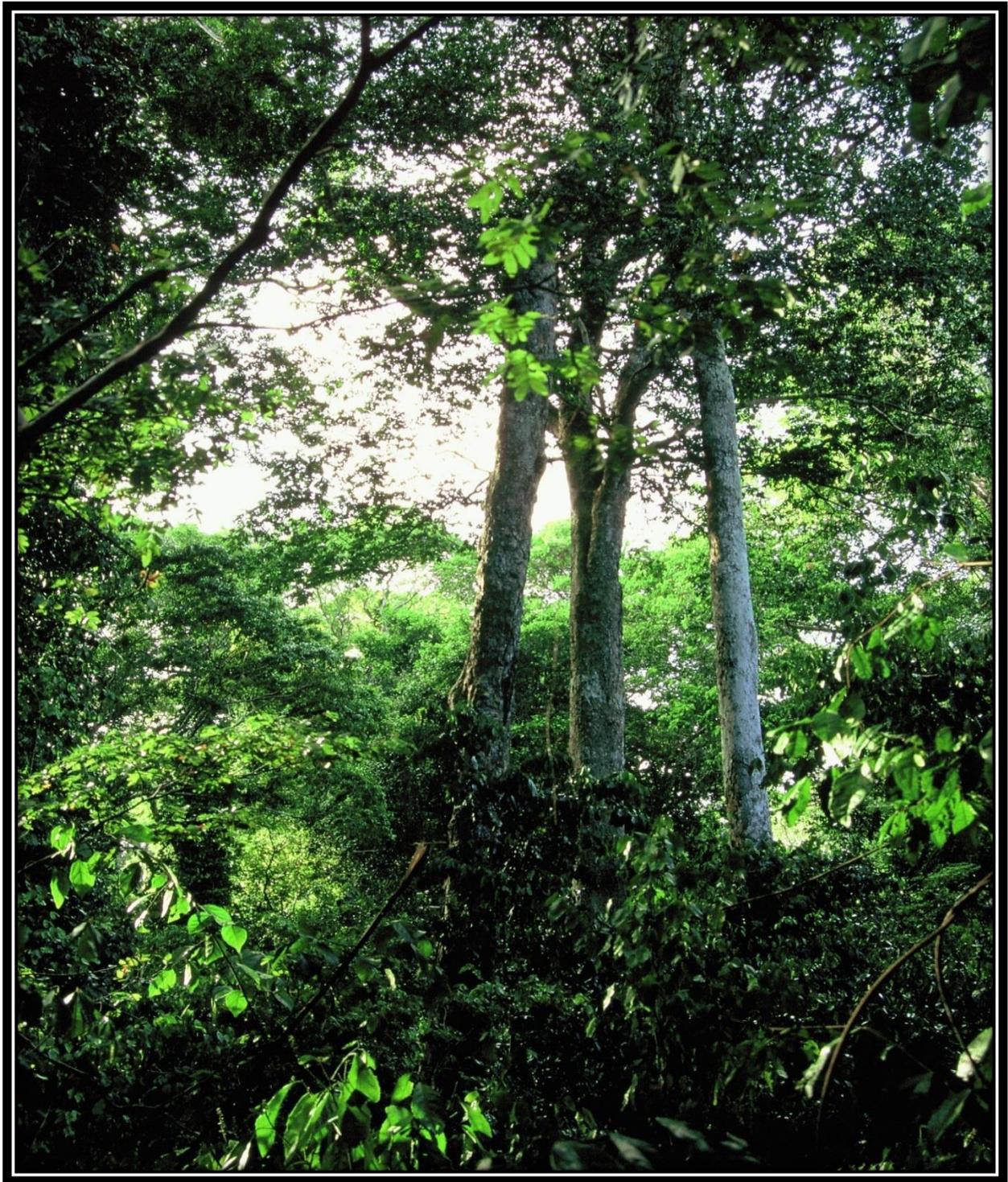
Lowland rain forests of Africa are characterized by three features: (1) only one gymnosperm tree genus (*Podocarpus* L'Héritier) still occurs rarely in lowland rain forest on the African mainland, *e.g.* at 600 m at Kouyi (just southeast of the Massif du Chaillu, Republic of the Congo, Maley 2001); (2) all single-dominant lowland rain forests as well as (3) all mixed lowland rain forests on the African mainland are dominated by the legumes of the “subfamily Caesalpinioideae” representing often large trees (Richards 1996, p. 311). One reason for such a strong dominance of legumes are traits related to growth in soils poor in nitrogen, phosphorus and other nutrient elements combined with the possible ecological importance of different mycorrhizal associations for these trees (Malloch *et al.* 1980). Most of these legume tree species have heavy seeds without an efficient dispersal mechanism. This is from the author's point of view another reason why Metarbelidae species that are associated to woody legumes have a sedendary behavior or slow dispersal abilities in lowland rain forests or in coastal forests of Eastern Africa, *e.g.* Kaya Muhaka and Gogoni Forest (Kwale District, Kenya).

If the author is correct, the following conclusion can be drawn: the earliest Metarbelidae that are linked to legume dominated tropical lowland rain forests evolved on the Afro-Arabian continent together with the earliest diversification events for the woody Leguminosae *ca.* 59 Ma (Couvreur *et al.* 2011) with the majority of caesalpinioids and all mimosoids that were diverse by mid Eocene *ca.* 40 Ma (Wojciechowski 2003). This diversification of the legumes was rapid since their origin *ca.* 59.9 Ma (Wojciechowski 2003). The latter view contrasts with the view of an earlier origin of woody Leguminosae *ca.* 65 Ma ago and a long period of diversification that ended *ca.* 50 Ma (Axelrod 1992). However, any co-radiation of a diverse Metarbelidae fauna in lowland rain forest ended probably during the same period of time *ca.* 50 to 40 Ma. A strong association of African tropical lowland Metarbelidae to woody legumes explains, with one reason, the great difference in diversity of Metarbelidae between the Afrotropical Region and Oriental Region (*cf.* next chapter). Additionally, the origin of the Leguminosae was most probably restricted to edaphically dry sites, *e.g.* with sclerophyll woodland or shrubland, and in terrains of diverse relief along the Tethyan Seaway (Axelrod 1992). The only biome that optimized the basal branches of the legume phylogeny is the semi-arid Succulent Biome (Schrire *et al.* 2005), a kind of

desert shrubland. This biome occurred along the Tethyan Seaway in present northwestern Africa as well as adjacent to the northwestern edge of the Southern African Plateau *ca.* 75–55 Ma (*cf.* Axelrod & Raven 1978). Hence, if a primary trend in legume evolution is that wet derived from dry (Brian Schrire pers. comm. 2008) implies that the earliest lowland Metarbelidae that were linked to legumes occurred in dry habitats of southwestern Africa (maybe also on the northwestern part of the Southern African Plateau) and “migrated” northwards where they later co-radiated with the developing legume-dominated lowland rain forest as well as with the developing legume-dominated woodland. The oldest record of woodland dominated by legumes is known from Mahenge (Tanzania) 46 Ma and was structurally similar to modern miombo with seven Leguminosae species and the earliest record for *Acacia* Mill. (Jacobs 2004).



**FIGURE 198a.** Legume-dominated “Wetter mixed semi-deciduous forest” (Lehmann & Kioko 2005), Kaya Muhaka (Kenya, Coast), “Ingo’s Site” (Site 1), with the highest diversity of Metarbelidae on 625 m<sup>2</sup> comprising six species (including four undescribed species) in five genera (including *Salagena*, males of Gen. Nov. ZG and three other new genera) recorded during 14 years (1994–2008). The most dominant tree species include six specimens: one large tree of *Parkia filicoidea* Oliv. (Mimosaceae, dbh 340 cm (!), diameter at base 650 cm, height 27.6 m, the lower stem is in the left centre of the picture); two trees of *Julbernardia magnistipulata* (Harms) Troupin. (Caesalpiniaceae, dbh 38,4–56.6 cm, height up to 16.5 m) and three trees of *Synsepalum brevipes* (Baker) T.D. Penn. (Sapotaceae, dbh 30.0–70.1 cm, height up to 20.1 m). The leaves in the foreground belong to the tree *Drypetes reticulata* Pax (Euphorbiaceae, dbh 14 cm, height 10.7 m). Picture by Ingo Lehmann in February, 1994.



**FIGURE 198b** Legume-dominated “Wetter mixed semi-deciduous forest” (Lehmann & Kioko 2005), Kaya Muhaka, “Bohemani Site” (Site 6), with high diversity of Metarbelidae on 625 m<sup>2</sup> comprising five species (including four undescribed species) in four new genera (including males of Gen. Nov. ZG) recorded during 14 years (1994–2008). The most dominant tree species comprise 15 specimens: nine trees of *Scorodophloeus fischeri* (Taub.) J. Léonard (Caesalpiaceae, dbh 50.2–146.1 cm, height 17.2–36.1 m, three stems are visible in the centre of the picture), four trees of *Craibia brevicaudata* (Vatke) Dunn (Papilionaceae, dbh 22.2–36.9 cm, height 8.7–12.1 m) and two trees of *Cynometra suaheliensis* (Taub.) Baker f.(Caesalpiaceae, dbh 8.5–46.9 cm, height 5.2–24.1 m). Picture by Ingo Lehmann in January, 1998.



**FIGURE 199.** Woody legumes are very rare in Kaya Kinondo, a “Groundwater forest on coral rag” (Lehmann & Kioko 2005); figured is “Antiaris Site” (Site 2) where only one undescribed species of Metarbelidae (males of Gen. Nov. ZG) occurs on 625 m<sup>2</sup> recorded during 14 years (1994–2008). The most dominant tree species comprise 12 specimens: three specimens of *Antiaris toxicaria* (Pers.) Lesch. (Moraceae, dbh 89.0–107.0 cm, height 25.0–33.1 m, with two large stems in the background of the picture), four trees of *Sorindeia madagascariensis* DC. (Anacardiaceae, dbh 8.8–50.3 cm, height 9.5–15.7 m, one tree is visible in the foreground) and five trees of *Drypetes reticulata* Pax (Euphorbiaceae, dbh 13.1–18.2 cm, height 6.5–16.7 m). Picture by Ingo Lehmann in January, 1998.

## 7.2 The Oriental Region

### 7.2.1 Dispersal patterns, the possible age of the local Metarbelidae fauna and reasons for their low diversity

#### 7.2.1.1 Dispersal of *Squamura* and Gen.Nov.ZB

A possible dispersal scenario from the Afro-Arabian continent via Madagascar to southeast Laurasia and the Sunda shelf, respectively, on driftwoods (*cf.* Trewick 2000; Coulson *et al.* 2002) was already presented for the genera *Squamura* and Gen.Nov.ZB in relation to their sister-taxon Gen.Nov.ZA (*cf.* Figures 6a, 6d, III and chapters 7.1.1.3, 7.1.1.6). Hence, both “Oriental genera” will be not further discussed here.

#### 7.2.1.2 Dispersal of species of Gen.Nov.U, V, X and the possible age of their stem lineage representatives

The ancestral area of the Oriental species in Gen.Nov.V has been reconstructed as the Guineo-Congolian regional centre of endemism. The same ancestral area has been reconstructed for the species in Gen.Nov.U from Nepal (*cf.* Figure 6d). The sister-taxon of the Oriental Gen.Nov.X + *acutistriata* (Mell, 1923) occurs with two species (Gen.Nov.Y) in the rain forest of Lower Guinea. Hence, one contact zone was via land, namely from the rain forests of the Afro-Arabian continent via Nepal – and possibly India and Sri Lanka – towards southeast Laurasia. India collided *ca.* 50 Ma with Eurasia (Torsvik *et al.* 2012). Since the species that the author studied from Sri Lanka (not included in this thesis) do not represent basal taxa, the author assumes that this contact was not via the Madagascar-India subcontinent (Lehmann 2009). India and the Seychelles drifted off Madagascar 85 Ma (Torsvik *et al.* 2012). Hence, a contact was only possible when the Afro-Arabian continent was connected with southern Asia during the late Middle Eocene 38.3 Ma (Scotese 2014). This connection might have been a filter route, a route that does not allow all fauna to pass, but filters out certain elements – a series of islands could act as such, since it more easily allows flying animals to pass than ground dwelling ones or a narrow land connection may act in the same way (Rienk de Jong pers. comm. 2016). This contact lasted at least until the active Africa-Arabia separation in the Red Sea and Gulf of Aden began *ca.* 30–29 Ma with the southern Red Sea already in existence as far south as 10°N (Wolfenden *et al.* 2005). Further major extensional deformations occurred at *ca.* 11 Ma and still further seafloor spreading in the Red Sea at 5–3 Ma (Calais *et al.* 2003) resulting in major environmental changes (Medio *et al.* 2000). The author assumes that since the beginning of the Africa-Arabia separation 29 Ma a contact of the Oriental

Metarbelidae species via land to species of mainland Africa was no longer possible. Hence, the Metarbelidae of the Oriental Region are older than 29 Ma.

The lowland rain forest on the Afro-Arabian continent that was reconstructed as the ancestral area for the Oriental species of the new genera U, V and X, originated as the archetype of the rain forest since the Turonian 93 Ma. It was only *ca.* 65 Ma (Richards 1996, p.13) or 53–45 Ma that this forest was recognizably like the African rain forest of today (Maley 1996, White 2001). Hence, the ancestors of the species of the new genera U, V and X must be younger than 65 Ma. These facts as well as the geological facts regarding the separation of Africa and Arabia suggest an age for the local Metarbelidae fauna of genera U, V and X. This age is probably between 29 to 38 Ma, but the age of their stem lineage representatives that occurred on the Afro-Arabian continent should be 29 to 65 Ma.

### 7.2.2 Reasons for a low diversity of Metarbelidae on the Sunda shelf

There remains the question why Metarbelidae (*cf.* chapters 1.1, 1.3 for notes on their ecology) of the Oriental Region that are at least as old as 29 Ma are still so poorly represented, *e.g.* with only five species on Borneo?

After New Guinea, Borneo represents the second largest tropical island on earth with 751.936 km<sup>2</sup> and its rain forest reaches its greatest luxuriance and floristic wealth harbouring up to 15.000 plant species including *ca.* 3.000 tree species (Slik *et al.* 2003; also Richards 1996). Borneo belongs to the Laurasian Sunda shelf (comprising also Sumatra, Malaya, Java and Palawan). The extreme floristic richness of these islands on the Sunda shelf, that are all of continental ancestry, is not due to the flowering plants having evolved there but due to two floristic elements of different origin (Whitmore 1984). These elements are the “*Laurasian element*” (including, *e.g.* *Artocarpus* J.R. Forster & G. Forster, *Pinus* L. and Dipterocarpaceae centred on the Sunda shelf) and the “*Gondwanic element*” *sensu* Whitmore (1984). Both elements are now considerably intermingled. “*Gondwanic elements*” comprise, *e.g.* conifers other than *Pinus* L. Low extinction rates in the rain forests, *e.g.* during the Quaternary, are probably a second reason for the very high plant species diversity on Borneo today (Whitmore 1984; Slik *et al.* 2003). Relicts of Gondwanic vegetation still occur according to Whitmore (1984), *e.g.* in heath forests (for example in coastal areas on Borneo and Malaya), in rain forests of eastern Malaysia (with *Araucaria* Juss.) as well as in montane rain forests of Borneo (with *Phyllocladus* L.C. Rich. & A. Rich., Podocarpaceae). The forests of the Sunda shelf were already established when they became separated from other tropical regions in the Middle Cretaceous *ca.* 99 Ma, and evidence suggests that during glacial periods in the Pleistocene, western Borneo consisted

mainly of savanna with rain forest patches along rivers and mountain slopes, while northern and eastern Borneo remained covered with rain forest (Slik *et al.* 2003). These rain forests survived probably also earlier climatic changes. It is possible that tropical rain forest-like habitats were present in the region *ca.* 100 Ma. Direct and indirect evidence suggests that the earliest tropical rain forests occurred on Laurasia and are linked to the earliest palm lineages because the latter were a key component in the composition and diversity of the earliest stages in the evolution of tropical rain forest (Couvreur *et al.* 2011).

The absence of species of the “Basal Group” from the Oriental Region supports the author’s view that the Metarbelidae did not originate in these earliest tropical rain forests of Laurasia. Several closely related species, *e.g.* of *Squamura* occur on various islands of the Sunda shelf today. This fact suggests that all present islands were once connected during a period of time when Metarbelidae did already occur in Laurasia. The southeast extremity of Laurasia was the present Sulawesi. This part of Laurasia collided several times with fragments of New Guinea/Australia only 15–3 Ma. Hence, Sulawesi (from where only one endemic Metarbelidae species is known) was once Laurasia. During the recent glacial periods of the Pleistocene, Borneo was connected by land bridges to the mainland of Southeast Asia as well as to Java and Sumatra and hence, Metarbelidae species could “migrate” on these land bridges on the Sunda shelf in recent times.

The moth fauna of Borneo was extensively studied by Jeremy Holloway. Interestingly, he published in 1986 only five species of Metarbelidae that occur on the island, comprising four lowland species (= not exceeding 800 m on Borneo) and one montane species (collected between 1.500–2.000 m).

There is no link between a very high plant species diversity of angiosperms and a very low or absent Metarbelidae diversity in coastal forests that grow up to *ca.* 500 m inland of the Indian Ocean in southeast Kenya (Lehmann & Kioko 2000, 2005; Lehmann 2008; *cf.* Figure 199). In regard to montane habitats of central Kenya, the author found that Metarbelidae diversity is very high in old gymnosperm forests (*ca.* 230–300 years old) dominated by *Juniperus procera* Hochst. (*cf.* Figure 3). The studied gymnosperm forests have only two or three other woody plant species and hence, a very low woody plant species diversity. It is obvious that a high diversity in woody plant species does not simply cause a high diversity in the Metarbelidae fauna and that a very low diversity in woody plant species does not simply cause a low diversity of Metarbelidae.

The example for Borneo is even more extreme since it indicates that Metarbelidae do not respond to a very diverse lowland rain forest woody flora comprising high diversities of angiosperm as well as gymnosperm tree species. A similar low diversity of Metarbelidae was found on Sumatra during extensive collecting trips and research by Eduard Diehl during the years 1981–2003 (Lutz Kobes pers. comm. 1996, 2016).

One reason for the low diversity of Metarbelidae in the very diverse lowland rain forests of Borneo and Sumatra is most probably the absence of dominant legumes and hence, is linked to major differences in the floristic composition of their habitats if compared to the habitats of lowland rain forest on the African mainland (cf. 7.1.3). For example, based on a detailed study by Slik *et al.* (2003), Dipterocarpaceae (ca. 22 %) and Euphorbiaceae (ca. 12 %) represent the most dominant tree families in the lowland rain forest of Borneo and “... legumes only rank 12<sup>th</sup>, and no legume genus even occurs among the 25 most common genera”. Whitmore (1984) stated additionally, that conifers are represented by numerous species in the rain forests of the Sunda shelf including several genera at low elevations, *e.g.* *Podocarpus* L’Héritier, *Dacrydium* Sol. and *Agathis* Salisb. Such conifer dominated habitats are absent in African lowland rain forest with a very few exceptions (cf. 7.1.3).

These interesting results suggest that further research is needed on the Sunda shelf to the question if any species of the “Basal Group” occurs, *e.g.* in heath forests or rain forests with *Araucaria* Juss.

However, from the author’s point of view, and supported by Figure 6d, originated the Metarbelidae on the Afro-Arabian continent and it would be a real surprise if species of the “Basal Group” occur in the Oriental Region.

## 8. CONSERVATION

The Metarbelidae of the forests on the Sunda shelf as well as in Upper Guinea are at present the most endangered.

Considering the still limited knowledge about Metarbelidae occurring in the Afrotropical and Oriental Region it is important to discover and describe their diversity in form of new genera, new species as well as present information about their forest habitats and their biology before they become extinct. The loss or the fragmentation and/or degradation of many primary forests, *e.g.* on the Sunda shelf, due to fires, ongoing high rates of wood extraction for the production of pulp and timber, ‘jungle rubber’ collection, the production of rubber and palm oil (including the planting of rubber and oil palm monocultures/plantations), agricultural expansion, smallholder clearance for tree crops, and infrastructure extension are main threats to all remaining forests in Indonesia that experiences the second highest rate of deforestation among tropical countries (Margono *et al.* 2012). For example, the natural forest cover on Sumatra was 71.2% in 1950 but decreased to 30% by 2010, particularly in the Lowlands; nearly half (47%) of all Sumatran *primary forests* was either cleared (in total 7.54 million hectare) or degraded (0.12 million hectare per year) during 1990 and 2010 (Margono *et al.* 2012). In other areas with near-endemic and rare species of Metarbelidae, *e.g.* central Nepal, the mining for marble around Godavari, is also a constant threat (Khanal *et al.* 2013).

In Upper Guinea, the Ivory Coast experiences the highest rate of deforestation among tropical countries since the 1970's with 6.5% forest loss per year (Chatelain *et al.* 2004). Hence, the large majority of forest has already disappeared, only 11.230 km<sup>2</sup> remained in 1990 compared to 150.000 km<sup>2</sup> in the early 20<sup>th</sup> century. The Taï National Park is sadly the last important forest that has survived on the Ivory Coast. Additionally, there are only few large forests in Liberia, a few in Ghana and very little in Togo.

The forested zone in the whole of Upper Guinea covered *ca.* 680.000 km<sup>2</sup> in the early 20th century (Sommer 1976) representing *ca.* 20% of the African forest cover. Only 415.940 km<sup>2</sup> forest remained *ca.* twenty years ago. More recent estimates suggest that only between 20% and 50% of the early 20th century forest cover remain in Upper Guinea (Chatelain *et al.* 2004).

Many species of Metarbelidae are forest and/or woodland dependent and hence, their future is not good as the two most extreme examples from the Ivory Coast and Indonesia suggest. However, at least several species can survive in very small but old forest patches, possibly for a long period of time, based on the author's experience in southeast and central Kenya.

The conservation of small relict natural forest patches as well as forest sites that are several hundred years old will help to protect species of Metarbelidae for future generations. Metarbelidae should remain as a typical element in the fauna of the Afrotropical Region and they should be protected as an interesting rare element of the fauna in the Oriental Region.

*In the present thesis research gaps are presented that remain to be filled in the future, e.g. the description and publication of at least 50 genera with their species, research on behavior of females and on habitats of Metarbelidae larvae.*

*However, this thesis will stand as a record of what the status of taxonomy and systematics of Metarbelidae was like in the past 135 years in the Afrotropical and Oriental Region (1882 to 2017).*



**FIGURE 200.** My companion and botanist Saidi Ali Chidzinga of the Coastal Forest Conservation Unit (Ukunda) is standing on a dead lying stem of *Erythrophleum suaveolens* (Guill. & Perr.) Brenan (Caesalpiniaceae). The stem is more than 12 years old since it was already found in Kaya Muhaka on “Ingo’s Site” in 1994 and might be (?), like other dead wood, a food plant resource for larvae of some species of Metarbelidae. Saidi helped me not only to record and to mark Lepidoptera, to identify plant species correctly but also measured together with me more than 1.700 living and dead trees as well as treelets in five coastal forests during 1994–2008. Picture by Ingo Lehmann in February, 2006.

## 9. ACKNOWLEDGEMENTS

This PhD thesis is a result of my studies on Metarbelidae for more than 24 years. There was extremely little knowledge and few scattered literature on this family worldwide when I began in 1994. Hence, without help of scientists, colleagues and friends, research on a whole family starting at zero point is impossible. This thesis would definitely not exist without my long-term field work, experience and research in Kenya on forest structures, plant species dominance and Lepidoptera always supported by the NMK (1989–2019) and various Ministries of the Government of Kenya (Nairobi). I am deeply grateful to the following friends, scientists and colleagues:

1. In five coastal lowland forests (1994–2008: Kaya Muhaka, Kaya Kinondo, Kaya Diani, Gogoni Forest Reserve and Shimoni Forest) significant support came from Dr. Richard Kiome Bagine (formerly Deputy Director and Chief Scientist of the Center for Biodiversity at the NMK), my companion and botanist Saidi Ali Chidzinga (CFCU, Ukunda, funded by WWF, *cf.* Figure 200), the botanist Quentin Luke (NMK/WWF), Matano Abdulrahman (CFCU/WWF), Juma Said Rasso (CFCU), the late Hamisi Juma Mududu (Kwale), Said Abdalla Matiko (CFCU), Saidi Hamadi Matata (forest guide), Mohammed Pakia (CFCU/University of Bayreuth) and Mbinda Jeremia Munge (CFCU). John Baya Mitsanze (Environment Education Officer, Kilifi) helped in producing the first documentaries for schools about my research. The Kaya elders Mzee Omari Bakara Mwananiki, Mzee Hamissi Kassim (Kaya Muhaka eldes) and Mzee Ali Abdullah Mnyenze (Kaya Kinondo elder) allowed access to sacred places in the Kayas. My field research in Kenya was combined with extensive research at the BMNH (London, U.K.). In this context I am grateful for always free accommodation provided by the late John Albert Jones (Dulwich Village, London) during 1994–2006 as well as to my former fiancée Grit Hecht (Schwerin) for help in 1994–2001, including financial support for my research in Kenya in 1995/1998.

2. In four montane forest/bushland areas of central Kenya (2015–2018: Ololua Forest, Karura Forest, Lolldaiga Hills forests, Mpala bushlands) significant support was provided by Robert James Wells and his son Harry Bunzaemon Mizutani Wells who gave free accommodation, guides, armed rangers, transport and a great hospitality on their Lolldaiga Hills Ranch and Wildlife Conservancy. Additionally, Mike Roberts (formerly General Manager of the Lolldaiga Hills Ranch) and his wife Stephanie provided a great hospitality and professionally organized light-trappings during many field trips; my companion Julius Mwenda Mathiu helped to identify and measure woody plant species on my sample sites; Lemputui and Loipotoi (armed anti-poaching rangers) provided safety. I am grateful to Luka Kaburu Kubunia, Philip Kaibunga Nabea and Selvester Kirimi for excellent cooking during my time on the ranch.

3. I am deeply thankful for the interest and first help to study butterflies and moths in Kenya through a letter written by Dr. Richard E. Leakey (formerly Director/Chief Executive NMK) in 1989. Based on his letter continuous support was provided by the NMK particularly in the following years through, *e.g.* Dr. Richard K.

Bagine (*cf.* number 1), Dr. Koen Maes (formerly Head of Department of Invertebrate Zoology) in 1999, Dr. Esther Kioko (*cf.* number 6), Dr. Wanja Kinuthia (formerly Head of Department of Invertebrate Zoology) who supported my research particularly in 2000–2005, and at present by Laban N. Njoroge (Head of Invertebrates and Zoology Section). I thank the late Joseph Mugambi Ruthiri (formerly curator of the Invertebrates and Zoology Section), who accompanied me always in Ololua Forest (Nairobi) and at the house of the late Karen Blixen (Nairobi) during my field work since 1994 and Mike Peter Clifton (Head of Department of Invertebrate Zoology in 1969–1987) who gave precious advice on old literature from the 1960's in 2016 and 2018.

4. I am grateful for my interesting field work in Karura Forest (Nairobi) that was guided and supported by Chantal Mariotte (Friends of Karura Forest Executive Board), Musyoki Alex Mutinda (NMK, Zoology Department), Antony Njoroge Kuria (Institute for Primate Research and Friends of Karura Forest), Peter Kinyua Muriithi (Nature Kenya and Friends of Karura Forest) and Bernard Akunda (guide of Karura Forest).

5. I thank Dr. Yvonne de Jong (Lolldaiga Hills Research Programme), Dr. Paula Kahumbu (WildlifeDirect, Nairobi) who helped in various ways to support my field work on the Laikipia Plateau, as well as Andrea Surmatt (MRC) who was of great help to measure trees and shrubs on very thorny sample sites at the Mpala Research Center (MRC). I am grateful to Linet Nekesa Barasa, formerly “Runda Estate” (Nairobi), to the staff of “The Trout-Tree” (Naro Moru) and “Punda Miliyas Camp” (Nakuru), in particular to Denis Leshoo Nkulet and Danny, who supported various light-trappings.

As a result of my field research in Kenya and my work in various museums, in particular long-term studies in the BMNH, the revision and re-classification of the Metarbelidae began officially in May 2009 at the ZFMK (Bonn). My growing knowledge on this family would not have been possible without the invaluable scientific as well as technical support, guidance and criticism of the following scientists, colleagues and friends. I extend my sincere thanks to:

6. Professor Dr. Johann-Wolfgang Wägele (Director of ZFMK), Dr. Dieter Stünig (formerly ZFMK), Dr. Hossein Rajaei (scientist at SMNS) for critical comments on my drafts, often long, invaluable discussions on various subjects of zoology and Metarbelidae; Professor Dr. Heike Wägele (ZFMK), Uta Heidenreich and Hans-Joachim Krammer (ZFMK) for their excellent pictures on the genitalia of various species; Karin Ulmen (ZFMK) for constant support in producing excellent SEM pictures of several genera.

Dr. Malte Sommerlatte and Hilary Sommerlatte (Gatuamba, Naro Moru), Dr. Thomas Butynski (Soita Nyiro Conservancy and Sustainability Centre Eastern Africa, Lolldaiga Hills Ranch and Wildlife Conservancy), Dr. Esther N. Kioko (Head of Zoology Department, NMK), Trish Luke and Quentin Luke (Karen, Nairobi), Dr. Dino J. Martins (Executive Director MRC) as well as Steve Collins (ABRI, Karen) for their constant significant support and long-term guidance of my research on Lepidoptera and their habitats in Kenya.

7. I received significant help for this thesis, sometimes through precious discussions on Metarbelidae and criticism on my former publications, from Dr. Jeremy Holloway (BMNH, London), Professor Dr. Joël Minet (MNHN, Paris, France), Dr. Jurate De Prins and Willy De Prins (Royal Belgian Institute of Natural Sciences, Brussels, Belgium), Dr. Douglas Kroon and his late wife Noelline Kroon (Sasolburg, Republic of South Africa), Dr. Lauri Kaila (Senior Curator Finnish Museum of Natural History, University of Helsinki, Finland), Dr. Maria Heikkilä (Zoology Unit, Finnish Museum of Natural History, Helsinki) and Dr. Martin Husemann (Head, Department of Entomology, ZMH, Hamburg).

8. Plant species identifications and discussions on botany were provided by Jonathan Timberlake (Royal Botanic Gardens Kew, Richmond, U.K.), Quentin Luke (NMK), Mike Bingham (Lusaka, Zambia), Dr. Şerban Procheş (University of KwaZulu-Natal, Durban, Republic of South Africa), Dr. Andreas Hemp (University of Bayreuth, Bayreuth, Germany), the late Darrel Plowes (Mutare, Zimbabwe) and Professor Dr. Eberhard Fischer (University of Koblenz-Landau).

9. Aspects of geology and geomorphology in regard to Metarbelidae would not have been possible without the great help and criticism of Dr. Friederike Ursula Bauer (University of Bergen, Bergen, Norway) and Dr. Andy E. Moore (Rhodes University, Grahamstown, Republic of South Africa).

10. I am very grateful for unpublished habitat information for species of genera presented herein to Anders Bjørnstad (Skien, Norway), the late Dr. Torben Larsen who also encouraged me to continue my work on Metarbelidae, Dr. Ian Gordon (Nature Kenya) for unpublished literature on Tanzanian sites and his support on earlier publications in the JEANH in 2008/2009, Raymond John Revell (Cambridge, U.K.) for habitat descriptions from Namibia, Mike Peter Clifton (Nairobi) for descriptions of habitats near Nairobi and Kibwezi that no longer exist, Dr. Wolfgang von Richter (formerly Gaborone, Botswana, at present Leipzig) who provided rare literature on Botswana, Dr. Robert Plowes (University of Texas, Austin, U.S.A.) who provided rare information on Old Umtali (Zimbabwe), Jürgen Lenz (formerly Harare, Zimbabwe, at present Leipzig) who provided attractive pictures (*cf.* Figures 2, 5) and information on collecting sites in Zambia and Zimbabwe, Rhett Butler (Harare) for information on the Matopos Hills (Zimbabwe) and Raymond James Murphy (Nkhorongo, Mzuzu, Malawi) for his detailed habitat descriptions and pictures of collecting sites in Zambia and Malawi.

For a loan of museum material or other important specimens as well as for information on types or other Metarbelidae, I am very grateful to Leif Aarvik (NHMO, Oslo, Norway), Dr. Johannes Bergsten (Stockholm, Sweden), Ben Brugge (Collection manager Entomology, Naturalis Biodiversity Center, Leiden, The Netherlands) and Rob de Vos (Curator moth collection), Dr. Ugo Dall'Asta (formerly RMCA, Tervuren, Belgium), Dr. Axel Hausmann (ZSM, Munich), Willem Hogenes (formerly ZMA, Amsterdam), David Carter and Martin Honey (formerly BMNH, London), Ole Karsholt (ZMUC, Copenhagen), Dr. Wanja Kinuthia (NMK, Nairobi), Dr. Martin Krüger

(Ditsong National Museum of Natural History, Pretoria), Dorothy Chipo Madamba (NMZB, Bulawayo, Zimbabwe), Geoff Martin (BMNH, London), Dr. Wolfram Mey (ZMHU, Berlin), Professor Dr. Joël Minet (MNHN, Paris), Dr. Wolfgang Nässig (SMNF, Frankfurt am Main), Dr. John E. Rawlins (Curator and Chair, Section of Invertebrate Zoology, Assistant Director of Research and Collections Carnegie Museum of Natural History, Pittsburgh, U.S.A.), Dr. Thomas Josef Witt and Dr. Wolfgang Speidel (MWM, Munich, Germany), Professor Dr. Roman Yakovlev (Altai State University, Barnaul, Russia) and Dr. Vadim V. Zolotuhin (Department of Biology, State Pedagogical University of Ulyanovsk, Ulyanovsk, Russia).

11. For always save driving in Kenya since 2015 I am grateful particularly to Patrick Njoroge Ndereba (Kanyoni, Nanyuki), Eliud Mbuthi (Nairobi), Abrar Faiz Said (Nairobi) and Peter Kinyua Muriithi (Nairobi).

12. I received various research permits for my PhD project in Kenya since 2015: I am very grateful to the National Commission for Science, Technology and Innovation for my Research Clearance Permit No.: NACOSTI/P/15/5928/901; to Emilio N. Mugo (Director of Kenya Forest Service, Nairobi) and Dr. Geoffrey Mwachala (Director of Research and Collections, NMK) for my permission to undertake research in Karura Forest; to Dr. Mzalendo N. Kibunja (Director General of NMK) for the renewal of my Institutional Affiliation – a fruitful collaboration for which I am grateful since 1989.

13. I am in particular grateful to Alick Gordon Roberts (Kiluma, Mogwooni Ranch), who was the first person that I met in my life (in 2017) who could describe the character of my ideal George Adamson based on his experience as an assistant to him during July 1964 to April 1965.

I am grateful to my late grandparents Charlotte and Willi Eduard Haberland (Finsterwalde/Niederlausitz) for their support during many field trips as a child to record Lepidoptera in the Niederlausitz in 1971–1982; to my parents Angelika and Günter Lehmann (Elkenroth) for their financial support to undertake field work in Kenya during my PhD project in 2015–2018; to Frank and Dorothe Herhaus (Wiehl, Germany) for their encouragement in regard to my interest in Kenya since 1984.

Last but not least, to my son Shimoni Lehmann (Hamburg) for his support in Kenya in 2015/2016 as well as to my former fiancée Mary Muthoni Mbugua (Nairobi) for her great support in Kenya, particularly in February, September and October, 2018.

## **IN MEMORIAM**

During my work on this thesis long-term friends and colleagues passed away: My mentor **Professor Dr. Lutz Walter Rudolf Kobes** (Göttingen, Germany) who supported my early research on Metarbelidae significantly during 1986 and 1997 died on 21<sup>st</sup> July 2016 (*cf. Stüning et al. 2017*).

My friend and companion **Joseph Mugambi Ruthiri** who supported my work at the NMK since 1993 and my work in Ololua Forest and at the house of the late Karen Blixen, the last time in March 2016, sadly died in Nairobi on 04<sup>th</sup> September 2016.

Finally, the botanist **Darrel Plowes** who contributed much information about the Mutare area and excellent pictures of the Bvumba Mountains (*cf. Figure 197*) sadly passed away in Mutare (Zimbabwe) on 19<sup>th</sup> October 2016.

## 10. REFERENCES

- Agenjo, R. (1966) Family Glyphipterigidae. *Graellsia* 22, Supplement [45, Brachodinae].
- Ali, J.R. & Huber, M. (2010) Mammalian biodiversity on Madagascar controlled by ocean currents. *Nature*, 463(7281), 653–656. doi:10.1038/nature08706
- Aurivillius, C. (1901) Diagnosen neuer Lepidopteren aus Afrika. Fam. Hollandiidae. *Entomologisk Tidskrift*, 22(2), 126–128.
- Aurivillius, C. (1910) Lepidoptera. Arbelidae. In: Sjöstedt, Y. (Ed.) *Wissenschaftliche Ergebnisse der schwedischen zoologischen Expedition nach dem Kilimandjaro, dem Meru und den umgebenen Massaisteppeen Deutsch-Ostafrikas 1905–1906*. Part 9, 49–50 + 1 b/w Figure.
- Axelrod, D.I. (1992) Climatic pulses, a major factor in legume evolution. In: Herendeen, P. S. & Dilcher, D. L. (Eds.) *Advances in Legume Systematics. Part 4: The fossil Record*. Royal Botanic Gardens, Kew, Richmond, Surrey, UK, 259–279.
- Axelrod, D.I. & Raven, P.H. (1978) Late Cretaceous and Tertiary vegetation history of Africa. In: Werger, M.J.A. (Ed.) *Biogeography and ecology of southern Africa. Monographiae Biologicae*, Volume 31, Dr. W. Junk, The Hague, 77–130.
- Bagdasaryan, G.P., Gerasimovski, V.I., Polyakov, A.I. & Gakasyan, R.K. (1973) Age of volcanic rocks in the rift zones of East Africa. *Geochemistry International*, 10, 66–71.
- Balinsky, B.I. (1962) Patterns of animal distribution on the African continent (summing-up talk). *Annals of the Cape Province Museum* 2, 299–310.
- Bauer, F.U., Glasmacher, U.A., Ring, U., Schumann, A. & Nagudi, B. (2010) Thermal and exhumation history of the central Rwenzori Mountains, Western Rift of the East African Rift System, Uganda. *International Journal of Earth Sciences (Geologische Rundschau)*, 99(7), 1575–1597.
- Bauer, F.U., Karl, M., Glasmacher, U.A., Nagudi, B., Schumann, A. & Mroszewski, L. (2012) The Rwenzori Mountains of western Uganda – Aspects of the evolution of their remarkable morphology within the Albertine Rift. *Journal of African Earth Sciences*, 73–74, 44–56.
- Bauer, F.U., Glasmacher, U.A., Ring, U., Karl, M., Schumann, A. & Nagudi, B. (2013) Tracing the exhumation history of the Rwenzori Mountains, Albertine Rift, Uganda, using low-temperature thermochronology. *Tectonophysics*, 599, 8–28. doi.org/10.1016/j.tecto.2013.03.032.
- Bauer, F.U., Glasmacher, U.A., Ring, U., Grobe, R.W., Mambo, V.S. & Starz, M. (2016) Long-term cooling history of the Albertine Rift: new evidence from the western rift shoulder, D.R. Congo. *International Journal of Earth Sciences (Geologische Rundschau)*, 105(6), 1707–1728. doi: 10.1007/s00531-015-1146-6
- Beentje, H.J. (1994) *Kenya trees, shrubs and lianas*. National Museums of Kenya, Nairobi, Majestic Printing Works Ltd., iii–ix + 1–722.
- Berger, L.A. (1957) Clé pour la détermination des Familles de Macrolépidoptères et des groupes supérieurs de Microlépidoptères. *Lambillionea*, 57, 72–84.

- Bergner, A.G.N., Strecker, M.R., Trauth, M.H., Deino, A., Gasse, F., Blisniuk, P. & Dühnforth, M. (2009) Tectonic and climatic control on evolution of rift lakes in the Central Kenya Rift, East Africa. *Quaternary Science Reviews*, 28(25–26), 2804–2816. doi:10.1016/j.quascirev.2009.07.008
- Bethune-Baker, G.T. (1909) Descriptions of new African Lepidoptera. Arbelidae. *Annals and Magazine of Natural History*, 8 (3), 425–426.
- Bibby, C.J., Collar, N.J., Crosby, M.J., Heath, M.F., Imboden, C., Johnson, T.H., Long, A.J., Stattersfield, A.J. & Thirgood, S.J. (1992) *Putting biodiversity on the map: priority areas for global conservation*. BirdLife International, International Council for Bird Preservation (ICBP), Cambridge, U.K., vi + 1–90.
- Blumenbach, J.F. (1797) Elephas. In: D. Joh. Fr. Blumenbach's *Handbuch der Naturgeschichte*. Fünfte Auflage nebst zwei Kupfertafeln, Göttingen, bey Johann Christian Dieterich, 124–125.
- Bonini, M., Corti, G., Innocenti, F., Manetti, P., Mazzarini, F., Abebe, T. & Pecskey, Z. (2005) Evolution of the Main Ethiopian Rift in the frame of Afar and Kenya rifts propagation. *Tectonics*, 24 (1), TC1007. doi:10.1029/2004TC001680
- Boisduval, M.J.A. (1828a) *Europaeorum Lepidopterorum Index Methodicus*. Part 2: Essai sur une Monographie des Zygénides, suivi du tableau méthodique, des Lépidoptères d'Europe. Méquignon-Marvis, Paris, 2 [as Castniaires].
- Boisduval, M.J.A. (1828b) *Europaeorum Lepidopterorum Index Methodicus*. Part 1: Sistens genera *Papilio*, *Sphinx*, *Bombyx* et *Noctua* Lin., Méquignon-Marvis, Paris, 29 [as Sesiariae].
- Bradley Martin, E. (1973) *The history of Malindi – A Geographical Analysis of an East African Coastal Town from the Portugues Period to the Present*. East African Literature Bureau, Nairobi, V–XVI+1–301.
- Burgess, N.D., D'Amico Hales, J., Underwood, E., Dinerstein, E., Olson, D., Itoua, I., Schipper, J., Rickketts, T. & Newman, K. (Eds.) (2004) *Terrestrial ecoregions of Africa and Madagascar: a conservation assessment*. World Wildlife Fund (United States), Island Press, Washington, xxiii + 1–499.
- Burgess, N.D., Butynski, T.M., Cordeiro, N.J., Daggart, N.H., Fjeldså, J., Howell, K.M., Kilahama, F.B., Loader, S.P., Lovett, J.C., Mbilinyi, B., Menegon, M., Moyer, D.C., Nashanda, E., Perkin, A., Rovero, F., Stanley, W.T. & Stuart, S.N. (2007) The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. *Biological Conservation*, 134, 209–231.
- Burgoyne, P.M., van Wyk, A.E., Anderson, J.M. & Schrire, B.D. (2005) Phanerozoic evolution of plants on the African plate. *Journal of African Earth Sciences*, 43(1–3), 13–52. <http://dx.doi.org/10.1016/j.jafrearsci.2005.07.015>
- Burke, K. (1996) The African Plate, 24th du Toit Memorial lecture. *South African Journal of Geology*, 99, 339–409.

- Burke, K. & Gunnell, Y. (2008) The African Erosion Surface: A Continental-Scale Synthesis of Geomorphology, Tectonics, and Environmental Change over the Past 180 Million Years. *The Geological Society of America Memoir*, 201, 1–66. doi:10.1130/2008.1201.
- Calais, E., DeMets, C. & Nocquet, J.-M. (2003) Evidence for a post-3.16-Ma change in Nubia–Eurasia–North America plate motions? *Earth and Planetary Science Letters*, 216(1–2), 81–92. doi: 10.1016/S0012-821X(03)00482-5.
- Caswell, P.V. (1953) *Geology of the Mombasa-Kwale area*. Colony and Protectorate of Kenya, Geological Survey of Kenya, Report No. 24, Nairobi, iii+1–69+Degree Sheet No. 69 (two coloured maps) + 6 b/w maps.
- Chapman, J.W., Drake, V.A. & Reynolds, D.R. (2011) Recent insights from radar studies of insect flight. *Annual Review of Entomology*, 56, 337–356. doi:10.1146/annurev-ento-120709-144820
- Chatelain, C., Dao, H., Gautier, L. & Spichiger, R. (2004) Forest cover changes in Côte d’Ivoire and Upper Guinea. In: Poorter, L., Bongers, F., Kouamé, F.Y.N’. & Hawthorne, W.D. (Eds.) (2004) *Biodiversity of West African Forests – An Ecological Atlas of Woody Plant Species*. CAB International, Wallingford, Oxon, U.K., 15–32.
- Chipangura, N. (2013) Old Umtali 1891–1897: Conservation, interpretation and understanding a colonial past using historic buildings as evidentiary sources. *International Research Journal of Arts and Social Sciences*, 2(2), 24–29.
- Clarke, G.P. (1998) A new regional centre of endemism in Africa. In: Huxley, C.R., Lock, J.M. & Cutler, D.F. (Eds.) *Chorology, Taxonomy and Ecology of the Floras of Africa and Madagascar—from the Frank White Memorial Symposium held in the Plant Sciences Department, Oxford University, on 26<sup>th</sup> and 27<sup>th</sup> September 1996 by the Linnean Society of London, the Royal Botanic Gardens, Kew and Wolfson College, Oxford*. Royal Botanic Gardens, Kew, 53–65.
- Cockburn, H.A.P., Brown, R.W., Summerfield, M.A. & Seidl, M.A. (2000) Quantifying passive margin denudation and landscape development using a combined fission-track thermochronology and cosmogenic isotope analysis approach. *Earth and Planetary Science Letters*, 179, 429–435.
- Coffin, M.F. & Rabinowitz, P.D. (1987) Reconstruction of Madagascar and Africa: Evidence from the Davie Fracture Zone and Western Somali Basin. *Journal of Geophysical Research*, 92(B9), 9385–9406.
- Coltorti, M. & Ollier, C.D. (2000) Geomorphic and tectonic evolution of the Ecuadorian Andes. *Geomorphology*, 32 (1–2), 1–19.
- Cortlett, R.T. (2014) *The ecology of tropical East Asia*. Oxford University Press, 2<sup>nd</sup> edition. Oxford & New York, 304 pp.
- Coulson, S.J., Hodkinson, I.D., Webb, N.R. & Harrison, J.A. (2002) Survival of terrestrial soil-dwelling arthropods on and in seawater: implications for transoceanic dispersal. *Functional Ecology*, 16, 353–356.

- Couvreur, T.L.P., Forest, F. & Baker, W.J. (2011) Origin and global diversification patterns of tropical rain forests: Inferences from a complete genus-level phylogeny of palms. *BMC Biology*, 9 (1), 44. doi:10.1186/1741-7007-9-44
- Crosskey, R.W. & White, G.B. (1977) The Afrotropical Region – a recommended term in zoogeography. *Journal of Natural History*, 11, 541–544.
- Dawson, J.B. (1992) Neogene tectonics and volcanicity in the North Tanzanian sector of the Gregory rift valley: contrasts with the Kenya sector. *Tectonophysics*, 204, 81–92.
- De Prins, J. & De Prins, W. (2018) *Afromoths, online database of Afrotropical moth species (Lepidoptera)*. World Wide Web electronic publication of the Belgian Biodiversity Platform. Available from: <http://www.afromoths.net> [accessed 5 October 2018].
- Dewar, R.E. & Richard, A.F. (2007) Evolution in the hypervariable environment of Madagascar. *Proceedings of the National Academy of Sciences of the United States of America*, 104 (34), 13723–13727.
- Distant, W.L. (1897) On a collection of Heterocera made in Transvaal. Fam. Arbelidae. *The Annals and Magazine of Natural History*, 6 (xx), 209.
- Dufils, J.-M. (2003) Remaining Forest Cover. In: Goodman, S.M. & Benstead, J.P. (Eds.), *The Natural History of Madagascar*. The University of Chicago Press, Chicago and London, 88–96.
- Dufrane, A. (1945) Lépidoptères du Kivu (3e note). *Bulletin at Annales de la Société entomologique de Belgique*, 81, 91–143.
- Dudgeon, G.C., Elwes, H.J. & Hampson, G.F. (1901), Family Ratardidae. In: A Catalogue of the Heterocera of Sikhim and Bhutan. *The Journal of the Bombay Natural History Society*, 13(4), 425.
- Ebinger, C.J. (1989) Tectonic development of the western branch of the East African rift system. *The Geological Society of America Bulletin*, 101(7), 885–903.  
doi: 10.1130/0016-7606(1989)101<0885:TDOTWB>2.3.CO;2
- Ebinger, C.J., Rosendahl, B.R. & Reynolds, D.J. (1987) Tectonic model of the Malawi Rift, Africa. In: Ben-Avraham, Z. (Ed.) Sedimentary basins within the Dead Sea Rift and other rift zones. *Tectonophysics*, 141, 215–235.
- Edwards, E.D., Gentili, P., Horak, M., Kristensen, N.P. & Nielsen, E.S. (1999) The Cossoid/Sesioid Assemblage. In: Kristensen, N.P. (Ed.), *Lepidoptera, Moths and Butterflies*. Volume 1: *Evolution, Systematics, and Biogeography*. Handbook of Zoology, volume IV, part 35. Walter de Gruyter, Berlin, New York, pp. 181–197.
- Evernden, J.F. & Curtis, G.H. (1965) The potassium-argon dating of late Cenozoic rocks in East Africa and Italy. *Current Anthropology*, 6, 343–385.
- Fairhead, J.D. & Girdler, R.W. (1969) How far does the rift system extend through Africa? *Nature*, 221, 1018–1020.
- Federman, S., Dornburg, A., Downie, A., Richard, A.F., Daly, D.C. & Donoghue, M.J. (2015) The biogeographic origin of a radiation of trees in Madagascar: implications for the assembly of a tropical forest biome. *BMC Evolutionary Biology*, 15, 216. doi 10.1186/s12862-015-0483-1

- Fletcher, T.B. (1922) Notes and observations. *The Entomologist*, LV (713), 231.
- Fletcher, D.S. (1968) Cossidae, Metarbelidae, Psychidae, Limacodidae, Drepanidae, Uraniidae, Lasiocampidae, Eupterotidae, Bombycidae, Saturniidae & Sphingidae. *Ruwenzori Expedition, 1952*, British Museum (Natural History), London, 1(8), 325–353 + Figures 1–22.
- Fonseca, J.F.B.D., Chamussa, J., Domingues, A.L., Helffrich, G., Antunes, E., van Aswegen, G., Pinto, L.V., Custódio, S. & Manhiça, V.J. (2014) MOZART: A Seismological Investigation of the East African Rift in Central Mozambique. *Seismological Research Letters*, 85(1), 108–116. doi: 10.1785/0220130082
- Gaede, M. (1929) 21. Family: Metarbelidae. In: Seitz, A. (Ed.) *The Macrolepidoptera of the World. Volume 14: The African Bombyces and Sphinges*, Alfred Kern, Stuttgart, 501–513 + plate 78.
- Gaede, M. (1929b) 22. Family: Cossidae. In: Seitz, A. (Ed.) *The Macrolepidoptera of the World. Volume 14: The African Bombyces and Sphinges*, Alfred Kern, Stuttgart, 542–543.
- Grünberg, K. (1911) Drei neue Metarbeliden von Kamerun. *Entomologische Rundschau*, 28(17), 134–135.
- Hampson, G.F. (1898) *Catalogue of the Lepidoptera Phalaenae in the British Museum*. London, British Museum (Natural History), Volume 1, 12, 16, 19.
- Hampson, G.F. (1910) Descriptions of new African moths. Arbelidae. *Annals and Magazine of Natural History*, 8(6), 117–128.
- Hampson, G.F. (1916) Fam. Arbelidae. In: Poulton, E.B. (ed.) On a collection of moths made in Somaliland by Mr. W. Feather. With descriptions of new species by Sir G.F. Hampson, L.B. Prout, J.H. Durrant and Dr. Karl Jordan. *Proceedings of the Zoological Society of London*, 1, 164–165, plate 2, Figure 127.
- Hampson, G.F. (1920) On new genera and species of Lepidoptera Phalaenae, with the characters of two new families. Family Teragridae. Genus *Stenagra* nov. *Novitates Zoologicae*, XXVI, 263–264.
- Hampson, G.F. (1920a) On new genera and species of Lepidoptera Phalaenae, with the characters of two new families. Family Teragridae. *Selagena albicilia*. *Novitates Zoologicae*, XXVI, 264.
- Hartnady, C.J.H. (2006) Seismotectonics of Southern Mozambique. 21<sup>st</sup> *Colloquium on African Geology (CAG21)*, Maputo (3–5 July 2006), Mozambique, Abstracts Volume, 408–410.
- Heikkilä, M., Mutanen, M., Wahlberg, N., Sihvonen, P. & Kaila, L. (2015) Elusive ditrysian phylogeny: an account of combining systematized morphology with molecular data (Lepidoptera). *BMC Evolutionary Biology*, 15 (1), 260. doi: 10.1186/s12862-015-0520-0

- Hemp, C., Grzywacz, B., Warchałowska-Śliwa, E. & Hemp, A. (2016) Topography and climatic fluctuations boosting speciation: biogeography and a molecular phylogeny of the East African genera *Afroanthracites* Hemp & Ingrisch and *Afroagraecia* Ingrisch & Hemp (Orthoptera, Tettigoniidae, Conocephalinae, Agraeciini). *Organisms Diversity & Evolution*, 16(1), 211–223.
- Heylaerts, F.J.M. (1890) Heterocera Exotica – Nouveaux Genre et espèces des Indes Orientales Néerlandaises. Cossina. – Gen. Squamura m. [de squama (écaille) et oupá (queue)]. *Annales de la Société entomologique de Belgique*, 34, xxvi–xxvii.
- Holland, W.J. (1893) Descriptions of new species and genera of West African Lepidoptera. Arbelidae. *Psyche – A Journal of Entomology*, 6, 534–535.
- Holloway, J.D. (1986) The moths of Borneo. Part 1: Key to Families; Families Cossidae, Metarbelidae, Ratardidae, Dudgeoneidae, Epipyropidae and Limacodidae. *Malayan Nature Journal*, 40, 1–165 + 21 b/w pls + 9 colour pls.
- Jacobs, B.F. (2004) Palaeobotanical studies from tropical Africa: relevance to the evolution of forest, woodland and savannah biomes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, London, 359(1450), 1573–1583. doi: 10.1098/rstb.2004.1533
- Janse, A.J.T. (1925) A revision of the South African Metarbelinae. *South African Journal of Natural History*, 5, 61–100 + 5 b/w pls.
- Jenoh, E.M., Robert, E.M.R., Lehmann, I., Kioko, E., Bosire, J.O., Ngisiange, N., Dahdouh-Guebas, F. & Koedam, N. (2016) Wide ranging insect infestation of the pioneer mangrove *Sonneratia alba* by two insect species along the Kenyan coast, *PLoS ONE*, 11 (5), e0154849. <http://dx.doi.org/10.1371/journal.pone.0154849>
- Jordan, K. (1907) New African Zygaenidae. *The Entomologist*, 40 (529), 121–127.
- Karsch, F. (1896) Die Hollandiiden oder die äthiopischen Arbeliden W.J. Holland's. *Entomologische Nachrichten*, xxii ( 9), 135–141.
- Keay, R.W.J. (1959) *An outline of Nigerian vegetation*. Third edition. Federal Ministry of Information, Printing Division, Lagos, 1–46.
- Keranen, K.M. & Klemperer, S.L. (2008) Discontinuous and diachronous evolution of the Main Ethiopian Rift: Implications for development of continental rifts. *Earth and Planetary Science Letters*, 265, 96–111. doi:10.1016/j.epsl.2007.09.038
- Keranen, K.M., Klemperer, S.L., Julia, J., Lawrence, J.F. & Nyblade, A.A. (2009) Low lower crustal velocity across Ethiopia: Is the Main Ethiopian Rift a narrow rift in a hot craton? *Geochemistry Geophysics Geosystems*, 10, 1–21. doi:10.1029/2008GC002293
- Key, R.M., Cotterill, F.P.D. & Moore, A.E. (2015) The Zambezi River: An archive of tectonic events linked to the amalgamation and disruption of Gondwana and subsequent evolution of the African plate. *South African Journal of Geology*, 118.4, 425–438. doi:10.2113/gssajg.118.4.425

- Khanal, B., Chalise, M.K. & Solanki, G.S. (2013) Population status and threats of *Phaedyra aspasia kathmandia* Fujioka 1970 (Lepidoptera: Nymphalidae), an endemic subspecies of butterfly in Godavari Forest of Central Nepal. *Journal of Natural History Museum, Tribhuvan University, Kathmandu*, 27, 87–91.
- Kinabo, B.D. (2007) Incipient continental rifting: insights from the Okavango Rift Zone, northwestern Botswana. *Doctoral Dissertations*. Paper 2191, University of Missouri-Rolla, xiv + 1–97.
- Kingsley, M.H. (1897) *Travels in West Africa. Congo Francais, Corisco and Cameroons*. London, MacMillan and Co., Limited, vii–xvi + 1–743.
- Klots, A.B. (1970) Lepidoptera. In: Tuxen, S.L. (Ed), *Taxonomist's Glossary of Genitalia in Insects*. Munksgaard, Copenhagen, 115–130.
- Kobes, L.W.R. & Ronkay, L. (1990) The Ratardidae of Sumatra. *Heterocera Sumatrana*, 6, 79–100.
- Kroon, D.M. (2001) Editorial. In: *Metamorphosis – Journal of the Lepidopterists' Society of Africa*, 12(3), 82.
- Lawver, L.A., Gahagan, L.M. & Dalziel, I.W.D. (1998) A tight fit-Early Mesozoic Gondwana, a plate reconstruction perspective. *Memoirs of National Institute of Polar Research. Special issue 53*, 214–229.
- Leach, W.E. (1815) *Edinburgh Encyclopaedia*, Volume 9, 131 [as Cossida].
- Lebrun, J. (1947) La végétation de la plaine alluviale au sud du lac Edouard. Institut des Parcs Nationaux du Congo Belge, Exploration du Parc National Albert, Miss J. Lebrun (1937–1938), Bruxelles, pp. 1–800.
- Le Gall, B., Tshoso, G., Jourdan, F., Fèraud, G., Bertrand, H., Tiercelin, J.J., Kampunzu, A.B., Modisi, M.P., Dymont, J. & Maia, M. (2002)  $^{40}\text{Ar}/^{39}\text{Ar}$  geochronology data from the giant Okavango and related mafic dyke swarms, Karoo igneous province, northern Botswana. *Earth and Planetary Science Letters*, 202, 595–606.
- Lehmann, I. (1997) *Metarbela haberlandorum* spec. nov., a new moth from Kenya (Lepidoptera: Metarbelidae). *Nachrichten Entomologischer Verein Apollo*, 18 (1), 45–53.
- Lehmann, I. (2007) Metarbelidae. In: Mey, W. (Ed.), *The Lepidoptera of the Brandberg Massif in Namibia. Part 2. Esperiana Memoir*, 4, 169–185 + plate 17.
- Lehmann, I. (2008) Ten new species of Metarbelidae (Lepidoptera: Cossioidea) from the coastal forests and the Eastern Arc Mountains of Kenya and Tanzania, including one species from two upland forests. *Journal of East African Natural History*, 97(1), 43–82.  
[http://dx.doi.org/10.2982/0012-8317\(2008\)97\[43:TNSOML\]2.0.CO;2](http://dx.doi.org/10.2982/0012-8317(2008)97[43:TNSOML]2.0.CO;2)
- Lehmann, I. (2009) Six new species of Metarbelidae (Lepidoptera: Cossioidea) from the Eastern Arc Mountains of Tanzania, including one new species from Marenji Forest in southeast coastal Kenya. *Journal of East African Natural History*, 97(2), 187–206. <http://dx.doi.org/10.2982/0012-8317-97.2.187>
- Lehmann, I. (2010a) A new genus of Metarbelidae (Lepidoptera: Cossioidea) from the Afrotropical Region with the description of seven new species. *Esperiana Memoir*, 5, 294–321 + pl. 21.

- Lehmann, I. (2010b) *A revision of the genus Arbelodes Karsch (Lepidoptera: Cossioidea: Metarbelidae) from southeast-central and southern Africa with the description of thirteen new species*. Published by the author, Hamburg & Wismar, 3–81+ 8 b/w pls., 5 colour pls.  
[Available from <http://www.biodiversitylibrary.org/bibliography/79419>], accessed August, 2018.
- Lehmann, I. (2011) *The description of a new genus and twenty-three new species of Metarbelidae (Lepidoptera: Cossioidea) from the lowland tropical rain forests of the Guineo-Congolian Region with notes on habitats and biogeography*. Published by the author, Hamburg, 1–67 + 10 b/w pls., 6 colour pls., 1 coloured map.  
[Available from <http://www.biodiversitylibrary.org/bibliography/79417>], accessed August, 2018.
- Lehmann, I. (2012) Description of a new genus and species of Metarbelidae (Lepidoptera, Cossioidea) from the Albertine Rift region of Tanzania, East Africa. *Norwegian Journal of Entomology*, 59, 234–240.
- Lehmann, I. (2013) *Description of two new genera and ten new species of Metarbelidae (Lepidoptera: Cossioidea) from western, north-central and eastern Africa with notes on habitats and biogeography*. Published by the author, Hamburg, 3–81+ 10 b/w pls., 5 colour pls., 2 coloured maps.  
[Available from <http://www.biodiversitylibrary.org/bibliography/79421>], accessed August, 2018.
- Lehmann, I. (2014) Description of two new genera and two new species of Metarbelidae (Lepidoptera, Cossioidea) from the Northeastern Congolian Lowland Forests Ecoregion (Central Africa). *Zootaxa*, 3895 (4), 570–580.  
<http://dx.doi.org/10.11646/zootaxa.3895.4.6>
- Lehmann, I. & Kioko, E. (2000) Preliminary survey on butterflies and moths and their habitats in two Kaya forests of the Kenya coast. *Metamorphosis – Journal of the Lepidopterists' Society of Africa*. Occasional Supplement, 4, 1–52.
- Lehmann, I. & Kioko, E. (2005) Lepidoptera diversity, floristic composition and structure of three Kaya forests on the south coast of Kenya. *Journal of East African Natural History*, 94, 121–163.  
[http://dx.doi.org/10.2982/0012-8317\(2005\)94\[121:LDFCAS\]2.0.CO;2](http://dx.doi.org/10.2982/0012-8317(2005)94[121:LDFCAS]2.0.CO;2)
- Lehmann, I. & Rajaei, H. (2013) Description of a new genus and three new species of Metarbelidae (Lepidoptera: Cossioidea) from East and Central Africa, with notes on biogeography. *Bonn zoological Bulletin*, 62 (1), 100–110.
- Lehmann, I., Roberts, M., Mathiu, J.M. & Butynski, T.M. (2018) Undescribed species and genera of Metarbelidae moths (Lepidoptera, Cossioidea) from Lolldaiga Hills Ranch, central Kenya. *Newsletter Lolldaiga Hills Research Programme*, January–February 2018, 3–4. [Available from <http://www.lolldaiga.com>], accessed March, 2018.
- Lister, L.A. (1987) The Erosion Surfaces of Zimbabwe. *Zimbabwe Geological Survey Bulletin*. Harare, No. 90, 1–163.

- Lovett, J.C. (1993) Climatic history and forest distribution in eastern Africa. *In: Lovett, J.C. & Wasser, S.K. (Eds.) Biogeography and ecology of the rain forests of eastern Africa*. Cambridge University Press, Cambridge, U.K., 23–29.
- Lovett, J.C. (1993b) Eastern Arc moist forest flora. *In: Lovett, J.C. & Wasser, S.K. (Eds.) Biogeography and ecology of the rain forests of eastern Africa*. Cambridge University Press, Cambridge, U.K., 33–55.
- Mabille, M.P. (1891) Notes lépidoptérologiques. *Annales de la Société entomologique de France*, 6(10) (*Bulletin entomologique* 23 juillet 1890), CXLVI–CXLIX.
- Maley, J. (1996) The African rain forest – main characteristics of changes in vegetation and climate from the Upper Cretaceous to the Quaternary. *In: Alexander, I.J., Swaine, M.D. & Watling, R. (Eds.) Essays on the ecology of the Guinea–Congo rain forest. Proceedings of the Royal Society of Edinburgh*, 104B, 31–73.
- Maley, J. (2001) The Impact of Arid Phases on the African Rain Forest Through Geological History. *In: Weber, W., White, L.J.T., Vedder, A. & Naughton-Treves, L. (Eds.) African Rain Forest Ecology and Conservation – An Interdisciplinary Perspective*. Yale University Press with support from the Wildlife Conservation Society, New Haven and London, 68–87.
- Malloch, D.W., Pirozynski, K.A. & Raven, P.H. (1980) Ecological and evolutionary significance of mycorrhizal symbioses in vascular plants (A Review). *Proceedings of the National Academy of Sciences of the United States of America (PNAS)*, 77(4), 2113–2118.
- Margono, B.A., Turubanova, S., Zhuravleva, I., Potapov, P., Tyukavina, A., Baccini, A., Goetz, S., Hansen, M.C. (2012) Mapping and monitoring deforestation and forest degradation in Sumatra (Indonesia) using Landsat time series data sets from 1990 to 2010. *Environmental Research Letters*, 7, 1–16. Doi:10.1088/1748-9326/7/3/034010
- McConnell, R.B. (1972) Geological Development of the Rift System of Eastern Africa. *Geological Society of America Bulletin*, 83, 2549–2572.
- Medio, D., Sheppard, C.R.C. & Gascoigne, J. (2000) The Red Sea. *In: McClanahan, T.R., Sheppard, C.R.C. & Obura, D.O. (Eds.) Coral Reefs of the Indian Ocean – their ecology and conservation*. Oxford University Press, Oxford and New York, 231–255.
- Mell, R. (1923) *Arbela acutistriata* sp. n. *In: Über südchinesische Arbeliden und Verwandte. Deutsche Entomologische Zeitschrift*, 165–166.
- Merla, G. & Minucci, E. (1938) Missione Geologica Nel Tigray. Volume Primo. La Serie Dei Terreni. Roma. Reale Accademia D'Italia. *Centro Studi Per L'Africa Orientale Italiana*, 3, 1–363.
- Mey, W. (2018) *Dukearbela translucens* gen. nov., spec.nov. – a remarkable taxon from South Africa (Lepidoptera: Metarbelidae). *Metamorphosis – Journal of the Lepidopterists' Society of Africa*, 29, 11–13.
- Mohr, P. (1983) Volcanotectonic aspects of the Ethiopian Rift evolution. *Bulletin des centres de recherches exploration-production Elf-Aquitaine*, 7, 175–189.

- Monod, T. (1957) Les grandes divisions chorologiques de l'Afrique. Conseil Scientifique pour l'Afrique au sud du Sahara, publication n°24. Rapport présenté à la reunion des specialists sur la phytogéographie (Yangambi 29/7-8/8 1956), Londres pp. 1-156.
- Moore, A., Blenkinsop, T. & Cotterill, F. (2008) Controls on post-Gondwana alkaline volcanism in Southern Africa. *Earth and Planetary Science Letters*, 268, 151-164.
- Moore, F. (1879) *Arbela* n.g. In: Descriptions of new Genera and Species of Asiatic Lepidoptera Heterocera. *Proceedings of the Zoological Society of London*, May 6, 411-412 + Plate XXXIV, Figure 3.
- Mougenot, D., Recq., M., Virlogeux, P. & Lepvrier, C. (1986) Seaward extension of the East African Rift. Letters to nature. *Nature*, 321(5), 599-603. doi:10.1038/321599a0
- Müller, T. (2006) The distribution, classification and conservation of rainforests in eastern Zimbabwe. *Occasional Publications in Biodiversity*. Biodiversity Foundation for Africa, Bulawayo, Zimbabwe, No. 19, 1-31 + 42 maps.
- Mutanen, M., Wahlberg, N. & Kaila, L. (2010) Comprehensive gene and taxon coverage elucidates radiation patterns in moths and butterflies. *Proceedings of the Royal Society B*, 277, 2839-2848. <http://dx.doi.org/10.1098/rspb.2010.0392>
- Nonnotte, P., Guillou, H., Le Gall, B., Benoit, M., Cotton, J. & Scaillet, S. (2008) New K-Ar age determinations of Kilimanjaro volcano in the North Tanzanian Diverging rift, East Africa. *Journal of Volcanology and Geothermal Research*, 173(1-2), 99-112. doi:10.1016/j.jvolgeores.2007.12.042
- Nyblade, A.A. & Brazier, R.A. (2002) Precambrian lithospheric controls on the development of the East African rift system. *Geology*, 30(8), 755-758. doi: 10.1130/0091-7613(2002)030<0755:PLCOTD>2.0.CO;2
- Nyblade, A.A. & Sleep, N.H. (2003) Long lasting epeirogenic uplift from mantle plumes and the origin of the Southern African Plateau. *Geochemistry Geophysics Geosystems*, 4(12), 1-29. doi.org/10.1029/2003GC000573
- Page, R.D.M. (2001) *Nexus Data Editor for Windows, version 0.5.0*.
- Partridge, T.C. & Maud, R.R. (1987) Geomorphic evolution of southern Africa since the Mesozoic. *South African Journal of Geology*, 90, 179-208.
- Pickford, M., Senut, B. & Hadoto, D. P.M. (1993) *Geology and paleobiology of the Albertine Rift valley in Uganda-Zaire. Volume I: Geology*. Occasional Publication 24, Centre International pour la Formation et les Echanges Géologiques, Orléans, France, 1-189.
- Pik, R., Marty, B., Carignan, J., Yirgu, G., & Ayalew, T. (2008) Timing of East African Rift development in southern Ethiopia: implication for mantle plume activity and evolution of topography. *Geology*, 36(2), 167-170. doi:10.1130/G24233A.1
- Plumptre, A.J., Davenport, T.R.B., Behangana, M., Kityo, R., Eilu, G., Ssegawa, P., Ewango, C., Meirte, D., Kahindo, C., Herremans, M., Kerbis Peterhans, J., Pilgrim, J.D., Wilson, M., Languy, M. & Moyer, D. (2007) The biodiversity of the Albertine Rift. *Biological Conservation*, 134, 178-194.

- Poorter, L., Bongers, F., Kouamé, F.Y.N'. & Hawthorne, W.D. (eds.) (2004) *Biodiversity of West African Forests – An Ecological Atlas of Woody Plant Species*. CAB International, Wallingford, Oxon, U.K., 1–521.
- Rabinowitz, P.D., Coffin, M.F. & Falvey, D. (1983) The Separation of Madagascar and Africa. *Science*, 220, 67–69.
- Rambaut, A. & Drummond, A.J. (2009) *Tracer version 1.5* [computer program] <http://beast.bio.ed.ac.uk>
- Rayner, R.J., Bamford, M.K., Brothers, D.J., Dippenaar-Schoeman, A.S., McKay, I.J., Oberprieler, R.G. & Waters, S.B. (1997) Cretaceous fossils from the Orapa Diamond Mine. *Palaeontologia africana – Annals of the Evolutionary Studies Institute University of Witwatersrand*, 33, 55–65.
- Regier, J.C., Zwick, A., Cummings, M.P., Kawahara, A.Y., Cho, S., Weller, S., Roe, A., Baixeras, J., Brown, J.W., Parr, C., Davis, D.R., Epstein, M., Hallwachs, W., Hausmann, A., Janzen, D.H., Kitching, I.J., Solis, M.A., Yen, S.-H., Bazinet, A.L. & Mitter, C. (2009) Toward reconstructing the evolution of advanced moths and butterflies (Lepidoptera: Ditrysia): an initial molecular study. *BMC Evolutionary Biology*, 9 (1), 1–280.
- Reeves, C. (2014) The position of Madagascar within Gondwana and its movements during Gondwana dispersal. *Journal of African Earth Sciences*, 94, 45–57. <http://dx.doi.org/10.1016/j.jafrearsci.2013.07.011>
- Richards, P.W. (1996) *The tropical rain forest – an ecological study*. Cambridge University Press, Cambridge, UK, Second edition, reprinted in 1998, xxiii+1–575.
- Ring, U. (2014) The East African Rift System. *Austrian Journal of Earth Sciences*, 107(1), 132–146.
- Ringrose, S., Huntsman-Mapila, P., Kampunzu, A.B., Downey, W., Coetzee, S., Vink, B., Matheson, W. & Vanderpost, C. (2005) Sedimentological and geochemical evidence for palaeo-environmental change in the Makgadikgadi subbasin, in relation to the MOZ rift depression, Botswana. *Palaeogeography Palaeoclimatology Palaeoecology*, 217(3–4), 265–287. doi: 10.1016/j.palaeo.2004.11.024
- Roberts, E.M., Stevens, N.J., O'Connor, P.M., Dirks, P.H.G.M., Gottfried, M.D., Clyde, W.C., Armstrong, R.A., Kemp, A.I.S. & Hemming, S. (2012) Initiation of the western branch of the East African Rift coeval with the eastern branch. *Nature Geoscience*, 5, 289–294. <http://dx.doi.org/10.1038/NGEO1432>
- Roessner, S. & Strecker, M.R. (1997) Late Cenozoic tectonics and denudation in the Central Kenya Rift: Quantification of long-term denudation rates. *Tectonophysics*, 278 (1–4), 83–94. doi: 10.1016/S0040-1951(97)00096-6
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and Model Choice Across a Large Model Space. *Systematic Biology*, 61(3), 539–542. doi:10.1093/sysbio/sys029

- Rota, J., Peña, C. & Miller, S.E. (2016) The importance of long-distance dispersal and establishment events in small insects: historical biogeography of metalmark moths (Lepidoptera, Choreutidae). *Journal of Biogeography*, 43(6), 1254–1265. doi:10.1111/jbi.12721
- Saalmüller, M. (1884) *Cossus Stumpffi*. In: Saalmüller, M. (ed.) *Lepidopteren von Madagascar. Neue und wenig bekannte Arten*. Erste Abtheilung: Rhopalocera, Heterocera: Shinges et Bombyces, 210–211.
- Said, A., Moder, C., Clark, S. & Ghorbal, B. (2015) Cretaceous-Cenozoic sedimentary budgets of the Southern Mozambique Basin: implications for uplift history of the South African Plateau. *Journal of African Earth Sciences*, 109, 1–10. <http://dx.doi.org/10.1016/j.jafrearsci.2015.05.007>
- Sayer, J.A., Harcourt, C.S. & Collins, N.M. (1992) *The Conservation atlas of tropical forests. Africa*. IUCN. Macmillan Publishers Ltd., U.K., viii+ 9–288.
- Scholz, C.H., Koczyński, T.A. & Hutchins, D.G. (1976) Evidence for incipient rifting in southern Africa. *Royal Astronomical Society Geophysical Journal*, 44, 135–144.
- Schoorl, J.W. jr. (1990) A phylogenetic study on Cossidae (Lepidoptera: Ditrysia) based on external adult morphology. Leiden, *Zoologische Verhandelingen*, 263, 3–295.
- Schoorl, J.M., Veldkamp, A., Claessens, L., van Gorp, W. & Wijbrans, J.R. (2014) Edifice growth and collapse of the Pliocene Mt. Kenya: Evidence of large scale debris avalanches on a high altitude glaciated volcano. *Global and Planetary Change*, 123, 44–54. doi:10.1016/j.gloplacha.2014.10.010
- Schrire, B.D., Lewis, G.P. & Lavin, M. (2005) Biogeography of the Leguminosae. In: Lewis, G., Schrire, B., Mackinder, B. & Lock, M. (Eds.) *Legumes of the world*. Royal Botanic Gardens, Kew, Richmond, Surrey, UK, 21–54.
- Schultze, W. (1908) *Arbelidae*. *Squamicapilla* gen. nov. In: New and little known Lepidoptera of the Philippine Islands. *The Philippine Journal of Science A. General Science* 3(1): 29–30, Plate 1, Figure 4.
- Scoble, M.J. (1995) *The Lepidoptera: form, function and diversity*. The Natural History Museum, London, in association with Oxford University Press, Oxford, U.K., xi + 1–404.
- Scotese, C.R. (2014) *Atlas of Plate Tectonic Reconstructions (Mollweide Projection)*. PALEOMAP Project PaleoAtlas for ArcGIS, Technical Report, Evanston, Illinois, Volumes 1–6, 1–17 + 27 coloured maps. doi: 10.13140/2.1.1046.4967
- Şengör, A.M.C. (2001) Elevation as an indicator of mantle-plume activity. In: Ernst, R.E. & Buchan, K.L. (Eds.) *Mantle plumes: Their identification through time*. *The Geological Society of America Special Papers*, 352, 183–225.
- Shackleton, R.M. (1978) Structural development of the East African Rift System. In: Bishop, W.W. (Ed.) *Geological background to fossil man. Recent research in the Gregory Rift Valley, East Africa*. Scottish Academic Press Ltd., Edinburgh, 19–28.

- Sibatani, A., Ogata, M., Okada, Y. & Okagaki, H. (1954) Male genitalia of Lepidoptera: Morphology and Nomenclature. I. Divisions of the valvae in Rhopalocera, Phalaenidae (= Noctuidae) and Geometridae. *Annals of the Entomological Society of America*, 47, 93–106.
- Slik, J.W.F., Poulsen, A.D., Ashton, P.S., Cannon, C.H., Eichhorn, K.A.O., Kartawinata, K., Lanniari, I., Nagamasu, H., Nakagawa, M., van Nieuwstadt, M.G.L., Payne, J., Purwaningsih, Saridan, A., Sidiyasa, K. D., Verburg, R.W., Webb, C.O. & Wilkie, P. (2003) A floristic analysis of the lowland dipterocarp forests of Borneo. *Journal of Biogeography*, 30(10), 1517–1531. doi:10.1046/j.1365-2699.2003.00967.x
- Sommer, A. (1976) Attempt at an assessment of the world's tropical moist forests. *Unasylva*, 28, 109–120.
- Stainton, J.D.A. (1972) *Forests of Nepal*. John Murray Publishers Ltd., London, xvi + 181 pp. + 156 colour photographs.
- Strand, E. (1909) Fam. Metarbelidae (Hollandiidae). In: Lepidoptera aus Deutsch-Ostafrika gesammelt von Herrn Oberleutnant Wintgens. *Deutsche Entomologische Zeitschrift „Iris“*, 22, 118–121.
- Strand, E. (1917) Neue Heteroceren aus Formosa. *Archiv für Naturgeschichte. Abteilung A.*, 82(3), 139–141.
- Strand, E. (1923) *Paralebedella* n. n.. In: Strand, E. (ed.) *Lepidopterorum Catalogus*. Dalla Torre von, K.W. & Strand, E. Lepidarbelidae, Volume 4 Pars 28, 5–10, W. Junk, Berlin.
- Stüning, D., Hausmann, A. & Wierig, E. (2017) In Memoriam Lutz Kobes (26.08.1933–21.07.2016). *Nachrichtenblatt der bayerischen Entomologen*, 66 (1/2), 34–40.
- Swofford, D.L. (2002). *PAUP. Phylogenetic Analysis Using Parsimony (and other methods), version 4.ob10*. Sinauer Associates, Sunderland, MA, U.S.A.
- Tinker, J., De Wit, M.C.J. & Brown, R. (2008a) Mesozoic exhumation of the Southern Cape, South Africa, quantified using apatite fission track thermochronology. *Tectonophysics*, 455, 77–93.
- Tinker, J., De Wit, M.C.J. & Brown, R. (2008b) Linking source and sink: evaluating the balance between onshore erosion and offshore sediment accumulation since Gondwana break-up, South Africa. *Tectonophysics*, 455, 94–103.
- Torsvik, T.H., Van der Voo, R., Preeden, U., Mac Niocaill, C., Steinberger, B., Doubrovine, P.V., van Hinsbergen, D.J.J., Domeier, M., Gaina, C., Tohver, E., Meert, J.G., McCausland, P.J.A. & Cocks, L.R.M. (2012) Phanerozoic polar wander, palaeogeography and dynamics. *Earth-Science Reviews*, 114, 325–368. doi:10.1016/j.earscirev.2012.06.007
- Trewick, S.A. (2000) Molecular evidence for dispersal rather than vicariance as the origin of flightless insect species on the Chatham Islands, New Zealand. *Journal of Biogeography*, 27, 1189–1200.

- Van der Beek, P.A., Summerfield, M.A., Braun, J., Brown, R.W. & Fleming, A. (2002) Modelling postbreakup landscape development and denudational history across the southeast African (Drakensberg Escarpment) margin. *Journal of Geophysical Research: Solid Earth*, 107, ETG 11-1-ETG 11-18. doi:10.1029/2001JB000744
- Van Dyck, H. (2011) Habitat-use in butterflies: how to move from structural to functional ecology. *Abstracts of the XVIIth European Congress of Lepidopterology*. Luxembourg, 9-13.
- van Nieukerken, E.J., Kaila, L., Kitching, I.J., Kristensen, N.P., Lees, D.C., Minet, J., Mitter, C., Mutanen, M., Regier, J.C., Simonsen, T.J., Wahlberg, N., Yen, S.-H., Zahiri, R., Adamski, D., Baixeras, J., Bartsch, D., Bengtsson, B.Å., Brown, J.W., Bucheli, S.R., Davis, D.R., De Prins, J., De Prins, W., Epstein, M.E., Gentili-Poole, P., Gielis, C., Hättenschwiler, P., Hausmann, A., Holloway, J.D., Kallies, A., Karsholt, O., Kawahara, A.Y., Koster, S., Kozlov, M.V., Lafontaine, J.D., Lamas, G., Landry, J.-F., Lee, S., Nuss, M., Park, K.-T., Penz, C., Rota, J., Schmidt, B.C., Schintlmeister, A., Sohn, J.-C., Solis, M.A., Tarmann, G.M., Warren, A.D., Weller, S., Yakovlev, R.V., Zolotuhin, V.V. & Zwick, A. (2011) Order Lepidoptera Linnaeus, 1758. In: Zhang, Z.Q. (Ed.), *Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness*. *Zootaxa*, 3148, 212-221.
- van Someren, V.G.L. (1963) Revisional notes on the African *Charaxes* (Lepidoptera: Nymphalidae). Part I. *Bulletin of the British Museum (Natural History) (Entomology)*, 13(7), 195-242 + 19 pls.
- Viette, P. (1981) Lépidoptères Hétérocères de l'archipel des Comores nouveaux ou peu connus, I. Famille Metarbelidae. *Bulletin de la Société entomologique de France*, 86(1-2), 31-32.
- Wägele, J.-W., (2005) *Foundations of Phylogenetic Systematics*. Verlag Dr. Friedrich Pfeil, München, 5-365.
- Wahlberg, N., Wheat, C.W. & Peña, C. (2013) Timing and Patterns in the Taxonomic Diversification of Lepidoptera (Butterflies and Moths), *PLoS ONE*, 8 (11), e80875. <http://dx.doi.org/10.1371/journal.pone.0080875>
- Walker, F. (1855) Genus *Teragra*. In: Walker, F. (Ed.) *List of the specimens of Lepidopterous insects in the collection of the British Museum*. Printed by the order of the Trustees, London, Part V. - Lepidoptera Heterocera, 1064.
- Walker, F. (1865) Genus *Salagena*. In: Walker, F. (Ed.) *List of the specimens of Lepidopterous insects in the collection of the British Museum*. Printed by the order of the Trustees, London, part XXXI, Supplement, 590-591.
- Wallace, A. R. (1860) On the Zoological Geography of the Malay Archipelago. *Journal of the Proceedings of the Linnean Society of London*. *Zoology*, 4, 172-184. doi:10.1111/j.1096-3642.1860.tb00090.x
- Wallace, A.R. (1876) The Oriental Region. In: *The geographical distribution of animals. With a study of the relations of living and extinct faunas as elucidating the past changes of the earth's surface*. New York, Harper & Brothers Publishers, Franklin Square. Volume I, Part III, Chapter XII, Pp. 314-386 including one coloured map.

- Wayland, E.J. (1921) Some account of the geology of the Lake Albert Rift Valley. *The Geographical Journal*, 58(5), 344–359.
- Wells, N. A. (2003) Some Hypotheses on the Mesozoic and Cenozoic Paleoenvironmental History of Madagascar. In: Goodman, S.M. & Benstead, J.P. (Eds.), *The Natural History of Madagascar*. The University of Chicago Press, Chicago and London, 16–34.
- Werger, M.J.A. (Ed.), (1978) Biogeography and ecology of southern Africa. *Monographiae Biologicae*, Volumes 31 and 32, Dr. W. Junk, The Hague, vii + 3–1439.
- White, F. (1965) The savanna woodlands of the Zambezi and Sudanian Domains: an ecological and phytogeographical comparison. *Webbia*, 19, 651–681.
- White, F. (1976) The vegetation map of Africa: the history of a completed project. *Boissiera*, 24, 659–666.
- White, F. (1979) The Guineo-Congolian Region and its relationships to other phytochoria. *Bulletin du Jardin Botanique National de Belgique – Bulletin van de Nationale Plantentuin van België*, 49, 11–55 (including appendix).
- White, F. (1981) The history of the Aromontane archipelago and the scientific need for its conservation. *African Journal of Ecology*, 19(1–2), 33–54.  
doi: 10.1111/j.1365-2028.1981.tb00651.x
- White, F. (1983) *The Vegetation of Africa: a Descriptive Memoir to Accompany the Unesco/AETFAT/UNSO Vegetation Map of Africa*. Natural Resources Research no. XX. Unesco, Paris, 1–356.
- White, L.J.T. (2001) The African rain forest – climate and vegetation. In: Weber, W., White, L.J.T., Vedder, A. & Naughton-Treves, L. (Eds.) *African Rain Forest Ecology and Conservation – An Interdisciplinary Perspective*. Yale University Press with support from the Wildlife Conservation Society, New Haven and London, 3–29.
- Whitmore, T.C. (1984) *Tropical rain forests of the Far East*. Clarendon Press, Oxford, i–xvi + 1–353.
- Wiltshire, E.P. (1988) Lepidoptera of Saudi Arabia: Fam. Metarbelidae, Geometridae, Arctiidae, Agaristidae, Noctuidae (part 6). In: Büttiker, W. & F. Krupp (Eds.), *Fauna of Saudi Arabia*, 9, p. 71, Figures 1, 28. Natural History Museum Basle and National Commission for Wildlife Conservation and Development Riyadh.
- Wojciechowski, M.F. (2003) Reconstructing the phylogeny of legumes (Leguminosae): An early 21<sup>st</sup> century perspective. In: Klitgaard, B.B. & Bruneau, A. (Eds.) *Advances in Legume Systematics. Part 10: Higher Level Systematics*. Royal Botanic Gardens, Kew, Richmond, Surrey, UK, 5–35.
- Wolfenden, E., Ebinger, C., Yirgu, G., Renne, P.R. & Kelley, S.P. (2005) Evolution of a volcanic rifted margin: Southern Red Sea, Ethiopia. *Geological Society of America Bulletin*, 117(7–8), 846–864. doi: 10.1130/B25516.1

- Woolley, A.R. (1987) Lithosphere metasomatism and the petrogenesis of the Chilwa Province of alkaline igneous rocks and carbonatites, Malawi. *Journal of African Earth Sciences*, 6(6), 891–898.
- Yu. Y., Harris, A.J., Blair, C. & He, X. (2015) RASP (Reconstruct Ancestral State in Phylogenies): a tool for historical biogeography. *Molecular Phylogenetics and Evolution*, 87, 46–49. doi: 10.1016/j.ympev.2015.03.008. Epub 2015 Mar 26.
- Zavada, M.S. (2004) The earliest occurrence of Angiosperms in southern Africa. *South African Journal of Botany*, 70(4), 646–653. doi:10.1016/S0254-6299(15)30205-2

## 11a. SUMMARY

This thesis represents the first revision of the family Metarbelidae Strand, 1909. The author's extensive research on Metarbelidae includes fieldwork made in nine lowland and montane forests of Kenya (1994–2008; 2015–2018) as well as an extensive study of specimens from museum and private collections (1994–2018). At the family-level some notes are presented on possible relationships to Cossidae, Dudgeoneidae and Ratardidae. The author presents morphological diagnoses of 60 genera of Metarbelidae, including 20 already published genera and 40 genera new to science from the Afrotropical and Oriental Region. 50 genera are distributed on the African mainland, two on Madagascar, three on the Arabian Peninsula, one on Nepal and four genera occur on the Sunda shelf. The genus *Stenagra* Hampson is excluded from the Metarbelidae. Six genera that were published as Metarbelidae were not studied as their type species were not available during the author's work at various museums. At the species-level, the sample contains 442 species from the whole Afrotropical Region as well as species from Nepal, Malaysia and the Sunda shelf. Other species, *e.g.* from Thailand and Sri Lanka were studied, but were not included in this sample. As a result of this study the systematics on the species level will undergo further change for *ca.* 120 already published species in the future.

As a first step, seven plesiomorphic characters were determined and are presented for the “Basal Group” (genera *Teragra*/Gen.Nov.A) of Metarbelidae as a basis for the further delimitation of clades using apomorphic characters. One of these plesiomorphies, the occurrence of a fully developed CuP vein in the forewing, has been only found in species that occur mainly to the South of the Zambezi River or close to this river.

The author presents the ground pattern with its autapomorphies and apomorphies for each genus, distribution maps and figures for all 60 genera. Some genera have a very small distribution range, *e.g.* *Ortharbela*, *Aethiopina*; few genera have a large distribution range, *e.g.* *Kroonia*, *Marshalliana*. Twenty genera have only strict endemic or near-endemic species, *e.g.* *Metarbela*, all genera on Madagascar, all genera on the Sunda shelf; some genera on the Arabian Peninsula. Species of those genera might be of particular interest from the nature conservation point of view since habitats with many endemics have a high conservation value. Areas with high endemism among Metarbelidae occur in the Afromontane Region (particularly in Eastern Africa), Lower Guinea, in the Somalia-Masai Region and on Madagascar. Endemic species of Gen.Nov.F occur in arid areas of Kenya and Somalia. They are one example that species of arid areas are local endemics. The author's view that many Metarbelidae of arid areas might be endemic is supported by the fact that there has been no species or any genus found yet that extends unbroken southwesterly from the Somali Peninsula to the Western Cape/Namibia, *e.g.* via the “drought corridor” *sensu* Balinsky (1962). This corridor existed several times during dry glacial periods.

Destruction of forests and/or woodlands by humans and/or fire favour the extinction of endemic species.

In a binary data matrix 161 apomorphies were scored using the Dudgeoneidae as outgroup. 50 homoplasies were found by the author before and were excluded from this data matrix. Based on the morphological data a phylogeny of Metarbelidae was constructed using Bayesian Inference and Maximum Parsimony. Among 161 apomorphies 60 of which represent parsimony-informative characters. The consistency index of 0.8154 showed relatively high consistency of the data. The first split separates the “Basal Group”, the second split separates three large groups of genera with 24 (“Afromontane Group”), 14 (“West Africa-Sunda Group”) and 14 (“Mali-Zambezia-Somalia-Malagasy Group”) genera; a fourth group comprises two sister-groups (“Lower Guinea-Sunda Group” and “*Salagena*-Arabia Group”); two genera, including *Saalmulleria*, remain as single genera without affiliation. A general feature among the parsimony-informative characters is that the simplest, soft, thinly sclerotized characters of the genitalia occur in species of the “Basal Group” and “Afromontane Group” mainly on the Southern African Plateau and in particular in the Afromontane archipelago-like regional centre of endemism *sensu* White (1983) of the eastern part of the Republic of South Africa. All habitats of the “Basal Group” are located in areas that are geomorphologically stable since at least 65 Ma and hence, provide habitats under long stable geological conditions, possibly with a climate that is also more stable.

There is high support for monophyly from Bayesian Inference as well as Maximum Parsimony (pp: all above 0.92; Bootstrap: all above 62 in MP) that all closely related species of nine genera (except *Saalmulleria*), that occur not on the African mainland, belong to genera that have their ancestors on the African mainland. Hence, also all species of the Oriental Region have their stem lineage representatives in the Afrotropical Region. Furthermore, the constructed dendrogram shows that genera which include only lowland species have common ancestors that first occurred in montane areas. This hypothesis is supported by parsimony-informative characters that become more sclerotized and more complex, particularly in species of the lowland rain forest and its transition zones, maybe as a kind of adaptation, *e.g.* a broad band that connects the valva ventrally. The split that separates the sister-group that includes species of one genus occurring on Madagascar and species of one genus occurring along the eastern coast of Africa is supported with high monophyly.

Ancestral area reconstruction with RASP predicted the ancestral distribution of many Metarbelidae (24 genera) in the Afromontane Region suggesting a high importance for the evolution of this family.

Further studies are needed on the Metarbelidae of the Oriental Region, and at least 50 genera with their mainly new species have to be described and published in the future to complete the revision on the family Metarbelidae.

However, this thesis will stand as a record of what the Metarbelidae were like in regard to their systematic and taxonomy in the past 135 years in the Afrotropical and Oriental Region (1882 to 2017).

## 11b. ZUSAMMENFASSUNG

Die vorliegende Dissertation stellt eine erste Revision der Familie Metarbelidae Strand, 1909 (Lepidoptera: Cossioidea Leach, 1815) vor. Zu den Familien der Cossidae, der Dudgeoneidae und der extrem seltenen Ratardidae werden Unterschiede und Gemeinsamkeiten auf der Grundlage von plesiomorphen und apomorphen Merkmalen genannt, die vom Autor an untersuchten Faltern festgestellt wurden. Die vom Autor durchgeführten intensiven Forschungen zu den Metarbelidae basieren einerseits auf langjährige Studien in Kenya, und zwar in neun Naturwäldern zu deren Waldstruktur, floristischer Artenzusammensetzung, der Dominanz von Baumarten sowie den Tag- und Nachtfalterarten. Dabei handelt es sich um fünf Tieflandwälder an der Küste des Indischen Ozeans (1994–2008: Kaya Muhaka, Kaya Kinondo, Kaya Diani, Gogoni Forest Reserve und Shimoni Forest) sowie um vier Bergwälder im zentralen Teil Kenyas (2015–2018: Karura Forest, Ololua Forest, Lolldaiga Hills forests und Mpala bushlands). Zum anderen wurden morphologische Diagnosen zu insgesamt 60 Gattungen der Metarbelidae der Afrotropischen und Orientalischen Region durchgeführt. Diese umfassen 50 Gattungen des afrikanischen Festlandes südlich der Sahara, zwei Gattungen auf Madagaskar, drei Gattungen auf der Arabischen Halbinsel, eine Gattung in Nepal sowie vier Gattungen auf dem Sunda shelf. Zusätzlich ist eine Art der Gattung *Stenagra* Hampson untersucht worden. Aufgrund der vorliegenden Ergebnisse wurde diese Gattung von der Familie Metarbelidae ausgeschlossen. Sechs weitere als Metarbelidae publizierte Gattungen konnten nicht untersucht werden, weil das entsprechende Typenmaterial dem Autor nicht zur Verfügung stand.

Seit 1994 wurden insgesamt 442 Arten, die aus mehreren europäischen und afrikanischen Museen sowie von privaten Sammlungen stammen, detailliert untersucht. Dazu sind von jeder Art die Aderung sowie die Genitalstrukturen mittels genauer Bleistiftzeichnungen und Fotos erfasst worden. Von allen Faltern liegen zudem Fotos vor. Die Arten sind in der gesamten Afrotropischen Region sowie in Nepal, Malaysia und auf dem Sunda shelf gesammelt worden. Obwohl zusätzlich noch weitere Arten z.B. aus Sri Lanka, Thailand und aus dem Norden Malaysias untersucht wurden, sind diese hier nicht vorgestellt worden, weil die Studien zu den Arten der Orientalischen Region noch nicht abgeschlossen sind. Als ein Ergebnis dieser ersten Revision wird sich die Systematik von ca. 120 bereits publizierten Arten ändern.

In einem ersten Schritt wurden insgesamt sieben plesiomorphe Merkmale der Metarbelidae herausgearbeitet, um die „basale Gruppe“ definieren zu können (Gattungen *Teragra* und Gen.Nov.A). Diese plesiomorphen Merkmale dienen der Abgrenzung aller übrigen monophyletischen Gruppen auf der Grundlage apomorpher Merkmale. Zu den sieben Merkmalen zählt beispielsweise das Vorhandensein einer intakten CuP-Ader auf dem Vorderflügel, die bisher nur an basalen Arten gefunden wurde, die südlich des Zambezi River auf dem Southern African Plateau oder in der Nähe dieses Flusses vorkommen.

Der Autor stellt für jede Gattung das Grundmuster mit den Autapomorphien und Apomorphien vor. Das Aussehen der Falter wird mit Fotos verdeutlicht. Falls möglich werden Männchen und Weibchen dargestellt. Die Verbreitung jeder Gattung wird anhand von Karten präsentiert. Auffällig ist, dass einige Gattungen ein sehr kleines Verbreitungsgebiet haben (z.B. die Gattungen *Ortharbela* und *Aethiopina*), und nur wenige Gattungen ein großes Verbreitungsareal aufweisen (z.B. die Gattungen *Kroonia* und *Marshalliana*). Es werden 20 Gattungen vorgestellt, die ausschließlich endemische Arten aufweisen. Dazu zählen z.B. *Metarbela*, alle Gattungen Madagaskars, Nepals und des Sunda shelf, einige Gattungen der Arabischen Halbinsel. Die endemischen Arten dieser Gattungen sind aus dem Blickwinkel des Naturschutzes von besonderem Interesse, weil Lebensräume mit vielen endemischen Arten schutzwürdig sind. Endemismus ist bei den Metarbelidae in folgenden Gebieten hoch: in der Afromontanen Region (insbesondere in Ostafrika), in Niederguinea, in der Somalia-Masai Region im Sinne von White (1983), und auf Madagaskar. Die Abholzung oder Degradierung von Naturwäldern und Baumsavannen sowie natürliche oder durch Menschen verursachte Brände begünstigen das Aussterben endemischer Metarbelidae. Die endemischen Arten der neuen Gattung F (Gen.Nov.F) kommen in ariden Gebieten Kenyas und Somalias vor. Vermutlich sind viele Metarbelidae arider oder semi-arider Gebiete endemisch. Diese Vermutung des Autors wird von der Tatsache gestützt, dass bisher keine Arten oder Gattungen der Metarbelidae gefunden wurden, die im gesamten „drought corridor“ im Sinne von Balinsky (1962) verbreitet sind. Dieser Korridor erstreckte sich in verschiedenen glazialen Trockenphasen ungebrochen von der Somalischen Halbinsel in südwestliche Richtung bis nach Namibia.

In einer Datenmatrix wurden 161 Apomorphien kodiert. Die Dudgeoneidae dienten dabei als Außengruppe. Insgesamt 50 Homoplasien sind von dieser Datenmatrix zuvor ausgeschlossen worden. Die Phylogenie der Metarbelidae wurde mit Hilfe von Maximum Parsimonie und der Bayes'schen Inferenz rekonstruiert. Von den 161 Apomorphien sind insgesamt 60 Parsimonie informativ. Der Konsistenz-Index ist mit 0.8154 relativ hoch. Dies bedeutet, dass in der Datenmatrix nur noch wenige Homoplasien vorhanden waren. Die erste Aufteilung im Stammbaum trennt die „basale Gruppe“; die zweite Aufteilung bildet drei große Gattungsgruppen mit 24 („Afromontane Gruppe“), 14 („West Afrika-Sunda Gruppe“) und 14 („Mali-Zambezia-Somalia-Madagaskar Gruppe“) Gattungen. Eine vierte Gruppe enthält zwei Schwestergruppen („Niederguinea-Sunda Gruppe“ und „*Salagena*-Arabien Gruppe“). Zwei Gattungen (Gen.Nov.N und *Saalmulleria*) konnten phylogenetisch nicht zugeordnet werden.

Ein Trend bei den Parsimonie informativen Merkmalen ist, dass diese keine zusätzlichen Strukturen aufweisen, also besonders einfach sind, leicht biegsam, dünnhäutig und somit wenig sklerotisiert sind, und zwar in den Arten der „basalen Gruppe“ sowie der „Afromontanen Gruppe“. Alle Lebensräume der Arten der „basalen

Gruppe“ befinden sich in Gebieten, die geologisch seit mindestens 65 Millionen Jahre stabil sind. Dies begünstigt auch ein stabileres Klima.

Eine Monophylie mittels Maximum Parsimonie und Bayes'scher Inferenz zeigt, dass alle Arten von Gattungen (ohne *Saalmulleria*), die heute nicht auf dem afrikanischen Festland vorkommen, ihre Vorfahren auf dem afrikanischen Festland haben. Dazu zählen auch die Stammlinienvertreter aller Arten der Orientalischen Region. Das konstruierte Dendrogramm macht darüber hinaus deutlich, dass heutige Arten des Tieflandes Vorfahren haben, die im Bergland vorkamen.

Die Aufspaltung der Schwestergruppe Gen.Nov.I (mit Vorkommen der Arten entlang der Ostküste Afrikas) und Gen.Nov.H (mit Vorkommen der Art auf dem westlichen Madagaskar) hat eine gut gestützte Monophylie.

Die hypothetischen ursprünglichen Verbreitungen der Metarbelidae wurden mit RASP rekonstruiert und zeigen, dass die Arten von 24 Gattungen ihr Stammgebiet in der Afromontanen Region haben. Dies macht deutlich, dass diese Region eine hohe Bedeutung für die Evolution der Metarbelidae besitzt.

In der Zukunft sind weitere Studien notwendig, um die Revision der Metarbelidae zu vervollständigen, wie z.B. die Beschreibung und Publikation aller Arten der hier als neu vorgestellten Gattungen und der Gattungen selbst.

Diese Dissertation stellt eine Aufnahme zum Wissensstand, Systematik und zur Taxonomie der Metarbelidae der letzten 135 Jahre dar (1882 bis 2017).

**12a. APPENDIX 12.1**

***APOMORPHIES OF THE METARBELIDAE  
IN 60 GENERA COMPRISING 442 SPECIES  
FROM THE AFROTROPICAL AND ORIENTAL REGION***

## ✚ HEAD

### ○ Antennae

- (1) Flagellum and branches covered with scales in male (homoplasy);
- (60) Male antenna very long (at least 50% of length of costa of forewing);
- (65) Male antenna with very long branches (at least 8 x width of shaft) (homoplasy);
- (66) Male antenna with long branches (5 – 7 x width of shaft) (homoplasy);
- (114) Male antenna with short, thick (well sclerotized), broad rectangular branches that are not fused at base towards tip;
- (115) Male antenna with short, thinly membranous, broad rectangular branches and (115a) branches are not fused at base for one-third of each branch length for the last *ca.* 25% of the antenna length (hence, the antenna becomes not more unipectinated towards tip and the branches do not look like a broad shaped “V” viewed posteriorly);
- (161) Male antenna has suddenly very short branches (at *ca.* half of antenna);
- (195) Male antenna filiform, slightly unipectinated at tip.

### ○ Labial palpi

- (2) Two-segmented in male (homoplasy);
- (36) Two-segmented with tiny third one on top in male (homoplasy).

### ○ Fronto-clypeus

- (3) Pits present in male (homoplasy);
- (37) Projections present in male (homoplasy).

## ✚ THORAX

### ○ Patagia and tegulae

- (48) Tegulae have a peculiar colour of a glossy rust (xanthine orange) in both sexes (homoplasy).

○ Forewing

- (4) M-vein in discal cell not forked in male (homoplasy);
- (5) M-vein in discal cell strongly reduced, almost entirely absent in male (homoplasy);
- (6) R<sub>1</sub>+R<sub>2</sub> on a very long stalk (stalk has the length of 60–70% of R<sub>3</sub>) in male;
- (7) R<sub>1</sub>+R<sub>2</sub> on a long stalk (stalk has the length of 40–50% of R<sub>3</sub>) in male and/or female;
- (8) R<sub>1</sub>+R<sub>2</sub> on a short stalk (stalk has the length of 30% of R<sub>3</sub>) in male;
- (9) R<sub>2</sub> absent (only 11 veins present) in both sexes (homoplasy);
- (10) a prominent, broad, dark streak on lower part of discal cell in both sexes (homoplasy);
- (11) CuP absent in male and/or female [most probably in both sexes];
- (12) 1A+2A not deeply forked at base in male (homoplasy);
- (13) Areole absent in both sexes (homoplasy);
- (40) Forewing and hindwing butterfly-like, almost of equal size in male;
- (49) V-shaped geometric design in subterminal and postmedial area of forewing and hindwing in both sexes (homoplasy);
- (57) Discal cell open towards termen in male;
- (68) 1A+2A not forked at base in male (homoplasy);
- (75) Areole long and narrow elongated in male (homoplasy);
- (76) Anterior cell (= upper part of discal cell) in forewing unusually small, namely only slightly larger than the elongated areole;
- (82) Areole very small in both sexes (homoplasy);
- (89) Areole tiny (pyriform or elongated), almost not visible in male;
- (118) Areole like in number 75 and M<sub>1</sub>, R<sub>5</sub>, R<sub>3</sub> and R<sub>2</sub> initiating from areole in male;
- (122) Very small discal cell in forewing (less than 15% of forewing size) with the anterior part of discal cell only half or slightly less of the length of antenna in both sexes;
- (131) Lower part of discal cell smaller than upper part, discal cell ca. 50–60% of length of forewing in male (homoplasy);
- (154) The whole forewing upperside light green mixed with cream;
- (157) Triangular-shaped forewings and triangular-shaped hindwings with straight termen in male;
- (162) Very long, pure white, hair-like scales, not or only slightly curled, have an upright position on upperside of forewing well above the normal scale-layer;

- (163) Very rare forewing pattern in both sexes where a broad grey band extends from termen into the discal cell in between  $M_2$  and  $M_1$  or  $M_2$  and  $R_5$  as well as a broad white or light cream band extends from  $R_5$  to costal margin and to  $R_1$ ;  $CuA_2$  is not distinctly marked in this pattern;
  - (165) Long narrow scales (not like number 162) occur densely below discal cell but not well above the normal scale layer on upperside in both sexes (homoplasy);
  - (166) Very long scales above normal scale layer, pure white, hair-like, not or only slightly curled, occur densely in a mainly horizontal and less upright position only below base of discal cell on upperside of forewing in both sexes;
  - (173)  $M_1$  initiates from the same point as  $R_5+R_4+R_3+R_2$  that are long stalked (homoplasy);
  - (178)  $1A+2A$  at base not connected by a short vein with  $CuP$  in both sexes (homoplasy);
  - (185) Narrow, elongated forewing with rounded apex and almost triangular hindwings in male;
  - (192) Very narrow, elongated and small upper discal and lower discal cell, both ends strongly acuminate and deeply bifurcated in both sexes;
  - (206) Scales of number 162 occur evenly distributed on the whole upperside of forewing in both sexes.
- Hindwing
- (14) M-vein in discal cell not forked in male (homoplasy);
  - (15)  $CuP$  absent in both sexes (homoplasy);
  - (16a) M-vein in discal cell absent in male (homoplasy);
  - (59)  $Sc+R_1$  crosses the base of upper median of discal cell in both sexes;
  - (72)  $RS+M_1$  are forked and initiate on a very long straight stalk (stalk at two-thirds of length of both veins) in male;
  - (78)  $RS+M_1$  are forked and initiate on a long stalk (stalk at one-third of length of both veins) and  $M_1$  is more or less strongly bent downwards in male (homoplasy);
  - (120) Largely transparent hindwing and forewing in male; transparent parts are covered with tiny scales at least half of them are transparent scales;
  - (132) Lower discal cell smaller, more narrow, than upper discal cell in male (homoplasy);
  - (180) Frenulum only in male but not in female present;
  - (193)  $RS$  from mid-point of a long vein that connects the upper half of discal cell with  $Sc+R_1$  in both sexes.

○ Legs

- (16b) One pair of spurs to the hindleg almost equal in length (homoplasy);
- (47) The tarsi have a peculiar colour of a glossy rust (xanthine orange) in both sexes;
- (50) Epiphysis present (homoplasy);
- (88) Two pairs of spurs to the hindleg but very unequal in length;
- (116) One pair of spurs to the hindleg but very unequal in length (homoplasy).

✚ ABDOMEN

○ Uncus (Male)

- (25) Uncus strongly thickened ventrally, looking like a strongly sclerotized lunule in lateral view;
- (26) Uncus longer than width of valva and narrow elongated;
- (27) Uncus longer than width of valva, narrow elongated and deeply bifurcated (*ca.* at least one-third of uncus length);
- (44) Uncus has a heavy appearance, it is strongly sclerotized with a more or less flat dorsal surface;
- (58) Two tips of uncus stronger sclerotized than remaining uncus, both tips small or strongly reduced but bifurcated and acuminate;
- (63) Large sack-like, membranous structure below base of uncus extending to its tip;
- (64) Two thorn-like processes below number 63;
- (69) Very long setae on ventral side of uncus, the setae almost touch the costa of valva in lateral view;
- (84) Each uncus lobe has on its dorsal side (almost entire surface) a sclerotized structure that looks like a hill;
- (86) Uncus strongly elongated, narrow or broad, but only thinly sclerotized, bifid at tip;
- (87) Uncus strongly elongated, always narrow, only thinly sclerotized, never bifid at tip;
- (90) Uncus more or less beak-like in lateral view;
- (99) Uncus has a tiny hole (< 10%) of its dorsal surface near the centre of uncus;
- (100) The uncus has a large hole dorsally that is larger than 60% of the dorsal surface and is located near the centre of the uncus;

- (101) Band-like appendice originates on each side of uncus base (homoplasy);
- (103) Triangular-shaped and narrow bifurcated uncus with acuminate tips;
- (110) Along the edges of uncus occur one or more hollow, narrow, tube-like structures (homoplasy);
- (117) A narrow uncus is strongly bent downwards in the middle (lateral view);
- (133) Uncus tip represents a broad “V”;
- (134) Entire broad uncus is much shorter than basal width of valva and has a tip like in number 133;
- (135) Entire broad uncus is longer or equal to basal width of valva and has a tip like in number 133;
- (151) Entire narrow uncus is longer or equal to basal width of valva and has a tip like in number 133;
- (172) Uncus extremely long and bent downwards in lateral view, extending well below the costa of valva;
- (177) Large uncus triangular-shaped and almost as large as valva (ventral view);
- (179) Uncus narrow and not bent downwards in the middle (lateral view) in combination with a juxta that is extremely large, almost 50% the size of valva;
- (183) Uncus and tegumen very long, namely *ca.* 2.3 x longer than basal width of valva;
- (190) Uncus triangular-shaped, extremely broad and large, twice as large as valva in ventral view, with two claw-like tips;
- (191) Huge strongly sclerotized elongated uncus (larger than valva), in lateral view almost as broad as basal width of valva with a deep graben-like structure ventrally.

○ Gnathos (Male)

- (17) Large, sclerotized and broad gnathos, in lateral view two-thirds of the size of valva, extending to basal costa of valva;
- (18) Two gnathal arms are sclerotized, fused or connected by a more or less long, narrow band ventrally, basally connected to the base of uncus;
- (19) Gnathal arms well developed and connected by a small, broad and short plate-like (rectangular) structure, namely by a small bulla, ventrally;
- (20) Gnathal arms well developed, almost triangular at lower half of their length with many deep folds distally and connected by a large, broad and short rectangular bulla ventrally;
- (21) Gnathal arms not connected ventrally;

- (22) Gnathal arms extremely long, almost touching upper part of juxta;
- (23) The whole gnathal arms are not thorn-like but each arm comprises a prominent thorn-like appendice that is *ca.* 60% in size of each gnathal arm;
- (24) The whole gnathal arms are not thorn-like but each arm comprises a small thorn-like appendice that is *ca.* 10% in size of each gnathal arm;
- (41) The end of each gnathal arm looks like a hand with tiny thorn-like appendices;
- (45) Gnathos large (at least 50% the size of valva in lateral view) and heavy in appearance, well sclerotized, tabular in shape dorsally;
- (91) Gnathos large, 40% or 50% of the size of valva, elongated, looking like a wing of a penguin, its rounded end is well above or below the costa of valva;
- (94) Gnathos large, 50% of the size of valva, elongated with many strong folds on its whole length, its rounded end is below basal costa of valva but well above juxta;
- (97) Whole gnathos thinly membranous, only half width of sacculus, long and stick-like, ventrally connected by a thin membrane that breaks up easily;
- (105) Gnathos absent;
- (109) Relict of gnathos present (homoplasy);
- (124) Gnathos only thinly membranous and appears soft, not well sclerotized, ventrally fused;
- (125) Gnathos of number 124 is short (ending well above costa of valva) and broad (40–50% of width of valva);
- (126) Gnathos of number 124 is long (ending below costa of valva) and narrow (20% of width of valva) on its whole length;
- (127) Relicts of two narrow gnathal arms are attached to the lower part of tegumen (not uncus!);
- (146) Relicts of two gnathal arms are looking like a T-shaped stick and are attached to the lower part of tegumen (homoplasy);
- (155) Gnathos of number 124 (only thinly membranous and appears soft, not well sclerotized, ventrally fused) is very long (ending at half width of valva) and broader at base;
- (156) Gnathal arm represents a strongly sclerotized thorn with a broader base and an acuminate tip and is connected by a band to the base of uncus; the gnathal arms are connected by a narrow band ventrally and end well above the costa of valva;
- (159) Small thorn-like gnathal arm (25% the size of valva) is connected to the base of uncus by a long broad band;
- (160) like in number 156 but the thorn-like gnathal arm is large (35% the size of valva) and connected to the base of uncus by a long and very narrow band;

- (175) one gnathal arm appears like there are two arms in lateral view (homoplasy);
  - (187) thick, prominent V-shaped, finger-like appendice occurs below number 127 and has many small setae on its entire surface (homoplasy);
  - (196) Gnathal arms thinly membranous, narrow and fused for at least one-third of their entire length;
  - (198) Gnathal arms sclerotized, narrow and only slightly connected ventrally but not fused;
  - (201) Gnathal arms thinly membranous, strongly reduced, bulla still present but tiny (homoplasy);
  - (202) Two prominent and long, narrow sinuate, serrate processes, thorn-like, are attached to the upper part of the semi-transtilla;
  - (208) Gnathal arm very large and almost as large as valva;
  - (241) Gnathal arms broad, rectangular (ca. 40% of size of valva) and connected basally with a narrow band that is acuminate at middle (hook-like).
- Tegumen and vinculum (Male)
- (31) Narrow vinculum (one-third or less of width of aedeagus), no saccus, and very broad tegumen (at least 4 x broader than vinculum);
  - (43) Large, well sclerotized, rectangular plate-like structure close to ventral end of vinculum;
  - (73) Large skin-like, slightly sclerotized, light grey transparent structure that extends from near ventral base of vinculum to lower half of tegumen (lateral view), it is covered on both sides with many tiny dark setae on its surface (cf. number 205 that is much shorter in lateral view) (homoplasy);
  - (102) Very long, narrow saccus (in lateral view), almost as long as ventral edge of a broad rectangular valva;
  - (112) Vinculum broad with an rectangular broad end below ventral base of valva; the end appears as vertical edge in lateral view;
  - (119) Strongly rounded edges of valva;
  - (182) Long (50% longer than basal width of valva) membranous structure below uncus (homoplasy);
  - (197) Very large hole extends from tegumen towards base of uncus (homoplasy);
  - (205) Large skin-like, slightly sclerotized, light grey transparent structure that extends from near ventral base of vinculum beyond aedeagus (lateral view), it is covered on both sides with many tiny dark setae on its surface (homoplasy).

○ Valva (Male)

- (28) Valva narrow, only twice or less as broad as gnathal arm in lateral view;
- (29) Valva long, almost as long as tegumen + vinculum, tip suddenly very narrow and elongated, tip might be as long as uncus in lateral view, end of tip slightly pointed;
- (30) Valva very long, longer than tegumen + vinculum, but tip not very narrow and elongated (homoplasia);
- (38) Small thorn-like process at ventral posterior end of valva, process soft, only slightly sclerotized, not hollow on entire length;
- (39) More or less large weakly sclerotized, skin-like, transparent projection along the costa and inner distal edge of valva;
- (42) Prominent elongated emargination that is edged by a prominent thorn-like structure below and above the emargination;
- (51) Two prominent, long, narrow acuminate, thorn-like appendices on valva arising externally from its base;
- (54) Well sclerotized thorn-like process(-es) at the posterior margin of valva are hollow inside.
- (55) Well sclerotized, hollow and long thorn-like process originates at the costal margin and is strongly bent downwards to the ventral edge of valva;
- (56) Valva consists of two long narrow lobes, sometimes with a small third one between both lobes;
- (67) A wide emargination (looking like a wide “V”) forms the posterior edge of valva;
- (70) Valvae not separated, but connected by a narrow strongly sclerotized band ventrally;
- (71) Valvae not separated, but connected by a broad strongly sclerotized band ventrally;
- (74) A spoon-like, strongly sclerotized appendice (without a keel line ventrally) is attached to the upper part of a thinly membranous valva;
- (79) Valvae are extremely thinly membranous and small but are attached to a strongly sclerotized large spoon-like appendice that has a keel line ventrally;
- (80) Valvae not separated, but almost entirely connected by broad sclerotized band ventrally;
- (83) large, hollow, strongly sclerotized thorn-like appendice on ventral inner side of valva (not an extension of the sacculus) that is broadly connected to the strongly sclerotized band that links both valva;
- (85) large, hollow, sclerotized rounded appendice on ventral distal side of valva (not an extension of the sacculus, or an extension of the sacculus) is connected to the plate that links both valva;

- (92) A band-like transtilla is present, connected by a narrow thin membrane, but a well sclerotized dorsal edge is tube-like with an hook-like appendice and is not connected to the membrane;
- (93) valva becomes suddenly narrow (decreasing by two-thirds of its width) at half of its length towards tip;
- (95) valva rectangular, 1.5 x taller than its width;
- (98) valvae thinly membranous, basally not connected, with a tiny thorn-like appendice on the ventral side distally;
- (104) valvae not separated, connected ventrally by a narrow band that is only thinly membranous (homoplasy);
- (106) an oval-shaped projection is present ventral distally that looks like a piece of fur with short setae on a straight surface;
- (107) an oval, large tail-like projection (it has 30% the size of the saccus) is present ventral distally and looks like a piece of fur with short setae;
- (108) a well sclerotized valva with an outer edge (including costal margin and distal margin) that is strongly arc-shaped;
- (111) A broadly rectangular, thinly-membranous valva has a narrow strongly sclerotized band along the whole basal width and a distal margin that is C-shaped;
- (113) valva rectangular, 1.5 x broader than tall, only thinly membranous;
- (121) valva connected ventrally by a very broad band (as broad as half of width of valva) that is thin and sclerotized;
- (123) soft, thinly membranous valva without any structures but few tiny setae, all edges are softer and with no setae, the whole valva breaks easily during preparation;
- (128) two large, triangular-shaped appendices on ventral part of valva, that are basally connected cover ca. 80% of the surface of one valva (homoplasy);
- (129) two large, hollow, rectangular-shaped appendices on ventral part of valva, that are basally connected, are as large as ca. 30–40% of the soft outer surface of one valva;
- (130) two large, hollow, triangular-shaped appendices on ventral part of valva, that are basally connected, are as large as ca. 35% of the soft outer surface of one valva;
- (136) the large, oval-shaped valva has many very long setae, soft or sclerotized, on the inner surface at least near costa;
- (137) the valva has the shape of number 95 (valva rectangular, 1.5 x taller than its width) and has a small sclerotized appendice that looks like a lunule ventral distally;
- (147) the whole male genitalia has a shape like a penguin in lateral view;

- (148) A very large and elongated (35% the size of valva) thorn-like semi-transtilla (with an acuminate end) originates from a skin-like, weakly sclerotized costal margin of valva;
- (149) large, ear-shaped valva with many soft and very long straight setae (not bent) on inner surface of valva and one patch of strongly sclerotized long straight setae near the base where usually a small relict of semi-transtilla occurs but the latter is entirely absent;
- (150) Two large hollow appendices, the upper one is narrow rectangular with a flat tip, the lower one is triangular with a rounded tip, on ventral part of valva, both appendices are basally connected, and as large as *ca.* 30% of the soft outer surface of one valva.
- (152) large, ear-shaped valva with many very long straight setae on almost whole inner surface of valva but without one patch of strongly sclerotized long setae near the base of a small relict of semi-transtilla;
- (158) Transtilla is very broad (*ca.* 30% of width of valva);
- (169) Extension of sacculus is strongly sclerotized and looks like a boat at end distally;
- (170) Extension of sacculus is strongly sclerotized, looks simple and like half of a boat with a strongly reduced boat tip at end distally;
- (171) Extension of sacculus is strongly sclerotized and looks like a mountain top at end distally;
- (176) Thorn-like process of posterior margin sclerotized, hollow, bent upwards and represents an extension of the sacculus;
- (184) very long, strongly sclerotized and bent setae on almost the whole inner side of valva and densest near the base of a small relict of semi-transtilla;
- (188) Egg-shaped small valva with a rounded tip;
- (200) A unique shape of valvae in ventral view: The whole valvae are vertical elongated with a large and elongated (25% the size of valva) semi-transtilla (with a squarish end) that has a very broad base (50% of costal margin) and that originates from a skin-like, weakly sclerotized, almost vertical costal margin; the distal margin is almost C-shaped;
- (210) Thorn-like costa with large hollow semi-transtilla with very broad base (homoplasy);
- (203) A large, broad, more or less V-shaped, thinly sclerotized simple plate (relict of a transtilla?) occurs above the juxta, sometimes extending in between upper basal parts of valvae;
- (204) Two long, sclerotized, narrow sinuate processes originate from the same point, a third long narrow sinuate process is close to, and all three processes are attached with a narrow band to the upper part of valva as well as somehow to the vinculum;
- (209) Valva strongly rectangular and twice as broad as tall.

- Aedeagus (Male)
  - (77) Extremely large aedeagus (as large as tegumen+vinculum), strongly S-shaped, covered with tiny setae distally (homoplasy);
  - (81) Extremely large aedeagus (larger as tegumen+vinculum) covered with tiny setae at centre and distally (homoplasy);
  - (189) Very long and narrow aedeagus, at least 2.5 x as long as width of valva, only slightly S-shaped;
  - (207) Extremely short (less than length of juxta) and broad aedeagus (only 2-5 x longer than broad) with a well developed and strongly sclerotized thorn-like appendice distally (thorn less than 1/3 of valva length in lateral view).
  
- Juxta (Male)
  - (186) Very large, pot-shaped juxta, almost as broad as width of a broad V-shaped uncus;
  - (199) Juxta comprises mainly two long thorns originating from a common broader base.
  
- Segment 8 and papillae anales (Female)
  - (46) Segment 8 with narrow gap-like shape dorsally, extending to 50% of its dorsal length;
  - (52) Long setae occur in groups of two or three on segment 8;
  - (53) Below segment 8 occur two large and strongly sclerotized oval or rounded plates that are connected by a narrow short band ventrally;
  - (143) segment 8 very large (4-5 times as large as papillae anales), strongly sclerotized, extending broadly above anterior apophysis and covering half of it dorsally;
  - (144) Segment 8 strongly reduced and linked to number 153;
  - (153) Segment 8 comprises only narrow band-like structures;
  - (181) Very large, two pear-shaped papillae anales in horizontal position.
  
- Ductus bursae and corpus bursae (Female)
  - (34) The whole ductus bursae is sclerotized and short (homoplasy);
  - (35) Only ductus bursae extremely short and reduced (homoplasy);
  - (96) The base of a long ductus bursae is sclerotized;
  - (138) Corpus bursae very small and pyriform;
  - (139) Corpus bursae small and 60% sclerotized;

- (140) The base of ductus bursae strongly sclerotized;
  - (141) Both, ductus bursae and corpus bursae strongly reduced and small;
  - (164) Corpus bursae not sclerotized, small, only one-third the size of segment 8.
- Anterior apophyses and posterior apophyses (Female)
- (32) Posterior apophyses extend as crescent-shaped flap onto the papillae anales;
  - (33) Extremely long (at least 3 x as long as width of segment 8) and extremely narrow anterior apophyses with a very small broad base;
  - (61) Anterior apophyses very narrow and rudimentary;
  - (62) Posterior apophyses very broad and large, at least 60% larger than anterior apophyses (homoplasy);
  - (142) Anterior apophysis in broader base with one oval-shaped, elongated, large hole;
  - (145) Anterior apophysis looks at base like a huge sail that is connected by a thin membrane dorsally;
  - (167) Posterior apophyses at base V-shaped, but “V” strongly unequal in length and with thorn-like end, somehow fork-like;
  - (168) Anterior apophyses narrow and short, length less than width of segment 8 (including the ventral plate), near base very broad with a small rounded hole at centre;
  - (174 and 194) Anterior apophyses extremely S-shaped.

## **12b. APPENDIX 12.2**

### **❖ CURRICULUM VITAE**

#### **Ingo Lehmann**

##### **EDUCATIONS**

- Birth in Finsterwalde/Niederlausitz (East Germany/GDR), **1964**
- Elementary and middle school education in Finsterwalde, **1971–1982**
- Political imprisonment for four years by GDR Government, **1982–1984**
- Redeemed from prison after 19 months by FRG Government, **March, 1984**
- High school education in Arnsberg (West Germany/FRG), **1984–1986**
- Study of Forestry in Göttingen (Lower Saxony), **1986–1990**
- Diploma thesis in Turkana, Embu and Kitui districts, Kenya, **August–October, 1989**
- Graduation in Göttingen, **1990**
- Internship at Forestry Department in Bielefeld (Westfalia), **1990–1991**
- Department of Nature Conservation in the Ministry of Environment of Mecklenburg-Western Pommerania, Schwerin, **since June, 1991**
- Research in five coastal forests of southern Kenya, Ukunda, supported by the Coastal Forest Conservation Unit (CFCU), **January, 1994–June, 2008**
- Head of the Society for the Protection of Avenues in Germany (ASG), Berlin, **2001–2009**
- PhD candidate in ZFMK/Bonn university, including fieldwork in four montane forests/shrublands of central Kenya supported by the National Museums of Kenya, (NMK), Nairobi, **April, 2009– June, 2019**

❖ **FIELDWORK IN KENYA FOR PhD STUDIES BASED ON RESEARCH PERMITS (2015 –2018)**

- Research for two weeks on marked study sites in Ololua Forest (Nairobi) on plant species dominance, forest structure and Lepidoptera (Metarbelidae), **March, 2015**
- Research for five weeks on marked study sites on Lolldaiga Hills Ranch and Wildlife Conservancy; Mpala Research Center (Laikipia) and near Nakuru on plant species dominance, forest structure and Lepidoptera (Metarbelidae), **February–March, 2016**
- Research for five weeks on marked study sites on Lolldaiga Hills Ranch and Wildlife Conservancy; Ololua Forest (Nairobi); Mpala Research Center (Laikipia) and Karura Forest (Nairobi) on plant species dominance, forest structure and Lepidoptera (Metarbelidae), **May–June, 2017**
- Research for three weeks on Lolldaiga Hills Ranch and Wildlife Conservancy on the author’s marked study sites, **January–February, 2018**

❖ **RESEARCH VISITS TO NATURAL HISTORY MUSEUMS (2009 –2016)**

- Zoological State Collection Munich, Germany, **June, 2009**
- The Natural History Museum, Paris, France, **July, 2009**
- Museum Witt, Munich, Germany, **September, 2009**
- Zoological Research Museum Alexander Koenig, Bonn, **September, 2009**
- Royal Museum for Central Africa, Tervuren, Belgium, **October, 2010**
- Zoological State Collection Munich, **March, 2014**
- National Museums of Kenya, Nairobi, Kenya, **March, 2015**
- State Museum of Natural History Stuttgart, Germany, **July, 2016**

❖ **DESCRIBED AND PUBLISHED NEW GENERA AND NEW SPECIES  
FROM THE AFROTROPICAL REGION (2010 –2014)**

06/2010

✚ *Kroonia* Lehmann, 2010, **new genus** from the Afrotropical Region

- *K. murphyi* Lehmann, 2010, **new species** from Malawi, Tanzania
- *K. adamauensis* Lehmann, 2010, **new species** from Cameroon
- *K. carteri* Lehmann, 2010, **new species** from Sénégal
- *K. politzari* Lehmann, 2010, **new species**, Democratic Republic of the Congo
- *K. dallastai* Lehmann, 2010, **new species** from Kenya
- *K. heikeae* Lehmann, 2010, **new species** from Namibia
- *K. honeyi* Lehmann, 2010, **new species** from Namibia

08/2010

✚ Revision of the genus *Arbelodes* Karsch, 1896, from the Karoo-Namib regional centre of endemism, Cape regional centre of endemism, Kalahari-Highveld regional transition zone, Afromontane archipelago-like regional centre of endemism, Zambezian regional centre of endemism and Tongaland-Pondoland regional mosaic

- *Arbelodes deprinsi* Lehmann, 2010, **new species** from the Rep. of South Africa
- *Arbelodes prochesi* Lehmann, 2010, **new species** from Zambia
- *Arbelodes sebelensis* Lehmann, 2010, **new species** from Botswana
- *Arbelodes claudiae* Lehmann, 2010, **new species** from Malawi, Zambia
- *Arbelodes mondeensis* Lehmann, 2010, **new species** from Rep. of South Africa
- *Arbelodes haberlandorum* Lehmann, 2010, **new species** Rep. of South Africa
- *Arbelodes shimonii* Lehmann, 2010, **new species** from the Rep. of South Africa
- *Arbelodes dicksoni* Lehmann, 2010, **new species** from the Rep. of South Africa
- *Arbelodes franziskae* Lehmann, 2010, **new species** from the Rep. of South Africa
- *Arbelodes agassizi* Lehmann, 2010, **new species** from the Rep. of South Africa
- *Arbelodes kruegeri* Lehmann, 2010, **new species** from the Rep. of South Africa
- *Arbelodes varii* Lehmann, 2010, **new species** from the Rep. of South Africa
- *Arbelodes dupreezi* Lehmann, 2010, **new species** from Namibia

11/2011

✚ *Haberlandia* Lehmann, 2011, **new genus** from the Guineo-Congolian regional centre of endemism, Lake Victoria regional mosaic, Guinea-Congolia/Zambezia regional transition zone

- *H. odzalaensis* Lehmann, 2011, **new species** from the Rep. of the Congo, and Central African Republic
- *H. lindacammae* Lehmann, 2011, **new species** from Gabon
- *H. legraini* Lehmann, 2011, **new species** from the Rep. of the Congo
- *H. shimonii* Lehmann, 2011, **new species** from Gabon
- *H. annetteae* Lehmann, 2011, **new species** from Central African Rep.
- *H. hilaryae* Lehmann, 2011, **new species** from Cameroon
- *H. lusamboensis* Lehmann, 2011, **new species**, Democr. Rep. of the Congo
- *H. entebbeensis* Lehmann, 2011, **new species** from Uganda
- *H. isakaensis* Lehmann, 2011, **new species**, Democr. Rep. of the Congo
- *H. rudolphi* Lehmann, 2011, **new species**, Democr. Rep. of the Congo
- *H. isiroensis* Lehmann, 2011, **new species**, Democr. Rep. of the Congo
- *H. ueleensis* Lehmann, 2011, **new species**, Democr. Rep. of the Congo
- *H. clenchi* Lehmann, 2011, **new species**, Democr. Rep. of the Congo
- *H. josephi* Lehmann, 2011, **new species**, Democr. Rep. of the Congo
- *H. ofriedi* Lehmann, 2011, **new species** from Ghana
- *H. rohdei* Lehmann, 2011, **new species** from Ghana
- *H. togoensis* Lehmann, 2011, **new species** from Togo
- *H. hollowayi* Lehmann, 2011, **new species** from the Ivory Coast
- *H. janzi* Lehmann, 2011, **new species** from the Ivory Coast
- *H. tempeli* Lehmann, 2011, **new species** from the Ivory Coast
- *H. taiensis* Lehmann, 2011, **new species** from the Ivory Coast
- *H. rabiusi* Lehmann, 2011, **new species** from Sierra Leone
- *H. hulstaerti* Lehmann, 2011, **new species**, Democr. Rep. of the Congo

12/2012

✚ *Bjoernstadia* Lehmann, 2012, **new genus** from the Albertine Rift

- *B. kasuluensis* Lehmann, 2012, **new species** from Tanzania

03/2013

✚ *Mountelgonia* Lehmann, 2013, **new genus** from the Afromontane archipelago-like regional centre of endemism in Kenya, Tanzania, Uganda, Rwanda, Burundi, Zambia

- *M. percivali* Lehmann, 2013, **new species** from Kenya, Uganda
- *M. lumbuaensis* Lehmann, 2013, **new species** from Kenya
- *M. abercornensis* Lehmann, 2013, **new species** from Zambia
- *M. thikaensis* Lehmann, 2013, **new species** from Kenya
- *M. urundiensis* Lehmann, 2013, **new species** from Burundi

03/2013

✚ *Moyencharia* Lehmann, 2013, **new genus** from the Guineo-Congolian regional centre of endemism, Guinea-Congolia/Sudania regional transition zone, Sudanian regional centre of endemism

- *M. mineti* Lehmann, 2013, **new species** from Chad
- *M. joeli* Lehmann, 2013, **new species** from Nigeria
- *M. winteri* Lehmann, 2013, **new species** from the Republic of South Sudan, Democr. Rep. of the Congo
- *M. herhausi* Lehmann, 2013, **new species** from Burkina Faso
- *M. sommerlattei* Lehmann, 2013, **new species** from Guinea

05/2013

✚ *Shimonia* Lehmann & Rajaei, 2013, **new genus** from the Afromontane archipelago-like regional centre of endemism in Kenya, Uganda; the Congo Basin of Congolia and the Guinea-Congolia/Zambezia regional transition zone

- *S. timberlakei* Lehmann & Rajaei, 2013, **new species**, Democr. Rep. of the Congo
- *S. fischeri* Lehmann & Rajaei, 2013, **new species**, Democr. Rep. of the Congo
- *S. oyiekeae* Lehmann & Rajaei, 2013, **new species**, Democr. Rep. of the Congo

**12/2014**

✚ *Dianfosseya* Lehmann, 2014, **new genus** from Congolia

- *D. leakeyi* Lehmann, 2014, **new species**, Democr. Rep. of the Congo

**12/2014**

✚ *Janegoodallia* Lehmann, 2014, **new genus** from Congolia

- *J. davenporti* Lehmann, 2014, **new species**, Democr. Rep. of the Congo

❖ **PEER-REVIEWED INTERNATIONAL PUBLICATIONS (2012 –2014)**

- Lehmann, I. (2012) Description of a new genus and species of Metarbelidae (Lepidoptera, Cossioidea) from the Albertine Rift region of Tanzania, East Africa. *Norwegian Journal of Entomology*, 59, 234–240.
- Lehmann, I. (2014) Description of two new genera and two new species of Metarbelidae (Lepidoptera, Cossioidea) from the Northeastern Congolian Lowland Forests Ecoregion (Central Africa). *Zootaxa*, 3895 (4), 570–580.  
<http://dx.doi.org/10.11646/zootaxa.3895.4.6>
- Lehmann, I. & Rajaei, H. (2013) Description of a new genus and three new species of Metarbelidae (Lepidoptera: Cossioidea) from East and Central Africa, with notes on biogeography. *Bonn zoological Bulletin*, 62 (1), 100–110.

❖ **OTHER PUBLICATIONS FOR THE PhD THESIS (2010 –2018 )**

- Lehmann, I. (2010a) A new genus of Metarbelidae (Lepidoptera: Cossioidea) from the Afrotropical Region with the description of seven new species. *Esperiana Memoir*, 5, 294–321 + pl. 21.
- Lehmann, I. (2010b) *A revision of the genus Arbelodes Karsch (Lepidoptera: Cossioidea: Metarbelidae) from southeast-central and southern Africa with the description of thirteen new species*. Published by the author, Hamburg & Wismar, 3–81+ 8 b/w pls., 5 colour pls.  
[Available from <http://www.biodiversitylibrary.org/bibliography/79419>], accessed August, 2018.
- Lehmann, I. (2011) *The description of a new genus and twenty-three new species of Metarbelidae (Lepidoptera: Cossioidea) from the lowland tropical rain forests of the Guineo-Congolian Region with notes on habitats and biogeography*. Published by the author, Hamburg, 1–67 + 10 b/w pls., 6 colour pls., 1 coloured map.  
[Available from <http://www.biodiversitylibrary.org/bibliography/79417>], accessed August, 2018.
- Lehmann, I. (2013) *Description of two new genera and ten new species of Metarbelidae (Lepidoptera: Cossioidea) from western, north-central and eastern Africa with notes on habitats and biogeography*. Published by the author, Hamburg, 3–81+ 10 b/w pls., 5 colour pls., 2 coloured maps.  
[Available from <http://www.biodiversitylibrary.org/bibliography/79421>], accessed August, 2018.
- Lehmann, I., Roberts, M., Mathiu, J.M. & Butynski, T.M. (2018) Undescribed species and genera of Metarbelidae moths (Lepidoptera, Cossioidea) from Lolldaiga Hills Ranch, central Kenya. *Newsletter Lolldaiga Hills Research Programme*, January–February 2018, 3–4. [Available from <http://www.lolldaiga.com>], accessed March, 2018.