Evolution and recent speciation in two disparate endemic South African insect genera: *Macroderes* (Coleoptera: Scarabaeidae) and *Nemopterella* (Neuroptera: Nemopteridae)

By

Ishtiag Hassan Abdalla Mohammed

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Dedication

To *the soul of my father, Hassan Abdalla,*

To *my mother, Safia Al Salahaby,*

To *my brothers and sisters*

To *all friends*

Evolution and recent speciation in two disparate endemic South African insect genera: *Macroderes* (Coleoptera: Scarabaeidae) and *Nemopterella* (Neuroptera: Nemopteridae).

Student: Ishtiag Hassan Abdalla Mohammed
Supervisors: Prof. Catherine L. Sole, Prof. Clarke H. Scholtz and Prof. Mervyn W. Mansell
Department: Zoology and Entomology,
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Abstract

Phylogenetic, taxonomic and biogeographic analyses were conducted to investigate the role of the paleoclimatic and geological oscillations on the diversification and evolutionary history of two disparate southern African insect genera: the dung beetle genus *Macroderes* Westwood, 1842 and the lacewing genus *Afroptera* Abdalla & Mansell, 2019.

The taxonomic revision of *Macroderes* resulted in the description of seven new species: *M. cederbergensis* Abdalla & Deschodt, 2018, *M. tortuosus* Abdalla & Scholtz, 2018, *M. gifboomi* Abdalla & Scholtz, 2018, *M. leipoldti* Abdalla & Deschodt, 2018, *M. oreatus* Abdalla & Deschodt, 2018, *M. porselinus* Abdalla, 2018 and *M. soleiana* Abdalla & Deschodt, 2018. One species, *Macroderes nitidus* Harold, 1877 is redescribed and its lectotype designated. The diagnostic characters as well as an updated geographic distribution of each species are considered. An identification key to the species in the genus, photographs of habitus, internal sac sclerite, pronotum, pronotal punctures and elytra are also provided.

The phylogenetic analyses, based on concatenated molecular and combined concatenated molecular and morphological datasets, suggest *Macroderes* as a monophyletic group within the Scarabaeinae with strong statistical support. Molecular dating estimation suggests that the genus emerged approximately 38.9 Mya. Rapid recent speciation occurred during the late Miocene and throughout the Plio-Pleistocene eras (5.0-0.1 Mya), which is ascribed to the effects of the

paleoclimatic and geological oscillations during the late Mio-Pliocene and the recurrent warming and cooling of the Pleistocene.

Taxonomic revisions of the genera *Nemopterella* Banks, 1910 and *Nemia* Navás, 1915 resulted in the split of *Nemopterella* into three: *Nemopterella sensu stricto* with type species *Nemopteryx africana* Leach, 1815 (= *Nemopterella africana*), *Afroptera* Abdalla & Mansell, 2019 with type species *Nemopterella munroi* Tjeder, 1967, and the monotypic genus *Siccanda* Abdalla & Mansell, 2019, with type species *Nemopterella arenaria* Tjeder, 1967. Eight new species are described in the genus *Afroptera* these are: *A. acuta* Abdalla & Mansell, 2019, *A. alba* Mansell & Abdalla, 2019, *A. brinkmani* Abdalla & Mansell, 2019, *A. balli* Abdalla & Mansell, 2019, *A. cylindrata* Abdalla & Mansell, 2019, *A. folia* Abdalla & Mansell, 2019, *A. koranna* Mansell & Abdalla, 2019 and *A. maraisi* Abdalla & Mansell, 2019. In addition, two new species are added to *Nemopterella*: *N. kabas* Mansell & Abdalla, 2019 and *N. cedrus* Mansell & Abdalla, 2019. *Nemia* remained unaffected by these changes.

The phylogenetic analyses based on concatenated molecular and combined concatenated molecular and morphological datasets *Afroptera* resulted in well-supported phylogeny and two major clades were identified. The Divergence time estimates suggest that *Afroptera* originated in the early Eocene (53.9 Mya) but commenced diversification in the late Eocene 36.5 Mya. Most descendant species underwent rapid recent speciation during the late Mio-Pliocene and through the Pleistocene 4.6-0.2 Mya.

Biogeographic analyses of *Macroderes* and *Afroptera* indicate that the genera have different spatiotemporal origins. The most common ancestor of *Macroderes* originated in the Cape Floristic Region or the Namaqualand-Namib Domain and the Cape Floristic Region (CFR) during the late Eocene 38.9 Mya and evolved in the Namaqualand-Namib Domain and CFR in the late mid-Miocene 14.5 Mya. By contrast, the most common ancestor of *Afroptera* is shown to have originated earlier, during the Early Eocene (53.9 Mya) in the Namaqualand-Namib Domain, the Cape Floristic Region and Namib Desert Eco-region and evolved in the Namaqualand-Namib Domain and Namib Desert Eco-region during late Eocene 36.5 Mya. Dispersal was found to be the most prominent ecological mechanism that led to the present-day distribution of extant species. The late Mio-Pliocene witnessed synchronised dispersal and

vicariant events for both genera resulting in synchronised lineage splitting in many of their populations; indicating that the genera experienced the same paleoclimatic and geological processes driving speciation. The extant species of both genera appear to have evolved during the Pleistocene.

Key words: *Macroderes, Afroptera*, phylogeny, taxonomy, historical biogeography, South Africa, Greater Cape Floristic Region (GCFR), Succulent Karoo Biome, Fynbos Biome

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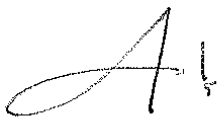
Declaration

I, **Ishtiag Hassan Abdalla Mohammed**, declare that the thesis, which I hereby submit for the degree of Doctor of Philosophy in Entomology at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Ishtiag Hassan Abdalla Mohammed



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CHAPTER I

General Introduction

Paleoclimatic and geological changes promote species diversification

The climatic variability of the Cenozoic era (66 Mya to the present) is believed to have had significant implications for speciation, migration, and extinction of species (Ruddiman 2014). Climatic oscillations of the Palaeogene (66–23 Mya) and Neogene periods (23–2.6 Mya), the repeated cycles of glaciations of the Quaternary period, and the climate fluctuations of the Holocene epoch, are believed to be associated with dramatic global and regional species turnover (Ruddiman 2014). Globally, it is believed that the alternating warming and cooling periods of the Palaeogene and Neogene indirectly affected the dispersal of mammalian lineages between continents through their effects on the climate of the inter-continental pathways (Ruddiman 2014). The Palaeogene's warm climate is said to have facilitated the dispersal of mammalian lineages from Asia to North America, using the northern corridor, which resulted in dramatic faunal turnover (Bowen *et al*. 2002). At the regional level, climatic fluctuations have been shown to have a strong impact on species' ranges, as clearly shown in the shrinking of African palm ranges during the drying periods of the Oligocene (Pan *et al.* 2006). The alternating glacial cycles of the Pleistocene also had strong impacts on species diversity (Huntley & Webb 1989). It is thought that the cooling and warming periods of that epoch caused major shifts in species' ranges, forcing them to contract into refugia, which may have resulted in fragmented populations, triggering species diversification (Carnaval *et al*. 2009; Hewitt 2000). Several studies have pointed to climatic instability during the Palaeogene and Neogene periods, and its role in the extinction of many species (*Sauer* 1988; Lewis *et al*. 2008; Crisp & Cook 2011).

Similarly, geological changes such as plate tectonics, continents splitting, and the formation of mountains, islands, and water bodies may be among factors that enhance species diversification (Coyne & Orr 2004). These factors may lead to topographical changes that result in the splitting of particular groups of species into isolated sub-groups, which undergo many genetic changes because of new conditions (Coyne & Orr 2004). The re-linking of landmasses that resulted from continental collisions may also encourage the emergence of new lineages through species

colonisation and extinction (Bossuyt & Milinkovitch 2001; Gillepsie & Roderick 2014). Many of today's distinct lineages are thought have arisen as a result of the continents' moving over time, eventually leading to isolated populations and many migratory waves (Holt *et al*. 2013). One of the most famous events that led to such speciation is the northward drift of the Indian plate towards the Eurasian plate (90 Mya). The massive dispersal waves of vertebrates towards the Asian continent led to the emergence of new lineages (Bossuyt & Milinkovitch 2001; Gillepsie & Roderick 2014). Plate tectonics may also indirectly promote species diversity through their effects on climate stability (Leprieur *et al.* 2016). The movement of landmasses due to plate tectonics (*e.g*., the African continent's northwards drift to latitudes 12° and 7° respectively) led to latitude shift and accordingly to climate instability, which ultimately led to species diversity (Sandel *et al.* 2011; Pellissier *et al.* 2014).

The Greater Cape Floristic Region (GCFR) as a centre of species diversification

The Greater Cape Floristic Region (GCFR) of south-western Africa comprises the Cape Floristic Region (CFR) and the Succulent Karoo, both of which are among some of the richest biodiversity hotspots in the world (Myers 1990; Born *et al.* 2007). The CFR is the essential heart of the GRCF owing to the unique composition of flora that distinguishes it from adjacent areas – apart from the Succulent Karoo, which shares many of the CFR's floral features despite the notable climatic and edaphic variations. The area extends in an 'L' shape, covering the winter rainfall area in the west and the non-seasonal rainfall area in the far south and southeast (Snijman 2013).

The extraordinary diversity of the GCFR flora has attracted the world's attention since the 17th century, with the first publications on rudimentary Cape flora by Thunberg (1794, 1813) followed by many studies in the 19th century by William Burchell, Carl Zeyher, Christian Ecklon, and Johann Dreg (Gunn & Codd 1981). Only a few studies tried to explain this unique diversity (Bolus 1886; Marloth 1929). Nevertheless, most of the creditable research that attempted to explain the high speciation rate in the Cape began shortly before the mid-nineteenth century, and has continued until now, but with different hypothesised explanations (Ellis & Verboom 2014). Huxley (1940) identified the role of gene flow cessation in species diversity, while other authors attributed the high diversity in the Cape to the impact of climate changes that resulted from the establishment of the cold Benguela current and the inception of the winter-

rainfall regime. This was coupled with the regression of the sea that led to the spread of aridity, resulting in major habitat shifts and resultant species diversity (Levyns 1954; Adamson 1958; Rouke 1972; Strid 1972; Bremer 1976; Goldblatt 1978; Linder 1985). In addition, this body of research built a better understanding of the association between the diversity of plant distribution across the Cape region and the effects of climate variability, with spatial isolation that resulted from edaphic and topographic heterogeneity (Ellis & Verboom 2014). Goldblatt (1978) concluded that the high species diversity in the Cape is a product of allopatric speciation resulting from excessive habitat shifts, due to climatic oscillations and topographic diversity. Several other factors have been suggested to be among the main driving forces of the diversification in the Cape area. Linder (1985) referred to the role of the distance of dispersal between populations. He argued that, although the distances are short, they might constitute a barrier separating populations, thereby halting gene flow and promoting allopatric speciation. Johnson (1992a, 1996, and 2010) claimed that the high floral diversity in the Cape resulted from divergent selection enforced by different pollinators. Cowling (1987) pointed to the significant impact of fire on the extinction and isolation of species, which might impede the flow of genes between populations and lead ultimately to allopatric speciation.

Historical biogeography

Historical biogeography seeks to correlate the evolutionary history of taxa with historical biogeographic events such as climate change, sea level fluctuations, erosion and weathering, recurrent volcanoes, earthquakes, tidal waves, and changes in atmospheric and soil chemistry. The earlier approach to the science considered dispersal as the only mechanism that could enhance the distribution of living organisms. However, it has recently become clear that plate tectonics, the rearrangement of continental land masses, and the opening and closing of oceans and seas have also had a significant role in shaping current distributions and the evolutionary history of living organisms (Posadas *et al.* 2006; Mantooth & Riddle 2011).

Evolutionary studies have contributed greatly to the field of historical biogeography through the inclusion of morphological and molecular information into phylogenetic analyses: the phylogenetic hypothesis (the cladogram), ancestral areas, dispersal-vicariance analysis, and reconciled trees (Posadas *et al.* 2006). One of the most important applications of molecular-based phylogenies is that of molecular clocks. By identifying the time of origin and the

divergence processes of a certain taxon, one can reject or accept the hypothesis of the driving factors leading to these processes (Posadas *et al.* 2006).

Historical biogeography can be categorized into many disciplines, including the following:

1 – Centre of origin and dispersal. This discipline assumes that all species originated in the same place and that, by chance, some individuals dispersed and evolved because of natural selection. This approach also assumes that dispersal and extension are the main drivers of the distribution of taxa (Matthew 1915).

2 – **Phylogenetic biogeography.** This discipline concerns the study of the history of monophyletic groups in time and space and is similar to the centre of origin and dispersal as it considers that dispersal and extension are the two main driving forces promoting the distribution of taxa. The approach is based on the formalisation of the phylogenetic assumptions for a given group to infer its biogeographic distribution (Hennig 1966; Brundin 1966).

3 – Ancestral areas. This discipline implicitly accepts the ideas of the centre of origin and phylogenetic biogeography approaches, and that dispersal and extension are engines of evolution. The ancestral area can be determined by the setup hypothesis of the historical distribution of certain taxa, and uses the topological information given by a cladogram (Bremer 1992).

4 – Panbiogeography. The aim of this approach is to identify the ancestral biotas and their histories. The approach therefore assumes dispersal, extension, and vicariance as the main drivers of the distribution of taxa (Croizat 1952, 1958, 1964).

5 – Cladistics biogeography. This discipline attempts to determine the history of areas by overlaying the distributional and phylogenetic data of taxa. The comparison of different areas in cladograms for different taxa will reflect the general patterns of the distribution of taxa that may be produced as result of allopatric speciation caused by vicariant events (Rosen 1978).

6 – Parsimony analysis of endemicity (PAE). This discipline aims to answer questions about the histories of the areas and localities of endemism (Rosen 1988).

7 – Event-based methods. The main concern of this discipline is to identify the historical distribution of particular taxa. Each biogeographic event (dispersal, extension, and vicariance) will consequently be modeled; the biogeographic distribution of certain taxa can be determined through phylogenetic information given from the application of the appropriate model (Ronquist 1997).

8 – Phylogeography. This discipline focuses on identifying the driving factors that have led to the geographical distribution of genealogical lineages. The approach adopts the use of animal mitochondrial DNA (mtDNA) and plant chloroplast DNA (cp DNA), and assumes the possibility of dispersal, extension, and vicariance (Avise *et al.* 1987).

9 – Experimental biogeography. This discipline answers questions about the histories of the regions, and includes dispersal, extension, and vicariance as factors that govern the geographic distribution of taxa (Haydon *et al.* 1994).

Molecular and morphological data as tools to infer evolutionary relationships

Determination of the taxonomic status of a taxon is based on the formulation of evolutionary hypotheses that can be derived directly from morphology as well as molecular data. The phylogenetic approach, based on biomolecules, has widely exploited changes in the composition of cellular molecules (DNA, RNA, and protein sequences) to infer the phylogenetic relationship between organisms (Patwardhan *et al.* 2014). These genetic differences between homologous sequences indicate genetic divergence due to molecular evolution over time (Patwardhan *et al.* 2014). At present, molecular sequences are considered the ideal tool to infer evolutionary relationships between taxa owing to their many advantages. On the one hand, molecular data are more abundant than fossil data, and can be obtained easily and quickly with high reliability. On the other hand, a huge amount of information is provided by genetic material because of the presence of several millions of base pairs in four different states, as well as the amino acids for proteins (Powell 1991). As the DNA is phylogenetically continuous and is present in all eukaryotic cells, it is easy to build evolutionary relationships, even for distantly related species.

The importance of morphological data in evolutionary studies has been discussed by many authors. Rokas *et al*. (2003) and Scotland *et al*. (2003) argued that this is the age of comparative genomics, and stressed the exclusion of morphological data in phylogenetic reconstruction. Taking a different view, Wiens (2004) refuted their claims and stressed the need for morphology in inferring phylogenetic relationships between organisms. Many taxa, including reptiles and amphibians, are represented by limited preserved specimens, many of which are stored in formalin (fixation) and are not easily collected because of their limited numbers and habitat distribution (Wiens 2004). In addition, many species of insects and plants are still only known from a single specimen collected decades ago (Wilson 1992; Donoghue & Alverson 2000).

Molecular phylogenies are often reconstructed with errors caused by many factors, such as long-branch attraction (Felsenstein 1978; Huelsenbeck & Crandall 1997), deviations between gene and species trees (Doyle 1992; Maddison 1997), and the routine problems of contamination and misidentification of specimens. However, the most undeniable advantage of morphological data is that it allows us to infer the phylogenetic relationship between fossils and living organisms (Wiens 2004). It is therefore important to have an accurate morphology-based phylogeny as a realistic examination of molecular outcomes (Doyle 1992; Hillis & Wiens 2000; Jenner2004). Both approaches are important, since the biological molecular structure of all organisms is similar, and the morphology of an organism is in fact the manifestation of its genomic, proteome, and transcriptome profiles. The combination of these two approaches can greatly support the determination of the evolutionary relationships between living organisms (Patwardhan *et al*. 2014).

Macroderes Westwood, 1842

The flightless dung beetle genus *Macroderes* Westwood (Scarabaeidae: Scarabaeinae, tribe *incertae sedis*), with 28 described species and three species that are still uncertain, remains controversial (Abdalla *et al.* 2018). Members of the genus are characterised by a small to medium, convex, bulky, black body (Frolov & Scholtz 2005). Geographical distribution of the genus is restricted to South Africa, especially in areas where winter and bimodal rainfall are prevalent in the south-western parts. The range of the species stretches between the Richtersveld in the north to Cape Agulhas in the south. Although Sharp (1880) reported the genus from the diamond fields of southern Namibia, there is only one species named from that area.

Systematics

Formerly, *Macroderes* was assigned to the tribe Dichotomiini based on the presence or absence of the transverse carina on the middle and hind tibiae, a characteristic that distinguishes the sister tribe Coprini from Dichotomiini (Frolov & Scholtz 2005). Dichotomiini lack this characteristic; however, the validity of Dichotomiini is no longer accepted by Montreuil (1998), who suggested transferring *Macroderes* to the sister tribe Coprini, and then synonymised Dichotomiini with Ateuchini as the valid tribe. Tarasov *et al.* (2016) reinstated the taxonomic position of the tribe within the subfamily Scarabaeinae. The study revealed a sister relationship between *Dichotomius* and *Ateuchus* (the type genus for the tribe Ateuchini (Laporte 1840), yet some of the Ateuchini

allies were morphologically different from *Dichotomius*, and thus the study suggested the splitting of Ateuchini into two tribes: Dichotomiini *sensu novo* with four genera, and Ateuchini with 20 genera. Nevertheless, the study was unable to assign the genus *Macroderes* to any of the Scarabaeinae tribes, and so left its taxonomic status unresolved (Tarasov *et al.* 2016).

Westwood (1842) described the genus *Macroderes* for the species *Onthophagus greeni* Kirby, followed by the work of Preudhomme de Bore (1880), who transferred *Scarabaeus bias* Oliver to *Macroderes* and added three new species. Another five new species were described by Harold (1877), Sharp (1880) and Kolbe (1908); and two new species were described by Péringuey (1901), who provided a key to five species. Frolov and Scholtz (2005) revised *Macroderes* and described six new species, *M. amplior*, *M. minutus*, *M. endroedyi*, *M. namakwanus*, *M. foveatus*, and *M. cornutus*. In addition, they designated the neotype of *M. bias* (Olivier) and established two new synonymies: *M. pilula* Sharp as a junior synonym of *M. bias* (Olivier), and *M. westwoodi* Preudhomme de Borre as a junior synonym of *M. undulatus* Preudhomme de Borre. They provided an identification key to the species in the genus, as well as notes on the biology and distribution of the species. The latest taxonomic revision (Abdalla *et al.* 2018) aimed to update the taxonomic status of the genus.

***Afroptera* Abdalla & Mansell, 2019**

The lacewing genus *Afroptera* Abdalla & Mansell, 2019 (Nemopteridae: Nemopterine) is a small to medium-sized genus of 28 species (Abdalla *et al*. 2019). The genus is basically endemic to South Africa, with some species' ranges extending into southern Namibia (Tjeder 1967; Abdalla *et al*. 2019), with a single species, *Afroptera alba* Mansell & Abdalla, 2019, recorded from Namibia (Abdalla *et al*. 2019). The genus is widely distributed in the Western and Northern Cape Provinces of South Africa (Tjeder 1967; Sole *et al*. 2013; Abdalla *et al*. 2019), where it is confined to the Succulent and Nama Karoo, Fynbos, Desert, and Savanna Biomes. The ranges are characterised by dry, sandy, or rocky habitats with low vegetation cover and rainfall (Tjeder 1967; Abdalla *et al*. 2019). Species in the genus are characterised by allopatric distributions with the majority of species recorded from single locality (Tjeder 1967; Abdalla *et al*. 2019).

The genus is recognised by the apical segment of the antenna that is completely or incompletely membranous (Abdalla *et al*. 2019). Species in the genus are very similar morphologically, to the

extent that it is difficult to distinguish the females from one another. Nevertheless, thorough examination of male specimens revealed many morphological characteristics that vary from one species to another and can be used to distinguish species. These include: size, colour, and pruniosity of the body, length of the antennae, shape of the last segment of the antennae, shape of the forewings, and the apical portion of the forewings; the colour of the thorax and abdomen setation, colour of the antennae, distance from the dark to the white areas of the hindwings, presence or absence of body stripes, a yellow hind margin of the vertex, and two rounded spots near the eye margin (Abdalla *et al*. 2019).

Systematics

The South African genus *Afroptera* was recently described following a taxonomic revision of the South African genera *Nemia* Navás, 1915 and *Nemopterella* Banks, 1910 by Abdalla *et al*. (2019). The systematics of *Nemopterella* has always been controversial, as the genus comprises a group of species with very complex characteristics. Navás (1910) first named the genus *Eretmoptera* with the type species *Nemopteryx africana* Leach, 1815. Banks (1910) changed the genus name to *Nemopterella* Banks, 1910 as the name *Eretmoptera* was preoccupied by *Eretmoptera* Kellogg, 1900 (Diptera). However, Navás observed that species in the genus have a different forewing venation, and consequently proposed the division of the genus into two genera: *Nemeva* with type species *Nemopteryx africana*, and *Nemia* with type species *Nemoptera costalis* Westwood, 1836. Tjeder (1967) rejected Navás' taxonomy, as it was based on characteristics that are widely found in Nemopteridae. Instead, he distinguished them by their abdomens, where the abdomen of *N. africana* bears a pair of pleuritocavae, while the abdomen of *N. costalis* lacked this organ. Tjeder consequently replaced the name *Nemeva* Navás with *Nemopterella*.

Historical biogeography of *Macroderes* and *Afroptera*

The biology and life histories of *Macroderes* and *Afroptera* are still largely unknown with the exception of field notes by Frolov & Scholtz (2005) and Mansell (Pers. Obs.) respectively. These notes show that the insects differ biologically and behaviourally. *Macroderes* is nocturnal and adapted to cool climates although some individuals may become active during rainy and cold winter days. Members in the genus inhabit areas with loamy, sandy soils rich in dense shrub vegetation associated with heuweltjies (ancient termite mounds) (Abdalla *et al*. 2018). The

feeding behaviour of the genus is not fully known, but laboratory feeding trials that used cattle and sheep dung demonstrated that *Macroderes* members dig vertical tunnels into the soil and spend the day there while the collection of the dung pellets starts at night. Species in the genus have been observed pulling the dung pellets back to their tunnels using their front legs. By contrast, species of *Afroptera* inhabit warm, low rainfall areas with high relative humidity. Members of the genus inhabit sandy and/or rocky habitats in addition to areas of rain shadow and poor vegetation cover or in bare soil between bushes. *Afroptera* species are mainly nocturnal and are attracted to light in large numbers. The adults only emerge at short specific times during summer, having spent the major part of their lives as larval carnivores. Larvae live freely in sandy soil, while the adults feed exclusively on pollen and nectar (Mansell & Ball Pers. Obs.).

The contemporary fragmented populations of *Macroderes* and *Afroptera* within the Northern and Western Cape provinces, particularly in the Succulent and Fynbos Biomes of South Africa, appear to have been influenced by paleoclimatic and geological oscillations of the late Cenozoic. The genera show overlapping, allopatric distribution within the region, indicating that the two genera have been similarly affected by common historical events and environmental factors. It was consequently hypothesised that if *Macroderes* and *Afroptera* were similarly affected by common historical events and environmental factors, they should exhibit similar biogeographic patterns and dates of lineage splitting. Plate tectonics, along with frequent sea-level fluctuations during the Miocene-Pliocene (5 Mya); glacial and interglacial cycles of the Pleistocene, would also have led to range shifts in the Cape area, leading to the fragmentation of species, geographically isolated populations and, consequently, to speciation within the two genera.

Relevance of the study

South Africa has two of the world's best known biodiversity hotspots: the Cape Floristic Region, and the Succulent Karoo with its expansion into Namibia. Biodiversity in these areas is at risk because of irresponsible human activities, including mining, improper agricultural practices and invasion of invasive plant species. Such factors may lead to the conversion and destruction of natural habitats, leading to extinction and the loss of biological diversity (Rouget *et al*. 2004; Khavhagali 2010). The genera *Macroderes* and *Afroptera* are characterised by wide, allopatric distributions in these regions, and the ranges of many species are vulnerable and under threat.

Currently, three species in *Macroderes*, *M. cornutus*, *M. endroedyi*, and *M. undulatus* are listed as threatened by the IUCN Red Data List (IUCN 2013). Implementing a successful and effective strategy for the conservation of the genera and their constituent species should be based on a thorough integrated knowledge of species classification, phylogenetics, geographical distribution and habitat preferences. Moreover, as the two insect genera, *Macroderes* and *Afroptera*, selected for this study, show overlapping patterns of distribution, understanding common evolutionary drivers acting on their populations will contribute greatly to our understanding of the evolutionary history of the Succulent and Fynbos biomes and other similar co-distributed taxa.

Objectives

The overall objective of this study was consequently, to investigate the influence of paleoclimatic and geological fluctuations on the comparative diversification and evolutionary history of the two disparate southern African genera, *Afroptera* Abdalla & Mansell, 2019 and *Macroderes* Westwood, 1842. This objective was attained by answering the following key questions in each chapter of this research thesis:

Chapter 2 – An update of the taxonomy of the genus *Macroderes* Westwood, 1842 (Coleoptera: Scarabaeidae: Scarabaeinae) with descriptions of new species from South Africa

***Key questions**:*

Q1.What is the updated taxonomic status of the genus *Macroderes*?

Q2.What is the current geographic distribution of the species in *Macroderes*?

Q3. Are there any undescribed species in the genus?

Chapter 3 – Phylogeny and divergence time of the southern African genus *Macroderes* Westwood, 1842 (Coleoptera: Scarabaeidae: Scarabaeinae)

***Key questions**:*

Q1. Does the genus *Macroderes* constitute a monophyletic group?

Q2. What are the phylogenetic relationships between the species of the genus?

Q3. What is the estimated divergence time of the genus?

Chapter 4 – Revision of the southern African genera *Nemopterella* Banks and *Nemia* Navás (Neuroptera: Nemopteridae: Nemopterinae), with descriptions of new genera and species

***Key questions**:*

Q1. What is the updated taxonomic status of *Nemopterella* Banks, 1910?

Q2. What is the updated taxonomic status *Nemia* Navás, 1915?

Q3.Are there any undescribed species in the two genera?

Q4. What is the updated distribution of the species in both genera?

Chapter 5 – Phylogeny and divergence time of the southern African lacewing genus *Afroptera* Abdalla & Mansell (Neuroptera: Nemopteridae: Nemopterinae)

***Key questions**:*

Q1. What are the phylogenetic relationships among the species of *Afroptera*?

Q2. What is the estimated divergence time of the genus?

Chapter 6 – Common trends in the historical biogeography and evolution of two southern African disparate insect, genera *Macroderes* (Scarabaeidae: Scarabaeinae) and *Afroptera* Abdalla & Mansell (Nemopteridae: Nemopterinae)

***Key questions**:*

Q1.What are the ancestral historical ranges of *Macroderes*?

Q2. What are the ancestral historical ranges of *Afroptera?*

Q3. What are the ecological mechanisms that are responsible for the diversification and current distribution of the species in both genera?

Q4. Do the historical drivers have a role in shaping the current overlapping geographical distribution of both genera?

Structure of the thesis

This thesis consists of seven chapters. Chapter 1 presents a general introduction, the objectives of the study, and the key questions for each chapter. Chapter 7 provides a brief synthesis of the results of all the chapters, and provides some suggestions for future work on these two groups of

insects. The other five research chapters comprise papers for publication, resulting in the unavoidable repetition of certain methodological aspects. The status of the publication of each research chapter is given below:

Chapter 2. **Abdalla, I.H.,** Deschodt, C.M., Scholtz, C.H. & Sole, C.L. (2018). An update to the taxonomy of the genus *Macroderes* Westwood 1842 (Coleoptera: Scarabaeidae: Scarabaeinae) with descriptions of new species from South Africa. *Zootaxa*, **4504** (1), 41-75.

Chapter 3. **Abdalla, I.H.,** Scholtz, C.H. & Sole, C.L. Phylogeny and divergence time of the southern African genus *Macroderes* Westwood 1842 (Coleoptera: Scarabaeidae: Scarabaeinae). To be submitted to *Systematic Entomology*.

Chapter 4. **Abdalla, I.H.,** Mansell, M.W. & Sole, C.L. (2019). Revision of the southern African genera *Nemopterella* Banks and *Nemia* Navás (Neuroptera: Nemopteridae: Nemopterinae), with descriptions of new genera and species. Zootaxa, **4635** (1), 1-89.

Chapter 5. **Abdalla, I.H.,** Mansell, M.W. & Sole, C.L. (in prep.). Phylogeny and divergence time of the Southern African lacewing genus *Afroptera* Abdalla & Mansell (Neuroptera: Nemopteridae: Nemopterinae). To be submitted to *Systematic Entomology*.

Chapter 6. **Abdalla, I.H.,** Scholtz, C.H., Mansell, M.W. & Sole, C.L. (in prep.). Common trends in the historical biogeography and evolution of two disparate southern African insect genera, *Macroderes* (Scarabaeidae: Scarabaeinae) and *Afroptera* Abdalla & Mansell (Nemopteridae: Nemopterinae). To be submitted to *Journal of Biogeography*.

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CHAPTER II

An update to the taxonomy of the genus *Macroderes* Westwood, 1842 (Coleoptera: Scarabaeidae: Scarabaeinae) with descriptions of new species from South Africa

Contents

Abstract

The genus *Macroderes* Westwood, 1842 (Scarabaeidae: Scarabaeinae, tribe *incertae sedis*) is practically endemic to South Africa with only one species found in southern Namibia. The ranges of the species are limited to the winter-rainfall and bimodal biomes of South Africa comprising the regions of Richtersveld as extreme points of its northerly distribution, and extending to the south through Namaqualand to Cape Agulhas. The taxonomy of the genus is revised. Fourteen valid species are recognised and three others are regarded as having doubtful validity. Seven new species are described, these are: *M. cederbergensis* Abdalla & Deschodt, new species, *M. tortuosus* Abdalla & Scholtz, new species, *M. gifboomi* Abdalla & Scholtz, new species, *M. leipoldti* Abdalla & Deschodt, new species, *M. oreatus* Abdalla & Deschodt, new species, *M. porselinus* Abdalla, new species, and *M. soleiana* Abdalla & Deschodt, new species. *Macroderes nitidus* Harold, 1877 is redescribed and its lectotype is designated. The diagnostic characters and an updated geographic distribution of each species are summarised. An updated key of the genus, photographs of habitus, sclerite of internal sac [of 14 of the 21 spp. illustrated], pronotum, pronotal punctures and elytra are also provided.

Key words: Taxonomy, Coleoptera, Scarabaeidae, Revision, New species, Northern Cape Province, Western Cape Province

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Introduction

The genus *Macroderes* Westwood, 1842 (Scarabaeidae: Scarabaeinae, tribe incertae sedis, see Tarasov & Dimitrov 2016) consists of 14 valid species and three others of doubtful validity (Davis *et al*. 2008). The genus is characterised by a convex black body and all species are wingless and range in size from small to medium (8-15 mm). The constituent species are distributed from the Richtersveld, which is thought to be the northern extreme of their range, southwards, through Namaqualand to Cape Agulhas. All species occur in the winter- and year-round rainfall areas of South Africa, placing the genus in the winter and bimodal center of distribution (Davis 2002). *Macroderes* is believed to be endemic to South Africa with most species being restricted to Namaqualand and the south-western Cape while a single species,

Macroderes bias (Olivier, 1789), is known from the south-eastern Cape. One species, *Macroderes pristinus* Sharp, 1880, is reported from what is now known as Diamond field 1 in southern Namibia (Frolov & Scholtz 2005).

All *Macroderes* species appear to have specific habitat requirements occurring in four biomes (Fynbos, Succulent Karoo, Albany Thicket and Grassland) although most occur in Fynbos and Succulent Karoo.

Macroderes is a cool-adapted genus and activity is limited to short periods from July to September, and then only for a few days after rain, while temperatures remain low (Frolov & Scholtz 2005). Although their exact habitat requirements have not been determined, Frolov & Scholtz (2005) noted that species are mostly allopatric with localised distribution patterns, often occurring in dense scrub associated with "heuweltjies" (mima-like earth mounds, Vissers & Toerien 1971; Cox *et al.* 1987; Lovegrove & Siegfried 1986; Fey 2010; Schmiedel *et al.* 2016).

It is known that the water-holding capacity and nutrient content of these heuweltjies is higher than in the surrounding areas (Fey 2010; Desmet 2007; Mucina & Rutherford 2006) and that they form foci for rodent activity (Fey 2010). The rodents are probably the main source of dung pellets as food for *Macroderes* species in a resource-scarce environment. The distribution of these heuweltjies (Fig. 1), as shown by Lovegrove & Siegfried (1986), matches well with the known generic distribution of *Macroderes*.

The majority of *Macroderes* species are known only from their type locality and have small or fragmented areas of occurrence (generally < than 20 000 km^2). This is because of their aptery, endemicity and specialised habitat requirements, most species would therefore qualify as "vulnerable B1 ac" when assessed under the IUCN red list categories (See IUCN Standards and Petitions Subcommittee (2013) for an explanation of the criteria).

Most studies concerning the genus *Macroderes* have focussed on the classification of the genus to species level using morphological characteristics such as the description of the body, pronotum, elytra, tibia and basal segment of tarsi. In 1880, Preudhomme de Bore reassigned *Scarabaeus bias* Olivier, 1789 to *Macroderes* and described three new species. An additional five species were described; one each by Harold (1877), Sharp (1880) and Kolbe (1908) and two by Péringuey (1901) who provided a key to the known species. All previous work on the genus

was revised by Janssens (1939) who described an additional species *M. arrowi* and provided a key to all known species.

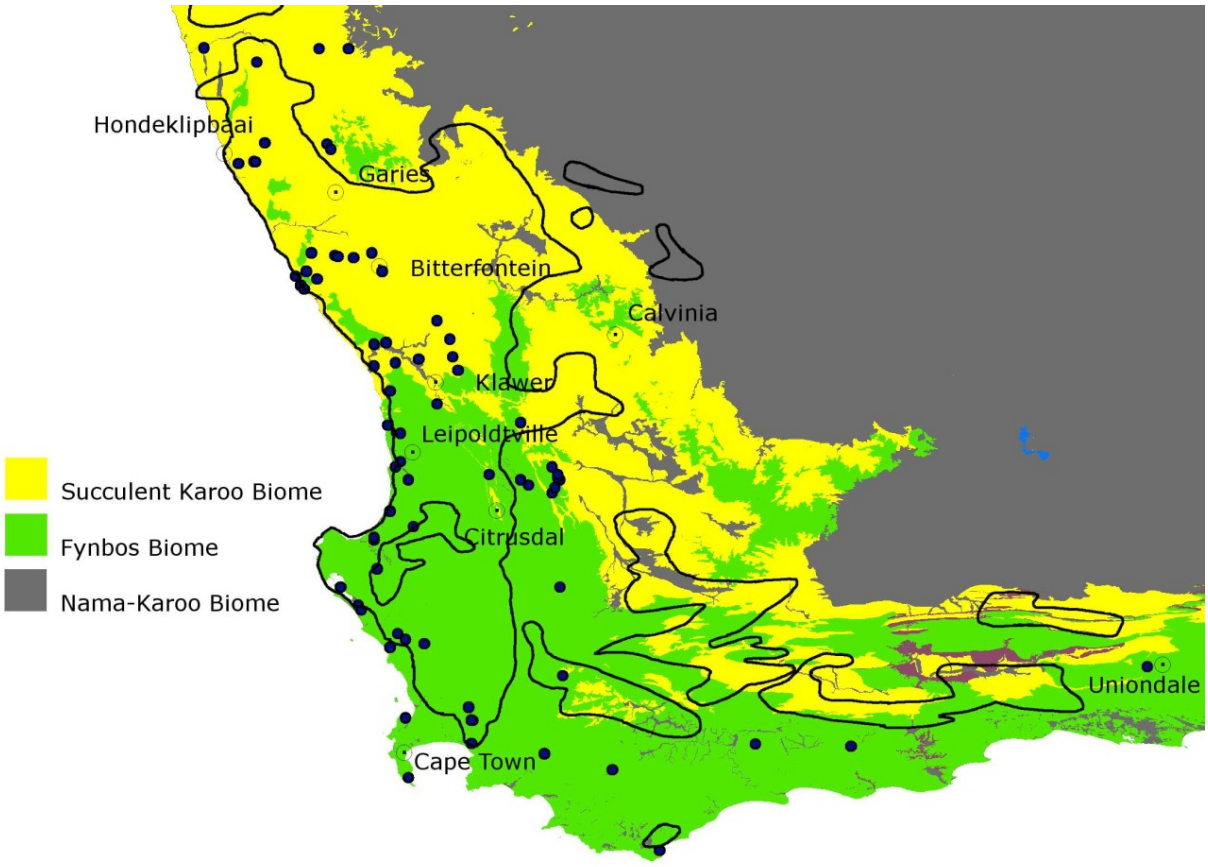


FIGURE 1. Distribution of Heuweltjies in the Succulent Karoo and Fynbos Biomes (according to Lovegrove & Siegfried, 1986, modified).

Frolov & Scholtz (2005) revised *Macroderes* and described six new species, *M. amplior*, *M. minutus*, *M. endroedyi, M. namakwanus*, *M. foveatus* and *M. cornutus*. In addition, they designated a neotype for *M. bias*. Furthermore, they established two new synonymies: *M. pilula* Sharp, 1880 as a junior synonym of *M. bias* and *M. westwoodi* Preudhomme de Borre, 1880 as a junior synonym of *M. undulatus* Preudhomme de Borre, 1880. They also provided a key to the species and notes on their biology and distribution. The current species in the genus are: *M. amplior*, *M.arrowi* Janssens, 1939, *M. bias, M. cornutus*, *M. endroedyi*, *M. fornicatus* Sharp, 1880, *M. foveatus*, *M. greeni* (Kirby, 1818), *M. minutus, M. mutilans* Kolbe, 1908, *M.*

namakwanus, M. nitidus Harold, 1877, *M. politulus* Preudhomme de Borre, 1880, *M. pristinus* and *M. undulatus* and *M. pristinus*.

In this paper we aim to update the current taxonomic status of the genus *Macroderes* by reviewing all the known species, outlining their geographic distribution and habitat preference and also by describing new species. *Macroderes nitidus* Harold, 1877 is redescribed from the type series and its lectotype is designated as the redescription by Frolov & Scholtz (2005) was based on material which is now considered as a new species, *M. soleiana* Abdalla & Deschodt, new species. The type series of *M. minutus* comprises two species, *M. minutus* and *M. cederbergensis* Abdalla & Deschodt, new species which is described here as new. In addition to that five new species are described which are: *M. gifboomi* Abdalla & Scholtz, new species, *M. leipoldti* Abdalla & Deschodt, new species, *M. oreatus* Abdalla & Deschodt, new species, *M. porselinus* Abdalla, new species, and *M. tortuosus* Abdalla & Scholtz, new species.

Material and Methods

For species identification the key, examination of type specimens and species descriptions in Frolov & Scholtz (2005) were used. Measurements of body size, length and width were taken with a caliper. Body length was taken from the fronto-clypeal suture to the elytral apex, and width measured across the widest point over the elytra. Male genitalia (internal sac sclerites of aedeagi) photographs were taken under a Leica M165 C microscope, using a Leica DMC 2900 digital camera. Photographs of the pronotum, elytral punctuation and puncture shapes were taken with a Zeiss Gemini Ultra plus Field Emission Scanning Electron microscope. Habitus images were made using a Canon 500D cameras mounted with a Canon MPE 65 mm lens and stacked with the Helicon remote and Helicon focus software packages. The distribution maps of the new species were drawn using the software ArcGIS 10.2 (ESRI 2013).
Specimen data labels are reported verbatim with authors' comments in square brackets. We used a comma (,) to separate data in different rows in the same label and single slash (/) to separate data in different labels from the same pin.

Specimens are deposited in the following institutions:
BMNH The Natural History Museum, London, United Kingdom;

IRSNB Institute Royal des Sciences Naturelles de Belgique, Brussels, Belgium;

MNHN Muséum National d'Histoire Naturelle, Paris, France;

SAMC IZIKO South African Museum (formerly South African Museum), Cape Town, South Africa;

SANC South African National Collection of Insects, Pretoria, South Africa;

TMSA Ditsong Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa;

UPSA University of Pretoria Scarab Collection, Pretoria, South Africa;

ZMHB Museum für Naturkunde, Leibniz Gemeinschaft, Berlin, Germany.

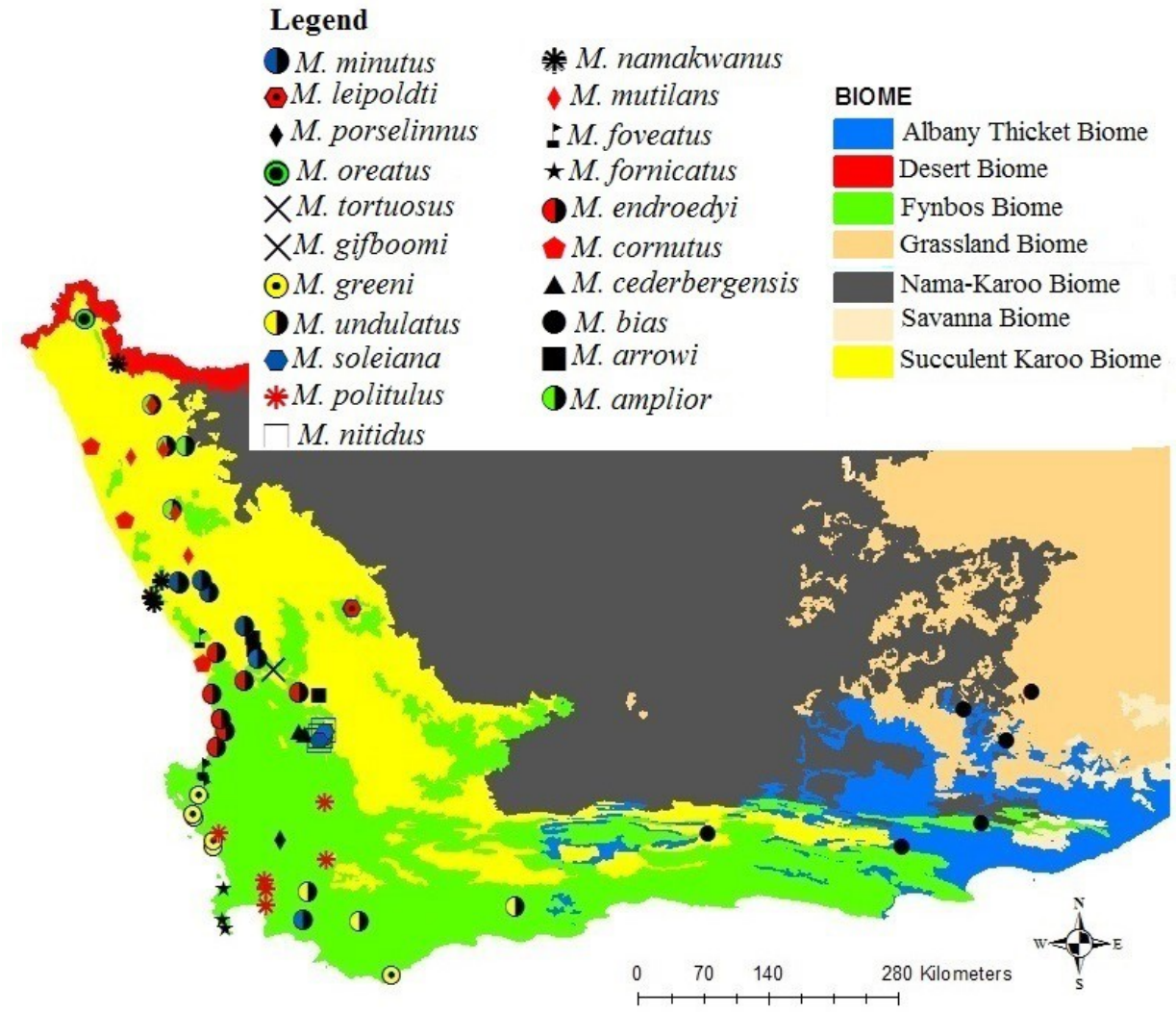


FIGURE 2. Distribution of *Macroderes* species. (Species listed in random order to aid finding them on the map).

Systematics

Macroderes amplior Frolov & Scholtz, 2005 (Figs. 3, 27, 64)

Macroderes amplior Frolov & Scholtz, 2005: 383.

Type locality. RSA, Western Cape Prov., 5 km W of Rietpoort, 30° 58' 36.58" S 017° 59' 55.69" E.

Type material examined. Holotype, m# (TMSA): "RSA, Western Cape Prov., 5 km W of, Rietpoort, A. Frolov & C. Deschodt leg." [printed] / "AF-0035(15), 3-11. IX. 2003, 30° 58'

36.58" S 017° 59' 55.69" E" [printed] / HOLOTYPUS, *Macroderes amplior,* Frolov & Scholtz, 2003 [red label, printed]". Paratypes: 1 m# and 10 f#f#, same data as holotype, 1 m# and 7 f#f# in UPSA, 3 f#f# in TMSA; 1 m# and 2 f#f# (TMSA): "RSA, Western Cape Prov, 5 km W of, Rietpoort, A. Frolov & C. Deschodt leg" [printed] / "AF-0036 (16),3-11. IX. 2003, 30° 58' 48.49" S 017° 59' 36.38" E" [printed] / PARATYPUS, *Macroderes amplior*, Frolov & Scholtz, 2003 [red label, printed]"; 1 m# (TMSA): "S. Afr, Namaqualand, Rietpoort farm, 30°. 59' S 18°. 06' E, [printed] / PARATYPUS, *Macroderes amplior*, Frolov & Scholtz, 2003 [red label, printed] / PARATYPUS, *Macroderes amplior*, Frolov & Scholtz, 2003 [red label, printed]"; 1 f# (SANC): "KOMAGGAS, NW, CP, (7 km N), 9. IX. 81, Red sand, Gravel Mountain, Karroo, Donkey & ALV. Davis [printed] / *Macorderes* sp., det. CSIRO. DBRU [printed] / PARATYPUS, *Macroderes amplior*, Frolov & Scholtz, 2003 [red label, printed]"; 1 m# and 1f# (SAMC): "RSA, Western Cape Prov, 5 km W of, Rietpoort, A. Frolov & C. Deschodt leg [printed] / "AF-0036 (16), 3-11-2003, 30° 58' 48.49" S 017° 59' 36.38" E" [printed] / Paratypus, *Macroderes amplior*, Frolov & Scholtz 2003 [red label, printed]".

Additional material examined. 1 f# (UPSA): "Rietpoort, 30.97729° S 18.00026° E, 30.viii.2004, C. Deschodt & M. Deschodt leg".

Size range. Males length: 11.8-13.2 mm, width: 8.5-9.0 mm; females length: 10.7-12.5 mm, width: 8.6-9.6 mm.

Differential diagnosis. Resembles *M. tortuosus* new species in having pronotum with elongated punctures (Fig. 64) and *M. mutilans* in the general body features, however, it can be distinguished from the former by having impunctate lateral borders of the pronotum and from the later by having rather undulate surface of elytra and also by having long lateral process of internal sac of aedeagus (Fig. 27).

Habitat and distribution. Rietpoort and Komaggas are two localities in the Namaqualand region (Fig. 2). The area is classified as a semi-arid region, typified by winter rainfall ranging from 50-400 mm per annum (Kelso & Vogel 2007) and a wide distribution of succulent vegetation.

Macroderes arrowi Janssens, 1939 (Figs. 4, 59, 70)

Macroderes arrowi Janssens, 1939: 26; Ferreira 1969: 320; Frolov & Scholtz 2005: 389.

Type locality. South Africa, Cape Prov., v Rhynsdorp [Vanrhynsdorp: 31°37' S 18°44' E].

Type material examined. None. Type (1 m#) deposited in IRSNB (Frolov & Scholtz 2005).

Additional material examined. 2 m#m# and 2 f#f# (UPSA): "RSA, Western Cape Prov., 11 km, N of Vanrhynsdorp, A. Frolov & C. Deschodt leg" / "AF-00 45 (25), 5-11. IX. 2003, 31° 30' 28.28" S 018° 43' 02.56" E", 2 f#f# (UPSA): "South Africa, Western Cape Prov, 124 km N of, Sandveld, 31.49859° S 018.71642° E, 15. 8. 2015, C. Deschodt & W. P. Strümpher leg."

Size range. Males length: 9.9-11.7 mm, width: 6.3-8.3 mm; females length: 9.7-10.5 mm, width: 6.5-7.7 mm.

Differential diagnosis. Due to the carinate margins of the elytra (Fig. 70) *M. arrowi* resembles *M. foveatus*, *M. cornutus* and *M. greeni*, however, it can be easily distinguished from the two former species as it lacks the deep triangular concavity at the base of the pronotum (Fig. 4) and from all by having a granular pronotum (Fig. 59) instead of rounded punctures found in *M. greeni* and longitudinal punctures in *M. cornutus* and *M. foveatus*.

Habitat and distribution. Only known from Vanrhynsdorp and Sandveld areas (Fig. 2). The two localities are situated in the Western Cape Province. Vanrhynsdorp is an arid area close to Namaqualand's coast. The area is covered by succulent vegetation and characterised by humid climate and low annual rainfall. Sandveld situated to the west of the Cedarberg Mountains and is characterised by a rich biodiversity of animals and plants.

Macroderes bias Olivier, 1789 (Figs. 9, 28, 55, 57, 61, 66)

Scarabaeus bias Olivier, 1789: 187.

Macroderes bias: Preudhomme de Borre 1880: 8; Péringuey 1901: 299; Janssens 1939: 28; Ferreira 1969: 320; Frolov & Scholtz 2005: 376.

Macroderes pilula Sharp, 1880: 38; Frolov & Scholtz 2005: 376 (junior synonym of *M. bias*).

Type locality. South Africa, Grahamstown [33° 18' S 26° 32' E].

Type material examined. None. Neotype designated by Frolov & Scholtz (2005) is deposited in IRSNB.

Additional material examined. 1 m# and1 f# (AMSA):"B[aviaans], Kloof, Jan. 1893, MRS. G. White"; 1 f# (AMSA): "TARKASTAD, 'KELSO', SHEEP DROPPINGS, JAN '62, [32° 00' 28.35" S 26° 16' 18.49" E]"; 1 f# (AMSA): "TARKASTAD, In veld, Jan '62"; 1 f# (AMSA): "LYEDOCH, BEDFORD, COW DUNG, JAN 62, [33° 58' 57.01" S 18° 46' 04.47" E]"; 1 m# (SANC): "UNIONDALE, E Cape, (10 kms NE), 4. 7. 76, 970 m, [33° 38' 55.5" S 23° 08' 17.52" E], Davis & Aschenborn / Ex Coll, CISRO, Div, Entomology, S. AFRICAN STATION / *Macroderes bias* (Oliver), Frolov, det. 2003"; 1 m# (SANC): "*Macroderes bias*"; 1 m# and 1 f# (SANC) without locality label; 1 m# and 1 f# (AMSA): "Grahama's Town, 11, 04, 05, [33° 19' 28.26" S 26° 37' 23.93" E] / *Macroderes bias* (Oliver), Frolov, det. 2003"; 1 m# and 1 f# (AMSA): "Cape Province, Strowan, Grahamstown, 11.IV.1969, [33° 18' S 26° 32' E], F.W.Gess"; 1 m# (SANC): "South Africa, Cape P, 46 Km, NW of Steytleville, 680 m, 05.v.1976, [33° 18' 49.12" S 24° 17' 54.55" E], Davis & Aschenborn / DBRU locality, 2307, Stony sandy loam, Scrub, cattle dung / *Macroderes* sp"; 1 m# (TMSA): "20. X. 1922, Dr. Brauns, Hamendoor, Camper, *Macroderes bias* (Oliver)?, Frolov, 2003". 1 f# (TMSA): "S. Afr, Cape, Toorberg E, 1522 m, 32°. 10' S – 24°. 02' E / 22 .11. 2007 / E-Y: 3759, under stones, Ruth Muller leg / TM, SOUTH AFRICA, TMSCO 9075 / *Macroderes bias* (Oliver), det. Adrian Davis, 2014"; 1 f# (TMSA): "SOUTH AFRICA, Cradock, Jan 1951, [32° 10' 51.50" S 25° 39' 03.57" E], G. S. Bosch / *Macroderes bias* (Oliver)?, Det. Frolov, 2003"; 1 f# (TMSA): "S. Afr, Cape Prov, Addo park, R. Wolmarans / 16-20. 12. 1996, PJ, 1-6, [33° 28' 53.91" S 25° 43' 47.23" E] / *Macroderes bias* (Olivier), det. A. Frolov, 2003"; 1 m# (SAMC): "Koeberg" / *Macroderes bias*, *Macroderes bias* (Olivier), Frolov & Scholtz, 2003"; 2 m#m# and 2 f#f# (SAMC): "Grahamstown, 11.VI.1905, [33° 19' 28.26" S 26° 37' 23.93" E], *Macroderes bias* (Olivier), Frolov & Scholtz, 2003".

Size range. Males length: 9.2-11.3 mm, width: 6.0-8.2 mm; females length: 8.2-12.5 mm, width: 6.3-8.3 mm.

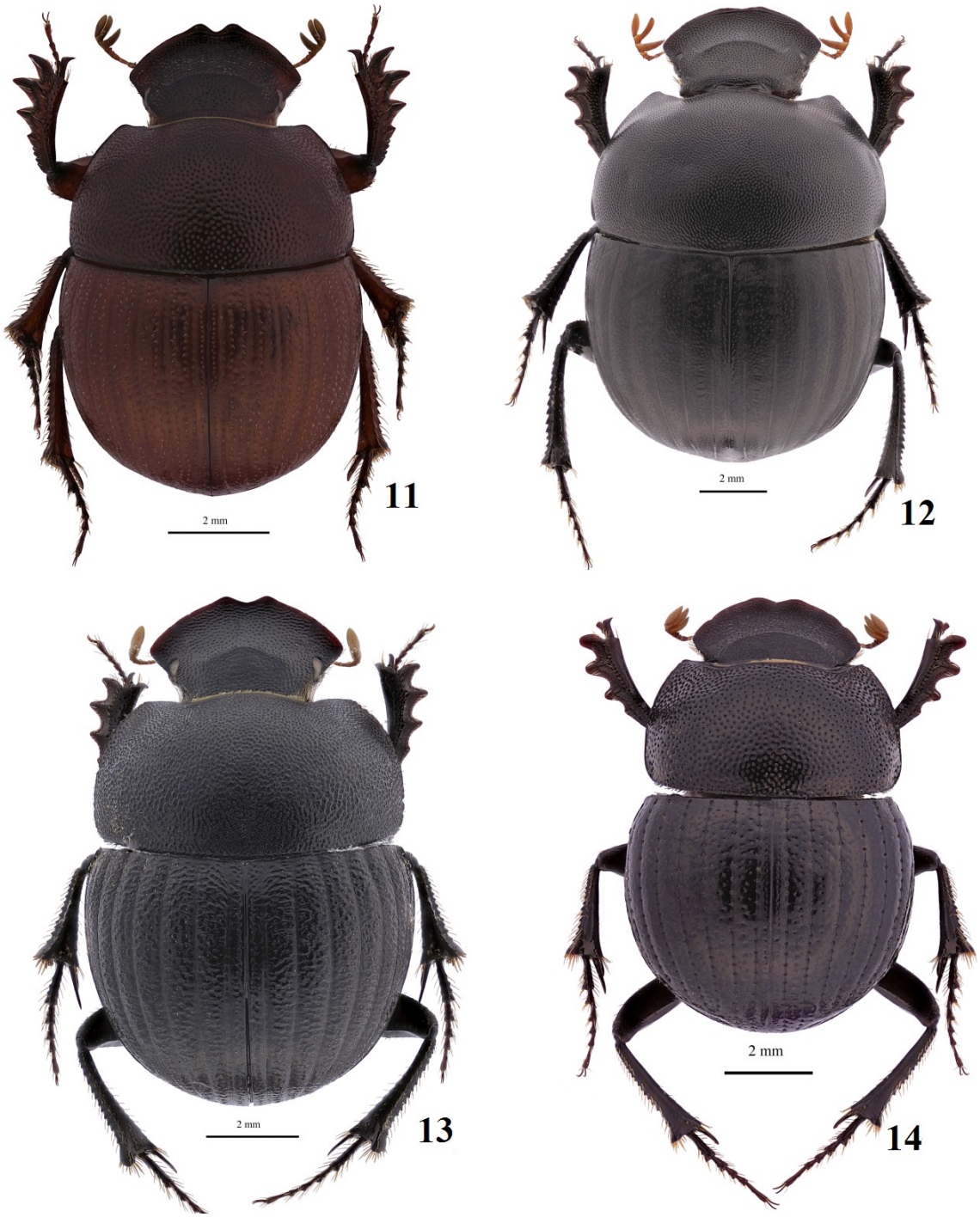
FIGURES 3-6. Habitus of *Macroderes* species. 3, *M. amplior* (Frolov & Scholtz, 2005) ♂; 4, *M. arrowi* (Janssens, 1939) ♂; 5, *M. cornutus* (Frolov & Scholtz, 2005) ♂; 6, *M. endroedyi* (Frolov & Scholtz, 2005) ♀.

Differential diagnosis. Due to its flatter intervals of elytra (Figs. 9, 66), *M. bias* is close to *M. mutilans* and *M. fornicatus*, nevertheless, it can be distinguished from both species by the closeness of stria 9 and stria 10 (Fig. 55) and from *M. mutilans* in that the lateral border of pronotum is punctate (Fig. 57) and the long sclerite of the internal sac (Fig. 28).

Habitat and distribution. Compared to the other species in the group this species has a wide distribution range in the Eastern Cape Province (Fig. 2). The range stretches over many bioregions encompassing the Eastern Fynbos-Renosterveld, Upper and Lower Karoo Bioregions and into the grassland Biome.

Remarks. *Macroderes bias* is the only species known from the Eastern Cape Province. Although the material studied have shown common characteristics such as the same even rounded shape of pronotum punctures, punctate lateral border of pronotum and the proximity of striae 9 and 10, there are distinct variations in the male pronotal shapes and elytral punctuation. Some males show strong antero-lateral excavation on the pronotum combined with an impunctate midline on the top, while others have a slight depression antero-laterally with their pronotum evenly punctuated. Also, the elytral interstriae in some males are flat and intensely punctuated while in others elevated medially and between the punctures. It seems that this species is one of a complex of species endemic to the region. Due to its rarity in collections it is difficult to judge these differential diagnostic characters as there are no new records of the species since the last study by Frolov & Scholtz (2005); with exception of a single female specimen collected in 2007 from Toorberg area which is not adequate to assign specific characters to for species identification. In addition to this, fresh material is needed for molecular analysis, which would allow us to infer phylogenetic relationships of the different species.

FIGURES 7-10. Habitus of *Macroderes* species. 7, *M. fornicatus* (Sharp, 1880) ♀; 8, *M. foveatus* (Frolov & Scholtz, 2005) ♀; 9, *M. bias* (Olivier, 1789) ♀; 10, *M. greeni* (Kirby, 1818) ♂.



FIGURES 11-14. Habitus of *Macroderes* species. 11, *M. minutus* (Frolov & Scholtz, 2005) ♀; 12, *M. mutilans* (Kolbe, 1908) ♂; 13, *M. namakwanus* (Frolov & Scholtz, 2005) ♂; 14, *M. nitidus* (Harold, 1877) ♀.

Macroderes cederbergensis Abdalla & Deschodt, new species (Figs. 20, 29, 76, 83, 94)

Macroderes minutus Frolov & Scholtz, 2005: 385 (partim).

Type locality. S.Africa, Western Cape Province, Cederberg Mts, Jeep Track, 32° 26' S 19° 13' E.

Type material. Holotype, m# (TMSA): "Cederberg Mts, Jeep Track, 32° 26' S 19° 13' E, 1.IX.1981, groundtraps with faeces and meat bait, 63 days, Endrödy-Younga leg [printed] / PARATYPUS, *Macroderes minutus*, Frolov & Scholtz, 2003 [red label, printed] / HOLOTYPE, *Macroderes cederbergensis,* Abdalla & Deschodt, 2018 [red label, printed]". Paratypes: 2 f#f# (TMSA): "Cederberg Mts, Jeep Track, 32° 26' S 19° 13' E, 1.IX.1981, groundtraps with faeces and meat bait, 63 days, Endrödy-Younga leg [printed] / PARATYPUS, *Macroderes minutus*, Frolov & Scholtz, 2003 [red label, printed] / PARATYPE, *Macroderes cederbergensis,* Abdalla & Deschodt, 2018 [red label, printed]"; 1 m#: "Cederberg Mts, Jeep Track, 32° 23' S 19° 24' E, 1.IX.1981, groundtrap with meat bait, 63 days, Endrödy-Younga leg [printed] / PARATYPUS, *Macroderes minutus*, Frolov & Scholtz, 2003 [red label, printed] / PARATYPE, *Macroderes cederbergensis,* Abdalla & Deschodt, 2018 [red label, printed]"; 1 m# and 1 f# (TMSA): "Cederberg Mts, Jeep Track, 32° 24' S 19° 10' E, 1.IX.1981, *Redunca rufo* [name could not be traced, probably *Pelea capreolus* (Forster, 1790) or Grey Rhebok] dung, Endrödy-Younga leg [printed] / PARATYPUS, *Macroderes minutus*, Frolov & Scholtz, 2003 [red label, printed] / PARATYPE, *Macroderes cederbergensis,* Abdalla & Deschodt, 2018 [red label, printed]"; 2 m#m# (TMSA) with the same data but collected from groundtraps with meat and feaces bait set up for 63 days.

Holotype description. Holotype, m# (Fig. 20). Body length 9.4 mm, width 6.8 mm.

Head. Genae right-angled. Frontal suture visible, not raised, strongly curved, no tubercle. Genal sutures barely discernible. Dorsal surface of clypeus behind frontal suture punctate punctures small, irregular and separated by 1-3 puncture diameters, area between punctures slightly rugose proximally of frontal suture. Dorsal part of eyes clearly visible.

Pronotum. Slightly convex. Anterior lateral angles almost right-angled, posterior lateral angles fairly rounded. No excavation antero-laterally. Lateral border not punctate. Dorsal surface smooth, with regular punctures separated by 0.5-1.5 puncture diameters (Figs. 76, 83).

Elytra. Elytral interstriae 1-8 flat, shagreened, irregularly punctate, punctures irregularly sized, separated by 0.5-3 puncture diameters, margins of punctures not carinate (Fig. 94). Striae

punctate with punctures separated by 2-4 puncture diameters. Sutural interstria narrow with single row of irregularly spaced punctures. Elytral stria 9 2/3 the length of elytron; interstria 10 about 5 times narrower than interstria 9 in the middle of elytron.

Aedeagus. The sclerite of internal sac curved, with small lateral process apically (Fig. 29).

Size range. Males length: 7.5-9.0 mm, width: 5.5-6.8 mm; females length: 7.8-9.5 mm, width: 6.0-6.3 mm.

Female. Female differs from male by having elytral interstriae 1-8 less shagreened; otherwise variation between male and female is slight.

Etymology. The specific epithet is derived from the Cederberg Range where the species occurs.

Differential diagnosis. It is close to *M. soleiana* new species but can be separated by having flatter elytral intervals (Figs. 20, 94) and the striae being slightly arcuate and not straight as in *M. soleiana* new species.

Habitat and distribution. This species was collected on the highest plateau in the Cederberg range (Fig. 2), above 1100 m a.s.l. (metres above sea level), characterised by clay soils and classified as Northern Inland Shale Band Vegetation (Mucina & Rutherford 2006). *Macroderes soleiana* new species occurs below 1100 m a.s.l.

Remark. See *M. minutus* for an explanation of the origin of the type series.

Macroderes cornutus Frolov & Scholtz, 2005 (Figs. 5, 30, 41, 47, 48, 50)
Macroderes cornutus Frolov & Scholtz, 2005: 391.

Type locality. South Africa, Namaqualand, Sand Kop 322 [29° 38' 31" S 17° 08' 53" E].

Type material examined. Holotype, m# (TMSA): “S. Afr: NAMAQUALAND, SAND KOP, 322, 29° 38' 31" S – 17° 08' 53" E, 19. VIII. 1996, leg. J. duG. HARRISON [printed] / UNIV, PRET, ZOO & ENTO, J. duG. HARRISON, 1996, SITE 61 NO c, VEGETATED DUNE, nr, Karoo Bush Rat Nest [printed] / HOLOTYPUS, *Macroderes cornutus*, Frolov &

Scholtz, 2003 [red label, printed]"; Paratypes: 1 m# and 3 f#f# (TMSA), same data as holotype. 1 f# (TMSA): "S. Afr, Namaq, Coast, Strandfontein farm, 30° 33' S 17° 22' E [printed] / 2.9.1977, EY: 1373, singled dunes, Endrödy-Younga leg [printed] / PARATYPUS, *Macroderes cornutus*, Frolov & Scholtz, 2003 [red label, printed]"; 4 m#m#: "RSA, Northern Cape Prov, 3 km, W of, Wallekraal, A. Frolov & Deschodt leg [printed] / "AF-003(11), 2-13. IX. 2003, 30 2214.74° S 017 2844. 93° E" [printed] / PARATYPUS, *Macroderes cornutus*, Frolov & Scholtz, 2003 [red label, printed]": 3 m#m# in (UPSA), 1 m# in (SANC).

Additional material examined. 1 f# (UPSA): "30.730175° S 17.523828° E, 15 August 2008".

Size range. Males length: 11.0-11.8 mm, width: 7.4-8.0 mm; females length: 10.4-11.6 mm, width 7.0-7.4 mm.

Differential diagnosis. *M. cornutus* resembles *M. foveatus* by having same deep triangular concavity in the base of pronotum (Figs. 5, 41). Also the presence of the large rounded tubercle in the middle of the frontal suture (Figs. 48, 50) makes this species one of the more easily recognizable *Macroderes* species.

Habitat and distribution. So far, this species is known only from the three localities in the Northern Cape Province. The localities stretch along the western coastline of South Africa within the Succulent karoo eco-region (Fig. 2). Generally, the area is characterised by its aridity and winter rains associated with cold frost.

Remarks. Due to the lack of adequate data regarding the species distribution and as it has a small distribution range this species is categorized as Data Deficient (Davis 2013). Some of the localities from which the species were collected are protected and managed by the government, however, as it is flightless and has a restricted distribution range it is well matched to two of three criteria from category B for threatened species, which would consider the species as NEAR Threatened in the IUCN Red List (Davis 2013).

FIGURES 15-18. Habitus of *Macroderes* species. 15, *M. politulus* (Preudhomme de Borre, 1880) ♂; 16, *M. undulatus* (Preudhomme de Borre, 1880) ♀; 17, *M. porselinus* (Abdalla, new species) ♂; 18, *M. gifboomi* (Abdalla & Scholtz, new species) ♂.

Macorderes endroedyi Frolov & Scholtz, 2005 (Figs. 6, 26, 45, 62, 72)

Macorderes endroedyi Frolov & Scholtz, 2005: 387.

Type locality. S. Afr, SW Cape, Nortier Farm, 32° 03' S–18° 19' E.

Type material examined. Holotype, m# (TMSA): "S. Afr, SW Cape, Nortier Farm, 32° 03' S – 18° 19' E [printed] / groundtrap with faeces bait [printed] / 25.8.1981, E-Y: 1845, groundtraps, Endrödy-Younga leg [printed] / HOLOTYPUS, *Macroderes endroedyi*, Frolov & Scholtz, 2003 [red label, printed]". Paratypes: 2 m#m# and 7 f#f# (TMSA): same data as holotype; 1 m# and 4 f#f# (TMSA): "S. Afr, SW Cape, Verlorevlei farm, 32°. 19' S – 18°. 29' E [printed] / 28. 8. 1981 / E-Y: 1856, groundtraps, 60 days, Endrödy-Younga leg [printed] / groundtrap with faeces bait [printed] / PARATYPUS, *Macroderes endroedyi*, Frolov & Scholtz, 2003 [red label, printed]"; 1 m# and 1 f# (TMSA): "RSA, W Cape, Papkuilsfontein farm, 32° 02' S 19° 10' E [printed] / 16.9.1994 / E-Y: 3007, groundtraps, 9 days, Endrödy-Younga leg [printed] / groundtraps with faces bait [printed] / PARATYPUS, *Macroderes endroedyi*, Frolov & Scholtz, 2003 [red label, printed]"; 3 m#m# and 9 f#f#: "RSA, Western Cape Prov, Kliphoek, A. Frolov & Deschodt leg [printed] / "AF-0047 (27), 6-10.IX. 2003, 31° 50' 20.6" S 018° 20' 08.55" E" [printed] / PARATYPUS, *Macroderes endroedyi*, Frolov & Scholtz, 2003 [red label, printed]": 1 m# and 1 f# in (TMSA), 2 m#m# and 8 f#f# in (UPSA). 1 f# (UPSA): "RSA, Western Cape Prov, Aurora, A. Frolov & Deschodt leg [printed] / "AF-0050 (30), 6-10. IX. 2003, 32° 42' 02.94" S 018° 29' 10.39" E" / PARATYPUS, *Macroderes endroedyi*, Frolov & Scholtz, 2003 [red label, printed]"; 2 m#m# and 3 f#f#: "RSA, Western Cape Prov, 4 Km S of, Trawal, A. Frolov & Deschodt leg [printed] / "AF-0048 (28), 6-10. IX. 2003, 31° 55' 43.13" S 018° 37' 56.33" E" / PARATYPUS, *Macroderes endroedyi*, Frolov & Scholtz, 2003 [red label, printed]": 1 m# and 1 f# in (UPSA), 1 m# and 2 f#f# in (TMSA). 2 m#m# and 6 f#f#: "RSA, Western Cape Prov, 6 Km NE of, Elandsbaai, A. Frolov & Deschodt leg [printed] / "AF-0049 (29), 6-10. IX. 2003, 32° 16' 57.40" S 018° 24' 51.98" E" / PARATYPUS, *Macroderes endroedyi*, Frolov & Scholtz, 2003 [red label, printed]"; 2 m#m# and 3 f#f# in (UPSA), 3 f#f# in (TMSA). 1 f# (TMSA): "S. Afr, SW Cape, Kliphout kop, 32°.17' S-18°.24' E [printed] / 26. 8. 1981, E-Y: 1852, groundtraps, 63 days, Endrödy-Younga leg [printed] / PARATYPUS, *Macroderes endroedyi*, Frolov & Scholtz, 2003 [red label, printed]"; 2 f#f# (TMSA): "S. Afr,

SW Cape, Seweputs Farm, 31°. 39' S – 18°. 22' E [printed] / 22. 8. 1981 / E-Y: 1832, Singled, night, Endrödy-Younga leg [printed] / PARATYPUS, *Macroderes endroedyi*, Frolov & Scholtz, 2003 [red label, printed]"; 1 m# (SAMC): "RSA, Western Cape Prov, 6 Km NE of, Elandsbaai, A. Frolov & C. Deschodt leg [printed] / "AF-0049 (29), 6-10. IX. 2003, 32° 16' 57.40" S 018° 24' 51.98" E" [printed] / Paratypus, *Macroderes endroedyi,* Frolov & Scholtz, 2003".

Additional material examined. 1 m# (UPSA):"South Africa, Western Cape Province, Elandsbaai, 32.27956° S 018.41713° E, 16. 8. 2015, C. Deschodt & W. P. Strümpher leg"; 3 f#f# (UPSA): "South Africa, Western Cape Province, Klawer, 31.92871° S 018.63217° E, 16.8. 2015, C. Deschodt & W. P. Strümpher leg".

Size range. Males length: 9.8-12.6 mm, width: 7.0-9.1 mm; females length: 9.7-13.7 mm, width: 7.4-8.8 mm.

Differential diagnosis. Externally the species is closely similar to *M. namakwanus* (Fig. 6) however, it can be easily distinguished by the following combinations of characteristics: irregular punctuation of pronotum disc (Fig. 62), elytral interstriae shagreened and covered by small shiny tubercles (Fig. 72), the sclerite of the internal sac of the aedeagus curved basely with a small lateral process (Fig. 26).

Habitat and distribution. This species was collected from a few localities occupying a small distribution range in the southwest of Western Cape Province (Fig. 2). Based on (Olson *et al.* 2001) terrestrial ecoregions of the world, the range of this species comprises the southwest part of the moister Fynbos and Renosterveld ecoregion and part of the montane Fynbos and Renosterveld in Cedarberg.

Remarks. Due to it is small, limited range, inability to fly and the vulnerable habitats it occurs in, the species has been assessed as NEAR Threatened in the IUCN Red List (Category B, Davis 2013).

Macroderes fornicatus Sharp, 1880 (Figs. 7, 54, 65, 67)

Macroderes fornicatus Sharp, 1880: 37; Péringuey 1901: 303; Janssens 1939: 28; Ferreira 1969: 320; Frolov & Scholtz 2005: 381.

Type locality. S. Afr., Western Cape Province, Cape Peninsula.

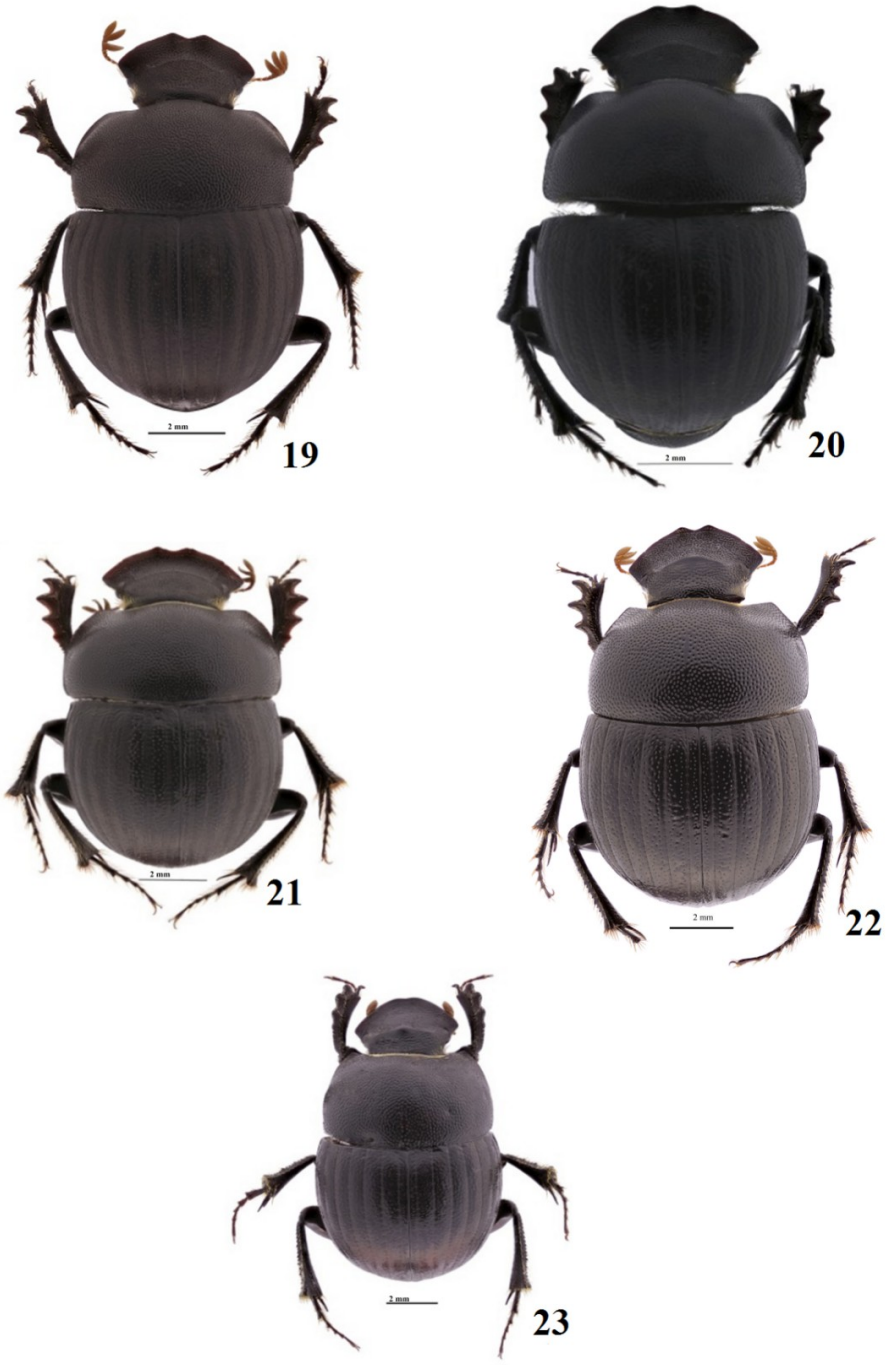
Type material examined. None. Type series is in MNHN (Frolov & Scholtz 2005).

Additional material examined. 1 m# (UPSA): "S. Africa, SW, Cape, Cape of Good Hope, NR, 34.1734° S 18.2546° E, 13 Oct. 1987, ALV Davis"; 1 m#: "S. Africa, SW, Cape, Good Hope, Nat. Res, 34.18° S 18.27° E, 15.VII .1987, ALV Davis / ex cattle dung baited pitfall, in 2-3 yr [year] fynbos / *Macroderes fornicatus* Sharp, Frolov det, 2003"; 1 m# with same data but date of collection: 3. VII. 1987. 2 f#f# (SANC): "UNIONDALE, E, CP, (10 Kms NE), 4.V.76, 970 m, Davis & Aschenborn / Ex Coll. CSIRO, Div, Entomology, S. AFRICAN STATION / *Macorderes* sp, det. CSIRO, DBRU"; 1 f# (UPSA): "RSA. Western Cape Province, Cape Peninsula, Cape Town, 34° 13' 19.21" S 18° 24' 38.49" E, 100 m, 17. vii. 2016, baited pitfall trap: pig dung, leg. C. Deschodt, W.P. Strümpher"; 1 m# (SAMC): "Tafelberg, 18. 4. 48 / *Macroderes fornicatus* Sharp / SAM-Col-A062970".

Size range. Males length: 8.2-11.2 mm, width: 5.4-7.3 mm; females length: 9.7-11.9 mm, width: 6.9-7.0 mm.

Differential diagnosis. Close to *M. mutilans* and *M. bias* in having flattened and matte elytral intervals (Fig. 67) but can easily be distinguished having stria 9 widely separated from stria 10 (Fig. 54).

Habitat and distribution. This species is known only from the Cape Peninsula (Fig. 2). The area forms part of the southwest Fynbos Bioregion located within the Peninsula Sandstone Fynbos vegetation unit (Mucina & Rutherford 2006). The unit extends from the top of Lions' Head and Table Mountain to Cape Point and Cape of Good Hope. The vegetation cover encompasses a mixture of proteoid and ericoid-leaved shrubland with mainly proteoid, ericaceous and restioid fynbos and some asteraceous fynbos. The mean annual precipitation ranges between 520 and 1690 mm (mean 780 mm) with a maximum peak from May to August.



FIGURES 19-23. Habitus of *Macroderes* species. 19, *M. oreatus* (Abdalla & Deschodt, new species) ♂; 20, *M. cederbergensis* (Abdalla & Deschodt, new species) ♂; 21, *M. soleiana* (Abdalla & Deschodt, new species) ♂; 22, *M. tortuosus* (Abdalla & Scholtz, new species) ♂; 23, *M. leipoldti* (Abdalla & Deschodt, new species) ♂.

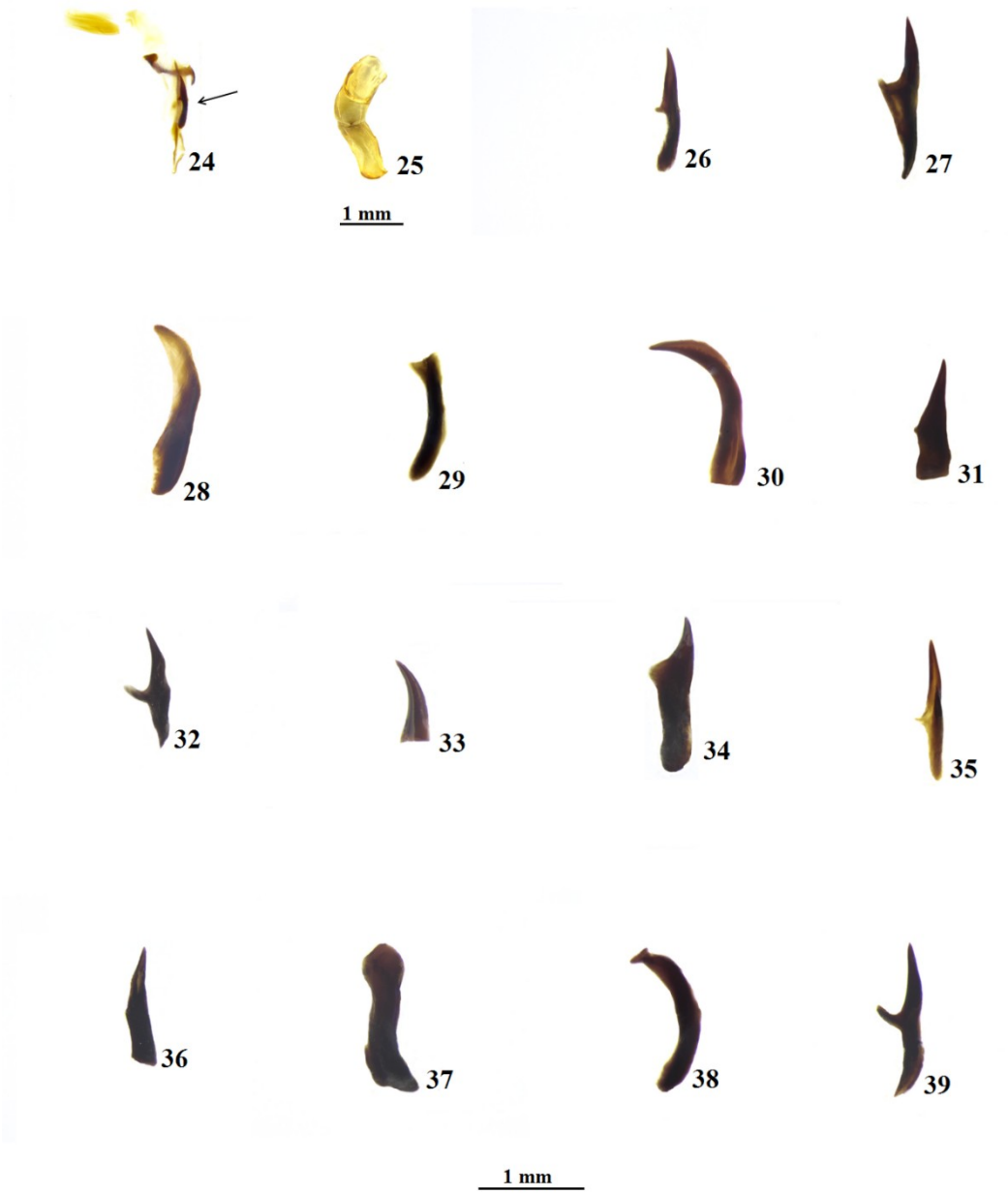


FIGURE S 24-39. Internal sac of aedeagus (24), aedeagus (25) and internal sac sclerite (26-39) of 14 of the 21 *Macroderes* species. 26, *M. endroedyi* Frolov & Scholtz, 2005; 27, *M. amplior* Frolov & Scholtz, 2005; 28, *M. bias* (Olivier, 1789); 29, *M. cederbergensis* Abdalla & Deschodt, new species; 30, *M. cornutus* Frolov & Scholtz, 2005; 31, *M. foveatus* Frolov & Scholtz, 2005; 32, *M. gifboomi* Abdalla & Scholtz, new species; 33, *M. leipoldti* Abdalla & Deschodt, new species; 34, *M. mutilans* Kolbe, 1908; 35, *M. namakwanus* Frolov & Scholtz, 2005; 36, *M. oreatus* Abdalla & Deschodt, new species; 37, *M. porselinus* Abdalla, new species; 38, *M. soleiana* Abdalla & Deschodt, new species; 39, *M. tortuosus* Abdalla & Scholtz, new species.

Macroderes foveatus Frolov & Scholtz, 2005 (Figs. 8, 31, 40, 46, 49, 51, 73)

Macroderes foveatus Frolov & Scholtz, 2005: 390.

Type locality. S. Afr., SW Cape, 3 km E of Veldrif, 32° 46' S 18° 14' E.

Type material examined. Holotype, m# (TMSA): "S. Afr, SW Cape, Veldrif, 3km E, 32° 46' S –18° 14' E [printed] / 31.8.1981, E-Y: 1870, ground traps, 59 days, Endrödy-Younga leg [printed] / groundtrap with meat bait [printed] / HOLOTYPUS, *Macroderes foveatus*, Frolov & Scholtz, 2003 [red label, printed]". Paratypes: 1 f# (TMSA) same data as holotype; 1 f# (TMSA): "S. Afr, S.W. Cape, Brakfontein farm, 32° 56' S 18° 15' E [printed] / 23.8.1983, E-Y: 1967, groundtraps, 72 days, Endrödy, Penrith leg [printed] / groundtrap with faeces bait [printed] / PARATYPUS, *Macroderes foveatus*, Frolov & Scholtz, 2003".

Additional material examined. 2 m#m# (UPSA): "RSA, Western Cape Province, Veldrif, 7 Km E, 19. vii. 2016, 32° 47' 38.18" S 18° 14' 53.42" E / baited pitfall trap: pig dung, C. Deschodt & W.P. Strümpher"; 1 f# (UPSA): "South Africa, Kommandokraal farm, 31.50317° S 018.20939° E, 14.8. 2015, C. Deschodt & W. P. Strümpher leg".

Size range. Males length: 10.2-10.4 mm, width: 6.2-7.4 mm; females length: 8.8-10.1 mm, width: 5.3-7.1 mm

Differential diagnosis. This species differs from all *Macroderes* species except *M. cornutus* in that the base of the pronotum bears deep triangular concavity (Figs. 8, 40).However, it can be separated by the combination of the following characteristics: lack of the rounded tubercle in the frontal suture that characterises *M. cornutus* (Figs. 49, 51), the internal sac sclerite bears small lateral processes (Fig. 31), less elongated punctures at each side of the pronotum (Fig. 46).

Habitat and distribution. This species is recorded from two localities in the southern western part of Western Cape Province along the west coast of South Africa (Fig. 2). Generally, the area is characterised by Mediterranean climate with warm, dry summers and moderate humid, rainy winters (Mucina & Rutherford 2006).

Macroderes gifboomi Abdalla & Scholtz**,** new species (Figs. 18, 32, 77, 84, 93)

Type locality. South Africa, Western Cape Province, Gifberg, 26 km SE of, Vanrhynsdorp, 31° 48' 5.22" S 18° 55' 7.16" E.

Type material. Holotype, m# (TMSA): "South Africa, Western Cape Province, Gifberg, 26 km SE of, Vanrhynsdorp, 31°48' 5.22" S 18° 55' 7.16" E, 26 km SE, Alt 377 m, 16.vi.2016, C. Scholtz [printed] / HOLOTYPE, *Macroderes gifboomi*, Abdalla & Scholtz, 2018, [red label, printed]". Paratypes: 1m# and 2f#f# (TMSA) same data as holotype; 4 m# (UPSA): "South Africa, Western Cape Province, Gifberg, 26 km SE of, Vanrhynsdorp, 31° 48' 5.22" S 18° 55' 7.16" E, Alt 377 m, 21.vii.2016, C. Deschodt & W.P. Strümpher [printed] / PARATYPE, *Macroderes gifboomi*, Abdalla & Scholtz, 2018, [red label, printed]".

Holotype description. Holotype, m# (Fig. 18). Body length 9.9 mm, body width 7.2 mm.

Head. Clypeus broad, semi-circular, bordered by two teeth on anterior edge which are wider than longer. Genae right angled. Frontoclypeal suture evident slightly curved without tubercle in the middle. Frons densely punctate with small round punctures. Clypeogenal suture present but poorly defined towards the clypeal edge. Clypeus densely punctate with fine punctures becoming rugose towards the clypeal frontal margin.

Pronotum. Form trapezoidal, smooth, shiny, width greater than length, with two distinct depressions anterolaterally. Lateral edges rounded delimited with fine borders. Borders impunctate, non-crenulated, base not bordered. Anterior angles obtuse, posterior angles right to obtuse. Pronotal surface lacking a longitudinal depression and uniformly covered with regular round punctures with yellow setae located peripherally (Figs. 77, 84). Punctures spaced by 2-4 times their own diameter.

Elytra. Elytral intervals convex, shiny, densely punctate with small round punctures. Punctures separated by shiny elevated areas by approximately 1-4 their own puncture diameter (Fig. 93). Striae punctate with small punctures with short yellow setae/spaced by 2-4 punctures diameter, stria 9 closest to stria 10 about 2/3 the length of elytra.

Aedeagus. Sclerite of internal sac with long lateral process and rather short and straight basal part (Fig. 32).

Size range. Males length: 9.4-10.1 mm, width: 6.7-7.1 mm; females length: 9.2-10.6 mm, width: 6.6-7.3 mm.

Female. Female differs from male by having well developed tubercle in the middle of the frontoclypeal suture and less excavated pronotum anteriolaterally.

Etymology. This species name reflects the Afrikaans name, *gifboom*, of the evergreen Fynbos shrub *Hyaenanche globosa* (Gaertn.) Lamb. & Vahl which is endemic to the Gifberg area.

Differential diagnosis. This species is similar to *M. nitidus* in having a pronotum with regular round punctures (Figs. 77, 84), however the pronotum is more convex and the whole body shinier than *M. nitidus* (Fig. 18).

Habitat and distribution. This species was collected from the base of the Gifberg (Fig. 2) at the northern end of the Bokkeveld Escarpment Mountain Plateau just south of Vanrhynsdorp. These mountains consist of Bokkeveld Sandstone Fynbos (Mucina & Rutherford 2006). The habitat is rocky with shallow soil, poor in mineral content.

Macroderes greeni Kirby, 1818 (Figs. 10, 44, 58, 91)
Onthophagus greeni Kirby, 1818: 397.
Macroderes greeni: Westwood 1847: 228; Preudhomme de Borre 1880: 9; Péringuey 1901: 298; Janssens 1939: 27; Ferreira 1969: 320; Frolov & Scholtz 2005: 388.

Type locality. Type with no locality data.

Type material examined. None. Type is in BMNH (Frolov & Scholtz 2005). [1 male according to Frolov & Scholtz 2005]

Additional material examined. 1 m# (TMSA): "S. Afr, SW Cape Prov, Abrahamskraal farm, 33°.14' S – 18°.09' E / 25.8.1983, E-Y: 1976, groundtraps, 70 days, Endrödy, Penrith leg /groundtraps with faeces bait / *Macroderes greeni* (Kirby), det. A. Frolov, 2003"; 3 f#f# (TMSA): "S. Afr, S.W Cape, Struisbaai, 34°.46' S – 20°.03' E / 28. 8. 1983 / E-Y: 1987,

groundtrap, 60 days, Endrödy, Penrith leg / groundtraps with faeces bait / *Macroderes greeni* (Kirby), det. A. Frolov, 2003"; 1 m# and 7 f#f# (SANC): "LANGEBAAN, C P, 12 Km, SE, Farm Geelbek, A.L.V. Davis, *Macroderes* sp, det. CSIRO. DBRU / *Macroderes greeni* (Kirby), Frolov, det, 2003 but with different dates of collecting: 1f#: 6.VII.1979; 1 m# and 2 f#f#: 13.VIII.1979; 1 f#: 23.V.1979; 1 f#: 30.V.1979. 1 f#: 1-29. X. 79; 1 f#: 26. VI. 1979; 2 m#m# and 4 f#f# (SANC): "S. Afr, SW, CP, Modderrivier farm, nr Atlantis, 33° 28' S 18° 20' E, 29°.VI.1987, ALV. Davis / ex cattle dung baited, pitfall in Strandveld / *Macroderes greeni* (Kirby), Frolov, det, 2003"; 1 f# (SAMC): "*Macroderes greeni* / *Macroderes greeni* (Kirby), det. Frolov, 2003"; 1 m# (SAMC): "Saldanha Bay / greeni Kirby / *Macroderes greeni* Kirby, det. Frolov, 2003 / SAM-A 043223"; 2 m#m# (SAMC): "Mamre-Mamlesburg Rd, Sep. 1938 / *Macroderes greeni* Kirby, det. Frolov, 2003 / SAM-Col-A02321".

Size range. Males length: 9.6-11.6 mm, width: 6.2-8.0 mm; females length: 10.3-11.4 mm, width: 6.3-7.8 mm.

Differential diagnosis. This species shares the elytral punctuation shape of *M. arrowi*, *M. foveatus* and *M. cornutus* (Fig. 91), however, it can be differentiated by the large and rounded punctures of the pronotum (Figs. 44, 58) and from the latter two species by lacking the triangular concavity in the base of the pronotum which characterise those two species.

Habitat and distribution. This species occupies a small range which extends along the south-western coast of South Africa from Cape Agulhas in the southeast and up to Saldanha Bay in the northwest (Fig. 2). The area is situated within the Southwest Fynbos Bioregion which is considered as the core of the Fynbos Biome (Mucina & Rutherford 2006). It is mostly sandstone area dominated by winter rains with mean annual precipitation of 695 mm.

Macroderes leipoldti Abdalla & Deschodt, new species (Figs. 23, 33, 81, 85, 95)

Type locality. S.Africa, Western Cape Province, Farm: Kelkiewyn, 31.21500° S 19.67958° E.

Type material. Holotype, m# (UPSA). S.Africa, Western Cape Province, "Farm: Kelkiewyn, 31.21500° S 19.67958° E, 781 m, 21.08.2008-13.09.2008, Pig dung baited glycol

traps. C. Deschodt [printed] / HOLOTYPE, *Macroderes leipoldti,* Abdalla & Deschodt, 2018 [red label, printed]". Paratypes: 3 f#f# (TMSA), same data as holotype.

Holotype description. Holotype, m# (Fig. 23). Body length 8.4 mm, width 6.1 mm.

Head. Clypeal surface smooth between punctures, sometimes becoming shagreened close to punctures. Punctures shallow. Frontal suture pronounced, slightly angled, almost tuberculate in middle.

Pronotum. Convex, lateral margins round. Slight indentation laterally. Lateral border not punctate. Dorsal surface punctate with punctures less than one puncture diameter apart (Fig. 81). Area between punctures smooth. Dorsal part of eyes clearly visible.

Elytra. Elytral interstriae 1-8 slightly raised, surface shagreened with irregularly spaced shallow punctures, margins of punctures not carinate (Fig. 95). Striae punctate with punctures separated by 3-4 puncture diameters. Sutural interstria narrow with single row of punctures close together, all other elytral interstriae wider. Stria 9 long, 3/4 the length of elytron, interstria 10 2-3 times narrower than interstria 9 in the middle of elytron.

Aedeagus. Sclerite of internal sac short and slightly curved before the apex, with rather broad basal part and without lateral process (Fig. 33).

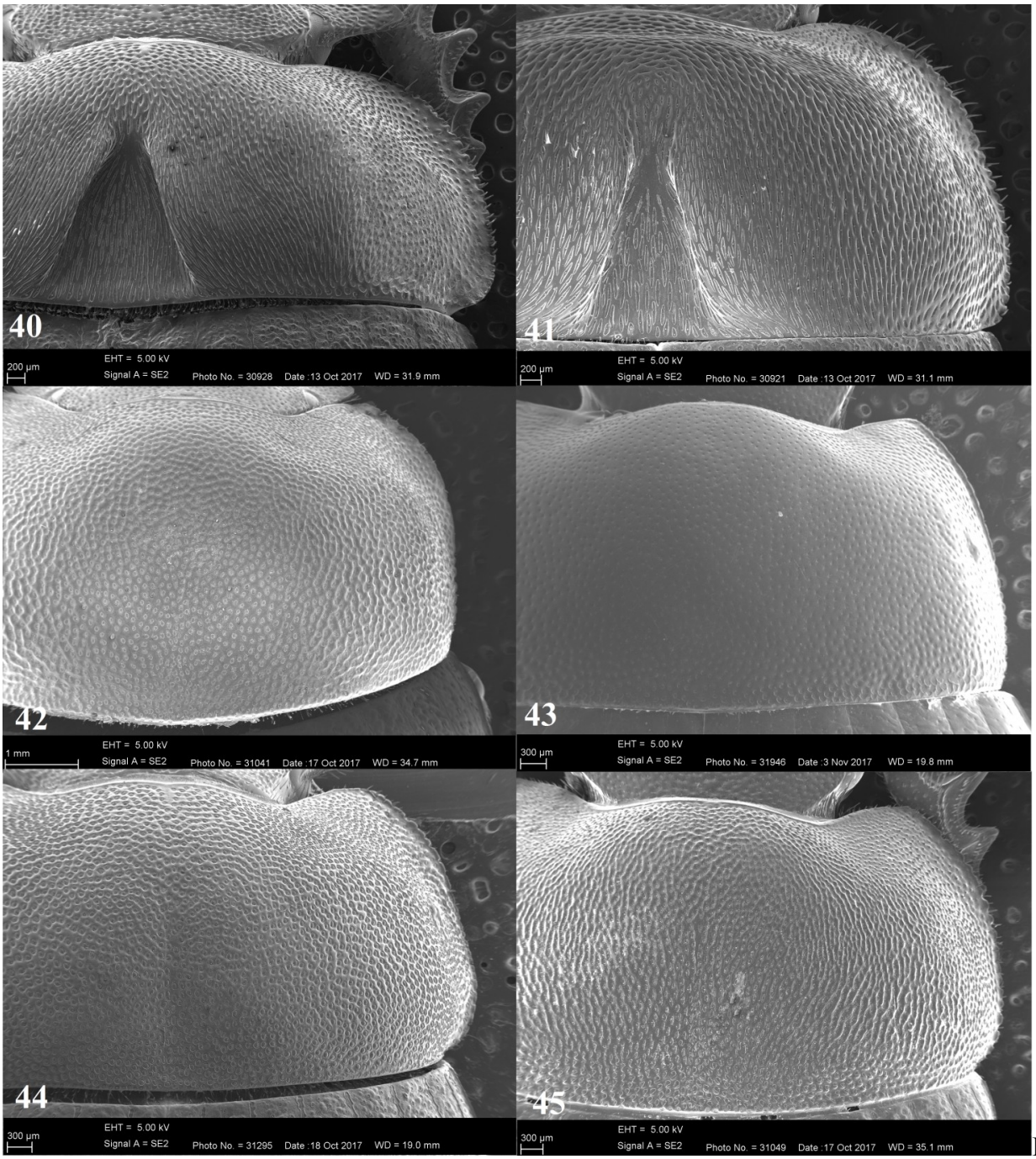
Size range. Female length: 8.0-8.4 mm, width: 5.7-6.1 mm.

Female. Female differs from male by the combination of the following characters: in the female the pronotum is less convex and appears broader anteriolaterally than in the male, and in the female the frontoclypeal suture is less developed than in the male with weakly developed tubercle in the middle.

Etymology. This species is named in honour of Dr. Christian F.L. Leipoldt, leading South African author, poet and an amateur botanist with a deep love of the Hantam Karoo.

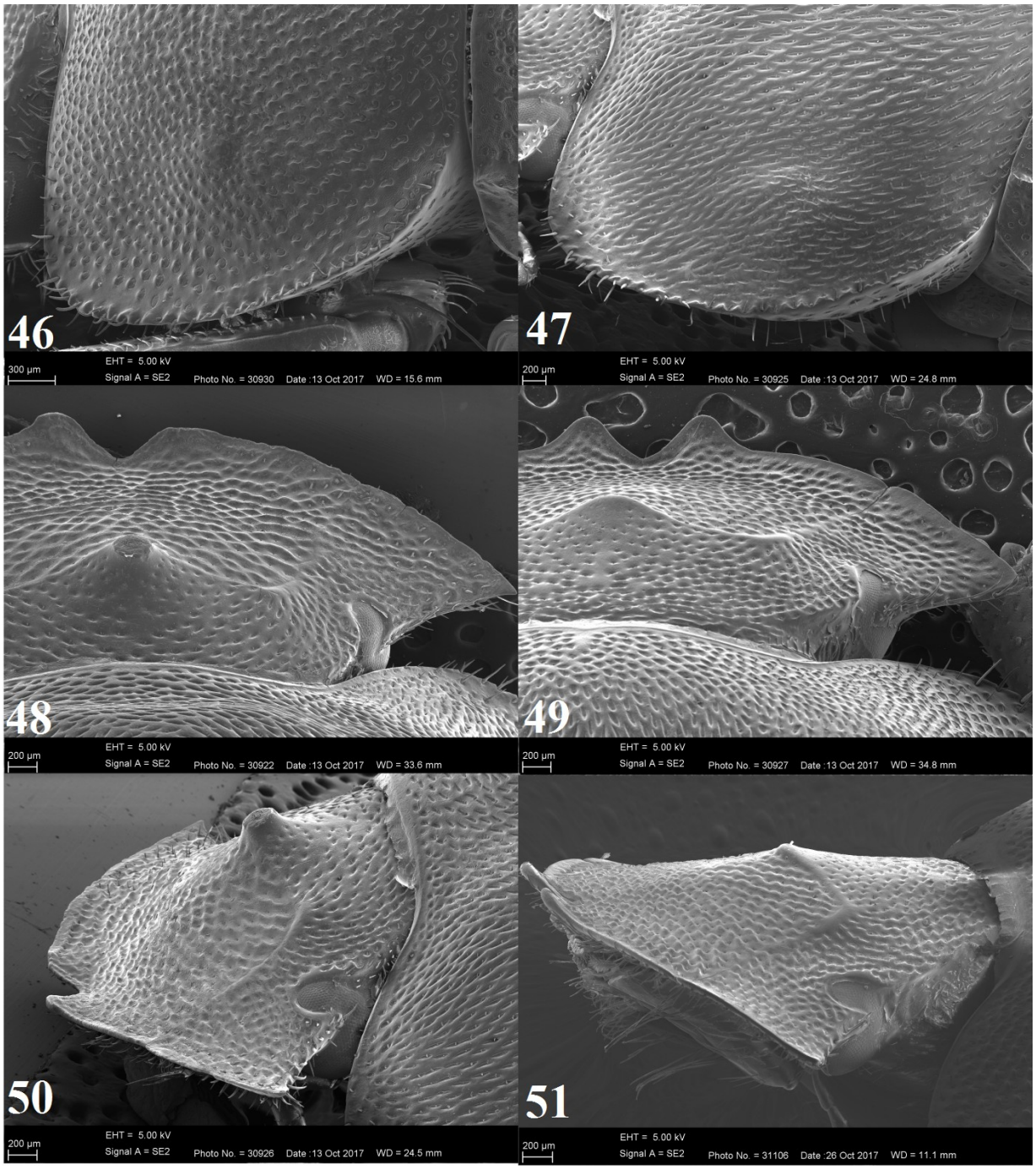
Differential diagnosis. This species is easily separated from others in the group by the puncture-associated seta being outside and close to the edge of the punctures. It is also short and

stubby. The pronotal punctures on the base are almost round and between 1.5 and 3 puncture diameters apart (Fig. 81).

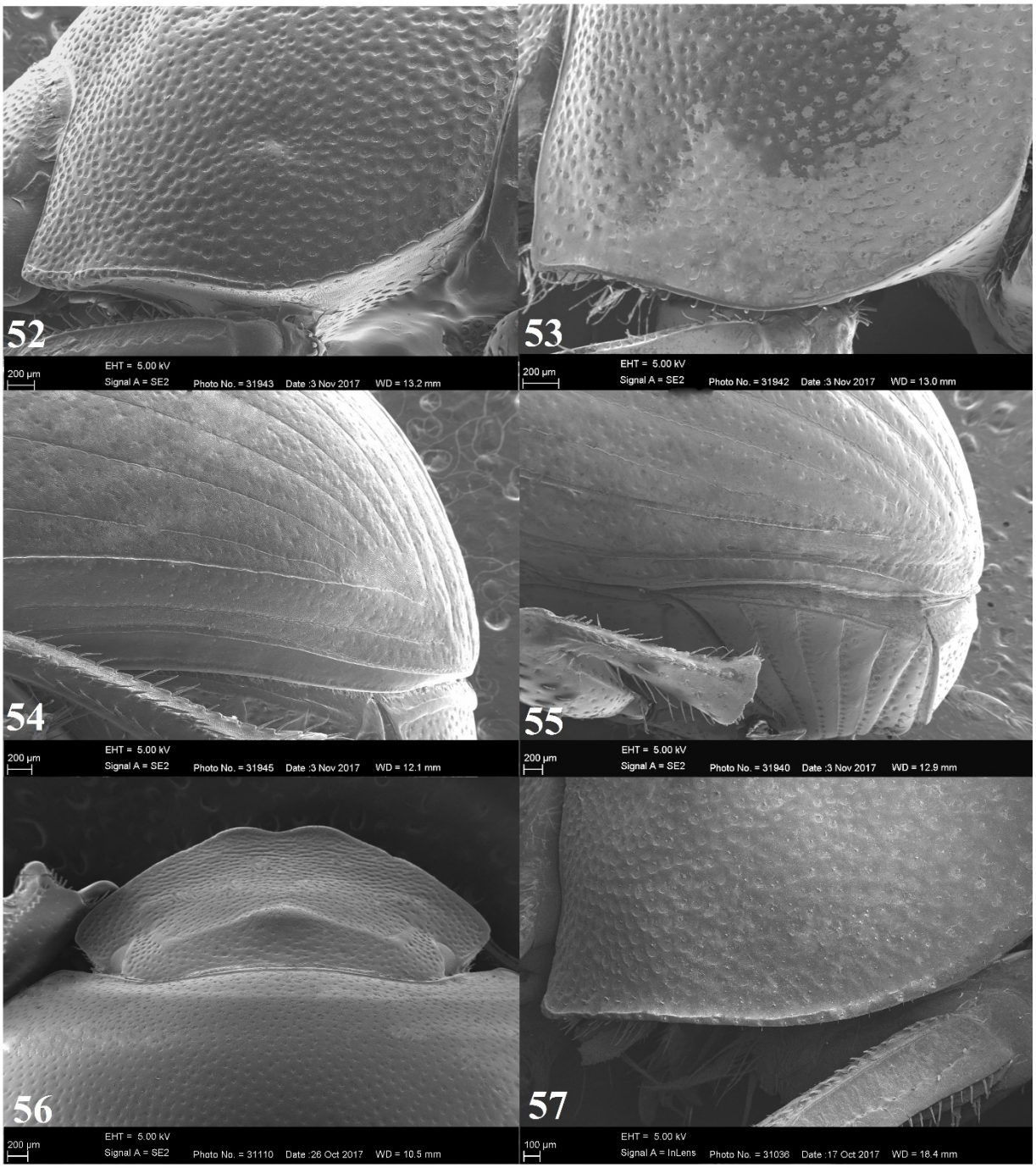


IGURES 40-45. Pronotum of *Macroderes* species. 40, *M. foveatus* Frolov & Scholtz, 2005; 41, *M. cornutus* Frolov & Scholtz, 2005; 42, *M. namakwanus* Frolov & Scholtz, 2005; 43, *M.*

politulus Preudhomme de Borre, 1880; 44, *M. greeni* (Kirby, 1818); 45, *M. endroedyi* Frolov & Scholtz, 2005.



FIGURES 46-51. Lateral side of pronotum (46, 47) and dorsal and lateral side of the head (48–51) of *Macroderes* species.46, 49, 51, *M. foveatus* Frolov & Scholtz, 2005; 47, 48, 50, *M. cornutus* Frolov & Scholtz, 2005.



FIGURES 52-57. Lateral side of pronotum (52, 53, 57), lateral elytra intervals (54, 55) and head in dorsal view (56) of *Macroderes* species. 52, *M. politulus* Preudhomme de Borre, 1880; 53, *M. minutus* Frolov & Scholtz, 2005; 54, *M. fornicatus* Sharp, 1880; 55, 57, *M. bias* (Olivier, 1789); 56, *M. undulatus* Preudhomme de Borre, 1880.

Habitat and distribution. This species occurs on the Hantam Plateau Dolerite Renosterveld (Fig. 2) as defined by Mucina & Rutherford (2006). However, the area where the species was collected should be defined as Hantam Karoo with loamy to sandy soils and a maximum of 175 mm of rain per year (Scholtz, personal observation).

Macroderes minutus Frolov & Scholtz, 2005 (Figs. 11, 53, 90)
Macroderes minutus Frolov &Scholtz, 2005: 385.

Type locality.RSA, Western Cape Prov., 15 km SW of Lutzville, 31° 40' 21.00" S 18° 13' 50.10" E.

Type material examined. Holotype, m# (TMSA): "RSA, Western Cape Prov., 15 km SW of Lutzville, A. Frolov & C. Deschodt leg [printed] / "AF-0046 (26), 6-1 0.IX.2003, 31° 40' 21.00" S 018° 13' 50.10" E" [printed] / HOLOTYPUS, *Macroderes minutus*, Frolov & Scholtz, 2003 [red label, printed]". Paratypes: 2 m#m# (UPSA, TMSA) with the same data as holotype; 1 m# (TMSA): "Zandkraal farm, 31° 42' S 18° 46' E, 12.IX.1987, coarse-sandy flat, Endrödy-Younga leg [printed] / PARATYPUS, *Macroderes minutus*, Frolov & Scholtz, 2003 [red label, printed]"; 1 m# (TMSA): "Namaqualand, Nuwerust farm, 31° 04' S 18° 17' E, 27.VIII.1979, singled on red sand, Endrödy-Younga leg [printed] / PARATYPUS, *Macroderes minutus*, Frolov & Scholtz, 2003 [red label, printed]"; 2 f#f# (UPSA): "5 km W of Rietpoort, 30° 58' S 17° 59' E, 3-11.IX.2003, Frolov & Deschodt leg [printed] / PARATYPUS, *Macroderes minutus*, Frolov & Scholtz, 2003 [red label, printed]"; 1 f# (TMSA): "10 km N of Bitterfontein, 30° 57' S 18° 13' E, 11.IX.1985, from sand pit, Endrödy-Younga leg [printed] / PARATYPUS, *Macroderes minutus*, Frolov & Scholtz, 2003 [red label, printed]"; 1 f# (UPSA): "25 km N of Vanrhynsdorp, 31° 23' S 18° 38' E, 5-11.IX.2003, Frolov & Deschodt leg [printed] / PARATYPUS, *Macroderes minutus*, Frolov & Scholtz, 2003 [red label, printed]".

Size range. Male length: 7.0-8.9 mm, width: 5.7-6.3 mm; females length: 8.5-8.9 mm, width: 5.0–5.9 mm.

Differential diagnosis. This species can be separated from others in the group by having ovoid pronotal punctures that are relatively close together (between 1 and 1.5 puncture diameters along the minor axis).

Habitat and distribution. This species occurs on the Namaqualand Strandveld vegetation type (Fig. 2). Specimens were collected in habitats featuring deep sand (Deschodt, personal observation).

Remarks. Frolov & Scholtz (2005) tentatively lumped specimens from extreme localities and vegetation types, such as Lutzville (Namaqualand Strandveld), Knersvlakte (Central Knersvlakte Vygieveld) and the top of the Cederberg range (Cederberg Sandstone Fynbos) together. Electron micrographs of specimens in the type series of *M. minutus* from different localities and further *M. minutus* material collected subsequent to the description of *M. minutus* were compared. It seems that the complex has been subjected to microhabitat speciation (speciation where species are still morphologically similar and geographical neighbours, but separated from each other by occupying different habitat types such as soil and/or vegetation type). Here we split the complex into three independent species (*M. minutus*, *M. cederbergensis* new species and *M. leipoldti* new species).

The holotype of *M. minutus* is from near Lutzville [31° 33' S 18° 20' E] and thus, specimens from there should be considered to be true *M. minutus*. Since the description of *M. minutus* in Frolov & Scholtz (2005) is based on the holotype, that species description is still applicable and need no changes, only the amended type series and short notes on its distribution are given here.

Macroderes mutilans Kolbe, 1908 (Figs. 12, 34, 74)
Macroderes mutilans Kolbe, 1908: 130; Péringuey 1908: 692; Janssens 1939: 29; Ferreira 1969: 322; Frolov & Scholtz 2005: 381.

Type locality. Brit, SW, Africa, Kl, Namaland, Steinkopf [29° 15' S 17° 44' E].

Type material examined. None. Type (1 f#) is in ZMHB (Frolov & Scholtz 2005).

Additional material examined. 3 m#m# and 9 f#f#:"RSA, Northern Cape Prov., 8 Km S of, Kamieskroon, A. Frolov & C. Deschodt leg / "AF-0030(10), 1-13. IX. 2003, 30° 17' 23.76" S 017° 57' 20.69" E" / *Macroderes mutilans* Kolbe, Frolov det, 2003", 1 m# and 1 f# (TMSA); 1 m# and 7 f#f# (UPSA); 1 m# and 1 f# (SANC); 9 m#m# and 15 f#f# with same data but the database and coordinates: 1 m# and 2 f# (UPSA): "AF-0030(10), 30° 15' 25.29" S 017° 55' 58.83" E", 8 m#m# and 13 f#f# (UPSA): "AF-0030(9), 30° 17' 17.37" S 017° 5'6 59.12" E"; 1 m# (TMSA): "10 m, E Springbok, Namaqualand, III.1958, G.van Son / *Macroderes mutilans* Kolbe, det. A. Frolov, 2003"; 1 m# (TMSA): "Springbok, CP, IX.65, L, Vari / *Macroderes mutilans* Kolbe, det A. Frolov, 2003"; 1m# (UPSA): "RSA, Northern Cape Province, Kamiesberg, 20 Km, NE of Garies, 30° 4' 28" S 018° 05' 9" E, 13.8.2015, baited pitfall trap: pig dung,. C. Deschodt & W.P. Strümpher leg"; 2 f#f# (UPSA): "RSA, Western Cape Province, 10 Km, West of Rietpoort, 30°.97 S 017°.99 E, 13.8. 2015, baited pitfall trap: pig dung, C. Deschodt & W.P. Strümpher leg"; 3 m#m# and 3 f#f# (UPSA): "RSA, Northern Cape Province, 51 km, S.W, Springbok, 29.74301° S 017.52547° E, 12. 8. 2015, baited pitfall trap: pig dung, C. Deschodt & W.P. Strümpher leg"; 1 m# (UPSA): "RSA, Northern Cape Province, Springbok, 4 Km W, 29.67914° S 017.85134° E, 12. 8. 2015, baited pitfall trap: pig dung, C. Deschodt & W.P. Strümpher leg"; 1 m# and 2 f#f# (UPSA): "Kamieskroon, 30.25747° S 17.93525° E, 28. viii. 2004, C. Deschodt & M. Deschodt leg"; 1 m# and 1f# (SAMC): "RSA, Northern Cape Prov, 8 Km S of, Kamieskroon, A. Frolov & C. Deschodt leg / "AF-0030 (10), 13. IX. 2003, 30° 17' 23.76" S 017° 57' 20.69" E" / *Macroderes mutilans* Kolbe, Frolov det, 2003 / SAM-Col-058293".

Size range. Males length: 9.6-12.6 mm, width: 7.2-8.9 mm; females length: 9-12.1 mm, width: 6.8–8.9 mm.

Differential diagnosis. Due to it is flatter elytra (Fig. 74) *M. mutilans* resembles *M. bias* and *M. fornicatus*, nevertheless, it can be easily distinguished from them by impunctate lateral border of pronotum and distinct differences in the shape of the internal sac sclerite (Fig. 34).

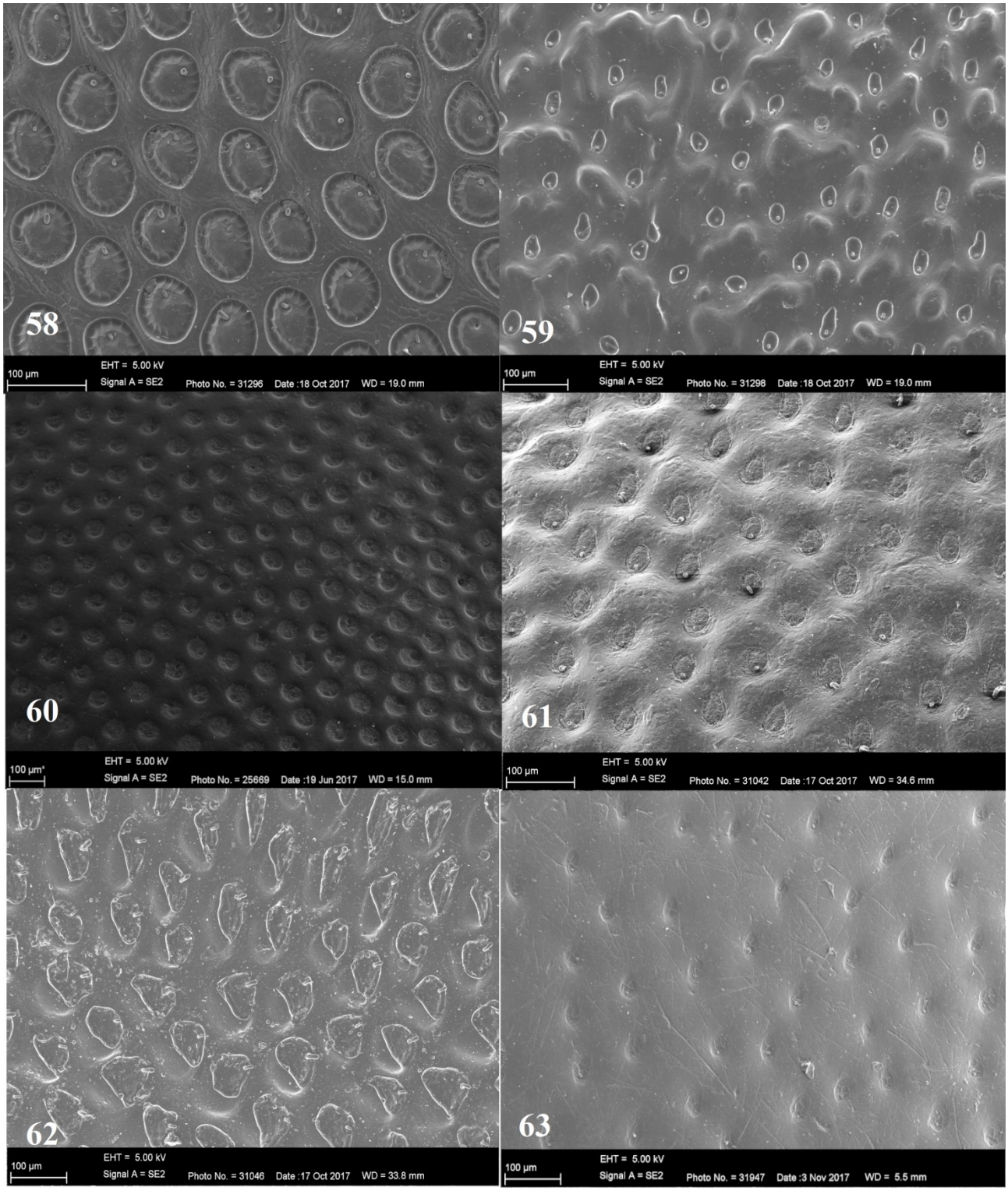
Habitat and distribution. This species was collected from localities confined to the Namaqualand region (Fig. 2). The area is part of the Succulent Karoo ecoregion which comprises two main bio-geographical domains: The Southern Karoo domain which is inland in South Africa and Namaqualand – Namibia domain which stretches from the west cost of

Namibia to the west coast of South Africa and includes the areas of Richtersveld, Sandveld, Hardveld and Kamiesberg. The area is semi desert, characterised by a succulent vegetation and winter rainfall.

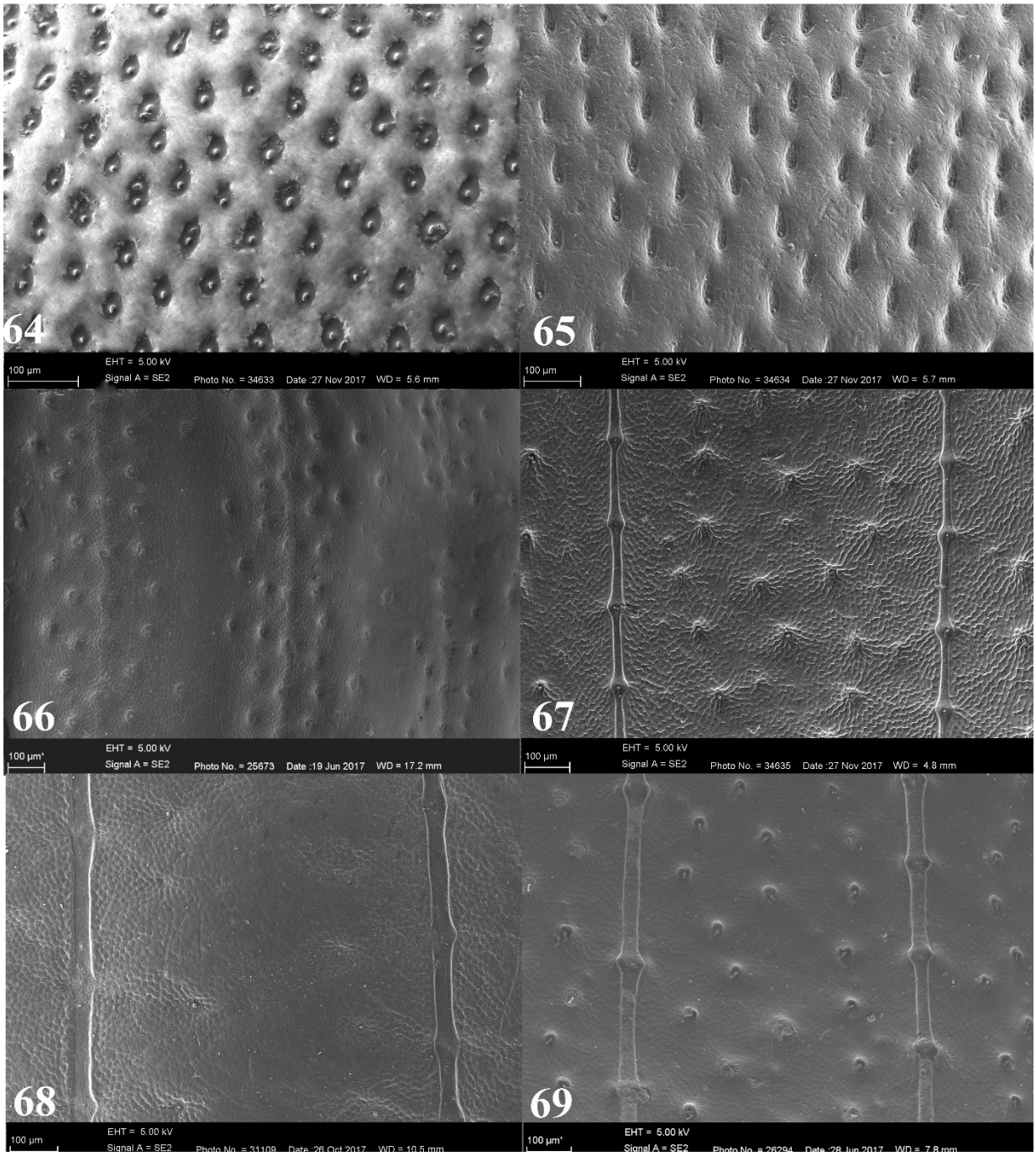
Macroderes namakwanus Frolov & Scholtz, 2005 (Figs. 13, 35, 42, 61, 75)
Macroderes namakwanus Frolov & Scholtz 2005: 388.

Type locality. RSA, Western Cape Prov., Hoekbaai, 31° 09' 26.07" S 017° 45' 55.70" E.

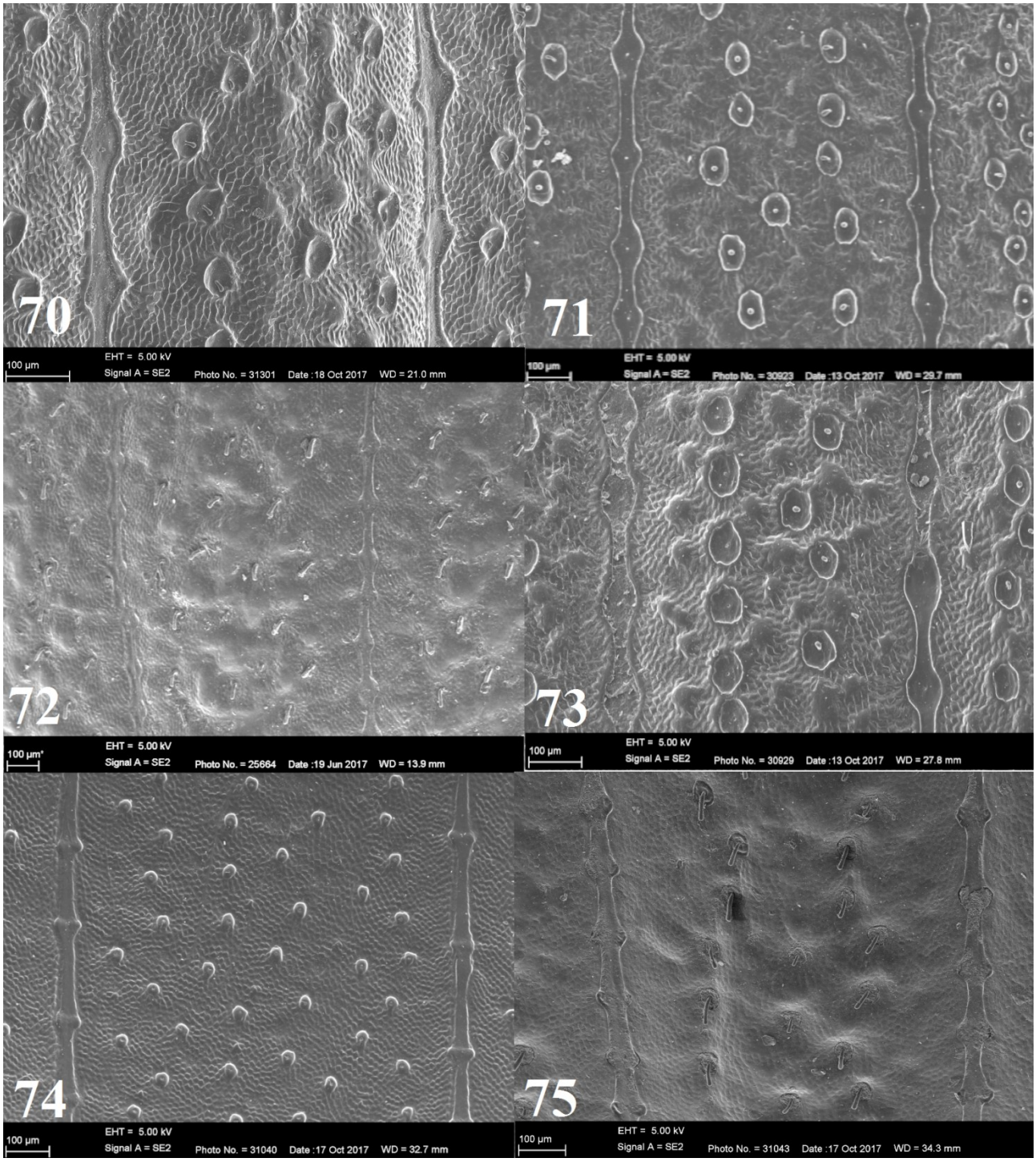
Type material examined. Holotype, m# (TMSA): "RSA, Western Cape Prov., Hoekbaai, A. Frolov & C. Deschodt leg [printed] / "AF-0039 (19), 4-11. IX. 2003, 31° 04' 26.07" S 017° 45' 55.70' E '" [printed] / HOLOTYPUS, *Macroderes namakwanus*, Frolov & Scholtz, 2003 [red label, printed]"; Paratypes: 1m# (TMSA): "S. Afr, Namaqualand, Brakriver mouth, 36°.06' S–17°.44' E [printed] / 25. 8. 1979 / E-Y: 1597, groundtraps, 63 days, Endrödy-Younga leg [printed] / PARTYPUS, *Macroderes namakwanus*, Frolov& Scholtz, 2003 [red label, printed]"; 1 m# (TMSA): "S. AFR, Namaqualand, Hoekbaai, 2 Km, E NE, 31°. 11' S 17°. 47' E [printed] / 27. 8. 1979 / E-Y: 1612, white sand, night, Endrödy-Younga leg [printed] / PARATYPUS, *Macroderes namakwanus*, Frolov & Scholtz, 2003 [red label, printed]"; 1 m# (TMSA): "S. Afr, Namaqualand, Kotzerus, 30° 57' S–17°.50' E [printed] / 23. 8. 1979 / E-Y: 1581, white dune, day , Endrödy-Younga leg [printed] / PARATYPUS, *Macroderes namakwanus*, Frolov & Scholtz, 2003 [red-printed]"; 1 f# (TMSA): "S. Afr, Richtersveld, Klein Helskloof, 28°.51' S – 17°.24' E [printed] / 8.9.1976 / E-Y: 1239, groundtraps, 32 days, Endrödy-Younga leg [printed] / groundtrap with faeces bait [printed] / PARATYPUS, *Macroderes namakwanus*, Frolov & Scholtz, 2003 [red label, printed]".



FIGURES 58-63. Punctuation of the base of pronotum of *Macroderes* species. 58, *M. greeni* (Kirby, 1818); 59, *M. arrowi* Janssens, 1939; 60, *M. bias* (Olivier, 1789); 61, *M. namakwanus* Frolov & Scholtz, 2005; 62, *M. endroedyi* Frolov & Scholtz, 2005; 63, *M. politulus* Preudhomme de Borre, 1880.



FIGURES 64-69. Punctuation of the base of pronotum (64, 65) and sculpture of second elytra intervals (66-69) of *Macroderes* species. 64, *M. amplior* Frolov & Scholtz, 2005; 65, 67, *M. fornicatus* Sharp, 1880; 66, *M. bias* (Olivier, 1789); 68, *M. undulatus* Preudhomme de Borre, 1880; 69, *M. nitidus* Harold, 1877.



FIGURES 70-75. Sculpture of second elytra intervals of *Macroderes* species. 70, *M. arrowi* Janssens, 1939; 71, *M. cornutus* Frolov & Scholtz, 2005; 72, *M. endroedyi* Frolov & Scholtz, 2005;73, *M. foveatus* Frolov & Scholtz, 2005; 74, *M. mutilans* Kolbe, 1908; 75, *M. namakwanus* Frolov & Scholtz, 2005.

Additional material examined. 2 m#m# and 3 f#f# (UPSA): "South Africa, Western Cape Province, 6 km N of, Kotzerus, 30° 69' 26.11" S 017° 86' 9.83" E, 12. 8. 2015, leg. C. Deschodt & W. P. Strümpher"

Size range. Males length: 10.4-12.8 mm, width: 7.0-8.7 mm; females length: 11.7-12.5 mm, width: 8.0-9.0 mm.

Differential diagnosis. *M. namakwanus* is in habitus similar to *M. endroedyi* (Fig. 13) however, it is differentiated by the combination of the following characteristics: Pronotum regularly punctate lacking the distinct tubercle in between (Fig. 61) and no shiny tubercles on the elytra (Fig. 75)

Habitat and distribution. See distribution under *M. mutilans* (Fig. 2)

Macroderes nitidus Harold, 1877 (Figs. 14, 69)

Macroderes nitidus Harold, 1877: 97; Preudhomme de Borre 1880: 11; Péringuey 1901: 302; Janssens 1939: 28; Ferreira 1969: 322; Frolov & Scholtz 2005: 384.

Type locality. S.Africa, Western Cape Province, O[o]rlog Rivier.

Type material examined. Lectotype, present designation, f# (ZMHB): "O[o]rlog Rivier, Meyer, Nr.57079 [pale blue label] / Lectotype, *Macroderes nitidus* Harold, 1877, des Deschodt & Abdalla, 2018 [red label, printed]". Paralectotypes: 6 f#f# (ZMHB): "Promont. b. sp. Meyer, Nr.50568 [printed] / "Paralectotype, *Macroderes nitidus* Harold, 1877, des Deschodt & Abdalla, 2018 [red label, printed]"; 5 f#f# (ZMHB): "O[o]rlog Rivier, Meyer, Nr.57079 [printed]" / Paralectotype*, Macroderes nitidus* Harold, 1877, des Deschodt & Abdalla, 2018 [red label, printed]".

Additional material examined. 5f#f# (UPSA): "RSA, Western Cape Province, Nieuwoudtville 12km E; 20.vii.2017, 31° 22' 37.69" S 19° 13' 51.51" E, 745 m, Baited pitfall trap: pig dung, leg. C. Deschodt, W.P. Strümpher".

Size range. Female length: 8.2-11.5 mm, width: 6.3-7.3 mm.

Differential diagnosis. This species appears similar to *M. soleiana* new species but is easily separated from it by being smooth and not shagreened on the interstriae (Fig. 67). The habitus is shiny black in appearance (Fig. 14).

Redescription. Lectotype, f# (Fig. 14). Body length 10.3 mm, body width 7.1 mm.

Head. Genae right-angled. Frontal suture indistinct, more pronounced medially. Genal sutures faint. Dorsal surface of clypeus punctate posterior of frontal suture, rugose anteriorly.

Pronotum. Convex. Base without depression in the middle. Anterior angles obtuse, posterior angles rounded. Lateral border not punctate. Dorsal surface with small, round, regular punctures; close together at base, becoming shallower and further apart anteriorly; surface smooth and shiny.

Elytra. Elytral interstriae 1–8 flat and shiny punctate, punctures shallow, punctures separated by 1–2 puncture diameters, margins smooth. Striae punctate with punctures separated by 2-4 puncture diameters, sides straight, narrower than punctures (Figs. 14, 69). Stria 9 is 3/4 the length of elytron, close to stria 10; interstria 9 1/4 as wide as interstria 8 in the middle.

Habitat and distribution. Mucina and Rutherford (2006) describe the area around Calvinia where the Oorlogskloof River flows and where the species was recovered as Hantam Karoo in the Succulent Karoo biome (Fig. 2). This area is around 1000 m a.s.l.

Remark. Frolov & Scholtz (2005) examined the type series of *M. nitidus*. They concluded that the Cederberg specimens were *M. nitidus*, included them as additional material examined, and based their redescription of *M. nitidus* partly on this material. Those specimens actually belong to *M. soleiana* new species described earlier in this paper.

The specimens in the type series (collected by Meyer) are probably from two localities: “Promont. b. sp.” and “Orlog Rivier”. Meyer practiced medicine at Calvinia [31° 28' S 19°46' E] and had sent plant and insect specimens collected from that area to Berlin (Gunn & Codd 1981). “Orlog Rivier” most likely refers to the Oorlogskloof River that flows past Calvinia. The locality Cap bon. spei [Cape of Good Hope] given in Harold (1877) is probably derived from the

Promont. b. sp. [Promontorii Bon Spei] specimens in the type series and most likely those specimens are also from the same area close to Calvinia. Following this information, Deschodt and Strümpher collected a series (5 mentioned above) of *M. nitidus* in an area close to the Oorlogskloof River [31° 22' 37.69" S 19° 13' 51.51" E] on 20th of July 2016 (Fig. 101). These recently collected specimens (in UPSA) and the type series housed in the ZMHB are the only specimens known for the species.

Macroderes oreatus Abdalla & Deschodt, new species (Figs. 19, 36, 78, 86, 96)

Macroderes sp.: Sole & Scholtz 2010: 636.

Type locality. S. Afr., Northern Cape Province, Richtersveld National Park, Armmanshoek, , 28.41756° S 17.07902° E.

Type material. Holotype: m# (TMSA): "Armmanshoek, Richtersveld NP, 28.41756° S 17.07902° E, 13.iv.2005 / 623 m, C. Deschodt & A. Deschodt [printed] / HOLOTYPE, *Macroderes oreatus*, Abdalla & Deschodt, 2018 [red label, printed]"; Paratypes: 5 f#f#, same data as holotype, 1f# (TMSA), 2f#f# (UPSA), 2f#f# (SANC).

Holotype description. Holotype, m# (Fig. 19). Body length 7.2 mm, width 4.9 mm. Specimen is teneral.

Head. Genae right-angled. Frontal suture distinct, curving slightly, no tubercle. Genal sutures barely discernible. Dorsal surface of clypeus behind frontal suture punctate punctures small, irregular and separated by 1-3 puncture diameters, gradually becoming rugose proximally.

Pronotum. Convex, lateral margins round. Anterior lateral angles almost right-angled, posterior lateral angles rounded. No excavation anterolaterally. Lateral border not punctate. Dorsal surface shagreened to matte, with regular punctures separated by 1-2 puncture diameters (Figs. 78, 86).

Elytra. Elytral interstriae 1-8 even, shagreened, irregularly punctate, punctures irregularly sized, separated by 0.5-2 puncture diameters, margins of punctures not carinate (Fig. 96). Striae

punctate with punctures separated by 2-4 puncture diameters. Sutural interstria narrow with single row of punctures up to apex, all other elytral interstriae wider, with 2-3 irregular rows of punctures. Stria 9 long, 3/4 the length of elytron; interstria 10 is 2-3 times narrower than interstria 9 in the middle of elytron.

Aedeagus. Sclerite of the internal sac straight, with weakly developed lateral process. (Fig. 36)

Size range. Female length: 7.0-7.2 mm; width: 4.5-4.9 mm.

Female. Female differs from male by having less developed frontal suture and the elytral striae 1-8 being less shagreened and shinier than in males.

Etymology. Oreads are Greek mythological mountain nymphs.

Differential diagnosis. Superficially similar to species from the *M. minutus* group but can be separated by the more oval body shape (Fig. 19) and by having a longer elytral stria 9.

Habitat and distribution. This species was collected in an isolated, mesic ravine (Armmanshoek) in the Vanderster Mountains in the Richtersveld National Park, South Africa (Fig. 2). Mucina & Rutherford (2006) classify this area as the Stinkfonteinberge Quartzite Fynbos vegetation type. The soils are predominantly loamy. It receives approximately 200 mm rain per year. Coastal fogs occur between 10 and 20 days a year.

Remarks. Three specimens were sequenced for five gene regions (A, cytochrome oxidase I; B, 16S ribosomal RNA; C, 28S rRNA domain 2; D, 28S rRNA domain 3; and E, the CPSase region of CAD (carbamoyl–phosphate synthetase 2, aspartate transcarbamylase, and dihydroorotase)). The sequences can be found in GenBank (submitted by Sole & Scholtz 2010) with the following accession numbers: specimen 1, A: GQ290039 B: GQ289687 C: GQ289821 D: GQ289905 E: GQ289974; specimen 2, A: GQ290040 B: GQ289688 C: GQ289822 D: GQ289906 E: no sequence; specimen 3, A: GQ290041 B: GQ289689 C: GQ289823 D: GQ289907 E: GQ289975. A label with GenBank accession numbers has been added to each of the three specimens. Specimens were dissected during DNA extraction and are kept in ethanol.

Macroderes politulus Preudhomme de Borre, 1880 (Figs. 15, 43, 52, 63, 92)

Macroderes politulus Preudhomme de Borre 1880: 11; Péringuey 1901: 302; Janssens 1939: 29; Ferreira 1969: 322; Frolov & Scholtz 2005: 383.

Type locality. South Africa, Caffr[ar]ia.

Type material examined. None. Type (1 male) is in IRSNB (Frolov & Scholtz 2005).

Additional material examined. 1 m# (SANC): "*Macroderes politulus*, Somerset E [East], [32° 45' 43.95" S 25° 32' 28.51" E], Jan. 84"; 2 m#m# and 1 f#f# (UPSA): "S. Africa, SW Cape, Oranjefontein farm, nr Darling, 33° 25' S 18° 26' E, 28.VIII.1987, ALV Davis / ex cattle dung baited pitfall in pasture"; 1 m# same data but the date of collection: 3.VII. 1987; 3 f#f# same data but the dates of collections as follows: 1 f#: 7.VII. 1987, 1 f#: 29.VII.1987, 1 f#: 17 Sept. 1987.

Size range. Males length: 9.0-12.2 mm, width: 6.3-8.6 mm; females length: 9.7-12.2 mm; width: 6.4-8.7 mm.

Differential diagnosis. This species is close to *M. porselinus* new species in having elongated punctures of the pronotum (Fig. 63) and a punctuated lateral border of pronotum (Fig. 43). It is separated from *M. porselinus* new species by its rather narrower and less convex pronotum.

Habitat and distribution. The range of the species is restricted to an area located within the Fynbos Biome and characterised by Renosterveld vegetation types in the Western Cape Province (Fig. 2). These habitats are represented as one of the most threatened areas due to the intensive cultivation and removal of indigenous plants (Mucina & Rutherford 2006), which in turn might threaten the associated fauna.

Macroderes porselinus Abdalla, new species (Figs. 17, 37, 79, 87, 97)

Type locality. South Africa, Western Cape Province, Porselinberg, 33° 27.597' S 18° 58.765' E.

Type material. Holotype, m# (TMSA): "South Africa, Western Cape Province, Porselinberg, 33° 27.597' S 18° 58.765' E, 03-2015, baited pitfall trap: pig dung, F. Roets leg / HOLOTYPE, *Macroderes porselinus*, Abdalla, 2018, [red label, printed]". Paratype: 1 f# (TMSA) same data as holotype.

Holotype description. Holotype, m# (Fig. 17). Body length 11.00 mm, body width 7.9 mm.

Head. Clypeus broad, semicircular, bordered, by two teeth on anterior edge wider than longer. Genae right angled. Frontoclypeal suture slightly curved without tubercle in the middle. Frons densely punctuate with small round punctures. Clypeogenal suture present but poorly defined towards the clypeal edge. Clypeus densely punctuate with fine punctures becoming rugose towards the clypeal frontal margin.

Pronotum. Form trapezoidal, convex and broad, matte, more or less shagreened, width greater than length, not excavated anterolaterally. Pronotal lateral edges rounded width twice as wide as length delimited with narrow borders. Borders crenulated, punctate and partially visible in dorsal view, base not bordered, anterior angle right slightly extended forwards, posterior angle obtuse. Pronotal base lacking a longitudinal depression. Pronotal surface densely punctate, medially punctures are elongate, becoming large, round towards the pronotal lateral edges and the base and smaller towards the pronotal frontal margin (Figs. 79, 87). Punctures with short yellow setae. Punctures spaced by more or less elevated areas about 1-1.5 times their own diameter.

Elytra. Elytra intervals convex, matte, rugose, granular, sparsely punctate with irregular large round punctures interspersed with smaller ones. Punctures separated by elevated areas about 2-5 times their puncture diameters. Striae narrow, punctate with small punctures spaced by 2-6 times their own diameter (Fig. 97). Stria 9 short, close to stria 10, 2/3 the length of the elytron.

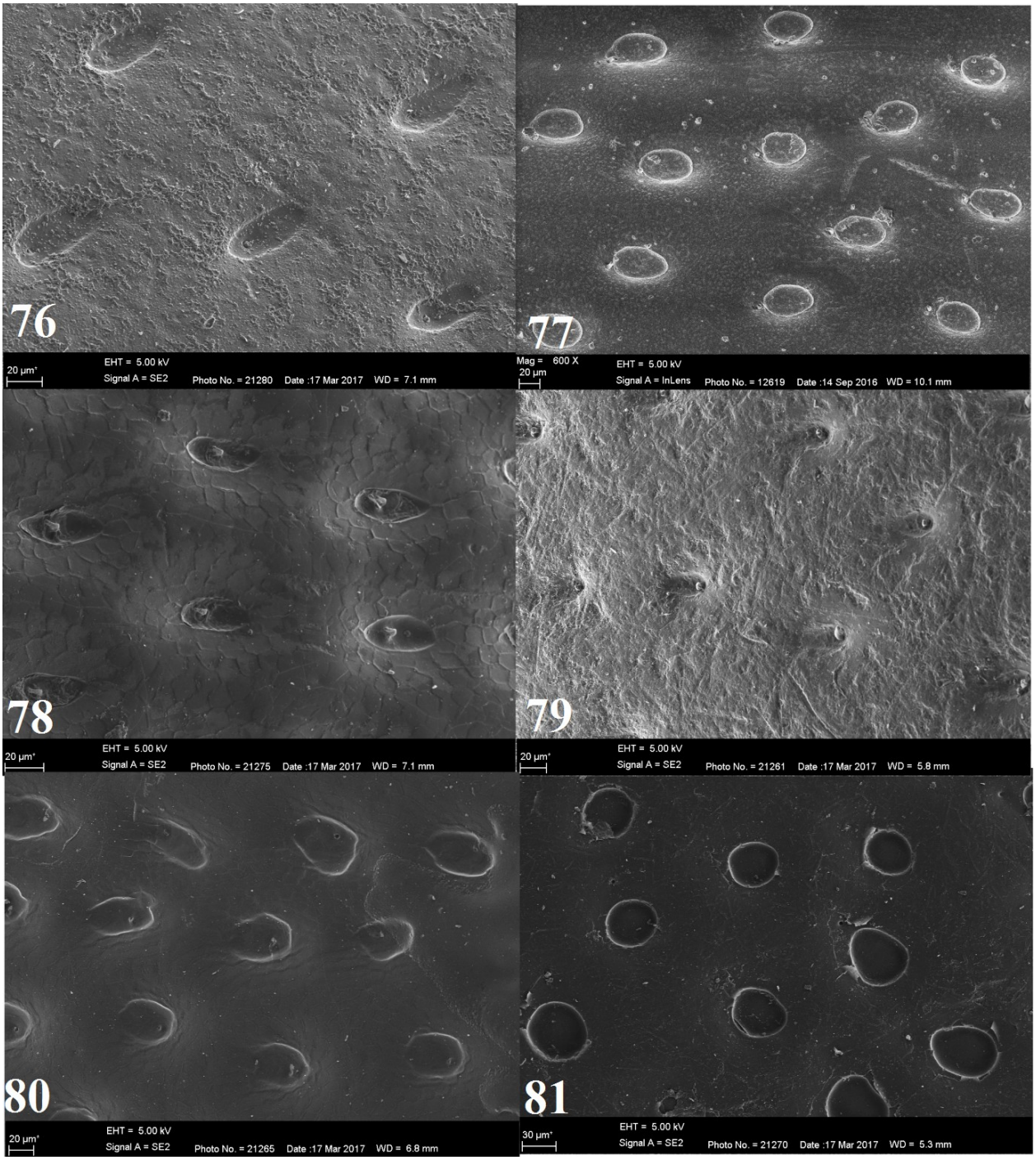
Aedeagus. Sclerite of internal sac straight, rather broad basally and without lateral process (Fig. 37).

Size range. Female length: 10.9 mm, width: 7.6 mm.

Female. Female differs from the male by having frontoclypeal suture with small developed tubercle in the middle.

Etymology. Named after the Porselinberg, the type locality of the species.

Differential diagnosis. This species is most similar to *M. politulus* in that its pronotum has elongate punctures (Figs. 79, 87) but it differs in that it has a convex and broad pronotum.



FIGURES 76-81. Punctuation of the base of pronotum of *Macroderes* species. 76, *M. cederbergensis* Abdalla & Deschodt, new species; 77, *M. gifboomi* Abdalla & Scholtz, new species; 78, *M. oreatus* Abdalla & Deschodt, new species; 79, *M. porselinus* Abdalla, new species ; 80, *M. soleiana* Abdalla & Deschodt, new species; 81, *M. leipoldti* Abdalla & Deschodt, new species.

Habitat and distribution. Porselinberg is a mountain in the Western Cape Province (Fig. 2). The land is mostly covered by croplands; however, there is some natural vegetation. Soil is sandy with a loamy texture (Mucina & Rutherford 2006).

Macroderes soleiana Abdalla & Deschodt, new species (Figs. 21, 38, 80, 88, 98)
Macroderes nitidus Harold, 1877: 384 (partim, sensu Frolov & Scholtz 2005)

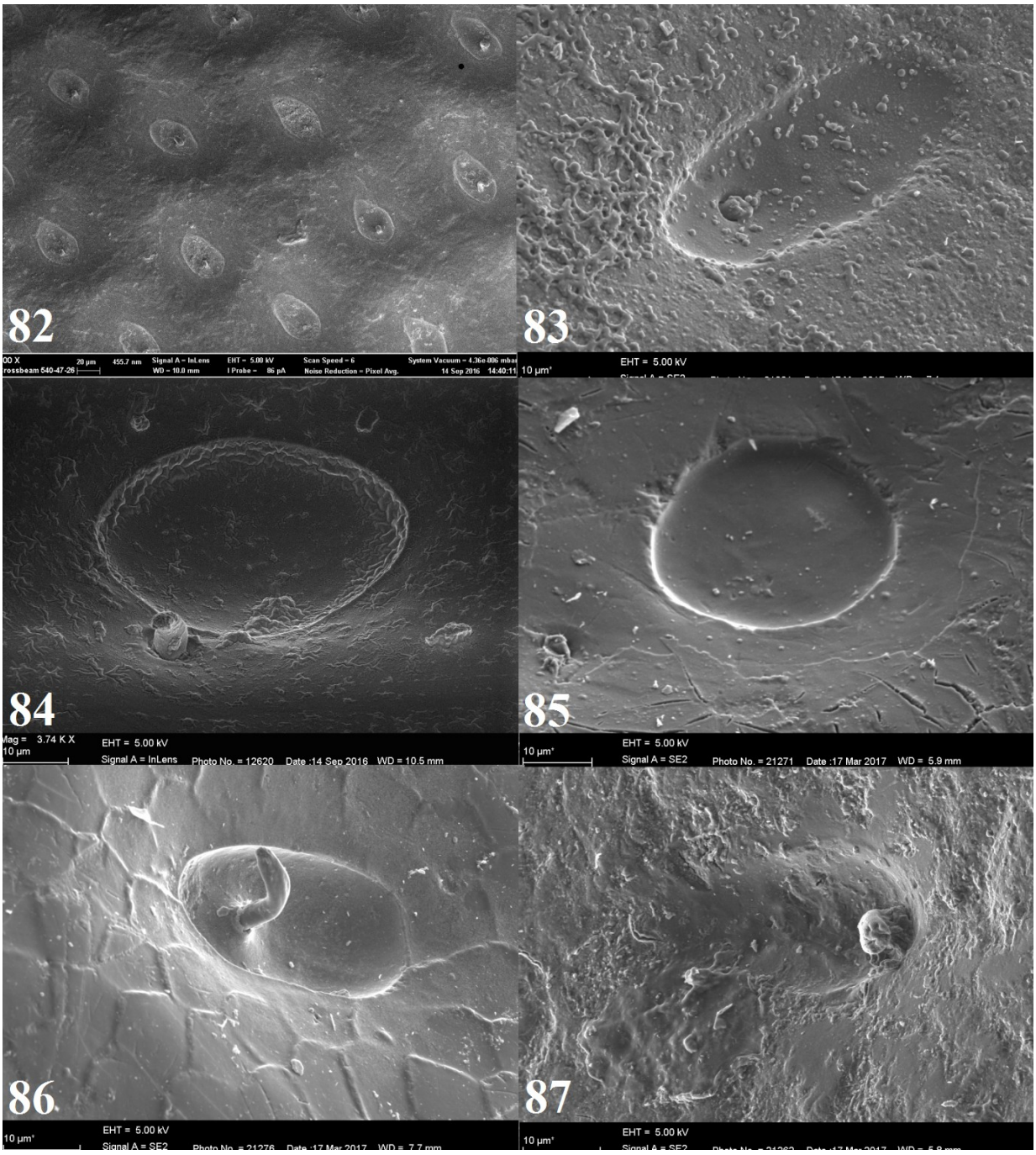
Type locality. South Africa, Western Cape Province, Cederberg Range, east track, 32° 29' S 19° 22' E.

Type material. Holotype, m# (TMSA): "South Africa, Western Cape Province, Cederberg Range , east track, 800 m, 32° 29' S 19° 22' E, 21.VIII.1983, groundtrap with feaces bait, 66 days, Endrödy-Younga and Penrith leg [printed] / HOLOTYE, *Macroderes soleiana,* Abdalla & Deschodt, 2018 [red label, printed]". Paratypes: 3 m#m# and 2 f#f# (TMSA), same data as holotype; 26 specimens with the same data as holotype but coordinates and elevation: 1 m#m# and 8 f#f# (TMSA): 32° 24' S 19° 25' E, 650 m, 1 m# and 2 f#f# (UPSA), 6 f#f# (TMSA); 2 m#m# and 3 f#f# (TMSA): 32° 27' S 19° 23' E, 1, 100 m; 4 m# and 5 f#f# (TMSA): 32° 23' S 19° 24' E, 650 m; 1 m# and 2 f#f# (TMSA): 32° 22' S 19° 24' E, 650 m; 7 m#m# and 6 f#f# (UPSA): "South Africa, Ramakraal, 32. 41883° S 019.43167° E, 17. 08. 2015, C. Deschodt & W. P. Strümpher leg [printed] / PARATYPE, *Macroderes soleiana*, Abdalla & Deschodt, 2018, [red label, printed]"; 1 m# and 2 f#f# (UPSA): "South Africa, Western Cape Province, Leopard Rock, 32.45506° S 019.40608° E,17.08.2015, C.Deschodt & W. P. Strümpher leg [printed] / PARATYPE , *Macroderes soleiana*, Abdalla & Deschodt, 2018 [red label, printed]"; 1 m# (UPSA): "Kleinlee [uu] lak, Matjiesrivier, NR , 32° 29' 01.0" S 19° 21' 36.5" E, 21-08-2015 [printed] / PARATYPE, *Macroderes soleiana*, Abdalla & Deschodt, 2018, [red label, printed]". 1 f# (UPSA): "Perdewater, Matjiesrivier, NR, 32° 26' 41.9" S 19° 21' 05.3" E [printed] / PARATYPE , *Macroderes soleiana*, Abdalla & Deschodt, 2018, [red label, printed]".

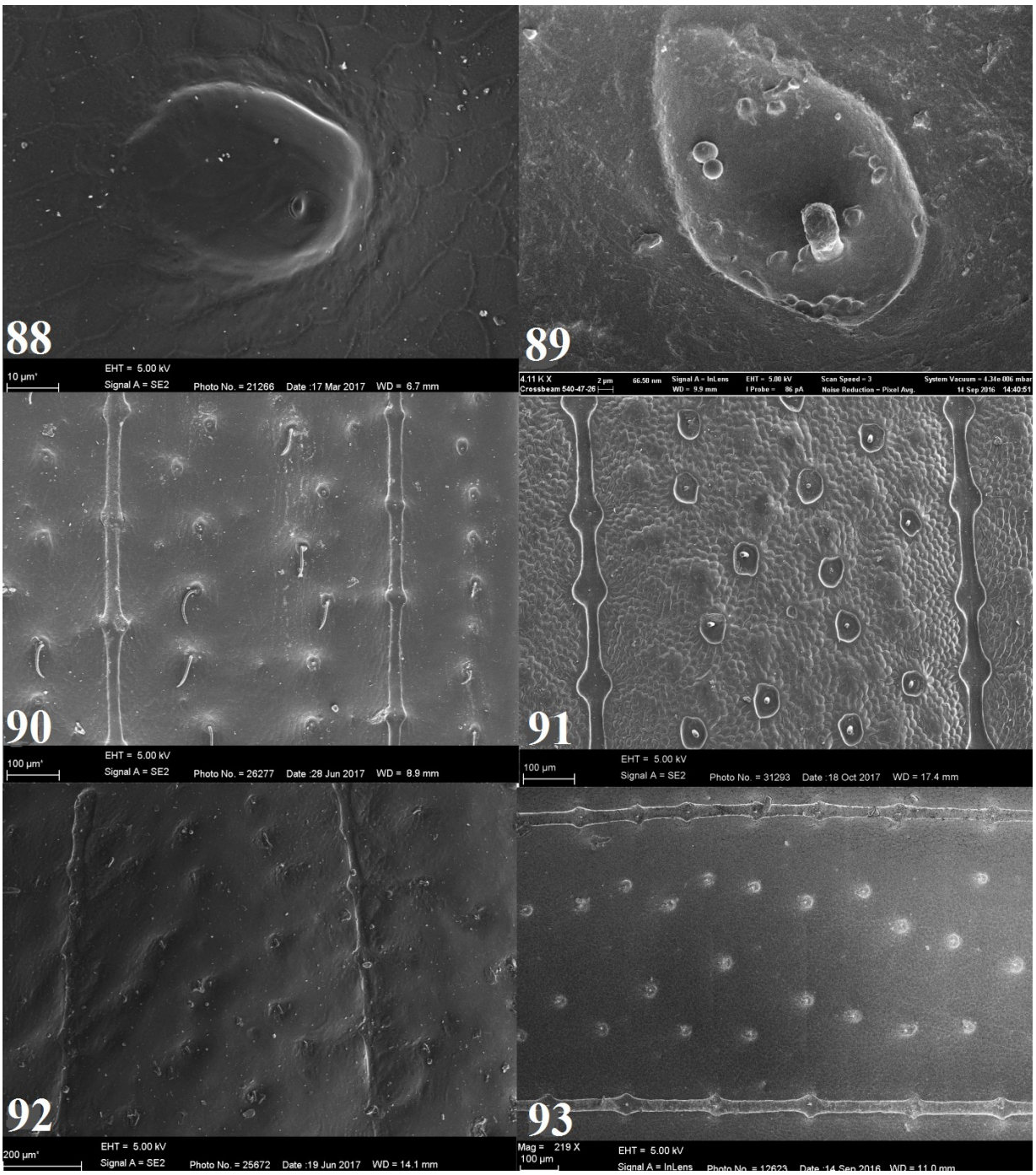
Holotype description. Holotype, m# (Fig. 21). Body length 8.8 mm, body width 6.2 mm.

Head. Genae sharp angled and sutures indistinct. Frontal suture distinct, angulate medially. Dorsal surface of clypeus rugose anterior of frontal suture, punctate posteriorly. Area between punctures shagreened.

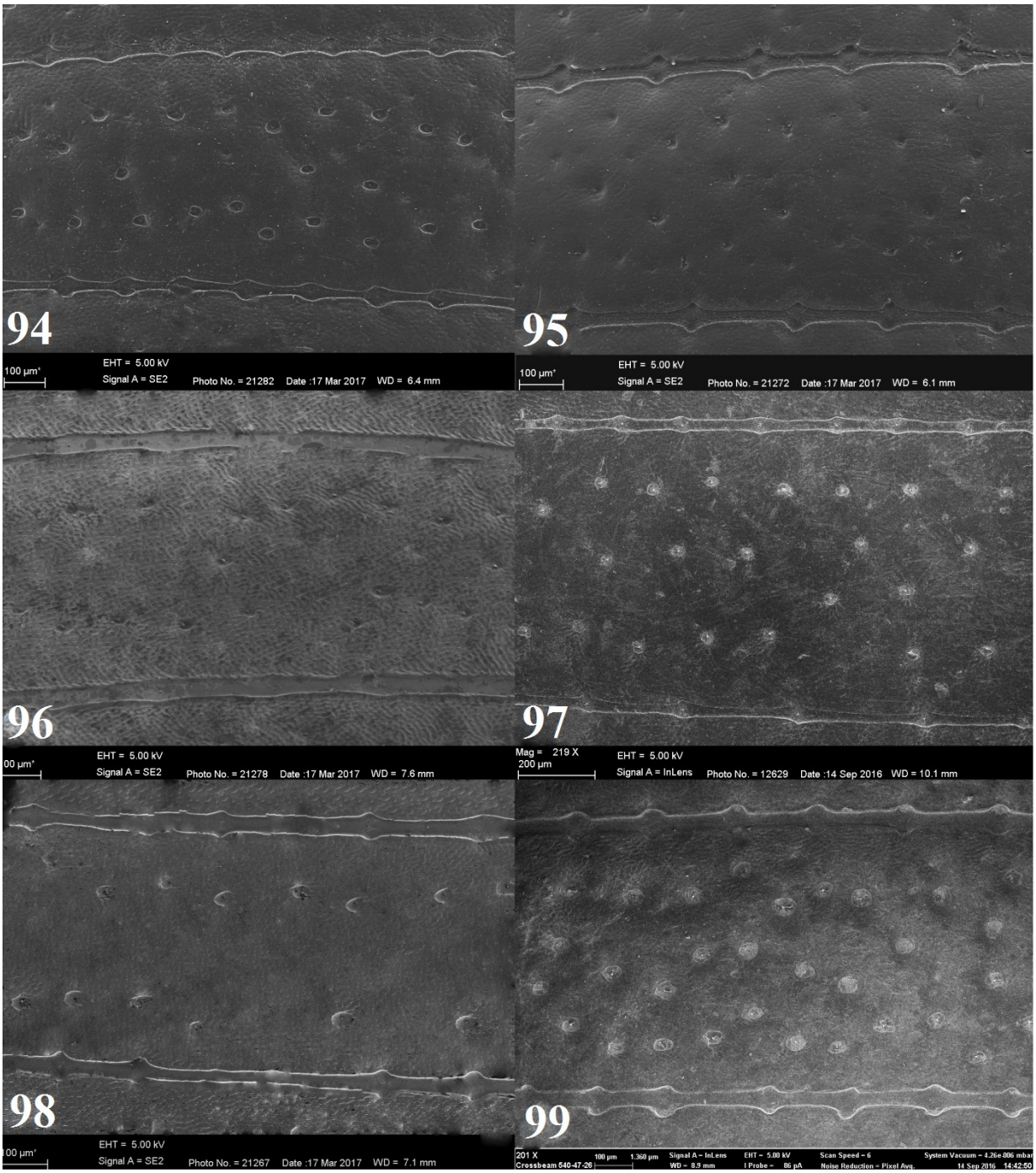
Pronotum. Convex, anterior angles rounded, posterior angles rounded. Lateral border not punctate. Dorsal surface regularly punctate punctures close together, separated by less than one puncture diameter (Figs. 80, 88).



FIGURES 82-87. Pronotum punctures shape of *Macroderes* species. 82, *M. tortuosus* Abdalla & Scholtz, new species; 83, *M. cederbergensis* Abdalla & Deschodt, new species; 84, *M. gifboomi* Abdalla & Scholtz, new species; 85, *M. leipoldti* Abdalla & Deschodt, new species; 86, *M. oreatus* Abdalla & Deschodt, new species; 87, *M. porselinus* Abdalla, new species.



FIGURES 88-93. Pronotum punctures shape (88, 89) and sculpture of second elytra intervals (90-93) of *Macroderes* species. 88, *M. soleiana* Abdalla & Deschodt, new species; 89, *M. tortuosus* Abdalla and Scholtz, new species; 90, *M. minutus* Frolov and Scholtz, 2005; 91, *M. greeni* (Kirby, 1818); 92, *M. politulus* Preudhomme de Borre, 1880; 93, *M. gifboomi* Abdalla & Scholtz, new species.



FIGURES 94-99. Sculpture of second elytra intervals of *Macroderes* species. 94, *M. cederbergensis* Abdalla & Deschodt, new species; 95, *M. leipoldti* Abdalla & Deschodt, new species; 96, *M. oreatus* Abdalla & Deschodt, new species; 97, *M. porselinus* Abdalla, new species; 98, *M. soleiana* Abdalla & Deschodt, new species; 99, *M. tortuosus* Abdalla & Scholtz, new species.

Elytra. Elytral interstriae 1-8 slightly raised, punctate, punctures shallow, punctures separated by 1–2 puncture diameters, each puncture with short associated seta. Elytral margins not carinate. Area between punctures shagreened. Striae clearly bordered, faintly shagreened, punctures faint (Fig. 98). Stria 9 disjunct, anterior 1/5 medially between stria 8 and 10, second 2/3 close to stria 10, interstria 10 almost covered by stria 9 in the anterior 1/3.

Aedeagus. The sclerite of internal sac elongate and strongly curved, without lateral process (Fig. 38).

Size range. Males length: 8.2-12.3 mm, width: 5.0-8.0 mm; females length: 10.0-12.5 mm, width: 7.0-8.1 mm.

Female. Beside the body length variations, female differs from male by having less developed frontoclypeal suture as well as the pronotal laterl marigins more clear in dorsal view than in male.

Etymology. This species is named after our colleague Prof. Catherine L. Sole of the Department Zoology and Entomology, University of Pretoria, in recognition of her leadership and her molecular work on the African dung beetles, lacewings and Baboon spiders.

Differential diagnosis. This species is most similar to *M. nitidus* and *M. cederbergensis* new species. It differs from the former in being more shagreened and less shiny on the elytral interstriae (Fig. 98) and from the latter by being larger and having the pronotal punctures smaller and farther apart (Figs. 80, 88).

Habitat and distribution. Cederberg Mountains (Fig. 2). Specimens have been collected between 600 and 1000 m a.s.l. and mainly in the Swartruggens Quartzite Fynbos vegetation type. This area receives between 200–620 mm of precipitation per year. The soils are sandy but skeletal (Mucina & Rutherford 2006).

Remark. Frolov & Scholtz (2005) used specimens from this species for their redescription of *M. nitidus*. Please, refer to the redescription of *M. nitidus* for more detailed explanation.

Macroderes tortuosus Abdalla and Scholtz, new species (Figs. 22, 39, 82, 89, 99)

Type locality. South Africa, Western Cape Province, Gifberg, 31°48' 5.22" S 18°55' 7.16" E.

Type material. Holotype, m# (TMSA): "South Africa, Western Cape Province, Gifberg, 26km SE of Vanrhynsdorp, 31° 48' 5.22" S 18° 55' 7.16" E, Alt 377 m, 16.vi.2016, C. Scholtz [printed] / HOLOTYPE, *Macroderes tortuosus,* Abdalla & Scholtz, 2018, [red label, printed]". Paratypes: 1m# and 2f#f# (TMSA) same data as holotype; 2 m#m# (TMSA): "South Africa, Western Cape Province, Gifberg, 26 km SE of, Vanrhynsdorp, 31° 48' 5.22" S 18° 55' 7.16" E, Alt 377 m, 21.vii.2016, C. Deschodt & W.P. Strümpher leg [printed] / PARATYPE, *Macroderes tortuosus,* Abdalla & Scholtz, 2018, [red label, printed]".

Holotype description. Holotype, m# (Fig. 22). Body length 10.6 mm, body width 7.7 mm.

Head. Clypeus broad, semi-circular, edges with narrow border and two teeth on anterior margin. Genae acute angled. Frons densely punctate with small round punctures. Frontoclypeal suture slightly curved without tubercle in the middle. Clypeogenal suture present but poorly defined towards the clypeal edge. Dorsal surface of clypeus densely punctate with more or less elongated punctures becoming rugose near the clypeal margin.

Pronotum. Form trapezoidal, shagreened, matte, excavated anterolaterally, lateral edges delimited by narrow borders, borders crenulated, punctate, base not bordered. Pronotum anterior angle obtusely angled, posterior rounded angled appears entire in dorsal view. Pronotal sides rugose with formation of distinct tubercles. Base lacking a longitudinal depression. Pronotal surface punctate with elongated, confluent, coarse punctures (Figs. 82, 89). The confluent punctures flowing together forming twisted-like channels. Punctures with short yellow setae. Punctures becoming smaller towards the pronotum anterior edge. Punctures spaced by elevated matte areas.

Elytra. Elytral intervals convex, strongly shagreened, matte, densely punctate with large roughly round punctures. Punctures associated with short yellow setae in the middle. Punctures separated by elevated matte areas. Striae with fine punctures spaced by 2–4 times their own diameter (Fig. 99). Stria 9 short, close to stria 10, 2/3 the length of the elytron.

Aedeagus. Sclerite of internal sac curved basally and with long lateral process, (Fig. 39).

Size range. Males length: 10.0-10.7 mm, width: 7.4-7.9 mm; females length: 8.7-9.8 mm, width: 6.4-7.2 mm.

Female. Female differs from male by having pronotum less excavated anterolaterally than in male.

Etymology. The name of this species is taken from the Latin adjective tortuosus (twisted) for many turns in the pronotum.

Differential diagnosis. This species is most similar to *M. amplior* in having pronotum with elongated punctures (Figs. 82, 89) but it is different from the latter in having close punctures and the pronotum lateral edges punctuate and crenulation clearly visible in dorsal view.

Habitat and distribution. This species was collected from the base of the Gifberg (Fig. 2) at the northern end of the Bokkeveld Escarpment Mountain Plateau just south of Vanrhynsdorp. These mountains consist of Bokkeveld Sandstone Fynbos (Mucina & Rutherford 2006). The habitat is very rocky with shallow soil, poor in mineral content.

Macroderes undulatus Preudhomme de Borre, 1880 (Figs. 16, 56, 68)
Macroderes undulatus Preudhomme de Borre, 1880:10; Péringuey 1901: 303; Janssen 1939: 27; Ferreira 1969: 323; Frolov & Scholtz 2005: 386.
Macroderes westwoodi Preudhomme de Borre, 1880: 9; Frolov &Scholtz 2005: 386 (junior synonym of *M. undulatus*).

Type locality. South Africa, Cape of Good Hope.

Type material examined. None. Type series is deposited in IRSNB (Frolov & Scholtz 2005).

Additional material examined. 10 f#f# (SANC):“VILLIERSDORP, SW. C.P., (15 Km SE), 13. VIII. 79, Davis & Payton leg / *Macorderes* sp, det. CSIRO DBRU”; 3 f#f# (SANC):

"VILLIERSDORP, SW. C[ape] P[rovince], (15 Km SE), 29.VI. [19]79, stony sandy loam, Fallow crop field C, Davis & Payton / *Macorderes* sp, det. CSIRO, DBRU"; 1 f# (SANC): "WORCESTER, C P, (5 min NW), 16. X. 71, Bornemissza & Kirk / ex coll. CSIRO, Div, Entomology, S. AFRICAN STATION"; 1 f# (SANC): "SWELLENDAM, CP, (29 Kms E), 3. V. 76, 250 m [a.s.l.], Davis & Aschenborn / Ex Coll. CSIRO, Div, Entomology, S. AFRICAN STATION / *Macorderes* sp, det. CSIRO, DBRU"; 1 f# (UPSA): "*Macroderes undulatus*, P. d , Borre, Frolov det"; 1 f# (SAMC): "Riversdale Mountains / SAM-Col-A043 226"; 1 f# (SAMC): "Rietpol [Rietpoort], C.P., Nov. 1937, *Macroderes undulatus* Borre / SAM-Col-A043218".

Size range. Females length: 10.0-11.7 mm, width: 7.2-8.1 mm.

Differential diagnosis. This unique species can be separated from its congeners by the presence of a small tubercle in the middle of the frontal suture (Fig. 56), elytra having smooth, elevated areas in the middle of each interstria with sparse punctuation (Fig. 68) and metasternum lacking any punctuation.

Habitat and distribution. The species was collected from uncertain localities in the southern part of the Western Cape Province (Fig. 2), however, in general the southern part of the Western Cape as described by Olsen *et al.* (2001) is a moist coastal hilly area delimited by the lowland Fynbos biome and Renosterveld eco-region in the north and the coast of Renosterveld in the east.

Remarks. According to Frolov & Scholtz (2005), the types of *M. westwoodi* and *M. undulatus* are curated in the same collection (J. Thompson's collection) and they might even have been collected from the same uncertain locality. The observations of Frolov & Scholtz (2005) on these two species emphasise their similarity in many morphological aspects; they are similar in general body shape, the presence of a tubercle on the frontal suture, the same pronotal punctures and weakly distinct punctures on the metasternum, although they are different in elytral sculpture. As we have not seen the types of *M. westwoodi* and *M. undulatus*, we agree with Frolov & Scholtz (2005) in synonymising *M. westwoodi* with *M. undulatus* as their reasoning stated above, regarding the subject is sound.

The species has been listed as threatened in the IUCN red list under the B1ab criterion due to it is limited and vulnerable range (Davis 2013).

Macroderes pristinus Sharp, 1880 (Figs. 100-102)

Macroderes pristinus Sharp, 1880: 38; Péringuey 1901: 304; Janssen 1939: 29; Ferreira 1968: 322; Frolov & Scholtz 2005: 392.

Type locality. South Africa, Diamond fields (present-day Diamond field 1 in southern Namibia).

Type material examined. Holotype, f# (MNHN): "*Macroderes pristinus,* Type, D [David]. S [Sharp], Diamonds fields-, S. a[A]frica [hand written]" / "EX. Musaeo, D [David]. Sharp 1890 [printed]" / "MUSEUM PARIS, 1952, COLL, R. OBERTHUR [printed]" / "HOLOTYPE [red label, printed] / HOLOTYPE, *Macroderes pristinus* Sharp 1880 [printed]". (Figs. 100-102).

Differential diagnosis. This species is similar to *M. bias* females through the combination of the following characters: punctate lateral borders of pronotum, elytra stria 9 contiguous to elytra stria 10, even punctuation of pronotum, anterolateral depressions of pronotum and the dense punctate and shagreened elytra, however, *M. pristinus* can be distinguished from *M. bias* by having a more punctuated, flatter elytra striae.

Remarks. We agree with Frolov & Scholtz (2005) in that this species is close to females of *M. bias* and probably the same species. We compared the holotype of *M. pristinus* with females of *M. bias* and insignificant differences are noted between the two species. The most significant difference is that the elytral striae in *M. pristinus* are much flatter and densely punctuated than those of *M. bias*. The examined material show many common characteristics summarized as follows: the punctate lateral borders of pronotum, elytra stria 9 close to elytra stria 10, regular rounded punctures of pronotum, the excavation of pronotum antero-laterally and the shagreened elytra with dense punctuation.

Although the validity of the species is questioned, it is not possible to transfer it to *M. bias* as the species has been described from a single female specimen and collected from a different site opposite to *M. bias* range of distribution.

Macroderes dubius Péringuey, 1901

Macroderes dubius Péringuey, 1901: 301; Janssens 1939: 29; Ferreira 1969: 320; Frolov & Scholtz 2005: 392.

Type locality. South Africa, Cape Colony (no exact locality).

Type material examined. None. No indication of where the type was deposited in Péringuey's original description.

Remarks. Unfortunately, we could not locate the holotype of this species, but according to Péringuey's (1901: 301) original description, body size is 11 mm in length and 7.5 mm in width and it resembles *M. politulus* in size, shape, head, and punctuation of the pronotum. Péringuey (1901) mentioned that this species differs from *M. politulus* by bearing a more convex and rounded pronotum without any observed excavation antero-laterally. In addition, the species has even elytral intervals covered by finer and shallower punctures than *M. politulus*, costate and punctate striae. He also observed an unusual elytral shape in the specimen he studied and attributed this to a malformation.

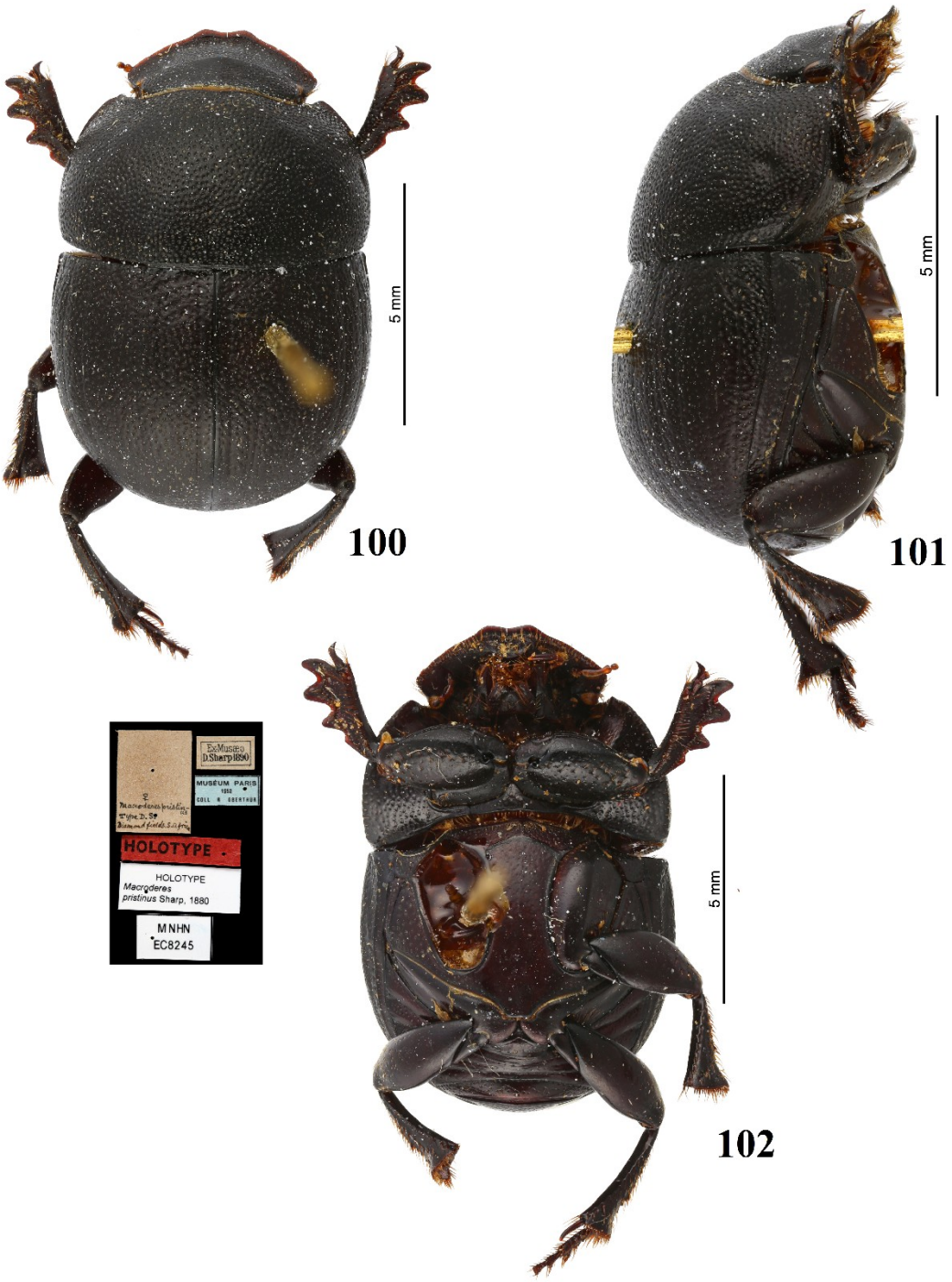
Macroderes spectabilis Péringuey, 1901

Macroderes spectabilis Péringuey, 1901: 300; Janssens 1939: 27; Ferreira 1969: 322; Frolov & Scholtz 2005: 392.

Type locality. South Africa, Cape Colony (no exact locality).

Type material examined. None. Type specimen may be lost, it was not found in any South African museum.

Remarks. We have not seen the type specimen of this species at any of the South African museums throughout our study, thus we support the assumption of Frolov & Scholtz (2005) that the type specimen of this species may be lost. However, Péringuey in his original description



FIGURES 100-102. Holotype of *M. pristinus* Sharp, 1880 and the labels associated with the specimen. 100, dorsal view; 101, lateral view; 102, labels and ventral view.

(1901: 300) mentioned that the length of the specimen is 12.75 mm and the width is 8.5 mm. The species is different from its congeners in that it has a remarkable retuse and lobate pronotum in front and the absence of elytral stria 9. In his description, Péringuey (1901) added that the species has dense, equally distant and close pronotal punctures with the presence of deep impression antero-laterally.

The absence of elytral stria 9 is not known among *Macroderes* species; however, other above mentioned characteristics put the species in close similarity to *M. bias*. Frolov & Scholtz (2005) suggested that the species might be "an aberrant specimen" of *M. bias* and attributed the absence of elytral stria 9 to uncompleted separation of the striae from each other.

Revised key to adult *Macroderes* species (modified from Frolov & Scholtz 2005)

1. Base of pronotum with deep triangular concavity occupying more than 1/2 length of pronotum (Figs. 5, 8, 40, 41)...…….....2

2. Base of pronotum without deep concavity……...3

3.Frontal suture without rounded tubercle (Figs. 49, 51). Sides of pronotum with irregular, somewhat rounded punctures (Fig. 46). Elytral intervals with denser and larger punctures (Fig. 73). Internal sac sclerite slender, with small but distinct lateral process (Fig. 31) ……*M. foveatus* Frolov & Scholtz, 2005

-Frontal suture with rounded tubercle flattened apically in males and acute in females (Figs. 48, 50). Sides of pronotum with elongated punctures (Fig. 47). Elytral intervals with sparser and smaller punctures (Fig. 71). Internal sac sclerite with wide basal part and without lateral process (Fig. 30)….……*M. cornutus* Frolov & Scholtz, 2005

4. Punctures of elytral intervals with somewhat carinate margins (Figs. 70, 91). Sides of pronotum crenulate in dorsal view (Figs. 40, 41, 44, 45) ……...……..4

- Elytral intervals with different sculpture. Sides of pronotum crenulate or entire in dorsal view…….……...…..……...5

5.Pronotum with round punctures (Figs. 44, 58). Coastal sand distribution localised south of Yzerfontein [33°21'S 18°09E'] (Fig. 2)……..……...….*M. greeni* (Kirby, 1818)

-Pronotum granular (Fig. 59). Endemic to Sandveld near Vanrhynsdorp [31°37'S 18°44'E] (Fig. 2)…….....*M. arrowi* Janssens, 1939

6.Lateral border of pronotum not punctate, margin appears entire in dorsal view (Fig. 53) ……..……..……..…..6

- Lateral border of pronotum with punctures (Fig. 52), margin appears entire (Fig. 43) or crenulate in dorsal view (Figs. 42, 45)……...……...19

7. Elytral intervals with matte areas separated by more or less developed smooth, elevated areas (Figs. 16, 68). Head with small tubercle in the middle of frontal suture (Fig. 56). Metasternum smooth, without distinct punctuation, sometimes very faint punctures visible…..……..….*M. undulatus* Preudhomme de Borre, 1880

-Elytral intervals with different sculpture. Head with more or less carinate frontal suture, without tubercle in the middle. Metasternum with distinct punctuation……..7

8.Elytra somewhat rugose (Fig. 3), matte. Sclerite of internal sac with long lateral process (Fig. 27)…….…….…..…..*M. amplior* Frolov & Scholtz, 2005

-Elytra interval more or less densely punctate but not rugose (Figs. 11, 12, 14). Shape of internal sac different.……...…….8

9.Pronotum smooth, shiny with regular punctuation……...……...…..…….……9

- Pronotum shagreened, matte, with different sculpture……...……10

10. Pronotum not excavated antero-laterally (Fig. 14)…….……....*M. nitidus* Harold, 1877

- Pronotum excavated anterolaterally (Fig.18)*M. gifboomi* Abdalla & Scholtz, new species

11. Elytra convex, pronotum with elongated confluent punctures (Fig. 82) ……...……...*M. tortuosus* Abdalla & Scholtz, new species

-Elytra flat, pronotum with different punctures shapes but not confluent……...11

12. Elytra matte, shagreened (Fig. 74)…...……...…...*M. mutilans* Kolbe, 1908

-Elytra shiny or matte…….…….…..…….....12

13. Body smaller (7.0–9.5 mm)……...…….……...…….13

-Body larger (9.5–12.5 mm).....…….…..……...……14

14. Body shape oval (Fig. 19), elytral stria 9 long…….
.....*M. oreatus* Abdalla & Deschodt, new species

- Body shape rather elongates (Fig. 11) elytral stria 9 short……...*M. minutus* Frolov & Scholtz, 2005

15. Pronotum surface flat (Figs. 9, 60), lateral border punctate (Fig. 57)...……..……15

- Pronotum surface convex, lateral border not punctate…….……...……..16

16. Elytral stria 9 almost adjacent to stria 10 (Fig. 55)……..…*M. bias* (Olivier, 1789)

-Elytral stria 9 widely separated from stria 10 (Fig. 54)…….....*M. fornicatus* Sharp, 1880

17. Elytral interstriae 1–8 flat (Figs. 20, 94), punctures at base of pronotum marginally bigger than the rest (Fig. 76)….....*M. cederbergensis* Abdalla & Deschodt, new species

-Elytral interstriae 1–8 more or less raised, pronotum base with different sculpture……...……...…..……..……..17

18. Dorsal surface of pronotum with elongated punctures (Figs. 79, 87), elytra rugose, and granular (Fig. 97)…….…....*M. porselinus* Abdalla, new species

-Dorsal surface of pronotum with regular punctures (Figs. 80, 81, 85, 88), elytra shagreened, (Figs. 95, 98)……..……18

19. Sclerite of internal sac long and strongly curved without lateral process (Fig. 38)…….. ……..*M. soleiana* Abdalla & Deschodt, new species

-Sclerite of internal sac short and slightly curved before the apex without lateral process (Fig. 33).……..……..*M. leipoldti* Abdalla & Deschodt, new species

20. Pronotum granular at least antero-laterally, lateral margin more or less crenulate in dorsal view…….…….…….....20

- Pronotum punctate, not granular (Fig. 63), lateral margin entire in dorsal view (Fig. 43), elytral intervals shiny at least in the middle……*M. politulus* Preudhomme de Borre, 1880

20 Base of pronotum with rounded, larger punctures (Fig. 61), Elytral intervals densely punctate, rugose, monotonously opaque (Fig. 75), sclerite of internal sac not curved basally (Fig. 35)…….…….....*M. namakwanus* Frolov & Scholtz, 2005

-Base of pronotum with sparser, somewhat irregular punctures, with more or less distinct tubercles in-between, appearing granular under dissecting microscope (Fig. 62). Elytral intervals more strongly shagreened, with small shiny tubercles (Fig. 72). Sclerite of internal sac curved basally with lateral process (Fig. 26) ……..*M. endroedyi* Frolov & Scholtz, 2005

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CHAPTER III

Phylogeny and divergence time of the southern African genus *Macroderes* Westwood, 1842(Coleoptera: Scarabaeidae: Scarabaeinae)

Abstract

The flightless genus *Macroderes* Westwood 1842 (Scarabaeidae: Scarabaeinae, tribe incertaesedis) is studied. The genus comprises a group of small to medium sized dung beetles with 21 valid species and three others of doubtful validity. Members in the genus are confined to bimodal and winter-rainfall regions of South Africa with one species that has been recorded from southern Namibia. The aims of this study are to test the monophyly of the genus, determine the phylogenetic relationships among the species and estimate their time of divergence. The phylogeny was constructed based on DNA sequence data from 2 ribosomal (16S rRNA and 28S rRNA) and 2 protein coding (CO1, CAD) genes, and 66 morphological characters. Analyses were performed using Parsimony, Maximum Likelihood and Bayesian approaches. *Macroderes* ages of divergence were estimated using Bayesian dating analyses with fossil calibrations. Monophyly of the genus is strongly supportedby both types of datasets and two major clades were recovered. The origin of the genus was estimated to be in the late Eocene (38.9 Mya), with the current known species diversification in the late Mio-Pliocene and throughout Pleistocene (5.0-0.1 Mya).

Key words. Scarabaeinae, *Macroderes,* molecular, morphology, phylogeny, divergence, South Africa.

Introduction

The Greater Cape Floristic Region (GCFR) is considered as one of the rich hotspots of biodiversity worldwide (Born *et al*. 2007). This vast area comprises the Cape Floristic Region (CFR) plus the Succulent Karro (Jürgens 1997; Lechmere-Oertel & Cowling 2001). The area falls within a Mediterranean type climate dominated by Fynbos and Succulent Karoo vegetation (Bayer 1984; Jürgens 1991, 1997). Due to its remarkable floral composition, the literature mostly deals with each region as an independent biodiversity hot spot (Myers *et al*. 2000; Mittermeier *et*

al. 2004). The CFR comprises a rich diversity of temperate floras (Cowling *et al*. 1996) while the Succulent Karoo harbors approximaly 30% of the total number of the succulent flora in the world (Driver *et al*. 2003; Mittermeier *et al*. 2004). It is suggested that the notable floral endemism in both regions is owed to climatic shift during the Mio-Pliocene boundary, when the Benguela current established, and lowered the world's temperature, leading to general cooling and aridification (Goldblatt & Manning 2002). This climatic anomaly is thought to be the major driving force that initiated rapid faunal and floral radiations (Linder *et al*. 1992; Midgley *et al*. 2001). If this is true for the Cape flora, it is probable that climatic shifts during that period also have influenced the evolutionary history of the Cape fauna (Tolley 2006). Indeed, many studies have revealed associations of paleoclimatic oscillations during the Plio-Pleistocene and diversification of the Cape fauna (Swart *et al*. 2009; McDonald & Daniels 2012; Sole *et al*. 2013). In this regard, the southern African genus *Macroderes* Westwood, 1842 (Scarabaeidae: Scarabaeinae: tribe incertaesedis) which is widely distributed in the bimodal and winter-rainfall regions of South Africa particularly in Fynbos and Succulent Karoo Biomes (Fig. 1) (Davis 2002; Frolov & Scholtz 2005) is relevant. Only one species, *M. pristinus* Sharp, is known from southern Namibia (Frolov & Scholtz 2005). The genus comprises 21 valid species, of which seven were discovered recently (Abdalla *et al.* 2018), and three species of doubtful validity (Frolov & Scholtz 2005). Adults of *Macroderes* are flightless of small to medium size (approximately 8–15 mm long) and usually with convex, black body (Frolov & Scholtz 2005). Most species in the genus have restricted distribution and are known only from their mostly small, type locality (Frolov & Scholtz 2005). Therefore, because of their flightless nature, localised distribution and specialised habitat requirements, most species should be considered as "vulnerable B1 ac" within the IUCN red list categories (IUCN 2013).

The biology and biogeography of the genus are poorly known, except for some notes on its biology by Frolov and Scholtz (2005). All species are associated with dense shrubs in loamy and sandy soils (Frolov & Scholtz 2005) and where heuweltjies are present (Abdalla *et al.* 2018). Members of the genus are suggested to be nocturnal, tolerate cold and their maximum activity is in winter (July-September) particularly after rain (Frolov & Scholtz 2005).

The genus was originally established by Westwood (1842) from one species *Onthophagus greeni* Kirby. Many years later, Preudhomme de Bore (1880) transferred *Scarabaeus bias* Olivier

to *Macroderes* and added three new species. Harold (1877), Sharp (1880) and Kolbe (1908) added five new species and two others were added by Péringuey (1901) who provided an identification key for five species. Latter, Janssens (1939) described another species, *M. arrowi,* and set up a key to all known species. The first detailed comprehensive revision was carried out by Frolov and Scholtz (2005). The revision included descriptions of seven new species (*M. amplior*, *M. minutus*, *M. endroedyi*, *M. namakwanus*, *M. foveatus* and *M. cornutus*) and synonymy of two others (*M. pilula* Sharp, 1880 as a junior synonym of *M. bias* and *M. westwoodi* Preudhomme de Borre, 1880 as a junior synonym of *M. undulatus* Preudhomme de Borre, 1880), as well as designation of a neotype for *M. bias*. In addition, the study provided information on the distribution of each species and some notes on biology of the genus. The most recent revision of the genus was by Abdalla *et al*. (2018). The revision covered all known species and added seven new species (*M. cederbergensis* Abdalla & Deschodt, *M. tortuosus* Abdalla & Scholtz, *M. gifboomi* Abdalla & Scholtz, *M. leipoldti* Abdalla & Deschodt, *M. oreatus* Abdalla & Deschodt, *M. porselinus* Abdalla, and *M. soleiana* Abdalla & Deschodt). Also, the study redescribed *Macroderes nitidus* Harold, 1877 and designated a lectotype for the species.

The present work is the first molecular and morphological phylogenetic study of the genus *Macroderes;* it aimed to:(1) test the monophyly of the genus; (2) reconstruct phylogenetic relationships among itsspecies; (3) estimate its time of divergence and test the hypothesis of climate-driven speciation.

Material & Methods

Taxon Sampling

Thirteen of 21 valid species of the genus *Macroderes* and one undescribed species were included for molecular characterisation. Species included are *M. mutilans*, *M. arrowi*, *M. soleiana*, *M. namakwanus*, *M. nitidus*, *M. gifboomi*, *M. endroedyi*, *M. minutus*, *M. foveatus*, *M. fornicatus*, *M. tortuosus*, *M. amplior*, *M. oreatus* and *Macroderes* sp. The out-group comprised three species *Anonychonitis freyi, Phalops* sp. and *Caccobius* sp. representative of three genera as they have been shown to have a sister relationship with the genus *Macroderes* (Mlambo *et al.,* 2015). The sequences of the out-groups were published by Mlambo *et al.* (2015) and of *M. oreatus, M. mutilans, M. minutus* and *M. amplior* by Sole *et al*. (2010) thus retrieved from GenBank.

Table 1. Species included in this study along with their collection locality and GenBank accession numbers.

No	In-group taxa	ID	Collecting locality	GenBank accession numbers			
				CO1	16S	CAD	28S
1	*M. amplior*	MARP01*	Rietpoort	GQ290050	GQ289698	GQ289978	GQ289834
2	*M. amplior*	MART02	Rietpoort	✓	MK584693	MK821252	MK584673
3	*M. arrowi*	MASV01	Sandveld	✓	MK584678	MK798027	-
4	*M. arrowi*	MASV02	Sandveld	✓	MK584679	-	-
5	*M. arrowi*	MASV03	Sandveld	✓	-	-	MK584667
6	*M. endroedyi*	MEEL01	Elands Baai	✓	MK584683	-	-
7	*M. endroedyi*	MEEL02	Elands Baai	✓	MK584684	-	MK584666
8	*M. endroedyi*	MEKL01	Klawer	✓	MK584685	-	-
9	*M. endroedyi*	MEKL02	Klawer	✓	MK584686	-	-
10	*M. endroedyi*	MEKL03	Klawer	✓	MK584687	-	MK584676
11	*M. fornicatus*	MFCP01	Cape Peninsula	✓	MK584688	MK798028	MK584664
12	*M. foveatus*	MFKK01	Kommandokraal farm	✓	MK584689	MK798029	MK584668
13	*M. foveatus*	MFVF02	Veldrift	✓	MK584690	MK798030	-
14	*M. foveatus*	MFVF03	Veldrift	✓	-	-	-
15	*M. gifboomi*	MGGB01	Gifberg	✓	MK584681	-	MK584665
16	*M. gifboomi*	MGGB02	Gifberg	✓	MK584682	-	-
17	*M. minutus*	MMRP01*	Rietpoort	GQ290051	GQ289699	GQ289977	GQ289835
18	*M. minutus*	MMRP02	Rietpoort	✓	MK584691	MK798034	MK584675
19	*M. minutus*	MMRO03	Rietpoort	✓	MK584692	MK798033	MK584674
20	*M. mutilans*	MMKK01*	Kamieskroon	GQ290028	GQ289673	GQ289959	GQ289808
21	*M. mutilans*	MMKK02*	Kamieskroon	GQ290029	GQ289674	GQ289960	GQ289809
22	*M. mutilans*	MMKK03*	Kamieskroon	GQ290030	GQ289675	GQ28996	GQ289810
23	*M. mutilans*	MMSB02	Springbok	MK559421	MK584694	MK798035	MK584671
24	*M. mutilans*	MMSB03	Springbok	✓	MK584695	MK798036	MK584672
25	*M. namakwanus*	MNKA01	Kotzerus	MK887210	MK584698	MK821251	MK584669
26	*M. namakwanus*	MNKA02	Kotzerus	MK887211	MK584699	-	MK584670
27	*M. namakwanus*	MNKA04	Kotzerus	✓	MK584700	-	-
28	*M. nitidus*	MNDN01	Nieuwoudtville	✓	MK584696	MK798031	-
29	*M. nitidus*	MNDN02	Nieuwoudtville	✓	MK584697	-	-
30	*M. oreatus*	MRNP01*	Richtersveld National Park	GQ290039	GQ289687	GQ289974	GQ289821
31	*M. oreatus*	MRNP02*	Richtersveld National Park	GQ290040	GQ289688	-	GQ289822
32	*M. oreatus*	MRNP03*	Richtersveld National Park	GQ290041	GQ289689	GQ289975	GQ289823
33	*M. soleiana*	MSRA01	Ramakraal	✓	MK584704	-	-
34	*M. soleiana*	MSRA06	Ramakraal	✓	MK584705	-	MK584663
35	*M. soleiana*	MSRA07	Ramakraal	✓	MK584706	-	MK584662
36	*M. soleiana*	MSEL01	Leopard Rock	✓	MK584702	MK798037	MK584660
37	*M.soleiana*	MSEL02	Leopard Rock	✓	MK584703	-	MK584661
38	*M.soleiana*	MSEL03	Leopard Rock	✓	-	-	-
39	*M. tortuosus*	MTGB01	Gifberg	✓	-	-	MK584677
40	*M. tortuosus*	MTGB02	Gifberg	✓	MK584680	-	-
41	*Macroderes* sp.	MNTV01	Piketberg	✓	MK584701	MK798032	-
Out-group							
42	*Anonychonitisfreyi*	ANY1*	Tswalu Kalahari Reserve	JN804610	JN804681	JN804568	JN804754

43	*Anonychonitisfreyi*	ANY2*	Tswalu Kalahari Reserve	JN804611	JN804682	JN804569	JN804755
44	*Caccobius*sp.	CCB1*	Kruger National Park	JN804614	JN804684	JN804571	JN804757
45	*Caccobius*sp.	CCB2*	Kruger National Park	JN804615	JN804685	-	JN804758
46	*Phalopsrufosignatus*	PLP1*	Kruger National Park	JN804660	JN804732	JN804599	JN804800
47	*Phalopsrufosignatus*	PLP2*	Kruger National Park	JN804661	JN804733	JN804600	JN804801

* Above specimen ID indicates sequences retrieved from GenBank

✓indicates GenBank accession numbers in processes

Morphological characters

All *Macroderes* species included in the molecular study were used for the morphological analyses. The total matrix consisted of 66 morphological characters (Appendix 2) based on the adult male external morphology and genitalia (Appendix 1). The morphological terminology follows Frolov & Scholtz (2005). All characters were equally weighted with characters states treated as unordered. To score inapplicable or unknown characters, dashes (-) and question mark (?) were used.

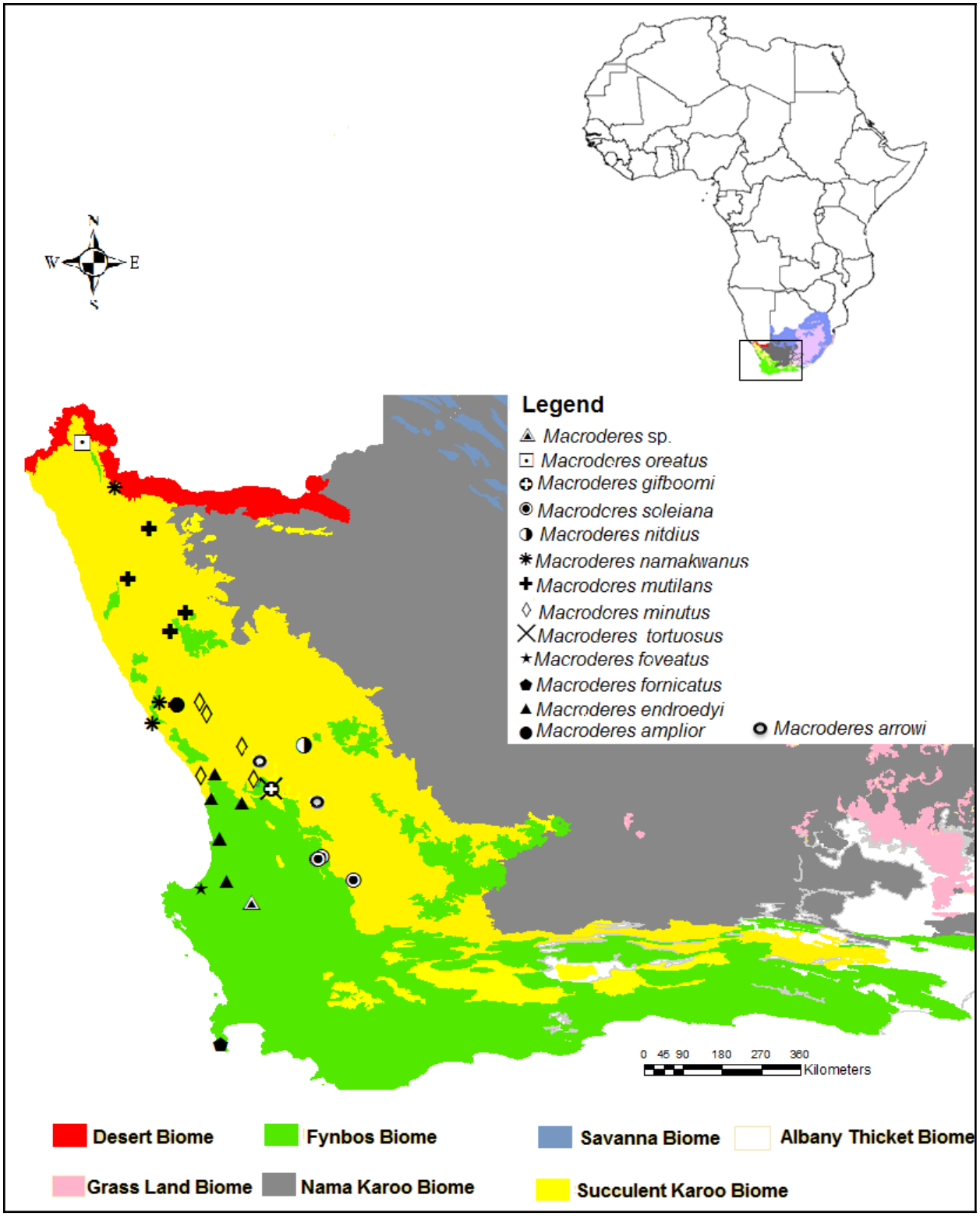

Fig 1. Distribution map of *Macroderes* species used in this study in South Africa.

DNA extraction and sequencing

Total DNA was extracted from muscle tissue of a hind leg using the Macherey Nagel (NucleoSpin® Tissue, Duren Germany) extraction kit following the instructions of the manufacturer. DNA sequence data were generated from four gene regions, including partial sequences from two ribosomal genes: 16S ribosomal RNA (16S rRNA), a portion of the nuclear rRNA large subunit -28S (28S rRNA) domain 2 and two protein-coding genes; Cytochrome Oxidase subunit I (COI) and carbamoyl-phosphate synthetase - aspartate transcarbamoylase-dihydroorotase (CAD). The PCR reactions were run using standardised primers presented in Table 2. The 16S fragments were amplified in a final volume of 50 µl containing approximately 50–100 ng genomic DNA template, 2.5 mM MgCl2, 20 pmol of each primer, 10 mM dNTP's (0.25 mM of each of the four nucleotides (Promega)) and 10 × buffer in the presence of 1 U of Taq. Amplification was done using the following PCR protocol: 90 sec at 94°C initial denaturing, 60 sec at 94°C, 90 sec at 48°C and 90 sec at 72°C for 35 cycles and a final extension of 72°C for 60 sec. The CO1, CAD and 28S Domain 2 regions were amplified in final volume 25 µl by using the Emerald Amp MAX HS PCR Mastermix (Takara Bio inc., Otsu, Shiga, Japan). The following PCR cycling conditions were used to obtain CO1 fragments: 90 sec at 94°C initial denaturing, 22 sec at 94°C, 30 sec at 48°C and 90 sec at 72°C for 33 cycles and a final extension of 72°C for 60 sec. A protocol of two amplification stages was applied to generate the CAD fragments. Stage one was performed by using the primer pair 54F and 680R with the following PCR protocol: initial denaturation for 4 min at 94 °C followed by 4 cycles (30s at 94°C, 30s at 52°C, 2 min at 72°C), thereafter 6 cycles (30 s at 94°C, 1 min at 47°C, 2 min at 72°C) and 36 cycles (30s at 94 °C, 20s at 42 °C, 2.5 min at 72°C) with a final extension of 3 min at 72 °C. Following this, 3 µl of the original amplified product was used in the same reaction mixture except at a 3 mM MgCl2 concentration using internal primers 338F/365F and 654R/654Rmod under the following conditions: initial denaturation for 4 min at 94 °C followed by 4 cycles (30s at 94°C, 30s at 51°C, 1 min 20 s at 72 °C), thereafter 36 cycles (30 s at 94 °C, 30 s at 45 °C, 1 min 20 s at 72 °C) with a final extension of 3 min at 72°C. For 28S domain2 a three step touchdown PCR program was used: initial denaturation for 20s at 96°C was followed by 3 cycles (15s at 96 °C, 20s at 52°C 1min at 72 °C), thereafter 7 cycles (12s at 96 °C, 18s at 51 °C, 60s at 72 °C) and 30 cycles (12s at 96 °C, 15s 50 °C ,50s at 72 °C) with final extension of I min at 72 °C.

The amplified genes' products were then purified using the Macherey Nagel (NucleoSpin® Tissue) purification's kit following the manufacturer's instructions. Purified products were sequenced in both directions using Big Dye Terminator v3.1 Cycle Sequencing Kit (PE Applied Biosystems, Foster City, CA, USA).

Table 2. Summary of Primers used for PCR amplification.

GENE	PRIMER NAME	SEQUENCE 5'-3'	REFERENCE
Cytochrome Oxidase I	C1-J-2183	AACATTTATTTTGATTTTTTGG	Simon *et al.* (1994)
	Tl2-N-3014	TCCAATGCACTAATCTGCCATATTA	Simon *et al.*(1994)
16S RNA	16Sb2	TTAATCCAACATCGAGG	Vogler *et al.* (1993)
	LRN-N-13398	CGCCTGTTTAACAAAAACAT	Simon *et al.*(1994)
28S RNA Domain 2	D2–3551	CGTGTTGCTTGATAGTGCAGC	Gillespie *et al.* (2005)
	D2–4057	TCAAGACGGGTCCTGAAAGT	Gillespie *et al.* (2005)
CAD	54F	GTNGTNTTYCARACNGGNATGGT	Moulton &Wiegman (2004)
	680R	AANGCRTCNCGNACMACYTCRTAYTC	Moulton & Wiegman (2004)
	338F	ATGAARTAYGGYAATCGTGGHCAYAA	Moulton &Wiegman (2004)
	365F	GAYATHTTYCCNGCNGGNTGGTC	Winterton *et al.* (2010)
	654R	TCYTTCCANCCYTTYARSGATTTRTC	Winterton *et al.* (2010)

Sequence alignment

Forward and reverse sequences were firstly visualised and edited in Chromas (version 2.0) and thereafter assembled in CLC Bio MAIN WORKBENCH version 6.9 (http://www.clcbio.com). Edited sequences then were aligned using the ClustalW method with default parameters as implemented in Mega version 7.0 (Kumar *et al.*, 2016). The aligned sequences were then checked manually. An appropriate IUB symbols were used to code the ambiguous sites after double-checking the electropherograms for recognisable sequencing artefacts. New sequences were deposited in GenBank.

Phylogenetic analyses

The phylogenetic relationships between the species of *Macroderes* were inferred from molecular and combined morphological/concatenated molecular datasets using the following reconstruction methods: Parsimony, Maximum Likelihood (ML), and Bayesian inference (BI). Both datasets were analysed under the Parsimony and Bayesian analyses while Maximum Likelihood analysis was only applied to the molecular dataset. Parsimony analyses were performed in PAUP* v. 4.0b10 (Swofford 2003). The heuristic search option was applied using tree bisection-reconnection (TBR) branch swapping, with 10 random addition sequences. Uninformative sites were excluded from the analysis and gaps were treated as missing data. Bootstrap support values (Felsenstein 1985) were calculated based on 1000 replicates.

Maximum Likelihood analyses were implemented in the computer program RaxML-HPC version 8.1.20. (Stamatakis 2014). The analyses were performed under the default GTR + GAMMA model of rate heterogeneity. To ensure that the tree space has been effectively sampled, the analyses were repeated five times with different starting seeds. To assign confidence scores to the best likelihood tree, bootstrap method (Felsenstein 1985) was performed by applying a 1000 rapid bootstrap replicate searches.

Bayesian analyses were implemented with Mr Bayes version 3.1.2 (Ronquist & Huelsenbeck 2003). Selection of best-fit models of nucleotide substitution for each data partition used in Bayesian analyses was based on the Bayesian Information Criteria (BIC, Schwarz 1978) as implemented in jModelTest (Posada 2008) (Table 3). Four Markov chains were run for 30 million generations with two independent runs and temperature of the heated chains set to 0.1. The stationary state of MCMC chains was examined by measuring the effective sample size (ESS) using the program TRACER v.1.6 (Rambaut & Drummond 2014). Trees were sampled every 200 generations and the first 37 500 (25%) trees were discarded as burn-in.

Estimation divergence times

Age of divergence based on the concatenated-molecular dataset was estimated using the software program BEAST version 1.4.8. (Drummond & Rambaut 2008), with the input file generated in BEAUti (Drummond & Rambaut 2008). We used the same evolutionary models as in the MrBayes analysis (Table 3). Substitution models were unlinked among the four partitions while the molecular clocks and tree topology linked for all partitions. The tree prior was set to a Yule

speciation model. The minimum divergence age of *Macroderes* was constrained to the Mid Miocene (13.5 Mya) based on the fossil *Onthophagus bisontinus* Heer, 1862 (13.5–14 Mya (Kälin *et al*. 2001; Berger *et al*. 2005). Calibrations were modelled under a lognormal distribution with an offset, mean and standard deviation so that 95% of the prior distributions fall within the minimum and maximum ages of the fossils. The setups of parameters of the lognormal distribution model were as follows: offset 13.5, mean 0, and standard deviation of 0.56. Two independent runs of MCMC were implemented for 15 million generations with generations sampled every 1000th. The first 20% of the runs were discarded as burn-in after checking for convergence and effective size (ESS) > 200 using TRACER version 1.6 (Drummond & Rambaut 2014). The logs files of the two runs were combined using the LOG COMBINER version 2.4.7 (Drummond & Rambaut, 2008). The resulting trees were also combined and interpreted in TREE ANNOTATOR version 2.4.7 (Drummond & Rambaut, 2008), and viewed in FigTree version 1.4.3 (Rambaut 2009).

Results

Molecular phylogeny

The final data matrix included 2632 base pairs (bp) of which: 830 for COI, ≈ 362 for 16S rRNA, ≈ 567 for 28S rRNA, and 873 for CAD. The concatenated molecular dataset resulted in 706 parsimonious informative sites. The analysis yielded 1014 equally parsimonious trees with tree length 1519 steps (Cl=0.6116, RI=0.7954, RC=0.486, HI=0.3884). The Bayesian tree along with the values of posterior probability (PP), Parsimony bootstrap (PB) and Maximum Likelihood bootstraps (MLB) for the concatenated molecular dataset is presented in Fig.2. Branches with bootstrap values ≥70% and posterior probabilities ≥ 0.95 were considered to be well-supported (Hillis & Bull, 1993; Alfaro & Holder, 2006).

All analyses strongly support the monophyly of the genus *Macroderes* (Fig. 2) with Bayesian posterior probability (PP) 1.00, Parsimony bootstrap (PB) 100% and Maximum likelihood Bootstrap (MLB) 100%. All analyses produced a tree with two major distinct Clades: Clade A (1.00 PP, 75 % PB, 92 % MLB) and Clade B (1.00 PP, 78 % PB, 80% MLB).

Within major Clade A many of the deeper nodes are either poorly/not supported by ML and Parsimony analyses. Three monophyletic sister sub-clades were recovered with varying support: Sub-clade A1 is supported by only Bayesian analysis (1.00 PP) and includes seven taxa that are individually well-supported. The only well-supported sister relationship is that between *Macroderes namakwanus* and *M. amplior* (1.00 PP, 98 % PB, 99 % MLB). Sub-clade A2 was moderately supported by Bayesian analysis (0.71 PP) and includes three species: *M. mutilans* (0.98 PP, 71% PB, 100% MLB), *M. gifboomi* and *M. nitidus* each with 1.00 PP, 100% PB, 100 % MLB. Sub-clades A1 and A2 were recovered sister to each other with high posterior probability (1.00) and moderate PB and MLB (53 %, 65 %), respectively. *Macroderes fornicatus* and *Macroderes* sp. together formed Sub-clade A3 with strong support (1.00 PP, 99 % PB, 100 % MLB) and sister to all other species in major Clade A with (1.00 PP, 75 % PB, 92 % MLB). Strong sister relationship was recovered within the major Clade B between *M. oreatus* and *M. minutus* (1.00 PP, 78 % PB, 80 % MLB).

Table 3. Estimated model parameters for COI, 16S, 28S and CAD for *Macroderes* using jMODELTEST.

Gene	**COI**	**16S**	**28S**	**CAD**
Length (bp)	830	362	567	873
Best-fit model	GTR+I+G	GTR+G	GTR+G	HKY+I
A frequency	0.3530	0.4092	0.2223	0.3252
C frequency	0.1135	0.1350	0.2801	0.1741
G frequency	0.1115	0.0781	0.2940	0.1982
T frequency	0.4220	0.3777	0.2036	0.3025
Gamma	0.7070	0.2510	1.1550	
p-inv	0.5150			0.6100

The Combined morphological/concatenated molecular phylogeny

Analyses of the combined morphological/concatenated molecular datasets using Parsimony produced 769 parsimony-informative sites of 2698 and 81 equally long parsimonious trees with tree length 1733 steps (CI = 0.5880; RI = 0.8020; HI=0.4120). The 50% majority-rule consensus tree with bootstrap support (PB) values is presented in Fig. 3. The analysis strongly supported the monophyly of *Macroderes* with high bootstrap support (100% PB). The resulting tree

topology comprised two major Clades (A: 86%) and (B: 83%) and this result is congruent with the tree topologies obtained from the BI, ML and PB analyses of the molecular dataset (Fig. 2). Overall the resultant parsimony analyses of the combined datasets is better-resolved than the parsimony analyses based on the molecular dataset alone. As with the combined molecular analysis (Fig. 2) the phylogenetic relationships of some deeper nodes in major Clade A were not supported, the analysis moderately supports the monophyly of the groups comprising *M. namakwanus*, *M. amplior* and *M. arrowi* with 58 % PB, *M. mutilans*, *M. gifboomi* and *M. nitidus* with 62% PB and a sister relationship between *M. endroedyi* and *M. tortuosus* with 63% PB. The phylogenetic relationship between *M. fornicatus* and *Macroderes* sp. was recovered as strongly supported with 99% PB. The overall groupings of the species across dataset analyses (concatenated molecular and concatenated molecular/morphology) remains consistent.

The combined morphological/concatenated molecular datasets under the Bayesian analyses recovered a robust phylogeny with the monophyly of the genus strongly supported (1.00 PP). Tree topology was identical to the tree topologies resulting from BI, ML and MP analyses of the molecular dataset with two major Clades (A & B). However, the major difference between the two phylogenies is represented in the position of *M. soleiana.* By adding the morphology *M. soleiana* moved from Sub-clade A1 to sub-clade A2 being sister to *M. mutilans, M. gifboomi* and *M. nitidus* with strong posterior probability support (1.00). All species across all analyses were well-supported.

Divergence Time estimation

The topology of the chronogram (Fig. 5) inferred by BEAST analysis is similar to the topology of the Bayesian analyses. The maximum crown age of *Macroderes* was estimated to be around the late Eocene (38.9 Mya: 95% HPD: 34.5–45 Mya). The initial diversification within the genus occurred in the late mid-Miocene around (14.5 Mya: 95% HPD: 13.9–15.8 Mya) when the major Clades (A & B) split from each other. Major Clade A started to radiate around the late Middle Miocene/early late Miocene around (12.2 Mya: 95% HPD: 10.9–13.8 Mya), while major Clade B started radiating approximately (11.5 Mya: 95% HPD: 10–13.3 Mya) during late Miocene. Within the major Clade A, times of divergence of all descendent sub–clades (A1, A2 and A3) were in the late Miocene (10.5 Mya: 95% HPD: 9.2–12.00 Mya), (10.3Mya: 95% HPD: 8.9–12

Mya) and (7.0 Mya: 95% HPD: 5.4–8.8 Mya), respectively. Most clades underwent recent rapid radiation during Plio-Pleistocene (5.0–0.1 Mya) giving rise to the extant species.

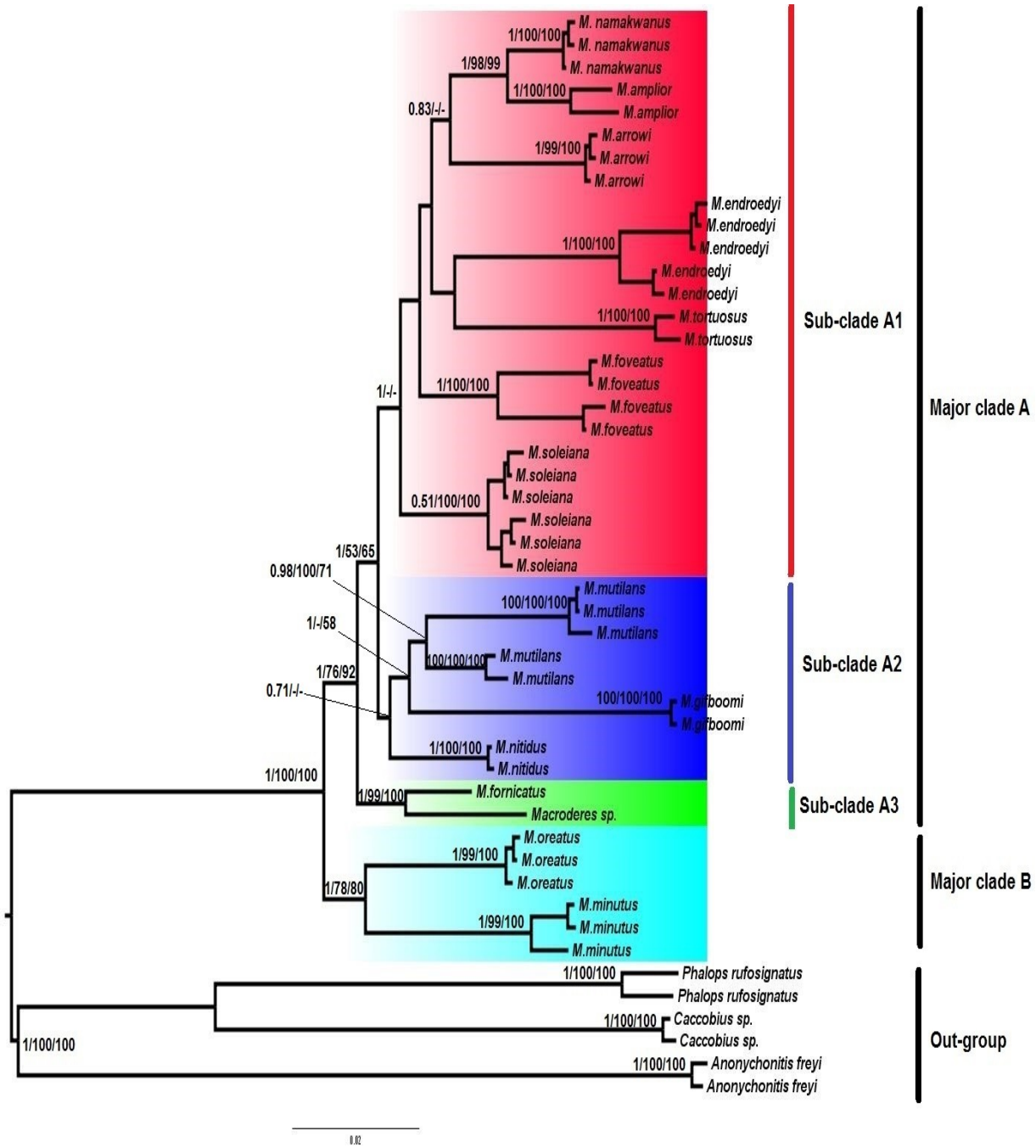

Fig 2. Fifty percent majority rule consensus tree resulting from Bayesian analysis of the combined (COI, CAD, 16S and 28S) with PP, MP and MLB given, respectively. Dashes (-) on nodes indicate weak/no support.

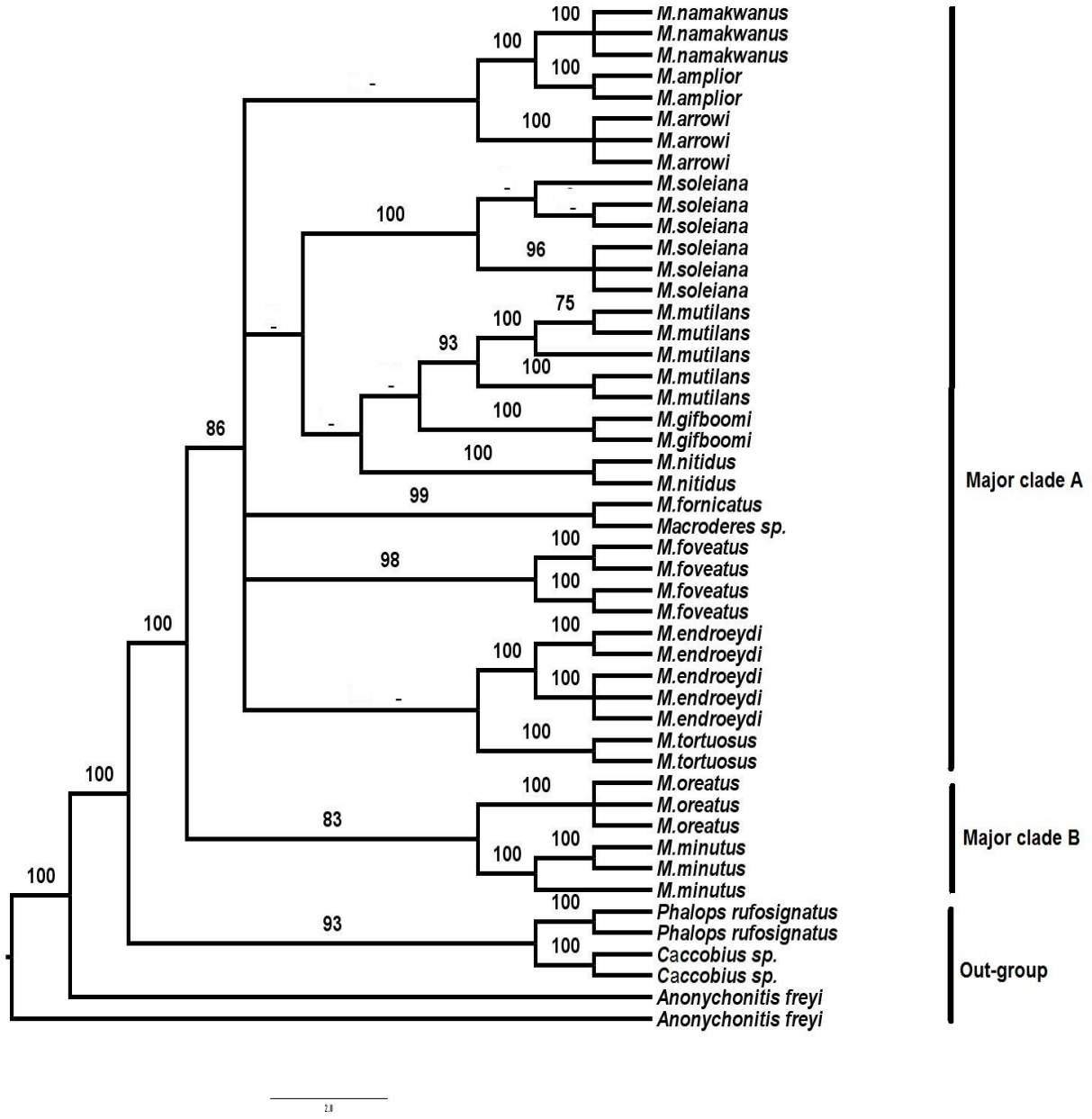

Fig 3. The most parsimonious tree of the combined morphological/concatenated molecular dataset with bootstrap support values on each branch. Dashes (-) on branches indicate weak/no support.

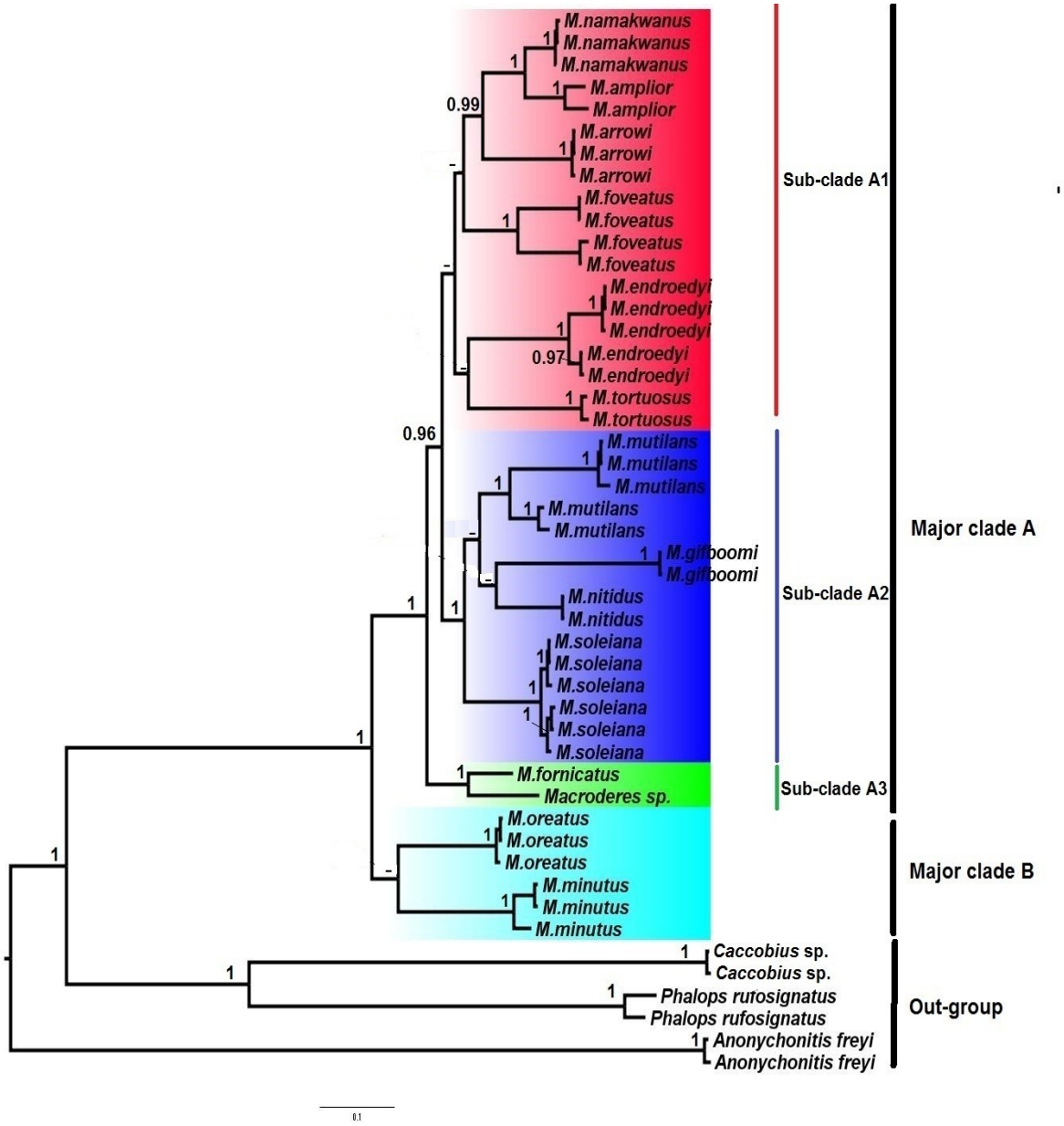

Fig 4. Fifty percent majority-rule consensus tree inferred from Bayesian analysis of the combined morphological/concatenated molecular dataset (COI, CAD, 16S and 28S) with posterior probabilities on each node. Dashes (-) on nodes indicate weak/no support.

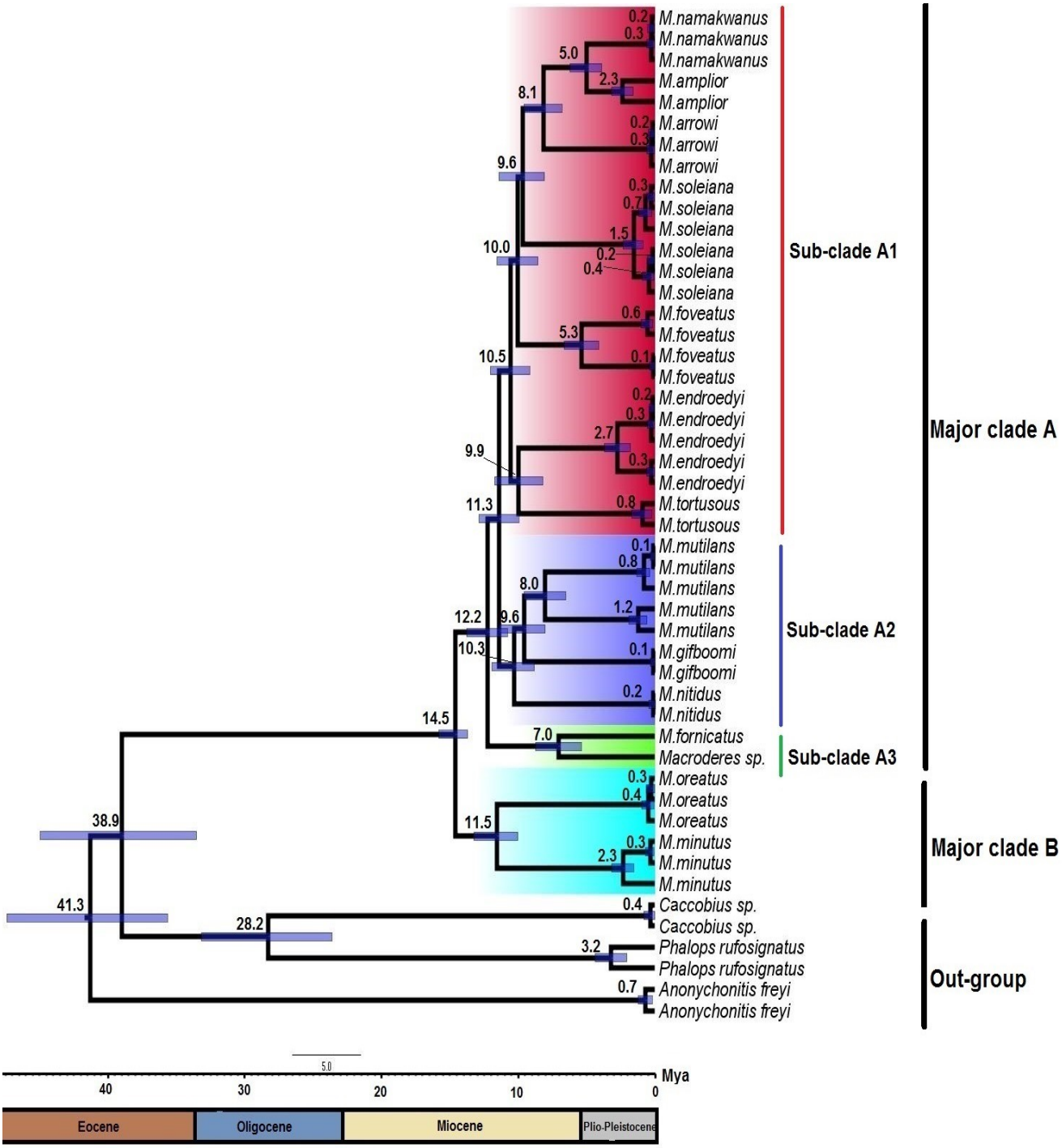

Fig 5. Chronogram resutling from BEAST analyses. Each node represents the mean divergence time estimate and blue bars represent the 95% highest posterior density intervals around mean nodal ages.

Discussion

Phylogenetic relationships

This is the first phylogenetic study conducted on the relationships of the genus *Macroderes* that combines both molecular and morphological evidence. *Macroderes* currently has 21 valid species and three of doubtful validity. Members are small to medium-sized species (8–15 mm) and characterised by a black convex and bulky body (Frolov & Scholtz 2005). Superficially, females are very similar to males and it is difficult to discriminate between them. However, the presence of an acute tooth at the apex of the males' tibiae facilitates their distinction (Frolov & Scholtz 2005). Also, separation of the species is difficult since externally all of them appear alike except for *M. foveatus* and *M. cornutus* which are very distinct from others in that they bear a deep triangular concavity on the base of the pronotum (Frolov & Scholtz 2005). However, thorough examination of micro-sculpture on the pronotum and elytra has revealed notable variations among the species that can be used as diagnostic characters (Frolov & Scholtz 2005). Moreover, the species exhibit significant differences in the shape of the sclerite of the internal sac of the aedeagus (Frolov & Scholtz 2005).

All analyses (BI, MP and MLB) supported the monophyly of *Macroderes*. The genus was split into two major clades with some deeper relationships of Clade A weakly supported by ML and MP analyses. Major Clade A is sub-divided into three sub-clades (A1, A2 and A3) which includes species characterised by large size when compared to the species in major clade B. Sub-clade A1 consists of the species *M. namakwanus, M. amplior, M. arrowi, M. foveatus, M. endroedyi, M. tortuosus* and *M. soleiana*. These species share several unambiguous morphological characteristics represented by matte, shagreened pronotum and their pronotum margins appear entire in dorsal view. Moreover, all species are characterised by having rugose, matte elytra and crenulate, punctate lateral margins of pronotum except for *M. soleiana*, which is characterised by impunctate lateral margin of pronotum which may explain why this species sorted separately as sister to all species in the sub-clade. *Macroderes namakwanus, M. amplior* and *M. arrowi* clustered together with strong support and are characterised by having a straight sclerite of the internal sac of aedeagus that bears Lateral process. Although *M. endroedyi* and *M. tortuosus* were moderately supported by Bayesian analysis, they share the curved shape of the sclerite of the internal sac of aedeagus. *Macroderes foveatus* sorted separately and is recovered as sister to all species in the sub-clade A1, and this is

maybe due to the presence of the deep longitudinal concavity on the base of pronotum which makes this species very distinctive from its congeners. The close phylogenetic relationship between *M. mutilans, M. gifboomi* and *M. nitidus* in sub-clade A2 is supported by their impunctate, not crenulate lateral margin of pronotum. Also, these species are characterised by having flat, dense punctate elytra. Within this sub-clade, *M mutilans* and *M. gifboomi* showed close affinity which maybe explained by the same shape of their pronotum which is excavated antero-laterally. The monophyly of the *M. fornicatus* and *Macroderes* sp. in sub-clade A3 is strongly supported by all analyses. This relationship can be supported by their strongly shagreened, matte elytra intervals, punctate and crenulate lateral margins of pronotum and also by the same micro-structures in the pronotum punctures.

In major Clade B *M. oreatus* is strongly recovered as sister taxon to *M. minutus*. This close phylogenetic relationship was also shown by the morphological classification (Abdalla *et al*. 2018). Of all *Macroderes* species, *M. oreatus* and *M. minutus* are characterised by their small body size and superficially they look very similar. Both species have the same shape of the internal sac of aedeagus which is almost straight and with a weakly developed lateral process.

Divergence time of the genus *Macroderes*

The evolutionary history of modern dung beetles in southern Africa is largely associated with the evolution of climate and geography of the region during the Tertiary (Davis 1990). The onset of winter-rainfall system in the late Miocene along the southwestern coast (Axelrod & Raven 1978; Deacon, 1983) followed by cooler and warm phases of Plio-Pleistocene caused aridity and major changes in vegetation cover (Axelrod & Raven 1978). Combined with the northward drift of the continent and recurrent uplifts of the Great Escarpment in the late Oligo-Miocene and later during Plio-Pleistocene these have also contributed to aridity of the region and elimination of tropical forest (Axelrod & Raven 1978). These factors collectively have led to extensive habitat shifts favouring species diversification (Davis 1990, Davis 1993, 1997).

Based on Bayesian divergence time estimation, the age of *Macroderes* is dated back to the late Eocene (38.9 Mya). This finding is consistent with the hypothesis proposed by Mlambo *et al.* (2015) that members of the subfamily Scarabaeinae were present in Africa since at least the Eocene (42; 95% HPD: 32–53 Mya). The first speciation events in the genus were in the late mid-Miocene (*ca.* 14.5 Mya) when major clade A started to diverge from major clade B. It appears that the radiation of the genus would therefore mostly have been affected by climatic changes during the so-called "Middle Miocene Transition Climate" that started at the end of the mid-Miocene (Flower & Kennett 1994). In this period, the world climate started to change from warmer to cooler, marked by a general decline in global temperature and sea level, which increased aridity and cooling (Flower & Kennett 1994). Most major speciation events in the genus occurred during the late Miocene (11.5–5.3 Mya), followed by rapid speciation during Plio-Pleistocene (5.0–0.1Mya) resulting in the emergence of the different species of today. By the late Miocene and early Pliocene, the polar ice sheet was well developed and this is thought to be the primary causal factor for the introduction of the South African winter-rainfall regime along the south-western coast (Stuut *et al*. 2004). The characterised dry, cooler climate of the late Miocene contracted the early Tertiary tropical forests that were replaced by woodland and Savanna (Axelrod & Raven 1978, Coetzee & Rodgers 1982, 1986; Tyson 1986). Also, this era witnessed the extinction of most old mammalian lineages that couldn't adapt to drought, and the appearance of modern mammal families is evident (Janis 1993). As diverse mammals appeared in Africa and plentiful amounts of dung were available (Cambefort 1991a), dung beetles developed different morphological, behavioural and ecological traits to utilise this patchy and

ephemeral resource (Philips *et al*. 2004). It has been suggested that this is maybe the reason behind the great diversity of modern dung beetles in Africa seen today (Maglio 1978; Bigalke 1978). The explosive, rapid radiation of *Macroderes* during Plio-Pleistocene periods could have been facilitated by both climatic and topographic shifts during that era. The Pliocene is characterised by two climatic systems of rainfall: winter rainfall climate in the Western Cape and Spring/Autumn bimodal rainfall in the Eastern Cape (Deacon 1983). It is thought that the westerly wind that accounted for the winter rainfall dominated the easterly wind that controlled the summer rainfall to the north of the winter rainfall region (Tyson 1986). The fluctuating northwards-southwards climatic belts during Pleistocene caused major shifts in the species habitats lead to isolation of populations, which consequently prompted *Macroderes* speciation (Tyson 1986; Davis 1990, 1993, 1997).

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Appendices

Appendix 1. Morphological characters list and their corresponding states used in this study.

[1]Species: (0) flight; (1) flightless.

[2] Body size: (0) small; (1) medium; (2) large.

[3] Body colour: (0) black; (1) others.

[4] Body shape: (0) hemispherical and convex; (1) convex and taper posteriorly; (2) elongate and flattened.

Frons

[5] Frontal suture bears: (0) a cute tubercle; (1) without tubercle; (2) horn.

[6] Frontal suture: (0) strongly curved; (1) slightly curved; (2) developed to horn.

[7] Frontoclypeal suture shape: (0) straight; (1) curved triangularly; (2) curved circularly.

[8] Frons punctuation: (0) densely; (1) sparsely; (2): more or less densely punctuated.

[9] Punctures of the frons: (0) rounded; (1) elongated.

Clypus

[10] Clypeus sinuation shape: (0) V shape; (1) obtuse; (2) clypus without sinuation.

[11] Frontal clypus teeth: (0) V shape; (1) obtuse; (2) without teeth.

[12] Clypus: (0) bordered; (1) not border.

[13] Clypus lateral borders sinuation: (0) present; (1) absent.

[14] Shape of clypus surface: (0) completely rugose; (1) shagreened; (2) smooth; (3) partially rugose; (4) partially carinate.

[15] Clypus punctuation: (0) densely; (1) sparsely; (2) very densely punctate.

[16] Shape of the clypeus punctures: (0) rounded; (1) elongated.

[17] Clypus lateral border: (0) round; (1) oblique.

[18] Clypeal ventral carina shape: (0) rounded; (1) triangular.

[19] Clypeus frontal teeth reflexed upwards: (0) present; (1) absent.

Gena

[20] Gena angles: (0) right; (1) acute; (2); obtuse (3) right to obtuse.

[21] Gena protruding: (0) present; (1) absent.

Pronotum

[22] Pronotum shape: (0) convex; (1) very convex; (2) slightly convex.

[23] Pronotum dorsal surface: (0) punctuate; (1) impunctate.

[24] Pronotum dorsal surface punctures shape: (0) rounded; (1) elongated; (2) irregular; (4) granular.

[25] Pronotum anterior-laterally excavation: (0) present; (1) absent.

[26] Pronotum base longitudinal depression: (0) present; (1) absent; (2) with different depression.

[27] Pronotum base: (0) boarded; (1) not boarded.

[28] Pronotum base punctuation: (0) sparsely; (1) densely.

[29] Pronotum sides punctures shape: (0) irregular; (1) regular.

[30] Pronotum sides: (0) crenulated in dorsal view; (1) not crenulated in dorsal view.

[31] Pronotum side's margin appears: (0) entire in dorsal view; (1) not entire in dorsal view.

[32] Pronotum lateral border punctuation: (0) present; (1) absent.

[33] Pronotum anterior angle: (0) obtuse; (1) rounded; (2) acute; (3) right.

[34] Pronotum posterior angle: (0) obtuse; (1) rounded; (2) acute; (3) right.

[35] Pronotum posterior angle: (0) clear in dorsal view; (1) unclear in dorsal view.

[36] Pronotum lateral and anterior margins: (0) with fine border; (1) with strong border; (2) without border.

[37] Pronotum posterior margin arcuate: (0) present; (1) absent.

[38] Pronotum lateral fovea: (0) present; (1) absent.

[39] Pronotum extended medially in anterior margin forming two distinct notches: (0) present; (1) absent.

Elytra

[40] Elytral intervals with: (0) larger denser punctures; (1) larger sparser punctures; (2) smaller denser punctures; (3) smaller sparser punctures.

[41] Elytra with: (0) sculpture; (1) without sculpture.

[42] Elytra intervals punctures: (0) with carinate margins; (1) without carinate margins.

[43] Elytra interval punctures surrounded by: (0) matte areas; (1) shiny area; (2) more or less shiny area.

[44] Elytra punctures separated by: (0) smooth elevated areas; (1) shagreened elevated areas.

[45] Elytra surface: (0) rugose; (1) shagreened; (2) smooth.

[46] Elytral intervals: (0) very convex; (1) slightly convex; (2) flat.

[47] Elytral intervals: (0) matte; (1) shiny; (2) more or less shiny.

[48] Elytra intervals sides: (0) rugose; (1) shagreened; (2) smooth.

[49] Elytral intervals punctuation: (0) densely; (1) sparse; (2) more or less densely punctuated.

[50] Elytral intervals with: (0) shiny tubercle; (1) without tubercle.

[51] Elytral intervals 1–8: (0) flat; (1) elevated.

[52] Elytral stria 9 and 10: (0) stria 9 almost adjacent to stria 10; (1) stria 9 widely separated from stria 10.

Pygidium

[53] Pygidium medial furrow: (0) broad; (1) narrow.

[54] Pygidium medial furrow: (0) long; (1) short.

[55] Pygidium medial furrow lateral edges: (0) completely fused together; (1) partially fused together; (2) open.

[56] Pygidium punctuation: (0) sparse; (1) dense.

[57] Pygidium punctures shape: (0) round; (1) elongate; (2) irregular shape.

[58] Pygidium shape: (0) swallowed; (1) flat.

Legs

[59] Fore tibia with: (0) 4 teeth; (1) 3 teeth

[60] The additional 4 teeth: (0) present; (1) absent

[61] Fore tibia teeth: (0) acute; (1) blunted.

[62] Apex of the fore tibia oblique: (0) present; (1) absent.

[63] Fore tibia tarsus: (0) present; (1) absent.

[64] Fore tibia in males with acute process next to the apical spur: (0) present; (1) absent.

Aedeagus

[65] Sclerite of internal sac: (0) straight basely; (1) curved.

[66] Aedeagus lateral process: (0) short medially; (1) long medially; (2) short apically; (3) long apically.

Appendix 2. Data matrix of 66 morphological characters of the genus *Macroderes* andthe out-group. Missing data are coded with "?"

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
M. namakwanus	1	1	0	0	1	1	1	1	1	1	1	0	1	3	0	1	0	0	0	0	0	0
M. amplior	1	1	0	0	1	1	1	1	1	1	1	0	1	3	0	1	0	0	0	0	0	0
M. fovatus	1	1	0	0	0	0	1	1	1	0	0	0	1	0	0	1	0	1	0	0	0	0
M. endroedyi	1	1	0	0	1	1	2	0	1	0	0	0	1	3	0	1	0	0	1	0	0	0
M. tortuosus	1	1	0	0	1	1	2	0	0	0	0	0	1	3	0	1	0	0	1	0	0	0
Macroderes sp.	1	1	0	0	1	1	1	0	1	1	1	0	1	3	0	1	0	1	0	3	0	0
M. fornicatus	1	1	0	0	1	1	0	0	0	0	1	0	1	3	0	1	0	1	0	3	0	0
M. gifboomi	1	1	0	0	1	1	2	0	0	1	1	0	1	0	0	0	0	0	1	0	1	0
M. mutilans	1	1	0	0	1	1	2	1	0	1	1	0	1	0	0	0	0	0	1	0	0	0
M. nitidus	1	1	0	0	1	0	2	0	0	1	1	0	1	0	0	0	0	0	1	0	1	0
M. arrowi	1	1	0	0	1	1	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0
M. soleiana	1	1	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	1	0	0	1	1
M. oreatus	1	0	0	0	1	1	2	0	1	0	0	0	1	3	0	1	0	1	1	0	0	0
M. minutus	1	0	0	0	1	1	2	0	1	1	0	0	1	3	0	1	0	1	1	0	0	0
***Caccobius* sp.**	0	0	1	1	1	3	2	1	0	1	1	0	1	1	1	0	0	1	0	2	1	2
Anonychonitis freyi	0	2	1	2	2	2	3	?	1	2	2	0	1	1	0	0	0	0	0	2	1	3
Phalops rufosignatus	0	0	1	1	1	1	0	0	1	1	1	0	0	1	0	1	1	1	0	1	0	0

Appendix 2 (continued).

Species	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
M. namakwanus	0	0	1	1	1	1	0	0	0	0	0	1	1	0	1	0	1	1	0	1	0	1
M. amplior	0	1	1	1	1	1	0	1	1	1	0	1	1	0	1	0	1	1	0	1	0	1
M. fovatus	0	1	1	0	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1
M. endroedyi	0	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	1	1	1	0	1
M. tortuosus	0	1	0	1	1	1	0	0	0	0	0	1	1	0	1	0	1	0	1	1	0	1
Macroderes sp.	0	0	1	1	1	1	0	0	0	0	0	1	0	0	1	0	1	2	1	1	0	2
M. fornicatus	0	1	0	1	1	1	0	0	0	0	0	1	1	0	1	0	1	2	1	1	0	2
M. gifboomi	0	0	0	1	0	1	1	1	1	1	0	1	1	0	1	0	1	0	1	1	0	2
M. mutilans	0	1	0	1	1	1	1	1	1	1	0	1	1	0	1	0	1	0	1	1	1	1
M. nitidus	0	0	1	1	1	0	1	1	1	1	0	1	1	0	1	0	1	0	1	1	0	2
M. arrowi	0	0	1	1	1	1	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	1
M. soleiana	0	0	1	1	1	0	0	1	1	1	1	1	0	0	1	0	1	2	1	1	0	1
M. oreatus	0	0	1	1	1	0	?	1	1	1	3	1	1	0	1	0	1	2	1	1	0	1
M. minutus	0	0	1	1	1	0	?	1	1	1	0	1	1	0	1	0	1	2	1	1	1	1
***Caccobius* sp.**	0	0	1	1	0	0	0	1	0	1	2	0	1	1	0	0	0	3	1	1	1	1
Anonychonitis freyi	0	2	1	2	1	1	0	1	0	1	2	0	0	0	0	0	0	0	1	1	0	1
Phalops rufosignatus	0	0	1	0	1	1	0	1	0	1	1	1	0	1	1	0	1	2	0	1	1	1

Appendix 2 (continued).

Species	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66
M. namakwanus	1	0	0	1	0	1	1	0	0	0	2	1	2	0	0	0	0	1	0	0	0	0
M. amplior	1	0	0	1	0	1	1	0	0	0	2	1	2	0	0	1	0	1	0	0	0	1
M. fovatus	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
M. endroedyi	1	0	0	1	0	0	1	0	0	1	2	0	1	0	0	0	0	1	0	0	1	0
M. tortuosus	1	0	0	1	0	1	1	0	0	1	2	0	1	0	0	0	0	1	0	0	1	0
Macroderes sp.	1	0	0	1	1	1	1	0	1	1	1	0	1	1	0	1	1	1	0	0	?	?
M. fornicatus	1	0	0	1	1	1	1	1	1	1	1	1	0	0	0	1	0	1	0	0	1	0
M. gifboomi	2	1	1	2	0	1	1	0	0	1	1	1	0	0	0	1	0	1	0	0	0	1
M. mutilans	1	2	0	1	0	1	0	0	1	1	1	0	0	0	1	0	1	1	0	0	0	0
M. nitidus	2	1	2	1	1	1	1	0	0	1	2	0	0	0	0	1	1	1	0	0	1	2
M. arrowi	1	0	0	1	0	0	1	0	1	1	2	0	2	1	0	0	0	1	0	0	0	0
M. soleiana	1	1	0	1	0	1	1	0	1	0	1	0	0	0	0	0	0	1	0	0	1	2
M. oreatus	1	2	0	1	0	1	0	0	0	0	2	1	1	0	1	0	0	1	0	0	0	3
M. minutus	2	2	1	1	0	1	0	1	0	0	2	0	1	0	0	0	0	1	0	0	0	3
***Caccobius* sp.**	2	2	0	2	1	1	0	?	2	1	1	0	0	0	0	1	1	1	0	0	?	?
Anonychonitis freyi	2	2	1	2	0	1	0	?	2	?	?	0	1	0	0	1	1	1	1	1	?	?
Phalops rufosignatus	1	0	1	1	0	0	1	?	2	?	?	1	1	0	0	1	1	1	0	1	?	?

CHAPTER IV

Revision of the southern African genera Nemopterella Banks and Nemia Navás (Neuroptera: Nemopteridae: Nemopterinae), with descriptions of new genera and species

Abstract

The southern African genera *Nemopterella* Banks, 1910 and *Nemia* Navás, 1915 (Neuroptera: Nemopteridae: Nemopterinae) are revised. *Nemopterella* is split into three genera: *Nemopterella sensu stricto* with type species *Nemopteryx africana* Leach, 1815 (= *Nemopterella africana*), *Afroptera* **gen. nov.**, with type species *Nemopterella munroi* Tjeder, 1967, and the monotypic genus *Siccanda* **gen. nov.**, with type species *Nemopterella arenaria* Tjeder, 1967. Eight new species are described in *Afroptera* **gen. nov.**: *A. acuta* Abdalla & Mansell **sp. nov.**, *A. alba* Mansell & Abdalla **sp. nov.**, *A. brinkmani* Abdalla & Mansell **sp. nov.**, *A. balli* Abdalla & Mansell **sp. nov.**, *A. cylindrata* Abdalla & Mansell **sp. nov.**, *A. folia* Abdalla & Mansell **sp. nov.**, *A. koranna* Mansell & Abdalla **sp. nov.**, *A. maraisi* Abdalla & Mansell **sp. nov.**, as well as two new species in the genus *Nemopterella*: *N. kabas* Mansell & Abdalla **sp. nov.**, and *N.cedrus* Mansell & Abdalla **sp. nov.**

Key words: Nemopteridae, *Nemopterella*, *Nemia*, new genera, new species, South Africa, Namibia

Introduction

The family Nemopteridae Burmeister, 1839 is renowned for the striking form of the hind wings that are extremely elongated, a very short metathorax (Tjeder 1967) and the elongated mouthparts of the adults. It comprises about 142 described species worldwide in two subfamilies, Crocinae (thread-winged lacewings) with 48 species and Nemopterinae (spoon and ribbon-winged lacewings) with 94 species (Sole *et al*. 2013).

The family is distributed in the drier regions of the world including The Oriental Region (1 Crocinae, 1 Nemopterinae), Palaearctic (17, 21), Nearctic (South America) (6, 1), Australia

(6, 3) and particularly, in Afrotropical Africa, including Socotra Island (18, 94), with high levels of endemism in southern Africa. There are no extant representatives in North America (Tjeder 1967; Mansell 1992), where the family is only represented by two fossil species: *Marquettia americana* (Cockerell 1907) and *Marquettia metzeli* (Pierce & Kirkby 1959), which are further discussed by Carpenter (1959).

Adult nemopterids are obligate nectar and pollen feeders with specially adapted elongate mouthparts (Popov 1963; Tjeder 1967; Picker 1987; Monserrat & Martinez 1995; Mansell, 1996; Monserrat 1996; Krenn *et al*. 2005, Krenn *et al.* 2008). These modifications are derived traits that have evolved from predatory biting and chewing mouthparts to the present form and function (Krenn *et al*. 2008). Unlike the adults, larvae of Nemopteridae are all specialised predators, with elongate mandibles and maxillary laciniae adapted for piercing and ingesting the internal tissues of small arthropods (Popov 1963, 1973).

The subfamily Crocinae is characterised by its thread-like hind wings that function as tactile sensors and in mate recognition systems (Mansell 1996; Monserrat 1996). It includes about 48 species mostly confined to arid desert zones on the southern fringes of the West Palaearctic, West Oriental Region, and dry areas of the Neotropical, Afrotropical and Australian Regions (Mansell 1996; Monserrat 1996). This distribution in the southern continents suggests a Gondwanan origin (Mansell 1986). An increasing amount of data on the biology and morphology of Crocinae has been provided by Tjeder (1967), Mansell (1976, 1977, 1980, 1981a, 1981b, 1983a, 1983b, 1986, 1996) and Monserrat (1983). Hölzel (1975) and Monserrat (1996) added information on the taxonomy, biogeography and phylogeny of the subfamily. The adults of Crocinae are mainly nocturnal and crepuscular while the larvae have specialized habitat preferences including small caves, under rock overhangs or hollow tree trunks (Sole *et al*. 2013). They are sometimes synanthropic, living in man-made structures such as ceilings, old fireplaces, window sills and ledges (Mansell Pers. Obs.). The flying, mating and ovipositional behaviour was described by Mansell (1996). Several observations of two species have been made of mating aggregations of about 20 individuals flying in small swarms under rock overhangs and small caves (Mansell Pers. Obs.).

By contrast, the subfamily Nemopterinae has spoon or ribbon-like hind wings that stabilize the insects during flight and for camouflage when at rest (Mansell 1996). It is thought that they also play a role in thermoregulation. However, laboratory investigations by Leon & Picker (1990) on *Palmipenna aeoleoptera* Picker revealed limitations in this regard. Despite these findings, field observations by Ball, Brinkman and Mansell (Pers. Obs.) on the genera

Sicyoptera Navás and *Barbibucca* Tjeder, and the species *Palmipenna pilicornis* Tjeder and *P. aeoleoptera* strongly support the thermoregulation hypothesis.

The subfamily Nemopterinae comprises 94 described valid species, with at least another 20 undescribed species in southern Africa.

The biology of the adults and preimaginal stages of Nemopterinae are still obscure (Tjeder 1967; Mansell 1973). Only a few studies have discussed the eggs, larvae and pupal stages (Mansell 1973; Monserrat 1996). The first record of a nemopterine larva from Africa was by Mansell (1973), revealing that larvae of *Derhynchia vansoni* Tjeder, a Kalahari endemic, live freely in sand and use their prothoracic legs for burrowing forwards into sand (Mansell 1973). The adults have a short and synchronous emergence period once a year (Tjeder 1967; Mansell 1973), with mass emergences occurring periodically. The environmental cues that stimulate such emergences have not been positively established, but are thought to be rainfall-related. Species of some genera are diurnal in habit (*Sicyoptera*, *Palmipenna* Tjeder, *Halterina* Navás, *Barbibucca*, *Knersvlaktia* Picker), while others (*Nemopterella*, *Nemia*, *Nemeura* Navás, *Semirhynchia* Tjeder, *Derhynchia* Tjeder) are crepuscular and nocturnal, and often attracted to light in large numbers. (Tjeder 1967, Mansell and Ball Pers. Obs.)

South Africa harbours most of the world Nemopteridae species with about 72 species (48% of the world fauna) known from the Cape region of which 57 species (38% of the world fauna) are mainly centred in the Western and Northern Cape Provinces (Sole *et al*. 2013). The genera, *Laurhervasia* Navás, *Concroce* Tjeder, *Thysanocroce* Withycombe (Crocinae), *Derhynchia, Sicyoptera*, *Palmipenna, Halterina, Barbibucca, Knersvlaktia, Nemia* and *Nemopterella* (Nemopterinae) are confined to southern Africa while a single genus (*Semirhynchia*) extends its range of distribution into southern Angola. Two genera (*Nemeura and Nemopistha* Navás) extend northwards into other parts of the Afrotropical Region (Tjeder 1967).

In South Africa, the distribution of the taxa in the family seems limited to small ranges or sometimes to single localities that are confined to arid and semi-arid habitats of low annual rainfall (254 mm) and high relative humidity, in areas characterised by sandy or stony landscapes with low vegetation cover (Tjeder 1967). The genera *Nemeura* and *Nemopistha* by contrast, occur in the north-eastern part of South Africa where rainfall is higher and sometimes surpasses 762–1016 mm (Tjeder 1967).

Taxonomic history

The genus *Nemopterella* (now *Nemopterella sensu stricto*) was originally described by Navás (1910), who designated *Nemopteryx africana* Leach, 1815, as type species of *Eretmoptera*.

However, the name *Eretmoptera* is preoccupied by a genus of Diptera (*Eretmoptera* Kellogg, 1900) and Banks (1910) proposed the name *Nemopterella* as a replacement name for *Eretmoptera*. Navás (1915) split the genus *Nemopterella* into two genera, *Nemeva* with type species *Nemopteryx africana* and *Nemia* with type species *Nemoptera costalis* Westwood, 1836. This taxonomy was based on variation in the forewing venation of the two genera. In *Nemia* the "*confluentiam cubitorum*", *i.e.* the veins CuA and CuP (Fig. 2) are fused before reaching the forewing margin. Tjeder (1967), in a comprehensive morphological study of the genera *Nemeva* and *Nemia*, refuted Navás' division as it was based on a character that is consistently found in most nemopterids and also in the type species of *Nemeva*. He then attempted to find additional substantive characters to differentiate between the two genera, and discovered a pair of large spongy structures, pleuritocavae, in the abdomen of the male of *N. africana* (Fig. 1 (a)) that are absent from the abdomen of the male of *N. costalis* (Fig. 1 (b)). He consequently synonymised *Nemeva* Navás with *Nemopterella*. The taxonomic status of the genus however, remained unclear owing to the discovery of new species that are very close morphologically to *Nemia* but have pleuritocavae which are characteristic of the males of *Nemopterella.*

In this study, we revise the South African genera *Nemia* and *Nemopterella*, as their past taxonomic treatment is still controversial due to a lack of reliable diagnostic features. Moreover, the two genera had not been revised since Tjeder (1967) and there was a large amount of accumulated material in various South African museums, which was in need of investigation. Some species were known only from a single locality or from single specimens, which necessitated their revision to determine their accurate range of distribution as well as their validity. In addition, there was also a need to provide a clear identification key to the species in each genus.

This taxonomic revision is based on morphological criteria. A concurrent molecular study of the genera *Nemia* and *Nemopterella* (Abdalla *et al*. in preparation) strongly supports the recognition of four distinct lineages. One lineage comprises most of the species in the genus *Nemopterella,* with the exception of *N. africana* and *N. arenaria*, which resolve separately, with each forming a separate well supported distinct lineage. The genus *Nemia* also forms a well-supported fourth separate lineage.

In view of the above, we concluded that the lineages constitute four distinct genera: *Nemopterella* with type species *Nemopterella africana* (Leach, 1815), comprising three species; *Nemia* (Navás, 1915) with type species *Nemia costalis* (Westwood, 1836) with six species and two new genera, the monotypic genus *Siccanda* **gen. nov.**, with type species

Nemopterella arenaria Tjeder, 1967, and *Afroptera* **gen. nov.**, with type species *Nemopterella munroi*Tjeder, 1967, comprising 28 species of which 20 were described by Tjeder (1967) and eight new species are described here. The geographic distribution and habitat preference for each species, with illustrated maps are provided. Identification keys to the species in *Afroptera* **gen. nov.**, and in *Nemopterella* are also provided. In addition, there are illustrations of habitus, thorax, antennae and forewings.

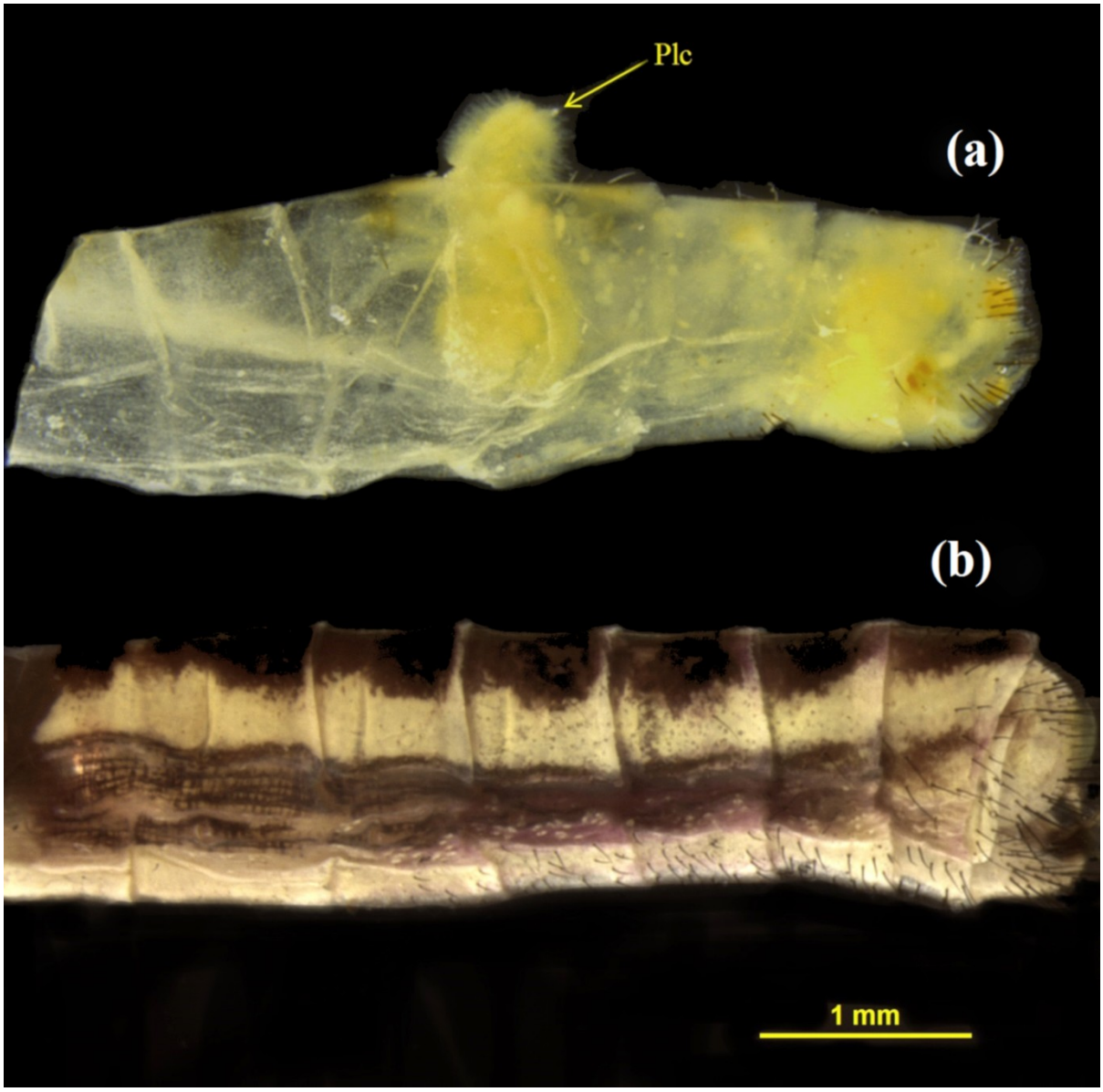


Figure 1(a) & (b); (a), *Nemopterella africana* (Leach). Abdomen lateral view with everted pleuritocavae (Plc); (b), *Nemia karrooa* (Péringuey). Abdomen lateral view lacking pleuritocavae.

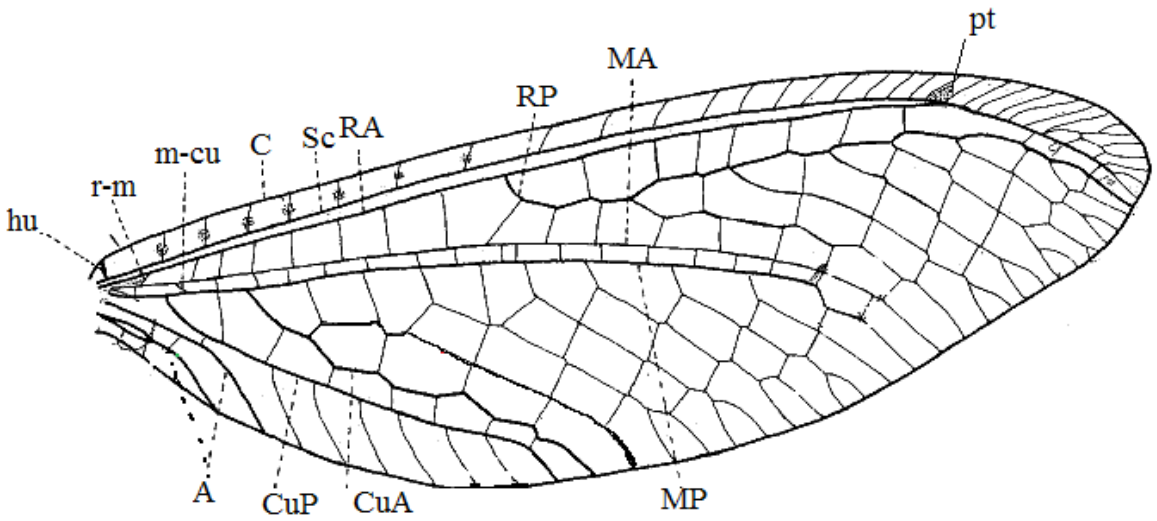


Figure 2. Wing venation of forewing. *Afroptera* pruinosa (Tjeder), after Tjeder (1967). Forewing terminology follows that of (Breitkreuz *et al.* 2017). Abbreviations: A = Anal, C = Costa, CuA = cubitus anterior, CuP = cubitus posterior, MA = media anterior, MP= media posterior, RA = radius anterior, RP = radial posterior, hu = humeral vein, r-m = oblique cross vein, m-cu = oblique vein, Sc = subcostal vein, Pt = Pterostigma. Abbreviations for wing venation used in text below.

Material and methods

This study is based on examination of material in the following institutions: South African National Collection of Insects, Pretoria, South Africa (SANC); Jonathan B. Ball Collection, Cape Town (JBBC); IZIKO South African Museum (formerly South African Museum), Cape Town, South Africa (SAMC); Ditsong Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa (TMSA); Naturhistorisches Museum Vienna; Austria (NHMW); Zoological Institute, Lund University Lund, Sweden (ZILS); Oxford University Museum of Natural History, Life Collection Oxford, England (OXUM); National Museum, Bulawayo, Zimbabwe (NMBZ).

Terminology follows that of Tjeder (1967). Some measurements were taken to approximate lengths as the abdomens of some specimens are curved posteriorly and difficult to measure. In addition, the wings are sometimes deformed apically, as well as antennae that are either curved to one side or the tip is lost. All measurements are in millimeters. Measurements of the

body, forewings, hind wings and antennae were obtained with a digital caliper. Body length was measured from the anterior margin of vertex to the apex of the abdomen.

Habitus and forewing photographs were taken using a Canon EOS550D camera coupled with a 100 mm Canon® macro lens. All photos were compiled using Helicon Focus automontage software. Images of antennae were taken using a Leica camera, version DMC-2900 attached to a Leica M 165C stereomicroscope.

Localities and label data are presented. We used square brackets to insert additional data, not reflected on the original label, and single slash (/) to separate data on different labels on the same pin.

Distribution maps are based on specimen locality information from labels or obtained from the Palpares Relational Database (Mansell & Kenyon 2002). Taxomomic data derived from this database can be viewed online in Mansell & Oswald (2019), and the specimen data on the websites of the Animal Demography Unit, University of Cape Town, http://vmus.adu.org.za/?vm=LacewingMAP, and the South African National Biodiversity Institute in Mansell (2016). Maps were generated using ArcGIS 10.4 software.

Accession numbers are provided for all material examined and recorded as in the above-mentioned database. The first four letters of each unique accession code reflect the institutional acronym as provided above.

Systematic account

Family Nemopteridae Burmeister, 1839

Subfamily Nemopterinae

Genus *Nemopterella* Banks, 1910

Synonymy

Eretmoptera Navás, 1910: 359 (Preoccupied by *Eretmoptera* Kellogg, 1900, Diptera)

Nemopterella Banks, 1910: 390; Navás 1911: 226.

Nemeva Navás, 1915: 35; Tjeder 1967: 454 (synonymy).

Type species. *Nemopteryx africana* Leach, 1815, by original designation.

Diagnosis. Medium to large species that can be distinguished by: (1) tip segment of antennae in the males as well as females terminates in an acute tooth (Fig. 8); (2) vertex of head broad with a pair of yellow or dark transverse spots along the postfrontal suture on the

frons above antennae (Fig. 9); (3) forewings with a whitish pterostigma (Fig. 7a); (4) anal area tinged brown or dark brown (Fig. 7b); (5) number of costal cells between 23–37; (6) the entire hind wing from base to the apical whitish area bears black setae (Fig. 10); (7) fifth abdominal tergite with a pair of pleuritocavae on each side (Fig. 3); (8) thorax and abdomen with distinct brown to dark brown longitudinal mid and lateral-stripes; (9) costal crossveins (Cx) and area between the Cx tinged brown to light brown.

Size (mm). Male: body length 7–12.7; forewing 20.5–32.2; hind wing 42.4–73.1; antenna 14.3–37.2; Female: body length 8.7–15.1; forewing 17.5–28.7; hind wing 34.5–62.3; antenna 13.2–20.2.

Redescription.

Head. Large with long rostrum (Fig. 9). Vertex broad with dark midline along epicranial suture and a pair of yellow or dark sub-triangular transverse spots along postfrontal suture on frons above antennae. Frons above antennae markedly elevated. Eyes large, widely separated. Antennae in males show intraspecific variation, some not reaching pterostigma others reaching just beyond pterostigma, while some extend beyond the wing (Figs 11–13). Tip segment ends in an acute tooth (Fig. 8). In females, antennae are short not reaching pterostigma and ending in acute tooth on the tip segment. In some species, the head bears distinct very sparse short black hairs over vertex and genae.

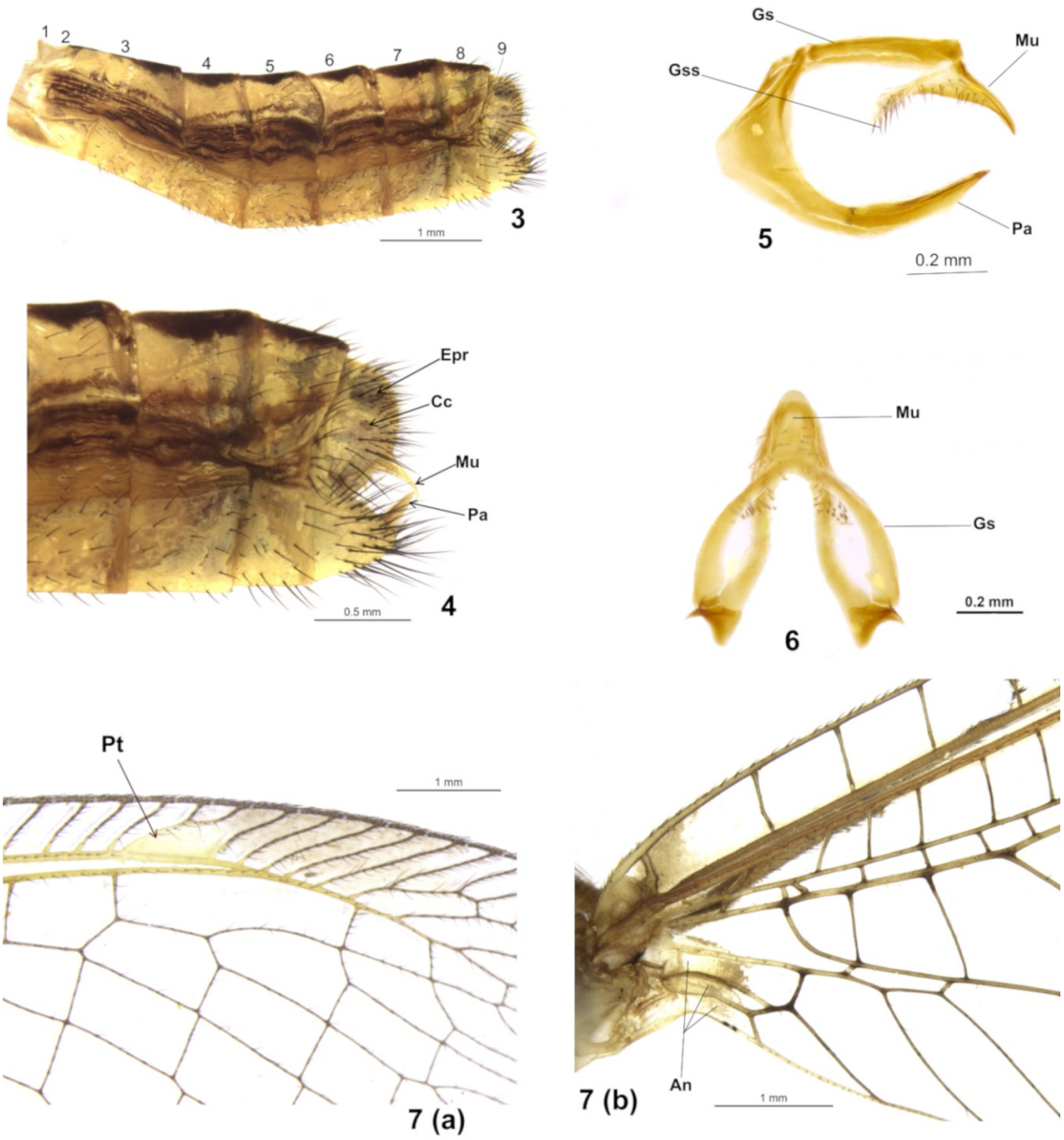
Thorax. Pruinose, with distinct longitudinal brown or dark brown mid and two lateral stripes. Pronotum short, narrow, elevated in the middle bending downwards laterally with saddle-like shape and elevated fore margin with upwardly reflexed hind margin. Mesonotum broad, metanotum shorter narrower than pronotum. Pubescence differs between sexes being longer, denser and softer in males than in females.

Forewings. Hyaline. Differing between sexes, slender in males and broader in females. Male forewings with an acute or sub-acute apex combined with a slight or shallow emargination before the apex or in some species with a rounded apex without distinct emargination. In females, forewings have a rounded apex without emargination. Pterostigma is mainly white (Fig. 7 (a)). Area between costa (C) and subcosta (Sc), as well as anal area tinged brown. In most species, the subcostal and radial areas tinged brown with adjacent costal cells beyond pterostigma tinged greyish brown. Costal crossveins (or costals) (Cx) vary from 23–37. *Hind wings* very narrow, ribbon-like, with four distinct portions: the proximal portion near wing base pale or fuscous in colour, the portion before the dark area pale whitish, the dark area brown or dark brown, apical portion white. Setation black from wing bases to apical white portion (Fig. 10). *Legs* slender, covered with black setae, in some species the

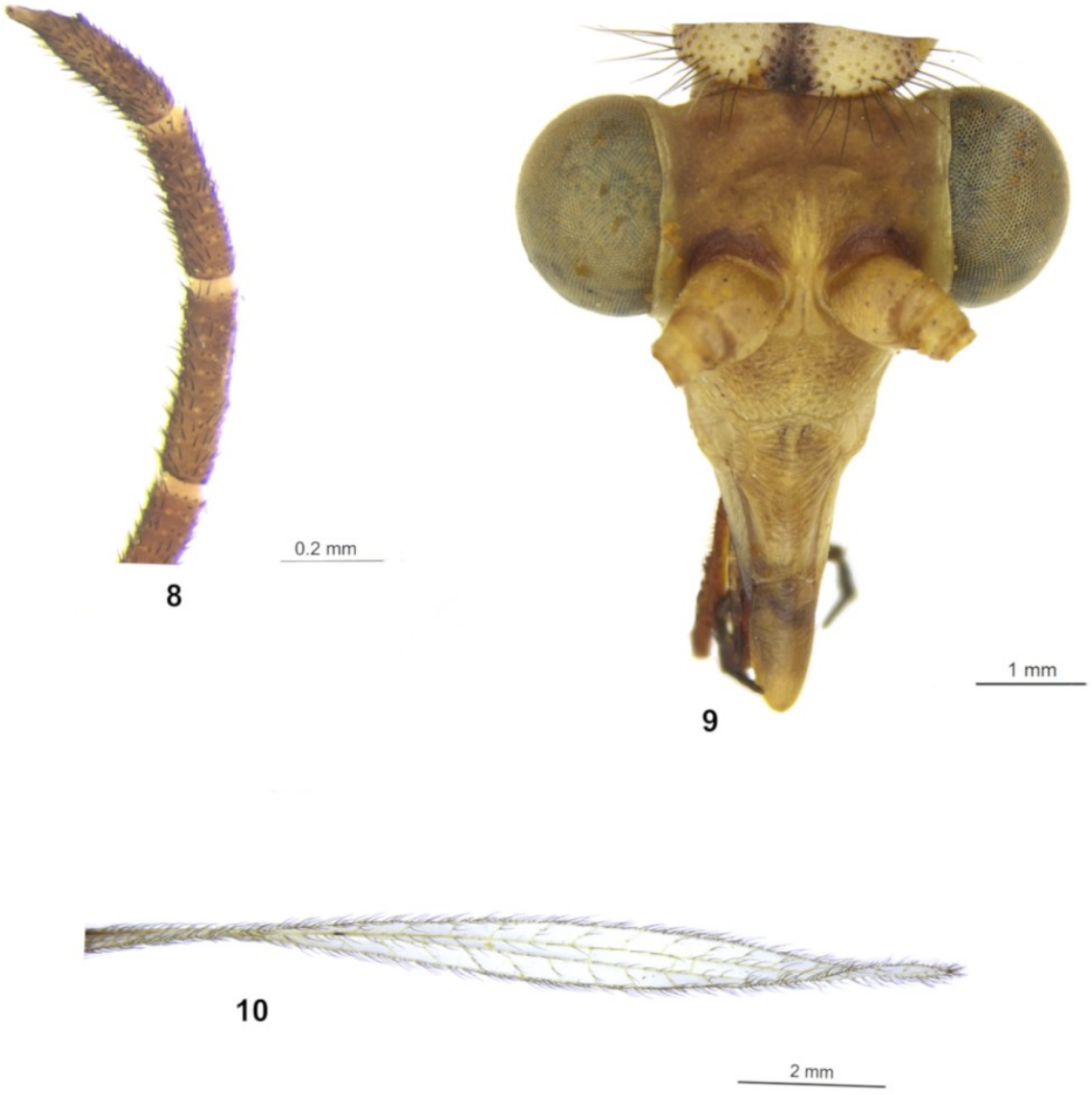
coxae covered with white setae; femora and tarsi either with or without tinged tips Tarsal segment 1 longer than segments 2–5 combined.

Abdomen. Cylindrical with short segments and very distinct brown or dark brown mid and lateral stripes (Fig. 3). In males, tergite 5 has short folds at hind margin with a pair of spongy structures, pleuritocavae, that open between tergites 5 and 6 (Fig. 1 (a)). Fore margin of tergite 6 is much larger than fore-margins of other abdominal tergites. These structures are absent from females. Setation of abdomen different in sexes, always longer and denser in males than females.

Genital structures of males and females are similar in the different species with no significant differences observed, so are of little value in distinguishing between species. In males, the gonarcus bears a long mediuncus and the gonolatus and gonosetae are present. Parameres long, fused apically (Figs 4, 5). Females with short gonapophyses laterales.



Figures 3–7 *Nemopterella africana* (Leach). 3, Abdomen male, lateral view; 4, Apex of male abdomen. 5, Parameres and gonarcus; 6, Gonarcus dorsal view showing bases of parameres. 7(a), Pterostigma in forewing; 7(b), Anal area. Abbreviations: 1–9 = Abdominal tergites, An = Anal area, Epr = Ectoproct, Cc = Callus cerci, Mu = Mediuncus, Pa = Parameres, Pt = Pterostigma, Gs = Gonarcus, Gss = Gonosetae.



Figures 8–10. *Nemopterella africana* (Leach). 8, Antennal apex; 9, Head; 10, Apical white portion of hind wing.

Key to species of male *Nemopterella*

1. Forewings with broad rounded apex, without emargination before apex (Fig. 19), hairs on thorax short, black (Fig. 15)…….....*Nemopterella cedrus* **sp. nov.**

- Forewings with acute or sub-acute apex, with emargination before apex, hairs on thorax long with different colours (Figs 14, 16)…….……..…….…….2

2. Forewings slender with sub-acute apex, costal cells before pterostigma tinged brown, costal cells beyond pterostigma shaded greyish brown (Fig. 17), male antennae extending beyond pterostigma, approximately the same length as forewing (Figs 11, 17) …….....*Nemopterella africana* (Leach)

- Forewings broad in the middle tapering towards apex, ending with sub-acute apex , costal cells before pterostigma shaded light brown, costal cells beyond pterostigma without shading (Fig. 18), male antennae extremely long, longer than forewings (Figs 13, 18) …..... …….....*Nemopterella kabas* **sp. nov.**

***Nemopterella africana* (Leach, 1815)**
(Figs 3, 4, 5, 6, 7, 8, 9, 10, 11, 14, 17, 31)

Synonymy

Nemopteryx africana Leach, 1815: 74.
Nemoptera africana (Leach): Westwood 1836: 75.
Nemoptera bacillaris Klug, 1836: 95; Walker 1853: 474.
Nematoptera bacillaris (Klug): Burmeister 1839: 986.
Nematoptera latipennis Burmeister, 1839: 986; Westwood 1841: 12.
Nematoptera africana (Leach): Westwood 1841: 12.
Halter africanus (Leach): Kirby 1900: 458.
Eretmoptera africana (Leach): Navás 1910: 359.
Nemopterella africana (Leach): Navás 1912: 9.
Nemeva africana (Leach): Navás 1915: 35.

Type locality. South Africa, *Western Cape Province*. Worcester, 33°38'23"S 19°26'41"E.

Type depository. BMNH.

Etymology. Unknown, most likely from the word Africa because the species originates from Africa.

Diagnosis. *Nemopterella africana* is externally similar to *N. kabas* **sp. nov**. It resembles *N. kabas* by having the same body patterns (Fig. 11). However, *N. africana* can easily be distinguished from *N. kabas* by a combination of the following characteristics: *N. africana*is is characterised by slender forewings with short rounded tip (Figs 11, 17) while in *N. kabas* the forewings are broader and taper towards acute apex (Figs 13, 18). Also, *N. africana* has

shaded costal cells beyond pterostigma (Fig. 17) while in *N. kabas* the costal cells are not shaded (Fig. 18). Moreover, *N. africana* has brown-tinged subcostal and radial areas (Fig. 17) while in *N. kabas* the subcostal and radial areas are not tinged (Fig. 18). Vertex in *N. africana* bears two dark transverse sub-triangular spots along the postfrontal suture (Fig. 5) while the transverse spots in *N. kabas* are yellow (Fig. 13). In addition, the male antennae in *N. africana* are long, extending beyond pterostigma and are approximately same length as forewing while in *N. kabas* the antennae are very long, longer than forewing.

Size (mm).Male: body length 9.7 (7–12.7); forewing 24.7 (20.5–27.6); hind wing 54.0 (42.4–61.8); antenna 17.6 (15.5–25.1). Female: body length 11.2 (8.7–15.1); forewing 25.3 (17.5–25.8); hind wing 50.1 (34.5–58.8); antenna 13.4 (14.5–19.8). (N = 143)

Type material. Holotype f# (not examined).

Material examined. SOUTH AFRICA, *Western Cape Province*, 22f#, NEUR09680, Doornfontein Farm, Tanqua Karoo, 32°35'S 19°33'E, 20–21.x.2006, 432 m, A.K.Brinkman; 1m#, NEUR09681, Dwarsrivier Farm, Clanwilliam Dist., 32°13'S 18°59'E, 26–27.x.2006, 337 m, A.K.Brinkman; 1m# 1f#, NEUR02145, Sanddrift Farm, Cedarberg Mts., 32°29'S 19°16'E, 19–24.xii.1994, E.Grobbelaar, Collected at light;2m# 4f#, NEUR00419, Citrusdal, [32°35'24"S 19°00'4"E], M.v.d.Berg, 12.xi.1981, ACH1184, Gevang by ligval / Nemopterella africana (Leach), det. M.W.Mansell; 1m# 5f#, NEUR00701, Biedouw Farm, Biedouw Valley, 32°08'S 19°14'E, 29.ix.1986, M.W.Mansell, J.H.Hoffmann / Collected at light; 1m#, NEUR11193, Clanwilliam, Owls Hoot B&B, 32°10'12"S 18°53'52"E, 87 m, 18.xi.2001, M.W.Mansell, J.B.Ball; 1m#, NEUR11809, Kelkiewyn Farm, Calvinia District, 31°12'01"S 19°41'33"E, 25.x.2011, 681 m, C.H.Scholtz; 1m# 7f#, NEUR09922, same locality and collector, but 1–3.xii.2008 / At light; 2f#, NEUR12305, Sarisam Farm, 30°34'50"S 17°32'15"E, 3–6.xii.2013, R.D.Stephen (All SANC). 1m# 1f#, SAM–NEU–A001248, Bulhoek, CLW. [Clanwilliam], [32°00'03"S 18°46'43"E], S.A.M., 12.56 / *Nemopterella africana* (Leach), det. Bo Tjeder, 1965; 1f#, SAM–NEU–A001247 / Upper Source Olifants River, Ceres, [33°22'00"S 19°19'00"E] / *Nemopterella africana* (Leach), det. Bo Tjeder, 1965 (All SAMC). 2m# 1f#, TMSA00736 and 5f#, TMSA00764, Diepkloof Farm near Clanwilliam, [32°01'32"S 18°51'20"E], 12.xii.03, to M.V. light, Farm staff / *Nemopterella africana* (Leach, 1815) f#, Det. M.W.Mansell 2013 (All TMSA). *Northern Cape Province,* 1f#, TMSA02059, Lekkersing [29°00'06"S 17°05'58"E], 17.xi.1933, G.van Son / *Nemopterella africana* (Leach), det. Bo Tjeder, 1965 (TMSA); 19m# 24f#, NEUR01471, Concordia, 29°32'41"S 17°56'04"E, 1000 m, 9–10.xi.1990, M.W.Mansell, R.B.Miller, L.A.Stange / Collected at light (SANC). 2f#, SAM–NEU–A001246 / Aggeneys,

Bushmanland, Btw Springbok and Pella [29°11'S 18°50'E] / *Nemopterella africana* (Leach), det. Bo Tjeder, 1966 (SAMC). 4m# 1f#, NEUR02142, Kliprand 40 km S., 30°58'S 18°40'E, 400 m, 3.xii.1988, M.D.Picker (SANC). NAMIBIA, *Karas Region*. 16m# 16f#, NEUR08900, Diamond Area no. 1, Klinghardtberge, 27°19'S 15°46'E, (2715 Bd), 20 / 21.x.1974, M.W.Mansell / Collected at mercury vapour light, arid rock terrain (SANC).

Distribution and habitat. This species has a wide distribution but is endemic to South Africa and Namibia (Fig. 31). In South Africa, the species is known from the Northern and Western Cape Provinces in localities mainly centred in the Succulent Karoo, Nama Karoo and Fynbos Biomes. In the Succulent Karoo, the species has been reported from the Rainshadow Valley Karoo Bioregion occurring in the Tankwa Karoo and Agter-Sederberg Shrubland vegetation units (Mucina & Rutherford 2006). Both regions are dry, characterised by winter rains. The former unit is dominated by scattered dwarf succulent shrubs while the latter is vegetated mostly with tall shrubs of a mixture of succulent and non-succulent elements. The species has also been recorded from the Namaqualand Hardeveld and Strandveld Bioregions, where it seems to be associated with two different vegetation units: Namaqualand Blomveld and Namaqualand Strandveld. The habitat in the former unit is represented by sparse dwarf shrubs with succulent or ericoid leaves, while in the latter it is dominated by low shrubs of creeping succulents, and perennial plants when there is rain. *Nemopterella africana* has also been recorded from the Richtersveld Bioregion where the species has been found associated with Lekkersing Succulent shrubs. (The description of the habitat in this unit is given under the distribution of *A. sabuleti*). Within the Fynbos Biome, the range of distribution is centred in the Olifants Sandstone Fynbos and the Sandstone Fynbos Bioregions. In the former bioregion, the species is associated with the Sandstone Fynbos vegetation unit where the habitat is predominated by proteoid and restioid fynbos with mixtures of Cape thicket, asteraceous fynbos and tall shrubs. In the latter bioregion, the species seems to be associated with the Cederberg Sandstone Fynbos vegetation unit. The habitat in this unit is represented by asteraceous, restioid and proteoid fynbos (Mucina & Rutherford 2006). Another population has been collected from the Shale Renosterveld and Sand Fynbos Bioregions where the species is associated with Ceres Shale Renosterveld and Leipoldtville Sand Fynbos vegetation types (Mucina & Rutherford 2006). In the Nama Karoo, the collection localities fall mainly within the Bushmanland Sandy Grassland in the Bushmanland Bioregion. (See the description of the habitat in this vegetation unit under the distribution of *A. munroi*). In Namibia, the distribution is known only from the extension of the Succulent Karoo Biome in southern

Namibia. It is a dry region represented by succulent vegetation and predominantly receives winter rains.

***Nemopterella cedrus* Mansell & Abdalla sp. nov.**
(Figs 12, 15, 19, 32)

Etymology. The specific epithet is a noun in apposition from the Latin name *Cedrus*, a cedar tree, *Widdringtonia cedarbergensis* (the Clanwilliam or Cape cedar), for which the Cedarberg mountain range is named, and where the type specimens were collected.

Type locality. South Africa, *Western Cape Province*. Cedarberg, Sanddrift 32°29'16"S 19°19'13"E.

Diagnosis. This species is distinguished from its congeners by its small size, short antennae and the rounded apex of the forewings (Figs 12, 19).

Description

Size (mm). Male: body length 10.0 (9.5–10.4); forewing 22.5 (21–23.7); hind wing 50.3 (47.2–53.5); antenna 16.3 (14.3–17.6). Female: body length 11.0 (9.7–12.9); forewing 23.0 (21.7–24.7); hind wing 45.8 (39–57.6); antenna 14.0 (13.2–15.8). Holotype m# (Fig. 12): body length 9.7; forewing 22.8; hind wing 50.2; antenna 17.1. (N = 12).

Head. Yellow. Vertex reddish brown with longitudinal dark brown midline along epicranial suture. Pair of ill-defined sub-triangular yellowish portions present lateral to epicranial suture on frons above antennae, their apices extended into torular area. In addition, a pair of yellow portions lateral to dark brown line. Frons below antennae tinged reddish brown. Genae cream coloured. Palpi blackish brown. Eyes small, widely separated. Antennae yellow proximally, dark brown distally with short black setae. Antennae short not reaching pterostigma. Apical segment blackish, ending in acute bare tooth.

*Thorax.*Yellow, slightly pruinose, with three distinct longitudinal dark brown mid and two lateral stripes, which extend onto the membranous area between pronotum and mesonotum (Fig. 15). Mid stripe extends backwards through prescutum, mesoscutellum and metanotum while lateral stripes are also visible along lateral sides of prescutum. Pronotum margins covered in erect, long black hairs more dense along fore margin, less dense along hind margin. Very fine somewhat long white hairs situated on disc between the two margins. Lateral sides of pronotum with long black hairs intermingled with long white hairs. Prescutum disc with robust, long dense black hairs while antero-lateral sides with long black hairs intermingled with sparse long white hairs. Sparse, stiff, short black hairs present on mesoscutum and mesoscutellum discs, being longer along hind margin of mesoscutellum. Mesoscutum

posterior lateral sides with two groups of greyish hairs. A few very short black hairs present near base of each forewing. Sparse long white hairs admixed with black hairs present along hind margin and laterally on sides of mesoscutellum. Metanotum with two tufts of very long white hairs intermingled with long black hairs.

Forewings. Broad with broad rounded tip (Figs 12, 19). Venation blackish brown. Costa greyish brown. Subcosta brown proximally, light yellow to whitish distally towards pterostigma. Radius (R) brown. Other veins blackish brown. Subcostal and radial areas tinged with brown. Basal cells between the anal veins 1, 2 and 3 tinged dark brown. Proximal Cx near wing base shaded dark brown. Pterostigma white, short at base. Costal cells beyond pterostigma tinged with brown. Thirty Cx before pterostigma in right wing, 29 in left. Ten crossveins between RA and Media anterior (MA) before origin of Radial posterior (RP) in right wing, 9 in left wing of the holotype. Twelve radial crossveins before pterostigma in both wings. *Hind wings* pale yellow proximally, whitish in the middle before the dark area. Longitudinal and crossveins pale yellow to creamy white near wing bases and whitish before the dark area, with brown membrane proximally and whitish distally towards the dark area. Dark area dark brown and approximately same length as white area. Whole wing clothed with black hairs even the white area except for areas near the bases of wings that have long white hairs. *Legs* yellow with short black setae and dark brown tips to femora.

Abdomen. Yellow, slightly pruinose. Dorsum with distinct broad, longitudinal, blackish brown mid and lateral stripes. Tergites with sparse, long white hairs, some long black hairs admixed with the white hairs on tergites 5–9. Venter yellow with sparse short black hairs. Apex yellow with dense, long black pubescence.

Variation. Some males have only white hairs on metanotum. In addition, the examined specimens differ in the number of costals as well as the number of radial crossveins.

Type material examined. SOUTH AFRICA, *Western Cape* Province, Holotype m#, NEUR12344, Sanddrift, Cedarberg, 32°29'16"S 19°19'13"E, 840 m, 2.xii.2015, C.H.Scholtz, H.de Klerk. *Paratypes*: 2m# 9f#, same data as holotype (All SANC).

Distribution and habitat. This species is endemic to the Western Cape Province where it is known from only one locality within the Fynbos Biome (Fig. 32). The collection site falls within the Cederberg Sandstone Fynbos vegetation unit in the Olifants Sandstone Fynbos Bioregion (Mucina & Rutherford 2006). See the description of habitat in the unit under the distribution of *N. africana*.

***Nemopterella kabas* Mansell & Abdalla sp. nov.**
(Figs 13, 16, 18, 32)

Etymology. The specific epithet is a noun in apposition derived from Kabas Farm, Pofadder District, where the type specimens were collected.

Type locality. SOUTH AFRICA, *Northern Cape Province*, Kabas Farm, Pofadder District, 29°02'S 19°26'E.

Diagnosis. Externally, the species is similar to *N. africana.* Similarity and differences between the two species are discussed in the diagnosis of *N. africana*.

Description

Size (mm). Male: body length 11.1 (9.7–12.6); forewing 28.3 (24.7–32.2); hind wing 60.4 (49.7–73.1); antenna 30.4 (24.7–37.2). Female: body length 12.3 (10.2–14.2); forewing 25.2 (21.2–28.7); hind wing 54.2 (44.2–62.3); antenna 18.9 (15–20.2). (N = 128). Holotype m# (Fig. 13): body length 11.9; forewing 28; hind wing 62.3; antenna 33.

Head. Frons, clypeus light yellow. Genae creamy. Palpi light brown. Vertex light reddish brown with dark brown midline along epicranial suture, also with pair of sub-triangular yellowish portions on raised area of frons above antennae. Two dark brown spots near eye margins either each side of vertex. The yellow hind margin of vertex shortened into two yellow portions laterally on each side of epicranial suture. Eyes large, brown, widely separated. Antennae extremely long, longer than forewings. Scape and pedicel brownish, flagellomeres yellow with sparse, short setae proximally and dark, dense setae distally. Apical segment dark brown, ending with acute tip.

*Thorax***.** Yellow, slightly pruinose with pronotum yellow to creamy white (Fig. 16). The longitudinal brown central and lateral stripes well defined on pronotum, prescutum and mesoscutum, being much darker on pronotum and mesoscutellum and lighter on prescutum, central stripe appears narrow on pronotum and on area between prescutum and mesoscutellum and narrow on postnotum of mesothorax and metanotum and enlarged over prescutum disc. Mesoscutellum central stripe appears broad as an ill-defined brown shading. The three stripes also visible over dorsal cervical sclerite between pronotum and prescutum. Pronotal margins with erect, extremely long dense black hairs intermixed with long fine pale white hairs, with white hairs being denser on hind margin than fore margin. Pronotal disc with long pale white hairs. Very long erect brown hairs admixed with very long white hairs also present distally on each lateral side of pronotum. Prescutum disc with very long, dense, erect dark brown hairs intermingled with some pale white hairs on frontal part of prescutum. Extremely long, dark

brownish hairs intermingled with long white hairs present antero-laterally on each side of prescutum. Long white hairs spread along lateral sides of prescutum. Mesoscutum disc with long, soft brown hairs admixed with a few long white hairs and two clusters of extremely long white hairs present posteriorly on each side of mesoscutum. Two clusters of short black hairs present on lateral sides of mesoscutum above forewing bases. Mesoscutellum with faint brown shading centrally. Two groups of long white hairs situated posteriorly on each side of mesoscutellum. Metanotum with two tufts of very long white hairs laterally on each side of metanotum.

Forewings. Elongate, broadened in middle, tapered towards apex with sub-acute tip and slightly emarginated before apex (Figs 13, 18). Venation brown. Costa whitish, Sc and RA yellow. Distal portion of Sc and R and below pterostigma whitish. Pterostigma short, white, broad at base. Proximal costal cells shaded with very light brown. Costal (Cx) bases before pterostigma white, remainder dark brown. Thirty four Cx before pterostigma in right wing, 35 in left. Thirteen crossveins between RA and MA before origin of RP in right wing, 12 in left. Eleven radial crossveins before pterostigma in right wing, 12 in left. *Hind wings* light yellow proximally, whitish before the dark area. Longitudinal and crossveins light brown to creamy-white proximally and whitish before the dark area. Dark area dark brown with longitudinal and cross veins of same colour; shorter than the white area. Two tufts of long white hairs at each wing base. *Legs*. Femora yellow with brown tips, tibia and tarsi whitish yellow with long black setae. Fore coxae with dark brown hairs intermingled with long white hairs, while mid and hind coxae bear white hairs with a few short black hairs.

Abdomen. Yellow, slightly pruinose laterally. Dorsum with distinct longitudinal dark reddish brown mid and lateral stripes. Tergites with sparse, very long white hairs, much denser and longer at sides of tergites and on third tergites. Sternites not striped. Sternites covered in sparse relatively long black hairs, sparse short white hairs present on sternites 2–3. Apex yellow with long black hairs.

Variation. In some male specimens there are short black hairs intermingled with the white hairs on tergites 5–8 and also some white hairs intermixed with the black hairs on sternites.

Type material examined. SOUTH AFRICA, *Northern Cape Province*. Holotype m#, NEUR09631, Kabas Farm, 10 Km NE Pofadder, 29°02'S 19°26'E [29°03'40"S 19°26'07"E], 800 m, 1.xi.1996, M.W.Mansell / Collected at light. *Paratypes*: 2m# 4f#, NEUR09631, same data as holotype; 7m# 6f#, NEUR09631, same locality but 1.x.1996, M.W.Mansell, C.H.Scholtz / collected at light; 11m# 22f#, NEUR09630, same locality but 27.x.1996 / M.W.Mansell, C.H.Scholtz / Collected at light; 13m# 13f#, NEUR09628, Bottom of

Kouboomkloof, 6 Km S W of Aggeneys, 29°13"30'S 18°47"20'E, 6.xi.1996, E.Holm, C.Deschodt / Collected at light; 1m#, NEUR08901, Richtersveld, Cornell's Kop, 145 m, 28°25'S 16°53'E, (2816Bd), 9.x.1974, M.W.Mansell / Collected at mercury vapour light, arid rocky terrain / *Nemopterella africana* (Leach, 1815) m#, Det. M.W.Mansell, 1986; 2m# 4f#, NEUR09826, Richtersveld, Swartpoort, 28°07'S 16°55'E, 100m, 7.x.1991, M.W.Mansell / Collected at light; 3f#, NEUR09827, Richtersveld, De Hoop Turnoff, 3 km E Die Koei, 28°17'S 17°02'E, 450 m, 6.x.1991, M.W.Mansell / Collected at mercury vapour light; 2f#, NEUR09825, Richtersveld, Jenkins Kop, 28°43'S 17°15' E, 600 m, 9.x.1991, M.W.Mansell, R.G.Oberprieler / Collected at mercury vapour light; 1f#, without accession No. Richtersveld, 27.xi.1986, G.Newlands; 1m#, without accession No. 9 m W Steinkopf [29°15'11"S 17°43'52"E], 17.xi.1962, H.D.Brown, W.Furst. NAMIBIA, *Karas Region*. 11m# 11f#, NEUR08944, Dabimub River Valley, 27°58'S 17°07'E, 28.x.1999, M.W.Mansell, C.H.Scholtz / At light; 2m#, NEUR09786, Orange/Boom Rivers Confluence, 28°03'S 17°04'E, 29.x.1999, M.W.Mansell, C.H.Scholtz; 4m# 8f#, NEUR09823, Obib Poort, 28°06'S 16°42'E, 1.xi.1999, M.W.Mansell, C.H.Scholtz / Mercury vapour light. All SANC.

Distribution and habitat. This species is endemic to South Africa and Namibia (Fig. 32). In South Africa, it occurs in the Northern Cape Province in localities mainly centred in the Succulent and Nama Karoo Biomes. In the Succulent Karoo Biome, the species has been collected from the Richtersveld Bioregion where it is associated withUpper Annisvlakte Succulent, Bushmanland Inselberg, Umdaus Mountains Succulent, Central Richtersveld Mountain and the Stinkfonteinberge Eastern Apron Shrublands vegetation units, and associated with the Namaqualand Blomveld vegetation unit in Namaqualand Hardeveld Bioregion (Mucina & Rutherford 2006). (See the description of the habitats in these units under the distribution of *A. parva, A. dyscrita, A. brinkmani, A. papio* and*A. munroi*). In the Nama Karoo Biome, the range of distribution is mainly centred in the Bushmanland Sandy Grassland vegetation unit, Bushmanland Bioregion (Mucina & Rutherford 2006). See the description of the habitats in these units under the distribution of *A. munroi*. The range of distribution of this species extends north into the extension of the Succulent Karoo Biome of southern Namibia.

Figure 11. *Nemopterella africana* (Leach), male habitus. Forewing length = 26.9 mm.

Figure 12. *Nemopterella cedrus* Mansell & Abdalla **sp. nov**., male habitus Forewing length = 22.8 mm.

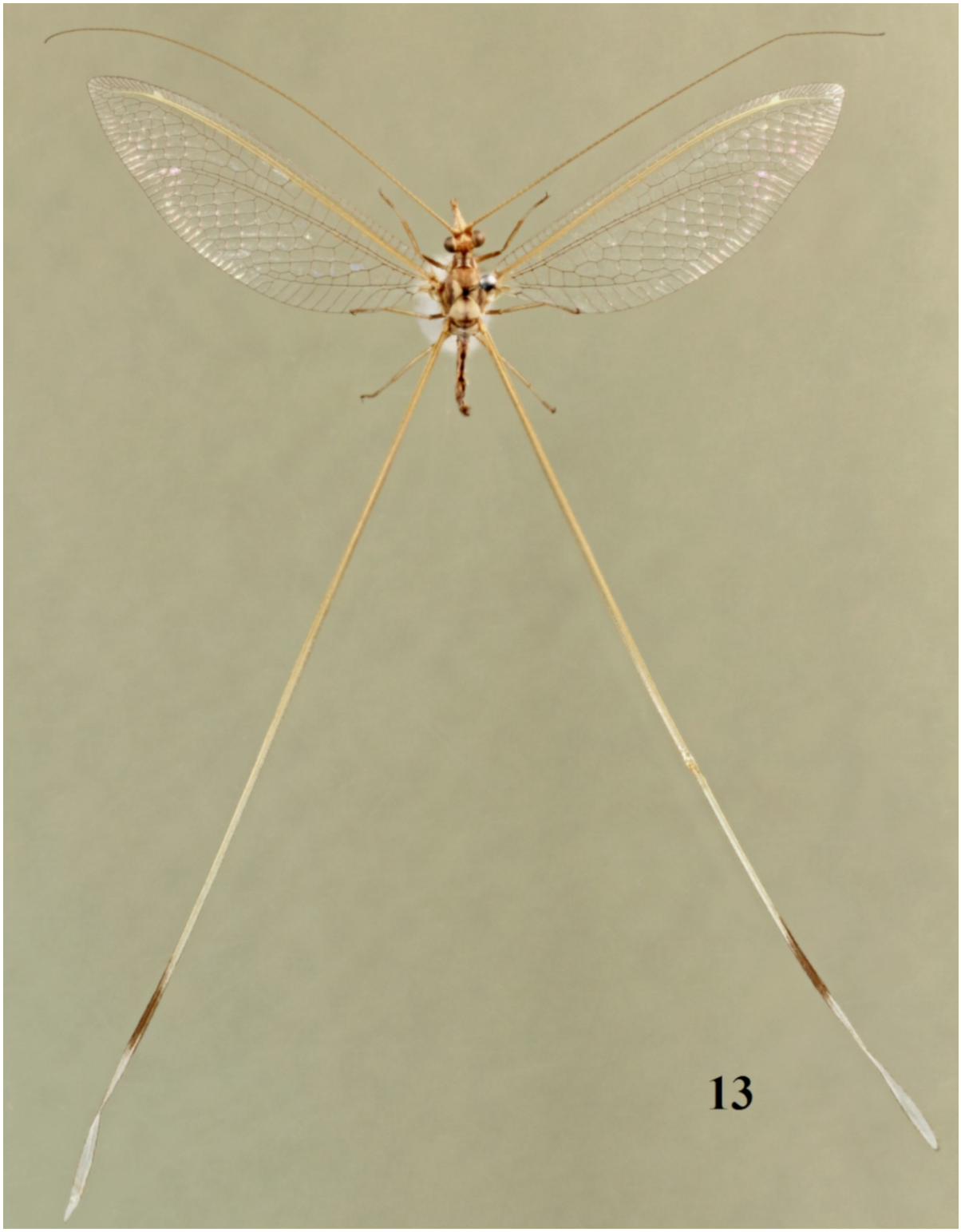
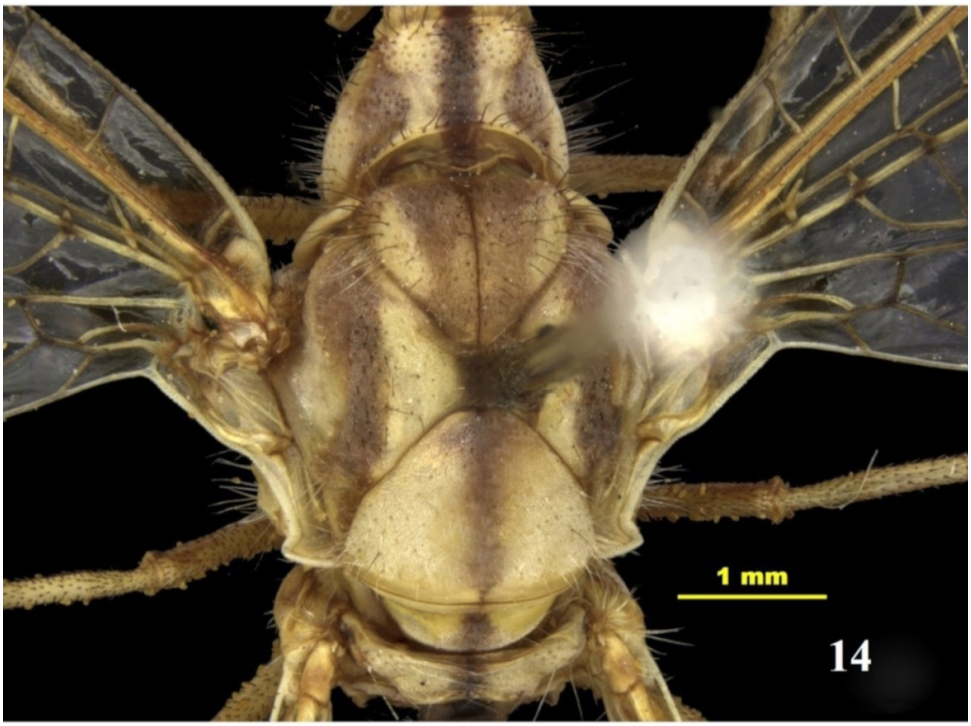
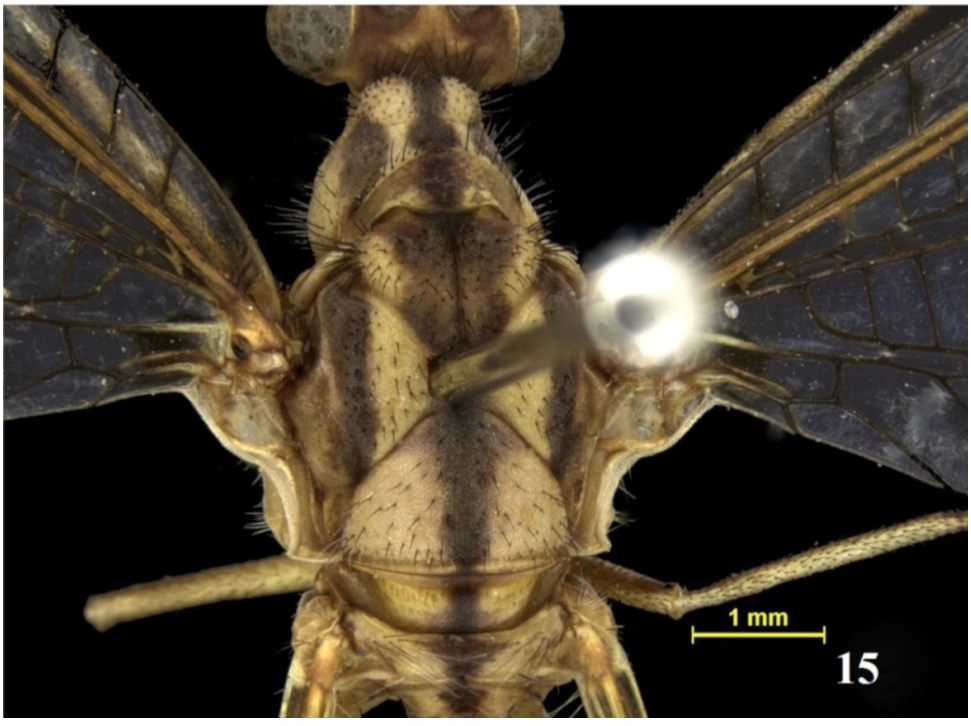


Figure 13. *Nemopterella kabas* Mansell & Abdalla **sp. nov**., male habitus. Forewing length = 28 mm.





Figures 14–15. *Nemopterella* spp. Thorax. 14, *Nemopterella africana*; 15, *Nemopterella cedrus*.

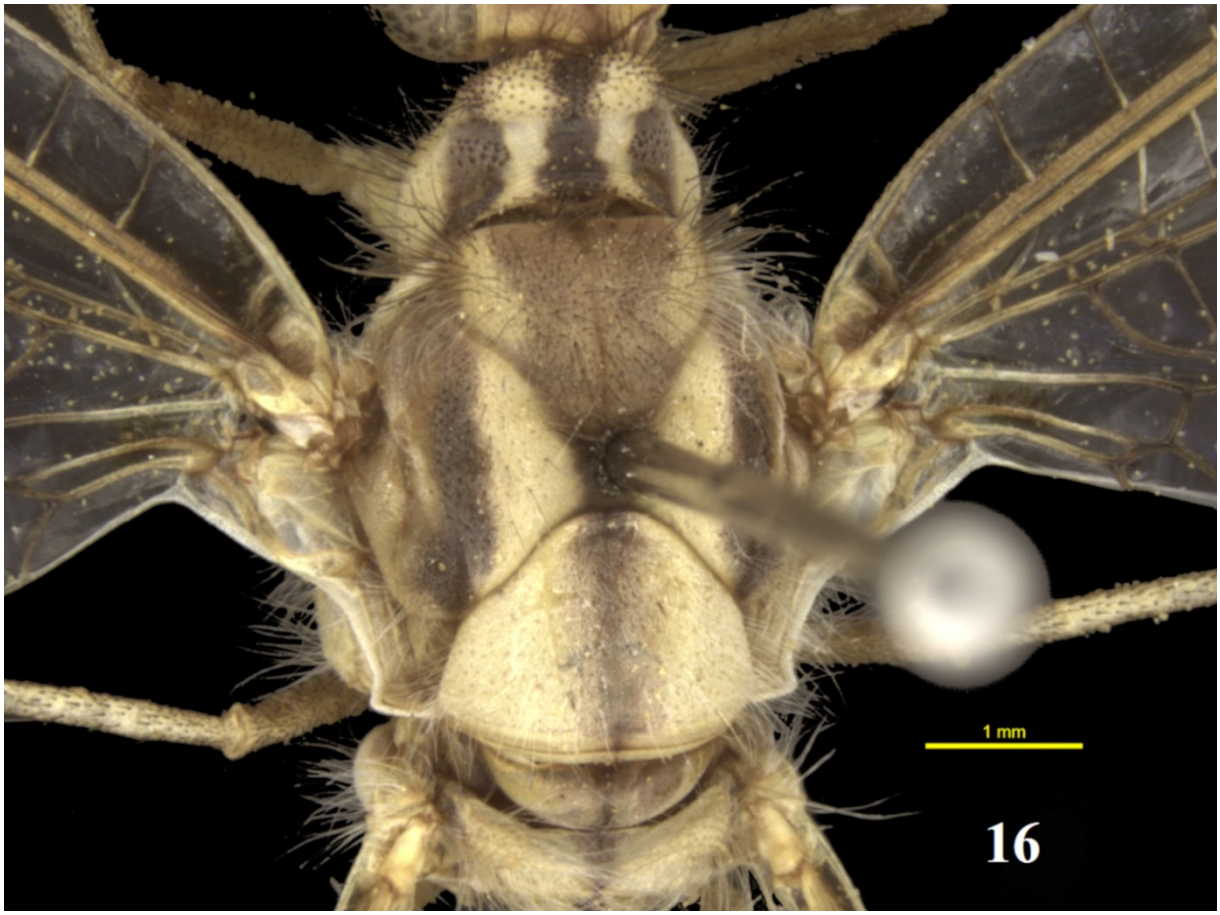
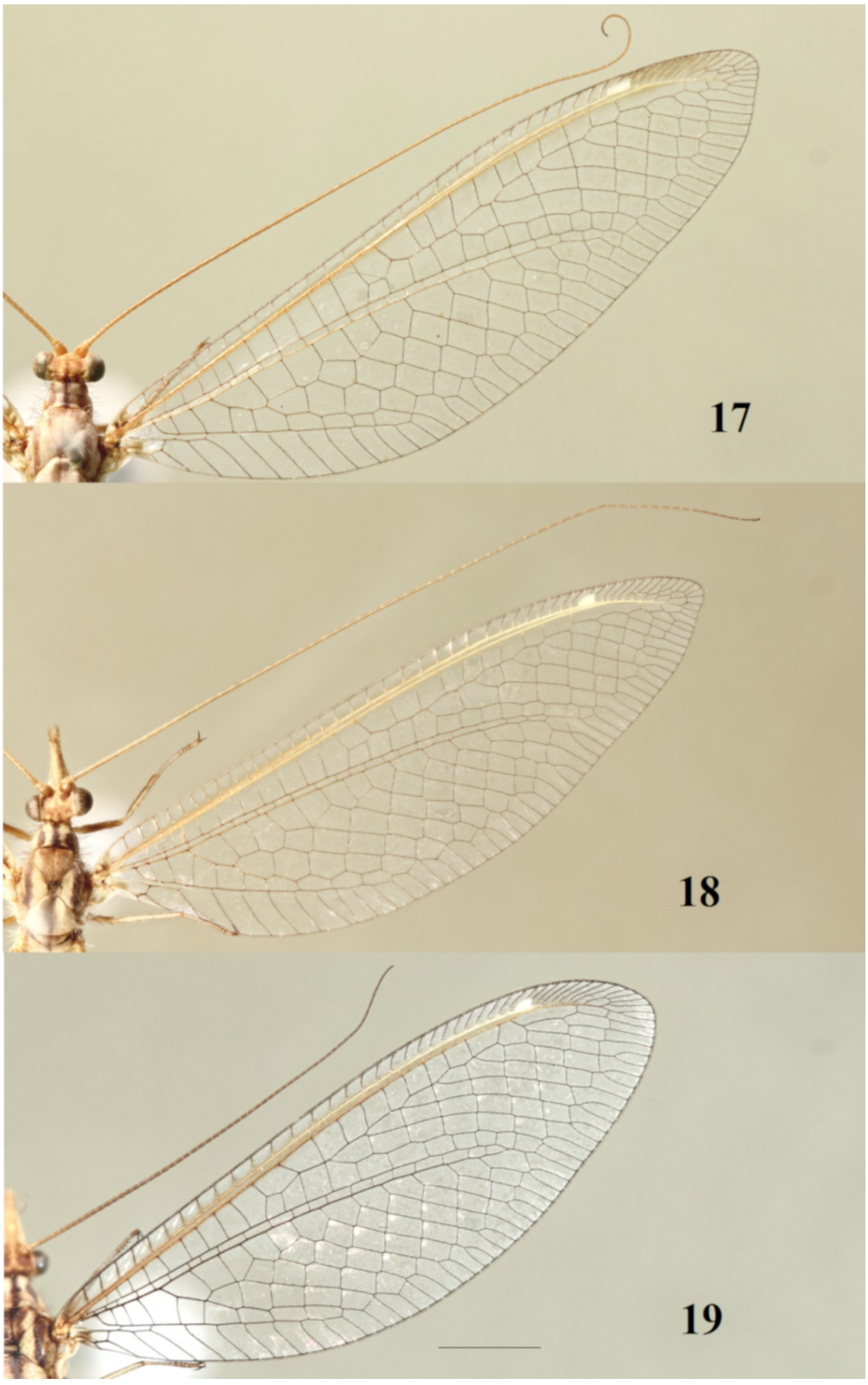


Figure 16. Thorax. *Nemopterella kabas*.



Figures 17–19. *Nemopterella* spp., male forewings. 17, *N. africana*; 18, *N. kabas*; 19, *N. cedrus* Scale = 1 mm.

Genus *Siccanda* Abdalla & Mansell gen. nov.

Synonymy

Nemopterella Banks, 1910: 454 (*partim*)

Etymology. The genus name is derived from the Latin adjective *siccaneus* (dry soil) for the dry areas where the species occurs. Gender feminine as derived from the name of the type species.

Type species. *Nemopterella arenaria* Tjeder, 1967 (Fig. 29), designated here.

Diagnosis. Small to medium-sized species, distinguished by: (1) faintly visible light yellowish pterostigma (Fig. 24b); (2) blackish greyish body (Fig. 29); (3) terminal segment of antennae ending with acute bare tooth (Fig. 25); (4) faint brown shading over Cx (Fig. 29); (5) between 20–32 Cx; (6) indistinct body stripes (Figs 20, 28, 29), (7) subcostal, radial and anal areas never tinged (Figs 24 a); (8) costal cells before and beyond pterostigma never tinged (Fig. 24b); (9) whitish apical portion of hind wings clothed with white hairs (Fig. 27); (10) tergite 5 of abdomen with pleuritocavae (Fig. 20); (11) Frons above antennae with pair of yellow transverse spots along the postfrontal suture (Fig. 26); (12) ventral side of the thorax tinged dark brown.

Description

Size (mm). Male: body length 7.8 (6.5–10); forewing 21.9 (20.3–26.9); hind wing 49.1 (43.4–62); antenna 20.4 (18.9–24.3); Female: body length 9.8 (9.2–10.6); forewing 21.2 (20.3–21.9); hindwing 45.1 (43.4–46.7); antenna 12.5 (11.1–12.8). (N = 47).

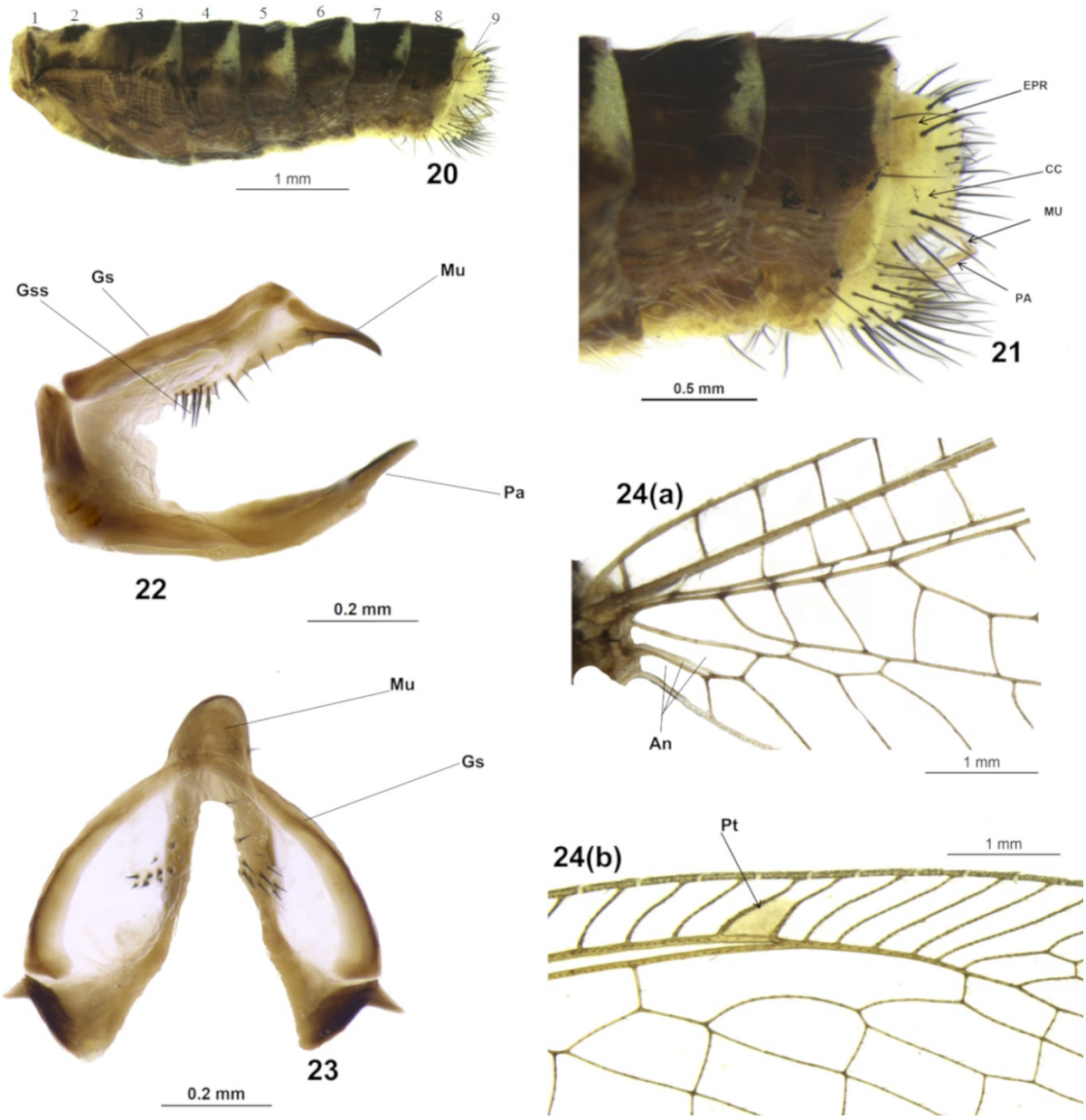
Head. Yellow, medium-sized with large prominent eyes that are relatively smaller and more widely separated in females than males. Vertex brown with yellow hind margin, distinctly broader in females than males. Frons above antennae markedly elevated with a pair of yellow transverse spots along postfrontal suture. Palpi brown. Antennae in males much longer than females, reaching beyond pterostigma, yellow proximally, darkened distally, covered in black setae becoming denser towards apex. Apical segment short, blackish, ending in acute bare tooth.

Thorax (Fig. 28).Shape as in *Nemopterella.* Markedly pruinose. Pronotum dark greyish brown without distinct stripes and with yellowish hind margin. Fore and hind margins covered in long, erect black hairs intermixed with long fine hairs. Fine, long white hairs situated behind the fore-margin hairs. Distal anterior lateral portions of pronotum covered in mixture of long black and white hairs. Setation in males much denser and longer than females. Mesonotum dark greyish with two greyish portions on anterior lateral sides of prescutum and

central greyish yellow portion between prescutum and mesoscutellum. Mesonotum ventral sides tinged greyish dark brown. Mesonotum very hairy particularly on prescutum disc, densely covered with long hairs, mainly black on prescutum and mesoscutum and white in mesoscutellum, also with some white hairs admixed with the black hairs on the antero-lateral sides of prescutum and on mesoscutum disc. Metanotum yellowish with two clusters of long white hairs laterally. *Legs* as in *Nemopterella* but coxae tinged dark brown.

Forewings (Fig. 29). Broader in females than males withfaintly greyish membrane. Males with slightly falcate apex and shallow emargination before apex, ending in a narrowly rounded apex while in females the apex is broadly rounded. Pterostigma small with light yellowish tinge. Costal cells, subcostal, radial and anal areas before and beyond pterostigma not tinged as in *Nemia* and N*emopterella*. Proximal Cx slightly shaded with brown. From 20–32 Cx present.

Abdomen (Fig. 20) as in *Nemopterell*a. Blackish with reddish yellow hind margins to tergites dorsally, without distinct stripes, yellowish ventrally. Setation different between sexes, long, dense and white in males, short, sparse and black in females.



Figures 20–24. *Siccanda arenaria* (Tjeder). 20, Abdomen, lateral view; 21, Apex of male abdomen; 22, Parameres and gonarcus; 23, Gonarcus dorsal showing bases of the Parameres; 24(a), Anal area; 24(b), Pterostigma in forewing. Abbreviations as in Figs 3–7.

Figures 25–27. *Siccanda arenaria* (Tjeder). 25, Antennal apex; 26, Head; 27, Apical white portion of hind wing.

***Siccanda arenaria* (Tjeder, 1967) comb. nov.**
(Figs 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 33)

Synonymy

Nemopterella arenaria Tjeder, 1967: 463.

Etymology. Unknown, but probably from the Latin *arenarius* (of sand) with reference to the dry sandy area in which this species occurs.

Type locality. SOUTH AFRICA, *Northern Cape Province*. Vioolsdrif, 28°50'S 17°39'E.

Type depository. TMSA

Diagnosis and description. As in genus.

Type material examined. SOUTH AFRICA, *Northern Cape Province*: Holotype m# (Fig. 29), TMSA02061, HOLOTYPE Neu 97, *Nemopterella arenaria* Tjeder (red–printed) / VIOOLSDRIF [28°50'S 17°39'E], 6-10.VIII.1961, van Son [G] & Vari [L] (white – printed) / Holotypus m#, *Nemopterella arenaria*, Bo Tjeder, 1966 (red – handwritten). (TMSA).

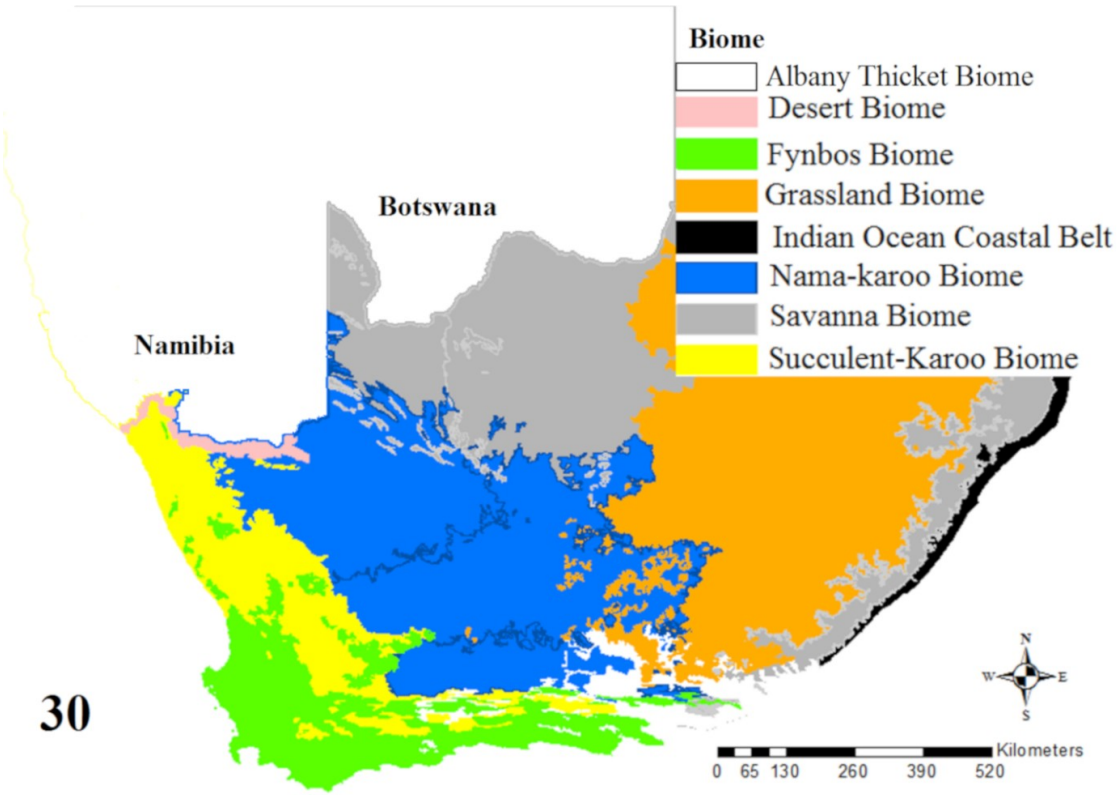
Other material examined. SOUTH AFRICA, *Northern Cape Province*: 8m#, NEUR10212, Keimoes, 28°44'07"S 20°56'19"E, 24.viii.2009, C.Deschodt, Handnetted; 13m# 1f#, NEUR11813, Koms Farm, 28°44'08"S 20°56'15"E, 730 m, 13.viii.2013, M.W.Mansell, J.B.Ball; 2m# 3f#, NEUR10212, same locality but 23.ix.2013, P.de Vos; 8m#, NEUR12534, same locality but 12–13.viii.2014, J.B.Ball, Handnetted; 2m#, NEUR09822, Namaqualand, Steinkopf [29°15'11"S 17°43'52"E], 3.ix.1986, R.Mijburgh (All SANC). NAMIBIA, *Karas District*: 6m#, TMSA02199, Farm Bergland, Gaapmouth into Fish River, 27°27'S 17°44'E, 826 m, 18.vii.2005, T.Bird / *Nemopterella arenaria* Tjeder, 1967 m#, det. M.W.Mansell 2014; 1m# 3f#, TMSA02196, Witput Farm, 27°26'S 17°42'E, 571 m, T.Bird / *Nemopterella arenaria* Tjeder, 1967 m#, det. M.W.Mansell 2014 (All TMSA).

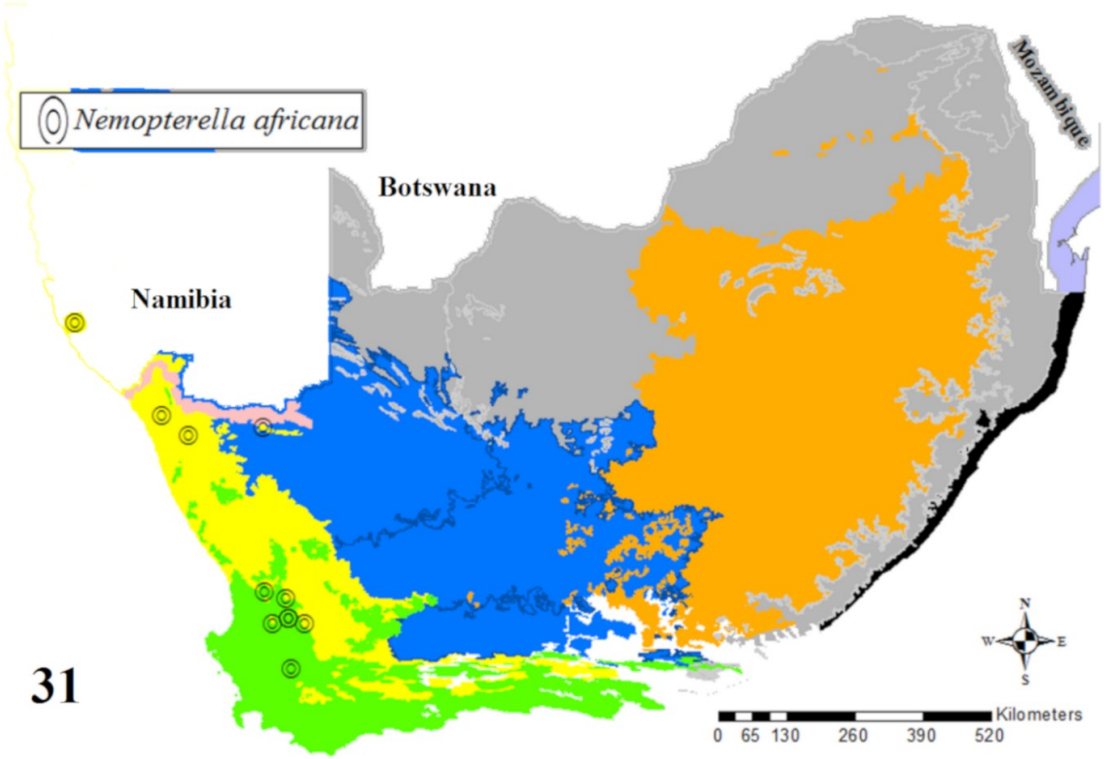
Distribution and habitat. This species is endemic to South Africa and Namibia (Fig. 33). In South Africa, the species is known from localities in the Northern Cape Province that mainly fall within the Nama Karoo and Desert Biomes. The collection sites are in the Lower Gariep Broken Veld and Northern Nababiepsberge Mountain Desert vegetation units in the Bushmanland and West Griqualandand Gariep Desert Bioregions (Mucina & Rutherford 2006). The habitat in the former vegetation unit is characterised by extreme aridity and summer rains. The topographic features are plains with sparse low hills and mountains; vegetated mostly by dwarf shrubs, perennial grasses, herbs and scattered low trees. While in the latter vegetation unit the habitat is montane interspersed by deep valleys, mostly vegetated by succulent trees, leaf-succulent shrubs and perennial herbs. It receives predominantly late summer / early autumn rains with mean annual precipitation 45–70 mm (Mucina & Rutherford 2006).

The species has also been recorded from sites located within the extension of the Nama Karoo Biome in Namibia.

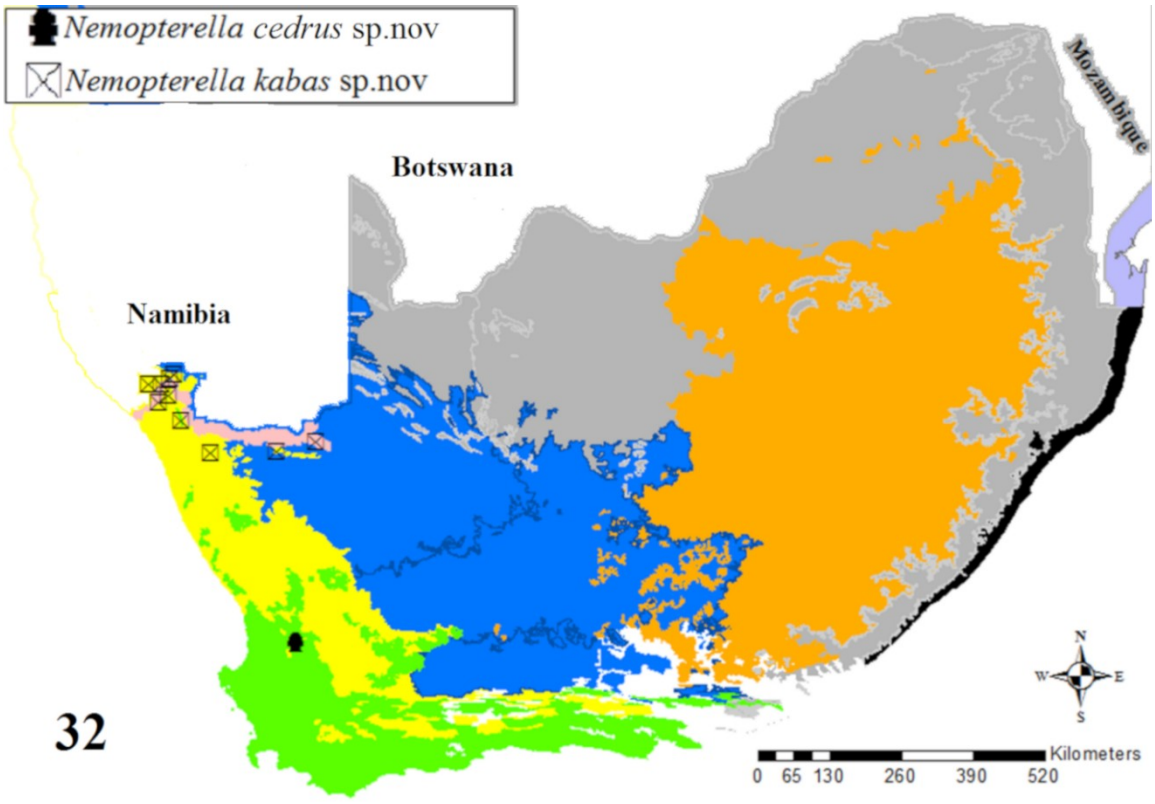
Figure 28. *Siccanda arenaria* (Tjeder). Thorax dorsal view.

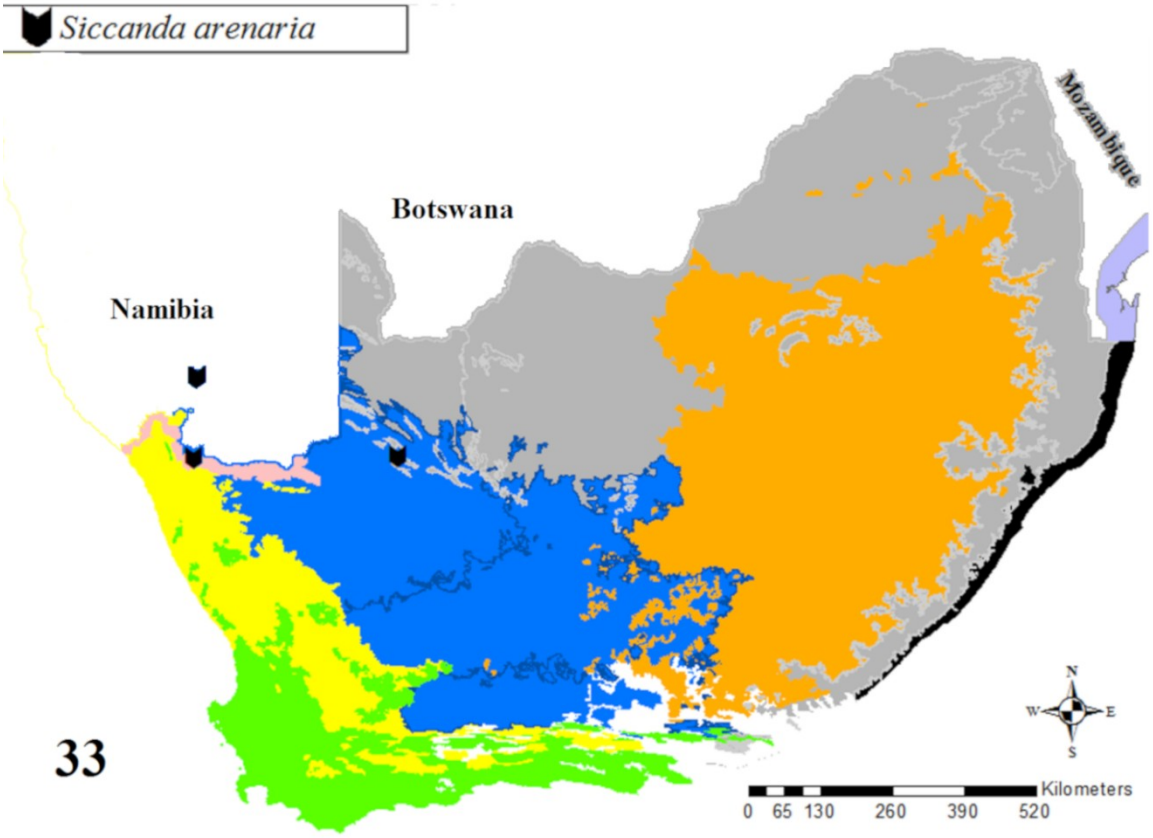
Figure 29. Holotype, *Nemopterella arenaria* Tjeder, type species of the *genus Siccanda with* associated labels.





Figures 30–31. 30, Terrestrial Biomes in South Africa; 31, distribution of *Nemopterella africana* (Leach).





Figures 32–33. Distributions of *Nemopterella* and *Siccanda* spp. 32, *N. cedrus* **sp. nov**and *N. kabas* **sp.nov**; 33, *Siccanda arenaria* (Tjeder).

Genus *Afroptera* Abdalla & Mansell gen. nov.

Etymology. The generic name is derived from the words Africa for the continent of Africa and part of the name Neuroptera since the genus is endemic to Africa.

The generic name *Afroptera* is feminine, despite the species name (*munroi*) being masculine, as it was named after Hugh Kenneth Munro (Tjeder 1967).

Type species (Fig. 111). *Nemopterella munroi* Tjeder, 1967, designated here.

Diagnosis. Small to medium-sized species distinguished by: (1) Forewings hyaline without spots or shading between Cx, shading over proximal Cx towards wing base (Fig. 38b); (2) Subcostal and radial areas never shaded (Fig. 38b); (3) Pterostigma distinct comprising a single costal cell with yellowish brown or dark brown colour (Fig. 38a), adjacent costal cells before and after pterostigma never tinged (Fig. 38a); (4) Number of costal cells less than 30; (5) Hind wings with whitish area bearing white setae (Fig. 41); (6) Apical segment of antennae partly or mainly membranous (Fig. 39); (7) Fifth abdominal segment with pair of pleuritocavae (Fig. 34); (8) Anal area never tinged (Fig. 38 b).

Description.

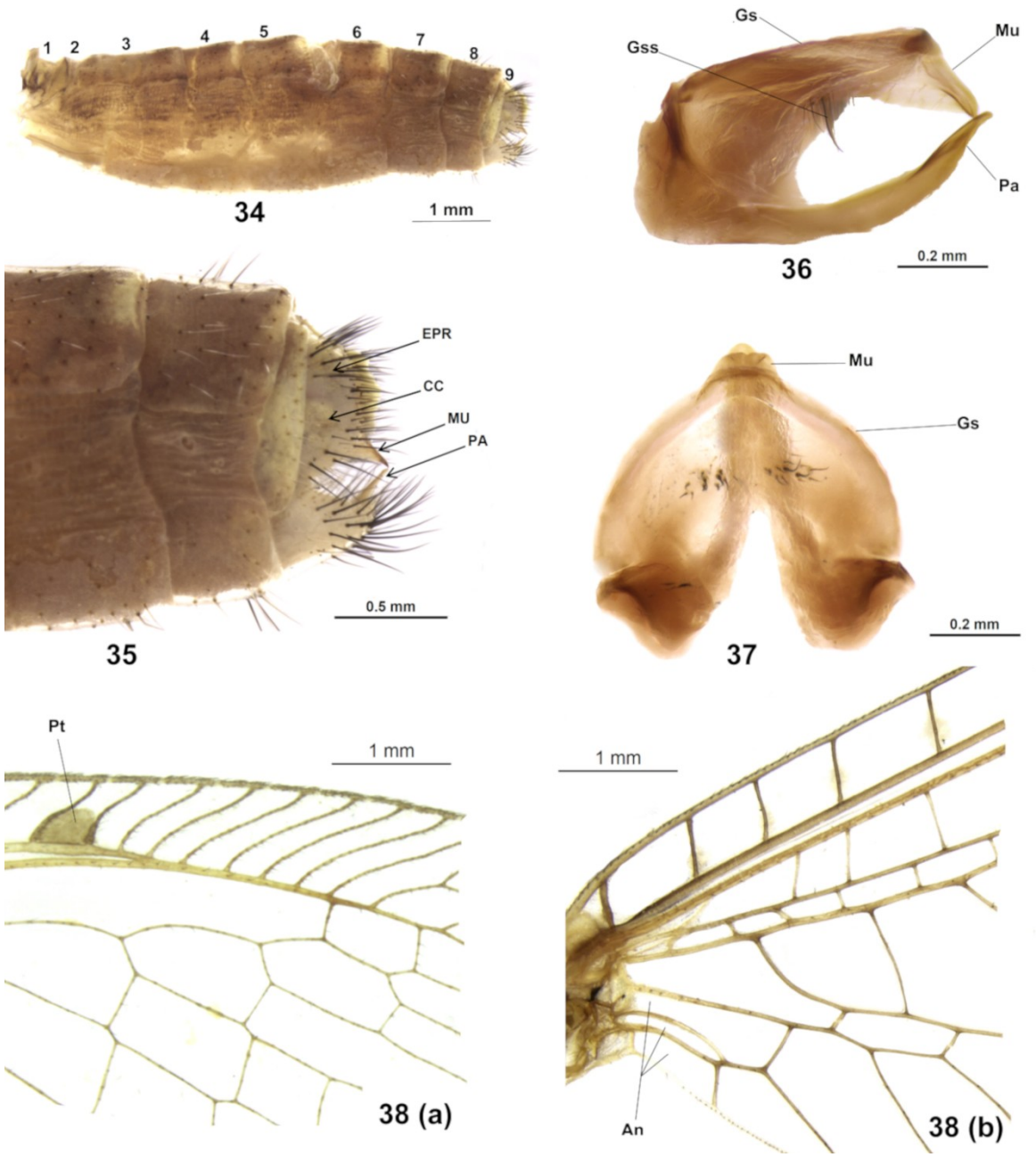
Size (mm). Male: body length 6.1–12.8; forewing 15.9–27.8; hindwing 31.7–64.8; antenna 11–27.4; Female: body length 8.5–14.1; forewing 17–26.3; hindwing 35.2–60.0; antenna 9.4–18.7.

Head. Small to medium-sized, without pubescence, with long rostrum, broad vertex and well defined epicranial and postfrontal sutures (Fig. 40). Vertex much broader in females than males. In some species, vertex may have two yellow rounded spots near eye margins. Frons above antennae slightly elevated without transverse yellow spots as manifest in *Nemia, Nemopterella* and *Siccanda.* Eyes protruding, either large where their diameter equals length of genae or small less than length of genae and always widely separated. In males, antennae maybe short not reaching pterostigma or long reaching beyond pterostigma or same length as forewings, covered with short setae arranged in circles over antennal surface. Apical segment of antennae partly or mainly membranous with narrow sclerotised, pigmented setaceous area at base of segment and along dorsal surface of membranous area (Fig. 39). In females, antennae short not reaching pterostigma with apical segment typically ending in short, acute membranous portion.

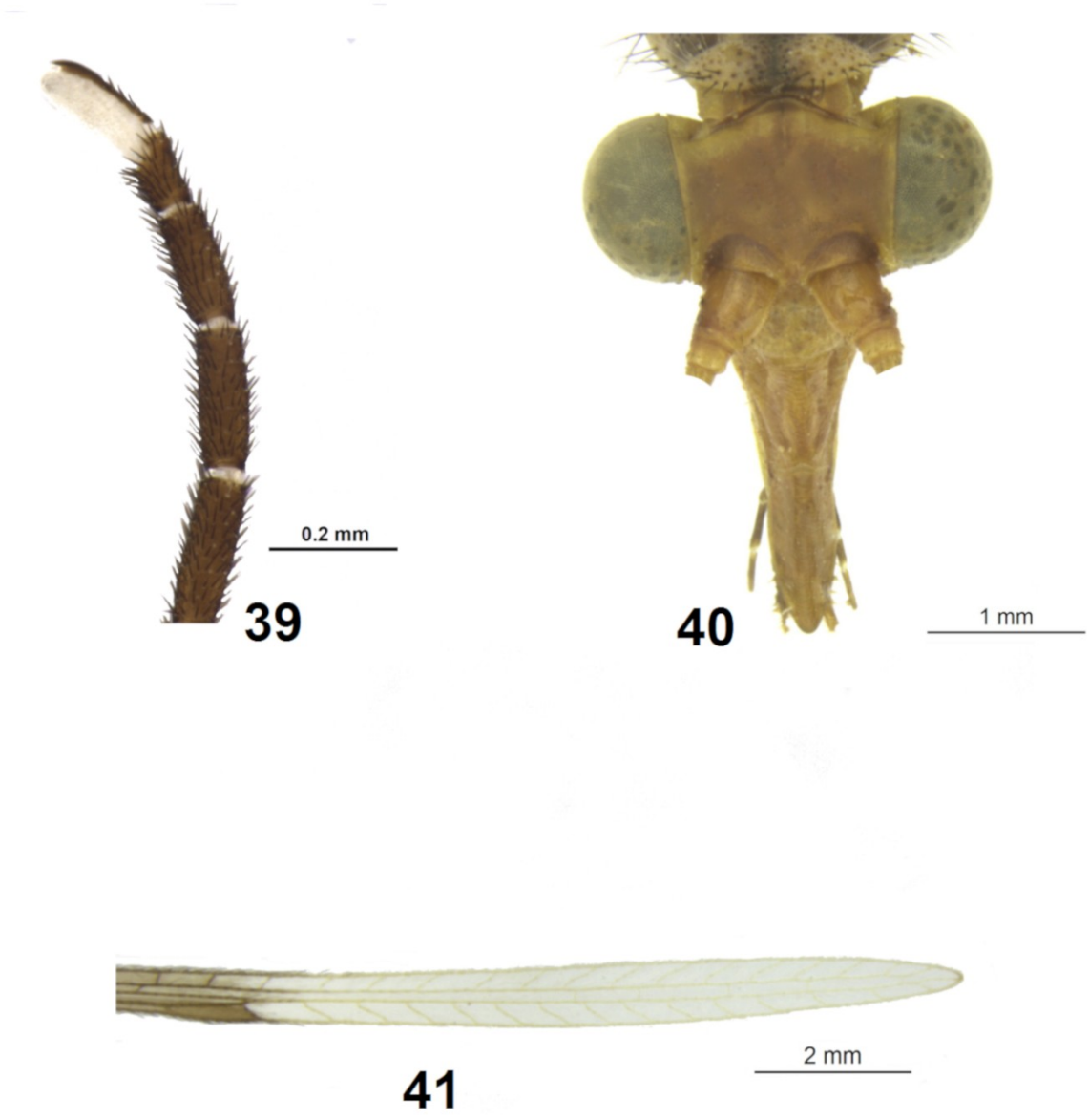
Thorax. As in *Nemopterella* but mid and lateral stripes indistinct or with unstriped thorax in some species. Thorax in males with long hairs while in females hairs are short and sparse. *Legs* as in *Nemopterella.*

Forewings. As in *Nemopterella* but proximal Cx in most species distinctly shaded brown or dark brown, with costal cells never shaded. Subcostal, radial and anal areas never tinged. Number of Cx less than 30. Pterostigma distinct comprising a single costal cell with brown or dark brown colour, adjacent costal cells before and after pterostigma usually not tinged except in some species females adjacent cells partly tinged. *Hind wings* with black setation from wing base to dark area with white setae in apical white portion.

Abdomen. As in *Nemopterella* but longitudinal midstripe only present in a few species, dorsum uniformly brown in most, dark brown or blackish with yellowish, reddish or reddish yellow hind margins to tergites (Fig. 34). Lateral abdominal stripes ill-defined in most cases or appearing as brown or greyish brown shading along lateral margins of tergite. Male and female genitalia as in *Nemopterella.*



Figures 34–38. *Afroptera munroi* (Tjeder). 34, Abdomen, lateral view; 35, Apex of male abdomen; 36, Parameres and gonarcus; 37, Gonarcus dorsal view showing bases of the parameres; 38(a), Pterostigma in forewing; 38(b), Anal area in forewing. Abbreviations as in Figs 3–7.



Figures 39–41. *Afroptera munroi* (Tjeder). 39, Antennal apex; 40, Head; 41, Apical white portion in hind wing.

Key to males of *Afroptera* species

1. Forewings without emargination before apex, apex rounded (Figs 81, 134, 148, 149)…2

- Forewings with slight or shallow emargination before apex, apex acute or sub-acute ….5

2. Small species (body length ≤ 8 mm, Figs 125, 130)…..…..……3

- Large species (body length ≥ 9 mm, Fig. 150)...……...4

3. Pronotum and mesonotum with distinct mid and lateral stripes (Fig. 100).....*A. parva* (Tjeder)

- Pronotum unstriped, mesonotum lacking the mid stripe (Fig. 101).....*A. exigua* (Tjeder)

4. Prescutum with black hairs (Fig. 52), thorax unstriped.....*A.koranna* **sp. nov.**

- Prescutum with white hairs (Fig. 97), thorax with three stripes…….....*A. remifera* (Tjeder)

5. Species extremely pruinose, body unstriped (Figs 43, 44, 113)……..……6

- Species slightly pruinose or without pruinose body, body stripes distinct or appearing as faint brown shading…….…...8

6. Species with greyish body appearance (Fig. 113).....*A. pruinosa* (Tjeder)

- Species with whitish body appearance (Figs 43, 44).....…….....7

7. Prescutum and mesonotum with white pubescence (Fig. 48), antennae whitish yellow proximally and darker distally, short not reaching pterostigma (Figs 43, 80), forewings with slight emargination before the apex, pterostigma long (Fig. 80).....*A. alba* **sp. nov.**

- Prescutum and mesonotum with black pubescence (Fig. 49), antennae yellow, long reaching pterostigma (Figs 44, 82), forewings with shallow emargination before apex, pterostigma short (Fig. 82).....*A. balli* **sp. nov.**

8. Small species (hindwing length < 49 mm, Figs 106, 107, 110)….....9

- Large species (hindwing length ≥ 49 mm) …….....11

9. Antennae long reaching beyond pterostigma (Figs 85, 106), forewings elongate, tapering towards apex with acute tip(Fig. 85).....*A. maraisi* **sp. nov.**

-Antennae short not reaching pterostigma (Fig. 110), forewings broad with short rounded apex (Figs 117, 120)…….....10

10. Head with yellowish brown vertex and rounded yellowish spots near eye margins (Fig. 142), prescutum with white pubescence (Fig. 105), antennae whitish yellow, apical segment very long much longer than penultimate segments (Figs 63, 110), hind wings with dark area shorter than white apical area (Fig. 110).....*A. apicalis* (Tjeder)

- Head with reddish vertex without yellowish spots near the eye margins (Fig. 141), prescutum with black pubescence (Fig. 103), antennae pale brown, apical segment large,

approximately same length as penultimate segment (Fig. 65), hind wing dark area as long as white apical area (Fig. 107)……..……....*A. aequabilis* (Tjeder)

11. Forewings elongate, with distinctly elongate rounded apex (Figs 79, 86).....12

- Forewings elongate or broad, with acute, or sub-acute apex.....13

12. Prescutum with long dense white hair on disc (Fig. 47)……...*A. acuta* **sp. nov.**

- Prescutum with long sparse black hair on disc (Fig. 46)……....*A. folia* **sp. nov.**

Prescutum with white pubescence (Figs 92, 93, 96, 99).....14

- Prescutum with black pubescence (Figs 50, 90, 91, 94, 95, 98, 102)…..…..…….....21

13. With white pubescence on abdominal tergites and sternites (Fig. 147)……..….....15

- With white pubescence on abdominal tergites and black hairs on sternites (Fig. 146)…...
……..……...……..*A. bitis* (Tjeder)

14. Species with light grey thorax (Figs 51, 92, 93)...…….……...16

- Species with yellow or yellowish brown thorax……...…….……...18

15. Vertex strongly concave, without yellow hind margin (Fig.143)…..*A. brinkmani* **sp. nov.**

- Vertex not concave, with yellow hind margin (Fig. 144)…….……...17

16. Pronotum dark shaded only centrally, lateral stripes on mesonotum faintly indicated (Fig. 92), hind wings dark area as long as white apical area (Fig. 111) …….....*A. munroi* (Tjeder)

- Pronotum and mesonotum with distinct mid and lateral stripes (Fig. 93), dark area of hind wing much shorter than white apical area (Fig. 108)...…..….*A. longicornis* (Tjeder)

17. Forewings broad (Figs 127, 135).…….…..*A. lanata* (Tjeder)

- Forewings elongate (Figs 137, 138, 139)…….……19

18. Head uniformly reddish yellow, antennae reddish yellow (Fig. 131)…….……20

- Head pale yellowish brown, antennae yellowish (Fig. 123)…..…....*A. segregata* (Tjeder)

20. Forewings with broad, short rounded apex and very slight emargination before apex (Figs 131, 139), the hind wing dark area approximaly as long as white apical area (Fig. 131).…….……..…..*A. peringueyi* (Tjeder)

- Forewings with short, narrow rounded apex and slight emargination before the apex (Figs 128, 137), the hind wing dark area shorter than white apical area (Fig. 128) …….....…..….....*A. papio* (Tjeder)

21. Abdomen with white hairs on dorsum and venter.……..…….……...22

- Abdomen with white hairs on dorsum and black hairs on venter……..……..….24

22. Antennae yellow proximally dark distally, pronotum only with mid stripe (Fig. 109)…..
…….……...*A. olivacea* (Tjeder)

- Antennae whitish yellow, pronotum with distinct mid and two lateral stripes.....23

23. Forewings very broad with short rounded tip (Fig. 133)…….*A. dyscrita* (Tjeder)
- Forewings falcate, with sub-acute tip…..……...*A. leptocera* (Navás)

24. Antennae long reaching beyond pterostigma (Figs 54, 112)…….…….....25
- Antennae short not reaching pterostigma (Fig. 126).…….....……..27

25. Mid and lateral stripes of pronotum and mesonotum of thorax distinct (Figs 90, 91, 94, 98)…….……26
- Mid and lateral stripes on pronotum abbreviated to brown spots, mid stripe on prescutum appears as faint brown shading (Fig. 50).....*A. cylindrata* **sp. nov.**

26. Vertex with pair of yellow spots near eye margins (Fig. 145).....*A. nigrosetosa* (Tjeder)
- Vertex without pair of yellow spots near eye margins...…….....*A. sabuleti* (Tjeder)

27. Forewings broad (Fig. 136).…….…….....*A. obtusa* (Tjeder)
- Forewings elongate (Fig. 140) ……..*A. pilosa* (Tjeder)

***Afroptera acuta* Abdalla & Mansell sp. nov.**
(Figs 42, 47, 56, 79, 154)

Etymology: The specific epithet from the Latin word *acuta* (acute, sharp) for the acute tip to the forewings.

Type locality. NAMIBIA, *Karas Region*. Orange / Boom River Confluence, 28°02'S 17°04'E.

Diagnosis. A large species. General body colour greyish (Fig. 42). This unique species can be readily distinguished from its congeners by the elongate forewings with remarkably elongated rounded tip (Figs 42, 79).

Description

Size (mm). Male: body length 9.6 (9–10.9); forewing 24 (22.4–25.4); hind wing 53.8 (46.4–56.5); antenna 21 (18.8–22.8), Female: body length 10.5 (9–12.5); forewing 20.9 (20–23.5); hind wing 45.2 (42.4–52.2); antenna 14.2 (12.9–16.4). Holotype m#, body length 9.0; forewing 22.4; hind wing 46.4; antenna 20.3.

Head. Clypeus yellow. Vertex yellowish brown with yellow hind margin and pair of rounded yellowish spots near eye margins. Palpi dark brown. Eyes large. Antennae yellow in proximal portion, light yellowish brown distally, extending beyond pterostigma, with short black setae (Fig. 42); apical segment longer than preapical segments and mostly membranous (Fig. 56).

Thorax. Greyish, distinctly powdered (Fig. 47). Longitudinal midstripe only traceable centrally on pronotum near hind margin as dark brown shading while lateral stripes shortened to brown transverse spots laterally on either side of pronotum near hind margin. Fore and hind margins of pronotum with erect, long black hairs intermixed with long white hairs. Fine and long white hairs scattered on disc. Long white hairs combined with long black hairs also present laterally. Longitudinal mid and the lateral stripes on mesonotum appear as faint brown shading. Prescutum entirely covered in dense long white hairs dorsally with two clusters of long, stiff white hairs present antero-laterally. Long, sparse white hairs cover mesoscutum disc with two tufts of sparse long white hairs present laterally along hind margin of mesoscutum. Mesoscutellum bearing a few short, white hairs on disc and two tufts of long white hairs laterally on each side of mesoscutellum. Metanotum with two groups of long white hairs laterally.

Forewings. Slender, elongate, with pronounced rounded apex and shallow emargination before apex (Fig. 79). Venation light brown. Costa whitish, proximal Cx shaded light brown. Costal cells increasing in size towards pterostigma. Pterostigma dark brown, broad at base, long but not reaching C. Twenty Cx before pterostigma in both wings. Ten crossveins between RA and MA before origin of RP in right wing, 9 in left. Eleven radial crossveins before pterostigma in right wing, 9 in left. *Hind wings* light brown to creamy white in proximal half before the dark area. Crossveins shaded brown. Longitudinal veins creamy white to light brown. The dark area brown, shorter than white area and apical area white haired. *Legs* yellow with black hairs.

Abdomen. Brown, pruinose, with yellowish brown hind margins to tergites. Tergites with long white hairs, denser and longer laterally on each tergite. Venter with sparse, short, white hairs. Apex with black hairs.

Variation. Some males have a very shallow emargination before apex of forewings.

Type material examined. NAMIBIA, *Karas Region*. Holotype m#, NEUR08943, Orange / Boom River Confluence, 28°02'S 17°04'E, 29.x.1999, M.W.Mansell, C.H.Scholtz. *Paratype*s: 5m# 4f#, same data as holotype. (All SANC).

Distribution and habitat. The range of distribution of this species is in the Desert Biome (Fig. 154). The collection locality falls within the Noms Mountain Desert vegetation unit in the Gariep Desert Bioregion (Mucina & Rutherford 2006). The area is situated in the southernmost part of Namibia, it is montane consisting of low mountains and sparse succulent shrub type vegetation. It receives winter and summer rains with a mean annual precipitation of 40–60 mm (Mucina & Rutherford 2006).

Figure 42. *Afroptera acuta* Abdalla & Mansell **sp. nov.,** habitus. Forewing length = 22.4 mm.

***Afroptera aequabilis* (Tjeder, 1967) comb. nov.**
(Figs 65, 103, 107, 117, 153)

Synonymy

Nemopterella aequabilis Tjeder, 1967: 483.

Etymology. Unknown.

Type locality. SOUTH AFRICA, *Northern Cape Province*. Prieska, 17 miles north, 29°25'15"S 22°48'06"E.

Type depository. TMSA.

Diagnosis. This species is most closely related to *A. apicalis*. Both species are small with a narrow rounded apex to forewing (Figs 117, 120). *Afroptera aequabilis* can be distinguished from *A. apicalis* by the following characteristics: *A. aequabilis* is characterised by having pale brownish antennae while the antennae in *A. apicalis* are whitish yellow; *A. aequabilis* has black hairs on the prescutum disc (Fig. 103) while in *A. apicalis* the prescutum disc is covered by white hairs (Fig. 105); *A. aequabilis* is characterised by having the dark area of the hind wing as long as white apical area (Fig. 107), while in *A. apicalis* the dark area is shorter than the white (Fig. 110).

Size (mm). Male: body length 10.3 (8.9–10.7); forewing 20.9 (18.2–22); hind wing 46.1 (36–48); antenna 14.4 (12–18.8). Female: body length 10.8 (9.4–11.3); forewing 20.3 (17–22); hind wing 43.4 (36–46); antenna 13.6 (10.4–14.9). (N = 46)

Type material examined. SOUTH AFRICA, *Northern Cape Province*. Holotype m#, TMSA02057, HOLOTYPE, Neu 062, *Nemopterella aequabilis* Tjeder (red, printed) / Prieska 17 m North of [29°25'15"S 22°48'06"E], 7–8.x.1954, A.J.T.Janse (white, printed) / Holotypus m#, *Nemopterella aequabilis* Tjed, Bo Tjeder 1966 (red–handwritten). *Paratype*s: 19f#, same data as holotype; 4f#, TMSA02058, Niekerkshoop [29°19'37"S 22°50'13"E], 18.x.1955, H.K.Munro (white, printed) / Paratypus *Nemopterella aequabilis* Tjed 1966' (red, handwritten). (All TMSA).

Other material examined. SOUTH AFRICA, *Northern Cape Province*: 4m# 19f#, TMSA02057, Prieska 17 m north of [29°25'15"S 22°48'06"E], 7.viii.1954, A.J.T.Janse / Det. M.W.Mansell 2013. (TMSA).

Distribution and habitat. *Afroptera aequabilis* is known only from the Nama Karoo Biome in the Northern Cape Province (Fig. 153). The distribution falls mainly within the Lower Gariep Broken Veld and Northern Upper Karoo vegetation units in Bushmanland and Upper Karoo Bioregions, respectively (Mucina & Rutherford 2006). The description of the habitat in the former vegetation unit is given under the distribution of *S. arenaria*. The habitat in the latter vegetation unit is in a flat area with sparse hills, vegetated mostly by dwarf karoo shrubs, grasses and *Acacia mellifera* sub sp. *detinens* with some low trees in the north and towards the Orange River (Mucina & Rutherford 2006).

***Afroptera alba* Mansell & Abdalla sp. nov.**
(Figs 43, 48, 57, 80, 154)

Etymology. The specific epithet is derived from the Latin word *alba* (white) for the characteristic pale coloration of this species.

Type locality. NAMIBIA, *Karas Region*. Kwessiewater Farm, 24°52'34"S 15°54'06"E.

Diagnosis. This unique species is easily differentiated from all other species in *Afroptera* by its small size, the whitish body appearance and unstriped body (Fig. 43).

Description

Size (mm). Male: body length 8.9 (8.6–9.3); forewing 20.5 (20–21.6); hind wing 46.6 (43.8–48.4); antenna 14.3 (12.8–15.3). Female: body length 9.7 (8.5–11.4); forewing 21 (20–22.8); hind wing 42.3 (39.6–46.9); antenna 10.3 (9.4–11.5). Holotype m#. Body length 9.5; forewing 22.4; hind wing 48.1; antenna 15.3. (N = 10)

Head. Frons, clypeus light yellow. Genae and maxilla creamy white. Palpi light brown. Vertex light yellowish brown. Eyes small, black, widely separated. Antennae short, not reaching pterostigma, whitish yellow proximally, darkish brown distally with black setae. Terminal segment mainly membranous and approximately same length as penultimate segment (Fig. 57).

Thorax. White, heavily powdered, without distinct longitudinal mid and lateral stripes (Fig. 48). Fore and hind margins of pronotum with long white hairs and no black hairs. Sparse smooth white hairs present behind anterior hairs on fore margin. Distal lateral sides also with long white hairs. Whole mesonotum with white pubescence, markedly longer and denser on antero-lateral portions and on disc of prescutum than mesoscutum and mesoscutellum. Sides of mesoscutum naked except for a few short white hairs posteriorly on each side. Two tufts of long white hairs also present laterally on hind margin of the mesocutllum. Metanotum with two groups of long white hairs laterally on each side.

Forewings. Broad with sub-acute apex and distinct emargination before the apex (Fig. 80). Pterostigma brown, long but not reaching C. Venation light brown. Costa whitish. Subcosta and RA creamy yellowish. Two thirds of Cx before pterostigma shaded with dark brown. Costal cells increasing in size towards pterostigma. Nineteen Cx before pterostigma in right wing, 20 in left. Nine crossveins between RA and MA before origin of RP in right wing, 8 in left. Ten radial crossveins before pterostigma in right wing, 9 in left. *Hind wings*

approximately double the length of forewings. Proximal portions and bases whitish yellow, creamy white to light brown in the middle with cells shaded brown. Area before dark area whitish with white cells. The dark area shorter than white area. Crossveins dark brown, longitudinal veins creamy white. *Legs* yellow with black setae, first tarsomere white, coxae pruinose, with short white hairs.

Abdomen. Predominantly white, highly pruinose with whitish yellow hind margin to tergites. The longitudinal mid and lateral stripes indistinct. Tergites covered in scattered long white hairs. Venter with short dense white hairs. Apex yellow with long black hairs.

Variation. The thorax in some female specimens with white hairs only, and some variation in the number of Cx.

Type material examined. NAMIBIA, *Karas Region*. Holotype m#, Kwessiewater Farm, Namib Rand Game Park, 24°52'34"S 15°54'06"E, 900 m, 2–10.x.2011, C.H.Scholtz. *Paratypes*: 4m# 5 f#, same data as holotype. (All SANC).

Distribution and habitat. *Afroptera alba* is endemic to Namibia where its distribution is in the Namib Desert Eco-region (Fig. 154). The collection site is in the Namib Desert west of the Great Escarpment. The area is mostly gravel plains, sand dunes and scattered mountain outcrops, vegetated mostly by grasses, shrubs, and ephemeral plants near the escarpment with sparse trees (Nicholson 2011).

Figure 43. *Afroptera alba* Mansell & Abdalla **sp. nov**., habitus. Forewing length = 22.4 mm.

***Afroptera apicalis* (Tjeder, 1967) comb. nov.**
(Figs 63, 105, 110, 120, 152)

Synonymy

Nemopterella apicalis Tjeder, 1967: 487.

Etymology. Unknown, probably from the Latin word "*apicalis*" (apical) for the very long terminal segment of the antennae.

Type locality. SOUTH AFRICA, *Northern Cape Province*. Marydale, 5 miles north, 29°20'19"S 22°05'50"E.

Type depository. TMSA.

Diagnosis. *Afroptera apicalis* is probably the sister species to *A. aequabilis.* Similarities and differences between the two species are given in the diagnosis of *A. aequabilis*.

Size (mm). Male: body length 9.5 (8.5–10.2); forewing 23.3 (19–24.6); hind wing 47.8 (40–50.7); antenna 17.4 (14–18.5); Female: body length 11 (8.8–13.2); forewing 22.4 (19–24.8); hind wing 48.4 (39–52.6); antenna 12.4 (10.1–14.8). (N = 17)

Type material examined. SOUTH AFRICA, *Northern Cape Province*. Holotype m# (Fig. 110), TMSA02060. HOLOTYPE Neu 090 *Nemopterella apicalis* Tjeder m# (red printed label) / MARYDALE, 5 m North of [29°20'19"S 22°05'50"E], 9–10.X.1954, A.J.T.Janse (white printed label) / Holotypus m# *Nemopterella apicalis* Tjed, Bo Tjeder 1966 (red handwritten label). *Paratype*: 1f# same data as holotype. (Both TMSA).

Other material examined. SOUTH AFRICA, *Northern Cape Province*. 1m# 4#, NEUR 11241 and 1m# 1f#, NEUR 11244, Lang Hoogte Mine Office, 29°32'19"S 17°23'27"E, 100 m, 27.xi.1996, A.J.van Wyk; 4m# 4f#, NEUR11243, same data but 1.xii.1996. (All SANC).

Distribution and habitat. This species is endemic to the Northern Cape Province of South Africa (Fig. 152). The present distribution is in two regions. One region falls within the Namaqualand Hardeveld Bioregion in the Succulent Karoo where the habitat is dry, typified by winter rains and vegetated by mostly dwarf succulent shrubs. The other region is located to the east of first one in the Bushmanland Bioregion in the Nama Karoo Biome where the habitat is also dry, receives predominantly summer rains and is dominated by grasses of the Bushmanland Arid Grassland type (Mucina & Rutherford 2006).

***Afroptera balli* Abdalla & Mansell sp. nov.**
(Figs 44, 49, 61, 82, 154)

Etymology. This new species is named for Jonathan B. Ball (Cape Town) for his significant contribution to knowledge of the Cape Nemopteridae and particularly this study, through the donation of many specimens collected by himself, Andre P. Marais and A.K. (Tony)

Brinkman, which enabled the molecular analyses and enhancement of distributional data through their systematic surveys.

Type locality. NAMIBIA, *Karas Region*. Sendlingsdrift Gate, 28°04'S 16°49'E.

Diagnosis. This species is very similar to *A. alba* with a whitish appearance but is easily distinguished by the combination of the following characters: *A. balli* is larger (Fig. 44), with much longer antennae that reach the pterostigma (Figs 44, 82), while in *A. alba* the antennae are shorter not reaching the pterostigma. A*froptera balli* is further characterised by blackish pubescence on the thorax (Fig. 49), while in *A. alba* the thorax bears white hairs. Also, *A. balli* has the Cx shaded light brown while in *A. alba* the Cx are shaded dark brown (Fig. 44).

Description

Size (mm). Female: body length 10.5 (9.9–11.5); forewing 23.9 (22.7–24.7); hind wing 52.2 (47.9–54.6); antenna 13.9 (13.1–15.4). Holotype m# (Fig. 44), body length 10.2; forewing 26.4; hind wing 63.1; antenna 22.9. (N = 5)

Head. Rich yellow, with light yellowish brown vertex. Eyes small, widely separated. Antennae yellow, long, reaching pterostigma, with black setae. Apical segment much longer than preapical segments, mainly membranous (Fig. 61).

Thorax. Whitish, pruinose (Fig. 49). Only the longitudinal midstripe discernible on pronotum and mesoscutellum while midstripe on prescutum and lateral stripes on mesoscutum indistinct. The midstripe on pronotum forms a dark brown portion centrally in posterior half of pronotum while lateral stripes appear as two small transverse brown spots laterally on each side of pronotum. Stiff long black hairs intermingled with a few soft long white hairs present on fore and hind margins of pronotum, with soft long dense white hairs present behind these. Distal anterior sides of pronotum bear erect black hairs intermingled with long white hairs. Prescutum covered dorsally by long black hairs and antero-laterally by two groups of long black hairs intermixed with long white hairs. Long soft white hairs present along lateral sides of prescutum. Mesoscutum covered on disc by sparse, long white hairs admixed with a few long black hairs. Two tufts of long white hairs present on each side of prescutum. Midstripe on mesoscutellum manifest as dark midline centrally. Mesoscutellum with sparse short white hairs and two tufts of long white hairs on each side. Metanotum markedly pruinose with two tufts of long white hairs on each side. *Legs* yellow with black setae, tip of femora and tibiae tinged light brown. Coxae pruinose but mid and hind coxae more pruinose than fore coxae.

Forewings. Elongate, tapering towards apex, sub-acute with emargination before apex (Fig. 82). Pterostigma light brown, short, not reaching C. Venation yellow. Costa whitish, SC and RA light brown. Proximal Cx shaded light brown. Costal cells increase in size towards

pterostigma. In holotype, 26 Cx before pterostigma in both forewings. Eleven crossveins present between RA and MA before origin of RP in both forewings. Eleven radial crossveins before pterostigma in right wing, 10 in left. *Hind wings* creamy white proximally, light brown before dark area. The portion just before dark area white. Longitudinal veins creamy white. Crossveins shaded faintly light brown. Dark area dark brown, shorter than white area.

Abdomen. Greyish, markedly powdered particularly at sides and venter, with longitudinal brown midstripe very distinct on tergites 3–7. Hind margin of tergites yellowish. Tergites with long white hairs, sternite 2 with short white hairs, sternites 3–9 black haired. Apex yellow, pruinose with stiff long black hairs.

Variation. No observed variation between female specimens.

Type material examined. NAMIBIA, *Karas Region*. Holotype m#, NEUR08932, Sendlingsdrift Gate, 28°04'S 16°49'E, 31.x.1999, M.W.Mansell, C.H.Scholtz. *Paratypes*: 4f#, same data as holotype. (All SANC).

Distribution and habitat. This species is known only from Namibia (Fig. 154). The range of distribution falls within the Nama Karoo Biome's extension into southern Namibia. The habitat is dry, vegetated mostly by low shrubs, grasses, succulents and annual forbs. It receives predominantly summer rains (Mucina & Rutherford 2006).

***Afroptera brinkmani* Abdalla & Mansell sp. nov.**
(Figs 45, 51, 66, 84, 143, 154)

Etymology. This species is named for A.K. (Tony) Brinkman (Cape Town, now Cambridge University, England) who collected part of the type series, and many other specimens that contributed to enhancing our knowledge of the Cape Nemopteridae.

Type locality. SOUTH AFRICA, *Northern Cape Province*.21 km S of Vioolsdrif, 28°56'22"S 17°44'55'E.

Diagnosis. Alarge greyish species, most similar to *A. munroi* in having long antennae extending beyond the pterostigma (Figs 45, 84), and long white pubescence on the thorax and abdomen (Fig. 51). It differs from *A. munroi* by a narrow concave area on the vertex without a yellow hind margin (Fig. 143). *Afroptera brinkmani* is characterised by more slender forewings that taper towards the apex with sub-acute apex (Fig. 84). Also, *A. brinkmani* has the dark area of the hindwings shorter than the white apical area (Fig. 45) while in *A. munroi* the dark area is approximaly as long as the white apical area.

Description (Fig. 45).

Size (mm). Male: body length 10.1 (8.5–11.4); forewing 26.6 (24.6–27.8); hind wing 58.5 (54.7–63.2); antenna 23.8 (21.3–25.9); Female: body length 11.2 (10–12.3); forewing 23.9 (22.8–25); hind wing 51.2 (50–53.2); antenna 16.1 (14.6–18.4). Holotype m#; body length 10.1; forewing 26.3; hind wing 58.1; antenna 25.9. (N = 33)

Head. Yellow with light brown narrow concave vertex (Fig. 143). Palpi dark brown to blackish. Eyes large, brown (Fig. 143). Antennae long, in some specimens longer than forewing, yellowish brown proximally, dark brown distally towards apex with dense long black setae. Apical segment longer than penultimate segment, mainly membranous (Figs 45, 66).

Thorax. Light grey, pruinose (Fig. 51). Pronotum with longitudinal midstripe attenuated to brown portion centrally in posterior half of pronotum. Lateral stripes shortened into two transverse spots lateral to midline. Fore and hind margins with long, rigid, black hairs intermixed with long white hairs. Soft, long white hairs spread behind fore margin hairs, also on disc and laterally on distal sides. Prescutum with indistinct brown midstripe. Long white hairs present on antero-lateral sides admixed with a few long black hairs. Long dense white hairs present on disc. Long white hairs spread laterally along each side of prescutum. Long white hairs scattered over mesoscutumdisc and two tufts of long white hairs, postero-lateral stripes distinctly brown. Area between prescutum and mesoscutellum dark. Long white hairs scattered over mesoscutellum disc, with indistinct mid-stipe appearing as faint brown midline. Metanotum with unusual, tangled long dense white hairs laterally on each side forming two distinct clusters.

Forewings. Elongate, tapering towards the acute apex, weakly emarginated before apex (Fig. 84). Venation brown. Costa whitish, SC and RA pale brown other veins light brown. Pterostigma dark brown, broad at base, short not reaching C. Proximal Cx shaded brown. In holotype, 26 Cx before pterostigma in both forewings. Ten crossveins between RA and MA before origin of RP in both forewings. Ten radial crossveins before pterostigma in right wing, 13 in the left. *Hind wings* whitish yellow. Dark area short compared to white area. Proximal crossveins shaded dark brown. Longitudinal veins whitish yellow. Stiff, long white hairs present at base of each wing. *Legs* light yellow with black hairs.

Abdomen. Greyish, pruinose, tergites with yellowish brown hind margins. Dorsum with dense long white hairs. Extremely long white hairs spread over hind and fore margins of third tergite. Venter markedly pruinose with short, sparse white hairs. Apex yellow with black hairs.

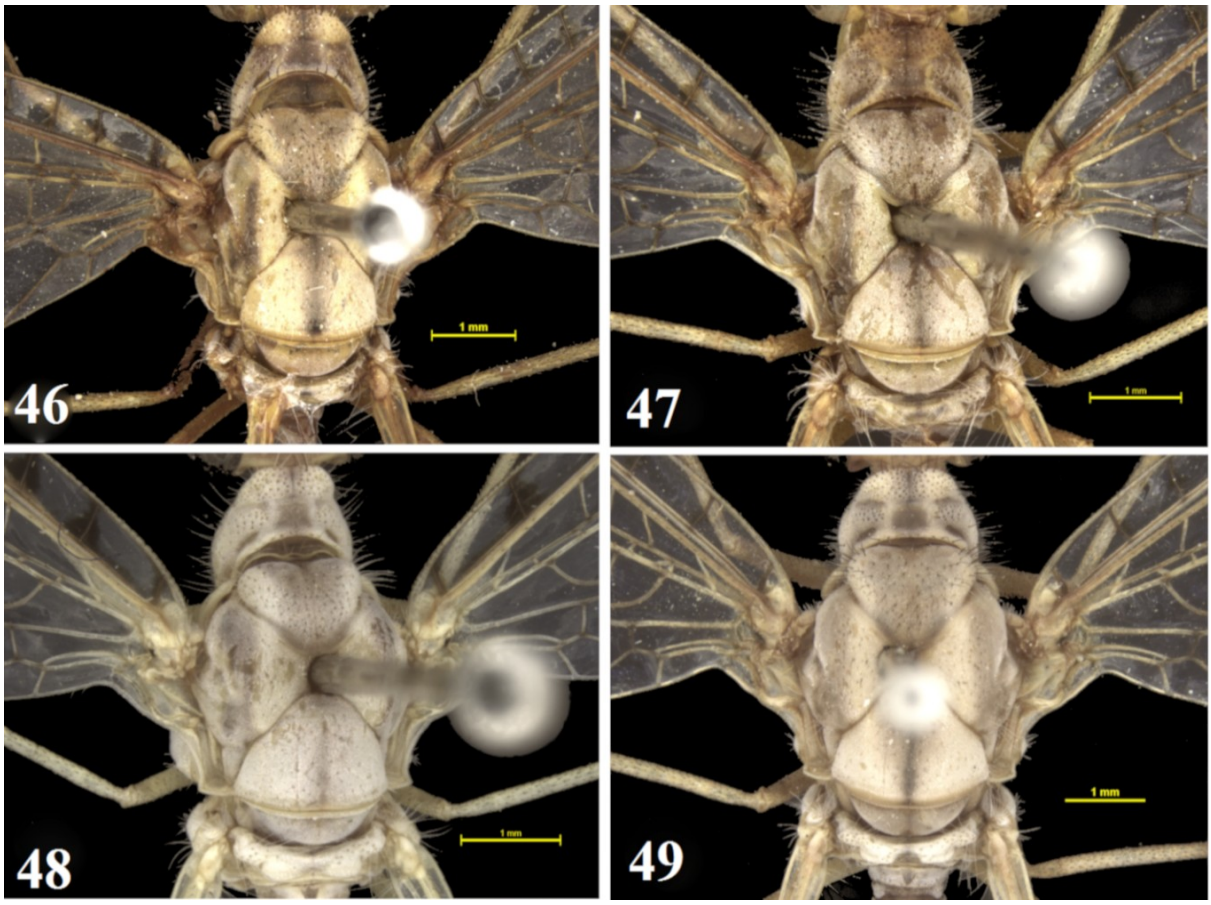
Variation. Some male specimens with shallow emargination before the apex in the forewings. In addition, some males with long antennae that slightly excede the length of the forewings.

Type material examined. SOUTH AFRICA,*Northern Cape Province*.Holotype m#, NEUR09618, 21 km S Vioolsdrif, 28°56'22"S 17°55'55"E, 22.x.2006, 600m, A.Swart. *Paratype*s: 3m# 4f #, same data as holotype; 16m# 9f#, NEUR12192, Swartkop Mine, 21 km S Vioolsdrif, 28°56'22"S 17°55'55"E, 675m, 29.ix.2007, A.K.Brinkman, light trap. (All SANC).

Distribution and habitat. This species is endemic to the Succulent Karoo and Desert Biomes of the Northern Cape Province, South Africa (Fig. 154). The ranges of distribution fall mainly within the Umdaus Mountains Succulent Shrubland and Northern Nababiepsberge Mountain Desert vegetation units respectively (Mucina & Rutherford 2006). In the former vegetation unit, the species seems to be associated with montane landscapes covered with scattered succulent shrubs and dominated by winter rains with mean annual precipitation (MAP) 100–200 mm. The latter habitat is described under the distribution of *S. arenaria.*

Figure 44. *Afroptera balli* Abdalla & Mansell **sp. nov.**, habitus. Forewing length = 26.4 mm.

Figure 45. *Afroptera brinkmani* Abdalla & Mansell **sp. nov.**, habitus. Forewing length = 26.3 mm.



Figures 46–49. Thorax of *Afroptera* spp. 46, *A. folia* **sp. nov**; 47, *A. acuta* **sp. nov**; 48, *A. alba* **sp. nov**; 49, *A. balli* **sp. nov.**

***Afroptera bitis* (Tjeder, 1967) comb. nov.**
(Figs 64, 89, 104, 146, 152)

Synonymy

Nemopterella bitis Tjeder, 1967: 465.

Etymology. From the town of Pofadder (type locality) that was named after a well-known and widespread African snake, *Bitis arietans*, whose common Afrikaans name is "Pofadder" or "puff adder" in English.

Type locality. SOUTH AFRICA, *Northern Cape Province*. Pofadder, 29°07'S 19°23'E.

Type depository. ZILS.

Diagnosis. Adults of *A. bitis* resemble those of *A. dyscrita* in their large body size and broad forewings (Fig. 89), but *A. bitis* can easily be distinguished from *A. dyscrita* by a combination of the following characters: *A. bitis* has dense white hairs over the whole thorax

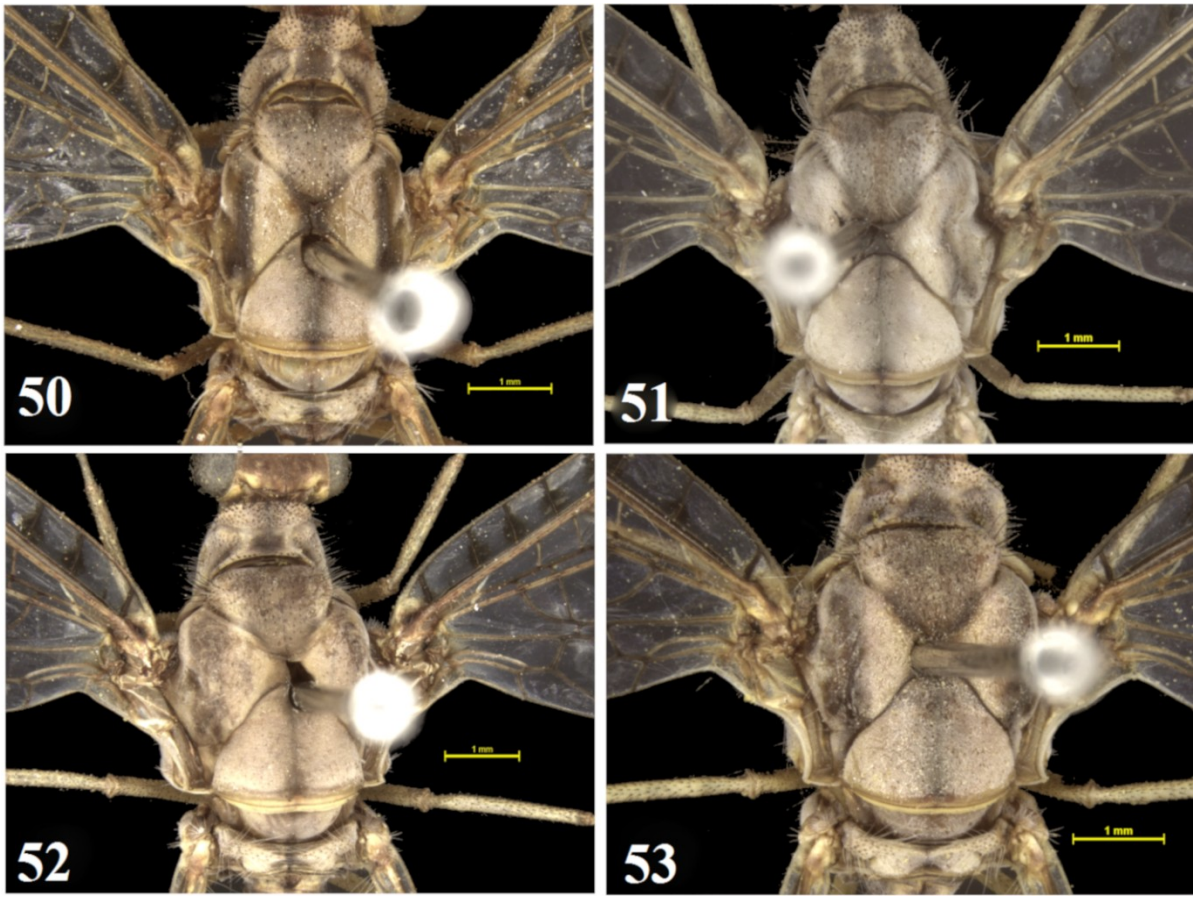
(Fig. 104) while in *A. dyscrita* the prescutum is covered in stiff black hairs (Fig. 102). Moreover, *A. bitis* has long antennae that reach the pterostigma (Fig. 89) while in *A. dyscrita* they do not (Fig. 129).

Size (mm). Male: body length 9.8 (8–11.7); forewing 23.6 (18.7–27.0); hind wing 55.7 (41.1–64.8); antenna 21.7 (17–25.5); Female: body length 11.2 (9.3–13.7); forewing 22.7 (19.2–26.3); hind wing 49.4 (42–55.6); antenna 15.2 (12.3–18.2). (N = 319).

Type material examined. SOUTH AFRICA, *Northern Cape Province*.Holotype m# (Fig. 89) labelled: Cape Prov, Pofadder, 9.XI.1950, P.Brinck, G.Rudebeck, På lijus [on light] / Holotypus m# *Nemopterella bitis* Tjed, Bo Tjeder 1966' (red printed label) / MZLU Type no. 3845:1 (ZILS). *Paratypes*: 4f#, TMSA02062, Paratype Neu 094, *Nemopterella bitis* Tjeder (yellow printed label) / Pofadder [29°07'34"S 19°23'44"E], 17.x.1954, A.J.T.Janse (white printed label) / Paratypus, *Nemopterella bitis* Tjed, Bo Tjeder, 1966 (red handwritten label). (TMSA).

Other material examined. SOUTH AFRICA, *Northern Cape Province*.2m#, TMSA00729, Richtersveld, 7 km SW Claim Peak, 28°26'S 17°10'E, 23.ix.1991, M.Krüger / *Nemopterella bitis* Tjeder, 1967, Det. M.W.Mansell 2013; 1m# 1f#, TMSA00753, Pofadder [29°07'34"S 19°23'44"E], 17.x.1954, A.J.T.Janse / *Nemopterella bitis* Tjeder, 1967, Det. M.W.Mansell 2013; 1m# 1f#, TMSA00758, Kenhardt 6 km W [29°20'57"S 21°09'03"E], 12.x.54, A.J.T.Janse. (All TMSA). 9m#, NEUR09772 and 16f#, NEUR09783, Kabas Farm, 10 km NE Pofadder, 29°02'S 19°26'E, 800m, 1.xi.1986, M.W.Mansell; 143m# 47f#, NEUR08925, Richtersveld, Die Koei, 28°17'S 16°59'E, 400m, 1–6.x.1991, M.W.Mansell, R.G.Oberprieler / Collected at light; 50m# 33f#, NEUR08927, Richtersveld, De Hoop turnoff, 3 km E Die Koei, 28°17'S 17°02'E, 450m, 6.x.1991, M.W.Mansell / Collected at light; 1f#, NEUR08928, Richtersveld, Hakkiesdoringhoek, 28°25'S 17°11'E, 500m, 2.x.1991, M.W.Mansell, R.G.Oberprieler. NAMIBIA, *Karas Region*. 7m# 2f#, NEUR10209, 'Boom River Canyon 4 km N Orange (ESE of Rosh Pinah), 28°00'S 17°03'E, 200m, 25.x.1996, E.Holm, at gas light.

Distribution and habitat. *Afroptera bitis* is endemic to the Northern Cape Province, South Africa, from localities mainly centred in the Richtersveld and Bushmanland Bioregions (Fig. 152). The Bioregions fall mainly within the Succulent and Nama Karoo Biomes. The habitats vary from arid mountainous desert with a succulent vegetation type and winter rains in the Richtersveld Bioregion to arid habitats dominated by shrubs and grass, characterized by late summer rains in Bushmanland (Mucina & Rutherford 2006).



Figures 50–53. Thorax of *Afroptera* spp. 50, *A. cylindrata* **sp. nov**; 51, *A. balli* **sp. nov**; 52, *A. koranna* **sp. nov.;** 53, *A. maraisi* **sp. nov.**

***Afroptera cylindrata* Abdalla & Mansell sp. nov.**

(Figs 50, 54, 60, 83, 154)

Etymology. The name of this species is derived from the Latin adjective *cylindrata* (cylindrical) for its markedly slender elongate forewings, which resemble a cylinder in profile.

Type locality. SOUTH AFRICA, *Northern Cape Province*. Richtersveld National Park, Cornell's Kop, 28°25'S 16°53'E.

Diagnosis. A medium-sized species (Fig. 54). General colouration yellow. This species can readily be distinguished from all other *Afroptera* species by the elongate slender forewings (Figs 54, 83).

Description

Size (mm). Male: body length 9.3 (8–10.7); forewing 23.6 (20.3–26.4); hind wing 53.4 (45–63.4); antenna 20.8 (18.5–22.8); Female: body length 10.9 (8.5–13.1); forewing 23.4 (22.4–

26.3); hind wing 50.2 (44.4–57.3); antenna 14.8 (12.5–18.7). Holotype m#: body length 9.2, forewing 22.6, hind wing 53.4, antenna 22. (N = 37)

Head. Frons and clypeus yellow. Vertex brown with pale yellowish hind margin. Palpi dark brown. Antennae brown proximally, dark brown distally, long, almost as long as forewings (Figs 54, 83), with black setae. Apical segment mainly membranous and longer than penultimate segment (Fig. 60).

Thorax. Yellow, pruinose (Fig. 50). Pronotum with ill-defined longitudinal mid and lateral stripes. Midstripe appears as central shading at hind margin of pronotum while the lateral stripes form two transverse brown spots posteriorly. Fore and hind margins with erect long black hairs, with smooth long white hairs spread behind fore margin hairs. Long white hairs admixed with long, black hairs cover distal anterior lateral sides of pronotum. Prescutum midstripe appears as faint brown shading centrally. Antero-lateral side of prescutum covered with long, rigid black hairs admixed with a few long white hairs, disc covered in dense long black hairs. Mesoscutum with distinct dark brown lateral stripes, disc covered with long (but not longer than on prescutum), stiff black hairs; pleurites pruinose with two clusters of smooth long hairs on each side of mesoscutum. Area between pre- and mesoscutum dark brown. Mesoscutellum with distinct dark brown longitudinal midstripe. Short white hairs spread over disc. Long white hairs present posterior-laterally. Metanotum with two clusters of long white hairs on each side.

Forewings. Elongate, slender, with acute apex, slightly emarginated before apex (Figs 54, 83). Venation brown. Costa whitish, other veins yellowish brown, proximal Cx shaded brown. Proximal costal cells increase in size towards pterostigma. Pterostigma brown, broad basally, long but not reaching C. In holotype, 23 Cx present before pterostigma in right wing, 24 in left. Nine crossveins between RA and MA before origin of RP in right wing, 12 in left. Eleven radial crossveins before pterostigma in right wing, 9 in left. *Hind wings* brown. Portion just before dark area lighter than proximal portion. Crossveins shaded light brown. Dark area dark brown, shorter than white area. *Legs* yellow with short yellow hairs. Coxae pruinose, with black hairs. Apices of femora tinged dark brown.

Abdomen. Greyish, pruinose, particularly laterally on tergites and venter. Dorsum dark brown with yellowish hind margin to tergites, with long white hairs. A few long black hairs intermingled with white hairs present on tergites 5–9. Venter with sparse short black hairs. Apex with long black hairs.

Variation. Some males have white hairs intermixed with black hairs on the thorax. Some males also have a more acute tip to the forewings.

Type material examined. SOUTH AFRICA, *Northern Cape Province*. Holotype m#, NEUR08906, Richtersveld, Cornells Kop, 28°25'S 16°53'E, (2816 Bd), 145m, 9.x.1974, M.W.Mansell, H.D.Brown / Collected at mercury vapour light, arid rocky terrain. *Paratypes*: 14m# 7f#, same data as holotype. (SANC). NAMIBIA, *Karas Region*. 8m# 5f# NEUR08931, Obib Poort, 28°06'S 16°42'E, 1.xi.1999, M.W.Mansell, C.H.Scholtz, light; 1m# 1f#, NEUR12587, Diamond Area no. 1, Klinghardtberge, 27°19'S 15°46'E, (2715 Bd), 20 / 21.x.1974, M.W.Mansell, H.D.Brown / Collected at mercury vapour light, arid rocky terrain. (All SANC).

Distribution and habitat. This species is known from three localities in the Northern Cape Province, South Africa and southern Namibia (Fig. 154). The range is mainly centred in the Richtersveld Bioregion of the Succulent Karoo Biome (Mucina & Rutherford 2006). (See description of the habitat under distribution of *A. parva*).

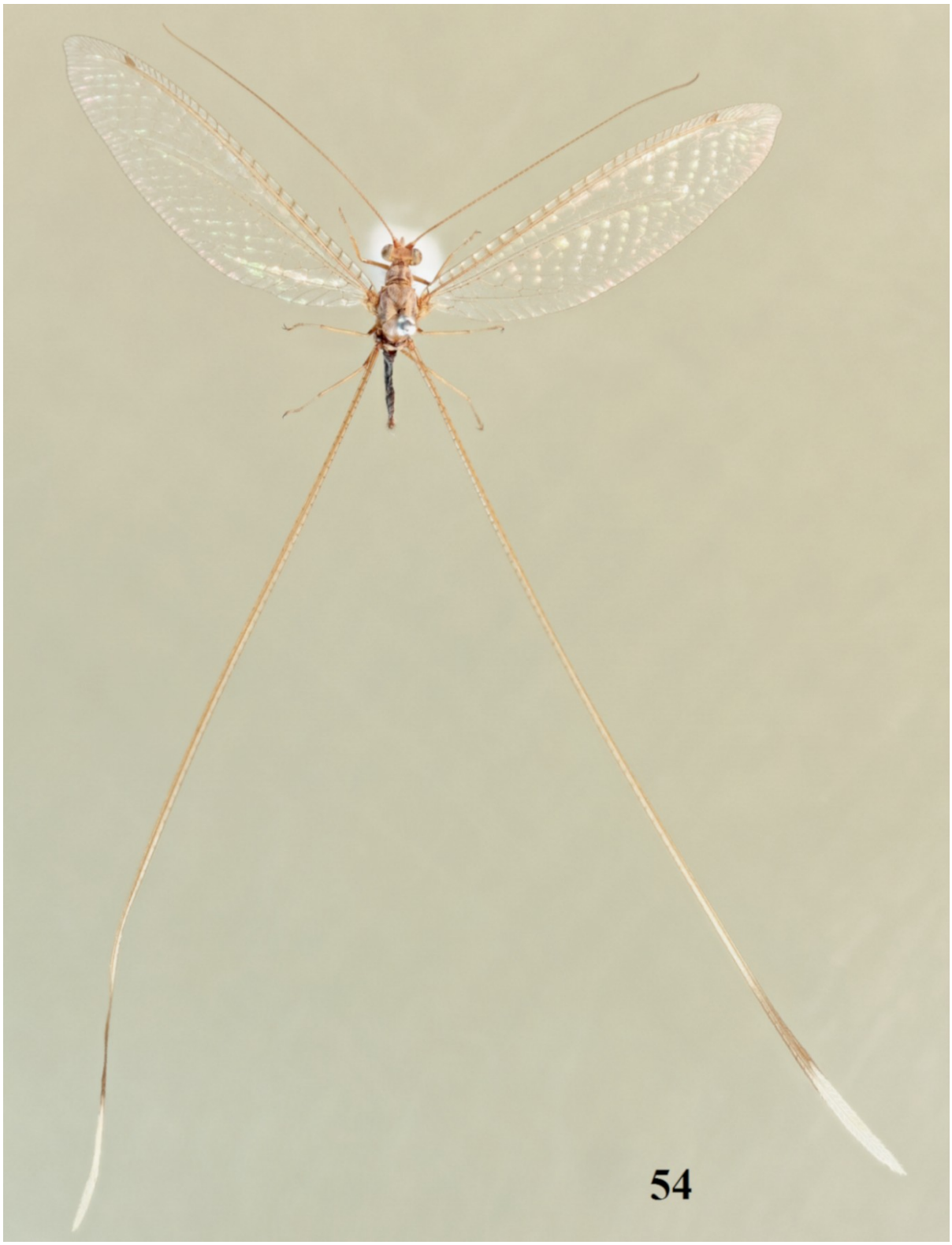


Figure 54. *Afroptera cylindrata* Abdalla & Mansell **sp. nov**., habitus. Forewing length = 22.6 mm.

***Afroptera dyscrita* (Tjeder, 1967) comb. nov.**
(Figs 77, 102, 129, 133, 151)

Synonymy

Nemopterella dyscrita Tjeder, 1967: 467.

Etymology. Unknown.

Type locality. SOUTH AFRICA, *Northern Cape Province*. Pofadder, 29°08'S 19°24'E.

Type depository. SAMC.

Diagnosis. *Afroptera dyscrita* is most closely related to *A. bitis*. Similarity and differences between these two species are provided in the diagnosis of *A. bitis*.

Size (mm). Male: body length 8.7 (8–10.3); forewing 21.4 (20.6–23.2); hind wing 46.2 (42.5–50.8); antenna 15.3 (14.6–16.7); Female: body length 10.9 (10–12.2); forewing 22.8 (21.1–25.9); hind wing 48.2 (43–54); antenna 15.2 (13.3–15.9). (N = 27)

Type material examined. SOUTH AFRICA, *Northern Cape Province*. Holotype m# (Fig. 129), SAM–NEU–A001249 / Holotypus *Nemopterella dyscrita* Tjed, Bo Tjeder 1966 (red handwritten label) / Pofadder, Bushmanland, Oct. 1939, Museum Staff (white printed label). Allotype f#, SAM–NEU–A001250 /Allotypus f# *Nemopterella dyscrita* Tjed, Bo Tjeder 1966 (red handwritten label), same data as holotype. (Both SAMC).

Other material examined. SOUTH AFRICA, *Northern Cape Province*. 9m# 16f#, NEUR09619, Kabas Farm, 10 km NE Pofadder, 29°02'S 19°26'E, 800m, 27.x.1996, M.W.Mansell, C.H.Scholtz. (SANC).

Distribution and habitat. This species is known from only one locality in the Northern Cape Province, South Africa (Fig. 151). The locality is situated in the north of the Bushmanland Bioregion within the Nama Karoo Biome where the habitat is arid consisting of isolated mountains and flat plains, dominated by Bushmanland Inselberg Shrubs that comprise succulent and non-succulent shrubcomponents. The area receives late summer rains with an average below 100 mm per year (Mucina & Rutherford 2006).

***Afroptera exigua* (Tjeder, 1967) comb. nov.**
(Figs 75, 101, 130, 134, 155)

Synonymy

Nemopterella exigua Tjeder, 1967: 493.

Etymology. Unknown, probably from the Latin word *exigua* (small) for its small size.

Type locality: SOUTH AFRICA, *Western Cape Province*. Klaarstroom, 33°19'51"S 22°32'05"E.

Type depository. SAMC.

Diagnosis. *Afroptera exigua* is very similar in appearance to *A. parva* and *A. koranna* **sp. nov.**, due to its small size, rounded apex of the forewings (Fig. 134), short antennae and black hairs on prescutum. It can however, be easily distinguished from the former species by the unstriped pronotum (Fig. 101), short apical antennal segment (Fig. 75) and darkened tips of femurs, and from the latter by having a different shape to the apical antennal segment and by the white pubescence on the mesoscutum and mesoscutellum instead of the black hairs that are present in *A. koranna* **sp. nov.**

Size (mm). Male: body length 7.7 (7–8.3); forewing 20 (17.5–22.5); hind wing 39.8 (35–44.6); antenna 13.5 (11–15.9). (N = 2).

Type material examined. SOUTH AFRICA, *Western Cape Province*. Holotype m# (Fig. 130), SAM–NEU–A001251 / Klaarstroom, Prince Albert District, [33°20'S 22°32'E], Mus Expd, Oct 1952 (white printed label) / Holotypus *Nemopterella exigua* Tjeder 1966 (red handwritten label). (SAMC).

Other material examined. SOUTH AFRICA, *Western Cape Province*. 1m#, NEUR12588, Middeldrif Farm, Laingsburg District, 33°03'13"S 21°16'14"E, 708m, at light, 18.x.2009, A.P.Marais; 1f#, NEUR12589, Wamakerskraal Farm, Laingsburg Dist., 33°01'24"S 21°36'43"E, 550m, 11.x.2008, J.B.Ball, A.P.Marais (SANC).

Distribution and habitat. *Afroptera exigua* has a limited distribution restricted to the Western Cape Province, South Africa (Fig. 155). The collection localities fall within the Rainshadow Valley and Lower Karoo Bioregions in the Succulent and Nama Karoo Biomes respectively (Mucina & Rutherford 2006). The habitat in the former bioregion is mostly flat to undulating land with Heuweltjies (small hills) formations and series of hills, dominated mostly by succulent shrubs, herbs and low shrubs. The area is characterised by low MAP (165 mm) because of the rainshadow of the Swartberg Mountains. While in the latter bioregion the species seems to be associated with dry habitats of undulating lands of mud and sandstone soils, mostly dominated by a Gamka Karoo vegetation type where the main components are dwarf spiny shrubs, Karoo shrubs and sparse low trees. The area receives autumn and summer rains with an average of 100–250 mm per year (Mucina & Rutherford 2006).

***Afroptera folia* Abdalla & Mansell sp. nov.**
(Figs 46, 55, 59, 86, 154)

Etymology. The specific epithet is derived from the Latin word *folia* (leaf) for the leaf-like shape of the forewings.

Type locality. SOUTH AFRICA, *Northern Cape Province*. Richtersveld, Blackie's Prospect, 28°18'S 17°07'E.

Diagnosis. Body colour yellow. This species is very similar to *A. acuta* **sp. nov.**,in having a similar long rounded apex to the forewings (Fig. 86) and pruinose thorax (Fig. 46). It can easily be distinguished from *A. acuta*by the following characters: *A. folia*is characterised by long black hairs on the prescutum and mesoscutum (Fig. 46) while in *A. acuta*the hairs are white, the forewings of *A. folia* are broader (Fig. 86) than those of *A. acuta*.*Afroptera folia* is further characterised by the yellowish brown abdomen while in *A. acuta* the abdomen is brown.

Description

Size (mm). Male: body length 10.1 (9–11.5); forewing 23.9 (22.5–26.8); hind wing 55.3 (49.8–63.5); antenna 22.1 (20.8–25.3); Female: body length 10.2 (9.4–10.9); forewing 21.3 (18.9– 23.6); hind wing 42.5 (37.3–47.7); antenna 13.7 (11.5–15.9). Holotype m# (Fig. 55); Body length 9.6; forewing 23.7; antenna 21.7; hind wing 52.9. (N = 8).

Head. Yellow. Vertex brown with yellow hind margin and two pale yellowish spots near eye margins. Palpi yellowish brown. Eyes large, widely separated. Antennae yellow proximally, yellowish brown distally, long, extending beyond pterostigma, covered in black setae longer in distal portion (Figs 55, 86). Apical segment longer than penultimate segment, mainly membranous (Fig. 59).

Thorax. Light yellow to creamy white, pruinose (Fig. 46). The midstripe on pronotum manifest as a brown central portion in posterior half of pronotum, while lateral stripes appear as two transverse brown spots lateral to midline. Fore and hind margins with erect long, black hairs intermixed with a few short white hairs. Very fine short white hairs spread behind black hairs on fore margin. Long erect black hairs spread with some long white hairs on each distal lateral side of pronotum. *Prescutum*with faintly visible midstripe appearing as light brown shading, discwith sparse, long black hairs, long black hairs present anterior-laterally admixed with a few long white hairs. Long white hairs also present along lateral sides of prescutum.

Area between prescutum and mesoscutum dark brown. Mesoscutum with distinct dark brown lateral stripes, covered in long sparse white hair, two tufts of long white hairs spread posteriorly at each side of mesoscutum. Mesoscutellum unstriped, with sparse, long white hairs, but not longer than prescutum hairs. Two tufts of short hairs present posteriorly on each side of the mesoscutellum. Two tufts of long white hairs present laterally on each side of metanotum. *Legs* yellow with black setae. Coxae with intermingled white and black setae. Dorsal surface of femur tinged brown.

Forewings. Elongate, with extended rounded apex and distinct broad emargination before apex (Fig. 86). Venation brown, C whitish, proximal Cx shaded brown, costal cells increase in size towards pterostigma. Pterostigma dark brown, short. In holotype male, 20 Cx before pterostigma in right wing, 21 in left. Nine crossveins between RA and MA before RA in both wings. Eleven radial crossveins before pterostigma in right wing, 10 in left. *Hind wings* yellowish brown proximally, brown in middle portion before dark area. Crossveins shaded light brown. Costal cells tinged brown. Longitudinal veins brown. Dark area dark brown, shorter than white area. *Legs* yellow with black hairs, femoral apices tinged dark brown.

Abdomen. Greyish, pruinose, tergites with yellow hind margins. Dorsum and venter with white hairs, denser, longer on dorsum than venter. Apex yellowish brown with long black hairs.

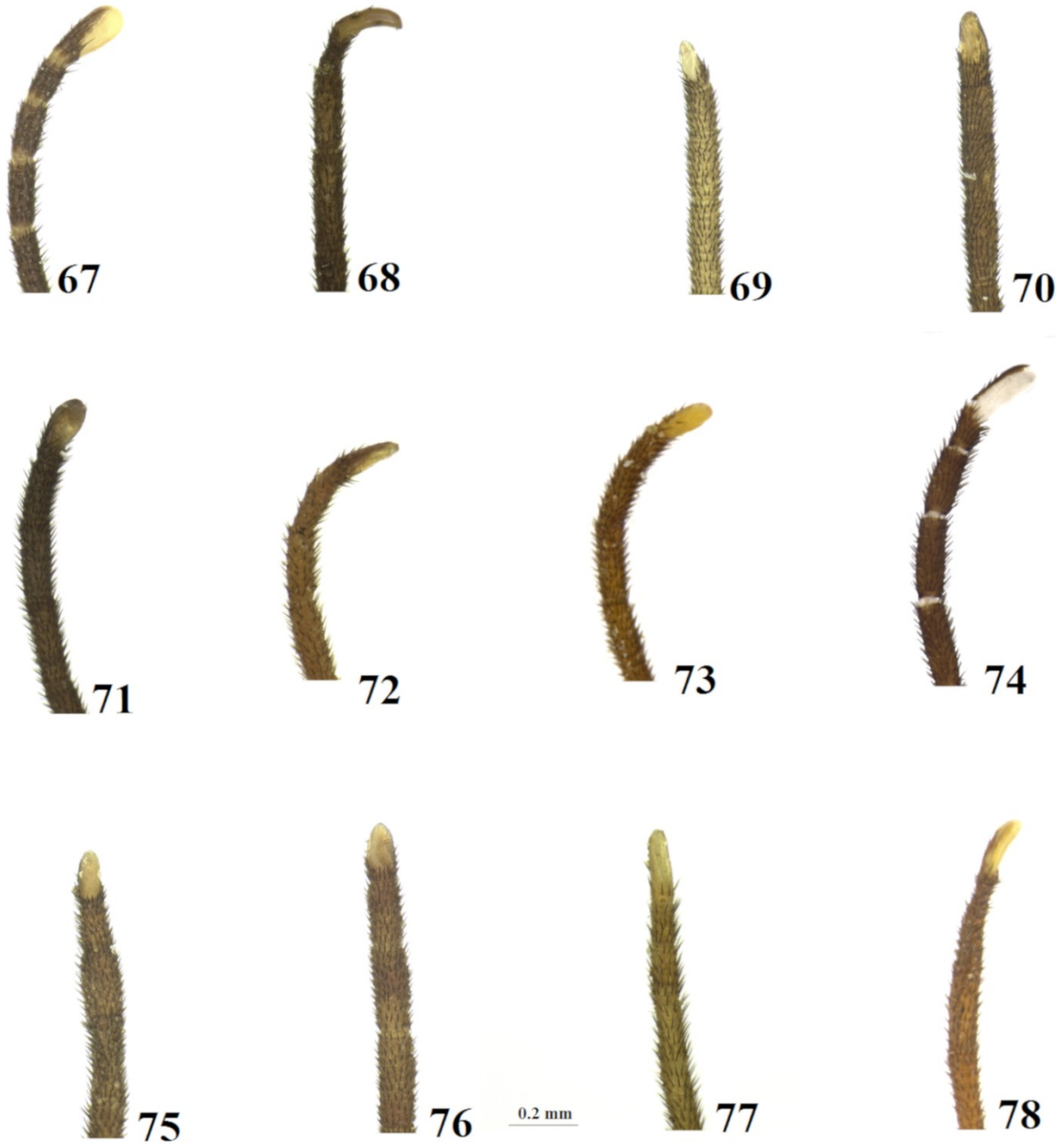
Variation.Some males have a shorter pterostigma than others.

Type material examined. SOUTH AFRICA, *Northern Cape Province*. Holotype m#, NEUR08905, Richtersveld, Blackie's Prospect, 145 m, 28°18'S 17°07'E, (2817Ac), 11.x.1974, M.W.Mansell. *Paratypes*: 5m# 2f#, same data as holotype. (All SANC).

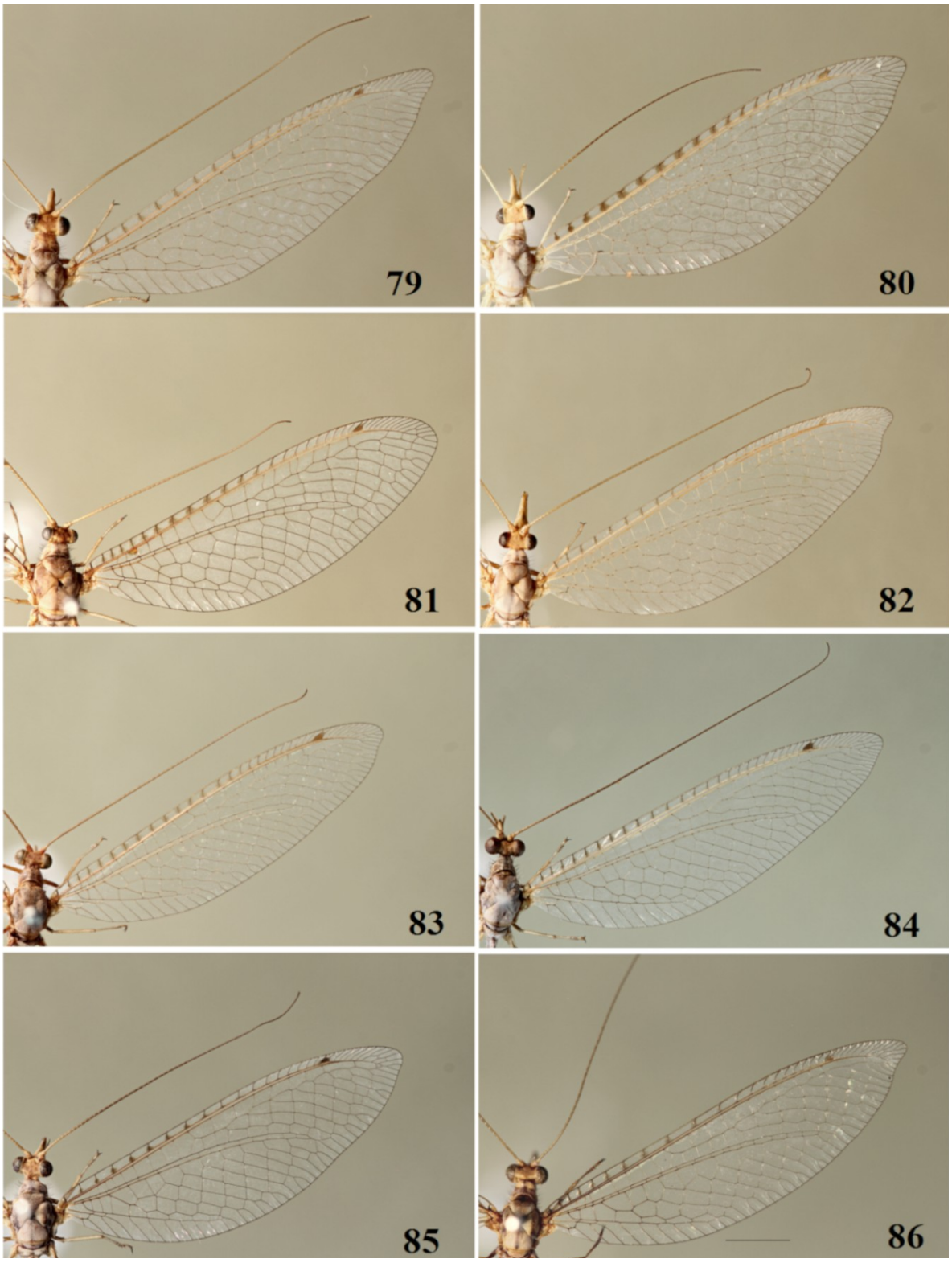
Distribution and habitat. This species is known from one locality in the Richtersveld Bioregion in the Succulent Karoo Biome (Fig. 154). The collection site falls within the Central Richtersveld Mountain Shrubland vegetation unit in the Richtersveld Bioregion. (See description of the habitat in this vegetation unit under the distribution of *A. munroi*).

Figure 55. *Afroptera folia* Abdalla & Mansell **sp. nov.,** habitus. Forewing length = 23.7 mm.

Figures 56–66. Antennae of *Afroptera* spp. 56, *A. acuta* **sp. nov.**; 57, *A. alba* **sp. nov.**; 58, *A. koranna* **sp. nov.**; 59, *A. folia* **sp. nov.**; 60, *A. cylindrata* **sp. nov.**; 61, *A. balli* **sp. nov.**; 62, *A. maraisi* **sp. nov.**; 63, *A. apicalis* (Tjeder); 64, *A. bitis* (Tjeder); 65, *A. aequabilis* (Tjeder); 66, *A. brinkmani* **sp. nov.**



Figures 67–78. Antennae of *Afroptera* spp. 67, *A. segregata* (Tjeder); 68, *A. peringueyi* (Tjeder); 69, *A. parva* (Tjeder); 70, *A. nigrosetosa* (Tjeder); 71, *A. pilosa* (Tjeder); 72, *A. sabuleti* (Tjeder); 73, *A. longicornis* (Tjeder); 74, *A. munroi* (Tjeder); 75, *A. exigua* (Tjeder); 76, *A. remifera* (Westwood); 77, *A. dyscrita* (Tjeder); 78, *A. leptocera*, (Navás).



Figures 79–86. *Afroptera* spp. Forewings of the males. 79, *A. acuta* **sp. nov.**; 80, *A. alba* **sp. nov.;** 81, *A. koranna* **sp. nov.;** 82, *A. balli* **sp. nov.;** 83, *A. cylindrata* **sp. nov.**; 84, *A. brinkmani* **sp. nov**.; 85, *A. maraisi* **sp. nov**.; 86, *A. folia* **sp. nov**. Scale = 1 mm.

***Afroptera koranna* Mansell & Abdalla sp. nov.**
(Figs 52, 58, 81, 87, 154)

Etymology. A noun in apposition, named for the Korannaberg Hills that harbour this species, and are a prominent feature of the Tswalu Kalahari Reserve, Northern Cape Province, South Africa. The Korannaberg, in turn, refers to the Koranna, a tribe of the Khoisan people, the original human inhabitants of southern Africa.

Type locality. South Africa, *Northern Cape Province*. Picnic Valley, Tswalu Kalahari Reserve, 27°17'46"S 22°27'42"E.

Diagnosis. This species is close to *A. pruinosa* by having a similar pruinose, unstriped thorax (Fig. 52). It can be distinguished from *A. pruinosa* by a combination of the following characters: *A. koranna* is characterised by rounded tips to forewings while the tip in *A. pruinosa* is rounded with slight emargination before the tip. Also, *A. koranna* has very short antennae, not reaching pterostigma (Figs 81, 87) while the antennae in *A. pruinosa* are long reaching beyond pterostigma. Moreover, *A. koranna* is characterised byhaving a reddish vertex with two yellowish spots near the eye margins instead of a yellowish vertex as in *A. pruinosa*,and also by the yellowish brown abdomen, which is blackish brown in *A. pruinosa*. The species is also very similar to *A. exigua* by having a rounded tip to forewings; it can be separated from *A. exigua* by the black pubescence on the mesoscutum and mesocutllum instead of the white pubescence that is present in *A. exigua.*

Description

Size (mm). Male: body length 9.0 (7.9–10.9); forewing 21.4 (17.9–23.6); hind wing 46.2 (38.7–51.5); antenna 14.3 (12.5–15.4); Female: body length 10.0 (9–11.2); forewing 20.9 (18.8–22.9); hind wing 43.8 (38–51.2); antenna 11.6 (9.9–12.7). Holotype m# (Fig. 87): Body length 10.1; forewing 23.6; hind wing 51.3; antenna 15.8. (N = 22).

Head. Frons, clypeus, genae reddish yellow. Palpi dark brown. Vertex reddish with yellow hind margin and two faint yellowish spots laterally near eye margins. Eyes small, widely separated. Antennae light yellow, short, not reaching pterostigma, clothed with black setae, scape reddish yellow, pedicel yellow (Figs 81, 87). Apical segment approximately same length as preapical segments but terminates in a small acute membranous tip, appearing dark because of dense hair (Fig. 58).

Thorax. Broad, predominantly yellowish brown, pruinose, unstriped (Fig. 52). Pronotum fore margin with long, stiff black hairs, and long, smooth hairs situated behind these, lateral sides with long black hairs intermingled with long white hairs. Hind margin covered in long black hairs. Smooth sparse short white hairs spread on disc. Prescutum with long, stiff black hairs on anterior-lateral sides intermingled with long white hairs, disc with short, sparse black hairs. Short white hairs also present along lateral sides of prescutum. Mesoscutum with short brown pubescence combined with short black hairs on disc. Sides largely pruinose, naked except for an assemblage of two groups of whitish hairs at each posterior side of mesoscutum. Mesoscutellum with short, sparse white hairs, two groups of short white hairs also present posteriorly on each lateral side. Metanotum greyish with two tufts of long white hairs laterally.

Forewings. Broad, short, with rounded apex. Pterostigma brown. (Fig. 81). Venation dark brown. Costa whitish yellow, SC and RA light brown, proximal Cx shaded brown. Costal cells increase in size towards pterostigma. In holotype, 22 Cx before pterostigma in both wings. Eight crossveins between RA and MA before origin of RP in right wing, 9 in left. Nine radial crossveins before pterostigma in both wings. *Hind wings* with longitudinal veins pale brown to creamy white in proximal portion, whitish in middle before the dark area. Crossveins brown, tinged dark brown in proximal portion, whitish in middle before the dark area. Dark area dark brown, approximately same length as white area. *Legs* yellow with black setae, mid and hind coxae pruinose, femoral extremities tinged brown.

Abdomen. Brown, pruinose, tergites with yellowish hind margins. Tergites covered in long white hairs. Venter pruinose with short sparse black hairs. Apex yellow with dense long black hairs.

Variation. Some males have white hairs instead of black on venter.

Type material examined. SOUTH AFRICA, *Northern Cape Province*.Holotype m#, NEUR12257, Picnic Valley, Tswalu Kalahari Reserve, 27°17'46"S 22°27'42"E, 1120m, 17.ix.2016, M.W.Mansell, C.L.Sole, W.Strümpher, Light Trap. *Paratypes*: 4m#, same data as holotype; 4m# 7f#, NEUR12256, Gosberg, Tswalu Kalahari Reserve, 27°15'16"S 22°27'43"E, 1169m, 16.ix.2016, same collectors, Light Trap; 6f#, NEUR12255, Dedeben, Tswalu Kalahari Reserve, 27°17'16"S 22°29'08"E, 1219m, 15.ix.2016, same collectors, Light Trap. (All SANC).

Distribution and habitat. This species is endemic to the Northern Cape Province, South Africa (Fig. 154) and known from localities centred in the Olifantshoek Plains Thornveld vegetation unit in the Savanna Biome (Mucina & Rutherford 2006). The habitat is dry, mostly flat land covered in *Acacia* and *Boscia* tree species intermixed with tall shrubs. Populations of

A. koranna however, are confined to the rocky Korannaberg mountain range, which extends into the Kalahari savannah. The area receives summer to autumn rains with MAP= 250–350 mm.

***Afroptera lanata* (Tjeder, 1967) comb. nov.**
(Figs 127, 135, 155)

Synonymy

Nemopterella lanata Tjeder, 1967: 485.

Etymology. Unknown, probably from the Latin word *lanata* (woolly) for its hairy thorax.

Type locality. South Africa, *Western Cape Province*. Riversdale Mountains, 34°00'S 21°15'E.

Type depository. SAMC.

Diagnosis. A large species, easily distinguished from its congeners by the markedly broad forewings (Figs 127, 135) and very hairy thorax.

Type material examined. SOUTH AFRICA, *Western Cape Province*. Holotype m#, SAM–NEU–A001258, Riversdale Mountains [34°00'S 21°15'E], (white printed label) / Holotypus m#, *Nemopterella lanata* Tjed, Bo Tjeder 1966 (red handwritten label). (SAMC).

Distribution and habitat. This species is known only from Riversdale Mountains in the Western Cape Province, South Africa (Fig. 155) where it was collected in the Mossel Bay Shale Renosterveld vegetation type in the Fynbos Biome (Mucina & Rutherford 2006). In general, this habitat comprises undulating hills together with flat lands rich in thicket elements, Renosterbos and succulent plants are also present. The area is characterised by high annual precipitation with an average of 270–620 mm per year.

Remarks. The species is known only by its male holotype.

***Afroptera leptocera* (Navás, 1910) comb. nov.**
(Figs 88, 95, 152)

Synonymy

Eretmoptera leptocera Navás 1910: 364.

Nemopterella leptocera Navás 1912: 9.

Etymology. Unknown.

Type locality. Namibia, Fort Numis (not located).

Type depository. NHMV.

Diagnosis. *Afroptera leptocera* is recognised by the pronounced blackish stripes on the thorax and the whitish yellow antennae.

Size (mm). Male: body length 9.1 (8.1–10); forewing 21.8 (20–23.1); hind wing 50.2 (45–54.3); antenna 19.1 (15–21.3); Female: body length 10.3 (8.4–12); forewing 21.4 (19–23.4); hind wing 45.7 (41–52); antenna 13 (10.5–14). (N = 22).

Type material examined. NAMIBIA.Holotype f# (Habitus Photo, Fig. 88). Holotypus (red printed label) / Damara L, Fort Numis?, No 6. *Halter* sp. Fleck' (white handwritten label) / *Eretmoptera leptocera* Nav. (white handwritten label) /Typus (red printed label).

Other material examined. NAMIBIA. 1m# 1f#, TMSA02064, 'Rehoboth [20°14'S 15°40'E], March 1938, H.W.Bell Marley / *Nemopterella leptocera* Nav., Det. Bo Tjeder 1966; 2f#, TMSA02065, BULLSPOORT [24°08'56"S 16°21'47"E], x.1952, S.W.A., R.G.Strey / *Nemopterella leptocera* Nav. det. Bo Tjeder 1966; 2f#, Ongvati River, Outjo Dist. [20°06′32″S 16°09′17″E], VIII.1950, R.G.Strey / *Nemopterella leptocera* Nav., Det. Bo Tjeder 1966; 1f#, TMSA02066, Warmfontein [27°05'45"S 19°14'52"E], 5.x.1950, R.G.Strey / *Nemopterella leptocera* Nav., Det. Bo Tjeder 1966; 3m#, TMSA02198 and 2f#, TMSA02197, Farm Bergland [27°28'S 17°40'E], Karas Dist., Gaapmouth into Fish River, 454m, 25.vii.2005, T.Bird / *Nemopterella leptocera* (Navás, 1910) m#, det. M.W.Mansell 2014. (All TMSA). 10f#, NEUR08940, Boom River Canyon Campsite, 28°00S 17°03E, 19.xi.1993, R. Stals. (SANC).

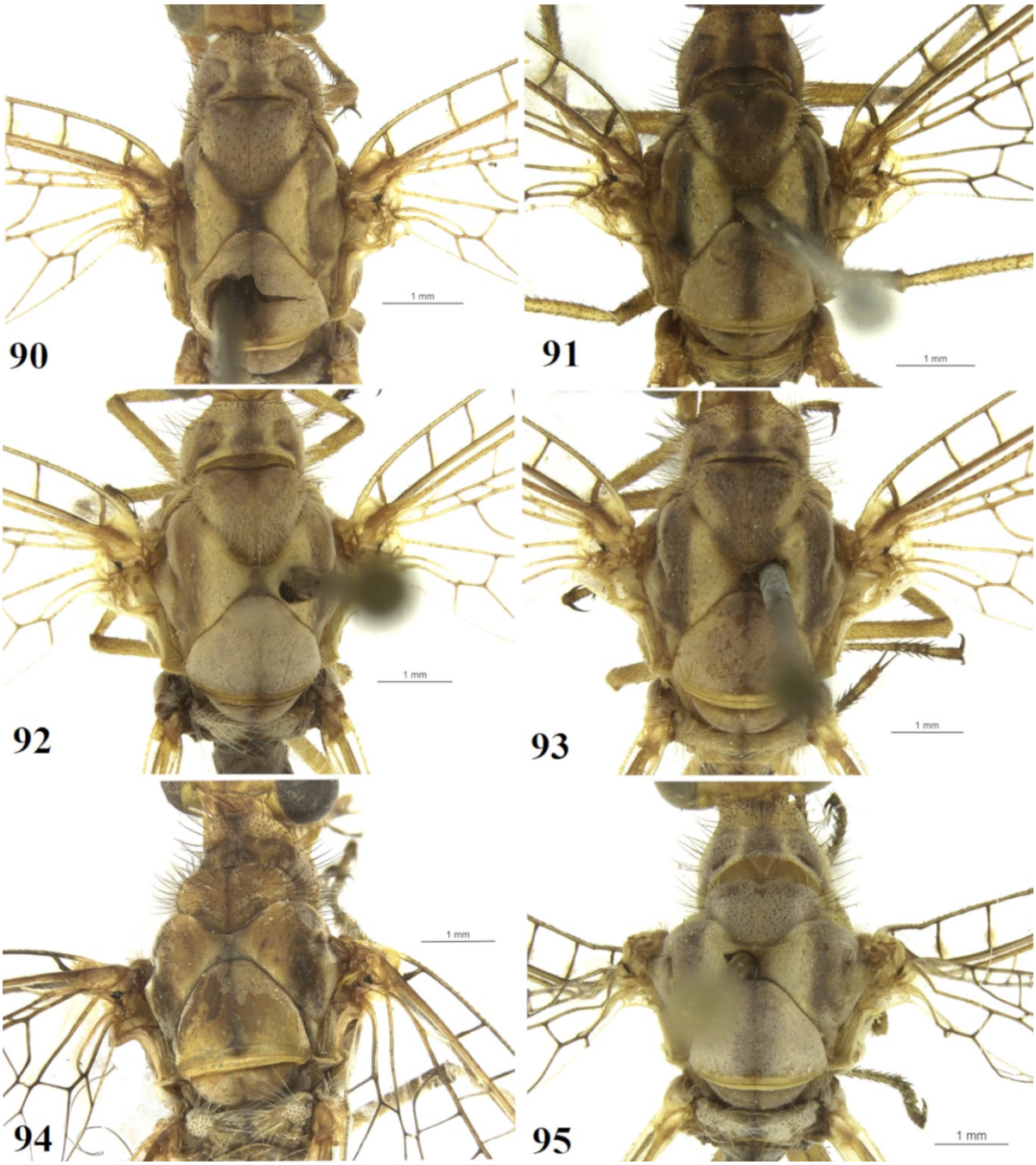
Distribution and habitat. This species seems to be endemic to Namibia where its main distribution falls within the Namibia Savanna Woodlands Ecoregion (Fig. 152). (See the description of the habitat under the distribution of *A. alba*).

Figure 87. *Afroptera koranna* Mansell & Abdalla **sp. nov**., male habitus. Forewing length = 23.6 mm.

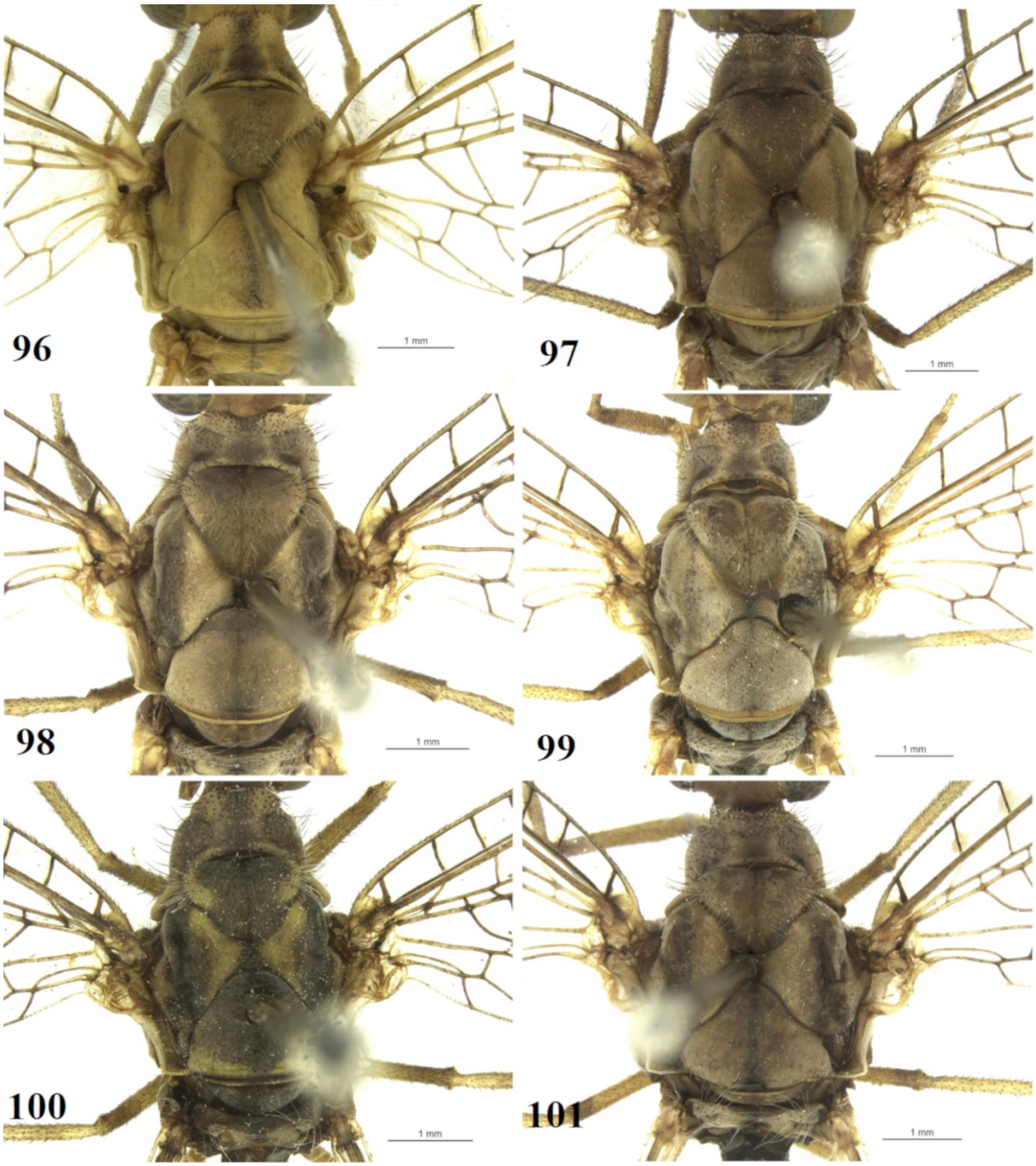
88

89

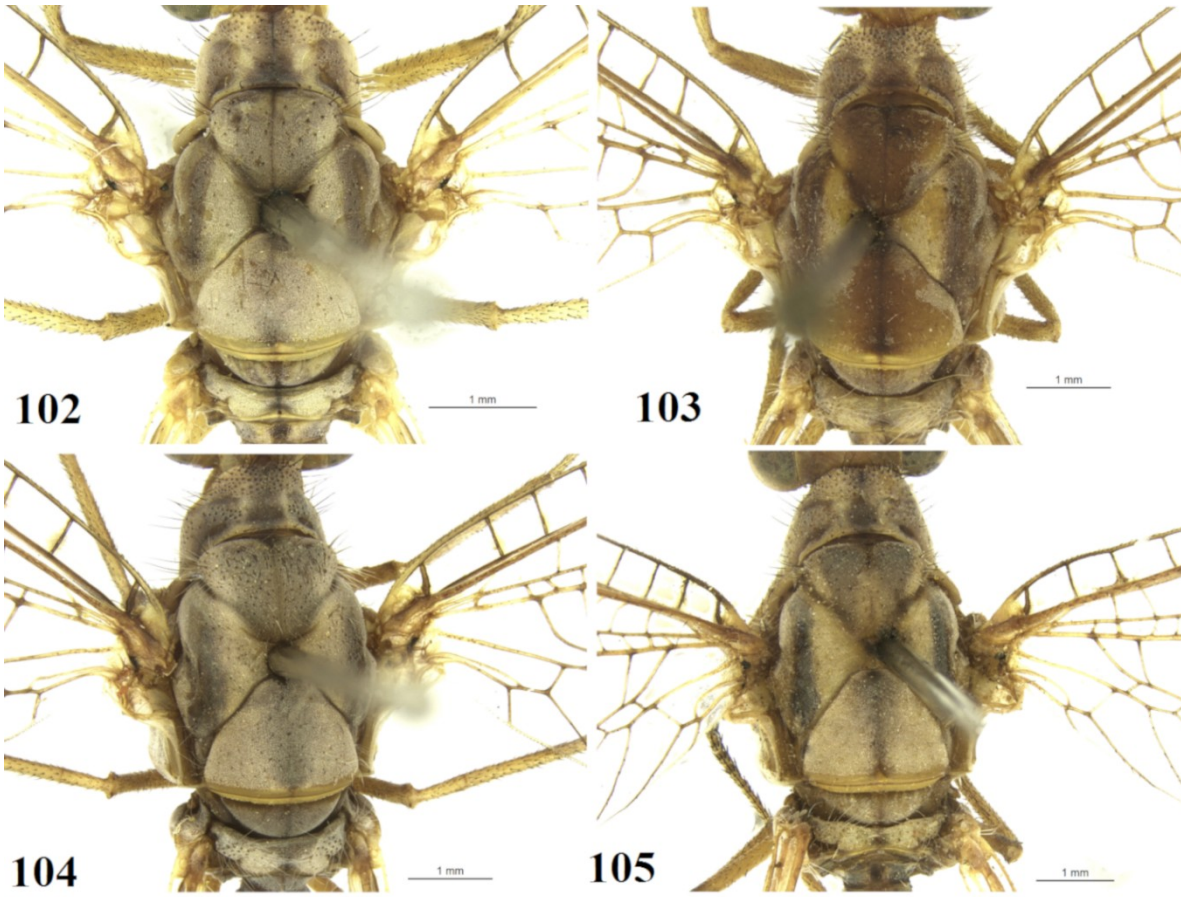
Figures 88–89. Holotypes of *Afroptera* spp. with associated labels. 88*, A. leptocera* (Navás) f#, 89, *A. bitis* (Tjeder) m#. (Photos: 88, NHMV; 89, ZILS).



Figures 90–95. *Afroptera* spp. Thorax. 90, *A. sabuleti* (Tjeder); 91, *A. nigrosetosa* (Tjeder); 92, *A. munroi* (Tjeder); 93, *A. longicornis* (Tjeder); 94, *A. obtusa* (Tjeder); 95, *A. leptocera* (Navás).



Figures 96–101. *Afroptera* spp. Thorax. 96, *A. segregata* (Tjeder); 97, *A. remifera* (Tjeder) 98, *A. pilosa* (Tjeder); 99, *A. peringueyi* (Tjeder); 100, *A. parva* (Tjeder); 101, *A. exigua* (Tjeder).



Figures 102–105. *Afroptera* spp. Thorax. 102, *A. dyscrita* (Tjeder); 103, *A. aequabilis* (Tjeder); 104, *A. bitis* (Tjeder); 105, *A. apicalis* (Tjeder).

***Afroptera longicornis* (Tjeder, 1967) comb. nov.**
(Figs 73, 93, 108, 115, 153)

Synonymy
Nemopterella longicornis Tjeder, 1967: 473.

Etymology. Unknown, probably derived from the Latin words *long* and *cornu* (horn) (long-horn) for its long antennae.

Type locality. South Africa, *Northern Cape Province*. Marydale, 29°20'19"S 22°05'50"E.

Type depository. TMSA.

Diagnosis. This species is most closely related to *A. munroi* based on external morphology. It is separable from *A. munroi*, by its longer antennae (Fig. 108) and the distinct lateral stripes on pronotum and mesonotum (Fig. 93). It is further characterised by the more rounded forewing apex with a slight emargination before the apex (Fig. 115).

Size (mm). Male: body length 9.2 (7.4–11.9); forewing 21.8 (19.7–26.4); hind wing 54.2 (44.8–63.7); antenna 21.9 (19.8–26.5); Female: body length 11.7 (10.2–13.3); forewing 23.3 (20.0–25.6); hind wing 50.8 (50–56); antenna 16.1 (13.2–17.1). (N = 136).

Type material examined. SOUTH AFRICA, *Northern Cape Province*.Holotype m# (Fig. 108), TMSA02067, HOLOTYPE Neu086, *Nemopterella longicornis* Tjeder (red printed label) / MARYDALE 5 m North [29°20'19"S 22°05'50"E], 9–10.X.1954, A.J.T.Janse (white printed label) / Holotypus m#, *Nemopterella longicornis* Tjed Bo Tjeder 1966 (red handwritten label). *Paratypes*: 2m# 1f#, same data as holotype. (All TMSA).

Other material examined. SOUTH AFRICA, *Northern Cape Province*.2m#, TMSA00751, MARYDALE, 5 m North [29°20'19"S 22°05'50"E], 9–10.x.1954, A.J.T.Janse / *Nemopterella longicornis* Tjeder, 1967, Det. M.W.Mansell 2013. (TMSA). 63m# 68f#, NEUR08942, Richtersveld, Jenkins Kop, 28°43'S 17°15'E, 600m, 9.x.1991, M.W.Mansell, R.G.Oberprieler, Mercury vapour light. (SANC).

Distribution and habitat. This species is only known from the Northern Cape Province, South Africa (Fig. 153). The ranges of distribution are mainly centred in the Bushmanland and Richtersveld Bioregions in the Nama and Succulent Karoo Biomes respectively (Mucina & Rutherford 2006). Both areas are dry, in the former, late summer–early autumn rains are dominant and vegetation cover primarily consists of grasses and succulent shrubs. While in the latter, winter rains are prevalent and the frequent fogs typify the area, which makes it more humid. The vegetation cover mainly comprises succulent shrubs and herbs.

Remarks. This species is sympatric with *A. apicalis* in Marydale.

***Afroptera maraisi* Abdalla & Mansell sp. nov.**
(Figs 53, 62, 85, 106, 154)

Etymology. This species is named for Andre P. Marais (Cape Town) for his systematic surveys of Nemopteridae that contributed significantly to this project, and to our knowledge of the Neuroptera of the Western and Northern Cape provinces of South Africa.

Type locality. South Africa, *Northern Cape Province*. Stofbakkies Farm, Prieska District, 29°39'02"S 22°44'19"E.

Diagnosis. A small species that resembles *A. aequabilis* in having a similar body size and appearance, but it can be separated by the elongate forewings that taper apically and end in an acute apex (Fig. 85), while in *A. aequabilis* the forewings are broad and end in a narrow rounded apex (Fig. 117). It also differs from *A. aequabilis* by having long antennae that reach beyond the pterostigma (Fig. 85, 106); while in *A. aequabilis* the antennae are short, not reaching the pterostigma.

Description

Size (mm). Male: body length 9.7 (9–10.2); forewing 23 (22.4–23.3); hind wing 48.0 (47.6–50.6); antenna 18.9 (16–20.4). Holotype m# (Fig. 106); Body length 8.4; forewing 22.8; hind wing 47.9; antenna 19.7. (N = 3).

Head. Frons, clypeus yellow. Vertex brown with two yellow areas laterally at hind margin and two ill-defined lateral yellow spots on each side near eye margins. Antennae long, reaching pterostigma, scape yellowish brown, pedicel yellow, proximal portion yellowish brown with scattered short setae, dark brown distally with long black setae (Fig. 106). Apical segment mostly membranous (Fig. 62). Eyes large with diameter approximaly same length as genae.

Thorax. Greyish, pruinose (Fig. 53). Pronotum with ill-defined stripes with only midstripe that is traceable as brownish grey shading posteriorly, while the lateral stripes form two lateral brown transverse spots. Pronotal margins with erect long black hairs intermixed with some long, soft white hairs; soft, white hairs situated behind black hairs on fore margin. Distal anterior lateral margins with very long black hairs admixed with white hairs, long, soft white hairs also present on disc. Midstripe on prescutum appears as light brown shading but indistinct on mesoscutellum. Stiff long black hairs present on anterior lateral portions of prescutum admixed with white long hairs. Long sparse black hairs present on disc, with long soft white hairs along lateral margins of prescutum. Mesoscutum with faint brown lateral stripes. Short white hairs on disc, two lateral long tufts of white hairs at each side. Mesoscutellum with scattered short white hairs over whole disc and two groups of long white hair at each side. Metanotum with very long white hairs laterally on hind margin. *Legs* yellow, with short setae. Femoral and tibial apices tinged dark brown, fore coxae with black and white setae.

Forewings. Appearing elongate, tapering towards apex, weakly emarginated before acute apex (Fig. 85). Pterostigma dark brown, broad at base, long but not reaching C. Costal cells before and beyond pterostigma slightly tinged brown. Venation dark brown. Costa whitish but appearing blackish due to dense black setae. Subcosta and RA light brown. Proximal Cx

shaded brown. Costal cells increase gradually in size towards pterostigma. Holotype with 18 Cx before pterostigma in right wing, 21 in left. Ten crossveins between RA and MA before origin of RP in right wing, 11 in left. Eight radial crossveins before pterostigma in right wing, 10 in left. *Hind wings* pale creamy white. Proximal portion appears brown. Longitudinal veins pale creamy white, while crossveins appear much darker. Median portion before dark area white, longitudinal veins and crossveins white, dark area dark brown, shorter than white area.

*Abdomen***.** Yellowish brown, tergites with yellowish hind margins. Longitudinal midstripe dark brown. Pleurites pruinose, tergites with dense, long white setae. Venter light reddish yellow, pruinose, with long white hairs but shorter than on tergites. Apex yellow with dense, long black setae.

Variation. Some males have a few black hairs intermingled with the white hairs on the abdomen.

Type material examined. SOUTH AFRICA, *Northern Cape Province*. Holotype m#, NEUR12582, Stofbakkies Farm, Prieska Dist. 29°39'02"S 22°44'19"E, 938m, 30.ix.2010, A.P.Marais. *Paratypes*: 3 m#, same data as holotype. (All SANC).

Distribution and habitat. The range of distribution of this species is in the Northern Cape Province (Fig. 154) where it is situated in the Lower Gariep Broken Veld bioregion in the Nama Karoo Biome (see description of the habitat under distribution of *S. arenaria*).

Figure 106. *Afroptera maraisi* **sp. nov.**, male habitus. Forewing length = 22.8 mm.

***Afroptera munroi* (Tjeder, 1967) comb. nov.**
(Figs 34, 35, 36, 37, 38, 39, 40, 41, 74, 92, 111, 116, 144, 147, 152)

Synonymy

Nemopterella munroi Tjeder, 1967: 470.

Etymology. The species was named after H.K.Munro (Plant Protection Research Institute, Pretoria) who collected the type specimens.

Type locality. South Africa, *Northern Cape Province*. Houmoed, 29°18'53"S 19°32'47"E.

Type depository. TMSA.

Diagnosis. *Afroptera munroi* resembles *A. longicornis* and *A. brinkmani* by having similar pubescence patterns on the thorax and abdomen. It can be distinguished from *A. longicornis* by its shorter antennae (Fig. 111), indistinct lateral stripes on pronotum and mesonotum (Fig. 92) and less rounded apex on the forewings (Fig. 116). It is distinguished from *A. brinkmani*by the smaller body size, less concave vertex and the yellowish hind margin of the vertex (Fig. 144).

Size (mm). Male: body length 10.2 (8.3–13.8); forewing 24.3 (21.1–27.6); hind wing 54.9 (42.7–63.5); antenna 20.9 (16.5–24.1); Female: body length 11 (9–12.3); forewing 23.5 (20.5–25.5); hind wing 49.8 (43.2–56.8); antenna 12.9 (9–12.3) (N = 139).

Type material examined. SOUTH AFRICA, *Northern Cape Province*.Holotype m#, TMSA02068, HOLOTYPE Neu 98, *Nemopterella munroi* Tjeder (red printed label) / Houmoed, N.W.Cape [29°18'53"S 19°32'47"E], 20.X.1955, H.K.Munro (white handwritten label) / Holotypus m#, *Nemopterella munroi* Tjed, Bo Tjeder 1966 (red handwritten label). (TMSA). *Paratypes*: 5m# 1f#, NEUR08902, Gelykswerf, Richtersveld, C.P.,x.1956, H.K.Munro (white printed label) / Paratypus, *Nemopterella munroi* Tjed., Bo Tjeder 1966 (red handwritten label). (SANC). 1m# 3f#, SAM–NEU–A001225, Aggeneys, Bushmanland Btw Springbok and Pella (white printed label) / Paratypus, *Nemopterella munroi*, Bo Tjeder 1966 (red handwritten label). (SAMC).

Other material examined. SOUTH AFRICA, *Northern Cape Province*.5m#, TMSA00759, Houmoed, [29°18'53"S 19°32' 47"E], 20.X.1955, H.K.Munro; 2m# 5f#, TMSA00730, Richtersveld, Omsberg Water, 23.ix.1991, M.Krüger (All TMSA). 1m# 1f#, NEUR08917, Richtersveld, Gelykswerf, x.1956, H.K,Munro; 16m# 6f#, NEUR08913, Richtersveld near Rosyntjieberg, 28°24'S 17°11'E, (2817Ac), 350m, 11.x.1974, M.W.Mansell, H.D.Brown; 4m# 2f#, NEUR12583, Kelkiewyn Farm, Calvinia District, 31°12'01"S 19°41'33"E, 22–23.x.2013, 681m, C.H.Scholtz; 3m# 1f#, NEUR12343, same locality, 1.x.2015, C.H.Scholtz / *Nemopterella munroi* Tjeder, 1967 m# Det. M.W.Mansell 2016; 2f#, NEUR11812, same locality, 1.x.2012, J.B.Ball, M.W.Mansell; 1m# 2f#, NEUR11811, same

locality, 25.x.2011, C.H.Scholtz; 3m# 1f#, NEUR10895, same locality, 26.ix.2010, C.H.Scholtz; 2m# 1f#, NEUR10226, Nuwelande Farm, Calvinia District, 31°10'50"S 19°40'08"E, 664m, 15.x.2009, J.de Klerk; 14m# 17f#, NEUR00710, Groblershoop, 26°53'44"S 21°59'04"E, 6–9.x.1986, C.G.E.Moolman, Collected at light; 1m#, NEUR09822, Namaqualand, Steinkopf [29°15'11"S 17°43'52"E], 3.ix.1986, R.Mijburgh. (All SANC). NAMIBIA, *Karas District*. 18m# 2f#, NEUR08904, S.W.AFRICA, Diamond Area no 1, nr Aurusberg, 300m, 27°32'S 16°10'E, (2716Ca), 22.x.1974, M.W.Mansell, H.D.Brown; 2m#, NEUR08903, same locality, 23.x.1974, M.W.Mansell; 10m# 7f#, NEUR08941, Hohenfels, 28°30'S 16°37'E, 100m, 21.x.–5.xi.1994, C.J.Klok. S.L.Chown, C.H.Scholtz. (All SANC).

Distribution and habitat. This species is known from the Northern Cape Province and Namibia (Fig. 152). The distribution is centred in the Succulent Karoo, Nama Karoo and Desert Biomes. In the Succulent Karoo Biome, the species range falls mainly within the Central Richtersveld Mountain Shrubland and Hantam Karoo vegetation units in the Richtersveld and Trans-Escarpment Succulent Karoo Bioregions, respectively (Mucina & Rutherford 2006). In the former vegetation unit, the topography of the area is steep and montane in some parts with deep canyons and large valleys in others. It is characterised by loamy sands, sandy and loam soils. It receives winter rains with an average of 60–299 mm per year (Mucina & Rutherford 2006). The vegetation cover mainly consists of succulent shrubs, low shrubs and herbs. The range of distribution also extends northwards into southern Namibia along the Orange River. The Hantam Karoo vegetation unit is dry and lies between Nieuwoudtville and Calvinia, vegetated with dwarf karoo shrubs and succulent plants. It receives predominantly winter rains with a MAP 190 mm (Mucina & Rutherford 2006). In the Nama Karoo Biome, the species seems to be associated with two different habitats in the Bushmanland Bioregion. It has been reported from the Bushmanland Sandy Grassland and Bushmanland Arid Grassland vegetation units where the vegetation cover comprises mainly *Stipagrostis* grassspecies (Mucina & Rutherford 2006).

***Afroptera nigrosetosa* (Tjeder, 1967) comb. nov.**
(Figs 70, 91, 112, 122, 145, 153)

Synonymy
Nemopterella nigrosetosa Tjeder, 1967: 480.

Etymology. Unknown, but probably derived from the Latin words *nigra* (black) and *setosus* (seta) (black setae) for the black pubescence on the prescutum and abdominal venter.

Type locality. South Africa, *Northern Cape Province*. Soebatsfontein, 30°07'08"S 17°35'27"E.

Type depository. TMSA.

Diagnosis. Morphologically similar to *A. sabuleti*, with slender forewings, blackish abdomen and the same pubescence patterns on the abdomen and thorax. However, *A. nigrosetosa* is typified by the yellowish brown vertex with a pair of round spots near the eye margins (Fig. 145), while in *A. sabuleti* the vertex is reddish yellow without spots.

Size (mm). Male: body length 9.8 (8.6–11.5); forewing 23.0 (20–25.8); hind wing 53.0 (45–60.9); antenna 19.3 (15.1–22.6). Female: body length 12.4 (11–14.1); forewing 22.9 (19.3–25.6); hind wing 51.6 (42.3–60.3); antenna 13.6 (12.9–15). (N = 56).

Type material examined. SOUTH AFRICA, *Northern Cape Province*.Holotype m# (Fig. 112), TMSA02069, HOLOTYPE Neu 043, *Nemopterella nigrosetosa* Tjeder (red printed label) / SOEBATSFONTEIN [30°07'08"S 17°35'27"E], 13–14.11’33, G.van Son (white printed label) / Holotypus m# *Nemopterella nigrosetosa* Tjed., Bo Tjeder 1966 (red handwritten label). *Paratypes*: 2m# 14f#, same data as holotype. (All TMSA).

Other material examined. SOUTH AFRICA, *Northern Cape Province*.2m# 26f#, TMSA00762, Soebatsfontein [30°07'08"S 17°35'27"E], 13–14.11.1933, G.van Son / *Nemopterella nigrosetosa* Tjeder, 1967, Det. M.W.Mansell 2013; 4f#, TMSA00767, same locality IV.54, A.J.T.Janse; 1m#, Omsberg Water, TMSA00769 , Richtersveld, 23.ix.1991, M.Krüger leg. (All TMSA); 5m#, NEUR09617, Lang Hoogte Mine Office, 29°32'S 17°23'E, 100m, 30.x.1996, A.J.van Wyk; 1m#, NEUR09768, same locality and collector, 9.x.1996; 1m#, NEUR09769, same locality, 16.x.1996, J.duG.Harrison; (All SANC).

Distribution and habitat. This species is only known from the Northern Cape Province (Fig. 153), and has been reported from localities mainly centred in the Namaqualand Hardeveld and Richtersveld Bioregions in the Succulent Karoo Biome (Mucina & Rutherford 2006). Generally, both areas are dry (semi-desert) typified by winter rains. The topography in the former bioregion is primarily undulating plains rich in heuweltjies, covered in low dwarf succulent shrubs of Heuweltjieveld vegetation type, while in the latter the habitats vary from rocky outcrops to sand dunes covered in leaf-succulent shrubs.

Remarks. This species is sympatric with *Nemia lata* Tjeder in the Soebatsfontein area.

***Afroptera obtusa* (Tjeder, 1967) comb. nov.**
(Figs 94, 126, 136, 156)

Synonymy

Nemopterella obtusa Tjeder, 1967: 477.

Etymology. Unknown, most likely from the Latin word *obtuse* (broad) due to its broad forewings.

Type locality. South Africa, *Western Cape Province*. Koup Siding, 33°07'31"S 21°16'11"E.

Type depository. SAMC.

Diagnosis. *Afroptera obtusa* and *A. pilosa* are morphologicallyvery similar, due largely to similar black pubescence on the thorax (Fig. 94), the yellow colour of the head and reddish yellow of the vertex. They can be distinguished from each other by broader forewings with a short rounded apex in *A. obtusa* (Fig. 136), whereas in *A. pilosa* the forewings are elongate and the apex is much narrower than *A. obtusa* (Fig. 140).

Type material examined. SOUTH AFRICA, *Western Cape Province*. Holotype m#, SAM–NEU–A001253, Koup Siding, Laingsburg [33°07'31"S 21°16'11"E], C.P. (white printed label) / Mus. Expd., / Oct.1952 (white printed label) / Holotypus m#, *Nemopterella obtusa* Tjed., Bo Tjeder 1966. (Red handwritten label). (SAMC).

Distribution and habitat. This species was collected from localities in the Western Cape Province (Fig. 156). The collection site is in the Koedoesberge-Moordenaars Karoo vegetation unit in the Succulent Karoo Biome (Mucina & Rutherford 2006). The habitat is hilly, with mud and sandstone soils in plains, with low succulent scrubs, scattered tall shrubs with white grass mostly on the plain. It receives predominately winter rains with an average above 200 mm per year (Mucina & Rutherford 2006).

***Afroptera olivacea* (Tjeder, 1967) comb. nov.**
(Figs 109, 119, 153)

Synonymy

Nemopterella olivacea Tjeder, 1967:482.

Etymology. Unknown, probably from the Latin word *olea* (olive) for the olivaceous colour of the thoracic pubescence.

Type locality. South Africa, *Northern Cape Province*. Schmidts Drift, 28°42'01"S 24°03' 27"E.

Type depository. TMSA.

Diagnosis. *Afroptera olivacea* is immediately recognisable by the dense olivaceous scale-like microtrichia on the thorax.

Size (mm).Female: body length 10.6 (10.3–10.9); forewing 20.7 (20.6–20.8); hind wing 44.2 (43.8–44.5); antenna 11.3 (10.7–11.7). (N = 2)

Type material examined. SOUTH AFRICA, *Northern Cape Province*. Holotype m# (Fig. 109), TMSA02071, HOLOTYPE, Neu 096 *Nemopterella olivacea* Tjeder (red printed label) / Schmidts Drift [28°42'01"S 24°03'27"E], 1.X.1954, G.van Son (white handwritten label) / Holotypus m#, *Nemopterella olivacea* Tjed., Bo Tjeder 1966 (red handwritten label). (TMSA).

Other material examined. SOUTH AFRICA, *Northern Cape Province*. 2f#, TMSA00748, Schmidts Drift [28°42'01"S 24°03'27"E], 1.x.1954, [G.van Son] / *Nemopterella olivacea* Tjeder, 1967, Det. M.W.Mansell 2013. (TMSA).

Distribution and habitat. This species is endemic to the Northern Cape Province of South Africa (Fig. 153). It is only known from one locality in the Eastern Kalahari Bushveld vegetation unit in the Savanna Biome (Northern Cape). The habitat is dry, with well-drained shallow, stony soil and angular rocks, predominantly covered by the Schmidtsdrif Thornveld vegetation type, which mainly comprises *Acacia mellifera* and *A. tortilis* trees. The area receives low late summer / early autumn rains with very dry winter (Mucina & Rutherford 2006).

***Afroptera papio* (Tjeder, 1967) comb. nov.**

(Figs 128, 137, 155)

Synonymy

Nemopterella papio Tjeder, 1967: 476.

Etymology. Named after the well-known South African primate, *Papio ursinus*, the “chacma” or “Cape baboon”; “bobbejaan” or “baviaan” in Afrikaans, the name of the type locality, Baviaanskop, Namaqualand, South Africa.

Type locality. South Africa, *Northern Cape Province*. Baviaans Kop, 28°56'06"S 17°49'28"E.

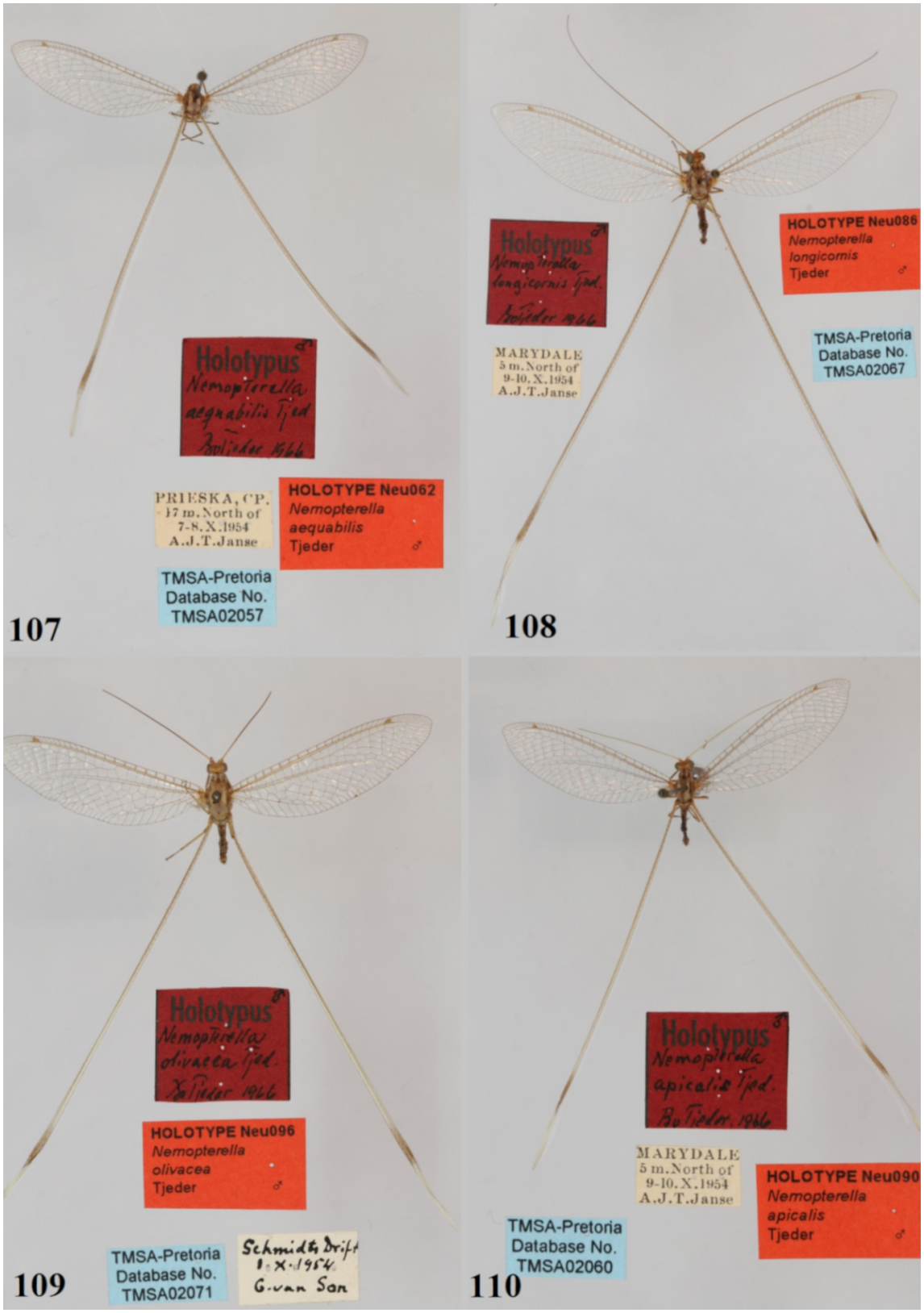
Type depository. SAMC.

Diagnosis. *Afroptera papio* could be confused with *A. sabuleti* but differs by having shorter antennae and white pubescence on the prescutum, instead of the black hairs as in *A. sabuleti*.

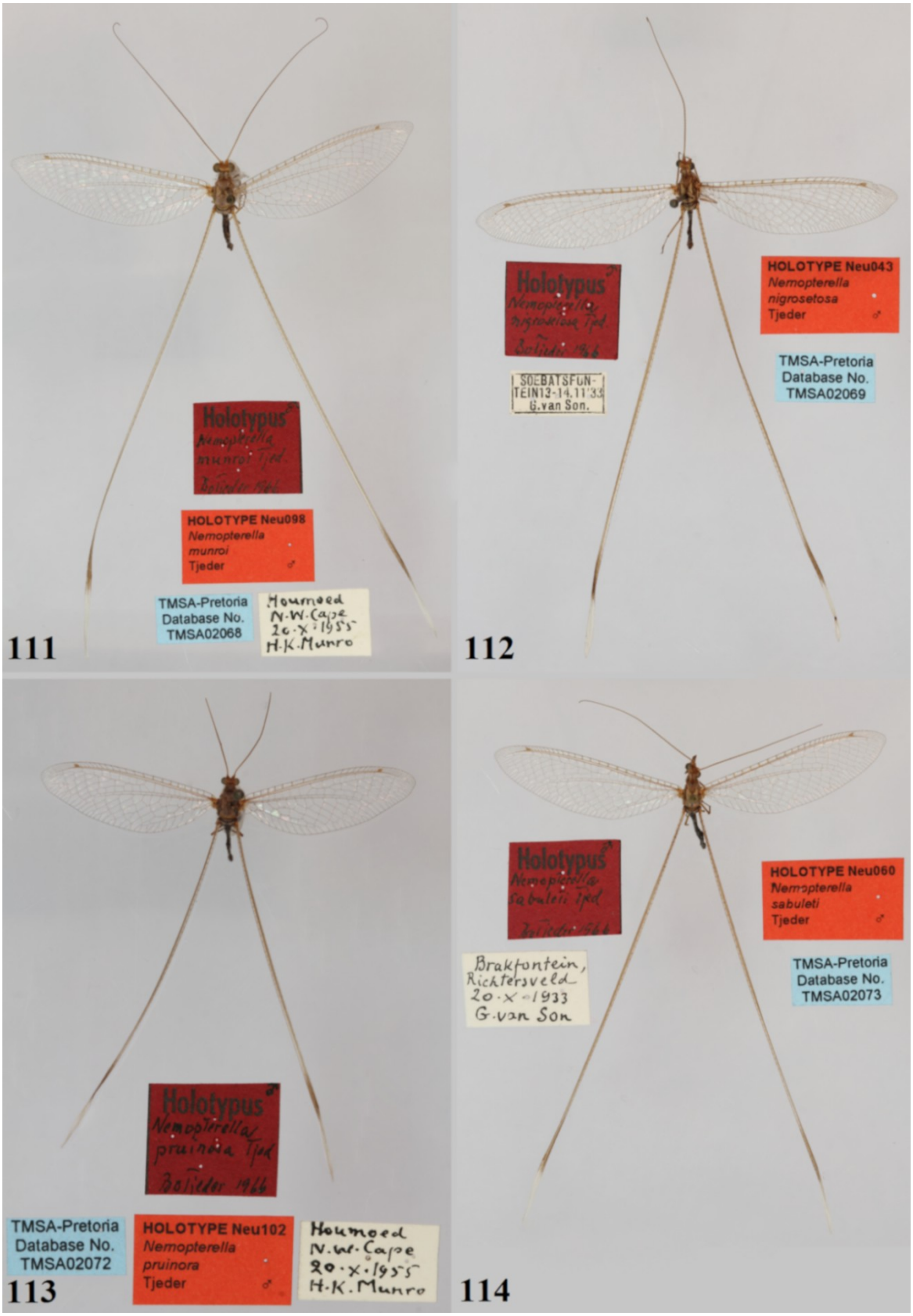
Type material examined. SOUTH AFRICA, *Northern Cape Province*. Holotype m# (Fig. 128), SAMC00173 / SAM–NEU–A001254 / Baviaans Kop, [28°56'06"S 17°49'28"E] near Jackalswater, Namaqualand, [Sept. 1939], [R.Smithers] (white handwritten label) / Holotypus m# *Nemopterella papio* Tjed., Bo Tjeder 1966 (red handwritten label). (SAMC).

Distribution and habitat. This species is known only by the male holotype from the Northern Cape Province, South Africa (Fig. 155). The record is from the Richtersveld Bioregion of the Succulent Karoo Biome (Mucina & Rutherford 2006). The species seems to occur in montane habitats, represented by the Umdaus Mountains Succulent Shrubland vegetation type where the main constituents are succulent trees, shrubs and herbs. The area receives mainly winter rains with an average of 100–200 mm per year.

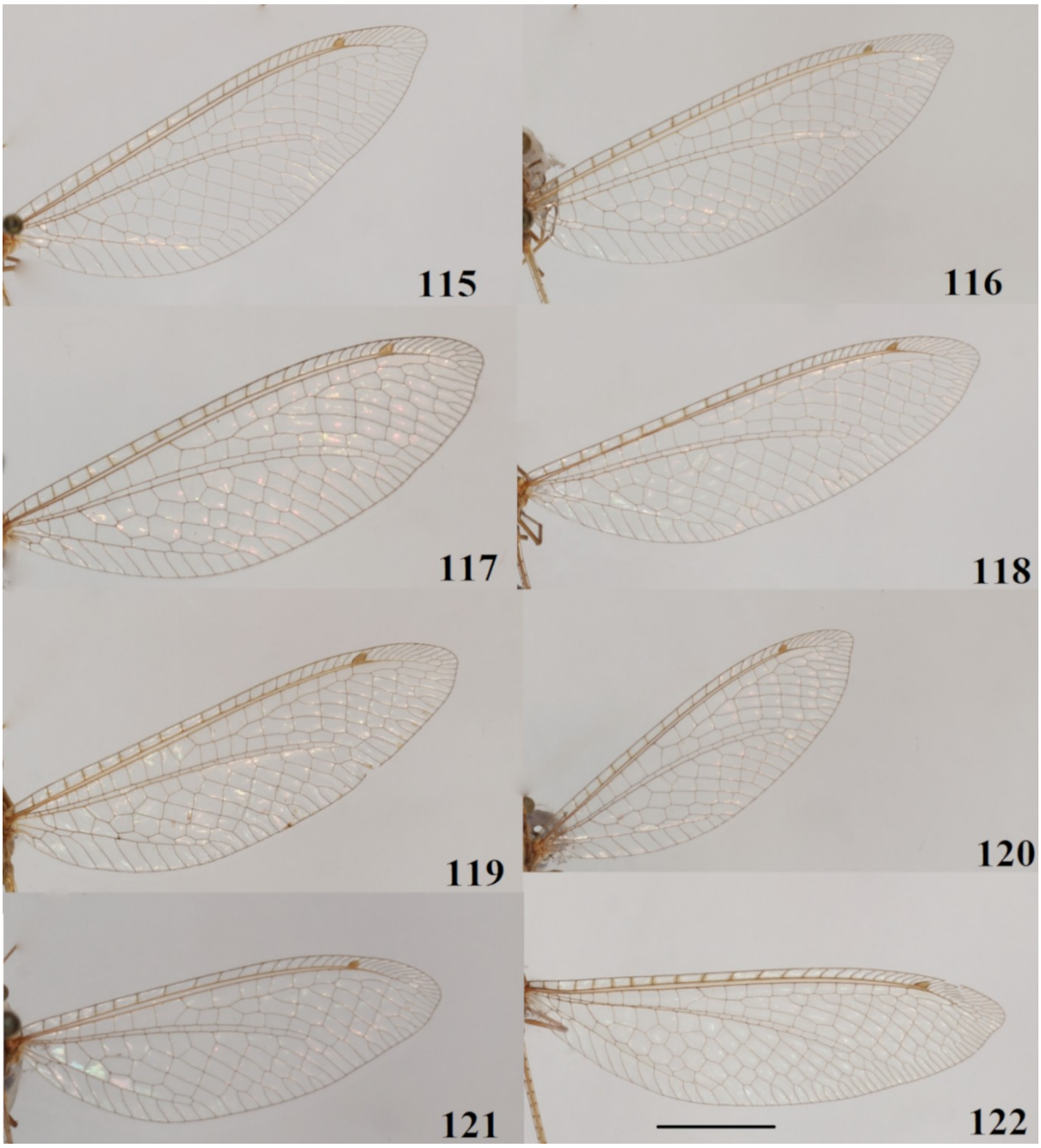
Remarks. The species is known only by the male holotype.



Figures 107–110. Holotypes of *Afroptera* spp with their associated labels. 107, *A. aequabilis* (Tjeder) m#; 108, *A. longicornis* (Tjeder) m#; 109, *A. olivacea* (Tjeder) m#; 110, *A. apicalis* (Tjeder) m#.



Figures 111–114. Holotypes of *Afroptera* spp with their associated labels. 111, *A. munroi* (Tjeder) m#; 112, *A. nigrosetosa* (Tjeder) m#; 113, *A. pruinosa* (Tjeder) m#; 114, *A. sabuleti* (Tjeder) m#.



Figures 115–122. *Afroptera* spp. Male forewings. 115, *A. longicornis* (Tjeder); 116, *A. munroi* (Tjeder); 117, *A. aequabilis* (Tjeder); 118, *A. sabuleti* (Tjeder); 119, *A. olivacea* (Tjeder); 120, *A. apicalis* (Tjeder); 121, *A. pruinosa* (Tjeder); 122, *A. nigrosetosa* (Tjeder). Scale = 1 mm.

***Afroptera parva* (Tjeder, 1967) comb. nov.**
(Figs 69, 100, 125, 148, 151)

Synonymy

Nemopterella parva Tjeder, 1967: 489.

Etymology. Probably from the Latin word *parva* (small) for its small size.

Type locality. South Africa, *Western Cape Province*. Waterval, Tanqua Karoo, 32°13'S 19°24'E.

Type depository. SAMC.

Diagnosis. A small species, antennae short, not reaching pterostigma, with short membranous antennal apex and rounded wing apices with no pre-apical emargination. *Afroptera parva* is closely related to *A. exigua*. Similarity and differences between these two species are provided in the diagnosis of *A. exigua*.

Size (mm).Male: body length 7.7 (6.1–9.2); forewing 18.7 (15.9–21.8); hind wing 39.6 (31.7–45.2); antenna 12.9 (11.2–14.6); Female: body length 9.9 (7.2–10.7); forewing 20.2 (17.4–21.2); hind wing 41.9 (35.2–47.9); antenna 12.8 (10.5–12.9). (N = 45).

Type material examined. SOUTH AFRICA, *Western Cape Province*. Holotype m# (Fig. 125), SAM–NEU–A001256 /Tankwa Karoo, Waterval [32°13S 19°24E], C.P. [Nov. 1952], [Museum Staff] (white printed label) / Holotypus m# *Nemopterella parva* Tjed., Bo Tjeder 1966 (red printed label). *Paratypes*: 2m#, SAM–NEU–A001256 and 1f#, SAM–NEU–A001255, same data as holotype. (SAMC).

Other material examined. SOUTH AFRICA, *Western Cape Province*. 2m#, NEUR00706, Mierkraal Farm, Biedouw Valley, 32°04S 19°24E, 29.ix.1986, M.W.Mansell, J.H.Hoffmann / Handnetted / *Nemopterella parva* Tjeder, 1967, Det. M.W.Mansell 1986; 4f#, NEUR09683, Doornfontein Farm, Tanqua Karoo, 32°35'S 19°33'E, 20–21.x.2006, 432m, A.K.Brinkman; 1m# 2f#, NEUR10228, Koup Siding, Laingsburg District, 33°07'40"S 21°16'36"E, 741m, At light, 17.x.2009, A.P.Marais; 1m# 4f#, NEUR09930, Wamakerskraal Farm, Laingsburg Dist., 33°02'03"S 21°35'36"E, 350m, 11.x.2008, J.B.Ball, A.P.Marais.*Northern Cape Province*. 1m#, NEUR09620, Richtersveld, 50 km NE Grootderm, 3.ix.1989, 29°19'00"S 16°55'00"E, J.G.H.Londt, B.R.Stuckenberg / Sandy valley below a rocky hillside, 350m; 4m# 4f#, NEUR08907, Richtersveld, Cornells Kop, 145m, 28°25'S 16°53'E, 2816Bd, 9.x.1974, M.W.Mansell, H.D.Brown / Collected at mercury vapour light, arid rocky terrain; 2m# 2f#, NEUR09770, Kabas Farm, 10 Km NE Pofadder, 29°02S 19°26E, 800m, 27.x.1996,

M.W.Mansell, C.H.Scholtz / Collected at light; 1m# 1f#, NEUR09784, same locality, 1.xi.1996, M.W.Mansell / Collected at light; 2f#, NEUR08924, Augrabies Falls Nat. Park, 28°35'S 20°21'E, x.1984, L.E.O.Braack / Collected at light; 3m#, NEUR08909, Richtersveld, Top of Hellskloof Pass, Paradysberg, 880m, 28°19'S 16°50'E (2816 Bd), 10.x.1974, M.W.Mansell, H.D.Brown; 1f#, NEUR12197, Koms Farm, Keimoes, 28°44'08"S 20°56'15"E, 730m, 24.x.2013, P.de Vos, House light; 1m# 1f#, NEUR12535, same locality 12–13.viii.2013, P.de Vos, Handnetted; 4f#, NEUR12584, same locality, 23.ix.2013, P.de Vos, Light. (All SANC).

Distribution and habitat. In South Africa, *N. parva* is known from the Northern and Western Cape provinces from localities mainly centred in the Succulent Karoo and Desert Biomes (Fig. 151). In the former biome, the collection sites fall mainly within the Rainshadow Valley Karoo, Namaqualand Sandveld and Richtersveld Bioregions (Mucina & Rutherford 2006). In the Rainshadow Valley Karoo Bioregion, one population is confined to the Agter-Sederberg Shrubland vegetation unit; where the vegetation mainly comprises succulent and non-succulent elements. Winter rains are predominant with an average of 250 mm per year. Another population occurs in the Tankwa Karoo vegetation unit where the habitat is typified by low winter rainfall (≤ 112 mm) and poor vegetation cover dominated by scattered low succulent shrubs, herbaceous climbers and annual flora (Mucina & Rutherford 2006). It has also been reported from the Koedoesberge-Moordenaars Karoo vegetation unit (see description of the habitat under the distribution of *N. obtusa*). Distribution in the Namaqualand Sandveld Bioregion is chiefly in Richtersveld Coastal Duneveld vegetation where there are sand dunes, large hills, extreme wind, frequent fog, winter rains, with succulent shrubs, woody succulent climber parasitic and herbs being important features of the habitat (Mucina & Rutherford 2006). In the Richtersveld Bioregion the collection site is on a wide plain of alluvial, loamy, sandy gravel soils dominated by the Upper Annisvlakte Succulent Shrubland vegetation type, where the main components are dwarf leaf succulent shrubs and geophytic herbs. The species has also been found in the Bushmanland Inselberg Shrubland vegetation unit (see description of the habitat in the unit under distribution of *A. dyscrita*). *Afroptera parva* is also known from the Namib Desert Bioregion in the Desert Biome. This range falls within the Western Gariep Hills Desert vegetation unit north of the Richtersveld where the species was collected in a hilly and open habitat, covered by leaf-succulent shrubs, low shrub, succulent and geophytic herbs. The area receives winter rains with an average of 45–60 mm per year (Mucina & Rutherford 2006).

***Afroptera peringueyi* (Tjeder, 1967) comb. nov.**
(Figs 68, 99, 131, 139, 155)

Synonymy

Nemopterella peringueyi Tjeder, 1967: 484.

Etymology. Named after Louis A. Péringuey, former Director of the South African Museum (Iziko Museums), Cape Town, who collected the type specimen.

Type locality. South Africa, *Western Cape Province*. Beaufort West, 32°21'00"S 22°35'00"E.

Type depository. SAMC.

Diagnosis. *Afroptera peringueyi* can be easily recognised among the *Afroptera* species by the uniformly yellowish red head and antennae (Fig. 131) and the reddish brown abdomen (Fig. 131).

Size (mm). Male: body length 8.3 (7–9.5); forewing 21.8 (20.6–22.9); hind wing 49.7 (45.5–52.0); antenna 18 (16.2–20.2). Female: body length 9.5 (8.8–10.8); forewing 20.9 (19.4–23.1); hind wing 44.3 (38.6–50.2); antenna 12.9 (11.4–15.5).(N = 36).

Type material examined. SOUTH AFRICA, *Western Cape Province*. Holotype m# (Fig. 131), SAM–NEU–A001257, CAPE, Beaufort West [32°21'00"S 22°35'00"E] (white handwritten label) / 'New type' (white handwritten label) / Holotypus m#, *Nemopterella peringueyi* Tjed., Bo Tjeder 1966 (red handwritten label). (SAMC).

Other material examined. SOUTH AFRICA, *Western Cape Province*. 18m# 4f#, NEUR01243, Karoo National Park, Stolshoek, 32°19'S 22°29'E, 950m, 22–23.xii.1989, M.W.Mansell, H.&U.Aspöck, / Collected at light; 1m#, NEUR01191, Prince Albert Dist, Tierberg Research Station, 33°08'S 22°17'E, 30.x.1988, W.R.J.Dean; 1m#, NEUR01455, Carnarvon, 30°59'S 22°08'E, 6.xi.1991, M.de Jager; 1m#, NEUR01454, Fraserburg, 12 Km E, 32°01'S 21°32'E, 11.i.1991, M.de Jager; 1f#, NEUR01354, Komkommerleegte Farm, 35 km E Fraserburg, 31°46'S 21°46'E, 1300 m, 16.xii.1989, M.W.Mansell, Handnetted during day; 3m# 3f#, NEUR01353, Uurhoogte, 11 Km E Fraserburg, 31°52'S 21°36'E, 1280m, 14–16.xii.1989, M.W.Mansell, H.&U.Aspöck; 1m# 3f#, NEUR08908, Wagon Wheel Motel, Beaufort West, 3222 BC, 11.xi.1986, C.Quickelberge, J.G.H.Londt / Collected at light. (All SANC).

Distribution and habitat. The species is endemic to the Western Cape Province where the ranges of distribution are mainly centred within the Succulent and Nama Karoo Biomes (Fig. 155). In the former biome, the distribution falls mainly within the Rainshadow Valley Karoo

Bioregion where the habitat is characterized by the Prince Albert Succulent Karoo vegetation type (see description of the habitat under the distribution of *A. exigua*). While in the latter, the distribution is confined to the Upper and Lower Karoo Bioregions where the habitat is represented by the Upper Karoo Hardeveld vegetation as described by Mucina & Rutherford (2006). The area comprises steep slopes and large stones, vegetated mostly with dwarf karoo scrub, tall shrubs, succulent shrubs, herbs and grasses. It receives autumn rains with an average of 150–350 mm per year. The habitat features of the lower Karoo are provided under the distribution of *A. exigua*.

***Afroptera pilosa* (Tjeder, 1967) comb. nov.**
(Figs 71, 98, 132, 140, 156)

Synonymy
Nemopterella pilosa Tjeder, 1967: 478.

Etymology. Unknown, but probably from the Latin word *pilosa* (hairy) for its hirsute thorax and abdomen.

Type locality. South Africa, *Western Cape Province*. Dikbome, 32°53'S 21°22'E.

Type depository. SAMC.

Diagnosis. Large species with striped thorax. Morphologically resembles *A. obtusa.* A comparison of these two species is provided in the diagnosis of *A. obtusa*.

Size (mm). Male: body length 9.7 (8.3–12.6); forewing 23.8 (21.5–27.4); hind wing 53.7 (48.1–62.1); antenna 19.8 (16.5–24.3); Female: body length 10.8 (8.7–12.1); forewing 22.8 (18.7–25); hind wing 46.8 (35.3–56.1); antenna 13.5 (10.8–16.2). (N = 48).

Type material examined. SOUTH AFRICA, *Western Cape Province*. Holotype m# (Fig. 132), SAM–NEU–A001273, Dikbome, Merweville Koup [32°53'S 21°22'E] C.P (white printed label) / Holotypus m#, *Nemopterella pilosa,* Bo Tjeder 1966 (red handwritten label). (SAMC).

Other material examined. SOUTH AFRICA, *Western Cape Province*. 4m# 2f#, NEUR12538, Wamakerskraal Farm, Laingsburg Dist, 33°01'24"S 21°36'43"E, 350m, 11.x.2008, J.B.Ball, A.P.Marais, At light / *Nemopterella pilosa* Tjeder, 1967, Det. M.W.Mansell 2017; 11m# 8f#, NEUR10048, Oorlogskloof Farm, Klaarstroom District, 33°21'48"S 22°43'34"E, 897m, 21.xi.2008, At light, A.P.Marais; 4m# 2f#, NEUR10229, Koup

Siding, Laingsburg District, 33°07'40"S 21°16'36"E, 741m, At light, 17.x.2009, A.P.Marais; 3f#, NEUR10121, Miertjieskraal Farm, Ladysmith District, 33°49'09"S 21°08'01"E, 299m, 26.xi.2008, At light, A.P.Marais; 2m# 5f#, NEUR12585, Middeldrif Farm, Laingsburg District, 33°03'13"S 21°16'14"E, 708m, At light, 18.x.2009, A.P.Marias. *Northern Cape Province*. 5m# 2f#, NEUR09742, Williston Farm, 30°51'S 21°26'E, 20.x.2001, H.S.Staude. (All SANC).

Distribution and habitat. *Afroptera pilosa* has been recorded from the Northern and Western Cape Provinces (Fig. 156). In the former province, it is confined to the Bushmanland Bioregion in the Nama Karoo Biome where the habitat comprises salty, mud-stone soils and receives predominantly late summer / early autumn rains with an average of 100–200 mm per year. Dwarf succulent and spiny shrubs are dominant. While in the latter province, the distribution is in the Rainshadow Valley Karoo, Lower Karoo and Renosterveld Bioregions of the Succulent Karoo, Nama Karoo and Fynbos Biomes, respectively. Two populations have been reported from the Rainshadow Valley Karoo; one seems to be associated with the Koedoesberge-Moordenaars Karoo vegetation type (see description of the vegetation type under distribution of *A. obtusa*). Another population has been recorded from Prince Albert Succulent Karoo vegetation unit to the west of Prince Albert (see description of the unit under distribution of *N. remifera*). In the Lower Karoo Bioregion the species has been found in association with Gamka Karoo vegetation type (see description of the vegetation type under distribution of *A. exigua*). In the Renosterveld Bioregion the vegetation cover is mostly comprises Montagu Shale Renosterveld type and includes *Acacia karoo*, succulent shrubs.

***Afroptera pruinosa* (Tjeder, 1967) comb. nov.**
(Figs 113, 121, 153)

Synonymy

Nemopterella pruinosa Tjeder, 1967: 486.

Etymology. Unknown, but probably from the Latin word *purinos* (smoke, frost, purinas) for its extensively powdered greyish body.

Type locality. South Africa, *Northern Cape Province*. Houmoed, 29°18'53"S 19°32'47"E.

Type depository. TMSA.

Diagnosis. *Afroptera pruinosa* is a small species with greyish pruinose thorax. Superficially similar to *A. koranna* through its small size, pruinose brown body, unstriped thorax and sparse short black hairs on the prescutum disc. It can be distinguished from *A.*

koranna by a combination of the following characters: *A. pruinosa* has a blackish brown abdomen with white hair on the dorsum and venter, while in *A. koranna* the abdomen is brown with white hair on the dorsum and black hair on the venter. *Afroptera pruinosa* also has forewings with a rounded apex but with a slight emargination before the apex (Fig. 121), while in *A. koranna* the apex is rounded without emargination.

Type material examined. SOUTH AFRICA, *Northern Cape Province*.Holotype m# (Fig. 113), TMSA02072, HOLOTYPE Neu 102, *Nemopterella pruinosa* Tjeder (red printed label) / Houmoed [29°18'53"S 19°32'47"E], N.W.Cape, 20.X.1955, H.K.Munro (white handwritten label) / Holotypus m#, *Nemopterella pruinosa* Tjed., Bo Tjeder 1966 (red handwritten label). (TMSA).

Distribution and habitat. This species is recorded from the Northern Cape Province and is known only from the type locality in the Nama Karoo Biome (Fig. 153). The locality falls within the Bushmanland Inselberg Shrubland vegetation unit in the Bushmanland Bioregion (Mucina & Rutherford 2006). See description of the habitat under distribution of *A. dyscrita*. The area receives late summer rains ranging between 70–120 mm from February to April.

Remarks. The species is represented by the male holotype only and occurs sympatrically with *A. munroi*.

***Afroptera remifera* (Westwood, 1874) comb. nov.**
(Figs 76, 97, 124, 149, 150, 151)

Synonymy
Nemoptera remifera Westwood, 1874: 179.
Halter remifera (Westwood): Kirby 1900: 458.
Eretmoptera remifera (Westwood): Navás 1910: 361.
Nemopterella remifera (Westwood): Navás 1912: 9.

Etymology. Unknown.

Type locality. South Africa, *Western Cape Province*. Uncertain locality: “Cape of Good Hope”. Klaarstroom, Prince Albert District, 33°20S 22°33E, subsequently designated as type locality by Tjeder (1967: 490).

Type depository. BMNH.

Diagnosis. This species can easily be distinguished from its congeners by the rounded apex of the forewings (Figs 149, 150), the very short antennae and the extremely small rounded apical antennal segment that ends in a distal membranous part (Figs 76, 149).

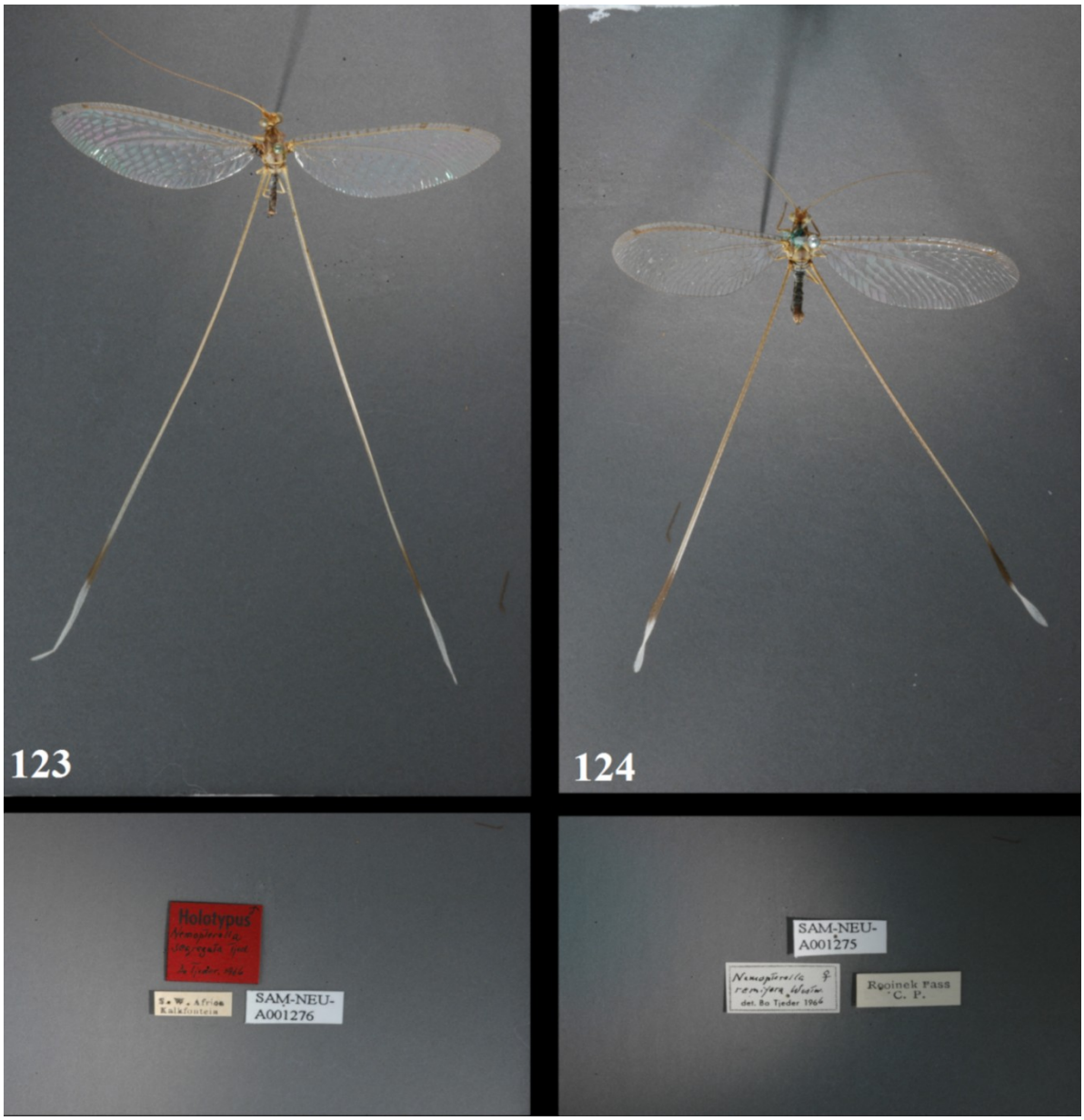
Size (mm). Male: body length 9.5 (7.5–11.5); forewing 21.4 (19–23.8); hind wing 46.5 (41–52); antenna 14 (13–15); Female: body length 11–12; forewing 21–23.5; hind wing 44–50; antenna 12–13. (N = 7).

Type material. Holotype f# (not examined).

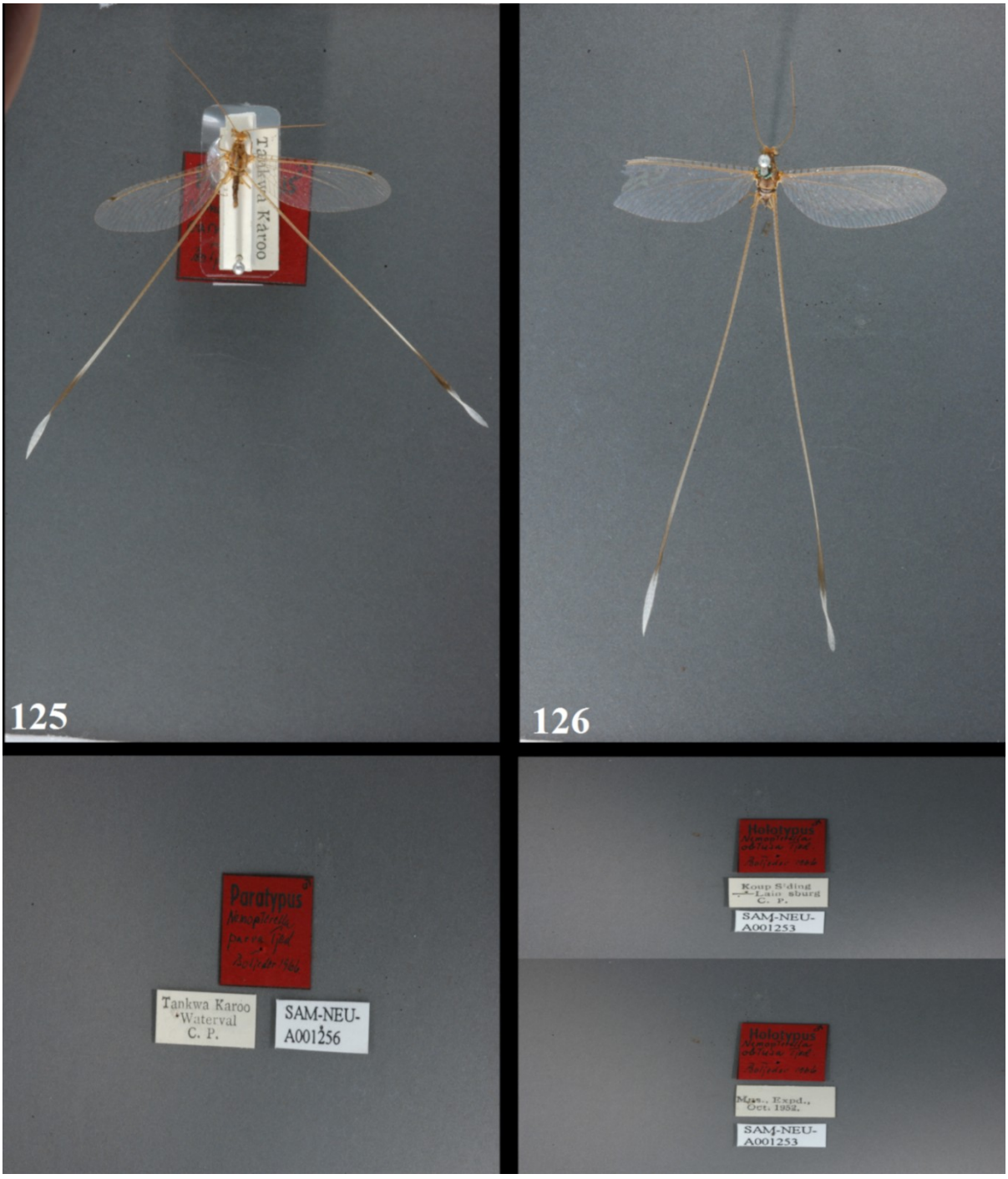
Other material examined. SOUTH AFRICA, *Western Cape Province*. 1m# 4f#, SAM–NEU–A001275, Rooinek Pass [33°19'56"S 20°55'34"E], C.P / *Nemopterella remifera* Westw., f#, det. Bo Tjeder 1966; 1f#, SAMC00177, Klaarstroom, Prince Albert [District], C.P / *Nemopterella remifera* Westw., det. Tjeder 1966. (All SAMC). 1m#, NEUR09829, Prince Albert Dist., Tierberg Research Station, 33°07'39"S 22°16'26"E, 4.x.1988, W.R.J.Dean, Light. (SANC).

Distribution and habitat. *Afroptera remifera* is currently known from localities in the Succulent Karoo Biome in the Western Cape Province, South Africa (Fig. 151). The ranges are mainly in the Rainshadow Valley Bioregion with features of the Prince Albert Succulent Karoo vegetation unit (Mucina & Rutherford 2006). See description of the habitat under the distribution of *A. exigua.*

Remarks. This species was originally described by Westwood (1874) and is in BMNH. Tjeder (1967), in his taxonomic notes, mentioned that he was informed by Dr. D.E.Kimmins that the female holotype is in bad condition, with damaged meso- and metanotum and one of the hind wings being complete. Tjeder therefore resorted to redescribing the species using a female specimen from Klaarstroom, Prince Albert District, after which Kimmins compared it with the type specimen and confirmed their similarity. Our revision of this species is consequently based on Tjeder's material that is in SAMC, Cape Town, South Africa.



Figures 123–124. *Afroptera* spp. 123, *A. segregata* (Tjeder), male holotype and associated labels; 124, *A. remifera* (Westwood), habitus f# and associated labels. Photos: Simon van Noort (SAMC).



Figures 125–126. *Afroptera* spp and their associated labels. 125, Paratype m#, *A. parva* (Tjeder); 126, Holotype m#, *A. obtusa* (Tjeder). Photos: Simon van Noort (SAMC).

***Afroptera segregata* (Tjeder, 1967) comb. nov.**
(Figs 67, 96, 123, 138, 151)

Synonymy

Nemopterella segregata Tjeder, 1967: 472.

Etymology. Unknown.

Type locality. Namibia. Kalkfontein, 28°01'S 18°45' E.

Type depository. SAMC.

Diagnosis. *Afroptera segregata* is similar to *A. munroi*, being of similar size, shape of the forewings and abdominal colour. It can be separated from *A. munroi* by being more yellowish in colour (Figs 96, 123), with much longer body pubescence.

Size (mm). Male: body length 10 (8.2–11.1); forewing 23.5 (20.9–26.3); hind wing 56.0 (47.5–63.4); antenna 22.4 (18.5–27.4). Female: body length 10 (7–11.5); forewing 21.8 (18.4–24.4); hind wing 47.0 (39–52.4); antenna 13.8 (12.6–15.9). (N = 31).

Type material examined. NAMIBIA. Holotype m# (Fig. 123), SAM–NEU–A001276 / S.W.Africa, Kalkfontein [28°01'S 18°45'E] (white printed label) / Holotypus *Nemopterella segregata* Tjed., Bo Tjeder 1966 (red handwritten label). *Allotype* f#, SAM–NEU–A001277 / S.W.Africa, Kalkfontein [28°'18°45'E], Oct. 1925, J.S.Brown (white handwritten label) / Allotypus f#, *Nemopterella segregata* Tjed., Bo Tjeder 1966 (red handwritten label). (Both SAMC).

Other material examined. NAMIBIA. 7m# 1f#, NEUR08922, Klinghards Mts 10 Km N Garusib, 27°17'S 18°55'E, 2.xi.1986, J. Jarvis; 1m#, NEUR08919, Lorelli, 20 Km SE Rosh Pinah [27°57'55"S 16°45'34"E], 15.x.1972, H.D.Brown, E.Koster, A.A.Prinsloo; SOUTH AFRICA, *Northern Cape Province*. 1m#, NEUR08915, Richtersveld, Paradysberg [28°19'40"S 17°02'14"E], 21.ix.1967, H.D.Brown; 10m# 5f#, NEUR08936, Richtersveld, Black Hills, 28°46'47"S 17°05'47"E, 400m, 10.x.1991, M.W.Mansell, R.G.Oberprieler; 4m#, NEUR08937, Richtersveld, Bloubos Ploegberg, 28°38'S 17°01'E, 400m, 8.x.1991, M.W.Mansell, R.G.Obrprieler. (All SANC).

Distribution and habitat. *Afroptera segregata* is known from South Africa and Namibia (Fig. 151). In South Africa, the known range of distribution is from the Richtersveld Bioregion in the Succulent Karoo Biome (Mucina & Rutherford 2006). The species seems to be associated with two different vegetation types: the Central Richtersveld Mountain Shrubland where the area is montane with succulent shrubs and herbs, and characterised by mild winter rainfall with an average of 60–200 mm per year. The species is also associated with the Goariep Mountain Succulent Shrubland where the habitat comprises the Goariep Mountain (Ploegberg), vegetated mostly by dense succulent shrubs and *Aloe*, and other types of trees.

The area receives winter rains with MAP 70 mm. In Namibia, the distribution is in the Kalahari xeric Savanna Ecoregion where the habitat is an open Savanna, known for its extreme aridity and poor nutrient sandy soils; vegetated mostly by grasses, *Acacia* and *Boscia* trees. The area receives summer rains with an average of 150–500 mm per year (Lovegrove 1993; Dennis *et al*. 1997). Another population was found confined to the extension of the Succulent Karoo Biome in southern Namibia, which falls within the Namaqualand-Namib Domain in southwestern Namibia (Jürgens 1991). The area is characterised by winter rains and succulent vegetation.

***Afroptera sabuleti* (Tjeder, 1967) comb. nov.**
(Figs 72, 90, 114, 118, 153)

Synonymy
Nemopterella sabuleti Tjeder, 1967: 474.

Etymology. Unknown, but most likely to have been derived from the Latin word *sabulet* (sandy, sandstone, smoothed) referring to the sandy habitat from which the species was collected.

Type locality. South Africa, *Northern Cape Province*. Richtersveld, Brakfontein, 28°56'S 17°06'E.

Type depository. TMSA.

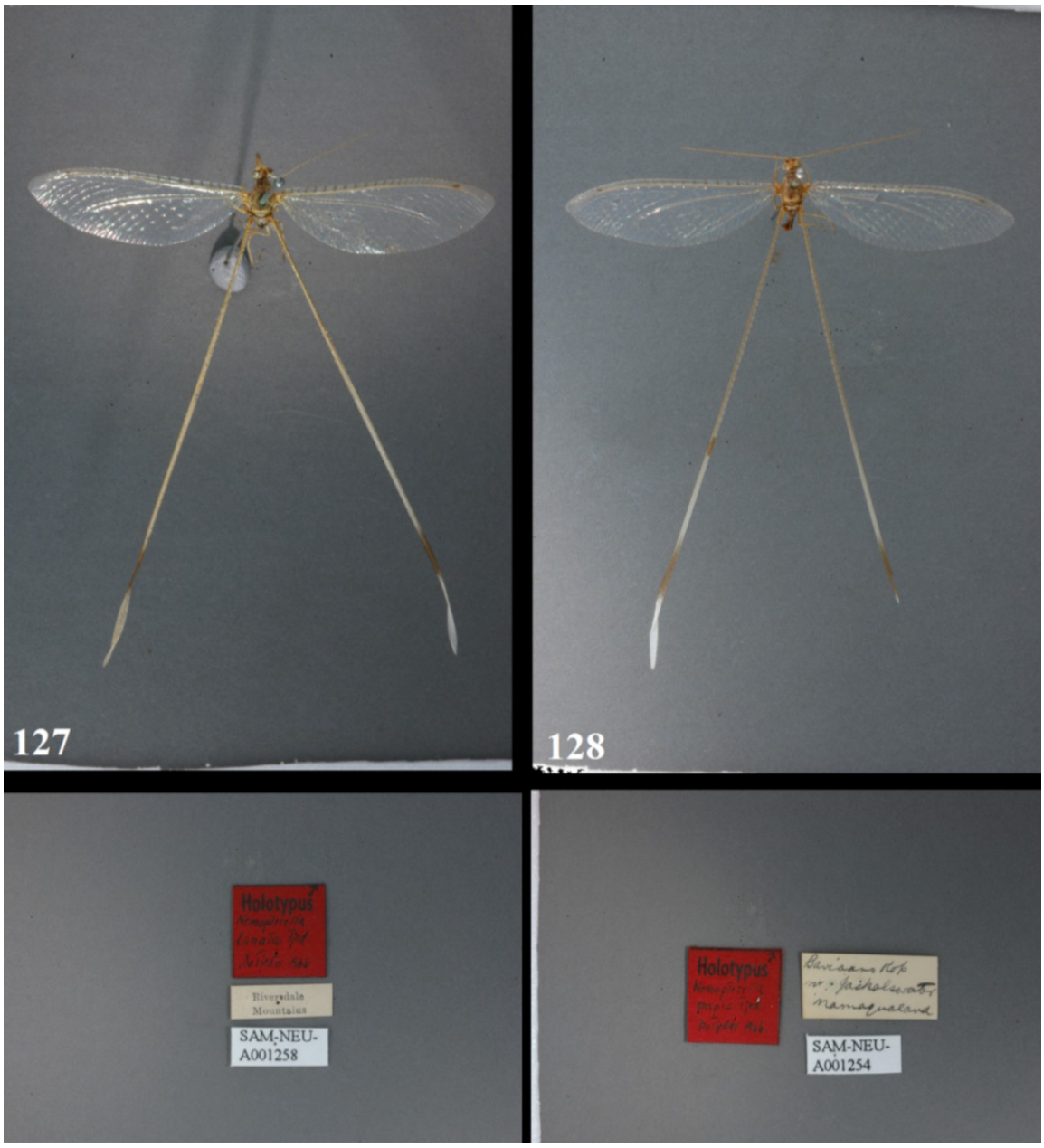
Diagnosis. This species is very similar to *A. munroi* and *A. nigrosetosa*. It can be separated from *A. munroi* by the following combination of characters: *A. sabuleti* has distinct brown thoracic stripes, while in *A. munroi* the thoracic stripes are faint, also the hairs on the prescutum disc of *A. sabuleti* are black, while in *A. munroi* they are white. *Afroptera sabuleti* is further characterised by the distinct yellow body colour, while in *A. munroi* the colour is less pronounced. *Afroptera sabuleti* also has slender, less acute forewings and smaller eyes. Comparisons between *A. sabuleti* and *A. nigrosetosa* are provided under the diagnosis of *A. nigrosetosa*.

Size (mm). Male: body length 10.4 (10–10.7); forewing 23.2 (22.9–23.4); hind wing: 54 (49.6–56); antenna 20.4 (19.2–21.6); Female: body length 10.9 (10.7–11); forewing 20.3 (19.7–24); hind wing 46 (43.2–54); antenna 11.3 (11–11.5). (N = 4).

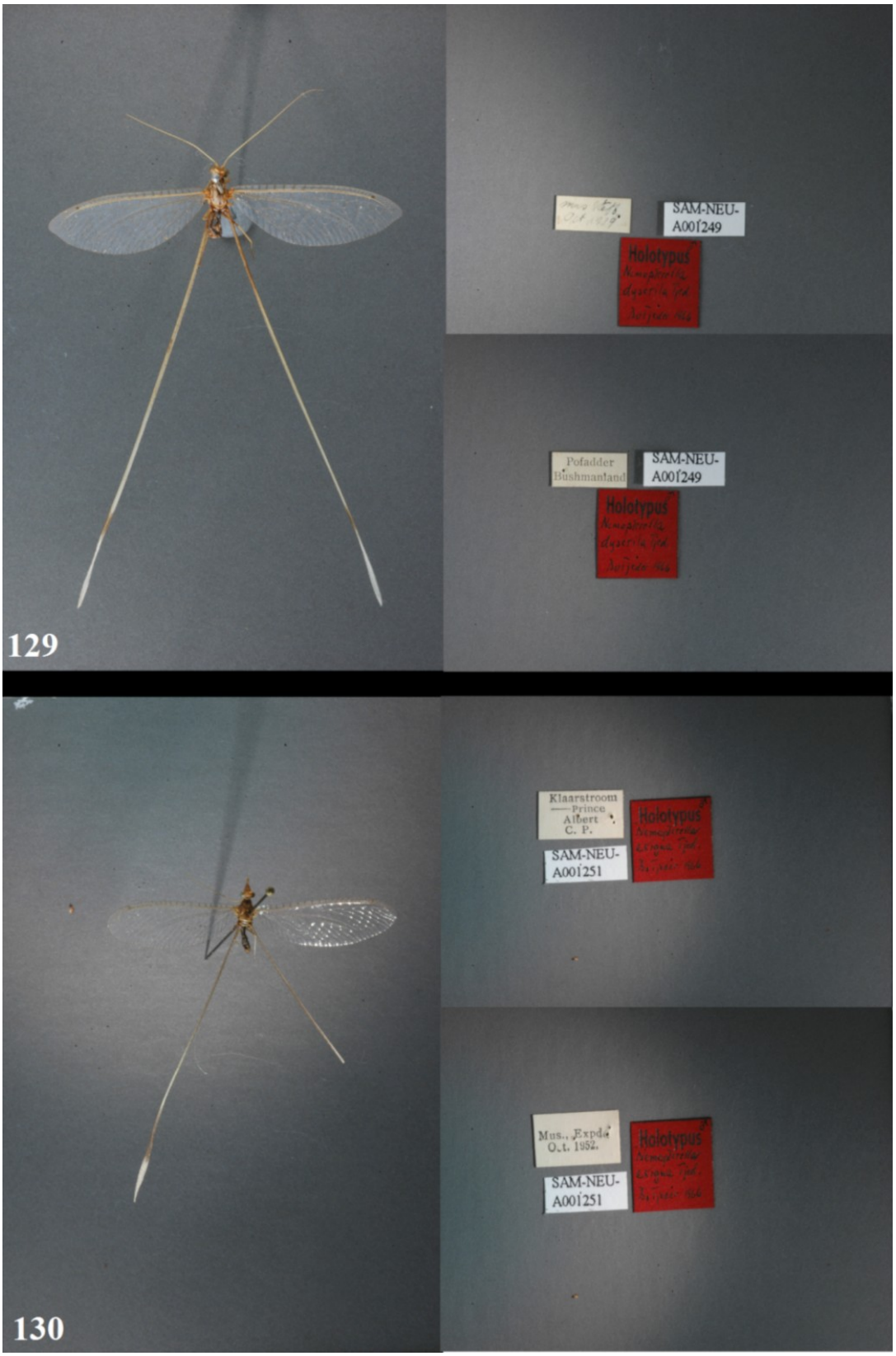
Type material examined. SOUTH AFRICA, *Northern Cape Province*. Holotype m# (Fig. 114), TMSA00728, HOLOTYPE Neu 060, *Nemopterella sabuleti* Tjeder (red printed label) / Brakfontein, Richtersveld [28°56'S 17°06'E], 20.X.1933, G.van Son (white handwritten label) / Holotypus m#, *Nemopterella sabuleti* Tjed., Bo Tjeder 1966 (red handwritten label). *Paratype*: 1f#, same data as holotype. (Both TMSA).

Other material examined. SOUTH AFRICA, *Northern Cape Province*.1m# 1f#, TMSA00770, Richtersveld, Eksteinfontein Valley, [28°50'S 17°15'E], 28.ix.1991, M.Krüger; 1m# 1f#, Richtersveld, Brakfontein [28°56'S 17°06'E], 20.x.1933, G.van Son. (All TMSA).

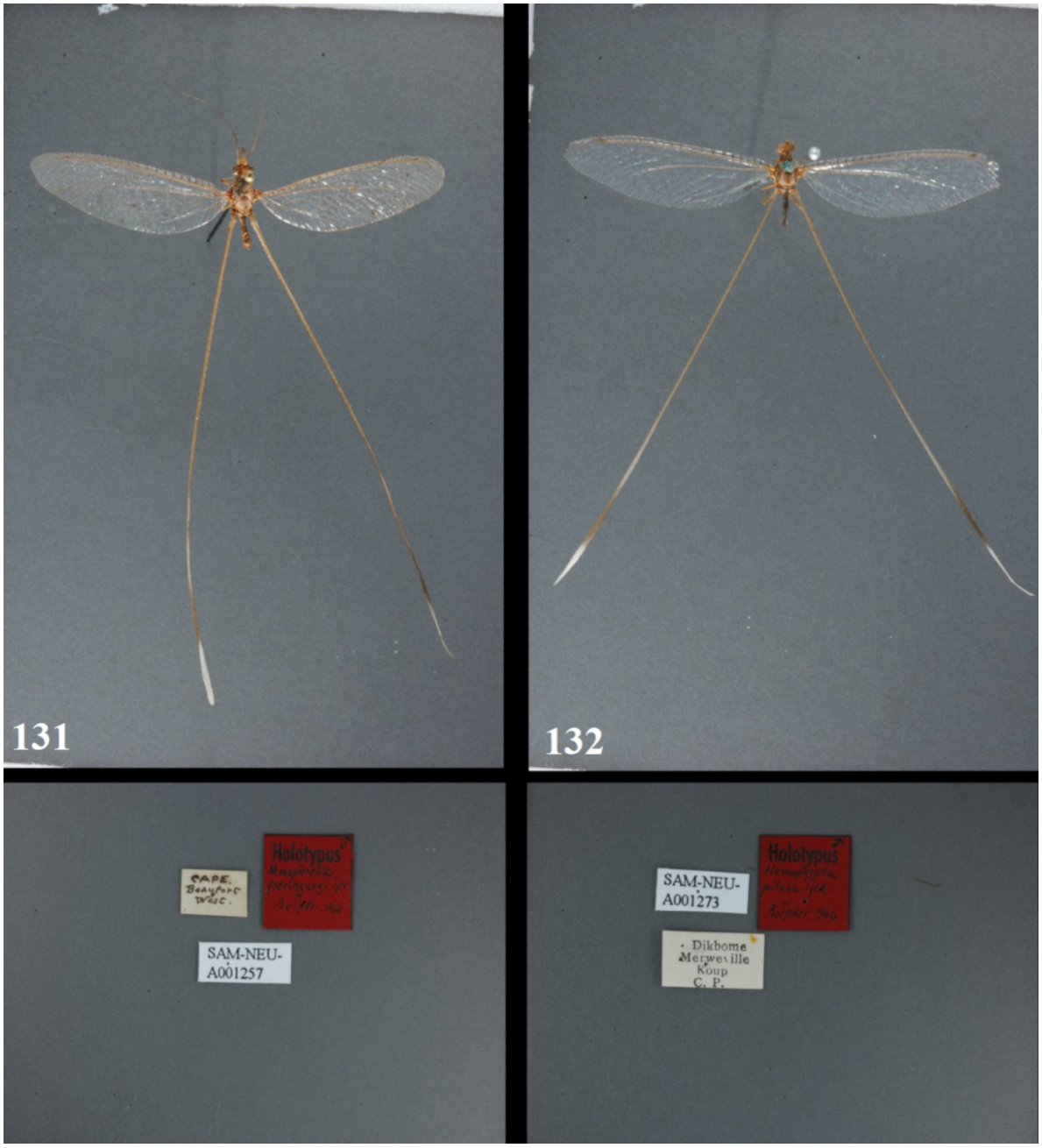
Distribution and habitat. This species is limited to a small range of distribution within the Succulent Karoo Biome in the Northern Cape Province (Fig. 153). The known distribution falls mainly within the Lekkersing Succulent Shrubland in the Richtersveld Bioregion (Mucina & Rutherford 2006). This habitat is dominated by dwarf leaf-succulents, small trees, herbaceous climbers and geophytic herbs. The area receives predominantly winter rains with an average of 60–120 mm per year (Mucina & Rutherford 2006).



Figures 127–128. Holotypes of *Afroptera* spp and their associated labels. 127, *A. lanata* (Tjeder) m#; 128, *A. papio* (Tjeder) m#. Photos: Simon van Noort (SAMC).

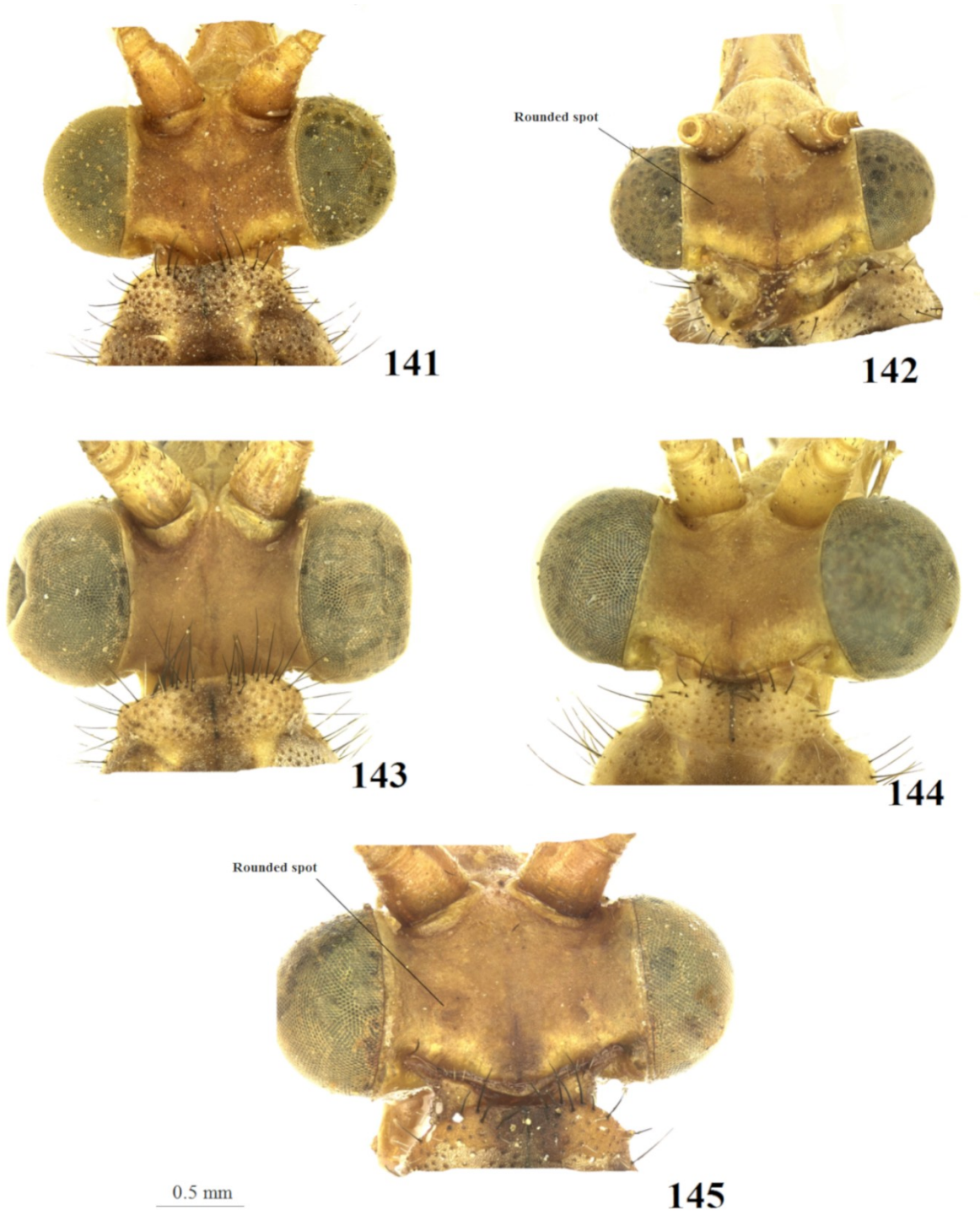


Figures 129–130. Holotypes of *Afroptera* spp and their associated labels. 129, *A. dyscrita* (Tjeder) m#; 130, *A. exigua* (Tjeder) m#. Photos: Simon van Noort (SAMC).

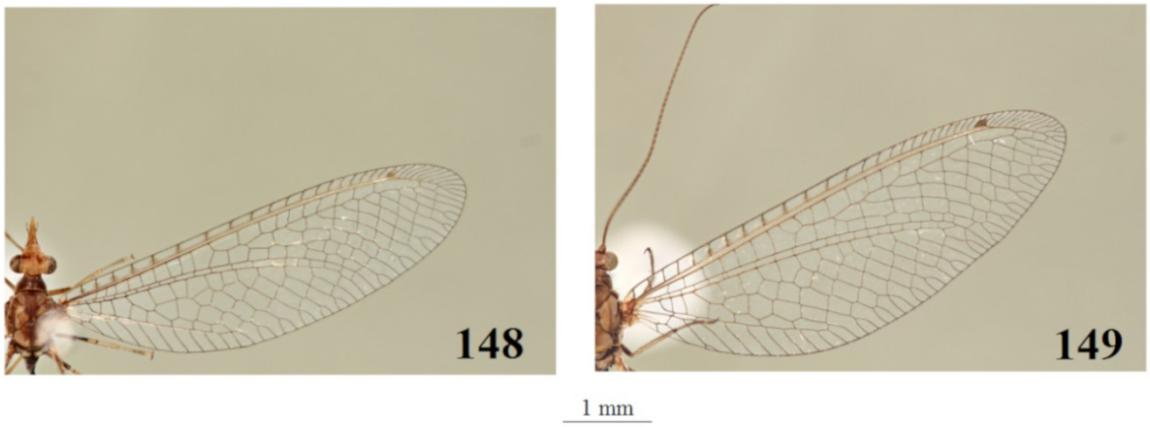


Figures 131–132. Holotypes of *Afroptera* spp and their associated labels. 131, *A. peringueyi* (Tjeder) m#; 132, *A. pilosa* (Tjeder) m#. Photos: Simon van Noort (SAMC).

Figures 133–140. *Afroptera* spp. Male holotypes: forewings. 133, *A. dyscrita* (Tjeder); 134, *A. exigua* (Tjeder); 135, *A. lanata* (Tjeder); 136, *A. obtusa* (Tjeder); 137, *A. papio* (Tjeder); 138, *A. segregata* (Tjeder); 139, *A. peringueyi* (Tjeder); 140, *A. pilosa* (Tjeder).

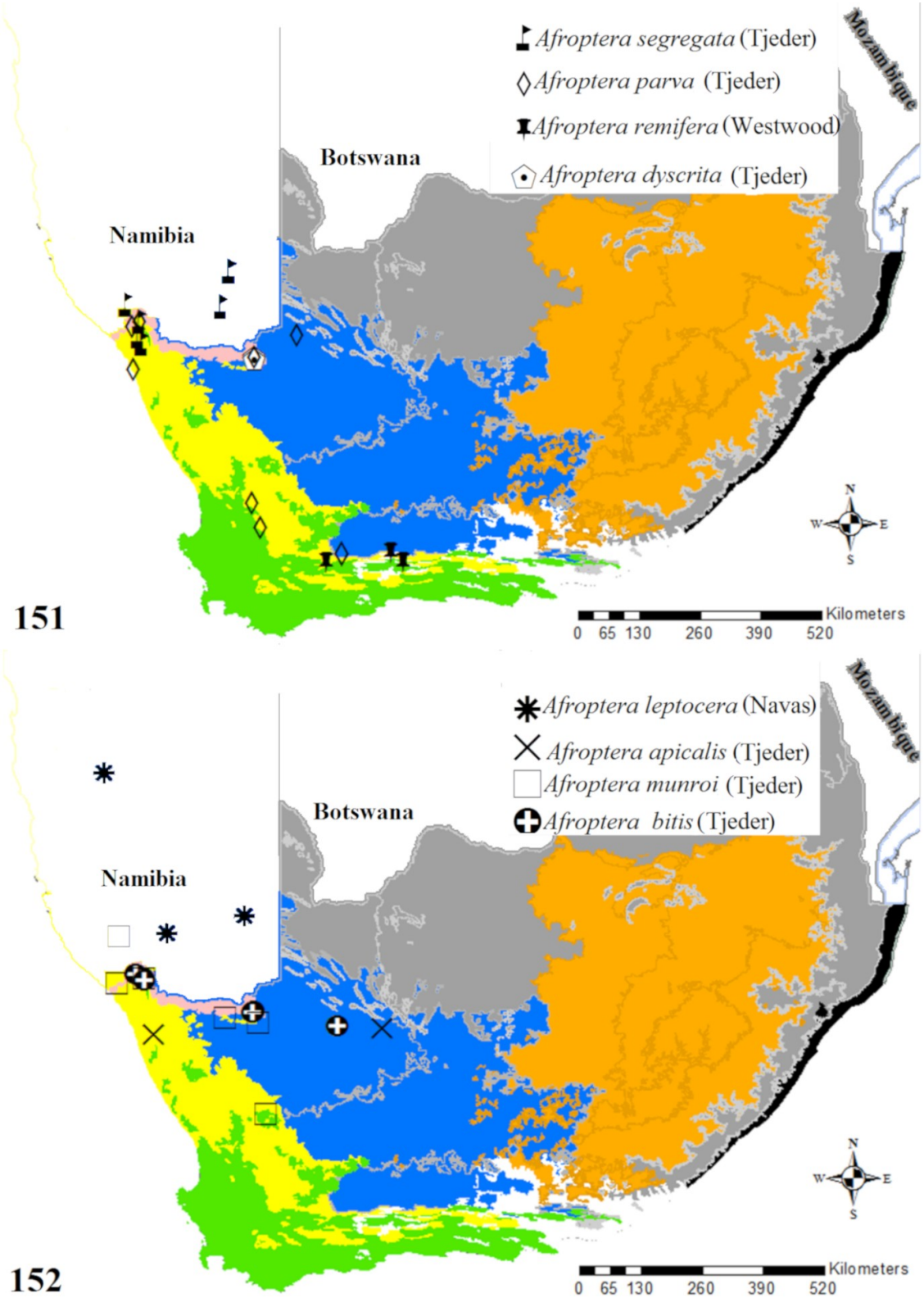


Figures 141–145. *Afroptera* spp. Vertex of Head. 141, *A. aequabilis*; 142, *A. apicalis*; 143, *A. brinkmani*; 144, *A. munroi*; 145, *A. nigrosetosa*.

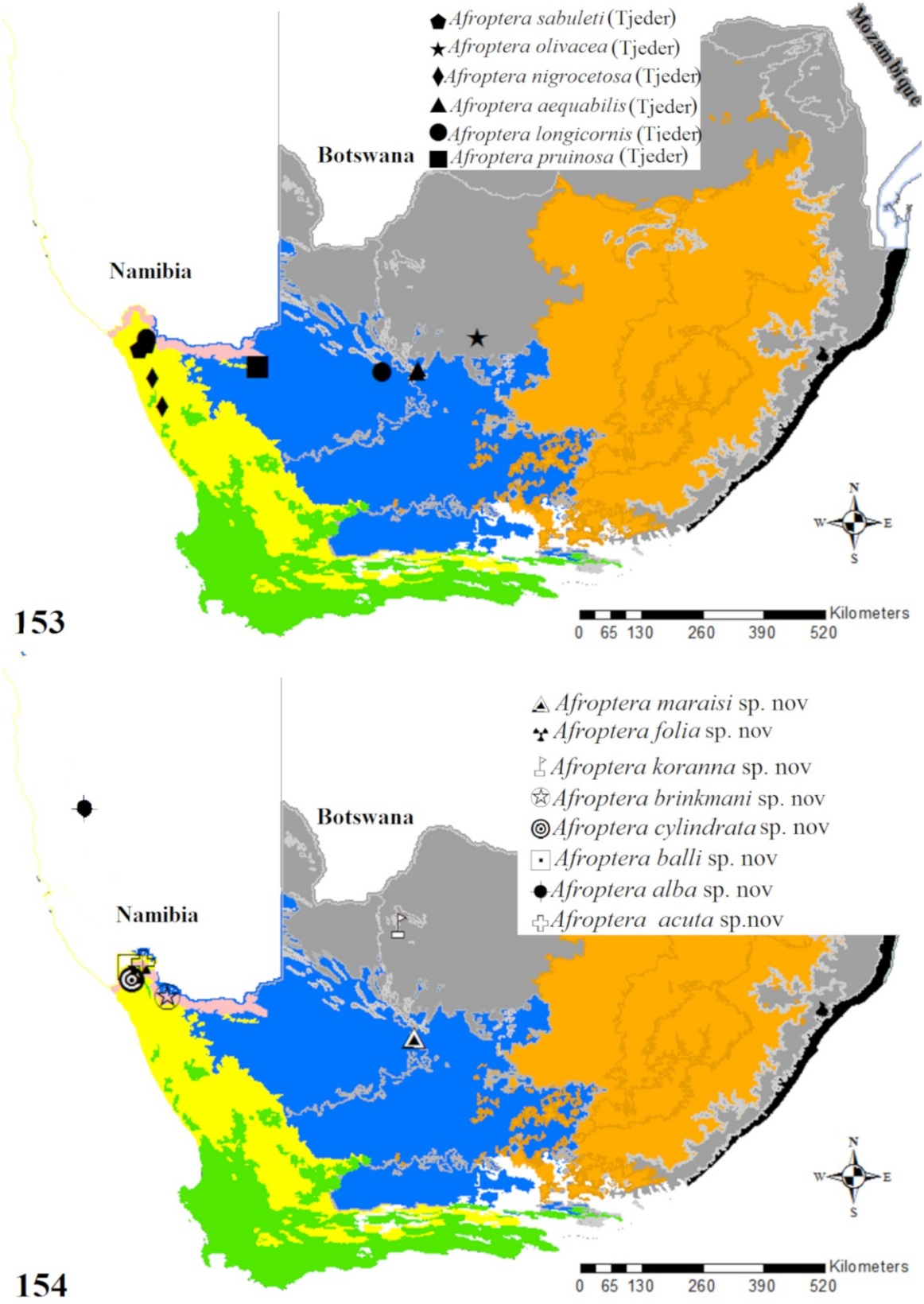


Figures 146–149. 146, Abdomen of *A. bitis* with white pubescence on dorsum and black on venter; 147, Abdomen of *A. munroi* with white pubescence on dorsum and venter; 148, Forewing of *A. parva;* 149, Forewing of *A. remifera*.

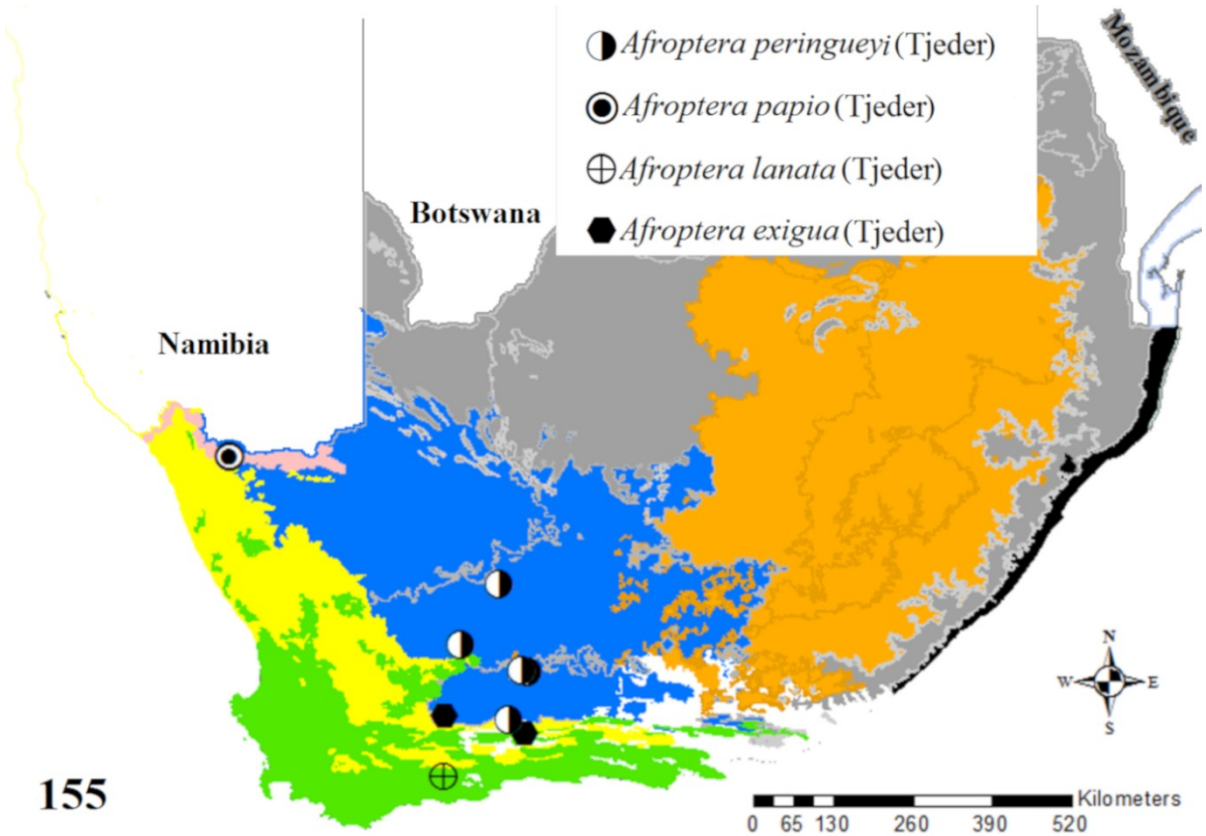
Figure 150. *Afroptera remifera* (Westwood). Male habitus. Forewing length = 23.8 mm.

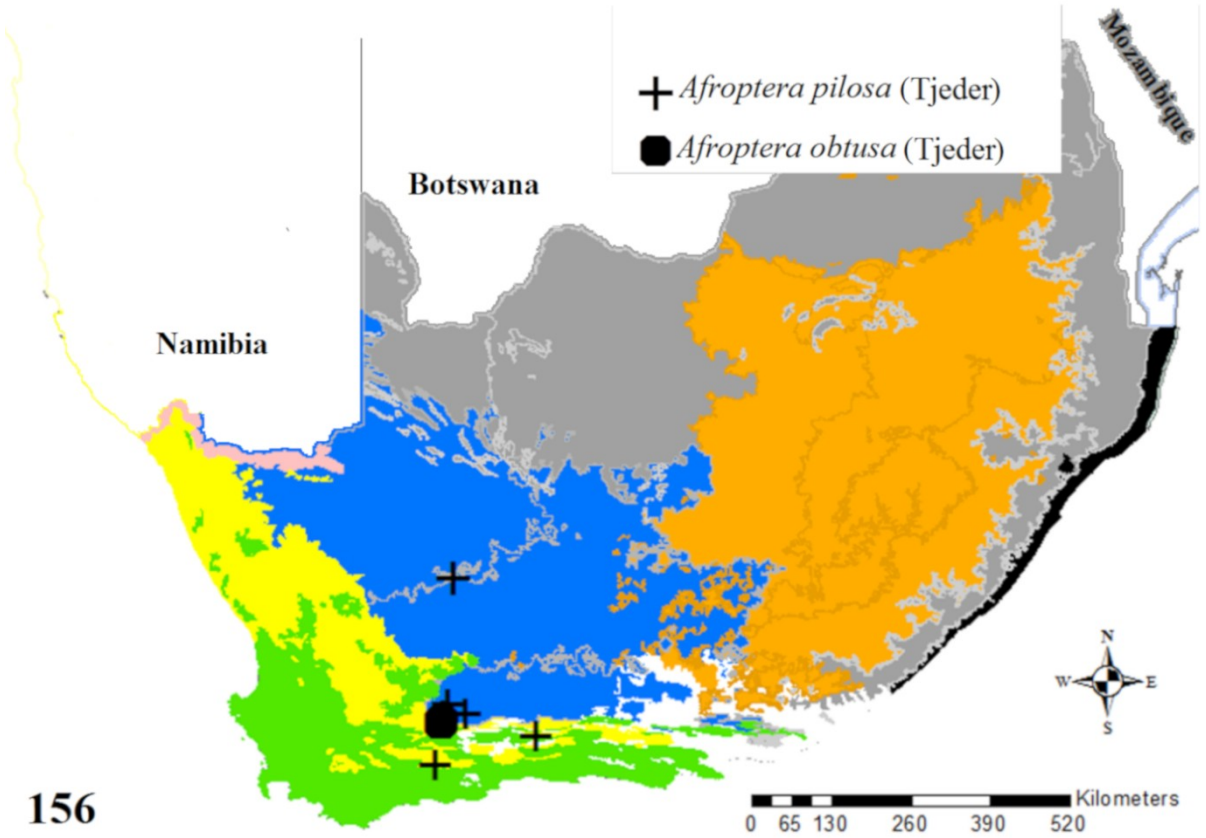


Figures 151–152. Distribution maps of *Afroptera* spp.



Figures 153–154. Distribution maps of *Afroptera* spp.





Figures 155–156. Distribution maps of *Afroptera* spp.

Genus *Nemia* Navás, 1915

Synonymy
Nemia Navás, 1915: 36

Type species: *Nemoptera costalis* Westwood, 1836. By original designation.

Diagnosis. *Nemia* can be readily separated from the genera *Nemopterella*, *Siccanda* and *Afroptera* by at least four key features: the apical antennal segment ends in a short sharp tooth-like point (not membranous); males lack abdominal pleuritocavae; the thorax and abdomen are characteristically striped, and the costal cells have dark marks on the membrane. For full description of the genus, see Tjeder 1967: 438.

***Nemia angulata* (Westwood, 1836)**
(Figs 157, 162, 167, 171)

Nemoptera angulata Westwood, 1836: 75.
Nematoptera angulata (Westwood): Westwood 1841: 12.
Nemoptera angula: Walker 1853: 475 (Incorrect subsequent spelling of *angulata*).
Halter costalis (Westwood): Kirby 1900: 458(*partim*).
Eretmoptera costalis (Westwood): Navás 1910: 361 (*partim*).
Nemopterella costalis (Westwood): Navás 1912: 9(*partim*).
Nemia angulata (Westwood): Tjeder 1967: 446.

Etymology. Unknown, but probably from the Latin word *angulatus* (angle) for the acute wing apex.

Type locality. South Africa, *Western Cape Province*. Cape of Good Hope. Subsequently designated type locality by Tjeder (1967): Pofadder, Northern Cape Province, South Africa, 29°09'S 19°25'E. (Fig. 157).

Type depository. OXUM.

Diagnosis. This species can be separated from its congeners by the remarkable acute apex of the forewings (Fig. 162).

Size (mm). Male: body length 12.7 (11–14.7); forewing 30.2 (27–35.5); hind wing 62.6 (59–79.9); antenna 35.2 (25–36.1); Female: body length 13 (11.7–14.2); forewing 26.1 (24.9–30.4); hind wing 60.1 (52.2–67.6); antenna 16.6 (15.9–20.9).(N = 31).

Type material. SOUTH AFRICA, *Western Cape Province*. Holotype m# (Photo), (Fig. 157), labelled: 'C.G.H.' [= Cape of Good Hope] (white handwritten label) / 'W' [Westwood] (blue diamond-shaped handwritten label) / *Nemopt. angulata* Westw., Trans Ent. S.1 Nat. Lib. Introd. to Entomol. pl. 27 1 (white handwritten label). (OXUM).

Other material examined. SOUTH AFRICA, *Northern Cape Province*. 5m# 2f#, TMSA00756, Kenhardt 6 m West of [29°24'23"S 21°06'01"E] 12.X.54, A.J.T.Janse / *Nemia angulata* (Westwood, 1836) f#, Det. M.W.Mansell, 2013; 3m#, TMSA02087, Marydale 5 mi North of [29°20'19"S 22°05'50"E], 9–10.x.1954, A.J.T.Janse / *Nemia angulata* Westw. det. Tjeder 1966; 3m# 1f#, TMSA02088, Brakfontein, Richtersveld [28°56'S 17°06'E], 20.x.1933, G.van Son / *Nemia angulata* Westw. det. Tjeder 1966; 1m# 1f#, TMSA00755, Farm Cnydas 12 km NW Lutzputs [28°09'S 20°34'E], 10.x.1980, Rautenbach, Wolhuter / *Nemia angulata* (Westwood, 1836) Det. M.W.Mansell 2013; 1m# 1f#, TMSA00756, Kenhardt West of, 1–14.X.1954, A.J.T.Janse / *Nemia angulata* (Westwood, 1836), Det. M.W.Mansell 2013. (All TMSA). 1m#, NEUR08896, Richtersveld, Blackie's Prospect, 8 km E Die Koei, 28°18'S 17°05'E, 320m, 3.x.1991, M.W.Mansell / Collected at light. (SANC). 1m#, A001233 [Van] Wyk[s] Vlei, 10.85 / *Nemia angulata* Westw., det Bo Tjeder 1966; 1m#, SAM–NEU–A001241, *Nemoptera bacillaris* Klug / Identified with *Nemoptera angulata* Westw. (SAMC). NAMIBIA, *Karas Region*. 3m#, NEUR08897, Obib Dunes 54 mi N.E. Oranjemund, S.W.Afr., 19.ix.1962, H.D.Brown, W.Furst; 2m# 1f#, NEUR08899, Diamond Area no.1, nr. Aurusberg, 500m, 27°32'S 16°10'E, (2716Ca), 22.x.1974, M.W.Mansell / Collected at mercury vapour light, arid rocky terrain; 1m#, NEUR03758, Rooiduine at Obib Mountains, 28°07'S 16°44'E, 1.xi.1999, M.W.Mansell / Handnetted on sand between *Euphorbia* bushes; 1f#, NEUR08898, Obib Mountains, 28°00'S 16°39'E, 19.xi.1992, no collector name. (All SANC). 1m#, SAM–NEU–A001232, S.W.Africa, Kalkfontein / *Nemia angulata* Westw., det. Bo Tjeder 1966. *Hardap Region*. 1f#, A001230, Rehoboth, S.W.A / *Nemia angulata* Westw., det. Bo Tjeder 1966; (SAMC).

Distribution and habitat. This species is endemic to South Africa and Namibia (Fig. 171). In South Africa, the range encompasses the northern part of Namaqualand and extends eastwards to include the northern portion of the Nama Karoo Biome. In Namibia, the range includes the south-western portion of the Namib Desert. The habitats in these areas are characterised by extreme aridity, although the area along the coast is more humid and is characterised by winter rains and succulent vegetation, while the Nama Karoo region is typified by summer rain and a Karoo vegetation type.

Figure 157. *Nemia angulata* (Westwood), holotype and associated labels (Photo: OXUM).

***Nemia costalis* (Westwood, 1836).**

(Figs 158, 165, 168, 172)

Synonomy

Nemoptera costalis Westwood, 1836: 75.

Nematoptera costalis (Westwood): Westwood 1841: 12.

Halter costalis (Westwood): Kirby 1900: 458.

Eretmoptera costalis (Westwood): Navás 1910: 361.

Nemopterella costalis (Westwood): Navás 1911: 226.

Nemia costalis (Westwood): Navás 1915: 36.

Nemopterella sp.: Acker 1958: 106, f.7–8, 10, 12–18, 20, 22.

Etymology. Unknown, probably from the characteristic costal area in the forewings.

Type locality. South Africa, *Western Cape Province*. Cape of Good Hope ("CGH"). Type locality subsequently designated by Tjeder (1967): Clanwilliam, 32°10'S 18°53'E.

Type depository. OXUM.

Diagnosis. *Nemia costalis* resembles *N. elongata* by the same head colouration and abdominal pubescence patterns. *Nemia costalis* can easily be distinguished from *N. elongata* by the broad forewings with rounded apex (Fig. 165), while in *N. elongata* the forewings are more slender and the apex is short and acute (Fig. 163).

Size (mm). Male: body length 10.9 (9.1–14.1); forewing 24 (21.6–28.4); hind wing: 52.2 (41.3–63.6); antenna 20.7 (14–24.2). Female: body length 10.4 (10.2–15); forewing 23.6 (20.4–27.9); hind wing 51 (41–61.4); antenna 15 (10.2–19.7). (N = 118).

Type material. SOUTH AFRICA, *Western Cape Province*.Holotype f# (photo), (Fig. 158), labelled: "C.G.H." [Cape of Good Hope] (White handwritten label) / 'W' [Westwood] (blue handwritten label) / *Nemopt. costalis* Westw., Trans. Ent. Soc. (white handwritten label). (OXUM).

Other material examined. SOUTH AFRICA, *Western Cape Province*.1f#, TMSA00739, Zeekoeivlei Farm near Clanwilliam [32°08'23"S 18°44'08"E], 29.x.2002, M.V. Light, Farm Staff *leg* / *Nemia costalis* (Westwood, 1836), Det. M.W.Mansell 2013; 2f#, TMSA00738, same locality and collectors, 29.xi.2002 / *Nemia costalis* (Westwood, 1836), Det. M.W.Mansell 2013; 1f#, TMSA00740, same locality and collectors, 21.xi.2002 / *Nemia costalis* (Westwood, 1836), Det. M.W.Mansell 2013; 2f#, TMSA02052, Clanwilliam [32°10'S 18°53'E], 11–12.XI.1949, Dr. C.Koch, *Nemia costalis* Westw., / det. Bo Tjeder 1966; 2f#, TMSA00765, Diepkloof Farm near Clanwilliam, 12.xii.2003 / M.V. Light, Farm Staff

Leg /*Nemia costalis* (Westwood, 1836), Det. M.W.Mansell 2013. (All TMSA). 25m# 26f#, NEUR00702, Biedouw Farm, Biedouw Valley, 32°08'S 19°14'E, 29.ix.1986, M.W.Mansell, J.H.Hoffmann, Light; 4m# 6f#, NEUR01473, Graafwater, 32°08'S 18°36'E, 190m, 15.xi.1990, M.W.Mansell, R.B.Miller, L.A.Stange; 3m# 3f#, NEUR09821, Seekoevlei Farm, Clanwilliam Dist., 32°09'S 18°45'E, 360 m, 27.xi.1996, R.G.Oberprieler; 2f#, NEUR08890, Williston, 14.ix.1985, C.Quickelberge, J.G.H.Londt, At night light trap; 1f#, NEUR09590, Clanwilliam [32°10'S 18°52'E], 10.xii.1996, E.Anderson; 1m#, NEUR09591, Elizabethfontein Farm, Cedarberg, 32°03'S 19°03'E, 25.xi.1996, J. Colville; 1f#, NEUR08888, 20 km SE Calvinia, 17.xi.1986, 3119Db, 1050 m, J.G.H.Londt, C.Quickelberge, Flat scrubland; 1m#, NEUR08889, 31 km N Matjiesfontein, 20.xi.1986, 3220Dc, 1230m, J.G.H.Londt, C.Quickelberge, Flat open area with flowers; 7m# 6f#, NEUR09682, Dwarsrivier Farm, Clanwilliam Dist., 32°13'S 18°59'E, 26–27.x.2006, 337m, A.K.Brinkman; 1f#, NEUR08891, Kromrivier Farm, 32°33'S 19°18'E (3219 Cb), 875m, 4–5.i.1975, M.W.Mansell; 1m# 11f#, NEUR1119, Clanwilliam, Owls Hoot B&B, 32°10'12"S 18°53'52"E, 87m, 18.xi.2001, M.W.Mansell, J.B.Ball. (All SANC). 2m#1f#, SAM-NEU–A001227, Olifantsriver between Citrusdal and Clanwilliam / *Nemia costalis* Westw., det. Bo Tjeder 1966; 1m#, SAM-NEU–A001228, Clanwilliam, Coefobes, 1959 / *Nemia costalis* Westw., det. Bo Tjeder 1966; 2m# 5f#, SAM-NEU–A001229, Bulshoek, Klaver, Clanw., Oct. 1950, Museum Staff / *Nemia costalis* Westw., det. Bo Tjeder 1966. (All SAMC).

Distribution and habitat. This species is confined to the Western Cape Province, South Africa (Fig. 172). The collection sites fall within the greater Cederberg Region. This area stretches from the town of Clanwilliam in the North to Citrusdal in the south in the Olifants River valley. The habitat in this region is typified by a Mediterranean climate with cold, wet winters and hot, dry summers (Cowling *et al*. 1996). The vegetation is composed of strandveld, renosterveld and fynbos.

Remarks. Westwood (1836) described *Nemoptera costalis* (=*Nemia costalis*) and *Nemoptera angulata* (=*Nemia angulata*) in the same paper as two distinct species. However, this classification was disputed by Hagen (1866) who synonymised *N.costalis* with *N.angulata* and, inversely, Kirby (1900) and Navás (1910) synonymised *N. angulata* with *N. costalis*. Tjeder (1967) recognised that they represented two distinct species and consequently redescribed both in his paper (Tjeder 1967).

Figure 158.*Nemia costalis* (Westwood), holotype and associated labels. (Photo: OXUM).

***Nemia elongata* Tjeder, 1967**
(Figs 159, 163, 170, 173)

Nemia elongata Tjeder, 1967: 444.

Etymology. Not stated, but certainly from the elongated shape of the forewings.

Type locality. South Africa, *Western Cape Province*. Vanrhynsdorp, 31°36'S 18°44'E.

Type depository. TMSA.

Diagnosis. Among the *Nemia* species, *N. elongata* can be readily recognised by its slender forewings that have a subacute apex (Fig. 163).

Size (mm). Male: body length 11.2 (10.2–13); forewing 26.4 (23.4–29.2); hind wing 61.5 (45–69.4); antenna 24.2 (20.5–26.7). Female: body length 12.9 (12–15.5); forewing 25.8 (24.8–27.8); hind wing 58.3 (57–61.8); antenna 17.8 (16–19.5). (N = 47).

Type material examined. SOUTH AFRICA, *Western Cape Province*. Holotype m#,TMSA02053, HOLOTYPE, Neu 108, *Nemia elongata* Tjeder (red printed label) / Vanrhynsdorp [31°36'S 18°44'E], XI.1933, G.van Son (white printed label) / Holotypus m#,

Nemia elongata Tjed., Bo Tjeder 1966 (red handwritten label). *Paratypes*: 4m# 5f#, Paratype Neu 110 *Nemia elongata* Tjeder (yellow printed label) / same data as holotype (white printed label) / Paratypus *Nemia elongata* Tjed., Bo Tjeder 1966 (red handwritten label). (All TMSA). 1f#, SAM–neu–A00 1231, Vanrhynsdorp [31°36'S 18°44'E], SAM museum (white handwritten label) / Paratypus *Nemia elongata*, Bo Tjeder 1966. (SAMC).

Other material examined. SOUTH AFRICA, *Western Cape Province*. 3m# 14f#, TMSA02087, Vanrhynsdorp [31°36'S 18°44'E], xi.1933, G.van Son /*Nemia elongata* Tjeder, 1967, Det. M.W.Mansell 2013. (TMSA).14m# 2f#, NEUR11751, Vanrhynsdorp Caravan Park, 31°36'55"S 18°44'07"E, 124m, 4–6.x.2011, Light trap, A.P.Marais; 1m#, NEUR09909, Vanrhynsdorp, 31°36'28"S 18°43'53"E, 24.xi.2008, C.H.Scholtz, At light; 2m#, NEUR09870, same locality and collector, 8.xi.2008, At light. (All SANC).

Distribution and habitat. This species is only known from Vanrhynsdorp in the Northern Cape Province, South Africa (Fig. 173). The town is within the Knersvlakte Bioregion (Mucina & Rutherford 2006) or Vanrhynsdorp centre. The area occupies the southern part of Namaqualand and is close to the west coast. Generally, the habitat is semi-arid, characterised by a winter rainfall regime and succulent vegetation.

***Nemia karrooa* (Péringuey 1911)**
(Figs 160, 164, 169, 174)

Nemoptera (*Eretmoptera*) *karrooa* Péringuey, 1911: 36.
Nemopterella karrooa (Péringuey): Navás 1912: 9.
Nemia karrooa (Péringuey): Tjeder 1967: 448.

Etymology. Derived the common name of the various *Pentzia* species (karoo bushes), the dominant shrubs that characterise the Karoo biomes of South Africa, and in which *N. karrooa* is widespread.

Type locality. South Africa, *Western Cape Province*. Tulbagh, 33°16S 19°06E.

Type depository. SAMC.

Diagnosis. This species shares the distinct dark thoracic stripes of *N. angulata* and *N. costalis* (Fig. 169). *Nemia karrooa* resembles *N. costalis* in having similar abdominal pubescence stripe patterns. It resembles *N. angulata* by the similar colouration of the forewing veins, costal membrane and subcostal and anal areas. It can be distinguished from the former

species by having a slightly broader forewing with less acute apex (Fig. 164), and from the latter by a much paler pterostigma and far less whitish pubescence on the thoracic pleurites.

Size (mm). Male: body length 12.3 (10.6–14.2); forewing 27.6 (24.4–30); hind wing 61.0 (58.8–69.9); antenna 25.5 (21.4– 28.5). Female: body length 13.2 (12.4–14.7); forewing 26.3 (25.6–27); hind wing 59.1 (58.3–60); antenna 17.8 (17–18.8). (N = 58).

Type material Examined. SOUTH AFRICA, *Western Cape Province*. Holotype f#, SAM–NEU–A001237, Tulbagh, R.Lightfoot 1910 (white handwritten label) / *Nemoptera tulbaghia* f# type, Py (white handwritten label) / Holotypus *Nemoptera* (*Eretmoptera*) *karrooa* Péringuey (red handwritten label) / *Nemia karrooa* Per., det. Bo Tjeder 1966 (white printed label). (SAMC).

Other material examined. SOUTH AFRICA, *Northern Cape Province*. 1m#, NEUR08895, 33f#, 9 Km W of Williston, 31°20'4"S 20°50'52"E, 10.xi.1998, J.G.H.Londt, 1080m, Karoo vegetation at foot of rocky ridge; 1m#, NEUR01476, Milddlepos, 32°54'S 20°14'E, 1120m, 16.xi.1990, M.W.Mansell, R.B.Miller, L.A.Stange; 1m#, NEUR01480, Sterkfontein Farm, Williston Dist, 31°48'S 20°31'E, 1200m, 17.xi.1990, M.W.Mansell, R.B.Miller, L.A.Stange; 1f#, NEUR01346, Westdene Farm, Richmond District, 31°24'S 23°44'E, 1320m, 14.xii.1989, M.W.Mansell, Handnetted; 1m# 3f#, NEUR12586, Kelkiewyn Farm, Calvinia District, 31°12'01"S 19°41'33"E, 22–23.x.2013, 661m, C.H.Scholtz. 7m# 3f#, NEUR118110, same locality and collector, 25.x.2011, At light. 1m# 5f#, NEUR09923, same locality and collector, 1–3.xii.2008, At light. (All SANC). *Western Cape Province*. 1m#, NEUR08894, Prince Albert Dist, Tierberg Research Station, 33°08'S 22°17'E, 26.xii.1989, W.R.J.Dean / Collected at light; 2m#, NEUR08893, same locality and collector, x.1989; 1m#, NEUR02164, same locality and collector, x.1990; 1m# 1f#, NEUR02117, Boonsteveld, 25 K. N Laingsburg [33°11'47"S 20°51'39"E], 10.xi.1985, M.D.Picker; 5m# 1f#, NEUR10118, Oorlogskloof Farm, Klaarstroom District, 33°21'48"S 22°43'34"E, 897m, 21.xi.2008, At light, A.P.Marais; 1m#, NEUR10119, Oukloof Farm, Prince Albert District, 33°16'23"S 22°08'12"E, 745m, 22–23.xi.2008, At light, A.P.Marais; 8m# 7f#, NEUR09864, Wamakerskraal Farm, Laingsburg District, 33°02'03"S 21°35'36"E, 350m, 11.x.2008, J.B.Ball, A.P.Mariais, Light. (All SANC). 1m#, A001338, Klaarstroom, Prince Albert / *Nemia karrooa* Per., det. Bo Tjeder 1966; 3m#, A001239, Dikbome, Merweville Koup, C.P / *Nemia karrooa* Per., det. Bo Tjeder 1966; 1m#, A001240, Koup Siding, Laingsburg [33°11'47"S 20°51'39"E], C.P. / *Nemia karrooa* Per., det. Bo Tjeder. (All SAMC).

Distribution and habitat. *Nemia karrooa* occurs in the Northern and Western Cape provinces, South Africa (Fig. 174). Compared to other species in the genus, this species has a

wide distribution. The range extends over the Fynbos, Succulent Karoo and Nama Karoo Biomes. The habitat consequently ranges from arid to semi-arid with different rainfall seasons and different vegetation cover according to biome type.

Remarks. The female holotype of *N. karrooa* was originally described by Péringuey(1911) and deposited in the South African Museum, Cape Town. When he examined the holotype Tjeder (1967), observed that it is labelled "*Nemoptera tulbaghia* f#./ type Per" with type locality "Tulbagh, R. Lightfoot 1910" instead of *Nemoptera karrooa* as Péringuey had named it in his paper. Tjeder assumed that the change in the species name from *tulbaghia* to *karrooa* may have been because Péringuey has been informed by Lightfoot (the collector of the species) that the type specimen had, in fact, been collected from Laingsburg in the Karoo region and not from Tulbagh, and Péringuey inadvertently did not change the label. Tjeder (1967) consequently amended the label to "Holotypus, *Nemoptera* (*Eretmoptera*) *karrooa* Péringuey" and then substituted the name *Nemoptera* with *Nemia* in his paper.

Figure 159. *Nemia elongata* Tjeder. Male holotype and associated labels.

Figure 160. *Nemia karrooa* (Péringuey). Female holotype and associated labels. Photo: Simon van Noort (SAMC).

***Nemia lata* Tjeder, 1967**
(Figs 161, 166, 171, 175)

Nemia lata Tjeder, 1967: 450

Etymology. Unknown, most likely from the Latin word *lata* (broad) for it is broad forewings and large body size.

Type locality. South Africa, *Northern Cape Province*. Soebatsfontein, 30°07'08"S 17°35'27"E.

Type depository. TMSA.

Diagnosis. *Nemia lata* is a distinct species that can be readily diagnosed by its large body size and the broad forewings that are sharply emarginated before the apex (Figs 161, 166).

Size (mm). Male: body length 12.3 (10.4–14.3); forewing 29.6 (22.2–34.5); hind wing 67.7 (50.5–78.1); antenna 29.9 (26.8–33.7); Female: body length 12.7 (11–15.9); forewing 28.1 (24.5–30.8); hind wing 62.8 (54.5–71); antenna 19.4 (15.1–23.5). (N = 93)

Type material examined. SOUTH AFRICA, *Northern Cape Province*. Holotype m#, TMSA02054 HOLOTYPE, Neu 119, *Nemia lata* Tjeder (red printed label) / SOEBATSFONTEIN [30°07'08"S 17°35'27"E], 13–14.11.1933 / G.van Son (white printed label) / Holotypus m# *Nemia lata* Tjed., Bo Tjeder 1966 (red handwritten label). *Paratypes*: 1m# 7f#, same data as holotype. (All TMSA). 1m#, SAM–NEU–A001242 O'kiep, 18.11. [18]85 (white handwritten label) / Paratypus *Nemia lata* Tjed., Bo Tjeder 1966 (red printed label); 1f#, SAM–NEU–A001243 (SAMC), same data but 14.11.[18]85. (Both SAMC).

Other material examined. SOUTH AFRICA, *Northern Cape Province*. 1m#, TMSA00766, Soebatsfontein [30°07'08"S 17°35'27"E], IV.[19]54, A.J.T.Janse / *Nemia lata* Tjeder, 1967, Det. M.W.Mansell 2013; 3m# 12f#, TMSA00761, same locality but 13–14.11 [19]33, G.van Son / *Nemia lata* Tjeder, 1967, Det. M.W.Mansell 2013; 1m#, TMSA00761, same locality and data / *Nemia lata* Tjeder, 1967, Det. M.W.Mansell 2013 / *Nemia* sp., Det. Bo. Tjeder 1966; 1f#, TMSA00754, Bitterfontein, 12.x.1983, R.Mijburg / *Nemia lata* Tjeder, 1967, Det. M.W.Mansell 2013. (All TMSA). 2m#, NEUR11242, Lang Hoogte Mine Office, 29°32'19"S 17°23'27"E, 100m, 27.x.1996, A.J.van Wyk; 1m#, NEUR08938, same locality and collector but 18.x.1996; 1m# 3f#, NEUR09624, same locality and collector but 19.x.1996 / Collected at light; 3m#, NEUR09623, same locality and collector but 12.xi.1996; 5m# 2f#, NEUR09622, same locality and collector but 4–5.xi.1996. 3m# 1f#, NEUR09629, same locality and collector but 6.xi.1996 / Collected at light; 3m#, NEUR09766 same locality but

16.x.1996, J. duG.Harrison / Collected at light; 5m# 1f#, NEUR09627, Strydrivier Farm, 22 km NE Kleinsee, 29°34'S 17°17'E, 1.xi.1996, J. duG.Harrison, C.H.Scholtz / Handnetted During day; 12m 6f#, NEUR009615, same locality but 31.x.1996, M.W.Mansell / Handnetted During day; 1m#, NEUR03762, Wallekraal, 30°23'S 17°30'E, 30.x.1999, R.D.Stephen; 3m# 4f#, NEUR00703 7 km N Soebatsfontein, 30°03'S 17°35'E, 6.x.1986, M.W.Mansell, J.H.Hoffmann, Handnetted: 8f#, NEUR03763, Garies Caravan Park, 30°33'S 17°59'E, 31.x.1999, R.D.Stephen. (All *Nemia lata* Tjeder, 1967, det. M.W.Mansell 1986). (All SANC).

Distribution and habitat. *Nemia lata* is confined to the Northern Cape Province, South Africa and occupies small range in north-western Namaqualand (Fig. 175). The range falls within the Namaqualand Sandveld Bioregion (Mucina & Rutherford 2006). The habitat in the area is characterised by winter rains and regular storms with low annual precipitation (50–80 mm). The vegetation cover is mainly succulent shrubs (Mucina & Rutherford 2006).

***Nemia zebra* Tjeder, 1967**
(Fig.176)

Nemia zebra Tjeder, 1967: 453.

Etymology. Unknown, but certainly because the striped white portion of the hind wings that resemble zebra markings.

Type locality: South Africa, *Western Cape Province*. Botesland Siding, 33°01'S 21°37'E.

Type depository. NMBZ.

Diagnosis. *Nemia Zebra* can be recognised by the remarkable crossed-striped apical parts of the hind wings, short antennae and the broad dark pterostigma.

Type material. Holotype m# (not examined).

Distribution and habitat. Only known from the type locality. Botesland is a railway siding on the railway line between Laingsburg and Beaufort West (Fig. 176). The area is situated in the Central Karoo Municipality in the Western Cape. The habitat is dry and characterised by karoo type vegetation and late summer rainfall.

Remarks. *Nemia zebra* is the only *Nemia* spp. that is known from Botesland area and is still only represented by the male holotype.

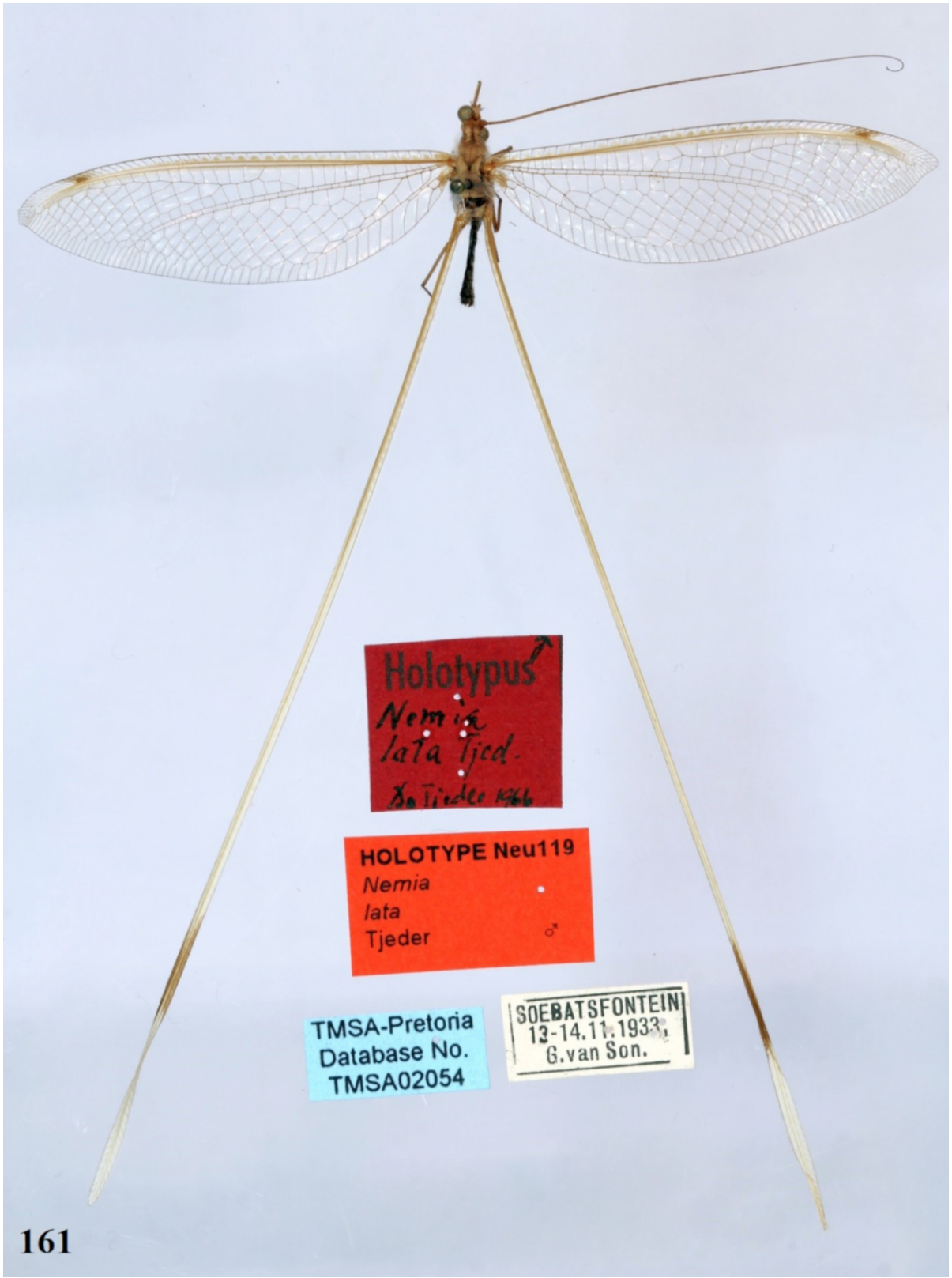
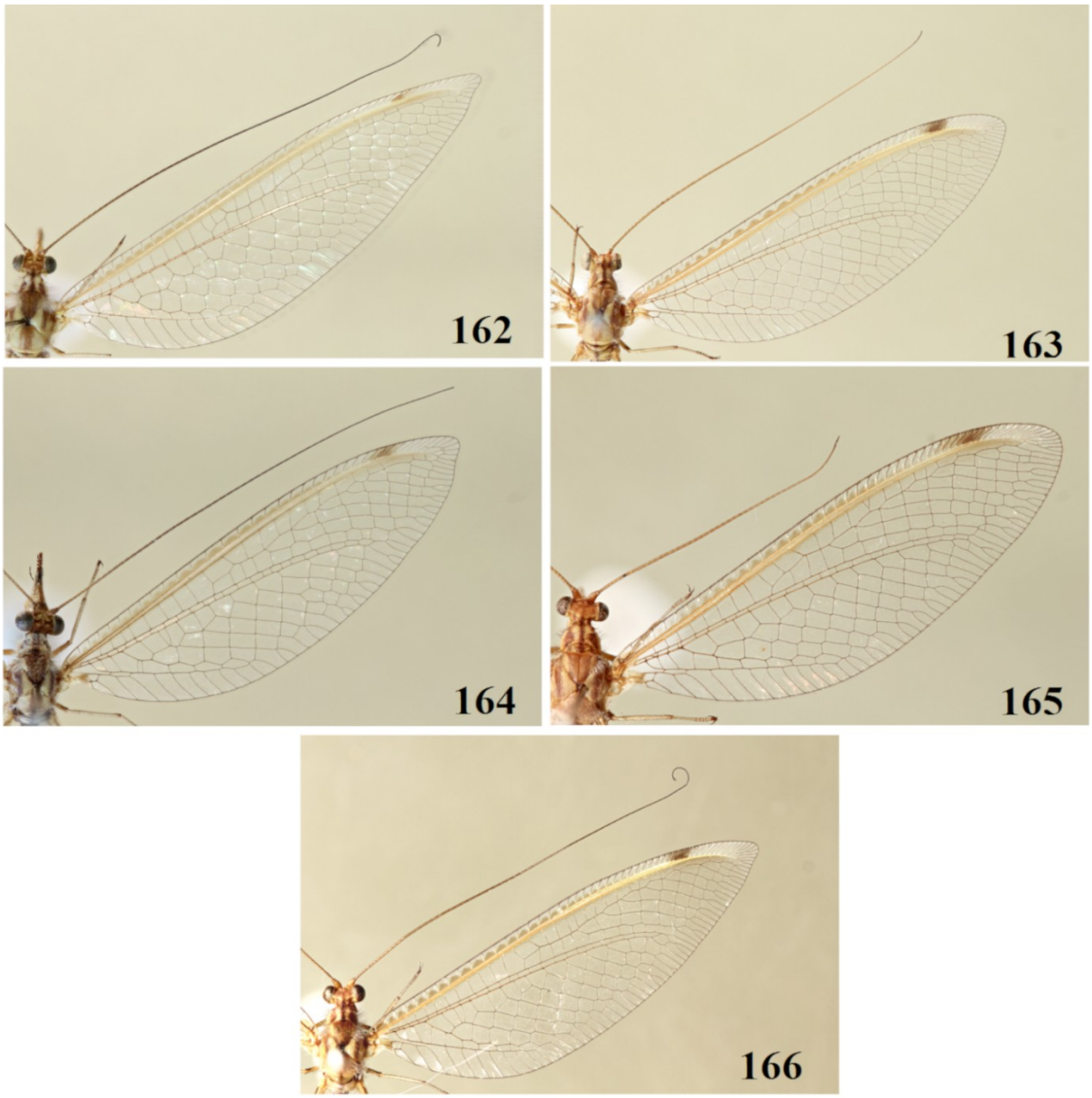
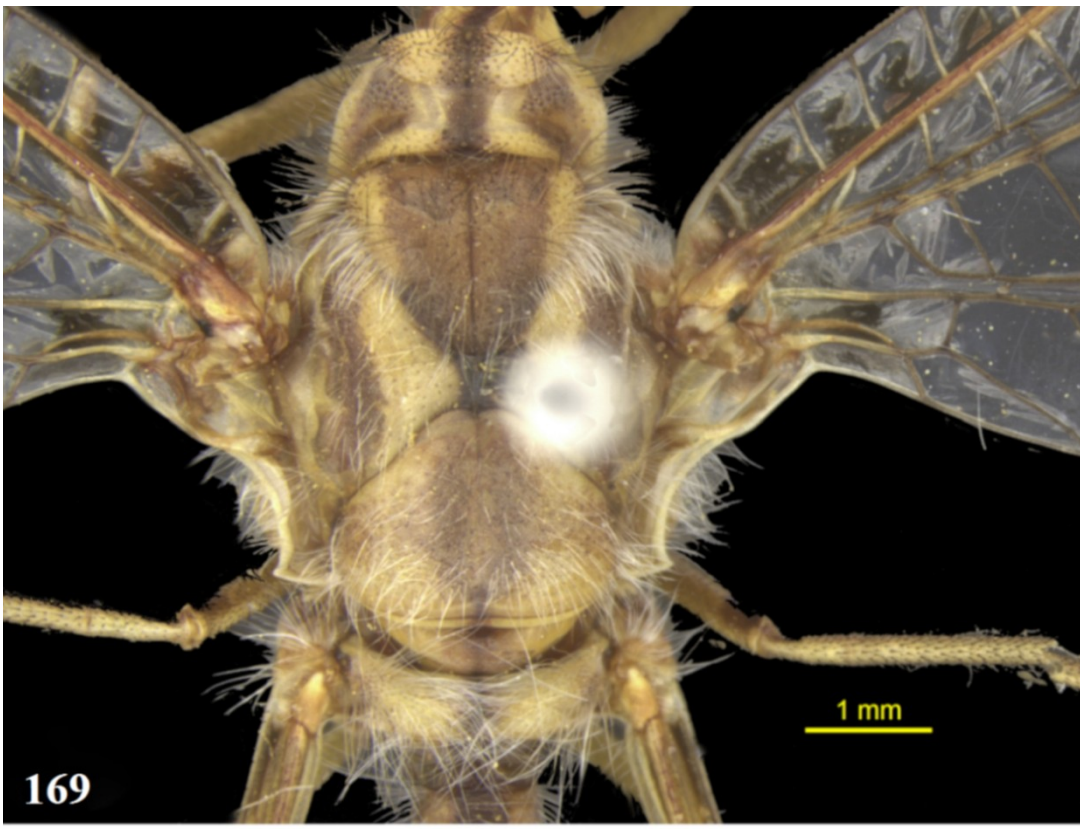


Figure 161. *Nemia lata* Tjeder. Male holotype and associated labels.



Figures 162–166. *Nemia* spp. Male forewings. 162, *N. angulata* (Westwood); 163, *N. elongata* Tjeder; 164, *N. karrooa* (Péringuey); 165, *N. costalis* (Westwood); 166, *N. lata* Tjeder.

Figures 167–168. *Nemia* spp. Thorax. 167, *N. angulata* (Westwood); 168, *N. costalis* (Westwood).


1 mm
169


1 mm
170

Figures 169–170. *Nemia* spp. Thorax. 169, *Nemia karrooa* (Péringuey); 170, *Nemia elongata* Tjeder.

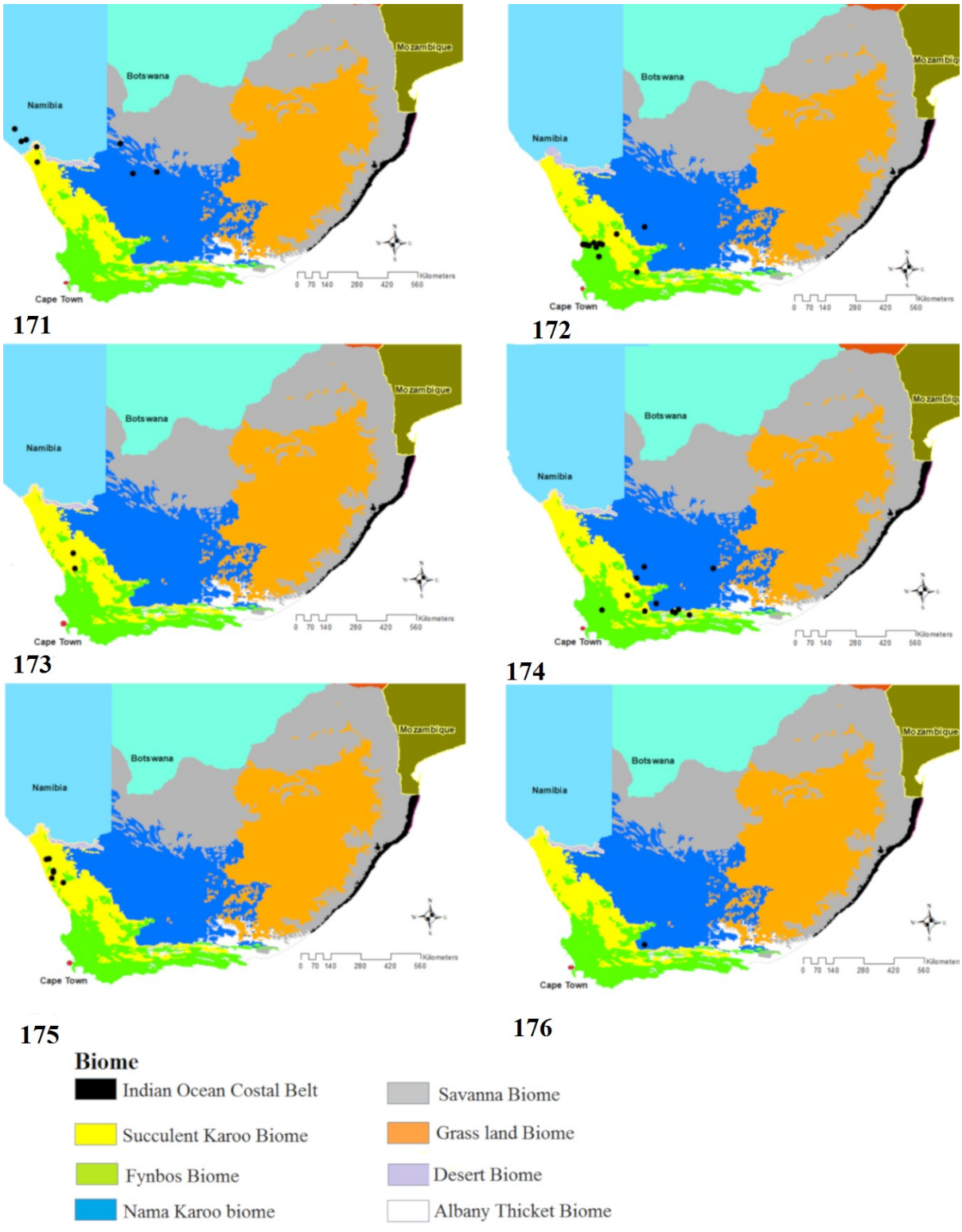


Figure 171–176. Distribution maps of *Nemia* spp. 171, *N. angulata* (Westwood); 172, *N. costalis* (Westwood); 173, *N. elongata* Tjeder; 174, *N. karrooa* (Péringuey); 175, *N. lata* Tjeder; 176, *N. zebra* Tjeder.

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CHAPTER V

Phylogeny and divergence time of the southern African lacewing genus *Afroptera* Abdalla & Mansell, 2019 (Neuroptera: Nemopteridae: Nemopterinae)

Abstract

The lacewing genus *Afroptera* Abdalla & Mansell, 2019 (Neuroptera: Nemopteridae: Nemopterinae) was studied. The genus comprises 28 species of which eight new taxa were recently described by Abdalla & Mansell (2019) and Mansell & Abdalla (2019). The genus is endemic to South Africa and Namibia with the main distribution in the south-western Cape, mainly in the Fynbos and Succulent Karoo Biomes. This study was to determine the phylogenetic relationships between the species of the genus and to estimate their divergence times. Molecular methods were based on partial sequences of three ribosomal genes (16S, 28S and 18S) and two protein-coding genes (COI, CAD), while the phylogeny, based on morphology, used 103 morphological characters. Both datasets recovered a well-supported phylogeny with two major clades (A and B). Divergence time estimates suggest that *Afroptera* originated in the Late Eocene (36.5 Mya) with most descendant species undergoing rapid speciation during the Pliocene and through the Pleistocene (4.6-0.2 Mya).

Key words. Phylogeny, Lacewings, phylogeny, molecular, *Afroptera,* Nemopterinae, South Africa, Western Cape,

Introduction

Nemopteridae (thread- spoon- and ribbon-winged lacewings) are unique by virtue of the unusual shape of their hind wings that are narrow and much longer than the forewings, and their short metathorax (Tjeder 1967). The family includes approximately 142 species mainly confined to arid habitats. They occur in The Middle East and India, Mediterranean Europe, South America, Australia, Socotra Island and Africa, with the greatest concentration in southern Africa (Sole *et al*. 2013). The family does not occur in North America, except for

two fossil records of the genus *Marquettia* Navás, 1913 (Carpenter 1959). The family comprises two subfamilies: Crocinae (thread-winged lacewings), which have filiform hind wings that act as tactile sensors enabling the insect to interact with its surroundings, and in mate recognition (Mansell 1996). This subfamily comprises about 43 species, primarily distributed in the arid and desert zones on the southern fringes of the Palaearctic and Oriental Regions and the Neotropical, Afrotropical and Australian Regions (Mansell 1996; Monserrat 1996). The adult and larval biology and morphology of Crocinae has been documented by Tjeder (1967), Mansell (1976, 1977, 1980, 1981a, 1981b, 1983a, 1983b, 1986, 1996) and Monserrat (1983), while the taxonomy, biogeography and phylogeny were treated by Hölzel (1975) and Monserrat (1996).

Nemopterinae (spoon- and ribbon-winged lacewings) by contrast, have broader hindwings with an apically dilated region, which provides stability during flight and in mating signals and camouflage (Mansell 1996). The subfamily has a similar distribution to that of Crocinae. The subfamily Nemopterinae was recovered as a monophyletic group by molecular analysis, including 10 of the 11 southern African genera, *Nemia* Navás, *Barbibucca* Tjeder, *Halterina* Navás, *Derhynchia* Tjeder, *Knersvlaktia* Picker, *Palmipenna* Tjeder, *Nemeura* Navás, *Sicyoptera* Navás, *Semirhynchia* Tjeder, and *Nemopterella* Banks (*Nemopistha* Navás could not be sequenced). *Nemia, Barbibucca, Derhynchia, Halterina, Palmipenna* and *Knersvlaktia* were found to be monophyletic while *Nemopterella* was paraphyletic (Sole *et al*. 2013). Divergence time of the subfamily was dated to the Late Jurassic (145.6 Mya) with most genera diversifying during the period *ca*. 44–11 Mya, while recent rapid speciation occurred in the Late Miocene (*ca*. 6–5 Mya). Among these genera, *Nemi*a and *Nemopterella* were always considered to be taxonomically controversial.

The new southern African genus *Afroptera* Abdalla & Mansell, (2019) was recently proposed after a comprehensive taxonomic revision of the two genera *Nemia* and *Nemopterella*. The taxonomy of these two genera was uncertain as there were no reliable diagnostic characters to distinguish them. The first taxonomic work on the two genera was by Navás (1910) when he proposed the genus *Eretmoptera* and designated *Nemopteryx africana* Leach, 1815, as type species of the genus. However, the name is a junior homonym of *Eretmoptera* (Diptera) (Kellogg 1900). Banks (1910) consequently proposed *Nemopterella* as the new replacement name for *Eretmoptera* Navás (Nemopteridae). A few years later, Navás (1915) split the genus *Nemopterella* into *Nemeva* Navás with type species *Nemopteryx*

africana and *Nemia* Navás with type species *Nemoptera costalis* Westwood, 1836. This classification was based on forewing venation patterns: in *Nemia*, the "*confluentiam cubitorum"*, *i.e.* veins Cu_{1a} and Cu_2 are fused before reaching the forewing margin. However, as more specimens were collected it transpired that this character was insufficient to distinguish the two genera, as it is frequently present in many other nemopterids, even in the type species of *Nemeva* (Tjeder 1967). Tjeder (1967) subsequently differentiated the genera based on more consistent characters. He discovered the presence of pleuritocavae in the abdomen of male *N. africana* that were absent from those of *N. costalis*, and used this character to differentiate *Nemia* and *Nemopterella*. He then synonymised *Nemeva* with *Nemopterella*. The taxonomic status of the genera however, remained unclear owing to the discovery of new species that were morphologically very close to *Nemia* yet had pleuritocavae, which are characteristic of males of *Nemopterella.*

The recent revision by Abdalla, Mansell & Sole (2019) suggested the separation of the two genera into four: *Nemopterella* Banks *sensu stricto* with three species, *Nemia* Navás with six species, *Siccanda* Abdalla & Mansell, 2019 with one species and *Afroptera* Abdalla & Mansell, 2019 with 28 species. The division was based on molecular evidence as well as morphologically diagnostic characters. These include: size of the body, shape of the tip segment of the antennae in both males and females, presence of a pair of transverse spots along the postfrontal suture on the frons above antennae, colour of the pterostigma of the forewing, forewing anal area tinged or not tinged, number of costal cells, pubescence patterns, colour of the hind wing from the base to the apical whitish area, presence of a pair of pleuritocavae in the male abdomen and striping of the body. The most significant diagnostic character however, for separating the genus *Afroptera* from the remaining genera is the membranous terminal segment of the antennae, which is characteristic of all the species in the genus *Afroptera*. The last segment is either entirely or partially membranous, while in the remaining genera it terminates in a tooth-like structure. The revision of the genus increased the number of known species to 28, eight of which were recently described (Abdalla, Mansell & Sole 2019).

As in most southern African Nemopterinae, members of *Afroptera* are distributed mainly in the Western and Northern Cape Provinces of South Africa (Tjeder 1967; Sole *et al*. 2013; Abdalla *et al*. 2019), with some species recorded further north in Namibia, and extending as far south as the Succulent Karoo and the Nama Karoo Biomes. The genus is considered to be

one of the most complex taxonomic groups since the species are morphologically very similar and there are no significant differences between the females of the different species. The identification of the species is consequently based largely on male specimens.. Little is known about the biology of the genus except that members of the genus are attracted to light in large numbers and adults feed exclusively on pollen and nectar, while the carnivorous larvae live freely in sand (Mansell Pers. Obs.).

The aims of this study were: (1) to establish a better understanding of the validity and the taxonomic status of the four genera of Nemopterinae using molecular data; (2) to resolve the phylogenetic relationship between the species of the genus *Afroptera*; (3) estimate the divergence times of its species; (4) test the hypothesis of whether the genus co-evolved with some of Cape flora in the Late Miocene/Pliocene, based on the similar recent diversification of the two groups.

Material and Methods

Sampling and taxon selection

Subfamily Nemopterinae

In-group taxa

The in-group taxa included in this study comprised all known southern African Nemopterinae genera: *Barbibucca*, *Derhynchia*, *Halterina*, *Knersvlaktia*, *Nemeura*, *Nemia, Palmipenna*, *Semirhynchia* and *Sicyoptera,* as well as the Australian *Chasmoptera* Westwood, in addition to the newly proposed *Nemopterella* Banks *senso stricto*, *Afroptera* Abdalla & Mansell*,* and *Siccanada* Abdalla & Mansell. The only genus not included in this study is *Nemopistha*.

Out-group taxa

A representative of the subfamily Crocinae, *Laurhervasia setacea* (Klug), was used as the out-group taxon.

Genus *Afroptera*

In-group taxa

In this study, we included 14 species from the genus *Afroptera* of which three were new, on the basis of availability of fresh material for molecular analysis. The sequences of the species *A. longicornis* and *A. munroi* were retrieved from GenBank.

Out-group taxa

Two species from the genus *Sicyoptera* and three species of *Palmipenna* were selected as out-groups as a close phylogenetic relationship between *Sicyoptera* and *Palmipenna* to *Afroptera* was indicated by a previous study (Sole *et al*. 2013). Previously published sequences of the out-group were from GenBank.

Table 1. Species included in this study, with collection locality and GenBank accession numbers.

No	Taxon	locality	Specimen ID	GenBank accession numbers				
				CO1	16S	CAD	28S	18S
1	A. bitis	Brulpoort Farm	ABBF01	MK798000	-	MK775345	MK684438	MK684407
2	*A. bitis*	Brulpoort Farm	ABBF02	MK798001	MK684474	MK775346	MK684440	MK684408
3	*A. bitis*	Brulpoort Farm	ABBF03	MK798002	MK684473	MK775347	MK684441	MK684412
4	*A. papio*	Swartkop Mine	APSW01	MK797996	MK684463	-	-	MK684410
5	*A. papio*	Swartkop Mine	APSW02	MK797997	MK684462	-	-	-
6	*A. papio*	Swartkop Mine	APSW03	MK797998	MK684464	-	MK684439	MK684410
7	*A. aequabilis*	Kransfontein Farm	AAKF01	MK798003	MK684460	MK775348	MK684442	MK684416
8	*A. aequabilis*	Kransfontein Farm	AAKF02	MK798004	MK684465	-	MK684446	MK684417
9	*A. aequabilis*	Kransfontein Farm	AAKF03	MK798005	MK684461	-	MK684447	MK684418
10	*A. sabuleti*	Marydale	ASMW01	MK798006	-	MK775349	MK684448	-
11	*A. sabuleti*	Marydale	ASMW02	MK798007	-	MK775351	MK684449	MK684419
12	*A. sabuleti*	Marydale	ASMW03	MK798008	-	MK775352	MK684450	MK684420
13	*A. pilosa*	Koup Station	APKS01	MK798009	-	MK775353	MK684459	MK684421
14	*A. pilosa*	Koup Station	APKS02	-	-	-	-	-
15	*A. pilosa*	Koup Station	APKS03	MK798010	-	-	-	MK684422
16	*A. peringueyi*	Middeldrift Farm	APMD02	-	MK684466	-	-	-
17	*A. peringueyi*	Middeldrift Farm	APMD03	MK798011	MK684467	-	MK684456	MK684423
18	*A. peringueyi*	Middeldrift Farm	APMD04	MK798012	-	-	-	MK684424
19	*A. munroi*	Swartkop Mine	AMMV01	MK798016	MK684479	MK775354	MK684457	MK684428
20	*A. munroi*	Swartkop Mine	AMMV02	MK798017	MK684480	-	MK684458	MK684429
21	*A. munroi*	Swartkop Mine	AMMV03	MK798018	MK684481	-	-	MK684430
22	*A. munroi*	Swartkop Mine	AMSW01	MK798013	MK684484	-	-	MK684425
23	*A. munroi*	Swartkop Mine	AMSW02	MK798014	MK684485	-	-	MK684426
24	*A. munroi*	Swartkop Mine	AMSW04	MK798015	MK684486	-	-	MK684427
25	*A. munroi*	Vioolsdrif	NMSK01*	JX294219.1	JX294160.1	-	JX294108	JX294273
26	*A. munroi*	Vioolsdrif	NMSK03*	JX294222.1	JX294162.1	-	JX294110	JX2942735
27	*A. obtusa*	Wolwefontein Farm	AOWF01	MK798024	MK684476	MK775359	MK684451	MK684435
28	*A. obtusa*	Wolwefontein Farm	AOWF02	MK798025	-	MK775360	-	-
29	*A. obtusa*	Wolwefontein Farm	AOWF03	MK798026	MK684475	MK775361	MK684452	MK684435
30	*A. lanata*	Wamakerskraal Farm	ALWK01	MK798019	MK684482	MK775355	-	-
31	*A. lanata*	Wamakerskraal Farm	ALWK02	MK798020	MK684483	-	-	MK684431
32	*A. maraisi*	Stofbakkies Farm	AMSF01	MK798021	-	MK775356	MK684453	MK684432
33	*A. maraisi*	Stofbakkies Farm	AMSF02	MK798022	MK684477	MK775357	MK684454	MK684433
34	*A. maraisi*	Stofbakkies Farm	AMSF03	MK798023	MK684478	MK775358	MK684455	MK684434
35	*A. koranna*	Tswalu Reserve	DTK01	MK797993	MK684468	-	MK684444	MK684413
36	*A. koranna*	Tswalu Reserve	DTK02	-	MK684472	-	MK684445	MK684415
37	*A. koranna*	Tswalu Reserve	NSS02	MK797994	MK684469	-	MK684443	MK684414
38	*A. longicornis*	Sterkfontein Farm	NLTS01*	JX294207	JX294149	-	JX294100	JX294262
39	*A. longicornis*	Sterkfontein Farm	NLTS02*	JX294208	JX294150	-	-	JX294263

40	*A. alba*	Kwessiewater Farm	AAKA01	MK797999	MK684470	MK775350	MK684437	MK684409
41	*A. olivacea*	Schmidts Drift	AOSC01	MK797995	MK684471	-	-	-
42	*N. africana*	Doornfontein	NKDTK01	JX294185.1	JX294126.1	-	JX294080.1	JX294240.1
43	*N. africana*	Doornfontein	NKDTK03	JX294186.1	JX294127.1	-	-	JX294241.1
44	*N. cedrus*	Cedarberg, Sanddrift	NCCS01	✓	✓	✓	✓	✓
45	*S. arenaria*	Koms farm	NAKA01	✓	✓	✓	✓	✓
46	*S. arenaria*	Koms farm	NAKA02	✓	✓	✓	✓	✓
47	*N. costalis*	Clanwilliam	NCCD02*	JX294188.1	JX294129.1	-	JX294082.1	JX294243.1
48	*N. costalis*	Clanwilliam	NCCD03*	JX294189.1	JX294130.1	-	JX294083.1	JX294244.1
49	*N. karrooa*	Middeldrift Farm	NKMD01	✓	✓	✓	✓	✓
50	*N. karrooa*	Middeldrift Farm	NKMD02	✓	✓	✓	✓	✓
51	*N. karrooa*	Middeldrift Farm	NKMD05	✓	✓	✓	✓	✓
52	*N. karrooa*	Marydale,Swartkopspan	NAMD01*	JX294205.1	JX294147.1	-	JX294098.1	JX294261.1
53	*N. karrooa*	Marydale, Swartkopspan	NAMD02*	JX294206.1	JX294148.1	-	JX294099.1	JX294260.1
54	*N. elongata*	Vanrhynsdorp	NEVD01	✓	✓	✓	✓	✓
55	*N. elongata*	Vanrhynsdorp	NEVD02	✓	✓	✓	✓	✓
56	*N. elongata*	Vanrhynsdorp	NEVD03	✓	✓	✓	✓	✓
57	*S. dilatata*	Galgeberg	SDGG01*	X294222.1	JX294163.1	-	-	JX294276.1
58	*S. dilatata*	Galgeberg	SDGG02*	JX294223.1	JX294164.1	-	JX294111.1	JX294277.1
59	*S. dilatata*	Galgeberg	SDGG03*	-	JX294165.1	-	JX294112.1	JX294278.1
60	*S. dilatata*	Galgeberg	SDGB01*	JX294226.1	JX294168.1	-	JX294115.1	JX294281.1
61	*S. cuspidata*	Worcester	SCBB01*	JX294225.1	JX294167.1	-	JX294114.1	JX294280.1
62	*Sicyoptera* sp. nov.	Welbedacht	SWB01*	JX294237.1	JX294179.1	-	JX294120.1	JX294292.1
63	*Sicyoptera* sp. nov.	Welbedacht	SWB02*	JX294238.1	JX294180.1	-	JX294121.1	JX294293.1
64	*Semirhynchia* sp. nov.	Clanwilliam	SMC02*	JX294209.1	JX294151.1	-	-	JX294264.1
65	*Semirhynchia* sp. nov.	Vanrhynsdorp - Kobee Pass	SV01*	JX294230.1	JX294172.1	-	JX294116.1	JX294285.1
66	*P. palmulata*	Kobee Pass	PPkP02*	JX294236.1	JX294178.1	-		JX294291.1
67	*P. palmulata*	Brandkop	PBK01*	JX294210.1	-	-	-	JX294265.1
68	*P. pilicornis*	Biedou Valley	PPB02*	JX294234.1	JX294176.1	-	-	JX294289.1
69	*P. pilicornis*	Biedou Valley	PPB03*	JX294235.1	JX294177.1	-	-	JX294290.1
70	*P. aeoleoptera*	Biedou' Valley	PAC02*	JX294231.1	JX294173.1	-	JX294117.1	JX294286.1
71	*P. aeoleoptera*	Biedou Valley	PAC03*	JX294232.1	JX294174.1	-	JX294118.1	JX294287.1
72	*P. aeoleoptera*	Biedou Valley	PAC10*	JX294233.1	JX294175.1	-	JX294119	JX294288
73	*N. gracilis*	Worcester	NGW01*	JX294191.1	JX294132.1	-	JX294085.1	JX294246.1
74	*N. gracilis*	Worcester	NGW02*	JX294192.1	JX294133.1	-	JX294086.1	JX294247.1
75	*N. gracilis*	Worcester	NGW03*	JX294193.1	JX294134.1	-	JX294087.1	JX294248.1
76	*B. biremis*	Graafwater	BBGW01*	JX294200.1	JX294142.1	-	JX294095.1	JX294256.1
77	*B. elegans*	Klompbome, Loeriesfontein	BEL01*	JX294202.1	JX294144.1	-	-	-
78	*B. elegans*	Klompbome, Loeriesfontein	BEL02*	JX294203.1	JX294145.1	-	JX294097.1	JX294258.1
79	*Barbibucca sp.*	Wallekraal	BWK01*	JX294199.1	JX294141.1	-	JX294094.1	JX294255.1
80	*Barbibucca sp.*	Knersvlakte	BKP01*	-	JX294181.1	-	JX294122.1	JX294294.1
81	*C. huitti*	Coorow, Western Australia	CS01*	JX294224.1	JX294166.1	-	JX294113.1	JX294279.1
82	*Derhynchia vansoni*	Tswalu - Gosa Dunes	DVT01*	JX294227.1	JX294169.1	-	-	JX294282.1
83	*Derhynchia vansoni*	Tswalu - Gosa Dunes	DVT02*	JX294228.1	JX294170.1	-	-	JX294283.1
84	*Derhynchia*	Tswalu - Gosa Dunes	DVT03*	JX294229.1	JX294171.1	-	-	JX294284.1

	vansoni							
85	*Halterina sp. nov.*	Zandrug 10km north Clanwilliam	HBCZ03*	JX294197.1	JX294138.1	-	JX294091.1	JX294252.1
86	*H .pulchella*	Koeberg	HPCT01*	JX294194.1	JX294135.1	-	JX294088.1	JX294249.1
87	*K. nigroptera*	Knersvlakte	KNK01*	JX294211.1	X294152.1	-	JX294101.1	JX294266.1
88	*K. nigroptera*	Knersvlakte	KNK02*	JX294212.1	JX294153.1	-	JX294102.1	-
89	*Knersvlaktia* sp. nov.	Vyftienmylberg	BVB01*	JX294216.1	JX294157.1	-	-	JX294270.1
Out-group								
90	Crocinae (*Laurhervasia setacea*)	Kelkiewyn Farm	LSKF01	JX294183.1	JX294124.1	-	JX294079.1	-
91	Crocinae (*Laurhervasia setacea*)	Piketberg 'Uitkyk'	CPC01*	JX294182.1	JX294123.1	-	JX294078.1	-

* Above specimen ID indicates sequences retrieved from GenBank.

✓indicates GenBank accession numbers in progress

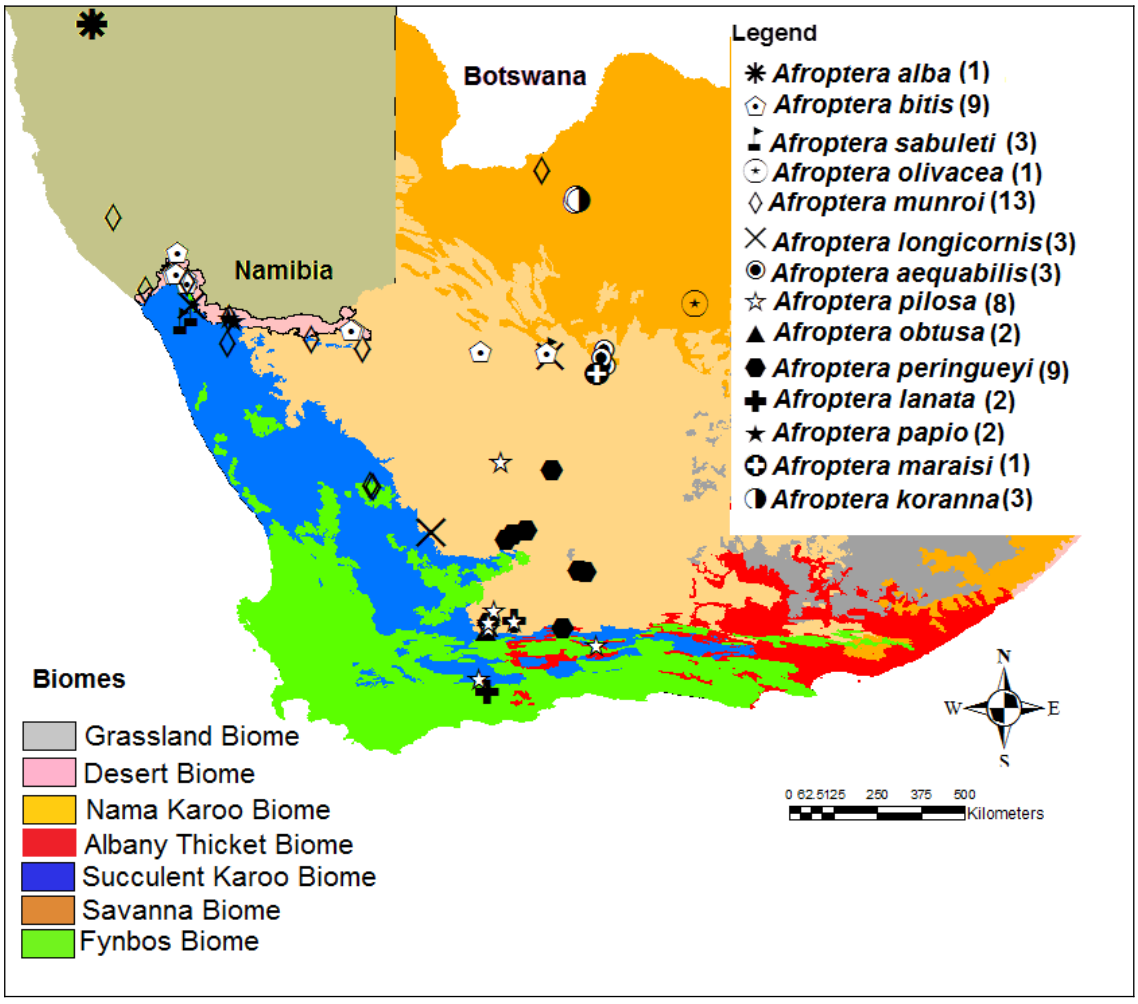

Fig 1. Distribution of the species of *Afroptera* included in the study, from South Africa and Namibia. Numbers in brackets indicate number of specimen records.

Morphological characters

A matrix of 103 morphological characters obtained from adult male external morphology include: head, thorax, legs, forewings, hind wings, and abdomen (Appendix 2). The matrix (Appendix 3) was created using the program MESQUITE (Maddison & Maddison 2003). All multistate characters treated as unordered and equally weighted. For unknown character states, characters were symbolised with '?' (See Appendix 2 for the morphological data matrix).

DNA extraction, amplification

Total genomic DNA was extracted from muscle tissue of a single hind leg of alcohol-preserved specimens and two legs from dried specimens by using the Macherey Nagel (NucleoSpin® Tissue) extraction kit. Five gene regions were selected to construct the phylogenetic relationships among the species of *Afroptera*. Partial sequences of three ribosomal genes; 16S rDNA, 18S rDNA and a portion of the nuclear rRNA large subunit 28S domain 2 and two protein-coding genes, Cytochrome Oxidase subunit I (COI) and carbamoyl-phosphate synthetase-aspartate transcarbamoylase-dihydroorotase (CAD). The oligonucleotide primers used to amplify the five gene regions are summarised in Table 2. To obtain fragments of all gene regions, the genes were amplified in final volume 25µl by using the Emerald Amp MAX HS PCRMastermix (Takara Bio Inc., Otsu, Shiga, Japan). Polymerase chain reaction (PCR) for 16S rDNA was carried out with the following cycling conditions: 90 sec at 94°C initial denaturing, 60 sec at 94°C, 90 sec at 48°C and 90 sec at 72°C for 35 cycles and a final extension of 72°C for 60 sec. The PCR cycling conditions for CO1 were: 90 sec at 94°C initial denaturing, 22 sec at 94°C, 30 sec at 48°C and 90 sec at 72°C for 33 cycles and a final extension of 72°C for 60 sec. For CAD, a re-amplification step was applied to amplify the desired fragments. A '3-cycle' touchdown PCR was used for the first amplification step using the oligonucleotides 54F and 680R. Initial denaturation for 4 min at 94°C followed by 4 cycles (30 sec at 94°C, 30 sec at 51°C, 2 min at 72°C). Thereafter 6 cycles (30 sec at 94°C, 1 min at 47°C, 1 min at 72°C) and 36 cycles (30 sec at 94°C, 20 sec at 42°C, 2.5 min at 72°C) with a final extension of 3 min at 72°C. Following this, 3µl of the original amplified product was used in the same reaction mixture using internal primers 338F/ 365F and 654R/654Rmod under the following conditions: initial denaturation for 4 min at 94 °C followed by 4 cycles (30 sec at 94°C, 30 sec at 51°C, 1 min 20 sec at 72°C). Thereafter 36 cycles (30 sec at 94°C, 30 sec at 45 °C, 1 min 20 sec at 72°C) with a final extension of 3 min at 72°C. Thermal cycling conditions for 28S domain 2 were as follows: initial denaturation for 90 sec at 94°C, followed by 35 cycles of 94°C for 60 sec, primer annealing at 50°C for 60 sec

and elongation at 72°C for 90 sec, followed by a final elongation at 72°C for 3 min. 18S rDNA was amplified using the following protocol: initial denaturation at 94°C for 2 min; 30 cycles of 95°C for 10 sec, 49°C for 10 sec, 72°C for 1 min; final extension at 72°C for 5 min.PCR products for all gene regions were purified using the Macherey Nagel (NucleoSpin® Tissue) purification kit following the manufacturer's instructions. The purified products were sequenced in both directions using Big Dye Terminator v3.1 Cycle Sequencing Kit (PE Applied Biosystems, Foster City, CA, USA). Cycle sequencing products were precipitated using a standard sodium acetate method.

Sequence alignment

Sequence chromatograms were firstly visualised and edited in Chromas (Version 2.0) and then the forward and reverse sequences were assembled in CLC BIO MAIN WORKBENCH version.6 (http://www.clcbio.com). Sequence alignment was implemented in Mega version 7 using ClustalW method (Kumar *et al*., 2016). Sequences for all gene regions were aligned with the default settings and then were checked manually. Ambiguous sites were coded using the appropriate IUB symbols after double-checking the electropherograms for recognisable sequencing artefacts. All sequences were deposited in GenBank.

Table 2. Primers used for PCR amplification.

GENE	PRIMER NAME	SEQUENCE 5'-3'	REFERENCE
Cytochrome Oxidase I	C1-J-2183	AACATTTATTTTGATTTTTTGG	Simon *et al.* (1994)
	Tl2-N-3014	TCCAATGCACTAATCTGCCATATTA	Simon *et al.* (1994)
16S RNA	16Sb2	TTAATCCAACATCGAGG	Vogler *et al.* (1993)
	LRN-N-13398	CGCCTGTTTAACAAAAACAT	Simon *et al*. (1994)
28S RNA Domain 2	D2–3551	CGTGTTGCTTGATAGTGCAGC	Gillespie *et al*. (2005)
	D2–4057	TCAAGACGGGTCCTGAAAGT	Gillespie *et al.* (2005)
18S RNA	18S-Intfw-Sti2	ATCAAGAACGAAAGTTAGAG	Haring & Aspöck (2004)
	18S-Rev1	ATGGGGAACAATTGCAAGC	Haring & Aspöck (2004)
CAD	54F	GTNGTNTTYCARACNGGNATGGT	Moulton &Wiegman (2004)
	680R	AANGCRTCNCGNACMACYTCRTAYTC	Moulton & Wiegman (2004)
	338F	ATGAARTAYGGYAATCGTGGHCAYAA	Moulton &Wiegman (2004)
	365F	GAYATHTTYCCNGCNGGNTGGTC	Winterton *et al.* (2010)
	654R	TCYTTCCANCCYTTYARSGATTTRTC	Winterton *et al*. (2010)

Phylogenetic reconstructions

To construct phylogenetic relationships between the species of *Afroptera*, two data partitions were analysed: Molecular and combined morphological/concatenated molecular datasets. The concatenated molecular dataset was analysed under three molecular algorithms: Parsimony (MP) using the computer software PAUP*4.0b10 (Swofford 2003), Maximum Likelihood (ML) using RAXML-HPC version 8.1.20 (Stamatakis 2014) and Bayesian Inference (BI) using MrBayes version 3.1.2 (Ronquist & Huelsenbeck 2003). The combined morphological/concatenated molecular dataset was analysed with Parsimony and Bayesian methods.

Bayesian inference (BI) was used also to infer the phylogenetic relationship between the genera of the subfamily Nemopterinae.

In the Parsimony analyses, a heuristic tree search protocol with 10 random addition sequences and tree bisection and reconnection (TBR) was employed. All characters were unordered and equally weighted, uninformative characters were excluded from the analysis, gaps were treated as missing data. The branch support was estimated by calculating bootstrap values (Felsenstein 1985) based on 1000 replicates.

For Maximum Likelihood analyses, Maximum Likelihood searches were conducted using RAXML-HPC version 8.1.20 (Stamatakis 2014). To acquire an optimal ML tree, tree searches was performed using the option ML+rapid bootstrapping under the GTRGAMMA model with 1,000 bootstrap pseudo-replicates.

Prior to Bayesian analyses, jModelTest (Posada 2008) was conducted to estimate the best fitting model of nucleotide evolution based on Bayesian Information Criteria (BIC) (Schwarz 1978) (Table 3). Markov Chain Monte Carlo (MCMC) consisted of two independent runs with one cold and three heated chains (0.01) for 30 million generations starting from random trees and sampling every 200 generations. The stationary probability distribution of Markov chains was verfied by measuring the effective sample size (ESS) using the program TRACER v.1.6 (Rambaut & Drummond 2014). The first 37500 (25%) trees were discarded as burn-in.

For the genera in Nemopterinae, the bayesian analysis was run following the same procedure mentioned above, but with MCMC run for 20 million generations and 25000 (25%) trees were discarded as burn-in.

Estimation divergence time

Species divergence times were estimated using the BEAST v.2.5.1 software package (Rambaut & Drummond 2014). The program BEAUti v 2.5.1 (Rambaut & Drummond 2014) was used to generate xml files that were then executable by BEAST. The combined dataset used five partitions, the substitution models were set as unlinked and the molecular clock and trees were set as linked. The favoured substitution models that were chosen by the jModelTest were assigned to each gene. The relaxed lognormal model was employed for molecular clock analysis. The tree prior was set to Yule speciation. A fossil record for the genus *Marquettia* from the Eocene-Oligocene boundary (33.9 mya) (Carpenter 1959) was used to constrain the minimum age of *Afroptera,* where we used the midpoint of 34 million years (my) as a hard-minimum age constraint in an exponential prior. Two independent runs were performed for 10 million generations. The log files of the two runs were combined using the program LOG COMBINER v 2.5.1 (Rambaut & Drummond 2014). The results were then checked for convergence and effective size (ESS) > 200 using TRACER v 1.6. (Rambaut & Drummond 2014). The first 20% of the logs were discarded as burn-in. The resulting trees were also combined, and then interpreted in TREE ANNOTATOR v 1.8.4, and viewed in FigTree v 1.4.3 (Rambaut 2009).

Results

Molecular phylogeny

Subfamily Nemopterinae

The total alignment matrix contained 3318 bp of which 736 bp were from CO1, 863 bp from CAD,≈ 336 bp from 16S, ≈ 791 bp from 18S and ≈ 592 bp from 28S.

The resultant Bayesian phylogram including all available genera supports Sole *et al.* (2013) in that the subfamily Nemopterinae constitutes a monophyletic group with strong Bayesian posterior probability (1.00 PP) (Fig. 2).The analysis revealed two major clades: clade A with (1.00 PP) and clade B with (1.00 PP). Clade A comprises well-supported monophyletic genera: *Afroptera* (1.00 PP)*, Siccanda* (1.00 PP), *Halterina* (1.00 PP), *Nemia* (1.00 PP), *Barbibucca* (1.00 PP), *Nemopterella* (*sensu stricto*) (1.00 PP), *Knersvlaktia* (1.00 PP) and *Palmipenna* (1.00 PP). Within clade A, the genera are clustered into two groups I and II: Clade I includes *Afroptera* which is sister to *Siccanda* and in turn they are sister to *Halterina*.

Clade II includes the sister genera *Nemia* and *Barbibucca* which are in turn are sister to *Nemopterella sensu stricto* and *Knersvlaktia*. The genus *Palmipenna* was recovered as being close relative to all genera in the clade. Clade B includes the genera: *Nemeura*, *Sicyoptera*, *Semirhynchia*, *Chasmoptera* and *Derhynchia*. The genus *Derhynchia* was recovered as the only monophyletic genus in the clade while the remainder of the genera are polyphyletic. The genus *Derhynchia* appears as sister to all genera in the clade.

Genus *Afroptera*

The total alignment matrix contained 3230 bp of which 736 bp were from CO1, 863 bp from CAD, ≈ 330 bp from 16S, ≈ 685 bp from 18S and ≈ 616 bp from 28S. Parsimony analysis for the concatenated molecular dataset resulted in 447 parsimony-informative sites and 10 most equally parsimonious trees with tree length 768 steps (CI = 0.7435; RI = 0.8219). The values of Bayesian Posterior Probability (PP), Parsimony (MP) and Maximum Likelihood bootstraps (MLB) for concatenated molecular datasets are summarised in a Bayesian consensus tree (Fig. 3). Nodes with bootstrap support values above 70% and/or posterior probability above 0.90 are considered as strongly supported nodes (Hillis & Bull 1993; Alfaro & Holder 2006).

All analyses (BI, PB and ML) for concatenated molecular dataset resulted in strong phylogenies with (Bayesian Posterior Probability 1.00 PP; Parsimony bootstrap (PB) 100% and Maximum Likelihood Bootstrap (MLB) 100 %). In addition, all analyses produced similar tree topologies that consisted of two major clades labelled A (1.0 PP; 91% PB; 93 % MLB) and B (1.00 PP; 91% PB; 97% MLB) with *A. alba* Mansell & Abdalla recovered as sister taxon (1.00 PP; 92% PB; 95% MLB) to all the other species (Fig. 3). Major clade A consisted of four sub-clades labelled A1, A2, A3 and A4 (Fig. 3). In BI and ML analyses, the phylogenetic relationships between the four sub-clades were well supported while in MP the sister relationship between the clades A1 and A2 was poorly supported. Sub-clade A1 is strongly supported (1.0 PP; 81% PB; 86 % MLB) with five species recovered representing three sister groups (Fig. 3). The first group comprises the species *A. bitis* (Tjeder, 1967), *A. olivacea* (Tjeder, 1967) and *A. sabuleti* (Tjeder, 1967) with moderate posterior probability (0.78 PP). Within the group, *A. bitis* and *A. olivacea* clustered together with low support (0.5*4* PP; 55% MLB) and in turn, they were placed sister to *A. sabuleti* with (1.00 PP; 75% PB; 87% MB). The second group comprises *A. maraisi* Abdalla & Mansell, 2019 that resolved separately forming a strong sister relationship with other species in the first group (1.00 PP;

75% PB; 87 % MLB). The third group includes *A. aequabilis* (Tjeder, 1967), which was also recovered separately and formed a strong sister relationship with the remainder of the species in the sub-clade A1 (1.00 PP; 81 % PB; 86 % MLB). Phylogenetic relationships among the species in sub-clade A2 were strongly supported by Bayesian analysis and moderately supported by PB and ML analyses (*1*.00 PP; 54% PB; 64% MLB) and two clusters were recovered. One cluster contains *A. longicornis* (Tjeder, 1967), *A. lanata* (Tjeder, 1967) and *A. peringueyi* (Tjeder, 1967) (1.00 PP; 83% PB; 84 % MLB) and in turn, they form a sister relationship with *A. pilosa* (Tjeder, 1967). The phylogenetic relationship between the species of sub-clade A1 and A2 was strongly supported by Bayesian analysis (1.00 PP) and moderately supported by Maximum Likelihood analysis (60% MLB). The sub-clade A3 was recovered with (1.00 PP; 92% MLB) and comprises a single species *A. papio* (Tjeder, 1967), while sub-clade A4 comprises *A. munroi* (Tjeder, 1967) (1.0 PP; 76% PB; 99% MLB). Strong phylogenetic relationships were recovered in the major clade B between *A. obtusa* and *A. koranna* Mansell & Abdalla, 2019, with (1.00 PP; 91% PB; 97% MLB)**.**

Combined morphological/concatenated molecular phylogeny

Parsimony analysis for the combined morphological/concatenated molecular datasets resulted in 540 parsimony-informative sites of 3332 and one most parsimonious tree with tree length 1166 steps (CI = 0.6467; RI = 0.7379). The strict consensus trees with bootstrap support (PB) values are presented in (Fig. 4).

Parsimony analyses for the combined morphological/concatenated molecular datasets resulted in a well-resolved monophyletic tree with high bootstrap support (100 % PB). The tree's topology is strongly congruent with tree topologies resulting from Bayesian and Maximum Likelihood analyses for molecular data. The phylogenetic relationship between sub-clades A1 and A2 resolved poorly in the parsimony analysis of the molecular data, but resolved strongly in the combined morphological/concatenated molecular dataset with bootstrap support (70 % PB). The most significant difference between the topologies of the two datasets is in the position of *A. maraisi* in the sub-clade A1. In the trees resulting from the molecular data, *A. maraisi* is sister to the group comprising *A. bitis*, *A. olivacea* and *A. sabuleti*, while in the tree from the combined morphological/concatenated molecular dataset *A. maraisi* appears as sister to *A. bitis,* although this relationship is weakly supported.

Bayesian analysis for the combined morphological/concatenated dataset also retrieved a very strong phylogeny with high posterior probability (Fig. 5; 1.00 PP) and two major clades (A & B) are manifest. The only difference between this phylogeny and that of the Bayesian analysis of the molecular dataset is in the position of *A. papio*, which is sister to *A. maraisi.*

Table 3. Estimated model parameters for COI, 16S, 28S 18S and CAD for *Afroptera* using JMODELTEST.

Gene	COI	16S	28S	18S	CAD
Length (bp)	736	330	616	685	863
Best-fit model	HKY +I+G	HKY+G	HKY+G	HKY+G	HKY+I
A frequency	0.3357	0.4351	0.3260	0.2551	0.3392
C freqency	0.1564	0.1287	0.1137	0.1744	0.1656
G frequency	0.1036	0.0566	0.11743	0.2417	0.1976
T frequency	0.4043	0.3797	0.3860	0.3288	0.2976
Gamma	1.0530	0.1560	0.1600	0.0270	
p-inv	0.6050				0.8880

Divergence time estimates

The BEAST chronogram is largely congruent with those resulting from Bayesian, Parsimony and Maximum Likelihood analyses for the concatenated molecular dataset. The divergence-time estimate tree is shown in Figure 6. The mean nodal Bayesian divergence time estimates indicated that the stem–node (the root) is estimated to be Early Eocene (53.9; 95% confidence interval: 34.4–81.7 Mya). The molecular clock approach dated the first diversification event within *Afroptera* to the Late Eocene around (36.5; 95% confidence interval: 45.0–33.0 Mya) when *A. alba* split from the rest of the species. Subsequent radiation events occurred in the Late Oligocene approximately (28.5; 95% confidence interval: 38.0–18.0 Mya) when the major clade A split from the major clade B. The radiation of clade A started in the Early Miocene (21.9 Mya; 95% confidence interval: 11.5–32.0 Mya) with the split of sub-clade A4 first, followed by the split of sub-clade A3 in the Middle Miocene around (16.6 Mya; 95% confidence interval: 6.3–25.3 Mya). The split between the sub-clades A1 & A2 occurred approximately (14.0 Mya; 95% confidence interval: 6.0–21.0 Mya). Rapid

speciation within these clades occurred in the Late Miocene through the Pliocene to the Pleistocene (10.4–0.2 Mya).

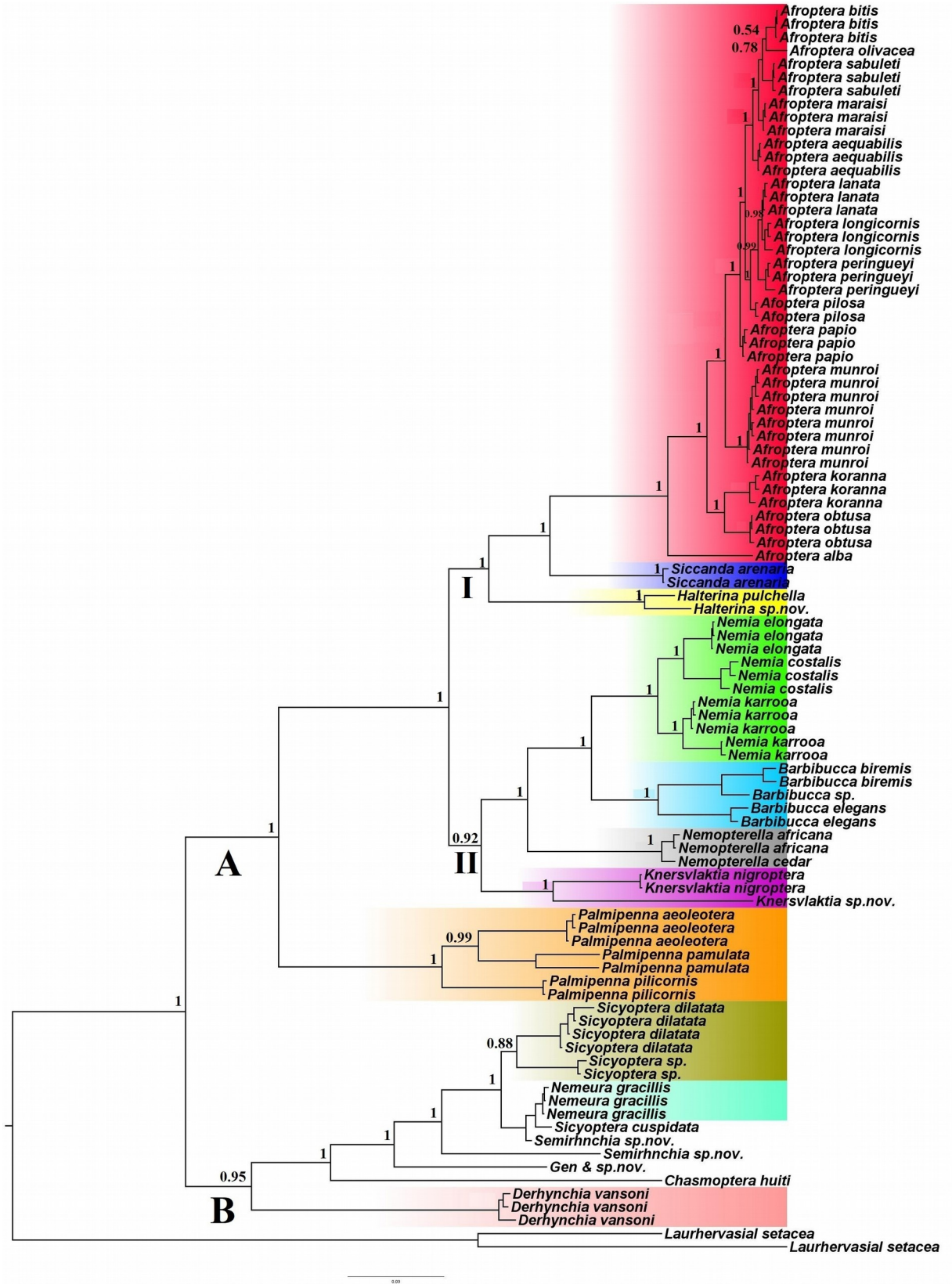

Fig 2. Cladogram of southern African Nemopterinae, including the new genera after splitting *Nemopterella* into *Afroptera*, *Siccanda* and *Nemopterella sensu stricto*. The cladogram is a

50% majority-rule consensus tree resulting from Bayesian analysis of the combined COI, CAD, 16S, 28S and 18S genes, with posterior probabilities (PP).

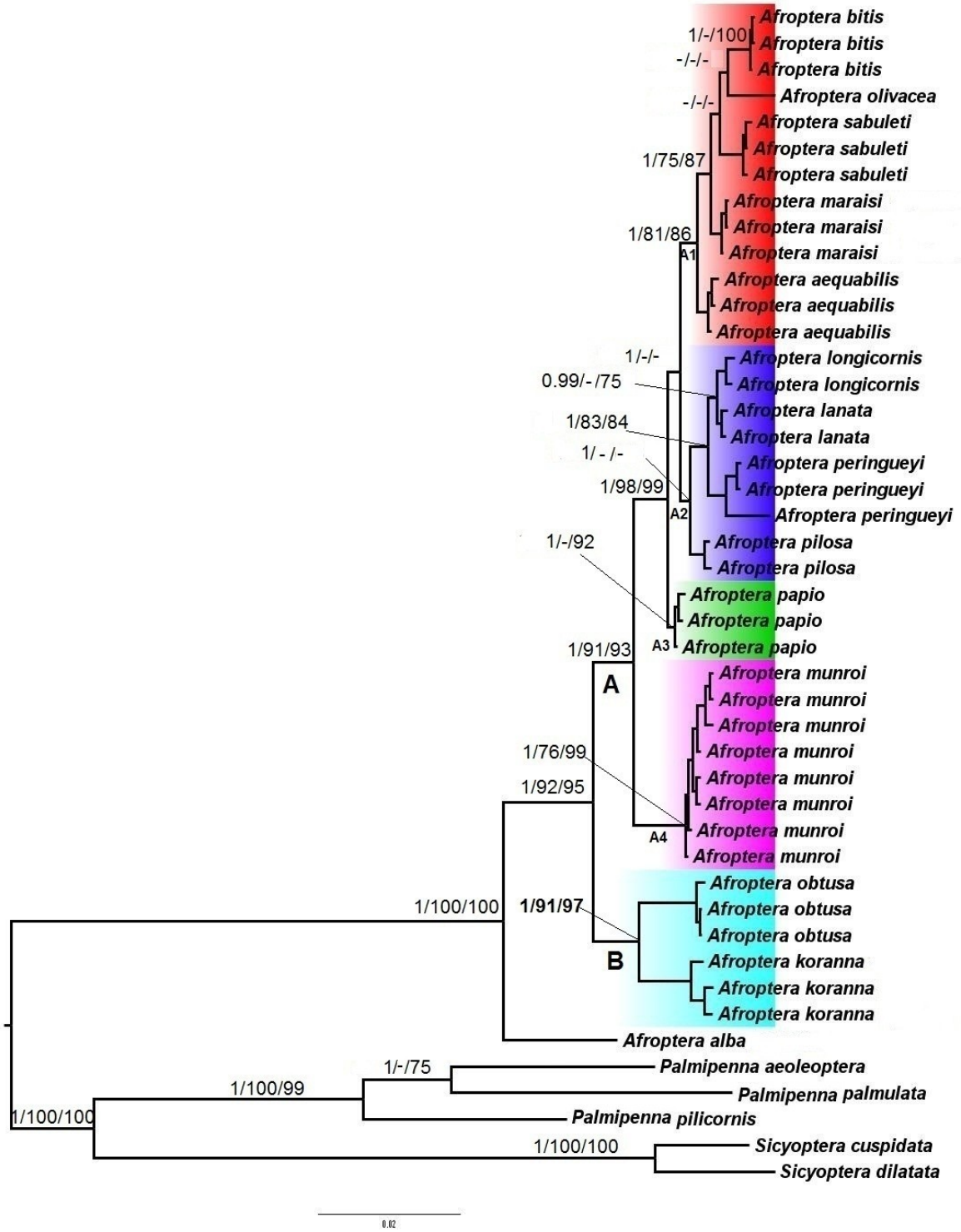

Fig 3. Fifty percent majority rule consensus tree resulting from Bayesian analysis of the combined (COI, CAD, 16S, 28S and 18S) with PP, MP and MLB given, respectively. Dashes (-) on nodes indicate weak/no support. Letters below branches indicate the clade's name.

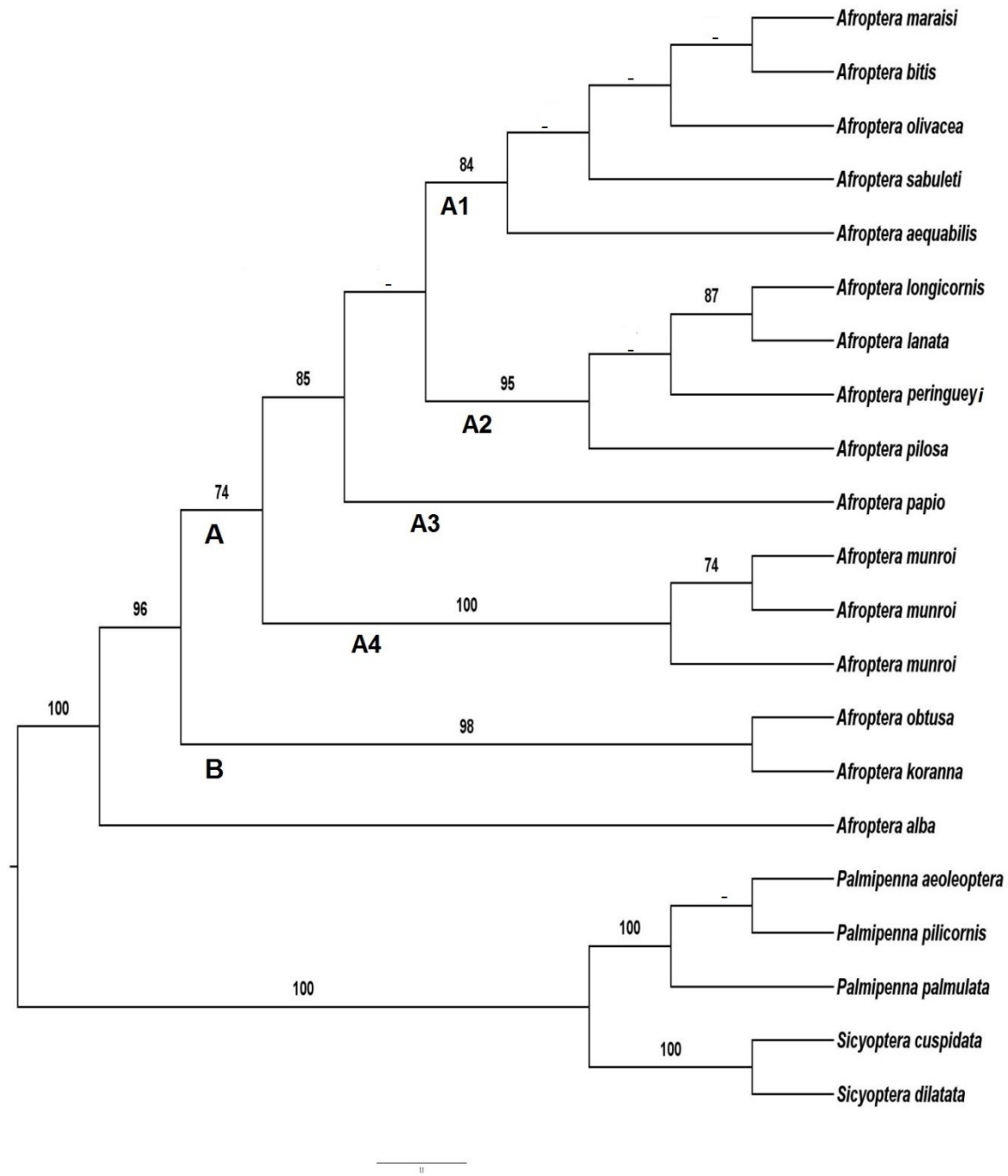

Fig 4. The single most parsimonious tree of the combined morphological/concatenated molecular dataset with bootstrap support values on each branch. Dashes (-) on branches indicate weak/no support.

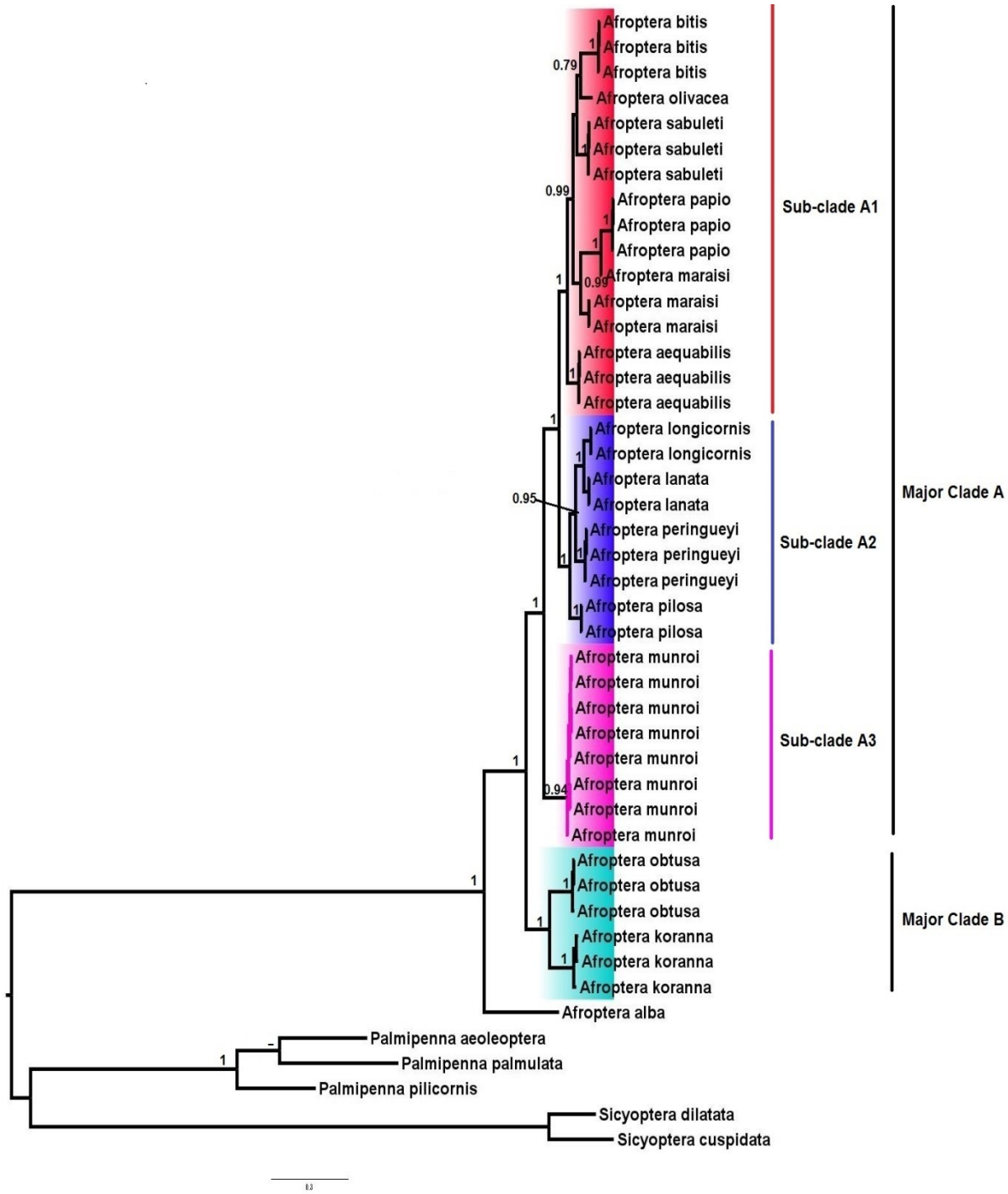

Fig 5. Fifty percent majority rule consensus tree inferred from Bayesian analysis of the combined morphological/concatenated molecular dataset (COI, CAD, 16S, 28S and 18S) with posterior probabilities on each node.

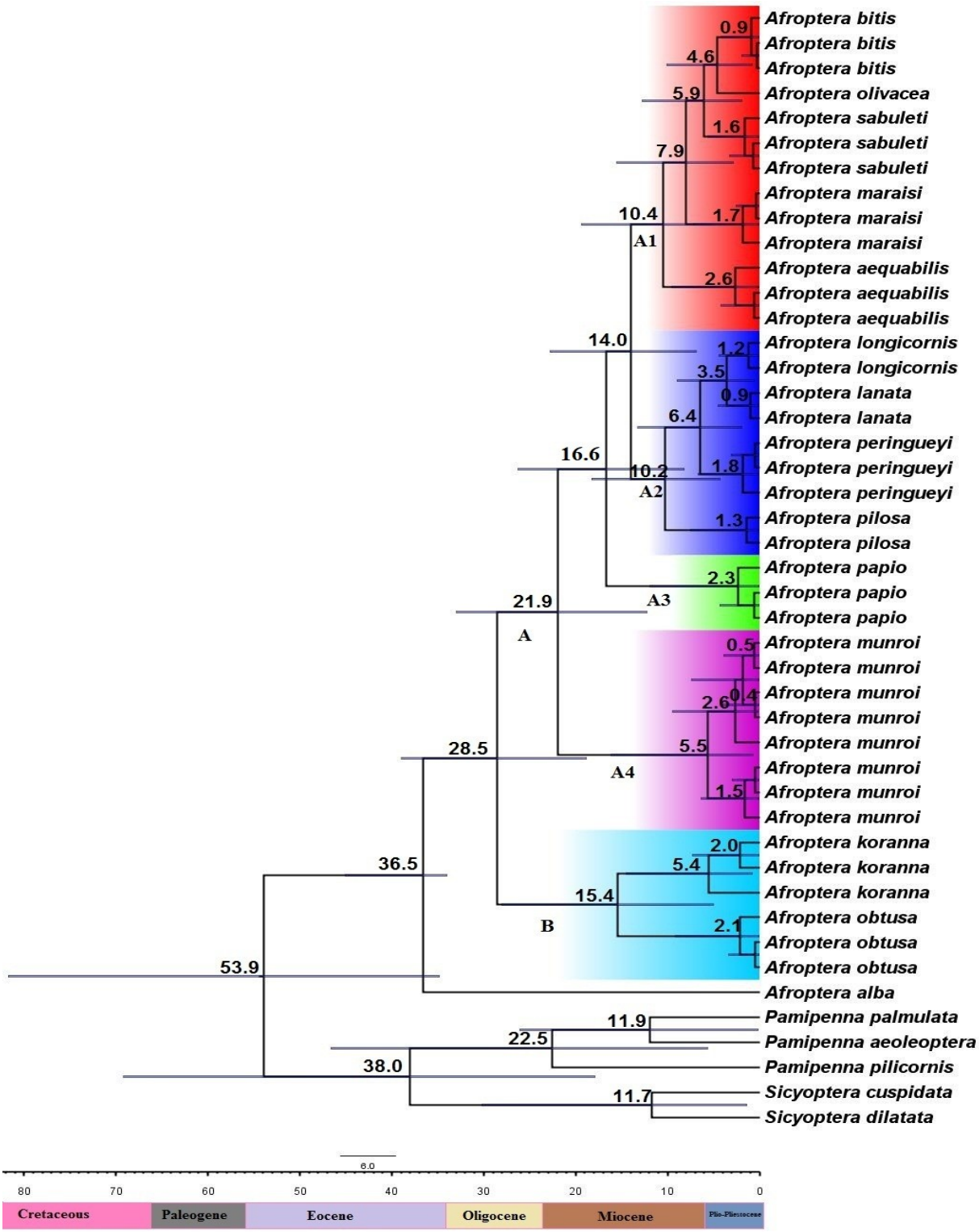

Fig 6. Chronogram resutling from BEAST analyses. Each node represents the mean divergence time estimate and blue bars represent the 95% highest posterior density intervals (HPD) around mean nodal ages. Letters on branches indicate the clade name.

Discussion

Phylogentic relationships

Genus *Nemopterella*

Nemia and *Nemopterella* have always been taxonomically complex genera regarding conclusive characters to differentiate them (Sole *et al.,* 2013). The classification of Tjeder (1967) was based on the presence or absence of pleuritocavae in the species of *Nemopterella* Banks and *Nemia* Navás, respectively. He accordingly assigned the name *Nemopterella* to all species that have pleuritocavae while those that lack the character were assigned to the genus *Nemia.*

Revision of the genus *Nemopterella* by Abdalla *et al.* (2019) indicated that the genus includes groups of species that are in fact morphologically different and consequently suggested the division of genus into three new genera: *Afroptera* Abdalla & Mansell, 2019; *Siccanda* Abdalla & Mansell, 2019 and *Nemopterella* Banks, *sensu stricto*. The key morphological character to distinguish the species of *Afroptera* from *Siccanda* and *Nemopterella sensu stricto* is the presence of the membranous part on the last segment of the antennae. The last segment of the antennae in *Siccanda* and *Nemopterella sensu stricto* terminates in an acute bare tooth (Abdalla *et al.* 2019)

In addition, *Siccanda* is further distinguished from *Afroptera* by a faintly visible light yellowish pterostigma, with the shading over the costals being weakly manifest. *Afroptera* is characterised by a distinct yellowish, brown or dark brown pterostigma and the shading over the costals is very distinct. In addition, *Siccanda* is characterised by a blackish grey body, while the bodies of *Afroptera* species are yellowish, yellowish brown or brown. In addition, in *Siccanda* the frons above the antennae has a pair of yellow transverse spots along the postfrontal suture and the ventral side of the thorax is tinged dark brown, while the species in *Afroptera* lack these characters. *Halterina* species are easily distinguished from those of *Afroptera* and *Siccanda.*

The second group comprising *Nemia*, *Barbibucca*, *Nemopterella sensu stricto*, *Knersvlaktia* and *Palmipenna* were statistically strongly supported as being monophyletic. The sister-group relationship between *Nemia* and *Barbibucca* is supported by the absence of pleuritocavae in both genera. *Barbibucca* is morphologically distinct from *Nemia* and

Nemopterella sensu stricto by having a very robust body and evenly broad hind wings. *Nemopterella sensu stricto* and *Nemia* are also morphologically different. According to Abdalla *et al*. (2019) the species comprising *Nemopterella sensu stricto* are distinguished by having the following characteristics: the presence of pleuritocavae in the fifth tergite of the male abdomen, while in *Nemia* the species lack this character. In addition, the species in *Nemopterella sensu stricto* are characterised by a whitish pterostigma in the forewings, while those of *Nemia* are characterised by a brown or dark brown pterostigma. Although there are distinctions between the two genera, they also manifest many common characteristics that place them into one group. Characteristics include: terminal segment of the antennae terminates in an acute tooth; vertex of head broad with a pair of yellow or dark transverse spots along the postfrontal suture on the frons above the antennae; anal area tinged brown or dark brown; number of costal cells sometimes exceeds 30; the entire hind wing from the base to the apical whitish area bears black setae; thorax and abdomen with distinct brown to dark brown longitudinal mid and lateral-stripes; costals and area between the costals tinged brown to light brown.

Genus *Afroptera*

This is the first molecular and morphological study carried out on the phylogeny of the new southern African genus *Afroptera*. All cladograms obtained from BI, MP and ML analyses revealed well-resolved trees and two major clades were recognised (labelled A & B) with *A. alba* being sister to all the species in the tree (Fig. 3). The major Clade (A) split into four sub-clades: A1 with five species, *A. bitis*, *A. olivacea*, *A. sabuleti*, *A. maraisi* and *A. aequabilis.* Sub-clade A2 comprises two clusters; one cluster consisted of *A. longicornis*, *A. lanata*, *A. peringueyi* and, in turn, they are sister to the cluster comprising *A. pilosa*. Another two sub-clades resolved each with single species: *A. papio* in sub-clade A3 and *A. munroi* in sub-clade A4. Major Clade B comprised two sister species *A. obtusa* (Tjeder, 1967) and *A. koranna* Mansell & Abdalla, 2019. .

The species in sub-clade A1 are very similar in their superficial appearance. They manifest many morphological characteristics that reveal them as close relatives. All the species are characterised by their large sizes, elongated forewings that end with sub-acute apex and the broad pterostigma in the forewings. All have the prescutum entirely covered with black hairs and the abdomen clothed in white hairs, except for *A. bitis* in which the black hairs are restricted to the anterior-lateral sides of the prescutum. The antennae of the species are long,

reaching the pterostigma of the forewing and always ending with the last segment entirely membranous except for *A. aequabilis* in which the antennae are relatively short but still with the last segment completely membranous. In this sub-clade the phylogenetic tree revealed very strong biogeographic patterns in which all the constituent species are confined to the Northern Cape Province.

Sub-clade A2 containing *A. longicornis*, *A. lanata*, *A. peringueyi* and *A. pilosa* was strongly supported by BI (1.00 PP) and weakly supported by PB and ML analyses (54% PB%; 64% MLB). All the species share the markedly striped mesonotum and the reddish yellow vertex of the head. The species, *A. longicornis*, *A. peringueyi* and *A. lanata* formed a well-supported sister-group. Morphologically these three species have mainly white hairs on the mesonotum and black hairs on the anterior lateral portions of the prescutum as well as white hairs on the dorsum and venter of the abdomen. Moreover, they have a brown pterostigma. *Afroptera papio* and *A. munroi* are single species that form sub-clades A3 and A4 respectively, and are sister to all species in the clade. Although *A. papio* and *A. munroi* are morphologically very close to the species in clade A by having elongated forewings and a similar size, *A. papio* is characterised by having the whole mesonotum and abdomen pubescence white without intermingling of black hairs. In addition, *A. munroi* is very distinct from all other species in the clade by having an indistinctly striped thorax and the middle and hind coxae of the legs are devoid of hairs. The close relationship between *A. obtusa* and *A. koranna* in major clade B is supported morphologically by having a reddish yellow vertex, short antennae, same patterns of pubescence on the thorax and abdomen, length of the hind wing's dark area being the same length as the white apical area and legs with a tinged tip to the femurs.

Afroptera alba appears as sister to all species in the major clades A and B. Morphologically, *A. alba* is very distinct from the other species. It is characterised by having a whitish appearance due to an extremely pruinose body, while the others appear yellow or greyish yellow. Environmental factors may account for the difference in body colour of the species in the two lineages. *Afroptera alba* is confined to a desert environment where the habitat is characterised by extreme aridity and heat. To tolerate heat, insects have evolved many physiological, behavioural and morphologically adaptive mechanisms (Sheikh *et al.* 2017). Pruinosity occurs on the body and wings of many insects (*e.g.* Odonata). Odonata use the pruinosity to reflect ultraviolet light and to cool their bodies by reflecting the sun's

radiation (Corbet 1999). As the desert is thermally stressful, characterised by low temperatures in winter and extreme heat in summer, it is conceivable that *A. alba* has evolved physiological and morphological adaptations by developing a pruinose body to survive extreme temperature fluctuations.

Divergence time estimation

The evolutionary histories and distribution of certain taxa are closely congruent with the historical and biogeographic events such as climate change, sea-level fluctuations, plate tectonics, orogenic events and frequent volcanic activity and earthquakes (Crisci *et al*. 2006; Posadas *et al*. 2006; Mantooth & Riddle 2011; Liu *et al*. 2013). On the one hand, topographic heterogeneity may influence species diversification by increasing habitat diversity and by limiting genetic flow between populations inhabiting different ecological niches (Verboom 2015). On the other, climatic oscillations and, in particular, those associated with glaciation periods are the primary factors that enhance species diversification and shaping of distributions (Potts 1996; Demenocal 2004).

Southern Africa has undergone a series of topological and climatic changes marked by plate tectonics, sea level fluctuations and extreme wet and dry periods (Siesser & Dingle 1981; Cowling *et al*. 2009). These changes may be associated with the uplift of the great southern African escarpment (Partridge 1998; Partridge & Mud 1987, 2000) and the global cooling climate that dominated the post to mid-Miocene (Tolley *et al*. 2008).

Species of the southern African genus *Afroptera* have wide but disjunctive distributions in the Fynbos and Succulent Karoo Biomes (Sole *et al*. 2013). Molecular dating of the genus has shown that initial diversification from its most common ancestor (MCA) occurred approximately during the Late Eocene (36.5 Mya) when *A. alb*a diverged from the rest of the group (Fig. 6). This conclusion concurs with Sole *et al*. (2013), who indicated that most genera in the subfamily Nemopterinae were widespread in the Middle Eocene–Middle Miocene (*ca.* 44–11 Mya). There is correlation between the commencement of divergence of the genus in this period and the origin of the circum-Antarctica current 26–35 Mya in the Late Eocene (Feakins & DeMenocal 2010).

The Tertiary epoch witnessed the start of the northward movement of the Australian plate and its separation from Antarctica (NRC 1995). It known that the two continents were

connected during the Paleogene and they remained attached even after the submergence of the shelves that connected them by the mid-Miocene (NRC 1995). However, by the late Eocene the movement of the plate towards the north accelerated, leading to the collision of the northern edge with the island arcs of the Sundra Plate in the Middle- to Late Miocene (Galloway & Kemp 1981). It is believed that the dramatic climate fluctuations near the end and after the Eocene epoch are due to the progressive separation of Australia and Antartica. It resulted in the onset of a circum-Antarctic current, which prevented warm water flowing from the north to Antarctica. The resulatnt cooling of surface water led to the formation of cool deep waters.

By the Late Eocene and Early Oligocene, the glacial ice sheet had developed on Antarctica and the sea level dropped (Zachos *et al*. 2001). During this period, the climate changed from warmer to cooler temperatures, leading to aridity (Zanazzi *et al*. 2007), seasonality and reduction of forest in the equatorial belt and expansion of grassland. In Africa, with the start of the Oligocene global cooling, there was a significant increase in continental erosion associated with the eastern African coastal uplift (Anka & Séranne 2004). These factors collectively engendered a cool climate and aridity along the western coast of southern Africa, leading to fragmented ecosystems and isolation of populations of fauna and flora, which engendered the diversification of many species.

Subsequent radiation in *Afroptera* occurred during the Late Oligocene (28.5 Mya) when the major clade (A) split from the major clade (B). The driving force behind this radiation is presumably the general climatic improvement in the Late Oligocene. By the advent of this period global CO2 levels decreased, the glacial ice sheets rapidly expanded and the global sea level dropped (Feakins & Demenocal 2010). The Benguela current consequently developed, leading to increased aridity with hyper-arid, sporadic habitats acting as centres for species radiation (Linder 2003; Sepulchre *et al*. 2006). The molecular dating results point to a marked increase in the speciation rate of *Afroptera* by the end of the Miocene (10.4–5.9 Mya), which may be correlated with the increased effect of the Benguela current as a result of the growth of the Antarctic ice sheet near the Late Miocene 8.9 Mya (Robert *et al*. 2005). In addition, the Pliocene uplift of the eastern edge of the southern African Escarpment 5.0 Mya (Partridge & Maud 1987) contributed to increasing aridity along the west coast and accordingly speciation, by preventing rain from the Indian Ocean from extending to the west coast, leaving only the winter rains from the Atlantic to dominate (Dupont *et al*. 2011). Molecular dating for most

descendent species of *Afroptera* showed explosive rapid diversification during the Pliocene and throughout the Pleistocene (4.6–0.2 Mya), which may have been facilitated by the prevalent Mediterranean climate in the region and the new arid and semi-arid habitats that dominated post Late Eocene (Cowling *et al*. 2009; Swart *et al*. 2009; Tolley *et al*. 2009). The rapid and recent origin of species owing to extensive habitat changes resulting from the climatic shifts has been documented for many Cape faunal and floral elements. For example, the most recent diversification of many of Cape clades is attributed to the effect of the Antarctic (Benguela) current 5.2 Mya (Axelrod & Raven 1978; Richardson *et al*. 2001; Demenocal, 1995, 2004; Linder 2003). Similarly, many evolutionary studies of fauna confined to the Cape region have correlated the recent speciation to climatic shifts in the era post late Miocene (Swart *et al*. 2009; Tolley *et al*. 2006; Linder *et al*. 2010; McDonald & Daniels 2012; Sole *et al*. 2013).

The close proximity of recently rapid radiation events in the Pliocene and through the Pleistocene for most current *Afroptera* species may explain their close morphological similarity since there was inadequate time for significant differentiation, which makes their distinction challenging in most cases.

The Cape flora consists of many plant families including Asteraceae, Fabaceae, Iridaceae, Ericaceae, Scrophulariaceae, Proteaceae, Restionaceae, Cyperaceae, Orobanchaceae, Rutaceae, Diosmeae, Polygalaceae, Rhamnaceae, Thymelaeaceae and Poaceae (Goldblatt 1978). Among which, Ruchioideae (Aizoaceae) is the second largest family in the southern African flora and the largest family in Namaqualand and in south-western Namibia with about 1600 species (Goldblatt 1978). Molecular dating of the Aizoaceae suggested that the family originated about 3.8–8.7 Mya (Klak *et al*. 2004). As the southern African Nemopterinae and Aizoaceae occur in the same areas of distribution, Sole *et al*. (2013) hypothesised that Nemopterinae may have a diet that relies on Aizoaceae and they may have co-evolved at the same time. The results of Sole *et al*. (2013) of divergence time of Nemopterinae have shown that most genera including *Nemia* and *Nemopterella* (currently *Afroptera, Nemopterella sensu stricto* and *Siccanda*) have undergone recent rapid adaptive radiations during the Late Miocene (*ca*. 6–4.5 Mya), which accords with our results. Although our results strongly strengthened the Sole *et al*. (2013) hypothesis, a recent unpublished study by Chirango (2014) on the gut contents of southern African nemopterids provided different insights on co-evolution. One of the aims of that study was to test the hypothesis of Sole *et al*. (2013) as to

whether the speciation of southern African Nemopteridae follows Aizoaceae radiation as an adaptive radiation; thereby hypothesising that Aizoaceae would be the main diet of this group. By collecting specimens from different types of vegetation and biomes, the study included two Crocinae genera (*Laurhervasia* Navás and *Concroce* Tjeder) and nine Nemopterinae genera (*Palmipenna, Nemopterella*, *Nemia*, *Knersvlaktia*, *Nemeura*, *Sicyoptera*, *Semirhynchia*, *Derhynchia* and *Nemopistha*). An analysis of gut contents in different genera showed that of the 11 genera examined, *Nemopterella* contained a variety of pollens that included about 24 pollen types, *Nemeura* 13 and *Palmipenna* and *Nemia* had 12 each, *Derhynchia* and *Concroce* did not contain any pollen component and the other genera contained 2–4 pollen types (Chirango 2014). The study also indicated that the plant family Asteraceae is the most abundant pollen type in nemopterid's gut contents. It was present in seven of the 11 genera examined and constituted about 100% of *Knersvlakti*a diet and 99% of *Palmipenna aeoleoptera* Picker, 1987, 90% of *Palmipenna pilicornis* Tjeder, 1967 and 57% of *Nemopterella* (Chirango 2014). *Nemia* was found to be the most reliant on Aizoaceae pollens, which reached 75%–94% of the diet. Aizoaceae pollen was less in *Sicyoptera* (15%), *Nemopterella* (10%) and in *Palmipenna* it was less than 10% (Chirango 2014). The study concluded that *Nemia* is the only Nemopteridae genus that may have co-evolved with Aizoaceae, while the remaining genera evolved independently, and their recent diversification was presumably to accommodate the high variety of food resources available (Chirango 2014).

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Appendices

Appendix 1. Morphological characters list and their corresponding states used in this study.

Head

[1] Head vertex coloration: (0) brown; (1) reddish brown; (2) reddish yellow; (3) reddish; (4) yellowish brown; (5) light brown.

[2] Vertex with: (0) markings; (1) without markings.

[3] The yellow hind margin on vertex: (0) present; (1) abbreviated into two yellow portions laterally; (2) absent.

[4] The dark brown mid line along the epicranial suture on vertex: (0) present; (1) absent.

[5] Vertex above antennae convex: (0) present; (1) absent.

[6] Vertex area: (0) broad; (1) narrow.

[7] The yellow transverse spots on the frons above the antennae: (0) present; (1) absent.

[8] The two yellow lateral spots on vertex near the eye margin: (0) present; (1) absent.

[9] Frons below antennae coloured: (0) present; (1) absent.

[10] Eyes: (0) large; (1) small.

[11] Eyes: (0) broadly separated; (1) narrowly separated.

[12] Antennae length: (0) long; (1) short.

[13] Antennae colour: (0) yellow; (1) whitish yellow; (2) brown; (3) dark yellowish; (3) Reddish yellow.

[14] Antennae tip segment: (0) ending in acute tip; (1) ending in membranous tip.

[15] Antennae tip segment: (0) completely membranous; (1) partially membranous; (2) not applicable.

Thorax

[16] Thorax: (0) striped; (1) un-striped; (2) striped partially.

[17] Pronotum pruinose: (0) lightly; (1) absent; (2) strongly.

[18] Pronotum colour: (0) yellow; (1) brown; (2) creamy; (3) greyish; (4) greyish brown; (5) yellowish brown; (6) white.

[19] Pronotum mid-stripe: (0) distinct; (1) indistinct; (2) faintly distinct; (3) appear as spots; (4) extremely distinct.

[20] Pronotum mid-stripe: (0) brown; (1) dark brown; (2) not applicable.

[21] Pronotum lateral-stripes: (0) distinct; (1) faintly distinct; (2) appear as lateral spots; (3) indistinct; (4) extremely distinct.

[22] Pronotum lateral-stripes: (0) brown; (1) dark brown; (2) indistinct.

[23] Pronotum lateral-stripes: (0) broad; (1) narrow; (2) oblique; (3) not applicable (4)

[24] Pronotum setation of fore margin and hind margin colouration: (0) entirely black; (1) entirely white; (2) admixed (3)

[25] Prescutum pruinose: (0) lightly; (1) absent; (2) strongly.

[26] Prescutum colour: (0) Brown; (1) yellow; (2) creamy; (3) greyish; (4) brownish grey; (5) greyish brown; (6) white.

[27] Prescutum with: (0) mid and tow lateral stripes; (1) with mid stripes only; (2) unstriped.

[28] Prescutum mid-stripe: (0) faint; (1) dark; (2) not applicable.

[29] Prescutum with a pair of yellowish lateral spots anteriorly: (0) present; (1) absent.

[30] Space between prescutum and mesoscutum: (0) yellow; (1) black; (2) white; (3) brown; (4) greyish.

[31] Prescutum anterior-lateral hairiness colour: (0) mainly white with few black hairs intermingled; (1) mainly black with few white hairs intermingled; (2) only white; (3) Only black; (4) mainly white with few brownish hairs intermingled.

[32] Prescutum hairiness on the disc: (0) uniformly white; (1) Uniformly black; (2) admixed.

[33] Prescutum hairiness along the sides: (0) white; (1) black.

[34] Prescutum hairiness: (0) short; (1) long; (2) very long.

[35] Prescutum hairiness: (0) dense; (1) sparse.

[36] Prescutum pruinose: (0) present; (1) absent.

[37] Mesoscutum mid-stripe: (0) distinct; (1) indistinct; (2) extremely distinct.

[38] Mesoscutum pruinose: (0) lightly; (1) absent; (2) strongly.

[39] Mesoscutum hairiness colour: (0) black; (1) white; (2) admixed.

[40] Mesoscutum hairiness: (0) sparse; (1) dense.

[41] Mesoscutum hairiness: (0) short; (1) long.

[42] Mesoscutum lateral sides: (0) naked; (1) clothed with hairs.

[43] Mesocutllum mid-stripe: (0) distinct; (1) indistinct; (2) faintly shaded; (3) faintly distinct; (4) extremely distinct.

[44] Mesocutllum hairiness colour: (0) white (1) black.

[45] Mesocutllum pruinose: (0) lightly; (1) absent; (2) strongly.

[46] Mesocutllum hairiness: (0) sparse; (1) dense.

[47] Metanotum pruinose: (0) lightly; (1) absent; (2) strongly.

[48] Metanotum colour: yellow (0) brown; (1) greyish; (2) white.

[49] Metanotum mid-stripe: (0) distinct; (1) indistinct; (2) extremely distinct.

[50] Metanotum hairiness colour: (0) white; (1) black.

[51] Metanotum hairiness: (0) short; (1) long; (2) extremely long.

Legs

[52] Legs coloration: (0) yellow; (1) brown; (2) blackish brown; (3) whitish yellow; (4) whitish yellow.

[53] Legs femur: (0) with whole tip tinged; (1) not tinged; (2) tinged as spots.

[54] Tibiae and last tarsal segment tips: (0) tinged; (1) not tinged ()

[55] Fore coxae hairs: (0) white hairs; (1) black hairs; (2) naked.

[56] Middle coxae hairs: (0) white hairs; (1) black hairs; (3) naked.

[57] Hind coxae hairs: (0) white hairs; (1)black hairs; (2) naked.

[58] Ventral side of thorax: (0) tinged dark; (1) not tinged.

Forewings

[59] Forewings tip: (0) rounded; (1) acute; (2) sub-acute; (3) short rounded; (4) narrowly rounded.

[60] Forewings emargination before the apex: (0) slightly; (1) largely; (2) not found.

[61] Forewings: (0) broad; (1) elongate.

[62] Forewings membrane: (0) hyaline; (1) tinged.

[63] Pterostigma colour: (0) white; (1) brown; (2) dark brown; (3) yellowish brown; (4) Yellowish.

[64] Pterostigma occupying: (0) single costal cell; (1) more than one costal cell.

[65] Costal area beyond pterostigma coloured: (0) whitish; (1) grey brown; (2) brown; (3) Dark brown; (4) Not coloured.

[66] Radial area below and beyond pterostigma tinged: (0) tined all; (1) not tinged; (2) tinged distally towards pterostigma.

[67] Cells before and beyond the pterostigma: (0) tinged; (1) not tinged.

[68] Forewings pterostigma: (0) broad basely; (1) not broad.

[69] Pterostigma: (0) long; (1) short.

[70] Costal colouration: (0) whitish; (1) brown; (2) yellowish.

[71] Costals: (0) shaded; (1) the shading between the costals.

[72] Subcostal area: (0) all tinged; (1) proximally hyaline and tinged distally; (2) not tinged

[73] Proximal Cu and anal area and forking points: (0) tinged; (1) not tinged.

[74] Costals number: (0) > 30; (1) < 30.

Hindwings

[75] Dark area: (0) distinct; (1) indistinct.

[76] Dark area: (0) shorter than the white area; (1) loner than the white area; (2) same length of white area.

[77] Hairiness colour in the white area: (0) white; (1) black.

[78] Hind wings colour before the dark area: (0) pale yellow; (1) pale brown; (2) yellowish brown; (3) pale; (4) dark; (5) greyish; (6) pale creamy white; (7) whitish yellow.

[79] Portion of hindwings before the dark area coloured: (0) white; (1) pale; (2) dark.

[80] Hindwings membrane: (0) hyaline; (1) tinged.

Abdomen

[81] Abdomen pruinose: (0) lightly; (1) absent; (2) strongly.

[82] Abdomen dorsum colouration: (0) yellow; (1) black; (2) brown; (3) yellowish brown; (4) Blackish brown; (5) reddish brown; (6) discoloured; (7) white.

[83] Abdomen venter colour: (0) yellow; (1) black; (2) brown; (3) reddish brown; (4) Yellowish brown; (5) blackish brown; (6) greyish; (7) whitish.

[84] Abdomen dorsum: (0) striped; (1) un-striped.

[85] Abdomen venter: (0) striped; (1) un-striped.

[86] Abdomen dorsal mid-stripe colour: (0) brown; (1) blackish brown; (2) reddish brown; (3) black; (4) not applicable.

[87] Abdomen lateral stripes: (0) distinct; (1) indistinct; (2) extremely distinct.

[88] Presence of pleuritocavae: (0) present; absent (1)

[89] Hairiness colour in dorsum: (0) white; (1) black; (2) mixed.

[90] Hairiness on dorsum: (0) sparse; (1) dense.

[91] Hairiness colour in venter: (0) white; (1) black; (2) mixed.

[92] Hairiness on venter: (0) sparse; (1) dense.

[93] Hairiness of terminal area: (0) black; (1) white; (2) admixed.

[94] Dark area: (0) narrow; (1) broad.

[95] Abdomen: (0) short; (1) long.

[96] Antennae with: (0) long setae; (1) short setae.

[97] Antennae: (0) thick; (1) thin.

[98] Hind wings white area: (0) present; (1) absent.

[99] Length of dark area more than the rest of the hind wing: (0) present; (1) absent.

[100] Dark area: (0) bifurcate; (1) oblique to one side; (2) not applicable.

[101] The dark area with: (0) yellow dot; (1) white dot; (2) not applicable.

[102] Species body appearance: (0) whitish; (1) greyish; (2) yellow.

[103] Species body pruinosity: (0) light; (1) very dense.

Appendix 2. Data matrix of 103 morphological characters of genera *Nemia, Nemopterella* andthe out-group. Missing data are coded with "?"

Taxon	Character No																																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
N. bitis	4	0	1	1	0	0	1	0	1	1	0	1	5	1	0	1	2	6	1	2	3	2	3	1	2	6	2	2	1	2	2	0	0	1	0
N. maraisi	0	1	0	0	1	0	1	1	1	0	0	0	0	1	0	1	0	0	0	1	3	2	3	2	0	3	2	2	1	4	2	0	0	1	0
N. aequabilis	0	1	0	0	1	0	1	1	1	0	1	0	0	1	0	1	0	3	0	1	1	2	3	0	0	3	2	1	1	3	3	0	0	1	0
N. sabuleti.	2	1	0	0	1	0	1	1	1	1	1	1	0	1	0	0	0	5	0	0	0	0	1	0	0	7	0	1	1	1	1	2	0	1	0
N. olivacea	2	1	0	0	1	0	1	0	1	1	1	1	0	1	1	1	0	5	1	2	3	2	3	0	0	7	2	2	1	1	1	2	0	1	0
N .longicornis	2	1	0	0	1	0	1	1	1	0	0	1	5	1	0	0	0	1	0	0	0	0	1	0	0	0	1	1	1	1	3	1	0	1	0
N. peringueyi	3	1	2	0	1	0	1	1	1	1	0	1	2	1	0	2	0	0	0	0	0	0	3	0	0	1	1	1	1	1	3	1	0	0	1
N. lanata	0	1	2	0	1	0	1	0	1	0	0	0	2	1	0	2	0	3	2	1	0	0	3	0	0	3	1	0	1	1	2	1	0	1	1
N. pilosa	4	1	0	0	1	0	1	1	1	0	0	0	0	1	0	2	0	0	0	0	3	2	3	0	0	1	1	0	1	1	3	1	0	1	0
N. koranna	1	1	0	0	1	0	1	1	1	0	0	0	4	1	0	2	0	0	0	0	0	0	3	0	0	1	1	1	1	1	3	1	0	1	0
N. obtusa	2	1	0	0	1	0	1	1	1	0	0	0	4	1	0	0	0	5	0	0	0	0	1	0	0	0	1	2	1	1	3	0	0	1	0
N. munroi	2	1	0	0	1	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1	0	0	0	1	0
N. papio	2	1	1	0	1	1	0	1	1	0	1	1	4	1	0	0	0	5	1	2	3	2	3	0	1	1	1	0	1	0	2	1	0	2	1
N. alba	2	1	0	0	1	0	1	1	1	0	0	0	0	1	0	0	0	2	0	0	0	0	1	0	0	0	1	2	1	1	3	0	0	1	0
P. pilicornis	0	1	0	1	0	1	1	0	1	0	1	2	0	2	1	1	5	1	2	3	2	3	1	1	0	2	2	1	2	4	0	0	1	0	1
P. palmulata	0	2	0	0	0	1	1	0	1	0	0	2	0	2	0	1	6	1	1	0	1	0	2	1	0	2	2	1	1	4	0	0	1	0	1
p. aeoleoptera	1	1	0	1	0	1	1	1	1	0	1	2	0	2	1	1	1	0	2	3	2	3	0	1	0	2	2	1	1	1	2	0	1	0	1
S. dilatata	1	2	1	0	1	1	1	0	1	1	0	5	0	2	0	1	1	0	2	3	2	0	0	0	6	2	2	0	1	4	1	1	1	1	1
S. cuspidata	1	2	1	0	0	1	1	0	0	0	0	2	0	2	1	0	1	1	1	3	2	3	1	0	0	2	2	1	1	0	0	0	0	1	0

Taxon	Character No

A. bitis	0	1	2	1	0	0	0	1	0	0	0	2	3	1	0	1	4	1	1	0	1	1	1	2	1	1	0	1	0	4	1	1	1	0	0
A. maraisi	0	1	0	1	0	1	1	1	0	0	0	0	2	1	0	1	0	1	1	0	0	0	1	2	1	1	0	1	0	4	1	1	0	0	2
A.aequabilis	0	0	0	1	0	0	1	2	0	0	0	0	0	1	0	1	0	2	1	1	2	2	1	2	1	1	0	1	0	4	1	1	0	1	2
A. sabuleti.	0	0	0	2	0	0	1	2	0	0	0	0	0	1	0	1	0	0	1	1	1	1	1	4	1	0	0	2	0	4	1	1	0	1	1
A. olivacea	0	1	0	2	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	1	0	2	0	0	2	0	4	1	1	0	1	1
A. longicornis	0	0	0	2	0	1	1	2	0	1	0	1	0	1	0	1	0	1	1	1	1	1	1	3	0	1	0	2	0	4	1	1	0	0	0
A. peringueyi	0	1	0	2	0	1	1	1	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	2	1	1	0	1	0	4	1	1	0	1	1
A. lanata	0	1	0	1	0	1	1	1	0	0	0	0	2	1	0	1	0	0	0	0	1	1	1	2	0	1	0	2	0	4	1	1	0	0	1
A. pilosa	0	0	0	1	0	1	1	1	1	0	0	0	0	1	0	1	0	1	1	1	1	1	1	2	1	1	0	2	0	4	1	1	0	0	2
A. koranna	0	0	0	2	0	1	1	0	0	0	0	0	0	1	0	1	0	0	1	1	1	1	1	2	1	1	0	1	0	4	1	1	0	1	2
A. obtusa	0	0	0	1	0	0	0	0	0	0	0	0	3	1	0	1	0	0	1	1	1	1	1	3	0	1	0	1	0	4	1	1	1	1	0
A. munroi	0	0	0	1	0	0	1	2	0	1	0	0	0	1	0	0	0	1	1	1	1	1	1	3	0	0	0	2	0	4	1	1	0	0	0
A. papio	1	0	1	1	1	1	1	0	0	1	0	1	0	1	0	1	0	0	1	1	1	1	1	2	1	2	0	1	0	4	1	1	1	1	1
A. alba	0	0	0	1	0	0	1	1	0	0	0	0	2	1	0	1	0	0	1	1	2	2	1	3	0	1	0	1	0	4	1	1	0	1	0
P. pilicornis	2	0	1	1	1	1	3	0	1	1	1	1	2	0	1	0	1	1	0	0	0	1	0	2	0	0	0	0	4	1	1	1	0	0	2
P. palmulata	1	1	1	1	1	0	1	0	1	0	1	1	1	0	1	0	1	1	1	1	1	1	0	2	0	0	6	0	4	1	1	1	1	0	2
p. aeoleoptera	1	1	2	1	1	1	1	2	1	1	1	1	1	1	0	0	1	1	1	1	1	1	0	2	0	0	0	0	4	1	1	0	1	0	2
S. dilatata	2	1	0	0	1	1	1	1	1	1	1	3	2	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	3	0
S. cuspidata	2	0	1	0	0	1	3	0	0	0	0	1	2	3	2	0	0	0	3	0	0	1	0	2	0	1	5	0	2	0	0	1	1	1	1

Appendix 2 (continued).

Appendix 2 (continued).

Taxon	Character No																															
	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103
A. bitis	0	2	1	1	0	0	0	7	0	1	2	7	7	1	1	4	3	0	0	0	0	0	0	0	0	1	1	0	1	2	2	0	0
A. maraisi	0	2	1	1	0	0	0	2	1	1	0	1	1	1	1	4	1	0	0	1	1	1	0	0	0	1	1	0	1	2	2	1	1
A. aequabilis	0	2	1	1	0	2	0	3	1	1	0	4	5	1	1	4	1	0	0	1	0	0	0	0	0	1	1	0	1	2	2	1	1
A. sabuleti.	0	2	1	1	0	2	0	1	0	0	0	3	6	0	1	3	1	0	2	1	1	0	0	0	0	1	1	0	1	2	2	1	1
A. olivacea	0	2	1	1	0	2	0	1	0	0	0	2	2	1	1	0	1	0	0	1	1	0	0	0	0	1	1	0	1	2	2	1	1
A.longicornis	0	2	1	1	0	2	0	3	0	0	1	4	5	1	1	4	1	0	2	1	1	1	0	0	0	1	1	0	1	2	2	1	1
A. peringueyi	0	2	1	1	0	2	0	2	1	1	0	4	5	0	1	3	1	0	0	1	0	0	0	0	0	1	1	0	1	2	2	2	1
A. lanata	0	2	1	1	0	0	0	2	1	1	0	3	3	1	1	4	1	0	0	1	0	0	0	0	0	1	1	0	1	2	2	1	1
A. pilosa	0	2	1	1	0	0	0	2	1	1	0	3	1	0	1	1	1	0	0	1	0	0	0	0	0	1	1	0	1	2	2	2	1
A. koranna	0	2	1	1	0	2	0	2	1	1	0	1	1	1	1	4	1	0	0	1	0	0	0	0	0	1	1	0	1	2	2	2	1
A. obtusa	0	2	1	1	0	2	0	3	0	0	1	5	3	1	1	4	1	0	0	1	0	1	0	0	0	1	1	0	1	2	2	1	1
A. munroi	0	2	1	1	1	2	0	3	1	0	1	2	4	0	1	4	1	0	0	0	0	1	0	0	0	1	1	0	1	2	2	1	1
A. papio	0	2	1	1	0	0	0	4	2	0	0	3	4	0	1	1	1	0	0	1	0	0	0	0	0	1	1	0	1	2	2	1	1
A. alba.	0	2	1	1	0	0	0	3	0	1	1	3	3	1	1	4	1	0	0	1	0	1	0	0	0	1	1	0	1	2	2	1	1
P. pilicornis	2	1	1	0	1	2	0	0	0	1	3	1	0	1	4	1	0	0	0	1	0	0	0	1	0	0	1	1	0	?	?	2	?
P. palmulata	2	1	1	0	0	1	1	1	1	1	4	1	0	1	1	1	1	0	1	1	1	0	0	0	0	0	1	0	0	?	?	2	?
p. aeoleoptera	2	1	1	0	1	2	1	3	1	1	2	1	0	1	4	1	0	0	0	1	0	0	0	0	0	1	0	1	0	?	?	2	?
S. dilatata	0	1	1	0	1	0	5	2	1	1	1	1	0	1	4	1	?	1	0	1	0	0	1	1	1	0	1	0	1	?	?	2	?
S. cuspidata	0	1	1	0	0	0	1	0	0	0	4	1	0	1	4	2	1	1	0	1	0	0	1	0	1	0	1	0	1	?	?	2	?

CHAPTER VI

Common trends in the historical biogeography and evolution of two southern African insect genera, *Macroderes* Westwood, 1842 (Scarabaeidae: Scarabaeinae) and *Afroptera* Abdalla & Mansell, 2019 (Nemopteridae: Nemopterinae)

Abstract

The Greater Cape Floristic Region (GCFR) is one of the most unique biodiversity hotspots worldwide because of its exceptionally rich species diversity. The endemic southern African insect genera *Macroderes* Westwood, 1842 and *Afroptera* Abdalla & Mansell, 2019 have wide but disjunctive distributions within this region. Species of the two genera revealed similar overlapping distribution patterns, suggesting that the same evolutionary history and paleoclimatic and geological processes may have influenced their current distribution and speciation events. The aim of this study was to infer the ancestral historical ranges of these genera, determine the ecological factors that triggered their speciation, and to test the hypothesis that the same biological, paleoclimatic and geological factors led to their current overlapping distributions. The historical ancestral ranges were reconstructed using S-DIVA analysis implemented in RASP (Reconstruct Ancestral State in Phylogenies). Results obtained revealed different spatio-temporal origins for these genera: *Macroderes* originated in the Cape Floristic Region and Namaqualand-Namib Domain during the late mid-Miocene (14.5 Mya), while *Afroptera* originated in the Namaqualand-Namib Domain and Namib Desert Eco-region during the late Eocene (36.5 Mya). Dispersal was indicated by S-DIVA to be the most important ecological factor responsible for the current distribution of the species in both genera. The results provide evidence of association between the latest dispersal and vicariance events that resulted in current allopatric distributions among the individual species of the two genera. The sudden rapid splitting of the major clades and sub-clades in both genera coincided with the initiation of the arid, cool climate of the late Miocene and early Pliocene in the south-western Cape. This was enhanced by the effects of the uplift-driven topographic and climatic changes of the Great Escarpment during Mio-Pliocene, and also by the alternating warmer and cooler periods of the

Pleistocene. The results revealed synchronised lineage splitting in many populations as well as dispersal and vicariance events particularly during the late Miocene and early Pliocene, indicating that the genera had been impacted by similar paleoclimatic and geological processes. The results also indicate that all the extant species of these genera evolved in parallel during the Pleistocene epoch.

Introduction

Determining factors that promoted contemporary biological diversity and distribution of taxa are vital to evolutionary studies. The disjunctive geographical distribution of taxa can be caused by two ecological mechanisms, vicariance and dispersal (Newton 2003). Vicariance is defined as the process by which the geographical range of an organism is fragmented into isolated ranges resulting from the appearance of geographical barriers, such as the formation of mountains, water bodies, islands and habitat fragmentation (Albert & Crampton 2010). The appearance of such barriers may lead to significant shifts in species' ranges, resulting in the separation of a population into allopatric sub-populations and, consequently, reducing gene flow between individuals of these sub-populations, which will engender the differentiation of new taxa. By contrast, dispersal occurs when an individual or individuals move from their provenance (parental area) to a new breeding site or from their current location to another through pre-existing geographical features (Newton 2003; Ronce 2007; Sanmartin 2004; Wilkinson 2001). Such movement of individuals will eventually result in completely isolated populations, preventing the exchange of genetic material and consequently, leading to allopatric speciation (Newton 2003).

The Greater Cape Floristic region (GCFR) (Fig. 1) is famous for its unprecedented floral and faunal endemism and is considered as one of the most important hotspots of biodiversity worldwide (Myers 1990; Born *et al*.2007). This region was formerly restricted to cover the Cape Floristic Region (CFR) (Fig. 1), but was later expanded to incorporate the Little Karoo, Namaqualand, Tanqua Karoo and Hantam-Roggeveld (Born *et al*. 2007), which were then grouped together to be known as the Succulent Karoo (Jürgens 1997; Milton *et al*. 1997; Lechmere-Oertel & Cowling 2001). Both regions, the CFR and the Succulent Karoo are usually considered as separate biodiversity hotspots (Myers *et al*. 2000). The paleoclimatic and

geological changes during the Cenozoic era (*ca.* 66 Mya) had a profound impact on the climate and topography of southern African and, in particular, the GCFR (DeMenocal 1995; Zachos *et al*. 2001; DeMenocal 2004; Trauth *et al*. 2009). Such changes left imprints on the biological diversity and are thought to have been the main driving forces of diversification and distribution of much of the fauna and flora in the region (Tolley *et al*. 2014). The arid, cool climate of the Mio-Pliocene (Deacon *et al*. 1992; Scott *et al*. 1997; Roberts *et al*. 2013) and repeated Pleistocene glacial cycles caused major range shifts resulting in range fragmentation and subsequently population isolation. This scenario of spatial isolation is strengthened by the topographic heterogeneity resulting from the recurrent erosional orogeny of the southern African Great Escarpment during the Mio-Pliocene epochs (Desmet & Cowling 1999; Cowling *et al*. 2005). The formation of this Escarpment dates back to the late Jurassic/early Cretaceous after the fragmentation of Gondwanaland (Partridge & Maud 1987; Gilchrist *et al*. 1994; McCarthy & Rubidge 2005; Moore *et al*. 2009). It runs along the edge of the African plateau, from the northwestern part of Angola, through Namibia and South Africa to the east and north-east of South Africa (Clark *et al*. 2011). It also passes across Lesotho, Swaziland and eastern parts of Zimbabwe and the western border of Mozambique (Clark *et al*. 2011).

The interaction between climatic and topographic factors is thought to have been the catalyst for range fragmentation and subsequent population isolation, prompting allopatric speciation of flora in the Cape region (Adamson 1958; Goldblatt 1978). This example of range fragmentation driven by allopatric speciation has been confirmed in many Cape faunal elements (Makokha *et al*. 2007; Swart *et al*. 2009; Tolley *et al*. 2006, 2008, 2009; Daniels *et al*. 2007, 2009; Sole *et al*. 2013; Barlow *et al*. 2013; Switala *et al*. 2014; Matenaar *et al*. 2018).

The insect genera *Macroderes* Westwood, 1842 (Scarabaeidae: Scarabaeinae) and *Afroptera* Abdalla & Mansell, 2019 (Nemopteridae: Nemopterinae) are primarily endemic to South Africa, with some species in both genera recorded from southern Namibia. The genera are characterised by numerous fragmented populations within the GCFR and Namibia. Members of both genera are adapted to the arid and semi-arid regions of South Africa and Namibia (Tjeder 1967; Frolov & Scholtz 2005; Sole *et al.* 2013; Abdalla *et al*. 2018; Abdalla *et al.* 2019). *Macroderes* ranges from southern Namibia and extends across the Richtersveld in Namaqualand in the north of South Africa to Cape Agulhas in the south within the CFR. One species, *Macroderes bias*

(Olivier, 1789) is recorded from the south-eastern Cape (Frolov & Scholtz 2005; Abdalla *et al*. 2018). Likewise, the distribution of *Afroptera* is very similar to that of *Macroderes*, as most of the ranges of the species are also confined to Namaqualand and extend southwards to the CFR with some species extending their ranges into the neighbouring Nama Karoo and Savanna Biomes (Tjeder 1967; Abdalla *et al.* 2019). Some *Afroptera* species occur in southern Namibia, their ranges extend as far south as the Succulent Karoo and the Nama Karoo Biomes (Tjeder 1967; Abdalla *et al.* 2019). These disjunctive and overlapping patterns of distribution of the two genera suggested their common historical biogeography. We hypothesised that the historical biogeographical patterns and diversification processes of the two genera were influenced by similar past climatic and geological changes during the Late Cenozoic, and consequently mirror each other's pattern of distribution.

The aims of this study were to first infer the ancestral historical ranges of both genera; second, to investigate the ecological mechanisms that are responsible for the diversification and the current distribution of the species of both genera; and third, to test the hypothesis of common historical climatic and geological factors that contributed to their current overlapping patterns of distribution.

Methodology

Taxon sampling, DNA amplification and gene sequencing

The selected in-group taxa of the genus *Macroderes* include thirteen described species of 21 and one undescribed species. Three species of *Anonychonitis* (Janssens, 1950), *Phalops* (Erichson, 1847) and *Caccobius* (Thompson, 1859), sister genera of *Macroderes* (Mlambo *et al*.2015) were chosen as out-groups. Their their corresponding sequences were obtained from GenBank. Sequences of *Macroderes oreatus* Abdalla & Deschodt, 2018 and some additional sequences of *M. mutilans* Kolbe, 1908, *M. minutus* Frolov & Scholtz, 2005 and *M. amplior* Frolov & Scholtz, 2005 were obtained from Sole *et al*. (2010).

Afroptera sequence sampling included 14 of the 28 described species. Two representatives from the genus *Sicyoptera* Navás, 1910 and three from *Palmipenna* Tjeder, 1967 were obtained

from Sole *et al*. (2013), and selected as out-groups. All species studied, along with their localities, are shown in Table (1) of chapters (III) and (V), respectively.

For the phylogenetic reconstruction of *Macroderes* and *Afroptera*, DNA extraction, amplification and sequencing of two protein-coding genes: Cytochrome Oxidase subunit I (COI) and carbamoyl-phosphate synthetase-aspartate transcarbamoylase-dihydroorotase (CAD) and partial sequences from two ribosomal genes: 16S ribosomal RNA (16S rRNA) and a portion of the nuclear rRNA large subunit -28S (28S rRNA) domain 2 were carried out following the same procedures as described in Chapters (III) and (V) respectively. An additional gene region, the ribosomal gene 18S rDNA, was used to infer interspecific phylogenetic relationships of *Afroptera* species (see chapter V).

Phylogenetic analyses

Two phylogenetic procedures were used to infer the phylogenetic relationships among the species of *Afroptera* and *Macroderes*: Bayesian inference (BI) and Maximum Likelihood (ML).

Bayesian analyses

The analyses were carried out using MrBayes version 3.1.2 (Ronquist & Huelsenbeck 2003). Prior to the analyses, the best-fit models of nucleotide substitution for each data partition were determined according to the Bayesian Information Criteria (BIC, Schwarz 1978) as implemented in jModelTest (Posada 2008). Two separate runs were performed with the following setup for each run: Four Markov chains with 30 million generations and the temperature of the heated chains was to 0.1. Trees were sampled every 200 generations and the first 37 500 (25%) trees were discarded as burn-in.

Maximum Likelihood

Analyses were carried out using Randomized Axelerated Maximum Likelihood (RaxML) version 8.1.20 (Stamatakis 2014). The best tree with highest maximum likelihood values was obtained after executing the analyses in five different instances using the option of ML and rapid bootstrapping under the General Time Reversible (GTR) model of nucleotide substitution with 1,000 bootstrap pseudo-replicates.

Divergence time estimation

For both genera, the age of divergence of each node was estimated using the software program BEAST version 1.4.8. (Drummond & Rambaut 2008), with the input file generated in BEAUti (Drummond & Rambaut 2008), following the procedure was outlined in chapters III and V.

Biogeographic inference

Ancestral biogeographical area reconstruction

To gain a better understanding of the biogeographic history of *Macroderes* and *Afroptera* lineages, the Statistical-Dispersal Vicariance Analysis method (S-DIVA) (Yu *et al.* 2010) was used as implemented in the software program RASP v3.2 (Reconstruct Ancestral State in Phylogenies) (Yu *et al*. 2015). The final MCC tree derived from BEAST analysis mentioned above of each genus was used to reconstruct the possible ancestral historical ranges after trimming duplicate representatives for each species. One species from the out-group was used to polarise the tree. The species of both genera were given a code as being present/absent based on their known contemporary distribution areas in South Africa and Namibia (Fig. 1). The areas are: (A), Namaqualand-Namib Domain (NND); (B), Hantam-Tanqua Roggeveld (HTR); (C), Cape Floristic Region (CFR); (D), Nama Karoo Biome (NKB); (E), Savanna Biome (SB); (F) Namib Desert Eco-region; (NDE). The maximum number of areas of distribution for *Macroderes* was set to two as some species were recorded from two areas, while that of *Afroptera* was set to three.

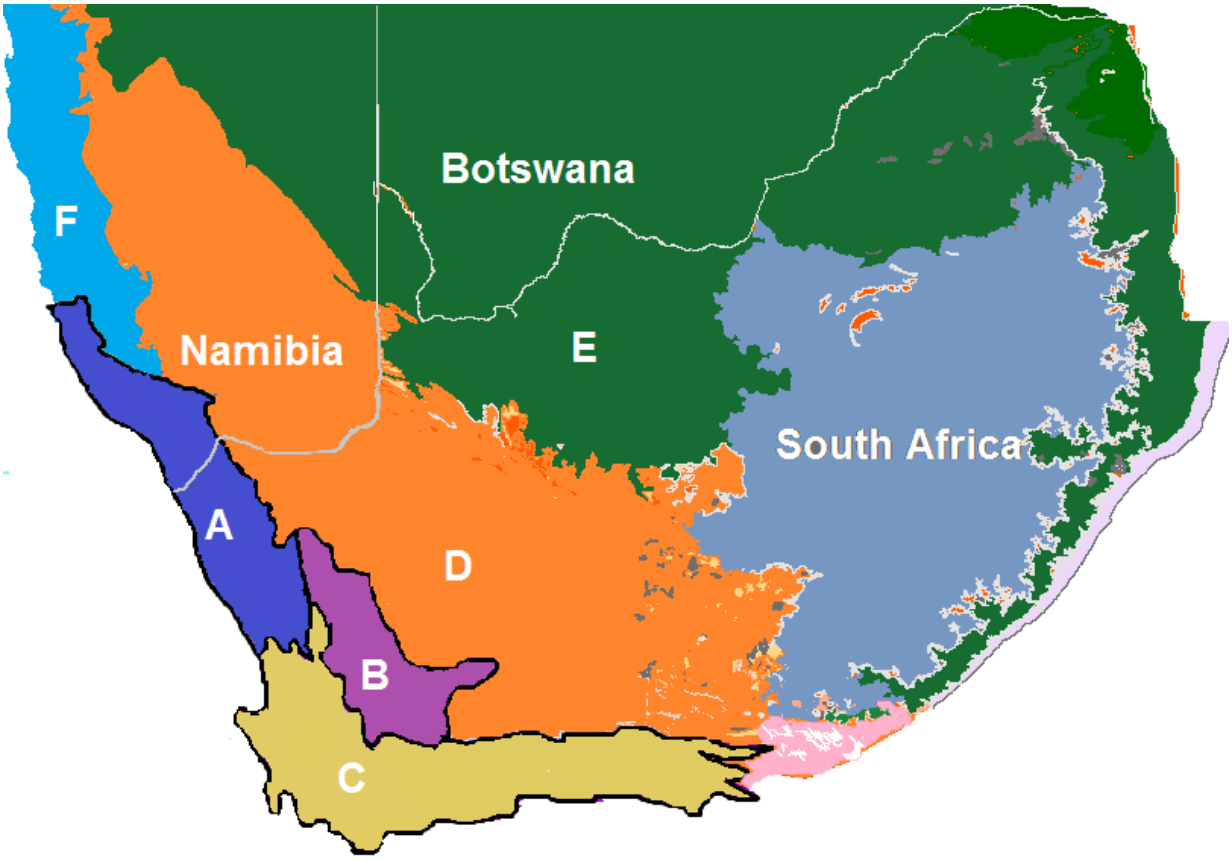

Figure 1. A colour-coded map showing the biomes in which the species of *Macroderes* and *Afroptera* occurred**. A**: Namaqualand-Namib Domain (NND), **B**: Hantam-Tanqua Roggeveld (THR), **C**: Cape Floristic Region (CFR), **D**: Nama Karoo Biome (NKB), **E**: Savanna Biome (SB), **F**: Namib Desert Eco-region (NDE).

Results

Phylogenetic relationships and Divergence time estimation of *Macroderes* and *Afroptera*

The phylogenetic relationships among the species of *Macroderes* and *Afroptera* and their time of divergence are shown in chapters (III) and (V) respectively.

Historical biogeography of *Macroderes*

The historical biogeographic origins of *Macroderes* and *Afroptera* are shown in Figs 2 and 3, respectively. Results of the S-DIVA analysis indicate that the most recent common ancestors of *Macroderes* probably originated in the Cape Floristic Region or the Namaqualand-Namib Domain and the Cape Floristic Region together (A or AC, node 18 in Fig. 2). The analysis suggests that the contemporary distribution of the genus was shaped by six dispersals and four vicariance events. A dispersal event at node 18 (Fig. 2) split the *Macroderes* into the Namaqualand-Namib Domain and CFR (AC, node 16) approximately 38.9 Mya. The most recent common ancestors of the genus split vicariously during the late mid-Miocene (14.5 Mya) into two major clades: A in the CFR (C, node 14 in Fig. 2) and B in the Namaqualand-Namib Domain (A, node 17). The most recent common ancestors of clade A underwent successive dispersals and cladogenesis events within the CFR at different times during the evolutionary history of the genus. Most of the resultant descendants of clade A occupied the CFR (C), representing the most recent common ancestors of the sub-clade A1 (node 8 in Fig. 2) and A3 (node 15 in Fig. 2). A few descendants of the clade, representing the most recent common ancestors of sub-clade A2 then dispersed to occupy the area between the Hantam-Tanqua Roggeveld and the CFR (BC, node 13 in Fig. 2). Part of sub-clade A1 dispersed to a region located between the Namaqualand-Namib Domain and CFR (AC, node 3, in Fig.2). The most recent common ancestors of these descendants (node 3) diverged vicariously into two lineages: one in the Namaqualand-Namib Domain (A, node 2 in Fig. 2) while the other inhabited the CFR (C, node 4 in Fig. 2). By the advent of the late Miocene, the most recent common ancestors of sub-clade A2 underwent subsequent sequential vicariance events in 10.3 Mya and in 9.6 Mya (node 13, 12 in Fig. 2). The first event resulted in the division of the most recent common ancestors of the sub-clade into two lineages, one in the Hantam-Tanqua Roggeveld (B), while the second dispersed to an area probably between Namaqualand-Namib Domain and CFR (AC, node 12 in Fig. 2). The second event led to the split of the most recent common ancestors of the second lineage (node 12) into two newly isolated groups; one in the Namaqualand-Namib Domain (A) and the other in the CFR (C).

Historical biogeography of *Afroptera*

A different biogeographic history was suggested by S-DIVA for the most recent common ancestor of *Afroptera*. The analysis suggests the Namaqualand-Namib Domain, CFR and Namib

Desert Eco-region (ACF node 15 in Fig. 3) as possible biogeographic centres of origin of the most recent common ancestor of the genus. Results of the S-DIVA analysis indicate dispersal as the most likely agent responsible for the present-day distribution of the genus, with 18 dispersal versus four vicariance events. A dispersal event at node 15 (Fig. 3) split the genus *Afroptera* into the Namaqualand-Namib Domain and Namib Desert Eco-region (AF, node 14) approximately 53.9 Mya. An early vicariance event in the late Eocene 36.5 Mya (node 14 in Fig. 3) led to the split of the *A. alba* lineage to the north, in the present-day Namib Desert Eco-region, from the most recent common ancestor of clades A and B in the south, in the Namaqualand-Namib Domain (A, node 12 in Fig. 3). Clade A diverged from clade B 28.5 Mya and occupied the Namaqualand-Namib Domain (A, node 10 in Fig. 3), while clade B dispersed to an area somewhere between the Namaqualand-Namib Domain and Savanna Biome (AE, node 13, Fig. 3). Part of clade A, represented by sub-clade A4, occupied the Namaqualand-Namib Domain (nodes 11 in Fig. 3), however, part of sub-clade A4 later dispersed into areas of the Namaqualand-Namib Domain, Hantam-Tanqua Roggeveld and Nama Karoo Biome (ABD). The majority of the descendants of clade A dispersed to occupy either the area of Namaqualand-Namib Domain and Nama Karoo Biome, or Namaqualand-Namib Domain (AD or A, node 9 in Fig. 3). Further dispersal of these descendants resulted in two isolated groups: the first represents the sub-clade A3 that occupied the area of the present-day Namaqualand-Namib Domain, while the second group dispersed into Namaqualand-Namib Domain and Nama Karoo Biome or Nama Karoo Biome or Namaqualand-Namib Domain (node 5 in Fig. 3). However, further dispersal of this last group resulted in two newly isolated lineages. The first comprised the most recent common ancestor of the sub-clade A1 which inhabited the present-day Namaqualand-Namib Domain and Nama Karoo Biome or Nama Karoo Biome (AD or D, node 4 in Fig. 3). The second then possibly dispersed into the Namaqualand-Namib Domain or Nama Karoo Biome, and includes ancestors of sub-clade A2 (nodes 8 in Fig. 3). The ancestors of sub-clade A1 underwent two successive dispersal events eastwards into the Nama Karoo Biome (D, in Fig. 3) and an additional third dispersal wave but to an area not fully identified by the analysis (ADE or AD or A, node 2 in Fig. 3). However, the ancestors of the last dispersal wave dispersed further and diverged into two isolated lineages: one settled in the Namaqualand-Namib Domain (A) while the area of the second lineage not fully determined by RASP remained ambiguous (ADE or DE or AE, node 1 in Fig. 3). A vicariance event (node 1 in Fig. 3) resulted in two isolated groups. The first settled in the Namaqualand-Namib Domain and Nama Karoo Biome (AD) while the

second colonised the Savanna Biome (E). The most recent common ancestor of sub-clade A2 in the Namaqualand-Namib Domain or Nama Karoo Biome (A or D, node 8 in Fig. 3) underwent three dispersal events during the evolutionary history of the sub-clade. This resulted in three isolated lineages: the first dispersed to the Namaqualand-Namib Domain, CFR and Nama Karoo Biome (ACD) while the second dispersed to the Namaqualand-Namib Domain and Nama Karoo Biome (AD, node 7 in Fig. 3). The third lineage dispersed to the Namaqualand-Namib Domain, CFR and Nama Karoo Biome or CFR and Nama Karoo Biome or Namaqualand-Namib Domain and CFR (ACD or CD or AC, node 6 in Fig. 3). A vicariance event in the most recent common ancestor of the third lineage (node 6 in Fig. 3) gave rise to two isolated lineages; one in the CFR (C) and another in the Namaqualand-Namib Domain and Nama Karoo Biome (AD).

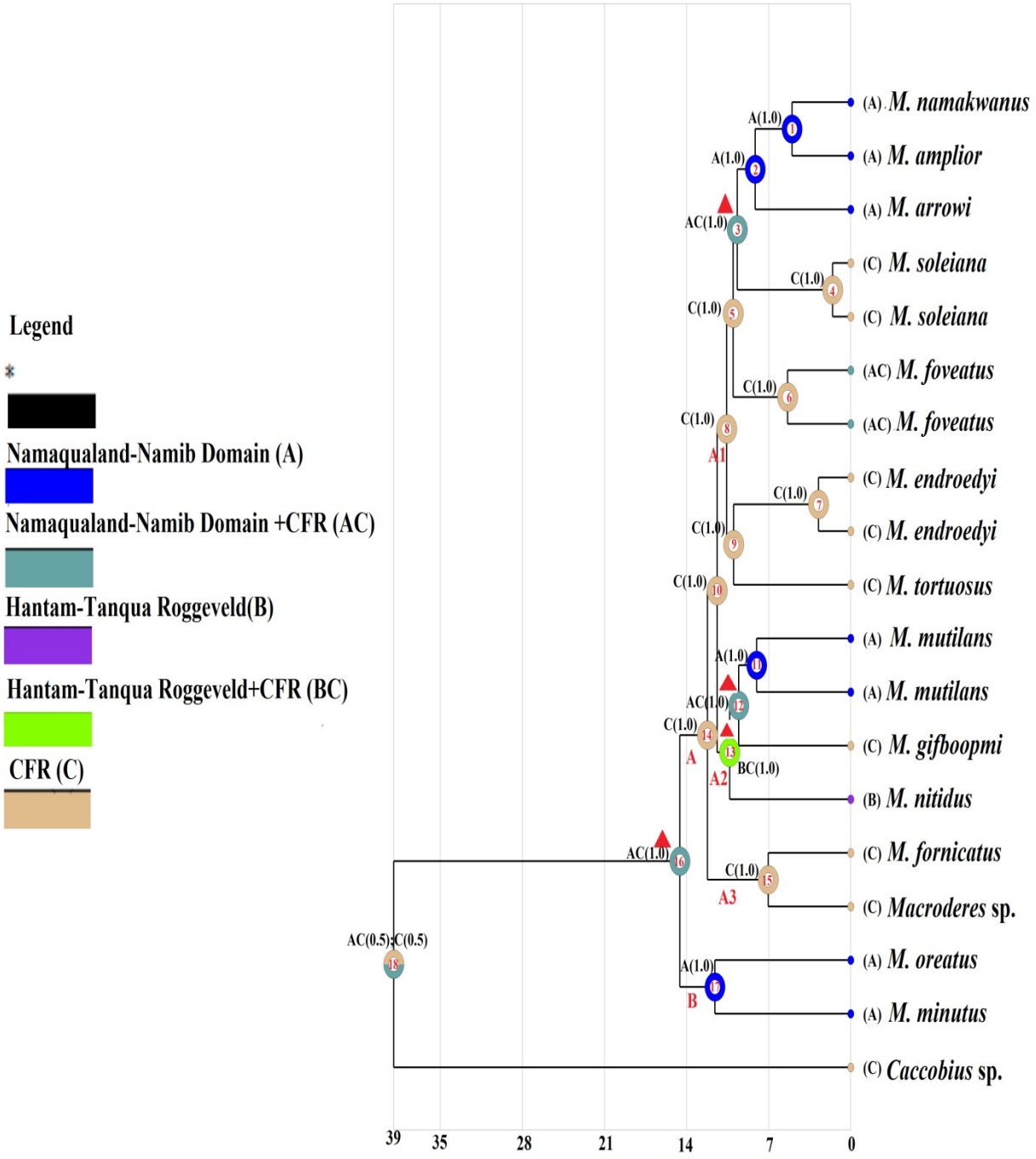

Figure 2. Ancestral area reconstruction of *Macroderes* using Statistical-Dispersal Vicariance Analysis (S-DIVA). The most likely ancestral ranges are indicated by colour-coded pie charts at each node. Capital letter/s on each node indicates the area code. Red triangles indicate vicariance events on these nodes. Legend for all areas of species distribution and the combinations of areas are shown on the left of the tree.

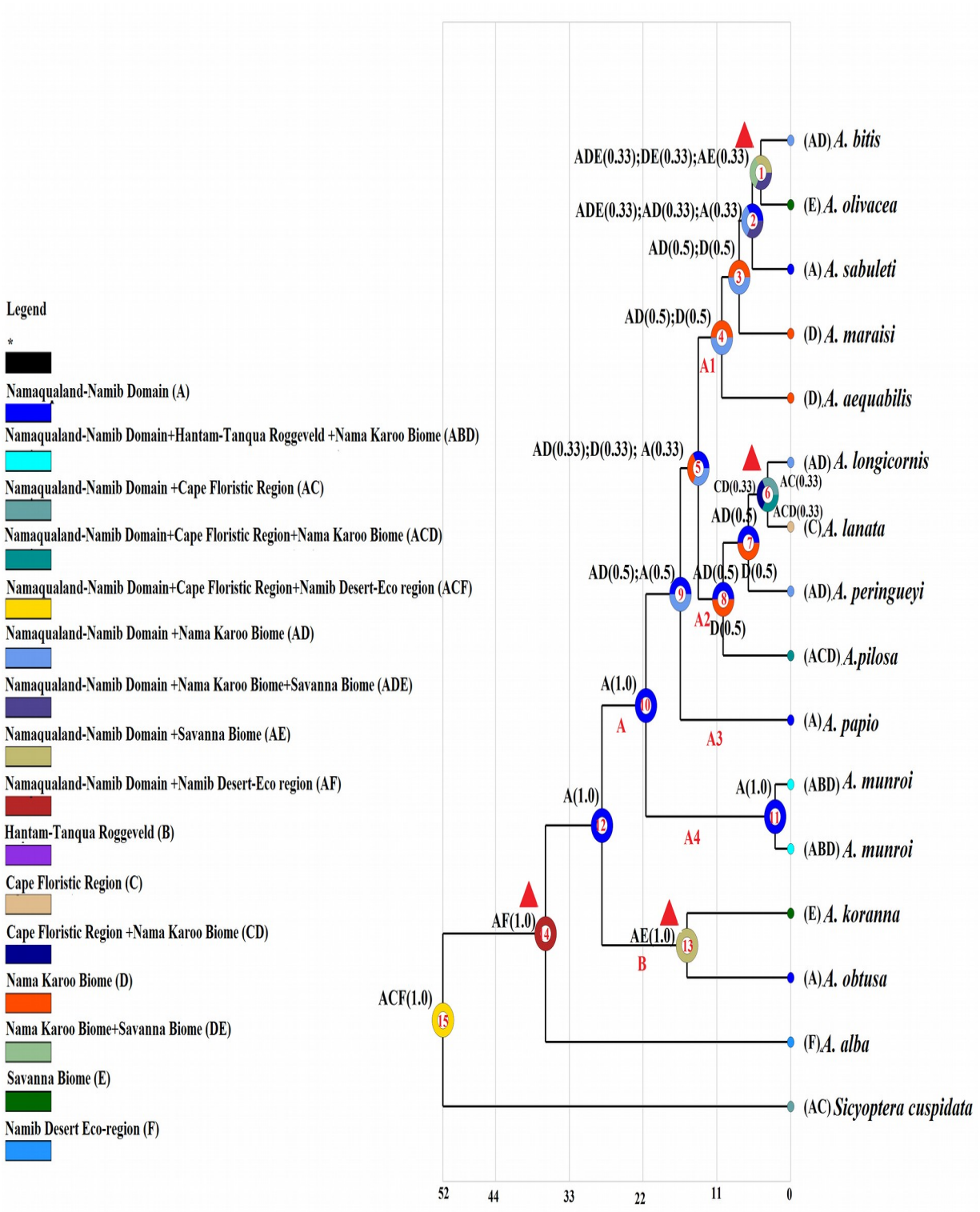

Figure 3. Ancestral area reconstruction for *Afroptera* species using Statistical-Dispersal Vicariance Analysis (S-DIVA). The most likely ancestral ranges are indicated by colour-coded pie charts at each node. Capital letter/s on each node indicate the area code. Red triangles

indicate vicariance events on these nodes. Legends for all areas of species distribution and the combinations of areas are shown to the left of the tree.

Discussion

Historical biogeography

Results of the historical biogeographic reconstruction revealed that the speciation processes and contemporary distribution of the species in *Macroderes* and *Afroptera* were engendered by dispersal rather than vicariance events. Although dispersal is not the principal distributional driving force in the southern hemisphere biotas (Sanmartin & Ronquist 2004), particularly for flightless taxa such as *Macroderes*, a recent study by Matenaar *et al*. (2018) has emphasised its importance.

Genus *Macroderes*

The results provided here indicate that the ancestor of *Macroderes* originated in the CFR or in the Namaqualand-Namib Domain and CFR (node 18 in Fig. 2). A dispersal event at the root of the tree (Fig. 2) led to the split of the genus approximately 38.9 Mya, which subsequently migrated into the Namaqualand-Namib Domain and CFR (AC, node 16 in Fig. 2). The vicariant splitting of the genus during the end of the late midMiocene (14.5 Mya) resulted in two major clades: clade A which settled in the CFR (C, node: 14) and clade B which inhabited the Namaqualand-Namib Domain (A, node: 17). This divergent event is in accordance with the Miocene uplift of the subcontinent that affected the topography of the GCFR by raising the Great Escarpment, leading to erosion along the south-western coast, and the incision of major river valleys in lowlands and mountains (Partridge & Maud 1987, 2000; Cowling *et al.* 2009). The uplift also edaphically affected the lowland habitats by eroding over the land surface leading to the development of a new clay soil layer (Cowling *et al.* 2009; Bytebier *et al*. 2011; Dupont *et al* 2011; Schnitzler *et al*. 2011; Schreiner *et al*. 2013). Such topographic and landscape changes could have influenced *Macroderes* habitats and consequently induced its diversification. The radiation of the major clades A and B of *Macroderes* in the late Miocene suggests their association with the late Miocene cool and arid climate that pervaded the Cape region (Tyson & Partridge 2000). In addition, ongoing effects of the uplift of the Great Escarpment, led to

progressive aridification, as a result of the rain shadow, which was intensified by the effects of the cold Benguela current (Partridge & Maud 1987). The ancestral state reconstruction indicates that the ancestors of clade A occupied the CFR, and as aridification intensified by the late Miocene, hospitable habitats became rare and fragmented, inducing the ancestors of clade A to disperse to more suitable regions and undergo a series of local cladogenesis events resulting in sub-clades A1, A2 and A3. Some descendants of sub-clade A1 and the populations of sub-clade A3 remained in the ancestral area adapting to the region. Other descendants of sub-clade A1 dispersed northward to settle somewhere between the Namaqualand-Namib Domain and CFR over two time intervals during the late Miocene, 10.0 Mya and 9.6 Mya, respectively. The environment became extremely arid by the late Miocene producing a further vicariant split of these populations into two: one population colonising the Namaqualand-Namib Domain while the other became established in the CFR. The late Miocene spanned alternating periods of retreat and upsurge of the Atlantic Ocean (Grützner *et al*. 2005). It is consequently possible that the recession of the ocean facilitated dispersal of populations through the lowlands (coastal plains and intermontane basins). During the upsurge periods when the coastal plains were inundated, *Macroderes* probably used the corridors provided by intrusion of mountain ranges into the lowland habitats to disperse, producing more disjunctive populations. It is likely that the genus dispersed along these corridors as they were characterised by higher precipitation and were considerably humid (Midgley *et al*. 2001; Campbell 1983; Deacon *et al.* 1992). Many recent studies on the Cape fauna and flora indicated that the CFR comprises several habitat patches that acted as refugia during adverse climatic conditions (Mucina & Rutherford 2006; Tolley *et al*. 2014; Switala *et al*. 2014; Matenaar *et al*. 2018). Significant dispersals and species differentiation of the genus took place during the Plio-Pleistocene. At that time, the climate became extremely arid and cool due to renewed glaciation of Antarctica and regression of sea levels along the South African coast (Tyson & Partridge 2000). As the sea retreated, large seashore areas became exposed, allowing for further population dispersals along the coastal region. The retreat of the ocean that occurred during the Plio-Pleistocene also left imprints along the west coast of southern Africa (Grützner *et al*. 2005). The accumulation of a calcareous sandy substrate along the west coast caused dramatic shifts in habitats and led to the development of new habitats rich in calcareous soils (Cowling *et al.* 2009), which were less favourable to *Macroderes* lineages. These new conditions would have promoted dispersal of the genus, which subsequently led to isolated populations providing an opportunity for adaptive, allopatric

speciation events. In addition, the Plio-Pleistocene transition period lacked the dry, cool features, with the Pliocene being warmer and wetter (Dupont *et al*. 2011). These changes in climate probably accounted for further migration waves of the genus, and consequently forced fragmentation and population diversification. The effect of the Plio-Pleistocene climate fluctuations triggered species diversification, something that has also been confirmed in many other Cape fauna and flora elements (Swart *et al*. 2009; Tolley *et al*. 2006; Linder *et al*. 2010; McDonald & Daniels 2012; Sole *et al*. 2013; Matenaar *et al*. 2018).

Factors impeding *Macroderes* dispersal

Macroderes lineages in sub-clade A3 in the CFR evolved to become *M. fornicatus* Sharp, 1880 in the Cape Peninsula and *Macroderes* sp. in the Piketberg Mountains (Fig. 4). These two areas are separated by the vast area of the Cape Flats. At the time of glacial cycles and the regression of the sea during the Pleistocene, aridification prevailed and this led to the deterioration of the Cape Flat's flora, which led to isolated and fragmented habitats. It has been shown that, during the progression of the Pleistocene, the region was inundated, creating a barrier preventing the dispersal of individuals, and consequently, hindered the exchange of genetic material (McDonald & Daniels 2012). This would have been enhanced by the effect of the Berg River valley (Fig. 4), which may also have acted as an additional geographical barrier blocking the dispersal of individuals of the two species moving from north to south and *vice versa*. Descendants of sub-clade A1 that colonised the CFR evolved to *M. soleiana* in the Cedarberg Mountains (Fig. 4). This range of mountains is well known for its hospitable habitats (Tolley *et al* 2014; Matenaar *et al.* 2018) and it provided a vital refuge for many animal taxa during the aridification periods of the Pliocene (Daniels *et al.* 2007; Daniels *et al.* 2009; Daniels *et al.* 2010). The Doring River valley to the north and the Olifants River valley (Fig. 4) to the west of the Cederberg Mountains constituted geographical barriers blocking the dispersal of *M. soleiana*, preventing the exchange of genetic material with its congeners in the north and west. There are two lineages in sub-clade A1, which inhabited the CFR and Namaqualand-Namib Domain in the late Miocene. The first lineage evolved during the Pleistocene resulting in *M. foveatus*, which occurs in areas along the West Coast and is currently known from the Veldrift area of the CFR to the south of the Olifants River valley and Kommandokraal Farm in the Namaqualand-Namib Domain to the north of the Olifants River. The Olifants River valley also seems to have played a role in preventing these two populations from exchanging genetic

material between each other, as well as with their congeners in the Namaqualand-Namib Domain and the CFR. The Verlorenvlei Estuary also served as a geographical barrier hindering gene flow between neighbouring populations of *M. endroedyi* in Elands Bay and *M. foveatus* in Veldrift. The second lineage split vicariously into two further lineages: the first to the north in the Namaqualand-Namib Domain, which during the Pleistocene evolved to produce the species *M. namakwanus*, *M. amplior* and *M. arrowi*. The second lineage was confined to the south in the CFR and differentiated into two species. *Macroderes tourtosus*, which currently inhabits the base of the eastern margin of the Gifberg Mountains and the second, *M. endroedyi* is currently known from two localities within the CFR. One in Klawer to the east of the Olifants River and the second inhabiting Elands Bay along the west coast to the west of the Olifants River. This conclusion is also supported by the presence of the Olifants River valley barrier, which separates the two populations, thereby hindering gene flow between them. The Gifberg Mountains are a geographical barrier preventing the dispersal of individuals of *M. tortuosus* to the east and *M. endroedyi* to the west and consequently prevents gene flow between these species. The most recent common ancestors of sub-clade A2 in the Hantam-Tanqua Roggeveld and CFR underwent two successive vicariance events. In the first, the ancestors split into two lineages, one in the Hantam-Tanqua Roggeveld while the other occupied the Namaqualand-Namib Domain and CFR. The subsequent vicariance event led to a split into two further descendant lineages. The first in the Namaqualand-Namib Domain while the other occupied the CFR. By the Pleistocene, all the descendants from the most common ancestors of sub-clade A2 had evolved to the current extant species of *M. nitidus*, *M. gifboomi* and *M. mutilans. Macroderes nitidus* occurred in what is now known as the Hantam-Tanqua Roggeveld. This region is part of the Succulent Karoo Hotspot and is recognised as a refuge for many plant and animal taxa (Clark *et al*. 2011). *Macroderes gifboomi* occupied the base of the eastern margin of the Gifberg Mountains. *Macroderes mutilans* colonised the Kamiesberg Mountain range, which stretches from Garies in the south to Springbok in the north about 140 km (Anderson & Hoffman 2005) (Fig. 4). In the Kamiesberg Mountain, *M. mutilans* exists in two populations; one confined to the northern part of the mountain to the west of Springbok while the second occupies the southern part of the mountain to the west of Kamieskroon. Many geographical barriers could have affected the dispersal of these two species, consequently preventing gene flow between them. The enormous distance between the two mountainous areas of the two populations of *M. mutilans* may act as a geographical barrier preventing the dispersal northwards as well as southwards and accordingly

obstructing gene flow. The effect of the long distances between mountains on delaying the dispersal of taxa has also been suggested for the flightless grasshopper genus *Betiscoides* (Lentulidae) (Matenaar *et al*. 2018). The dispersal of *M. nitidus* to the west and *M. gifboomi* to the east was blocked by the Oorlogskloof and Troe-Troe Rivers (Fig. 4). The dispersal of *M. nitidus* northward, where *M. mutilans* succeeded, was probably hindered by the vast arid plains of the Knersvlakte in the area between the Bokkeveld and Kamiesberg Mountains (Kounov *et al.* 2008). The presence of such a vast, arid flat area with poor vegetation cover and habitats could have acted as a geographical barrier, particularly for taxa that are confined to mountainous regions (Daniels *et al*. 2010; Portik *et al*. 2011). In addition to the Hol, Vars and Sout Rivers, the Troe-Troe (Fig. 4), may have acted as a geographical barrier deterring the dispersal of *M. mutilans* populations in the north and *M. gifboomi* populations to the south. The Kamiesberg Mountain range may also have been a geographical barrier preventing the dispersal of *M. oreatus* populations in the extreme north of the Namaqualand to the *M. minutus* territory in the extreme south of the Namaqualand-Namib Domain and *vice versa*.

Genus *Afroptera*

The analysis indicated that the most recent common ancestor of *Afroptera* had been present in the Namaqualand-Namib Domain, CFR and Namib Desert Eco-region since the early Eocene. This result indicates a different ancestral origin from that of *Macroderes* and, consequently, suggests different historical processes that led to the diversification of the two genera. The analysis supports a dispersal event during the early Eocene, into the Namaqualand-Namib Domain and Namib Desert-Eco region. The initial diversification of *Afroptera* took place in the late Eocene when the most recent common ancestor of *A. alba* split vicariously restricting this species to the north in the Namib Desert Eco-region of Namibia, while the remainder of the species were confined to the south in the Namaqualand-Namib Domain of present-day South Africa. It is possible that the vicariance event that led to this separation was associated with continued continental erosion resulting from the African uplift during late Eocene (Anka & Séranne 2004).

The ancestral state reconstruction analysis suggests that a dispersal event during the Oligocene led to the split of clade A, which remained in the Namaqualand-Namib Domain, from clade B, which migrated eastwards to colonise the Namaqualand-Namib Domain and Savanna Biome. At that time, the lowlands of Africa (coastal plains and intermontane basin) were covered by

accumulated silcrete layers following volcanic activities on the Deccan plateau in northern India during the Palaeocene (Partridge 1998). During the Oligocene, rivers of the Cape region were languid and winding, and characterised by vast wetlands, with many areas covered by infertile alluvial sands and gravels. In addition, expansion of the Antarctic glacial ice sheet reduced the sea level by about 500 m (Rogers 1987; Siesser & Dingle 1981; Feakins & Demenocal 2010), exposing large coastal areas leading to the accumulation of sand dunes along the coast. It is suggested that the cool, arid climate of the Oligocene (Zachos *et al.* 2001) contributed to the movement of these sands to form widespread sand plains (Cowling *et al.* 2009). It is possible that this hyper-arid environment reduced and shrank floral communities (on which *Afroptera* relied as a food source) thereby leading to extensive fragmentation of these floral habitats, forcing the genus to disperse with the flora as an adaptive strategy. Dispersal of the most recent common ancestor of clade B to the Namaqualand-Namib Domain and Savanna Biome had little impact on the diversity of the genus, as most ancestors did not radiate extensively, with only two species currently comprising this clade. *Afroptera. obtusa* is confined to sandy, rocky habitats in the Namaqualand-Namib Domain, and *A. koranna*, which occurs in dry, mountainous habitats in the Savanna Biome. It is possible that, to avoid these adverse conditions, and because of its terrestrial mode of life and weak flight ability, the genus exploited mountain ranges and hills as corridors to expand their ranges northwards into the Kalahari Savanna biome. The biogeographical reconstruction of *Afroptera* indicates that the most recent common ancestor of clade A, which encompasses the majority of species in the genus, underwent several radiation waves during the early and mid-Miocene, expanding its distribution from the Namaqualand-Namib Domain further eastward into the Nama Karoo Biome. Descendants of the clade provided most of the ancestors of sub-clades A4 but remained in the Namaqualand-Namib Domain. By the advent of the Plio-Pleistocene; they gave rise to *A. munroi* which dispersed further to occupy the Namaqualand-Namib Domain, Hantam area and Nama Karoo Biome.

The majority of lineages that represent the most recent common ancestors of sub-clades A1, A2 and A3 dispersed to colonise either the Namaqualand-Namib Domain and Nama Karoo Biome, or only the Namaqualand-Namib Domain. These lineages underwent further migration waves and diverged into three descendants: one colonised the Namaqualand-Namib Domain representing the most recent common ancestor of the sub-clade A3. The second represented the most recent common ancestor of sub-clade A2 that inhabited the Namaqualand-Namib Domain, while the third lineage, which includes the most recent common ancestors of the sub-clades A2,

migrated into the Namaqualand-Namib Domain and Nama Karoo Biome. These dispersal events were probably related to habitat shifts that are associated with the initiation of the Post-African I erosion cycle in the Miocene (Cowling *et al*. 2009). At that time, the Cape lowlands were covered by silcrete layers, with the appearance of many areas with different soil textures varying from clay soils to montane quartz and sandstones among others (Cowling *et al.* 2009). The varied habitats formed by these edaphic substrates affected the Cape flora by triggering floral dispersal, which subsequently enhanced the dispersal of *Afroptera* in the form of adaptive radiations. The effects of the edaphic heterogeneity in dispersing the Cape fauna is also confirmed by recent studies on the grasshopper genus *Betiscoides* (Lentulidae) (Matenaar *et al*. 2018), and this may also be the case in *Afroptera*. It has been shown that edaphic heterogeneity may cause changes in soil pH and waterlogging, which will directly threaten the plants and enhance their dispersal, as is known for many Cape plants (Linder 2003; Araya *et al*. 2011). Werger (1978a, 1978b) asserted that there is a floral affinity between the Cape Region and the Nama Karoo Biome, particularly in the south-western part of the biome. This argument is supported by the presence of fynbos elements in the Nama Karoo Biome dating back to 70 Mya (Scholtz 1985). Many studies indicated that the current karroid vegetation of the Nama Karoo Biome evolved later in response to the arid, cool climate of the late Miocene (Coetzee 1978b), which means that, during the Oligocene, the Nama Karoo Biome still preserved some fynbos elements that were favoured by the species of *Afroptera*. A recent study has also indicated that the Nama Karoo Biome harbours many refugial patches (Clark *et al.* 2011).The late Miocene witnessed synchronised and extensive dispersal waves of sub-clades A1 and A2 (*ca.* 10.4 and 10.2 Mya), respectively. The most recent common ancestor of sub-clade A1 underwent three major dispersal waves during the late Miocene: two waves towards the Nama Karro Biome took place about 10.4-7.9 Mya. The descendants of these waves evolved to *A. aequabilis* and *A. maraisi*, respectively by the Pleistocene. The third migration wave occurred approximately 7.9 Mya but its destination not fully established by the analysis. However, the ancestors of this last wave underwent two dispersal events, one towards the Namaqualand-Namib Domain and by the Pleistocene had evolved to *A. sabuleti*, while the direction of the second wave remained uncertain as indicated by the analysis (ADE or DE or AE, node 1 in Fig. 3). A vicariance event in the latter lineage (node 1 in Fig 3) resulted in two descendants: the first one colonised the Namaqualand-Namib Domain and Nama Karoo Biome and by the Pleistocene gave rise to *A. bitis*, while the second inhabited the Savanna Biome and evolved to *A. olivacea.* The most recent

common ancestor of sub-clade A2, which occurred in the Namaqualand-Namib Domain and Nama Karoo Biome, underwent different dispersal waves during the late Miocene resulting in three isolated descendants. During the early stages of the sub-clade one descendant probably dispersed into the Namaqualand-Namib Domain, CFR and Nama Karoo Biome and by the Pleistocene era had given rise to *A. pilosa*. The second descendant dispersed to inhabit the Namaqualand-Namib Domain and Nama Karoo Biome and by the Pleistocene gave rise to *A. peringueyi*. The third lineage possibly evolved in the Namaqualand-Namib Domain, CFR and Nama Karoo Biome or CFR and Nama Karoo Biome or Namaqualand-Namib Domain and CFR during the Pleistocene. A vicariance event during the Pliocene (3.5 Mya) split this lineage into two isolated descendants. The first was confined to possibly Namaqualand-Namib Domain and Nama Karoo Biome and by the Pleistocene evolved into *A. longicornis*, while the second lineage occupied the CFR and during the Pleistocene evolved to *A. lanata.* The arid, cool climate of the late Mio-Pliocene, together with the repeated uplift of the Great Escarpment and the periodic glacial cycles of the Pleistocene, were possibility the main driving forces of the radiation and diversification of the Cape flora. It is stated that the progressive aridification associated with these periods prompted dramatic habitat shifts and fragmentation, and led to the dispersal of many Cape floral lineages (Linder 2003; Linder & Verboom 2015). All these historical climate changes left an important impact on the evolution and the biogeography of *Afroptera*. Since the Nemopterinae are pollen and nectar feeders, the dispersal and expansion of its ranges in the Nama Karoo and Savanna Biomes out of the Cape region could have followed the Cape floral range expansion. A study by Mucina & Rutherford (2006) indicated that the southern and western parts of the Nama Karoo Biome comprise succulent and fynbos components, represented by the families Aizoaceae and Asteraceae, with some fynbos generic elements also present in the Savanna Biome. Indeed, the dispersal of ancestors of clade A and the subsequent dispersal waves of its descendant sub-clades within the Namaqualand-Namib Domain, Nama Karoo Biome and Savanna Biome has significantly expanded the distribution of the genus and increased its diversity, as most of the extant species proliferated within these regions in different habitats types.

Factors impeding *Afroptera* dispersal

The weak flight ability and terrestrial biology of the genus *Afroptera* could be some of the most important factors restricting genus dispersal, consequently leading to isolated niches with fragmented, localised populations and restricted gene flow (Tjeder 1967). River valleys, water bodies and mountains may also act as geographical barriers hampering species dispersal, and reducing gene flow among populations. The dispersal of *A. alba* from the Namib Desert Eco-region southward in southern Africa may have been prevented by the Orange River valley (Fig. 4). It seems that the majority of *Afroptera* species that are endemic to present-day South Africa could not migrate northwards due to this natural barrier, although there are some exceptions such as *A. munroi* and *A. segregata* that succeeded in dispersing and have representatives in both South Africa and Namibia. This water body also constituted a barrier that blocked the dispersal of *A. koranna* and *A. olivacea* from the Savanna Biome southward towards the Nama Karoo Biome or westwards to the Namaqualand-Namib Domain. It also deterred the dispersal of *A. aequabilis* and *A. maraisi* from the Nama Karoo Biome and the dispersal of *A. obtusa* from the Namaqualand-Namib Domain to the north towards the Savanna Biome. The dispersal of *A. sabuleti* from the Namaqualand-Namib Domainto the north is restricted by the presence of the Holgat River (Fig. 4), while the Kamiesberg Mountain range as well as the Doring River form the southern boundary and limited further dispersal of the species. The Kamiesberg Mountain also seems to have significantly impacted the distribution of *A. papio* and *A. longicornis* southwards towards the CFR, while it had little effect on the dispersal of *A. munroi* and *A. bitis* from the Namaqualand-Namib Domain as some populations of both species occur in the Nama Karoo Biome and in the Hantam-Tanqua Roggeveld. The mountain ranges of Rooiberg, Gamakaberg and Swartberg (Fig. 8) probably halted the migration of *A. lanata* from the Riversdale Mountains in the CFR to the north towards the Namaqualand-Namib Domain and Nama Karoo Biome.

The populations of *A. pilosa* inhabit three adjacent bioregions within the Namaqualand-Namib Domain, CFR and Nama Karoo Biome. Although these regions include several water bodies represented by the: Gamka and Dwyka Rivers in the Nama Karoo Biome, Buffels, Brand, Doring, and the Groot Rivers in the Namaqualand-Namib Domain (Fig. 4), they don't seems to have influenced the dispersal of the species between these regions. The Gamka River seems to

have halted the dispersal of *A. peringueyi* from the Namaqualand-Namib Domain towards the CFR in the west.

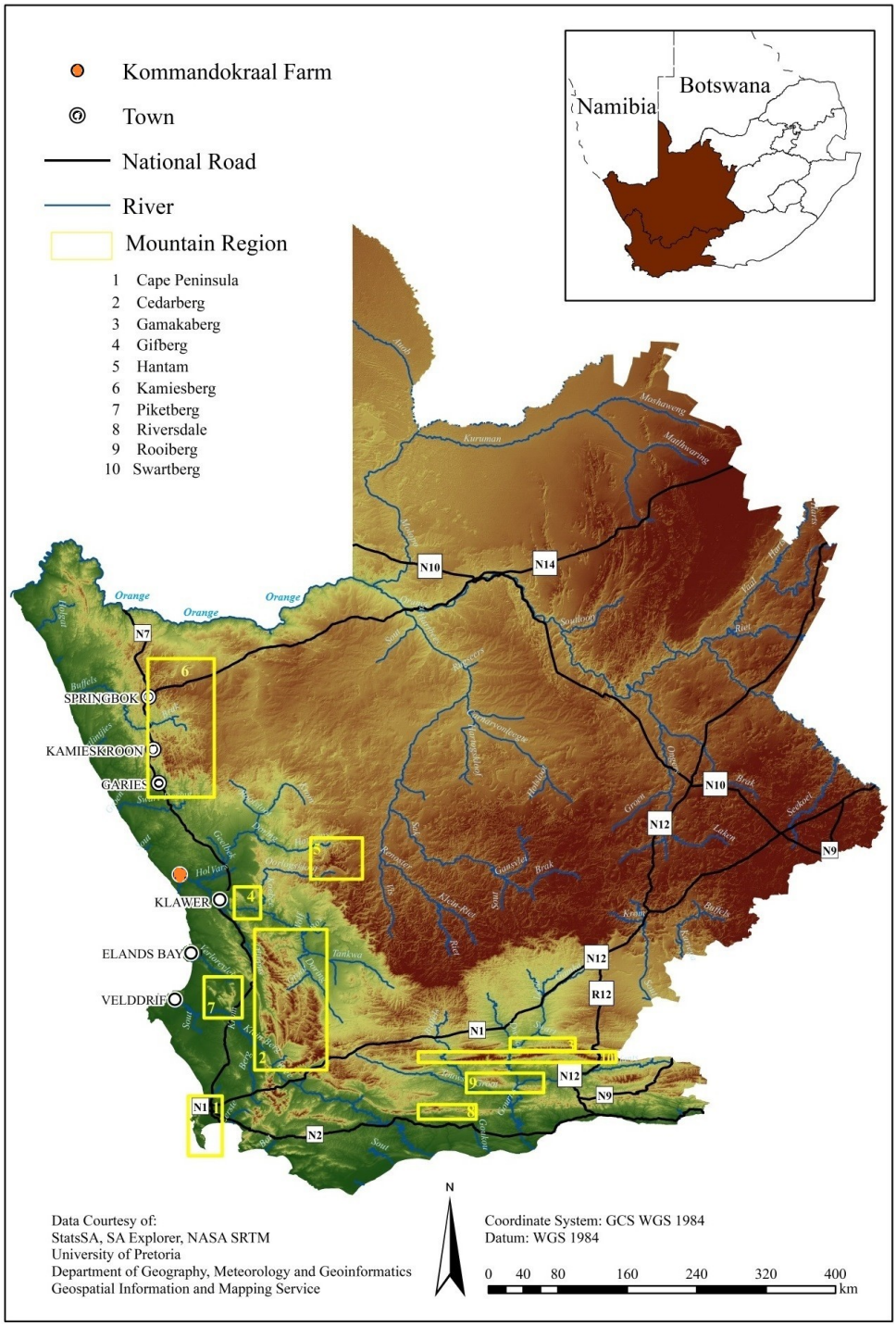

Figure 4. Major Mountains Ranges and rivers associated with *Macroderes* and *Afroptera* distribution in the Northern and Western Cape Provinces of South Africa.

Common trends in the historical biogeography of *Macroderes* and *Afroptera*.

The historical biogeographic analysis of *Macroderes* and *Afroptera* revealed that some extant species of these genera are sympatric in the Namaqualand-Namib Domain, Cape Floristic Region and the Hantam-Tanqua and Roggeveld. According to the S-DIVA results, the genus *Afroptera* has occupied the Namaqualand-Namib Domain and Namib Desert Eco-region since the late Eocene (36.5 Mya), while the genus *Macroderes* inhabited the Namaqualand-Namib Domain and Cape Floristic Region recently in the late mid-Miocene (14.5 Mya). According to these findings, it is clear that the most recent common ancestor of *Afroptera* is ancient and its existence in the Namaqualand-Namib Domain predates the existence of the most recent common ancestors of *Macroderes.* In addition, most descendant lineages of *Afroptera* that are represented by the most recent common ancestor of major clades A and B had colonised the Namaqualand-Namib Domain by the Oligocene (28.5 Mya), while those of *Macroderes* colonised the region late in the late Miocene. By contrast, the presence of *Macroderes* in the CFR dates back to the late Miocene (12.2 May) compared to the presence of *Afroptera* lineages which recently appeared in the region during the Pliocene. Despite differences in the spatio-temporal origin of the most common ancestors of *Afroptera* and *Macroderes*, and according to the above-mentioned observations, the genera exhibit many common trends through their evolutionary history. It is obvious that there is a correlation between the latest dispersal and vicariance events and derived-allopatric distribution, and the explosive rapid speciation of the major clades and sub-clades of both genera at the onset of the arid, cool climate of the late Mio-Pliocene and through Pleistocene in the Cape region. The inferred ancestral distribution results indicate that *Macroderes* lineages that currently occur in the Namaqualand-Namib Domain or CFR occupied the regions because of vicariance events or dispersal waves during the periods of the mid and late Miocene and in the Pliocene, resulting in the emergence of the extant species in the region. Likewise, the lineages of *Afroptera* that currently occupy these regions entered or recolonised the regions either through dispersal waves throughout the periods of the early to late Miocene or vicariance events during late Miocene and in the Pliocene. For example, the most recent common ancestor of *M. namakwanus*, *M. amplior*, *M. arrowi*, *M. mutilans* and *M. foveatus* of the genus *Macroderes* and *A. sabuleti*, *A. bitis, A. pilosa, A. peringueyi, A. lanata* and *A. longicornis* from *Afroptera* colonised or re-colonised the Namaqualand-Namib Domain simultaneously, either as a result of dispersal or vicariance events during the late Mio-Pliocene. The most recent common ancestor of *M. minutus* and *M. oreatus,* and the most recent common ancestor of *A. obtusa* also

occupied Namaqualand-Namib Domain following vicariance events approximately during the same period in the mid-Miocene. The results of this study also indicate that all extant species of *Macroderes* and *Afroptera* evolved in parallel during the Pleistocene. It is clear that there is synchronisation in timing of the lineage splitting as well as the time of dispersal and vicariance events. These results lead to the conclusion that the populations of both genera encountered similar paleoclimatic and geological processes. This synchronisation in timing of the two ecological processes, dispersal and the vicariance events during late Mio-Pliocene epochs is supported by the fact that the African uplift coincides with the Benguela Current, which played an important role in increasing cooling during the late Mio-Pliocene eras (Jung *et al.* 2014).

Other factors influencing the distribution of *Macroderes* and *Afroptera*

The biogeographic analysis indicates that *Afroptera* has a comparatively wider distribution than that of *Macroderes*. By contrast, the species of *Macroderes* are confined to the Fynbos and Succulent Karoo Biomes (Figs 6 & 7). These dissimilarities in distributions are attributed to many biotic and abiotic factors that may account for species distribution. *Macroderes* is a genus adapted to cool climates and its species are restricted to the winter and bimodal rainfall regions of South Africa where it is associated with loamy, sandy soils that are rich in dense shrubs. Activity of *Macroderes* species is limited to short periods during the cool rainy days in winter, from July to September, and a few days after rains (Frolov & Scholtz 2005). The current distribution of *Macroderes* within the Cape region is concentrated in the western coastal plains and to the interior along the western part of the Great Escarpment (Frolov & Scholtz 2005; Abdalla *et al*. 2018). In these regions, the genus is associated with “heuweltjies” (ancient termite mounds) and its distribution follows the heuweltjies in the Succulent Karoo and Fynbos Biomes (Abdalla *et al*. 2018). Heuweltjies are distributed throughout the Succulent Karoo and Fynbos Biomes and are one of the region’s features (Merryweather 1965; Coaton & Sheasby 1974; Lovegrove & Seigfried 1986). They are characterised by having high silt content and the capacity to retain water long after rains (Fey 2010; Desmet 2007; Mucina & Rutherford 2006). They also serve as shelters for rodents (Fey 2010) which are the main sources of dung pellets (Abdalla *et al.* 2018). It is most likely that heuweltjies constitute suitable habitats for the sustainability of the genus by providing humidity, particularly during the dry summer months, as well as by providing the dung pellets consumed by the genus as food (Abdalla *et al*. 2018). Species of *Afroptera* also have primary habitat requirements. As in most southern African

Nemopterinae, species of the genus occur in the driest regions of the Western and Northern Cape provinces and Namibia, occurring in sandy and rocky habitats with low rainfall but high relative humidity and poor vegetation cover (Tjeder 1967). The species in the south-western Cape live in bare soil areas between shrubs and bushes or at the foot of rocky escarpments and where there is rain shadow (Tjeder 1967). These habitat features of low rainfall and low vegetation cover are also characteristic of the Nama Karoo and Savanna Biomes (Mucina & Rutherford 2006). Another factor that could be invoked to explain the restricted distribution of *Macroderes* is its low vagility and flightlessness. *Macroderes* is a flightless genus (Frolov & Scholtz 2005; Abdalla *et al*. 2018) and its ability to move and disperse long distances is limited (Davis 2013). Members of the genus are confined to small ranges of distribution that may result in localised, allopatric populations, limiting the chances of genetic exchange. By contrast, although *Afroptera* are weak fliers (Tjeder 1967), their ability to fly has contributed to its wider distribution relative to that of *Macroderes*.

Based on the above conclusions, it seems that the biology of the two genera had little impact on shaping their current overlapping distributions. It is also clear that the dispersal of the Cape flora has significantly affected the diversity and dispersal of *Afroptera*, while in *Macroderes* it has not had a significant impact, as *Macroderes* are dung feeders. We can consequently assume that the paleoclimatic and topographic changes in the late Mio-Pliocene and Pleistocene are the main driving forces responsible for the current, overlapping distributions of the two genera.

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CHAPTER VII

Summary

According to available data (Tjeder 1967; Frolov & Scholtz 2005; Sole *et al*.2013; Abdalla *et al*. 2018; Abdalla *et al*. 2019), the species of the southern African genera *Macroderes* Westwood, 1842 and *Afroptera* Abdalla & Mansell, 2019 are characterised by allopatric distributions within the Western and Northern Cape Provinces of South Africa. They manifest patterns of overlapping distribution with each other within these regions. This suggests that the current populations of the two genera may have been influenced by the same evolutionary drivers. The overall objective of the research presented in the different chapters of this thesis was consequently, to explore the role of the paleoclimatic and geological changes during the late Cenozoic epoch on the diversification and the evolutionary history of the two genera. To achieve this, knowledge of the taxonomy of each genus, as well as a full understanding of their phylogenetic relationships and their historical biogeography was required. This chapter presents a summary of the key findings of each research chapter.

Chapter 2

The existing taxonomic status of the species of *Macroderes* was unresolved, as the last taxonomic revision was by Frolov & Scholtz in (2005). One of the objectives of this study was to update the taxonomy of the genus. *Macroderes* comprised 28 valid species with the validity of three other species still being uncertain. From the total number of the currently known species, seven new species are described, another redescribed, with its Lectotype designated in the present study. The revision provided complete diagnostic characters as well as an update on the geographic distribution and habitat of each species. In addition, an updated key to the species was completed with photographs of habitus, sclerite of internal sac, pronotum, pronotal punctures and elytra.

Chapter 3

No previous work had addressed the phylogeny and divergence time of *Macorderes*. The present study is the first attempt to construct the phylogenetic relationships among the species of the genus, and the timing of the speciation events..

The study included concatenated molecular and combined morphological/molecular datasets. The results of the analyses of both datasets strongly confirmed that *Macroderes* constitutes a monophyletic group with two major clades. The study also revealed high genetic distances between the populations of *M. mutilans*, *M. endroeydi* and *M. foveatus*, which require further morphological examination to determine their taxonomic status. The divergence-time estimate analyses indicated that the genus originated during the late Eocene (38.9 Mya) but commenced diversification in the late mid-Miocene (*ca*.14.5 Mya) with the currently known species radiating in the late Mio-Pliocene and through the Pleistocene (*ca*. 5.0-0.1 Mya).

Chapter 4

The taxonomy of the southern African genera *Nemia* Navás, 1915 and *Nemopterella* Banks, 1910 had remained uncertain. This was due to lack of reliable diagnostic characters to distinguish species of the two genera, and a revision of their taxonomy was consequently required. The present revision represents the most comprehensive taxonomic study of these two genera since Tjeder's 1967 monograph more than 5 decades ago. In addition to the taxonomic analysis, information on the distribution of the species and descriptions of their habitats were added. The generic classification was based on both morphological and molecular criteria. In accordance with the results obtained, we split the two genera into four. *Nemopterella sensu stricto* with type species *Nemopteryx africana* Leach, 1815 (= *Nemopterella africana*), *Afroptera* Abdalla & Mansell, 2019, with type species *Nemopterella munroi* Tjeder, 1967, the monotypic *Siccanda* Abdalla & Mansell, 2019, with type species *Nemopterella arenaria* Tjeder, 1967 and *Nemia* Navás, 1915, with type species *Nemia costalis* (Westwood, 1836), which comprises six species. In addition, eight new species were described in *Afroptera* and two new species in *Nemopterella.* Identification keys to the species in the genera *Afroptera* and *Nemopterella* were provided.

Chapter 5

The new genus *Afroptera* was recently described (Abdalla & Mansell, 2019). The phylogenetic relationships between the species in *Afroptera* were based on both concatenated molecular and combined morphological/molecular datasets. Both datasets recovered a well-supported phylogeny with two major clades, with a single species, *Afroptera alba* Mansell & Abdalla, 2019

recovered as the sister group. The estimated age of the genus was approximated to the Late Eocene (*ca*. 36.5 Mya), with most descendant species undergoing rapid speciation during the late Mio-Pliocene and through the Pleistocene (*ca*. 4.4-0.2 Mya), with very similar timing to those of *Macroderes*.

Chapter 6

One of the objectives of this study was to investigate the potential ancestral range of *Macroderes* and *Afroptera* and the ecological factors responsible for the current allopatric and overlapping distribution of the two genera. The results indicated that the genera had different origins, with *Macroderes* originating in the Cape Floristic Region and Namaqualand-Namib Domain during the late mid-Miocene (14.5 Mya), while *Afroptera* originated in the Namaqualand-Namib Domain and Namib Desert Eco-region at the late Eocene (36.5 Mya). Dispersal appeared to be the main ecological mechanism that accounted for the current species distribution for both genera. The results showed that the two genera exhibited many common evolutionary trends in that there was association between the latest dispersal and vicariance events that, in turn, led to the current allopatric distribution of species in the two genera, and the rapid radiation of major clades and sub-clades in both genera. This coincided with the aridification period and cool climate during the late Mio-Pliocene in the south-western Cape, enhanced by the effects of the uplift-driven topographic and climatic changes of the Great Escarpment during the same eras, and the recurrent warmer and cooler periods of the Pleistocene. During the late Mio-Pliocene there was synchronised lineage divergence as well as dispersal waves and vicariance events that suggest similar paleoclimatic and geological processes that acted on these populations. The results also indicated that all extant species of both genera evolved in parallel during the Pleistocene epoch.

Suggestions for further research

Future work on these two groups of insects should focus on investigations of their biology, as the available data do not cover this vital part adequately. In addition, this study was based on limited samples and could not include all species of the described genera. To obtain a comprehensive picture of the phylogenetic relationships between the species and to gain a better understanding of their historical biogeography it is recommended that all the extant described species be

included. There is a need to clarify the position of *Afroptera* and *Siccanda* within the Nemopterinae. Finally, the inclusion of the paleoclimatic and distribution modelling approach would be of great value in understanding how these factors enhanced speciation on both genera.