REVISION OF THE SOUTH AFRICAN GEOGARYPIDAE (ARACHNIDA: PSEUDOSCORPIONES)

by

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DECLARATION

I declare that this thesis hereby handed in for the qualification MAGISTER SCIENTIAE at the University of the Free State is my own independent work and that I have not previously submitted the same work for qualification in/at another University/Faculty.

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ABSTRACT

Despite a recent order-level revision published by Harvey (1992b), where, through the use of 126 morphological characters, 24 families were recognized, detailed morphological and ecological data is still sorely lacking for the vast majority of pseudoscorpions, including the poorly-known South African fauna. Taking this into consideration, the need for detailed revisions of our indigenous fauna was recognized. To this end, the family Geogarypidae, originally a subfamily of Garypidae, but recently elevated to full familial status (Harvey 1986), was chosen to spearhead this endeavour as our indigenous fauna only consisted of eight described species in two genera (*Afrogarypus* Beier, 1931 and *Geogarypus* Chamberlin, 1930). This study is the first holistic approach to the classification of South African pseudoscorpions, taking both morphological as well as molecular phylogenetic (COI and 28S) data into consideration. Results showed the morphology and phylogenetics complemented each other and that there are 18 distinct species of Geogarypidae within South Africa, nine of which are new to science namely, *A. carmenae* sp. nov., *A. castigatus* sp. nov., *A. megamolaris* sp. nov., *G. deceptor* sp. nov., *G. liomendontus* sp. nov., *G. modjadji* sp. nov., *G. octoramosus* sp. nov., *G. tectomaculatus* sp. nov. and *G. variaspinosus* sp. nov. These are divided into three major clades, one corresponding to *Geogarypus* and two to *Afrogarypus*. Four species previously from *Geogarypus* were found to belong to the *Afrogarypus* clades and are transferred. The data also supports the separation of *G. olivaceus* (Tullgren, 1907) and *G. flavus* (Beier, 1947) (synonymised by Beier in 1964), with the latter revalidated. Lastly, the two subspecies *A. excelsus excelsus* (Beier, 1964) and *A. excelsus excellens* (Beier, 1964) are synonymised under *A. excelsus* (Beier, 1964) stat. nov.

Key words: Geogarypidae, morphology, phylogenetics, South Africa, Pseudoscorpiones

OPSOMMING

Ten spyte van 'n onlangse orde-vlak hersiening gepubliseer deur Harvey (1992b), waar, deur die gebruik van 126 morfologiese karakters, 24 families herken was, ontbreek gedetailleerde morfologiese en ekologiese data oor die meerderheid van vals-skerpioene, insluitend die swak bekende Suid-Afrikaanse fauna. Laaste in ag geneem, was die behoefte vir gedetailleerde hersienings oor ons inheemse fauna duidelik. Die familie Geogarypidae, oorspronklik 'n subfamilie van Garypidae, wat onlangs tot vol familiestatus verhef is (Harvey 1986), was gekies om die poging te lei aangesien ons inheemse fauna slegs uit agt beskryfde spesies in twee genera (*Afrogarypus* Beier, 1931 en *Geogarypus* Chamberlin, 1930) bestaan. Hierdie studie verteenwoordig die eerste holistiese benadering tot die klassifikasie van Suid-Afrikaanse vals-skerpioene, deur beide morfologiese en molekulêre filogenetiese (28S en COI) data in ag te neem. Resultate het getoon dat die morfologie en filogenie mekaar komplimenteer en dat daar 18 unieke spesies Geogarypidae binne Suid-Afrika voorkom, nege voorheen onbekend tot die wetenskap naamlik, *A. carmenae* sp. nov., *A. castigatus* sp. nov., *A. megamolaris* sp. nov., *G. deceptor* sp. nov., *G. liomendontus* sp. nov., *G. modjadji* sp. nov., *G. octoramosus* sp. nov., *G. tectomaculatus* sp. nov. and *G. variaspinosus* sp. nov. Die spesies is verdeel in drie klades, een wat ooreenstem met *Geogarypus* en twee wat ooreenstem met *Afrogarypus.* Vier spesies voorheen in *Geogarypus* is gevind wat om aan die *Afrogarypus* klades te behoort, en word oorgeplaas. Die data ondersteun verder die skeiding van *G. olivaceus* (Tullgren, 1907) en *G. flavus* (Beier, 1947) (gesinonimiseer deur Beier in 1964), met die laasgenoemde weer bekragtig. Laastens word die twee subspesies, *A. excelsus excellens* (Beier, 1964) en *A. excelsus excelsus* (Beier, 1964), gesinonimiseer onder *A. excelsus* (Beier, 1964) stat. nov.

Sleutelwoorde: Geogarypidae, morfologie, filogenetika, Suid Afrika, Pseudoscorpiones

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FOREWORD

The following dissertation was created with the aim of spearheading one of the most exciting and ambitious research projects in the history of South African pseudoscorpion taxonomy, namely to revise the entirety of South African pseudoscorpion fauna and bring the aforementioned field into the 21st century. Throughout the completion of this dissertation, two main issues became apparent that the above mentioned project hopes to address by its completion.

First and foremost, it highlighted the complexity of pseudoscorpion taxonomy and systematics and how daunting it can be for a novice, like myself, to find a foothold in this field. The difficulty in acquiring literature pertaining to South African pseudoscorpions, combined with the fact that there are no practising taxonomists in the country specializing in the Pseudoscorpiones, makes it particularly hard to get comfortable with pseudoscorpion identification. This dissertation aims to not only provide a comprehensive study on the taxonomy of the Geogarypidae of South Africa, but also serves as a stepping stone into the taxonomic study of the Pseudoscorpiones in general. To this end, both photographic and diagrammatic aids are given to the reader, making it as easy as possible for novice taxonomists to accurately, and confidently, identify the species under question in this work. To aid in this endeavour, where possible, only techniques that would be readily available to the average taxonomist was used to identify character states used in the identification key.

Secondly, due to the fact that none of the previously described Geogarypidae species of South Africa were identified by local taxonomists, most of the type specimens reside elsewhere in overseas institutions. This, combined with the reluctance of many curators to ship valuable type specimens overseas, makes it difficult to acquire and view original type specimens when doing revisions (a problem encountered more than once in this project). To this end, particular effort was made to collect sufficient new material of both already described and novel species, which will be deposited in the National Museum in Bloemfontein. This centralization of endemic pseudoscorpion types (holo-, syn-, neo- and paratypes) aims to ease the burden of locating and transporting specimens from multiple institutions worldwide, when working on endemic pseudoscorpion fauna.

In conclusion, the taxonomic work that follows not only aims to modernize the taxonomy of the South African Geogarypidae, but also serves to introduce novice taxonomists to the field of pseudoscorpion taxonomy.

CHAPTER 1 - INTRODUCTION

1.1 *The Pseudoscorpiones*

Pre-Devonian in origin, the Pseudoscorpiones are one of the oldest extant lineages (Shear, Schawaller & Bonamo 1989; Schawaller 1991; Judson 2012) and over the past 392 Ma have diverged into more than 3400 known species in 26 families (Harvey 2013). Due to their small size and lack of medical and agricultural importance, the study of the Pseudoscorpiones has been carried out by only a small group of dedicated scientists. This group has mostly consisted of taxonomists, with these arthropods only beginning to gain the interest of a wider audience of researchers during recent decades.

Their unusual appearance and secretive nature has been recorded as far back as Aristotle (Harvey & Judson 1998), though even Linnaeus failed to clearly define the group, instead grouping the first two described species (*Acarus crancroides* Linnaeus, 1758 and *A. scorpioides* Linnaeus, 1758) together with mites and harvestmen (Harvey & Judson 1998). During the late 19th century and early 20th century, authors such as Simon (1879), Balzan (1892), Hansen (1893) and With (1906) contributed greatly to our knowledge of pseudoscorpions, though it was only later in 1931, with his seminal paper, that Joseph C. Chamberlin devised the first detailed classification system based on comparative morphological characters of the order. For the first time, detailed morphological knowledge was available through the delineation of suborders, families and genera, as well as through the use of a broad range of new identification characters. Despite minor alterations to this system by authors such as Beier (1932a,b), it has remained largely unaltered and is still used today.

Historically, most research on the group concentrated primarily on the taxonomic resolution of species, together with species catalogues. Recently, pseudoscorpion research has begun to venture away from pure taxonomy to more ecological fields. Their use as both bio-indicators in the monitoring of field margins (Bell *et al.* 1999), as well as in the ecological management of forest soils (Deleporte & Tillier 1999; Yamamoto, Nakagoshi & Touyama 2001), has been recently shown. Some species are also being investigated for their potential use as biological control agents (Donovan *et al.* 2009), while the group also serves as an important model for understanding mitochondrial gene evolution (Arabi *et al.* 2012; Ovchinnikov & Masta 2012).

1.2 *General morphology*

All pseudoscorpions are predatory in nature, and through the study of many fossilized specimens from 50 ma old Baltic and younger Dominican and Mexican ambers (Schawaller 1980; Shear, Schawaller & Bonamo 1989; Judson 2003, 2009), this has been the case for millions of years. Most are less than five millimetres in length, though they range from less than one millimetre in some Chthoniidae to just over ten millimetres in females of *Garypus titanius* Beier, 1961 (Beier 1961). They superficially resemble true scorpions, but lack the elongated metasoma (tail) and telson (sting) (Harvey 2002, 2007). They do, however, share the six-segmented pedipalps, with the tibia and tarsus modified into a chela with a movable finger. The chela house some of the pseudoscorpion's most sensitive sensory structures and are used primarily for environmental awareness and subduing prey, with members of the suborder Iocheirata possessing venom teeth on either one or both of the chelal fingers. The carapace may possess either one or two pairs of eyes on the anterior lateral margins, though some troglobitic species either lack eyes completely, or possess them in a reduced form (Muchmore & Pape 1999; Harvey & Du Preez 2014).

The chelicerae are two-segmented and attached under the anterior margin of the carapace. Each contains a specialized grooming structure on the moving finger called the serulla exterior, together with a spinneret or galea used to construct silken retreats. These retreats are then used for moulting, shelter from the environment, as well the formation of the brood-sac by females. Overall dorso-ventrally flattened, the segmented abdomen can vary in shape from elongated to sub-ovalate. The 12-segmented abdomen is covered dorsally by tergites and ventrally by sternites. The abdominal plates are connected laterally by an exposed pleural membrane. The genitalic and respiratory openings are located ventrally, with sternites two and three forming the genital opperculum, while the spiracles open laterally of sternites three and four. The anus is located posteriorly on the abdomen. The four pairs of walking legs usually have six segments, though many species have a reduced number of five in the front two pairs of legs. Each leg ends with a pair of claws and an arolium. The exterior surface of a pseudoscorpion can either be granulated, sculptured or predominantly smooth (Weygoldt 1969).

1.3 *Ecology*

Pseudoscorpions occur in almost every part of the world, though most species are found within the tropics and subtropics. Their unique morphology makes these secretive generalists a very important predatory component of many terrestrial habitats, where they can readily be found among humid soil (Fig. 1), leaf litter, compost piles, under stones (Fig. 2), bark (Fig. 3) and logs, as well as harsh environments such as intertidal zones (Hoff 1949; Haddad & Dippenaar-Schoeman 2009;

Batuwita & Benjamin 2014). Although most species are ground dwellers, many arboreal representatives such as *Lophochernes mucronatus* (Tullgren, 1907) are also present (Dippenaar-Schoeman & Harvey 2000). On the other hand, *Chelifer cancroides* (Linnaeus 1758), a cosmopolitan species, can often be found within manmade structures (Levi 1948, Buddle 2005).

Some species furthermore occupy very specific niches, such as caves (Muchmore & Pape 1999; Ćurčić *et al.* 2002; Harvey & Du Preez 2014; Harvey & Wynne 2014). Insectophilous species include *Ellingsenius fulleri* (Hewitt & Godfrey, 1929), which is strictly associated with bees (Judson 1990), and the myrmecophilous *Marachernes bellus* Harvey, 1992 (Harvey 1992a). Many species have also formed commensal relationships with a myriad of avian and mammalian species. Turienzo, Di Iorio & Mahnert (2010), as well as Christophoryová *et al.* (2011), identified many species associated with the nests of birds. Still other species are associated with bats (Harvey & Parnaby 1993), packrats (Villegas-Guzmán & Pérez 2005) and even moles and mice (Durden 1991), where they use the nests as shelter and feed on ecto-parasites such as mites and larval fleas.

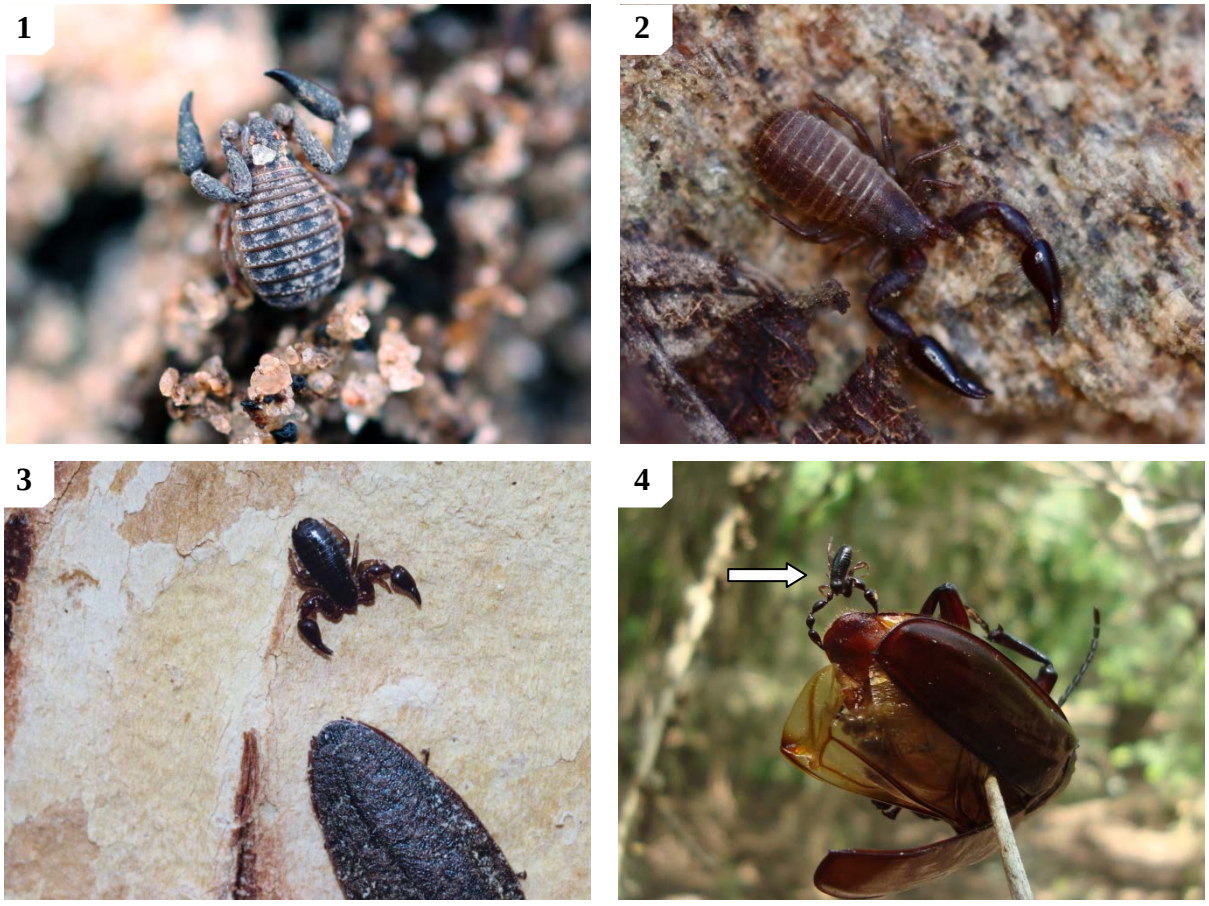
One of the better documented habits of pseudoscorpions is their phoretic association with many flying insects (Aguiar & Bührnheim 1998), whereby the pseudoscorpion attaches itself to a host insect by grasping it with its chela (Fig. 4), and travels along with its host to a new location where it would then detach. The exact reasons for this behaviour are still being debated, though the most popular theory is that it enhances their dispersal (Zeh & Zeh 1992).

When it comes to environmental interactions, the many sensory hairs located on the chela play a central role. Photoreception plays less of a role, as each eye only contains a few inverted sensory cells, meaning that object recognition is most likely not present, with the eyes merely playing a role in gauging the quantity of light (Weygoldt 1969). Like most arachnids, pseudoscorpions are generalist predators, feeding on small soil invertebrates such as mites, springtails, flies and ants. The chela are predominantly used in prey capture, where the pseudoscorpion stalks its prey and quickly grasps it , usually with both chela. The prey is held until all movement has ceased. The item is then brought to the chelicerae where a small incision is made in the cuticle. The pseudoscorpion then proceeds to inject digestive enzymes while macerating the prey with its chelicerae. Finally, the digested contents are absorbed, leaving only a small undigested globule to be discarded. During feeding the prey item is only held by the chelicerae (Levi 1948; Weygoldt 1969).

1.4 *Mating and social interactions*

In Pseudoscorpiones mating occurs through indirect spermatophore transfer, with no copulation between males and females. Male pseudoscorpions deposit spermatophores produced

from their gonopore onto the substrate, which the females then use to take up sperm. It is believed that pseudoscorpions may be the first group of arthropods that developed this behaviour (Kew 1912). Sperm transfer is via one of two means: in families such as Chthoniidae and Geogarypidae the male merely deposits a spermatophore on a suitable substrate, either with or without the presence of a female. The female is then tasked to locate the spermatophore chemotactically. Some species construct a chemical trail by spinning silken threads that lead to the spermatophore, aiding the female in her location of the sperm. Members of the Cheliferidae and Chernetidae, on the other hand, perform elaborate mating dances that can last up to three hours, with the male finally positioning the female over his spermatophore, thus ensuring the transfer of his genes (Weygoldt 1965, 1966a, b, c, 1970). De Andrade & Gnaspini (2003) and Klausen (2005) note that the spermatophore itself is usually very simple in structure, comprising a simple stalk bearing a globular sperm package on its tip.



Figs. 1-4. Pseudoscorpion habitats and behaviour. **1**. Garypidae sp. amongst moist soil particles; **2**. Atemnidae sp. taking shelter under a stone; **3**. Withiidae sp. exposed after removing bark; **4**. Prioninae beetle with phoretic *Titanatemnus natalensis* Beier, 1932 (Atemnidae). Photographs courtesy of Dr. Charles R. Haddad.

After insemination the eggs mature internally within the female. Before laying eggs most females set out to build a brood nest. The nest is most often made within a crevasse or depression in the substrate and covered with nearby debris for camouflage. The female will then stay within the

nest until the protonymphs are able to disperse. The eggs are laid within a secretion that hardens to form a brood-sac that is attached to the female's gonopore and is in open connection to the female's genital atrium. The eggs themselves are poor in yolk, thus brood care is provided by the female in the form of a nourishing liquid, produced in the ovaries, that she excretes into the brood sac. The developing embryos then use a unique pumping organ to absorb the nutritive fluid (Weygoldt 1969).

Pseudoscorpions go through four instars, divided by three post-embryonic moults. Protonymphs emerge from the eggs and cling to the female for some time before dispersing. They possess tube-like mouthparts and are still cared for by the female. Finally the protonymphs disperse and moult into free-living, predatory deutonymphs. These moult into tritonymphs and finally into adults, characterized by fully developed genital structures. Adults do not moult again and may live for several months to a year or two, with females able to produce multiple brood-sacs within this time (Buddle 2005). Pseudoscorpion nymphs resemble adults but are usually paler due to the lack of sclerotization. Each instar can be identified by the number of trichobothria present on the movable finger of the chela. Protonymphs have one, deutonymphs usually have two, tritonymphs usually have three and adults usually have four.

Due to their solitary lifestyle, pseudoscorpions generally avoid interacting socially, as there is often inter- and intraspecific aggressive behaviour. There are, however, a few social species that go beyond merely aggregating in large numbers. *Paratemnoides elongatus* (Banks, 1895), for example, exhibits one of the highest levels of social organisation currently known among pseudoscorpions, with communal spinning by immatures as well as communal moulting. Adults and tritonymphs also engage in cooperative predation, which enables the colony to capture prey many times their own size (Zeh & Zeh 1990).

Tizo-Pedroso & Del-Claro (2005) observed other behaviour of particular interest, namely the occurrence of matriphagy in *P. nidificator* (Balzan, 1888). Here the females, which are responsible for all brood care, would allow nymphs to attack and feed on them during periods of food deprivation. They hypothesized that this behaviour could lead to a decrease in cannibalism among nymphs, as well as contribute towards the evolution of social behaviour in the species.

1.5 *Taxonomy and phylogeny*

The classification of these remarkable creatures had scientists of the 18th century quite baffled, with Linnaeus relating their peculiar morphology to those of mites, crabs and scorpions. According to Harvey (2007) first species were described by Linnaeus in 1758 in the genus *Acarus*, thus grouping them with mites. Geoffroy, in 1762, moved these species to the genus *Chelifer*, but his

original paper was invalidated because he had not adhered to Linnaean binominal nomenclature (Harvey 2007). The genus *Chelifer* was finally validated in 1989 (International Commission on Zoological Nomenclature 1989).

During the next century only a handful of additional genera were added, by authors such as Illiger, Koch, Gervais and Menge (Harvey 2007). By the early 20th century, contributions by authors such as Banks (1895), Tullgren (1907a, b) and Ellingsen (1912) greatly expanded the taxonomic knowledge and species numbers of pseudoscorpions, though it was only with the publication of the seminal piece by Chamberlin (1931) that a standardised classification system was created. In his work he divided the Pseudoscorpionida into three suborders, namely the Heterosphyronida, Diplosphyronida and Monosphyronida, based on the fusion profiles of the tarsi and metatarsi of species. Beier (1932a, b) made minor adjustments to the system and proposed his own three suborders: Chthoniinea, Neobisiinea and Cheliferinea. Muchmore (1982) rejected the subordinal classification and instead divided the Pseudoscorpionida directly into six superfamilies: Chthonioidea, Neobisioidea, Garypoidea, Cheiridioidea, Feaelloidea and Cheliferoidea. At this point more than 2000 species of pseudoscorpions were known.

The next major breakthrough came when Harvey (1992b) provided a phylogeny based on 126 morphological characters and proposed a new classification recognising two suborders (Epiocheirata and Iocheirata) and 24 families. He based his suborders on either the presence or lack of a venom apparatus on the chelal fingers. He furthermore placed the Feaelliodea (Feaeillidae and Pseudogarypidae) as the sister group of the Chthonioidea (Harvey 1992b).

Changes to the latter classification since its publication included disputes by Judson (2000) about the validity of the Cheiridioidea, and its subsequent removal from synonymy with the Garypoidea. The Cheiridioidea is now considered the sister group to the Cheliferoidea. Further alterations, according to Harvey (2013), include the removal of the Pseudotyrannochthoniinae from the Chthoniidae in 1993 and the Garypininae from Olpiidae in 2004. Both were elevated to full familial status, resulting in 26 presently recognized families.

The first molecular phylogeny of the major pseudoscorpion clades was presented by Murienne, Harvey & Giribet in 2008. Though many superfamilies were successfully resolved, the Neobisiodea, Garypoidea and Cheliferoidea were not monophyletic. Furthermore they found that the Feaelloidea constituted the sister group to all other pseudoscorpions, while the Chthonioidea constituted the sister group to the remaining families.

Family level identifications are primarily done through the use of morphological characters such as trichobothrial and setal arrangements, chela and carapace morphology, leg segmentations and eye patterns (Harvey 1992b). Genus and species level identifications rely on finer structures such as chela teeth arrangements or the morphology and structures of the chelicerae (Bishop 1967; Engel 2012). Unlike the study of the Araneae, the structure of the male and female genitalia, as well as male spermatozoa, are infrequently used in species descriptions (Legg 1974a, b). Due to the complex structures of particularly the male genitalia, authors such as Legg (2008) consider them valuable taxonomic tools, with Proctor (1993) already using them to resolve trichotomy in cheliferoid pseudoscorpions.

1.6 *Pseudoscorpion research in South Africa*

At the start of the 20th century the data available on pseudoscorpions from Southern Africa was sparse at best, with *Cordylochernes octentoctus* (Balzan, 1892), *Withius simoni* (Balzan, 1892) and *W. tenuimanus* (Balzan, 1892) being the only South African endemics known (Ellingsen 1912). Historically, most of the early research, specifically species descriptions, was done by foreign scientists. The works of Tullgren (1907a, b), Ellingsen (1912) and to a lesser extent Hewitt & Godfrey (1929) saw an abundance of new species descriptions, both from field expeditions as well as examination of museum specimens. However, it was Max Beier who was by far the greatest contributor to the field, describing approximately 80% of the currently known species in the region from 1947 to 1966 (Beier 1947, 1955, 1964, 1966).

After 1964 the discovery of new species decreased drastically, with the last South African species described by Mahnert (1988). In was only during the second half of the 20th century that researchers based in South Africa, such as Lawrence (1967) from the Natal Museum, Pietermaritzburg, started to publish checklists of species found within the region. Dippenaar-Schoeman & Harvey (2000) published a complete checklist and catalogue of species found in South Africa, and in subsequent years several checklists of nature reserves would follow (Haddad *et al.* 2006; Haddad & Dippenaar-Schoeman 2009). In recent years South African specimens also contributed to karyotype studies (Šťáhlavský *et al.* 2006), as well as phylogenetic analyses (Murienne, Harvey & Giribet 2008; Van Heerden, Taylor & Van Heerden 2013).

South Africa currently has 152 known species in 17 families, with over 70% of these species endemic to the country, ranking the region eighth in the world with regards to pseudoscorpion species richness (Dippenaar-Schoeman & Harvey 2000; Harvey 2013). The most recently discovered species was described by Manhert (1988), and since then the main focus of research has been to create checklists of the region. Following advances in pseudoscorpion taxonomy, both morphologically

(Harvey 1992) as well as phylogenetically (Murienne, Harvey & Giribet 2008), a decision was made to follow on their success and start revisions of our indigenous fauna.

The family Geogarypidae was chosen to spearhead this endeavour as it has been previously revised by Harvey (1986). The South African fauna consists of nine species in two genera (*Afrogarypus* Beier, 1931 and *Geogarypus* Chamberlin, 1930), with one species, *A. excelsus* (Beier, 1964), consisting of two subspecies. The taxonomy of the family will be dealt with in detail in chapter 3. Difficulty soon arose in the acquisition of the type specimens. Since the indigenous fauna was described over a 60 year period by three foreign authors, many types were not lodged in South African collections. Although the types for *G. flavus*, *G. minutus*, *G. olivaceus* and *G. robustus* were located, the remaining types could not and are presumed to be lost or destroyed during World War II. A few are lodged in collections oversees, and since the curators were understandably unwilling to ship such valuable material, not all the types could be examined, although curators kindly provided high resolution images of some types for comparison.

1.7 *Aims*

Taking the above into consideration a three-phase plan was devised to meet the project goals of revising the Geogarypidae of South Africa:

Phase I - field work

The collection of as many specimens as possible from as many varying habitats around the country as time would allow. Attention would be given to the type localities of the described species, as to maximize the chance of acquiring them.

Phase II - morphological study

Detailed morphological analysis would be performed on all the distinct morphospecies found during the previous phase through the use of lactic acid clearing, stereomicroscopy and scanning electron microscopy (S.E.M.), which would allow for detailed species descriptions to be done.

Phase III - molecular phylogeny

A genetic analysis of all morphospecies acquired during Phase I, with the aim of constructing a phylogenetic tree of all the distinct species.

The above project plan is intended to provide a holistic view of the taxonomy of the Geogarypidae of South Africa through the incorporation of both morphological as well as molecular phylogenetic characters in species descriptions. The project will then also pave the way for future

work to be done on the remaining families. In short, the aim of this dissertation is to start with the complete revision of all South African pseudoscorpions, beginning with the family Geogarypidae.

CHAPTER 2 - MATERIALS AND METHODS

2.1 *Specimen sampling*

Between September 2011 and December 2013 multiple expeditions were conducted to a total of 53 sampling locations across eight of the nine provinces of South Africa. Due to habitat homologies with much of the Free State and Northern Cape (Mucina & Rutherford 2006), the North West Province was not sampled. A single geogarypid museum sample was found for the province, and future work will include sampling in this region to fill the information gap.

Since most of the type localities are situated within the Afromontane belt and coastal fynbos areas (Tullgren 1907a, b; Ellingsen 1912; Beier 1947, 1955, 1964), the majority of sampling was concentrated within these habitats. Effort was made to also sample as many diverse habitats as possible across South Africa to not only ensure accurate determination of species ranges and habitat preferences, but to also increase the likelihood of sampling new species.

Specimens were sampled using:

2.1.1 *Leaf litter sifting*

Sifting of leaf litter was done using a sieve containing a metal mesh with 5mm spacing. The technique consisted of collecting leaf litter, as well as other detritus material, from the environment and sifting the material over a white sheet. Any pseudoscorpions could then easily be identified, collected and placed in 1.5 ml cryovials with 99% ethanol for storage.

2.1.2 *Canopy fogging*

Fogging of the canopies of trees located at most of the sampling locations was conducted using a Stihl SR430 blower. A solution of Tobaccoguard®, a pyrethroid based ULV spray, and D.B.M. Double Strength, an organophosphate based emulsifiable concentrate, mixed in a ratio of 100:1, acted as the knock-down agent. White sheets mounted and spread on metal rods were placed under the target trees and covered an area of 54 m^2 beneath the canopies. A total of one hour was allowed for the knockdown agent to work on each tree sampled, whereafter the specimens were collected from the sheets using household Electrolux handheld vacuum cleaners, fitted internally with a fine material mesh to stop any specimens from entering the motor and blades. The material was then emptied into 250 ml plastic bottles and filled with 99% ethanol. The bottles were later emptied

into white plastic sorting trays in the laboratory and pseudoscorpions were collected and separated by morphospecies into 1.5 ml cryovials containing fresh 99% ethanol.

2.1.3 *Hand collecting*

Hand collecting was done when moving from one sampling location to another in an area. For this study, hand collecting consisted of lifting stones, logs and other debris in search of specimens. Occasionally shrubs were also sampled by vegetation beating using a 35 cm diameter sweep net and beating stick.

All specimen vials collected from an area were provided with detailed labels containing locality and sampling data. Locality co-ordinates were obtained using a Garmin GPSmap 62 handheld GPS (accuracy of 3-6m).

2.2 *Morphological analysis*

Geogarypidae specimens collected during fieldwork were firstly separated into morphospecies. Using specimens from the type localities as well as available literature (Tullgren 1907a, b; Ellingsen 1912; Beier 1947, 1955, 1964) the nine described species were identified. All specimens not matching the known species descriptions were initially identified to genus level, and only designated as new species after both morphological and molecular analysis. Additional specimens were either loaned from or examined at their respective institutions to aid in this study.

The following institutions either supplied, or currently house specimens referred to in this study (curators given in parenthesis):

AMG	Albany Museum, Grahamstown, South Africa (John Midgley)
NCA	National Collection of Arachnida, ARC - Plant Protection Research Institute, Pretoria, South Africa (Ansie Dippenaar-Schoeman)
NMBA	National Museum, Bloemfontein, South Africa (Leon Lotz)
NMSA	KwaZulu-Natal Museum, Pietermaritzburg, South Africa (Burgert Muller)
NMZA	Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe (Moira Fitzpatrick)
SAMC	Iziko South African Museum, Cape Town, South Africa (Dawn Larsen)
WAM	Western Australian Museum, Perth, Australia (Mark Harvey)
ZMH	Zoological Museum of Hamburg, Hamburg, Germany (Markus Koch)

During discussions with the Ditsong Museum, Gauteng and visits to the National Museum, Bloemfontein, no pseudoscorpion specimens belonging to the Geogarypidae could be located. Most of

the slides from AMG were damaged during a fire in 1941, which resulted in poor specimen visibility. Although specimens could be identified, the sexes of most could not be determined. Where locality co-ordinates could not be located either on labels or in an institution's database, they were traced by georeferencing, mainly using the Global Gazetteer version 2.2 (http://www.fallingrain.com) and Google Earth (https://www.google.com/earth/). Such localities are indicated by square brackets in the lists of material examined. Distribution maps were generated using the software program Quantum GIS Dufour version 2.0.1 (http://www.qgis.org/en/site/).

The morphological techniques used included:

2.2.1 *Whole specimen analysis*

Specimens were placed within a small glass Petri dish containing 99% ethanol and examined. Extended focal range images of entire specimens were taken using a Nikon Coolpix 8400 camera mounted on a Nikon SMZ800 stereomicroscope, and stacked using the 64bit software program Adobe Photoshop CS5 (http://www.adobe.com/products/photoshop.html) to increase depth of field. Due to the lack of fidelity caused by blooming, some of the smaller species were photographed on light backgrounds, while the rest of the species were photographed with a black background.

2.2.2 *Lactic acid clearing*

Before clearing, male and female representatives of each species were first transferred into glycerin and left overnight. This step prevented the exemplars from floating to the top during the clearing step, resulting in uneven to no clearing. Specimens were then transferred into small glass vials containing 90% lactic acid and left overnight to clear. For some heavily sclerotized specimens, such as those of *Afrogarypus impressus* (Tullgren, 1907), it was necessary to clear the specimens for two days. After clearing, the specimens were dissected according to Hu & Zhang (2012) by removing the chelicerae, pedipalps, leg I and leg IV using size 0 insect pins. The individual structures were then temporarily mounted in the same lactic acid on standard microscope slides. Following Harvey (2010), small pieces of nylon fishing line were used to elevate the cover slip above the structures. This prevented the structures from being crushed, while providing room for the rotation of the structures by movement of the cover slip. Fishing line thicknesses used were: 0.12 mm for chelicerae, 0.26 mm for pedipalps and legs and 0.45 mm for the carapace and abdomen. The slides were then mounted on an Axiophot stereoscopic microscope (Zeiss, Germany) fitted with an AxioCam ICc 5. Images and measurements were done using the 64bit software AxioVision Special Edition version 4.9.1 (http://www.zeiss.co.za/microscopy/en_za/home.html). Extended focal range images of the studied structures were produced by stacking in Adobe Photoshop CS5. These images were then printed and traced to produce the line drawings used for the species descriptions.

2.2.3 *Scanning electron microscopy (S.E.M.)*

Specimens were cleaned of soil and other debris using a Branson® 3200 ultrasonic bath at 30 second intervals for three minutes while suspended in 10 ml glass vials containing 100% ethanol. S.E.M. images were produced on a Shimadzu SSX-550 S.E.M. (Kyoto, Japan). Specimens were first dehydrated using 100% ethanol and then critical point dried using a Tousimis critical point dryer (Rockville, Maryland, U.S.A.) and carbon dioxide drying gas. After being mounted on stubs using thin double-sided tape, the specimens were gold sputter coated at 50-60nm thickness in a BIO-RAD (Microscience division) coating system (London, U.K.). All images were produced at 5.00kV. All stubs were donated to the Microscopy Division at the University of the Free State on their request.

Terminology mostly follows Harvey (1992b) with the exception of the chelicerae which follows Judson (2007). Ratios are given as $^{\text{Length}}$ / $_{\text{Width}}$. The following abbreviations are used in the figures and text:

Chela trichobothria

b	=	basal
sb	=	sub-basal
st	=	sub-terminal
t	=	terminal
ib	=	interior basal
isb	=	interior sub-basal
ist	=	interior sub-terminal
it	=	interior terminal
eb	=	exterior basal
esb	=	exterior sub-basal
est	=	exterior sub-terminal
et	=	exterior terminal

Chelicerae

es	=	exterior seta
bs	=	basal seta
sbs	=	sub-basal seta
is	=	interior seta
ls	=	laminal seta
gs	=	galea seta
se	=	serula exterior
si	=	serula interior
le	=	lamina exterior
r	=	rallum
g	=	galea

2.3 *Molecular methods*

Using Murienne, Harvey & Giribet (2008) as a reference guide, the following steps were followed to determine the phylogenetic relationships between the South African species of Geogarypidae using molecular techniques. The above mentioned paper used three molecular markers consisting of two nuclear ribosomal genes (complete 1.8 kb 18S rRNA and a 1kb fragment of 28S rRNA) and one mitochondrial protein-coding gene (cytochrome c oxidase subunit one).

In this study 18S rRNA was discarded due to its potential for weak resolution at species level branches (Steiner & Müller 1996) and the fact that it has to be sequenced in three fragments of 900bp each, which was restricted due to funding limitations. It was therefore decided to rather focus on the

remaining two genes, namely the nuclear gene 28S rRNA (28S hereafter) and the mitochondrial gene cytochrome c oxidase subunit one (COI hereafter).

One female specimen per morphospecies was designated for genetic analysis and stored in 1.5 ml cryovials in 100% ethanol at -80^{o}C until DNA extraction. After DNA extraction the genomic DNA of each specimen was again stored at -80^{o}C until amplification. All Polymerase Chain Reaction (PCR) products were stored at -20^{o}C until sent for sequencing.

2.3.1 *DNA extraction, amplification and sequencing*

Initial DNA extraction was performed at the WAM (Perth, Australia) using a modified version of the salting out procedure of Miller, Dykes & Polesky (1988), as this was the standard procedure used at the facility. Unfortunately, not only was the procedure a time-consuming endeavour, taking three days to yield deproteinized genomic DNA, but failed to yield any genomic DNA in over 50% of samples.

Final DNA extraction was then performed by using the same method as Murienne, Harvey & Giribet (2008). Tissue lysis and DNA purification was done using a DNEasy® tissue kit (Qiagen, R.S.A.), following the manufacturer's protocol. Total genomic DNA was extracted by incubating crushed, whole specimens in the lysis buffer overnight. The purified genomic DNA was then used as a template for PCR amplification.

Primer-pairs used in this study:

Gene	**Primers**	**Sequence**	**Reference**
28S	28SpsF1	5'- ATTA CCC GCC GAA TTT AAGC -3'	Murienne *et al.* 2008
	28SpsR1	5'- TCG GAG GGA ACC AGC TAC -3'	
COI	LCO1490	5'- GGTC AAC AAA TCA TAA AGA TAT TGG -3'	Folmer *et al.* 1994
	HCO2198	5'- TAAA CTT CAG GGT GAC CAA AAA ATCA -3'	

The above primers resulted in the amplification of the first c. 1000bp of the 28S rRNA (domain 1 of the 28S secondary structure) as well as COI. Cytochrome c oxidase subunit I amplification was done at the WAM using a BIO-RAD T100™ thermal cycler. Unpurified PCR products were sent to the Australian Genome Research Facility (Perth Node) for sequencing. Polymerase chain reactions for 28S were done at the Tick Pesticide Resistance Biotechnology Laboratory at the University of the Free State using a Corbett Research Gradient Palm-Cycler™, with the unpurified PCR products sent to Inqaba Biotechnical Industries in Pretoria for sequencing. Amplification reactions of 25µl contained 2.5µl of template DNA, 0.5µl of both the forward and reverse primers at 1µM each and 21.5µl TopTaq Master Mix (Qiagen, R.S.A.).

The PCR process involved the following:

Step	Process	Temperature	Time	Repeats
1	Denaturation	95°C	5 minutes	1x
2	Denaturation	95°C	30 seconds	
3	Annealing	45°C (28S); 46.2°C (COI)	30 seconds	34x
4	Extension	72°C	1 minute	
5	Final Extension	72°C	10 minutes	1x
6	Hold	20°C	∞	1x

Double stranded PCR products were verified via agarose gel electrophoresis (1% agarose) and sent for sequencing unpurified.

2.3.2 *Sequence editing and phylogenetic analysis*

Cromatograms in .abi format were edited in Geneious R6 version 6.0.4 (http://www.geneious.com/). Sequence terminals were trimmed of low quality bases and overlapping segments were assembled. Before alignment, BLAST searches were done via the NCBI website (http://ncbi.nlm.nih.gov/) to check for putative contamination.

The same software was used to perform Geneious, MUSCLE and ClustalW alignments, as well as concatenation for the combined phylogenetic tree. For outgroups, sequences for *Afrochthonius godfreyi* (Ellingsen, 1912) (Pseudotyrannochthoniidae), *Anagarypus heatwolei* Muchmore, 1982 (Garypidae) and *Synsphyronus apimelus* Harvey, 1987 (Garypidae) were obtained from GenBank. *Afrochthonius godfreyi* acted as root taxon, while the two garypid species served as the sister group to the Geogarypidae to assess whether or not the group is monophyletic. Alignments were produced for COI, 28S as well as the concatenated COI-28S tree.

Tests for maximum likelihood, neighbour-joining, minimum evolution and maximum parsimony were performed using Mega 5 version 5.2.2 (http://www.megasoftware.net/) on all the above mentioned alignments to produce the best fitting trees for COI, 28S and the combined COI-28S tree. Mega 5 was chosen due its ease of use and incorporation of multiple phylogenetic tests, thus eliminating the need for multiple programs and the use of multiple file formats (Hall 2013). All tests were done with 1000 Bootstrap replications. A final Bayesian analysis was also run on the concatenated COI-28S tree using the MrBayes version 3.2.5 software package and the resulting consensus tree was viewed and edited in Fig Tree version 1.4.2. Trees were then edited in Adobe Photoshop CS5 to italicize species names, before being saved as .png files.

CHAPTER 3 - SYSTEMATICS OF THE GEOGARYPIDAE

3.1 *Introduction*

Fossil Geogarypidae bearing all the characteristic morphological traits of their modern descendents have been collected from both Baltic (Henderickx 2005) and Rovno (Henderickx & Perkovsky 2012) ambers dating from the late Eocene to early Oligocene epochs, strongly suggesting that members of this family have been around for at least 50 million years.

Most modern species are generally tropical, subtropical or temperate, distributed north and south throughout the equatorial belt (Harvey 2013), and can commonly be found in leaf litter and under stones in habitats ranging in elevation from 0 - 3200m above sea level (Beron 2002). Most species are regional endemics with small distribution ranges, but due to human traffic, species such as *Geogarypus mirei* Heurtault, 1970 have extended their range beyond their natural dispersal capabilities (Mahnert 2011). Historically, most research focused on species descriptions, but they have recently been investigated as potential biological control agents in certain crops (Devasahayam & Koya 1994).

Originally a subfamily of the Garypidae, Geogarypinae was elevated to full familial status by Harvey (1986). Previously all species were placed in the genus *Geogarypus* Chamberlin, 1930, which had been divided into the three subgenera *Geogarypus* (*Afrogarypus*), *Geogarypus* (*Geogarypus*) and *Geogarypus* (*Indogarypus*) by Beier (1931, 1947, 1955, 1957, 1964). These subgenera were subsequently elevated to generic level by Harvey (1986) and are currently recognized as *Afrogarypus* Beier, 1931, *Geogarypus* and *Indogarypus* Beier, 1957. The family is currently represented by 67 species worldwide, of which 23 species have been described from the Afrotropical Region, five in *Geogarypus* and 18 in *Afrogarypus*.

While *Indogarypus* is restricted to India and Sri-Lanka (Harvey 1986), both *Afrogarypus* and *Geogarypus* have much wider distributions, with both genera being represented by multiple species in South Africa (Tullgren 1907a, b; Ellingsen 1912; Beier 1947, 1955, 1964). There are currently eight recognized species and two subspecies in South Africa, namely, *Afrogarypus excelsus excelsus* (Beier, 1964); *A. excelsus excellens* (Beier, 1964); *A. impressus* (Tullgren, 1907); *A. subimpressus* (Beier,

1955); *Geogarypus minutus* (Tullgren, 1907); *G. olivaceus* (Tullgren, 1907); *G. purcelli* (Ellingsen, 1912); *G. robustus* Beier, 1964 and *G. triangularis* (Ellingsen, 1912).

3.2 *Taxonomy*

3.2.1 Family **Geogarypidae** Chamberlin, 1930

Garypinae Simon, 1879: 42; Tömösváry, 1882: 208; Balzan, 1892: 534.
Garypidae (Simon); Hansen, 1893: 231; Ellingsen, 1904: 2; With, 1906: 89.
Geogarypinae Chamberlin, 1930: 609; Beier, 1932a: 227; Murthy & Ananthakrishan, 1977: 104 [**Type-genus** *Geogarypus* Chamberlin, 1930]
Geogarypidae (Chamberlin); Harvey, 1986: 754; Harvey, 1992b: 1420.

3.2.1.1 *Diagnosis*

According to Harvey (1992b) the Geogarypidae possess the following apomorphies: pit-like structures present on the exterior margin of fixed chelal finger and the presence of a simple, single-bladed rallum without any spinules.

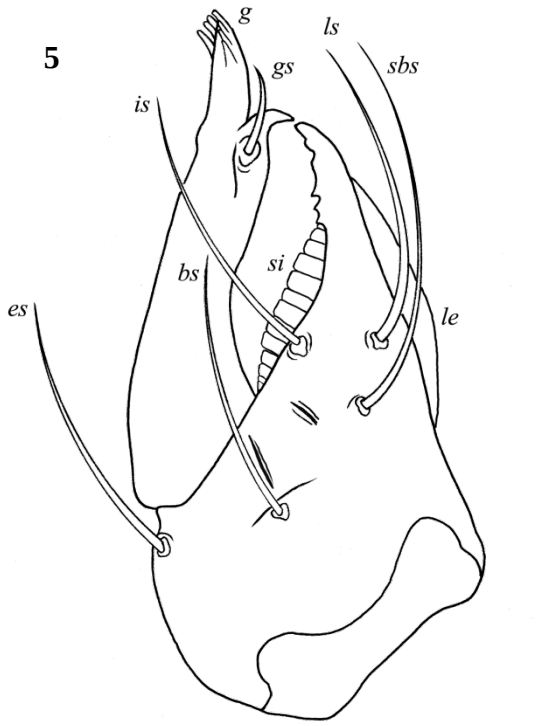
Further diagnostic characters include the possession of a sub-triangular carapace lacking any alae; two pairs of eyes situated on ocular tubercles located roughly one third the length of the carapace from its anterior margin; the presence of a venom apparatus on both chelal fingers; and most species, with the exception of *Geogarypus connatus* Harvey, 1986 and *A. castigatus* sp. nov., possessing diplotarsate adults.

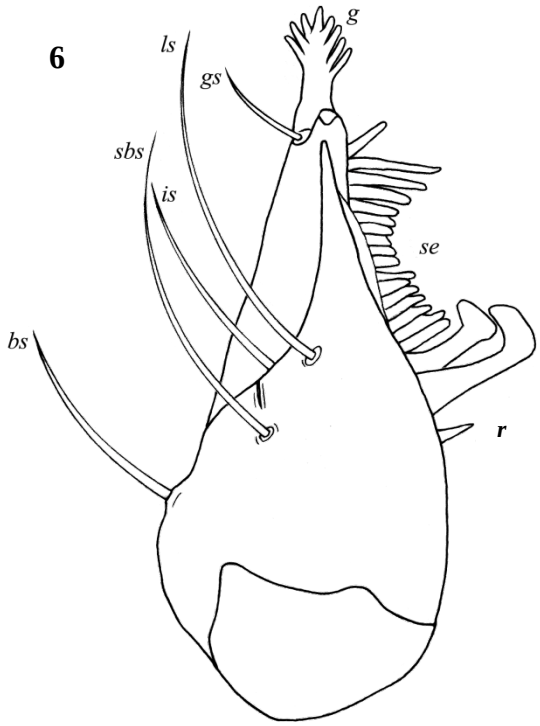
Members of the Geogarypidae can furthermore be separated from the family in which they were previously placed, the Garypidae, by the following: the presence of a spiracular stigmatic helix; a cheliceral rallum composed of a single blade lacking any spinules; coxa IV roughly as wide as coxa I; possessing a subterminal anal plate, without a lateral rim, that is not distinctly oval (Harvey 1986); and sternite XII without setae (this study).

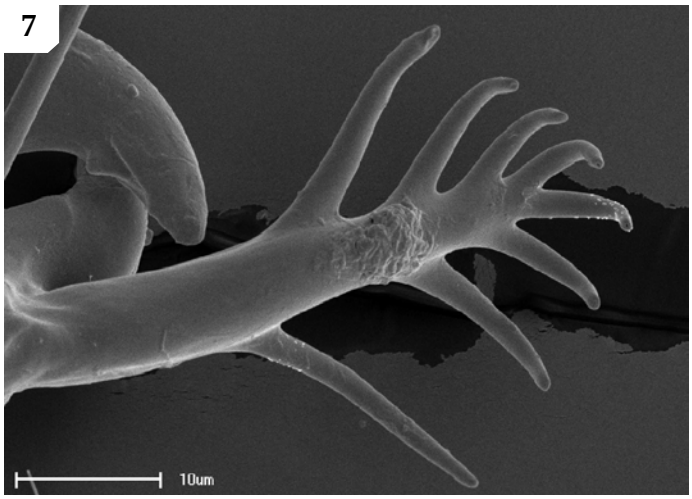
3.2.1.2 *Description*

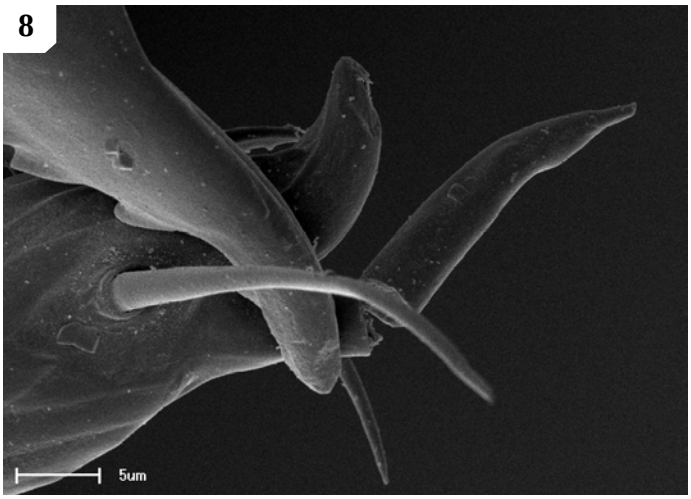
Geogarypidae colouration varies from uniformly brown, as in *A. triangularis* (Ellingsen, 1912) comb. nov., to the presence of different sized light cream patches on both the carapace, for example *Geogarypus deceptor* sp. nov., and abdominal ternites, as in *G. flavus* (Beier, 1947) stat. nov. All South African geogarypids possess darkened spots medially on abdominal tergites I and II, as well as paired spots on tergites IV to X. Tergite III lacks a dark spot, but may present cream patches.

Chelicerae have five acuminate setae on the cheliceral palm (Fig. 5), with seta *es* originating at the base of the movable finger, *bs* located on a ridge, centrally on the dorsal surface, setae *sbs*, *ls* and *is* grouping at the base of the fixed cheliceral finger and *gs* located just above the base of the galea, on the movable finger. Lamina exterior and serrula interior present on fixed chelal finger. Serrula exterior present on the movable finger, consisting of multiple lamellae; two lamellae closest to the rallum sickle-shaped (Fig. 6). The rallum is comprised of a simple, single blade without any spinules. Galea either complex, with multiple rami curving ventrally (♀) (Fig. 7), or simple, consisting of a single spinneret usually without spinules (♂) (Fig. 8).



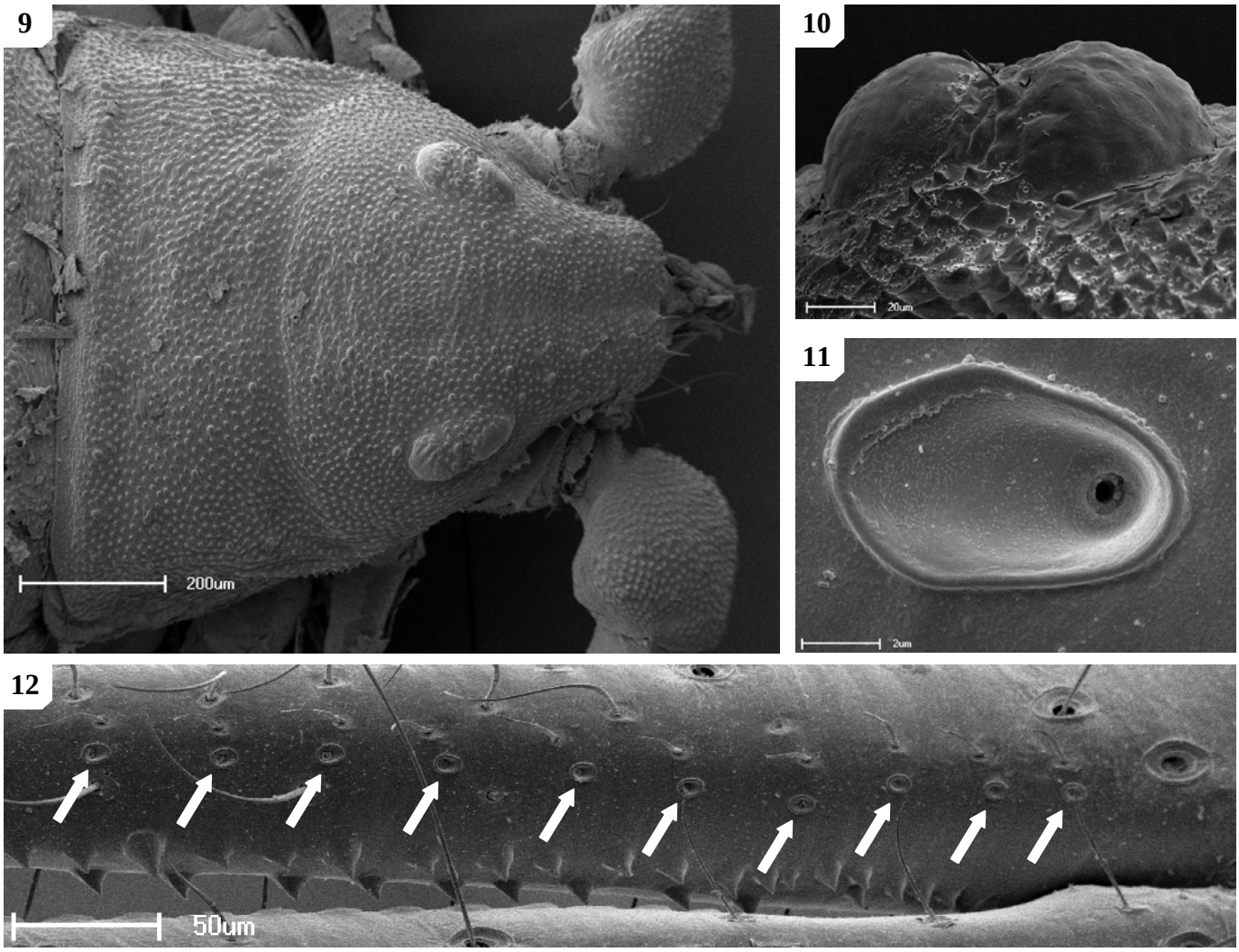






Figs. 5-8. General morphology of geogarypid chelicerae galea. **5**. Left chelicerae (female) dorsal view; **6**. Same, prolateral view; **7**. *Geogarypus octoramosus* sp. nov., female galea; **8**. Same, male galea.

Carapace strongly sub-triangular in shape, constricting into a cucullus anteriorly, granulate in texture and with a narrow furrow located posterior to the eyes (Fig. 9). Two pairs of corneate eyes situated on ocular tubercles located roughly one third the length of the carapace from its anterior margin (Fig. 10). Pedipalpal coxae with distinct shoulder, trochanter with ventral apophysis. Femora and patellae granulate in texture, without any sensory trichobothria. Lyrifissures situated dorsally, usually on a raised surface, near base of the patellae. Surface of the chelal hand granulate, becoming smooth at base of chelal fingers. Venom apparatus and lamina defensor present on both chelal fingers. Fixed finger either with or without accessory teeth, usually with eight trichobothria, but *A. castigates* sp. nov. with seven. Movable finger with four trichobothria. All trichobothria acuminate, with usual areolate shape. Fixed finger possessing a row of pit-like structures with raised rims on the exterior dorsal surface, each containing a central pore (Figs. 11 & 12).



Figs. 9-12. Scanning electron micrographs of *Afrogarpus excelsus* stat. nov. morphology. **9**. Female carapace dorsal view; **10**. Female ocular tubercle; **11**. Male pit structure on retrolateral surface of fixed chela finger with pore; **12**. Male fixed chelal finger showing pit structures on retrolateral surface.

Coxae of legs IV not significantly wider than coxae of legs I. Legs heterofemorate, with all joints of leg I and II movable. Legs I and II usually diplotarsate, though those of *A. castigatus* sp. nov. monotarsate, with arolium longer than claws. Abdomen sub-ovate in shape and broader than carapace. Tergites and sternites usually not divided, but a faint suture may be present ventrally, especially near the genital opercula. Pleural membrane wrinkled-plicate, with numerous investing setae present, set in small cuticular plates. In *A. triangularis* (Ellingsen, 1912) comb. nov. and *A. castigatus* sp. nov. males the cuticular plates are enlarged to form lateral sclerites. Spiracles open laterally of sternites III and IV, each with associated setae and a stigmatic helix (Harvey 1986). Female genital opening not visible, sternite III not curved, with few setae (Fig. 13). Genital opercula of males with visible opening, sternite III curving posteriorly around opening, usually with many associated setae (Fig. 14). Anal cone situated sub-terminally, formed by fusion of tergite XII and sternite XII. Tergite XII bearing two associated setae, sternite XII with none.

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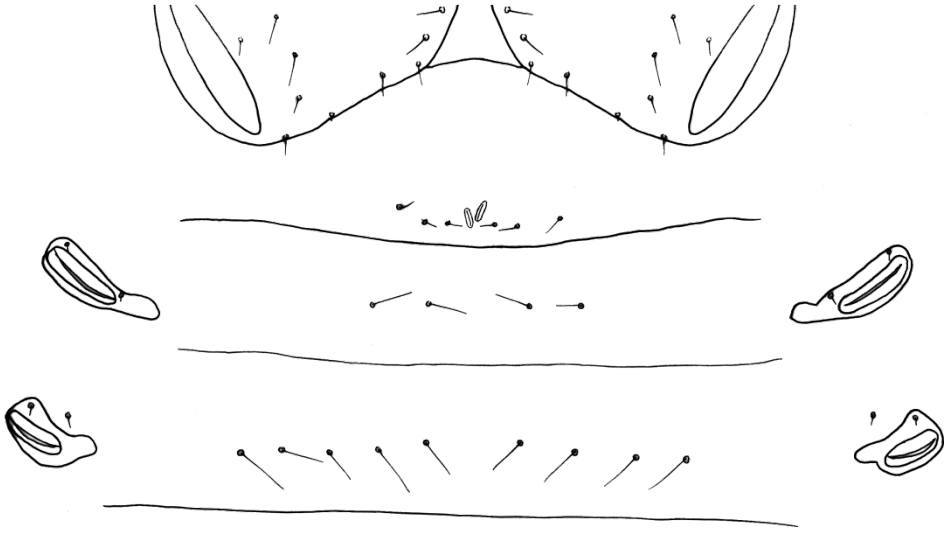

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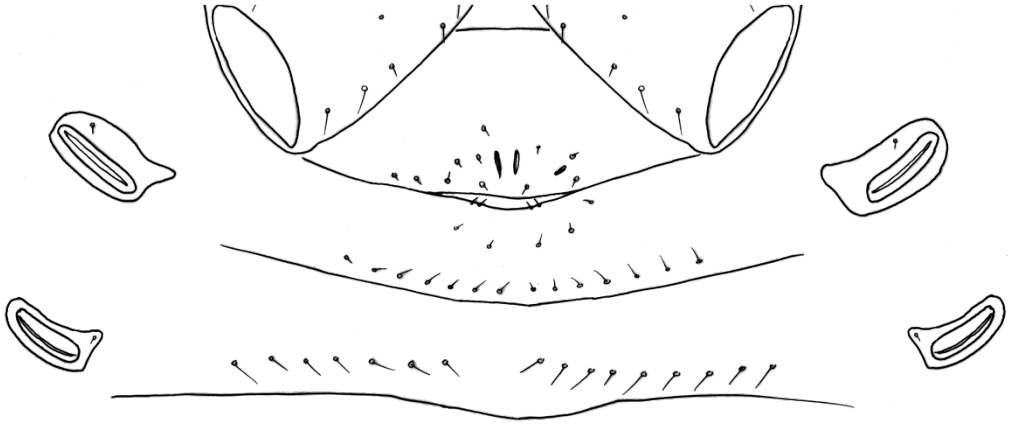


Figs. 13-14. General morphology of geogarypid genital opercula. **13**. Female genital area with spiracles; **14**. Same, male.

3.2.2 *The genera of South African Geogarypidae*

3.2.2.1 Genus ***Afrogarypus*** Beier, 1931

Afrogarypus Beier, 1931: 317; Harvey, 1986: 758; Harvey, 1992: 1420

[**Type species**: *Garypus senegalensis* Balzan, 1892].

Geogarypus (*Afrogarypus*) Beier, 1932a: 236; Beier, 1947: 320; Beier, 1955: 301.

3.2.2.1.1 *Diagnosis*

Originally distinguished by the presence of a deep dorsal sulcus on the chelal hand and lack of accessory teeth (Harvey 1986); data generated in this study necessitates an update of the diagnosis of the genus. The following alterations are proposed:

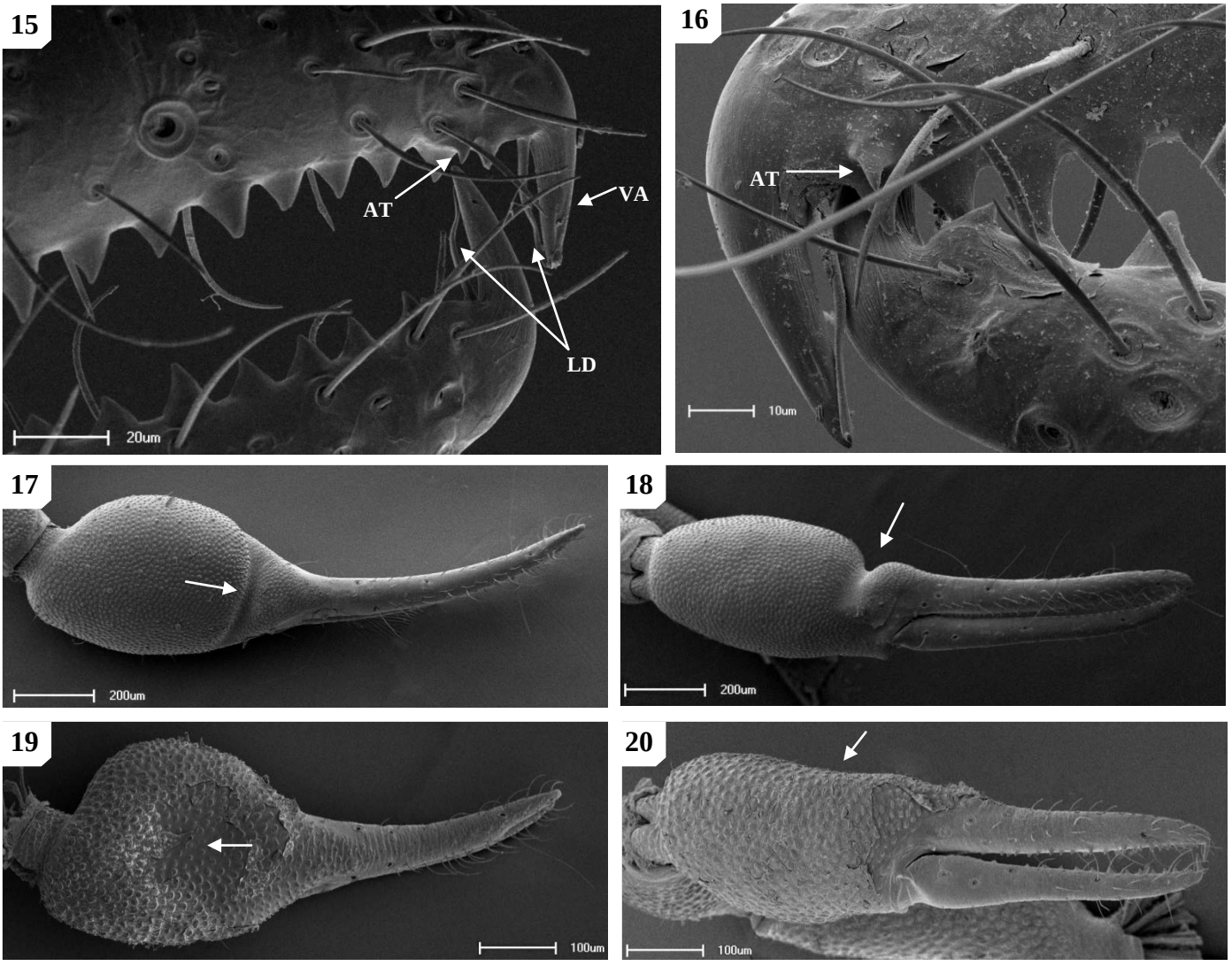
i – Phylogenetic analysis indicated that *A. minutus* (Tullgren, 1907) comb. nov., *A. purcelli* (Ellingsen, 1912) comb. nov., *A. robustus* (Beier, 1947) comb. nov. and *A. triangularis* (Ellingsen, 1912) comb. nov. (originally all in *Geogarypus*) group within the *Afrogarypus* clade. Morphological analysis of the above species showed the presence of a shallow depression on the dorsal surface of the chelal hand, a character not present on any of the species in the *Geogarypus* clade.

ii – Morphological analysis of species within the South African *Afrogarypus* clade indicated that the genus indeed possesses accessory teeth. Some of the examined *Afrogarypus* species, such as *A. excelsus* (Beier, 1964) stat. nov. and *Geogarypus* species, such as *Geogarypus octoramosus* sp. nov. also share a small accessory tooth just above the first teeth on the exterior dorsal surface of the fixed chelal finger (Figs. 15 & 16). The presence of accessory teeth is thus not a synapomorphy of any of the genera and it is proposed that the presence of accessory represents the pleisiomorphic state.

Species of the genus *Afrogarypus* can thus be distinguished from other South African Geogarypidae by the presence of either a well developed sulcus (Figs. 17 & 18), or a concave depression on the dorsal surface of the chelal hand (Figs. 19 & 20), resulting in a dorsal bulge at the base of the fixed chelal finger. With the exception of *Afrogarypus castigatus* sp. nov. which possess a reduced compliment of 7/4 all the South African members of the genus possess the full 8/4 complement of trichobothria. Accessory teeth are present in some species.

3.2.2.1.2 *Discussion*

South African *Afrogarypus* possess some of the most morphologically distinct chela of all the Geogarypidae, with the presence of a dorsal sulcus being the most distinct feature. Phylogenetic analysis and subsequent combinations into the genus suggests that all but two of the originally described South African Geogarypidae, namely *G. olivaceus* and *G. flavus* (Beier, 1947) stat. nov., belong to this genus.



Figs. 15-20. Scanning electron micrographs of South African Geogarypidae morphology. **15**. *G. octoramosus* sp. nov., **16**-**18**, *A. excelsus* (Beier, 1964) stat. nov., **19**-**20**. *A. triangularis* (Ellingsen, 1912) comb. nov. **15**, **16**. Exterior lateral view of the distal ends of the chela fingers, showing venom apparatus [VA], lamina defonsor [LD] and accessory tooth [AT]; **17**, **19**. Dorsal view of female right chela; **18**, **20**. Same, retrolateral view.

3.2.2.1.3 *Species included*

A. carmenae sp. nov.; *A. castigates* sp. nov.; *A. excelsus* (Beier, 1964) stat. nov.; *A. impressus* (Tullgren, 1907); *A. megamolaris* sp. nov.; *A. minutus* (Tullgren, 1907) comb. nov.; *A. purcelli*

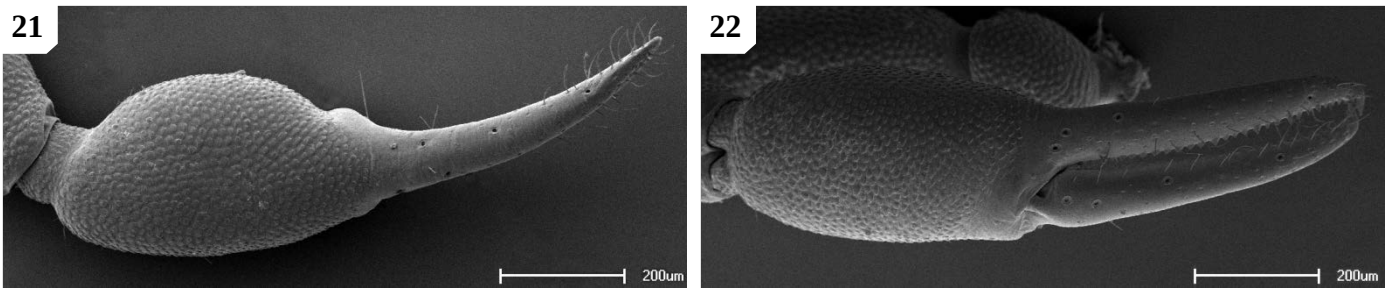
(Ellingsen, 1912) comb. nov.; *A. robustus* (Beier, 1964) comb. nov.; *A. subimpressus* (Beier, 1955) and *A. triangularis* (Ellingsen, 1912) comb. nov.

3.2.2.2 Genus ***Geogarypus*** Chamberlin, 1930

Geogarypus Chamberlin, 1930: 609; Beier, 1932b: 227; Beier, 1963: 241; Murphy & Ananthakrishan, 1977: 104; Harvey, 1986: 760; Harvey, 1992b: 1420
[**Type species**: *Garypus minor* Koch, 1873].

3.2.2.2.1 *Diagnosis*

With the revised diagnosis presented in this study, *Geogarypus* can easily be distinguished from the members of *Afrogarypus* by the lack of any dorsal sulcus or concave depression on the chelal hand, instead presenting a continuous convex dorsal surface from the chelal stem to the base of the fixed finger (Figs. 21 & 22). Accessory teeth may be present or absent.



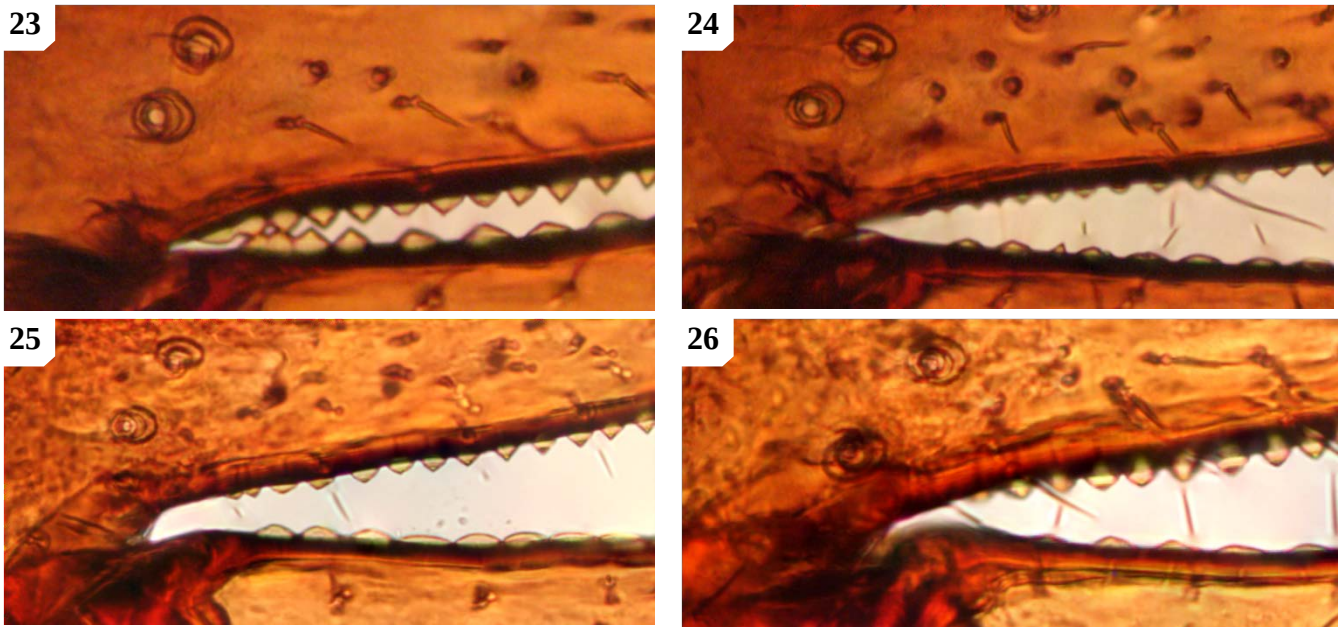
Figs. 21-22. Scanning electron micrographs the female right chela of *G. octoramosus* sp. nov. **21**. Dorsal view; **22**. Retrolateral view.

3.2.2.2.2 *Discussion*

The oldest of the Geogarypidae genera, the only previously described South African species to remain in *Geogarypus* are *G. olivaceus* and *G. flavus* (Beier, 1947) stat. nov. Pedipalps of the species are surprisingly uniform in shape, with the most distinct differences found between the morphology of the chelal teeth of females. Males of this genus can be troublesome to distinguish due to the many variations one finds in both size and colouration of a single species. As such, characters used within the proceeding identification key mainly rely on characters found in females. An example of the above can be seen when comparing the teeth at the base of the chelal fingers of both females (Figs. 23 & 25) and males (Figs. 24 & 26) of *G. olivaceus* (Tullgren, 1907) and *G. flavus* (Beier, 1947) stat. nov.

3.2.2.2.3 *Species included*

G. deceptor sp. nov.; *G. flavus* (Beier, 1947) stat. nov.; *G. liomendontus* sp. nov.; *G. modjadji* sp. nov.; *G. octoramosus* sp. nov.; *G. olivaceus* (Tullgren, 1907); *G. tectomaculatus* sp. nov.; *G. variaspinosus* sp. nov.



Figs. 23-26. Tooth morphology at the base of the chelal fingers of *Geogarypus* spp showing distinct differences in females, with males mainly differing with regard toteeth size between species. **23**. Female *G. olivaceus*; **24**. Same, male; **25**. Female *G. flavus* (Beier, 1947) stat. nov.; **26**. Same, male.

3.3 *Key to the Geogarypidae genera and species of South Africa*

1 Fixed chelal finger with trichobothria *isb*; legs I and II diplotarsate.....……...…..…..2

1' Fixed chelal finger without trichobothria *isb*; legs I and II monotarsate.
(***Afrogarypus castigates* sp. nov.**)……...……...……..…….....**p 32**

2. Dorsal surface of chela hand with a well developed sulcus or concave region…….…....3

2’ Dorsal surface of chela hand convex in shape from stem to base of fixed finger.
(*Geogarypus*)…….……...……11

3(1) Dorsal surface of chela hand with a well developed sulcus.
(*Afrogarypus* in part)…….…….....4

3’ Dorsal surface of chela hand with a concave region, but not a distinct sulcus…….……..7

4(3) Dorsal sulcus narrow and deep; dorsal surface of chela before sulcus elevated above bulge at the base of the fixed finger…….....…...5

4’ Dorsal sulcus wide and more shallow; dorsal surface of chela before sulcus on the same level as the bulge at the base of the fixed finger…….....……..6

5(4) Chelal fingers distinctly longer than hand with stem.
(***Afrogarypus excelsus*** **stat. nov.**)……...……...……..…….**p 37**

5’ Chelal fingers shorter than hand with stem.
(***Afrogarypus impressus***)……...……...…….**p 44**

6(4’) Interior surface of chelal hand strongly covex; female galea with eight rami.
(***Afrogarypus subimpressus***)……..……...…..**p 73**

6’ Interior surface of chelal hand almost straight, giving the chela a chisel shape; female galea with nine rami.
(***Afrogarypus megamolaris*** **sp. nov.**)…….……...….**p 50**

7(3) Chelal fingers distinctly longer than hand with stem.
(***Afrogarypus purcelli*** **comb. nov.**)……..……...……...……..….**p 61**

7’ Chelal fingers as long as hand with stem or shorter……...……...8

8(7’) Chelal fingers more or less as long as hand with stem……...……...…....9

8’ Chelal fingers distinctly shorter than hand with stem……...…....…10

9(8) First tooth behind venom apparatus noticeably more sclerotised and slightly larger than the teeth just after it; female galea with nine rami.
(***Afrogarypus carmenae*** **sp. nov.**)…….….**p 27**

9’ Chelal teeth not as above; female galea elongate and with eight rami.
(***Afrogarypus minutus*** **comb. nov.**)……...…**p 56**

10(8’) Chela long and slender; trichobothrial distribution normal, not grouping together.
(***Afrogarypus robustus*** **comb. nov.**)……....…....…..…...**p 67**

10’ Interior surface of chelal hand strongly convex, giving the chela a triangular appearance; trichobothria *eb*, *esb*, *est*, *ib*, *isb*, *b*, *sb* and *st* grouping proximally within the first third of the finger length, separated roughly by another third of the finger length from the distal group, consisting of trichobothria *ist*, *it*, *et* and *t*.
(***Afrogarypus triangularis*** **comb. nov.**)…….....……...**p 78**

11(2’) Female galea with nine rami…….....…….12

11’ Female galea with fewer than nine rami…….....……...17

12(11) Movable chelal finger with a distinct lone tooth at its base.
(***Geogarypus deceptor* sp. nov.**)…….....….**p 84**

12’ Movable chelal finger without a basal tooth separated from rest of teeth.....13

13(12') All teeth separate with no fusion.....14

13' Some teeth fused at the base of the chelal fingers.....16

14(13) Male and female with ≥ 40 teeth on the fixed chelal finger; first three basal teeth on movable finger separated by one tooth distance from each other; male galea with one or more spinules.
(***Geogarypus flavus* stat. nov.**).....**p 90**

14' Male and female with < 38 teeth on the fixed chelal finger; first three basal teeth on female movable finger adjacent to each other, without any gaps.....15

15(14') First three basal teeth on female movable finger grouped very close to each other, almost fused; said basal teeth originating above trichobothria *b* in females.
(***Geogarypus olivaceus***).....**p 111**

15' First three basal teeth on female movable finger grouped close at the base of the teeth, but teeth distinctly separate; said basal teeth originating between trichobothria *b* and *sb* in females.
(***Geogarypus tectomaculatus* sp. nov.**).....**p 116**

16(13') First four basal teeth on both female chelal fingers fused.
(***Geogarypus liomendontus* sp. nov**).....**p 96**

16' Only first three basal teeth fused on fixed chelal finger of female; no fused teeth on movable finger, though first three basal teeth grouped close together.
(***Geogarypus modjadji* sp. nov.**).....**p 100**

17(11') Female galea with eight rami.
(***Geogarypus octoramosus* sp. nov.**).....**p 105**

17' Female galea with variable number of rami, ranging from five to seven.
(***Geogarypus variaspinosus* sp. nov**).....**p 122**

3.4 *Afrogarypus carmenae* sp. nov.

Holotype: ♀, SOUTH AFRICA, Western Cape, Clanwilliam, Gecko Creek Wildlife Lodge, 32° 23'S, 18° 59'E, 331m a.s.l., Bushveld, Leaf litter sifting, leg. J.A. Neethling, 21.XII.2012 (NMBA P00228).
Paratypes: 1♀, 3♂, Same data as holotype (NMBA P00229).

3.4.1 *Etymology*

Named after Carmen Luwes who, throughout the study, helped to collect many of the new species described in this thesis.

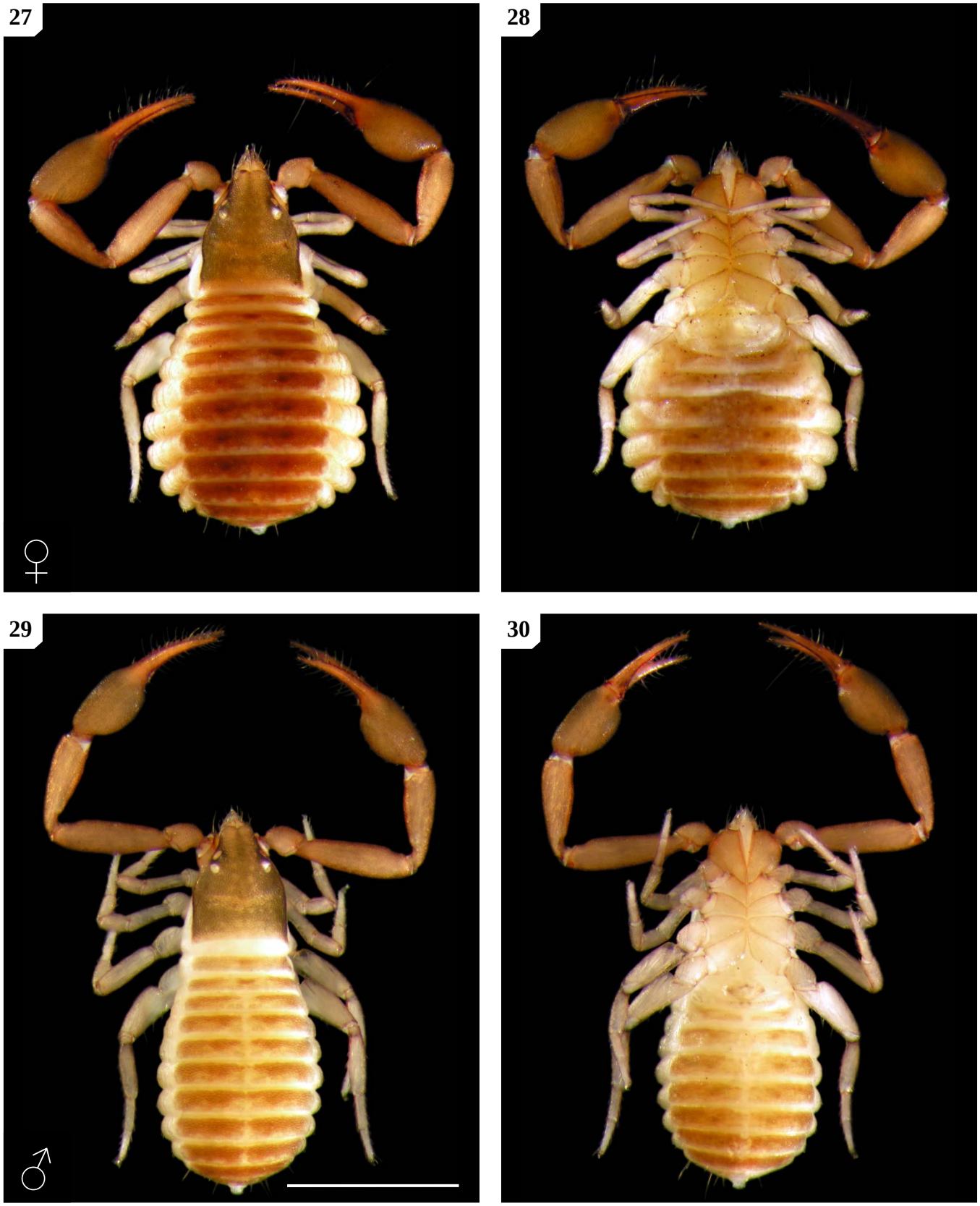
3.4.2 *Diagnosis*

Medium sized species, pedipalpal femur length 0.76mm (♀), 0.63mm (♂), chela length (with stem) 1.13mm (♀), 0.96mm (♂), movable finger length 0.55mm (♀), 0.49mm (♂). Both males and females can reach a total length (cucullus to posterior abdominal margin) of 2.14mm. Carapace uniform brown to light-brown in both sexes (Figs. 27 & 29). All pedipalp segments similar in colouration to the carapace. Concave depression present on dorsal surface of chelas. Abdominal tergites mostly brown with dark patches, though males can possess cream coloured markings. Abdominal sternites light brown in both sexes, weakly sclerotised in females (Fig. 28) and strongly sclerotised throughout in males (Fig. 30). Pedipalp coxa brown in colour with distinct shoulder, legs I-IV as well as remaining coxa tan to pale yellow. Though mostly equal in length, females tend to be more bulky with larger abdomens, while males are slimmer and more elongate.

Specimens of *Afrogarypus carmenae* sp. nov. resemble *A. purcelli* comb. nov. in general appearance, but can be distinguished by lacking the inclusion on the prolateral surface of the chela present in *A. purcelli* comb. nov.

3.4.3 *Description*

Carapace: Strongly sub-triangular, narrow furrow posterior to the eyes (Fig. 41). Overall brown to light-brown in both sexes, medial furrow and posterior margin somewhat lighter. Uniformly granular throughout, heavily constricted anteriorly into cucullus, constriction beginning at medial furrow. Two pairs of corneate eyes situated on ocular tubercles, located ca. one third away from anterior edge. Four prominent setae located on anterior edge, row of 10 setae, seated within rims, located on posterior margin. Numerous small setae present on the carapace. Carapace ratio: 1.08 (♀), 1.22 (♂).



Figs. 27-30. Digital microscope photographs of *Afrogarypus carmenae* sp. nov., Female (**27**, **28**) and Male (**29**, **30**). **27**, **29**. Dorsal view; **28**, **30**. Ventral view. Scale bar: 1.00mm.

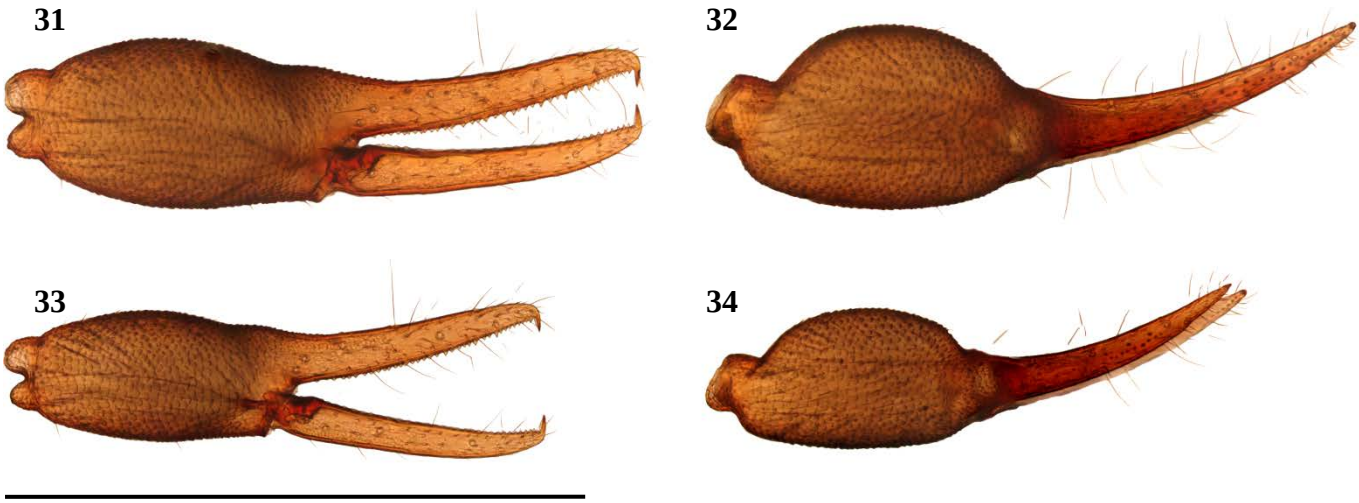
Abdomen: Abdominal tergites brown to light-brown with dark and cream patches in both sexes, granular. Tergites I and II with large median dark spot each. Tergite III without dark patches. Tergites IV-X with paired faint dark patches, just lateral of the midline. Light coloured specimens present faint, almost absent, spots. Tergites XI and XII without patches. Sternites light brown with faint dark patches in both sexes, weakly sclerotised in females, well sclerotised throughout in males. Pleural membrane wrinkled-placate, cream.

Pedipalp: Trochanter rounded, slightly elongate in shape, granular, same colour as carapace. Small setae scattered over entire surface, exception of stem. Ventral apophysis present. Pedipalp femur (Fig. 36) same colour, granular. Narrow at base, widening evenly before it is constricted at distal end. Femur ratio: 3.57 (♀), 3.64 (♂). Pedipalp patella (Fig. 36) same colour as previous, granular. Narrow, slightly angled at base, widening evenly into elongate cone. Lyriform fissures visible just anterior of base, located on a bulge, dorso-prolaterally on patella. Patella ratio: 3.04 (♀), 3.07 (♂).

Chela: (Figs. 31-36) Uniformly brown, may be slightly darker than rest of pedipalps. Granular from stem to base of fingers. Both fingers smooth, slightly shorter than hand-stem complex. Concave depression present on dorsal surface of chela, resulting in small bulge at base of fixed finger. Chela hand weakly convex on the prolateral edge, retrolateral edge mostly straight. Fixed chela finger with eight trichobothria, movable chela finger with four, both fingers narrow, curving slightly to interior. Venom apparatus present on both fingers. Trichobothria *eb* and *esb* situated on retrolateral surface of the fixed chelal finger, located just above base of finger, one trichobothrial width between them. Trichobothria *ib* located on prolateral surface, anterior and dorsal of *esb*, *est* located opposite and anterior, with one trichobothrial width, of *ib*. Trichobothria *isb* located roughly halfway along fixed finger, situated dorsally, *ist* is located on prolateral surface, approximately one third from anterior edge of fixed chelal finger. Trichobothria *it* located dorsally, roughly one fifth from anterior edge of fixed chelal finger, *et* located on retrolateral surface, just distal of *it*. Regarding movable finger, trichobothria *b* and *sb* located on retrolateral surface, just forward of finger base. Trichobothria *st* located on same surface, situated between *est* and *isb*, *t* located between *ist* and *it*. Chelal teeth acute, slightly retrorse. Fixed finger with 39 teeth (♀), 35 (♂). First tooth just before venom apparatus slightly enlarged, strongly sclerotised, followed by seven (♂) or eight (♀) smaller, closely spaced, roughly equal sized teeth before the first large accessory tooth (Fig. 42). Further teeth slightly retrorse and acute, arranged roughly in two rows. Movable finger with 31 teeth (♀), 29 (♂), tooth just before venom apparatus being very small. Following eight (♀) or 10 (♂) teeth after small tooth acute, retrorse, further teeth reduced into small teeth plates. In females, last five teeth regenerate into distinct group, spaced tightly against each other. In males, rear teeth may regenerate slightly, or remain as acute points. Chela ratio: 3.41 (♀), 3.80 (♂).

Chelicera: Hand with five setae as in Fig. 5. Fixed cheliceral finger with six teeth arranged as in Fig. 37. Galea complex, with nine rami in a fan shape as in Fig. 38 (♀) or simple, no rami (♂) (Fig. 39). Rallum composed of a single blade in both sexes. Serrula exterior with 19 lamella (♀) or 17 (♂). Lamina exterior present in both sexes.

Coxae and legs: Pedipalp coxae light brown, shoulder distinct. Legs I-IV, including coxae, tan to pale yellow. Trochanters of legs I and II compact and small, larger and elongate on legs III and IV. Femora of legs I and II longer than patella and tibia respectively (Fig. 43). Metatarsi and tarsi not fused, joint is movable (diplotarsate). Tarsal claws simple and curved, arolium much longer than claws, not divided. Femur-patella joint of leg IV immovable, tibia mostly straight (Fig. 42), metatarsi and tarsi not fused, with movable joint. Claws and arolium similar to those of legs I-III.



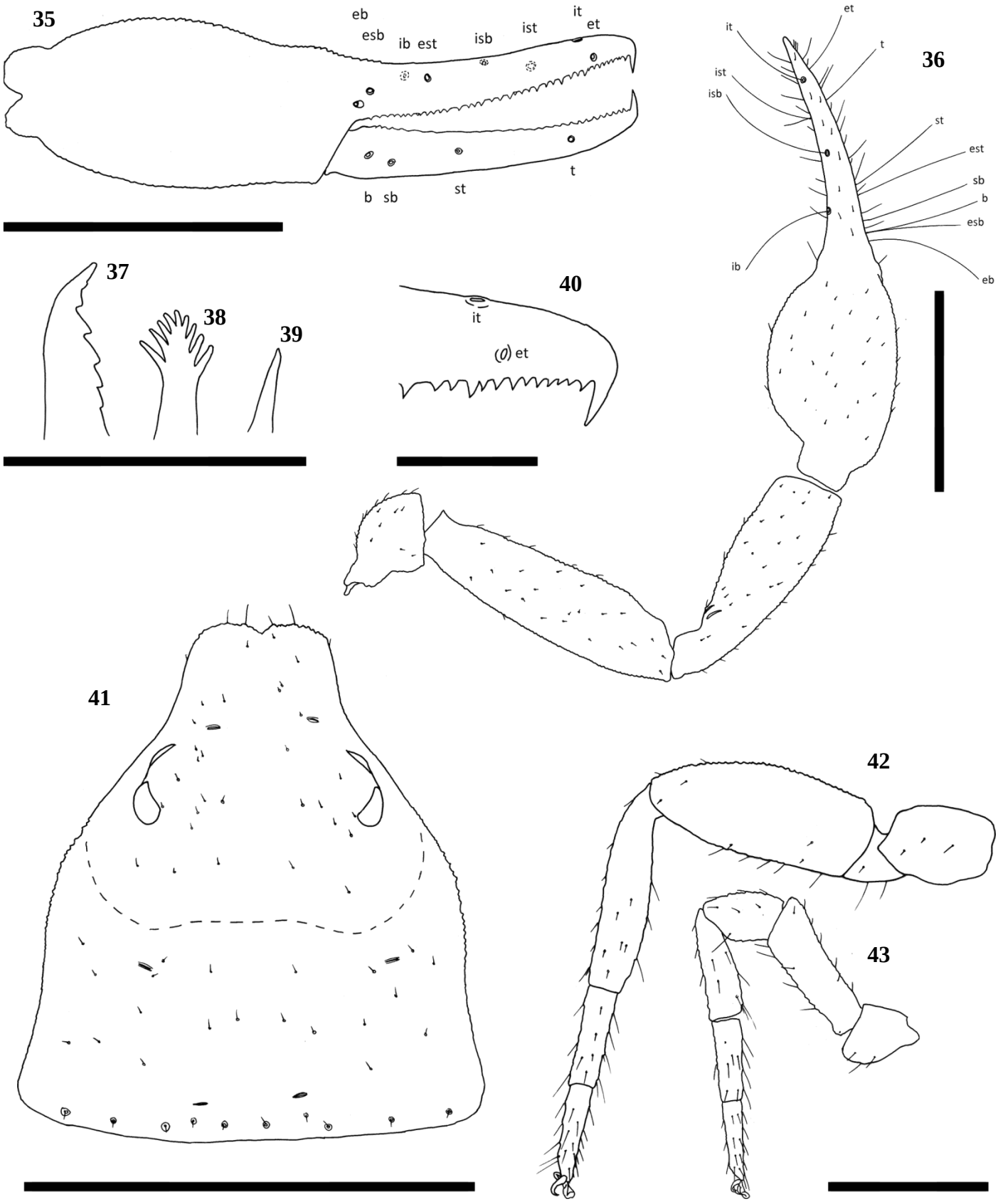
Figs. 31-34. Digital microscope photographs of *Afrogarypus carmenae* sp. nov. right chela: Female (**31**, **32**) and Male (**33**, **34**). **31**, **33**. Retrolateral view; **32**, **34**. Dorsal view. Scale bar: 1.00mm.

3.4.4 *Remarks*

Many museum exemplars were found to be misidentified as either immature *Afrogarypus robustus* comb. nov. or *A. purcelli* comb. nov. The type specimens were sampled together with a group of 13 individuals congregating under shaded vegetation along a rocky ridge. No immature specimens were ever sampled. The species has been collected in Fynbos and Nama Karoo habitats.

3.4.5 *Additional material examined*

SOUTH AFRICA: *Western Cape*: 1♀, 2♂, Bredasdorp, De Hoop Nature Reserve, 34° 28'S, 20° 30'E, 26m a.s.l., Coastal Fynbos, Leaf litter sifting, leg. J.A. Neethling & C. Luwes, 24.XII.2013 (NMBA P00227);



Figs. 35-43. *Afrogarypus carmenae* sp. nov. **35-38**, **40-43**. Female; **39**. Male; **35**. Right chela, retrolateral view; **36**. Right pedipalp, dorsal view; **37**. Chelicera movable finger, dorsal view; **38**, **39**. Galea; **40**. Right chela fixed finger, anterior teeth arrangement; **41**. Carapace, dorsal view; **42**. Right leg IV, prolateral view; **43**. Right leg I, prolateral view. Scale bars: Figs. 35, 36, 41-43: 0.50mm; Figs. 37-39: 0.10mm.

1♀, Same locality, Potberg, 34° 22'S, 20° 32'E, 180m a.s.l., leg. C.R. Haddad, 7.IV.2004 (WAM T79013); 1♀, Cape Town, Table Mountain, 33° 58'S, 18° 23'E, 15.I.2007 (WAM T85959); 1♀, Clanwilliam, Van Rhynsdorp Road [32° 10'S, 18° 52'E], leg. Leipoldt, XII.1997 (SAMC 9112); 1♀, 1♂, Hermanus, Fernkloof Nature Reserve, 34° 24'S, 19° 16'E, leg. R. Lyle, 29.IX.2007 (WAM T81146, T86777); 1♀, Kleinmond [34° 20'S, 19° 01'E], leg. H.G. Robertson, 4.XI.1995 (SAMC ENW-COO 6599); 1♀, 1♂ Laingsburg, Anysberg Nature Reserve [33° 28'S, 20° 35'E], leg. C.R. Haddad, 24.IX.2007 (WAM T86782, T86784); 1♀, Pringle Bay, Cape Hanglip [34° 23'S, 18° 50'E], leg. R.F. Lawrence, XII.1962 (NMSA 7897); 1♀, 1♂, Simon's Town, Cape of Good Hope Nature Reserve, Smitswinkelvlakte [34° 17'S, 18° 26'E], leg. H.G. Robertson, X.1998 (SAMC ENW-COO 5405, 5406); 2♀, Same locality, Teeberg [34° 14'S, 18° 24'E], leg. H.G. Robertson, X.1998 (SAMC ENW-COO 5409, 5435); 1♀, Stellenbosch [33° 55'S, 18° 52'E], leg. J. Botha, 19.V.1990 (NCA 90.286).

3.5 *Afrogarypus castigatus* sp. nov.

Holotype: ♀, SOUTH AFRICA, KwaZulu-Natal, St. Lucia, St. Lucia Coastal Forest, 28° 23'S, 32° 24'E, 20m a.s.l., Coastal forest, Canopy fogging *Trichilia emetica* (Natal Mahogany), leg. J.A. Neethling & C. Luwes, 13.V.2012 (NMBA P00219).
Paratypes: 1♀, 3♂, SOUTH AFRICA, KwaZulu-Natal, St. Lucia, iSimangaliso Wetland Park, Crocodile Centre, 28° 21'S, 32° 25'E, 24m a.s.l., Indigenous forest patch, Canopy fogging *Breonadia salicina* (Matumi), leg. J.A. Neethling & C. Luwes, 14.V.2012 (NMBA P00220).

3.5.1 *Etymology*

Castigatus (Latin *adj*. meaning compact). The species is named for its unusual morphological features, including reduced trichobothrial count on the fixed chelal finger and monotarsate legs I and II.

3.5.2 *Diagnosis*

Small species, pedipalpal femur length 0.49mm (♀), 0.45mm (♂), chela length (with stem) 0.75mm (♀), 0.68mm (♂), movable finger length 0.28mm (♀), 0.27mm (♂). Females reach lengths (cucullus to posterior abdominal margin) of 1.55mm, while males, on average, reach 1.35mm in length. Carapace dark brown in both sexes, with the medial furrow and posterior light-brown to cream in colour (Figs. 44 & 46). All pedipalp segments follow the same colouration as the carapace. Concave depression present on dorsal surface of chelas. Abdominal tergites light-brown to cream with dark patches in both sexes. Abdominal sternites light-brown to cream in both sexes, with no

markings; weakly sclerotised in females and partly to well sclerotised in males (Figs 45 & 47). Legs I and II monotarsate and cream to light-brown in both sexes, with corresponding coxae cream in colour.

Currently the smallest geogarypid species in South Africa, with very little sexual dimorphism in morphology and colouration, though males tend to be smaller than females. The species resembles small *Afrogarypus triangularis* comb. nov. and *A. subimpressus* in overall appearance, but can easily be distinguished by having a reduced trichobothrial compliment of 7/4, due to the absence of trichobothria *isb*, as well as having monotarsate leg pairs I and II. The species resembles *A. triangularis* comb. nov. in particular, due to the presence of a very convex prolateral surface on the chela, a concave dorsal chelal depression and the presence of pleural sclerites on the abdomen of adult males.

3.5.3 *Description*

Carapace: Strongly sub-triangular, broader than long in both sexes, with narrow furrow posterior to the eyes (Fig. 60). Generally dark brown in colour, medial furrow and posterior of carapace light-brown to cream in both sexes. Uniformly granular, heavily constricted anteriorly into cucullus, constriction beginning at the medial furrow. Two pairs of corneate eyes situated on ocular tubercles, located ca. one third away from anterior edge. Four prominent setae located on anterior edge, row of nine setae located on posterior margin. Numerous small setae present on carapace. Carapace ratio: 0.89 (♀), 0.86 (♂).

Abdomen: Very compact and almost circular in appearance. Abdominal tergites granular, light-brown to cream, with darker patches in both sexes. Tergites I and II with large median dark spot each, flanked by light-coloured patches, in turn flanked by light-brown patches at lateral edges. Tergite III without dark medial patch, cream, flanked at lateral edges by light-brown markings. Tergites IV-X with paired, faint dark patches just lateral of midline, flanked at lateral edges by light-brown markings. Tergites XI and XII without dark patches. Males possess lateral sclerites on pleural membrane (Fig. 61) as follows; one each below tergites III and IV, two below tergite V, four sclerites in two rows of two below tergite VI, four sclerites in single row below tergite VII, five sclerites in two rows of three and two below tergite VIII, three in single row below tergite IX, one below tergite X. Sternites light-brown to cream in both sexes, no markings, weakly sclerotised in females, partly to well sclerotised in males. Pleural membrane wrinkled-placate, cream, with light-brown lateral sclerites, in males.

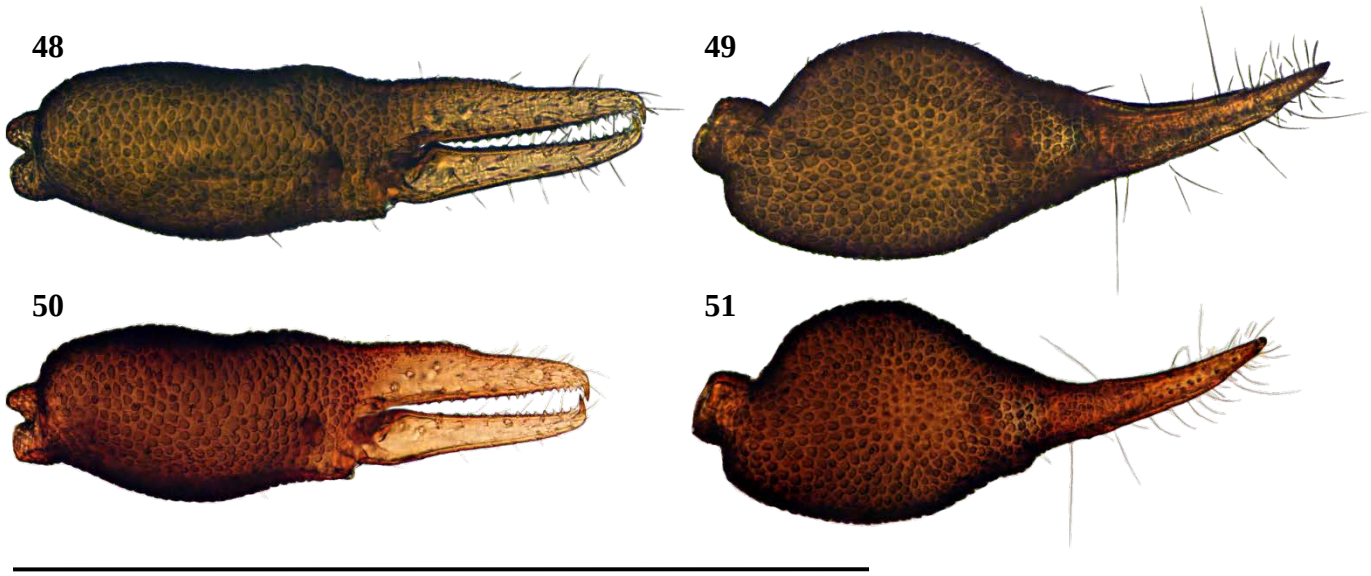
Figs. 44-47. Digital microscope photographs of *Afrogarypus castigatus* sp. nov., Female (**44**, **45**) and Male (**46**, **47**). **44**, **46**. Dorsal view; **45**, **47**. Ventral view. Scale bar: 1.00mm.

Pedipalp: Trochanter rounded in shape, granular, coloured same as carapace. Small setae scattered over entire surface, with the exception of the stem. Apophysis located ventrally. Pedipalp femur (Fig. 55) same colour and granular. Narrow at stem, widening quickly to form base, then widening slightly before constricting again at end. Femur ratio: 3.14 (♀), 3.03 (♂). Pedipalp patella (Fig. 55) same colour as femur, granular. Narrow, very angled at base, widening evenly into short cone. Lyriform fissures visible just anterior of base, located on bulge, dorso-prolaterally on patella. Patella ratio: 2.33 (♀), 2.20 (♂).

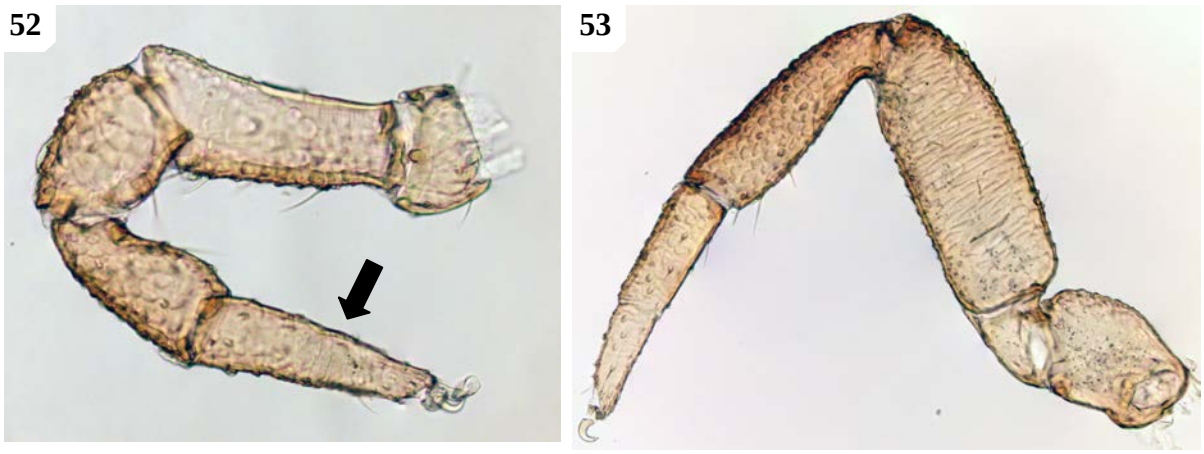
Chela: (Figs. 48-51, 54, 55) Same colour as carapace, uniformly granular from stem to base of the movable fingers, granular over first third of dorsal surface of fixed finger. Both fingers much shorter than hand-stem complex. First third of fixed chelal finger with characteristically swollen dorsal area. Concave depression present on dorsal surface of chela, resulting in small bulge at base of fixed finger. Chela hand strongly convex on prolateral edge, retrolateral edge slightly convex. Fixed chela finger with seven trichobothria (*isb* absent), movable chela finger with four, both fingers narrow, curving slightly to the interior. Venom apparatus present on both fingers. Trichobothria *eb* and *esb* situated on retrolateral surface of fixed chelal finger, just above base of finger, one trichobothrial width between them. Trichobothria *ib* on prolateral surface, distal of *esb* by just more than one trichobothrial width; *est* opposite, directly anterior of *ib*. Trichobothria *isb* absent, *ist* on prolateral surface, approximately half way from anterior edge of fixed chelal finger, situated close to chelal teeth. Trichobothria *it* located dorsally, just over quarter finger length from anterior edge of fixed chelal finger, *et* on retrolateral surface, just distal of *it*. On the movable finger, trichobothria *b*, *sb* and *st* group with equal distances from each other below group formed by *eb*, *esb* and *est*. Trichobothria *t* located roughly one third finger length from anterior edge of movable finger. Chelal teeth acute and retrorse. Fixed finger with 19 teeth in both sexes. First three teeth just before the venom apparatus slightly fused and raised (Fig. 56), remaining teeth spaced widely apart, decreasing in size to base of fixed finger. Movable finger with 16 teeth (♀), 15 (♂), two teeth just before venom apparatus being small and raised. Remaining teeth retrorse, facing backward, decreasing in size to base of moving finger. Chela ratio: 2.78 (♀), 2.55 (♂).

Chelicera: Hand with five setae as in Fig. 5. Fixed cheliceral finger with four teeth arranged as in Fig. 57. Galea complex with nine rami as in Fig. 58 (♀), or simple with no rami (♂) (Fig. 59). Rallum composed of single blade in both sexes. Serrula exterior with 15 lamella in both sexes. Lamina exterior present in both sexes.

Coxae and legs: Pedipalp coxae same colour as carapace, with distinct shoulder. Legs I and II monotarsate (Figs. 52 & 62), cream to light-brown in both sexes, corresponding coxae cream. Legs III and IV diplotarsate (Figs. 53 & 63), with same colouration as front legs.



Figs. 48-51. Digital microscope photographs of *Afrogarypus castigatus* sp. nov. right chela: Female (**48**, **49**) and Male (**50**, **51**). **48**, **50**. Retrolateral view; **49**, **51**. Dorsal view. Scale bar: 1.00mm.



Figs. 52-53. Digital microscope photographs of *Afrogarypus castigatus* sp. nov. female leg morphology. **52**. Monotarsate leg I; **53**. Diplotarsate leg IV.

3.5.4 *Remarks*

The only South African species with a reduced trichobothrial compliment, it is none the less not the only geogarypid displaying such a reduction. *Geogarypus connatus* (Harvey, 1986) from Australia, as well as *G. bucculentus* (Beier, 1955) from the Juan Fernandez Islands, Chile, also present the absence of trichobothria *isb* (Harvey 1987b). *Afrogarypus castigatus* sp. nov. and *G. connatus* furthermore possess adults with monotarsate legs I and II, while *G. bucculentus* adults are diplotarsate. Given their geographic locations, the three species may form a monophyletic group that originated in Gondwanaland (Harvey 1987b; Harvey 1996). Phylogenetic analysis of a broad distributional range of geogarypids will likely yield interesting results.

3.5.5 *Additional material examined*

SOUTH AFRICA: *KwaZulu-Natal*: 4♀, 6♂, St. Lucia, iSimangaliso Wetland Park, Meersig, 28° 14'S, 32° 29'E, 14m a.s.l., Wetland, Canopy fogging *Syzygium cordatum*, leg. J.A. Neethling & C. Luwes, 14.V.2012 (morphologic dissection, phylogenetic analysis & S.E.M.).

3.6 *Afrogarypus excelsus* (Beier, 1964) **stat. nov.**

Geogarypus excelsus Beier, 1964: 61, Fig.. 22 [**Holotype** ♀, South Africa, Eastern Cape, Grahamstown [33°18'S, 26°31'E], leg. J. Hewitt, deposited in NMZA, not examined].

Geogarypus excelsus excellens Beier, 1964: 62, Fig.. 23 [2♀, 1♂, 2 Deutonymphs, **Syntypes**, No collection information, NMZA, not examined; 4♀, 4♂, 1 Tritonymph, **Paratypes**, No collection information, NMZA, not examined].

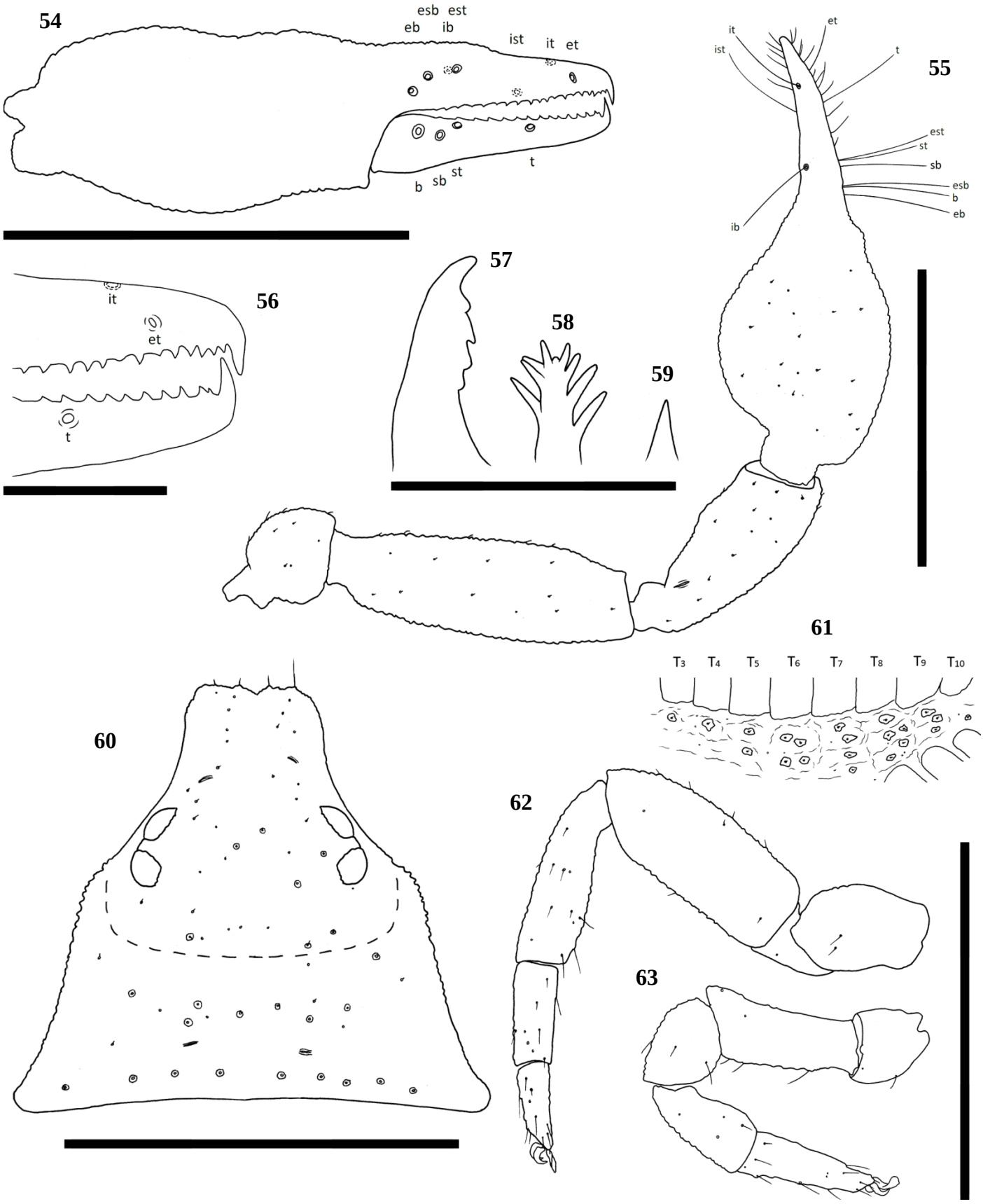
Geogarypus (*Afrogarypus*) *excelsus excellens* (Beier, 1964): Beier, 1966: 461.

Afrogarypus excelsus excelsus (Beier, 1964): Harvey, 1986: 758; Harvey, 1991: 250; Dippenaar-Schoeman & Harvey, 2000: 93 [**stat. nov.**].

Afrogarypus excelsus excellens (Beier, 1964): Harvey, 1986: 758; Harvey, 1991: 250; Dippenaar-Schoeman & Harvey, 2000: 93 [**syn. nov.**].

3.6.1 *Diagnosis*

Large species, pedipalpal femur length 0.92mm (♀), 0.81mm (♂), chela length (with stem) 1.52mm (♀), 1.32mm (♂), movable finger length 0.79mm (♀), 0.67mm (♂). Females can reach a total length (cucullus to posterior abdominal margin) of 2.96mm, with males reaching up to 2.27mm. Carapace dark brown with light brown markings in the form of an hourglass located on the posterior margin and stretching up to the mid area (Figs. 64 & 66). All pedipalp segments dark brown in colour. Abdominal tergites brown with dark patches, abdominal sternites light brown to tan and weakly sclerotised (♀) (Fig. 65), brown with dark patches and heavily sclerotized (♂) (Fig. 67). Pedipalp coxae brown in colour with distinct shoulder, legs I-IV as well as remaining coxae tan. As with many pseudoscorpions, the male of the species tends to vary in terms of size and colouration, while adult females tend to be similarly sized within a population. Males are generally smaller and can easily be identified by their dark, sclerotised sternites and thin, elongate pedipalps compared to those of the female.



Figs. 54-63. *Afrogarypus castigatus* sp. nov. **54-58**, **60**, **62**, **63**. Female; **59**, **61**. Male. **54**. Right chela, retrolateral view; **55**. Right pedipalp, dorsal view; **56**. Anterior retrolateral view of chela fingers; **57**, Distal end of chelicera movable finger, dorsal view, **58**, **59**. Galea; **60**. Carapace, dorsal view. **61**. Abdominal pleural sclerites; **62**. Leg IV, prolateral view; **63**. Leg I, prolateral view. Scale bars: Figs. 54, 55, 60, 62, 63: 0.50mm; Figs. 57-59. 0.05mm; Fig. 56: 0.10mm.

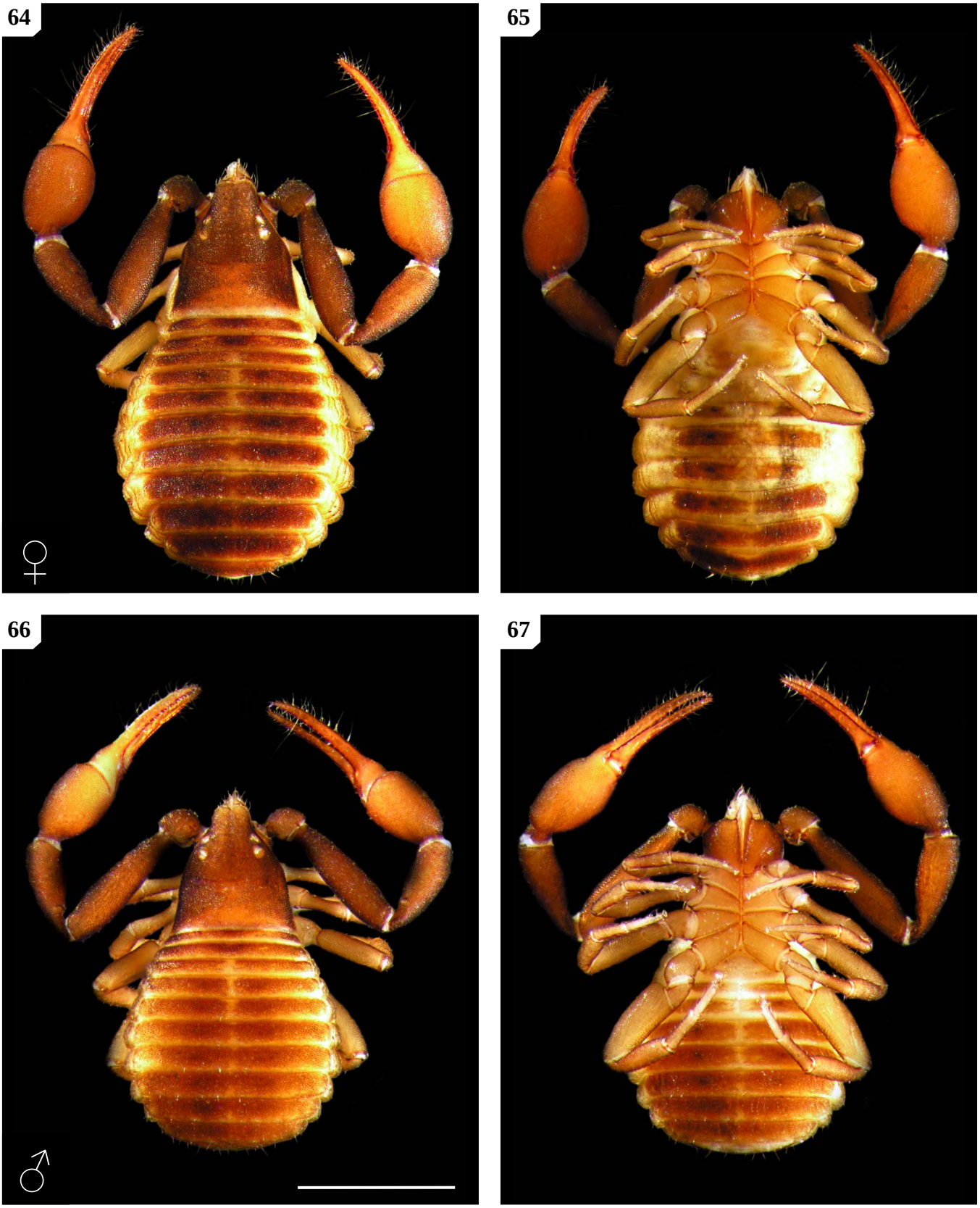
Afrogarypus excelsus stat. nov. closely resembles *A. impressus*, but differs in regard to the chela ratio, finger length, as well as their chelal teeth morphology. The most characteristic difference is that the chelal fingers of *A. excelsus* stat. nov. are longer than the hand-stem complex, while they are shorter than the complex in *A. impressus*. Together with *A. impressus*, *A. excelsus* stat. nov. is the only other large South African geogarypid to exhibit the presence of a well developed, deep dorsal sulcus. *Afrogarypus subimpressus* and *A. megamolaris* sp. nov. also demonstrate a developed dorsal sulcus, but it is not nearly as well defined as those found within the former species. The latter two species further differ in regard to size, as well as having chelal teeth that are spaced widely apart.

3.6.2 *Description*

Carapace: Strongly sub-triangular, narrow furrow posterior to the eyes (Fig. 76). Dark brown in the anterior, until beginning of the furrow, light brown marking in shape of an hourglass in posterior half. Uniformly granular, except for posterior margin. Heavily constricted anteriorly into cucullus, constriction beginning just anterior of the medial furrow. Two pairs of corneate eyes situated on ocular tubercles, located ca. one third away from anterior edge. Four prominent setae located on anterior edge, row of eight setae located on posterior margin. Numerous small setae present on carapace, some situated within large rims similar to those of trichobothria. Carapace ratio: 1.06 (♀), 1.01 (♂).

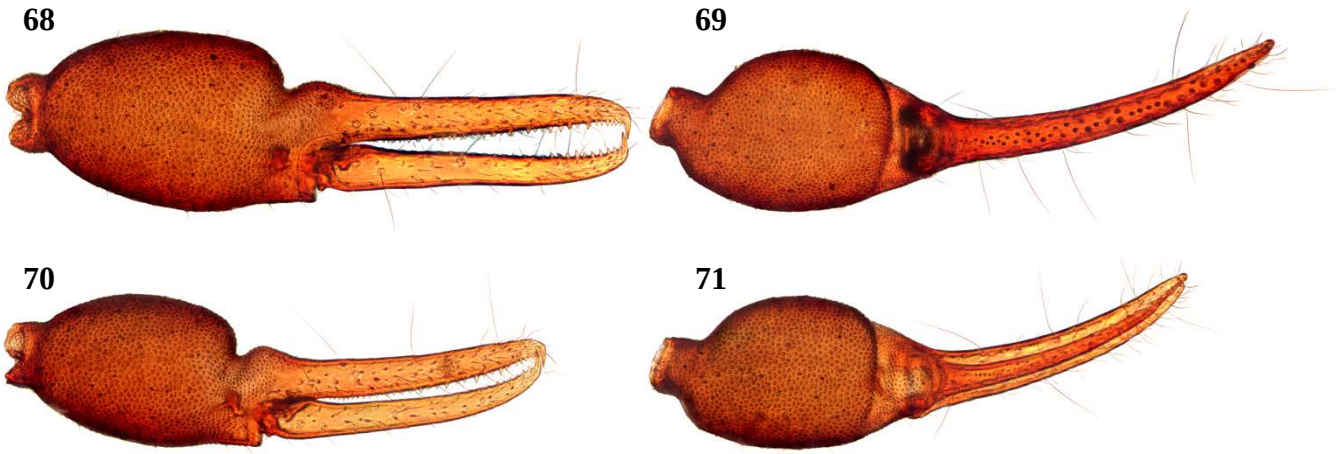
Abdomen: Abdominal tergites brown (♀), light brown (♂), with dark patches. Tergites I and II with large medially located dark spot each. Tergite III without dark patches. Tergites IV–X (♀) with paired dark patches, lateral of the midline, can be slightly lighter in colour (♂ may lack these paired patches). Tergites XI–XII without any patches. Sternites light brown to tan, weakly sclerotised (♀), brown with dark patches, heavily sclerotized (♂). Pleural membrane wrinkled-placate with invested setae.

Pedipalp: Trochanter rounded, granular, uniformly dark brown with small setae located on the dorsal and dorso-lateral sides. Apophysis located ventrally. Pedipalp femur (Fig. 73) dark brown, granular. Narrow at base, widening evenly until just posterior of anterior margin, where it is constricted. Femur ratio: 3.52 (♀), 3.64 (♂). Pedipalp patella (Fig. 73) dark brown, granular, narrow at base, widening quickly until anterior edge. Lyriform fissures visible just anterior of base, located on a bulge, dorso-prolaterally on patella. Patella ratio: 3.32 (♀), 3.13 (♂).



Figs. 64-67. Digital microscope photographs of *Afrogarypus excelsus* stat. nov., Female (**64**, **65**) and Male (**66**, **67**). **64**, **66**. Dorsal view; **65**, **67**. Ventral view. Scale bar: 1.00mm

Chela: (Figs. 68-73) Uniformly brown, granular from stem to base of fingers. Both fingers smooth. Well developed dorsal sulcus present, located just posterior of the base of the fixed finger. Dorsal bulge located just anterior of sulcus. Fixed chela finger with eight trichobothria, movable chela finger with four. Both fingers long and narrow, curving to interior. Fingers just as long as, or slightly longer than, hand with stem. Venom apparatus present on both fingers. Trichobothria *eb* and *esb* situated ca. one trichobothrial width from each other, located respectively retrolaterally and dorso-retrolaterally off base of fixed finger; *ib* situated ca. one quarter anterior of finger base, located dorso-prolaterally; *est* opposite, just anterior of *ib*; *isb* situated almost dorsally, located ca. halfway along fixed finger, closer to *est* than to *ist*; *ist* located ca. one quarter from the anterior edge of the fixed finger, situated prolaterally; *it* located dorsally, two widths along finger from *ist*; *et* located two widths from *it*, sits opposite on the same horizontal line with *ist*. Regarding the movable finger, *b* located just anterior of finger base, situated dorso-retrolaterally on finger in line vertically with *eb*; *sb* located ca. two trichobothrial widths from *b*, situated slightly ventrally; *st* located ca. halfway along movable finger, closer to *sb* than *t* and situated slightly more dorsally; *t* located ca. one quarter from anterior edge of movable finger, just forward of *ist*. Chelal teeth acute and retrorse, some curving back slightly. Fixed finger with 41 teeth (♀), 39 (♂). Six small, closely spaced teeth just behind venom apparatus, followed by large tooth (Fig. 59). Further teeth are arranged in two rows, reducing in size proximally, still acute. Movable finger with 26 teeth (♀), 25 (♂). Movable finger's teeth nearly contiguous, reduced to small projections proximally, after first nine (♀) or seven teeth (♂). Chela ratio: 3.87 (♀), 3.54 (♂).



Figs. 68-71. Digital microscope photographs of *Afrogarypus excelsus* stat. nov. right chela: Female (**68**, **69**) and Male (**70**, **71**). **68**, **70**. Retrolateral view; **69**, **71**. Dorsal view. Scale bar: 1.00mm .

Chelicera: Hand with five setae as in Fig. 5. Fixed cheliceral finger with five teeth arranged as in Fig. 78. Galea complex, with nine rami arranged evenly across the tip (♀) (Fig. 79), simple, with no

rami (♂) (Fig. 80). Rallum composed of single blade in both sexes. Serrula exterior with 13 lamella (♀) or 17 (♂). Lamina exterior present in both sexes.

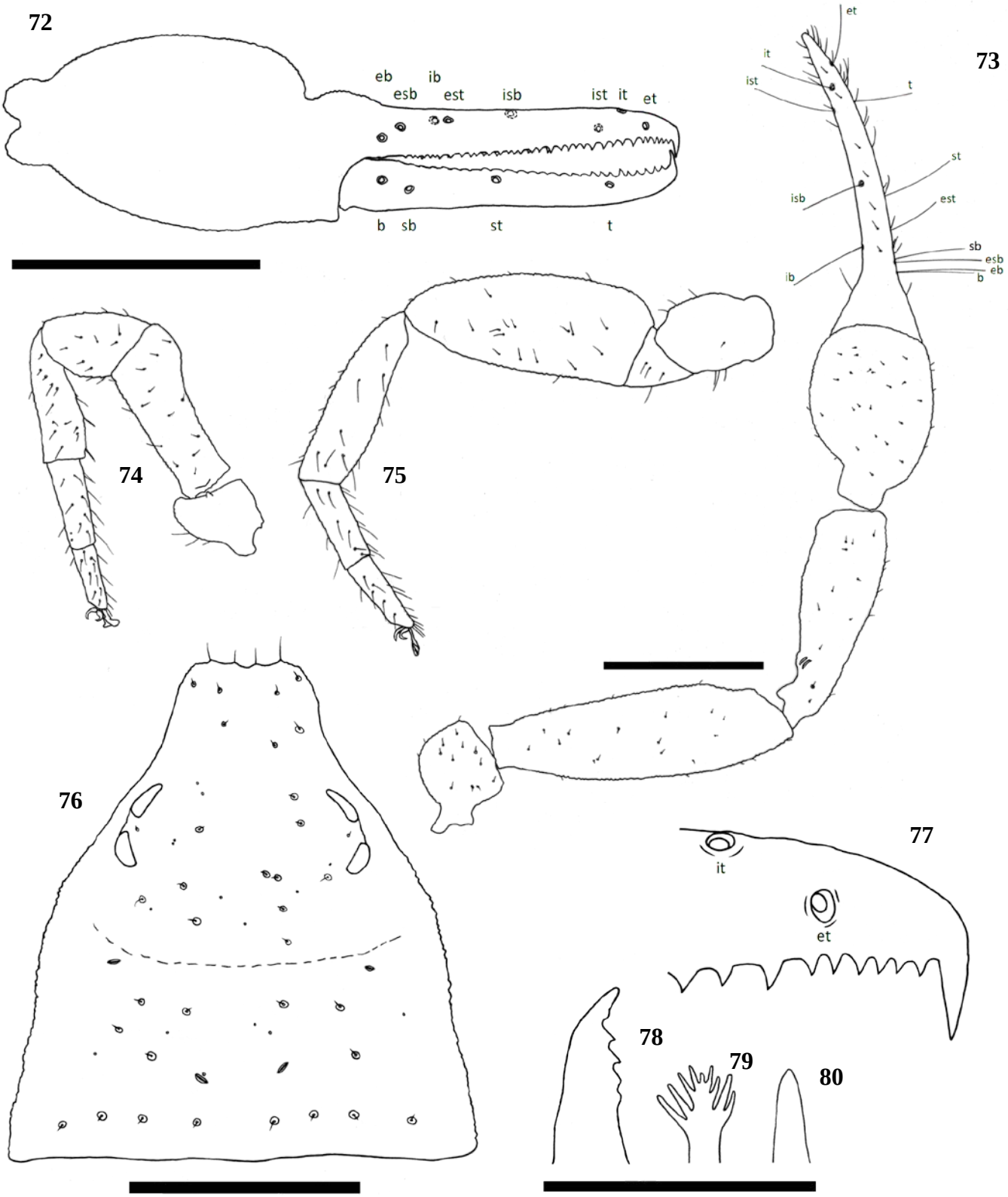
Coxae and legs: Pedipalp coxae brown, with distinct shoulder. Multiple long setae present along inner medial ridges. Coxae of legs I–IV, as well as all leg segments, tan. Trochanters of legs I and II compact and small, larger and elongate on legs III and IV. Femora of legs I and II longer than patellae and tibiae respectively (Fig. 74). Metatarsi and tarsi not fused, joint movable. Tarsal claws simple and curved, arolium much longer than claws, not divided. Femur-patella joint immovable in leg IV, tibia slightly curved, metatarsi and tarsi not fused and joint is movable (Fig. 75). Claws and arolium similar to those of legs I–III.

3.6.3 *Remarks*

The last of the South African geogarypid species to be described in the mid twentieth century, *Afrogarypus excelsus* stat. nov. was originally separated into two subspecies, namely *A. excelsus excelsus* (Beier, 1964) and *A. excelsus excellens* (Beier, 1964). Beier based his decision on specimens with no collection information that he found together in the same series as the species holoype. These specimens differed from the holotype of *A. excelsus* by the following; slimmer and slightly more elongate chela, trichobothria *ist* on the fixed chela finger being slightly closer to *it* and thus forming a proximal group with *et*, and trichobothria *st* on the movable chela finger being slightly closer to *sb* than to *t*, where it is evenly spaced between the two in the holotype of *A. excelsus* Beier, 1964. Specimens adhering to both subspecies descriptions were collected together from multiple locations, including Fort Fordyce Nature Reserve and Pirie Forest Reserve. Phylogenetic analyses of these specimens clearly show that they are the same species, and thus the slight differences in morphology can be contributed to intraspecific variation. The two subspecies are thus synonymised under *A. excelsus* stat. nov.

3.6.4 *Additional material examined*

SOUTH AFRICA: *Eastern Cape*: 5♀, 2♂, 2 Deutonymphs, Fort Beaufort, Fort Fordyce Nature Reserve, Afromontane forest, 32° 41'S, 26° 29'E, 1090m a.s.l., leg. J.A. Neethling & C. Luwes, 29.XI.2012 (NMBA P00190); 1♀, Grahamstown [33° 18'S, 26° 31'E], leg. J. Hewitt, VIII.1918 (AMG slide); 3♀, 4♂, 2 egg sacks, Grahamstown, Pine Plantation [33° 18'S, 26° 31'E], leg. C. Kewi, 2.XII.1918 (AMG slide); 1♀, King William's Town, Pirie Forest Reserve [32° 43'S, 27° 16'E], leg. R. Godfrey, 27.VIII.1908 (AMG slide); 2♀, 2♂, Somerset East, Besters Hoek Nature Reserve, Dry-shrub forest, 32° 42'S, 25° 33'E, 860m a.s.l., leg. J.A. Neethling & C. Luwes, 2.XII.2012 (morphological dissection and S.E.M. material); 2♀, 2♂, Somerset East, Bosberg [32° 41'S, 25° 32'E],



Figs. 72-80. *Afrogarypus excelsus* stat. nov. **72-79**. Female; **80**. Male. **72**. Right chela, retrolateral view; **73**. Right pedipalp, dorsal view; **74**. Right leg I, prolateral view; **75**. Right leg IV, prolateral view; **76**. Carapace, dorsal view; **77**. Right chela fixed finger, anterior teeth arrangement; **78**. Chelicera movable finger, dorsal view; **79**, **80**. Galea. Scale bars: Figs. 72-76: 0.50mm; Figs. 77-80: 0.10mm.

leg. R.F. Lawrence, III.1964 (NMSA 5126); 1♀, Somerset East, Zuurberg Pass, Afromontane forest clusters, 33° 17'S, 25° 42'E, 772m a.s.l., leg. J.A. Neethling, 15.IX.2011 (phylogenetic analysis); 13♂, Stutterheim, Sandile's Rest Lodge, Afromontane forest, 32° 39'S, 27° 17'E, 902m a.s.l., leg. J.A. Neethling, 20.IV.2013 (NMBA P00191).

3.6.5 *Additional material not examined*

SOUTH AFRICA: *Eastern Cape*: 3♀, 3♂, Somerset East, Bosberg [32° 41'S, 25° 32'E], III.1964 (examined by Beier 1966).

3.7 *Afrogarypus impressus* (Tullgren, 1907)

Garypus impressus Tullgren, 1907b: 228, fig. 7 [**Holotype** ♀, South Africa, KwaZulu-Natal, Amanzimtoti [30°3'S, 30°53'E], leg. I. Trägårdh, 18.I.1905, collection unknown, not examined; **Paratypes**, Hluhluwe-Imfolozi Game Reserve, Junction of Black and White Imfolozi Rivers [28°13'S, 31°57'E], leg. I. Trägårdh, 28.VIII.1905, collection unknown, not examined; Van Reenen, [28°22'S, 29°23'E], leg. I. Trägårdh, 24.VI.1905, collection unknown, not examined]; Ellingsen, 1912: 86, 107.

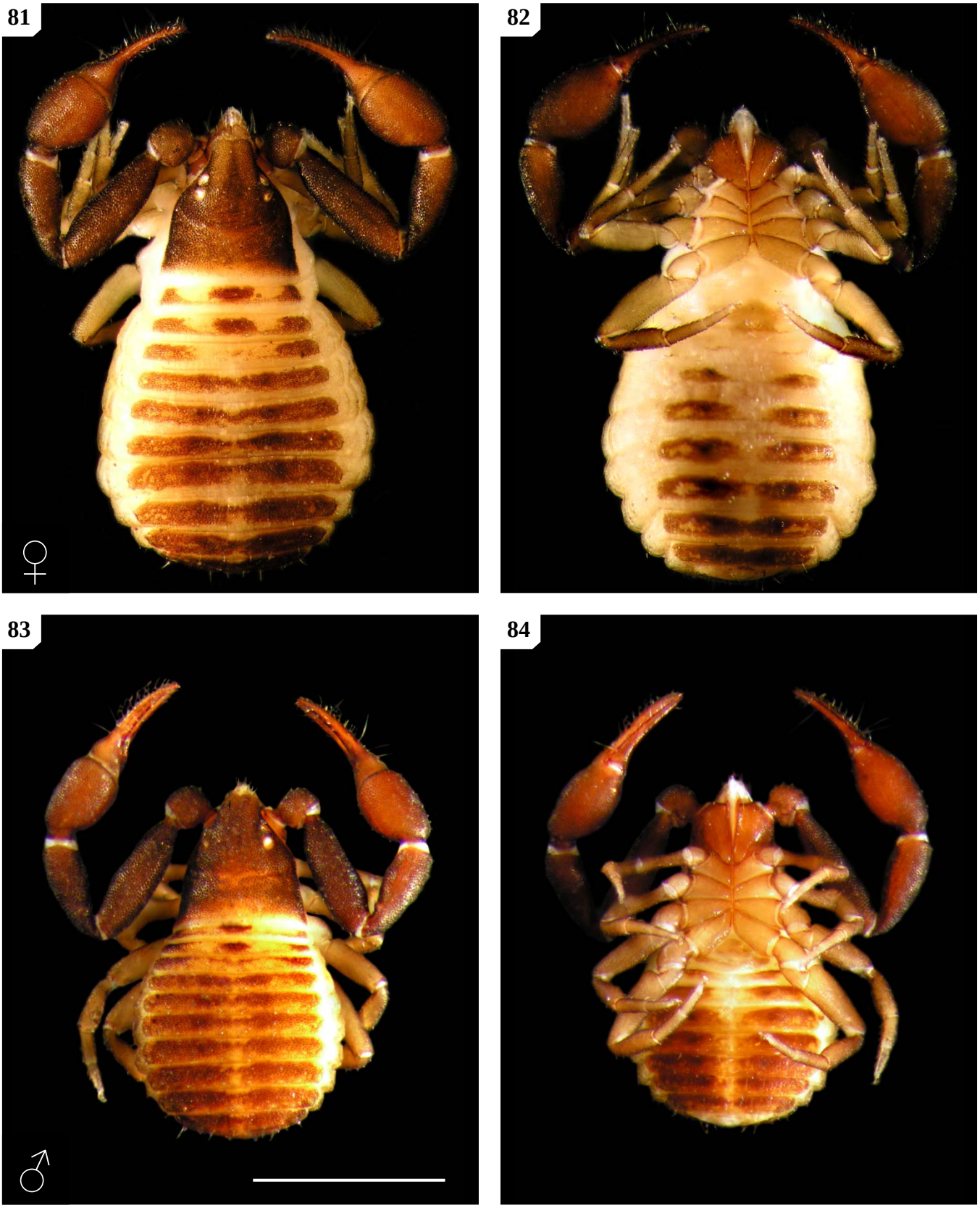
Geogarypus impressus (Tullgren, 1907): Chamberlin, 1930: 609; Roewer, 1936: fig. 77; Beier, 1964: 60; Lawrence, 1967: 89; Spaull, 1979: 117.

Geogarypus (*Afrogarypus*) *impressus* (Tullgren, 1907): Beier, 1932b: 236, fig. 265; Roewer, 1937: 270, fig. 222b; Beier, 1947: 320; Beier, 1955: 301, fig. 21a; Beier, 1958: 171; Beier, 1966: 461.

Afrogarypus impressus (Tullgren, 1907): Harvey, 1986: 758; Harvey, 1991: 250; Dippenaar-Schoeman & Harvey, 2000: 93.

3.7.1 *Diagnosis*

Large species, pedipalpal femur length 0.73mm (♀), 0.60mm (♂), chela length (with stem) 1.06mm (♀), 0.90mm (♂), movable finger length 0.43mm (♀), 0.42mm (♂). Females can reach a total length (cucullus to posterior abdominal margin) of 3.25mm, with males reaching up to 2.84mm. Carapace dark brown, medial furrow and posterior margin light brown (Figs 81 & 83). All pedipalp segments dark brown in colour. Well developed sulcus present on dorsal surface of chela. Abdominal tergites mostly brown with dark patches, abdominal sternites pale and weakly sclerotised anteriorly to brown and well sclerotised posteriorly (♀) (Fig 82), brown with faint, paired, darker patches and well sclerotised throughout (♂) (Fig 84). Pedipalp coxa brown in colour with distinct shoulder, legs I-IV as well as remaining coxa tan to pale yellow. Both sexes of the species are quite variable in size, though males from a particular locality still tend to be smaller than the females from the same area.



Figs. 81-84. Digital microscope photographs of *Afrogarypus impressus*, Female (**81**, **82**) and Male (**83**, **84**). **81**, **83**. Dorsal view; **82**, **84**. Ventral view. Scale bar: 1.00mm.

Closely resembling *A. excelsus* stat. nov. in both size and colouration, the two species are the only large geogarypids that possess a deep, well developed dorsal sulcus on each chela. *Afrogarypus impressus* can reliably be differentiated from *A. excelsus* stat. nov. by the ratios of their chelal fingers to the hand-stem complex, where the fingers are longer than the complex in *A. excelsus* stat. nov. and shorter than the complex in *A. impressus*. Further differences include a broader and shorter carapace in *A. impressus*, the front four teeth on the fixed finger grouping on a bulge, as well as chela that are broader compared to their length than those found in *A. excelsus* stat. nov. The anterior tergites of *A. impressus* furthermore possess distinct cream patches absent in *A. excelsus* stat. nov.

3.7.2 *Description*

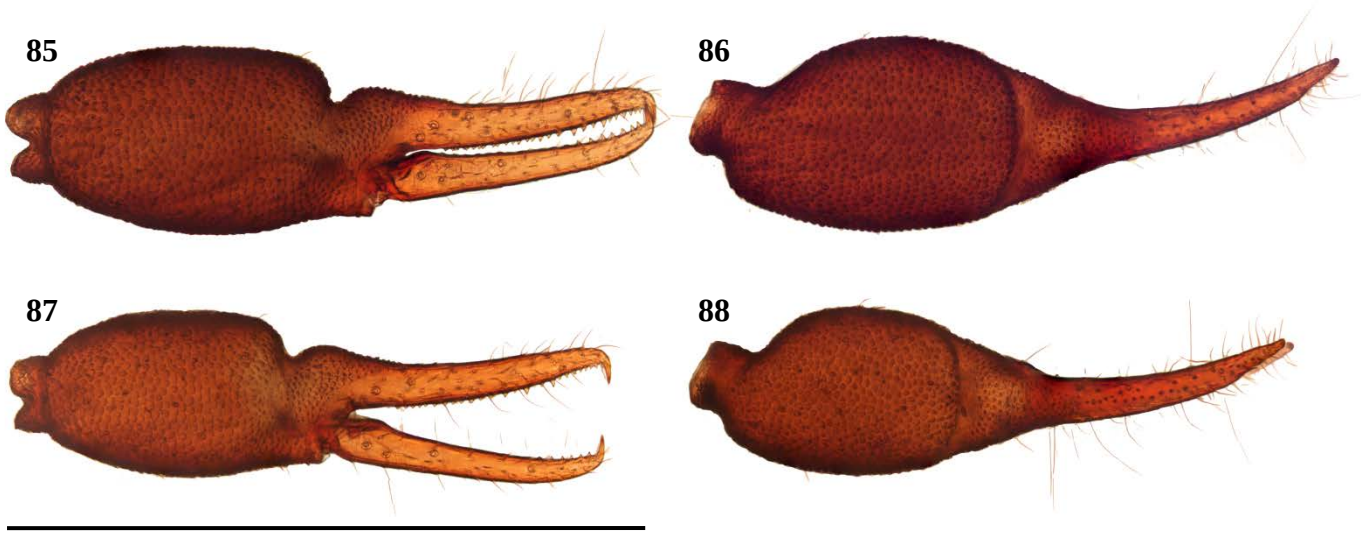
Carapace: Strongly sub-triangular, with narrow furrow posterior to the eyes (Fig. 93). Uniformly dark brown, medial furrow and posterior margin light brown. Uniformly granular, heavily constricted anteriorly into cucullus, constriction beginning between medial furrow and posterior pair of eyes. Two pairs of corneate eyes situated on ocular tubercles, located ca. one third away from the anterior edge. Four prominent setae located on anterior edge, row of eight setae, seated within large rims, located on the posterior margin. Numerous small setae present on carapace, some situated within large rims. Carapace ratio: 0.97 (♀), 0.98 (♂).

Abdomen: Abdominal tergites brown (♀), light brown (♂), with dark patches. Tergites I and II with large median dark spot each. Tergite III without dark patches. Tergites IV-X with paired dark patches just lateral of midline, may be just as dark, or slightly lighter than those on tergites I and II. Tergites XI and XII without patches. Sternites pale, weakly sclerotised anteriorly, brown and well sclerotised posteriorly (♀). Brown, with faint, paired darker patches, well sclerotised throughout (♂). Pleural membrane wrinkled-placate with invested setae.

Pedipalp: Trochanter rounded, somewhat square in shape, granular, uniformly dark brown. Small setae scattered over entire surface, with exception of stem. Apophysis located ventrally. Pedipalp femur (Fig. 90) dark brown, granular, narrow at base. Widens evenly, interior margin then constricts anteriorly to form narrow end. Femur ratio: 3.33 (♀), 3.55 (♂). Pedipalp patella (Fig. 90) dark brown and granular. Narrow at base, widening quickly into cone. Lyriform fissures visible just anterior of base, located on bulge, dorso-prolaterally on patella. Patella ratio: 2.78 (♀), 2.81 (♂).

Chela: (Figs. 85-90) Uniformly brown, granular from stem to base of fingers. Both fingers smooth. Well developed dorsal sulcus located just posterior of base of fixed finger. Dorsal bulge located at base of fixed chela finger. Fixed chela finger with eight trichobothria, movable chela finger with four, both fingers narrow, curving to interior. Fingers shorter than hand without stem. Venom apparatus

present on both fingers. Trichobothria *eb* and *esb* located retrolaterally, at base of fixed chela finger, situated ca. one trichobothrial width from each other; *ib* situated dorso-prolaterally, just distally of *esb*; *est* opposite and just anterior of *ib*; *isb* located pro-dorsally, aligned vertically with *st*, grouping close to *est*; *ist* located ca. one third from anterior edge of fixed finger, situated prolaterally; *it* located one quarter finger length from anterior edge, situated dorsally; *et* located distally from *it*, almost equidistant from *it* as *ist* from *it*. Regarding the movable finger, *b* located just anterior of finger base, situated dorso-retrolaterally on the finger in line vertically with *eb*; *sb* is located just anterior of *b*, situated slightly more ventrally on the finger, mostly aligned with *esb*; *st* is located ca. one third along movable finger, closer to *sb* than *t*; *t* located ca. one third from the anterior edge of the movable finger, just forward of *ist*. Chelal teeth acute and retrorse, some curving back slightly. Fixed finger with 31 teeth (♀), 25 (♂). Four closely spaced teeth, arranged on a slight bulge, just behind venom apparatus, followed by somewhat larger tooth (Fig 92). Further teeth arranged, roughly, in two rows and reduce in size proximally, but remain acute. Movable finger with 17 teeth (♀), 6 (♂). In the female, movable finger's teeth are nearly contiguous, reduced to small projections posteriorly after first seven teeth. In the male, only six well defined teeth visible posterior of the venom apparatus. Chela ratio: 3.21 (♀), 3.49 (♂).



Figs. 85-88. Digital microscope photographs of *Afrogarypus impressus* right chela: Female (**85**, **86**) and Male (**87**, **88**). **85**, **87**. Retrolateral view; **86**, **88**. Dorsal view. Scale bar: 1.00mm.

Chelicera: Hand with five setae as in Fig. 5. Fixed cheliceral finger with five teeth arranged as in Fig. 93. Galea complex, with nine rami arranged closer together on one side as in Fig. 96 (♀), simple, with no rami (♂) (Fig. 97). Rallum composed of single blade in both male and female. Serrula exterior with 17 lamella (♀) or 18 (♂). Lamina exterior present in both sexes.

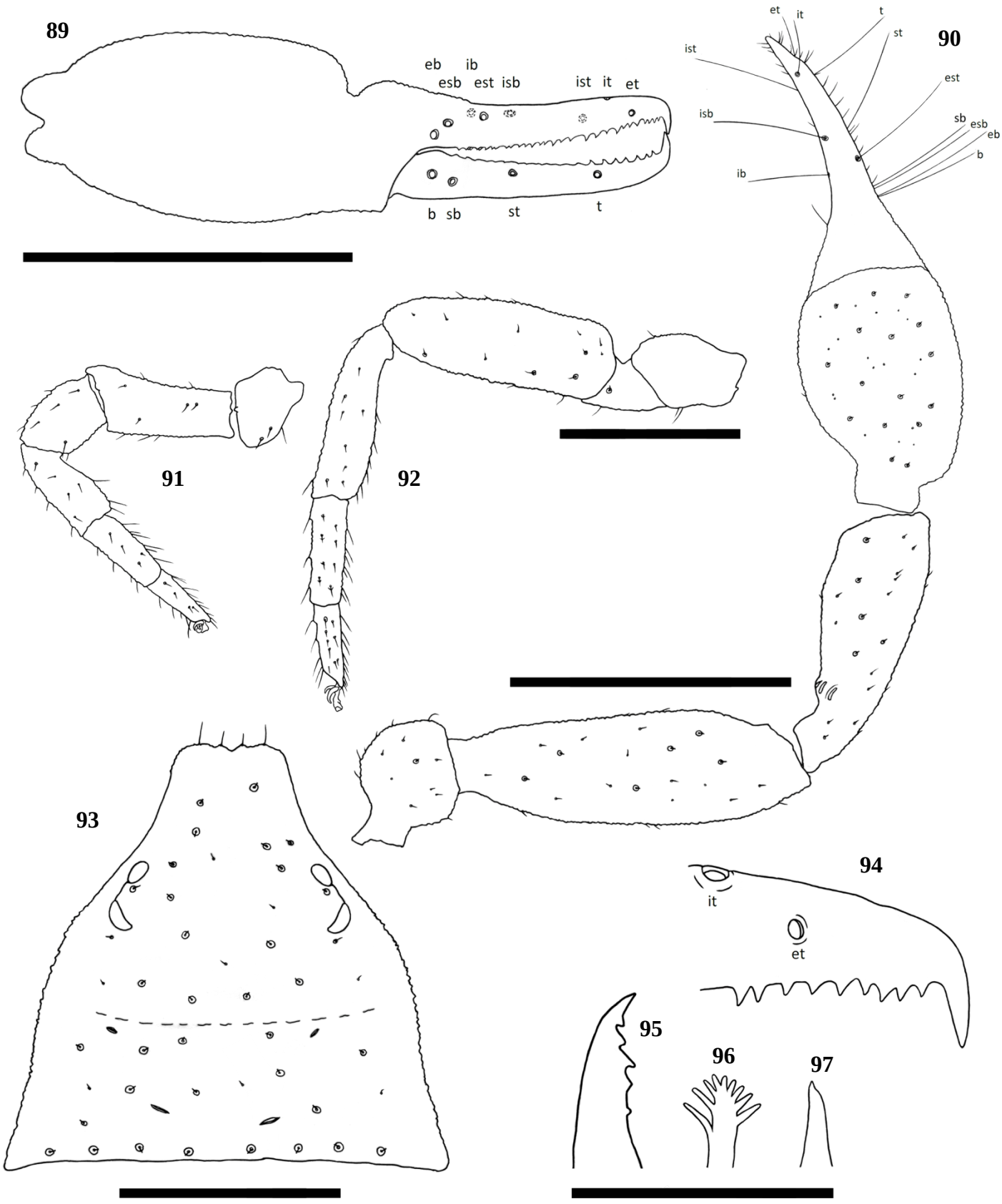
Coxae and legs: Pedipalp coxae brown, shoulder distinct. Multiple long setae present along inner medial ridges. Coxae of legs I-IV, as well as all leg segments, tan. Trochanters of legs I and II compact and small, larger and elongate on legs III and IV. Femora of legs I and II longer than patellae and tibiae respectively (Fig. 91). Metatarsi and tarsi not fused, joint movable. Tarsal claws simple and curved, arolium much longer than claws, not divided. Femur-patella joint immovable in leg IV, tibia mostly straight (Fig. 92), metatarsi and tarsi not fused, joint movable. Claws and arolium similar to those of legs I-III.

3.7.3 *Remarks*

One of the first three geogarypid species to be described from South Africa along with *A. minutus* comb. nov. and *Geogarypys olivaceus*. Tullgren (1907b) failed to mention where he lodged the type specimens. It was assumed that they would reside in ZMH along with the types for *A. minutus* comb. nov. and *Geogarypys olivaceus*, but this was not the case. Beier (1932b) gave a short description of specimens he studied that were lodged in the Museum für Naturkunde of Berlin. It is possible that the original types also reside here, though this has yet to be verified.

3.7.4 *Additional material examined*

SOUTH AFRICA: *Eastern Cape*: 1♀, Grahamstown, Paradise Kloof [33° 18'S, 26° 31'E], leg. J. Hewit, I.1919 (AMG Slide); 1♂, Kei Mouth, coastal forest, 32°41'S, 28°22'E, 21m a.s.l., leg. C.R. Haddad, 8.XII.2005 (WAM T79019); 1♀, 2 Deutonymphs, King William's Town, Pirie Forest Reserve [32° 43'S, 27° 16'E], leg. R. Godfrey, IX.1913 (NMSA 16050); 2♂, Stormsrivier, Stormsrivier Forest Nature Reserve, indigenous forest, 33° 59'S, 23° 54'E, 185m a.s.l., leg. J.A. Neethling, 5.XII.2012 (NMBA P00171); 1♀, 6♂, Stormsrivier, Tsitsikamma National Park, coastal forest, 34° 01'S, 23° 53'E, 47m a.s.l., leg. J.A. Neethling & C. Luwes, 22.XII.2013 (NMBA P00170); 2♀, 3♂, Same locality, Stormsrivier Mouth, 34° 01'S, 23° 54'E, 39m a.s.l. leg. J.A. Neethling & C. Luwes, 22.XII.2013 (morphological dissection); 2♂, 4 Tritonymphs, Same locality [34° 01'S, 23° 54'E], leg. R.F. Lawrence & J.Y. Lawrence, I.1961 (NMSA 7866).
KwaZulu-Natal: 7♀, 3♂, Durban [29° 51'S, 31° 01'E], leg. W.G. Rump, VIII.1940 (NMSA 5132); 1 Protonymph, Izindophi, Middle Drift, Tugela River [28° 53'S, 31° 01'E], leg. R.F. Lawrence, X.1940 (NMSA 5131); 1♂, Margate [30° 51'S, 30° 22'E], leg. W.G. Rump, IV.1940 (NMSA 5130); 18♀, 13♂, 1 Deutonymph, 2 Tritonymphs, Pietermaritzburg, Table Mountain [29° 36'S, 30° 36'E], leg. R.F. Lawrence, I.1940 (NMSA 5127); 1♀, 2♂, 1 Deutonymph, 2 Tritonymphs, Summerveld, Shongweni Resource Reserve [29° 50'S 30° 43'E], leg. W.G. Rump, VII.1940 (NMSA 5128).
Western Cape: 1♀, George, Groenkop, Groeneweide Forest [33° 56'S, 22° 32'E], leg. J.H. Koen, VII.1986 (NCA 97/313); 1♀, 1♂, George, Saasveld Pass, indigenous forest, 33° 58'S, 22° 31'E, 149m



Figs. 89-97. *Afrogarypus impressus*. **89-96**. Female; **97**. Male. **89**. Right chela, retrolateral view; **90**. Right pedipalp, dorsal view; **91**. Right leg I, prolateral view; **92**. Right leg IV, prolateral view; **93**. Carapace, dorsal view; **94**. Right chela fixed finger, anterior teeth arrangement; **95**. Chelicera movable finger, dorsal view; **96**, **97**. Galea. Scale bars: Figs. 89-93: 0.50mm; Figs. 94-97: 0.10mm.

a.s.l., leg. J.A. Neethling, 7.XII.2012 (phylogenetic analysis); 1♀, George, Wadville Forest, indigenous evergreen forest, 33° 55'S, 22° 39'E, 380m a.s.l., leg. H.G. Robertson, 13.X.1996 (SAMC ENW-COO 5420); 1♀, 1♂, Hoekwil, Woodville Big Tree, 33° 56'S, 22° 38'E, 262m a.s.l., leg. J.A. Neethling, 8.XII.2012 (lactic acid clearing); 1♀, Knysna, Diepwalle Forest, indigenous forest [33° 57'S, 23° 09'E], leg. J.H. Koen, III.1984 (NCA 97/281); 2♀, Knysna, Lily Vlei Nature Reserve, Gouna State Forest, indigenous forest [33° 56'S, 23° 02'E], leg. J.H. Koen, VII.1983 (NCA 97/371); 1♀, 2♂, Mossel Bay, St. Blaize Hiking Trail, coastal fynbos, 34° 11'S, 22° 08'E, 89m a.s.l., leg. J.A. Neethling, 8.XII.2012 (NMBA P00169); 2♀, 2♂, Rheenendal, Jubilee Creek Nature Reserve, 33° 53'S, 22° 58'E, Afromontane forest, 923m a.s.l., leg. J.A. Neethling & C. Luwes, 26.XII.2013 (NMBA P00172); 1♀, Suurbraak, Grootvadersbosch Nature Reserve, dry shrub forest, 33° 58'S, 20° 49'E, 422m a.s.l., leg. J.A. Neethling, 13.XII.2012 (phylogenetic analysis).

3.7.5 *Additional material not examined*

SOUTH AFRICA: *KwaZulu-Natal*: 1♂, Royal Natal National Park, Gaints Castle Game Reserve, Mahai Rest Camp, The Cascades [28° 41'S, 28° 56'E], 2.IV.1951 (examined by Beier 1955, collection unknown); St. Lucia, iSimangaliso Nature Reserve, Lake Sibayi shoreline [27° 21'S, 32° 43'E] (examined by Beier 1958, collection unknown).
Northern Cape: 2 immatures, Steinkopf [29° 15'S, 17° 44'E], leg. Schultze (examined by Beier 1947, deposited in ZMH).

3.8 *Afrogarypus megamolaris* sp. nov.

Holotype: ♀, SOUTH AFRICA, Limpopo Province, Louis Trichardt [Makhado], Medike Mountain Reserve, 22° 59'S, 29° 37'E, 903m a.s.l., Montane Bushveld, Leaf litter sifting, leg. J.A. Neethling, 9.XI.2012 (NMBA P00206).
Paratype: 1♂, Same data as holotype (NMBA P00207).

3.8.1 *Etymology*

Named for the enlarged basal teeth on both chelal fingers of the females.

3.8.2 *Diagnosis*

Small species, pedipalpal femur length 0.45mm (♀), 0.49mm (♂), chela length (with stem) 0.77mm (♀), 0.68mm (♂), movable finger length 0.39mm (♀), 0.36mm (♂). Females can reach up to 1.80mm and males up to 1.53mm in total length (cucullus to posterior abdominal margin). Carapace

uniform brown to dark brown in both sexes (Figs. 98 & 100), though the medial furrow and posterior margin may be slightly lighter in colour than the rest of the carapace. All pedipalp segments similar in colouration to the carapace. Well developed, broad and shallow sulcus present on the dorsal surface of chelas. Abdominal tergites generally brown with dark patches, though small cream coloured markings may be present on each side of the paired dark spots. Abdominal sternites light brown with cream markings in both sexes, weakly sclerotised in females (Fig. 99) and strongly sclerotised throughout in males (Fig. 101). Pedipalp coxa has same colouration as carapace and possesses a distinct shoulder. Legs I-IV as well as remaining coxa tan to pale yellow.

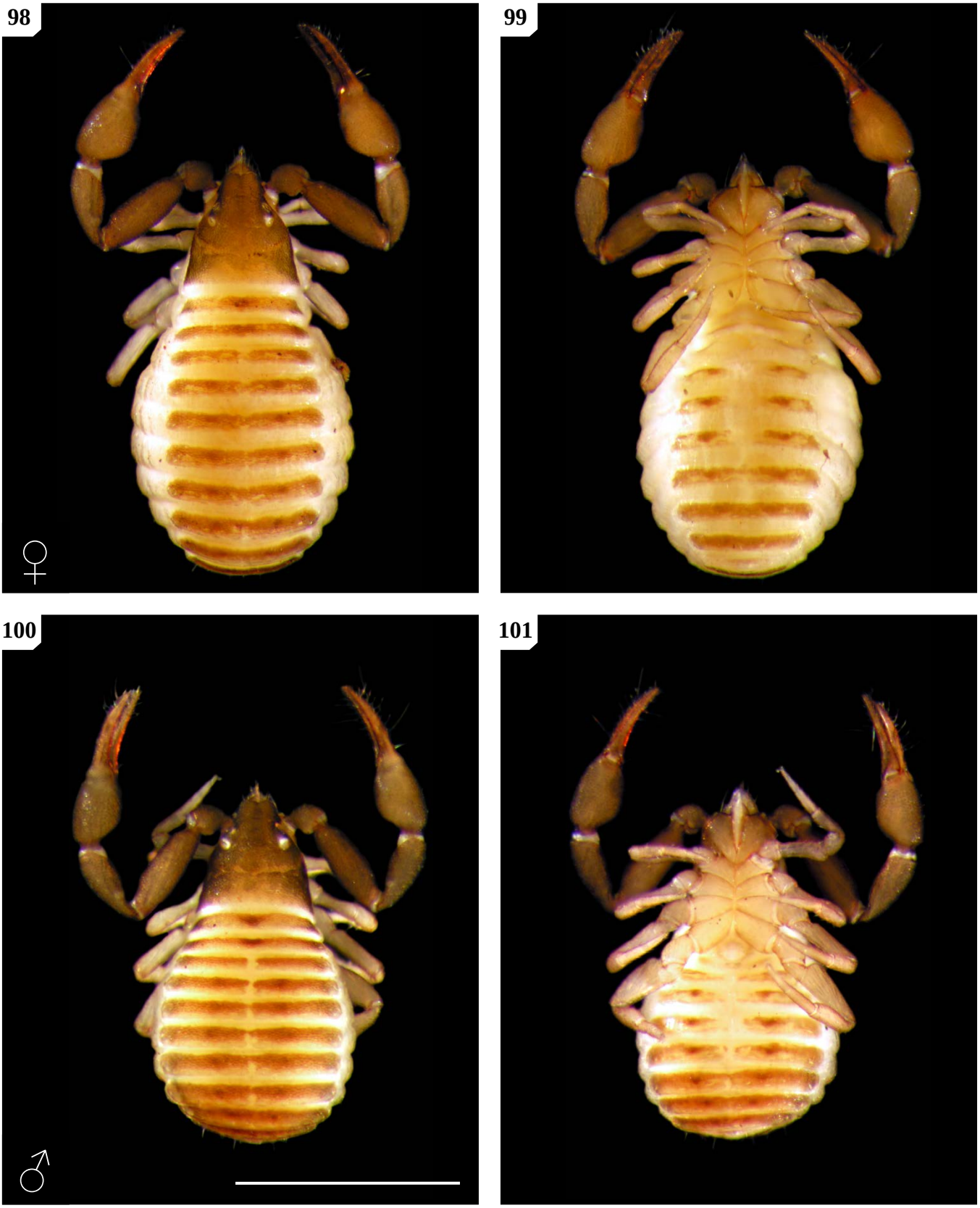
The species resembles *Afrogarypus minutus* comb. nov. in general size and appearance, but can easily be distinguished by the presence of a well developed dorsal sulcus on the chela hand, while *A. minutus* comb. nov. only possesses a shallow concave area.

3.8.3 *Description*

Carapace: Strongly sub-triangular, narrow furrow posterior to the eyes (Fig. 116). Uniformly brown to dark brown in both sexes, medial furrow and posterior margin somewhat lighter. Uniformly granular, heavily constricted anteriorly into cucullus, constriction beginning at the medial furrow. Row of eight setae located on the posterior edge. Two pairs of corneate eyes situated on ocular tubercles, located ca. one third away from the anterior edge. Carapace ratio: 0.89 (♀), 0.88 (♂).

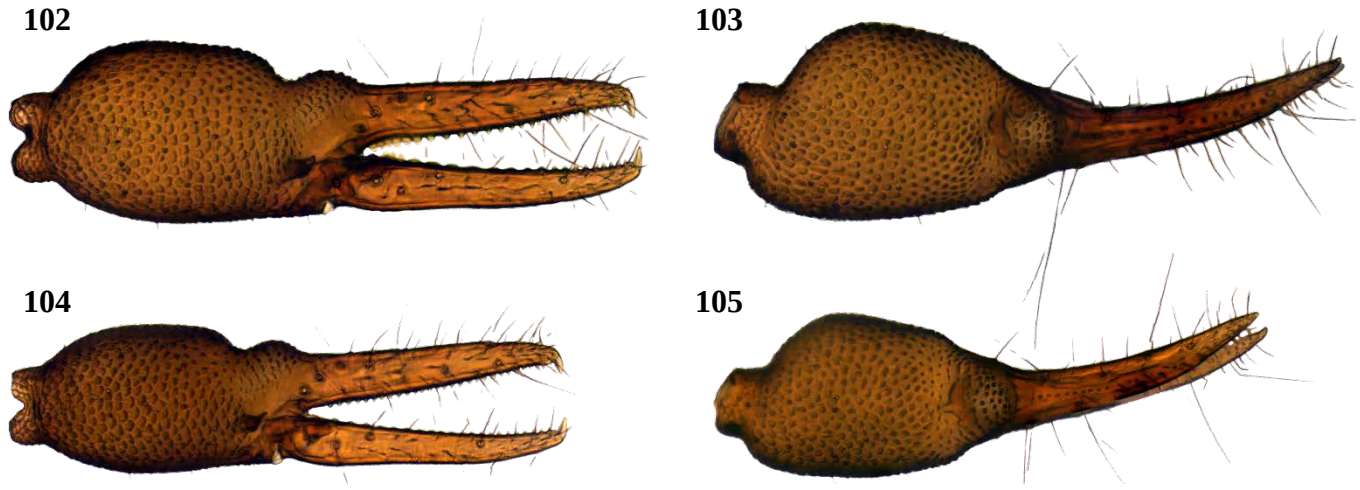
Abdomen: Abdominal tergites uniformly brown, with dark patches (small cream patches may be present, flanking paired dark spots) in both males and females, granular. Tergites I and II each with large median dark spot. Tergite III without dark patches. Tergites IV-X with paired, faint dark patches mediolaterally. Tergites XI and XII without patches. Sternites light brown with faint dark patches in both sexes, weakly sclerotised in females, well sclerotised in males. Pleural membrane wrinkled-placate, cream.

Pedipalp: Trochanter rounded, compact in shape, granular, coloured same as carapace. Small setae scattered over entire surface, except the stem. Apophysis located ventrally. Pedipalp femur (Fig. 109) same colour, granular. Narrow at stem, widening quickly at base, widening further slightly before constricting again at the end. Femur ratio: 2.78 (♀), 3.04 (♂). Pedipalp patella (Fig. 109) same colour as femur, granular. Narrow and slightly angled at base, widening evenly into cone. Lyriform fissures visible just anterior to base, located on a bulge, dorso-prolaterally on patella. Patella ratio: 2.40 (♀), 2.94 (♂).



Figs. 98-101. Digital microscope photographs of *Afrogarypus megamolaris* sp. nov., Female (**98**, **99**) and Male (**100**, **101**). **98**, **100**. Dorsal view; **99**, **101**. Ventral view. Scale bar: 1.00mm.

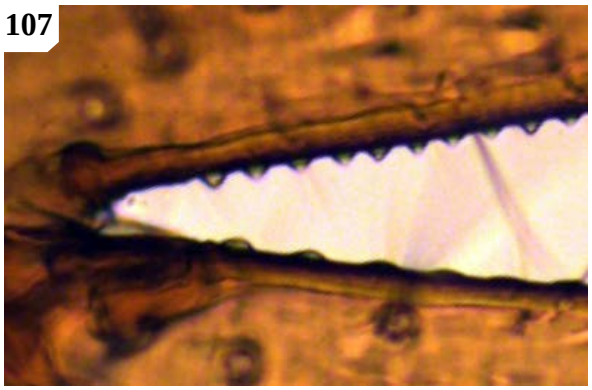
Chela: (Figs. 102-105, 108, 109) Same colour as rest of pedipalp, granular from stem to base of fingers. Both fingers smooth, just as long to slightly longer than hand-stem complex. Well developed, broad, shallow sulcus present on dorsal surface of chelal hand. Chela hand rounded at back on prolateral edge, tapering in toward base of fingers with a straight edge. Retrolateral edge mostly straight. Fixed chela finger with eight trichobothria, movable chela finger with four, both fingers narrow, curving slightly to interior. Venom apparatus present on both fingers. Trichobothria *eb* and *esb* situated as normal on retrolateral surface of fixed chelal finger, located just above base of finger, one trichobothrial width between them. Trichobothria *ib* located on the prolateral surface, anterior and dorsal of *esb*. Trichobothria *est* located opposite and anterior of *ib* by slightly more than one trichobothrial width. Trichobothria *isb* located just before halfway along fixed finger, situated dorsally, while *ist* located on interior lateral surface, over one third from anterior edge of fixed chelal finger, situated near to the teeth. Trichobothria *it* located dorsally, roughly one quarter distance from anterior edge of fixed chelal finger, *et* located on retrolateral surface, slightly distal and almost beneath *it*. Trichobothria *b*, *sb* and *st* group together in triangle within the first third of movable finger, *t* located distally, almost directly in line with *it*. Chelal teeth acute, most slightly retrorse. Fixed finger with 27 teeth (♀), 30 (♂). First six teeth from the anterior end small, increasing slightly in size before the first large accessory tooth (Fig. 92). Further teeth slightly retrorse and acute, arranged, mostly, in single row. Movable finger with 21 teeth (♀), 22 (♂) tooth just before venom apparatus very small. Teeth after small tooth acute and retrorse, degenerating into small points closer to base of finger. In females, first six basal teeth on fixed chelal finger, and first three on movable finger very enlarged, grouping tightly next to each other (Figs. 106 & 110). In males, teeth remain small and acute (Figs. 107 & 111) Chela ratio: 3.18 (♀), 3.28 (♂).



Figs. 102-105. Digital microscope photographs of *Afrogarypus megamolaris* sp. nov. right chela: Female (**102**, **103**) and Male (**104**, **105**). **102**, **104**. Retrolateral view; **103**, **105**. Dorsal view. Scale bar: 1.00mm.

Chelicera: Hand with five setae located as in Fig. 5. Fixed cheliceral finger with five teeth arranged as in Fig. 113. Female galea complex, with nine rami in a fan shape (Fig. 114), male galea simple, no rami (Fig. 115). Rallum composed of single blade in both sexes. Serrula exterior with 13 lamella (♀) or 12 (♂). Lamina exterior present in both sexes.

Coxae and legs: Pedipalp coxae light brown, shoulder distinct. Coxa of legs I-IV, as well as all leg segments, tan to pale yellow. Leg morphology standard and diplotarsate for both leg I (Fig. 117) and leg IV (Fig. 118).



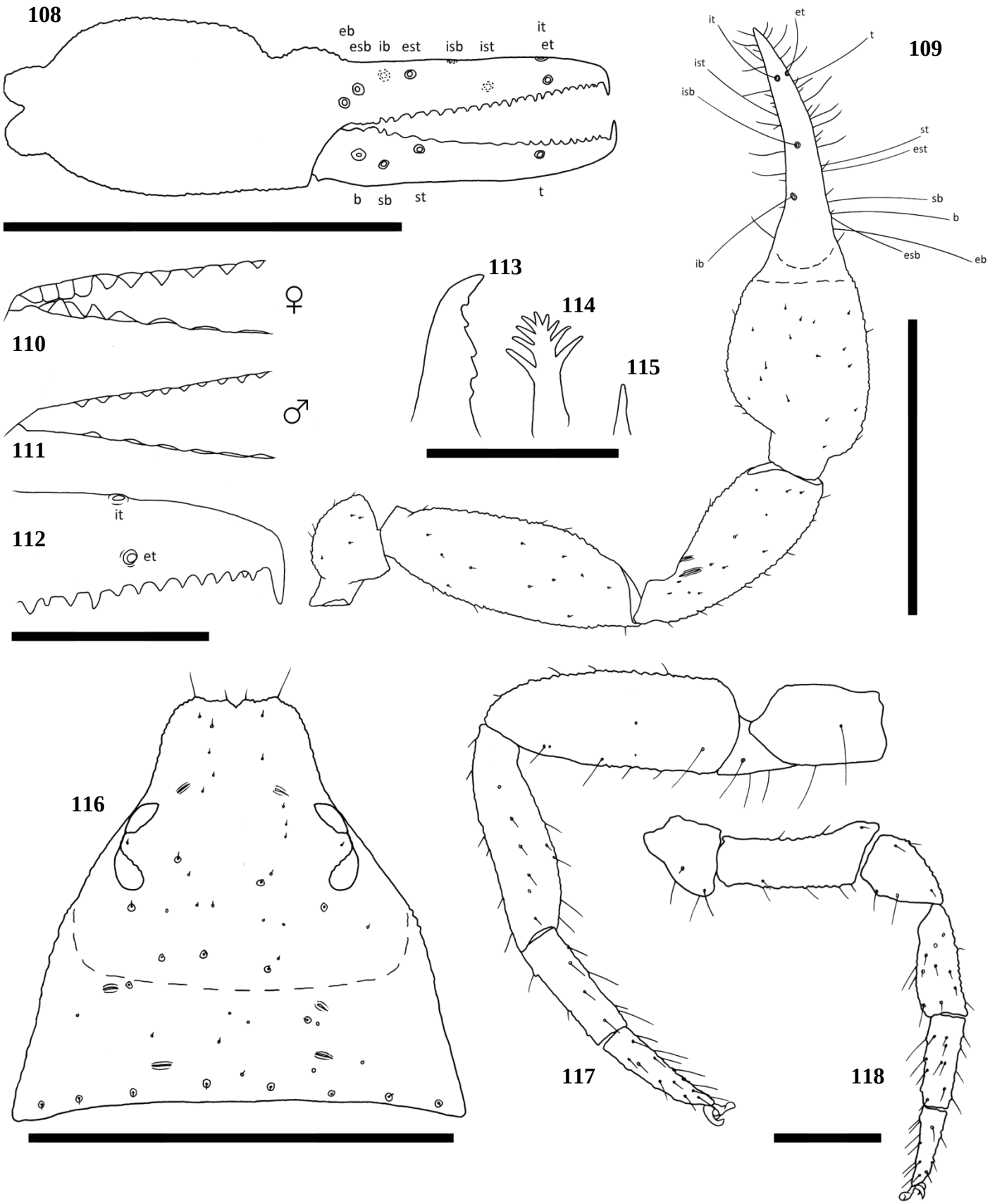
Figs. 106-107. Tooth morphology at the base of the chelal fingers of *Afrogarypus megamolaris* sp. nov. Female (**106**) and Male (**107**), showing distinct differences between the genders.

3.8.4 *Remarks*

Specimens of this species were primarily collected from the type locality, though museum specimens added further locality data. It is my opinion that this species could have accounted for many *A. impressus* misidentifications within the north-eastern areas of South Africa due to the presence of a dorsal sulcus, as such misidentifications were present in museum samples (NMSA 16051) that corresponded to sample data in Beier (1966) and Lawrence (1967).

3.8.5 *Additional material examined*

SOUTH AFRICA: *Gauteng Province*: 2 Adults, Pretoria, Groenkloof [25° 46'S, 28° 13'E], 15.IX.1921 (AMG slide); 1♀, Pretoria, Roodeplaat, Pretoria Plant Research Institute [25° 36'S, 28° 21'E], leg. M.S. Harvey, 24.III.2001 (WAM T67019).
Mpumalanga Province: 1♀, Kruger National Park, Malelane Camp [25° 29'S, 31° 31'E], leg. R.F. Lawrence, 3.XII.1963 (NMSA 16051).



Figs. 108-118. *Afrogarypus megamolaris* sp. nov. **108-110**, **112-114**, **116-118**. Female; **111**, **115**. Male. **108**. Right chela, retrolateral view; **109**. Right pedipalp, dorsal view; **110**, **111**. Basal teeth arrangement; **112**. Anterior teeth arrangement on fixed chelal finger; **113**. Chelicera movable finger, dorsal view; **114**, **115**. Galea; **116**. Carapace, dorsal view; **117**. Right leg IV, prolateral view; **118**. Right leg I, prolateral view. Scale bars: Figs. 108, 109, 116: 0.50mm; Figs. 112-115, 117, 118: 0.10mm.

3.9 *Afrogarypus minutus* (Tullgren, 1907) **comb. nov.**

Garypus minutus Tullgren, 1907a: 65, fig. 21 [**Holotype** ♀, South Africa, Eastern Cape, Port Elizabeth [33°56'S, 25°34'E], leg. H. Brauns, 15.XII.1898, deposited in ZMH, examined]; Tullgren, 1907b: 229; Ellingsen, 1912: 87, 108.

Geogarypus minutus (Tullgren, 1907): Chamberlin, 1930: 609; Beier, 1964: 60; Harvey, 1986: 760; Harvey, 1991: 257; Dippenaar-Schoeman & Harvey, 2000: 93; Turienzo, Di Iorio & Mahnert, 2010: 561, 564 [**comb. nov.**].

Geogarypus (*Geogarypus*) *minutus* (Tullgren, 1907): Beier, 1932a: 231, fig. 257; Roewer, 1937: 269; Beier, 1958: 171.

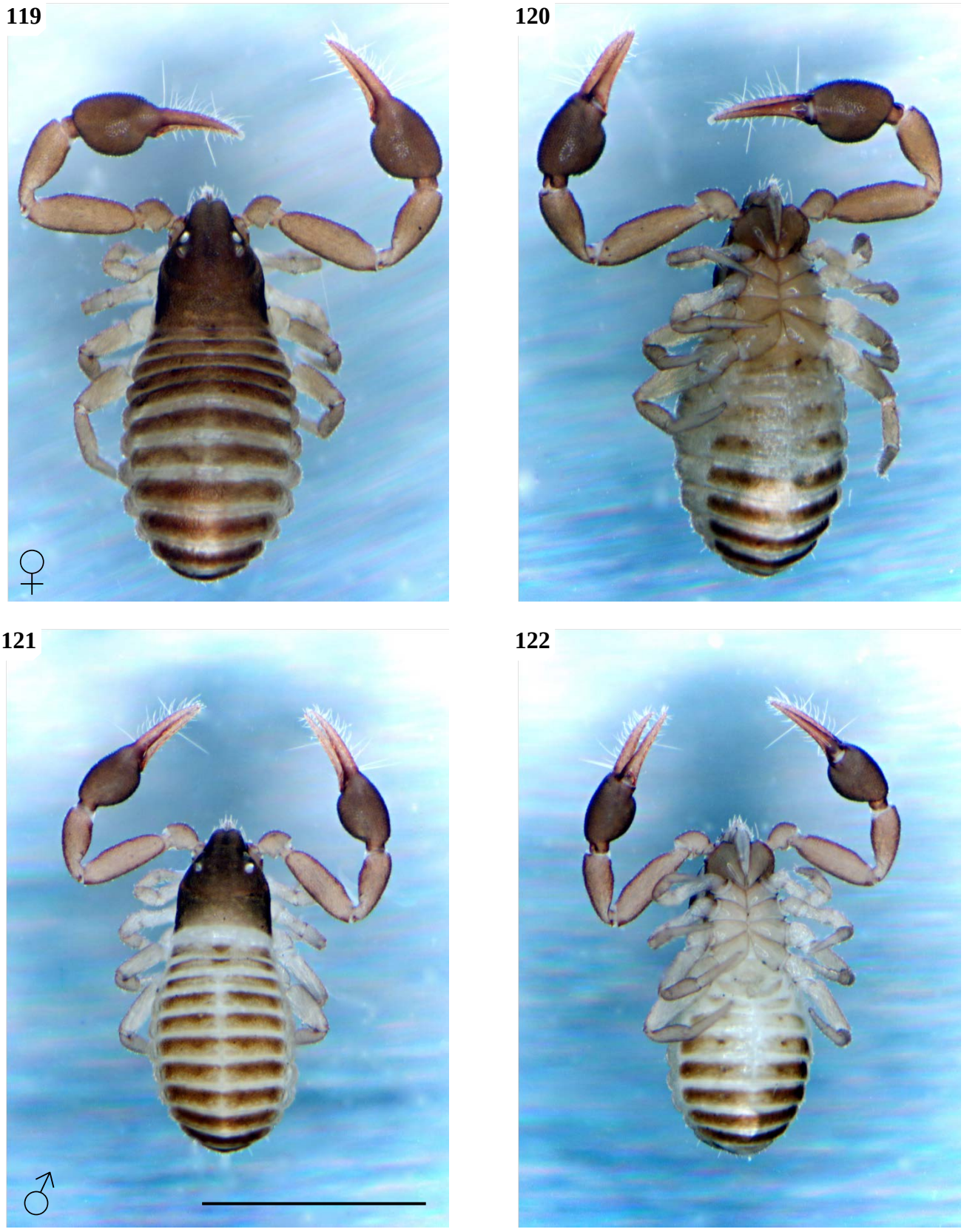
3.9.1 *Diagnosis*

Small species, pedipalpal femur length 0.52mm (♀), 0.41mm (♂), chela length (with stem) 0.82mm (♀), 0.71mm (♂), movable finger length 0.41mm (♀), 0.35mm (♂). Females can reach a length (cucullus to posterior abdominal margin) of 1.60mm, with males reaching 1.45mm. Carapace dark brown throughout in both sexes, though in some specimens the medial furrow and posterior edge of the carapace may be lighter (Figs. 119 & 121). Pedipalp trochanter, femur and patella light-brown in colour, with pedipalp coxa and chela dark brown. Concave depression present on dorsal surface of chelas. Abdominal tergites generally dark brown in females, dark brown with cream patches in males. Abdominal sternites cream to dark brown in both sexes, and weakly sclerotised (♀) (Fig. 120) and well sclerotised (♂) (Fig. 122). Pedipalp coxa possessing a distinct shoulder, legs I-IV cream in colour (both sexes), with the leg coxa yellow to light-brown in females and cream in males.

The specimens closely resemble smaller individuals of *A. triangularis* comb. nov., but can be distinguished by the shape of the chela and the lack of lateral sclerites on the abdomens of males. The chela of *A. minutus* comb. nov. do not possess the strongly convex interior lateral surface that gives the chela of *A. triangularis* comb. nov. their distinct shape, and instead have a less convex shape. The prolateral surface of some specimens' chela was found to be almost straight, giving the chela a distinct rectangular shape.

3.9.2 *Description*

Carapace: Strongly sub-triangular, narrow furrow posterior to the eyes (Fig. 135). Dark brown throughout in both sexes, medial furrow and posterior edge may be paler. Uniformly granular, strongly constricted anteriorly into cucullus, constriction beginning at the medial furrow. Two pairs



Figs. 119-122. Digital microscope photographs of *Afrogarypus minutus* comb. nov., Female (**119**, **120**) and Male (**121**, **122**). **119**, **121**. Dorsal view; **120**, **122**. Ventral view. Scale bar: 1.00mm.

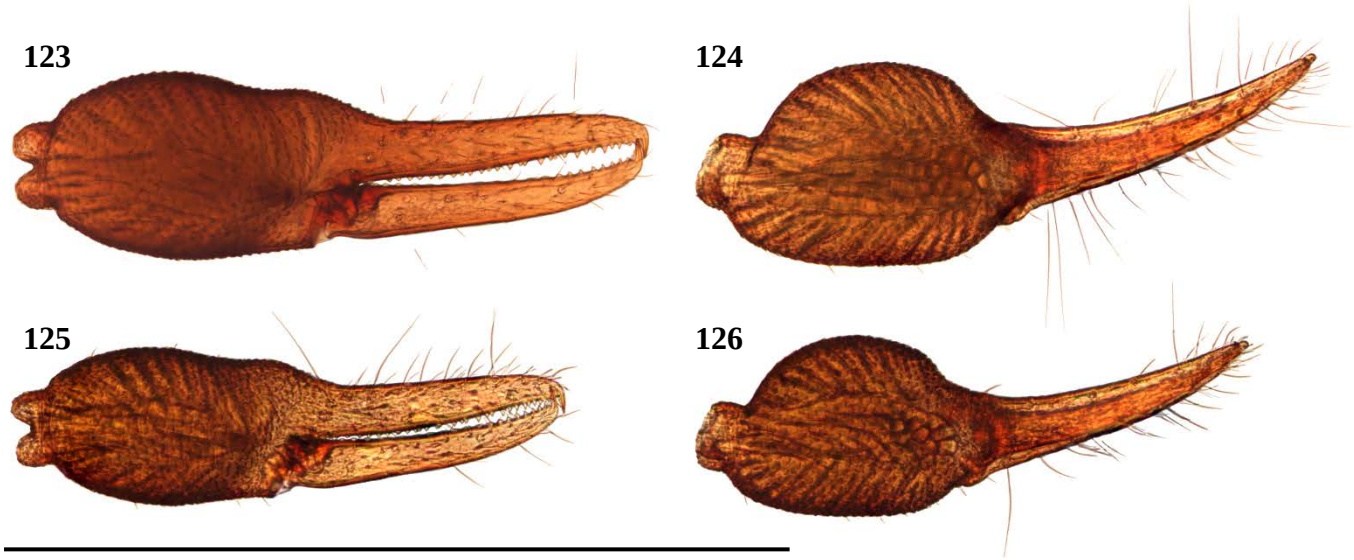
of corneate eyes situated on ocular tubercles, located ca. one third away from anterior edge. Four prominent setae located on anterior edge, row of seven setae located on posterior margin. Numerous small setae present on the carapace. Carapace ratio: 1.04 (♀), 1.18 (♂).

Abdomen: Abdominal tergites granular, uniformly dark brown in females, dark brown with cream patches in males. Tergites I and II with large median dark spot each. Tergite III without dark patches. Tergites IV-X with faint paired dark patches mediolaterally. Tergites XI and XII without patches. Sternites cream to dark brown in both sexes, weakly sclerotised in females, well sclerotised in males. Pleural membrane wrinkled-placate, cream.

Pedipalp: Trochanter rounded in front, overall rectangular in shape, granular and uniformly light brown. Small setae scattered over entire surface, except the stem. Apophysis located ventrally. Pedipalp femur (Fig. 128) light brown, granular. Narrow at stem, widening quickly to form base then widening evenly before constricting again at distal end. Femur ratio: 3.27 (♀), 2.77 (♂). Pedipalp patella (Fig. 128) same colour as femur, granular. Narrow, angled at base, widening quickly into short cone. Lyriform fissures visible just anterior of base, located on bulge, dorso-prolaterally on patella. Patella ratio: 2.59 (♀), 2.85 (♂).

Chela: (Figs. 123-128) Uniformly dark brown, almost same colour as carapace, granular from stem to base of fingers. Both fingers smooth. Concave depression present on dorsal surface of chela, resulting in bulge at base of fixed finger. Chela hand somewhat convex on prolateral edge, retrolateral surface mostly straight. Prolateral surface of some specimens also almost straight, giving chela distinct rectangular shape. Fixed chela finger with eight trichobothria, movable chela finger with four, both fingers narrow, curving slightly to interior. Fingers slightly longer than hand with stem. Venom apparatus present on both fingers. Trichobothria *eb* and *esb* located retrolaterally at base of fixed chela finger, situated ca. one trichobothrial width from each other. Trichobothria *ib* situated dorso-prolaterally, one trichobothrial width anterior of *esb*. Trichobothria *est* located retrolaterally, one trichobothrial width forward of *ib*. Trichobothria *ist* situated dorso-prolaterally just over one third finger length from base of fixed finger. Trichobothria *it* located one quarter finger length from anterior edge and situated dorsally; *et* located retrolaterally and distally from *it*. Regarding the movable finger, trichobothria *b, sb* and *st* located in first third of movable finger, just anterior to finger base and are situated retrolaterally, *b* is furthermore situated in line vertically with *eb*. Trichobothria *t* located lest than one third from anterior edge of movable finger, positioned between *ist* and *it*. Chelal teeth acute and retrorse, some curving back slightly. Fixed finger with 29 teeth (♀), 28 (♂). First four to five teeth after venom apparatus small, roughly equal in size, situated just in front of first large accessory tooth (Fig. 131). Further teeth slightly to distinctly retrorse and acute, arranged roughly in two rows. Movable finger with 20 teeth (♀), 22 (♂). In both sexes, first eight teeth

following the venom apparatus acute and retrorse, rest of the teeth degenerating into small teeth points. Six basal teeth in females regenerate (Fig. 129), with the first three regenerating in males (Fig. 130). Chela ratio: 3.09 (♀), 2.97 (♂).



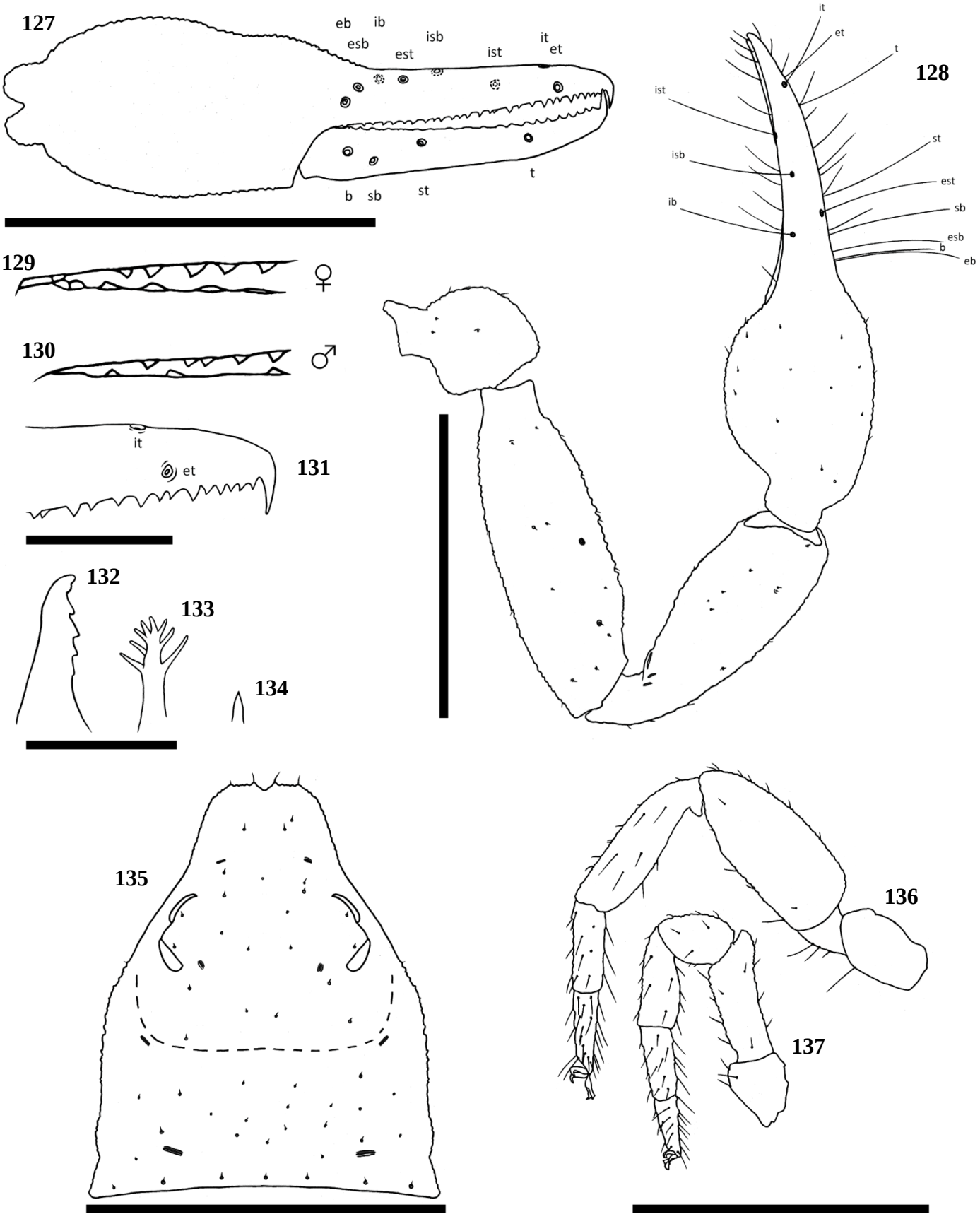
Figs. 123-126. Digital microscope photographs of *Afrogarypus minutus* comb. nov. right chela: Female (**123**, **124**) and Male (**125**, **126**). **123**, **125**. Retrolateral view; **124**, **126**. Dorsal view. Scale bar: 1.00mm.

Chelicera: Hand with five setae located as in Fig. 5. Fixed cheliceral finger with five teeth arranged as in Fig. 132. Female galea complex and elongate with eight rami (Fig. 133), small, simple, with no rami in males (Fig. 134). Rallum composed of single blade in both sexes. Serrula exterior with 16 lamella (♀) or 14 (♂). Lamina exterior present in both sexes.

Coxae and legs: Pedipalp coxae same colour as carapace, with distinct shoulder. Legs I-IV cream in both sexes, leg coxae yellow to light-brown in females, cream in males. Leg morphology standard and diplotarsate with regard to both leg I (Fig. 136) and leg IV (Fig. 137).

3.9.3 - *Remarks*

This is one of the first three geogarypid species described for South Africa by Tullgren (1907a). The species was originally the smallest of all South African geogarypids, though it now places second after *Afrogarypus castigatus* sp. nov., which has an average length of 1.40mm. *A. minutus* comb. nov. is here transferred to the *Afrogarypus* due, firstly, to its phylogenetic placement within the *Afrogarypus* clade and, secondly, to the presence of a concave dorsal depression on the chela hand, which it shares with the other species that were originally placed within the *Geogarypus* but now group within the genus *Afrogarypus*. The distribution of this species has only been confirmed from the Eastern Cape and eastern Western Cape. The potential exists that the



Figs. 127-137. *Afrogarypus minutus* comb. nov. **127-129**, **131-133**, **135-137**. Female; **130**, **134**. Male. **127**. Right chela, retrolateral view; **128**. Right pedipalp, dorsal view; **129**, **130**. Basal teeth arrangement, **131**. Anterior teeth arrangement on fixed chelal finger; **132**. Chelicera movable finger, dorsal view; **133**, **134**. Galea; **135**. Carapace, dorsal view; **136**. Right leg IV, prolateral view; **137**. Right leg I, prolateral view. Scale bars: Figs. 127, 128, 135-137: 0.50mm; Fig. 131: 0.10mm; Figs. 132-134: 0.05mm.

unexamined material may include misidentifications that could potentially alter the distribution proposed in this thesis.

3.9.4 - *Additional material examined*

SOUTH AFRICA: *Eastern Cape*: 1♀, Graaff-Reinet, Asante Sana Game Reserve, Waterkloof, 32° 15'S, 24° 56'E, leg. J. Midgely, 25.IX.2009 (NCA 2012/3500); 2 Adults, Grahamstown [33° 18'S, 26° 31'E] (AMG slide); 1 Adult, Port Alfred [33° 36'S, 26° 53'E], leg. J. Hewitt (AMG slide); 2♀, 2♂, Port Elizabeth, Island Nature Reserve, 33° 59'S, 25° 21'E, 268m a.s.l., Indigenous bush, Leaf litter sifting, leg. J.A. Neethling, 15.XII.2013 (NMBA P00186); 2 Adults, Tsolo, Somerville Mission Station [31° 12'S, 28° 39'E], leg. R. Godfrey, VI.1912 (AMG slide).
Western Cape: 2♀, 1♂, Knysna, Brenton-on-Sea, 34° 04'S, 23° 00'E, 228m a.s.l., Coastal Fynbos, Leaf litter sifting, leg. J.A. Neethling, 20.XII.2013 (NMBA P00185); 3♀, 1 Protonymph, 2 Deuto- nymphs, Knysna, Brenton-on-Sea [34° 04'S, 23° 00'E], leg. H.G. Robertson, 19-23.XI.1998 (SAMC ENW-COO 5846, 5848, 5855, 5856, 5859); 1♀, Mossel Bay [34° 11'S, 22° 08'E], leg. W.F. Purcell, 1896 (SAMC 588).

3.9.5 *Additional material not examined*

SOUTH AFRICA: *KwaZulu-Natal*: Durban, Stamfort Hill [29° 50'S, 31° 02'E], leg. I. Trägårdh, 31.I.1905 (examined by Tullgren 1907b, deposited in ZMH); Van Reenen [28° 23'S, 29° 23'E], leg. I. Trägårdh, 23.IV.1905 (examined by Tullgren 1907b, deposited in ZMH).
Western Cape: 2♀, Caledon [34° 14'S, 19° 26'E], leg. W.F. Purcell (examined by Ellingsen 1912); 1♀, Clanwilliam, Waterfall Kloof [32° 04'S, 19° 05'E], leg. R. Pattison (examined by Ellingsen 1912); 1 Immature, George, Montagu Pass [33° 54'S, 22° 25'E], leg. W.F. Purcell (examined by Ellingsen 1912); 1♂, Robertson [33° 48'S, 19° 53'E], leg. W.F. Purcell (examined by Ellingsen 1912); 1♀, Swellendam, Zondereinde Mountains [34° 01'S, 20° 26E'], leg. W.F. Purcell (examined by Ellingsen 1912).

3.10 *Afrogarypus purcelli* (Ellingsen, 1912) **comb. nov.**

Garypus purcelli Ellingsen, 1912: 110 [**Holotype** ♀, 1 Immature, South Africa, Western Cape, Beaufort West [32° 21'S, 22° 35'E], leg. W.F. Purcell, collection unknown, not examined].

Geogarypus (*Geogarypus*) *purcelli* (Ellingsen, 1912): Beier, 1932a: 235; Roewer, 1937: 270; Beier, 1955: 300, fig. 19.

Geogarypus purcelli (Ellingsen, 1912): Beier, 1964: 59; Beier, 1966: 461; Harvey, 1986: 760; Harvey, 1991: 259; Dippenaar-Schoeman & Harvey, 2000: 93 [**comb. nov.**].

3.10.1 *Diagnosis*

Medium to large species, pedipalpal femur length 0.73mm (♀), 0.62mm (♂), chela length (with stem) 1.31mm (♀), 1.07mm (♂), movable finger length 0.69mm (♀), 0.57mm (♂). Females can reach a length (cucullus to posterior abdominal margin) of 2.22mm, with males reaching 2.14mm. Carapace uniform brown to light-brown in both sexes (Figs. 138 & 140). Pedipalp segments same colour as carapace, while chela may be slightly darker. Concave depression present on dorsal surface of chelas, with a distinct inclusion present on the prolateral surface just before the base of the fingers. Abdominal tergites mostly brown with dark patches and a medial cream patch on most tergites, abdominal sternites brown and relatively well sclerotised (♀) (Fig. 139), well sclerotised throughout (♂) (Fig. 141). Pedipalp coxa same colour as carapace with distinct shoulder, legs I-IV cream in colouration (both sexes), with leg coxa pale yellow to light-brown.

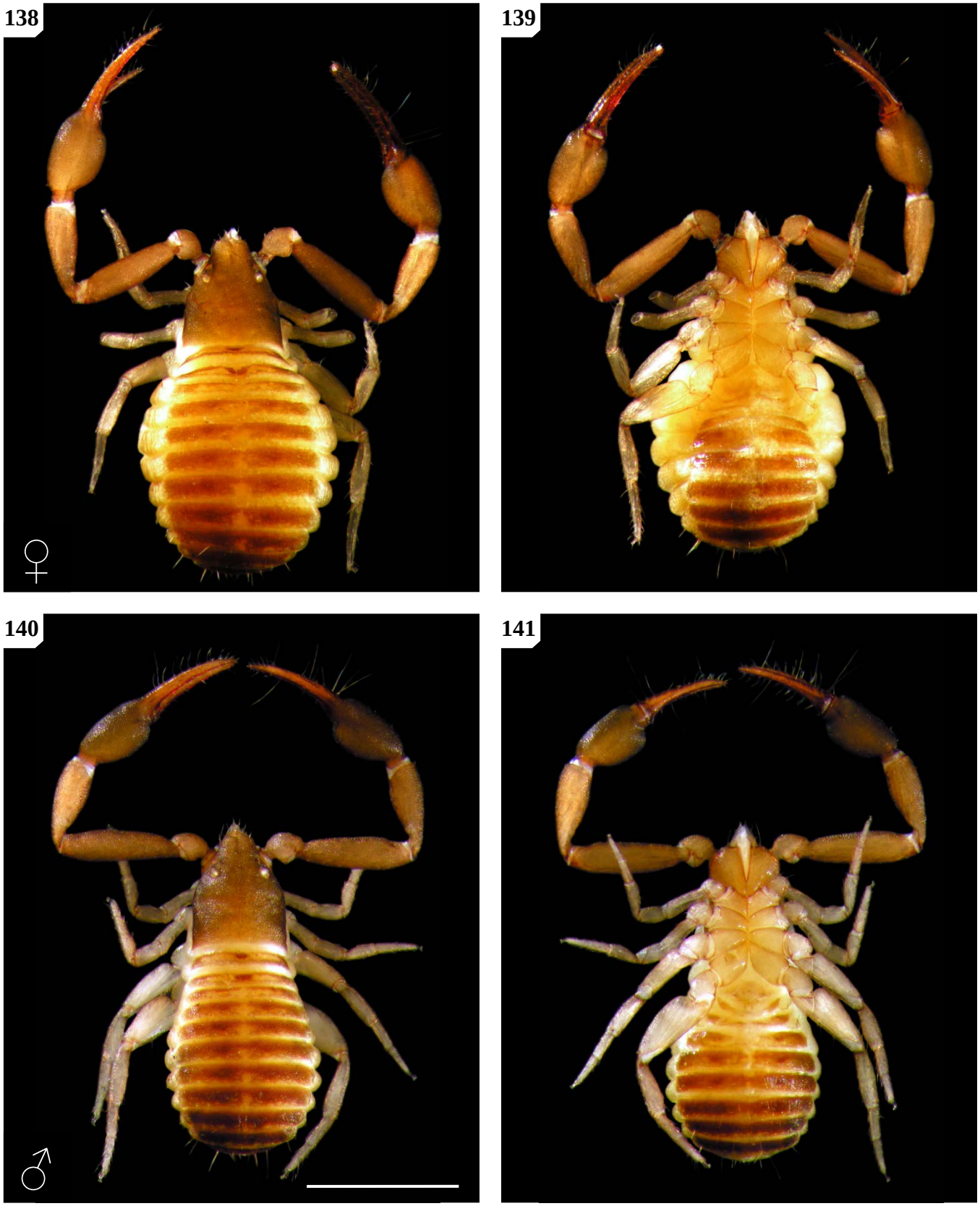
Although somewhat larger, *A. purcelli* comb. nov. resembles *A. carmenae* sp. nov. in general morphology. The two can be distinguished by either the presence or lack of the inclusion on the prolateral surface of the chela, present in *A. purcelli* comb. nov. and absent in *A. carmenae* sp. nov. Mature females are generally larger than males and more robust, while the males are more elongate.

3.10.2 *Description*

Carapace: Strongly sub-triangular, longer than broad in both sexes, narrow furrow posterior to the eyes (Fig. 152). Carapace uniformly brown to light-brown in both sexes, granular. Heavily constricted anteriorly into cucullus, constriction beginning at medial furrow. Two pairs of corneate eyes situated on ocular tubercles, located ca. one third away from anterior edge. Four prominent setae located on anterior edge, row of eight setae, seated with rims, located on posterior margin. Numerous small setae present on carapace. Carapace ratio: 1.09 (♀), 1.19 (♂).

Abdomen: Abdominal tergites brown with dark patches and medial cream patch on most plates. Tergites I and II with large median dark spot each, flanked by cream patches. Tergite III without dark patches, but with cream patches. Tergites IV–X with faint paired dark patches mediolaterally. Tergites XI and XII lack dark patches. Tergites IV–IX with medial cream patch. Sternites relatively well sclerotised in females, well sclerotised in males. Brown to light-brown throughout, with paired dark patches mediolaterally. Pleural membrane wrinkled-placate, cream.

Pedipalp: Trochanter rounded, slightly elongate, granular, somewhat lighter in colour than carapace. Small setae located on dorsal and dorso-lateral sides. Apophysis located ventrally. Pedipalp femur



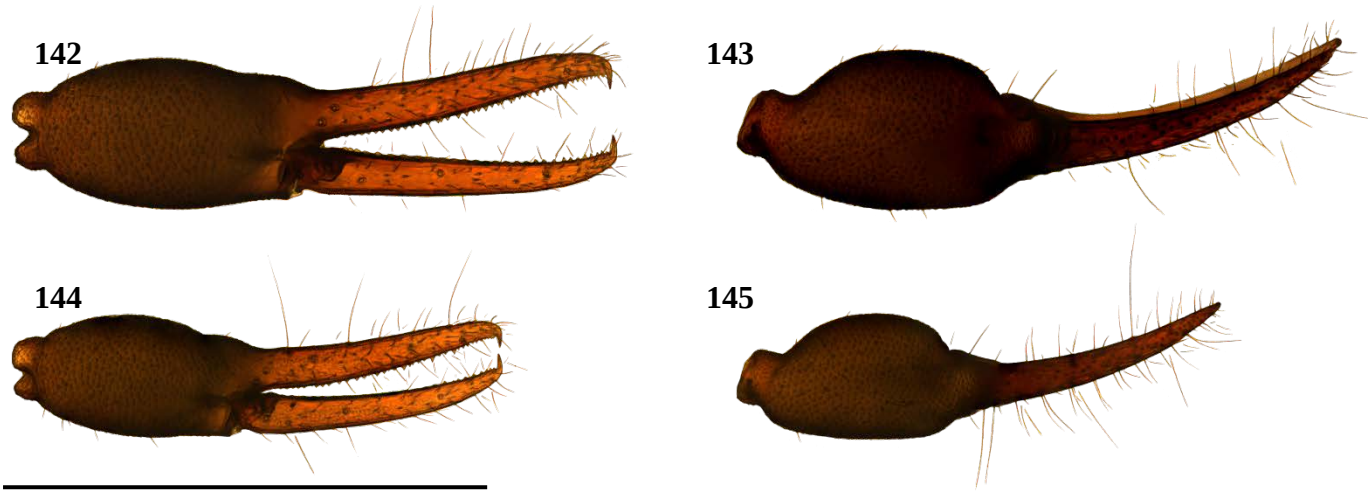
Figs. 138-141. Digital microscope photographs of *Afrogarypus purcelli* comb. nov., Female (**138**, **139**) and Male (**140**, **141**). **138**, **140**. Dorsal view; **139**, **141**. Ventral view. Scale bar: 1.00mm.

(Fig. 147) and patella same colour as trochanter, granular. Femur narrow at base, widening evenly until just posterior of anterior margin, where there is a sudden constriction. Femur ratio: 3.61 (♀), 3.16 (♂). Pedipalp patella (Fig. 147) narrow, slightly angled at base, widening evenly into elongate cone. Lyriform fissures visible just anterior of base, located on a bulge, dorso-prolaterally on patella. Patella ratio: 3.09 (♀), 2.64 (♂).

Chela: (Figs. 142-147) Slightly darker than rest of pedipalp in both sexes, granular from stem to base of fingers. Both fingers smooth, distinctly longer than hand-stem complex. Dorsal depression present on chelal hand, resulting in bulge at base of fixed chelal finger. Prolateral surface slightly convex, ending in sharp inclusion at the base of chelal fingers, distinct to species. Fixed chela finger with eight trichobothria, movable chela finger with four. Both fingers long and narrow, curving to interior. Venom apparatus present on both fingers. Venom apparatus on female movable finger extends slightly past anterior edge of fixed chelal finger (Fig. 147). Trichobothria *eb* and *esb* situated just over one trichobothrial width from each other, located retrolaterally at base of fixed finger, while *ib* is located dorso-prolaterally, three trichobothrial widths distal of *esb*. Trichobothria *est* is located just short of one third finger length on retrolateral surface, with *isb* situated distally by three trichobothrial widths on opposite surface. Trichobothria *ist* located one third finger length from anterior finger edge, roughly in middle of prolateral surface; *it* located on dorsal surface, one sixth finger length from anterior finger edge, while *et* is situated just anterior on retrolateral surface. Four trichobothria on the movable finger positioned with *b* ventrally in line with *eb* and *sb* ventrally in line with *ib*. Trichobothria *st* positioned in line ventrally with *isb*, while *t* located roughly one quarter finger length from anterior edge of the movable finger. Chelal teeth acute and retrorse. Fixed finger with 43 teeth (♀), 39 (♂). Eight to nine small, closely spaced teeth just behind venom apparatus, followed by large accessory tooth (Fig. 151). Further teeth arranged roughly in two rows, decreasing in size to base of finger. Movable finger with 29 teeth (♀), 25 (♂). First tooth behind venom apparatus small, followed by large teeth that degenerate into small points. In females, first five basal teeth regenerate into acute and retrorse structures, basal three spaced tightly next to each other. Only slight teeth regeneration in males. Chela ratio: 3.74 (♀), 3.90 (♂).

Chelicera: Hand with five setae located as in Fig. 5. Fixed cheliceral finger with five teeth arranged as in Fig. 148. Female galea complex, with nine rami (Fig. 149). Male galea simple, with no rami (Fig. 150). Rallum composed of single blade in both sexes. Serrula exterior with 19 lamella (♀) or 18 (♂). Lamina exterior present in both sexes.

Coxae and legs: Pedipalp coxae same colour as trochanters, with distinct shoulder. Legs I-IV cream in both sexes, with leg coxae yellow to light-brown. Leg morphology standard and diplotarsate with regard to both leg I (Fig. 153) and leg IV (Fig. 154).



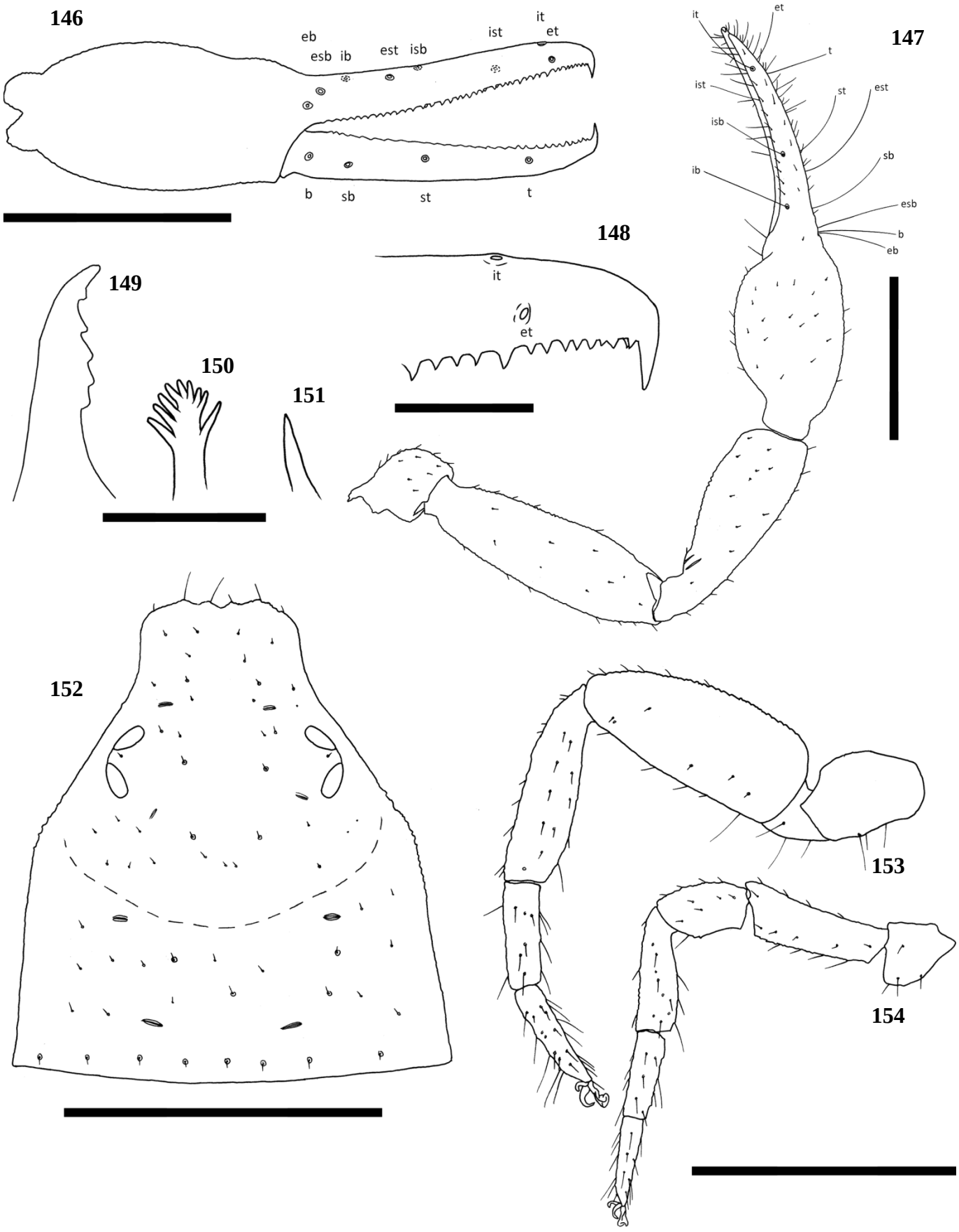
Figs. 142-145. Digital microscope photographs of *Afrogarypus purcelli* comb. nov. right chela: Female (**142**, **143**) and Male (**144**, **145**). **142**, **144**. Retrolateral view; **143**, **145**. Dorsal view. Scale bar: 1.00mm.

3.10.3 *Remarks*

Afrogarypus purcelli comb. nov. is transferred to the genus due to the presence of a concave dorsal depression on the chelal hand, a character shared by *A. robustus* comb. nov., *A. minutus* comb. nov. and *A. triangularis* comb. nov. These species, originally placed in *Geogarypus*, group within the *Afrogarypus* clade in the molecular phylogeny, supporting their transfer. According to Ellingsen's (1912) original description the type material for this species was housed with those for *A. triangularis* comb. nov. in the SAMC, though the types of neither species could be located during a visit to the museum. Failure to trace the types by the time this study is published will result in neotypes to be assigned. The outlying record from Louis Trichardt (Makhado) in Limpopo could possibly be a misidentification, as no specimens belonging to the species were found during fieldwork at the locality. Since no specimens were collected from the type locality, all identifications are regarded as tentative until new material can be collected.

3.10.4 *Additional material examined*

SOUTH AFRICA: *KwaZulu-Natal*: 1♀, Emangusi, Tembe Elephant Park, 26° 58'S, 32° 24'E, 112m a.s.l., Sand forest, leg. C.R. Haddad, 12.IV.2006 (WAM T81144).
Western Cape: 1♀, Arniston, Marcus Bay [34° 39'S, 20° 14'E], leg. H.A. Fry, 1900 (SAMC 13992); 8♂, Bredasdorp, De Hoop Nature Reserve, 34° 29'S, 20° 31'E, 26m a.s.l., Coastal Fynbos, Leaf litter sifting, leg. J.A. Neethling & C. Luwes, 24.XII.2013 (NMBA P00189); 1♂, Same locality, Koppie Alleen, 34° 28'S, 20° 30'E, 53m a.s.l., Rocky shore, leg. C.R. Haddad, 10.IV.2004 (WAM T79012); 1♂, Same locality, Lekkerwater Road, 34° 24'S, 20° 33'E, 134m a.s.l., Grassland, leg. C.R. Haddad,



Figs. 146-154. *Afrogarypus purcelli* comb. nov. **146-149**, **151-154**. Female; **150**. Male. **146**. Right chela, retrolateral view; **147**. Right pedipalp, dorsal view; **148**. Chelicera movable finger, dorsal view; **149**, **150**. Galea; **151**. Right chela fixed finger, anterior teeth arrangement; **152**. Carapace, dorsal view; **153**. Right leg IV, prolateral view; **154**. Right leg I, prolateral view. Scale bars: Figs. 146, 147, 152-154: 0.50mm; Fig. 151: 0.10mm; Figs: 148-150. 0.05mm.

26.IX.2007 (WAM T86767); 2♂, Same locality, Potberg, 34° 22'S, 20° 32'E, leg. C.R. Haddad, 7.IV.2004 (WAM T79013).

3.10.5 *Additional material not examined*

SOUTH AFRICA: *Limpopo Province*: 93♀+♂, Louis Trichardt [Makhado], Mountain Top [23° 03'S, 29° 54'E], leg. R.F. Lawrence, II.1960 (examined by Beier 1964, deposited in NMZA).
Western Cape: 1♂, Bredasdorp, 7 Miles SW [34° 36'S, 19° 57'E], 30.XII.1950 (examined by Beier 1955); 1♀, Bredasdorp, De Hoop Nature Reserve, 20 Miles ENE, Windhoek farm [34° 27'S, 20° 24'E], 2.I.1951 (examined by Beier 1955).

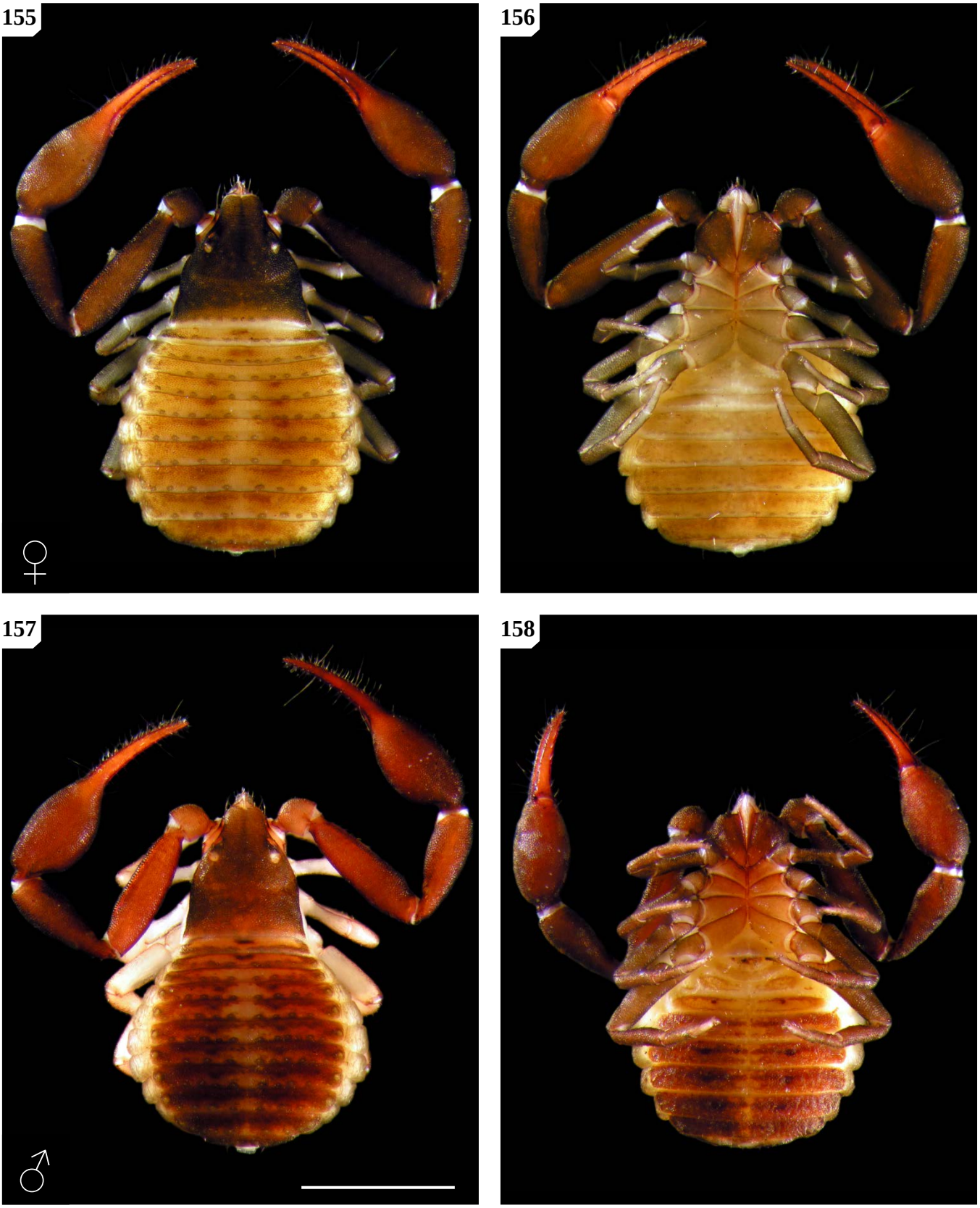
3.11 *Afrogarypus robustus* (Beier, 1947) **comb. nov.**

Geogarypus (*Geogarypus*) *robustus* Beier, 1947: 319, fig. 25 [**Lectotype** ♀ and **paralectotype**, ♂, here designated, South Africa, Western Cape, Cape Town, Newlands, Fernwood [33° 59'S, 18° 27'E], leg. R.F. Lawrence (SAMC B8519), examined; **Paratype** 1♀, South Africa, Western Cape, Cape Town, St James [34° 07'S, 18° 27'E], leg. R.F. Lawrence (SAMCB 8518), examined]; Beier, 1955: 301.

Geogarypus robustus (Beier, 1947): Harvey, 1986: 760; Harvey, 1991: 259, Dippenaar-Schoeman & Harvey, 2000: 93 [**comb. nov.**].

3.11.1 *Diagnosis*

Large species, pedipalpal femur length 1.07mm (♀), 0.95mm (♂), chela length (with stem) 1.54mm (♀), 1.48mm (♂), movable finger length 0.68mm (♀), 0.69mm (♂). Females can reach a length (cucullus to posterior abdominal margin) of 2.34mm, with males reaching 2.23mm. Carapace very dark, almost black, in females with medial furrow and posterior margin somewhat lighter in colour, while the male carapace is brown to red-brown (Figs. 155 & 157). Female pedipalps dark in colouration, with chela slightly lighter, male pedipalps are the same colour as the carapace. Concave depression present on dorsal surface of chelas. Abdominal tergites yellow to light-brown with dark patches in females, red-brown with dark patches and a medial cream coloured patch in males. Sternites well sclerotised in both sexes, yellow to light-brown throughout in females (Fig. 156), red-brown with dark patches and a cream-coloured medial line in males (Fig. 158). Pedipalp coxa same colour as carapace with a distinct shoulder, legs I-IV grey in females, while those of males from cream to dark brown.



Figs. 155-158. Digital microscope photographs of *Afrogarypus robustus* comb. nov., Female (**155**, **156**) and Male (**157**, **158**). **155**, **157**. Dorsal view; **156**, **158**. Ventral view. Scale bar: 1.00mm.

Afrogarypus robustus comb. nov. is particularly unique morphologically, with the abdomen being especially wide. Though easily distinguishable from all the other South African Geogarypidae under a microscope, they do superficially resemble *A. impressus* to the naked eye, but of course lack a well developed sulcus on the chelal hand. The species is the most sexually dimorphic geogarypid in South Africa with regard to colouration, with females taking on a two-tone appearance (dark carapace and pedipalps, light coloured abdomen and legs) and males being more uniformly coloured.

3.11.2 *Description*

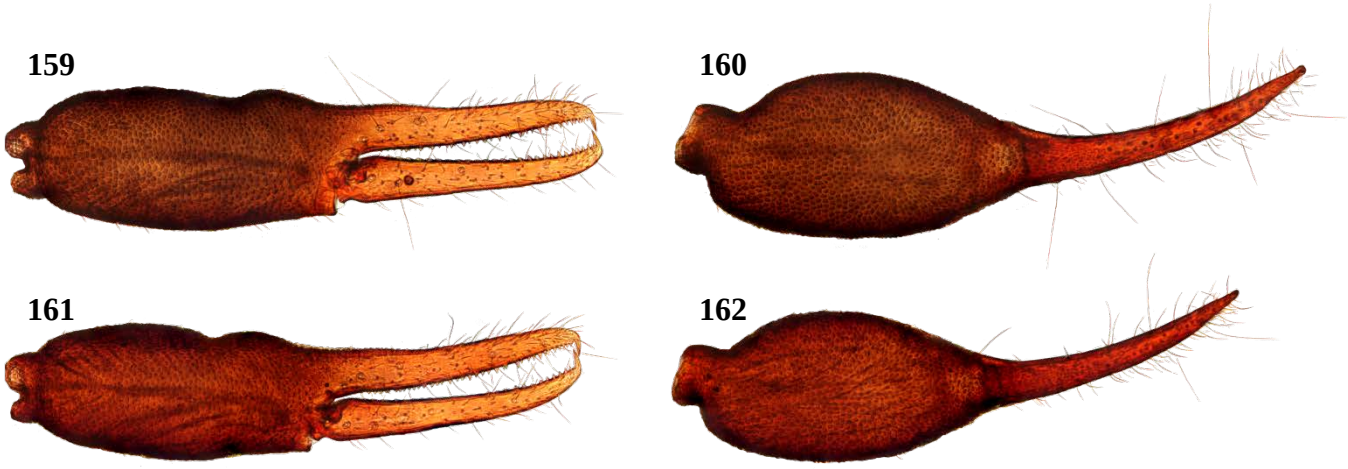
Carapace: Strongly triangular in females and sub-triangular in males, with narrow furrow posterior to the eyes (Fig. 169). Much broader than long in females, with carapace of males being either just as broad as long or slightly longer than broad. Very dark to almost black, with slightly lighter furrow and posterior carapace margin in females. Uniformly brown to red-brown in males. Uniformly granular in both sexes, heavily constricted anteriorly into cucullus, constriction beginning at medial furrow. Two pairs of corneate eyes situated on ocular tubercles, located ca. one third away from anterior edge. Four prominent setae located on anterior edge, row of nine setae, seated with rims, located on posterior margin. Numerous small setae present on carapace, some situated within rims. Carapace ratio: 0.86 (♀), 1.07 (♂).

Abdomen: Abdominal tergites yellow to light-brown with dark patches in females. Red-brown with dark patches and median cream patch in males. Tergites I and II with large median dark spot each. Tergite III without dark patches. Tergites IV–X with paired dark patches just lateral of midline, while tergites XI and XII lack patches. Setae of posterior setal rows of tergites, in both sexes, are situated on large pale plates with dark edges, making these plates distinctly visible. Sternites well sclerotised in both sexes, yellow to light-brown throughout (♀), while red-brown with dark patches and cream midline (♂). Pleural membrane wrinkled-placate, cream.

Pedipalp: Trochanter rounded, granular, slightly lighter than carapace. Small setae located on the dorsal and dorso-lateral sides. Apophysis located ventrally. Pedipalp femur (Fig. 164) same colour as trochanter, granular, narrow at base, widening evenly until just posterior of anterior margin where there is a sudden constriction. Femur ratio: 3.69 (♀), 3.52 (♂). Pedipalp patella (Fig. 164) same colour and granulation as femur, narrow, slightly angled at base, widening evenly into elongate cone. Lyriform fissures visible just anterior of base, located on bulge, dorso-prolaterally on patella. Patella ratio: 3.30 (♀), 3.20 (♂).

Chela: (Figs. 159-164) Somewhat lighter than rest of pedipalp in females, same colour as rest of pedipalp in males. Both sexes granular from stem to base of fingers. Both fingers smooth, distinctly

shorter than hand-stem complex. Dorsal depression present on chelal hand, resulting in bulge at base of fixed chelal finger. Fixed chela finger with eight trichobothria, movable chela finger with four. Both fingers long and narrow, curving to interior. Venom apparatus present on both fingers. Venom apparatus on female movable finger extends slightly past anterior edge of fixed chelal finger (Fig. 164). Trichobothria *eb* and *esb* situated just over one trichobothrial width from each other, located retrolaterally at base of fixed finger. Trichobothria *est* located retrolaterally within first third of fixed finger length, distal of *esb*, *ib* is situated almost exactly opposite, slightly more anterior on prolateral surface of finger. Trichobothria *isb* located roughly halfway along dorsal surface of finger, situated slightly prolaterally; *ist* located one third finger length from anterior finger edge, situated in middle of prolateral surface. Trichobothria *it* located approximately one quarter finger length from finger's anterior edge, situated on dorsal surface, *et* located anteriorly on retro-dorsal surface. Regarding the movable finger, *b* and *sb* are located on retrolateral surface, just anterior of finger base, separated by two trichobothrial widths. Trichobothria *st* located just short of halfway along movable finger. Trichobothria *t* located one quarter finger length from anterior finger edge, situated in line ventrally with *it*. Chelal teeth acute, some retrorse and curving back slightly. Fixed finger with 40 teeth (♀), 38 (♂). Four to five small, closely spaced teeth just behind venom apparatus, followed by large accessory tooth (Fig. 168). Further teeth arranged in two rows. Movable finger with 27 teeth (♀), 28 (♂). First two teeth behind venom apparatus small, followed by large teeth that degenerate into small points, basal tooth regenerated into an acute, wide, backwards facing point. Chela ratio: 3.58 (♀), 3.72 (♂).



Figs. 159-162. Digital microscope photographs of *Afrogarypus robustus* comb. nov. right chela: Female (**159**, **160**) and Male (**161**, **162**). **159**, **161**. Retrolateral view; **160**, **162**. Dorsal view. Scale bar: 1.00mm.

Chelicera: Hand with five setae located as in Fig. 5. Fixed cheliceral finger with five teeth arranged as in Fig. 165. Female galea complex, with nine rami (Fig. 166). Male galea simple, with no rami

(Fig. 167). Rallum composed of single blade in both sexes. Serrula exterior with 17 lamella (♀) or 16 (♂). Lamina exterior present in both sexes.

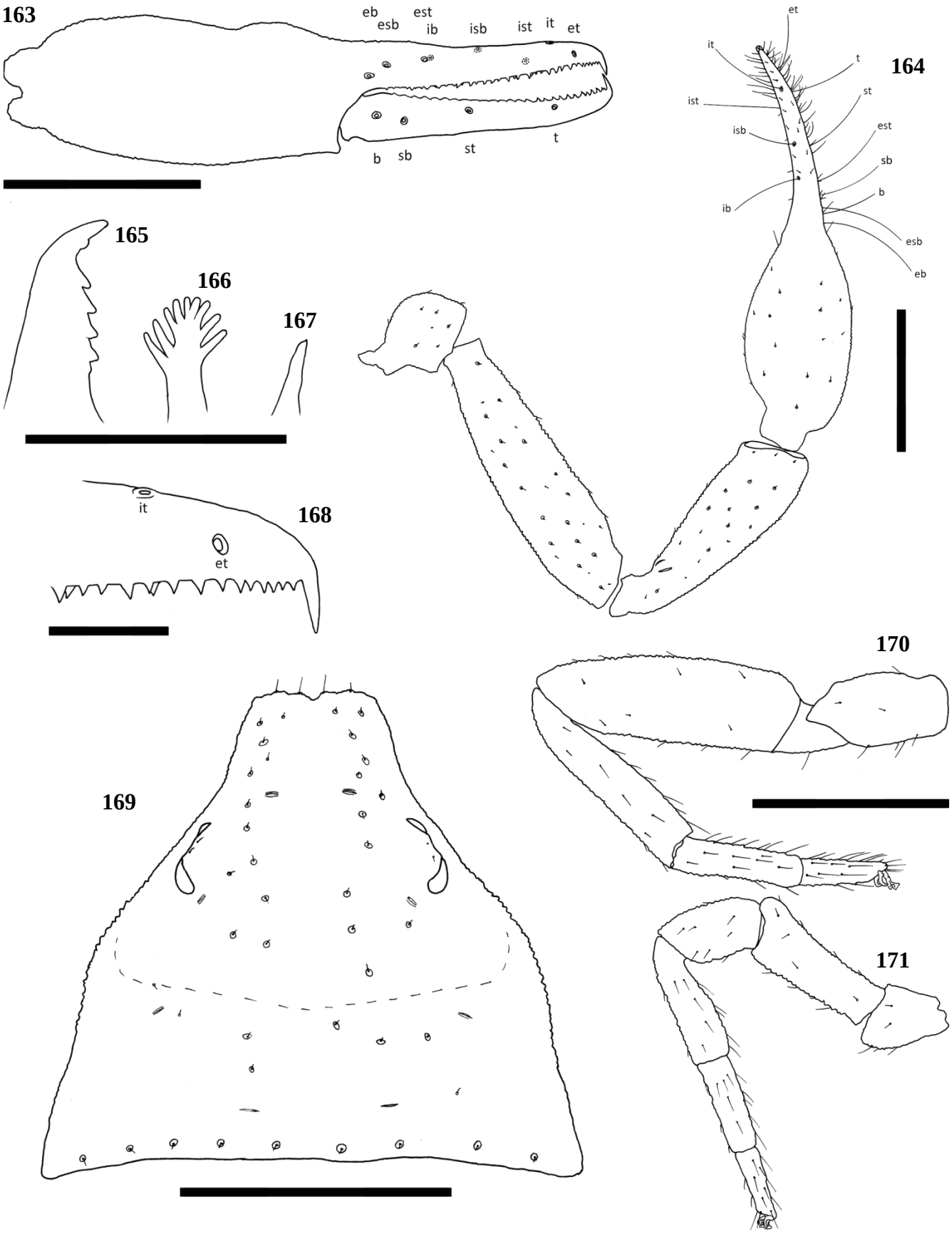
Coxae and legs: Pedipalp coxae same colour as carapace, with distinct shoulder. Legs I-IV grey in females, either cream or dark brown in males. Leg coxae yellow to light-brown in females, cream or red-brown in males. Leg morphology standard and diplotarsate with regard to both leg I (Fig. 170) and leg IV (Fig. 171).

3.11.3 *Remarks*

The largest geogarypid in South Africa, with *Geogarypus tectomaculatus* sp. nov. second. The concave depression on the chela was of particular interest to Beier (1947), and served one of the species' most distinguishing morphological characters. When examining the type material it was noted that Beier (1947) mentioned four adult specimens in the type series, though there were only two specimens in the vial, one female and one male, which are here designated as the lectotype and paralectotype, respectively. The female specimen was in good condition, though severely bleached; the male specimen on the other hand was severely damaged. The paratype was in good condition, though bleached as well. As with *A. purcelli* comb. nov., *A. minutus* comb. nov. and *A. triangularis* comb. nov., the species is here transferred to *Afrogarypus* due to the presence of a concave dorsal depression on the chelal hand and its grouping within the *Afrogarypus* clade in the molecular phylogeny.

3.11.4 *Additional material examined*

SOUTH AFRICA: *Western Cape*: 1 immature, Cape Town, Kirstenbosch National Botanical Gardens, 33° 59'S, 18° 26'E, 136m a.s.l., Cultured gardens, leg. J. Pryke, 2.VIII.2005 (WAM T85960); 1♀, Cape Town, Kirstenbosch National Botanical Gardens, Skeleton Gorge Trail, 33° 59'S, 18° 25'E, 359m a.s.l., Afromontane Forest, Leaf litter sifting, leg. J.A. Neethling, 11.XII.2012 (NMBA P00184); 2♀, 3♂, Same data as previous (lactic acid clearing and phylogenetic analysis); 1 immature, Cape Town, Table Mountain, 33° 58'S, 18° 26'E, 360m a.s.l., Disturbed Fynbos, leg. J. Pryke, 18.I.2007 (WAM T85958); 1♀, Same locality, Natwal Forest South, 34° 00'S, 18° 23'E, leg. J. Pryke, 11.I.2006 (WAM T85954); 1♀, Same locality, Natwal Forest South, 34° 00'S, 18° 25'E, 322m a.s.l., Exotic forest, leg. J. Pryke, 3.VII.2006 (WAM T85955); 1♀, 1♂, Same locality, Natwal Forest South, 34° 00'S, 18° 23'E, leg. J. Pryke, 13.X.2006 (WAM T85956).



Figs. 163-171. *Afrogarypus robustus* comb. nov. **163-166**, **168-171**. Female; **167**. Male. **163**. Right chela, retrolateral view; **164**. Right pedipalp, dorsal view; **165**. Chelicera movable finger, dorsal view; **166**, **167**. Galea; **168**. Right chela fixed finger, anterior teeth arrangement; **169**. Carapace, dorsal view; **170**. Right leg IV, prolateral view; **171**. Right leg I, prolateral view. Scale bars: Figs. 163, 164, 169-171: 0.50mm; Figs 165-168: 0.10mm.

3.11.5 *Additional material not examined*

SOUTH AFRICA: *Western Cape*: 1♂, Cape Town, Table Mountain, Wynberg Hollow gorge [33° 58'S, 18° 25'E], 730m a.s.l., 18.XII.1950 (examined by Beier 1955).

3.12 *Afrogarypus subimpressus* (Beier, 1955)

Geogarypus (*Afrogarypus*) *subimpressus* Beier, 1955: 302, fig. 21 right, 22 [**Holotype** ♂, South Africa, Western Cape, Simon's Town, Cape Point Nature Reserve [34° 21'S, 18° 28'E], unknown collector, 10.XII.1950, deposited in NMZA, not examined; **Paratypes** 2♂, 2 immatures, Same data as previous, deposited in NMZA, not examined].

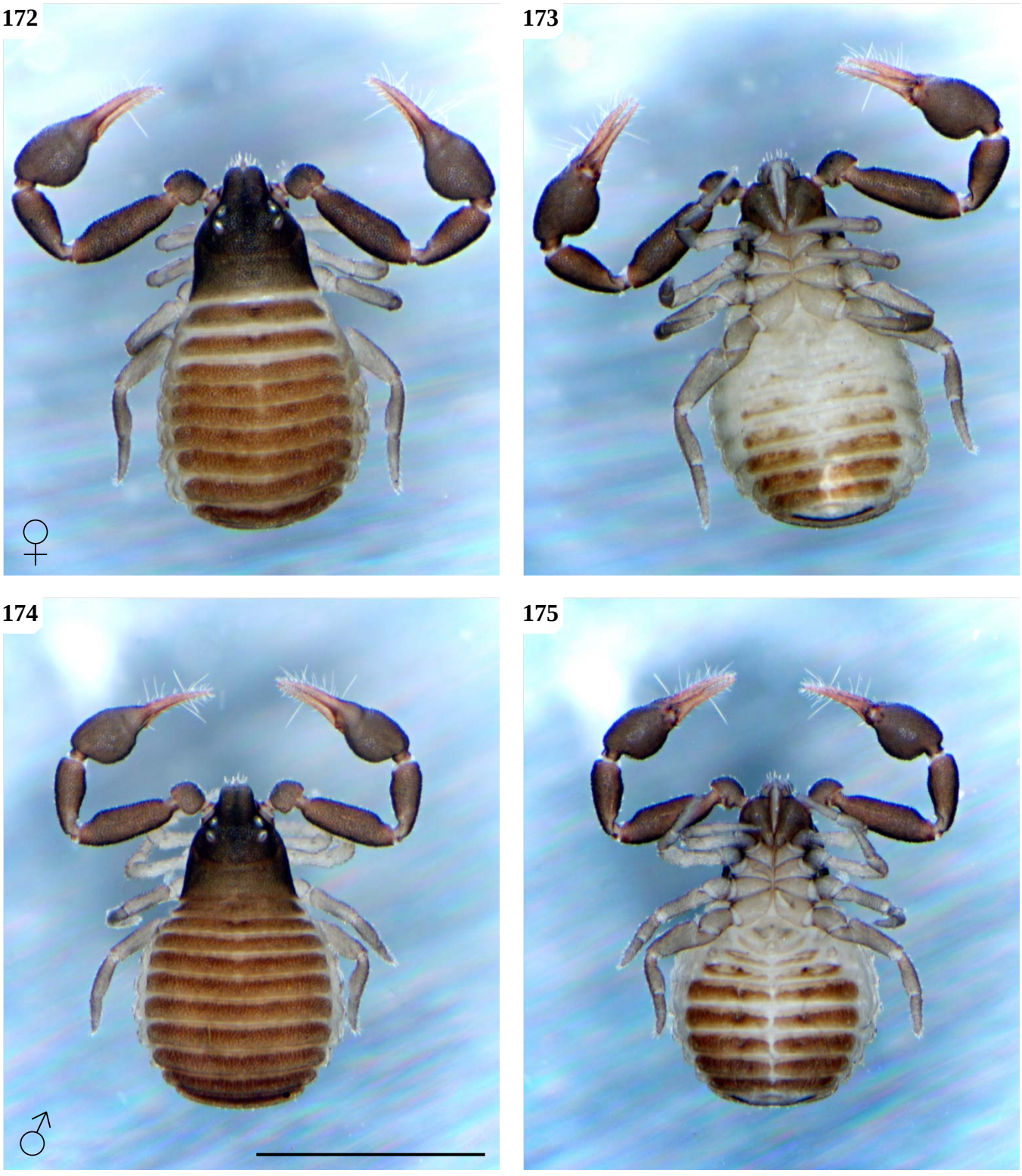
Geogarypus subimpressus (Beier, 1955), Beier, 1964: 60.

Afrogarypus subimpressus (Beier, 1955), Harvey, 1986: 758; Harvey, 1991: 251; Dippenaar-Schoeman & Harvey, 2000: 93.

3.12.1 *Diagnosis*

Small species, pedipalpal femur length 0.55mm (♀), 0.44mm (♂), chela length (with stem) 0.75mm (♀), 0.61mm (♂), movable finger length 0.34mm (♀), 0.29mm (♂). Females can reach a total length (cucullus to posterior abdominal margin) of 1.63mm, with males reaching up to 1.46mm. Carapace dark brown, with slightly lighter posterior in both sexes (Figs. 172 & 174). All pedipalpal segments same colour as carapace. Well developed, broad sulcus present on dorsal surface of chelal hand. Abdominal tergites of both sexes uniformly brown, with very faded dark patches. Sternites of females weakly sclerotised anteriorly, becoming more sclerotised posteriorly (Fig. 173), male sternites well sclerotised throughout (Fig. 175). Pedipalp coxae same colour as carapace and possessing a distinct shoulder, legs I-IV pale grey, with the remaining coxa pale brown in colour.

Somewhat resembling *Afrogarypus castigatus* sp. nov. in terms of its compact build and colouration, *A. subimpressus* can easily be distinguished by possessing the normal 8/4 trichobothria ratio, diplotarsate front legs and the presence of a well developed sulcus on the dorsal surface of its chela. The dorsal sulcus can be compared with the one found in *A. megamolaris* sp. nov. in that it is broader and more shallow that those found in *A. excelsus* stat. nov. and *A. impressus*. *Afrogarypus subimpressus* can be distinguished from *A. megamolaris* sp. nov. with regards to its carapace ratio, which is lower than 1 (thus the carapace is broader than long) as well as possessing a prolateral chelal hand surface that is strongly convex, while that in *A. megamolaris* sp. nov. is relatively straight.



Figs. 172-175. Digital microscope photographs of *Afrogarypus subimpressus*, Female (**172**, **157**) and Male (**174**, **175**). **172**, **174**. Dorsal view; **173**, **175**. Ventral view. Scale bar: 1.00mm.

3.12.2 *Description*

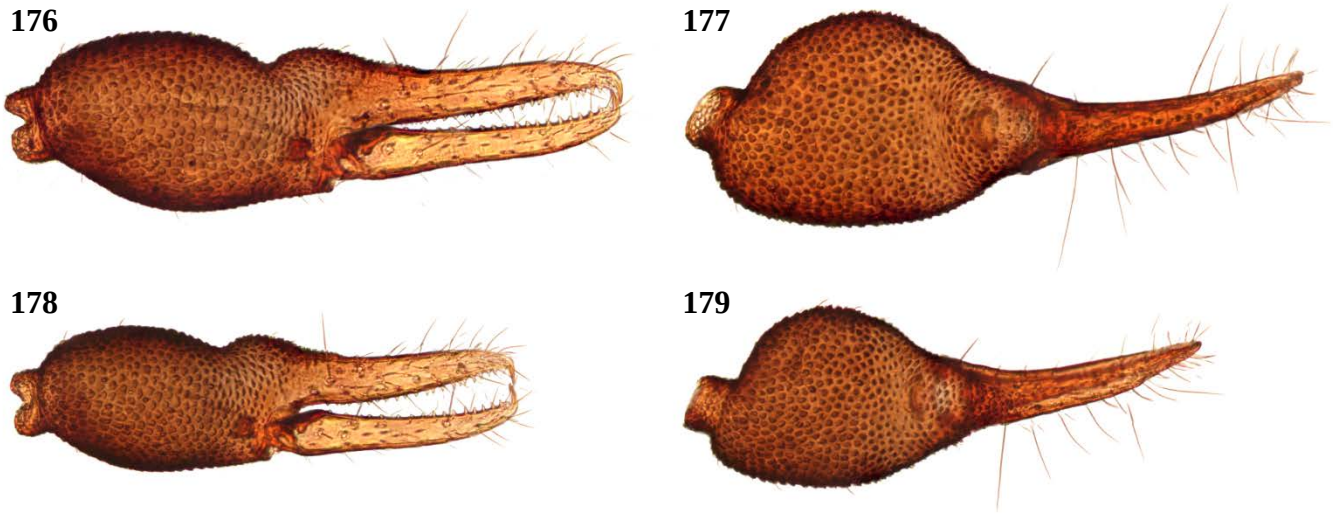
Carapace: Strongly sub-triangular, narrow furrow posterior to the eyes (Fig. 186). Uniformly dark brown with slightly lighter posterior margin in both sexes. Uniformly granular, heavily constricted anteriorly into cucullus, constriction beginning at the medial furrow. Two pairs of corneate eyes situated on ocular tubercles, located ca. one third away from the anterior edge. Four prominent setae located on anterior edge, multiple setae located on posterior margin. Numerous small setae present on carapace. Carapace ratio: 0.89 (♀), 0.97 (♂).

Abdomen: Tergites uniformly brown, faint dark patches present in both sexes, granular. Tergites I and II with large median dark brown spot each. Tergite III without dark patches. Tergites IV-X with paired, faint dark patches situated laterally of the midline. Tergites XI and XII without patches. Sternites dark brown in both sexes. Weakly sclerotised anteriorly in females, uniformly sclerotised in males. Pleural membrane wrinkled-placate, pale.

Pedipalp: Trochanter rounded in shape, uniformly dark brown, granular, small setae scattered over entire surface, except the stem. Apophysis located ventrally. Pedipalp femur (Fig. 181) dark brown, granular. Stem very narrow, widening quickly to form the base, widens only slightly distally before constricting again at the end. Femur ratio: 3.40 (♀), 3.15 (♂). Pedipalp patella (Fig. 181) dark brown and granular. Narrow, sharply angled at base, widening quickly into cone. Lyriform fissures visible just anterior to the base, located on bulge, dorso-prolaterally on patella. Patella ratio: 2.56 (♀), 2.68 (♂).

Chela: (Figs. 176-181) Uniformly dark brown, granular from stem to base of fingers. Both fingers smooth, curving very slightly to interior. Well developed, broad, shallow sulcus present on dorsal surface of chelal hand. Chela hand strongly convex on prolateral edge, retrolateral edge mostly straight. Fixed chela finger with eight trichobothria, movable chela finger with four. Fingers just shorter than hand-stem complex, venom apparatus present on both. Trichobothria *eb, esb* and *est* located retrolaterally in diagonal line at base of fixed chela finger. Trichobothria *eb* and *esb* situated ca. one trichobothrial width from each other, *est* situated two trichobothrial widths from *esb*. Trichobothria *ib* situated prolaterally, just anterior of *esb*; *isb* located prolaterally, just anterior of *est.* Trichobothria *ist* situated prolaterally and just over one third away from anterior edge of fixed finger; *it* located one quarter finger length from anterior edge, situated dorsally; *et* located retrolaterally, just anterior of *it*. Trichobothria *b, sb* and *st* located in triangular pattern just anterior of finger base, situated retrolaterally on finger, *b* situated in line vertically with *eb*. Trichobothria *t* located ca. one quarter from anterior edge of movable finger, halfway between *ist* and *et.* Trichobothria divided in

proximal and distal group, proximal group consisting of *eb*, *esb*, *ib*, *esb*, *isb*, *b*, *sb* and *st*, distal group containing *ist*, *it*, *et* and *t*. Chelal teeth acute, slightly retrorse, beginning large anteriorly and gradually decreasing in size to base of finger. Fixed finger with 27 teeth (♀), 24 (♂). First two teeth just before the venom apparatus grouped close together, small (Fig. 182). Further teeth slightly to distinctly retrorse, acute, arranged roughly in two rows. Movable finger with 18 teeth (♀), 17 (♂). The first two teeth following venom apparatus situated on raised ridge. Rest of teeth quickly increase in size posteriorly, distinctly retrorse, further teeth gradually decreasing in size, spaced further apart. Chela ratio: 2.79 (♀), 2.68 (♂).



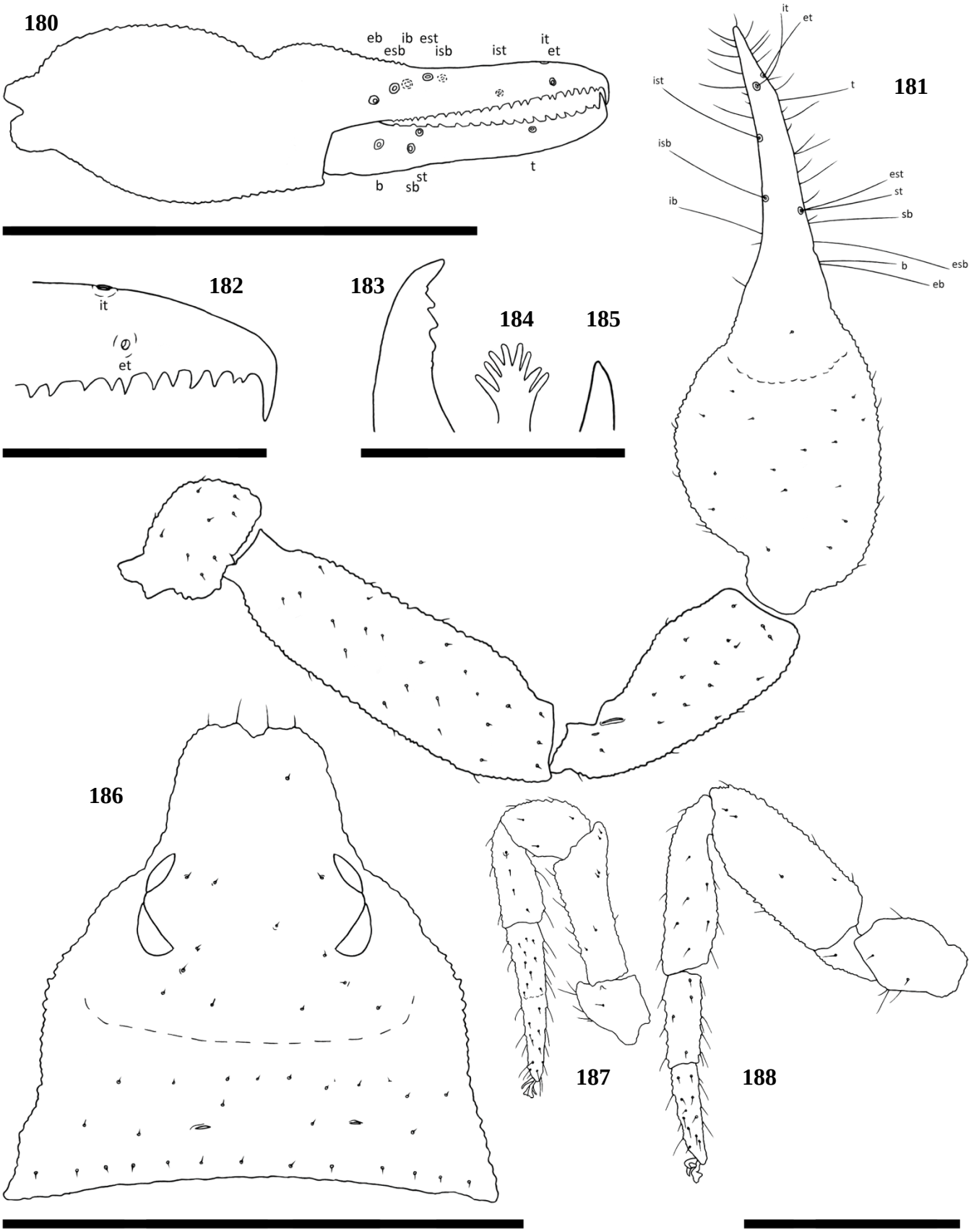
Figs. 176-179. Digital microscope photographs of *Afrogarypus subimpressus* right chela: Female (**176**, **177**) and Male (**178**, **179**). **176**, **178**. Retrolateral view; **177**, **179**. Dorsal view. Scale bar: 1.00mm.

Chelicera: Hand with five setae situated as in Fig. 5. Fixed cheliceral finger with five teeth arranged as in Fig. 183. Female galea complex, with eight rami in a fan shape (Fig. 184). Male galea simple, no rami (Fig. 185). Rallum composed of single blade in both sexes. Serrula exterior with 15 lamella (♀) or 12 (♂). Lamina exterior present in both sexes.

Coxae and legs: Pedipalp coxae dark brown, possessing distinct shoulder. Legs I-IV light grey. Joint between metatarsus and tarsus of legs I and II almost completely fused, immovable, slight fusion line visible (Fig. 187). Leg pairs III and IV diplotarsate (Fig. 188).

3.12.3 *Remarks*

When Beier (1955) described the species, it was only known from the Cape Peninsula, though it has since been shown to have a much greater distribution. Due to the presence of a well developed



Figs. 180-188. *Afrogarypus subimpressus*. **180-184**, **186-188**. Female; **185**. Male. **180**. Right chela, retrolateral view; **181**. Right pedipalp, dorsal view; **182**. Right chela fixed finger, anterior teeth arrangement; **183**. Chelicera movable finger, dorsal view; **184**, **185**. Galea; **186**. Carapace, dorsal view; **187**. Right leg I, prolateral view; **188**. Right leg IV, prolateral view. Scale bars: Figs. 180, 181, 186-188: 0.50mm; Figs. 182-185: 0.10mm.

dorsal sulcus, then only known from *Afrogarypus impressus*, and owing to its diminutive size, Beier opted to name the species *A. subimpressus*, combining both the size and relationship to *A. impressus* in one name. The species has been in *Afrogarypus* since its description, though then *Afrogarypus* was still a sub-genus of *Geogarypus*. It was consequently retained in *Afrogarypus* in the revision done by Harvey (1986), and given its current status as *Afrogarypus subimpressus*.

3.12.4 *Additional material examined*

SOUTH AFRICA: *Northern Cape*: 1♂, Hanover, 31° 15'S, 24° 24'E, leg. J.M. Waldock, 17.IV.2001 (WAM T67018).
Western Cape: 1♀, 3♂, Beaufort West, Karoo National Park, Klipspringer Pass, 32° 19'S, 22° 27'E, 1126m a.s.l., leg. J.A. Neethling, 14.XI.2013 (NMBA P00175); 2♂, 1 immature, Cape Town, Table Mountain, 33° 58'S, 18° 23'E, leg. J. Pryke, 17.X.2005 (WAM T85951, T85952 & T85953); 1 Deutonymph, Knysna, Brenton-on-Sea [34° 03'S, 22° 59'E], leg. H.G. Robertson, 23.XI.1998 (SAMC ENW-COO5851); 2♀, 3♂, Simon's Town, Cape Point Nature Reserve, Cape Point, 34° 21'S, 18° 29'E, 118m a.s.l., leg. J.A. Neethling, 26.IV.2013 (NMBA P00174); 3♀, 3♂, Same data as previous (morphological dissection and phylogenetic analysis); 1♀, 2♂, Same locality, Olifantsbos, 34° 15'S, 18° 22'E, 9m a.s.l., leg. J.A. Neethling, 12.XII.2012 (NMBA P00176); 1♀, 2 Deutonymphs, Same locality, Olifantsbos, 34° 15'S, 18° 23'E, leg. H.G. Robertson, X.1998 (SAMC ENW-COO 5432); 3♀, 3♂, 2 Deutonymphs, Same locality, Smitswinkelvlakte [34° 16'S, 18° 25'E], leg. H.G. Robertson, X.1998 (SAMC ENW-COO 5404, 5407, 5408 & 5436).

3.12.5 *Additional material not examined*

SOUTH AFRICA: *Unknown*: 2♀, 1♂, No collection information (examined by Beier 1964, deposited in NMZA).

3.13 *Afrogarypus triangularis* (Ellingsen, 1912) **comb. nov.**

Garypus minutus var. *triangularis* Ellingsen, 1912: 110 [**Holotype** Unknown gender, South Africa, Eastern Cape, King William's Town, Izeli [32° 48'S, 27° 23'E], No further data, collection unknown, not examined; **Paratypes** 1 specimen, Frankfort, Frankfort Hill [32° 43'S 27° 27'E], No further data, collection unknown, not examined; 1 specimen, Butterworth, Blythswood, Bushman's Rock [32°13'S, 27°58'E], No further data, collection unknown, not examined; 2 specimens, Bloemfontein, Naval Hill [29° 06'S, 26° 14'E], No further data, collection unknown, not examined].
Geogarypus (*Geogarypus*) *minutus* var. *triangularis* (Ellingsen, 1912): Beier, 1932b: 23.

Geogarypus triangularis (Ellingsen, 1912): Roewer, 1937: 269; Beier, 1964: 59, fig. 20; Harvey, 1986: 760; Harvey, 1991: 260; Dippenaar-Schoeman & Harvey, 2000: 93 [**comb. nov.**].

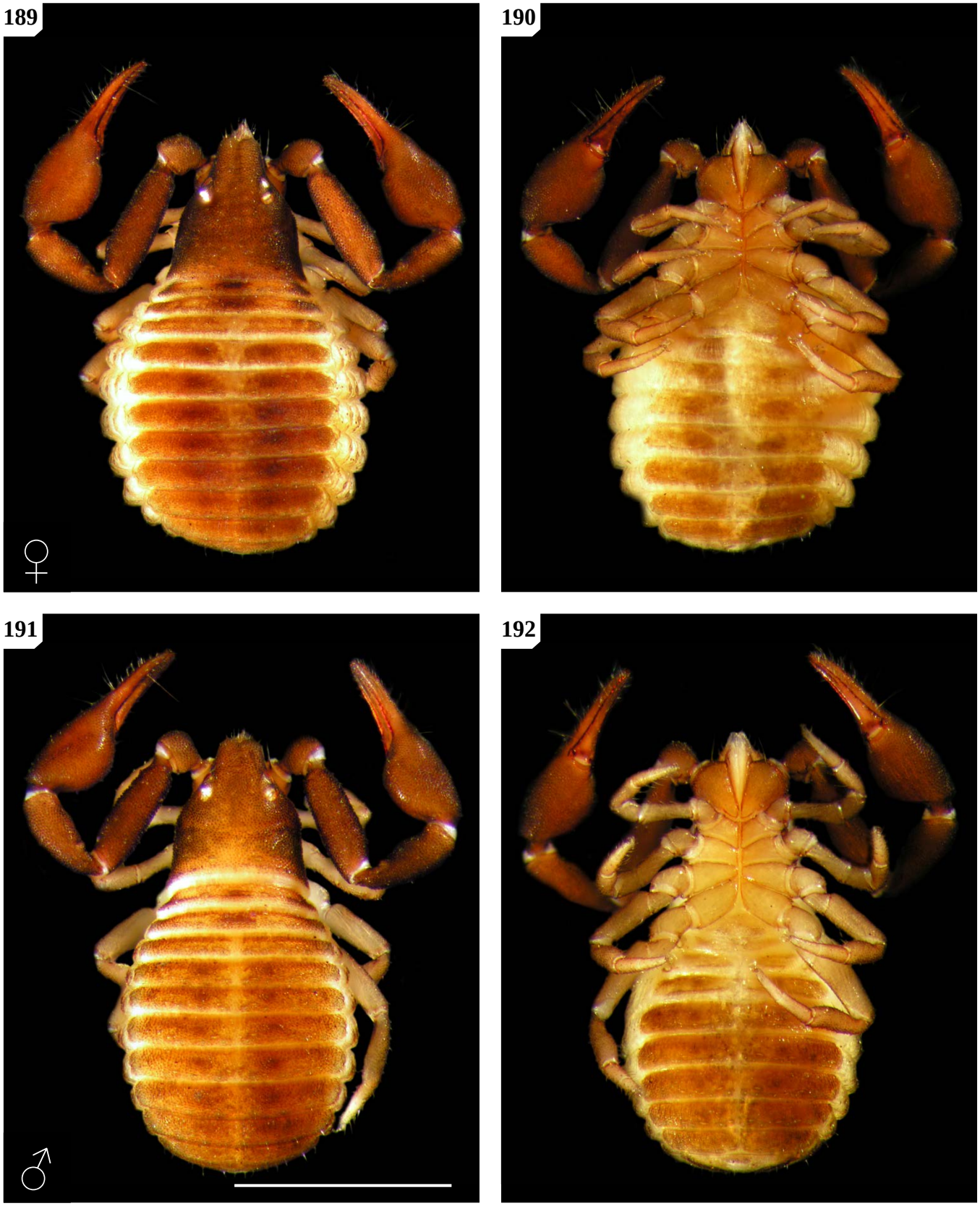
3.13.1 *Diagnosis*

Medium species, pedipalpal femur length 0.65mm (♀), 0.59mm (♂), chela length (with stem) 0.98mm (♀), 0.89mm (♂), movable finger length 0.44mm (♀), 0.43mm (♂). Females can reach a total length (cucullus to posterior abdominal margin) of 2.10mm, with males reaching up to 2.08mm. Carapace uniform dark brown in females, brown with medial furrow and posterior margin light brown in males (Figs. 189 & 191). All pedipalp segments brown in colour. Concave depression present on dorsal surface of chelas. Abdominal tergites mostly brown with dark patches, abdominal sternites light brown and weakly sclerotised (♀) (Fig. 190), light brown and well sclerotised throughout (♂) (Fig. 192). Males with distinct lateral schlerites between tergites and sternites. Pedipalp coxa brown in colour with distinct shoulder, legs I-IV as well as remaining coxa tan to pale yellow. Both sexes are quite variable in size, though males from a particular location still tend to be smaller than the females from the same area.

Smaller *A. triangularis* comb. nov. specimens closely resemble *A. minutus* comb. nov. with regards to size and coloration, but can still be distinguished by the triangular shape of the chela hand (only somewhat convex or rectangular in *A. minutus* comb. nov.). Females can furthermore be identified by the differences in galea structure, while adult males can easily be differentiated by the presence of lateral sclerites on the abdomen. Together with *Afrogarypus castigatus* sp. nov., they are the only known South African geogarypids that possess lateral abdominal sclerites, a trait they share with members of the Feaellidae. In both *A. triangularis* comb. nov. and *A. castigatus* sp. nov. only mature males have these sclerites present.

3.13.2 *Description*

Carapace: Strongly sub-triangular, narrow furrow posterior to the eyes (Fig. 201). Uniformly dark brown in females, overall brown with light-brown medial furrow and posterior margin in males. Uniformly granular, heavily constricted anteriorly into cucullus, constriction beginning at the medial furrow. Two pairs of corneate eyes situated on ocular tubercles, located ca. one third away from anterior edge. Four prominent setae located on anterior edge, row of 12 setae, seated within rims, located on posterior margin. Numerous small setae present on carapace. Carapace ratio: 1.03 (♀), 1.02 (♂).



Figs. 189-192. Digital microscope photographs of *Afrogarypus triangularis* comb. nov., Female (**189**, **190**) and Male (**191**, **192**). **189**, **191**. Dorsal view; **190**, **192**. Ventral view. Scale bar: 1.00mm.

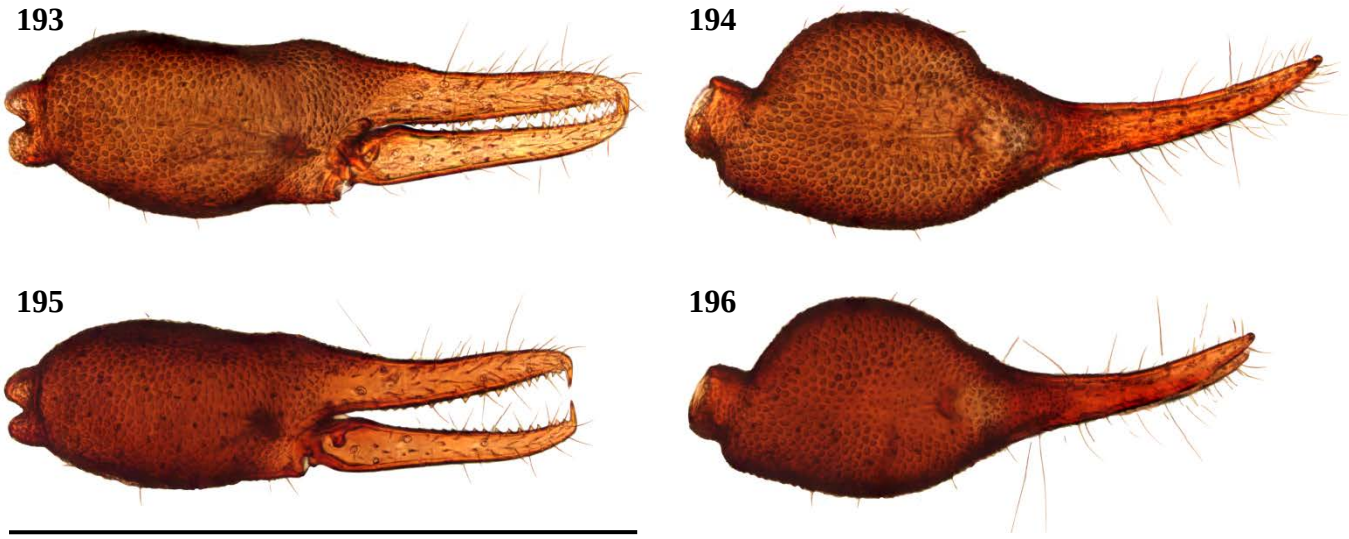
Abdomen: Abdominal tergites granular, brown with dark patches in both sexes. Tergites I and II with large medial dark spot each. Tergite III without dark patches. Tergites IV-X with paired, faint dark patches just lateral of midline. Tergites XI and XII without dark patches. Sternites light brown, weakly sclerotised (♀). Darker brown, well sclerotised throughout (♂). Pleural membrane wrinkled-placate, males with 17 lateral sclerites (Fig. 202) on each side of abdomen, arranged as follows: one sclerite beneath tergite III, two beneath tergite IV, three beneath tergite V, two beneath tergite VI, three beneath both tergites VII and VIII, two beneath tergite IX , one beneath tergite X.

Pedipalp: Trochanter rounded in shape, granular, uniformly dark brown. Small setae scattered over entire surface, except the stem. Apophysis located ventrally. Pedipalp femur (Fig. 198) dark brown and granular. Narrower at base, widening evenly before constricting again at end. Femur ratio: 3.29 (♀), 3.28 (♂). Pedipalp patella (Fig. 198) dark brown and granular. Narrow, sharply angled at base, widening quickly into cone shape. Lyriform fissures visible just anterior of base, located on bulge, dorso-prolaterally on patella. Patella ratio: 2.55 (♀), 2.53 (♂).

Chela: (Figs. 193-198) Uniformly brown, granular from stem to base of fingers. Both fingers smooth. Concave depression present on dorsal surface of chela, resulting in bulge at base of fixed finger. Chela hand strongly convex on prolateral edge, blunt constriction just posterior to base of fingers giving chela somewhat triangular appearance. Fixed chela finger with eight trichobothria, movable chela finger with four, both fingers narrow, curving slightly to interior. Fingers just shorter than hand-stem complex. Venom apparatus present on both fingers. Trichobothria *eb*, *esb* and *est* located retrolaterally in diagonal line at base of fixed chela finger, situated ca. one trichobothrial width from each other. Trichobothria *ib* situated dorso-prolaterally, nearly exactly opposite of *est*; *isb* located dorso-prolaterally, one trichobothrial width forward of *ib.* Trichobothria *ist* situated prolaterally, one third away from anterior edge of fixed finger; *it* located one quarter finger length from anterior edge, situated dorsally; *et* located retrolaterally and distally from *it*, nearly equidistant from *it* as *ist* from *it*. Trichobothria *b*, *sb* and *st* located in triangular pattern just anterior to finger base, situated retrolaterally on finger, *b* situated in line vertically with *eb*. Trichobothria *t* located ca. one third from the anterior edge of movable finger, in line vertically with *ist*. Trichobothria can be divided into two groups, with proximal group consisting of *eb*, *esb*, *ib*, *esb*, *isb*, *b*, *sb* and *st*, distal group containing *ist*, *it*, *et* and *t*. Chelal teeth acute, mostly retrorse, some curving back. Fixed finger with 22 teeth (♀), 19 (♂). First tooth just before venom apparatus not retrorse, almost pointing anteriorly (Fig. 203). Further teeth slightly to distinctly retrorse and acute, arranged roughly in two rows. Movable finger with 16 teeth (♀), 18 (♂). First five teeth following the venom apparatus in females, gradually increase in size, rest of teeth gradually decrease in size, spacing further apart. In males, first 11 teeth roughly same size, remaining seven teeth being reduced to acute points. Chela ratio: 2.80 (♀), 2.74 (♂).

Chelicera: Hand with five setae as in Fig. 5. Fixed cheliceral finger with five teeth arranged as in Fig. 204. Female galea complex with nine rami, basal pair situated small distance from remaining group as in Fig. 205. Male galea simple, no rami (Fig. 206). Rallum composed of single blade in both sexes. Serrula exterior with 16 lamella (♀) or 13 (♂). Lamina exterior present in both sexes.

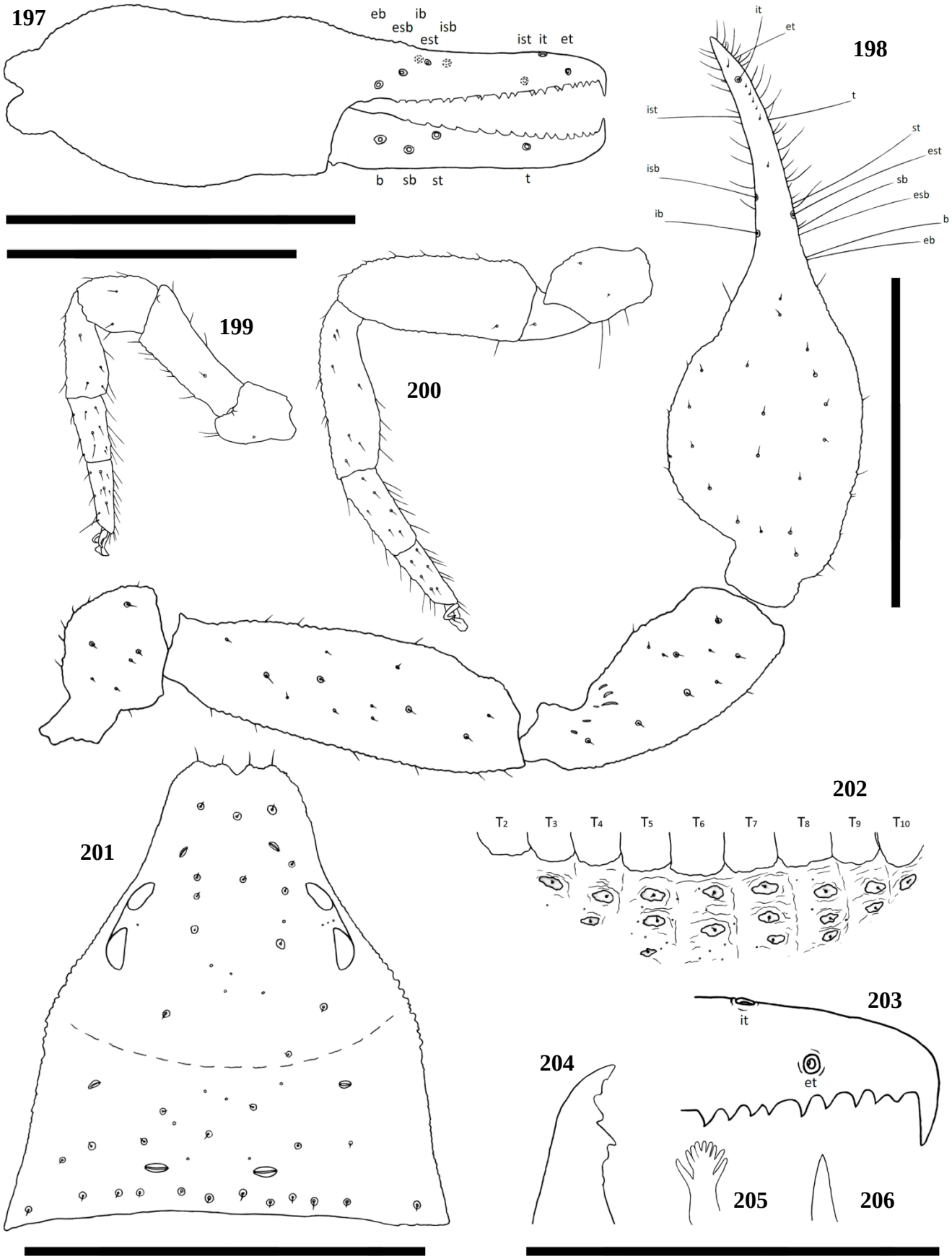
Coxae and legs: Pedipalp coxae brown in colour, shoulder distinct. Multiple long setae present along inner medial ridges. Coxae of legs I-IV, as well as all leg segments, tan. Trochanters of legs I and II compact and small, larger and more elongate on legs III and IV. Femora of legs I and II longer than patellae and tibiae respectively (Fig. 199). Metatarsi and tarsi not fused, joint movable. Tarsal claws simple, curved, arolium much longer than claws, not divided. Femur-patella joint of leg IV immovable, tibia mostly straight (Fig. 200), metatarsi and tarsi not fused, joint movable. Claws and arolium similar to those of legs I-III.



Figs. 193-196. Digital microscope photographs of *Afrogarypus triangularis* comb. nov. right chela: Female (**193**, **194**) and Male (**195**, **196**). **193**, **195**. Retrolateral view; **194**, **196**. Dorsal view. Scale bar: 1.00mm.

3.13.3 *Remarks*

Originally regarded as a variant of *A. minutus* comb. nov. by Ellingsen (1912) due to their similarities, he separated *A. triangularis* comb. nov. due to its distinctive triangular chela. The species then continued to hold its variant status until it was given a proper redescription by Beier (1964), where he elevated it to full species status as *Geogarypus triangularis*. As the species possesses a concave dorsal depression on the chelal hand and groups within the *Afrogarypus* clade in the molecular phylogeny, similar to *A. purcelli* comb. nov., *A. minutus* comb. nov and *A. robustus* comb. nov., its transfer to *Afrogarypus* is proposed here.



Figs. 197-206. *Afrogarypus triangularis* comb. nov. **197-201**, **203-205**. Female; **202**, **206**. Male. **197**. Right chela, retrolateral view; **198**. Right pedipalp, dorsal view; **199**. Leg I, prolateral view; **200**. Leg IV, prolateral view; **201**. Carapace, dorsal view; **202**. Male abdominal pleural sclerites; **203**. Chela fixed finger, anterior teeth arrangement; **204**. Chelicera movable finger, dorsal view; **205**, **206**. Galea. Scale bars: Figs. 197-201: 0.50mm; Figs. 203-206: 0.10mm.

The original variant was identified from a group of nine immature specimens that Ellingsen received from Reverend Robert Godfrey's collection, originally housed within the SAMC. He unfortunately never mentions the gender or the depository numbers of the variants, only stating the sampling locations of the nine specimens. After extensive searching within the collections housed in the SAMC, neither the type specimens for *A. triangularis* comb. nov., nor those of *A. purcelli* comb. nov. (also originally housed in the museum) could be located. Even after collaborated searches in prominent museum collections overseas, the type specimens of these two species could not be located. However, adequate material has been collected from the vicinity of the type locality to verify the status and identity of the species. Failure to track down the types by the time this study is published, neotypes will be assigned. The Bloemfontein, Free State, record is suspected to be a misidentification, as no specimens of the species could be located on Naval Hill and surrounding areas, even after multiple attempts by the author and Dr. L.N. Lotz of NMBA.

3.13.4 *Additional material examined*

SOUTH AFRICA: *Eastern Cape*: 1♀, Burgersdorp [30° 59'S 26° 19'E], leg. R.F. Lawrence, X.1944 (NMSA 677); 3♀, 4♂, Cradock, Mountain Zebra National Park, bushveld, 32° 13'S, 25° 28'E, 1240m a.s.l., leg. J.A. Neethling & C. Luwes, 29.III.2012 (NMBA P00187); 13 Adults, Grahamstown, Grey Dam [33° 19'S 26° 31'E], leg. J. Hewitt, 3.X.1918 (AMG Slide); 2 Adults, Same locality, leg. J. Hewitt, XII.1918 (AMG Slide); 11♀, 8♂, Hogsback, Hogsback Arboretum, invaded forest, 32° 35'S, 26° 56'E, 1247m a.s.l., leg. J.A. Neethling & C. Luwes, 2.IV.2012 (NMBA P00182); 7♀, 6♂, King William's Town, Mount Coke State Forest, indigenous forest, 32° 59'S, 27° 28'E, 420m a.s.l., leg. J.A. Neethling, 30.XI.2013 (NMBA P00183); 2♀, 2♂, Same data as previous (morphological dissection and phylogenetic analysis).

3.13.5 *Additional material not examined*

SOUTH AFRICA: *Eastern Cape*: 1♀, Grahamstown, Coldsprings, Southern slope [33° 06'S, 26° 41'E], V.1920 (examined by Beier 1964, deposited in NMZA); 1♀, Port Elizabeth [33° 56'S, 25° 34'E], leg. F. Emden (examined by Beier 1964, deposited in NMZA).
Unknown: 7♀, 5♂, No collection information, (examined by Beier 1964, deposited in NMZA).

3.14 *Geogarypus deceptor* sp. nov.

Holotype: ♀, SOUTH AFRICA, KwaZulu-Natal, St. Lucia, iSimangaliso Wetland Park, Cape Vidal, 28° 08'S, 32° 33'E, 62m a.s.l., Coastal forest, Leaf litter sifting, leg. J.A. Neethling & C. Luwes, 12.V.2012 (NMBA P00221). **Paratypes:** 1♀, 2♂, Same data as holotype (NMBA P00222).

3.14.1 *Etymology*

The Latin noun *deceptor* means deceiver and refers specifically to all the examined museum exemplars, which either lacked a species level identification, or were misidentified as *Geogarypus olivaceus*.

3.14.2 *Diagnosis*

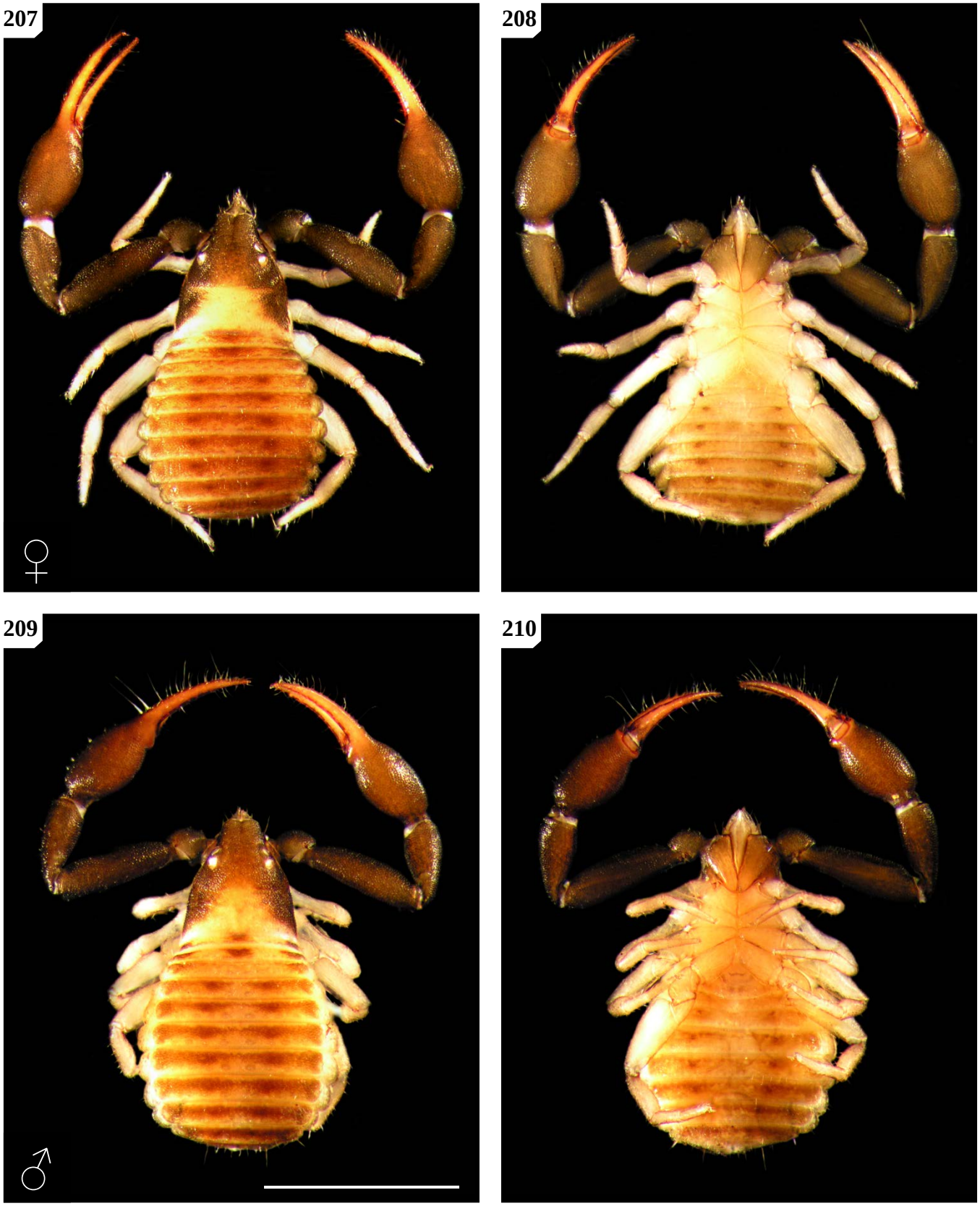
Medium species, pedipalpal femur length 0.76mm (♀), 0.69mm (♂), chela length (with stem) 1.28mm (♀), 1.09mm (♂), movable finger length 0.62mm (♀), 0.53mm (♂). Both males and females can reach an average length (cucullus to posterior abdominal margin) of 1.65mm. Carapace dark brown with a large cream coloured patch on the posterior in both sexes (Figs. 207 & 209). Pedipalp segments same colour as carapace, with the dorsal surface of the chela hand convex from the stem to the base of the chelal fingers. Abdominal tergites brown to light-brown in colour, with dark and cream patches in both sexes, while the abdominal sternites are light-brown with distinct dark spots in both sexes (Figs. 208 & 210). Pedipalp coxa same colour as carapace with distinct shoulder, legs I-IV with corresponding coxae cream to tan in colour in both sexes.

The species closely resembles both *G. liomendontus* sp. nov. and *G. modjadji* sp. nov. in both morphology and colouration, but can be distinguished from them by the lack of any fused chelal teeth, as well as possessing an isolated basal tooth close to the base of the movable chelal finger. Although both sexes can reach the same average length, females nonetheless possess longer appendages than the males.

3.14.3 *Description*

Carapace: Strongly sub-triangular, narrow furrow posterior of the eyes (Fig. 224). Carapace dark brown, large dorsal cream patch behind medial furrow, uniformly granular in both sexes. Heavily constricted anteriorly into cucullus, constriction beginning at medial furrow. Two pairs of corneate eyes situated on ocular tubercles, located ca. one third away from anterior edge. Four prominent setae located on anterior edge, row of ten setae located on posterior margin. Numerous small setae present on carapace. Carapace ratio: 0.99 (♀), 1.09 (♂).

Abdomen: Abdominal tergites brown to light-brown with both dark and cream patches on most plates. Tergites I and II with large median dark spot each, flanked by cream patches. Tergite III without dark patches, almost entirely cream. Tergites IV–X with cream posterior margins together with paired dark patches just lateral of the midline. Tergites XI and XII lack dark patches. Setae of posterior setal rows



Figs. 207-210. Digital microscope photographs of *Geogarypus deceptor* sp. nov., Female (**207**, **208**) and Male (**209**, **210**). **207**, **209**. Dorsal view; **208**, **210**. Ventral view. Scale bar: 1.00mm.

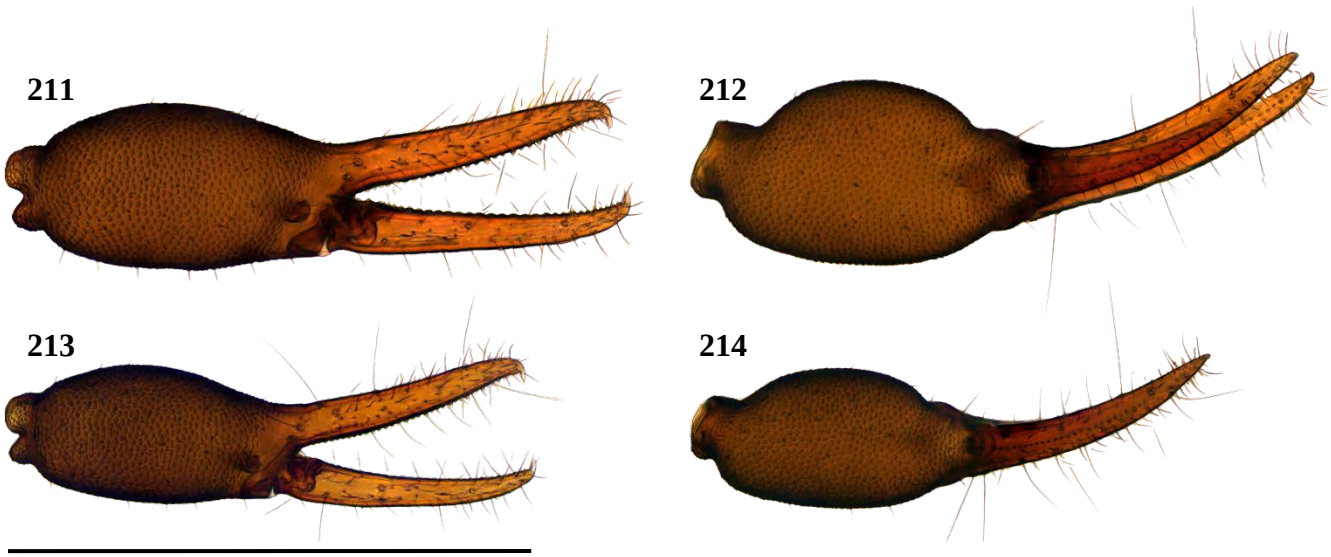
of tergites situated on small pale plates with dark edges, making plates distinctly visible. Sternites light-brown, well sclerotised in both sexes, paired dark spots located laterally of midline. Pleural membrane wrinkled-placate, cream.

Pedipalp: Trochanter rounded anteriorly, granular, same dark colouration as carapace. Small setae located on dorsal surface, ventral apophysis present. Pedipalp femur (Fig. 218) and patella same colour as trochanter, granular. Femur narrow at base, widening evenly until just posterior of anterior margin, where there is a sudden constriction. Femur ratio: 3.27 (♀), 3.77 (♂). Pedipalp patella (Fig. 218) narrow, slightly angled at base, widening evenly into cone. Lyriform fissures visible just anterior of base, located on bulge, dorso-prolaterally on patella. Patella ratio: 2.66 (♀), 2.39 (♂).

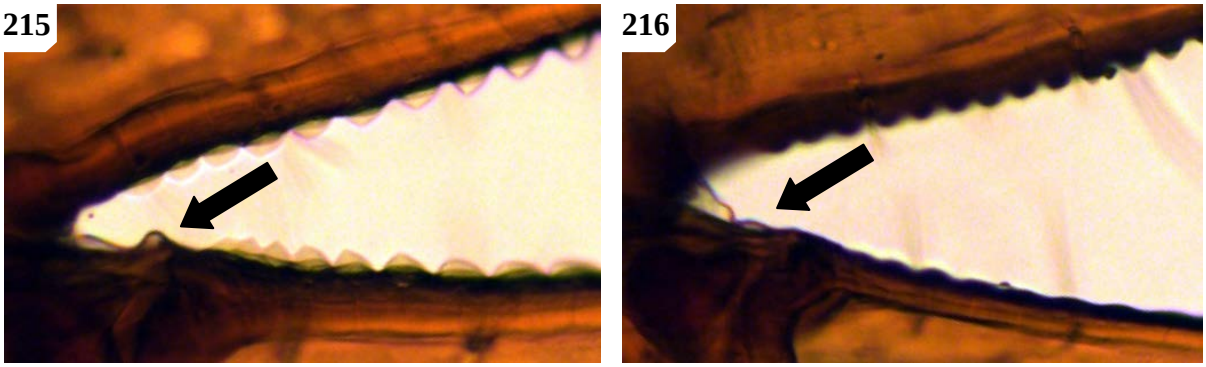
Chela: (Figs. 211-214, 217, 218) Chela palm same colour as rest of the pedipalp, fingers lighter in both sexes, granular from stem up to base of fingers. Both fingers smooth, slightly shorter than hand-stem complex. Dorsal surface of chelal hand uniformly convex in shape from stem to base of chelal fingers. Both pro- and retrolateral surfaces slightly convex, prolateral surface more so. Fixed chela finger with eight trichobothria, movable chela finger with four. Both fingers long and narrow, curving to interior. Venom apparatus present on both fingers. Trichobothria *eb* and *esb* one trichobothrial width from each other, located retrolaterally at base of fixed finger, *ib* located dorso-prolaterally, two trichobothrial widths distal of *esb*. Trichobothria *est* located one quarter finger length on retrolateral surface, with *isb* situated distally, located two fifths finger length from base of fixed finger on dorsal surface. Trichobothria *ist* located one third finger length from anterior finger edge, roughly in middle of the prolateral surface, *it* located on dorsal surface, just over one quarter finger length from anterior finger edge; *et* situated anteriorly on retrolateral surface. Trichobothria *b* and *eb* on movable finger situated somewhat forward of finger base, *b* ventrally in line with *esb*. Trichobothria *st* is positioned in line ventrally with *isb*, *t* located roughly one quarter finger length from anterior edge of movable finger. Chelal teeth acute and retrorse. Fixed finger with 32 teeth (♀), 37 (♂). All teeth are situated in one row, several large teeth located equally along finger length (Fig. 220). Movable finger with 29 teeth (♀), 30 (♂). Basal teeth on female movable finger regenerate into acute points, both sexes possessing an isolated tooth at base of movable finger (Figs. 215, 216, 219). Chela ratio: 3.32 (♀), 3.73 (♂).

Chelicera: Hand with five setae located as in Fig. 5. Fixed cheliceral finger with five teeth arranged as in Fig. 219. Female galea complex with nine rami (Fig. 222). Male galea simple, with two spinules (Fig. 223). Rallum composed of single blade in both sexes. Serrula exterior with 17 lamella in both sexes. Lamina exterior present in both sexes.

Coxae and legs: Pedipalp coxa same colour as carapace, with distinct shoulder, legs I-IV with corresponding coxa cream to tan in both sexes. All legs diplotarsate (Figs. 225 & 226).



Figs. 211-214. Digital microscope photographs of *Geogarypus deceptor* sp. nov. right chela: Female (**211**, **212**) and Male (**213**, **214**). **211**, **213**. Retrolateral view; **212**, **214**. Dorsal view. Scale bar: 1.00mm.



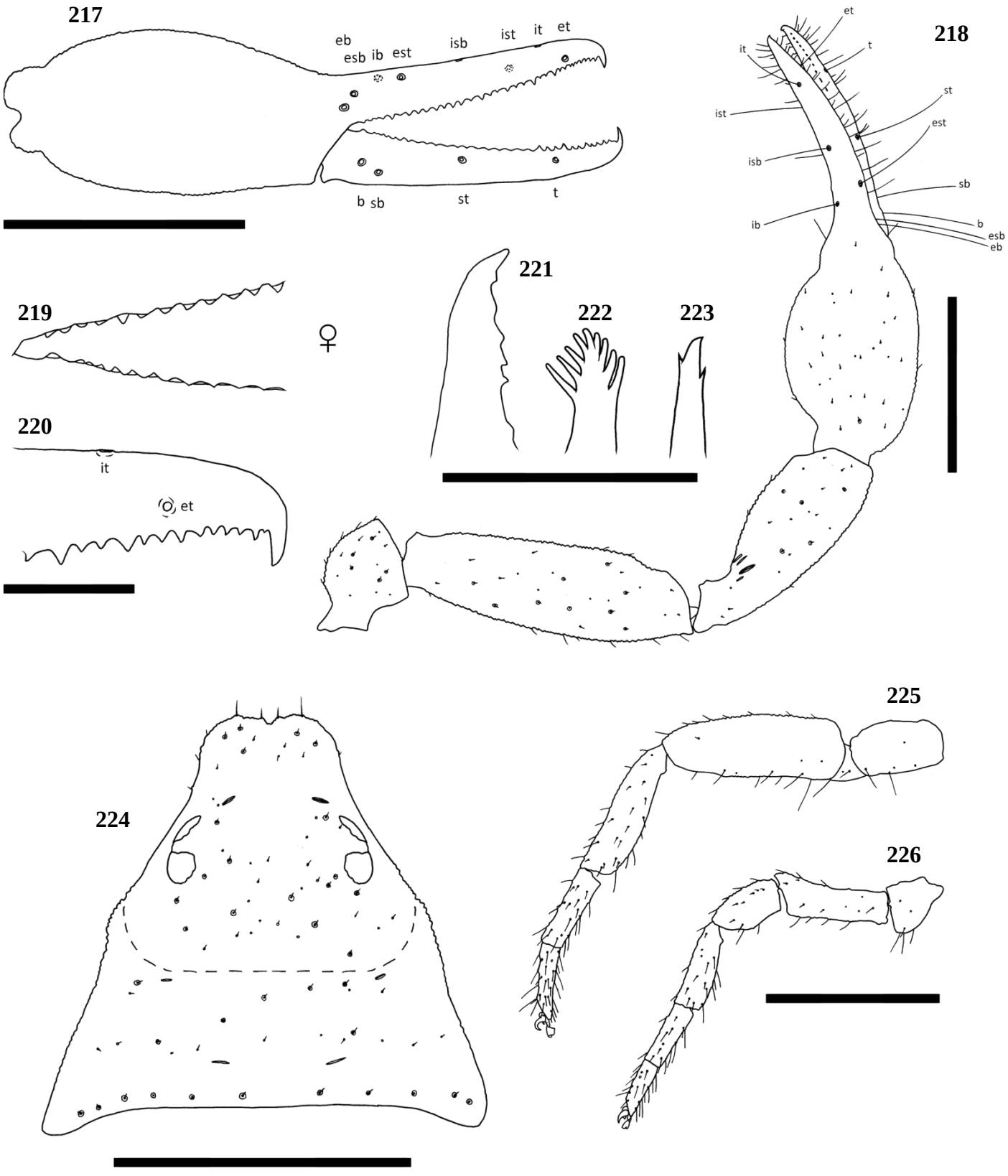
Figs. 215-216. Digital microscope photographs of *Geogarypus deceptor* sp. nov., arrows indicating isolated basal chelal tooth of female (**215**) and male (**216**).

3.14.4 *Remarks*

This is the only South African species that possesses an isolated basal tooth on the movable chela finger. Although not many museum exemplars were found, all were either unidentified or misidentified as *G. olivaceus*.

3.14.5 *Additional material examined*

SOUTH AFRICA: *KwaZulu-Natal*: 2♀, 1♂, Jozini, Jozini Town Outskirts, 27º 29'S, 32º 01'E, 454m a.s.l., Indigenous bush patch, Leaf litter sifting, leg. J.A. Neethling & C. Luwes, 19.V.2012 (NMBA



Figs. 217-226. *Geogarypus deceptor* sp. nov. **217-222**, **224-226**. Female; **223**. Male. **217**. Right chela, retrolateral view; **218**. Right pedipalp, dorsal view; **219**. Basal teeth arrangement; **220**. Anterior teeth arrangement on fixed chelal finger; **221**. Chelicera movable finger, dorsal view; **222**, **223**. Galea; **224**. Carapace, dorsal view; **225**. Right leg IV, prolateral view; **226**. Right leg I, prolateral view. Scale bars: Figs. 217-220, 224-226: 0.50mm; Figs. 221-223: 0.10mm.

P00218); 3♀, 2♂, Mbazwana, iSimangaliso Wetland Park, Sodwana Bay National Park, 27° 32'S, 32° 41'E, 11m a.s.l., Coastal bush, Leaf litter sifting, leg. J.A. Neethling & C. Luwes, 18.V.2012 (NMBA P00217); 2♀, 1♂, Ndumo Game Reserve, 26° 55'S, 32° 16'E, 120m a.s.l., Under rocks, leg. C.R. Haddad, 7.I.2007 (WAM T67148, T79040, T79039); 1♀, Same locality, Crocodile Farm, 26° 54'S, 32° 19'E, 57m a.s.l., leg. C.R. Haddad, 7.II.2005 (WAM T79038); 3♀, Umhlali, Sheffield Beach [29° 29'S, 31° 15'E], leg. R.F. Lawrence, VII.1958 (NMSA 5163); 2♀, 5♂, 1 Deutonymph, St. Lucia, Dukuduku Forest [28° 22'S, 32° 20'E], leg. R.F. Lawrence & J.Y. Lawrence, XII.1960 (NMSA 7864); 3♀, 5♂, St. Lucia, St. Lucia Coastal Forest, 28° 23'S, 32° 24'E, 20m a.s.l., Coastal forest, Leaf litter sifting, leg. J.A. Neethling & C. Luwes, 13.V.2012 (morphological dissection and phylogenetic analysis); 2♀, Tembe Elephant Park, 27° 03'S, 32° 27'E, 68m a.s.l., Closed woodland, leg. C.R. Haddad, 6.I.2002 (WAM T86753).

Mpumalanga: 2♀, Kruger National Park, Pretoriuskop Rest Camp, [25° 10'S, 31° 16'E], leg. R.F. Lawrence, XII.1960 (NMSA 16048); 1♀, 1♂, Nelspruit, Lowveld National Botanical Gardens, 25° 27'S, 30° 58'E, 642m a.s.l., Indigenous forest patch, Leaf litter sifting, leg. J.A. Neethling, 1.X.2012 (NMBA P00214).

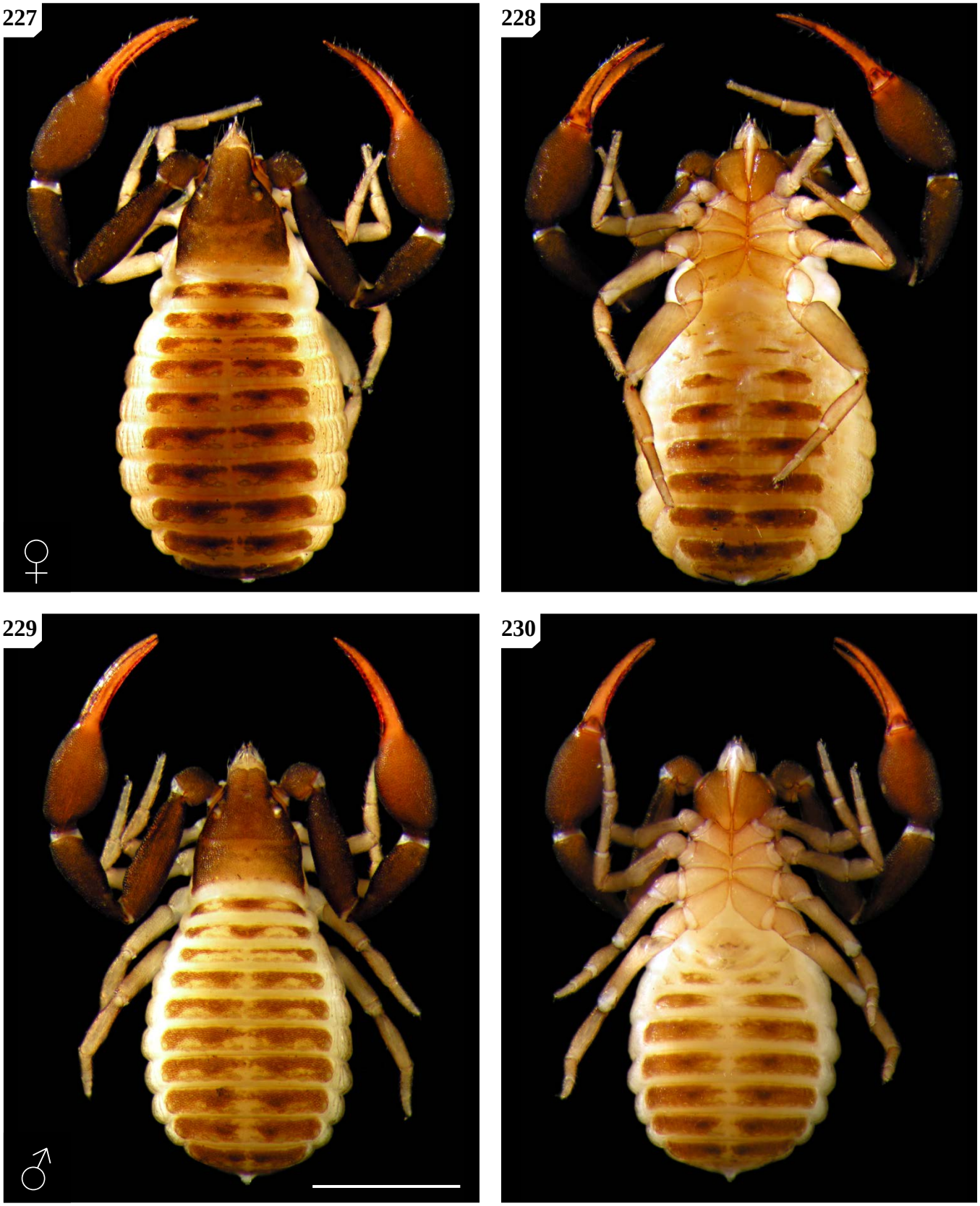
3.15 *Geogarypus flavus* (Beier, 1947) **stat. nov.**

Geogarypus (*Geogarypus*) *flavus* Beier, 1947: 318, fig. 24 [**Holotype** ♀, South Africa, Western Cape, Plettenberg Bay, Keurbooms River [33° 59'S, 23° 24'E], leg. K.H.B. (SAMC B6922), examined]; Beier, 1958: 170.

Geogarypus olivaceus (Tullgren, 1907): Beier, 1964: 59 (syn.)

3.15.1 *Diagnosis*

Large species, pedipalpal femur length 0.94mm (♀), 0.90mm (♂), chela length (with stem) 1.54mm (♀), 1.36mm (♂), movable finger length 0.79mm (♀), 0.69mm (♂). Females can reach a length (cucullus to posterior abdominal margin) of 2.92mm, with males reaching 2.74mm. Carapace dark brown in both sexes, with a lighter coloured band around the medial furrow and posterior edge of the carapace (Figs. 227 & 229). Pedipalp segments same colour as carapace, with the dorsal surface of the chela hand convex from the stem to the base of the chelal fingers. Abdominal tergites mostly brown to dark brown with dark and cream patches, while the abdominal sternites are brown to light-brown with dark spots and well sclerotised in both sexes (Figs. 228 & 230). Pedipalp coxa same colour as carapace with distinct shoulder, legs I-IV with corresponding coxa yellow to light-brown in both sexes.



Figs. 227-230. Digital microscope photographs of *Geogarypus flavus* stat. nov., Female (**227**, **228**) and Male (**229**, **230**). **227**, **230**. Dorsal view; **228**, **230**. Ventral view. Scale bar: 1.00mm.

Longer and more narrow, but less bulky than *Afrogarypus robustus* comb. nov., *G. flavus* stat. nov. is one of the largest geogarypid species in South Africa. Large specimens closely resemble *G. tectomaculatus* sp. nov. in general size, morphology and colouration, while smaller specimens resemble *G. olivaceus*. In both instances, *G. flavus* stat. nov. can be distinguished by having small and separated basal chelal teeth, while the basal teeth of *G. olivaceus* and *G. tectomaculatus* sp. nov. are larger and spaced tightly next to each other.

3.15.2 *Description*

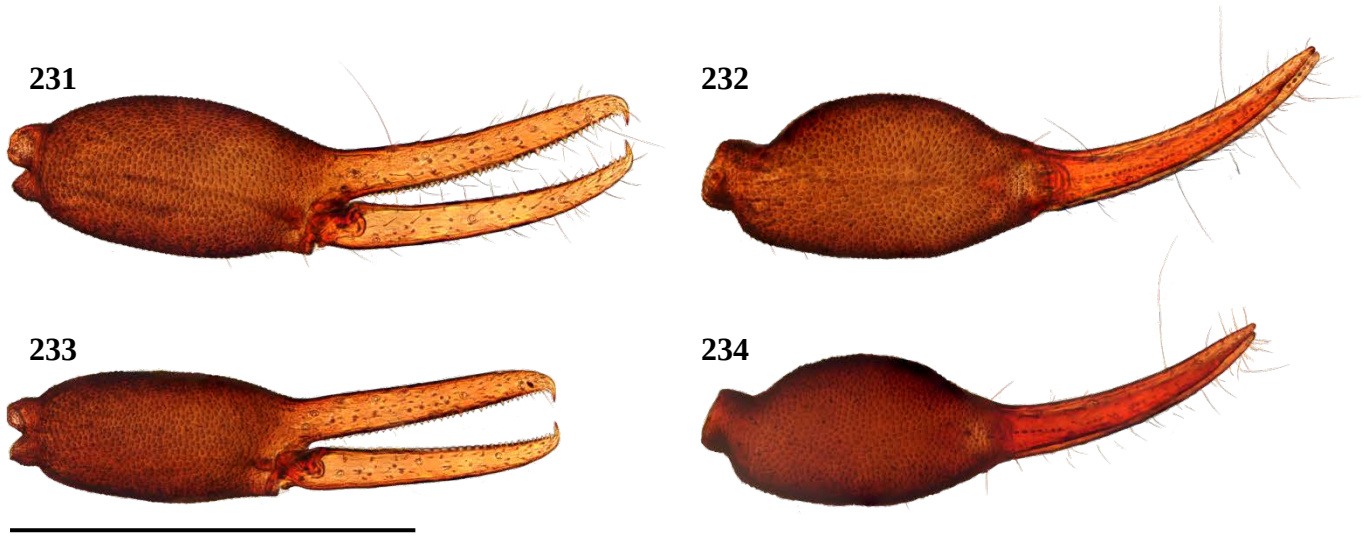
Carapace: Strongly sub-triangular, longer than broad in both sexes, with narrow furrow posterior to the eyes (Fig. 242). Carapace dark brown, uniformly granular in both sexes, lighter coloured band around medial furrow and posterior edge. Heavily constricted anteriorly into cucullus, constriction beginning at medial furrow. Two pairs of corneate eyes situated on ocular tubercles, located ca. one third away from anterior edge. Four prominent setae located on anterior edge, row of ten setae located on posterior margin. Numerous small setae present on carapace. Carapace ratio: 1.06 (♀), 1.13 (♂).

Abdomen: Abdominal tergites brown to dark brown, both dark and cream coloured patches on most plates. Tergites I and II with large median dark spot each, flanked by cream patches. Tergite III without dark patches, with median cream band extending almost entire length of tergum. Tergites IV–X with medial cream patch and paired dark patches just lateral of midline, flanked laterally by cream patches. Tergites XI and XII lack dark patches. Setae of posterior setal rows of tergites, predominantly in females, situated on large pale plates with dark edges, making these plates distinctly visible. Sternites well sclerotised in both sexes, paired dark spots located laterally of cream midline. Pleural membrane wrinkled-placate, cream.

Pedipalp: Trochanter rounded anteriorly, granular, same colouration as carapace. Small setae located on dorsal and dorso-lateral sides, apophysis located ventrally. Pedipalp femur (Fig. 236) and patella same colour as trochanter, granular. Femur narrow at base, widening evenly until just posterior of anterior margin, where there is a sudden constriction. Femur ratio: 3.39 (♀), 3.52 (♂). Pedipalp patella (Fig. 236) narrow, slightly angled at base, widening evenly into a cone. Lyriform fissures visible just anterior to base, located on bulge, dorso-prolaterally on patella. Patella ratio: 2.60 (♀), 2.77 (♂).

Chela: (Figs. 231-236) Mostly same colour as rest of pedipalp, can be slightly lighter in both sexes. Granular from stem up to base of fingers. Both fingers smooth, just as long as hand-stem complex. Dorsal surface of chelal hand uniformly convex from stem to base of chelal fingers. Both pro- and retrolateral surfaces slightly convex. Fixed chela finger with eight trichobothria, movable chela finger with four. Both fingers long, narrow, curving to the interior. Venom apparatus present on both fingers.

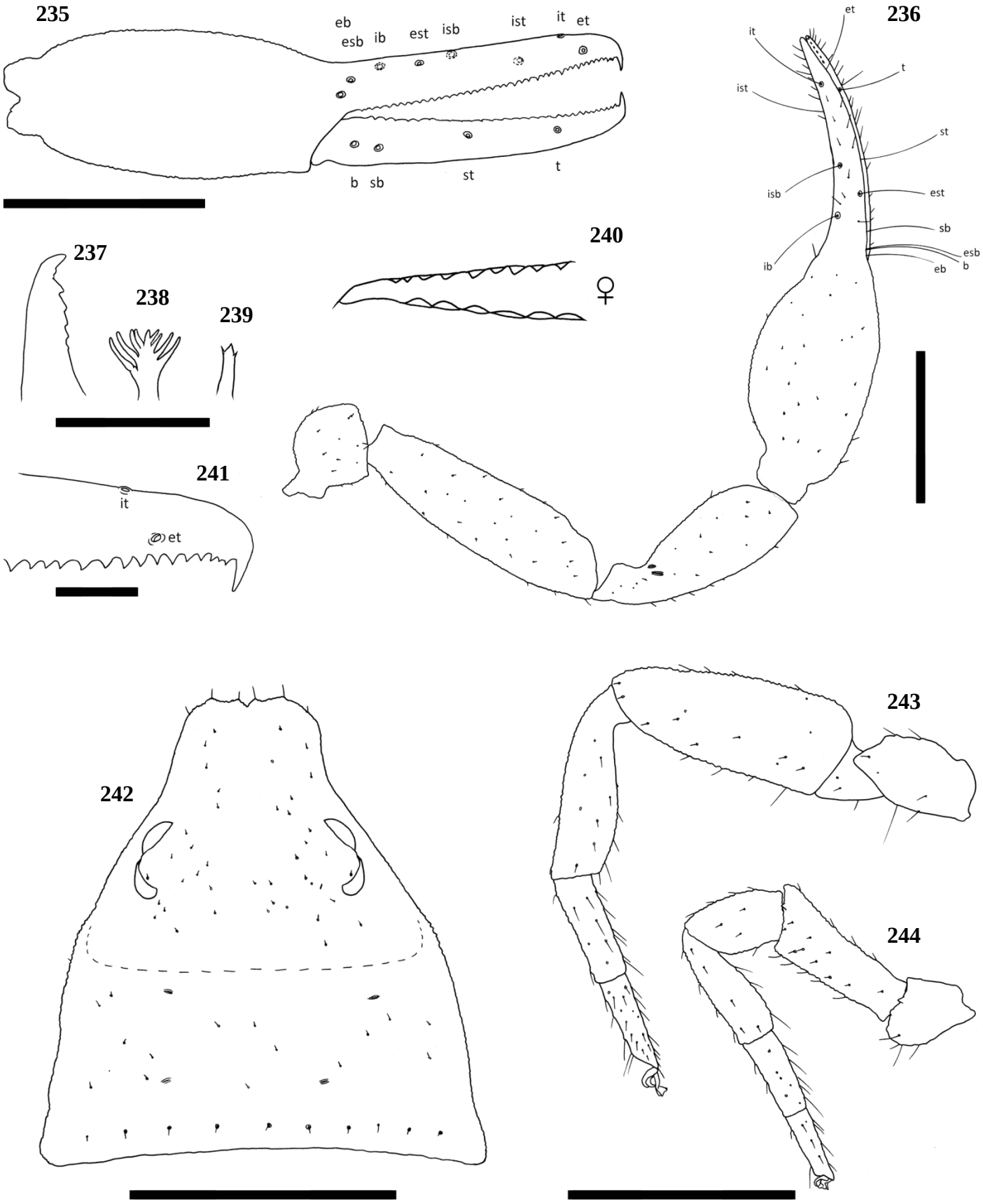
Trichobothria *eb* and *esb* situated one trichobothrial width from each other, retrolaterally at base of fixed finger, *ib* located dorso-prolaterally, three trichobothrial widths distal of *esb*. Trichobothria *est* located one third finger length on retrolateral surface, *isb* situated distally by three trichobothrial widths on opposite surface. Trichobothria *ist* located one third finger length from anterior finger edge, roughly in middle of prolateral surface; *it* located on dorsal surface, one fifth finger length from anterior finger edge, *et* situated just anterior on retrolateral surface. Trichobothria *b* and *eb* on movable finger, somewhat forward of finger base, *b* ventrally in line with *esb*. Trichobothria *st* positioned roughly halfway along movable finger, *t* located roughly one quarter finger length from anterior edge of movable finger. Chelal teeth acute and retrorse. Fixed finger with 41 teeth (♀), 40 (♂). First three teeth behind venom apparatus raised, forming distinct group (Fig. 241). Formation then followed by remaining fixed chelal teeth, within a single row, only decreasing slightly in size to base (Fig. 240). Movable finger with 30 teeth (♀), 31 (♂). First tooth behind venom apparatus small, followed by larger teeth that degenerate into small points. In both sexes the first few basal teeth on movable finger regenerate into wide teeth points. Chela ratio: 3.71 (♀), 3.58 (♂).



Figs. 231-234. Digital microscope photographs of *Geogarypus flavus* stat. nov. right chela: Female (**231**, **232**) and Male (**233**, **234**). **231**, **233**. Retrolateral view; **232**, **234**. Dorsal view. Scale bar: 1.00mm.

Chelicera: Hand with five setae located as in Fig. 5. Fixed cheliceral finger with six teeth arranged as in Fig. 237. Female galea complex with nine rami (Fig. 238), simple, with two spinules in males (Fig. 239). Rallum composed of single blade in both sexes. Serrula exterior with 19 lamella in both sexes. Lamina exterior present in both sexes.

Coxae and legs: Pedipalp coxae same colour as trochanters, with distinct shoulder. Legs I-IV with corresponding coxae yellow to light-brown. All legs diplotarsate (Figs. 243 & 244).



Figs 235-244. *Geogarypus flavus* stat. nov. **235-238**, **240-244**. Female; **239**. Male. **235**. Right chela, retrolateral view; **236**. Right pedipalp, dorsal view; **237**. Chelicera movable finger, dorsal view; **238**, **239**. Galea; **240**, Chela basal teeth arrangement; **241**. Right chela fixed finger, anterior teeth arrangement; **242**. Carapace, dorsal view; **243**. Right leg IV, prolateral view; **244**. Right leg I, prolateral view. Scale bars: Figs. 235, 236, 242-244: 0.50mm; Figs. 237-239, 243: 0.10mm.

3.15.3 *Remarks*

The species is here removed from synonymy with *Geogarypus olivaceus* and revalidated on account of the distinct morphological differences between the species, as well as the supporting molecular phylogenetic evidence.

3.15.4 *Additional material examined*

SOUTH AFRICA: *Eastern Cape*: 2 Adults, Port Alfred [33° 36'S, 26° 53'E], leg. J. Hewitt (AMG slide).

KwaZulu-Natal: 4 Adults, 2 Immatures, Durban [29°51'S, 31° 02'E], Mango plantation, leg. L. Bevis, 13.II.1921 (3x AMG slides); 2♀, 1♂, Same locality, leg. W.G. Rump, VIII.1940 (NMSA 648); 1♂, Same locality, Umbilo [29° 54'S, 30° 59'E], leg. L. Bevis, 27.II.1921 (NMSA 16046); 3♀, 2♂, Estcourt [29° 00'S, 29° 53'E], leg. R.F. Lawrence, VIII.1941 (NMSA 5126); 1♀, 1♂, Greytown, Mazongwaan Forest [29° 04'S, 30° 36'E], leg. R.F. Lawrance, XI.1940 (NMSA 5123); 1♀, Ixopo [30° 09'S, 30° 04'E], leg. C. F. Newson, X.1962 (NMSA 7889); 2♀, 1♂, Kranskop [28° 58'S, 30° 52'E], leg. R.F. Lawrence, I.1940 (NMSA 642); 1♀, 1 Deutonymph, Margate [30° 51'S, 30° 23'E], leg. W.G. Rump, IV.1940 (NMSA 643); 1♂, Mooi River, Rosetta [29° 18'S, 29° 59'E], leg. W.G. Rump, I.1942 (NMSA 662); 1♀, 1♂, Pietermaritzburg, [29° 36'S, 30° 23'E], leg. R. Godfrey, X.1930 (NMSA610); 8♀, 12♂, 4 immatures, Pietermaritzburg, KwaZulu-Natal National Botanical Gardens, 29° 35'S, 30° 20'E, 873m a.s.l., Grassland, leg. M.S. Harvey, 5.IV.2001 (WAM T63156, T63157); 5♀, 4♂, Same locality, 29° 36', 30° 21'E, 720m a.s.l., High moisture indigenous forest, Leaf litter sifting, leg. J.A. Neethling, 23.XI.2012 (NMBA P00178); 3♀, 4♂, Pietermaritzburg, Road to Bulwer [29° 42'S, 30° 29'E], leg. R.F. Lawrence, XII.1936 (NMSA 611); 2♀, Same locality, Swartkop [29° 37'S, 30° 14'E], leg. R.F. Lawrence, VI.1957 (NMSA 5153); 2♀, 3♂, Same locality, Table Mountain [29° 37'S, 30° 36'E], leg. W.G. Rump, VII.1940 (NMSA 645); 1♀, Same locality, Town Bush [29° 36'S, 30° 23'E], leg. R.F. Lawrence, I.1940 (NMSA 5124); 1♀, Same locality, leg. R.F. Lawrence, X.1960 (NMSA 7863); 2♀, Port Edward [31° 03'S, 30° 13'E], leg. R.F. Lawrence, XII.1943 (NMSA 671); 2♀, Same locality, leg. R.F. Lawrence, VI.1944 (NMSA 675); 2♀, Port Shepstone, Oribi Gorge [30° 41'S, 30° 18'E], leg. R.F. Lawrence, X.1936 (NMSA 5125); 3♀, 5♂, Umzinto, Vernon Crookes Nature Reserve, 30° 16'S, 30° 37'E, 445m a.s.l., High moisture indigenous forest, Leaf litter sifting, leg. J.A. Neethling, 26.XI.2012 (NMBA P00177).

Western Cape: 1♀, 2♂, George, Saasveld Pass, 33° 58'S, 22° 32'E, 149m a.s.l., Indigenous forest, Leaf litter sifting, leg. J.A. Neethling & C. Luwes, 7.XII.2012 (morphological dissection); 4♀, 3♂, Hoekwil, Woodville Big Tree, 33° 56'S, 22° 39'E, 262m a.s.l., Indigenous forest, Leaf litter sifting, leg. J.A. Neethling & C. Luwes, 8.XII.2012 (phylogenetic analysis); 1♀, 6♂, Rheenendal, Jubilee

Creek Nature Reserve, 33° 53'S, 22° 58'E, 923m a.s.l., Afromontane forest, Leaf litter sifting, leg. J.A. Neethling & C. Luwes, 26.XII.2013 (NMBA P00173).
Unknown: 2♀, No collection data (NMSA 16049).

3.15.5 *Additional material not examined*

SOUTH AFRICA: *KwaZulu-Natal*: 2♀, Richards Bay [28° 47'S, 32° 02'E], leg. R.F. Lawrence, XII.1943 (NMSA 670, examined by Beier 1958, not traced).

3.16 *Geogarypus liomendontus* sp. nov.

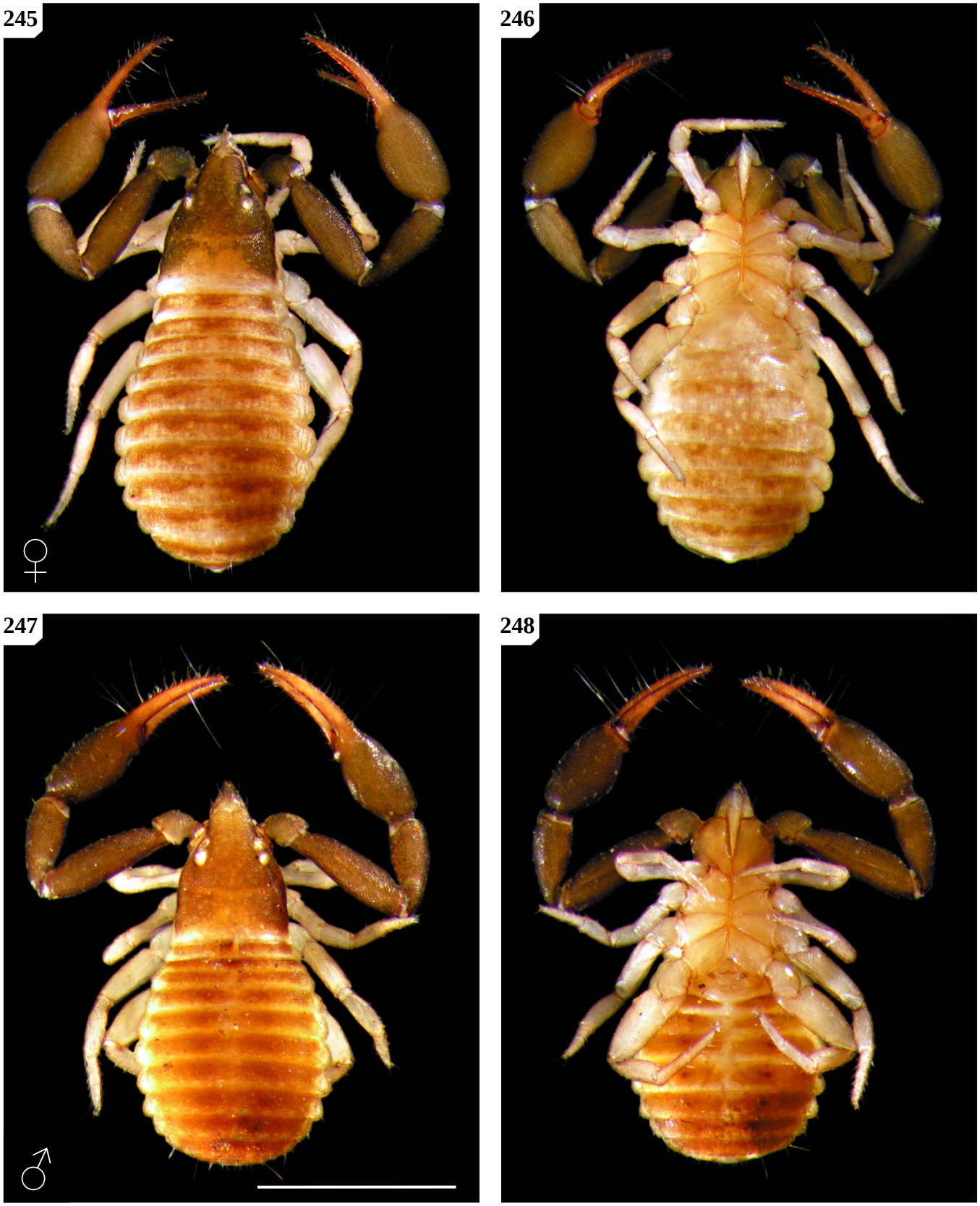
Holotype: ♀, SOUTH AFRICA, Limpopo, Tshwenyane, Abel Erasmus Pass, 24° 28'S, 30° 36'E, 760m a.s.l., Indigenous mountain bush patch, Leaf litter sifting, leg. J.A. Neethling, 4.X.2012 (NMBA P00208).
Paratype: 1♂, Same data as holotype (NMBA P00209).

3.16.1 *Etymology*

The name for the species is a compound of the Greek words; *lioméno* (λιωμένο), meaning fused, and *dónti* (δόντι), meaning tooth, and refers to the rows of fused basal teeth found on both chelal fingers of the female.

3.16.2 *Diagnosis*

Medium species, pedipalpal femur length 0.68mm (♀), 0.64mm (♂), chela length (with stem) 1.21mm (♀), 1.11mm (♂), movable finger length 0.60mm (♀), 0.57mm (♂). Females can reach a length (cucullus to posterior abdominal margin) of 2.11mm, with males averaging 1.80mm in length. Carapace dark brown, with light-brown colouration along the medial furrow and a large light-brown patch on the posterior in both sexes (Figs. 245 & 247). Pedipalp segments same colour as carapace, with the dorsal surface of the chela hand convex from the stem to the base of the chelal fingers. Abdominal tergites light-brown in colour with cream markings and faint dark patches in both sexes, while the abdominal sternites are either cream to light-brown with very faint dark patches and weakly sclerotised (♀) or brown to light-brown with distinct dark patches and well sclerotised (♂) (Figs. 246 & 248). All pedipalp segments with the same dark colouration of the carapace, while legs I-IV, with corresponding coxae, are cream to tan in both sexes.



Figs. 245-248. Digital microscope photographs of *Geogarypus liomendontus* sp. nov., Female (**245**, **246**) and Male (**247**, **248**). **245**, **247**. Dorsal view; **246**, **248**. Ventral view. Scale bar: 1.00mm.

The species closely resembles both *Geogarypus deceptor* sp. nov. and *G. modjadji* sp. nov. in both morphology and colouration, but can be distinguished from them by possessing rows of fused basal teeth on both chela fingers in the female. Since males of the species lack these rows of fused teeth, they remain cryptic and challenging to separate from the males of related species on chelal morphology alone, requiring examination of micro-anatomical features such as those found on the chelicerae.

3.16.3 *Description*

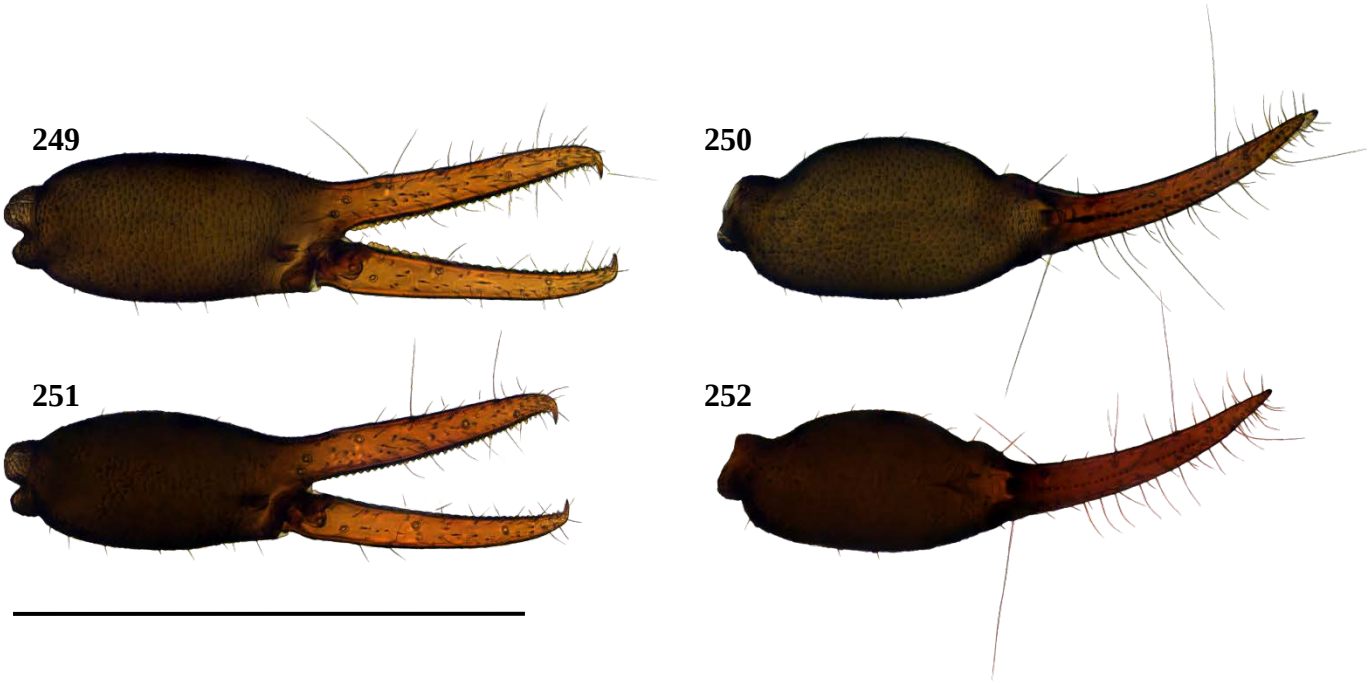
Carapace: Strongly sub-triangular, with narrow furrow posterior to the eyes (Fig. 262). Anterior half dark brown, light-brown along medial furrow, large light-brown triangular patch on posterior, uniformly granular in both sexes. Heavily constricted anteriorly into cucullus, constriction beginning at medial furrow. Two pairs of corneate eyes situated on ocular tubercles, located ca. one third away from anterior edge. Four prominent setae located on anterior edge, row of ten setae located on posterior margin. Numerous small setae present on carapace. Carapace ratio: 1.05 (♀), 1.09 (♂).

Abdomen: Abdominal tergites brown to light-brown, cream markings on posterior margin of most plates, particularly those of females. Faint dark patches present. Tergites I and II with faint median dark spot each, flanked by cream patches. Tergite III without dark patches. Tergites IV–X with cream posterior margins and paired dark patches lateral of the midline. Patches may appear absent and usually only seen on closer examination. Tergites XI and XII lack dark patches. Sternites light-brown, weakly sclerotised in females, brown, well sclerotised in males. Both sexes with paired dark spots located laterally of midline. Pleural membrane wrinkled-placate, cream.

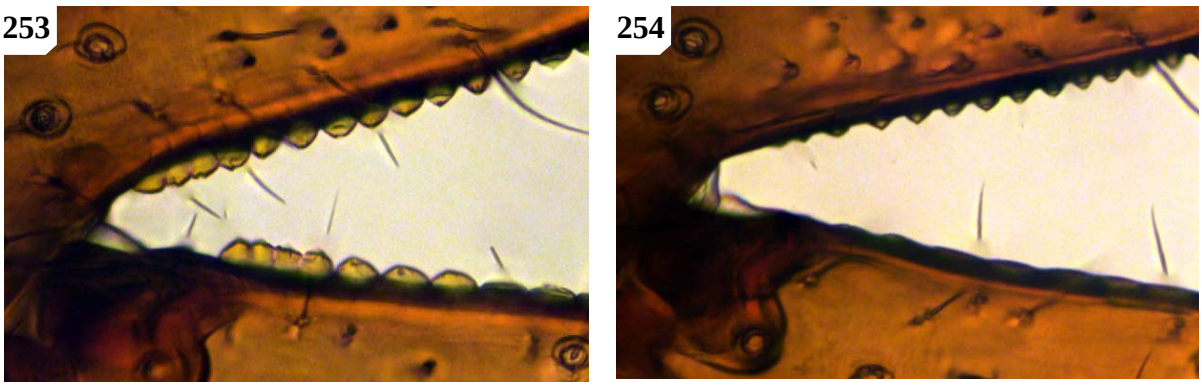
Pedipalp: Trochanter rounded anteriorly, slightly curved, granular, bearing the same colouration as the carapace. Small setae located on dorsal surface, apophysis located ventrally. Pedipalp femur (Fig. 256) and patella same colour as trochanter, granular. Femur narrow at base, widening evenly until just posterior of anterior margin, where there is a sudden constriction. Femur ratio: 3.60 (♀), 3.15 (♂). Pedipalp patella (Fig. 256) narrow, slightly angled at base, widening evenly into cone. Lyriform fissures visible just anterior of base, located on bulge, dorso-prolaterally on patella. Patella ratio: 2.61 (♀), 2.53 (♂).

Chela: (Figs. 249-252, 255, 256) Chelal hand same colour as rest of pedipalp, fingers lighter. Chela granular from stem to base of fingers. Both fingers smooth, just as long as hand-stem complex. Dorsal surface of chelal hand uniformly convex from stem to base of chelal fingers. The prolateral surface of chela only slightly convex, retrolateral surface roughly straight. Fixed chela finger with eight trichobothria, movable chela finger with four. Both fingers long and narrow, curving to interior.

Venom apparatus present on both fingers. Trichobothria pattern almost identical to that of *G. deceptor* sp. nov., with the exception that *est* is located just anterior and almost opposite of *ib*. Fixed finger with 35 teeth (♀), 38 (♂). All teeth situated in one row, several large teeth located equally along finger length (Fig. 258). Movable finger with 27 teeth (♀), 28 (♂). Anterior edge of the female's movable finger extends slightly beyond that of fixed chelal finger. Unique to females of this species is the presence of large fused teeth plates at the base of both chela fingers (Figs. 253 & 257). Plate on fixed finger consists of fusion of first four basal teeth, teeth immediately after grouping tightly next to each other. Plate on movable finger also consists of fusion of first four basal teeth. Males do not possess fused plates, with no increase in basal teeth size present (Fig. 254). Chela ratio: 3.78 (♀), 3.83 (♂).



Figs. 249-252. Digital microscope photographs of *Geogarypus liomendontus* sp. nov. right chela: Female (**249**, **250**) and Male (**251**, **252**). **249**, **251**. Retrolateral view; **250**, **252**. Dorsal view. Scale bar: 1.00mm.



Figs. 253-254. Digital microscope photographs of tooth morphology at the base of the chelal fingers of *Geogarypus liomendontus* sp. nov., showing distinct differences between female (**253**) and male (**254**).

Chelicera: Hand with five setae located as in Fig. 5. Fixed cheliceral finger with six teeth arranged as in Fig. 259. Female galea complex with nine rami (Fig. 260), simple in males (Fig. 261). Rallum composed of single blade in both sexes. Serrula exterior with 13 lamella in females, 16 in males. Lamina exterior present in both sexes.

Coxae and legs: Pedipalp coxae slightly lighter than carapace, with distinct shoulder. Legs I-IV with corresponding coxa cream to tan in both sexes. All legs diplotarsate (Figs. 263 & 264).

3.16.4 *Remarks*

The species is unique in that the females possess a plate consisting of large fused teeth at the base of both chelal fingers. Although *G. modjadji* sp. nov. females also possess fused teeth, these are only present at the base of fixed chelal finger.

3.16.5 *Additional material examined*

SOUTH AFRICA: *Limpopo*: 1♀, 1♂, Tshwenyane, Abel Erasmus Pass, 24° 28'S, 30° 36'E, 760m a.s.l., Indigenous mountain bush patch, Leaf litter sifting, leg. J.A. Neethling, 4.X.2012 (phylogenetic analysis).
Mpumalanga: 2♀, 1♂, Nelspruit, R539, 25° 24'S, 30° 44'E, 785m a.s.l., Highveld Afromontane forest, Leaf litter sifting, leg. J.A. Neethling, 29.IX.2012 (morphological dissection).

3.17 *Geogarypus modjadji* sp. nov.

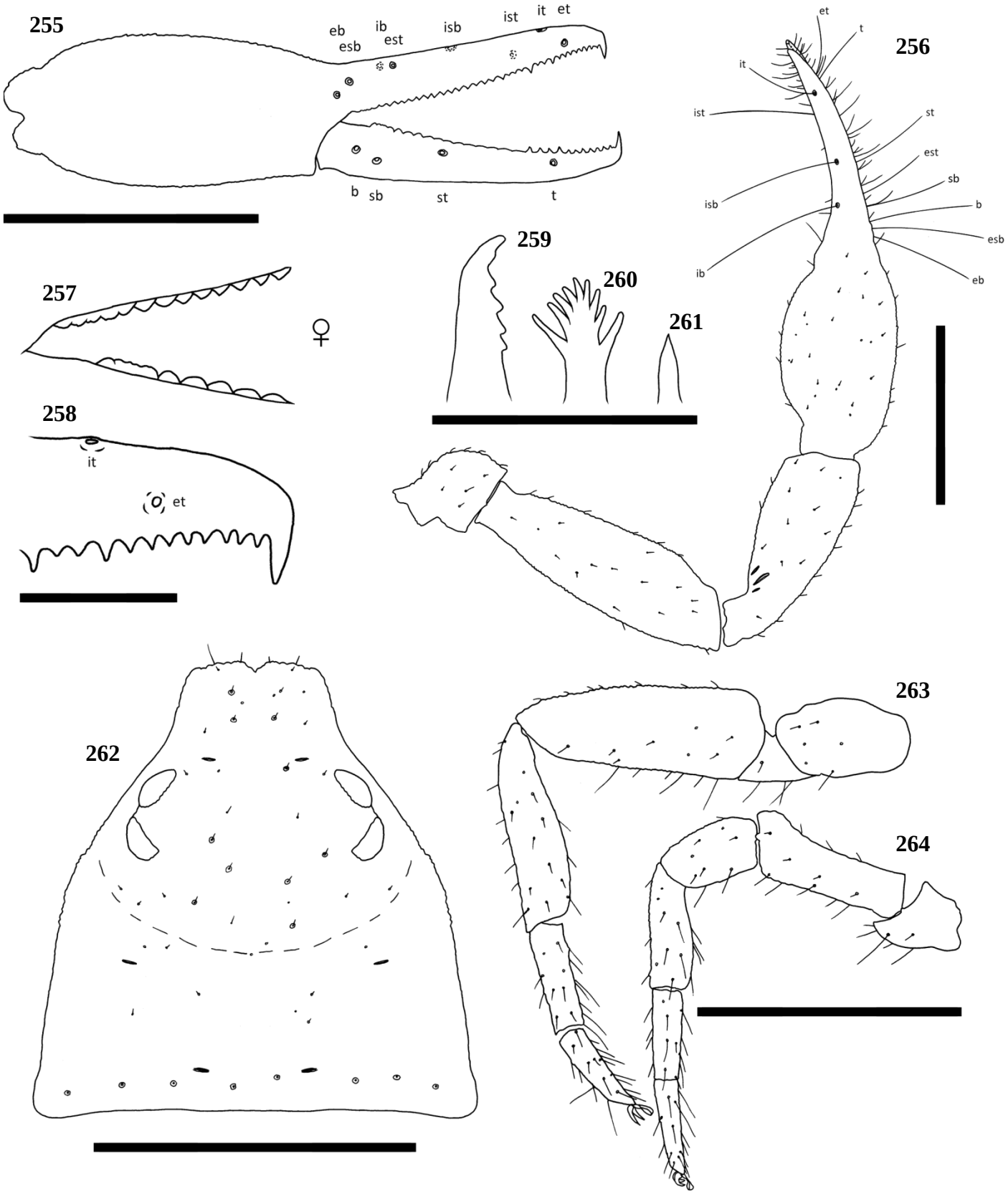
Holotype: ♂, SOUTH AFRICA, Limpopo, Modjadjikloof, Modjadjikloof Nature Reserve, 23° 38'S, 30° 22'E, 902m a.s.l., Dry-shrub cycad forest, Leaf litter sifting, leg. J.A. Neethling, 5.XI.2012 (NMBA P00210).
Paratypes: 2♂, Same data as holotype (NMBA P00211).

3.17.1 *Etymology*

The species name refers to the type locality.

3.17.2 *Diagnosis*

Medium species, pedipalpal femur length 0.77mm (♀), 0.70mm (♂), chela length (with stem) 1.38mm (♀), 1.23mm (♂), movable finger length 0.70mm (♀), 0.60mm (♂). Female reach an average



Figs. 255-264. *Geogarypus liomendontus* sp. nov. **255-260**, **262-264**. Female; **261**. Male. **255**. Right chela, retrolateral view; **256**. Right pedipalp, dorsal view; **257**. Basal teeth arrangement; **258**. Anterior teeth arrangement on fixed chelal finger; **259**. Chelicera movable finger, dorsal view; **260**, **261**. Galea; **262**. Carapace, dorsal view; **263**. Right leg IV, prolateral view; **264**. Right leg I, prolateral view. Scale bars: Figs. 255, 256, 262-264: 0.50mm; Figs. 258-261: 0.10mm.

length (cucullus to posterior abdominal margin) of 2.37mm, while males average 2.03mm. Carapace dark brown to almost black with a large cream patch on the posterior in both sexes (Figs. 265 & 267). Pedipalp segments same colour as carapace, with the dorsal surface of the chela hand convex from the stem to the base of the chelal fingers. Abdominal tergites brown to light-brown, with dark and cream patches in both sexes, while the abdominal sternites are light-brown with distinct dark spots in both sexes (Figs. 266 & 268). Pedipalp coxae lighter in colour than the carapace, with distinct shoulder, legs I-IV with corresponding coxae cream to tan in colour in both sexes.

The species closely resembles both *G. liomendontus* sp. nov. and *G. deceptor* sp. nov. in morphology and colouration, but can be distinguished from them by females only possessing fused teeth at the base of the fixed chela finger. *Geogarypus modjadji* sp. nov. is also the largest of the three species with both sexes averaging over 2.00mm. Males of *G. liomendontus* sp. nov. and *G. deceptor* sp. nov. both average below 2.00mm in length.

3.17.3 *Description*

Carapace: Strongly sub-triangular, with narrow furrow posterior to the eyes (Fig. 280). Carapace dark brown to black, with large, triangular cream patch on posterior half, extending from posterior edge up to medial furrow. Uniformly granular in both sexes, heavily constricted anteriorly into cucullus, constriction beginning at the medial furrow. Two pairs of corneate eyes situated on ocular tubercles, located ca. one third away from anterior edge. Four prominent setae located on anterior edge, row of ten setae located on posterior margin. Numerous small setae present on carapace. Carapace ratio: 1.04 (♀), 1.18 (♂).

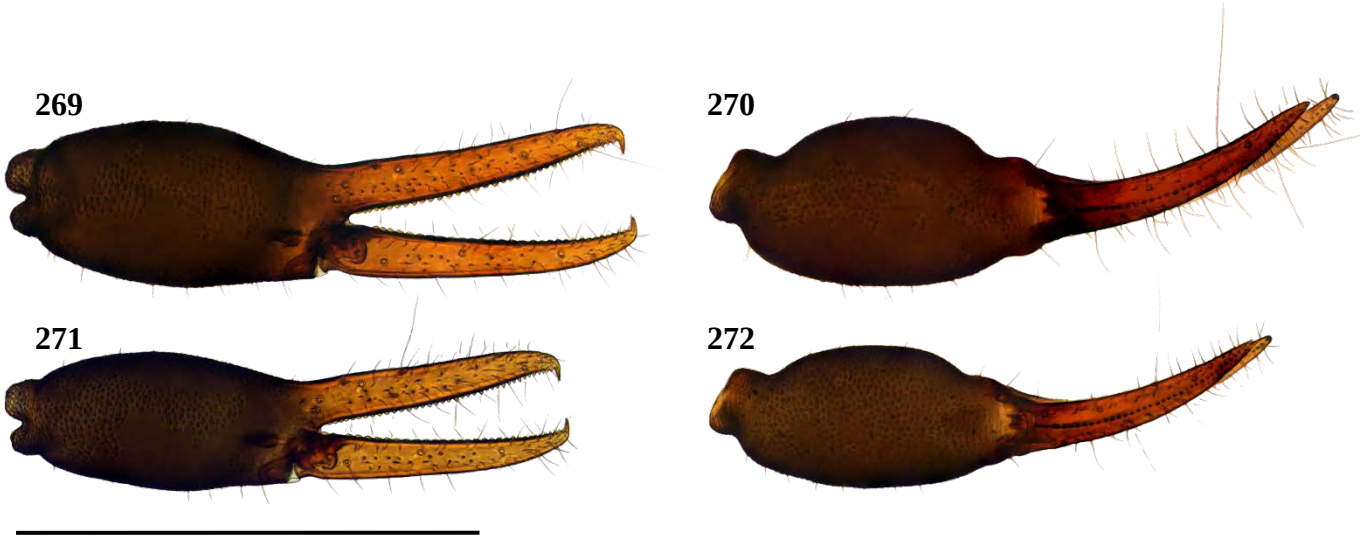
Abdomen: Abdominal tergites brown to light-brown, dark and cream patches present on most plates. Tergites I and II with large median dark spot each, flanked by cream patches. Tergite III without dark patches, but with a large medial cream patch. Tergites IV–IX with paired dark patches just lateral of midline, flanked by cream patches, with midline also cream. Tergites IX–XII uniformly brown, lacking any discernable dark or light patches. Setae of posterior setal rows of tergites are situated on small pale plates with dark edges, making these plates distinctly visible. Sternites light-brown and well sclerotised in both sexes, paired dark spots located laterally of the midline. Pleural membrane wrinkled-placate, cream.

Pedipalp: Trochanter rounded anteriorly, regular in shape, granular, with same dark colouration as carapace. Small setae located on dorsal and dorso-lateral sides, apophysis located ventrally. Pedipalp femur (Fig. 274) and patella same colour as trochanter and granular. Femur narrow at base, widening evenly until just posterior of anterior margin, where there is a sudden constriction. Femur ratio: 3.31

Figs. 265-268. Digital microscope photographs of *Geogarypus modjadji* sp. nov., Female (**265**, **266**) and Male (**267**, **268**). **265**, **267**. Dorsal view; **266**, **268**. Ventral view. Scale bar: 1.00mm.

(♀), 3.16 (♂). Pedipalp patella (Fig. 274) narrow, slightly angled at base, widening evenly into a cone. Lyriform fissures visible just anterior of base, located on bulge, dorso-prolaterally on patella. Patella ratio: 2.88 (♀), 2.64 (♂).

Chela: (Figs. 269-274) Chelal hand same colour as rest of pedipalp, fingers lighter. Chela granular from stem to base of fingers. Both fingers smooth, just as long as hand-stem complex. Dorsal surface of chelal hand uniformly convex from stem to base of chelal fingers. Prolateral surface slightly convex, retrolateral surface roughly straight. Fixed chela finger with eight trichobothria, movable chela finger with four. Both fingers long, narrow, curving to interior. Venom apparatus present on both fingers. Trichobothrial pattern nearly identical to both *G. deceptor* sp. nov. and *G. liomendontus* sp. nov., but with the following differences: trichobothria *eb* and *esb* separated by just less than one trichobothrial width , *est* situated anterior of *ib* by one trichobothrial width. Chelal teeth acute and retrorse. Fixed finger with 38 teeth (♀), 39 (♂). All teeth situated in one row, several large teeth located equally along finger length (Fig. 276). Movable finger with 31 teeth (♀), 30 (♂). Teeth on the movable finger degenerate into small points after about 12 teeth from anterior edge, regenerating near base of movable finger in both sexes. Three basal teeth of fixed chelal finger of females fused (Fig. 275), those of the male grouped tightly next to each other, but not fused. Chela ratio: 3.63 (♀), 3.88 (♂).



Figs. 269-272. Digital microscope photographs of *Geogarypus modjadji* sp. nov. right chela: Female (**269**, **270**) and Male (**271**, **272**). **279**, **271**. Retrolateral view; **270**, **272**. Dorsal view. Scale bar: 1.00mm.

Chelicera: Hand with five setae located as in Fig. 5. Fixed cheliceral finger with six teeth arranged as in Fig. 277. Female galea complex with nine rami (Fig. 278), simple in males (Fig. 279). Rallum composed of single blade in both sexes. Serrula exterior with 18 lamella in females, 17 in males. Lamina exterior present in both sexes.

Coxae and legs: Pedipalp coxae slightly lighter than carapace, with distinct shoulder, legs I-IV with corresponding coxae cream to tan in both sexes. All legs diplotarsate (Figs. 281 & 282).

3.17.4 *Remarks*

Currently only known from the type locality.

3.17.5 *Additional material examined*

SOUTH AFRICA: *Limpopo*: 3♀, 2♂, Modjadjikloof, Modjadjikloof Nature Reserve, 23° 38'S, 30° 22'E, 902m a.s.l., Dry-shrub cycad forest, Leaf litter sifting, leg. J.A. Neethling, 5.XI.2012 (morphological dissection & phylogenetic analysis).

3.18 *Geogarypus octoramosus* sp. nov.

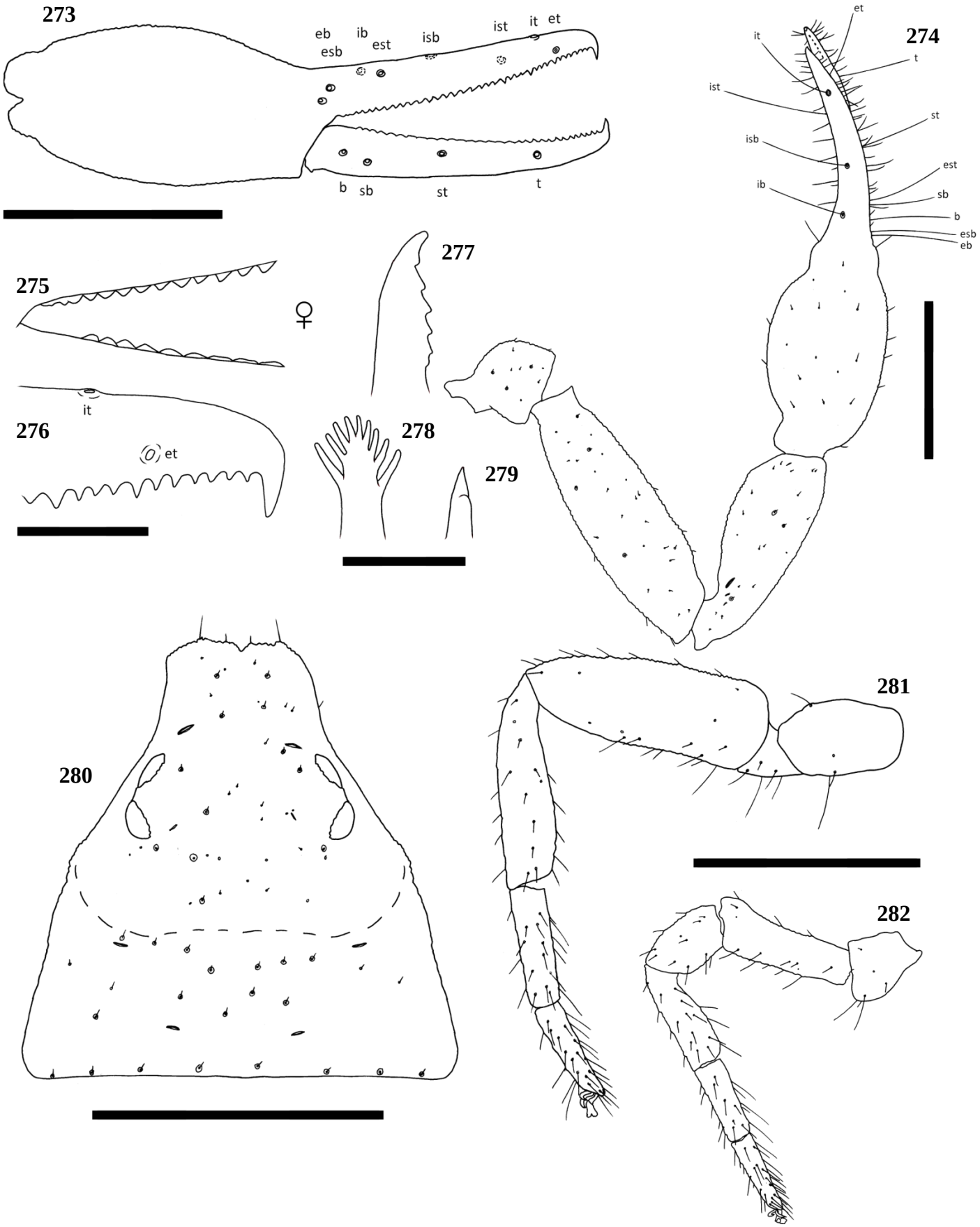
Holotype: ♀, SOUTH AFRICA, KwaZulu-Natal, Vryheid, Vryheid Mountain Nature Reserve, 27° 45'S, 30° 48'E, 1363m a.s.l., Thicket, Leaf litter sifting, leg. J.A. Neethling & C. Luwes, 22.V.2012 (NMBA P00215).
Paratypes: 4♀, 1♂, Same data as holotype (NMBA P00216).

3.18.1 *Etymology*

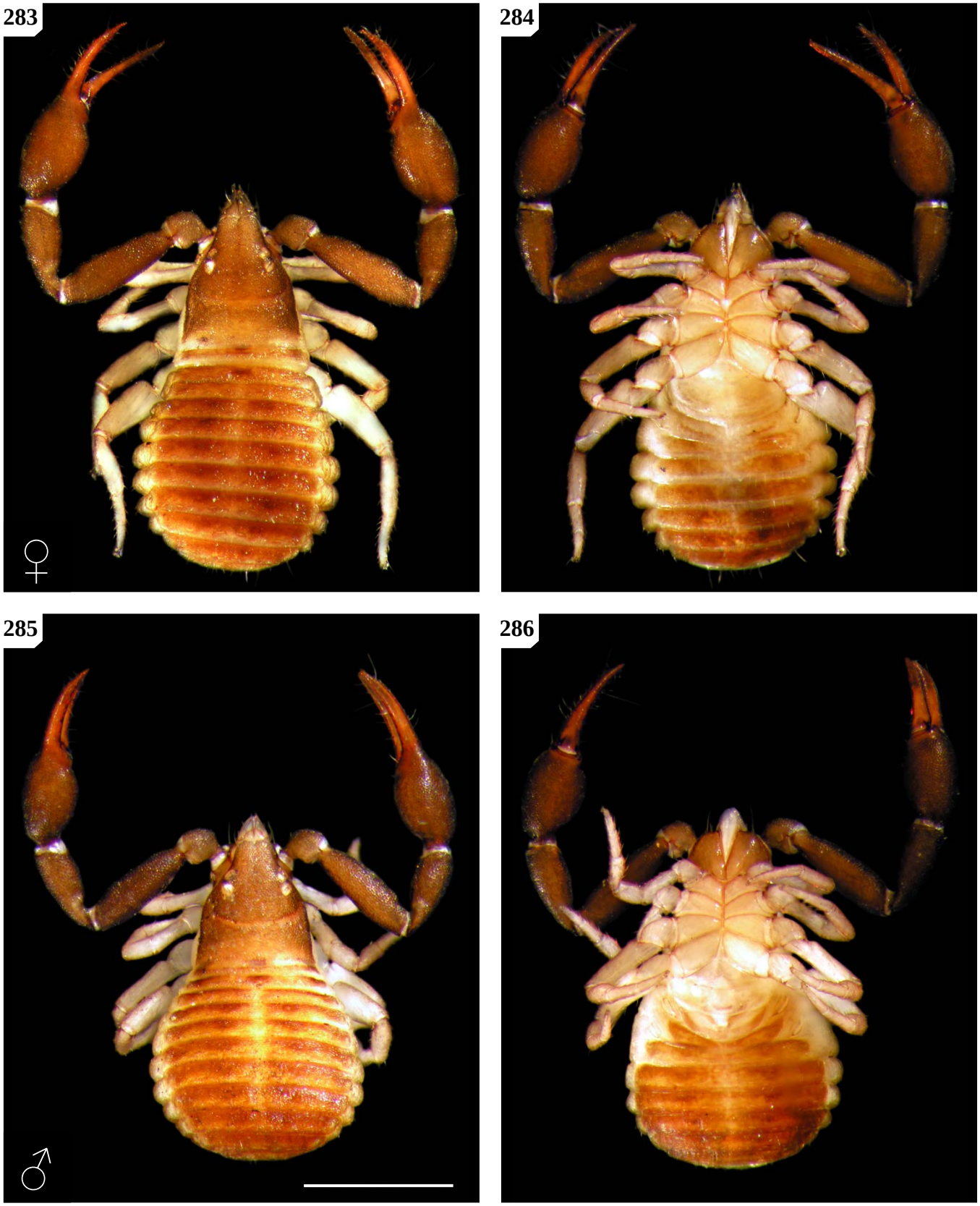
The species name refers to the reduced number of eight rami on the female galea.

3.18.2 *Diagnosis*

Medium species, pedipalpal femur length 0.73mm (♀), 0.62mm (♂), chela length (with stem) 1.27mm (♀), 1.07mm (♂), movable finger length 0.64mm (♀), 0.55mm (♂). Females reach a length (cucullus to posterior abdominal margin) of 2.24mm, while males average 2.11mm. Carapace brown, with the medial furrow and posterior edge slightly lighter in both sexes (Figs. 283 & 285). All pedipalp segments same colour as carapace, with the dorsal surface of the chela hand convex from the stem to the base of the chelal fingers. Abdominal tergites uniformly brown, with dark patches in both sexes and paler line medially. Abdominal sternites in both sexes are brown to light-brown with faint dark spots (Figs. 284 & 286). Legs I-IV with corresponding coxa tan to light-yellow in both sexes.



Figs. 273-282. *Geogarypus modjadji* sp. nov. **273-278**, **280-282**. Female; **279**. Male. **273**. Right chela, retrolateral view; **274**. Right pedipalp, dorsal view; **275**. Basal teeth arrangement; **276**. Anterior teeth arrangement on fixed chelal finger; **277**. Chelicera movable finger, dorsal view; **278**, **279**. Galea; **280**. Carapace, dorsal view; **281**. Right leg IV, prolateral view; **282**. Right leg I, prolateral view. Scale bars: Figs. 273, 274, 280-282: 0.50mm; Figs. 276-279: 0.10mm.



Figs. 283-286. Digital microscope photographs of *Geogarypus octoramosus* sp. nov., Female (**283**, **284**) and Male (**285**, **286**). **283**, **285**. Dorsal view; **284**, **286**. Ventral view. Scale bar: 1.00mm.

The species closely resembles *G. variaspinosus* sp. nov. in general morphology and colouration, but can easily be distinguished by having eight rami on the female galea, whereas females of *G. variaspinosus* sp. nov. have five to seven rami, but never eight.

3.18.3 *Description*

Carapace: Strongly sub-triangular, with narrow furrow posterior to the eyes (Fig. 298). Uniformly brown with medial furrow and posterior edge slightly lighter in both sexes. Granular in both sexes, heavily constricted anteriorly into cucullus, constriction beginning at the medial furrow. Two pairs of corneate eyes situated on ocular tubercles, located ca. one third away from anterior edge. Four prominent setae located on anterior edge, row of ten setae located on posterior margin. Numerous small setae present on carapace. Carapace ratio: 0.96 (♀), 1.02 (♂).

Abdomen: Abdominal tergites uniformly brown with faint dark patch on most plates. Tergites I and II with large median dark spot each. Tergite III lacks dark patches. Tergites IV–IX with paired dark patches just lateral of midline, tergites IX–XII lack discernible patches. Sternites of both sexes brown to light-brown, well sclerotised. Most sternites furthermore possess paired dark spots mediolaterally. Pleural membrane wrinkled-placate, cream.

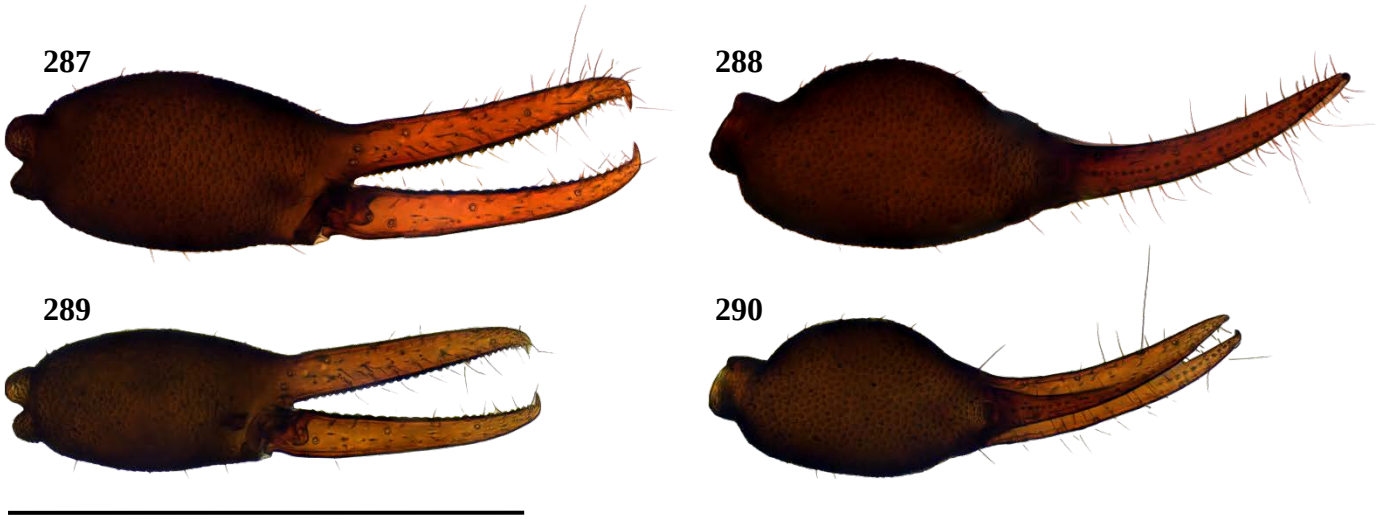
Pedipalp: Trochanter rounded anteriorly, regular in shape, granular, with same colouration as carapace. Small setae located on dorsal and dorso-lateral sides, apophysis located ventrally. Pedipalp femur (Fig. 292) and patella same colour as trochanter, granular. Femur narrow at base, widening evenly until just posterior of anterior margin, where there is a sudden constriction. Femur ratio: 3.18 (♀), 3.10 (♂). Pedipalp patella (Fig. 292) narrow and slightly angled at base, widening evenly into cone. Lyriform fissures visible just anterior of base, located on bulge, dorso-prolaterally on patella. Patella ratio: 2.54 (♀), 2.53 (♂).

Chela: (Figs. 287-292) Same colouration as rest of pedipalp in both sexes. Granular from stem to base of fingers. Both fingers smooth, just as long to slightly longer than hand-stem complex. Dorsal surface of chelal hand uniformly convex from stem to base of chelal fingers. Prolateral surface convex, retrolateral surface less so. Fixed chela finger with eight trichobothria, movable chela finger with four. Both fingers long, narrow, curving to interior. Venom apparatus present on both fingers. Trichobothrial pattern nearly identical to those of *G. deceptor* sp. nov., *G. liomendontus* sp. nov. and *G. modjadji* sp. nov., but differs with Trichobothria *b* and *sb* positioned closer to base of movable finger. Chelal teeth acute and retrorse. Fixed finger with 34 teeth (♀), 32 (♂). Four teeth behind venom apparatus on fixed chelal finger of equal size and spacing , followed by a large tooth. Teeth situated in one row, several large teeth located equally along the finger length (Fig. 294). Movable

finger with 25 teeth in both sexes. Teeth on movable finger degenerate into small points after about 10 teeth from anterior edge, regenerating near base of movable finger, particularly in females (Fig. 293). Chela ratio: 3.34 (♀), 3.33 (♂).

Chelicera: Hand with five setae located as in Fig. 5. Fixed cheliceral finger with six teeth arranged as in Fig. 295. Female galea complex with eight rami (Figs. 7 & 296), simple in males (Fig. 297). Rallum composed of single blade in both sexes. Serrula exterior with 18 lamella in females, 17 in males. Lamina exterior present in both sexes.

Coxae and legs: Pedipalp coxae same colour as carapace, with distinct shoulder. Legs I-IV with corresponding coxa tan to light-yellow in both sexes All legs diplotarsate (Figs. 299 & 300).



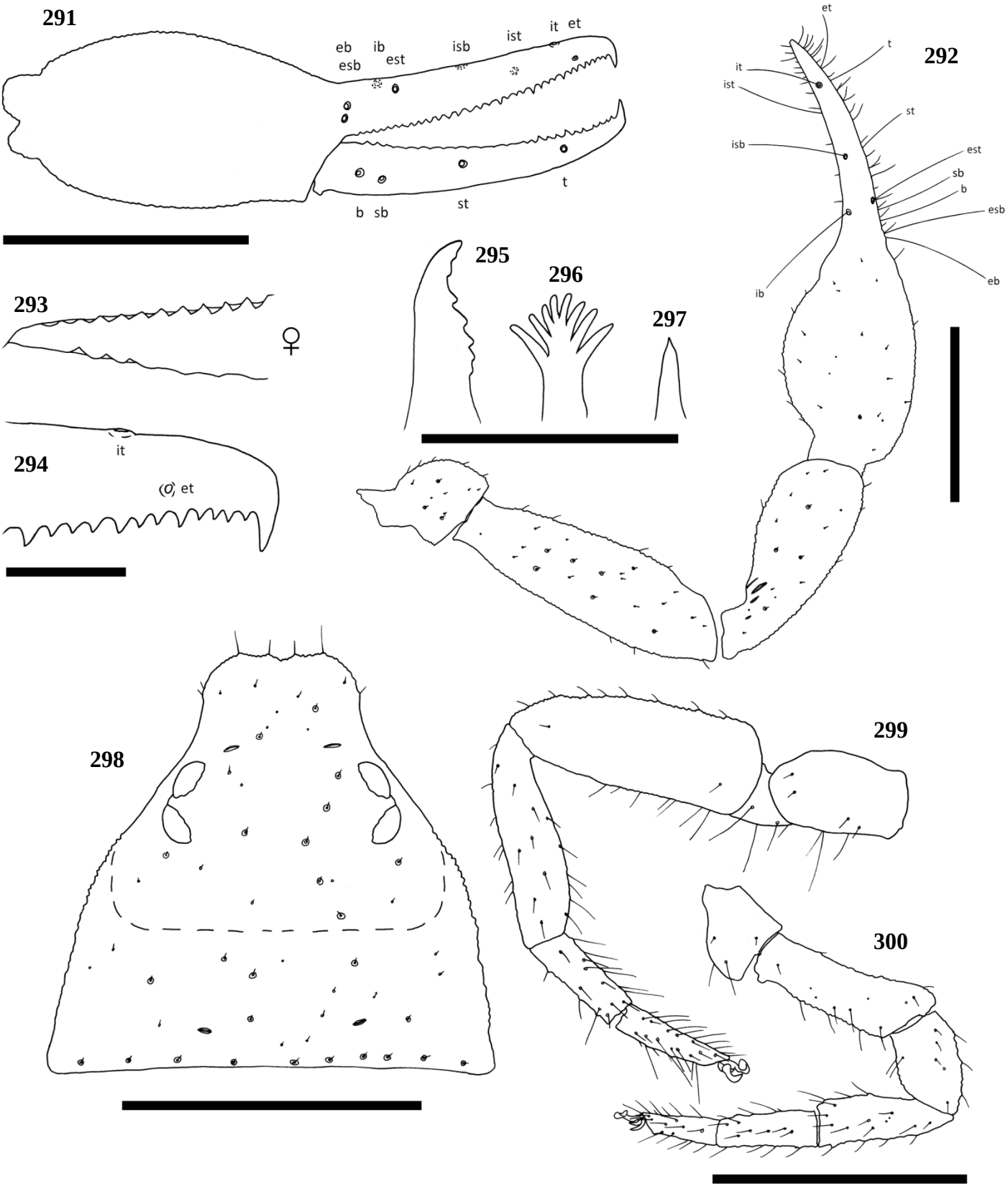
Figs. 287-290. Digital microscope photographs of *Geogarypus octoramosus* sp. nov. right chela: Female (**287**, **288**) and Male (**289**, **290**). **287**, **289**. Retrolateral view; **288**, **290**. Dorsal view. Scale bar: 1.00mm.

3.18.4 *Remarks*

The reduced number of rami (eight) in females of this species was found to be constant through all populations, unlike those of *G. variaspinosus* sp. nov. that can vary between the chelicerae of an individual.

3.18.5 *Additional material examined*

SOUTH AFRICA: *Free State*: 1♀, Harrismith, Platberg Nature Reserve, 28° 16'S, 29° 10'E, 1964m a.s.l., *Eucalyptus* plantation, Leaf litter sifting, leg. J.A. Neethling & L. Lotz, 15.III.2012 (NMBA P00226).



Figs. 291-300. *Geogarypus octoramosus* sp. nov. **291**-**296**, **298**-**300**. Female; **297**. Male. **291**. Right chela, retrolateral view; **292**. Right pedipalp, dorsal view; **293**. Basal teeth arrangement; **294**. Anterior teeth arrangement on fixed chelal finger; **295**. Chelicera movable finger, dorsal view; **296**, **297**. Galea; **298**. Carapace, dorsal view; **299**. Right leg IV, prolateral view; **300**. Right leg I, prolateral view. Scale bars: Figs. 291, 292, 298-300: 0.50mm; Figs. 294-297: 0.10mm.

KwaZulu-Natal: 1♀, Emangusi, Tembe Elephant Park, 27° 02'S, 32° 25'E, 95m a.s.l., Sand forest, leg. C.R. Haddad, 8.I.2001 (WAM T86752); 1♀, Paulpietersburg, Paulpietersburg Outskirts, 27° 20'S, 30° 29'E, 1225m a.s.l., Grassland, Leaf litter sifting, leg. J.A. Neethling & C. Luwes, 23.V.2012 (S.E.M.); 3♀, 3♂, Vryheid, Vryheid Mountain Nature Reserve, 27° 45'S, 30° 48'E, 1363m a.s.l., Thicket, Leaf litter sifting, leg. J.A. Neethling & C. Luwes, 22.V.2012 (morphological dissection, phylogenetic analysis and S.E.M.)

3.19 *Geogarypus olivaceus* (Tullgren, 1907)

Garypus olivaceus Tullgren, 1907a: 63, fig. 20; [**Holotype** ♀, South Africa, Free State, Bothaville [27° 23'S, 26° 38'E], leg. H. Brauns, 9.X.1899, deposited in ZMH, examined]; Tullgren, 1907b: 229.

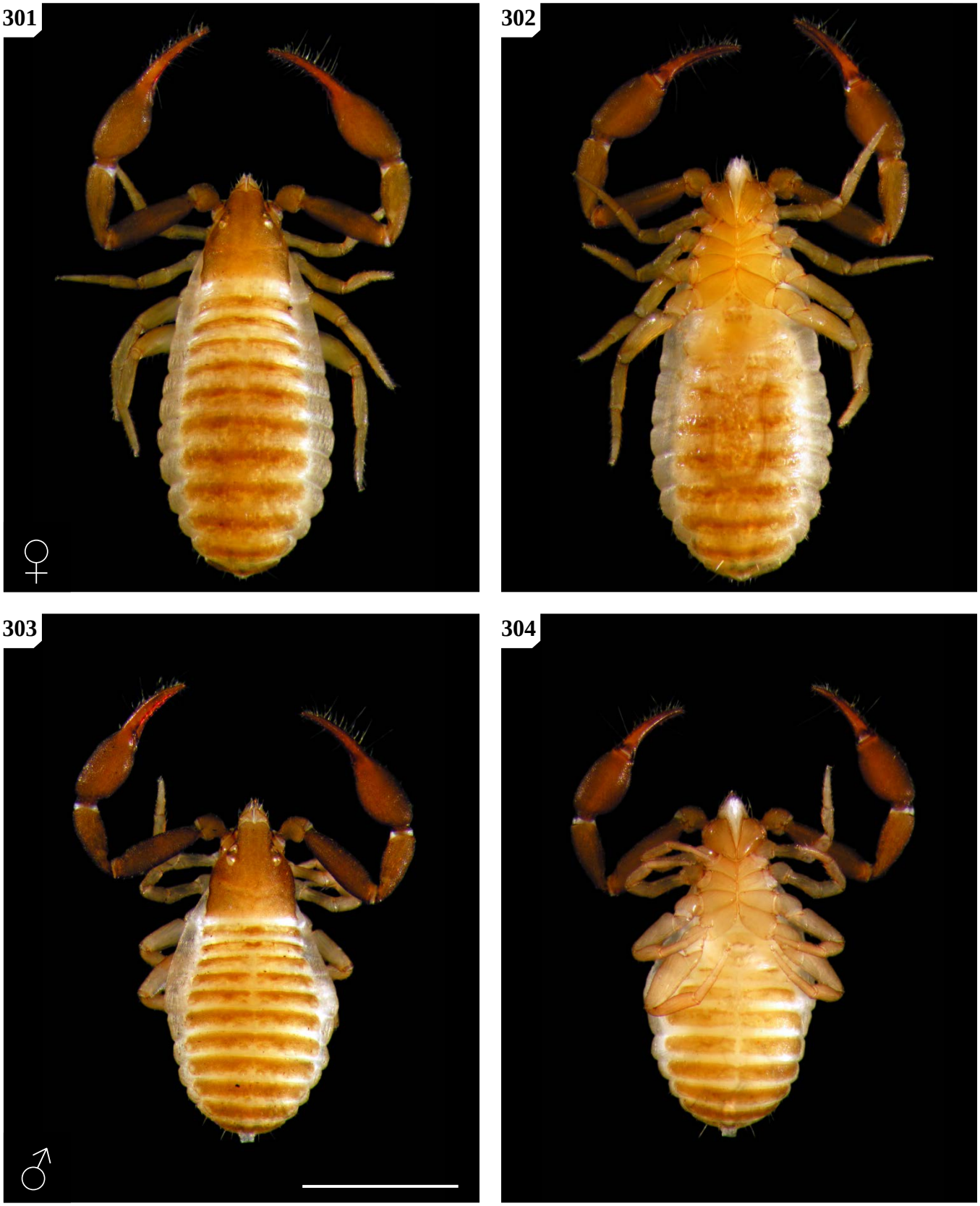
Geogarypus (*Geogarypus*) *olivaceus* (Tullgren, 1907): Beier, 1932a: 230, fig. 256; Roewer, 1937: 269; Beier, 1955: 301, fig. 20; Beier, 1958: 170.

Geogarypus olivaceus (Tullgren, 1907): Weidner, 1959: 115; Beier, 1964: 59; Beier, 1966: 461, 470; Lawrence, 1967: 89; Harvey, 1986: 760; Harvey, 1991: 258; Dippenaar-Schoeman & Harvey, 2000: 93.

3.19.1 *Diagnosis*

Medium species, pedipalpal femur length 0.60mm (♀), 0.57mm (♂), chela length (with stem) 1.11mm (♀), 1.05mm (♂), movable finger length 0.55mm (♀), 0.53mm (♂). Females can reach a length (cucullus to posterior abdominal margin) of 2.24mm, with males averaging 2.02mm. Carapace uniform light-brown in both sexes (Figs. 301 & 303). Pedipalp segments same colour as carapace, with the dorsal surface of the chela hand convex from the stem to the base of the chelal fingers. Abdominal tergites light-brown, with dark and cream patches in both sexes, while the abdominal sternites are light-brown and weakly sclerotised in females and well sclerotised in males (Figs. 302 & 304). Pedipalp coxae same colour as carapace, with distinct shoulder, legs I-IV, including coxae, yellow to tan in both sexes.

The species closely resembles smaller specimens of *Geogarypus flavus* in general morphology and colouration, which resulted in their synonymization by Beier (1964). The species can be separated on grounds of their basal chelal teeth morphology, with *G. olivaceus* having large and closely spaced basal teeth (Figs. 23 & 24), while *G. flavus* stat. nov. possesses smaller and more widely spaced teeth (Figs. 25 & 26).



Figs. 301-304. Digital microscope photographs of *Geogarypus olivaceus*, Female (**301**, **302**) and Male (**303**, **304**). **301**, **303**. Dorsal view; **302**, **304**. Ventral view. Scale bar: 1.00mm.

3.19.2 *Description*

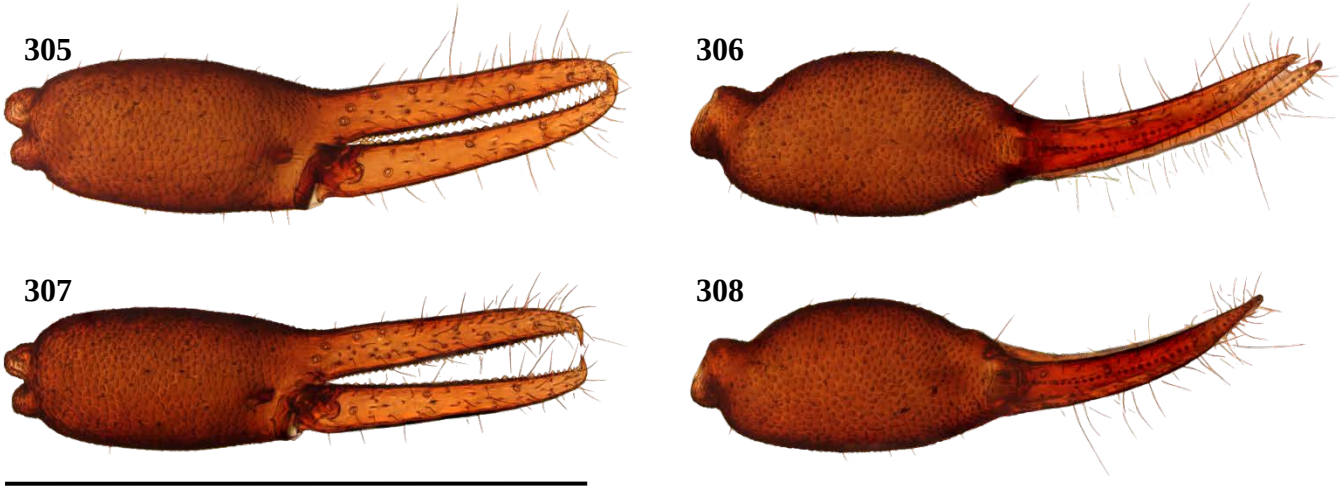
Carapace: Strongly sub-triangular, longer than broad in both sexes, with narrow furrow posterior to the eyes (Fig. 316). Carapace uniform light-brown, granular in both sexes. Strongly constricted anteriorly into cucullus, constriction beginning at medial furrow. Two pairs of corneate eyes situated on ocular tubercles, located ca. one third away from anterior edge. Four prominent setae located on anterior edge, row of eight setae situated along posterior edge of carapace, with small setae present and spread over carapace. Carapace ratio: 1.14 (♀), 1.08 (♂).

Abdomen: Abdominal tergites light-brown with both dark and cream patches on most plates. Tergites I and II with large median dark spot each, flanked by cream patches. Tergite III without dark patches, but with medial cream spot. Tergites IV–X with paired dark patches just lateral of midline. Tergites IV and V with medial cream spot. Tergites XI and XII lack any patches. Sternites light-brown, weakly sclerotised in females, strongly sclerotised in males. Abdomen of both sexes narrow and elongate. Pleural membrane wrinkled-placate, cream.

Pedipalp: Trochanter rounded anteriorly, granular, with same colouration as carapace. Small setae located on dorsal and dorso-lateral sides, ventral apophysis present. Pedipalp femur (Fig. 310) and patella same colour as trochanter, granular. Femur narrow at base, widening evenly until just posterior of anterior margin, where there is a sudden constriction. Femur ratio: 3.20 (♀), 3.04 (♂). Pedipalp patella (Fig. 310) narrow, slightly angled at base, widening evenly into cone. Lyriform fissures visible just anterior of base, located on bulge, dorso-prolaterally on patella. Patella ratio: 2.67 (♀), 2.51 (♂).

Chela: (Figs. 305-310) Same colouration as rest of pedipalp in both sexes, granular from stem to base of fingers. Both fingers smooth, just as long as hand-stem complex. Dorsal surface of chelal hand uniformly convex from stem to base of the chelal fingers. Pro- and retrolateral surfaces convex, with prolateral surface slightly more so. Fixed chela finger with eight trichobothria, movable chela finger with four. Both fingers long, narrow, curving to interior. Venom apparatus present on both fingers. Trichobothria *eb* and *esb* situated less than one trichobothrial width from each other, retrolaterally at base of fixed finger, *ib* located dorso-laterally on prolateral surface, one trichobothrial width distal of *esb*. Trichobothria *est* on retrolateral surface, three trichobothrial widths distal of *ib*, *isb* situated an equal distance from *est* as *est* from *ib* on opposite surface. Trichobothria *ist* over one third finger length from anterior finger edge, roughly in middle of prolateral surface, *it* on dorsal surface, one fifth finger length from anterior finger edge. Trichobothria *et* just anterior of *it* on retrolateral surface. Trichobothria *b* and *eb* somewhat forward of finger base, *b* ventrally in line with *esb*. Trichobothria *st* located halfway along movable finger, *t* located in middle between *st* and anterior edge of movable finger. Chelal teeth acute and retrorse. Fixed finger with 37 teeth (♀), 35 (♂). First tooth behind the

venom apparatus very small, followed by larger tooth (Fig. 314), remaining fixed chelal teeth situated in a single row, not decreasing in size basally, forming broader, less pointed teeth grouped tightly together. Movable finger with 29 teeth (♀), 28 (♂). First two teeth behind venom apparatus small and grouped close together, followed by larger teeth that degenerate into small points. Basal teeth regenerate, grouping tightly together, almost seeming fused in females (Fig. 315). In males, lesser degree of basal teeth regeneration, teeth remain separated. Chela ratio: 3.68 (♀), 3.73 (♂).



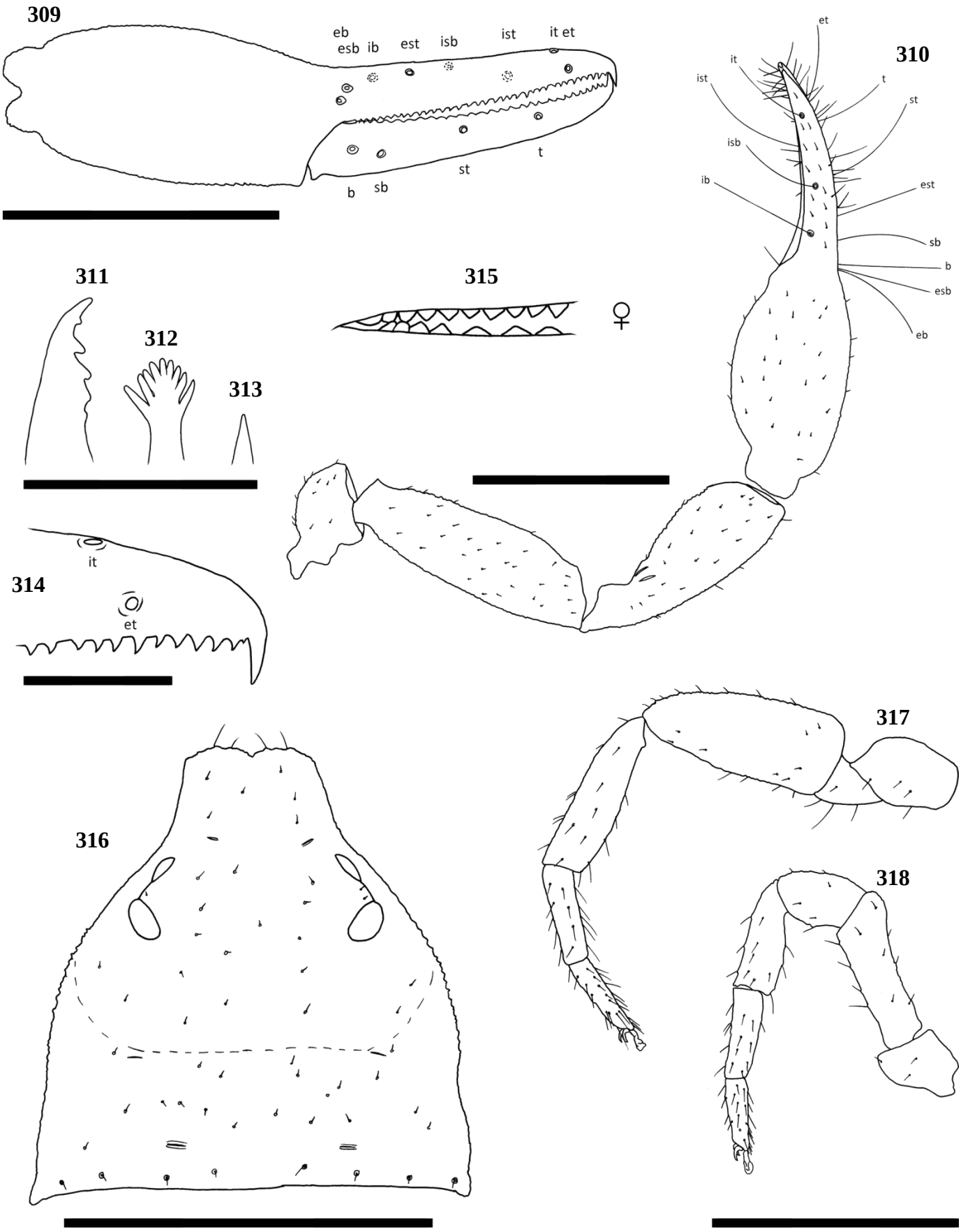
Figs. 305-308. Digital microscope photographs of *Geogarypus olivaceus*. right chela: Female (**305**, **306**) and Male (**307**, **308**). **305**, **307**. Retrolateral view; **306**, **308**. Dorsal view. Scale bar: 1.00mm.

Chelicera: Hand with five setae located as in Fig. 5. Fixed cheliceral finger with five teeth arranged as in Fig. 311. Female galea complex with nine rami (Fig. 312), simple in males (Fig. 313). Rallum composed of single blade in both sexes. Serrula exterior with 16 lamella in both sexes. Lamina exterior present in both sexes.

Coxae and legs: Pedipalp coxae same colour as carapace, with distinct shoulder. Legs I-IV, including coxae, yellow to tan in both sexes. All legs diplotarsate (Fig. 317 & 318).

3.19.3 *Remarks*

One of the first geogarypids to be described from South Africa by Tullgren (1907a). Given the morphological differences between *G. olivaceus* and *G. flavus*, together with the phylogenetic support obtained in this study, *G. flavus* stat. nov. is removed from synonymy with *G. olivaceus* and revalidated. The Western Cape distribution records for this species could potentially be misidentifications, as no specimens were collected in the province during field work undertaken as part of this study.



Figs. 309-318. *Geogarypus olivaceus*. **309-312**, **314-318**. Female; **313**. Male. **309**. Right chela. retrolateral view; **310**. Right pedipalp, dorsal view; **311**. Chelicera movable finger, dorsal view; **312**, **313**. Galea; **314**. Right chela fixed finger, anterior teeth arrangement; **315**. Female chela basal teeth arrangement; **316**. Carapace, dorsal view; **317**. Right leg IV, prolateral view; **318**. Right leg I, prolateral view. Scale bars: Figs. 309, 310, 316-318: 0.50mm; Figs. 311-314: 0.10mm.

3.19.4 *Additional material examined*

SOUTH AFRICA: *Free State*: 1♀, 1♂, Bloemfontein, Free State National Botanical Gardens, 29° 03'S, 26° 13'E, 1397m a.s.l., Grassland, leg. C.R. Haddad, 29.I.2005 (WAM T79036, T79037); 2♀, 2♂, Same locality, Grassland, Leaf litter sifting, leg. J.A. Neethling & C. Luwes, 2.II.2012 (NMBA P00188); Bloemfontein, Maselspoort, 29° 02'S, 26° 24'E, leg. C.R. Haddad, 4.II.2005 (WAM T79035); 3♀, 1♂, Bothaville, 27° 24'S, 26° 38'E, 1262m a.s.l., Woodland patch, Leaf litter sifting, leg. J.A. Neethling, 5.II.2012 (morphological dissection and phylogenetic analysis); 1♀, 5♂, Brandfort, Amanzi Private Game Reserve, 28° 36'S, 26° 26'E, 1430m a.s.l., Bushveld, Leaf litter sifting, leg. J.A. Neethling, 21.I.2014 (NMBA P00181).
KwaZulu-Natal: 1♀, Newcastle, Muller's Pass [27° 52'S, 29° 43'E], leg. R.F. Lawrence, III.1947 (NMSA 686); 1♂, Pomeroy, Gordon Memorial Mission [28° 34'S, 30° 26'E], leg. R. Godfrey, 11.IX.1930 (NMSA 16047).
North West: 1♂, Brits [25° 38'S, 27° 47'E], leg. R. Watmough, 6.I.1989 (NCA 89/1005).

3.19.5 *Additional material not examined*

SOUTH AFRICA: *KwaZulu-Natal*: Durban, Stamfort Hill [29° 50'S, 31° 02'E], leg. I. Trägårdh, 9.VII.1905 (examined by Tullgren 1907b); St. Lucia, Dukuduku Forest [28° 22'S, 32° 20'E], leg. I. Trägårdh, 27.VII.1905 (examined by Tullgren 1907b); 4♀, 6♂, 1 Tritonymph, Same locality, leg. R.F. Lawrence, XII.1960 (examined by Beier 1964); St. Lucia, Lake Sibayi [27° 22'S, 32° 43'E], leg. I. Trägårdh, 1.X.1905 (examined by Tullgren 1907b).
Mpumalanga: 1♀, Barberton [25° 47'S, 31° 03'E], leg. V. Fitzsimons, 15.X.1938 (examined by Beier 1964); 3♀, Kruger National Park, Malelane Camp [25° 29'S, 31° 31'E], leg. R.F. Lawrence, 3.XII.1963 (examined by Beier 1966); 1♀, 1♂, Kruger National Park, Pretoriuskop Camp [25° 10'S, 31° 16'E], leg. R.F. Lawrence, 2.XII.1963 (examined by Beier 1966).
Western Cape: 1♀, 1♂, Prins Albert, Swartberg Pass, Platberg [33° 21'S, 22° 03'E], 1525m a.s.l., 06.I.1951 (examined by Beier 1955); 1♀, Rooi-Els [34° 18'S, 18° 49'E], leg. J.R. Grindley, 17.XII.1962 (examined by Beier 1966).

3.20 *Geogarypus tectomaculatus* sp. nov.

Holotype: ♀, SOUTH AFRICA, Mpumalanga, Graskop, R532 Rock Formations, 24° 54'S, 30° 52'E, 1500m a.s.l., Highveld Grassland, Leaf litter sifting, leg. J.A. Neethling, 2.X.2012 (NMBA P00212).
Paratypes: 3♀, 2♂, Same data as holotype (NMBA P00213).

3.20.1 *Etymology*

The species name is a combination of the Latin words *tectum*, meaning roof and *macula*, meaning spot or blemish. The name refers to the tergite markings, particularly of the females, that differ from the other South African geogarypid species in appearing as small distinct spots, rather than large patches.

3.20.2 *Diagnosis*

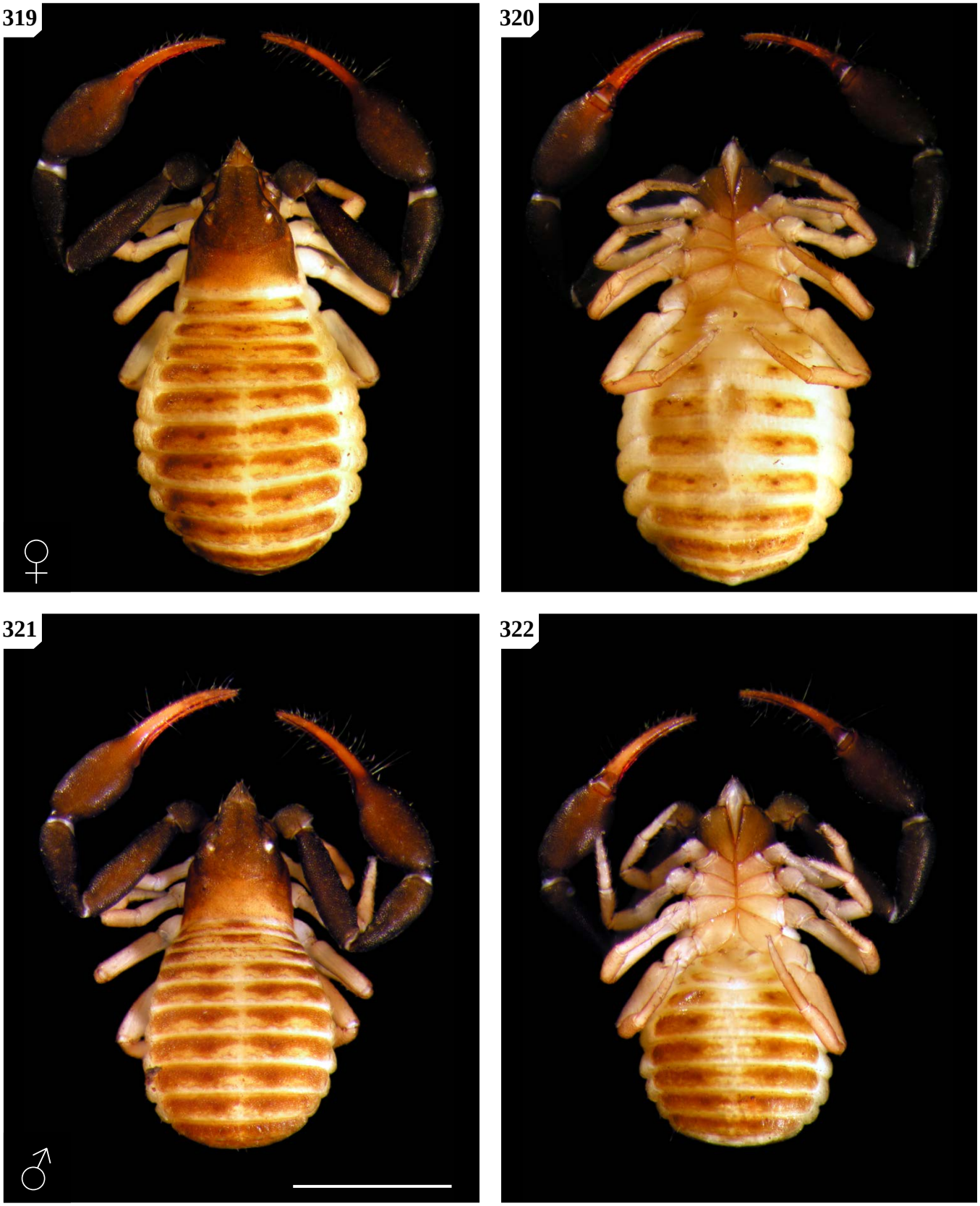
Large species, pedipalpal femur length 0.86mm (♀), 0.83mm (♂), chela length (with stem) 1.44mm (♀), 1.40mm (♂), movable finger length 0.70mm (♀), 0.72mm (♂). Females reach an average length (cucullus to posterior abdominal margin) of 2.59mm, while males average 2.20mm. The carapace is dark brown in both sexes, with the posterior half being slightly lighter (Figs. 319 & 321). Pedipalp segments are the same colour as the carapace, with the dorsal surface of the chela hand convex from the stem to the base of the chelal fingers. Abdominal tergites brown with cream patches and dark spots in both sexes, while the abdominal sternites are brown to light-brown with dark spots in both sexes (Figs. 320 & 322). Legs I-IV, including, coxae tan to pale yellow in both sexes.

Closely resembling *Geogarypus flavus* stat. nov., *G. tectomaculatus* sp. nov. can be distinguished by having fewer chelal teeth as well as possessing relatively large basal teeth that are grouped tightly next to each other, while *G. flavus* stat. nov. has smaller basal teeth that are separate from one another.

3.20.3 *Description*

Carapace: Strongly sub-triangular, slightly longer than broad in both sexes, with narrow furrow posterior to eyes (Fig. 333). Posterior half somewhat lighter than anterior half. Heavily constricted anteriorly into cucullus, constriction beginning at medial furrow. Two pairs of corneate eyes situated on ocular tubercles, located ca. one third from anterior edge. Four prominent setae located on anterior edge, row of ten setae located on posterior margin. Numerous small setae present on carapace. Carapace ratio: 1.02 (♀), 1.06 (♂).

Abdomen: Abdominal tergites brown with cream patches and dark spots on most plates. Tergites I and II with median dark spot each, flanked by cream patches. Tergite III without dark patches, but with central cream coloured band extending almost entire length of tergum. Tergites IV–X with medial cream patch, with paired dark spots just lateral of midline, flanked laterally by small cream patches.



Figs. 319-322. Digital microscope photographs of *Geogarypus tectomaculatus* sp. nov., Female (**319**, **320**) and Male (**321**, **322**). **319**, **321**. Dorsal view; **320**, **322**. Ventral view. Scale bar: 1.00mm.

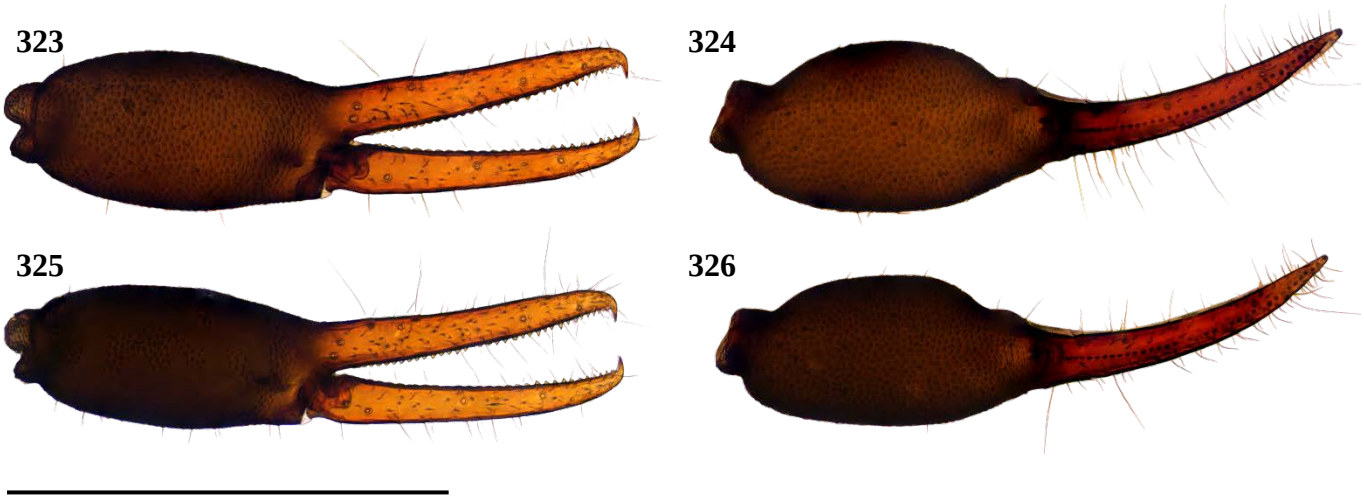
Dark spots are distinct in females, sometimes fainter and larger in males. Tergites XI and XII lack patches. Setae of posterior setal rows of tergites, predominantly in females, situated on pale plates with dark edges, making plates distinctly visible. Sternites well sclerotised in both sexes, with paired dark points located laterally of cream medial line. Pleural membrane wrinkled-placate, cream.

Pedipalp: Trochanter rounded anteriorly, granular, with same colouration as carapace. Small setae located on dorsal and dorso-lateral sides, ventral apophysis present. Pedipalp femur (Fig. 328) and patella granular, same colour as trochanter. Femur narrow at base, widening evenly until just posterior of anterior margin, where it is suddenly constricted. Femur ratio: 3.60 (♀), 3.87 (♂). Pedipalp patella (Fig. 328) narrow, slightly angled at base, widening evenly into cone. Lyriform fissures visible just anterior to base, located on bulge, dorso-prolaterally on patella. Patella ratio: 2.91 (♀), 2.76 (♂).

Chela: (Figs. 323-328) Same colour as rest of pedipalp in both sexes, granular from stem up to base of fingers. Both fingers smooth, just as long as hand-stem complex. Dorsal surface of chelal hand uniformly convex in shape from stem to base of chelal fingers. Both pro- and retrolateral surfaces slightly convex in shape, prolateral surface more so than retrolateral. Fixed chela finger with eight trichobothria, movable chela finger with four trichobothria. Both fingers long, narrow, curving to interior. Venom apparatus present on both fingers. Trichobothria *eb* and *esb* situated just under one trichobothrial width from each other, located retrolaterally at base of fixed finger, *ib* located dorso-laterally on prolateral surface, four trichobothrial widths distal of *esb*. Trichobothria *est* located one trichobothrial width distal, opposite from *ib* in females, three trichobothrial widths distal in males, resulting in *est* positioned just proximal of *isb*. Trichobothria *isb* located almost dorsally, roughly halfway along finger in females, one third finger length from base of fixed finger in males, while *ist* located one third finger length from anterior finger edge, roughly in middle of the prolateral surface in both sexes. Trichobothria *it* located on dorsal surface, roughly one quarter finger length from anterior finger edge, *et* situated anteriorly on retrolateral surface. Trichobothria *b* and *eb* on movable finger situated somewhat forward of finger base, *b* ventrally in line with *esb*. Trichobothria *st* positioned just before halfway along movable finger, *t* located midway between *st* and anterior edge of movable finger. Chelal teeth acute, retrorse, curving back slightly. Fixed finger with 34 teeth (♀), 36 (♂). First three teeth behind venom apparatus small, grouping together to form distinct group (Fig. 332). This group is followed by remaining fixed chelal teeth, situated in single row, only decreasing slightly in size to base, with distinctly larger teeth located throughout length of fixed finger. Movable finger with 28 teeth (♀), 30 (♂). In both sexes basal teeth on movable finger regenerate into distinct teeth, following small tooth points. Chela ratio: 3.67 (♀), 4.04 (♂).

Chelicera: Hand with five setae located as in Fig. 5. Fixed cheliceral finger with six teeth arranged as in Fig. 329. Female galea complex with nine rami (Fig. 330), simple with single spinule in males (Fig. 331). Rallum composed of single blade in both sexes. Serrula exterior with 15 lamella in both sexes. Lamina exterior present in both sexes.

Coxae and legs: Pedipalpal coxae same colour as carapace, with distinct shoulder. Legs I-IV, including coxae, tan to pale yellow in both sexes. All legs diplotarsate (Figs. 334 & 335).



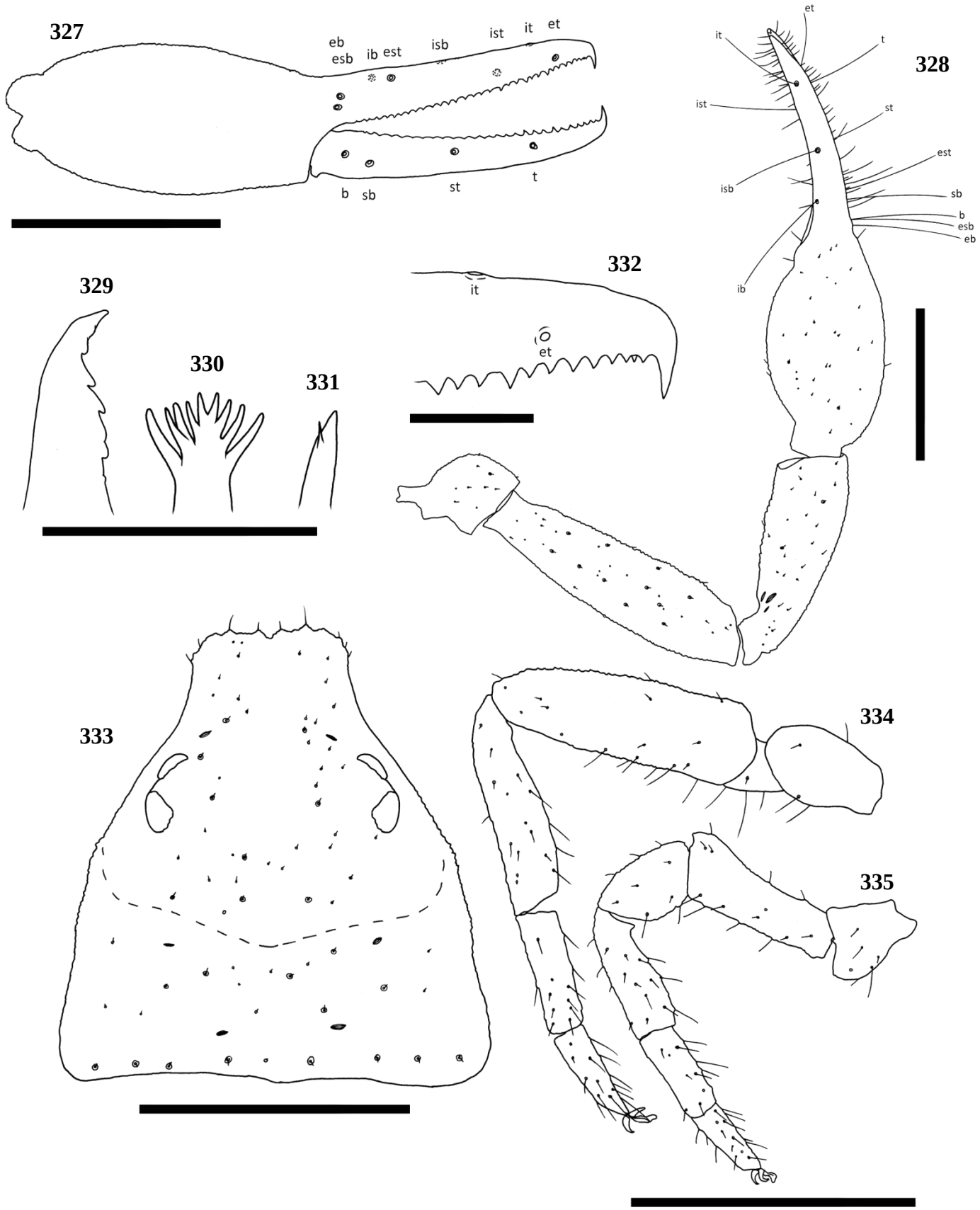
Figs. 323-326. Digital microscope photographs of *Geogarypus tectomaculatus* sp. nov. right chela: Female (**323**, **324**) and Male (**325**, **326**). **323**, **325**. Retrolateral view; **324**, **326**. Dorsal view. Scale bar: 1.00mm.

3.20.4 *Remarks*

The second largest geogarypid species in South Africa, being just slightly smaller than *Afrogarypus robustus* comb. nov. Males of the species also possess the largest chela ratios, with chela that are four times as long as wide.

3.20.5 *Additional material examined*

SOUTH AFRICA: *Mpumalanga*: 1♀, Graskop, God's Window, 24° 52'S, 30° 53'E, 1705m a.s.l., Highveld bush with indigenous forest patches, Leaf litter sifting, leg. J.A. Neethling, 28.IX.2012 (morphological dissection); 3♀, 1♂, Same locality, Wonderview, 24° 52'E, 30° 54'E, 1723m a.s.l., Highveld bush, Leaf litter sifting, leg. J.A. Neethling, 30.IX.2012 (morphological dissection & phylogenetic analysis); 1♂, Sabie, Bergvliet State Forest, 25° 10'S, 30° 48'E, Pitfall trapping, leg. A. van den Berg, 27.XI.1986 (NCA 87/444).



Figs. 327-335. *Geogarypus tectomaculatus* sp. nov. **327-330**, **332-335**. Female; **331**. Male; **327**. Right chela, retrolateral view; **328**. Right pedipalp, dorsal view; **329**. Chelicera movable finger, dorsal view; **330**, **331**. Galea; **332**. Right chela fixed finger, anterior teeth arrangement; **333**. Carapace, dorsal view; **334**. Right leg IV, prolateral view; **335**. Right leg I, prolateral view. Scale bars: Figs. 327, 328, 333-335: 0.50mm; Fig. 331: 0.10mm.

3.21 *Geogarypus variaspinosus* sp. nov.

Holotype: ♀, SOUTH AFRICA, Northern Cape, Olifantshoek, 27° 56'S, 22° 44'E, 1294m a.s.l., Rocky veld, Leaf litter sifting, leg. J.A. Neethling, 16.VI.2013 (NMBA P00223).
Paratypes: 2♂, Same data as holotype (NMBA P00225).

3.21.1 *Etymology*

The species name refers to the variable number of rami that can occur on the galea of a female.

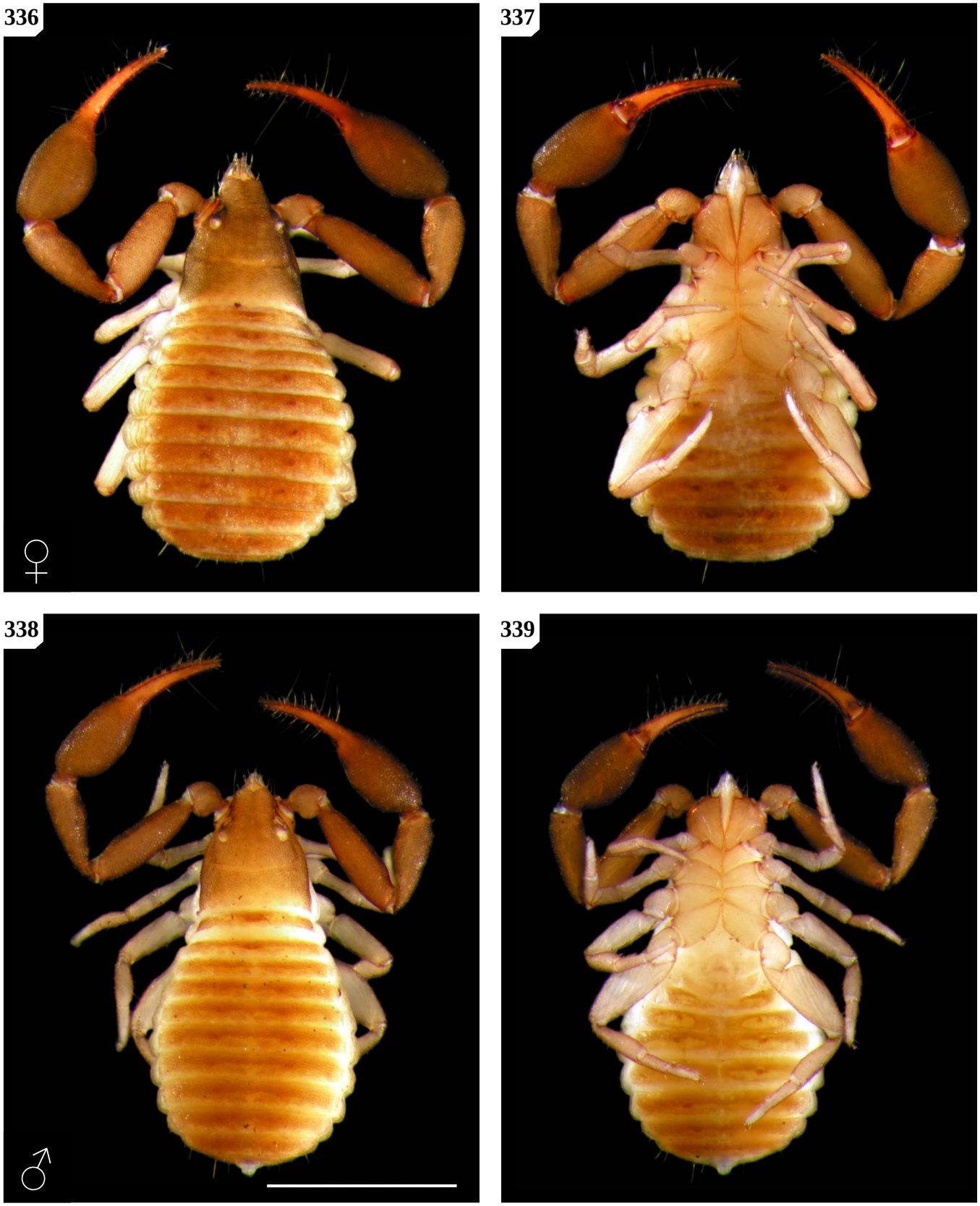
3.21.2 *Diagnosis*

Medium species, pedipalpal femur length 0.79mm (♀), 0.74mm (♂), chela length (with stem) 1.29mm (♀), 1.08mm (♂), movable finger length 0.64mm (♀), 0.52mm (♂). Females reach a length (cucullus to posterior abdominal margin) of 2.05mm, while males average 1.99mm. Carapace overall brown, with the medial furrow and posterior edge slightly lighter in both sexes (Figs. 336 & 338). All pedipalp segments same colour as carapace, with the dorsal surface of the chela hand convex from the stem to the base of the chelal fingers. Abdominal tergites uniformly brown to light-brown, with dark patches in both sexes, while the abdominal sternites are light-brown with faint dark spots (Figs. 337 & 339). Legs I-IV, including coxae, tan in both sexes.

The species closely resembles both *Geogarypus octoramosus* sp. nov. in general morphology and colouration, but can be distinguished by the variable number of rami found on the galea of females, which are always fewer than eight (five to seven). Males are difficult to distinguish from related congeners, but resemble smaller, lighter females.

3.21.3 *Description*

Carapace: Strongly sub-triangular, longer than broad in both sexes, with narrow furrow posterior to eyes. Carapace uniformly brown, granular, furrow and posterior edge slightly paler. Heavily constricted interiorly into cucullus, constriction beginning at medial furrow. Two pairs of corneate eyes situated on ocular tubercles, located ca. one third away from anterior edge (Fig. 352). Four prominent setae located on anterior edge, row of ten setae located on posterior margin. Carapace ratio: 1.04 (♀), 1.05 (♂).



Figs. 336-339. Digital microscope photographs of *Geogarypus variaspinosus* sp. nov., Female (**336**, **337**) and Male (**338**, **339**). **336**, **338**. Dorsal view; **337**, **339**. Ventral view. Scale bar: 1.00mm.

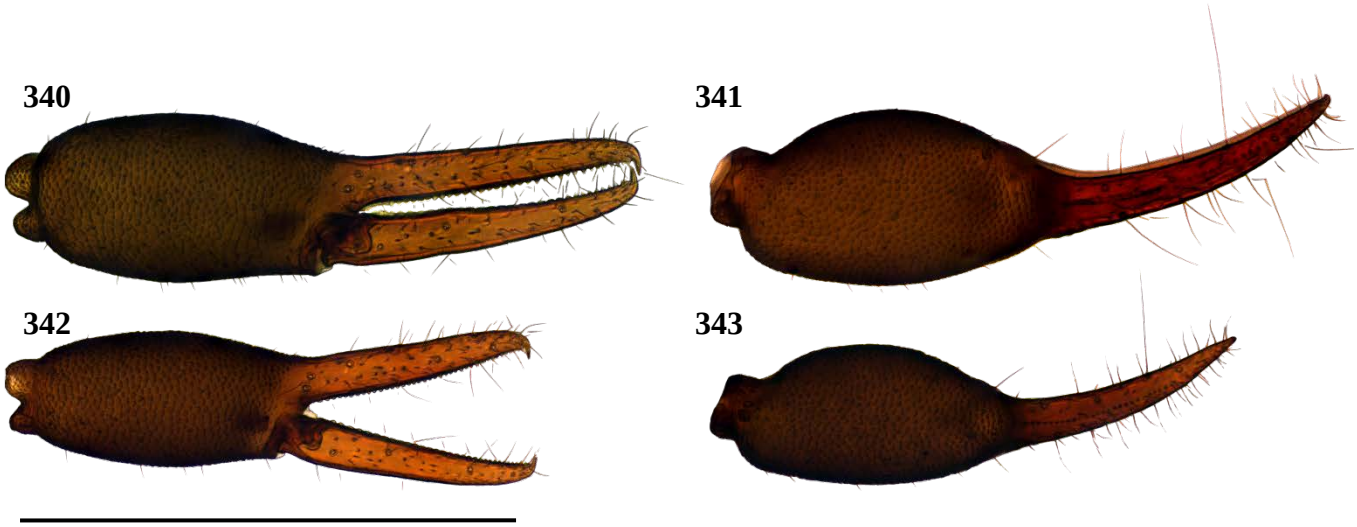
Abdomen: Abdominal tergites overall light-brown, dark patches and faint cream markings present. Tergites I and II with large medial dark spot each. Tergite III lacks dark patches. Tergites IV–X with paired dark patches just lateral of the midline. May appear very faint in some specimens. Tergites XI and XII lack dark patches. Sternites light-brown, well sclerotised in both sexes. Paired dark spots, located laterally of midline, present. Pleural membrane wrinkled-placate, cream.

Pedipalp: Trochanter rounded anteriorly, slightly curved, granular, same colour as carapace. Small setae located on dorsal and dorso-lateral sides, ventral apophysis present. Pedipalp femur (Fig. 345) and patella same colour as trochanter, granular. Femur narrow at base, widening evenly until just posterior of anterior margin, where it is constricted. Femur ratio: 3.39 (♀), 3.62 (♂). Pedipalp patella (Fig. 345) narrow and slightly angled at base, widening evenly into cone. Lyriform fissures visible just anterior of base, located on a bulge, dorso-prolaterally on patella. Patella ratio: 2.90 (♀), 2.97 (♂).

Chela: (Figs. 340-345) Same colouration as rest of pedipalp in both sexes, granular from stem up to base of fingers. Both fingers smooth, as long to slightly shorter than hand-stem complex. Dorsal surface of chelal hand uniformly convex in shape from the stem to the base of the chelal fingers. Both pro- and retrolateral surfaces slightly convex in shape, prolateral surface slightly more so. Fixed chela finger with eight trichobothria, movable chela finger with four trichobothria. Both fingers long and narrow, curving to the interior. Venom apparatus present on both fingers. Trichobothria *eb* and *esb* situated one trichobothrial width from each other, located retrolaterally at base of fixed finger, *ib* located dorso-prolaterally, four trichobothrial widths distal of *esb*. Trichobothria *est* located on retrolateral surface, just anterior of *ib*, *isb* situated an equal distance from *est* as *est* is from *esb*, on opposite surface. Trichobothria *ist* located one third finger length from anterior finger edge, somewhat ventral on prolateral surface, *it* located on dorsal surface, one fifth finger length from anterior finger edge. Trichobothria *et* situated just anterior of *it*, on retrolateral surface. Trichobothria *b* and *eb* are situated somewhat forward of finger base, *b* ventrally in line with *esb*. Trichobothria *st* variable, positioning from one third finger length from base of finger to just under halfway along length of movable finger. Trichobothria *t* is located one quarter finger length from anterior edge of movable finger. Chelal teeth acute, retrorse, some curving back slightly. Fixed finger with 38 teeth (♀), 40 (♂). First two teeth behind venom apparatus small, followed by larger tooth (Fig. 347). Rest of fixed finger teeth situated in single row, not decreasing in size to base of finger. In females basal seven teeth are fused, followed by teeth that group tightly next to each other. Movable finger with 31 teeth (♀), 32 (♂). First two teeth behind the venom apparatus of movable finger small, grouped close together, followed by larger teeth that degenerate into tooth plates. In females basal teeth regenerate and group tightly together, almost seeming fused (Fig. 346). In males lesser degree of basal teeth regeneration, teeth remain situated widely apart. Chela ratio: 3.57 (♀), 3.75 (♂).

Chelicera: Hand with five setae located as in Fig. 5. Fixed cheliceral finger with six teeth arranged as in Fig. 348. Female galea complex with variable number of rami, ranging from five to seven (Figs. 349 & 350). Male galea simple, without spinules (Fig. 351). Rallum composed of a single blade in both sexes. Serrula exterior with 16 lamella in both sexes. Lamina exterior present in both sexes.

Coxae and legs: Pedipalpal coxae same colour as carapace, with distinct shoulder. Legs I-IV, including coxae, tan in colour in both sexes.. All legs diplotarsate (Figs. 353 & 354).



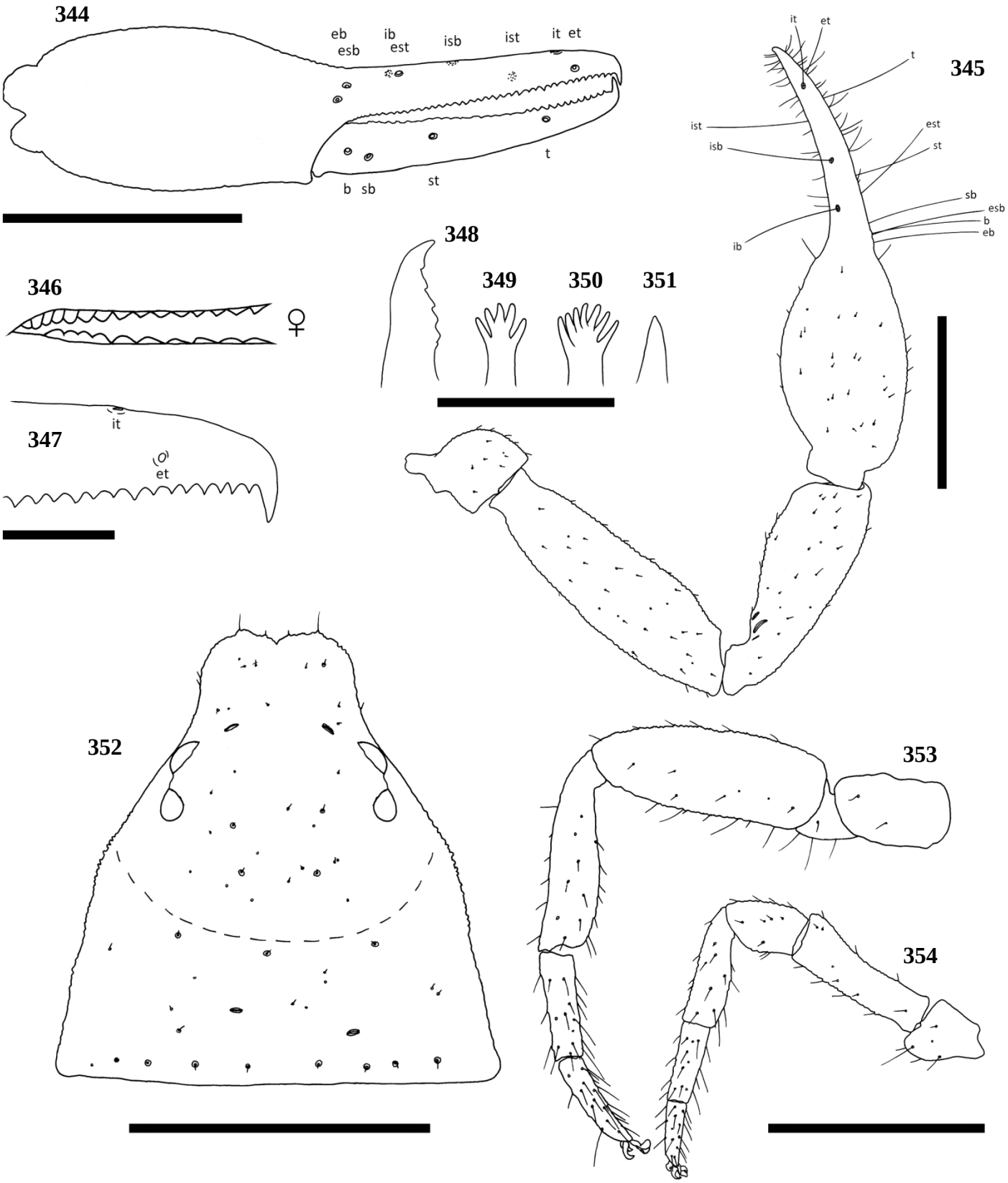
Figs. 340-343. Digital microscope photographs of *Geogarypus variasponosum* sp. nov. right chela: Female (**340**, **341**) and Male (**342**, **343**). **340**, **342**. Retrolateral view; **341**, **343**. Dorsal view. Scale bar: 1.00mm.

3.21.4 *Remarks*

Geogarypus variaspinosus sp. nov. is unique in that in all the females that were studied presented chelicerae with galeae that differed in the number of rami present. Of particular interest is that in many specimens the number of rami varied even between the left and right sides, but always numbered between five and seven.

3.21.4 *Additional material examined*

SOUTH AFRICA: *Northern Cape*: 1♀, 1♂, Douglas, Sunset View River Guesthouse, 29º 04'S, 23º 44'E, 985m a.s.l., Bushveld, Leaf litter sifting, leg. J.A. Neethling, 19.VI.2013 (NMBA P00224); 4♀, 4♂, Olifantshoek, 27º 56'S, 22º 44'E, 1294m a.s.l., Rocky veld, Leaf litter sifting, leg. J.A. Neethling, 16.VI.2013 (morphological dissection and phylogenetic analysis).



Figs. 344-354. *Geogarypus variaspinosus* sp. nov. **344-350**, **352-354**. Female; **351**. Male. **344**. Right chela, retrolateral view; **345**. Right pedipalp, dorsal view; **346**. Basal teeth arrangement; **347**. Anterior teeth arrangement on fixed chelal finger; **348**. Chelicera movable finger, dorsal view; **349**, **350**, **351**. Galea; **352**. Carapace, dorsal view; **353**. Right leg IV, prolateral view; **354**. Right leg I, prolateral view. Scale bars: Figs. 344, 345, 352-354: 0.50mm; Figs. 347-351: 0.10mm.

CHAPTER 4 - BIOGEOGRAPHY

4.1 *Introduction*

Worldwide, the Geogarypidae are represented by 67 recognized species recorded from 69 countries, distributed mostly along the equatorial belt (Petrov 1997; Harvey 2000; Harvey 2013). They can be found in habitats ranging in altitude from 0-3200m above sea level (Beron 2002). South Africa currently has the highest number of described species (n=9), followed by Kenya (n=8) and India (n=7). The family also contains one of the most widespread pseudoscorpion species, *Geogarypus longidigitatus* (Rainbow, 1897), which can be found across 150^{o} of longitude, throughout the Pacific region from Thailand to the Easter Islands (Harvey 2000). Although predominantly tropical and temperate in nature, most Geogarypidae dwell in leaf litter in forested areas. Their adaptability has allowed some species to inhabit more peculiar habitats, including hostile intertidal zones (Haddad & Dippenaar-Schoeman 2009) and birds' nests (Turienzo, Di Iorio & Mahnert 2010).

Within the Geogarypidae, the genus *Geogarypus* Chamberlin, 1930 is the most widespread, with species being recorded from Southern Europe, Africa, Asia, Australia, and as far south as Argentina in South America (Harvey 1981; Harvey 1986; Harvey 1987b; Mahnert *et al.* 2011). The remaining genera, on the other hand, are more restricted in their distribution, with *Afrogarypus* Beier, 1931 only being recorded from Africa and surrounding islands such as the Seychelles (Spaull 1979), *Indogarypus* Beier, 1955 being restricted to India and Sri Lanka (Harvey 1986), and *Castigarypus* gen. nov. being endemic to eastern South Africa (current study).

4.2 *South African biomes*

South Africa's geography is characterized by a high interior plateau bordered by high mountain ranges stretching from the south, inland of the eastern coast, and ending in the Northern Soutpansberg Mountains in the north-east (Fig. 355). Like many southern landmasses, South Africa differs from most northern lands by retaining considerable tracts of ancient landscape. Although most of its geological architecture was only formed following the Gondwanaland breakup, many elements were inherited from earlier times (Cowling, Richardson & Pierce 2004).

The climate in South Africa is characterized by increasing aridity in an east to west plane, with the highest precipitation occurring in the coastal regions along the mountain ranges. These areas regularly receive annual rainfall above 1000mm. Some of the most western parts of the subcontinent receive less than 250mm annually, while the interior generally varies in rainfall from 300-800mm annually (Mansell & Erasmus 2002). Two of the world's floristic regions can be found within South Africa, namely the Paleotropical (comprising mainly open woodland, savanna and grassland vegetation) and the Cape Floristic Region (comprising fynbos vegetation), with the latter being endemic to the southern part of South Africa (Cox 2001).

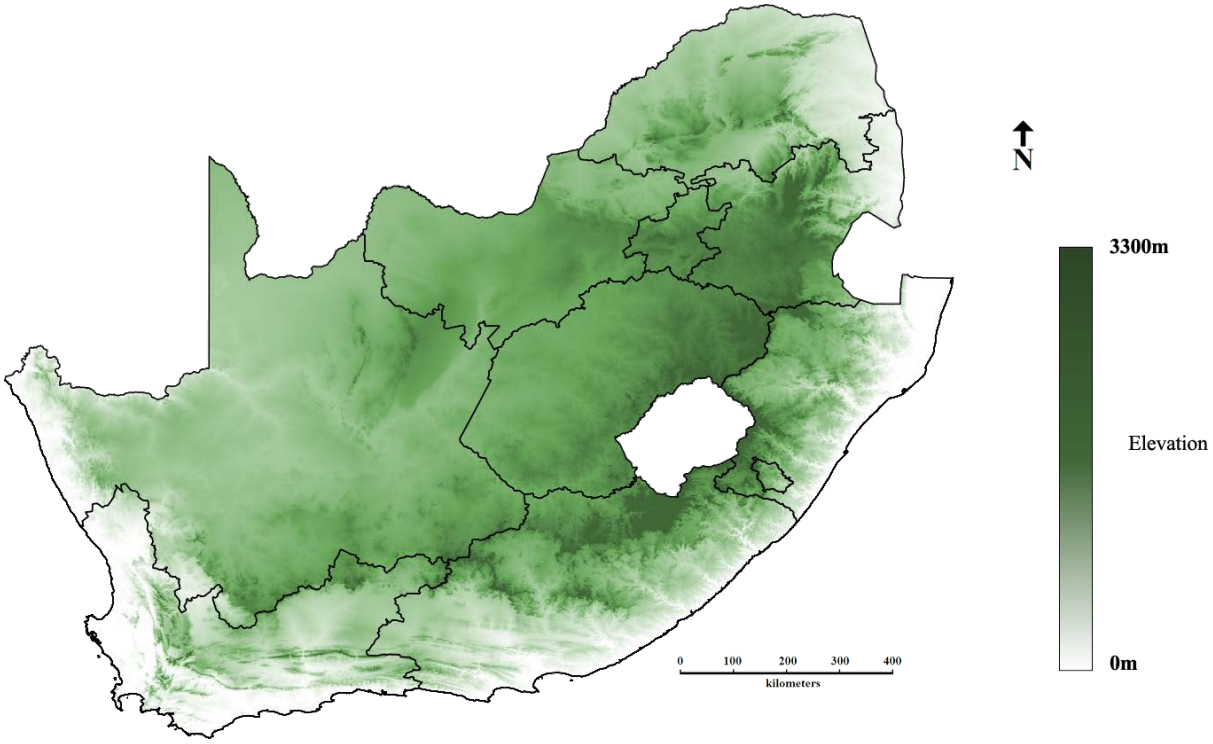


Fig. 355. Topographical map of South Africa highlighting the low altitude coastal areas that are bordered by high mountain ranges, that in turn form the rim of the high altitude central plateau. Map shapefile acquired from http://www.diva-gis.org/gdata (accessed 25.I.2015).

Mucina & Rutherford (2006) recognized eight distinct biomes within South Africa, which include the Albany thicket, desert, indigenous forest, fynbos, grassland, Nama-Karoo, savanna and succulent Karoo biomes (Fig. 356).

The Albany thicket was only recently classified as a distinct biome. The biome occurs where the rainfall is insufficient to sustain true forests, but where fire protection is present in a degree that allows for the growth of dense stands of trees and shrubs. These trees are not tall enough to be classified as true forests, nor does the ground stratum contain enough grasses to be classified as savanna. This biome is dominant along the Afromontane coastal belt, and stretches from the central

coast of KwaZulu-Natal all the way to Swaziland. Also referred to as a transitional thicket, the biome contains many vegetation types found in adjacent biomes, and is dominated by evergreen, sclerophyllous or succulent trees, shrubs and vines.

The true desert biome of southern Africa is primarily located in Namibia, although the southernmost edge does extend within north-western South Africa, and can be found in the lower Orange River valley near the Springbokvlakte area of the Richtersveld. The climate is more extreme than that of the Nama- or succulent Karoo, and annual rainfall can vary from 10-70mm, with very arid summer conditions. Vegetation consists mainly of annual plants such as low grasses that sprout after rains (Mucina & Rutherford 2006).

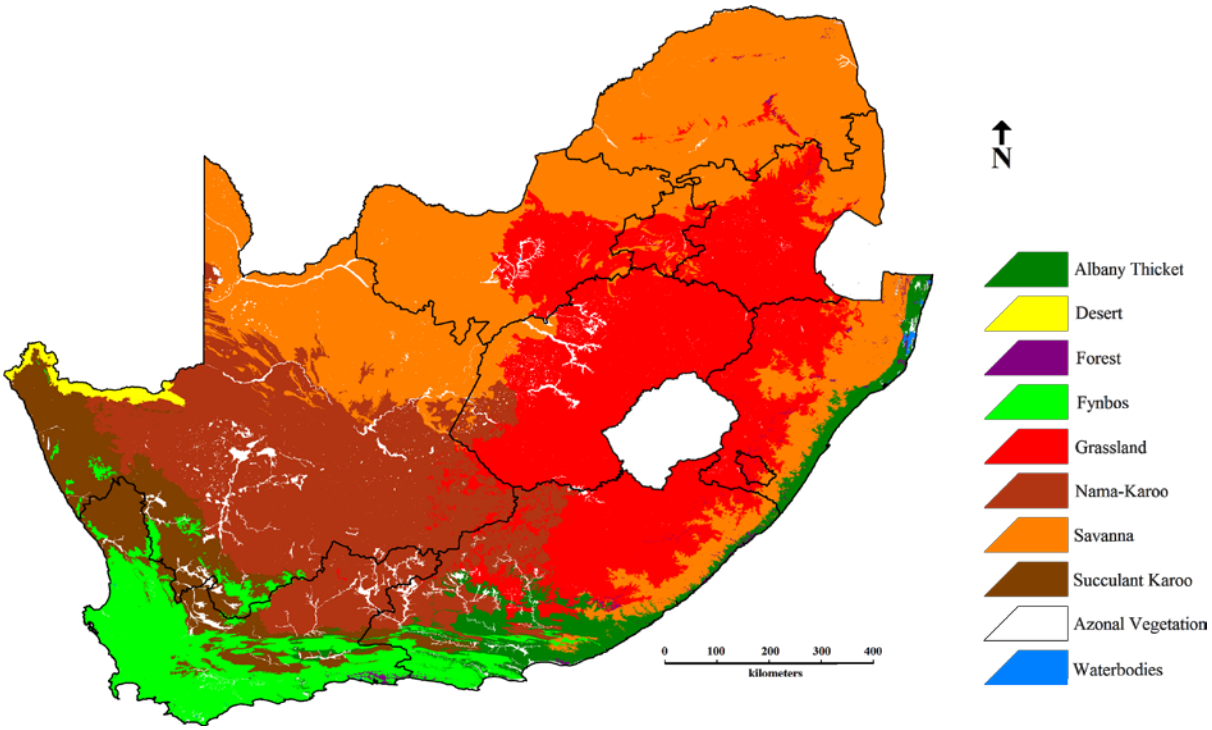


Fig. 356. Vegetation map of South Africa, depicting the biomes as delineated by Mucina & Rutherford (2006). Vegetation map shapefile acquired from http://bgis.sanbi.org/vegmap/biomes.asp (accessed 12.X.2014).

Indigenous forests in South Africa tend to occur in patches (Fig. 357) in areas that receive more than 500mm of rain in winter and 750mm in summer. Found at elevations ranging from 0-2100m above sea level, they typically occur along mountains and within gorges, and these patches rarely cover more than 1km^2.

South African indigenous forests can be divided into three broad types, namely Afromontane forests (usually associated with montane areas), coastal forests, and sand forest (endemic to the Maputaland centre of endemism in northern KwaZulu-Natal and southern Mozambique). Each of

these forest types is unique in terms of geology and plant composition (Mucina & Rutherford 2006). They are characterized by high humidity, a dense and continuous evergreen canopy and shaded ground cover. Due to their shaded nature, ground level vegetation is usually poorly developed, though many species of ferns and herbaceous plants flourish in these conditions. Due to its patchy nature, the forest biome is, by percentage cover, the smallest of the South African biomes, covering only about 0.30% of the country.

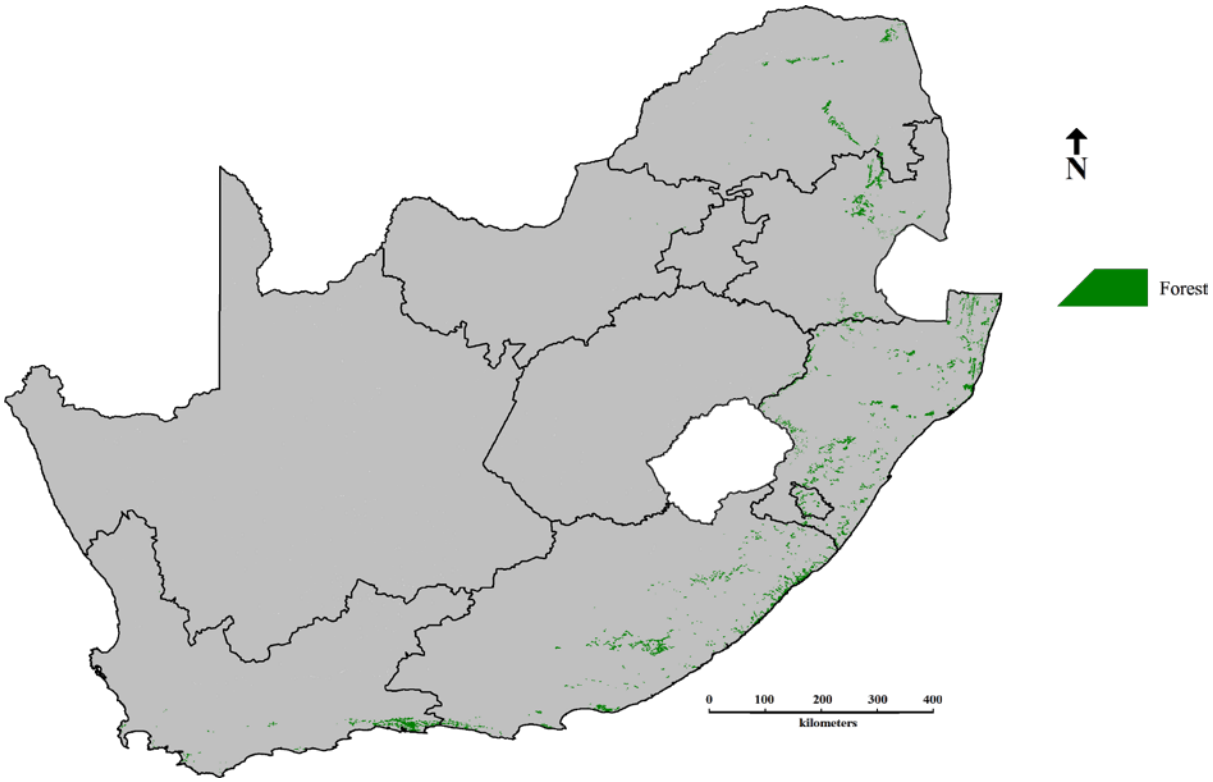


Fig. 357. The Forest biome of South Africa, as delimited by Mucina and Rutherford (2006), illustrating the fragmented nature of the vegetation. Vegetation map shapefile acquired from http://bgis.sanbi.org /vegmap/biomes.asp (accessed 12.X.2014).

Unique to South Africa, and in particular the Cape Floristic Region (CFR), is the fynbos biome. The smallest of the six floral kingdoms, the CFR is the only one to be situated, in its entirety, within one country. Characterized by its high species richness and endemicity, with 70% of the 9000 known plants found within the biome being endemic (Goldblatt & Manning 2002), the region not only compares to some of the richest ecosystems on earth, but surpasses some of them.

The biome contains two subgroups of vegetation, namely the Renosterveld, which is dominated by plants belonging to the Asteraceae family, and the fynbos component found predominantly on well-leeched, infertile soils. The latter is made up of a combination of restioid, ericoid and proteoid components (Cowling, Richardson & Pierce 2004). Many endemic organisms found within the biome have very short distribution ranges, with 24 centres of endemism described

from with the biome. The region has furthermore been listed as an endemic bird area, a centre of plant diversity, as well as identified as a global biodiversity hotspot (Pressey, Cowling & Rouget 2003). Due to its fragile nature, many authors, such as Cowling *et al.* (2003), have proposed plans for its conservation by the year 2020.

Found primarily on the central plateau of South Africa, Lesotho and Swaziland, as well as the inland areas of KwaZulu-Natal and the Eastern Cape, the grassland biome is characterized by a flat and rolling topography that ranges in elevation from near sea level to well over 3000m. Trees are mostly absent, except along hillsides, rivers and scattered woodlands, and the biome is dominated by a single layer of grasses and forbs (Mucina & Rutherford 2006). Annual rainfall averages between 400-600mm, and primary driving forces in limiting the spread of woody plants are rainfall, fire and frost. Currently, much of the biome has been destroyed due to activities such as afforestation, cultivation, overgrazing, and urban expansion (Bredenkamp & Van Rooyen, 1996), and as such the grasslands, particularly of the Free State, are some of the most threatened habitats in South Africa (Kaiser, Avenant & Haddad 2008).

The Nama Karoo is the second largest biome in South Africa and is characterized by the dominance of grassy- and dwarf shrubland. Annual summer rainfall varies between 100mm and 500mm, and is the main factor in determining the distribution of the biome. It is located in the western half of the central South African plateau, and consists primarily of lime-rich, weakly developed soil over rock. The Succulent Karoo is a distinct biome, and not a subset of the Nama Karoo. Its distribution is determined by annual winter rainfall, which varies from 20-290mm, and has characteristic summers that can be extremely arid. The biome is located on a gently undulating plane that is mostly below 800m in altitude, and occurs in the dry western and south-western parts of the country (Figs. 355 & 356). The vegetation is dominated by dwarf and succulent shrubs.

The largest of the South African biomes is the savanna. Characterized by a distinct upper layer of woody plants with a grassy ground layer, it is divided into eutrophic and dystrophic subtypes (Hoare & Frost 2004). It is also the dominant biome in the neighbouring countries of Botswana, Mozambique, Namibia and Zimbabwe. The eutrophic savanna is mainly dominated by microphyllous *Acacia* trees, while the dystrophic savanna is dominated by longer-lived, broad-leaf trees.

In terms of diversity, particular importance is placed on the above mentioned CFR hotspot and the Maputaland-Pondoland-Albany (MPA) hotspot (Fig. 358). The latter is the second richest floristic region after the CFR and incorporates six of the eight biomes in South Africa. It covers an area of approximately 275000km^2 below the Great Escarpment along the eastern coast (Perera, Ratnayake-Perera & Procheş 2011).

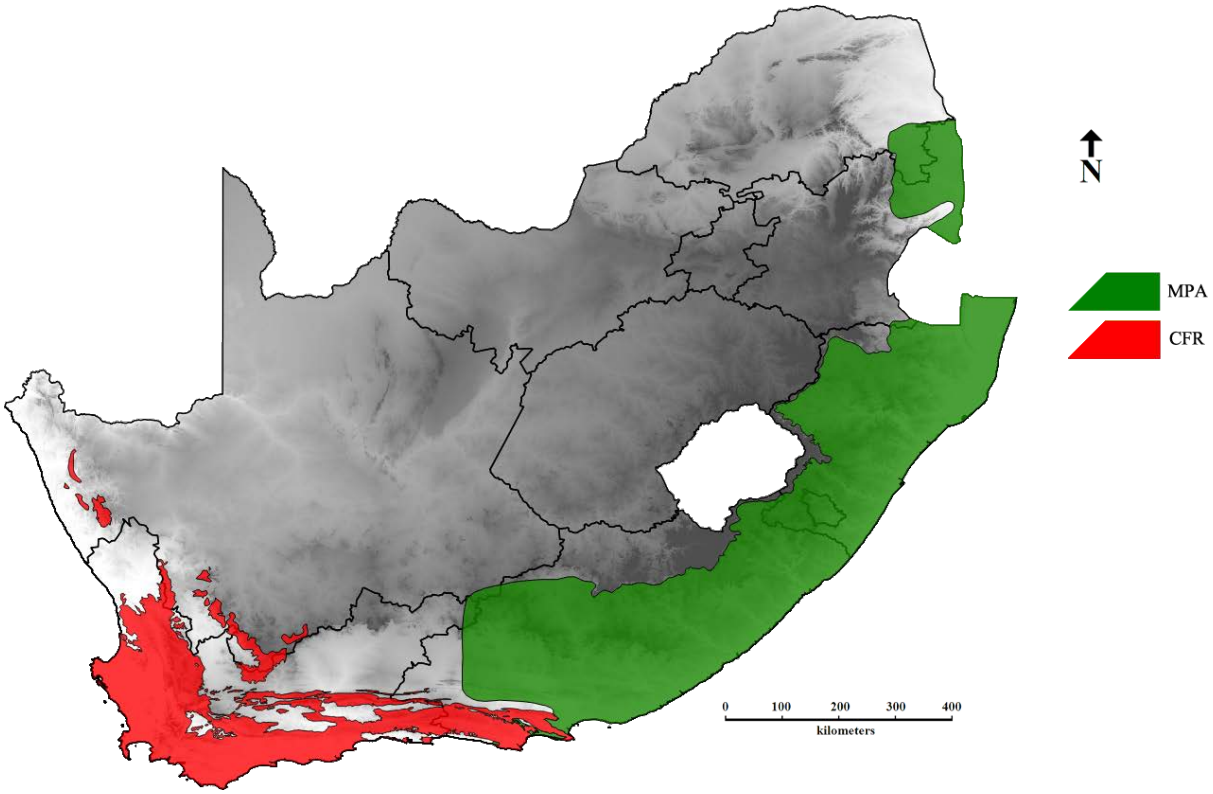


Fig. 358. Topographical map of South Africa highlighting the distributions of the Cape Floristic Region (CFR) and the Maputaland-Pondoland-Albany (MPA) hotspot. Shapefile acquired from http://www.conservation.org/where/priority_areas/hotspots/Pages/hotspots_main.aspx (accessed 12.X.2014).

4.3 *Species biogeography and ecology*

When studying the distribution of the South African Geogarypidae (Fig. 359), it is immediately apparent is that there is a noticeable north-south division in the distribution of records of *Afrogarypus* Beier, 1931 and *Geogarypus* Chamberlin, 1930, with the first predominantly occurring in the southern part of the country and the latter in the northern part. The recently discovered *Castigarypus* gen. nov. can be regarded as a short-range endemic genus, presently only known from the coastal and wetland areas of the southern iSimangaliso Wetland Park. Distribution of the genera is furthermore concentrated along the higher rainfall areas found on the coastal side of the mountain ranges, especially within the fynbos, Albany thicket and indigenous forest biomes.

The large gaps located within the mainland are possibly due to poor sampling, particularly the Northern Cape and North-West provinces. When comparing the above figure with those by Griswold (1991) and Haddad (2014), many of the groupings formed by the Geogarypidae fall perfectly within three known areas of endemism, which are the CFR, the Knysna indigenous forests, and the MPA centre of endemism. When comparing the individual species (Figs. 360-377), one can see that most species' distributions fall entirely within the centres of endemism, with many appearing to be endemics to their areas. That said, other species such as *Afrogarypus impressus* (Tullgren, 1907) and

A. minutus (Tullgren, 1907) comb. nov. possess distribution ranges that cover large areas of southern and south-eastern South Africa, though some of the records are currently unconfirmed and may prove to be misidentifications.

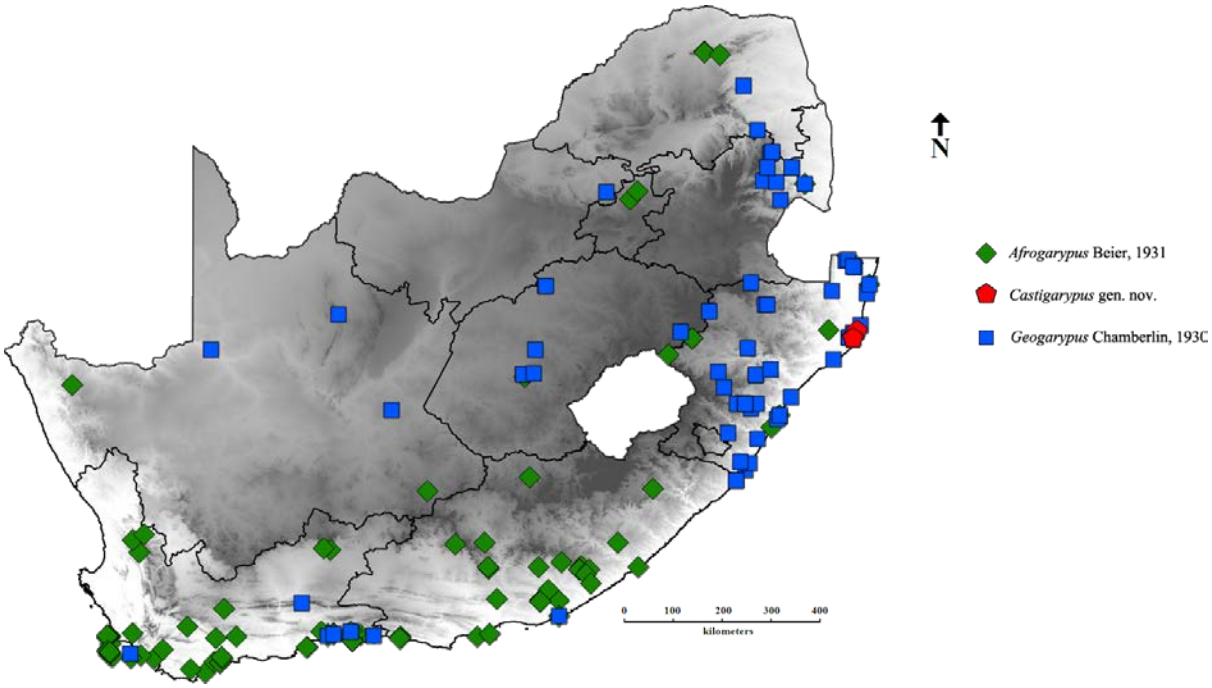


Fig. 359. The distribution of the three Geogarypidae genera found in South Africa, illustrating a noticeable north-south division between the distribution of *Afrogarypus* Beier, 1931 and *Geogarypus* Chamberlin, 1930 records.

4.4 *Afrogarypus carmenae* sp. nov.

Distributed entirely within the CFR (Fig. 360), *A. carmenae* sp. nov. can be found in the leaf litter of mesic mountain fynbos within the central parts of the Western Cape and in leaf litter of coastal fynbos around the southern edges of the province. Most exemplars were collected from the Cape of Good Hope Nature Reserve, though never in high numbers. In contrast, those collected from the inland Cederberg areas near Clanwilliam were found in greater numbers in deep leaf litter collected amongst rocks under dense shrubs. Specimen records indicate that the species can be collected throughout the year.

Habitat & Biology: Leaf litter of mesic mountain and coastal fynbos, particularly from deep leaf litter that is only slightly moist. Elevation: 7-334m.

4.5 *Afrogarypus castigatus* sp. nov.

The species has thus far only been collected from the coastal forests and wetlands in the southern part of the iSimangaliso Wetland Park, located at the north-eastern area of the MPA centre of endemism, South-eastern Maputaland (Fig. 369). The species is furthermore significant in that it appears to be the only obligate arboreal geogarypid in South Africa, collected only from indigenous trees within its distribution range. *Geogarypus deceptor* sp. nov. occurs within the same area as *A. castigatus* sp. nov., but is only found within leaf litter, while *A. castigatus* sp. nov. was never collected from leaf litter. It is therefore considered to be a short-range endemic to the area.

Habitat & Biology: Found exclusively under the bark and within crevices on trees of the species *Breonadia salicina* (Matumi), *Trichilia emetica* (Natal Mahogany) and *Syzygium cordatum* (Umdoni Waterberry) . The only specimens collected thus far were sampled during May. Elevation: 14-24m.

4.6 *Afrogarypus excelsus* (Beier, 1964) **stat. nov.**

The species is limited to the south-central region of the Eastern Cape (Fig. 361), with its distribution falling completely within the MPA centre of endemism. The region is characterized by its myriad of isolated mountains and gorges, each with accompanying indigenous forest patches. It is within these forest patches, as well as surrounding vegetation stands, where *A. excelsus* stat. nov. is most often found. Currently no specimens have been collected from the grassy areas between these forest stands, and as such it is unclear whether populations are confined to these forests or not.

Habitat & Biology: Leaf litter of indigenous high moisture Afromontane forests and dense vegetation stands, particularly around rock formations. All exemplars were collected during the months of November to March. Elevation: 500–1200m.

4.7 *Afrogarypus impressus* (Tullgren, 1907)

Preferring deep, moist leaf litter, *A. impressus* occurs throughout the Afromontane forests along the coastal provinces, but has also been recorded from more arid regions in the Northern Cape and Mpumalanga. Its distribution is furthermore not confined to South Africa, with the species being reported from as far north as the coral atoll of the outer Seychelles island of Aldabra in the Indian Ocean (Spaull 1979). The species has a mostly coastal distribution (Fig. 362) with few inland records, with the exception of the unconfirmed records from the Van Reenen area in the Drakensberg Mountains, which may be misidentifications of *G. octoramosus* sp. nov., which has been collected from the nearby Platberg Nature Reserve. A large proportion of localities fall within both the Knysna

and Tsitsikamma indigenous forests, contained within the CFR, with several also located within the MPA centre of endemism in the Eastern Cape and KwaZulu-Natal. Since its initial collection from leaf litter in the Amanzimtoti region on the 18th of January 1905 (Tullgren 1907b), the species has become one of the most extensively recorded geogarypid species from within South Africa. Most of these localities fall within the 0-300m elevation range.

Habitat & Biology: Leaf litter of indigenous high moisture Afromontane forests along the South African coast, particularly around rock formations. Found under rocks in more arid regions in the Northern Cape and savannas in Mpumalanga. Elevation: 50 – 1600m. Of special interest is that Ellingsen (1912) published notes he received from the Rev. B. Godfrey on parts of the life history of the species. This makes *A. impressus* the only South African geogarypid with published biological data. According to the notes, the species is ground-living and lives under stones in forests. Its nests are attached to stones, hemispherical in shape and lined with both silk and ground particles. Moulting has been recorded in the months of April and September, with females both gravid and with brood-sacs recorded in December (Ellingsen 1912).

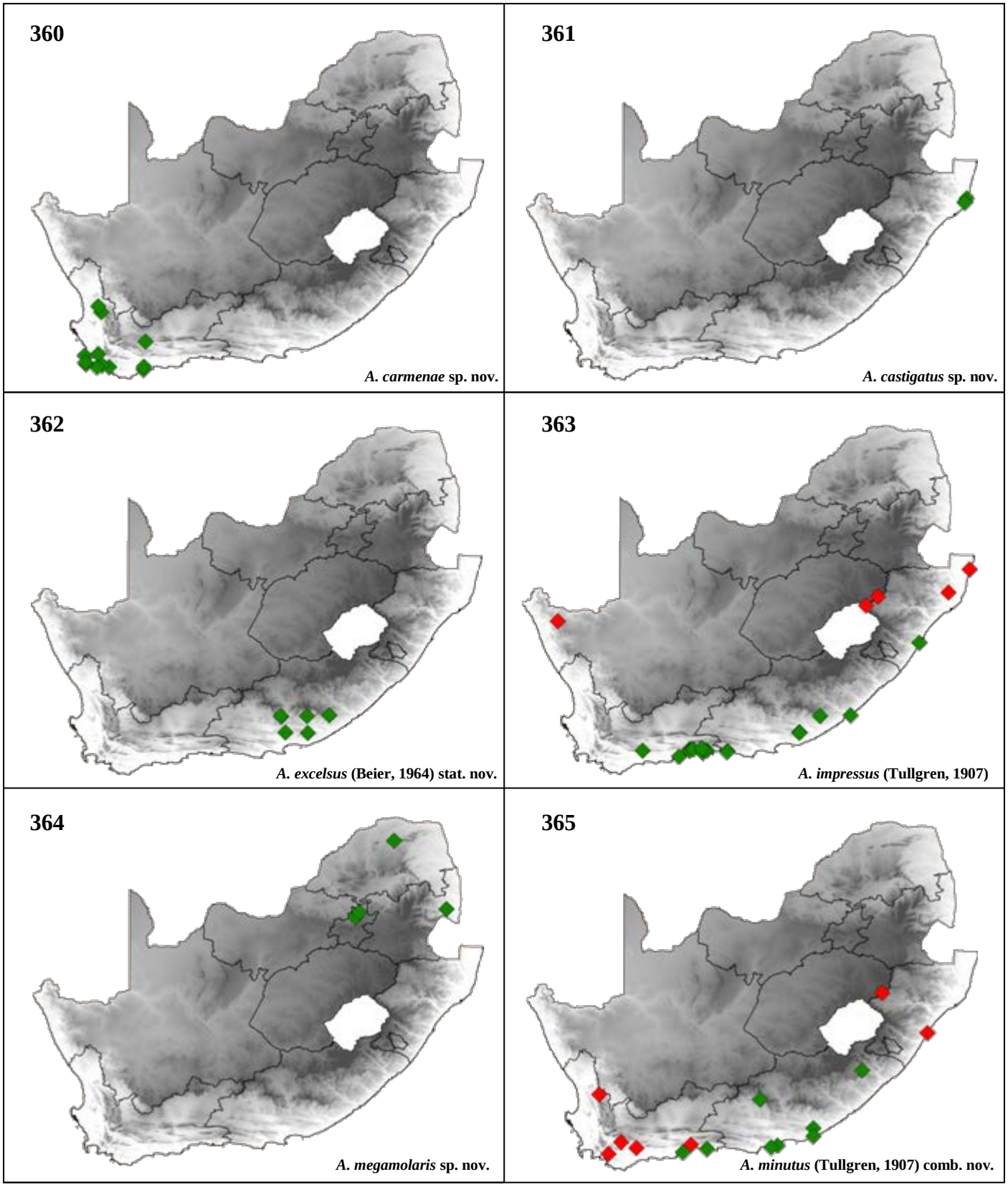
4.8 *Afrogarypus megamolaris* sp. nov.

Known from only a handful of localities, including one that is within the Transvaal-Drakensberg endemism area, as proposed by Griswold (1991). The species' distribution spans three provinces (Fig. 363), with all localities located within the savanna biome. Specimens tend to be difficult to find as they seem to prefer deep, moist, shaded and compact leaf litter that collected alongside large rock formations within the drier northern savanna.

Habitat & Biology: Deep, moist and compact leaf litter, especially next to large shaded rock formations, such as those of the Soutpansberg Mountains. Specimens have all been collected during the warmer months of September to March. Elevation: 300-1400m.

4.9 *Afrogarypus minutus* (Tullgren, 1907) **comb. nov.**

Members of this species have been recorded primarily along the coastal areas of the Western Cape, Eastern Cape and KwaZulu-Natal, with some of the distribution records being within both the CFR and MPA centres of endemism (Fig. 364). Specimens have been sampled from leaf litter of coastal fynbos, Albany thicket and indigenous forests, though most specimens were sampled from the first two biomes.



Figs. 360-365. Distribution maps for: **360**. *Afrogarypus carmenae* sp. nov.; **361**. *A. castigatus* sp. nov.; **362**. *A. excelsus* Beier, 1964 stat. nov.; **363**. *A. impressus* (Tullgren, 1907); **364**. *A. megamolaris* sp. nov.; **365**. *A. minutus* (Tullgren, 1907) comb. nov., where green indicates confirmed localities and red unconfirmed data.

Habitat & Biology: Moist and dry leaf litter from fynbos and Albany thicket shrubs, primarily along the coastal areas of the CFR and MPA centres of endemism. Specimens have been recorded throughout the year, though most were sampled during December. Elevation: 50-2100m.

4.10 *Afrogarypus purcelli* (Ellingsen, 1912) **comb. nov.**

Mostly occurring within the southern coastal region of the Western Cape sympatrically with *A. carmenae* sp. nov. (Fig. 365), the species has nonetheless also been recorded from the Tembe Elephant Park in KwaZulu-Natal, with unconfirmed reports from Louis Trichardt in Limpopo. The reason for the species' absence in the large area between the CFR and its northern distribution is unclear at the moment. It is possible, however, that the unknown number of specimens collected from Louis Trichardt in Limpopo that Beier (1964) attributed to this species could be misidentifications of a yet unknown species, as the location falls within the Transvaal-Drakensberg endemism area.
Habitat & Biology: Western Cape exemplars were collected from leaf litter of the same mesic mountain and coastal fynbos as *A. carmenae* sp. nov. during December. Specimens from the northern distributions were collected from leaf litter in savanna. Elevation: 40-950m.

4.11 *Afrogarypus robustus* (Beier, 1947) **comb. nov.**

A short-range endemic species from the CFR, all known specimens were collected from either indigenous or mixed-indigenous forest patches on and around Table Mountain (Fig. 366). The species is thus entirely constricted to the Table Mountain area of endemism, as proposed by Griswold (1991). This is only the second pseudoscorpion definitively restricted to Table Mountain, in addition to *Chthoniella cavernicola* Lawrence, 1935 (Picker & Samways 1996).

Habitat & Biology: Moist or dry leaf litter next to logs and rock formations in indigenous forests located primarily within gorges on Table Mountain, such as Skeleton Gorge at the Kirstenbosch Botanical Gardens. All specimens have been sampled between the months of August and January. Elevation: 50-900m.

4.12 *Afrogarypus subimpressus* (Beier, 1955)

Originally only known from its type locality (Beier 1955), the distribution of the species has since increased to include regions of the eastern Western Cape and adjoining Northern Cape (Fig. 367). Primarily found within the Cape Point Nature Reserve in the fynbos biome of the CFR, the species can also be found in leaf litter under shrubs in grassland areas located further inland.

Habitat & Biology: Primarily in moist leaf litter under fynbos vegetation, particularly adjacent to coastal rock formations. Specimens have been recorded from April to December, with most specimens sampled from October to December. Elevation: 10-1400m.

4.13 *Afrogarypus triangularis* (Ellingsen, 1912) **comb. nov.**

Occurring primarily within the Eastern Cape, the species has also been recorded from the Free State (Fig. 368). Semi-arboreal in nature, *A. triangularis* were collected in canopy fogging samples taken from *Podocarpus falcatus* (Yellowwood) and other indigenous trees found within forests throughout the Eastern Cape, where they have also been reported from bird nests (Ellingsen 1912). Individuals may also be collected from moist leaf litter in these areas. In grasslands, the species can be found within grass tussocks and shaded leaf litter. Interestingly, most locations either fall within the 600-700m or 1200-1400m elevation ranges.
Habitat & Biology: Semi-arboreal species preferring canopies of indigenous trees in forest stands within the Eastern Cape, as well as associated leaf litter, and from shaded leaf litter and grass tussocks in grassland habitats. Elevation: 60 – 1485m.

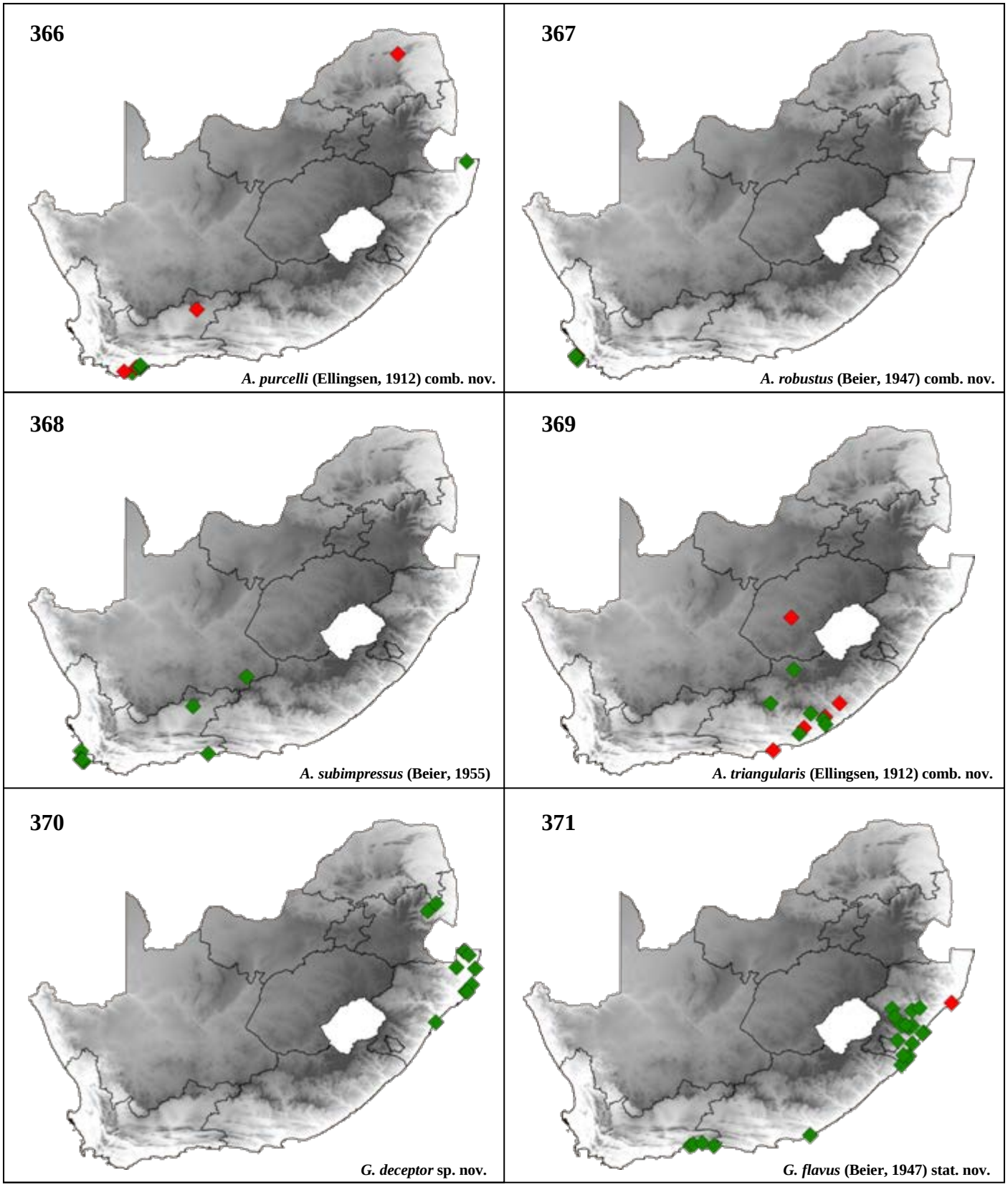
4.13 *Geogarypus deceptor* sp. nov.

Occurring mainly within the north and north-eastern parts of the MPA centre of endemism, this species can be found amongst leaf litter in habitats ranging from coastal forests, wetlands, closed woodlands and savanna. The species mainly occurs in the northern parts of KwaZulu-Natal to the centre of Mpumalanga (Fig. 370).

Habitat & Biology: Specimens have primarily been collected from dry leaf litter in coastal forests and woodland areas, but has also been located from very moist leaf litter in the indigenous forest patch located at the Highveld Botanical Gardens. Specimens have been recorded throughout the year. Elevation: 30-620m.

4.15 *Geogarypus flavus* (Beier, 1947) **stat. nov.**

The distribution of the species is split between two main populations (Fig. 371), with a single locality record between them. The southernmost population falls neatly within the Knysna indigenous forest area of endemism, while the northern population is contained completely within the MPA centre of endemism in KwaZulu-Natal. A common species of the coastal Afromontane belt, most specimens were collected from high moisture leaf litter in indigenous forest patches.



Figs. 360-365. Distribution maps for: **366**. *A. purcelli* (Ellingsen 1912) comb. nov.; **367**. *Afrogarypus robustus* (Beier, 1947) comb. nov.; **368**. *A. subimpressus* (Beier, 1955); **369**. *A. triangularis* (Ellingsen, 1912) comb. nov.; **370**. *Geogarypus deceptor* sp. nov.; **371**. *G. flavus* (Beier, 1947) stat. nov., where green indicates confirmed localities and red unconfirmed data.

Habitat & Biology: High moisture leaf litter from indigenous forest patches, particularly deep, loose litter next to large rocks. Specimens have been recorded throughout the year, with most sampled during the summer months of December to February. Elevation: 10-1100m.

4.16 *Geogarypus liomendontus* sp. nov.

Only known from two localities, both situated in isolated gorges just outside the northern edge of the MPA centre of endemism (Fig. 372). Both gorges were predominantly arid, and contained dense indigenous tree stands growing next to very steep rock faces.

Habitat & Biology: All specimens were collected from cool, dry and shaded leaf litter located either against the trunks of trees or occasionally from deposits of litter between groups of rocks. Elevation: 760-785m.

4.17 *Geogarypus modjadji* sp. nov.

Currently only known from its type locality (Fig. 373), extensive sampling at other locations near the type locality failed to yield any further specimens. The locality is unique in that it contains the world's largest concentration of a single species of cycad, known as the Modjadi palm (*Encephalartos transvenosus*). The area consists of a 305ha reserve situated within a gorge, with a central stream that is mostly shaded by an isolated forest made up of the cycads, which are up to 13m tall (Grobbelaar, Meyer & Burchmore 1988). Due to the unique nature and isolation of this habitat, it is believed that *G. modjadi* sp. nov. constitutes a short-range endemic species, unique to this distinct cycad forest.

Habitat & Biology: Moist leaf litter in undergrowth of cycad forest, particularly deposits among rock formations. Specimens were collected during the month of November. Elevation: 900m.

4.18 *Geogarypus octoramosus* sp. nov.

Found primarily at the northern reaches of KwaZulu-Natal, the distribution of the species falls just outside of the MPA centre of endemism (Fig. 374). Although most of the locality data is situated either within the grassland or Albany thicket biomes, most of the specimens were collected from leaf litter under thickets located either on top of rocky hills or next to rocky outcrops in the veld at altitudes above 1000m. Other specimens were located in either *Eucalyptus* plantations or Sand Forest.

Habitat & Biology: Cool and semi-moist, shaded leaf litter, especially under thickets growing between rocky outcrops that result in leaf litter collecting in the crevices. Specimens have been recorded from January to May. Elevation: 100-1900m.

4.19 *Geogarypus olivaceus* (Tullgren, 1907)

One of the few South African geogarypid species with substantial inland records, *G. olivaceus* can be found in five provinces, with a distribution stretching as far south as the coast of the Western Cape and as far north as the Kruger National Park in Mpumalanga (Fig. 375). Specimens can easily be found within the grassland biome of central South Africa, particularly in the leaf litter of the African Wild Olive tree (*Olea europaea africana*) that commonly grows along rocky hills in the Free State at altitudes above 1100m.

Habitat & Biology: Records show that the species is present throughout the year, with most being collected from cool, shaded and semi-moist to dry leaf litter in the central grassland biome of South Africa. Elevation: 20-1400m.

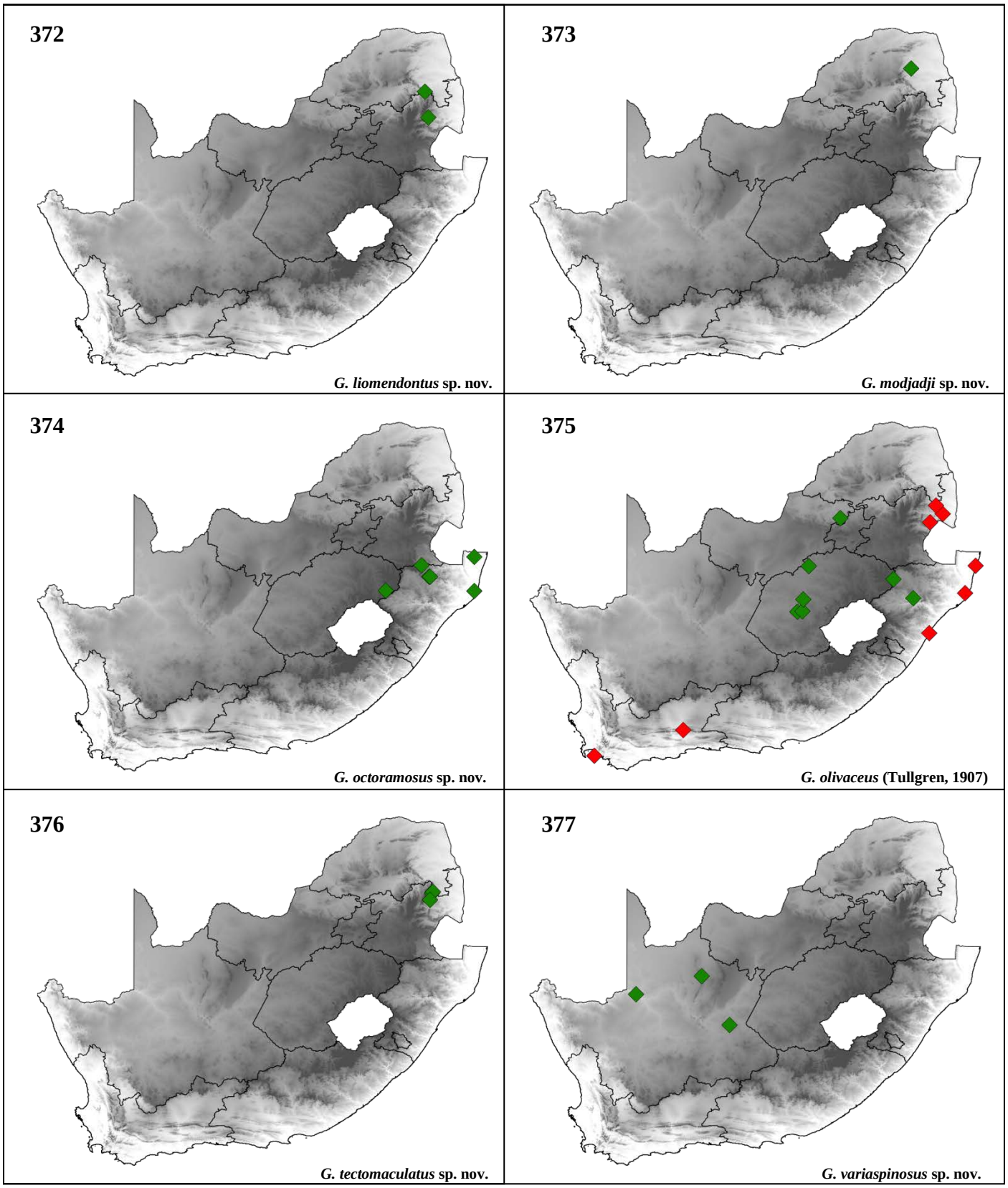
4.20 *Geogarypus tectomaculatus* sp. nov.

Another potential short-range endemic, *G. tectomaculatus* sp. nov. seems to be confined to rocky outcrops found along the edges of ridges in the highlands of Mpumalanga (Fig. 376). These particular rock formations form many crevices and shaded areas that allow shrubs to grow and deposit deep layers of leaf litter in an otherwise open, grass dominated biome. It is within these deposits of leaf litter that this new species is most often found.

Habitat & Biology: Most often found within cool, dry and shaded leaf litter deposited in crevices around rock formations in open grassland. Specimens can also be found in more moist leaf litter of scattered indigenous forest patches. Collection records range from September to October. Elevation: 1200-1700m.

4.21 *Geogarypus variaspinosus* sp. nov.

The only species found entirely within the Northern Cape (Fig. 377), they inhabit the leaf litter of shrubs on rocky hills and along rivers of both the Nama-Karoo and the adjacent savanna biomes of the province. The species seems to be more xerophilic than the other South African Geogarypidae, in that they can often be found in very dry and sandy leaf litter.



Figs. 360-365. Distribution maps for: **372**. *Geogarypus liomendontus* sp. nov.; **373**. *G. modjadji* sp. nov.; **374**. *G. octoramosus* sp. nov.; **375**. *G. olivaceus* (Tullgren, 1907); **376**. *G. tectomaculatus* sp. nov.; **377**. *G. variaspinosus* sp. nov., where green indicates confirmed localities and red unconfirmed data.

Habitat & Biology: Other than its occurrence in, often, very dry leaf litter found within the arid Northern Cape, little is known about the biology of this new species. All collection records for this species fall with the winter month of June. Elevation: 900-1300m.

CHAPTER 5 - PHYLOGENETICS

5.1 *Introduction*

The phylogeny of the Pseudoscorpiones has been a hotly debated topic amongst experts in the field since the late 19th century (Wheeler & Hayashi 1998), historically being placed as a sister group to the Solifugae in the clade Haplocnemata. That said, the internal phylogeny of the Pseudoscorpiones has not received nearly the same amount of attention, with most of the early studies focussing on the non-numerical analysis of morphological features (Murienne, Harvey & Giribet 2008).

The systematics of the group was modernized by the seminal works of Chamberlin (1929, 1930, 1931), where he divided the Pseudoscorpiones into three suborders, Monosphyronida, Diplosphyronida and Heterosphyronida. Beier (1932a,b) adopted Chamberlin's scheme and proposed the equivalent suborders of Cheliferinea, Neobisiinea and Chthoniinea. These classification systems remained the norms in America and Europe, respectively, until the first cladistic analysis of the group was done by Harvey (1992b), where, through the use of 126 characters, 24 families were recognized. He furthermore placed these families within two suborders based on either the presence (Iocheirata) or lack (Epiocheirata) of a venom apparatus on the chelal fingers.

With the advent of modern molecular techniques, the phylogeny of the group was once again subjected to scrutiny. Although molecular work was done on single species by authors such as Wilcox *et al.* (1997) and Wheeler & Hayashi (1998), phylogenetic analysis of pseudoscorpion groups has only recently been done (Zeh, Zeh & Bonilla 2003; Moulds *et al.* 2007). The most significant study is the work done by Murienne *et al.* (2008), where through the use of two nuclear and one mitochondrial genes, the phylogenetic relationships of the major pseudoscorpion clades were investigated, firmly introducing the group to the molecular age. Many of the superfamilies proposed in Harvey's (1992b) morphological cladistic analysis were found to be monophyletic, although the superfamilies Neobisiodea, Garypoidea and Cheliferoidea were not. Their study thus supported an observation made by Mallat & Giribet (2006), finding that although phylogenetic relationships derived from gene-sequences generally agree with traditional morphologically derived relationships, the former can sometimes show startling differences, necessitating revisions of species' morphology to account for their genetic relationships. The same results were obtained in this study, as can be seen

by the multiple new combinations, status updates and new species discovered after molecular phylogenetic analysis of the morphospecies recognized in chapter 3.

Both 18S rRNA and 28S rRNA have been extensively used throughout the years to infer the phylogenetic relationships among arthropods (Wheeler & Hayashi 1998; Mallat & Giribet 2006) and recently among pseudoscorpions as well (Murienne, Harvey & Giribet 2008). In this study 18S rRNA was discarded, both due to the potential for weak resolution at species level branches (Steiner & Müller 1996), and cost involved. Therefore, only COI and 28S genes were used, as they better reflect species level relationships.

One of the most popular genes currently used to infer phylogenetic relationships, the Cytochrome C Oxidase Subunit I (COI) gene, has been used by many authors in recent years in phylogeographic studies of pseudoscorpion populations (Wilcox *et al.* 1997; Zeh *et al.* 2003; Moulds *et al.* 2007; Murienne *et al.* 2008; Pfeiler *et al.* 2009; Van Heerden, Taylor & Van Heerden 2013).

5.2 *Amplification results*

Of the 18 morphospecies sequenced, 17 yielded 28S rRNA PCR products and 17 yielded COI PCR products. After multiple PCR parameter adjustments, as well as genomic DNA extractions, we were unable to obtain 28S rRNA products for *Afrogarypus minutus* (Tullgren, 1907) comb. nov. or COI products for *A. megamolaris* sp. nov., resulting in their absence from the corresponding trees (Figs. 378 & 379). Since both of the abovementioned species yielded results for at least one gene, they could still be incorporated within the concatenated tree (Fig. 380), and showed the same placement as other species with similar morphology. Positive PCR products of the 28 rRNA gene yielded sequences with post-trim and assembling lengths of 998-1077bp, while the COI products yielded sequences 674-682bp in length. All sequences were deposited in GenBank under the accession numbers shown in Table 1.

5.3 *28S rRNA results*

Phylogenetic analysis of the 28S rRNA gene sequences of the South African Geogarypidae using multiple alignment and tree construction models yielded trees that differed only slightly in topology, with the tree constructed using Geneious alignment and Neighbour Joining being chosen as the most congruent (Fig. 378).

Table 1. GenBank accession numbers for the nuclear 28S rRNA and mitochondrial COI sequences obtained during the study.

Species	GenBank Accession Numbers		Specimen Locality
	28S rRNA	COI	
***Afrogarypus* Beier, 1931**			
A. carmenae sp. nov.	KP297847	KP331813	Clanwilliam
A. castigatus sp. nov.	KP297858	KP331824	St. Lucia
A. excelsus (Beier, 1964) stat. nov.	KP297844	KP331810	Fort Fordyce NR
A. impressus (Tullgren, 1907)	KP297845	KP331811	Tsitsikamma NR
A. megamolaris sp. nov.	KP297854	-	Louis Trichard
A. minutus (Tullgren, 1907) comb. nov.	-	KP331815	Brenton-on-Sea
A. purcelli (Ellingsen, 1912) comb. nov.	KP297850	KP331817	De Hoop NR
A. robustus (Beier, 1947) comb. nov.	KP297851	KP331818	Kirstenbosch BG
A. subimpressus (Beier, 1955)	KP297846	KP331812	Cape Point NR
A. triangularis (Ellingsen, 1912) comb. nov.	KP297852	KP331819	King Williams Town
***Geogarypus* Chamberlin, 1930**			
G. deceptor sp. nov.	KP297853	KP331820	St. Lucia
G. flavus Beier, 1947 stat. nov.	KP297848	KP331814	Jubilee Creek NR
G. liomendontus sp. nov.	KP297843	KP331809	Abel Erasmus Pass
G. modjadji sp. nov.	KP297855	KP331821	Modjadjis Kloof NR
G. octoramosus sp. nov.	KP297859	KP331825	Vryheid
G. olivaceus (Tullgren, 1907)	KP297849	KP331816	Bothaville
G. tectomaculatus sp. nov.	KP297857	KP331823	Graskop
G. variaspinosus sp. nov.	KP297856	KP331822	Douglas

The resulting 28S rRNA tree shows the presence of four major clades within the South African Geogarypidae, two clades corresponding with *Afrogarypus* Beier, 1931 and two clades corresponding to *Geogarypus* Chamberlin, 1930. The most distinctive feature of the tree is the inclusion of *G. minutus* (Tullgren, 1907), *G. purcelli* (Ellingsen, 1912), *G. robustus* Beier, 1947 and *G. triangularis* (Ellingsen, 1912) in the *Afrogarypus* clade. The two subspecies, *A. excelsus excellens* (Beier, 1964) and *A. excelsus excelsus* (Beier, 1964), are shown to be very closely related, with almost no genetic variation between the two, even after magnification of the tree to enhance the branch lengths. *Geogarypus flavus* (Beier, 1947), originally described as a separate species but later synonymised with *G. olivaceus* (Tullgren, 1907) by Beier (1955), is once again resolved as a separate species, with the two species falling into different *Geogarypus* clades.

The tree also supported the presence of nine new species, with *A. carmenae* sp. nov., *A. castigatus* sp. nov. and *A. megamolaris* sp. nov. representing three new species of *Afrogarypus*, and *G. deceptor* sp. nov., *G. liomendontus* sp. nov., *G. modjadji* sp. nov., *G. octoramosus* sp. nov., *G. tectomaculatus* sp. nov. and *G. variaspinosus* sp. nov. placed in *Geogarypus*.

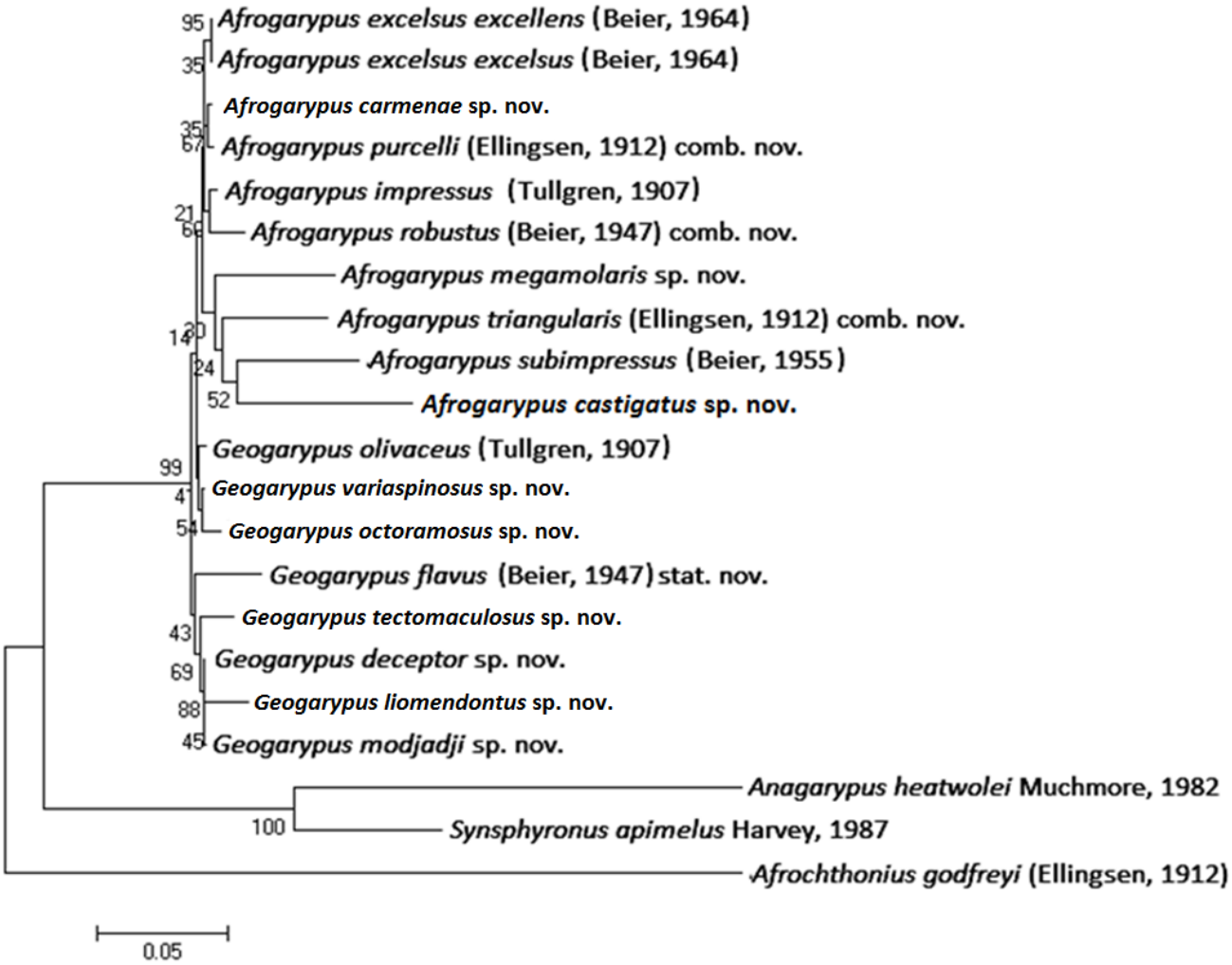


Fig. 378. Neighbour Joining tree with 1000 Bootstrap repetitions of 28S rRNA sequences depicting the phylogenetic relationships of the South African Geogarypidae.

Morphologically, species forming the four major clades share the following similarities:

i – The species comprising the first *Afrogarypus* clade, consisting of *A. excelsus excellens*, *A. excelsus excelsus*, *A. carmenae* sp. nov., *A. purcelli* (Ellingsen, 1912) comb. nov., *A. impressus* (Tullgren, 1907) and *A. robustus* (Beier, 1947) comb. nov., all contain chela with only slightly convex interior hand surfaces, chelal fingers with many small teeth, as well as either a well developed, deep dorsal sulcus or concave dorsal region on the chela hand.

ii – The species in the second *Afrogarypus* clade, consisting of *A. megamolaris* sp. nov., *A. triangularis* (Ellingsen, 1912) comb. nov., *A. subimpressus* (Beier, 1955) and *A. castigatus* sp. nov., contain chela where the interior surface of the hand is enlarged to a globular strongly convex shape, with the exception of *A. megamolaris* sp. nov. They furthermore contain chelal fingers with fewer but more prominent teeth, and the presence of either a broader, shallower dorsal sulcus or a concave

dorsal region. *A. triangularis* comb. nov. and *A. castigatus* sp. nov. also show the presence of lateral abdominal sclerites in the males.

iii – The species comprising the first *Geogarypus* clade, consisting of *G. olivaceus*, *G. octoramosus* sp. nov. and *G. variaspinosus* sp. nov. contain carapaces and tergites that are both uniformly brown, with slight lighter markings in only a small number of samples. Males of the species all possess simple galea with no spinules, while the females of *G. octoramosus* sp. nov. and *G. variaspinosus* sp. nov. have galea with fewer than nine rami.

iv – In the second *Geogarypus* clade, *G. flavus* stat. nov. and *G. tectomaculatus* sp. nov present tergites with distinct cream-coloured patches, female galea that are very broad, and male galea that possess spinules. *Geogarypus deceptor* sp. nov., *G. liomendontus* sp. nov. and *G. modjadji* sp. nov. furthermore possess distinct cream-coloured patches on the posterior half of their carapaces, with all females possess regular shaped galea. *Geogarypus deceptor* sp. nov. and *G. modjadji* males also possess galea with spinules.

5.4 *COI results*

Using the same parameters as the 28S rRNA analysis, the COI gene sequences of the South African Geogarypidae once again yielded trees that differed only slightly in topology, with the tree constructed using Geneious alignment and Neighbour Joining again being chosen as the most congruent (Fig. 379).

The COI tree differs from the 28S rRNA tree with regard to the topographical placement of particularly the new species, but supports many of the main results. These include the placement of *G. minutus*, *G. purcelli*, *G. robustus* and *G. triangularis* in the *Afrogarypus* clade; the placement of *A. excelsus excellens* and *A. excelsus excelsus* as barely distinguishable sister taxa, and the revalidation of *G. flavus* stat. nov. as a distinct species. The nine new species are still distinct and, with the exception of *A. castigatus* sp. nov., grouping within the same genus clades as in the 28S rRNA results. Of particular note is the placement of *A. castigatus* sp. nov. as a sister group to all the other South African Geogarypidae. Given the species' unusual morphological adaptations, this placement is not unexpected. One troubling aspect of the tree is the very low Bootstrap values at some of the nodes, particularly between the taxa of the *Geogarypus* clade. Saturation of the COI gene is a possible explanation, as the mitochondrial genome evolves much faster than the nuclear genome (Burger, Gray & Lang 2003).

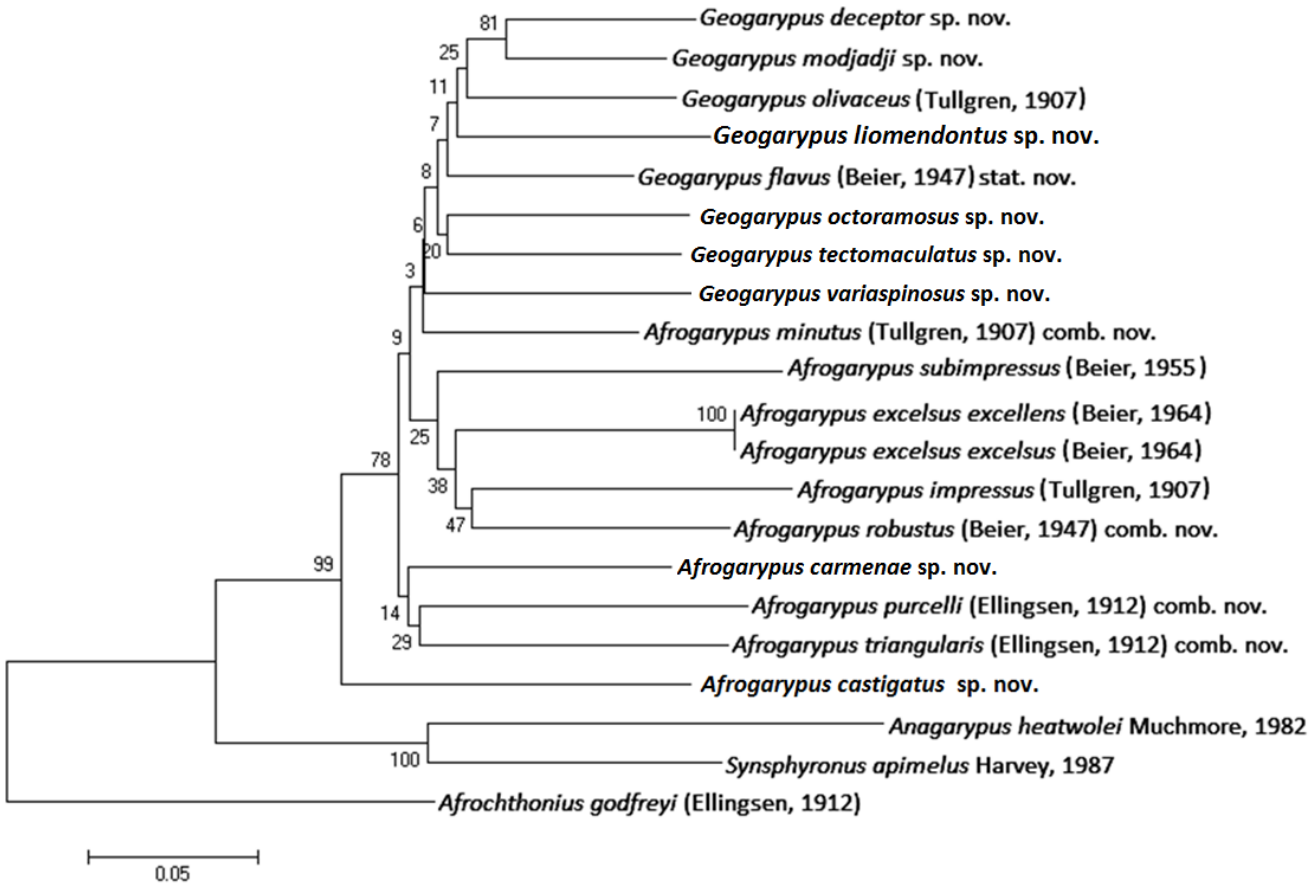


Fig. 379. Neighbour Joining tree with 1000 Bootstrap repetitions of COI sequences depicting the phylogenetic relationships of the South African Geogarypidae.

5.5 *Concatenated results*

Super-gene alignments are one of two fundamentally different techniques used to construct phylogenetic trees from multiple genes, the other being the use of consensus trees. Gadagkar, Rosenberg & Kumar (2005) found that a combination of concatenation and Neighbour Joining analysis consistently yielded more accurate trees than consensus analysis. It was thus decided to follow the same technique and construct a tree from concatenated sequences of both the 28S rRNA and the COI genes to increase the accuracy of the phylogenetic analysis. After concatenation the new super-genes were aligned using Geneious and the first consensus tree was constructed using Neighbour Joining with 1000 Bootstrap replicates.

The resulting tree (Fig. 380) shows that the Geogarypidae forms a monophylic clade separate of the Garypidae and yielded the presence of four distinct clades, one corresponding to *Geogarypus* and three corresponding to *Afrogarypus*. The major trends of the separate 28S and COI trees are once again present and resulted in the following changes and additions:

i – *Afrogarypus minutus* comb. nov., *A. purcelli* comb. nov., *A. robustus* comb. nov. and *A. triangularis* comb. nov. are transferred to *Afrogarypus*. These combinations are supported by the presence of a concave area on the dorsal surface of the chela, present only within these species and *A. castigatus* sp. nov. This results in two of the *Afrogarypus* clades possessing species with well developed dorsal sulci (Fig. 380B & D), as well as shallow concave depressions (Fig. 380C & E).

ii – *Afrogarypus excelsus excellens* and *A. excelsus excelsus* are synonymised under *Afrogarypus excelsus* (Beier, 1964) stat. nov., due to the evident lack of any significant branching, and thus genetic variation between the subspecies. The slight morphological differences used by Beier (1964) to distinguish between the subspecies can likely be attributed to intraspecific variation within the species. A well documented case supporting intraspecific variation can be seen in the study done by Zeh & Zeh (1992) on the intra-brood variability in the morphology of male *Semeiochernes armiger* (Balzan, 1892) (Chernetidae).

iii – Given both its phylogenetic separation and distinct morphological characters, *Geogarypus flavus* stat. nov. is removed from synonymy with *G. olivaceus* and revalidated as a distinct species.

iv – Despite its unique morphological adaptations and its phylogenetic separation, *A. castigatus* will be treated as a species within the *Afrogarypus*, due to the species posessing a concave dorsal area on the chela, consistent with that of other species within the genus. Its morphological synapomorphies: the presence of monotarsate leg pairs I and II, and a reduced trichobothrial compliment due to the absence of trichobothria *isb*, characters make this species unique among the South African fauna, and can possibly be explained as a simple case of paedomorphosis in a small species, as both of the morphological reductions have been recorded in, and seem commonplace, in Garypidae (Harvey 1987a).

v – The following nine new species are recognized due to being both phylogenetically and morphologically distinct: *A. carmenae* sp. nov., *A. castigatus* sp. nov.; *A. megamolaris* sp. nov., *G. deceptor* sp. nov., *G. liomendontus* sp. nov., *G. modjadji* sp. nov., *G. octoramosus* sp. nov., *G. tectomaculatus* sp. nov. and *G. variaspinosus* sp. nov.

The particularly low Bootstrap values at some of the nodes necessitated a careful study of morphological features to help validate the phylogenetic findings. Fortunately, the low values were present between taxa with very distinct morphological differences, including the historically described species. Since the 28S rRNA tree presented significantly higher Bootstrap values, the low values are attributed to those of the COI tree cascading into the concatenated tree. As previously stated, saturation of the mitochondrial genome is the most likely cause. Murienne *et al.* (2008) also

recommended the incorporation of pseudoscorpion specific genes, or the design of specific primers instead of using universal varieties.

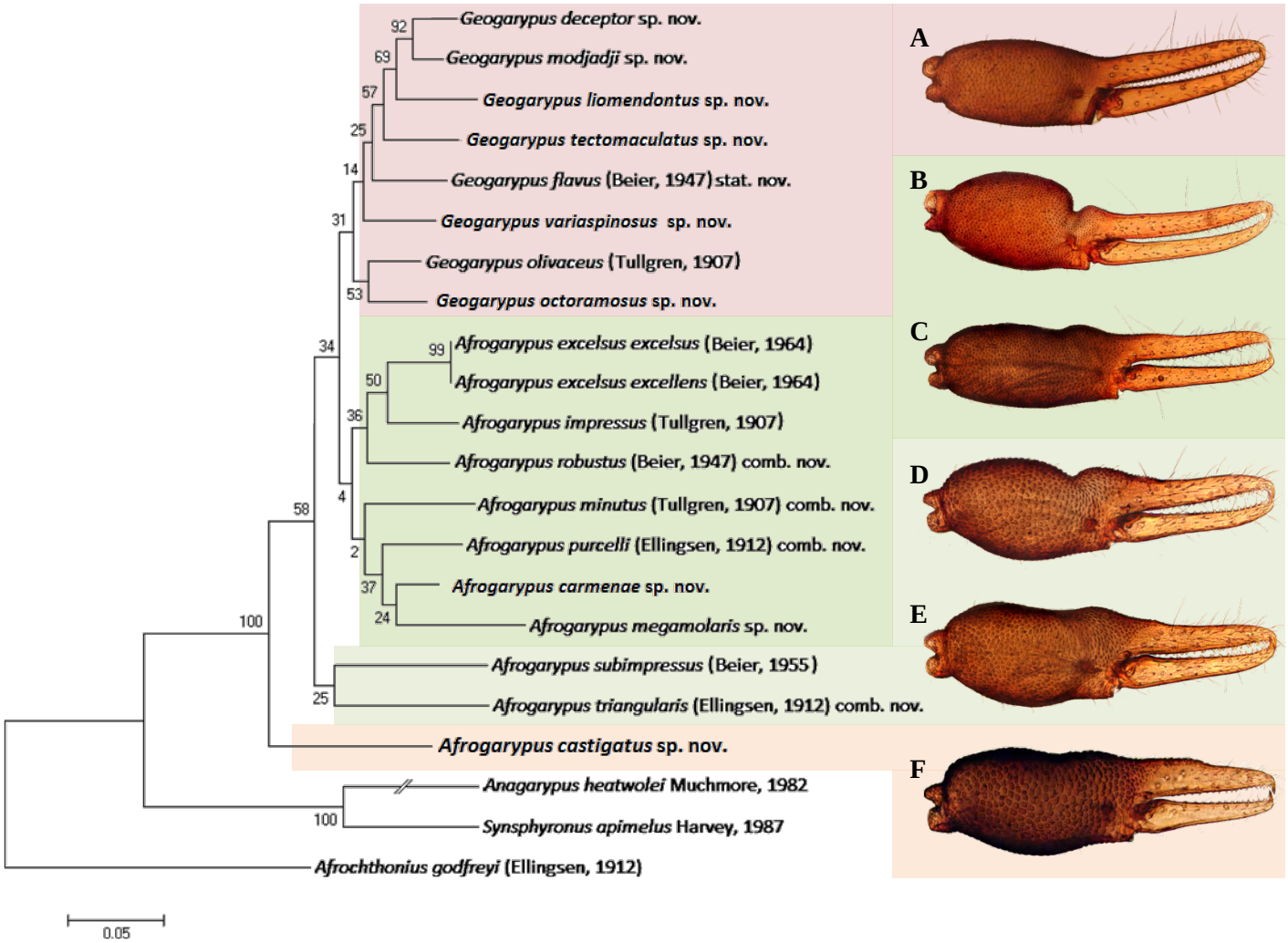


Fig. 380. Neighbour Joining tree depicting the phylogenetic relationships between taxa of the South African Geogarypidae, constructed via the use of concatenated sequences of both 28S rRNA and COI genes, with representative chela of each major clade. **A**. *Geogarypus olivaceus* (Tullgren, 1907); **B**. *Afrogarypus excelsus* (Beier, 1964) stat. nov.; **C**. *A. robustus* (Beier, 1947) comb. nov.; **D**. *A. subimpressus* (Beier, 1955); **E**. *A. triangularis* (Ellingsen, 1912) comb. nov.; **F**. *Castigarypus primus* sp. nov.

Regarding the Bayesian analysis of the concatenated data (Fig. 381), the results correlate well with the previous trees and is most similar to the 28rRNA consensus tree. It results in three major clades, one corresponding to *Geogarypus* and two corresponding to *Afrogarypus*. Both genera are again represented as paraphyletic and well defined by shared characters. *Afrogarypus* again includes the species of *Afrogarypus minutus* comb. nov., *A. purcelli* comb. nov., *A. robustus* comb. nov. and *A. triangularis* comb. nov., originally in *Geogarypus*, together with *A. carmenae* sp. nov., *A. castigatus* sp. nov. and *A. megamolaris* sp. nov. which represent new species. All the species share the presence of either a well developed dorsal sulcus or a concave dorsal depression. The rest of the species group

within the *Geogarypus* clade and share chela that possess a convex dorsal surface. Of importance is the presence of two trichotomous splits within the tree, one within each clade, indicating that the concatenated sequences were insufficient in perfectly resolving the species. This again highlights the need for the use of new genes and loci to sufficiently resolve the phylogenetic relationships of modern pseudoscorpions.

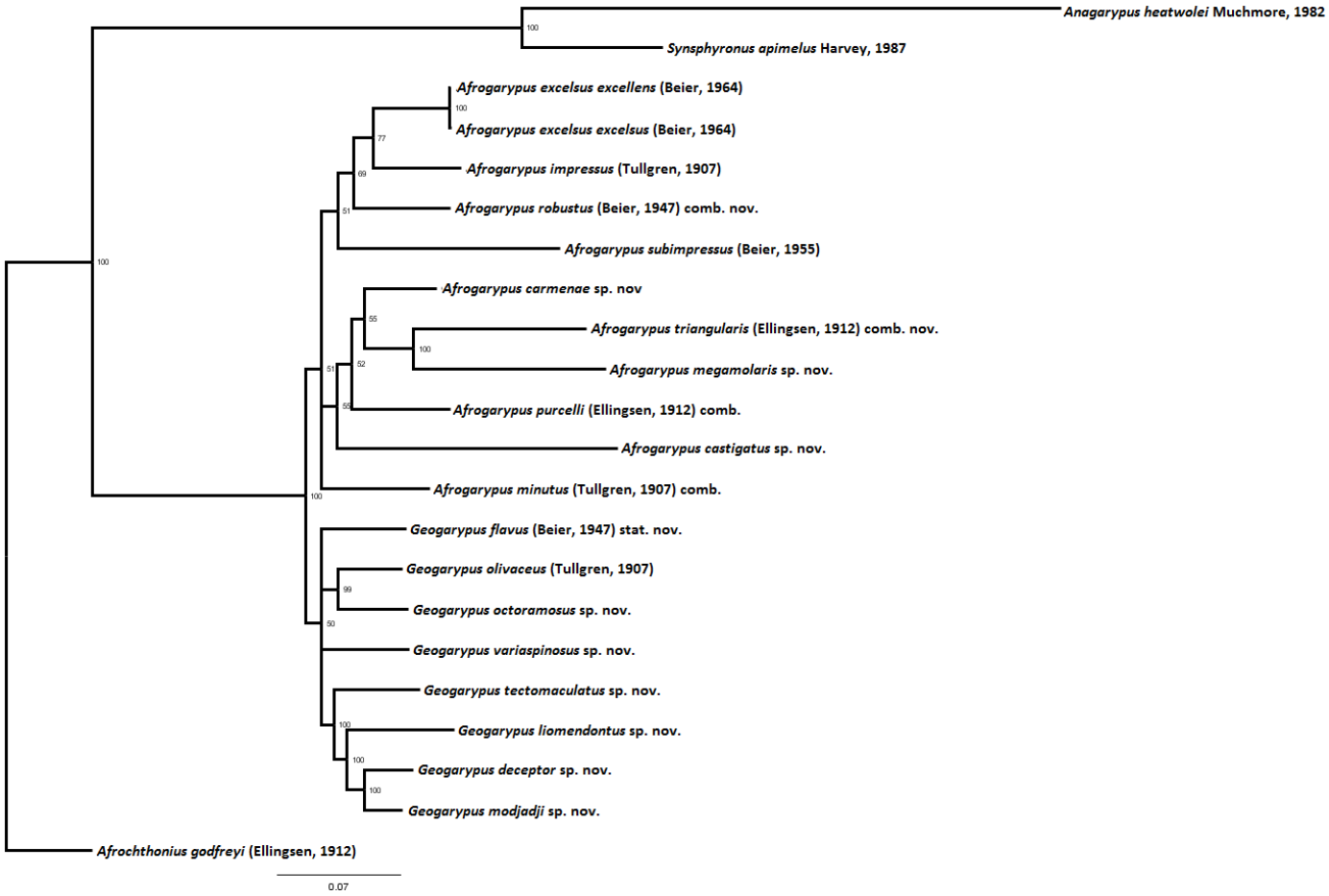


Fig. 381. Bayesian analysis consensus tree depicting the phylogenetic relationships between taxa of the South African Geogarypidae, constructed via the use of concatenated sequences of both 28S rRNA and COI genes.

5.6 *Discussion*

By incorporating a genetic section into this study, valuable insight was achieved with regards to the variability of morphological characters and their value in distinguishing between closely related species. Narrowing down the limits of these variations were major factors contributing to both the synonymization of the *A. excelsus* stat. nov. subspecies, as well as the revalidation of *G.*

flavus stat. nov. The above analysis furthermore resulted in the identification of cryptic species such as *Geogarypus deceptor* sp. nov. that, on multiple occasions, was found to be misidentified as either *G. flavus* stat. nov. or *G. olivaceus* in museum collections. *Geogarypus modjadji* sp. nov., another cryptic species which very closely resembles *G. liomendontus* sp. nov., was also originally identified by its phylogenetic distinction. This resulted in the recognition of distinct differences in the basal teeth morphology of their chelal fingers that can now be used to accurately distinguish the two species.

The study also presented the difficulty of finding and using distinct morphological characters in male Geogarypidae to identify species, as the most defining characters are found in females. Zeh & Zeh (1994) faced a similar situation in their study, where the uniformity of pseudoscorpion males masked the population's genetic diversity. This issue can best be resolved using techniques to identify micro-morphological characters that can aid in distinguishing between the males of cryptic geogarypids (Muster, Schmarda & Blick 2004), as well as DNA bar-coding.

In conclusion, the phylogenetic analysis of the South African Geogarypidae highlighted, amongst other things, the hazards of using pure morphological techniques to infer relationships between pseudoscorpion species. When it comes to the systematics of the Pseudoscorpiones, previous studies have shown that the sole use of either phylogenetic or morphological techniques lack the resolution to identify all the complicated relations among species (Zeh & Zeh 1992; Wilcox *et al.* 1997). Van Heerden *et al.* (2013) suggested that a combination of phylogenetic analysis and morphological analysis using micro-morphological characters could best be used to infer relationships between pseudoscorpion species. The current study fully supports this holistic view to pseudoscorpion systematics.

CHAPTER 6 - CONCLUDING REMARKS

6.1 *General discussion*

With the discovery of nine new species, bringing the total number of South African species to 18, South Africa currently holds the record as the most diverse country regarding Geogarypidae fauna. It is clear that large areas of central, northern and western South Africa require more intensive sampling, as few records are present from especially the Northern Cape, North West, Free State, Gauteng and Limpopo provinces. The use of canopy fogging also proved invaluable to collect Geogarypidae specimens from habitat strata not accessible using more conventional sampling methods (leaf litter sifting, sweep netting, beating and hand collecting), yielding valuable insight into habitat flexibility of this family.

The most curious of the species discovered was *A. castigatus* sp. nov., the first South African geogarypid with both monotarsate front legs as well as a reduced trichobothrial count. Interestingly, members of the Geogarypidae sharing these reduced features were already known, as Harvey (1986) described an Australian species (*Geogarypus connatus* Harvey, 1986) during his revision of the Geogarypidae that also possesses monotarsate leg pairs I and II, as well as the absence of tricobothria *isb*. Furthermore, all collection records of *G. connatus* were from under bark, indicating that the species may also be an obligate arboreal inhabitant, like *Afrogarypus castigatus* sp. nov. Phylogenetic analysis of the South African and Australian geogarypid fauna will likely yield very interesting results, including the possibility that *G. connatus* and *A. castigatus* sp. nov. may be related, indicating a Gondwanaland origin to the clade. Furthermore, new combinations of species into *Afrogarypus* necessitated an update of the diagnostic features of the South African genera. *Geogarypus* is defined by a uniformly convex dorsal chela hand surface and with a usual trichobothrial compliment of 8/4. *Afrogarypus* possess either a well developed sulcus or concave depression on the dorsal surface of the chelal hand, as well as the usual trichobothrial compliment of 8/4, with the exception of *A. castigatus* sp. nov., which presents distinct monotarsate anterior legs and the absence of trichobothria *isb*, resulting in a reduced trichobothrial compliment of 7/4.

The currently known distribution of Geogarypidae in South Africa correlate very closely with known centres of endemism, such as the Cape Floristic Region and the Maputaland-Pondoland-Albany centre of endemism, and agrees with distribution patterns of other arachnids (Kuntner *et al.* 2008; Lotz 2009; De Bivort & Giribet 2010; Haddad & Wesolowska 2013; Wesolowska & Haddad

2013; Haddad 2014). Griswold (1991) eluded that the speciation seen today within South African Afromontane spiders could have originated by the fragmentation of once persistent forest cover into isolated patches during periods of aridity, the most significant of these periods occurring during the Miocene-Pliocene and Pleistocene epochs. These isolation events would have had the same effects on the distribution and speciation of the Geogarypidae present at the time, and are most likely a major factor in explaining the distribution of modern geogarypid species within isolated forest patches of the Maputaland-Pondoland-Albany centre of endemism along the eastern parts of South Africa.

The genetic analysis done in this study represents only the second phylogenetic analysis of any South African pseudoscorpions, with the first study being recently published by Van Heerden, Taylor & Van Heerden (2013) on members of the Olpiidae. Phylogenetic analysis of South African geogarypids followed many patterns observed by other authors working on similar pseudoscorpion groups, and yielded valuable information on the Geogarypidae as a whole. Most importantly, the phylogenetic results corroborated the morphological analysis, and yielded the first holistic view on the systematics of the South African species of a family of pseudoscorpions. Although the phylogenetic analysis proved to be successful, difficulties with low Bootstrap values and the lack of gene amplification in *Afrogarypus minutus* (Tullgren, 1907) stat. nov. and *A. megamolaris* sp. nov. highlighted areas that need further research, including the identification of pseudoscorpion specific genes and the development of group-specific primers.

The study furthermore highlighted the lack of pseudoscorpion expertise within South Africa, as could be seen by both the lack of even family-level identifications for many museum exemplars, as well as the many misidentifications in the collections of our national museums. The difficulty of both tracking down and loaning type specimens was exacerbated by the apparent loss of the type specimens of *Afrogarypus impressus* (Tullgren, 1907), *A. purcelli* (Ellingsen, 1912) comb. nov. and *A. triangularis* (Ellingsen, 1912) comb. nov. Literature indicated that the *A. impressus* type was housed together with the types for *A. minutus* and *Geogarypus olivaceus* (Tullgren, 1907), and although the last two types could be located within the Zoological Museum, Hamburg, the type of the first species was not present (Dr. Markus Koch, personal communication). The same issue arose after a literature study suggested that the types for the Ellingsen species were housed within the Iziko South African Museum, Cape Town. After extensive searching, only the types for *A. robustus* (Beier, 1947) and *G. flavus* (Beier, 1947) could be located, and none of Ellingsen's types. Presently, the missing types are feared to be lost, though searching will continue until publication of this study. Harvey (1994) experienced a similar issue, but was fortunate enough to rediscover the lost types in the Department of Entomology of the University of Queensland. If the types cannot be located, suitable neotypes will be designated and deposited within the collections of the National Museum in Bloemfontein, South Africa.

6.2 *Conclusion*

The study presented in this thesis aimed to provide the first holistic approach into the systematics of the South African species of a pseudoscorpion family, and thereby spearheads an endeavour to revise the endemic fauna as a whole. In this regard, the study was successful, achieving the aims set forth at the beginning of the thesis. The holistic approach yields a more complete taxonomic view than either the morphological or phylogenetic analyses on their own. The discovery of nine new Geogarypidae species also suggests that similar results could be expected with the revisions of other pseudoscorpion families in South Africa. To this end, this study will act as a ground-breaking reference with regard to the techniques that can be used, possible difficulties that can be expected, as well as setting the basis for future technical improvements.

CHAPTER 7 - LITERATURE CITED

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