



The Hercules pseudoscorpions from Madagascar: A systematic study of Feaellidae (Pseudoscorpiones: Fealloidea) highlights regional endemism and diversity in one of the "hottest" biodiversity hotspots

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Abstract

Madagascar is amongst the "hottest" biodiversity hotspots with extreme levels of diversity and endemism. Throughout the last decades, there has been substantial progress in documenting the Malagasy invertebrate fauna but no study has ever focused on pseudoscorpions (Arachnida: Pseudoscorpiones) in the arachnid fauna. Here we review the Malagasy fauna of Hercules pseudoscorpions (family Feaellidae), which are common in soil habitats of arid biomes across Madagascar. Using morphology and molecular data, we recover three reciprocally monophyletic clades that correspond to three new genera in well-defined biogeographical regions and identify twelve new species: *Antsirananaella* **gen. nov.** for *Antsirananaella lorenzorum* **sp. nov.**, *Antsirananaella leniae* **sp. nov.**, *Antsirananaella faulstichi* **sp. nov.** and *Antsirananaella marlae* **sp. nov.**; *Mahajanganella* **gen. nov.** for *Mahajanganella fridakahloae* **sp. nov.**, *Mahajanganella heraclis* **sp. nov.** and *Mahajanganella schwarzeneggeri* **sp. nov.**; *Toliaranella* **gen. nov.** for *Toliaranella fisheri* **sp. nov.**, *Toliaranella griswoldi* **sp. nov.**, *Toliaranella mahnerti* **sp. nov.**, *Toliaranella meridionalis* **sp. nov.** and *Toliaranella pumila* **sp. nov.** Local endemism in this fauna is high and most species have small distributions, ranging from 20 km to 350 km linearly. Genetic distances between populations are also high, suggesting restricted dispersal or selection against dispersal in this fauna. Species' ranges seem to be delimited by geological barriers including volcanic fields (Ambre-Bobaomby in the north of Madagascar), mountain ranges (foothills of the Central Highland Plateau), and rivers (Manankolana, Mandrare, Manombo and Onilahy Rivers and their anabranches), but mainly by different biome habitats. Overall, Madagascar emerges as a global "hotspot" of feaellid radiation and these animals may be used in future studies to test biogeographical hypotheses across xeric biomes on this island.

Keywords

biodiversity, false scorpions, new species, systematics, taxonomy

1. Introduction

Madagascar is one of the world's priority conservation hotspots and amongst the most biodiverse countries with extreme levels of endemism and high species diversity across rich vegetation zones, including tropical rainforest in the east, spiny desert in the south and dry deciduous rainforest in the west (Mittermeier et al. 2004). Sadly, more than 90% of original habitats are already lost and major habitat types are irreversibly damaged (Ganzhorn et al. 2008). Madagascar's high levels of biodiversity and endemism are correlated with landscape heterogeneity, bioclimatic zonation and a long history of isolation that includes rifting from West Gondwana (Africa and South America) beginning as early as 166 Ma and ending by 116 Ma, and from India-Seychelles 85–90 Ma, during the break-up of Gondwana (Ali and Aitchison 2008; Vences et al. 2009). Ecological disparities between the arid west and humid east, montane and lowland rainforest refugia, and habitats separated by canyon and riverine barriers have driven adaptive trait diversification among the island's fauna and flora, allowing species to occupy new niches as they emerged (Wood et al. 2015). In addition to ongoing deforestation and overharvesting, anthropogenic climate change is increasingly threatening the remaining natural habitats and accelerating biodiversity loss in this natural laboratory (Morelli et al. 2020).

In the past two decades, there has been major progress in documenting the Malagasy invertebrate fauna at the taxonomic level, including many arachnid lineages (e.g., Griswold et al. 2012; Saucedo et al. 2015; Wood and Scharff 2018). Several studies have addressed patterns and causes of invertebrate speciation (e.g., Miraldo et al. 2011; Wesener et al. 2011; Agnarsson et al. 2015), but no data are presently available for pseudoscorpions, a meso-diverse arachnid lineage, following the more diverse spiders and mites, which are found in all ground habitats on Madagascar (WPC 2022). No detailed taxonomic studies have ever been conducted on Malagasy pseudoscorpions and 15 species are presently recognized in eight families – a relatively small number compared to regions such as

Kenya (133 species) or South Africa (ca. 140 species). In a brief contribution, Heurtault (1986) listed eight of the presently 25 recognized pseudoscorpion families on Madagascar and identified twelve putatively endemic genera in these families but also wrote that “Les Pseudoscorpions (...) ne présentent pas de cas “d’explosion” ou de “pulvérisation” spécifique” (“The pseudoscorpions do not represent a case of explosive speciation”) in contrast to many other faunal groups. She was also amongst the first to note the presence of the pseudoscorpion family Feaellidae Ellingsen, 1906 on Madagascar and mapped a record from Toliara Province but did not describe any species, however.

Feaellid pseudoscorpions have a unique morphology that includes a dorsoventrally compressed body, a thick and granulate cuticle, the presence of 2–6 lobes on the anterior margin of the carapace, and raptorial pedipalps with heavily armed and robust pedipalpal femora, resulting in a somewhat hulky appearance, hence the name “Hercules pseudoscorpions” that is introduced here to symbolize this morphology for non-arachnologists. Together with their sister-family, the Pseudogarypidae Chamberlin, 1923, this family constitutes one of the two basal suborders of pseudoscorpions, Atoposphyronida Harvey 2019, which is characterized by the unique presence of carapaceal lobes, spiracles near sternites IV and V, a heavily sclerotized anal plate, and the absence of venom glands in the chelal fingers (Harvey 1992; Benavides et al. 2019). Atoposphyronida may have originated in the Permian or even Carboniferous (Benavides et al. 2019). Today, the Feaellidae are restricted to the Mediterranean and tropical biomes of former Gondwanan landmasses (Fig. 1), although compression and amber fossils from the Triassic and Paleogene of Europe highlight a once wide distribution (Henderickx and Boone 2014, Kolesnikov et al. 2022). The taxonomy of Feaellidae is still in flux and there is no recent generic revision but six genera and subgenera are presently recognized in two extant subfamilies. Cybellinae Judson, 2017 includes a single genus, *Cybella* Judson, 2017 with four species from subterranean habitats in the Southeast Asian countries of Cambodia, Malaysia and Vietnam (Judson 2017; Har-

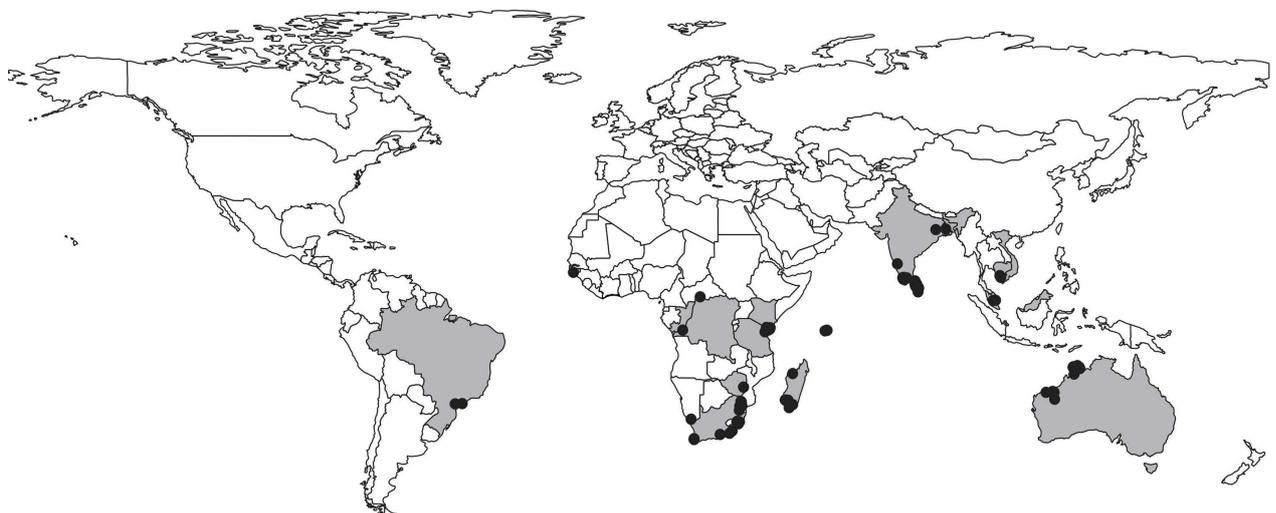


Figure 1. Global distribution of the pseudoscorpion family Feaellidae Ellingsen, 1906.

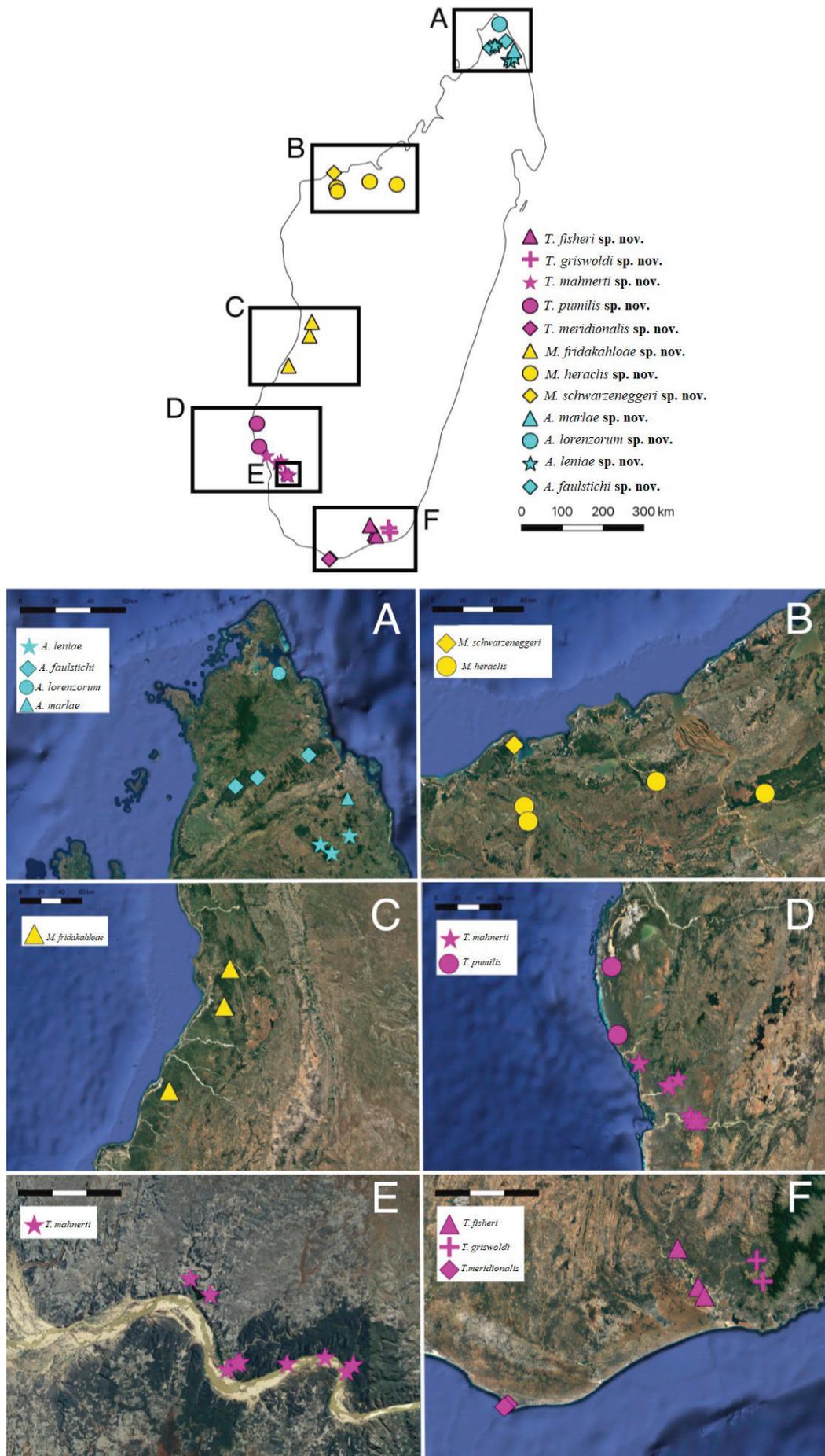


Figure 2. Distribution of examined Malagasy genera: *Antsirananaella*, gen. nov. (turquoise), *Mahajanganella*, gen. nov. (yellow) and *Toliaranella*, gen. nov. (pink).

vey 2018). The second subfamily, Feaellinae Ellingsen, 1906, includes the monotypic *Iporangella* Harvey et al., 2016 from the Brazilian Atlantic rainforests, and *Feaella* Ellingsen, 1906, which is divided into three subgenera based on the number of carapaceal lobes: *Feaella* (*Feaella*) Beier, 1955 with three species from tropical Africa (Guinea-Bissau, Côte d'Ivoire, Congo and Kenya) having six carapaceal lobes; *Feaella* (*Tetrafeaella*) Murthy and Ananthkarishnan, 1977 with twelve Recent species from southern Africa, India, Sri Lanka, the Seychelles, Maldives, Western Australia and a Baltic amber fossil (Harvey et al. 2016a, 2016b; Novák et al. 2020; Harvey 2022); and *Feaella* (*Difeaella*) Beier, 1966 with a single species from Kruger National Park, South Africa (Beier 1966). Although all species in the subgenus *Feaella* (*Tetrafeaella*) have four carapaceal lobes, it is likely that this subgenus is polyphyletic as it includes species from diverse climates (Mediterranean, tropical) and habitats (e.g., rocky outcrops in Western Australia, savannah and coastal habitats in continental Africa; Beier 1955; Harvey et al. 2016a), and with diverse morphologies.

Before the onset of phylogenetics, most feallid species were considered widespread, e.g., *Feaella* (*Feaella*) *mirabilis* Ellingsen, 1906 across western and central Africa (Heurtault-Rossi and Jézéquel 1965; Heurtault 1983) or *Feaella* (*Tetrafeaella*) *indica* (Chamberlin, 1931) across Bangladesh, India and Sri Lanka (Chamberlin 1931; Batuwita and Benjamin 2014). However, recent molecular studies have indicated extreme local endemism in a morphologically cryptic fauna with slow rates of evolution, implying that many species hypotheses will have to be revised (Harvey et al. 2016a; Novák et al. 2020). In contrast to the historical literature, Feallidae may in fact turn out to be a highly suitable group for vicariance biogeography because they seem to disperse poorly and occur almost exclusively on continental landmasses despite a record from the Maldives that might indicate trans-oceanic dispersal (Novák et al. 2020). Certainly, the present distribution is indicative of diversification from continental drift and the Late Cretaceous (Cenomanian: 99 Ma), Burmese amber fossil, *Protofeaella peetersae* Henderickx and Boone, 2014 shares prime synapomorphies of feallids, providing unequivocal evidence for an ancient radiation beyond age estimates provided by molecular clock analyses (Henderickx and Boone 2016).

The presence of feallids in Madagascar went largely unnoticed even in the arachnological community apart from sporadic records (Vachon 1960; Heurtault 1986) but comprehensive biodiversity surveys conducted by Brian L. Fisher and his team have established records of Hercules pseudoscorpions from all of Madagascar's drier vegetation zones but not from eastern forests. Unlike other regions of the world where feallids are highly elusive and rarely collected, Hercules pseudoscorpions are amongst the more abundant pseudoscorpions in sclerophyll and savannah habitats and have been frequently collected in pitfall traps, often in large numbers. However, occurrences seem to be localized and strictly tied to specific microhabitats or localities. Following our detailed study, the Malagasy fauna also falls into distinct morphological

clades that show strict regional zonation: a northern clade (in the former Antsiranana Province), a western clade (in the former Mahajanga and Toliara Provinces), and a southern clade (in the former Toliara Province) (Fig. 2). These three clades share the presence of four carapaceal lobes and hence resemble *Feaella* (*Tetrafeaella*) rather than *Feaella* (*Feaella*) or *Feaella* (*Difeaella*). However, considering that each of these three clades present unique diagnostic characters, are genetically well-differentiated and correspond to specific regions of Madagascar, they are each recognized here as new genera.

This study aims to: (1) document the Malagasy fauna of Hercules pseudoscorpions both at the generic and species level across dry and subarid bioclimatic zones in Madagascar; (2) provide the first comprehensive monograph of a Malagasy pseudoscorpion lineage to date; (3) use taxonomic data to discuss endemism and distributional patterns with regards to hotspot biogeography of other invertebrates; and (4) discuss potential reasons for the unprecedented levels of feallid diversity in Madagascar.

2. Methods

2.1. Morphology

All specimens were collected between 2002–2006 and are deposited in the California Academy of Sciences (CAS), San Francisco and the Museum of Nature Hamburg – Zoology (formerly Zoological Museum Hamburg (ZMH)). Specimens sequenced as outgroups are lodged in the Western Australian Museum (WAM), Perth. Most Malagasy specimens were collected by Dr. Brian Fisher during extensive surveys of Malagasy invertebrates and preserved in 75% ethanol. Specimens were sexed, identified and sorted using a Leica M125C stereomicroscope. Dissected parts were kept in microvials. Measurements (in mm) were taken with a Leica M205A stereomicroscope and Leica Application Suite X Version 3.0.1. Digital images were taken with a custom-made BK Plus Lab System by Dun, Inc. using a Canon EOS 7D Mark II camera, an attached 5×-magnification microscopic lens in a P-51 CamLift-System installation controlled by P-51 Camlift Controller ver. 2.8.0.0 and by Capture One ver. 9.3. Scanning electron images were taken from temporarily mounted specimens using a Hitachi TM4000Plus scanning electron micrograph. Since many specimens were coated with a thick layer of dirt or particles, ultrasound cleaning was used to improve imaging results, however, success was limited. Drawings were made by hand using original images that were checked against primary specimens after illustration. Maps were created using QGIS Version 3.0 (<https://www.qgis.org>) and coordinates taken from original labels. Images, trees and maps were edited with Adobe Photoshop Version CC 2017.

Table 1. Details of the species sequenced for H3 and GenBank accession codes.

Species	Collection Number	Locality	GenBank Accession Code
Heterosphyronida			
<i>Allochthonius coreanus</i> Morikawa, 1970	WAM T120699	South Korea	OP589972
<i>Pseudotyrannochthonius giganteus</i> Beier, 1971	WAM T120449	Australia: Western Australia	OP589948
<i>Ehippochthonius boldorii</i> (Beier, 1934)	WAM T120677	Germany: Saxony	OP589971
<i>Ehippochthonius tetrachelatus</i> (Preysslner, 1790)	WAM T120678	Germany: Saxony-Anhalt	OP589973
<i>Mundochthonius ussuricus</i> Beier, 1979	WAM T120369	Russia: Primorsky Krai	OP589945
<i>Tyrannochthonius terribilis malaccensis</i> Beier, 1952	WAM T114617	Malaysia: Selangor	OP589946
Atoposphyronida			
<i>Neopseudogarypus scutellatus</i> Morris, 1948	WAM T104213	Australia: Tasmania	OP589951
<i>Pseudogarypus bicornis</i> (Banks, 1895)	WAM T114846	U.S.A.: Oregon	OP589950
<i>Feaella (Tetrafeaella) cf. anderseni</i> (Harvey, 1989)	WAM T120617	Australia: Western Australia	OP589952
<i>Feaella (Tetrafeaella) cf. mucronata</i> (Tullgren, 1907)	WAM T120637	South Africa: Eastern Cape	OP589949
<i>Antsirananaella lorentorum</i> sp. nov.	CAS 9071844	Madagascar: Antsiranana region	OP589964
<i>Antsirananaella faulstichi</i> sp. nov.	CAS 9071843	Madagascar: Antsiranana region, Reserve special d'Ankarana	
<i>Antsirananaella leniae</i> sp. nov.	CAS 9072445	Madagascar: Antsiranana region, Foret d'Antsahabe	OP589968
	CAS 9072435	Madagascar: Antsiranana region, Foret d'Binara	OP589966
	CAS 9072455	Madagascar: Antsiranana region, Foret d'Bekaraoka	OP589967
<i>Antsirananaella marlae</i> sp. nov.	CAS 9072444	Madagascar: Antsiranana region, Foret d'Ampondrabe	OP589965
<i>Mahajanganella heraclis</i> sp. nov.	CAS 9071835	Madagascar: Province Mahajanga, Parc National d'Ankarafantsika	OP589970
<i>Mahajanganella fridakahloae</i> sp. nov.	CAS 9071518	Madagascar: Province Toliara, Foret de Kirindy	OP589969
<i>Mahajanganella schwarzeneggeri</i> sp. nov.	CAS 9071739 (not sequenced)	Madagascar: Province Mahajanga, Parc National de Baie de Baly	
<i>Toliaranella pumila</i> sp. nov.	CAS 9071606	Madagascar: Province Toliara, Foret de Tsinjoriaky	OP589953
	CAS 9071743	Madagascar: Province Toliara, Foret de Beroboka	
<i>Toliaranella fisheri</i> sp. nov.	CAS 9071590	Madagascar: Province Toliara, Foret de Bealoka	OP589962
	CAS 9071578	Madagascar: Province Toliara, Foret de Mahavelo	OP589963
<i>Toliaranella griswoldi</i> sp. nov.	CAS 9071500	Madagascar: Province Toliara, Parc National d'Andohahela	OP589960
	CAS 9071509	Madagascar: Province Toliara, Foret d'Andohahela	OP589959
<i>Toliaranella mahnerti</i> sp. nov.	CAS 9071763	Madagascar: Province Toliara, Antafoky	OP589955
	CAS 9071770	Madagascar: Province Toliara, Sept Lacs region	OP589954
	CAS 9071522	Madagascar: Province Toliara, Mandarano	OP589957
	CAS 9071753	Madagascar: Province Toliara, Mandarano	OP589958
	CAS 9072461	Madagascar: Province Toliara, Mandarano	OP589956
<i>Toliaranella meridionalis</i> sp. nov.	CAS 9071748	Madagascar: Province Toliara, Reserve Speciale de Cap Sainte Marie	OP589961

Abbreviations. **OR** (outer row); **MR** (middle row); **IR** (inner row); **af** (anterior furca); **al** (anteriolateral); **am** (anteriomedial); **pf** (posterior furca); **pl** (posteriolateral); **pm** (posteriomedial)

2.2 DNA Extraction, Sequencing and Taxon Sampling

DNA extraction and Sanger sequencing was trialed for representative specimens (one per locality) but because all specimens were collected almost two decades ago, amplification of mitochondrial or ribosomal markers failed. Still, we were able to amplify a fragment of the

nuclear protein-coding Histone 3a locus (H3), using primers and protocols from a previous study (Harms et al. 2019). Amplification of this short gene fragment (324 bp in total) was successful for eighteen Malagasy samples, representing eighteen localities (Table 1). Two additional *Feaella (Tetrafeaella)* specimens were also sequenced, including *Feaella (T.) cf. anderseni* (Harvey, 1989) from the Bonaparte Archipelago in Western Australia and *Feaella (T.) cf. mucronata* (Tullgren, 1907) from Eastern Cape, South Africa. We also sequenced ten representative outgroup taxa including two species of Pseudogarypidae [*Pseudogarypus bicornis* (Banks, 1895) and *Neopseudogarypus scutellatus* Morris, 1948], the sister family of Feaellidae, and eight species of Heterosphyro-

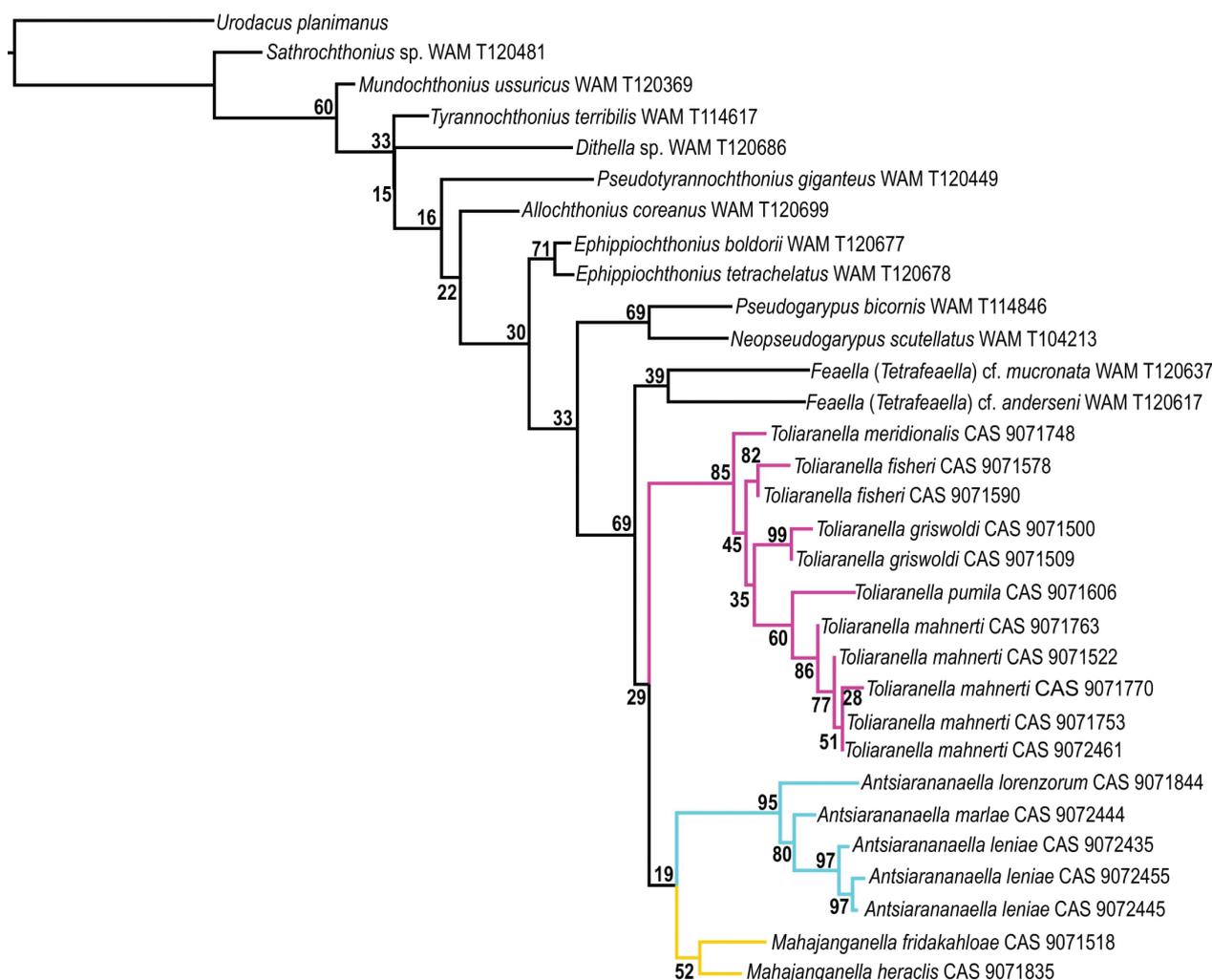


Figure 3. Phylogeny of Malagasy Feaellidae Ellingsen, 1906 obtained by maximum likelihood analysis of the H3 locus (340 aligned sites) for 31 terminals. Nodes above branches indicate bootstrap support values.

nida including taxa from both families, Chthoniidae Day, 1889 and Pseudotyranochthoniidae Beier, 1932, representing the second most plesiomorphic suborder within Pseudoscorpiones. A sequence of a scorpion, *Urodacus planimanus* Pocock, 1893, was downloaded from GenBank and included as the root for phylogenetic analyses (Table 1).

2.3. Phylogenetic Analyses

The H3 dataset comprising the eighteen Malagasy feaellids, two *Feaella* species and eleven outgroup taxa for a total of 31 terminals, was aligned using MAFFT version 7 online server (<https://mafft.cbrc.jp/alignment/server/>), applying the G-INS-i method of alignment, which assumes global homology (Katoh et al. 2002, Katoh and Toh 2008, Katoh and Standley 2013). The total length of the aligned H3 locus was 340 bp. A -f -a maximum likelihood tree search was performed with 1000 bootstrap iterations, applying a MULTIGAMMA model, and using the RAXML (Stamatakis 2006, 2014) graphical user interface raxmlGUI 2.0 (Edler et al. 2020) in the CIPRES Science Gateway V. 3.3. (Miller et al. 2010).

Mean uncorrected pairwise (p) genetic distances were calculated among all feaellid taxa using MEGA v. 11 (Tamura et al. 2021).

3. Results

3.1. Phylogenetic Analyses

Maximum likelihood analysis of the H3 dataset recovered Feaellidae as monophyletic with *T. cf. mucronata* and *T. cf. anderseni* forming a clade, sister to the Malagasy feaellids, which in turn, formed three geographically delimited clades (Fig. 3): a northern clade represented by five terminals from dry Diana and Sava Regions (formerly Antsiaranana Province), a central clade represented by two terminals from the dry Boeny and Menabe Regions (formerly Mahajanga and upper Toliara Provinces), and a southern clade represented by eleven terminals from the sub-arid Androy, Anosy and Atsimo-Andrefana Regions (formerly Toliara Province). Bootstrap support values were moderate to high for all three clades: 52%, 85% and

95% for the central, southern and northern clades, respectively.

Uncorrected *p*-distances between Malagasy terminals ranged from 0% (MGF 034 and MGF 033) to 15.2% (between Sept Lacs and Forêt de Bekaraoka). Mean uncorrected *p*-distances between the Malagasy species and two *Feaella* species was 15.5% and among the Malagasy clades were as follows: central-southern clades (11.4%), northern-central clades (12.0%) and northern-southern clades (13.1%). Mean uncorrected *p*-distances within each clade were 5% for the northern and southern clades, and 6% for the central clade. Subdivision into three geographically delimited clades is also mirrored by morphological differences, primarily morphometrics and chaetotaxy of the pedipalps, which are commonly used in pseudoscorpion taxonomy for species delimitation. Based on results of the phylogenetic analyses, genetic distances and supporting morphological data, these three geographically-delimited Malagasy clades are recognized as genera below.

3.2 Systematics

Family Feaellidae Ellingsen, 1906

Subfamily Feaellinae Ellingsen, 1906

All genera and species described below can be placed in the subfamily Feaellinae based on the presence of pleural platelets, the absence of the cheliceral rallum and an unmodified coxa III. Cybellinae lack pleural platelets, coxa III is modified, and the rallum comprises two blades (Judson 2017; Harvey 2018).

Note that there are significant morphological differences between the species included in the three different subgenera of *Feaella* which are retained here for practical reasons but almost certainly polyphyletic and in need of revision. The status and composition of *Feaella* (*Tetrafearella*) is problematic due to many poorly described species, including the type species *Feaella* (*T.*) *indica* Chamberlin, 1931, and the knowledge that the Australian fauna is misplaced in the genus (Harvey et al. 2016a).

The newly defined genera also differ from all previously described genera of Feaellinae and can be differentiated using characters in the key below:

Key to genera and subgenera of Feaellinae

- 1a Carapace with 2 or 4 anterior lobes 2
- 1b Carapace with 6 anterior lobes *Feaella* Beier, 1955
- 2a Carapace with 2 anterior lobes 3
- 2b Carapace with 4 anterior lobes 4
- 3a Specialized setae on the retrolateral face of the movable pedipalpal finger absent *Iporangella* Harvey et al., 2016
- 3b Specialized setae on the retrolateral face of the movable pedipalpal finger present *Feaella* (*Difearella*) Beier, 1966
- 4a Coxa I with 3–4 coxal spines *Feaella* (*Tetrafearella*) Beier, 1955 from Australia
- 4b Coxa I with 1–2 coxal spines 5
- 5a Coxa I with deep basal depression stretching widely into coxa II, framed by large irregularly sized spines; sternum heavily granulated (Fig. 25B, C) *Feaella* (*Tetrafearella*) from Africa
- 5b Coxa I with shallow basal depression framed by irregularly sized spines from coxa II; sternum slightly or moderately granulated 6
- 6a. Movable chelal finger with 5 specialized setae between trichobothrium *b* and terminal teeth arranged in a transverse row *Antsirananaella*, **gen. nov.**
- 6b. Movable chelal finger with 5 specialized setae between trichobothrium *b* and terminal teeth arranged in a compact group 7
- 7a. Cuticle of coxa I with perforated pit organ in a basal depression *Toliaranella*, **gen. nov.**
- 7b. Cuticle of coxa I without perforated organ in a basal depression *Mahajanganella*, **gen. nov.**

***Antsirananaella* gen. nov.**

<https://zoobank.org/NomenclaturalActs/F84D7A46-D14E-4E58-998D-AFDC59A6C824>

Type species. *Antsirananaella lorenzorum* **sp. nov.**

Diagnosis. *Antsirananaella* **gen. nov.** differs from other Malagasy genera, *Toliaranella* **gen. nov.** and *Mahajanganella* **gen. nov.**, by the following characters: the pres-

ence of five specialized setae on the retrolateral face of the movable chelal finger that are arranged in a row between trichobothrium *b* and the terminal chelal teeth (arranged in a group in *Toliaranella* **gen. nov.** and *Mahajanganella* **gen. nov.**); the presence of five terminal teeth (including one large tooth) on the fixed chelal finger and seven on the movable chelal finger (number of terminal teeth varying from 7–9 teeth in fixed and movable fingers in other Malagasy genera); anteromedial lobes of carapace closer to each other and slightly longer than anterolateral lobes

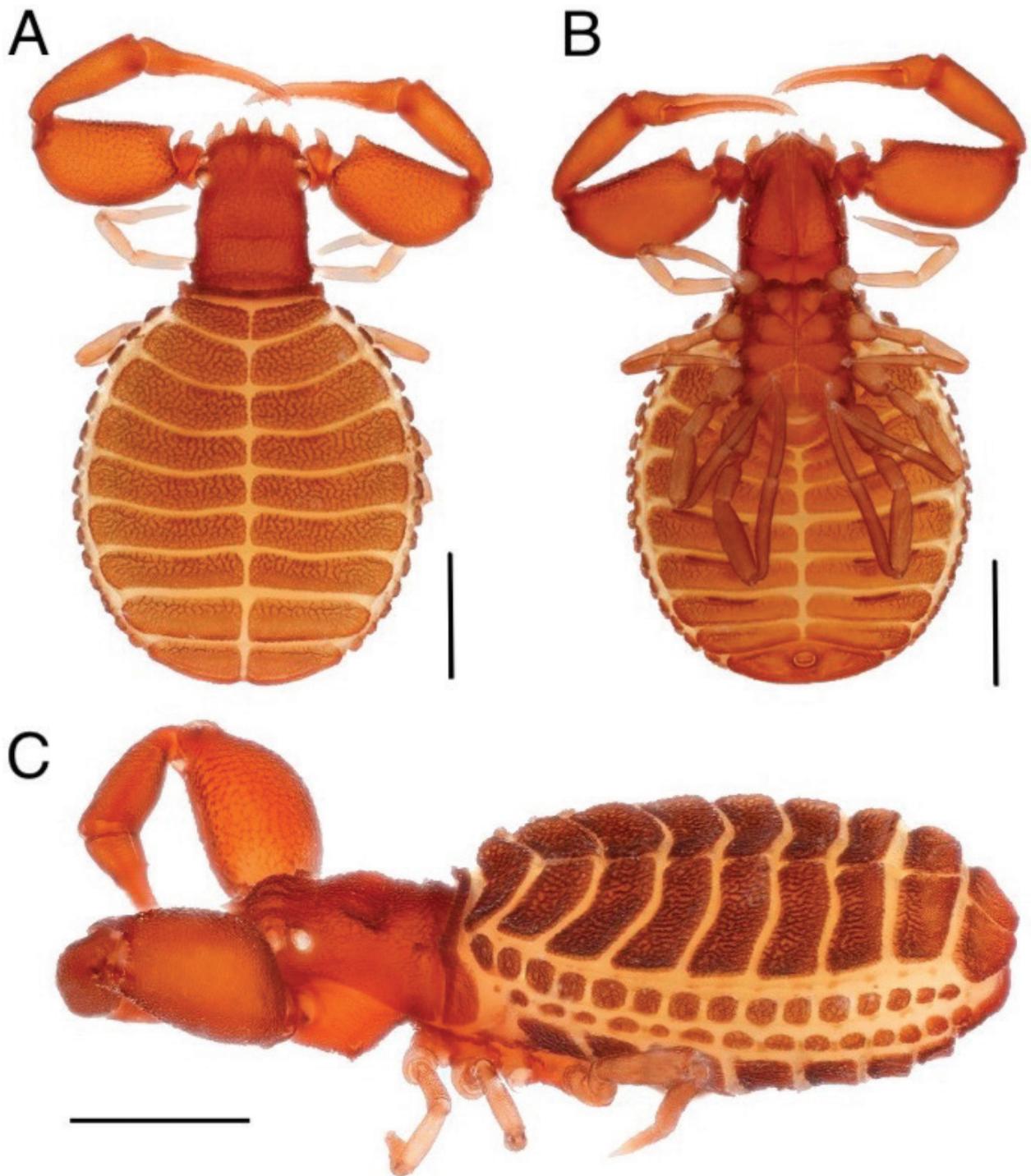


Figure 4. *Antsirananaella*, **gen. nov.**, habitus. Specimen used for imaging: *A. leniae* **sp. nov.** holotype (CAS 9072445). **A** dorsal; **B** ventral; **C** lateral. Scale bar: 0.5 mm.

(all four lobes equidistant in other Malagasy genera); and larger body size (1.80–2.17/2.17–2.47 ♂/♀ in *Antsirananaella* **gen. nov.** and ca. 1.56–1.89/1.96–2.33 ♂/♀ in all other genera). *Antsirananaella* **gen. nov.** differs from *Cybella* (Southeast Asia) by having platelets on the pleural membrane (absent in *Cybella*), from *Iporangella* (Brazil) by the presence of specialized setae on the movable chelal finger (absent in *Iporangella*), from *Feaella* (*Difeaella*) (South Africa) and *Feaella* (tropical Africa) by the presence of four anterior carapaceal lobes (two and six, respectively), from *Feaella* (*Tetrafeaella*) in conti-

ental Africa by having a less pronounced depression on the base of coxa I and on top of coxa II (distinctly more pronounced in *Feaella* (*T.*) cf. *mucronata* in Figs 25–27), and from the Australian species presently attributed to *Feaella* (*Tetrafeaella*) by having fewer coxal spines (one pair versus three or four in the Australian taxa).

Etymology. This genus is named after the former Antsiranana Province, the area where the specimens were found. The gender is feminine.

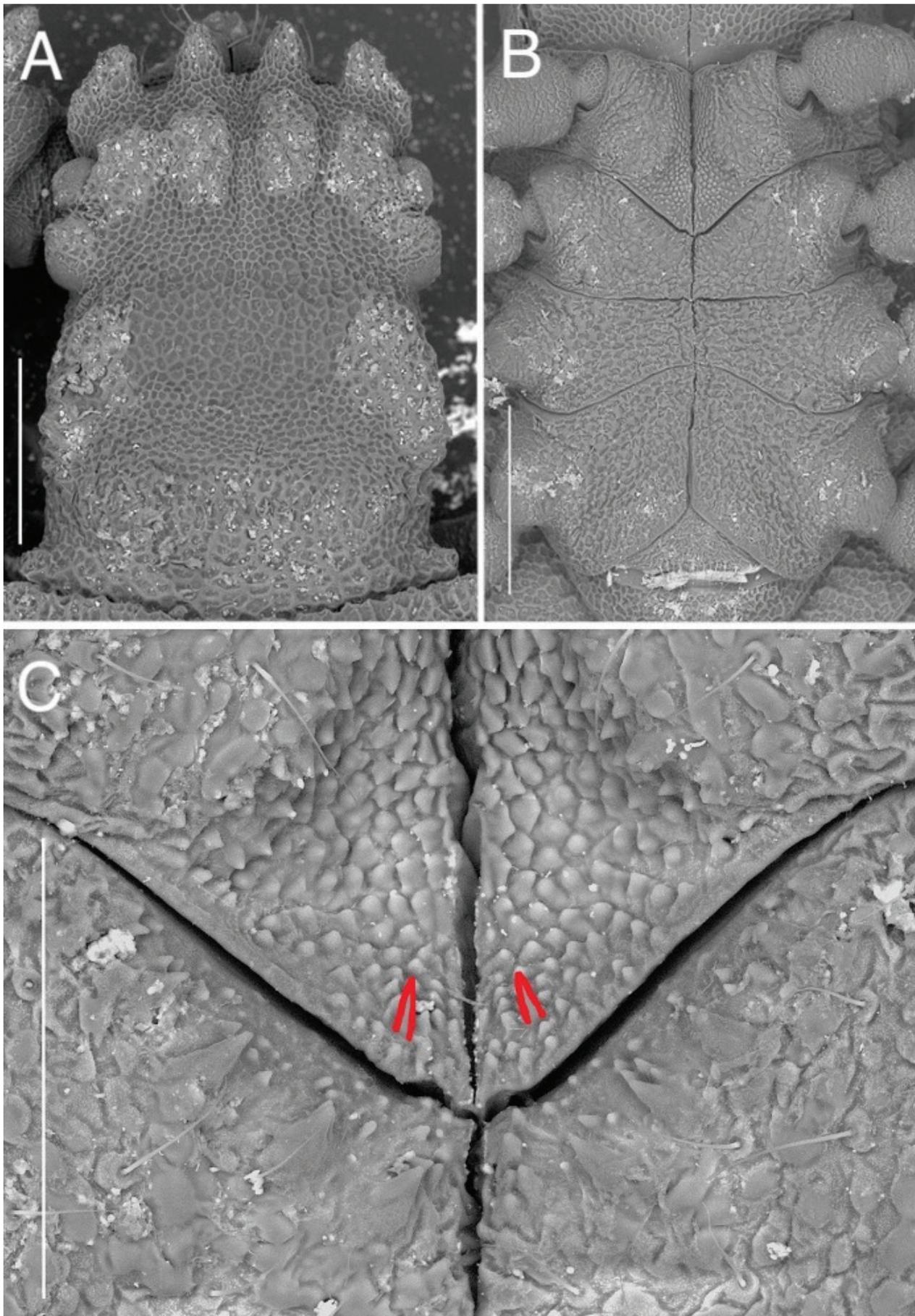


Figure 5. *Antsirananaella* gen. nov., scanning electron micrographs. Specimen used for imaging: *A. leniae* sp. nov. male paratype (ZMH-A0016685). **A** carapace, dorsal; **B** sternum, ventral; **C** coxal spines (highlighted in red). Scale bars: 0.2 mm (**A**, **B**); 0.1 mm (**C**).

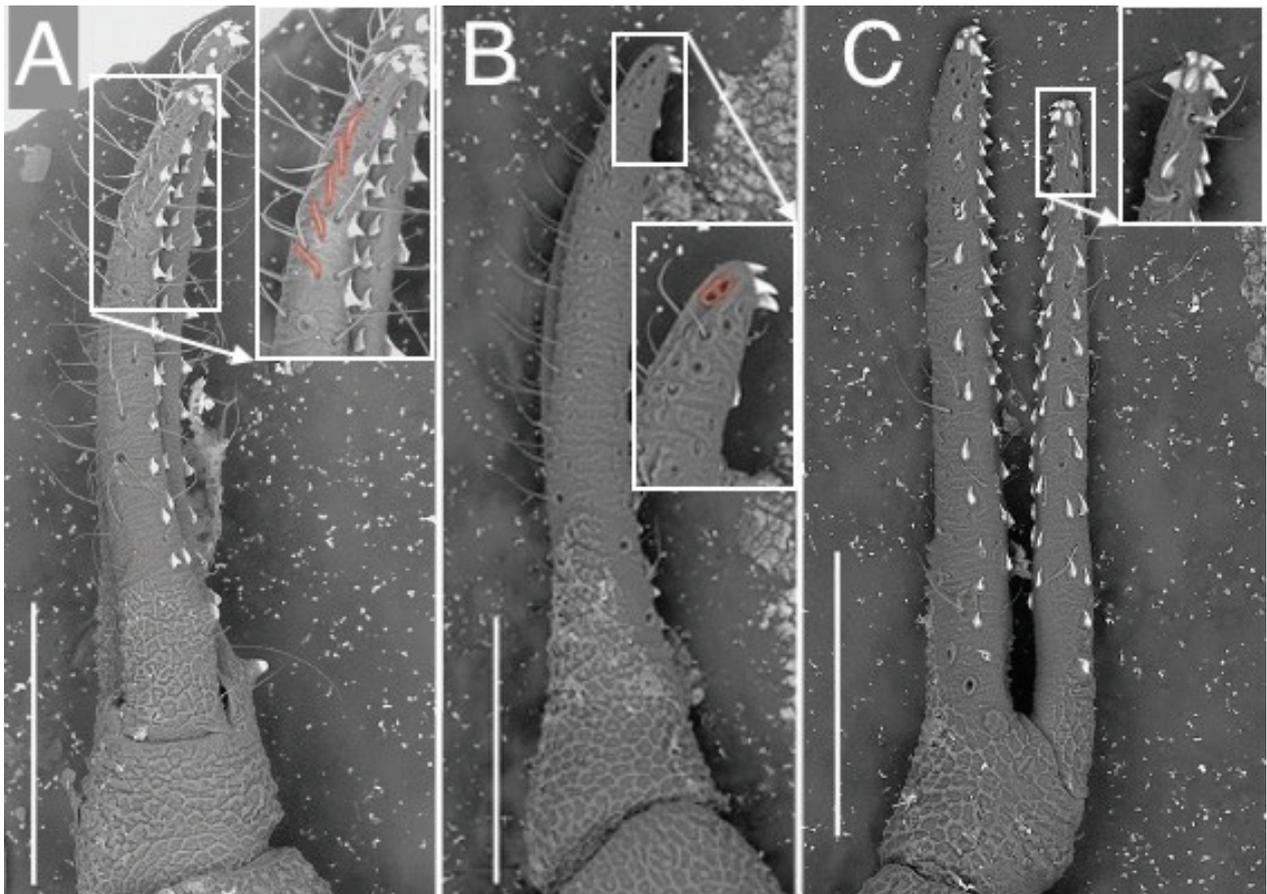


Figure 6. *Antsirananaella*, gen. nov., scanning electron micrographs. Specimen used for imaging: *A. faulstichi* sp. nov. allotype (ZMH-A0016680). **A** right chela from ventral with specialized setae in a row in detail; **B** left chela with double trichobothrium *dt* in detail; **C** left chela from medial with terminal teeth in a compact group in detail. Scale bar: 0.2 mm.

Description. The following description is based on examination of all species in *Antsiranana*. Typical feaelid habitus with a spherical abdomen, short and robust pedipalps, four prominent carapaceal lobes and dark reddish-brown body colour. — *Carapace*: (Figs 5A, 7A, 8A, 9A, 10A): With four distinctly pointed anterior lobes; anteriolateral lobes slightly broader and wider than anteriomedial ones; anteriomedial lobes distinctly longer and closer to each other than anteriolateral ones; two pairs of eyes with lenses, equal in size, second pair partly covered by cuticula; four prominent posterior lobes (*pm*, *pl* in Figs 7A, 8A, 9A, 10A) and two longitudinal furrows more distally (*af*, *pf* in Figs 7A, 8A, 9A, 10A); with two medio-lateral mounds; and two postero-lateral processes. — *Pedipalp*: With a distinct conical protuberance on trochanter (Figs 4A, B, 7D, 8D, 9D, 10D); femur broad and with one prolateral triangular process plus a retrolateral hump, patella cone-shaped. Chelal hand very small and with one large medial tooth at the base of each finger. Fixed finger with 9 trichobothria including *dt*, movable finger with 4 trichobothria (Figs 6A, B, C, 7C, 8C, 9C, 10C). Movable finger with 5 specialized setae on ventral face, arranged in a transverse row between *b* and terminal teeth (Fig. 6A). Chelal teeth large and retrorse, arranged in three rows on both chelal fingers. Terminal teeth situated in compact groups facing medial, four equally sized teeth and one

larger tooth on fixed finger, seven equally sized teeth on movable finger (Figs 6A, B, C, 7C, 8C, 9C, 10C). With 2 sensory setae (*dt* in Figs 6B, 7C, 8C, 9C, 10C) on dorsal tip of fixed finger. — *Chelicera*: Palm with five long and several short setae; *is* and *ls* close; *sbs* proximal on fixed finger; movable finger with 1 subdistal seta (*gs*); *es* on palm close to base of movable finger; galea absent; spinneret conical; serrula exterior with 16–20 blades; no rallum could be found in any of the Malagasy species because of dirt; movable finger short and without teeth. — *Coxal region* (Fig. 5B, C): Pedipalpal coxae with one spike laterally near base (Fig. 5B); coxae I with a basal depression and one small coxal spine only (Fig. 5B); coxae II with irregular shaped spines various in number framing depression of coxa I (Fig. 5B); all coxae reaching towards midline and with coxa IV bigger in size than coxa I–III; cuticle within depression strongly granulate. — *Legs* (Figs 4B, 7B, 8B, 9B, 10B): Trochanter I and II rather circular, trochanter III and IV rather elliptical; femur I and II slightly longer than patella I and II; femur III and IV shorter than patella III and IV; all tarsi long and slender, without specialized tactical trichobothria; subterminal tarsi with two curved and smooth claws; all setae acuminate; arolium much shorter than claws and with fimbriate distal margin; claws divided. — *Abdomen* (Fig. 4A, B, C): Paired tergites and sternites medially divided; anal plate strongly sclerotized and with a cir-

cular raised rim in the center; pleural membrane with two rows of pleural platelets, 15 in the dorsal row, 14 in the ventral row. — *Genital region* (Figs 4B, 5B): Details like outer genital setae and inner structures not visible because of dirt on all specimens.

Included species. *Antsirananaella lorenzorum* **sp. nov.**; *Antsirananaella faulstichi* **sp. nov.**; *Antsirananaella leniae* **sp. nov.**; and *Antsirananaella marlae* **sp. nov.**

Distribution. *Antsirananaella* **gen. nov.** is endemic to dry deciduous forests in Diana and Sava Regions (formerly Antsiranana Province) of northern Madagascar and separated by other Malagasy genera by more than 500 km of terrain. The climate is arid or “transition tropical” with temperatures ranging from 10.5–41.5 °C. Annual precipitation ranges from 400–1000 mm.

Antsirananaella lorenzorum **sp. nov.**

<https://zoobank.org/NomenclaturalActs/F05A19A5-EDFC-4A4F-AA68-5A8C3B54DBDD>

Type material examined. MADAGASCAR: Antsiranana Province [Diana Region]: Holotype ♂ (CAS 9071844 [BLF3182]), allotype ♀ (ZMH-A0016678), paratypes: 2 ♀ (CAS 9071844 [BLF3182]), 1 ♀ (ZMH-A0016679), 12°19'22"S 49°20'17"E, December 2003, B.L. Fisher.

Diagnosis. Differs from all congeners by body length (1.94/2.33 ♂/♀ versus 1.80/2.17 ♂/♀ in *A. leniae* **sp. nov.**, and 2.14/2.47 ♂/♀ in *A. faulstichi* **sp. nov.**); smallest ratio of pedipalpal femora (1.70/1.74 ♂/♀ versus 1.80/1.84 ♂/♀ in *A. marlae* **sp. nov.**, and 1.75/1.79 ♂/♀ in *A. faulstichi* **sp. nov.**); pedipalpal chaetotaxy with *sb* not on same sagittal level as *est* but slightly more distal (on same sagittal level in *A. marlae* **sp. nov.** and *A. leniae* **sp. nov.**), *it* between *eb* and *et* closer to *eb* than to *et* (equidistant in *A. leniae* **sp. nov.**), *et* situated midway between *dt* and *eb* on fixed finger (situated in distal third between *dt* and *eb* in *A. marlae* **sp. nov.** and *A. faulstichi* **sp. nov.**).

Etymology. This species is a patronym for the senior author's family that include parents Sylvia and Günther Lorenz and brother Henrik.

Description. The following description is based on holotype and allotype. — *Carapace* (Fig. 7A): 1.38 (♂), 1.35–1.47 (♀) times longer than broad. — *Pedipalp* (Fig. 7C): Trichobothrial pattern: *esb* and *est* in the proximal half of the retrolateral face; *ib*, *isb* and *ist* situated basally as a slightly curved line, *isb* and *ib* closer to each other than *isb* and *ist*; *eb* and *it* situated sub-distally and very close to each other, with *it* more distal and more medial than *eb*; *et* situated distally and approximately the same distance to *dt* than to *eb*; *dt* situated very distal in a plain pit; *st* situated sub-basally at the same sagittal level as *esb*; *st* and *est* also on the same level as *ist*; *t* distinctly closer

to *sb* than to *b*; *sb* distinctly closer to *t* than to *st*. Chelal fixed finger with 10 teeth in the OR, 20 in the MR and 15 in the IR; movable finger with 11 teeth in the OR, 14–15 teeth in the MR, and 14 teeth in the IR. — *Dimensions* (mm): *Holotype* ♂: Body length 1.94; abdomen length 1.33; abdomen width 1.12 (without pleura), 1.24 (with pleura); carapace length 0.58; carapace width 0.42. *Pedipalp*: trochanter 0.22; femur length 0.54; femur width 0.32; patella 0.46; chela (without pedicel) 0.54; hand length (without pedicel) 0.12; width 0.14; movable finger length 0.42. Leg I: trochanter 0.11; femur 0.19; patella 0.17; tibia 0.17; tarsus 0.27. Leg IV: trochanter 0.17; femur 0.13; patella 0.28; tibia 0.29; tarsus 0.35. *Allotype* ♀: Same as male except body length 2.26; abdomen length 1.59, width 1.36 (without pleura), 1.49 (with pleura); carapace length 0.66, width 0.49. *Pedipalp*: trochanter 0.30, femur length 0.75, width 0.44, patella length 0.61, chela (without pedicel) 0.64, hand length (without pedicel) 0.14, width 0.18. Leg I: trochanter 0.14, femur 0.25, patella 0.22, tibia 0.20, tarsus 0.29. Leg IV: trochanter 0.23, femur 0.15, patella 0.36, tibia 0.42, tarsus 0.39.

Variation. Body length 1.94 (♂), 2.26–2.45 (♀); abdomen length 1.33 (♂), 1.59–1.71 (♀); abdomen width (without pleura) 1.12 (♂), 1.27–1.40 (♀); abdomen width (with pleura) 1.24 (♂), 1.41–1.58 (♀), 1.19 (♂), 1.20–1.27 (♀) times longer than broad; carapace length 0.58 (♂), 0.66–0.75 (♀), width 0.42 (♂), 0.48–0.51 (♀), 1.38 (♂), 1.36–1.47 (♀) times longer than broad. *Pedipalp*: trochanter 0.22 (♂), 0.27–0.30 (♀); femur 0.54 (♂), 0.71–0.79 (♀) in length, 0.32 (♂), 0.40–0.47 (♀) in width, 1.70 (♂), 1.68–1.80 (♀) times longer than broad; patella 0.46 (♂), 0.58–0.63 (♀) long; chela (without pedicel) 0.54 (♂), 0.61–0.67 (♀); hand (without pedicel) 0.12 (♂), 0.13–0.14 (♀) in length, 0.14 (♂), 0.17–0.18 (♀) in width, 0.86 (♂), 0.76–0.82 (♀) times longer than broad; movable finger 0.42 (♂), 0.47–0.54 (♀), 2.77 (♂).

GenBank Code. OP589964. The species differs from all congeners by more than 6.9% in the H3 dataset.

Habitat. Dry deciduous forest between the coast and a rising limestone plateau.

Distribution. Only known from the type locality (BLF3182) in Diana Region (formerly eastern Antsiranana Province), northern Madagascar.

Antsirananaella faulstichi **sp. nov.**

<https://zoobank.org/NomenclaturalActs/ABF2723E-BF6D-4D6E-861C-3D31B73DD563>

Type material examined. MADAGASCAR: Antsiranana Prov. [Diana Region]: Holotype ♂ (CAS 9071843 [BLF3012]), allotype ♀ (ZMH-A0016680), paratypes: 7 ♂, 1 ♀ (CAS 9071843 [BLF3012]), 3 ♂ (ZMH-A0016681 – ZMH-A0016683), Reserve special d'Ankarana, 12°51'49"S 49°13'33"E, December 2003, B.L. Fisher.

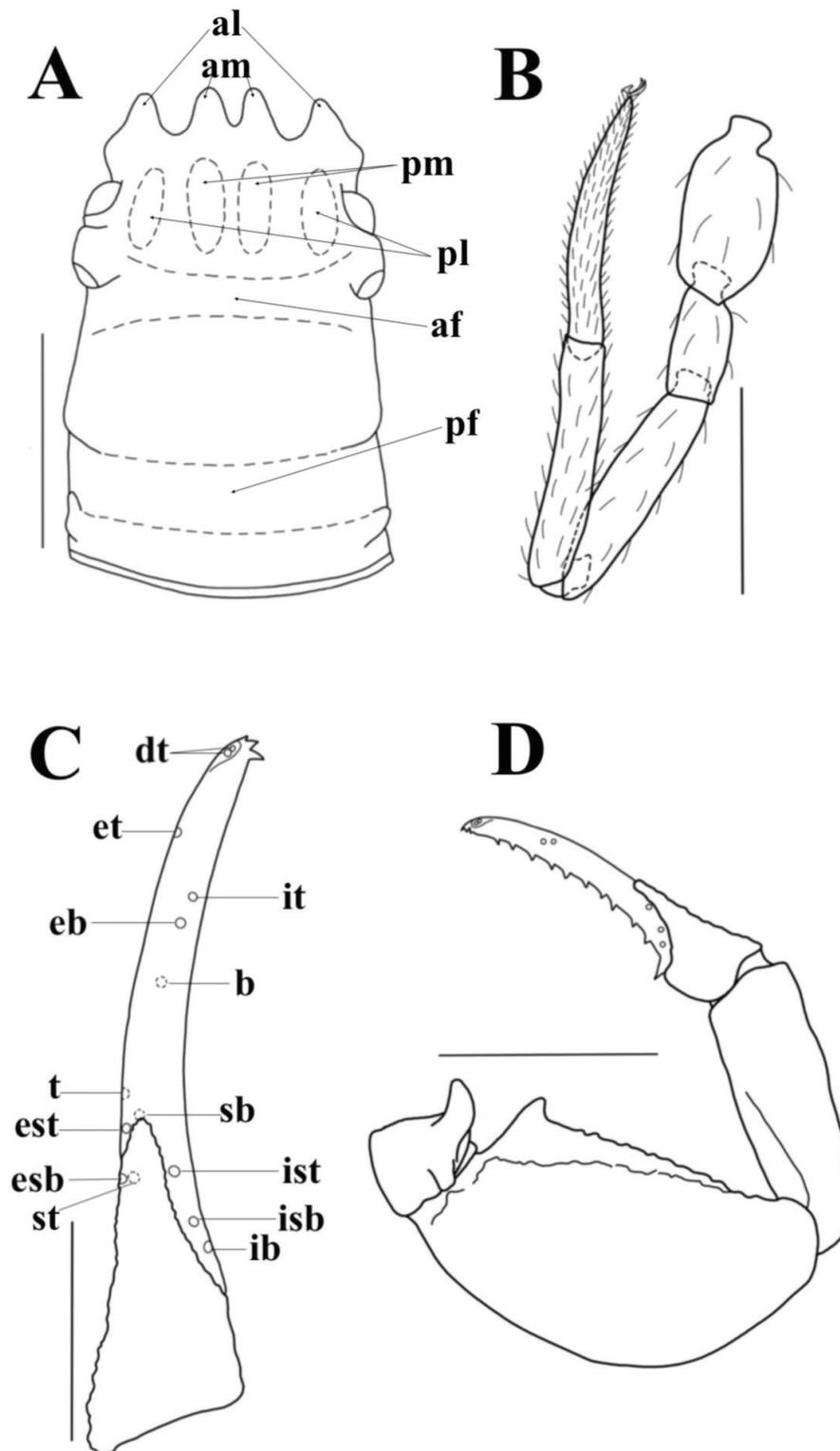


Figure 7. Drawings of *Antsirananaella lorenzorum* sp. nov.. **A** carapace, dorsal; **B** leg IV; **C** left chela from dorsal with trichobothrial pattern; **D** right pedipalp from dorsal. Scale bars: 0.2 mm (A–C); 0.4 mm (D).

Additional material examined. MADAGASCAR: Antsiranana Prov. [Diana Region]: 8 ♂, 4 ♀, 7 nymphs (CAS 9072436 [BLF11400]), Reserve Analamerana, 12°44'48"S 49°29'41"E, 5 December 2004, B.L. Fisher; 1 ♂ (CAS 9008191 [BLF2972]), Reserve Speciale de l'Ankarana, 12°54'32"S 49°06'35"E, 10–16 February 2001, Fisher, Griswold et al.; 1 ♀ (CAS 9071838 [BLF2858]), Reserve Speciale de l'Ankarana, 12°54'32"S 49°06'35"E, 10–16 February 2001, Fisher, Griswold et al.; Antsiranana Prov. [Sava Region]: 1 nymph (CAS 9072439

[BLF9656]), Foret de Binara, 13°15'48"S 49°36'12"E, 3 December 2003, B.L. Fisher.

Diagnosis. Smallest body sizes of all species of *Antsirananaella* gen. nov. (e.g., body length 1.80/2.17 ♂/♀ versus 1.94–2.17/ 2.21–2.47 ♂/♀; carapace length 0.55/0.65 ♂/♀ versus 0.58–0.69/ 0.70–0.77 ♂/♀). Unique cheotaxy: *sb* not on the same sagittal level as *est* but slightly more

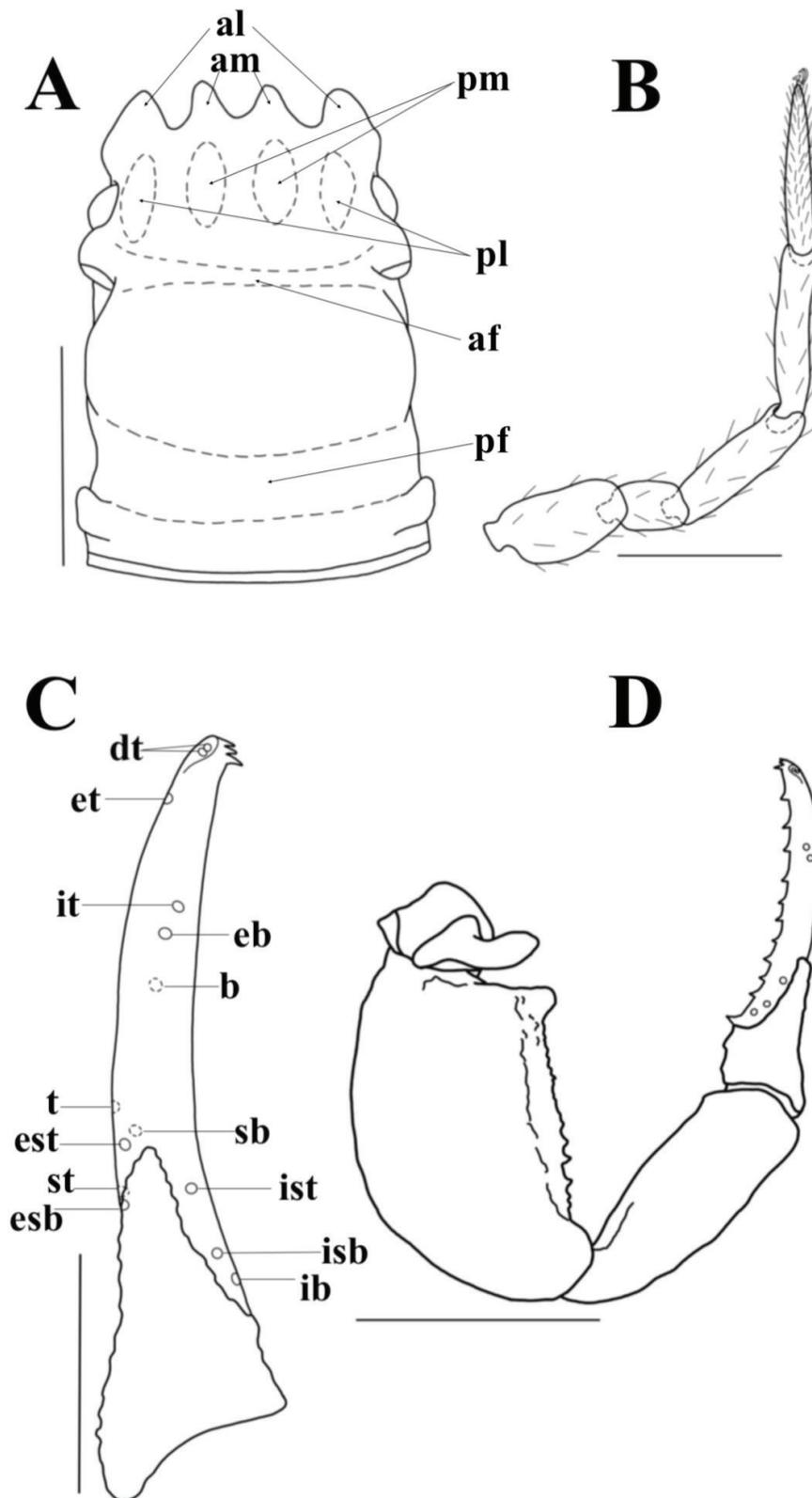


Figure 8. Drawings of *Antsirananaella faulstichi* sp. nov.. **A** carapace, dorsal; **B** leg IV; **C** left chela from dorsal with trichobothrial pattern; **D** right pedipalp from dorsal. Scale bars: 0.2 mm (A–C); 0.4 mm (D).

distal (on the same sagittal level in *A. marlae* sp. nov. and *A. leniae* sp. nov.); *it* between *eb* and *et* closer to *eb* than to *et* (equidistant in *A. leniae* sp. nov.); *et* in the distal third between *dt* and *eb* on the fixed finger (midway in between them in *A. lorenzorum* sp. nov. and *A. leniae* sp. nov.).

Etymology. This species is named after my former Latin teacher, Gerhard Faulstich, who might be one of the wisest men ML has ever known.

Description. The following description is based on holotype and allotype. — *Carapace* (Fig. 8A): 1.36–1.55

(♂), 1.43–1.50 (♀) times longer than broad. — *Pedipalps* (Fig. 8C): Trichobothrial pattern: *sb* on the movable finger distinctly distal to *est* on the fixed finger; *it* between *eb* and *et* on the fixed finger closer to *eb* than to *et*; *et* situated in the distal third between *dt* and *eb* on the fixed finger. Chelal fixed finger with 12 teeth in the OR, 16 in the MR and 15 in the IR; movable finger with 13 teeth in the OR, 13 in the MR and 16 in the IR. — *Dimensions* (mm): *Holotype* ♂: Body length 1.98; abdomen length 1.35, width (without pleura) 1.16, 1.25 (with pleura); carapace length 0.62, width 0.42; Pedipalp: trochanter 0.25; femur length 0.57, width 0.35; patella 0.46; chela (without pedicel) 0.57; hand length 0.13, width 0.15; movable finger 0.44; Leg I: trochanter 0.11, femur 0.20, patella 0.16, tibia 0.18, tarsus 0.27; Leg IV: trochanter 0.18, femur 0.12, patella 0.33, tibia 0.29, tarsus 0.32. *Allotype* ♀: Body length 2.28; abdomen length 1.53, width (without pleura) 1.34, 1.45 (with pleura); carapace length 0.73, width 0.51; Pedipalp: trochanter 0.32; femur length 0.71, width 0.38; patella 0.56; chela 0.65; hand length 0.14, width 0.18; movable finger 0.50; Leg I: trochanter 0.13; femur 0.25; patella 0.22; tibia 0.20; tarsus 0.33; Leg IV: trochanter 0.23; femur 0.14; patella 0.36; tibia 0.36; tarsus 0.36.

Variation. Body length 1.95–2.02 (♂), 2.14–2.28 (♀); abdomen length 1.29–1.37 (♂), 1.46–1.53 (♀), width (without pleura) 1.12–1.23 (♂), 1.24–1.34 (♀), 1.20–1.30 (♂), 1.33–1.45 (♀) (with pleura); 1.09–1.22 (♂), 1.14–1.18 (♀) times longer than broad; carapace length 0.58–0.66 (♂), 0.69–0.73 (♀), width 0.42–0.45 (♂), 0.46–0.51 (♀), 1.36–1.51 (♂), 1.43–1.50 (♀) times longer than broad. Pedipalp: trochanter 0.24–0.31 (♂), 0.26–0.32 (♀); femur length 0.57–0.67 (♂), 0.65–0.71 (♀), width 0.31–0.36 (♂), 0.36–0.38 (♀); 1.62–2.00 (♂), 1.81–1.87 (♀) times longer than broad; tibia 0.46–0.51 (♂), 0.52–0.56 (♀); chela (without pedicel) 0.55–0.58 (♂), 0.62–0.65 (♀); movable finger 0.44–0.47 (♂), 0.49–0.50 (♀); hand length (without pedicel) 0.10–0.13 (♂), 0.10–0.14 (♀), width 0.12–0.16 (♂), 0.16–0.18 (♀); 0.63–1.00 (♂), 0.63–0.78 (♀) times longer than broad.

GenBank Code. Genetic data is unavailable for this species.

Habitat. Tropical dry forest at 290 m altitude.

Distribution. Known from the type locality (BLF3012) and four additional locations (BLF11400, BLF2858, BLF2972 and BLF9656) in the Diana and Sava Regions (formerly Antsiranana Province).

Antsirananaella leniae sp. nov.

<https://zoobank.org/NomenclaturalActs/A7899CB9-382D-40C3-9CA9-5BE4D5D8F64D>

Type material examined. MADAGASCAR: Antsiranana Province [Sava Region]: Holotype ♂ (CAS 9072445 [BLF10116]), allotype ♀ (ZMH-A0016684), paratypes: 7 ♂, 3 ♀ (CAS 9072445 [BLF10116]), 5 ♂, 3 ♀ (ZMH-A0016685 – ZMH-A0016692), Forêt d’Antsahabe, 13°12’42”S 49°33’24”E, 12 December 2003, B.L. Fisher.

Additional material examined. MADAGASCAR: Antsiranana Province [Sava Region]: 10 ♂, 8 ♀, 15 nymphs (CAS 9072435 [BLF9556]), Forêt de Binara, 13°15’18”S 49°37’00”E, 1 December 2003, B.L. Fisher; 1 ♂, 6 ♀, 8 nymphs (CAS 9072455 [BLF9872]), Forêt de Bekarao-ka, 13°10’00”S 49°42’36”E, 7 December 2003, B.L. Fisher.

Diagnosis. Very similar to *A. lorenzorum* sp. nov. but has the largest female body size of *Antsirananaella* gen. nov. (e.g., body length 2.47 (♀) versus 2.17 (♀) in *A. faulstichi* sp. nov., 2.21 (♀) in *A. marlae* sp. nov., 2.33 (♀) in *A. lorenzorum* sp. nov.; carapace length 0.77 (♀) versus 0.65 (♀) in *A. faulstichi* sp. nov., 0.70 (♀) in *A. lorenzorum* sp. nov., 0.71 (♀) in *A. marlae* sp. nov.); most slender chelal hand of females in *Antsirananaella* gen. nov. (0.85 (♀) × longer than wide versus 0.71–0.81 in other species of *Antsirananaella* gen. nov.). Difference in trichobothrial pattern: *sb* on the same sagittal level as *est* (more distal in *A. lorenzorum* sp. nov. and *A. faulstichi* sp. nov.); *it* between *eb* and *et* equidistant to both of them (closer to *eb* than to *et* in all other species of *Antsirananaella* gen. nov.); *et* midway between *dt* and *eb* on fixed finger (in the distal third between them in *A. marlae* sp. nov. and *A. faulstichi* sp. nov.).

Etymology. This species is a patronym for DH’s beloved daughter.

Description. The following description is based on holotype and allotype. — *Carapace* (Fig. 9A): 1.36–1.51 (♂), 1.33–1.45 (♀) times longer than broad. — *Pedipalps* (Fig. 9C): Trichobothrial pattern: *sb* on the movable finger and *est* on the fixed finger on the same sagittal level; *it* between *eb* and *et* on the fixed finger with the same distance to *eb* and *et*. Chelal fixed finger with 12 teeth in the OR, 19 in the MR and 11 in the IR; movable finger with 11 teeth in the OR, 17 in the MR and 13–17 in the IR. — *Dimensions* (mm): *Holotype* ♂: Body length 2.21; abdomen length 1.54, width (with pleura) 1.34, 1.22 (without pleura); carapace length 0.68, width 0.45; Pedipalp: trochanter 0.27; femur length 0.63, width 0.34; patella 0.50; chela (without pedicel) 0.58; hand length (without pedicel) 0.11, width 0.15; movable finger 0.54; Leg I: trochanter 0.10; femur 0.27; patella 0.19; tibia 0.20; tarsus 0.29; Leg IV: trochanter 0.18; femur 0.13; patella 0.34; tibia 0.35; tarsus 0.38. *Allotype* ♀: Body length 2.46; abdomen length 1.71, width (without pleura) 1.51, (with pleura) 1.66; carapace length 0.72, width 0.54; Pedipalp: trochanter 0.36; femur length 0.79, width 0.44; patella 0.62; chela (without pedicel) 0.70; hand length 0.15, width 0.19; movable finger 0.54; Leg I: trochanter 0.14, femur 0.29, patella 0.17, tibia 0.20, tarsus 0.28; Leg IV: trochanter 0.23, femur 0.15, patella 0.41, tibia 0.48, tarsus 0.43.

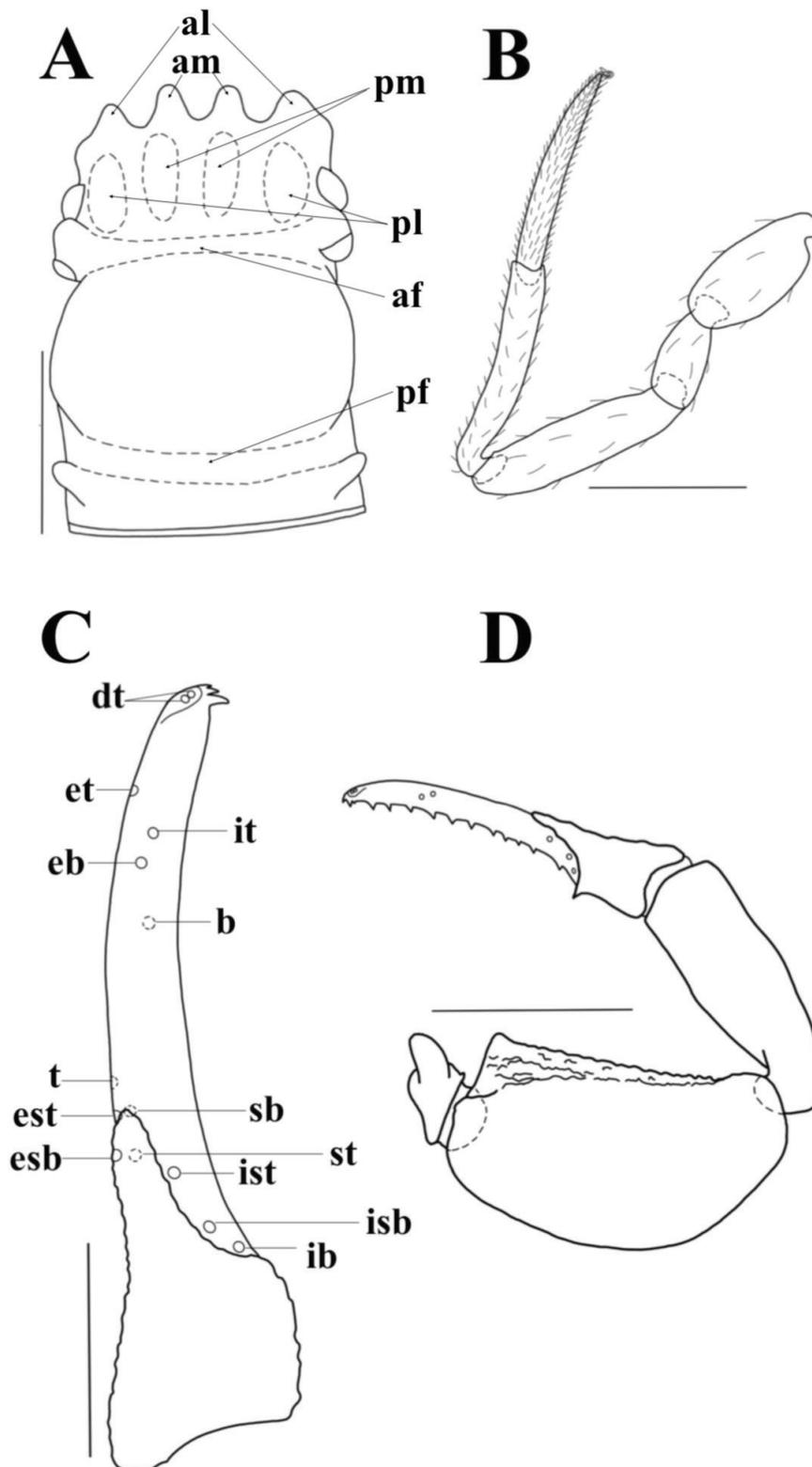


Figure 9. Drawings of *Antsirananaella leniae* sp. nov.. **A** carapace dorsal; **B** leg IV; **C** left chela from dorsal with trichobothrial pattern; **D** right pedipalp from dorsal. Scale bars: 0.2 mm (A–C); 0.4 mm (D).

Variation. Body length 2.01–2.24 (♂), 2.18–2.70 (♀); abdomen length 1.36–1.54 (♂), 1.46–1.89 (♀), width 1.17–1.39 (♂), 1.26–1.59 (♀) (without pleura), 1.32–1.42 (♂), 1.39–1.78 (♀) (with pleura), 1.00–1.26 (♂), 1.11–1.23 (♀) times longer than broad. Pedipalp: trochanter 0.21–0.28 (♂), 0.27–0.36 (♀); femur length 0.59–0.65 (♂), 0.71–0.87 (♀), width 0.33–0.35 (♂), 0.40–0.46 (♀);

1.71–1.91 (♂), 1.68–1.89 (♀) times longer than broad; tibia 0.48–0.52 (♂), 0.57–0.66 (♀); chela 0.55–0.62 (♂), 0.65–0.72 (♀); movable finger 0.44–0.55 (♂), 0.50–0.56 (♀); hand length (without pedicel) 0.11–0.15 (♂), 0.14–0.17 (♀), width 0.15–0.17 (♂), 0.18–0.19 (♀); 0.69–0.94 (♂), 0.74–0.89 (♀) times longer than broad.

GenBank Code. OP589966, OP589967, OP589968. The species differs from all congeners by more than 4.8% in the H3 dataset.

Habitat. Tropical dry forest at 550 m altitude. All specimens were found in sifted litter (leaf mold, rotten wood).

Distribution. Presently known from three localities: type locality (BLF10116) and two additional localities (BLF9556 and BLF9872) in the Sava Region (formerly Antsiranana Province).

Antsirananaella marlae sp. nov.

<https://zoobank.org/NomenclaturalActs/C563A8D4-7620-426E-8A7E-A257C1984516>

Type material examined. MADAGASCAR: Antsiranana Province [Sava Region]: Holotype ♂ (CAS 9072444 [BLF9974]), allotype ♀ (ZMH-A0016693), paratypes: 3 ♀, 2 ♂ (CAS 9072444 [BLF9974]), 2 ♀, 2 ♂ (ZMH-A0016694 – ZMH-A0016697), Forêt d'Ampondrabe, 26.3km 10° NNE Daraina, 175 m, 12°58'12"S 49°42'00"E, 10 December 2003, B.L. Fisher.

Diagnosis. Differs from congeners by large body size (e.g., male body length 2.17 versus 1.80–2.14, male carapace length 0.69 versus 0.55–0.66); a slender carapace (1.47 times longer than broad versus 1.36–1.40); medio-lateral mounds more pronounced than in *A. lorenzorum* sp. nov.; a slender pedipalpal femur (1.80 ♂), 1.84 ♀) times longer than broad versus 1.70–1.79 ♂), 1.74–1.80 ♀); pedipalpal trichobothrial pattern: *sb* on movable finger on same sagittal level as *est* on fixed finger (slightly more distal in *A. lorenzorum* sp. nov. and in *A. faulstichi* sp. nov.), *et* situated in the distal third between *dt* and *eb* on fixed finger (situated midway between *dt* and *eb* on fixed finger in *A. lorenzorum* sp. nov. and in *A. leniae* sp. nov.); *it* between *eb* and *et* situated closer to *eb* than to *et* (equidistant in *A. leniae* sp. nov.).

Etymology. The specific epithet is a patronym in honour of Marla Elisa Nibasumba, the senior author's godchild.

Description. The following description is based on holotype and allotype. — *Carapace* (Fig. 10A): 1.43–1.49 ♂), 1.30–1.46 ♀) times longer than broad. — *Pedipalps* (Fig. 10C): Trichobothrial pattern: *sb* on the movable finger and *est* on the fixed finger on the same sagittal level. *et* situated in the distal third between *dt* and *eb* on the fixed finger. Chelal fixed finger with 11 teeth in the OR, 21 teeth in the MR, and 12 teeth in the IR; movable finger with 11 teeth in the OR, 13 teeth in the MR, and 13 teeth in the IR. — *Dimensions* (mm): *Holotype* ♂: Body length 1.81; abdomen length 1.25; abdomen width 0.99 (without pleura), 1.11 (with pleura); carapace length 0.55; carapace width 0.37. Pedipalp: trochanter 0.24; femur length 0.54; femur width 0.29; patella 0.43; chela (without pedicel) 0.49; hand length (without pedicel) 0.11; width 0.13; movable finger length 0.40. Leg I: tro-

chanter 0.10; femur 0.13; patella 0.16; tibia 0.14; tarsus 0.25. Leg IV: trochanter 0.16; femur 0.11; patella 0.29; tibia 0.28; tarsus 0.31. *Allotype* ♀: Body length 2.30; abdomen length 1.60; abdomen width 1.21 (without pleura), 1.44 (with pleura); carapace length 0.67; carapace width 0.46. Pedipalp: trochanter 0.31; femur length 0.68; femur width 0.39; patella length 0.54; chela (without pedicel) 0.60; hand length (without pedicel) 0.14; hand width 0.18; movable finger length 0.48. Leg I: trochanter 0.11; femur 0.24; patella 0.22; tibia 0.15; tarsus 0.25. Leg IV: trochanter 0.21; femur 0.14; patella 0.35; tibia 0.41; tarsus 0.39.

Variation. Body length 1.70–1.91 ♂), 2.05–2.19 ♀); abdomen length 1.14–1.32 ♂), 1.37–1.46 ♀), width 0.98–1.07 ♂), 1.18–1.25 ♀) (without pleura), 1.02–1.18 ♂), 1.29–1.38 ♀) (with pleura), 1.17–1.28 ♂), 1.14–1.24 ♀) times longer than broad; carapace length 0.52–0.58 ♂), 0.63–0.67 ♀), width 0.36–0.39 ♂), 0.46–0.48 ♀), 1.43–1.49 ♂), 1.30–1.36 ♀) times longer than broad; Pedipalp: trochanter 0.22–0.25 ♂), 0.27–0.30 ♀); femur length 0.52–0.56 ♂), 0.70–0.71 ♀), width 0.29–0.32 ♂), 0.38–0.40 ♀), 1.73–1.86 ♂), 1.78–1.87 ♀) times longer than broad; tibia 0.39–0.46 ♂), 0.54–0.55 ♀); chela 0.45–0.51 ♂), 0.56–0.60 ♀); movable finger 0.37–0.41 ♂), 0.46–0.49 ♀); hand length (without pedicel) 0.10–0.12 ♂), 0.12–0.14 ♀), width 0.12–0.14 ♂), 0.15–0.17 ♀), 0.79–0.92 ♂), 0.75–0.88 ♀) times longer than broad.

GenBank Code. OP589965. The species differs from all congeners by more than 4.8% in the H3 dataset.

Habitat. Isolated tropical dry forest at a moderate elevation (100–500 m) located northwest of Ambarilao. The forest leads up to the mountain ranges of the Central Highlands. The specimens were found in sifted litter (leaf mold, rotten wood).

Distribution. Only known from the type locality (BLF9974) in Sava Region (formerly eastern Antsiranana Province) of northern Madagascar.

Mahajanganella gen. nov.

<https://zoobank.org/NomenclaturalActs/CACF3D4C-1557-46AB-AB1D-F2C9829023A4>

Type species. *Mahajanganella heraclis* sp. nov.

Diagnosis. *Mahajanganella* gen. nov. is morphologically unique by having the following characters, which differ from other fealloid members in Madagascar: 5 specialized setae on the retrolateral face of the movable chelal finger arranged in a group between trichobothrium *b* and terminal teeth (arranged in a row in *Antsirananaella* gen. nov.); smaller overall size than *Antsirananaella* gen. nov.; stronger granulate cuticle than *Antsirananaella* gen. nov.; all four anterior lobes of carapace with the

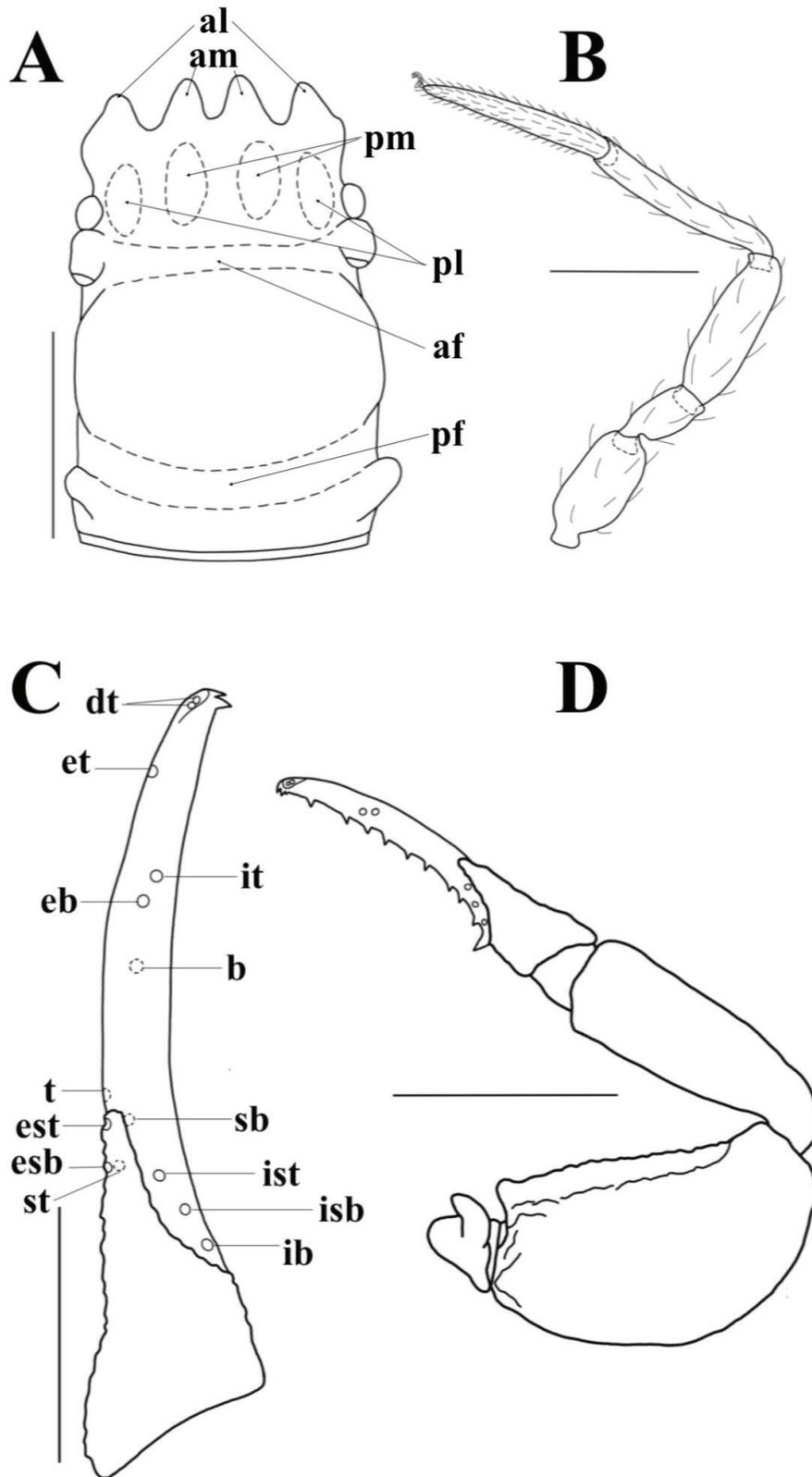


Figure 10. Drawings of *Antsirananaella marlae* sp. nov.: **A** carapace dorsal; **B** leg IV; **C** left chela from dorsal with trichobothrial pattern; **D** right pedipalp from dorsal. Scale bars: 0.2 mm (A–C); 0.4 mm (D).

same distance to each other (smaller distance between anteriomedial lobes than to anteriolateral ones in *Antsirananaella* gen. nov.). Like *Antsirananaella* gen. nov. and *Toliaranella* gen. nov., it differs from *Cybella* by having platelets on the pleural membrane (absent in *Cybella*), from *Iporangella* by the presence of specialized setae on

the movable chelal finger (absent in *Iporangella*), from *Feaella* (*Difeaella*) and *Feaella* (*Feaella*) by the presence of four anterior carapaceal lobes (two and six, respectively), from *Feaella* (*Tetrafeaella*) in continental Africa by having a less pronounced depression on the base of coxa I and on top of coxa II (distinctly more pronounced in *Fe-*

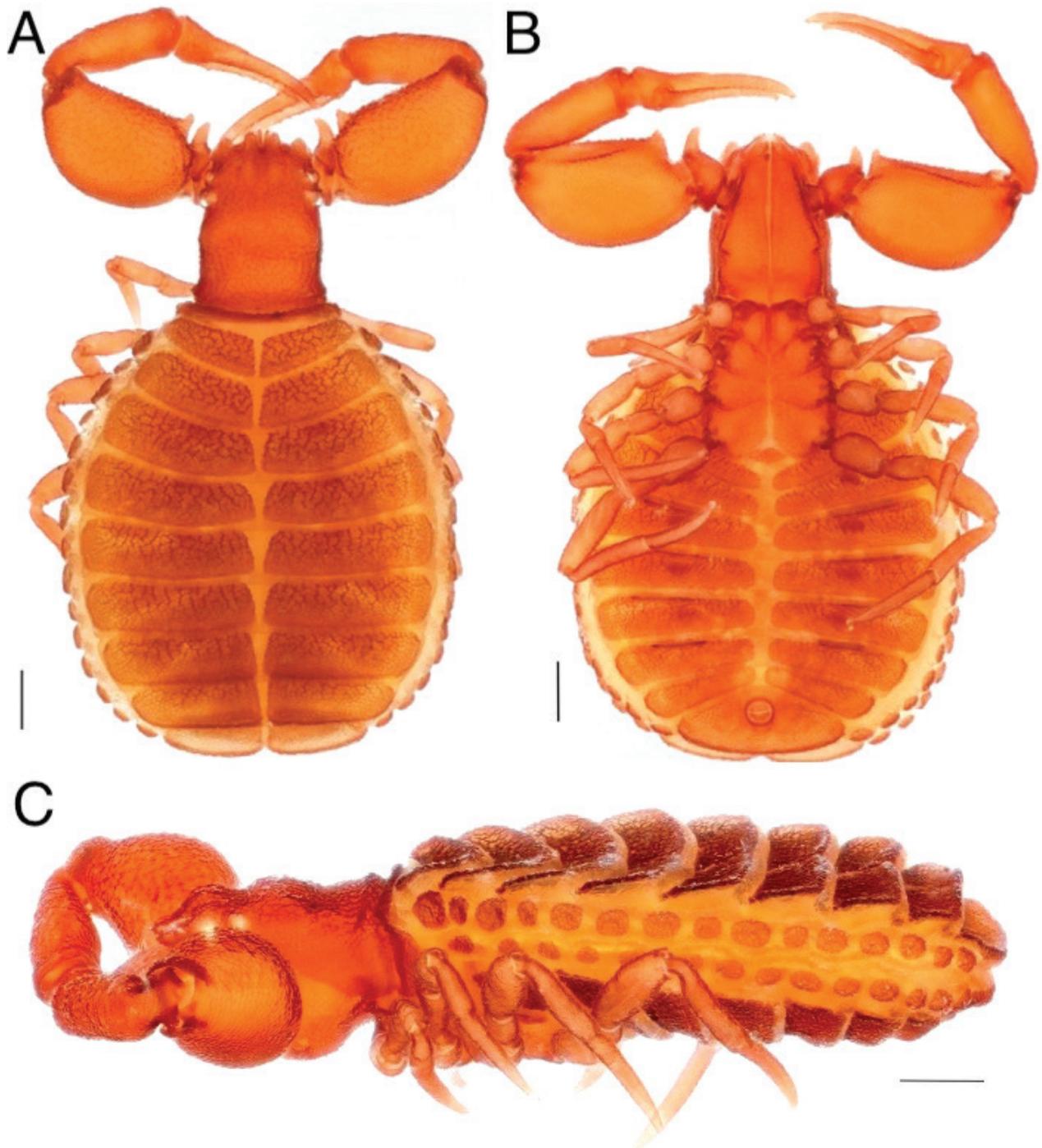


Figure 11. *Mahajanganella* gen. nov., habitus. Specimen used for imaging: *M. schwarzeneggeri* sp. nov. allotype (ZMH-A0016716). **A** dorsal; **B** ventral; **C** lateral. Scale bar: 0.2 mm.

aella (*T.*) cf. *mucronata*), and from the Australian species presently attributed to *Feaella* (*Tetrafeaella*) by having fewer coxal spines (one pair versus three or four in the Australian taxa).

Etymology. The genus is named after the former Mahajanga Province, where many of these feaellids occur. The gender is feminine.

Description. The following description is based on holotype and allotype of *M. heraclis* sp. nov. — *Carapace* (Figs 12A, 14A, 15A, 16A): Moderate granulate and all

four anterior lobes with same distance to each other. — *Pedipalp* (Figs 11A, B, 13A, B, C, 14C, D, 15C, D, 16C, D): Trichobothrial pattern: *esb* between *st* and *ist* on the sagittal level with *ist* slightly more distal and *st* slightly more proximal than *esb*; *t* distinctly closer to *sb* than to *b*; *sb* distinctly closer to *t* than to *st*; *it* on the fixed finger between *eb* and *et* distinctly closer to *eb* than to *et*. Movable finger with five specialized setae on the ventral face, arranged in a group and slightly more distally situated than *b* (Fig. 13A). Terminal teeth varying in number, both in fixed and the movable fingers each with 7–8 terminal teeth (one large tooth included on fixed finger). — *Cheli-*

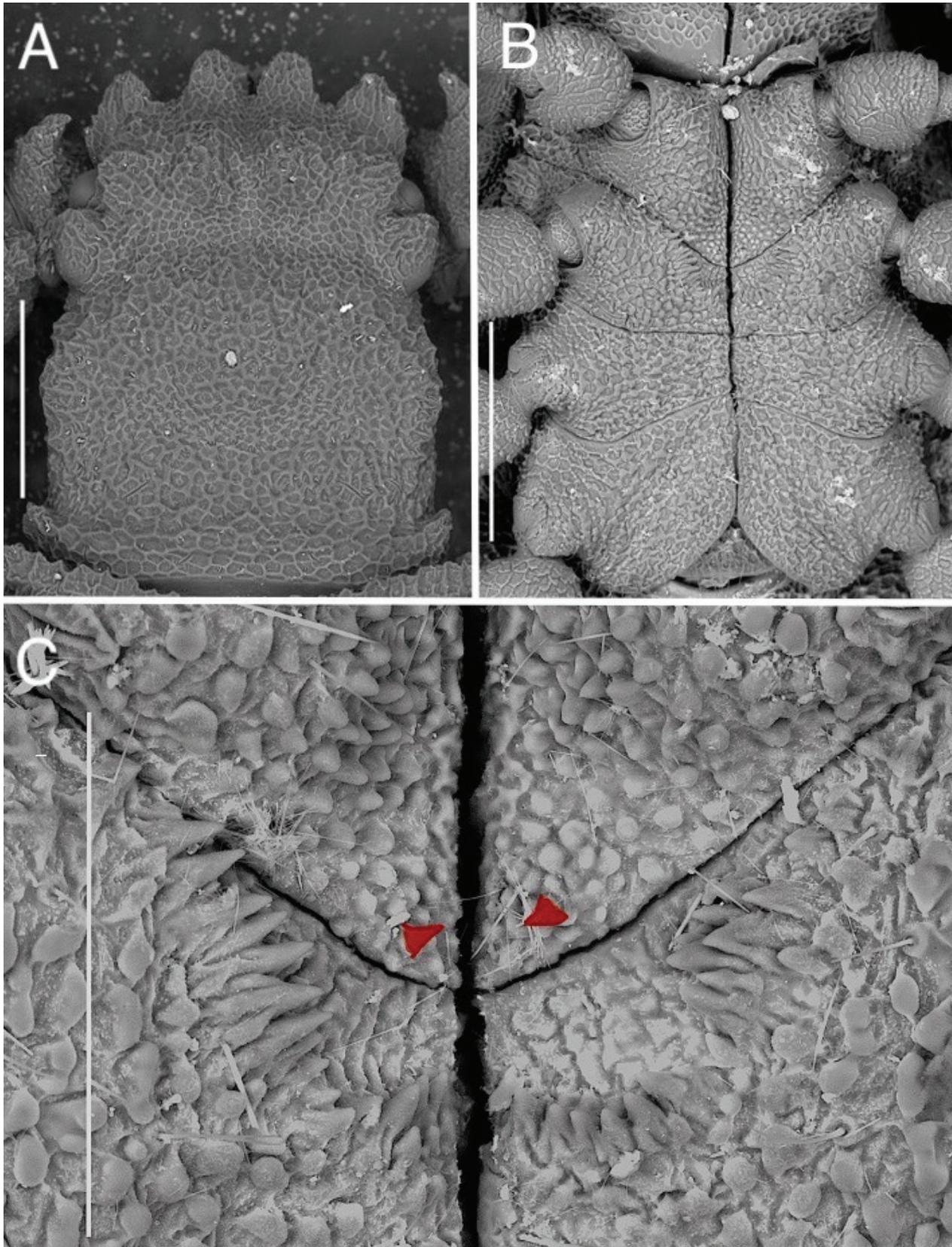


Figure 12. *Mahajanganella* gen. nov., scanning electron micrographs. Specimens used for imaging: **A** *M. fridakahloae* sp. nov. female paratype (ZMH-A0016709); **B, C** *M. schwarzeneggeri* sp. nov. male paratype (ZMH-A0016717). **A** carapace, dorsal; **B** sternum ventral; **C** coxal spines (highlighted in red). Scale bars: 0.2 mm (**A, B**); 0.1 mm (**C**).

cera: Most specimens were too dirty to get secure information about characters. *Coxal region* (Fig. 12B, C), *legs* (Figs 11B, 14B, 15B, 16B), *abdomen* (Fig. 11A, B, C)

and *genital region* (Fig. 12B) with the same characters as *Antsirananaella* gen. nov.

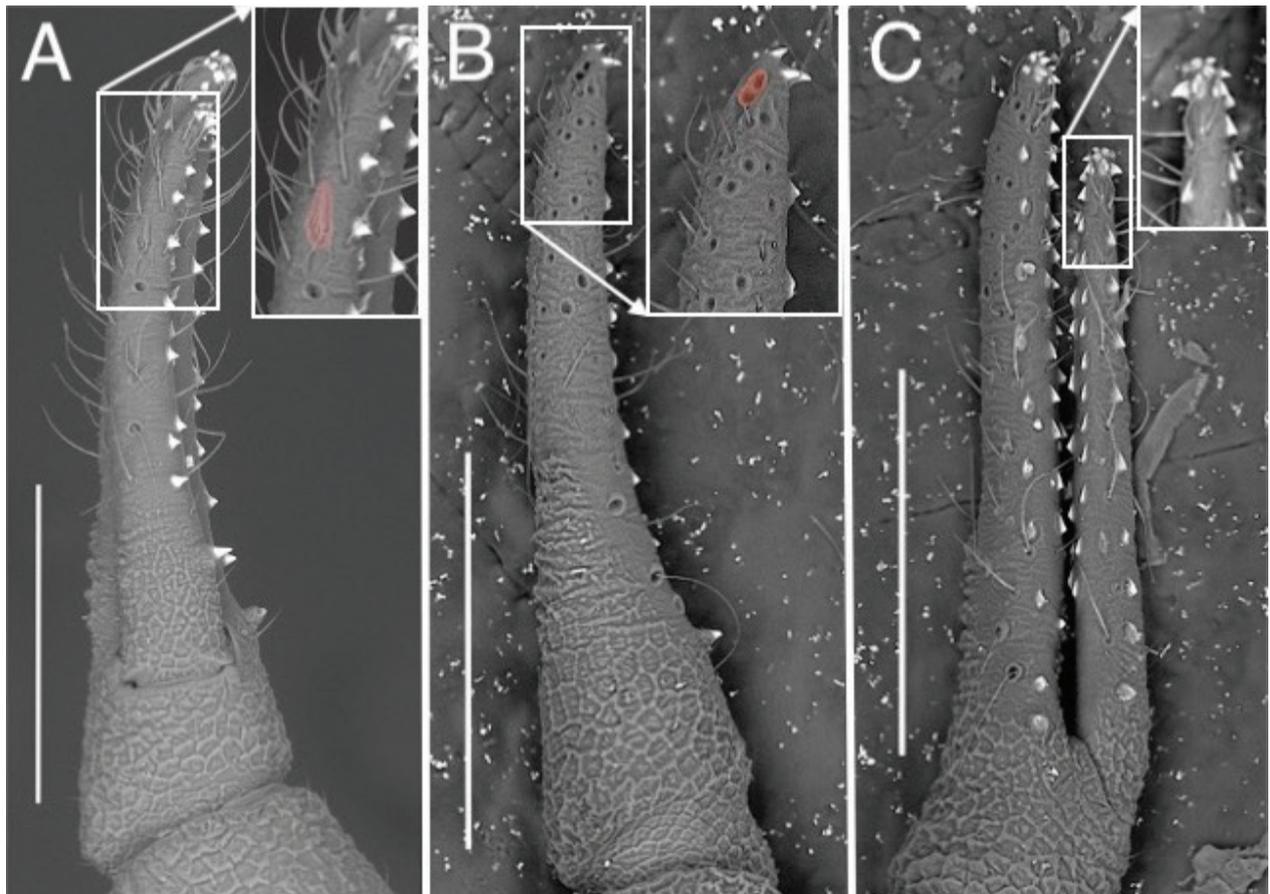


Figure 13. *Mahajanganela* gen. nov., scanning electron micrographs. Specimens used for imaging: **A** *M. heraclis* sp. nov. male paratype (ZMH-A0016701); **B** *M. fridakahloae* sp. nov. male paratype (ZMH-A0016715); **C** *M. schwarzeneggeri* sp. nov. male paratype (ZMH-A0016717). **A** right chela from ventral with specialized setae in a group in detail (highlighted in red); **B** left chela with double trichobothrium *dt* in detail (highlighted in red); **C** left chela from medial with terminal teeth in a compact group in detail. Scale bar: 0.2 mm.

Included species. *Mahajanganela fridakahloae* sp. nov.; *Mahajanganela heraclis* sp. nov.; and *Mahajanganela schwarzeneggeri* sp. nov..

Distribution. Specimens of *Mahajanganela* gen. nov. have been found in dry localities (dry tropical forests) in the Boeny and Menabe Regions (formerly Mahajanga and Toliara Provinces) along the western coast of Madagascar.

***Mahajanganela heraclis* sp. nov.**

<https://zoobank.org/NomenclaturalActs/0FA0CC57-7AD9-44FA-81AA-23ADAE328DD2>

Type material examined. MADAGASCAR: Province de Mahajanga [Boeny Region]: Holotype ♂ (CAS 9071835 [BLF3599]), allotype ♀ (ZMH-A0016698), paratypes: 6 ♂, 6 ♀, (CAS 9071835 [BLF3599, BLF3597]), 4 ♂, 4 ♀ (ZMH-A0016699 – ZMH-A0016706), Parc National d'Ankarafantsika, Forêt de Tsimaloto, 16°13'41"S 46°8'37"E, 2–8 April 2001, B.L. Fisher, Griswold et al.

Additional material examined. MADAGASCAR: Mahajanga Province [Boeny Region]: 23 ♂, 18 ♀, 29 nymphs (CAS 9008212 [BLF3571]), Parc National d'Ankarafantsika, 16°17'56"S 46°48'47"E, 26 March–1 April 2001, Fisher, Griswold et al.; 4 ♂, 2 ♀, 11 nymphs (CAS 9072477 [BLF6506]), Parc National de Namoroka, 16°22'36"S 45°19'36"E, 8–12 November 2002, Fisher, Griswold et al.; 2 ♂, 2 nymphs (CAS 9071651 [BLF6446]), Parc National de Namoroka, 16°28'00"S 45°21'00"E, 4–8 November 2002, Fisher, Griswold et al.

Diagnosis. Largest female body length of *Mahajanganela* gen. nov. (2.15 versus 2.03–2.08); robustest pedipalps of this new genus measured in ratios (e.g., femur 1.64/1.62 ♂/♀ times longer than broad versus 1.69–1.75/1.69–1.74 ♂/♀); e.g., femur 1.14 ♂ and ♀ times longer than tibia versus 1.27/1.21–1.27/1.27 ♂/♀; e.g., femur 1.02/1.06 ♂/♀ longer than chela versus 1.12/1.19–1.14/1.19 ♂/♀); anteriomedial lobes distinctly pointed and moderate carapace cuticle above second eyes (in other species of *Mahajanganela* gen. nov. distinctly more granulate carapace especially above second eyes).

Etymology. This species is named after the divine hero Herakles (lat. Hercules) who, in Greek mythology, is known for his power and courage. He is often portrayed

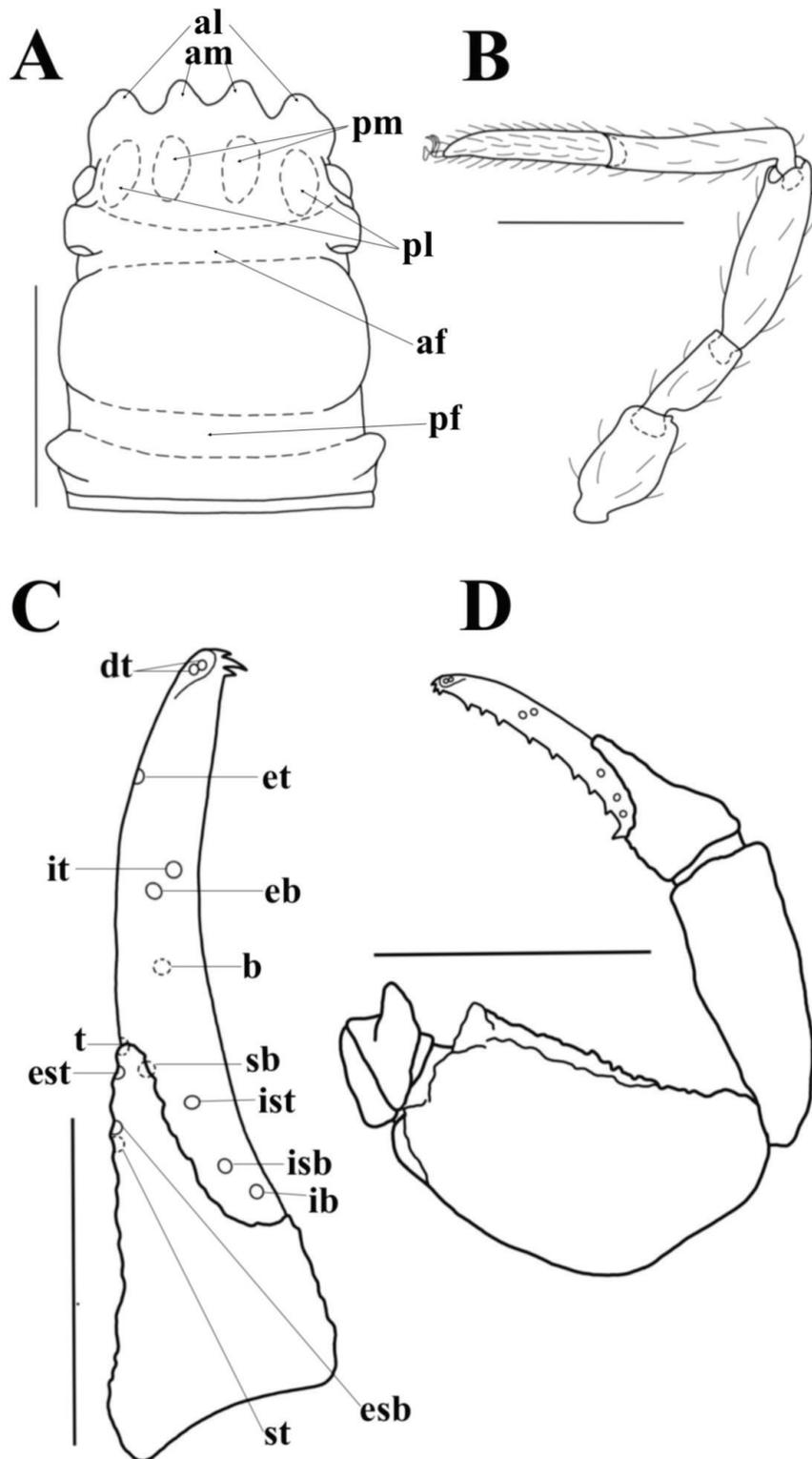


Figure 14. Drawings of *Mahajanganella heraclis* sp. nov.: **A** carapace from dorsal; **B** leg IV; **C** left chela from dorsal with trichobothrial pattern; **D** right pedipalp from dorsal. Scale bars: 0.2 mm (A–C); 0.4 mm (D).

with a mace, which resembles the strong pedipalps of this species. It is to be treated as a noun in apposition.

Description. The following description is based on holotype and allotype. — *Carapace* (Fig. 14A): 1.28–1.49 (♂), 1.21–1.36 (♀) times longer than broad. — *Pedipalp* (Fig. 14C, D): Femora very robust 1.50–1.68 (♂), 1.56–1.69 (♀) times longer than broad. See trichobothrial pat-

tern in genus description. Chelal fixed finger with 10 teeth in the OR, 15 in the MR and 11 in the IR; movable finger with 9 teeth in the OR, 12 in the MR and 8 in the IR. Terminal teeth with 7 equally sized and 1 larger tooth on the fixed finger, and 8 equally sized teeth on the movable finger. — *Dimensions* (mm): *Holotype* ♂: Body length 1.74; abdomen length 1.17, width (without pleura) 0.95, (with pleura) 1.08; carapace length 0.50, width 0.38. Pedipalp:

trochanter 0.25; femur length 0.47, width 0.28; patella 0.39; chela (without pedicel) 0.43; hand length 0.10, width 0.13; movable finger 0.35. Leg I: trochanter 0.08; femur 0.17; patella 0.17; tibia 0.12; tarsus 0.22. Leg IV: trochanter 0.14; femur 0.12; patella 0.23; tibia 0.21; tarsus 0.22. *Allotype* ♀: Body length 2.19; abdomen length 1.57, width (without pleura) 1.25, (with pleura) 1.41; carapace length 0.55, width 0.45. Pedipalp: trochanter 0.25; femur length 0.52, width 0.32; patella 0.47; chela (without pedicel) 0.48; hand length 0.10, width 0.15; movable finger 0.42. Leg I: trochanter 0.09; femur 0.22; patella 0.16; tibia 0.17; tarsus 0.30. Leg IV: trochanter 0.16; femur 0.14; patella 0.34; tibia 0.33; tarsus 0.30.

Variation. Body length 1.67–1.84 (♂), 2.06–2.22 (♀); abdomen length 1.13–1.26 (♂), 1.42–1.59 (♀); width (with pleura) 1.04–1.13 (♂), 1.32–1.46 (♀); width (without pleura) 0.92–1.05 (♂), 1.14–1.30 (♀); 1.13–1.28 (♂), 1.17–1.32 (♀) times longer than broad; carapace length 0.50–0.58 (♂), 0.55–0.61 (♀); width 0.37–0.40 (♂), 0.43–0.48 (♀); 1.28–1.49 (♂), 1.21–1.36 (♀) times longer than broad. Pedipalp: trochanter 0.17–0.25 (♂), 0.22–0.26 (♀); femur length 0.41–0.47 (♂), 0.50–0.57 (♀); width 0.26–0.28 (♂), 0.30–0.36 (♀); 1.50–1.37 (♂), 1.56–1.68 (♀) times longer than broad; patella 0.38–0.41 (♂), 0.39–0.50 (♀); chela (without pedicel) 0.42–0.45 (♂), 0.46–0.53 (♀); hand length 0.08–0.10 (♂), 0.09–0.11 (♀); width 0.12–0.13 (♂), 0.14–0.16 (♀); 0.62–0.83 (♂), 0.56–0.73 (♀) times longer than broad; movable finger 0.31–0.35 (♂), 0.37–0.42 (♀); femur 1.05–1.21 (♂), 1.08–1.16 (♀) times longer than patella; femur 0.95–1.09 (♂), 1.02–1.12 (♀) times longer than chela.

GenBank Code. OP589970. The species differs from all congeners by more than 6.5% in the H3 dataset.

Habitat. The specimens were found in sifted litter of tropical dry forest at an elevation of 135 m.

Distribution. Presently known only from the type locality (BLF3599) and from three additional locations (BLF3571, BLF6506 and BLF6446) in the Boeny Region (formerly Mahajanga Province).

Mahajanganela fridakahloae sp. nov.

<https://zoobank.org/NomenclaturalActs/A3F1CCB0-3681-4847-B58E-EFC5B252CB82>

Type material examined. MADAGASCAR: Province de Toliara [Menabe Region]: Holotype ♂ (CAS 9071518 [BLF4605]), allotype ♀ (ZMH-A0016707), paratypes: 9 ♂, 6 ♀ (CAS 9071518 [BLF4605]), 4 ♂, 4 ♀ (ZMH-A0016708 – ZMH-A0016715), Forêt de Kirindy, 20°02'42"S 44°39'44"E, 28 November–2 December 2001, B.L. Fisher, Griswold et al.

Additional material examined. MADAGASCAR: Province de Toliara [Menabe Region]: 2 ♂, 1 ♀, 4 nymphs (CAS 9071535 [BLF4432]), Parc National de Tsingy de Bemaraha, 19°42'34"S 44°43'5"E, 16–20

November 2001, Fisher, Griswold et al.; 17 ♂, 7 ♀, 16 nymphs (CAS 9071781 [BLF4726]), Toliara Province [Menabe Region]: Parc National de Kirindy Mite, 20°47'43"S 44°08'49"E, 6–10 December 2001, Fisher, Griswold et al.

Diagnosis. Very similar to the type species but remarkably more granulated cuticle on the carapace, especially above the posterior pair of eyes; anterior lobes on the carapace are not pointed but rounded at the tip.

Etymology. This species is named after the Mexican artist Frida Kahlo de Rivera († 1954) whose unmistakable character were her striking eyebrows, which she included in many of her self-portraits. The species is reminiscent of her because of the strongly granulated cuticle above the second pair of eyes, which resemble ‘eyebrows’.

Description. The following description is based on holotype and allotype. — *Carapace* (Fig. 15A): Cuticle strongly covered with granulate especially above the second eye pair which makes it look like an additional lateral pair of mounds behind the anterior margin; anterior lobes on carapace not pointed but rounded at the tips; 1.26–1.42 (♂), 1.18–1.34 (♀) times longer than broad. — *Pedipalps* (Fig. 15C, D): See trichobothrial pattern in genus description. Chelal fixed finger with 9–12 teeth in the OR, 14–15 in the MR and 8–12 in the IR; movable finger with 6–9 teeth in the OR, 9–11 in the MR and 9–10 in the IR; fixed finger with 6 equally sized and one larger terminal tooth, movable finger with 7 equally sized terminal teeth. — *Dimensions* (mm): *Holotype* ♂: Body length 1.71; abdomen length 1.15, width (with pleura) 1.01, width (without pleura) 0.90; carapace length 0.49, width 0.39. Pedipalp: trochanter 0.24; femur length 0.50, width 0.27; patella 0.34; chela (without pedicel) 0.41; hand length 0.08, width 0.12; movable finger 0.34. Leg I: trochanter 0.09; femur 0.14; patella 0.13; tibia 0.12; tarsus 0.21. Leg IV: trochanter 0.14; femur 0.10; patella 0.24; tibia 0.25; tarsus 0.23. *Allotype* ♀: Body length 2.22; abdomen length 1.58, width (with pleura) 1.35, width (without pleura) 1.14; carapace length 0.60, width 0.45. Pedipalp: trochanter 0.26; femur length 0.54, width 0.35; patella 0.44; chela (without pedicel) 0.49; hand length 0.10, width 0.14; movable finger 0.37. Leg I: trochanter 0.10; femur 0.17; patella 0.19; tibia 0.14; tarsus 0.22. Leg IV: trochanter 0.18; femur 0.13; patella 0.29; tibia 0.30; tarsus 0.31.

Variation. Body length 1.71–1.86 (♂), 1.92–2.26 (♀); abdomen length 1.15–1.27 (♂), 1.50–1.67 (♀); width (with pleura) 1.01–1.08 (♂), 1.20–1.41 (♀); width (without pleura) 0.90–0.99 (♂), 1.03–1.17 (♀); 1.22–1.35 (♂), 1.23–1.43 (♀) times longer than broad; carapace length 0.50–0.55 (♂), 0.52–0.61 (♀); width 0.38–0.41 (♂), 0.42–0.47 (♀); 1.26–1.42 (♂), 1.18–1.34 (♀) times longer than broad. Pedipalp: trochanter 0.19–0.24 (♂), 0.20–0.27 (♀); femur length 0.44–0.51 (♂), 0.53–0.60 (♀); width 0.26–0.30 (♂), 0.32–0.36 (♀); 1.57–1.85 (♂), 1.54–1.75 (♀) times longer than broad; patella 0.34–0.40 (♂), 0.44–0.47 (♀); chela (without pedicel) 0.39–0.45

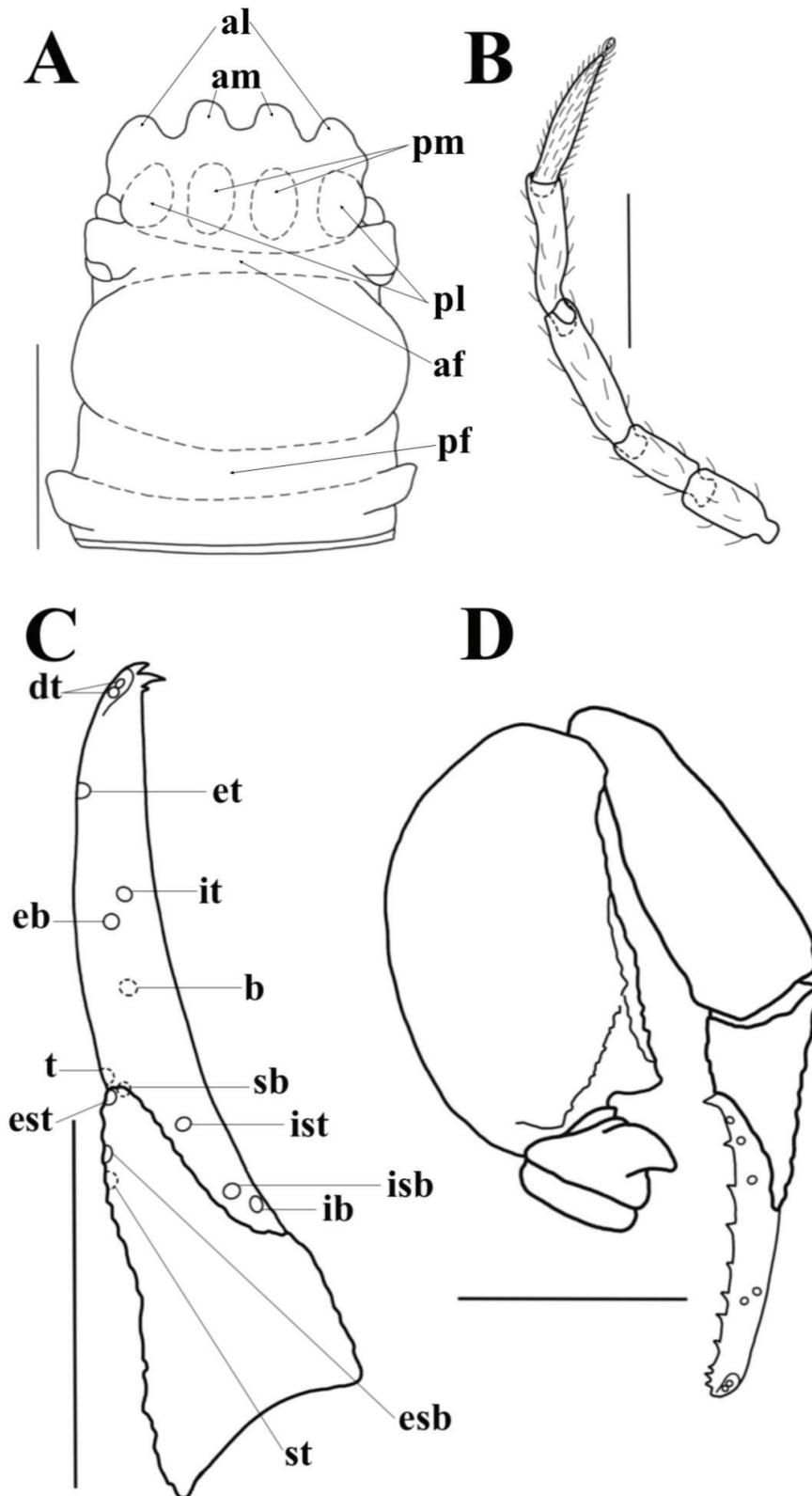


Figure 15. Drawings of *Mahajanganelle fridakahloae* sp. nov.: **A** carapace from dorsal; **B** leg IV; **C** left chela from dorsal with trichobothrial pattern; **D** right pedipalp from dorsal. Scale bars: 0.2 mm (A–C); 0.4 mm (D).

(♂), 0.44–0.49 (♀); hand length 0.07–0.11 (♂), 0.90–0.12 (♀); width 0.12–0.13 (♂), 0.13–0.16 (♀); 0.54–0.92 (♂), 0.56–0.80 (♀) times longer than broad; movable finger 0.32–0.34 (♂), 0.37–0.40 (♀); femur 1.16–1.47 (♂), 1.20–1.36 (♀) times longer than patella; femur 1.04–1.22 (♂), 1.13–1.34 (♀) times longer than chela.

Habitat. Specimens were found in tropical dry forest in sifted litter (leaf mold, rotten wood) at an elevation of 100–150 m.

GenBank Code. OP589969. The species differs from all congeners by more than 6.5% in the H3 dataset.

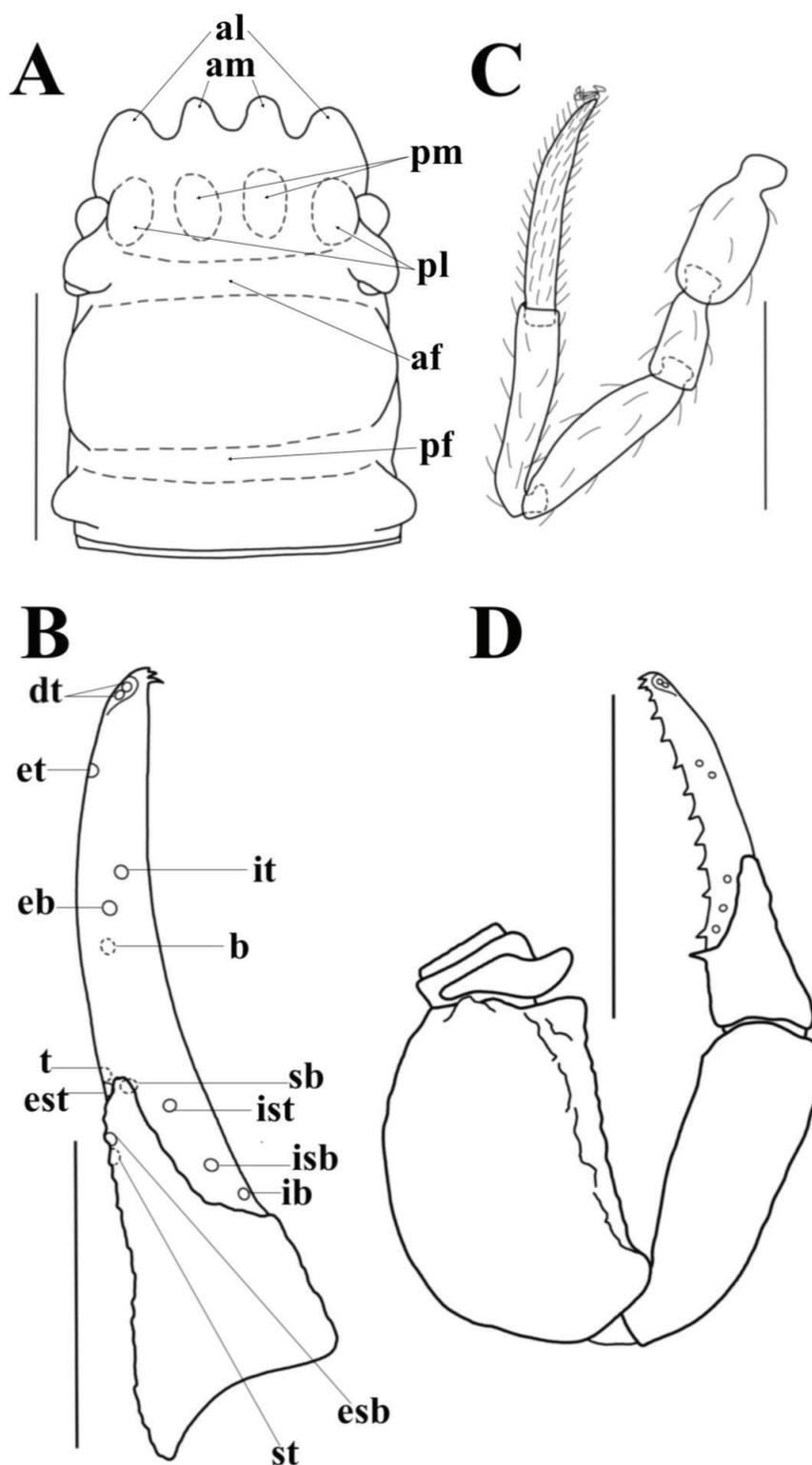


Figure 16. Drawings of *Mahajanganella schwarzeneggeri* sp. nov.: **A** carapace from dorsal; **B** leg IV; **C** left chela from dorsal with trichobothrial pattern; **D** right pedipalp from dorsal. Scale bars: 0.2 mm (A–C); 0.4 mm (D).

Distribution. Known from the type locality (BLF4605) and two additional localities (BLF4432 and BLF4726) in the Menabe Region (formerly Toliara Province) of western Madagascar.

***Mahajanganella schwarzeneggeri* sp. nov.**

<https://zoobank.org/NomenclaturalActs/8DD8CBE7-C8F5-46BE-8FBC-2ABDB7030F69>

Type material examined. MADAGASCAR: Mahajanga Province [Boeny Region]: Holotype ♂ (CAS 9071739 [BLF6812]), allotype

♀ (ZMH-A0016716), paratypes: 1 ♂ (ZMH-A0016717), 1 ♀ (CAS 9071739 [BLF6812]), Parc National de Baie de Baly; 16°00'36"S 45°15'54"E, 26–30 November 2002, B.L. Fisher, Griswold et al.

Diagnosis. Very similar to *Mahajanganella heraclis* sp. nov. but smaller female body size (body length 2.03 versus 2.15 in *M. heraclis* sp. nov.), and most slender carapace (1.47 (♂)/1.41 (♀) × longer than broad versus 1.35 (♂)/1.29 (♀) in *M. heraclis*); most slender femora of *Mahajanganella* gen. nov. (1.57/1.74 ♂/♀ × longer than broad versus 1.64/1.62 ♂/♀ in *M. heraclis* sp. nov.).

Etymology. This species is a patronym honoring Arnold Schwarzenegger, a famous former bodybuilder from Austria, known as an actor in the movie “Terminator”, former governor of California and now supporting conservation programs.

Description. The following description is based on holotype and allotype. — *Carapace* (Fig. 16A): 1.47 (♂), 1.38–1.43 (♀) times longer than broad. — *Pedipalps* (Fig. 16C, D): see trichobothrial pattern in genus description. Chelal fixed finger with 8 teeth in the OR, 13–17 in the MR and 9–12 in the IR; movable finger with 8–9 teeth in the OR, 11–13 in the MR and 9–12 in the IR; terminal teeth build a group of 6 equally sized and 1 larger tooth on the fixed finger and 8 equally sized teeth on the movable finger. — *Dimensions* (mm): *Holotype* ♂: Body length 1.93; abdomen length 1.34; width (with pleura) 1.17; (without pleura) 1.07; carapace length 0.56; width 0.38. *Pedipalp*: trochanter 0.23; femur length 0.56; width 0.32; patella 0.44; chela (without pedicel) 0.47; hand length 0.09; width 0.13; movable finger 0.36. *Leg I*: trochanter 0.09; femur 0.21; patella 0.14; tibia 0.15; tarsus 0.26. *Leg IV*: trochanter 0.15; femur 0.13; patella 0.29; tibia 0.24; tarsus 0.31. *Allotype* ♀: Body length 2.04; abdomen length 1.44; width (with pleura) 1.30; (without pleura) 1.18; carapace length 0.60; width 0.42. *Pedipalp*: trochanter 0.27; femur length 0.56; width 0.34; patella 0.48; chela (without pedicel) 0.51; hand length 0.10; width 0.15; movable finger 0.39. *Leg I*: trochanter 0.09; femur 0.21; patella 0.20; tibia 0.13; tarsus 0.28. *Leg IV*: trochanter 0.16; femur 0.13; patella 0.34; tibia 0.31; tarsus 0.33.

Variation. Body length 1.85–1.93 (♂), 2.02–2.04 (♀); abdomen length 1.25–1.34 (♂), 1.43–1.44 (♀); width (with pleura) 1.14–1.17 (♂), 1.29–1.30 (♀); width (without pleura) 1.03–1.07 (♂), 1.17–1.18 (♀); 1.21–1.25 (♂), 1.22 (♀) times longer than broad; carapace length 0.56 (♂), 0.58–0.60 (♀); width 0.38 (♂), 0.42 (♀); 1.47 (♂), 1.38–1.43 (♂) times longer than broad. *Pedipalp*: trochanter 0.23 (♂), 0.25–0.27 (♀); femur length 0.52–0.56 (♂), 0.56–0.58 (♀); width 0.29–0.32 (♂), 0.33–0.34 (♀); 1.75–1.79 (♂), 1.65–1.76 (♀) times longer than broad; patella 0.42–0.44 (♂), 0.48 (♀); chela (without pedicel) 0.44–0.47 (♂), 0.51 (♀); hand length 0.09–0.10 (♂), 0.09–0.10 (♀); width 0.13–0.14 (♂), 0.15 (♀); 0.67–0.69 (♂), 0.67–0.71 (♀) times longer than broad; movable finger 0.36 (♂), 0.39–0.40 (♀); femur 1.24–1.27 (♂), 1.17–

1.21 (♀) times longer than patella; femur 1.18–1.19 (♂), 1.10–1.14 (♀) times longer than chela.

GenBank Code. Genetic data is unavailable for this species.

Habitat. Specimens were found in sifted litter in tropical dry forest at an elevation of 10 m very close to the coastline.

Distribution. Known only from the type locality (BLF6812) in the Boeny Region (formerly Mahajanga Province) of western Madagascar.

Toliaranella gen. nov.

<https://zoobank.org/NomenclaturalActs/F9EDCC8D-D7A5-41F4-B101-DA7320782EBA>

Type species. *Toliaranella pumila* sp. nov.

Diagnosis. *Toliaranella* gen. nov. differs from all other Malagasy feaellids by the presence of a perforated organ above the coxal spines and smallest body size of any Malagasy groups. Like *Antsirananaella* gen. nov. and *Mahajanganella* gen. nov., it differs from *Cybella* by having platelets on the pleural membrane (absent in *Cybella*), from *Iporangella* by the presence of specialized setae on the movable chelal finger (absent in *Iporangella*), from *Feaella* (*Difeaella*) and *Feaella* (*Feaella*) by the presence of four anterior carapace lobes (two and six, respectively), from *Feaella* (*Tetrafeaella*) in continental Africa by having a less pronounced depression on the base of coxa I and on top of coxa II (distinctly more pronounced in *Feaella* (*T.*) cf. *mucronata*) and from the Australian species presently attributed to *Feaella* (*Tetrafeaella*) by having fewer coxal spines (one pair versus three or four in the Australian taxa).

Etymology. This genus is named after the former Toliara Province, where all specimens were collected. The gender is feminine.

Description. The following description is based on holotype and allotype. — *Carapace* (Figs 18A, 20A, 21A, 22A, 23A, 24A): Strongly granulate, all four anterior lobes with same distance to each other and rounded at tips. — *Pedipalps* (Figs 17A, B, 19A–C, 20C, D, 21C, D, 22C, D, 23C, D, 24C, D): Terminal teeth with 7–8 teeth on both the fixed and the movable fingers (including 1 large tooth on fixed finger). — *Coxal region* (Figs 17B, 18B, C): *Pedipalpal* coxae each with one spike laterally near base; coxae I with basal depression, each side with one small coxal spine; slightly more cranial of coxal spine one novel organ on each side: rose-shaped, not granulate but perforated organ (Fig. 18B, C) filling the base of the depression; coxae II with irregular shaped spines framing depression of coxae I.

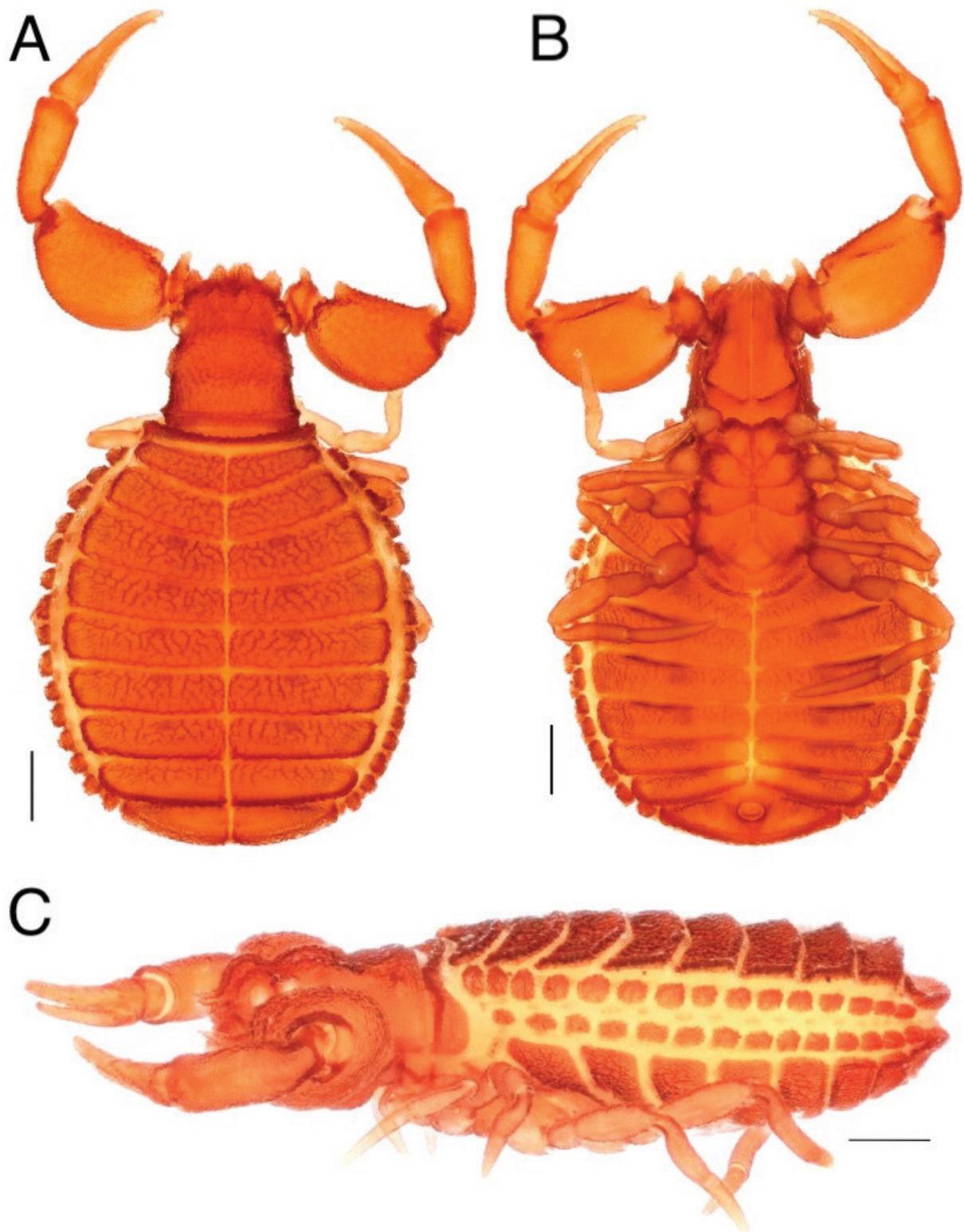


Figure 17. *Toliaranella* gen. nov.. Specimen used for imaging: *T. griswoldi* sp. nov. holotype (CAS 9071500). **A** dorsal overview; **B** ventral overview; **C** lateral overview. Scale bar: 0.2 mm.

Included species. *Toliaranella fisheri* sp. nov.; *Toliaranella griswoldi* sp. nov.; *Toliaranella mahnerti* sp. nov.; *Toliaranella meridionalis* sp. nov.; and *Toliaranella pumila* sp. nov.

Distribution. Members of this genus are localized to the southern part of Madagascar in the Androy, Anosy and

Atsimo-Andrefana Regions (formerly Toliara Province) where the main landscape is covered by arid spiny bush vegetation.

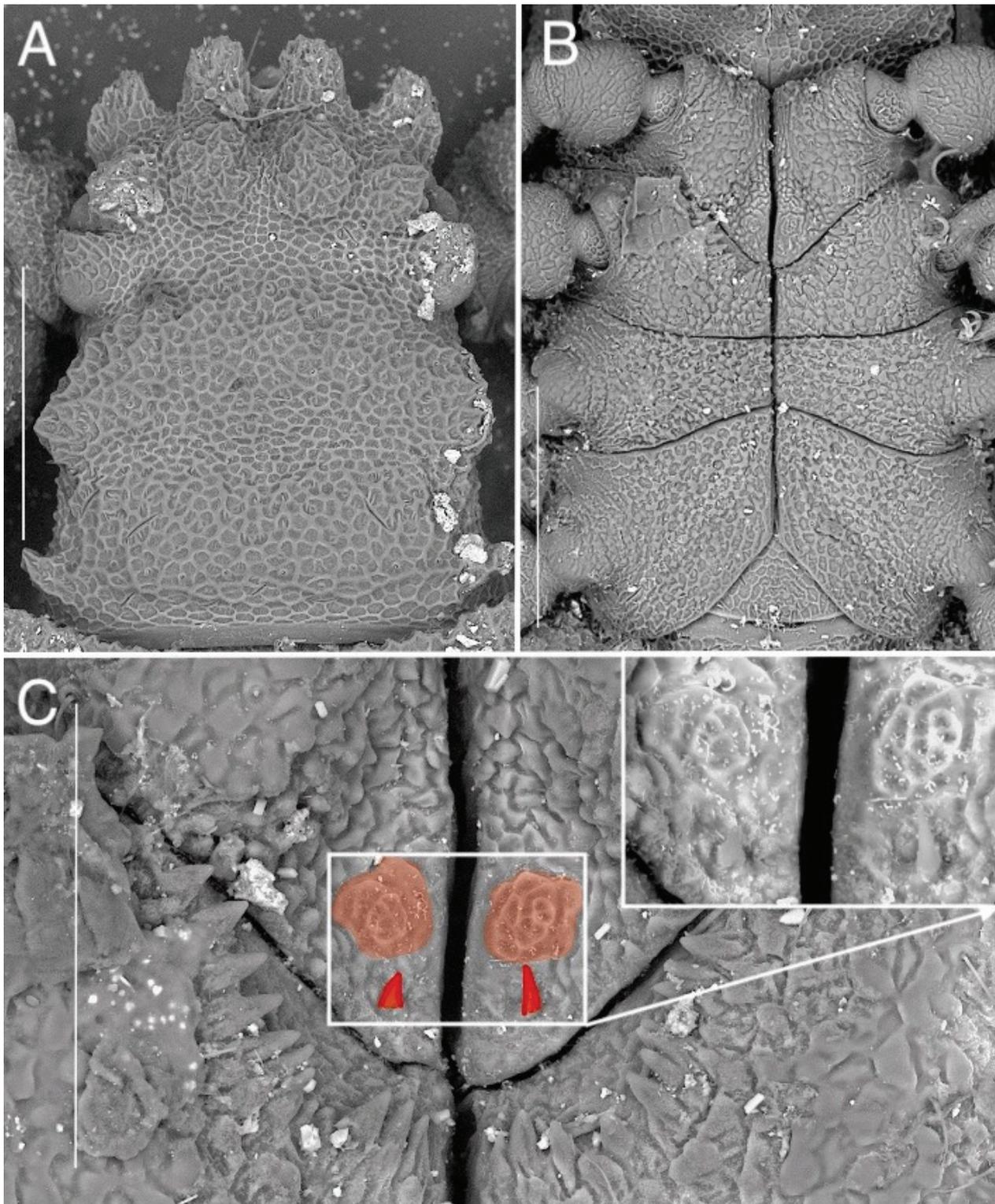


Figure 18. *Toliaranella* gen. nov., scanning electron micrographs. Specimens used for imaging: **A** *T. griswoldi* sp. nov. male paratype (ZMH-A0016740); **B, C** *T. meridionalis* sp. nov. male paratype (ZMH-A0016753). **A** carapace, dorsal view; **B** sternum ventral overview; **C** coxal spines and perforated organ in detail (highlighted in red). Scale bars: 0.2 mm (A, B); 0.1 mm (C).

***Toliaranella pumila* sp. nov.**

<https://zoobank.org/NomenclaturalActs/2EF7F29D-DD-BE-4DBF-A92E-C6B64346FCCF>

Type material examined. MADAGASCAR: Holotype ♂ (CAS 9071606 [BLF5966]), allotype ♀ (ZMH-A0016718), paratypes: 25

♂, 4 ♀ (CAS 9071606 [BLF5966]), 8 ♂, 3 ♀ (ZMH-A0016719 – ZMH-A0016729), Toliara Province, Forêt de Tsinjoriaky, 22°48'08"S 43°25'14"E, 6 March 2002, B.L. Fisher.

Additional material examined. MADAGASCAR: Toliara Province [Atsimo-Andrefana Region]: 25 ♂, 10 ♀, 39 nymphs (CAS 9071598 [BLF 6070]), 6 ♂, 1 ♀, 5 nymphs (CAS 9071743 [BLF 6068]), Foret

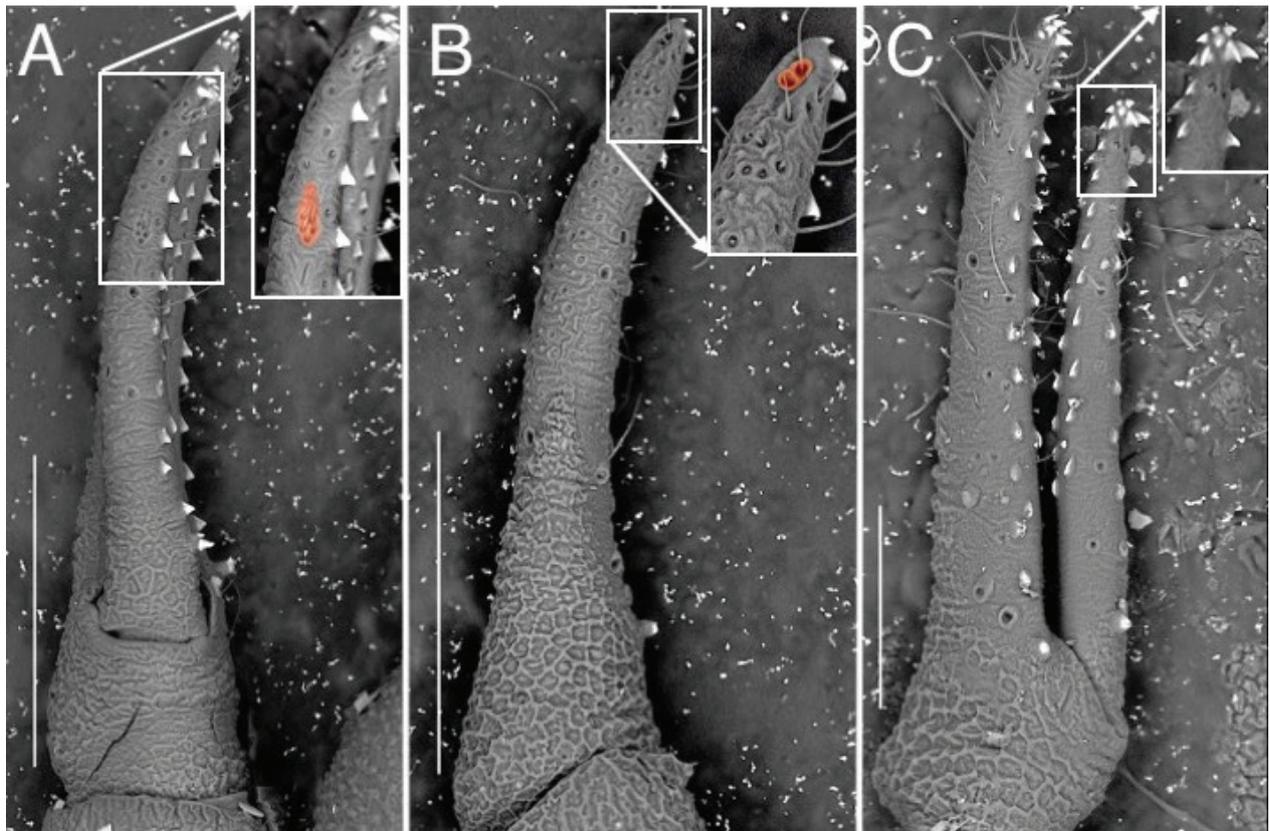


Figure 19. *Toliaranella*, gen. nov., scanning electron micrographs. Specimen used for imaging: *T. pumila* sp. nov. male paratype (ZMH-A0016722). **A** right chela from ventral with specialized setae in a group in detail (highlighted in red); **B** left chela with double trichobothrium *dt* in detail (highlighted in red); **C** left chela from medial with terminal teeth in a compact group in detail. Scale bar: 0.2 mm.

de Beroboka, 22°13'59"S 43°21'59"E, 12–16 March 2002, Fisher, Griswold et al.

Diagnosis. Smallest body sizes of *Toliaranella* species and of all Malagasy feaellids (e.g., body length 1.56/1.96 ♂/♀ versus 1.60–1.85/2.04–2.33 ♂/♀); Pedipalps: femur length 0.44/0.53 ♂/♀ versus 0.45–0.55/0.56–0.67 ♂/♀; most robust male pedipalpal femur of *Toliaranella* (femur 1.63 × longer than broad versus 1.65–1.72); cheotaxy: *est* on fixed finger on same sagittal level as *sb* on movable finger (*est* more distal than *sb* in *T. griswoldi* sp. nov. and *T. fisheri* sp. nov.).

Etymology. This species is named after the latin ‘*pumilus*, -a, -um’ which means “dwarf”. The specific epithet references the small size of all specimens.

Description. The following description is based on holotype and allotype. — *Carapace* (Fig. 20A): 1.29–1.44 (♂), 1.24–1.47 (♀) times longer than broad. — *Pedipalp* (Fig. 20C, D): Femora very robust (1.55–1.69 (♂), 1.43–1.80 (♀) times longer than broad; trichobothrial pattern: same as in *Mahajanganella* gen. nov., except: *est* on fixed finger on same sagittal level as *sb* on movable finger. Chelal fixed finger with 9–10 teeth in the OR, 12–15 in the MR and 8–12 in the IR; movable finger with 6–10 teeth in the OR, 9–11 in the MR and 9–10 in the

IR; fixed finger with 6 equally sized and one larger terminal tooth, movable finger with 7 equally sized terminal teeth. — *Chelicera*, *legs*, *abdomen* and *genital region*: With same characters as all members before. — *Coxal region*: See genus description. — *Dimensions* (mm): *Holotype* ♂: Body length 1.47; abdomen length 1.02, width (with pleura) 0.93, width (without pleura) 0.86; carapace length 0.45, width 0.32. Pedipalp: trochanter 0.21; femur length 0.45, width 0.27; patella 0.35; chela (without pedicel) 0.38; hand length 0.08, width 0.11; movable finger 0.30. Leg I: trochanter 0.08; femur 0.12; patella 0.15; tibia 0.11; tarsus 0.22. Leg IV: trochanter: 0.13; femur 0.11; patella 0.23; tibia 0.21; tarsus 0.26. *Allotype* ♀: Body length 2.08; abdomen length 1.51, width (with pleura) 1.39, width (without pleura) 1.15; carapace length 0.55, width 0.40. Pedipalp: trochanter 0.26; femur length 0.58, width 0.36; patella 0.42; chela (without pedicel) 0.43; hand length 0.11, width 0.13; movable finger 0.35. Leg I: trochanter 0.09; femur 0.18; patella 0.19; tibia 0.15; tarsus 0.26. Leg IV: trochanter 0.15; femur 0.13; patella 0.27; tibia 0.28; tarsus 0.33.

Variation. Body length 1.47–1.66 (♂), 1.83–2.11 (♀); abdomen length 1.02–1.16 (♂), 1.33–1.51 (♀); width (with pleura) 0.93–0.98 (♂), 1.13–1.39 (♀); width (without pleura) 0.83–0.88 (♂), 0.96–1.15 (♀); 1.19–1.32 (♂), 1.25–1.47 (♀) times longer than broad; carapace

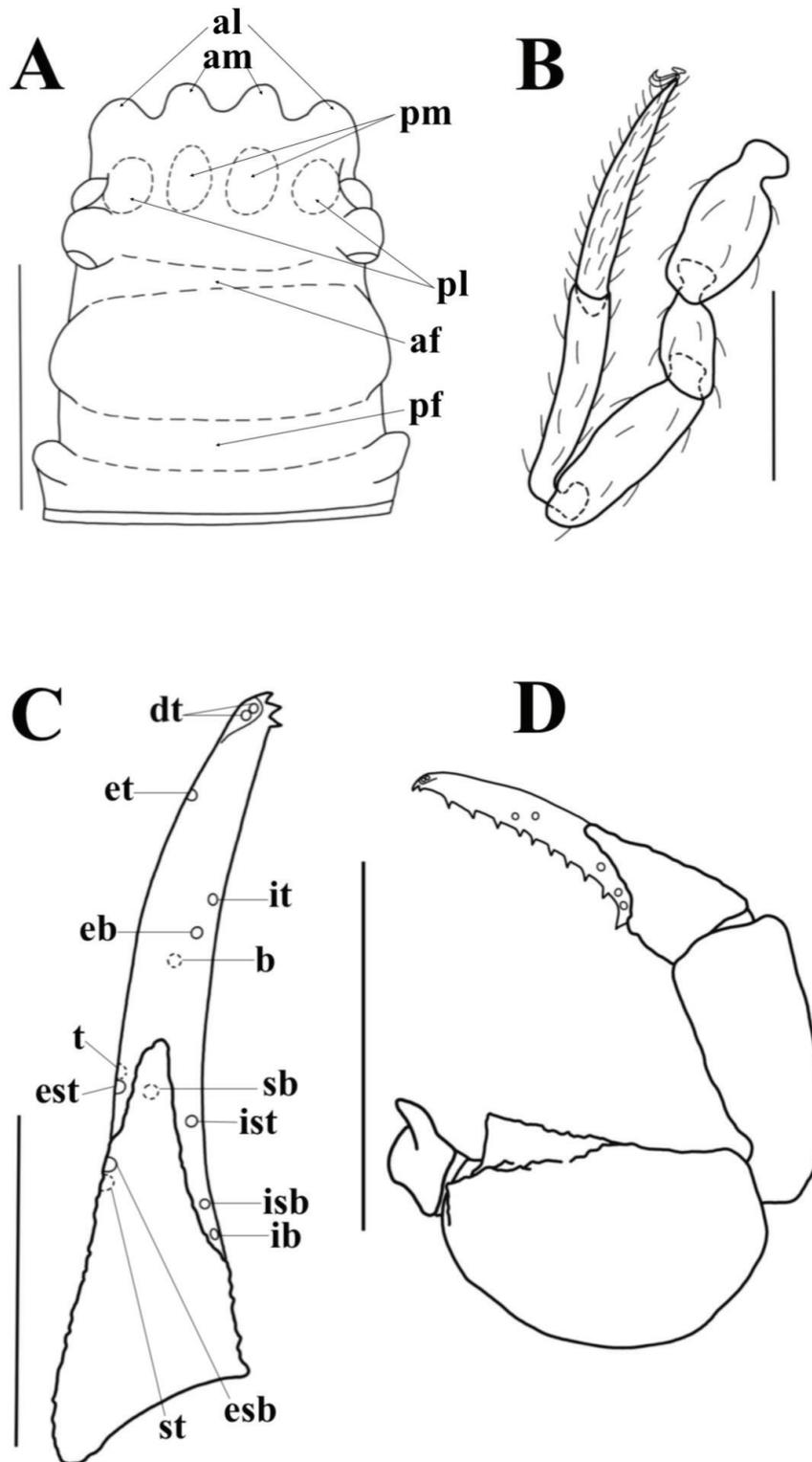


Figure 20. Drawings of *Tolaranella pumila* sp. nov.: **A** carapace from dorsal; **B** leg IV; **C** left chela from dorsal with trichobothrial pattern; **D** right pedipalp from dorsal. Scale bars: 0.2 mm (A–C); 0.4 mm (D).

length 0.43–0.47 (♂), 0.48–0.55 (♀); width 0.32–0.35 (♂), 0.36–0.41 (♀); 1.29–1.41 (♂), 1.24–1.47 (♀) times longer than broad. Pedipalp: trochanter 0.18–0.22 (♂), 0.22–0.27 (♀); femur length 0.42–0.46 (♂), 0.48–0.58 (♀); width 0.25–0.30 (♂), 0.30–0.36 (♀); 1.50–1.84 (♂), 1.43–1.80 (♀) times longer than broad; patella 0.33–0.35 (♂), 0.40–0.43 (♀); chela (without pedicel) 0.37–0.39

(♂), 0.42–0.46 (♀); hand length 0.07–0.10 (♂), 0.09–0.12 (♀); width 0.11–0.12 (♂), 0.13–0.14 (♀); movable finger 0.30–0.31 (♂), 0.35–0.37 (♀).

GenBank Code. OP589953. The species differs from all congeners by more than 5.3% in the H3 dataset.

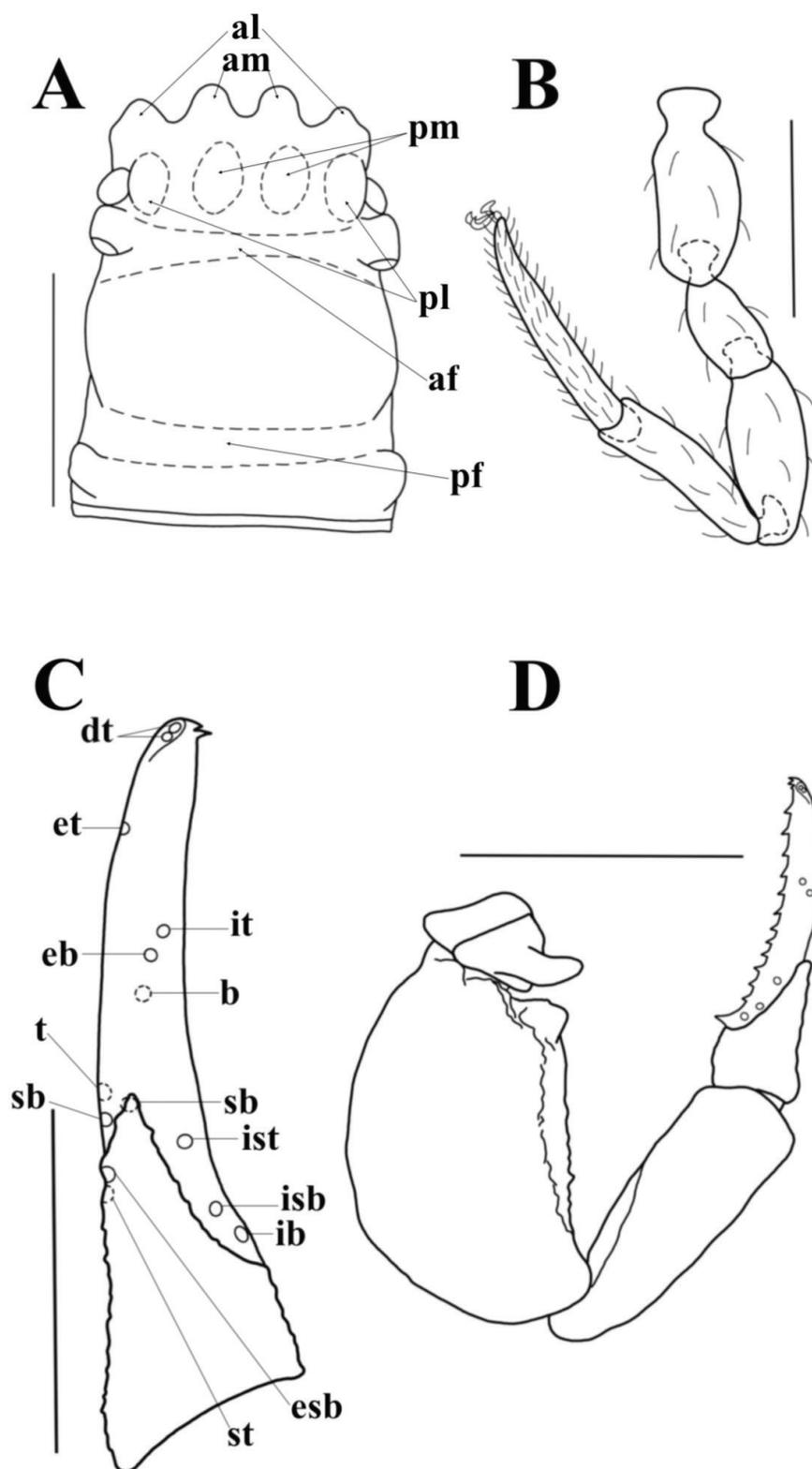


Figure 21. Drawings of *Tolaranella fisheri* sp. nov.: **A** carapace from dorsal; **B** leg IV; **C** left chela from dorsal with trichobothrial pattern; **D** right pedipalp from dorsal. Scale bars: 0.2 mm (A–C); 0.4 mm (D).

Habitat. Specimens were found in sifted litter of tropical dry forest (leaf mold, rotten wood) at an elevation of 375 m.

Distribution. Presently known from the type locality (BLF9556) and one additional locality (BLF6070) in the Atsimo-Andrefana Region (formerly Toliara Province).

***Tolaranella fisheri* sp. nov.**

<https://zoobank.org/NomenclaturalActs/D3AA212A-7763-41C7-A683-62F9FAC74FFC>

Type material examined. MADAGASCAR: Toliara Province [Anosy Region]: Holotype ♂ (CAS 9071590 [BLF5316]), allotype ♀ (ZMH-

A0016730), paratypes: 6 ♂, 7 ♀, (CAS 9071590 [BLF5316]), 4 ♂, 4 ♀ (ZMH-A0016731 – ZMH-A0016738), Reserve Prive Berenty, Foret de Bealoka, 24°57'25"S 46°16'17"E, 3–8 February 2002, B.L. Fisher, Griswold et al.

Additional material examined. MADAGASCAR: Toliara Province [Anosy Region]: 1 ♂, 1 nymph (CAS 9071750 [BLF5314]), Reserve Prive Berenty, Foret de Bealoka, 24°57'25"S 46°16'17"E, 3–8 February 2002, B.L. Fisher, Griswold et al. 76; ♂, 55 ♀, >100 nymphs (CAS 9071589 [BLF5426]), Reserve Prive Berenty, Foret de Malaza, Mandrare River, 25°00'28"S 46°18'22"E, 6 February 2002, Fisher, Griswold et al.; 1 ♂, 2 ♀, 2 nymphs (CAS 9071578 [BLF5278]), Foret de Mahavelo, Isantoria River, 24°45'13"S 46°09'5"E, 31 January 2002, Fisher, Griswold et al.

Diagnosis. Most similar to *T. griswoldi* sp. nov., but females with most slender femora of this new genus (1.71 × longer than broad versus 1.62–1.69) and different body size.

Etymology. This species is a patronym honoring Brian Fisher who collected many Malagasy feaellids.

Description. The following description is based on holotype and allotype. — *Carapace* (Fig. 21A): 1.25–1.39 (♂), 1.27–1.39 (♀) times longer than broad. — *Pedipalps* (Fig. 21C, D): See trichobothrial pattern in description of *T. griswoldi* sp. nov. Chelal fixed finger with 10 teeth in the OR, 13–16 in the MR and 10–13 teeth in the IR; movable finger with 8–10 teeth in the OR, 9–12 in the MR and 8–11 teeth in the IR. Fixed finger with 6–7 equally sized and one large terminal tooth, movable finger with 7 terminal teeth equal in size. — *Dimensions* (mm): *Holotype* ♂: Body length 1.56; abdomen length 1.10, width (with pleura) 1.00, width (without pleura) 0.85; carapace length 0.44, width 0.34. Pedipalp: trochanter 0.24; femur length 0.43, width 0.27; patella 0.36; chela (without pedicel) 0.39; hand length 0.09, width 0.12; movable finger 0.32. Leg I: trochanter 0.07; femur 0.16; patella 0.14; tibia; 0.13; tarsus 0.22. Leg IV: trochanter 0.15; femur 0.10; patella 0.25; tibia 0.26; tarsus 0.26. *Allotype* ♀: Body length 2.15; abdomen length 1.49, width (with pleura) 1.35, width (without pleura) 1.13; carapace length 0.57, width 0.44. Pedipalp: trochanter 0.24; femur length 0.60, width 0.33; patella 0.45; chela (without pedicel) 0.50; hand length 0.11, width 0.15; movable finger 0.41. Leg I: trochanter 0.10; femur 0.20; patella 0.16; tibia 0.15; tarsus 0.28. Leg IV: trochanter 0.19; femur 0.13; patella 0.30; tibia 0.31; tarsus 0.35.

Variation. Body length 1.54–1.72 (♂), 1.83–2.15 (♀); abdomen length 1.07–1.16 (♂), 1.30–1.54 (♀); width (with pleura) 0.97–1.05 (♂), 1.16–1.38 (♀); width (without pleura) 0.83–0.92 (♂), 1.00–1.17 (♀); 1.23–1.29 (♂), 1.27–1.40 (♀) times longer than broad; carapace length 0.44–0.50 (♂), 0.51–0.58 (♀); width 0.34–0.38 (♂), 0.39–0.44 (♀); 1.25–1.39 (♂), 1.27–1.39 (♀) times longer than broad. Pedipalp: trochanter 0.23–0.27 (♂), 0.22–0.27 (♀); femur length 0.43–0.48 (♂), 0.51–0.60

(♀); width 0.26–0.29 (♂), 0.29–0.35 (♀); 1.59–1.78 (♂), 1.56–1.84 (♀) times longer than broad; patella 0.36–0.39 (♂), 0.41–0.47 (♀); chela (without pedicel) 0.39–0.43 (♂), 0.44–0.50 (♀); hand length 0.08–0.11 (♂), 0.10–0.12 (♀); width 0.11–0.13 (♂), 0.13–0.15 (♀); 0.67–0.92 (♂), 0.67–0.86 (♀) times longer than broad; movable finger 0.31–0.35 (♂), 0.36–0.41 (♀).

GenBank Code. OP589962, OP589963. The species differs from all congeners by more than 3.7% in the H3 dataset.

Habitat. Specimens were found in sifted litter (leaf mold and rotten wood) in gallery forest and spiny forest thicket at an elevation of 35–115 m.

Distribution. Known from three localities along the Mandrare River in the Anosy Region (formerly Toliara Province) in southern Madagascar.

Toliaranella griswoldi sp. nov.

<https://zoobank.org/NomenclaturalActs/08C129BA-3575-4C-44-94B4-64C8CF38E3FC>

Type material examined. MADAGASCAR: Toliara Province [Anosy Region]: Holotype ♂ (CAS 9071500 [BLF4810]), allotype ♀ (ZMH-A0016739), paratypes: 11 ♂, 1 ♀ (CAS 9071500 [BLF4810]), 4 ♂, 2 ♀ (ZMH-A0016740 – ZMH-A0016745), Parc National d'Andohahela, Forêt de Manantalinjo, 24°49'1"S 46°36'36"E, 12–16 January 2002, B.L. Fisher, Griswold et al.

Additional material examined. MADAGASCAR: Toliara Province [Anosy Region]: 4 ♂, 4 ♀, 9 nymphs (CAS 9071509 [BLF4984]), Parc National d'Andohahela, Forêt d'Ambobihory, 24°55'48"S 46°38'44"E, 16–20 January 2002, Fisher, Griswold et al.; 1 ♂, 1 ♀ (CAS 9071516 [BLF4815]), Parc National d'Andohahela, Foret de Manantalinjo, 24°49'1"S 46°36'36"E, 12–16 January 2002, Fisher, Griswold et al.

Diagnosis. Differs from *T. pumila* sp. nov. in different cheotaxy: *est* on fixed finger situated between *sb* and *t* of the movable finger on sagittal level (*est* on same sagittal level with *sb* in *T. pumila* sp. nov.); most compact carapace of the southern feaellid members (1.27/1.23 ♂/♀ times longer than broad versus 1.31–1.37/1.31–1.39 ♂/♀).

Etymology. This species is a patronym honoring Charles Griswold who collected many Malagasy feaellids.

Description. The following description is based on holotype and allotype. — *Carapace* (Fig. 22A): Very compact, heavily granulate, 1.20–1.31 (♂), 1.18–1.31 (♀) times longer than broad. — *Pedipalps* (Fig. 22C, D): Similar trichobothrial pattern as *T. pumila* sp. nov. but the following difference: *est* on fixed finger situated between *sb* and *t* of the movable finger on sagittal level. Chelal fixed finger with 9–10 chelal teeth in the OR, 12–14 in the MR and 9–11 in the IR; movable finger

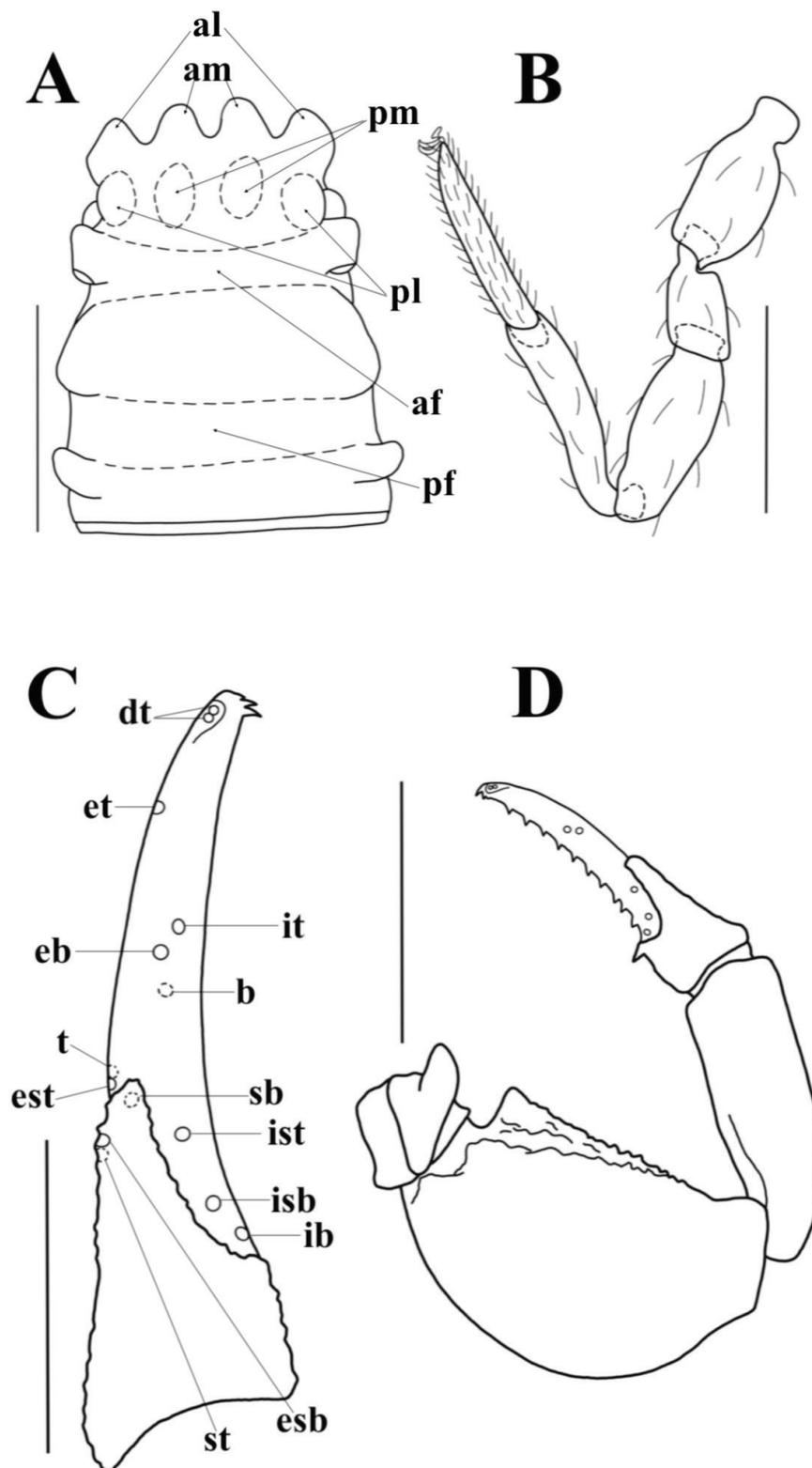


Figure 22. Drawings of *Tolaranella griswoldi* sp. nov.: **A** carapace from dorsal; **B** leg IV; **C** left chela from dorsal with trichobothrial pattern; **D** right pedipalp from dorsal. Scale bars: 0.2 mm (A–C); 0.4 mm (D).

with 6–8 in the OR, 7–11 in the MR and 7–8 in the IR. Fixed finger with 6–7 terminal teeth equal in size and one large one, movable finger with 7–8 equally sized terminal teeth. — *Dimensions* (mm): *Holotype* ♂: Body length 1.62; abdomen length 1.13, width (with pleura) 1.05, width (without pleura) 0.91; carapace length 0.46, width 0.35. Pedipalp: trochanter 0.22; femur length 0.49,

width 0.27; patella 0.35; chela (without pedicel) 0.35; hand length 0.10, width 0.11; movable finger 0.26. Leg I: trochanter 0.07; femur 0.14; patella 0.13; tibia 0.11; tarsus 0.21. Leg IV: trochanter 0.13; femur 0.10; patella 0.21; tibia 0.20; tarsus 0.26. *Allotype* ♀: Body length 2.04; abdomen length 1.47, width (with pleura) 1.33, width (without pleura) 1.11; carapace length 0.53, width

0.45. Pedipalp: trochanter 0.25; femur length 0.59, width 0.35; patella 0.46; chela (without pedicel) 0.44; hand length 0.10, width 1.14; movable finger 0.35. Leg I: trochanter 0.11; femur 0.16; patella 0.14; tibia 0.16; tarsus 0.25. Leg IV: trochanter 0.18; femur 0.14; patella 0.27; tibia 0.31; tarsus 0.30.

Variations. Body length 1.54–1.67 (♂), 1.96–2.24 (♀); abdomen length 1.08–1.18 (♂), 1.41–1.63 (♀); width (with pleura) 0.98–1.09 (♂), 1.27–1.41 (♀); width (without pleura) 0.84–0.95 (♂), 1.10–1.19 (♀); 1.20–1.29 (♂), 1.27–1.37 (♀) times longer than broad; carapace length 0.42–0.48 (♂), 0.53–0.57 (♀); width 0.35–0.38 (♂), 0.41–0.45 (♀); 1.20–1.31 (♂), 1.18–1.29 (♀) times longer than broad. Pedipalp: trochanter 0.19–0.22 (♂), 0.24–0.26 (♀); femur length 0.40–0.49 (♂), 0.54–0.59 (♀); width 0.25–0.28 (♂), 0.33–0.37 (♀); 1.60–1.81 (♂), 1.53–1.69 (♀) times longer than broad; patella 0.33–0.36 (♂), 0.45–0.48 (♀); chela (without pedicel) 0.35–0.38 (♂), 0.43–0.47 (♀); hand length 0.08–0.11 (♂), 0.10–0.11 (♀); width 0.11–0.13 (♂), 0.13–0.14 (♀); 0.73–0.91 (♂), 0.71–0.79 (♀) times longer than broad; movable finger 0.26–0.30 (♂), 0.35–0.37 (♀).

GenBank Code. OP589959, OP589960. The species differs from all congeners by more than 3.7% in the H3 dataset.

Habitat. Specimens were found in sifted litter of spiny forest thicket and tropical dry forest at an elevation of 150–300 m.

Distribution. Currently known from the type locality (BLF4810) and two additional localities of (BLF4984 and BLF4815) in the Anosy Region (former Toliara Province) in southern Madagascar.

***Toliaranella mahnerti* sp. nov.**

<https://zoobank.org/NomenclaturalActs/1D33F3C8-65A5-43D1-9524-ED771C402BC9>

Type material examined. MADAGASCAR: Toliara Province [Atsimo-Andrefana Region]: Holotype ♂ (CAS 9071763 [MGF001]), allotype ♀ (ZMH-A0016746), paratypes: 4 ♂, 2 ♀ (CAS 9071763 [MGF001]), 3 ♂, 1 ♀ (ZMH-A0016747 – ZMH-A0016750), Antafoky, 23°28'45"S 44°3'58"E, 9 February 2002, Frontier Project.

Additional material examined. MADAGASCAR: Toliara Province [Atsimo-Andrefana Region]: 3 nymphs (CAS 9071531 [MGF004]), Antafoky, 23°29'16"S 44°04'39"E, 9 February 2002, Frontier Project; 3 ♂, 1 ♀, 6 nymphs (CAS 9071523 [MGF020]), Sept Lacs, 23°31'42"S 44°09'20"E, 8 March 2002, Frontier Project; 5 ♂, 3 ♀, 6 nymphs (CAS 9071770 [MGF028]), Sept Lacs, 23°31'29"S 44°09'33"E, 10 March 2002, Frontier Project; 3 ♂, 3 ♀, 10 nymphs (CAS 9071522 [MGF030]), Manderano, 23°31'38"S 44°05'15"E, 10–14 March 2002, Frontier Wilderness Project; 6 ♂, 6 ♀, 8 nymphs (CAS 9071753 [MGF033]), Manderano, 23°31'27"S 44°05'34"E, 29 May–1 June 2002, Frontier Wilderness Project; 3 ♂, 4 ♀, 5 nymphs

(CAS 9072461 [MGF034]), Manderano, 23°31'24"S 44°05'40"E, 8–12 June 2002, Frontier Wilderness Project; 1 ♂, 2 nymphs (CAS 9071731 [MGF037]), Sept Lacs, 23°31'15"S 44°8'35"E, 20–24 August 2002, Frontier Wilderness Project; 3 nymphs (CAS 9071780 [MGF040]), 1 nymph (CAS 9072465 [MGF043]), Fiherenana, 23°10'37"S 43°57'39"E, 21–24 October 2002, Frontier Wilderness Project; 2 ♂, 2 ♀, 2 nymphs (CAS 9071745 [MGF050]), Fiherenana, 23°14'07"S 43°52'15"E, 1–4 December 2002, Frontier Wilderness Project; 2 ♂, 1 ♀, 3 nymphs (CAS 9071774 [MGF056]), Ranobe, 23°02'03"S 43°36'43"E, 5–9 February 2003, Frontier Wilderness Project; 2 ♂, 1 nymph (CAS 9071517 [MGF061]), Lake Ranobe, 23°02'23"S 43°36'39"E, 17–21 February 2003, Frontier Wilderness Project; 3 ♂, 4 ♀, 1 nymph (CAS 9072418 [MGF064 (14120(1))]), Lake Ranobe, 23°02'21"S 43°36'42"E, 25–28 April 2003, Frontier Wilderness Project; 1 nymph (CAS 9071722 [MGF070]), Lake Ranobe, 23°02'44"S 43°36'58"E, 17–21 May 2003, Frontier Wilderness Project; 1 ♀, 1 nymph (CAS 9071644 [MGF074]), Fiherenana, 23°13.351'S 43°52.853'E, 5–7 August 2003, Frontier Wilderness Project; 1 nymph (CAS 9071649 [MGF077]), Fiherenana, 23°10.619'S 43°57.685'E, 18–19 August 2003, Frontier Wilderness Project; 1 ♂, 1 ♀ (CAS 9072464 [MGF092]), Ranobe, 23°02.667'S 43°36.917'E, 26–29 January 2004, Frontier Wilderness Project; 21 ♂, 8 ♀, 47 nymphs (CAS 9071597 [BLF5850]), Foret de Mite, 23°31'27"S 44°07'17"E, 27 February–3 March 2002, Fisher, Griswold et al.

Diagnosis. Very similar to *T. pumila* sp. nov. but larger (e.g., body length 1.76/2.23 ♂/♀ versus 1.56/1.96 ♂/♀ in *T. pumila* sp. nov.; femur length 0.49/0.61 ♂/♀ versus 0.44/0.53 ♂/♀ in *T. pumila* sp. nov.); more slender femora (1.66/1.69 ♂/♀ times longer than broad versus 1.63/1.63 ♂/♀ in *T. pumila* sp. nov.).

Etymology. This species is a patronym honoring Volker Mahner who worked on African pseudoscorpions.

Description. The following description is based on holotype and allotype. — *Carapace* (Fig. 23A): 1.33–1.42 (♂), 1.32–1.37 (♀) times longer than broad. — *Pedipalps* (Fig. 23C, D): See trichobothrial pattern in description of *T. pumila* sp. nov.; Chelal fixed finger with 10–11 chelal teeth in the OR, 12–16 in the MR and 8–14 in the IR; movable finger with 6–8 in the OR, 9–11 in the MR and 8–10 teeth in the IR; 7 equally sized and one larger terminal tooth on fixed finger and 8 equally sized terminal teeth on movable finger. — *Dimensions* (mm): *Holotype* ♂: Body length 1.77; abdomen length 1.21, width (with pleura) 1.13, width (without pleura) 0.99; carapace length 0.52, width 0.39. Pedipalp: trochanter 0.26; femur length 0.49, width 0.30; patella 0.41; chela (without pedicel) 0.44; hand length 0.10, width 0.13; movable finger 0.36. Leg I: trochanter 0.08; femur 0.17; patella 0.15; tibia 0.15; tarsus 0.24. Leg IV: trochanter 0.15; femur 0.12; patella 0.26; tibia 0.23; tarsus 0.30. *Allotype* ♀: Body length 2.34; abdomen length 1.70, width (with pleura) 1.13, width (without pleura) 1.22; carapace length 0.59, width 0.43. Pedipalp: trochanter 0.26; femur length 0.61, width 0.37; patella 0.47; chela (without pedicel) 0.48; hand length 0.12, width 0.15; movable finger 0.39. Leg I: trochanter 0.10; femur 0.17; patella 0.20, tibia 0.18;

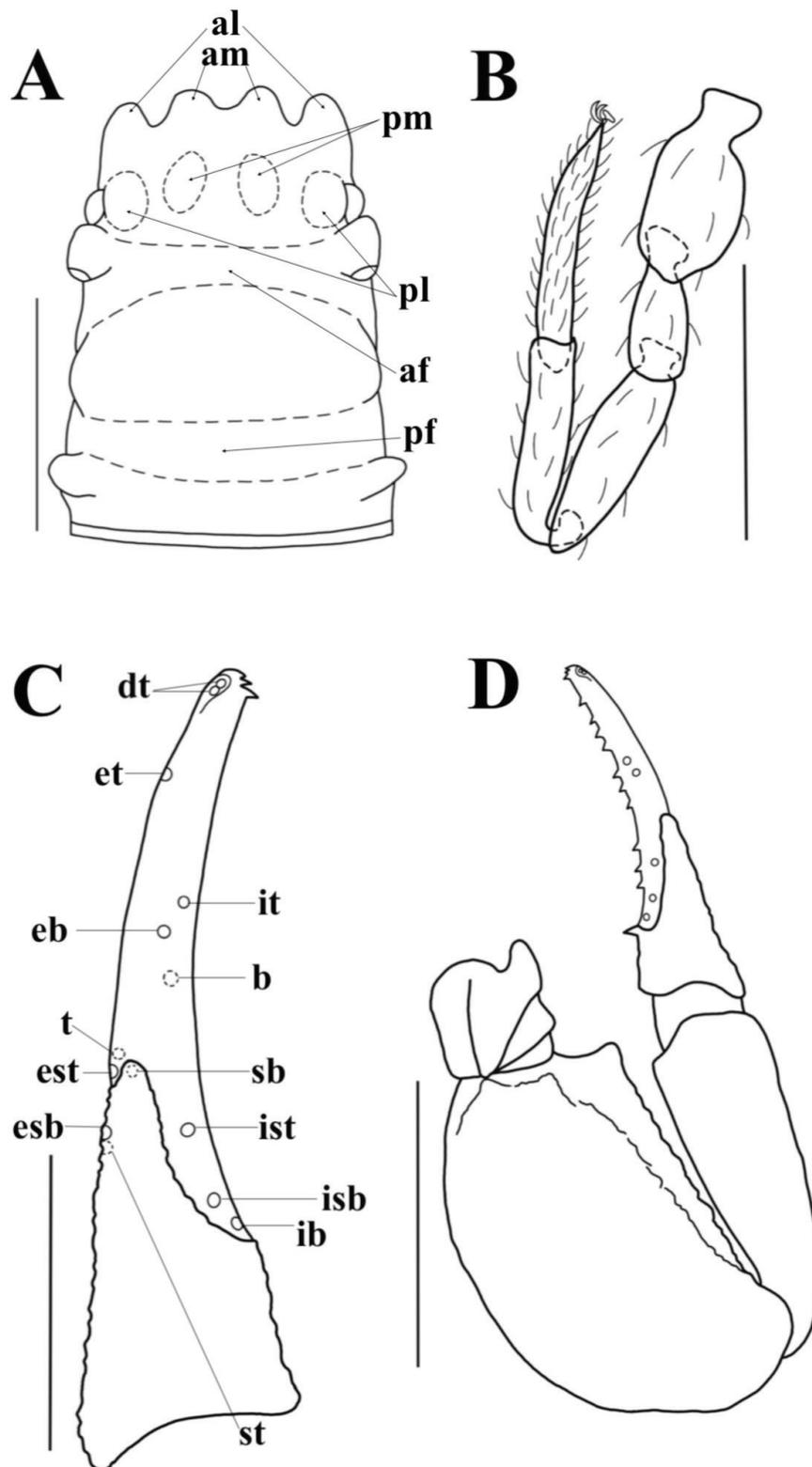


Figure 23. Drawings of *Tolaranella mahnerti* sp. nov.: **A** carapace from dorsal; **B** leg IV; **C** left chela from dorsal with trichobothrial pattern; **D** right pedipalp from dorsal. Scale bars: 0.2 mm (A–C); 0.4 mm (D).

tarsus 0.27. Leg IV: trochanter 0.18; femur 0.14; patella 0.31; tibia 0.32; tarsus 0.34.

Variation. Body length 1.64–1.88 (♂), 2.04–2.54 (♀); abdomen length 1.14–1.25 (♂), 1.44–1.86 (♀); width (with pleura) 1.03–1.15 (♂), 1.29–1.51 (♀); width (without pleura) 0.87–0.99 (♂), 1.14–1.31 (♀); 1.21–1.33

(♂), 1.26–1.42 (♀) times longer than broad; carapace length 0.50–0.53 (♂), 0.56–0.60 (♀); width 0.35–0.39 (♂), 0.42–0.44 (♀); 1.33–1.43 (♂), 1.32–1.40 (♀) times longer than broad. Pedipalp: trochanter 0.21–0.26 (♂), 0.24–0.29 (♀); femur length 0.46–0.52 (♂), 0.56–0.65 (♀); width 0.28–0.32 (♂), 0.34–0.37 (♀); 1.53–1.79 (♂), 1.61–1.78 (♀) times longer than broad; patella 0.37–0.41

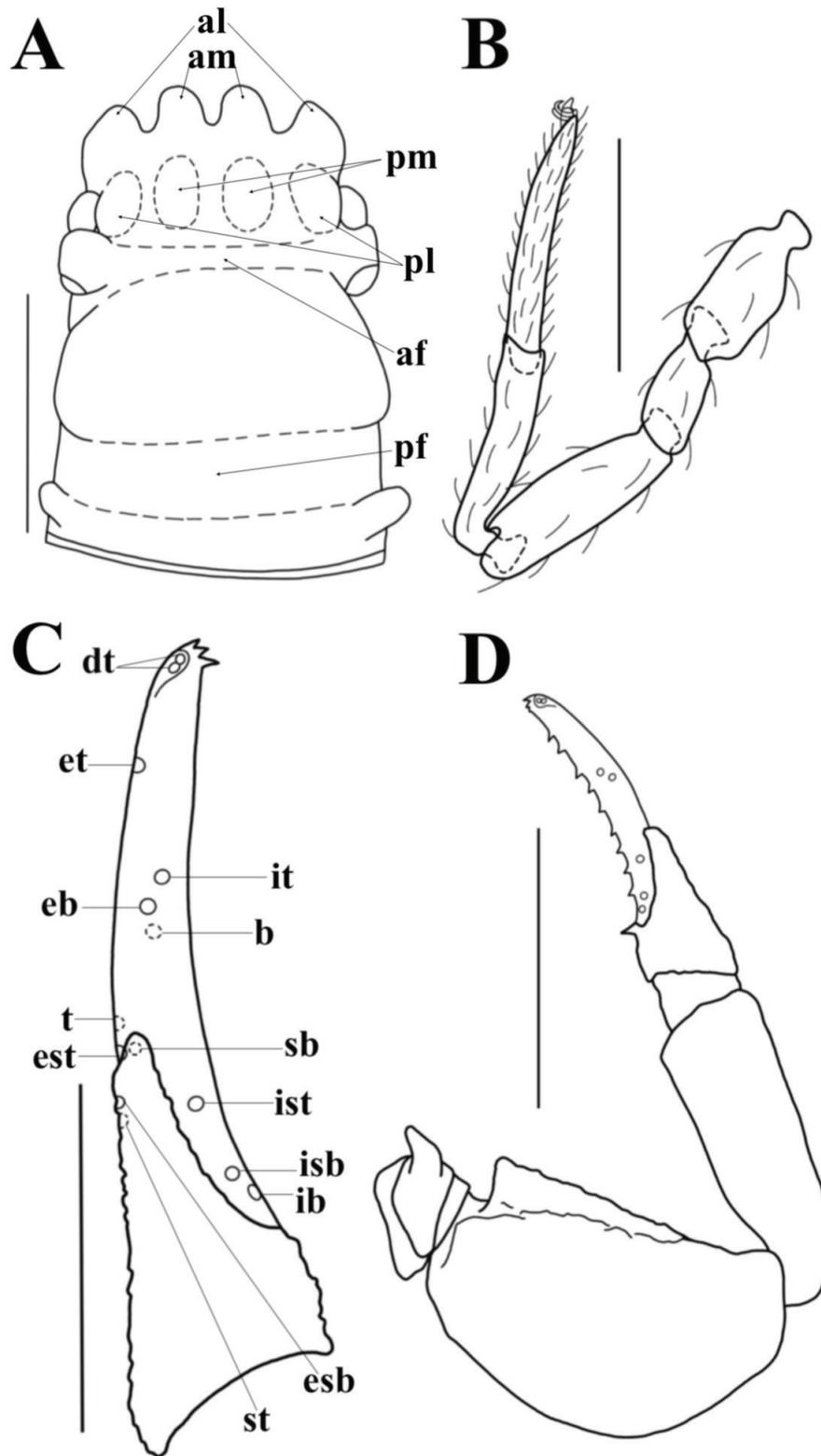


Figure 24. Drawings of *Toliaranela meridionalis* sp. nov.: **A** carapace from dorsal; **B** leg IV; **C** left chela from dorsal with trichothrial pattern; **D** right pedipalp from dorsal. Scale bars: 0.2 mm (A–C); 0.4 mm (D).

(♂), 0.47–0.50 (♀); chela (without pedicel) 0.41–0.45 (♂), 0.48–0.52 (♀); hand length 0.07–0.11 (♂), 0.11–0.14 (♀); width 0.11–0.13 (♂), 0.14–0.15 (♀); 0.58–0.92 (♂), 0.79–0.93 (♀) times longer than broad; movable finger 0.33–0.36 (♂), 0.39–0.41 (♀).

Habitat. Specimens were found in leaf litter in spiny forest thicket, degraded and undegraded gallery forest, and in disturbed and undisturbed riparian forest; elevation 20–160 m. All close to a river stream.

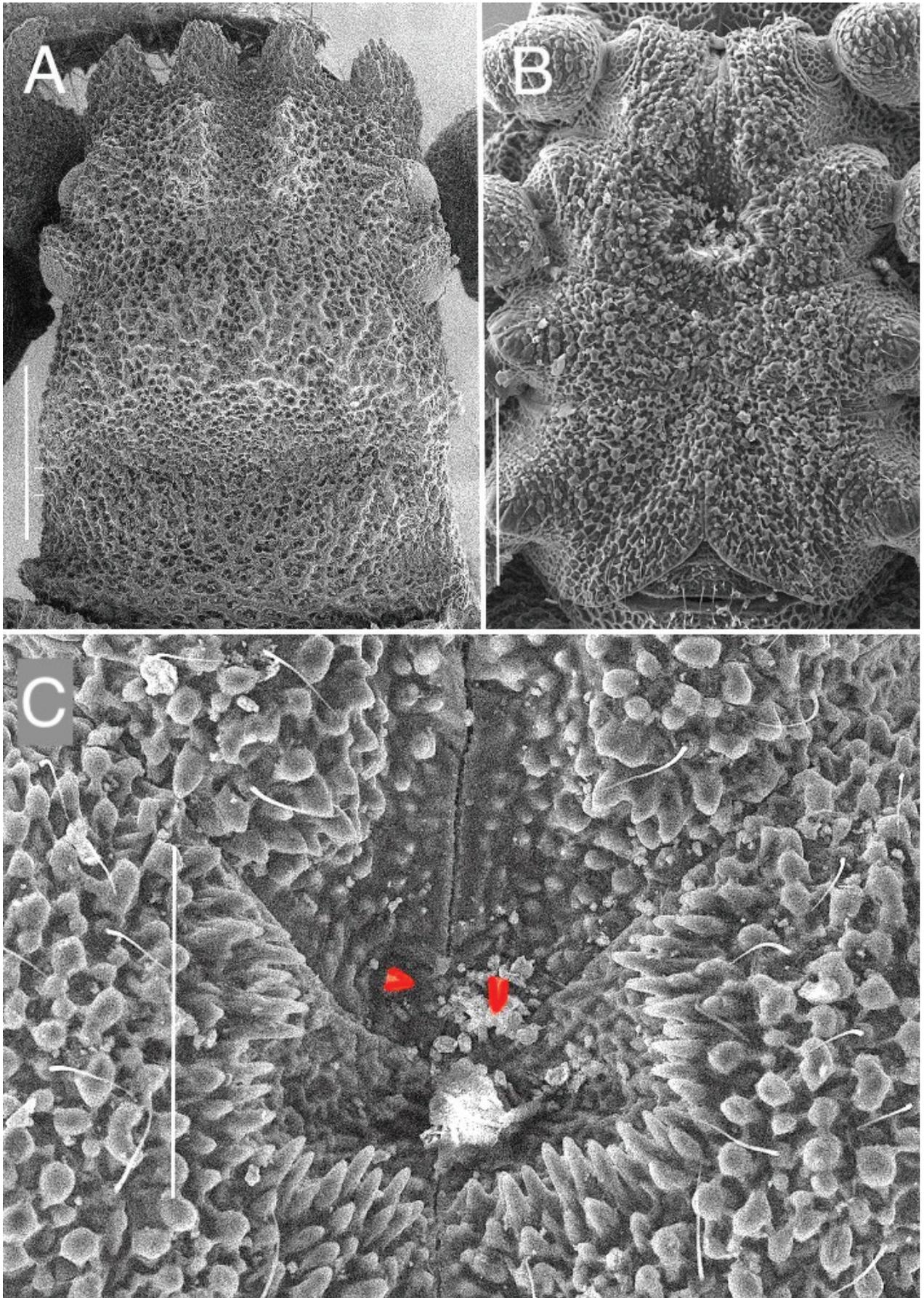


Figure 25. *Feaella (Tetrafeaella) cf. mucronata* (Tullgren, 1907), scanning electron micrographs. Specimen used for imaging: *F. cf. mucronata* female paratype (ZMH-A0010793). **A** carapace, dorsal view; **B** sternum ventral overview; **C** coxal spines in detail (highlighted in red). Scale bars: 0.2 mm (**A**, **B**); 0.1 mm (**C**).

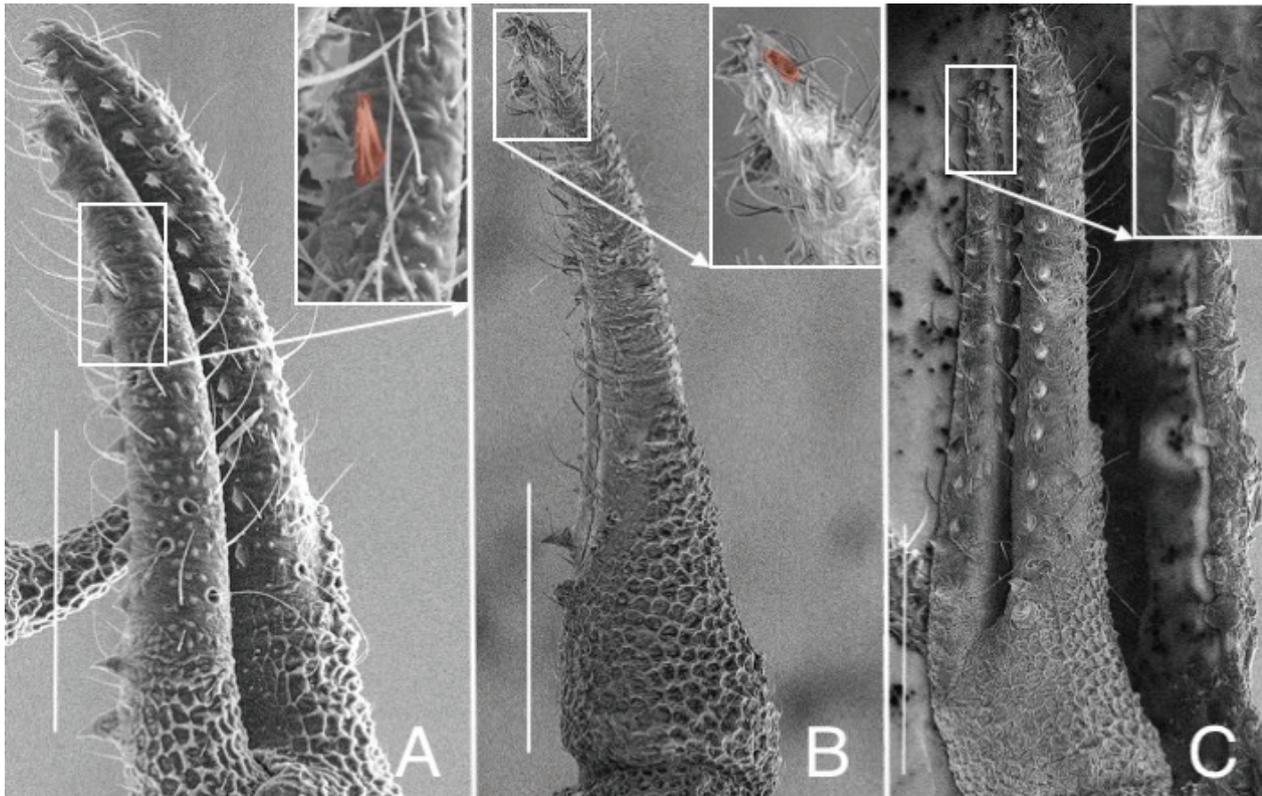


Figure 26. *Feaella (Tetrafeaella) cf. mucronata* (Tullgren, 1907), scanning electron micrographs. Specimen used for imaging: *F. cf. mucronata* female paratype (ZMH-A0010793). **A** right chela from ventral with specialized setae in a group in detail (highlighted in red); **B** left chela with double trichobothrium *dt* in detail (highlighted in red); **C** left chela from medial with terminal teeth in a compact group in detail. Scale bar: 0.2 mm.

GenBank Code. OP589954, OP589955, OP589956, OP589957, OP589958. The species differs from all congeners by more than 5.2% in the H3 dataset.

Distribution. Presently known from 17 localities in the Atsimo-Andrefana Region (formerly Toliara Province): type locality (MGF001) in southwestern Madagascar close to the Onilahy River delta and additional localities in the radius of 9 km upstream along the right side of the Onilahy River and around the Fiherenana River (MGF004, MGF020, MGF028, MGF030, MGF033, MGF034, MGF037, MGF043, MGF040, MGF050, MGF056, MGF061, MGF064, MGF070, MGF074, MGF077, MGF092).

Toliaranella meridionalis sp. nov.

<https://zoobank.org/NomenclaturalActs/97CDC6A3-72B1-4EF6-A8D7-CCC4FF4D7BB4>

Type material examined. MADAGASCAR: Toliara Province [Androy Region]: Holotype ♂ (CAS 9071748 [BLF5570]), allotype ♀ (ZMH-A0016751), 4 ♂ paratypes (CAS 9071748 [BLF5570 and BLF5650]), 2 ♂ (ZMH-A0016752, ZMH-A0016753), Reserve Speciale de Cap Sainte Marie, 25°35'40"S 45°8'49"E, 13–19 February 2002, B.L. Fisher, Griswold et al.

Additional material examined. MADAGASCAR: Toliara Province [Androy Region]: 8 ♂, 14 ♀, 5 nymphs (CAS 9071596 [BLF5500]), Reserve Speciale de Cap Sainte Marie, 25°34'54"S 45°10'6"E, 11–15 February 2002, Fisher, Griswold et al.

Diagnosis. Largest body size of the southern Malagasy feaellids (e.g., body length 1.85/2.33 ♂/♀ versus 1.56–1.80/1.96–2.23 ♂/♀; carapace length 0.53/0.64 ♂/♀ versus 0.45–0.51/0.52–0.58 ♂/♀; femur length 0.55/0.67 ♂/♀ versus 0.44–0.53/0.53–0.61 ♂/♀)

Etymology. This species is named after the type locality, which is the southernmost point of Madagascar.

Description. The following description is based on holotype and allotype. — *Carapace* (Fig. 24A): 1.25–1.38 (♂), 2.64 (♀) × longer than broad. — *Pedipalps* (Fig. 24C, D): See trichobothrial pattern in description of *T. pumila* sp. nov. Chelal fixed finger with 9–11 teeth in the OR, 13–14 in the MR and 10 in the IR; movable finger with 8–9 teeth in the OR, 11–14 in the MR and 9 teeth in the IR; terminal teeth: 7 equally sized and one large one on the fixed finger, 7 teeth on the movable finger equal in size. — *Dimensions* (mm): *Holotype* ♂: Body length 1.82; abdomen length 1.29, width (with pleura) 1.18, width (without pleura) 1.04; carapace length 0.50, width 0.40. Pedipalp: trochanter 0.24; femur length 0.59, width 0.34; patella 0.44; chela (without pedicel) 0.43; hand length 0.10, width 0.13; movable finger 0.34. Leg I: tro-

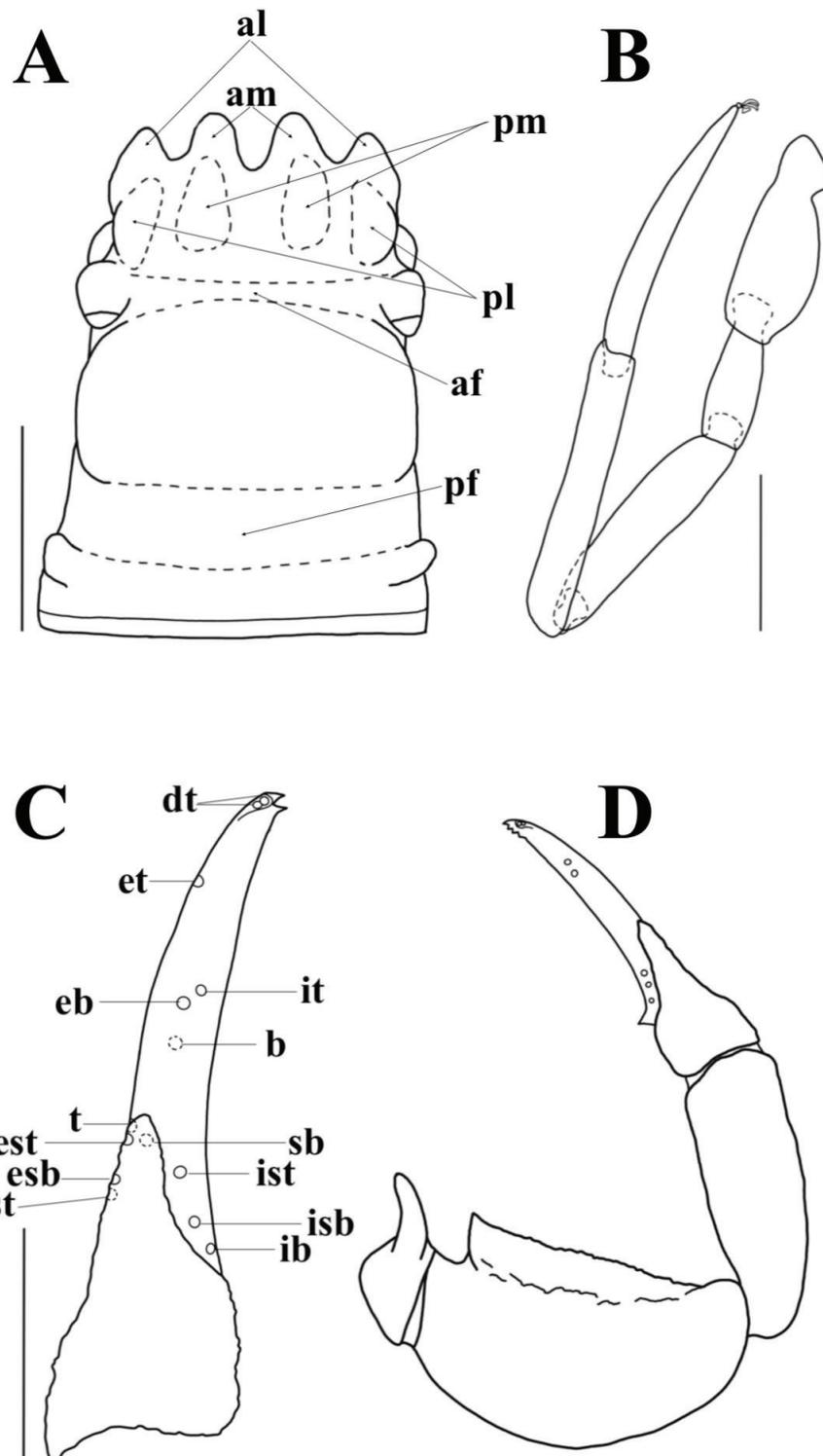


Figure 27. Drawings of *Feaella* (*Tetrafeaella*) cf. *mucronata* (Tullgren, 1907): **A** carapace from dorsal; **B** leg IV; **C** left chela from dorsal with trichobothrial pattern; **D** right pedipalp from dorsal. Scale bars: 0.2 mm (**A–C**); 0.4 mm (**D**).

chanter 0.10; femur 0.13; patella 0.17; tibia 0.17; tarsus 0.22. Leg IV: trochanter 0.16; femur 0.12; patella 0.26; tibia 0.24; tarsus 0.30. *Allotype* ♀: Body length 2.33; abdomen length 1.69, width (with pleura) 1.50, width (without pleura) 1.30; carapace length 0.64, width 0.46. Pedipalp: trochanter 0.27; femur length 0.67, width 0.40; patella 0.52; chela (without pedicel) 0.50; hand length 0.11, width 0.16; movable finger 0.41. Leg I: trochanter 0.11; femur 0.20; patella 0.21; tibia 0.15; tarsus 0.29. Leg

IV: trochanter 0.18; femur 0.16; patella 0.35; tibia 0.34; tarsus 0.34.

Variation. *Allotype* ♀: Body length 1.75–1.90 (♂), 2.33 (♀); abdomen length 1.17–1.36 (♂), 1.69 (♀); width (with pleura) 1.11–1.24 (♂), 1.50 (♀); width (without pleura) 1.01–1.09 (♂), 1.30 (♀); 1.16–1.26 (♂), 1.30 (♀) × longer than broad; carapace in length 0.50–0.55 (♂), 0.64 (♀); width 0.40–0.42 (♂), 0.46 (♀); 1.25–1.38 (♂),

1.39 (♀) × longer than broad. Pedipalp: trochanter 0.21–0.29 (♂), 0.27 (♀); femur length 0.52–0.59 (♂), 0.67 (♀); width 0.32–0.35 (♂), 0.40 (♀); 1.59–1.74 (♂), 1.68 (♀) × longer than broad; patella 0.43–0.47 (♂), 0.52 (♀); chela (without pedicel) 0.42–0.45 (♂), 0.50 (♀); hand length 0.90–0.12 (♂), 0.11 (♀); width 0.13–0.14 (♂), 0.16 (♀); 0.64–0.86 (♂), 0.69 (♀) × longer than broad; movable finger 0.32–0.36 (♂), 0.41 (♀).

GenBank Code. OP589961. The species differs from all congeners by more than 3.3% in the H3 dataset.

Habitat. Specimens found in sifted litter from spiny forest thicket very close to the coastline at an elevation of 160 m.

Distribution. Known from the two southernmost localities (type locality and BLF5500) among all Malagasy feaellids in the Androy Region (formerly Toliara Province).

4. Discussion

4.1. Biogeography

The only available studies specifically addressing Malagasy pseudoscorpions are short notes (Vachon 1960, Heurtault 1986) pointing out that all families present, including Feaellidae, do not seem to have undergone excessive *in-situ* speciation and that many genera are shared with continental Africa, southern India, Australia or Southeast Asia (Heurtault 1986). The present contribution is the first detailed study on a pseudoscorpion lineage in Madagascar and we point out that, after detailed examination, it is evident that at least the Feaellidae of Madagascar are a highly endemic fauna at both the generic and species level. We argue that this is most likely true for other pseudoscorpion families occurring on Madagascar but none of these have been revised taxonomically. Although there appear to be no families restricted to the island, endemism might in fact be substantial at the genus and species level and initial assessment of low endemism may result from the general problems of pseudoscorpion taxonomy, such as cryptic morphologies that change little over time, perhaps because of niche conservatism and retention of ancestral ecological characters in soil-dwelling fauna (Wiens and Graham 2005). Undoubtedly detailed morphological studies in conjunction with genetic data will be necessary to fully unravel the evolutionary history of the Malagasy pseudoscorpion fauna.

Feaellids are an ancient lineage with a fossil origin that dates back to the Late Triassic and Late Cretaceous (Henderickx and Boone 2016; Harms and Dunlop 2017; Kolesnikov et al. 2022) and molecular clock estimates suggest the lineage originated in the Paleozoic (Benavides et al. 2019). No molecular phylogeny currently exists for the family Feaellidae but it can be hypothesized that the origins of Malagasy *Hercules* pseudoscorpions

is Gondwanan, similar to other ancient invertebrate lineages in soil habitats such as pill millipedes (Wesener et al. 2010). Under a continental vicariance scenario, we predict this fauna to be closely allied with that of the Seychelles and southern India, followed by southern Africa, and then tropical Africa (Yoder and Nowak 2006) – a scenario that could be tested in a molecular phylogenetic framework because feaellids occur in all three of these regions and at least those from India, Maldives and the Seychelles are morphologically quite similar (e.g., Mahnert 1978; Novák et al. 2020) but differ from those in Brazil and Australia (e.g., Harvey et al. 2016a, b) and also Southeast Asia (Judson 2017). We hypothesize further that a dated molecular phylogeny should reflect continental vicariance to some degree, although we cannot rule out the possibility that some of the new genera described herein are older. Not only are feaellids an ancient Pangaeian lineage, but the molecular data presented here and elsewhere (Harvey et al. 2016a) clearly refute a historical concept based on morphology that considers many feaellid species to be widespread. In line with recent molecular studies on other soil-dwelling pseudoscorpions (e.g., Cosgrove et al. 2016; Harms 2018; Harms et al. 2019), the case is rather the opposite and feaellids appear to show extreme microendemism, habitat restriction and pronounced population structuring despite the absence of morphological disparity, perhaps comparable to some mygalomorph spiders that typically thrive in localized populations with limited dispersal between them (Greenberg et al. 2021) or mite harvestmen occurring also in soil habitats (De Bivord and Giribet 2010; Jay et al. 2016). Vicariance at various spatial scales (continental, regional and local) and different time periods seems to be a major factor that needs to be tested, although at least some feaellids occur in coastal habitats (Beier 1955) and might disperse, as recently suggested for a species found in the Maldives (Novák et al. 2020). Overall, our data are congruent with a hypothesis of pronounced endemism at all spatial scales, vicariance as a common cause for diversification, and small species ranges in specific habitats in the presence of relative morphological stasis that may be caused by niche conservatism. Feaellids therefore emerge as a new model group to test hypotheses pertaining to vicariance biogeography.

4.2. *In-situ* speciation and causes

Vences et al. (2009) reviewed possible diversification mechanisms for Madagascar and distinguished between ecogeographical constraints (meaning adaptive radiation in response to climatic shifts), speciation in rainforest refugia, montane refugia, riverine barriers, and river catchments as testable scenarios. Many studies on invertebrates have emphasized the importance of mountain or rainforest refugia (Wesener et al. 2011; Wood et al. 2015) and pointed out that *in-situ* speciation in such refugia, together with time and adaptive niche radiation, has been fundamentally important in diversification. Many taxonomic revisions have also focused on taxa that are

exclusively or predominantly found in the high-altitude forests of the east (Griswold 1997; Griswold et al. 2012; Wood and Scharff 2018) and documented substantial microendemism. For more arid habitats, a study by Wesener (2009) found that endemism in pill millipedes from dry forests was not as pronounced as that of species occurring in mesic habitats. Comprehensive taxonomic revisions on goblin spiders (Family Oonopidae Simon, 1890) have also documented major endemism at the generic level for the Malagasy fauna (Álvarez-Pardilla et al. 2012; Saucedo et al. 2015), but wide species distributions in arid habitats that roughly correspond with the generic distributions in our dataset. Perhaps the highest similarity is with the distribution of the goblin spider genus *Opopaea* Simon, 1891, where species endemism is high even in arid habitats (Andriamalala and Hormiga 2013). So, what is driving the high diversity of feaellids in Madagascar?

Adaptive radiation in response to climatic zonation is a likely hypothesis for the three feaellid genera described in our paper. *Antsiarananaella* **gen. nov.** is clearly restricted to the dry deciduous savannah forests of the north, a biome that is well known as a center of endemism in both vertebrates and invertebrates (e.g., Brown et al. 2016). The Irodo and Loky Rivers seem to be major barriers here that define species ranges to some extent and divide the ranges of *A. faulstichi* **sp. nov.** and *A. leniae* **sp. nov.** and *A. marlae* **sp. nov.** although forest cover and topography also seem to be important. The distribution of *Mahajan-ganella* **gen. nov.** encompasses the dry deciduous forests of the western Malagasy biome and species seem a little more widespread and river drainages do not seem as important here, although our species hypotheses are primarily based on morphology and we cannot rule out the possibility that more widespread species such as *M. heraclis* **sp. nov.** might show significant genetic structuring or cryptic speciation. *Toliaranella* **gen. nov.** is restricted to the subarid biome of the south, which is primarily covered by arid spiny bush vegetation. Our maps and genetic data (whenever available) clearly show that river drainages can define species ranges, such as with *T. mahner-ti* **sp. nov.** that is found in the Fiherenana and Onilahy drainages but nowhere else. The Mandrare drainage also has a distinct species (*T. fisheri* **sp. nov.**) although some species such as *T. meridionalis* **sp. nov.**, are found in coastal drainages of the Cape St. Marie Special Reserve in the south. It appears that ecogeographical constraints are effective at the generic level in Malagasy Hercules pseudoscorpions, whereas river catchments and sclerophyll forest refugia offer a testable framework to derive species limits in this fauna. It might also be pointed out that feaellids are absent from two of the major Malagasy biomes which is the central highlands and the evergreen forests to the east. These are also the regions that receive the highest annual rainfall with >1500 ml per year, whereas areas occupied by feaellids altogether receive less than 1000 ml. It appears that Malagasy feaellids are absent from rainforest habitats, unlike the fauna of central and western Africa or species recorded from Brazil that have been collected from rainforest habitats (e.g., Harvey et

al. 2016b) or Southeast Asia where the only records are from caves (Judson 2017; Harvey 2018). Ecologically this fauna seems to be more closely aligned with that of eastern Africa where feaellids have been collected from dry leaf litter in savannah or near-coastal habitats (Beier 1966; Mahnert 1982; Henderickx 2009). Interestingly, some other pseudoscorpion lineages in Madagascar show exactly the opposite pattern, such as the family Pseudoty-rannochthoniidae Beier, 1932 that seems to be restricted to the central highlands and the evergreen forests according to survey records. Revising these taxonomically could complement our understanding of the Malagasy pseudoscorpion fauna and help generate a more comprehensive picture of pseudoscorpion diversification patterns on the island.

4.3. Conservation

Madagascar is amongst the “hottest” biodiversity hotspots and the conservation of the remaining natural or semi-natural habitats is crucial to ensure lineage survival under intense anthropogenic pressure. It is therefore relevant to note that none of the species described in this study come from strictly protected areas or reserves such as Tsingy de Bemaha Reserve, Betampona Reserve, Tsaratanana Reserve, or Zahamena Reserve, but that some species occur in areas that have gained some conservation status after the specimens were collected: Ankarafantsika National Park (since 2002) and Tsingy de Namoroka National Park (since 2002) for *M. heraclis* **sp. nov.** (collected in 2001), and Montagne des Français Protected Area (since 2013) for *A. lorenzorum* **sp. nov.** Feaellids habitats are also conserved in the Baie de Baly National Park (*M. schwarzeneggeri* **sp. nov.**), Kirindy Mitea National Park (*M. fridakahloae* **sp. nov.**), the Analamerana Reserve (*A. faulstichi* **sp. nov.**), Andranomena Reserve (*M. fridakahloae* **sp. nov.**), Cap Sainte Marie Reserve (*T. meridionalis* **sp. nov.**), and Ankarana Special Reserve (since 1956 for *A. faulstichi* **sp. nov.**). We emphasize here that many other species with narrow distributional ranges occur in habitats that do not have any conservation status at present, such as *T. fisheri* **sp. nov.** Conservation incentives should target these species and their habitats whenever possible.

4.4. Systematics & Taxonomy

In this paper, we describe three new genera of Hercules pseudoscorpions, each restricted to a specific biome and climate of Madagascar, and each of these containing multiple species with short ranges. Aside from biogeographical and conservation aspects, our study also highlights the need to revise generic concepts in the family Feaellidae, specifically the genus *Feaella* in the Afrotropics that is presently divided into the subgenera: *Feaella* (*Feaella*), *Feaella* (*Tetrafeaella*) and *Feaella* (*Difeaella*) based on the number of anterior lobes of the carapace ranging from two to six (Beier 1966; Mahnert 1978). The most com-

mon combination is four lobes as in *Feaella* (*Tetrafeael-la*) and this condition is shared by all Malagasy species although these species are dissimilar from the type species, *Feaella* (*Tetrafeaela*) cf. *mucronata* (Figs 25, 26, 27) from Amanzimtoti in South Africa, both morphologically and genetically. Species from Australia, the Seychelles, the Maldives and the Indian subcontinent are also presently classified into the subgenus *Tetrafeaela*, which makes little sense biogeographically and it is evident that the distinguishing character (number of lobes) is of limited phylogenetic relevance.

It is not the aim of this study to test the generic limits within Feaellidae. However, a phylogenetic analysis with a detailed morphological investigation, including scanning electron microscopy and perhaps even micro-computed tomography, should be undertaken to resolve the phenetic classification. Our study may provide an avenue insofar as we define new genera and have identified morphological characters that had been overlooked or not given widespread attention, such as the sensory apparatus and setae, chelal tooth morphology, and cuticle sculpturing, which is an obvious feature in all feaellids that generally have a thick and armed body cuticle. Focusing on minute details unfortunately seems to be important in a morphologically highly conserved pseudoscorpion lineage where species are similar across continents despite significant genetic divergences (e.g., Harvey 2016a). Analyzing the causes for such a conserved morphology and the resulting morphological crypsis of lineages, both at the species and generic level, might be an interesting task for the future, not only for Feaellidae, but also for some other pseudoscorpion lineages because strong selective pressures might exist limiting morphological change over millions of years and across continents. Alternatively, this pattern may also represent an exceptional case of ecological niche conservation reflected by morphological stasis. Since feaellids are an ancient invertebrate lineage with possible origins in the Carboniferous (Benavides et al. 2019), the low morphological diversity might be a result of the latter, but virtually nothing is known about feaellid biology and ecology and that discussion is left for the future.

5. Acknowledgements

We thank Brian Fisher and Charles Griswold (California Academy of Sciences) for their outstanding contribution to biodiversity research in Madagascar, to Lauren Esposito and Darrell Ubick for facilitating the loan of specimens from the California Academy of Sciences, to Christoph Abel (Universität Hamburg) for assistance with molecular laboratory work, and to Nadine Dupérré (LIB Hamburg) for help with imaging work and sample curation.

6. References

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