

Synopsis of valid species-group taxa for freshwater Gastropoda recorded from the European Neogene

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Academic editor: Martin Haase | Received 30 June 2014 | Accepted 12 August 2014 | Published 15 August 2014

<http://zoobank.org/7321348E-A155-49FC-B93B-12B3A72E2EAB>

Citation: Neubauer TA, Kroh A, Harzhauser M, Georgopoulou E, Mandic O (2014) Synopsis of valid species-group taxa for freshwater Gastropoda recorded from the European Neogene. ZooKeys 435: 1–6. doi: 10.3897/zookeys.435.8193

Abstract

Here we present a complete list of all valid species-group taxa of freshwater gastropods reported from Miocene and Pliocene deposits in Europe. The last comparable work dates back to the 1920s and covered about 1,600 names. The extensive literature research underlying the present work revealed considerable changes in the taxonomic and systematic frameworks of Neogene freshwater gastropods and yielded a total number of 2,156 accepted taxa. Each taxon is accompanied by a full citation of its first description; where the information is available, page number and illustration reference are provided. First descriptions available as open-access full-text sources on the web were linked via hyperlink to the first page of the publication.

Keywords

Freshwater mollusks, species list, taxonomy, online sources, Miocene, Pliocene

Introduction

The latest available synopsis for continental gastropods of the Paleogene and Neogene of Europe is the over 3000-page-thick Fossilium Catalogus of Wenz (1923–1930), who managed to include data of almost all the literature published before

1923. For the freshwater Neogene (i.e., Miocene and Pliocene, 23.03–2.588 Ma, Gradstein et al. 2012) this resulted in a number of about 1,600 accepted species-group names. Since then numerous new papers and monographs have been published, which introduced new names, new combinations, and/or synonymized others and re-arranged many of the systematic classifications (e.g., Pavlović 1927, 1931; Jekelius 1932, 1944; Wenz 1938–1944; Papp 1953, 1954; Sauerzopf 1953; Bartha 1954, 1956; Schlickum 1964, 1976; Gillet and Marinescu 1971; Roshka 1973; Schütt 1976; Willmann 1981; Lubenescu and Zazuleac 1985; Anistratenko 1993; Rust 1997; Harzhauser and Binder 2004; Harzhauser et al. 2002; Gozhik and Datsenko 2007; Neubauer et al. 2011, 2013a, 2013b, 2014a, 2014b). Consequently, the inventory has changed substantially since Wenz.

This data paper presents a list of all accepted species-group names of the European Neogene freshwater gastropods, each with the current generic combination and reference to the first description. In many cases we referred to the latest available combination, but did not aim for a critical evaluation of these; this contribution is not meant as taxonomic revision.

Methods

The presented data derive from 459 literature sources. Nearly all of the first descriptions have been seen and verified by the authors (97.4%). We checked for correct spelling and nomenclatural validity (to exclude *nomina nuda*). Where feasible, we tried to include the full citation with indication of page number and illustrations (if present). Despite much effort it was not possible to acquire all of the mentioned publications. In such cases reference and indication of pages/illustrations were taken from Wenz (1923–1930) or other reliable sources where possible. For 9 taxa (0.4%) precise data is missing; for 11 taxa (0.5%) information is incomplete because the respective publication was only partially accessible to the authors (Gozhik and Prysazhnjuk 1978). An absent indication of illustration does not necessarily imply that there is no depiction in the original publication. Additionally hyperlinks to open-access online sources (e.g., Biodiversity Heritage Library, Internet Archive, Digital Library of the State Museum of Upper Austria, Gallica – Bibliothèque nationale de France, Google Books) are included for many of the publications.

Data setup

The list contains 2,156 accepted species-group taxa recorded for the Miocene and Pliocene. Since stratigraphical boundaries changed in the past decades and the age attributions of many gastropod-bearing localities have been revised since then, many taxa originally recorded for "Miocene" or "Pliocene" localities have been shown to belong to earlier or younger strata and vice versa. Although we tried to find out the

most recent and accurate age attributions for the localities containing the relevant taxa, there are still doubtful cases where species may prove not to derive from Neogene sediments. Erroneous records of extant species in Neogene deposits were not considered herein.

It was not possible to trace the correct authorship for the species *Melanopsis atanasii*, *Caspia dacica*, and *Prososthenia pertica*. The publications mentioned in the species list (Pană 1989; Pană et al. 1981) probably display the first descriptions, but erroneously cite wrong authorships (maybe referring to unpublished manuscripts). None of both works contain any reference to a publication matching the given authority, nor do they list compatible records in synonymy lists. For these three cases the probably correct authorships are stated; those given by the respective authors are included in square brackets.

The dataset includes the following fields:

Taxon: Fully spelt species-group name in the current combination, variably with indication of subgenus if stated that way in the literature

Genus: Genus name; again, sometimes with indication of subgenus

Species/subspecies: Epithet of species and subspecies, if available; given in its currently accepted combination and rank

Authority: Authorship and year of the taxon; in parentheses when not in original combination

Source: Full reference to the first description of the taxon

Page/Illustration: Indication of page number and illustration, if available

Seen: To indicate if the authors have personally checked the publication (v – seen, p – information partially available, n – not seen)

Source hyperlink: Hyperlink to first page of reference, if available

Although much time was spent to acquire all the relevant literature, this list may be incomplete. Moreover, not every described species is incorporated here, since the list only includes accepted names. Unaccepted names, such as primary homonyms, junior synonyms, nomina nuda, nomina dubia, or nomina inquirenda are not covered. For those older than 1923 see Wenz (1923–1930). Readers are invited to contact the authors for cases, where names – especially those thought to refer to accepted species-group taxa – are neither found in the here presented species list nor in Wenz or other sources.

Where a species contained one or several subspecific taxa (or they are currently ranked as such), the nominal subspecies was excluded from the list, so as not to overstate the actual number of accepted names.

Acknowledgments

The authors would like to thank following persons for assistance during literature research: Joaquín Albesa (Universidad de València), Vitaliy V. Anistratenko (Schmal-

hausen Institute of Zoology of the Ukrainian National Academy, Kiev), Daniela Esu (University of Rome), Gerhard Haszprunar (The Bavarian State Collection of Zoology, Munich, and Ludwig Maximilians University Munich), Sonja Herzog-Gutsch (Natural History Museum Vienna), Rodica Macaleș (National Institute of Hydrology and Water Management, București), Imre Magyar (Hungarian Natural History Museum, Budapest), Valentin A. Prysazhnjuk (Ukrainian Academy of Sciences, Kiev), Davit Vasilyan (Universität Tübingen). Daniela Esu (University of Rome) is thanked for her constructive review. This work contributes to the project "Freshwater systems in the Neogene and Quaternary of Europe: Gastropod biodiversity, provinciality, and faunal gradients" financed by the Austrian Science Fund (FWF project no. P25365-B25).

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Supplementary material I

List of valid species-group taxa for Neogene freshwater Gastropoda of Europe

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Data type: Table (Microsoft Excel 97-2003 format)

Explanation note: For details see chapter on data setup above.

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Link: doi: 10.3897/zookeys.435.8193.app1

Two new species of *Pergalumna* (Acari, Oribatida, Galumnidae) from Costa Rica, including a key to all species of the genus from the Neotropical region

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Academic editor: Vladimir Pesic | Received 5 July 2014 | Accepted 7 August 2014 | Published 15 August 2014

<http://zoobank.org/0F770825-247A-4DA7-BED3-1E686D83E6F2>

Citation: Ermilov SG, Alvarado-Rodríguez O, Retana-Salazar OP (2014) Two new species of *Pergalumna* (Acari, Oribatida, Galumnidae) from Costa Rica, including a key to all species of the genus from the Neotropical region. ZooKeys 435: 7–23. doi: 10.3897/zookeys.435.8213

Abstract

Two new species of oribatid mites of the genus *Pergalumna* (Oribatida, Galumnidae), *P. elongatiporosa* **sp. n.** and *P. striatiprodorsum* **sp. n.**, are described from leaf litter of a secondary forest in Costa Rica. *Pergalumna elongatiporosa* **sp. n.** is most similar morphologically to *P. horvathorum* P. Balogh, 1997 and *P. sura* P. Balogh, 1997, however, it differs from both by the body size, body surface ornamentation and morphology of notogastral porose areas *A1* and *A3*. *Pergalumna striatiprodorsum* **sp. n.** is most similar morphologically to *P. hawaiiensis hawaiiensis* (Jacot, 1934) and *P. strigulata* Mahunka, 1978, however, it differs from *P. hawaiiensis* by the length of interlamellar setae and surface ornamentation of the prodorsum; from *P. strigulata* by the surface of ornamentation of the notogaster, length of interlamellar setae and morphology of bothridial setae. An identification key to known species of *Pergalumna* from the Neotropical region is given.

Keywords

Oribatid mites, new species, *Pergalumna*, key, Costa Rica, Neotropical region

Introduction

Pergalumna is a large genus that was proposed by Grandjean (1936) with *Oribata nervosa* Berlese, 1914 as type species. Currently, it comprises more than 130 species having a cosmopolitan distribution collectively (Subías 2004, updated 2014). The generic characters of the genus are summarized by Ermilov et al. (2013a), an identification key to some species has been presented by Balogh and Balogh (2002).

In the course of taxonomic identification of Costa Rican oribatid mites collected in 2013, we found two new species of the genus *Pergalumna*. The main goal of our paper is to describe these species. Earlier, only three species were known from Costa Rica (P. Balogh 1997; Schatz 2006, 2007; Ermilov et al. 2014): *P. horvathorum* P. Balogh, 1997, *P. silvatica* Hammer, 1961 and *P. sura* P. Balogh, 1997. An identification key to known species of *Pergalumna* from the Neotropical region is given in the present work.

Materials and methods

Three specimens (holotype: male; two paratypes: one male and one female) of *Pergalumna elongatiporosa* sp. n. and nine specimens (holotype: female; eight paratypes: five males and three females) of *P. striatiprodorsum* sp. n. are from: Costa Rica, 9°50'24"N, 83°53'17"W, Cartago, Dulce Nombre, Paraíso, Jardín Botánico Lankester, 1400 m a.s.l., in leaf litter in secondary forest, 14.V.2013, collected by O. Alvarado-Rodríguez and A.P. Retana-Salazar.

Holotypes and paratypes were mounted in lactic acid on temporary cavity slides for measurement and illustration. The body length was measured in lateral view, from the tip of the rostrum to the posterior edge of the ventral plate. The notogastral width refers to the maximum width in dorsal aspect. Lengths of body setae were measured in lateral aspect. All body measurements are presented in micrometers. Formulae for leg setation are given in parentheses according to the sequence trochanter–femur–genu–tibia–tarsus (femulus included). Formulae for leg solenidia are given in square brackets according to the sequence genu–tibia–tarsus. General terminology used in this paper follows that of Grandjean (summarized by Norton and Behan-Pelletier 2009).

Taxonomy

Pergalumna elongatiporosa sp. n.

<http://zoobank.org/E008B3A2-4238-4C4E-B918-8B9E10E48686>

Figs 1–4

Diagnosis. Body size: 332–352 × 246–266. Body surface and pteromorphs microgranulate. Rostral, lamellar and interlamellar setae well developed, barbed. Bothridial setae setiform, ciliate unilaterally. Anterior notogastral margin not developed. Three

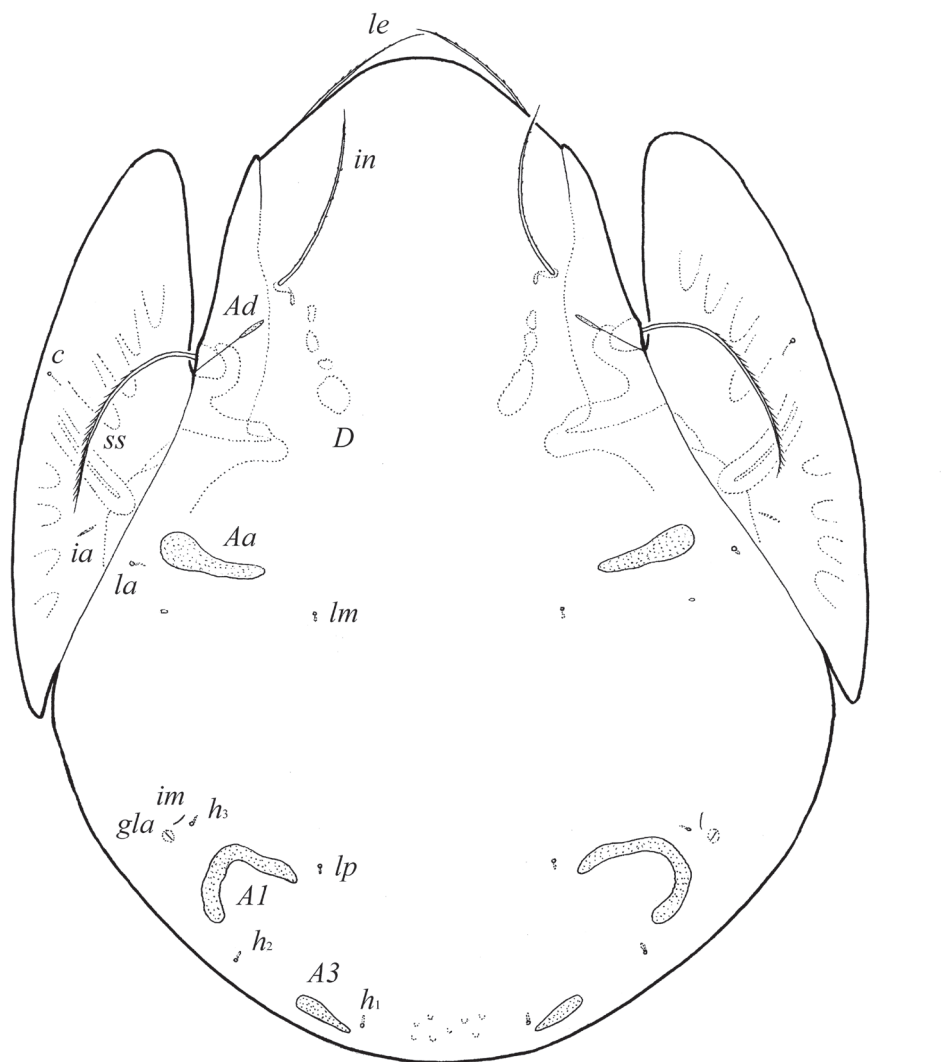


Figure 1. *Pergalumna elongatiporosa* sp. n.: dorsal view. Scale bar 100 μ m.

pairs of porose areas: *Aa* and *A3* elongate triangular, *A1* long, band-shaped, specifically curving, *Aa* located between notogastral alveoli *la* and *lm*. Median pore and postanal porose area absent. Aggenital and ano-adanal setae simple, short. Solenidion φ on tibia IV inserted in proximal part.

Description. *Measurements.* Body length: 332 (holotype, male), 340–352 (two paratypes: one male and one female); notogaster width: 246 (holotype), 246–266 (two paratypes).

Integument. Body color brown to black-brown. Body surface and pteromorphs with dense microgranules (their diameter up to 2). Pteromorphs with poorly visible wrinkles.

Prodorsum. Rostrum broadly rounded. Rostral (*ro*, 24–28), lamellar (*le*, 49–53) and interlamellar (*in*, 69–77) setae setiform, barbed. Bothridial setae (*ss*, 90–102) setiform, densely ciliate unilaterally. Exobothridial setae absent. Lamellar and sublamellar lines distinct, parallel, curving backwards. Insertions of lamellar setae distanced from the lamellar lines. Porose areas *Ad* small, elongate oval (8–12 × 2–4), located latero-posteriorly to interlamellar setae.

Notogaster. Anterior notogastral margin not developed. Dorsophragmata (*D*) long. Notogastral setae represented by 10 pairs of alveoli. Three pairs of porose areas well

visible, with distinct margins: *Aa* weakly triangular, transversally oriented ($36\text{--}57 \times 8\text{--}12$), *A1* long, band-shaped, specifically curving ($57\text{--}69 \times 8\text{--}13$), *A3* elongate, narrowly triangular ($28\text{--}32 \times 8\text{--}16$). Porose areas *Aa* located between notogastral alveoli *la* and *lm*. Median pore absent. All lyrifissures distinct; *im* and opisthonotal gland openings (*gla*) located latero-anteriorly to *A1*.

Gnathosoma. Morphology of subcapitulum, palps and chelicerae typical for *Pergalumna* (see Engelbrecht 1972; Ermilov et al. 2010; Ermilov and Anichkin 2011). Subcapitulum longer than wide ($90\text{--}94 \times 77\text{--}86$). Subcapitular setae setiform, slightly barbed; *a* ($14\text{--}16$) longer than *m* (10) and *b* (8). Two pairs of adoral setae (*or*₁, *or*₂, 8) setiform, hook-like distally, barbed. Palps (73) with setation 0–2–1–3–9(+ω). Solenidion attached to eupathidium, both located on dorsal tubercle. Chelicerae ($118\text{--}123$) with two setiform, barbed setae; *cha* ($28\text{--}32$) longer than *chb* (20). Trägårdh's organ distinct.

Epimeral and lateral podosomal regions. Apodemes 1, 2, sejugal and 3 well visible. Six pairs of setiform epimeral setae observed; setal formula: 1–0–2–3. Setae *4a*, *4b* (4) thin, smooth, shorter than *1b*, *3b*, *3c*, *4c* ($8\text{--}10$), slightly barbed. Pedotecta II (Pd II) scale-like, rounded in ventral view. Discidia (*dis*) pointly triangular. Circumpedal carinae (*cp*) distinct, directed posterior of setae *3b*.

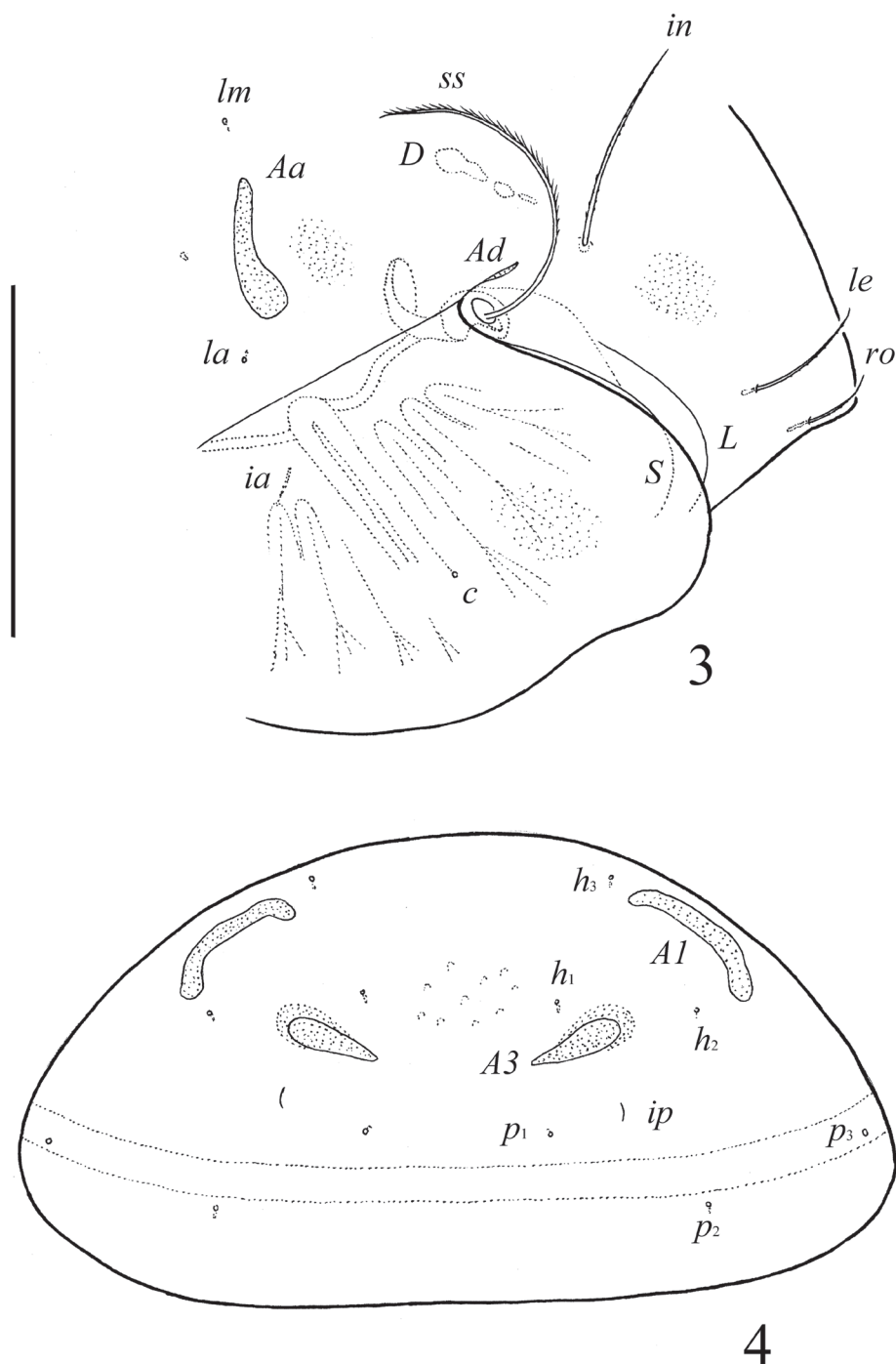
Anogenital region. Six pairs of genital (*g*₁, *g*₂, 8; *g*₃–*g*₆, 4), one pair of aggenital (*ag*, 4), two pairs of anal (*an*₁, *an*₂, 4) and three pairs of adanal (*ad*₁–*ad*₃, 4) setae minute, thin, smooth. Anterior parts of genital plates with two setae. Adanal setae *ad*₃ inserted laterally or antero-laterally to lyrifissures *iad*. Postanal porose area absent.

Legs. Morphology of leg segments, setae and solenidia typical for *Pergalumna* (see Engelbrecht 1972; Ermilov et al. 2010; Ermilov and Anichkin 2011). Formulae of leg setation and solenidia: I ($1\text{--}4\text{--}3\text{--}4\text{--}20$) [$1\text{--}2\text{--}2$], II ($1\text{--}4\text{--}3\text{--}4\text{--}15$) [$1\text{--}1\text{--}2$], III ($1\text{--}2\text{--}1\text{--}3\text{--}15$) [$1\text{--}1\text{--}0$], IV ($1\text{--}2\text{--}2\text{--}3\text{--}12$) [$0\text{--}1\text{--}0$]; homology of setae and solenidia indicated in Table 1. Solenidion φ on tibia IV inserted in proximal part.

Type deposition. The holotype is deposited in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia; one paratype is deposited in the collection of the Tyumen State University Museum of Zoology, Tyumen, Russia; one paratype is deposited in the collection of the Centro de Investigación en Estructuras, Microscópicas (CIEMIC), Ciudad de la Investigación, Universidad de Costa Rica, San José, Costa Rica.

Etymology. This specific name “*elongatiporosa*” refers to the elongate porose areas *A1*.

Remarks. In having the setiform bothridial setae, well developed interlamellar setae, absence of anterior notogastral margin and presence of three pairs of porose areas (*Aa* transversally elongated), *Pergalumna elongatiporosa* sp. n. is most similar to *P. horvathorum* P. Balogh, 1997 and *P. sura* P. Balogh, 1997 (see also Ermilov et al. 2014) from the Neotropical region. However, it differs from both by the smaller body size ($332\text{--}352 \times 246\text{--}266$ versus $394\text{--}410 \times 295$ in *P. horvathorum* and $443\text{--}498 \times 315\text{--}377$ in *P. sura*), microgranulate body surface (versus smooth in *P. horvathorum* and *P. sura*), band-shaped, specifically curving porose areas *A1* (versus elongate oval in *P. horvathorum* and triangular in *P. sura*) and elongate triangular porose areas *A3* (versus absent in *P. horvathorum* and oval in *P. sura*).



Figures 3–4. *Pergalumna elongatiporosa* sp. n.: **3** dorso-lateral view of prodorsum and anterior part of notogaster and pteromorph (gnathosoma and legs not illustrated) **4** posterior view of notogaster. Scale bars 100 μ m.

Table 1. Leg setation and solenidia of *Pergalumna elongatiporosa* sp. n. (same data for *P. striatiprodorsum* sp. n.)

Leg	Trochanter	Femur	Genu	Tibia	Tarsus
I	v'	d, (l), bv''	(l), v', σ	(l), (v), ϕ ₁ , ϕ ₂	(ft), (tc), (it), (p), (u), (a), s, (pv), v', (pl), l'', ε, ω ₁ , ω ₂
II	v'	d, (l), bv''	(l), v', σ	(l), (v), ϕ	(ft), (tc), (it), (p), (u), (a), s, (pv), ω ₁ , ω ₂
III	v'	d, ev'	l', σ	l', (v), ϕ	(ft), (tc), (it), (p), (u), (a), s, (pv)
IV	v'	d, ev'	d, l'	l', (v), ϕ	ft'', (tc), (p), (u), (a), s, (pv)

Roman letters refer to normal setae (ε to famulus), Greek letters to solenidia. Single prime (') marks setae on anterior and double prime (') setae on posterior side of the given leg segment. Parentheses refer to a pair of setae.

Pergalumna striatiprodorsum sp. n.

<http://zoobank.org/2DBFC49F-0502-4A55-AC59-6E1E45C8358C>

Figs 5–8

Diagnosis. Body size: 630–697 × 448–514. Body surface and pteromorphs microgranulate; surface of prodorsum with numerous longitudinal stria. Rostral, lamellar and bothridial setae of medium size, setiform, barbed; interlamellar setae short, slightly thickened, barbed. Anterior notogastral margin not developed. Three pairs of porose areas oval; *Aa* located between notogastral alveoli *la* and *lm*, close to *lm*. Median pore absent. Aggenital and ano-adanal setae simple, short. Postanal porose area present, elongated.

Description. *Measurements.* Body length: 697 (holotype, female), 630–697 (eight paratypes: five males and three females); notogaster width: 514 (holotype), 448–514 (eight paratypes).

Integument. Body color brown to black-brown. Body surface, pteromorphs and subcapitular mentum with dense microgranules (their diameter up to 2). Surface of prodorsum with numerous longitudinal stria. Pteromorphs with poorly visible wrinkles.

Prodorsum. Rostrum broadly rounded. Rostral (41–53), lamellar (57–69) and bothridial (106–114) setae setiform, barbed. Interlamellar setae short (12–16), setiform, slightly thickened, barbed. Exobothridial setae absent. Lamellar and sublamellar lines distinct, parallel, curving backwards. Insertions of lamellar setae distanced from the lamellar lines. Porose areas *Ad* elongate oval (20–28 × 4–8), located latero-posteriorly to interlamellar setae.

Notogaster. Anterior notogastral margin not developed. Dorsophragmata of medium size. Notogastral setae represented by 10 pairs of alveoli. Three pairs of porose areas well visible, with distinct margins: *Aa* rounded (14–16) or oval, weakly transversally oriented (14–20 × 12–16), *A1* oval, weakly elongated diagonally (24–41 × 12–20), *A3* rounded (12–16) or oval (12–16 × 10–12). Porose areas *Aa* located between notogastral alveoli *la* and *lm*, but clearly closer to *lm*. Median pore absent. All lyrifissures distinct; *im* located latero-anteriorly to *A1*. Opisthonotal gland openings located laterally to *A1*.

Gnathosoma. Morphology of subcapitulum, palps and chelicerae typical for *Pergalumna* (see Engelbrecht 1972; Ermilov et al. 2010; Ermilov and Anichkin 2011).

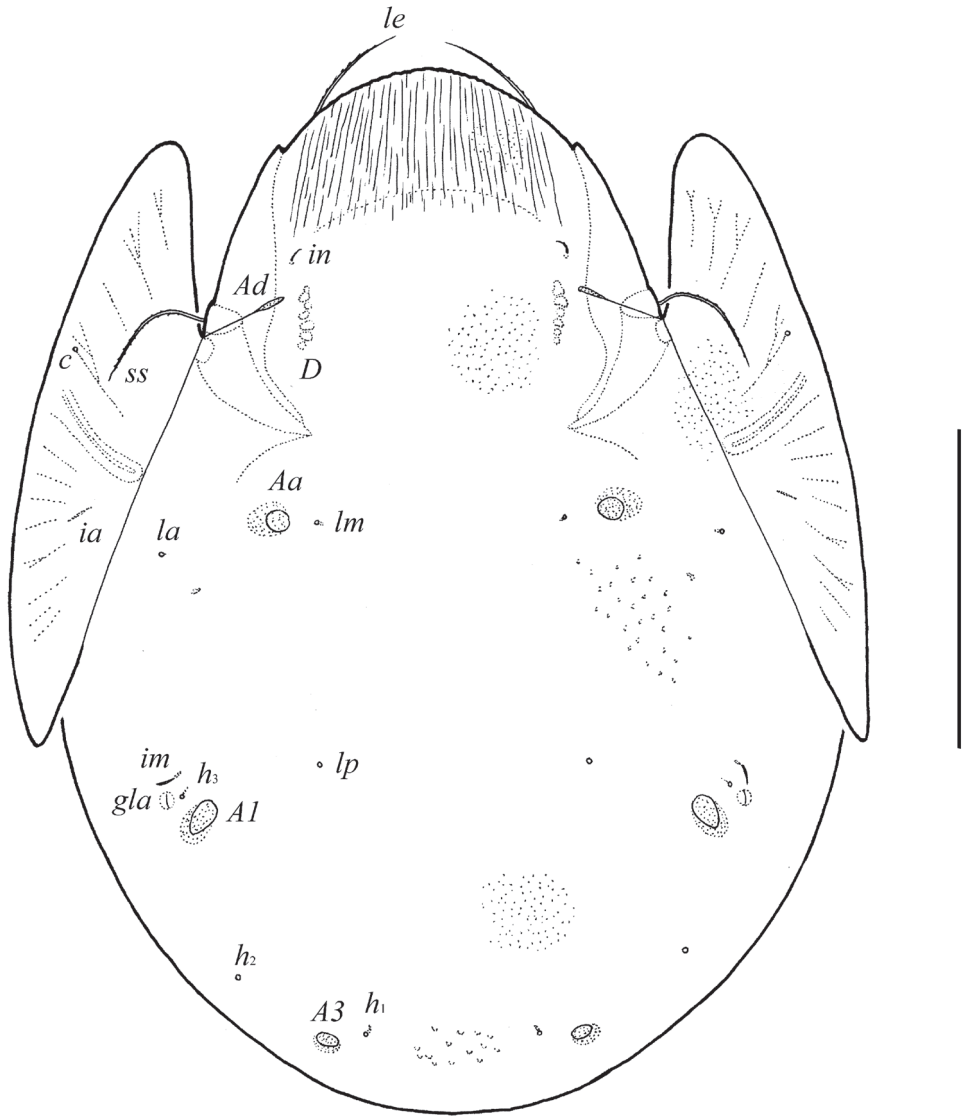


Figure 5. *Pergalumna striatiprodorsum* sp. n.: dorsal view. Scale bar 200 μ m.

Subcapitulum longer than wide (155–159 \times 131–143). Subcapitular setae setiform, slightly barbed; *a* (24) longer than *m* (16) and *b* (14–16). Two pairs of adoral setae (12–14) setiform, hook-like distally, barbed. Palps (123–127) with setation 0–2–1–3–9(+ ω). Solenidion attached to eupathidium, both located on dorsal tubercle. Chelicerae (196–205) with two setiform, barbed setae; *cha* (53) longer than *chb* (32–36). Trägårdh's organ distinct.

Epimeral and lateral podosomal regions. Apodemes 1, 2, sejugal and 3 well visible. Six pairs of setiform epimeral setae observed; setal formula: 1–0–2–3. Setae *4a*, *4b*

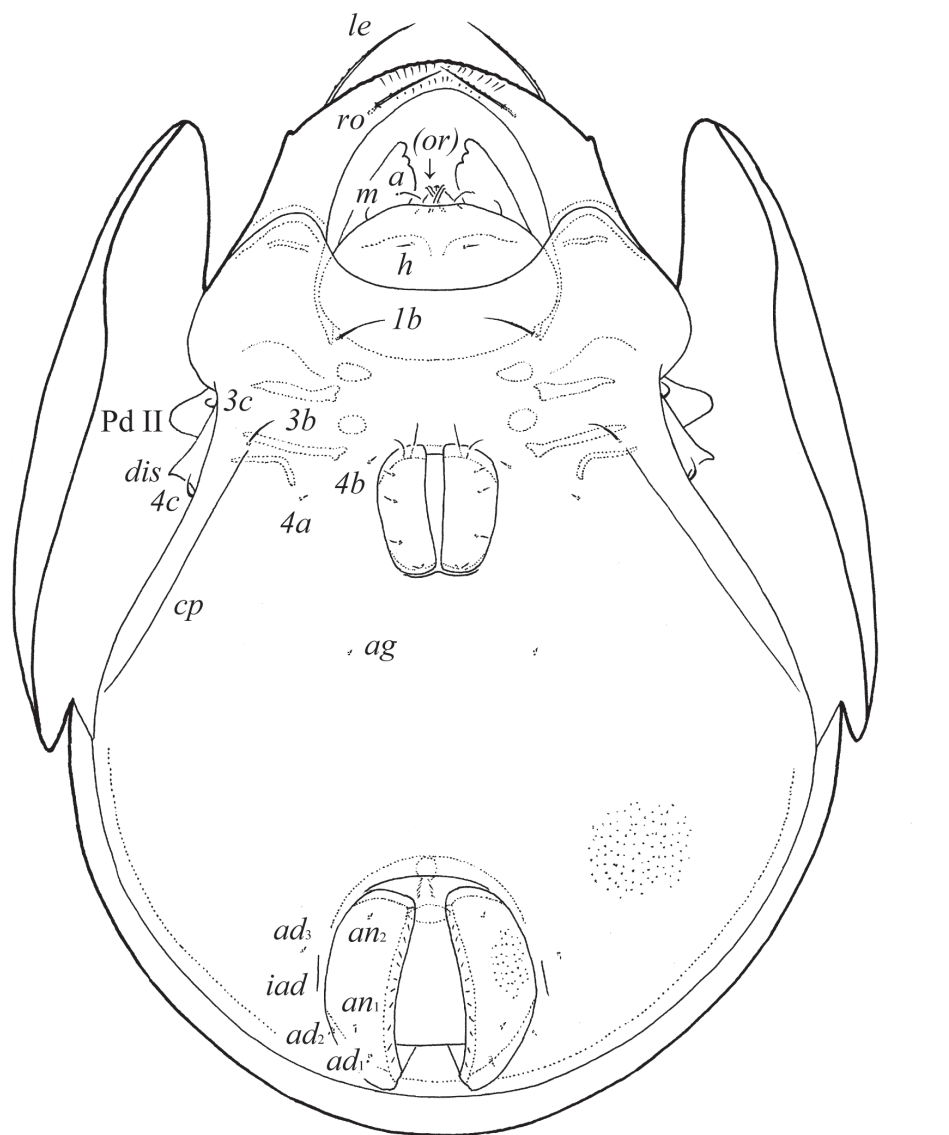
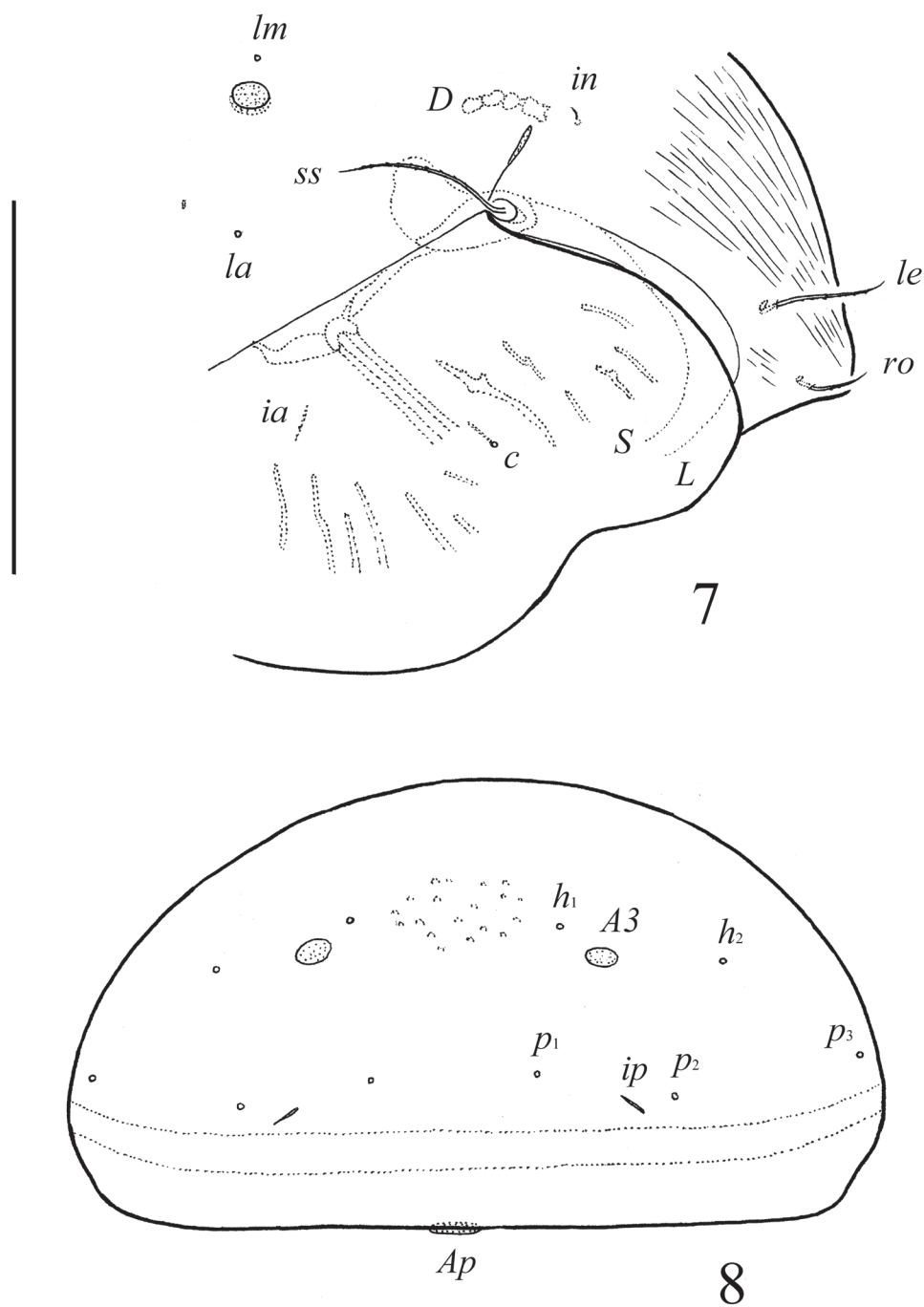


Figure 6. *Pergalumna striatiprodorsum* sp. n.: ventral view (legs not illustrated). Scale bar 200 μ m.

(6–8) thin, smooth, shorter than *3b* (20–24) and *1b*, *3c*, *4c* (32–36), slightly barbed. Pedotecta II scale-like, rounded in ventral view. Discidia pointly triangular. Circum-pedal carinae distinct, directed posterior of setae *3b*.

Anogenital region. Six pairs of genital (g_1 , 16–18; g_2 , 12–14; g_3 – g_6 , 8–10), one pair of aggenital (6–8), two pairs of anal (6–8) and three pairs of adanal (6–8) setae setiform, thin, smooth. Anterior parts of genital plates with two setae. Adanal setae ad_3 inserted laterally to lyrifiessures *iad*. Postanal porose area present, elongate oval (20–28 \times 6–8).



Figures 7–8. *Pergalumna striatiprodorsum* sp. n.: **7** dorso-lateral view of prodorsum and anterior part of notogaster and pteromorph (gnathosoma and legs not illustrated) **8** posterior view of notogaster. Scale bars 200 μ m.

Legs. Morphology of leg segments, setae and solenidia typical for *Pergalumna* (see Engelbrecht 1972; Ermilov et al. 2010; Ermilov and Anichkin 2011). Formulae of leg setation and solenidia: I (1–4–3–4–20) [1–2–2], II (1–4–3–4–15) [1–1–2], III (1–2–1–3–15) [1–1–0], IV (1–2–2–3–12) [0–1–0]; homology of setae and solenidia indicated in Table 1.

Type deposition. The holotype is deposited in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia; seven paratypes are deposited in the collection of the Tyumen State University Museum of Zoology, Tyumen, Russia; one paratype is deposited in the collection of the Centro de Investigación en Estructuras, Microscópicas (CIEMIC), Ciudad de la Investigación, Universidad de Costa Rica, San José, Costa Rica.

Etymology. This specific name “*striatiprodorsum*” refers to the striate prodorsum.

Remarks. In having the striate prodorsum, setiform bothridial setae, absence of anterior notogastral margin and presence of three pairs of oval porose areas (*Aa* oval, rounded, located close to *lm*), *Pergalumna striatiprodorsum* sp. n. is most similar to *P. hawaiiensis hawaiiensis* (Jacot, 1934) from the Pacific Islands and *P. strigulata* Mahunka, 1978 from Mauritius. However, it differs from *P. hawaiiensis* by the short interlamellar setae (versus medium size in *P. hawaiiensis*) and striate prodorsum (versus only anterior part of prodorsum with stria in *P. hawaiiensis*); from *P. strigulata* by the absence of stria on notogaster (versus notogaster striate in *P. strigulata*), short interlamellar setae (versus medium size in *P. strigulata*) and barbed bothridial setae (versus smooth in *P. strigulata*).

Among Neotropical species *Pergalumna striatiprodorsum* sp. n. is most similar morphologically to *P. decorata* Balogh & Mahunka, 1977. However, it differs from the latter by the absence of anterior notogastral margin (versus anterior margin present in *P. decorata*), barbed bothridial setae (versus smooth in *P. decorata*), absence of stria on notogaster (versus notogaster striate in *P. decorata*) and microgranulate body surface and pteromorphs (versus with larger foveoles in *P. decorata*).

Key to known species of *Pergalumna* from the Neotropical region¹

- | | | |
|---|--|----|
| 1 | Bothridial setae with clear head..... | 2 |
| – | Bothridial setae setiform | 13 |
| 2 | Anterior margin of notogaster developed | 3 |
| – | Anterior margin of notogaster not developed | 9 |
| 3 | Surface of prodorsum with numerous longitudinal stria or rugae | 4 |

1 We did not include two Neotropical species, *Pergalumna obvia* (Berlese, 1914) and *P. curva ventralis* (Willmann, 1931) (sensu Subías 2004, updated 2014), in the key. We consider *Pergalumna obvia* as representative of the genus *Galumna* Heyden, 1826 without additional studying of the type material (see Ermilov et al. 2013b). *Pergalumna curva ventralis* has no lamellar lines (see Hammer 1958, 1961, 1972), therefore we consider this species as representative of the genus *Allogalumna* Grandjean, 1936 (see generic diagnosis for *Allogalumna* in Ermilov et al. 2013a).

- Surface of prodorsum without stria and rugae.....5
- 4 Surface of notogaster striate; interlamellar setae of medium size; notogaster with four pairs of porose areas (*A2* present); body length: 330–460
.....*Pergalumna striata* (Pérez-Íñigo & Baggio, 1980) (see also Pérez-Íñigo and Baggio 1994). Distribution: Brazil
- Surface of notogaster foveolate; interlamellar setae absent; notogaster with three pairs of porose areas (*A2* absent); body size: 486–527 × 405–437
.....*Pergalumna complicata* Balogh & Mahunka, 1978 (see Fig. 23A–B, not Fig. 24A–E, in Balogh and Mahunka 1978). Distribution: Brazil
- 5 Centro-anterior part of notogaster with specific ornamentation (longitudinal line with lateral lineate branches); lamellar setae minute; notogastral porose areas *Aa* elongated transversally, very narrow; body size: 282–298 × 199–215
.....*Pergalumna ornamenta* Ermilov, Starý, Sandmann, Marian & Maraun, 2013. Distribution: Ecuador
- Centro-anterior part of notogaster without specific ornamentation; lamellar setae of medium size or long; notogastral porose areas *Aa* triangular, boot-shaped, rounded or oval.....6
- 6 Interlamellar setae long; notogastral porose areas *Aa* triangular or boot-shaped7
- Interlamellar setae minute; notogastral porose areas *Aa* rounded or oval8
- 7 Median pore located posterior to the virtual line connecting porose areas *A2*; notogastral porose areas *A1* and *A2* small; lyrifissures *im* located between setal alveoli *lm* and *lp*; body length: 470–600
.....*Pergalumna bryani bryani* (Jacot, 1934) (see also Hammer 1973). Distribution: Pacific Islands and Galapagos Islands
- Median pore located little posterior to the virtual line connecting porose areas *A1*; notogastral porose areas *A1* and *A2* of medium size; lyrifissures *im* located laterally to *A1*; body size: 620 × 430
.....*Pergalumna comparanda* (Berlese, 1920) (see also Mahunka 1992). Distribution: Argentina
- 8 Bothridial setae pointed distally; notogastral porose areas *A3* elongated, longer than *A1* and *A2*; body length: 820
.....*Pergalumna andicola* Hammer, 1961. Distribution: Peru
- Bothridial setae rounded distally; notogastral porose areas *A1*, *A2* and *A3* rounded, similar in size; body length: 730
.....*Pergalumna anellata* Hammer, 1961. Distribution: Peru
- 9 Interlamellar setae long10
- Interlamellar setae minute or represented by alveoli11
- 10 Bothridial head barbed medio-distally, stalk smooth; rostral setae inserted laterally; pteromorphal wrinkles indistinct; body size: 320–400 × 270
.....*Pergalumna numerosa* (Sellnick, 1923) (see also see also Pérez-Íñigo and Baggio 1994). Distribution: Brazil
- Bothridial head and stalk barbed; rostral setae inserted ventro-laterally; pteromorphal wrinkles clearly visible; body size: 338–392 × 258–320
.....*Pergalumna bellesii* Pérez-Íñigo & Baggio, 1997. Distribution: Brazil

- 11 Basal part of prodorsum with longitudinal stria; notogaster with four pairs of porose areas; lamellar setae of medium size; body length: 600.....
*Pergalumna montana* Hammer, 1961. Distribution: Peru and Venezuela
- Basal part of prodorsum without longitudinal stria; notogaster with three pairs of porose areas; lamellar setae short.....12
- 12 Notogastral porose areas *Aa* oval; median pore present; bothridial setae well barbed; body length: 492–576.....*Pergalumna nasica* Pérez-Íñigo & Baggio, 1980. Distribution: Brazil and Argentina
- Notogastral porose areas *Aa* triangular; bothridial setae indistinctly barbed; median pore absent; body length: 468 × 360*Pergalumna cardosensis* Pérez-Íñigo & Baggio, 1986. Distribution: Brazil and Peru
- 13 Anterior margin of notogaster developed14
- Anterior margin of notogaster not developed17
- 14 Surface of prodorsum and notogaster nearly smooth; body size: 520–676 × 502.....*Pergalumna foveolata* Hammer, 1973 (see also Bayartogtokh and Chattarjee 2010). Distribution: Polynesia, India and Brazil
- Surface of prodorsum with longitudinal stria or large foveoles; surface of notogaster striate15
- 15 Surface of prodorsum with longitudinal stria; interlamellar setae minute; notogastral porose areas *Aa* located closer to setal alveoli *lm* than to *la*; body size: 637–653 × 469–494.....*Pergalumna decorata* Balogh & Mahunka, 1977. Distribution: Neotropical region
- Surface of prodorsum with large foveoles; interlamellar setae of medium size; notogastral porose areas *Aa* equal distanced from setal alveoli *la* and *lm*....16
- 16 Rostrum pointed; anal plates striate; body size: 810–860 × 780–810.....
*Pergalumna decoratissima* Pérez-Íñigo & Baggio, 1986. Distribution: Neotropical region
- Rostrum rounded, with lateral tooth on each side; anal plates not striate; body size: 780–962 × 630–747*Pergalumna pardecoratissima* Ermilov & Kalúz, 2012. Distribution: Ecuador
- 17 Surface of prodorsum with three striate bands (one basal, transverse and two dorso-lateral, longitudinal striate bands)18
- Surface of prodorsum without three striate bands19
- 18 Rostrum pointed; posterior part of notogaster with striate bands; body size: 415–464 × 282–332.....*Pergalumna boliviana* Ermilov, 2013 (see Ermilov and Niedbala 2013). Distribution: Bolivia
- Rostrum rounded; posterior part of notogaster without striate bands; body size: 278 × 213.....*Pergalumna passimpunctata* Balogh & Mahunka, 1969 (see also Ermilov and Niedbala 2013). Distribution: Brazil
- 19 Surface of prodorsum with numerous longitudinal stria.....20
- Surface of prodorsum without stria.....21
- 20 Whole surface of prodorsum striate; interlamellar setae minute; notogastral porose areas *Aa* rounded; body size: 630–697 × 448–514.....
*Pergalumna striatiprodorsum* sp. n. Distribution: Costa Rica

- Only basal part of prodorsum striate; interlamellar setae of medium size; notogastral porose areas *Aa* elongated transversally; body length: 750.....
- 21 ...*Pergalumna magnipora magnipora* (Hammer, 1961). Distribution: Peru22
- Interlamellar setae of medium size or long22
- 22 – Interlamellar setae minute or represented by alveoli30
- 22 Rostrum tridentate; body size: 384 × 360 *Pergalumna plumata* Pérez-Íñigo & Baggio, 1986. Distribution: Neotropical region
- Rostrum rounded23
- 23 Notogastral porose areas *A1* of specific structure24
- Notogastral porose areas *A1* rounded or oval25
- 24 Body surface microgranulate; notogastral porose areas *Aa* weakly triangular, *A1* long, band-shaped, specifically curving; body size: 332–352 × 246–266..
-*Pergalumna elongatiporosa* sp. n. Distribution: Costa Rica
- Body surface smooth; notogastral porose areas *Aa* elongate oval, *A1* with rounded anterior part (with distinct margins) and triangular posterior part (without distinct margins); body size: 448–498 × 315–348..... *Pergalumna sura* P. Balogh, 1997 (see also Ermilov et al. 2014). Distribution: Neotropical region
- 25 Interlamellar setae longer than bothridial setae.....26
- Interlamellar setae shorter than bothridial setae27
- 26 Adanal setae of medium size, *ad*₃ inserted posteriorly to lyrifissures *iad*; surface of prodorsum with small tubercles; body size: 1062–1261 × 713–863
- *Pergalumna paralongisetosa* Ermilov & Kalúz, 2012. Distribution: Ecuador
- Adanal setae minute, *ad*₃ inserted laterally to lyrifissures *iad*; surface of prodorsum without tubercles; body size: 697–713 × 498–506
- 27 *Pergalumna ecuadorensis* Ermilov & Kalúz, 2012. Distribution: Ecuador
- 27 Notogastral porose areas *A1* clearly larger than other porose areas; body length: 400
- *Pergalumna melloi* Pérez-Íñigo & Baggio, 1994. Distribution: Brazil
- Notogastral porose areas *A1* not larger than other porose areas28
- 28 Two pairs of notogastral porose areas (*A1*, *A2*) observed, *A1* very narrowly band-shaped; body size: 394–410 × 295..... *Pergalumna horvathorum* P. Balogh, 1997. Distribution: Neotropical region
- Three or four pairs of notogastral porose areas observed, *A1* rounded or oval...29
- 29 Three pairs of notogastral porose areas (*A3* not observed) present; median pore absent; body size: 390–420 × 342–360
- *Pergalumna pauliensis* Pérez-Íñigo & Baggio, 1991. Distribution: Brazil
- Four pairs of notogastral porose areas (including *A3*) present; median pore present; body size: 410–490 × 315–365.....
- 30 *Pergalumna aequalis* (Sellnick, 1923). Distribution: Neotropical region
- Notogastral porose areas *Aa* rounded31
- Notogastral porose areas *Aa* elongated transversally32

- 31 Rostrum pointed; notogastral porose areas *A1* and *A3* oval or rounded; body length: 620 ***Pergalumna bifissurata* Hammer, 1972**. Distribution: Polynesia and Galapagos Islands
- Rostrum rounded; notogastral porose areas *A1* and *A3* elongated; body length: 500–540 ***Pergalumna australis* Pérez-Íñigo & Baggio, 1980**. Distribution: Brazil and Ecuador
- 32 Four pairs of notogastral porose areas present; interlamellar setae represented by alveoli; body size: 276–348 × 228–300
..... ***Pergalumna parva* Pérez-Íñigo & Baggio, 1986**. Distribution: Brazil
- Three pairs of notogastral porose areas present (*A2* absent); interlamellar setae represented by microsetae **33**
- 33 Lamellar setae longer than rostral setae; surface of anterior part of prodorsum granulate; body size: 863–1000 × 680–697 ***Pergalumna silvatica* Hammer, 1961** (see also Ermilov et al. 2014). Distribution: Neotropical region
- Lamellar setae shorter than rostral setae; surface of prodorsum not granulate; body size: 468 × 408
..... ***Pergalumna aegra* Pérez-Íñigo & Baggio, 1986**. Distribution: Brazil

Acknowledgements

We cordially thank Dr. Elizabeth A. Hugo-Coetzee (National Museum, Bloemfontein, South Africa) and one anonymous reviewer for the valuable comments.

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Revision of the family Carabodidae (Acari, Oribatida) VII. Redefinition of the genus *Malgasodes*; redescription of *M. curvisetus* Mahunka, 2000; and complementary description of *M. hungarorum* Mahunka, 2010. Phylogenetic relationships between *Malgasodes*, *Bovicarabodes*, *Afticarabodes*, *Congocephus* and *Cavaecarabodes* are discussed

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Academic editor: Vladimir Pesic | Received 9 June 2014 | Accepted 29 July 2014 | Published 15 August 2014

<http://zoobank.org/FF225E27-FA3D-4D87-A933-80C59DDF0D67>

Citation: Fernandez N, Theron P, Rollard C, Castillo ER (2014) Revision of the family Carabodidae (Acari, Oribatida) VII. Redefinition of the genus *Malgasodes*; redescription of *M. curvisetus* Mahunka, 2000; and complementary description of *M. hungarorum* Mahunka, 2010. Phylogenetic relationships between *Malgasodes*, *Bovicarabodes*, *Afticarabodes*, *Congocephus* and *Cavaecarabodes* are discussed. ZooKeys 435: 25–48. doi: 10.3897/zookeys.435.8071

Abstract

The genus *Malgasodes* is redefined; the type species *M. curvisetus* Mahunka, 2000, is redescribed by means of studies using optic and Scanning Electron Microscopy (SEM), and a complementary description of *M. hungarorum* Mahunka, 2000 is included. Comparison of genera *Malgasodes* Mahunka, 2000, *Bovicarabodes* Fernandez, Theron, Rollard, 2013a, *Cavaecarabodes* Fernandez, Theron, Rollard, Rodriguez Castillo, 2014, *Afticarabodes* Fernandez, Theron, Rollard, 2013b, and *Congocephus* Balogh, 1958 is made. Problems concerning chaetotaxy, regressive evolution and neotrichy are explained and phylogenetic relationships between *Malgasodes*, *Bovicarabodes*, *Afticarabodes*, *Congocephus* and *Cavaecarabodes* are discussed.

Keywords

Acari, Oribatida, Carabodidae, *Malgasodes*, taxonomy, phylogenetic relationships

Introduction

For several years we have been working on a revision of the family Carabodidae. Many years ago, upon commencing our work on this family, we studied large collections of material, principally from Madagascar, Gabon, Namibia, South Africa and Argentina; later, other collections were studied with material from Antilles, Vietnam, Central African Republic, Morocco, Congo, Thailand, Korea, China, Costa Rica, Brazil, Paraguay, etc.

We rapidly understood how essential it was to study type material deposited in different Museums; and in general collaboration was very good, but in some instances type material was not available on loan (National Natural History Museum, Budapest), leading to problems in the development of our study. A significant quantity of unavailable material is from Madagascar. We were fortunate as more than 4000 specimens from Madagascar were obtained from the Betsch and Paulian expedition team (Fernandez and Cleve 2010) and we managed to find specimens of all species unavailable on loan from Madagascar within these samples.

In this paper, we report on *Malgasodes curvisetus* (from the Madagascar collection at the MNHN) and *Malgasodes hungarorum* made available on loan from the Natural history Museum of Geneva, thus the totality of the species of this genus, with optic microscopy and SEM.

Identification of *M. curvisetus* was easy, due to several characteristics pointed out in the original description by Mahunka (2000), such as shape of interlamellar, lamellar, rostral, and notogastral setae; shape of sensillus and elevated interlamellar process.

We critically compared this genus with *Bovicarabodes* (Fernandez et al. 2013a) *Afticarabodes* (Fernandez et al. 2013b), *Cavaecarabodes* (Fernandez et al. 2014) and *Congocephus* Balogh, 1958.

Materials and methods

Specimens studied with light microscopy were macerated in lactic acid and observed in the same medium using the open-mount technique (cavity slide and cover slip) described by Grandjean (1949) and Krantz and Walter (2009). Drawings were made using an Olympus BHC compound microscope (Olympus, Rungis, France) equipped with a drawing tube. To aid observations, some specimens were stained with chlorazol black E (Coineau 1974). Specimens studied with the aid of scanning electron microscopy (SEM) were prepared as follows: specimens preserved in ethanol were carefully rinsed by sucking them into a Pasteur pipette several times, then transferring them for 2 hours to buffered glutaraldehyde (2.5%) in Sørensen phosphate buffer (pH 7.4; 0.1 M). After postfixation for 2 hours in buffered 2% OsO₄ solution and rinsing in buffered solution, all specimens were dehydrated in a series of graded ethanols and dried in a critical point apparatus. Specimens were mounted on Al-stubs with double-sided

sticky tape, after which they were gold-coated in a sputter apparatus (Alberti and Fernandez 1988; Alberti and Fernandez 1990a, 1990b; Alberti et al. 1991; Fernandez et al. 1991; Alberti et al. 1997; Alberti et al. 2007).

Measurements taken: total length (tip of rostrum to posterior edge of notogaster) and width (widest part of notogaster) in micrometres (μm). The description of leg chaetotaxy (SEM, standard, polarized and phase contrast microscopes) of *Malgasodes curvisetus* should be considered provisory as detailed study of leg chaetotaxy during ontogenetic development is necessary. Setal formulae of the legs include the number of solenidia (in parentheses); tarsal setal formulae include the famulus (ε).

Morphological terminology

Morphological terms and abbreviations used are those developed by F. Grandjean (1928–1974) (cf. Travé and Vachon 1975), Norton and Pelletier (2009) and Fernandez et al. (2012, 2013a, 2013b).

Evans (1992) and Murley (1951) (In: Evans *op.cit.*) were followed for setal types and ornamentation of cuticular surfaces respectively. Aligned irregular furrows (*a.i.ff*); bothridial ring (*bo.ri*); bothridial tooth (*bo.to*); circumgastric depression (*s.c*); elevated interlamellar process (*e.i.p*); notogastral anterior depression (*n.a.d*); posterior prodorsal depression (*p.p.d*); superior cornea of naso (*csø*).

Taxonomy

Genus *Malgasodes* Mahunka, 2000

Mahunka (2000, 87 p) established the genus, with *M. curvisetus* as type species (87–90 p, Figures 1–6).

Redescription. Diagnosis. Prodorsum with elevated processes; without posterior prodorsal depression. Lamellae dorsolateral. Bothridia with smooth bothridial ring and bothridial tooth. Notogaster with conspicuous anterior notogastral depression, fourteen pairs of setae, four pairs of setae inside anterior notogastral depression; four pairs around notogastral depression; two pairs posterior and externally to depression; four pairs marginally to notogaster. Interlamellar and notogastral setae long, simple (except four marginal pairs). Supratutorial depression, Pedotecta I, II, discidium, humeral apophysis present. Notogastral border tectum not prolonged by a limbus, notogastral and ventral plate separated.

Epimeral chaetotaxy 3-1-3-3. Anterior genital furrow present. Four pairs of genital setae; aggenital setae posterior to genital opening. Three pairs of adanal setae; anal plate slightly tipped. Two pairs of anal setae.

Type species

Malgasodes curvisetus Mahunka, 2000

Figures 1–17

Diagnosis. Redescription. Shape: elongate ovoid.

Integument. Prodorsum and notogaster smooth; only zone surrounding superior eye cornea, bothridium, and lateral body with small protuberances.

Setation. *simple, small:* subcapitular, epimeric, genital, aggenital, anal, adanal; *simple, large, long sharply curving tip:* notogastral, surrounding, posterior to and inside notogastral anterior depression and *in* setae; *sausage-shaped, roughly-spiculate surface:* *le* setae; *phylliform, small,* elevated central zone: *ro* setae; *phylliform medium sized:* h_3 , p_1 , p_2 , p_3 .

Prodorsum. Triangular to polyhedral. Intact elevated interlamellar process; *in* setae situated on elevated interlamellar process. Setae *in*, *ro*, *le* different shapes and lengths: $in > le > ro$; *in* setae directing posteriorly, exceeding the prodorsal margin. Rostral margin rounded. Shallow lamellar furrow discernible in the proximity of lamellar tip; lamellar tip triangular, small, shark tooth-like shape; superior cornea of naso, clearly visible; sensillus uncinat, curving upward. Notogastral anterior depression zone rectangular; posterior to this rectangular zone, an ovoid zone; dorsosejugal furrow hardly discernible, narrow, curving slightly backward. Circumgastric depression present, hardly discernible. Two pairs of notogastral setae situated posterior to notogastral anterior depression, extending forward. Four pairs inside notogastral anterior depression, with two pairs situated near dorsosejugal furrow, extending backward; four pairs bordering notogastral anterior depression, extending forward; four pairs marginally to notogaster, directing backward; three pairs of lyrifissures present, one pair at level of h_3 setae; one pair anterior to p_3 setae and *ips* between p_1 and p_2 setae.

Apodemes *apo.1*, *apo.2*, *apo.sj* and *apo.3* clearly visible; at level *apo.1*, in medial zone, rounded structure visible. Four pairs of linearly placed genital setae. Aggenital setae posterolaterally, three pairs of adanal setae; small, elongate bean-shaped lyrifissures *iad*. Two pairs of anal setae. Smooth surface between genital and anal openings.

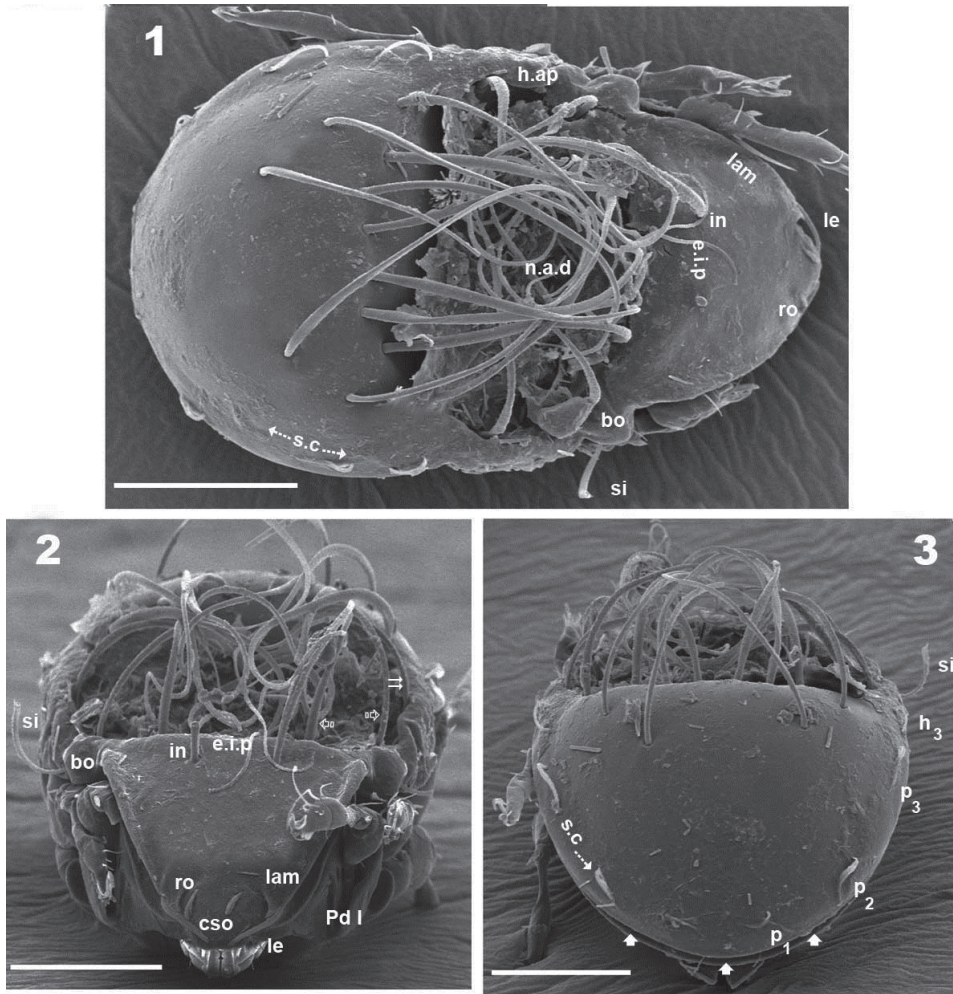
Material examined. Scanning Electron Microscopy and optic observation: 6 specimens; Madagascar R.C.P 2010. «Région Fort-Dauphin Madagascar Sud-est.» «R.C.P 2010-Piste de Ste Luce-Forêt littorale-Altitude 10 mètres» 9-12-1971. Coll. J-M.BETSCH. Three specimens deposited in Muséum National d'Histoire Naturelle, (MNHN) Paris, France.

Adult description. Female. Measurements: 372 μm (400–351) \times 260 μm (239–281) (three specimens). All specimens were female.

Shape: elongate ovoid (Figures 1, 4, 5).

Colour: yellow to light brown; slightly shiny, when observed in reflected light.

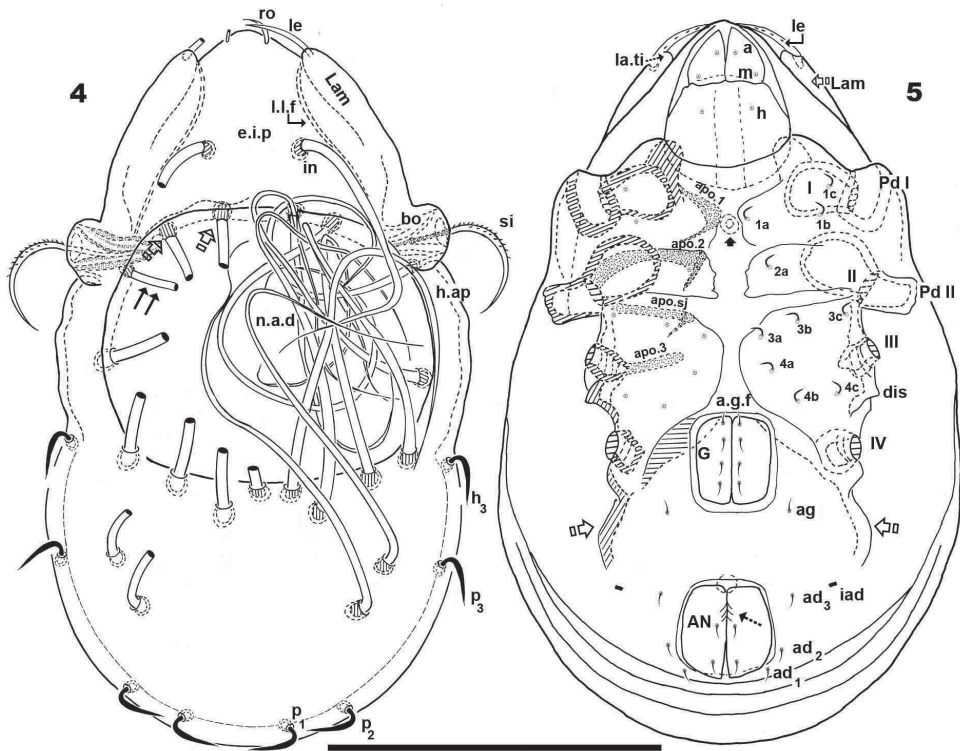
Cerotegument. Present in the notogastral anterior depression (*n.a.d*), retained by the setae and on humeral apophysis. On other body parts and legs nonexistent or disappeared during observation in lactic acid; similar in SEM observations (Figures 1, 6).



Figures 1–3. *Malgasodes curvisetus* Mahunka, 2000, adult. SEM observations. **1** dorsal view **2** frontal view **3** posterior view. Notes: Abbreviations: see “Material and methods”. Scale bar: **1–3** = 100 μ m.

Integument. Prodorsum: elevated interlamellar process (*e.i.p*) smooth (Figures 1, 2, 6); zone surrounding CSO, *bo*, and lateral body zone with small protuberances (Figures 7, 8, 10). Notogaster: smooth (Figures 1, 3, 6).

Setation (legs not included). Five types: 1) *simple, small*: subcapitular, epimeric, genital, aggenital, anal, adanal (Figure 5); 2) *simple, large, long sharply curving tip*: notogastral setae around, behind and inside *n.a.d*, and *in* setae (Figures 1, 2, 3, 4, 6); 3) *sausage-shaped, roughly-spiculate surface*: *le* (Figure 7); 4) *phylliform, small*, with elevated central zone, delimited on both sides by longitudinal depression; central elevated zone with longitudinal furrow in central zone giving a particular aspect in frontal view (Figure 10): *ro* setae (Figures 2, 7, 17); 5) *phylliform, medium size*: notogastral *h₃*, *p₁*, *p₂*, *p₃* (Figures 1, 3, 4, 6, 12, 14).

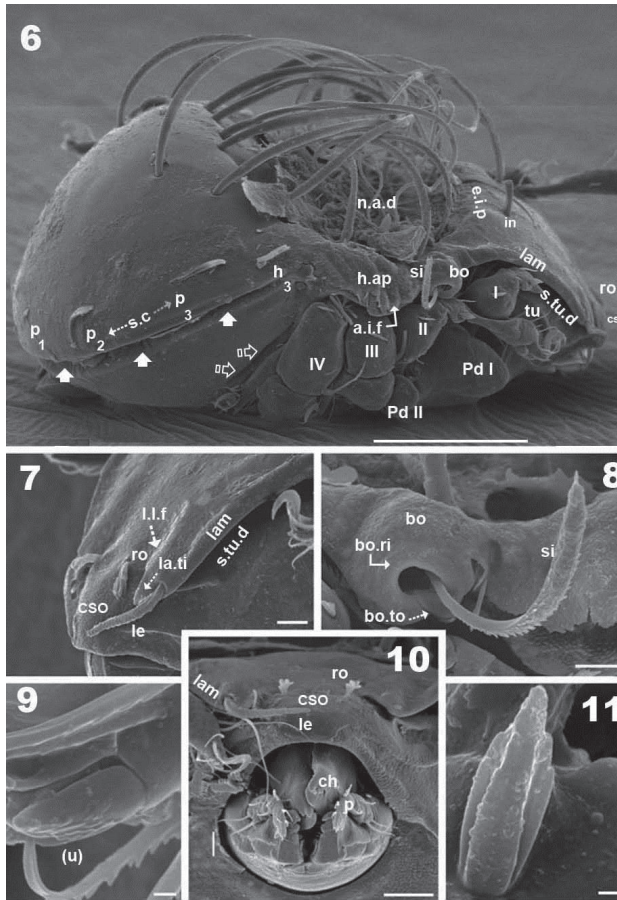


Figures 4–5. *Malgasodes curvisetus* Mahunka, 2000, adult. Optic observations. **4** dorsal view **5** ventral view. Notes: Abbreviations: see “Material and methods”. Scale bar **4**, **5** = 250 μ m.

Prodorsum. Triangular to slightly polyhedral (dorsal view) (Figures 1, 4); triangular in lateral and frontal view (Figures 2, 6, 12). Entire elevated interlamellar process (*e.i.p*) (Figure 2) situated at lower level than superior notogastral limit (Figures 2, 3, 6, 12).

Posterior prodorsal depression (*p.p.d*) absent (Figures 1, 6). Setae *in* situated on *e.i.p* (Figures 1, 2, 4, 6, 12), similar characteristics to long simple notogastral setae situated near and inside *n.a.d*; in all cases the *in* setae directing backward and entangled with cited notogastral setae (Figures 1, 2, 4, 6, 12).

Three pairs of prodorsal setae (*in*, *ro*, *le*) very different in shape and length (see Setation): *in* > *le* > *ro*; *ro* setae small, inserted posteriorly to *le* insertion, directing forward (Figures 1, 2, 4, 7, 10, 12, 14); *in* setae inserted on *e.i.p* antiaxially to medial plane and slightly externally to *ro* insertion level; posteriorly directed, far exceeding the prodorsal margin extending to *n.a.d* (Figures 1, 2, 4, 12, 19); *le* setae (Figures 1, 2, 4, 7, 10, 12, 14) laterally situated on lamellar apical zone but far from lamellar tip (*la.ti*), directing forward with tips converging to medial plane; *le* setae always found on prodorsal surface. Rostral margin rounded (Figures 1, 2, 4, 7, 10). Lamellae running laterally; shallow lamellar furrow (*l.l.f*) only discernible in proximity of *la.ti* (Figure 17); *la.ti* more



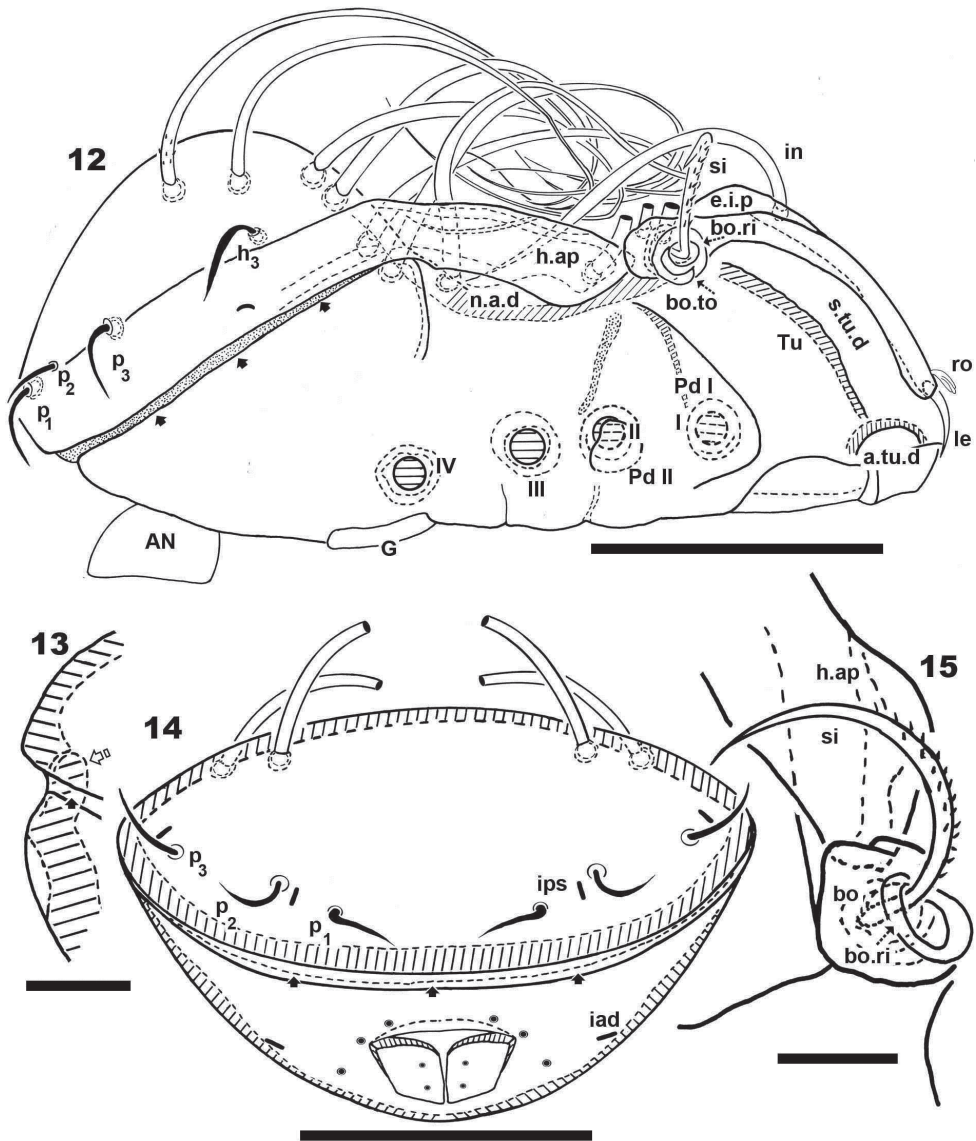
Figures 6–11. *Malgasodes curvisetus* Mahunka, 2000, adult. SEM observations. **6** lateral view **7** prodorsum, anterior part, lateral view **8** sensillus and anterior zone humeral apophysis **9** tarsus I, (*u*) seta, lateral view **10** rostrum and subcapitulum, frontal view **11** leg 1, segment I, genu. Notes: Abbreviations: see “Material and methods”. Scale bar: **6** = 100 μm ; **7**, **8**, **10** = 10 μm ; **10**, **9**, **11** = 1 μm .

or less triangular, small, sharply tipped (Figure 17). In frontal view (Figures 2, 10) the superior cornea of naso (*csn*) is clearly visible as a convex elevation situated anterior to the *ro* setal insertion; upward curving sensillus (*si*) uncinat with small barbs (Figure 2, 4, 6, 8, 12, 15)

Bothridium (*bo*), round–ovoid; bothridial ring (*bo.ri*) smooth, with bothridial tooth (*bo.to*), clearly visible (Figure 8, 12, 15).

Notogaster. In dorsal view, zone of *n.a.d* rectangular; posterior to this zone, ovoid (Figures 1, 4); in lateral view anterior part (zone of *n.a.d*) depressed, concave whilst rest of notogaster convex (Figure 6, 12); *d.sj* hardly discernible, narrow, curving slightly backward.

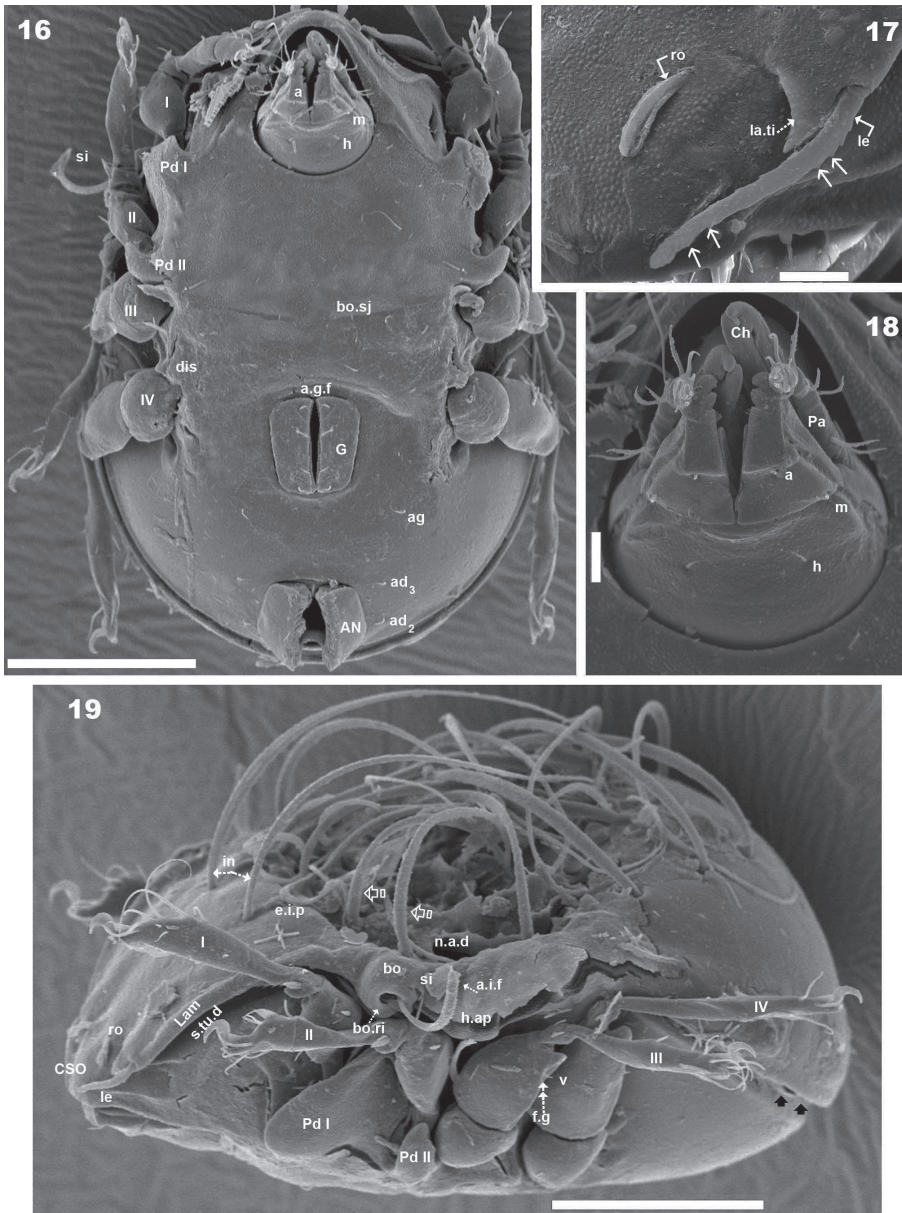
Notogaster smooth (Figures 1, 3, 6, 12). Anterior notogastral depression (*n.a.d*) ovoid, conspicuous, large, extending forward (Figures 1, 4, 6, 12).



Figures 12–15. *Malgasodes curvisetus* Mahunka, 2000, adult. Optic observations. **1** dorsal view **2** ventral view **3** frontal view. Notes: Abbreviations: see “Material and methods”. Scale bar: **12** = 250 μm ; **13** = 2 μm ; **14** = 200 μm ; **15** = 4 μm .

Circumgastric depression (*s.c*) present, hardly discernible (Figure 1, 3), situated at notogastral lateral setal insertion level (p_1 , p_2 , p_3 , h_3).

Fourteen pairs of notogastral setae, two pairs situated posterior to *n.a.d*, extending forward, exceeded *d.sj*; four pairs inside *n.a.d*, of which two pairs situated near *d.sj* extending backward (indicated in Figure 4, 19 with X); two pairs situated far from *d.sj*,



Figures 16–19. *Malgasodes curvisetus* Mahunka, 2000, adult. SEM observations. **16** ventral view **17** lamellae and lamellar tip **18** subcapitulum **19** lateral view, rotated. Abbreviations: see “Material and methods”. Scale bar: **16**, **19** = 100 μ m; **17**, **18** = 10 μ m.

extending forward, exceeding *d.sj* (one of them indicated in Figure 4, 19 with J); four pairs situated marginally to *n.a.d*, extending forward, exceeding *d.sj* and four pairs, situated marginally to notogaster, directing backward, these pairs we named *h₃*, *p₁*, *p₂*, *p₃* (Figures 1, 3, 4, 6, 12, 14, 19).

Lyrifissures difficult to observe; three pairs present, first pair situated at level of h_3 setae (Figure 12), another situated anterior to p_3 setae and ips situated between p_1 and p_2 . Lyrifissures not visible in SEM, only under optic observation (Figures 12, 14).

Humeral apophysis ($h.ap$) clearly discernible principally in lateral view (Figures 1, 4, 6, 8, 12, 19), antiaxially aligned irregular furrows ($a.i.f$) present, permitting concealment of si during protection mechanism deployment (Figures 6, 19, indicated by arrows). Cerotegumental layer often covering $h.ap$ (Figures 6, 8, 19). The $h.p$ and the posterior bothridial zone in the junction zone between both structures, posterior bothridial tip overlapping $h.ap$ anterior margin (Figure 6, 12, 19). Tectum border remarkable, not prolonged by a limbus, but by transverse cuticular structure (Figure 13 indicated by X) delimiting a space between notogastral and ventral shield (indicated by arrows. Figures 6; 12, 13, 19).

Lateral region. Tutorium (tu) clearly visible as a strongly curving cuticular thickening. Between lamellae and tutorium a deep supratutorial depression ($s.tu.d$) running parallel to both structures (Figures 6, 7, 12, 19). Bothridia cup-shaped with smooth bothridial ring ($bo. ri$); $bo.ri$ incomplete with bothridial tooth ($bo.to$) clearly visible (Figures 8, 12, 15, 19); sensillus (si) uncinat with small barbs, curving upward (Figures 8, 15) tip usually pointed, more coarsely barbed on lateral edge.

Lamellae with $la.ti$, short, “shark tooth-like” (Figures 7, 17); le setae sausage-shaped (Figure 17), roughly-spiculate surface, clearly visible (Figure 17 indicated by arrowh); ro phylliform, with rounded elevated central zone, delimited on each side by, depressed longitudinal furrow (Figure 17); $n.a.d$ well discernible due to transparency (Figure 12); two pairs of setae (probably c_1 , c_2) situated in the anterior part of $n.a.d$ and close to $d.sj$, (Figures 4, 6, 12, 19 indicated by X), observing $d.sj$, complicated by presence of cerotegument and setae, requiring observation from different angles. Two other pairs of setae situated inside $n.a.d$; first pair laterally and close to two anterior setae, at level of bothridia (Figures 4, 12, 19 indicated by J); the second pair hardly discernible, easily confused with other setae, situated marginally to $n.a.d$. Lateral view permitting clear understanding, of different setae directions and perceiving the complexity found at $n.a.d$ level (Figures 6, 12, 19).

Pedotectum I, prominent extended lamina. Pedotectum II, small polyhedral lamina, rounded edges. Humeral apophysis more or less triangular; basally slightly convex, immediately becoming concave; posterior bothridial zone overlapping anterior tip (Figure 12); aligned irregular furrows ($a.i.f$) delimited by rod-like cuticular structures (Figures 6, 19, indicated by arrow), crossing $h.ap$.

SEM observations made from two different lateral angles (Figures 6, 19) in order to clarify the relative position, shape and disposition of different prodorsal and notogastral structures and setae. In order to show positioning of legs during “legs folding process” specimens are shown with legs in place and alternatively with distended legs. Only one lyrifissure visible at level of h_3 setae Discidium not discernible. Only one depression, situated behind leg IV, used conceal tibia and tarsus (paraxial side) (Figure 6 indicated by X) during leg folding process (see Fernandez et al. 2013b).

Posterior view. Posterior view (Figure 14) clarifying position of marginal setae p_1 , p_2 , p_3 , lyrifissures and the two pairs of notogastral setae situated posterior to $n.a.d$,



Table 1. *Malgasodes curvisetus* Setae and Solenidia.

Leg I	Femur	Genu	Tibia	Tarsus	Claw
Seta	<i>d,(l),v</i>	<i>(l),v</i>	<i>d,(l),v</i>	<i>ft'',ε,(tc),(it),(p),(u),(a),s,(pv)</i>	1
Solenidia	-----	σ	-ϕ ₁ , ϕ ₂	----ω ₁ , ω ₂	
Leg II					
Seta	<i>da,dp,l',v</i>	<i>(l),v</i>	<i>d(v)</i>	<i>(pv),s,(a),(u),(p),(it),(tc),(ft)</i>	1
Solenidia	-----	-σ-	-ϕ-	ω ₁ , ω ₂	
Leg III					
Seta	<i>d,l',v</i>	<i>l'</i>	<i>(v)</i>	<i>ft',(pv),s,(a),(u),(tc),(p),(it)</i>	1
Solenidia	-----	-σ-	-ϕ-	-----0-----	
Leg IV					
Seta	<i>d,v</i>	<i>d,l'</i>	<i>v</i>	<i>ft'',(a),(pv),(tc),(p),(u),s</i>	1
Solenidia	-----	---0	--ϕ-	-----0-----	

unique pairs visible in posterior view. Lyrifissure *ips* can be uniquely identified on account of placement between setae *p*₁ and *p*₂; the other, probably *ih*, situated between *p*₃ and *h*₃.

In this position the zone between ventral and notogastral plates is easily discernible, separated due to particular tectal border (indicated in Figure 14 by ·).

Ventral region. Subcapitulum with three pairs of setae (*a*, *m*, *h*) clearly visible; insertion zone *m* and *a* setae simple, smooth (Figures 16, 18). Epimera hardly discernible; only *bo.sj* clearly visible as shallow furrow crossing the medial plane (Figure 16).

Apodemes *apo.1*, *apo.2*, *apo.sj* and *apo.3* clearly visible (Figure 5). In median zone, at level of *apo.1*, rounded more sclerotized structure visible (in optic observation), but smooth under SEM observation. Epimeral chaetotaxy 3-1-3-3.

Genital plate more or less similar in size to anal plate (Figure 5); anal plate small, sharply tipped (Figure 16); paraxial border of anal plates with small teeth (Figure 5, indicated by 5) on anterior third.

Anterior to genital plate a furrow (*a.g.f*) clearly visible. Four pairs of linear genital setae. Aggenital setae posterolaterally, posterior opening of genital border (Figure 5) situated at same level or slightly antiaxially to *ad*₃ setal insertion. Three pairs of adanal setae; small elongate bean-shaped lyrifissures *iad* clearly visible, situated antiaxially and far from *ad*₃. Two pairs of anal setae. Smooth surface between and lateral to genital and anal openings (Figure 16); depression at level of leg IV (involved in leg folding process. See lateral region). Short, curving, cuticular thickening behind acetabulum IV (Figure 5 indicated by X).

Legs. Legs presenting all characteristics observed in other Carabodidae, but lateral setae of genua are particular (Figure 11). The (*u*) pair of all tarsi are without barbs but rugous, particular (Figure 9).

All structures related to leg folding are present (Fernandez et al.2013a) and clearly visible (Figures 6, 12, 16, 19).

Setal formulae I (1-4-3-4-15-1) (1-2-2); II (1-4-3-3-15-1) (1-1-2); III (2-3-1-2-14-1) (1-1-0); IV (1-2-2-1-12-1) (0-1-0).

Remarks. Anterior part of *n.a.d* extending to *d.sj*, together with notogastral setae situated in this zone preventing clear observation. The *e.i.p.* is an elevated process situated not far from *d.sj*. The posterior part of *e.i.p* descending steeply at *d.sj* level. We consider *p.p.d* to be absent.

Two pairs of setae situated close to *d.sj* are probably *c₁* and *c₂* setae, but without immature stases it was impossible to establish with certainty.

Border of tectum in *Malgasodes* is unlike all others; in that it is not prolonged by a limbus, and that a space exists between the ventral plate and the notogaster.

Various inclinations in lateral view are provided to permit better understanding of the disposition of notogastral setae and the steeply descending posterior part of *e.i.p* towards *d.sj*.

Complementary description

Malgasodes hungarorum Mahunka, 2010

Figures 24–27

Remarks. Only one bleached specimen was available for study. The condition of this material was poor, for this reason a decision was made to add only characteristics and figures considered inadequate in the original description by Mahunka (2000). The ventral zone (text and figure) contained adequate information; some omitted aspects will be addressed in text. In contrast the dorsal and lateral descriptions and figures require redescription and new figures.

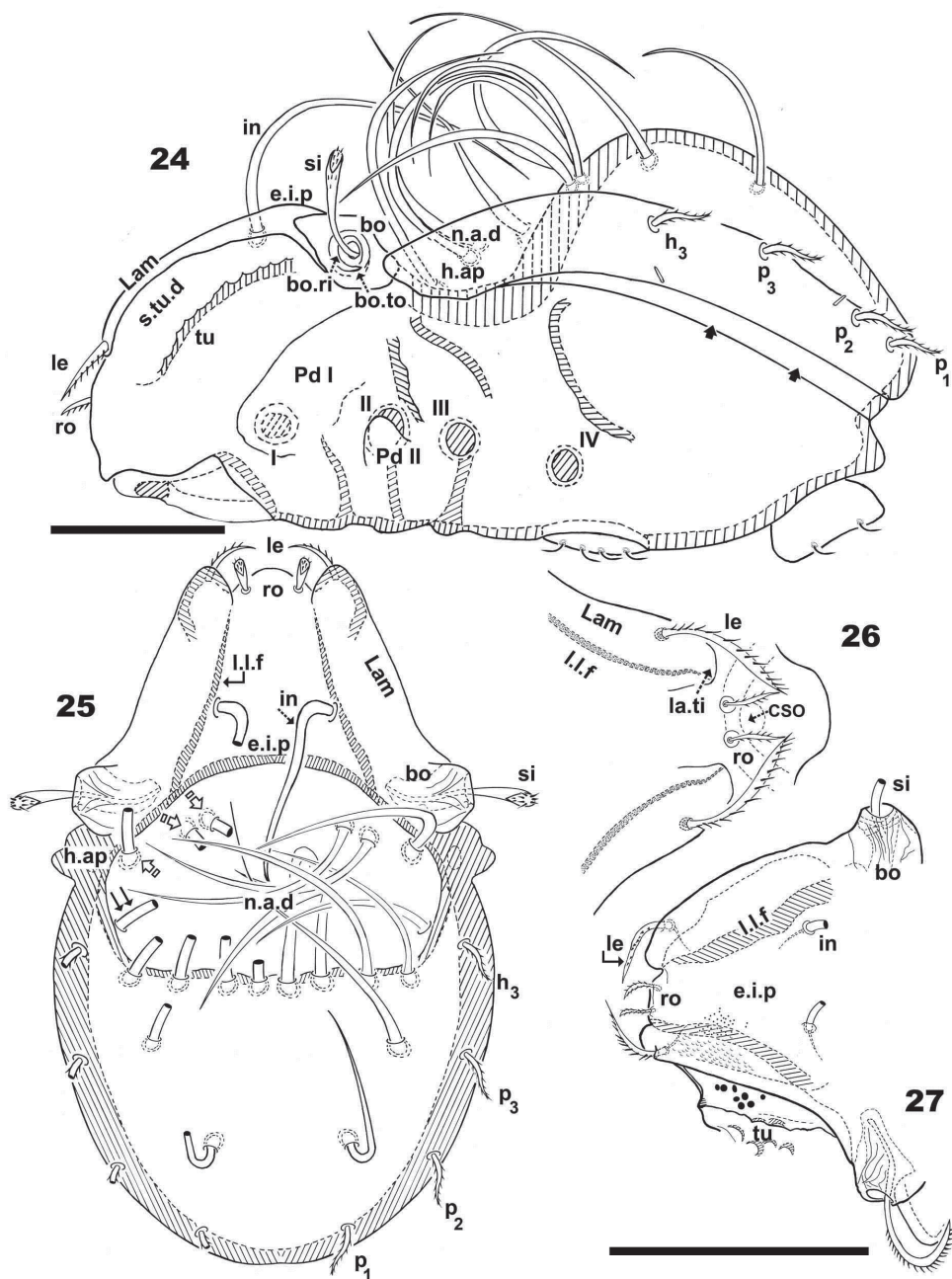
Diagnosis. Ovoid. Notogaster, prodorsum smooth; anterior zone *lam*, lateral body zone, small protuberances

Rostrum rounded to polyhedral. Complete elevated interlamellar process. Posterior prodorsal depression not present; *in* setae simple, medium length, situated on elevated interlamellar process, directing posteriorly; *ro* small, phylliform, slightly barbate, directing forward; *le* sausage-shaped, slightly barbate, directing forward; *in* > *le* > *ro*.

Lamellae laterally; shallow lamellar furrow well discernible dorsally; lamellar tip rounded to polyhedral. Superior cornea of naso clearly visible; sensillus uncinat, small barbs, curving upward; bothridial ring smooth, bothridial tooth present. Anterior notogastral depression well discernible, conspicuous; ovoid-shaped anterior zone, polyhedral posterior border. Circumgastric depression present, hardly discernible.

Fourteen pairs of notogastral setae, two pairs outside posterior notogastral anterior depression directing forward; four pairs inside notogastral anterior depression, three pairs near dorso-sejugal furrow, fourth pair distant; four pairs marginally to notogastral anterior depression; four pairs marginally to notogaster; two pairs lyrifissures present. Humeral apophysis easily discernible.

Tutorium strongly curving cuticular thickening; supratutorial depression clearly visible.



Figures 24–27. *Malgasodes hungarorum* Mahunka, 2000, adult. Optic observations. **24** lateral, slightly inclined view **25** dorsal view **26** prodorsum anterior part, dorsal view, inclined anteroposterior **27** prodorsum dorsal, inclined laterally. Abbreviations: see “Material and methods”. Scale bar: **24–25** = 60 μ m; **26, 27** = 55 μ m.

Pedotectum I, prominent extended lamina. Pedotectum II, small, polyhedral; two lyrifissures present; discidium not discernible; sejugal zone depressed; semicircular ridges at acetabulum IV level. Epimeral setae simple, fine; epimeric formulae 3-1-3-3; *Ic* small. Aggenital furrow present; anogenital region with ribs and crest; genital setae 4 pairs; aggenital 1 pair; anal 2 pairs; aggenital 3 pairs; *iad* present, situated far from anal opening.

Material examined. Paratype: Madagascar, Tomasina Province, Mananara Nord Biosphere Reserve and National Park, Lowland rainforest, NW slope Behafotra Hill; 250–300 m alt. 16°27. 1–3'S, 49°47.6'E. 14–15 August 1988. N° 9877. Leg. T. Pócs. Deposited in the Museum of Natural History, Geneva (MNHG).

Measurements: 301 µm × 198 µm.

Shape: ovoid (Figure 25).

Colour: Yellow to light brown; slightly shiny, when observed in reflected light.

Cerotegument. Not observed.

Integument. Notogaster and prodorsum smooth; anterior zone of *lam* and lateral body zone with small protuberances (Figures 24, 25, 27).

Prodorsum. Triangular to slightly polyhedral (dorsal view) (Figures 25, 27); curving in lateral view (Figure 24). Complete *e.i.p* (Figures 24, 25).

Posterior prodorsal depression (*p.p.d*) absent (Figures 24, 25). Setae *in*, medium length, situated on *e.i.p*, similar to long simple notogastral setae situated adjacent to and inside *n.a.d*, in all cases *in* setae directing backward and entangled with the cited notogastral setae (Figures 24, 25).

Three pairs of prodorsal setae (*in*, *ro*, *le*) (Figures 24–27), very different in shape and length: *in* > *le* > *ro*; *ro* setae small, phylliform, slightly barbate, directing forward; *in* setae inserted on *e.i.p* antiaxially to medial plane and slightly externally to *ro* insertion level, close to *l.l.f*; directing posteriorly, exceeding the prodorsal margin, extending to *n.a.d*; *le* setae sausage-shaped, slightly barbate, observation difficult (depending on position/angle of observation), laterally situated on lamellar apical zone, but far from *la.ti*, directing forward. Rostral margin rounded to polyhedral (Figures 25, 26).

Lamellae running laterally; *l.l.f* well discernible (Figures 25, 26, 27); *la.ti* rounded to polyhedral. Superior cornea of naso (*cs*) clearly visible as convex elevation situated anterior to *ro* setae insertion level (Figures 26); upward curving sensillus (*si*), uncinuate with small barbs (Figure 27).

Round-ovoid *Bo* with longitudinal ridges; *bo.ri* smooth, clearly visible *bo.to* (Figure 24).

Notogaster. Dorsal view: ovoid with polyhedral anterior zone of *h.ap*. (Figure 25). Lateral view, anterior part (zone of *n.a.d*) depressed, concave and rest convex (Figure 24); *h.ap* prominent expansion, large rounded tip (Figures 26, 27).

Notogaster smooth (Figure 25). Anterior notogastral depression (*n.a.d*) easily discernible, conspicuous, large, extending forward, ovoid anterior zone, polyhedral posterior border (Figure 25).

Circumgastric depression (*s.c*) present, hardly discernible, situated paraxially to lateral notogastral setal insertion (p_1 , p_2 , p_3 , h_3).

Fourteen pairs of notogastral setae, two pairs situated posterior to *n.a.d*, one far from posterior border of *n.a.d*; both pairs directing forward, not exceeding *d.sj*; four pairs inside *n.a.d*, three pairs situated near *d.sj* extending backward or laterally (indicated in Figure 25 with X); fourth pair situated far from *d.sj*, extending forward or laterally, not exceeding *d.sj* (indicated in Figure 25 with J); four pairs situated marginally to *n.a.d*, extending forward; four pairs, situated marginally to notogaster, directing backward, these four pairs are possibly named as h_3 , p_1 , p_2 , p_3 (Figure 25).

Lyrifissures difficult to observe; two pairs present, first pair situated at level of h_3 setae, the other situated between p_3 and p_2 (Figure 24).

Humeral apophysis (*h.ap*) clearly discernible (Figures 24, 25). Posterior bothridial zone overlapping anterior tip of *h.ap* (Figures 24, 25).

Remarkable border tectum, not prolonged by a limbus, space existing between the notogastral and ventral plates (Figures 24, indicated by arrows ·).

Lateral region. Tutorium (*tu*) clearly visible as a strongly curving cuticular thickening. Between lamellae and tutorium, deep supratutorial depression (*s.tu.d*) running parallel to both structures (Figure 24). Bothridia cup-shaped with smooth bothridial ring (*bo. ri*); *bo.ri* incomplete with *bo.to* clearly visible (Figures 24); *si* uncinat with small barbs, curving upward (Figure 27, pointed tip).

Lamellae with *la.ti*, round-polyhedral (Figures 26, 27); *le* setae sausage-shaped, rough-barbate surface, viewing angle slightly changing observation (see both sides of drawing Figure 27); *ro* small, philliform, barbate (Figures 26, 27); *n.a.d* clearly discernible; *d.sj* hardly visible. Lateral view greatly assists in understanding of different setae directions, and perceiving complexity found at *n.a.d* level (Figure 24).

Pedotectum I, prominent extended lamina, rounded apex. Pedotectum II, small polyhedral lamina, rounded edges. Humeral apophysis triangular; basally slightly convex and immediately concave; anterior tip overlapping posterior bothridial zone (Figure 24).

Only two pairs of lyrifissures visible at level of h_3 setae and between p_3 and p_2 . Discidium not discernible. Sejugal zone depressed. Semicircular ridges at level of acetabulum IV (Figure 24).

Ventral region. Well described by Mahunka (2000: page 89 and Figure 6) only adding: the *a.g.d* is clearly visible.

The comparison

Bovicarabodes Fernandez, Theron & Rollard, 2013a, *Afticarabodes* Fernandez, Theron & Rollard, 2013b, *Cavaecarabodes* Fernandez, Theron & Rollard, 2013c, *Congocephus* Balogh, 1958, *Malgasodes* Mahunka, 2000.

Introduction

Many years of study and previous publications lead us to the point where we are able to compare these genera. Several new collections with large numbers of specimens have become available, but it will take several years to describe this new material. A decision was made to first complete the comparison of the cited genera before commencing further descriptions.

In previous publications, we described *Bovicarabodes*, *Afticarabodes*, *Cavaecarabodes*, and studied and redescribed most of the species of *Congocephus*. All genera present several characteristics in common such as: notogastral anterior depression, posterior prodorsal depression, superior cornea of naso, elevated interlamellar process, notogastral setae situated around the notogastral anterior depression; humeral apophysis; anterior genital furrow. We observed two evolutive phenomena: regression and neotrichy in *Cavaecarabodes anouchkae* and *Congocephus germani*, respectively.

Malgasodes presents particular characteristics and some characters in common with genera mentioned above. Firstly we explain the situation of *Malgasodes*, after which we complete the comparison.

Malgasodes consists of only two species (Subias 2013) *M. curvisetus* Mahunka, 2000 and *M. hungarorum* Mahunka, 2000, both from Madagascar, described in the same with *M. curvisetus* as type species (Holotype and paratype deposited in Hungarian Natural History Museum, Budapest) and *M. hungarorum* (Holotype and 4 paratypes deposited in the Hungarian Natural History Museum, Budapest, and 1 paratype in the Musée d'Histoire Naturelle, Genève (MHNG)).

We studied specimens of both *M. hungarorum* (paratype) on loan from MHNG and *M. curviseta* unavailable from the Hungarian Natural History Museum, Budapest, but fortunately found in the Madagascar collection of Professor J-M Betsch (between 1968 and 1973), deposited in Museum National d'Histoire Naturelle, Paris, France (MNHN).

In the original description of *Malgasodes*, Mahunka (2000: 87) indicated: "Notogaster with a wide deep, roughly semicircular, hollow anteriorly, well framed laterally and posteriorly". "Fourteen pairs of notogastral setae: ten pairs long medially directed, recurved and four pairs short, phylliform, in marginal position. Of these 14 pairs, eight pairs arise around hollow, two pairs arise posteriorly and remaining four pairs present in posteromarginal position".

However, in Figure 1 (page 88) it is clear that four pairs of the eight indicated arise from and originate inside the *n.a.d* ("hollow" *sensu* Mahunka) and are not all situated around the *n.a.d*. In our studies we confirmed that four pairs are inside *n.a.d* (see redescription of *M. curvisetus* and *M. hungarorum*).

In the comparison with other genera Mahunka indicated "Its allies are in the genre *Congocephus* Balogh, 1958 and *Baloghodes* Mahunka, 1986. However, *Congocephus* is clearly distinguished from *Malgasodes* by the form of the ventral structure, mainly the ventral plate and the position of the lyrifissures *iad*. Species of the genus *Baloghodes* are characterized by the absence of the anteromedian hollow and covered lateral margin".

Table 2. Comparison between *Bovicarabodes*, *Afticarabodes*, *Cavaecarabodes*, *Congocephus*, *Malgasodes*.

	<i>Bovicarabodes</i>	<i>Afticarabodes</i>	<i>Cavaecarabodes</i>	<i>Congocephus</i>	<i>Malgasodes</i>
<i>n.a.d</i>	present	present	present	present	present
<i>p.p.d</i>	present	present	present	present	absent
Notogastral setae outside <i>n.a.d</i>	14 pairs	14 pairs	14 pairs	14 pairs	10 pairs
Notogastral setae inside <i>n.a.d</i>	0	0	0	0	4 pairs
Orthotrichy bideficient	present	present	present ³	present ¹	present
Notogastral setae identify	All	All	All	All	<i>p</i> ₁ <i>p</i> ₂ <i>p</i> ₃ <i>b</i> ₃
Notogastral setae setiform	0	0	0	1-2 pairs ²	10 pairs
<i>e.i.p</i>	present	present	present	present	present
Prodorsum	Paired horns and two cavities	Almost vertical; two ears	simple	simple	simple
Lyri fissures present	five pairs	five pairs	five pairs	five pairs	three pairs
Disposition notogastral setae	normal	normal	normal	normal	particular

1 *Congocephus germani* neotrichy situated at C setae alignment
2 *Congocephus germani* 8 pairs setiform setae, all situated at neotrichal level
3 *Cavecarabodes anouchkae* reduction in notogastral setae C, with only 12 pairs of setae

Mahunka only considered the ventral characteristics in *Congocephus* but there are other more important characteristics (see Table 2).
The comparison with *Baloghodes* is hard to understand as *Baloghodes* differs greatly from *Malgasodes*.

The posterior prodorsal depression

There are often small differences between immature stases of oribatids during ontogeny, and these differences obey precise rules, for example the number of genital setae is fewer in protonymph than in deuteronymph, which is fewer than in the tritonymph (3 pairs, 4 pairs and 5 pairs), but adult stases differ greatly from immature stases. Studies were not found on ontogenetic development in groups of Carabodidae where the posterior prodorsal depression is present in adult stases, but some exist for *Carabodes* (Grandjean 1949, Andre 1975, Bellido 1978, Ermilov 2011, Reeves 1992) and *Yoshiobodes* (Reeves 1997).
In 1949 Grandjean provided information on orthogenetic development of *Carabodes labyrinthicus*, while immature stases of the same species were studied by Andre in more detail in 1975. Evidently immature stases are very different to adults. Immature stases of Carabodidae are non-sclerotized with soft and fragile bodies. We searched through previous studies to determine if some characteristics could be found in the groups under study.
Species in these studies relate to genera without posterior prodorsal depressions (*p.p.d*), or notogastral anterior depressions (*n.a.d*) in adult stases, but there are very interesting structures on the immature prodorsum of *C. willmanni* Bernini, 1975 and *Y. irmayi* (Balogh & Mahunka, 1969) (Reeves 1997).

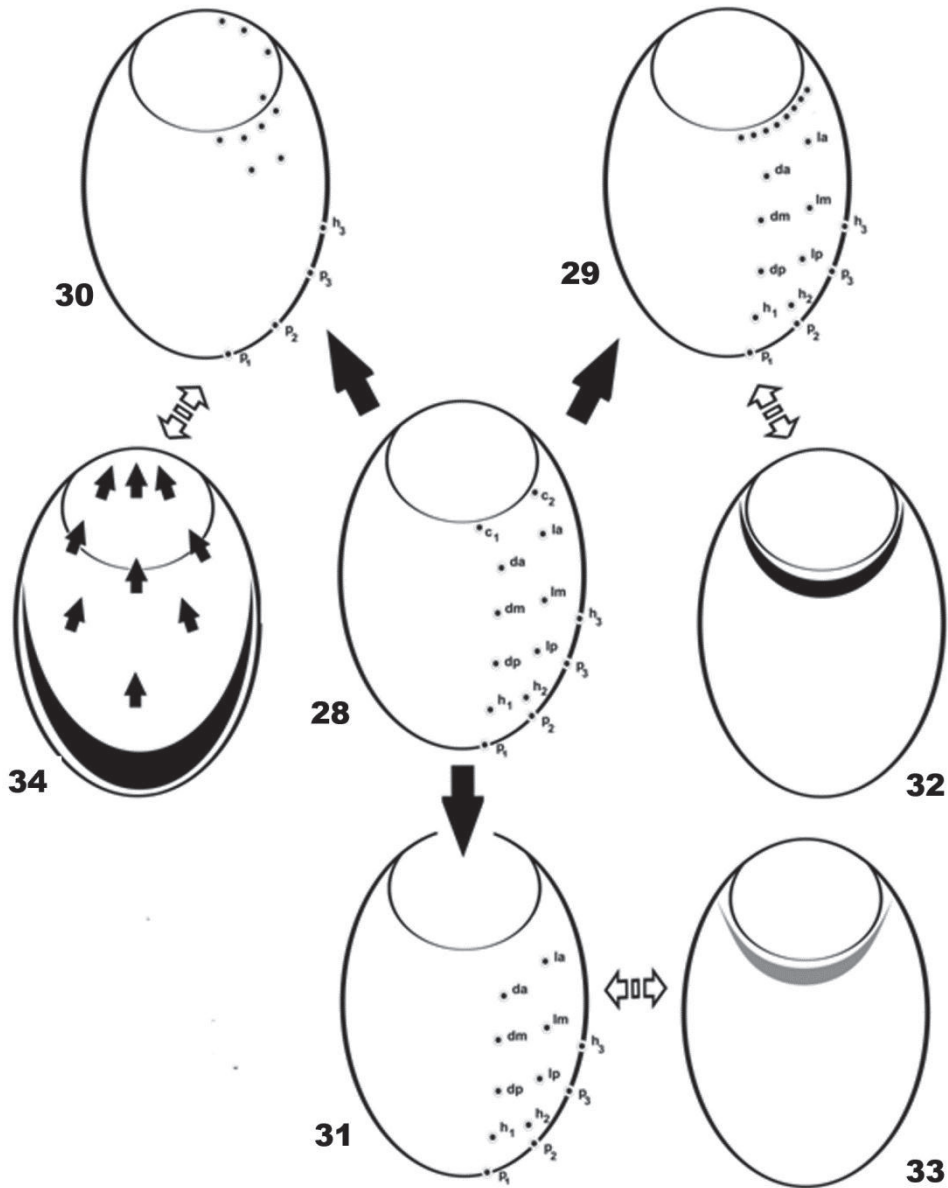


Figure 28–34. Setal distribution. **28** *Cavaecarabodes*, *Bovicarabodes*, *Aficarabodes*, *Congocepheus* **29** *Congocepheus germani* **30** *Malgasodes curvisetus* **31** *Congocepheus anouchkai* **32** neotrichal zone *Congocepheus germani* **33** regression area of setae *Congocepheus anouchkai* **34** migration process (with arrows) and area of marginal setae h_3, p_1, p_2, p_3 of *Malgasodes curvisetus* and *M. hungarorum*.

In *C. willmanni* Bernini, 1975 (Bellido 1978: 423) the prodorsum presents a foveate sclerite situated between lamellar and interlamellar setae (Figure 6, 7 in Bellido *op.cit*); this structure can be observed in the larva, but in the protonymph the

sclerite is clearly differentiated as a bowl-like structure, and in the deutonymph this zone acquires coloration (considered melanisation), and sclerotization (Bellido 1978: 423).

Reeves (1997), indicated (page 320) “The scalloped edged depression on the prodorsum of protonymphs, deutonymphs and tritonymphs appears similar to the foveate sclerite found in immature described by Bellido (1978) of *Carabodes willmanni* Bernini.”

In other cases, such as *Carabodes subarticus* (Ermilov 2011 – in russian) the figures of immatures are very deformed, and the presence of the sclerotized field between interlamellar and lamellar setae is only indicated in the description of the deutonymph. On figures 3.1 and 4.1, a structure exists between the interlamellar setae and posterior to the lamellar setae, probably the structure referred to by Bellido and Reeves.

The descriptions of Andre (1975) and Reeves (1992) do not show this structure in immature stases. Bellido (1978: 424) indicated that the existence of this prodorsal microsclerite permits easy differentiation between *C. willmanni* and *C. labyrinthicus*.

We were only able to study adults, not having immatures available, but we consider that the posterior prodorsal depression is probably the same depression found on the immature stases of *Carabodes* and *Yoshiobodes*, and in adult stases on *Congocephus*, *Bovicarabodes*, *Cavaecarabodes* and *Afticarabodes*.

Another important element is that the prodorsal structure of the prodorsal zone in *Ysiobodes* was not discussed by the author in text (Figure 9 dorsosejugal region, page 321), similar to *Carabodes interruptus* (Fig. 26) and *Carabodes pentasetosus* (Fig. 34) (in Reeves 1992) where a depression, probably a prodorsal posterior depression of reduced size, exists in the medial region of the prodorsum of the adult, but for these two species no reports on ontogenetic stages exist.

The anterior notogastral depression

All genera cited in this comparison present an anterior notogastral depression and a particular relation between this depression and notogastral setae.

In genera *Bovicarabodes*, *Afticarabodes*, *Cavaecarabodes* and *Congocephus* notogastral setae are related to the anterior notogastral depression, but setae are never found inside it; in the case of *Malgasodes*, the situation is very different and four pairs of setae are observed inside the *n.a.d.*

The presence of the notogastral anterior depression and the setal disposition around and/or inside it, involves a very interesting problem overlooked in descriptions of several genera of the family Carabodidae.

In the following genera setae are never found inside the *n.a.d.*: *Bovicarabodes*, with *B. deharvengi*, *B. levyi* and *B. fort-dauphiny*; *Afticarabodes*, with only *A. anjavidilavai*; *Cavaecarabodes* with *Ca. pulchritudo*, *Ca. hauseri* (Mahunka 1989), *Ca. orientalis* (Mahunka, 1987), *Ca. anouchkae*; *Congocephus*, with *Co. heterotrichus* Balogh, 1958; *Co. germani*; *Co. gabonensis* Fernandez, Theron, Rollard & Tiedt, 2013; *Co. involutus* Mahunka, 1997; *Co. ektactesi* Fernandez, Theron, Rollard & Tiedt, 2013; and *Co. taurus* Balogh, 1961.

Of these *Co. germani* is unique in presenting significant neotrichy (20 pairs of notogastral setae), but setae surround the *n.a.d.*, and are never observed inside it.

In *Malgasodes*, the situation is very different. The notogastral anterior depression is present, but the distribution of notogastral setae is unlike all others, with a particular distribution: four pairs of marginal setae p_1 , p_2 , p_3 and h_3 in the normal position; four pairs marginal to and two pairs posterior to *n.a.d.*; finally four pairs inside *n.a.d.*, of which two pairs are close to *d.sj*, these are probably c_1 and c_2 setae. Lyrifissure numbers are reduced.

The disposition of the notogastral setae is very particular, demonstrating displacement of most of the setae directing to the *n.a.d.* (Figure 34), and making accurate notation of the setae near impossible.

We have not been able to advance further, as ontogenetic studies are required; but this displacement process is found near the dorsosejugal furrow (*dis* or *das*) and this may indicate a very interesting evolutionary problem related to segmentation of the opisthosoma, the segmentary origin of the prodorsum and with terminology of the body in general.

Notogastral setae

The genera *Bovicarabodes*, *Afticarabodes*, *Cavaecarabodes*, *Congocephus* and *Malgasodes* display holotrichy bideficiency (14 pairs of setae) (Figure 8), while in *Malgasodes* the setal distribution is very particular (Figure 30). In some species of *Congocephus* and *Cavaecarabodes*, the evolutionary process is very interesting; in the case of *Congocephus* we studied six species: *Co. heterotrichus* Balogh, 1958; *Co. germani* Fernandez, Theron & Rollard, 2014; *Co. gabonensis* Fernandez, Theron, Rollard & Tiedt, 2013; *Co. involutus* Mahunka, 1997; *Co. ektactesi* Fernandez, Theron, Rollard & Tiedt, 2013; *Co. taurus* Balogh, 1961, and several particularities were observed, as discussed in Fernandez et al. (2014). The neotrichy found in *Co. germani* (Figure 29) with a well-established neotrichous territory (Figure 36) (see Fernandez et al. 2014) and the distribution of setae around the border of *n.a.d.* is very interesting. In this case setae involved in neotrichy are evidently the alignment *c*.

Another very interesting condition is the reduction process found in *Cavaecarabodes anouchkae* (Figure 31) where there are only twelve pairs of setae, with reduction of c_1 and c_2 setae. The area of setal reduction is indicated in Figure 33.

A completely different situation occurs between the genera *Congocephus* and *Malgasodes*.

In *Congocephus* the setae involved in neotrichy are easily identified by a “neotrichous territory” that follows the border of *n.a.d.* However, in the case of *Malgasodes*, a reduction process has occurred where two or three lyrifissures have disappeared. A particular process exists where the setae are directed towards the *n.a.d.* (Figure 34), and a large zone of the notogaster is therefore void of setae due to setal migration. Four pairs of setae migrate to inside the *n.a.d.*, with two pairs extending to near the *d.sj* furrow; four pairs are found near the border of *n.a.d.*; two pairs situated slightly posterior to

n.a.d and four pairs are situated in the posterior marginal zone of notogaster. Despite no modification in the number of setae (always orthotrichy bideficiency) the migration process impedes identification of the setae involved in the process; most probably the two pairs situated near *d.sj* furrow are c_1 and c_2 , but it is impossible to affirm. The displacement of setae does not involve all of them, because setae p_1 , p_2 , p_3 and h_3 , situated on the marginal zone, are not affected by this process. More complex still, the setae involved are probably from two different segments. The migration process found in *Malgasodes* is very remarkable and necessitates further ontogenetic study.

Acknowledgement

This work is based on research supported in part by the National Research Foundation of South Africa (UID) 85288. Any opinion, findings and conclusions or recommendations expressed in the material are those of the authors and therefore the NRF does not accept any liability in regard thereto.

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Description of the male of *Tityus kuryi* Lourenço, 1997 and notes about males of *Tityus stigmurus* (Thorell, 1877) and *Tityus serrulatus* Lutz & Mello, 1922 (Scorpiones, Buthidae)

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Academic editor: Jose O. Camara | Received 26 November 2013 | Accepted 22 July 2014 | Published 15 August 2014

<http://zoobank.org/AC7E6851-6CA1-4552-9943-05916C0A9FB9>

Citation: Santos MDS, Porto TJ, Lira-da-Silva RM, Brazil TK (2014) Description of the male of *Tityus kuryi* Lourenço, 1997 and notes about males of *Tityus stigmurus* (Thorell, 1877) and *Tityus serrulatus* Lutz & Mello, 1922 (Scorpiones, Buthidae). ZooKeys 435: 49–61. doi: 10.3897/zookeys.435.6694

Abstract

The male of *Tityus kuryi* Lourenço, 1997 is described for the first time. Despite being very similar to the female, the male presents more robust metasomal segments. Additionally, the distribution of the sexual populations of another two species of the *T. stigmurus* complex is reported herein: *T. serrulatus* Lutz & Mello, 1922 and *T. stigmurus* (Thorell, 1877). Males of *T. serrulatus* were, until now, restricted to the Minas Gerais State (Southwestern region of Brazil), and with new records reported here, its known distribution now encompasses the Northeastern region of Brazil. Males of *T. stigmurus* were previously recorded only for two municipalities in the State of Bahia, and here we present eight new records for Bahia State and one for Pernambuco State. We present a key to related species of the *T. stigmurus* complex based on morphology and coloration pattern.

Keywords

Sexual population, scorpions, *Tityus*, Brazil

Introduction

The description of males in population of scorpions is an important contribution, not only as regards taxonomic knowledge of the species, but also to enable understanding of its reproductive strategy. *Tityus kuryi* Lourenço, 1997 was described based on a single adult female collected in Palmeiras Municipality, in the Chapada Diamantina region, Bahia State, Brazil (Lourenço 1997). Although this species has previously been described, the male has not been described yet. In the last taxonomic review, Souza et al. (2009) included *T. kuryi* in the *Tityus stigmurus* complex, together with other five related species: *Tityus aba* Candido, Lucas, Souza, Diaz & Lira-da-Silva, 2005; *T. martinpaechi* Lourenço, 2001; *T. melici* Lourenço, 2003; *T. serrulatus* Lutz & Mello, 1922 and *T. stigmurus* (Thorell, 1887). This was due to the fact that they share the spinoid granules of the posterior dorsal region of the metasomal segments III and IV (Souza et al. 2009).

The two more widely distributed species from the *Tityus stigmurus* complex are parthenogenetic: *T. serrulatus* and *T. stigmurus* (Matthiessen 1962, Ross 2010). Both species are considered scorpions of medical importance (Brasil 2009). Despite their recognized asexual reproductive strategy, especially observed in urban areas, sexual populations have been recognized in Brazil, where males were described (Souza et al. 2009). Males of these two species were first reported by Lourenço and Cloudsley-Thompson in 1999 stating sexual populations in Minas Gerais and Pernambuco states. In the last review of the *T. stigmurus* complex, Souza et al. (2009) redescribed the males of *T. serrulatus* and *T. stigmurus* with greater number of details, especially in relation to dimorphism. These last authors based their study on specimens of *T. serrulatus* from Espinosa Municipality, Minas Gerais State, and on specimens of *T. stigmurus* from Camaçari and Paulo Afonso Municipalities, Bahia State. As far as we know, these are the only published records of males from both species.

In this paper, we describe the male of *T. kuryi* and report new records of *T. serrulatus* and *T. stigmurus* males, widening the known distribution of their sexual populations.

Materials and methods

Specimens of *Tityus kuryi* (n = 9), *T. serrulatus* (n = 1595) and *T. stigmurus* (n = 380) present in the scientific collection of the “Museu de Zoologia da Universidade Federal da Bahia (MZUFBA)” were analyzed. Along with these, another 280 specimens of *T. stigmurus* present in the reference collection of the “Centro de Informações Anti-veneno do Estado da Bahia” (CIAVE), Health Department of Bahia State, were also studied. Of the nine *T. kuryi* examined, four of them were kept in captivity for a year and a half (August 2009 to February 2011), a fact that allowed us to identify the spermatophore and to confirm the presence of two males.

The measurements were obtained following the methodology of Sissom et al. (1990) and using a digital Starrett 727 caliper. Trichobothrial notations follow Va-

chon (1974) while morphological terminology mostly follows Hjelle (1990), except for pedipalp carinae (Stahnke 1970). Observations of the morphology were made using a LEICA Z4 stereomicroscope. The photos of the specimens were taken with a Nikon D7000 camera, Micro Nikkor 85mm and Micro Nikkor 105mm lenses. The photos and measurements of the hemispermaphore were taken using the software program Motic Images 2000 version 1.2 by means of a PC connected to a Motic Digital stereomicroscope SMZ 168. The map of geographic distribution was produced with the ArcGis 10.0 software.

The males of *Tityus serrulatus* and *T. stigmurus* were identified based on observation of the external morphological characteristics, as diagnosed by Souza et al. (2009). The identification of the male of *T. kuryi* was based on observation of the courtship behavior, copulation and deposition of spermatophore (MZUFBA 2569), carried out in captivity occurred in May 2010. The hemispermaphore here described was dissected and deposited in the arachnid collection (MZUFBA 2570).

Abbreviations

- MZUFBA** Museu de Zoologia da Universidade Federal da Bahia (Zoology Museum of the Federal University of Bahia), Salvador, Bahia, Brazil.
- CIAVE** Centro de Informações Anti-veneno do Estado da Bahia (Anti-Poison Information Center of Bahia), Salvador, Bahia, Brazil.

Taxonomy

Family Buthidae C. L. Koch, 1837

Genus *Tityus* C. L. Koch, 1836

***Tityus kuryi* Lourenço, 1997**

Figs 1–14; Table 1

Material examined. Brazil, Bahia State, Palmeiras Municipality, Vale do Capão, 12°37'04"S; 41°29'20"W, 850 m, 24/XII/2006 (T.J. Porto leg.), adult male (MZUFBA 2569); Brazil, Bahia State, Palmeiras Municipality, Vale do Capão, 12°37'11"S; 41°29'23"W, 850 m, 24/XII/2006 (T.J. Porto leg.), adult male (MZUFBA 2570); Brazil, Bahia State, Palmeiras Municipality, Vale do Capão and Cachoeira da Fumaça, 12°31'44"S; 41°33'32"W, 04/VI/1999, 23/II/2007 and 17/VII/2009 (C. M. Pinto-Leite & G. Carvalho leg.), five adult females (MZUFBA 1000, 1602, 2166, 2505, 2529); Brazil, Bahia State, Ibicoara Municipality, 13°24'4"S; 41°16'5"W, I/2005 and VII/ 2011, two adult females (MZUFBA 2451, 2572).

Diagnosis. Scorpion of medium to large size, ranging from 55 to 78mm in total length. General coloration dark reddish with blackish spots on the pedipalps, legs,

lateral surfaces of mesosomal tergites and ventral submedian carinae of all metasomal segments, as well as transversal blackish spots on the posterior margin of sternites. Carinae moderately to strongly marked; granulations moderately to weakly marked. Fixed and movable fingers with 16–17 oblique rows of granules. Pectines with 24–25 teeth in males, 23–26 in female. Secondary sexual dimorphism evident.

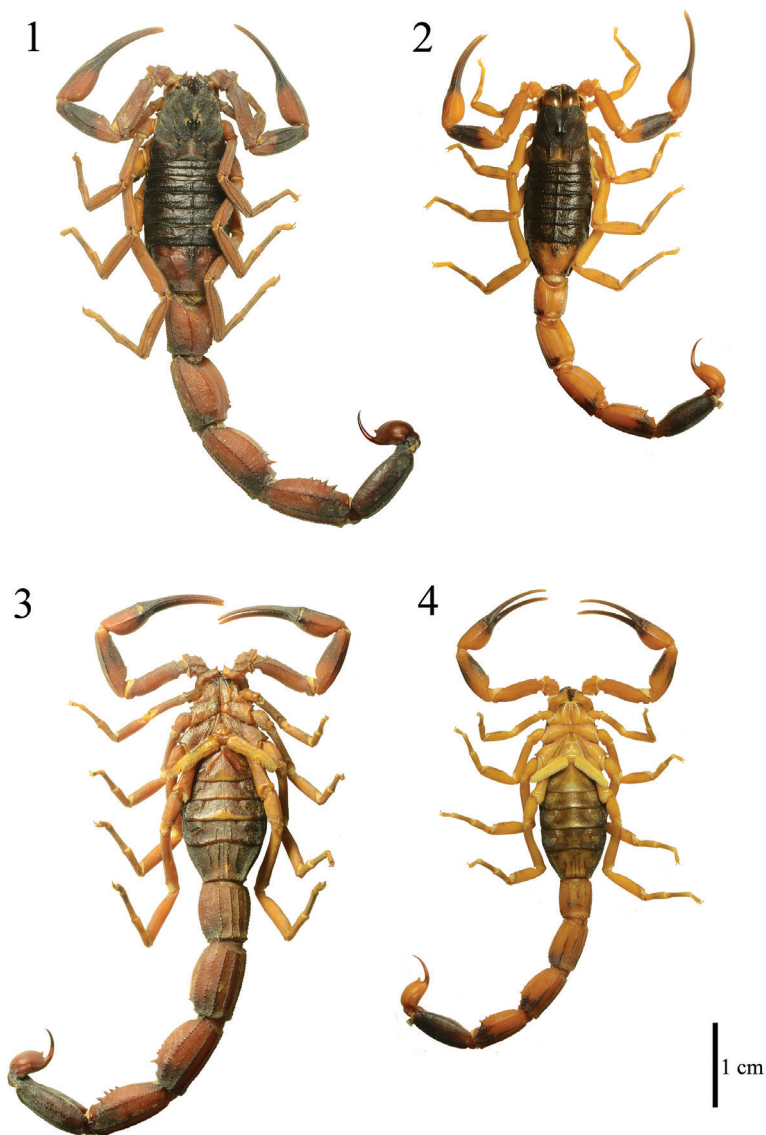
Comparisons with related species. *Tityus kuryi* Lourenço, 1997, belongs to the “*Tityus stigmurus*” species complex. The male of *T. kuryi* can be distinguished from the other males of the species complex, particular from *T. aba*, *T. stigmurus* and *T. martinpaechi*, by the absence of three longitudinal dark brown stripes on mesosomal tergites. Furthermore, in *T. aba* and *T. martinpaechi*, the pedipalp of the males is much thinner than of females, which also occurs in *T. melici* although there is no metasomal dimorphism in it (Souza et al. 2006, Souza et al. 2009). *T. kuryi* show pedipalps with no dimorphism (Figs 1–4). However, the male metasoma is more robust than the female, the same pattern of differentiation that can be observed in other species of the *T. stigmurus* complex, such as *T. serrulatus* and *T. stigmurus* (Souza et al. 2009).

Key to related species of the *T. stigmurus* complex

- 1 Metasomal segments III and IV without or with 1 to 3 granules modified as spines.....2
- Metasomal segments III and IV with 5 to 7 granules modified as spines.....5
- 2 Longitudinal dark stripes over tergites present3
- Tergites densely pigmented, without longitudinal stripes.....*Tityus melici*
- 3 One longitudinal dark stripe evident over tergites.....*Tityus stigmurus*
- Three longitudinal dark stripe evident over tergites4
- 4 Prosoma predominantly dark, pedipalps and legs without spots, pectines with 25–25 teeth*Tityus aba*
- Prosoma with dark inverted triangle, pedipalps and legs pigmented, pectines with 23–23 teeth*Tityus martinpaechi*
- 5 Coloration dark reddish, pedipalps and legs pigmented*Tityus kuryi*
- Coloration yellowish, pedipalps and legs without spots.....*Tityus serrulatus*

Description. Based on male MZUFBA 2569.

Coloration: Reddish brown with numerous dark areas (Fig. 1). Carapace dark with some light-brown areas (Fig. 5). Ocular tubercle dark. Mesosoma dark in tergite VI, tergite VII with a darker central region and lighter red-brown lateral region (Fig. 1); metasomal segments I–IV reddish brown with dark areas posteriorly in the lateral region and on the submedian ventral carinae (Figs 1 and 3); a dark spot occupying almost the entire segment V (Fig. 12). Telson: vesicle reddish brown, lighter than the metasomal segment V, with two small spots at the base; aculeus with dark spots at the base, red-brown medially and blackened distally (Fig. 12). Coxosternal region yellow with black spots in the coxapophyse I and II (Fig. 3); sternite III light brown, sternites IV–VI darker with the posterior medial region light brown, sternite VII darker with



Figures 1–4. *Tityus kuryi*. Male (MZUFBA 2569 - Palmeiras, Bahia, Brasil): dorsal (1) and ventral (3) views. Mature female (MZUFBA 2451 - Ibicoara, Bahia, Brazil): dorsal (2) and ventral (4) views.

medially light brown T-shaped spots (Fig. 3). Chelicerae dark with a light brown base; apex of the fingers brown. Pedipalps reddish brown with dark spots in the patella (Figs 9–10) and chela (Figs 7–8); fingers generally dark but distally light brown. Legs light brown with dark spots on tibia and tarsi (Fig. 1).

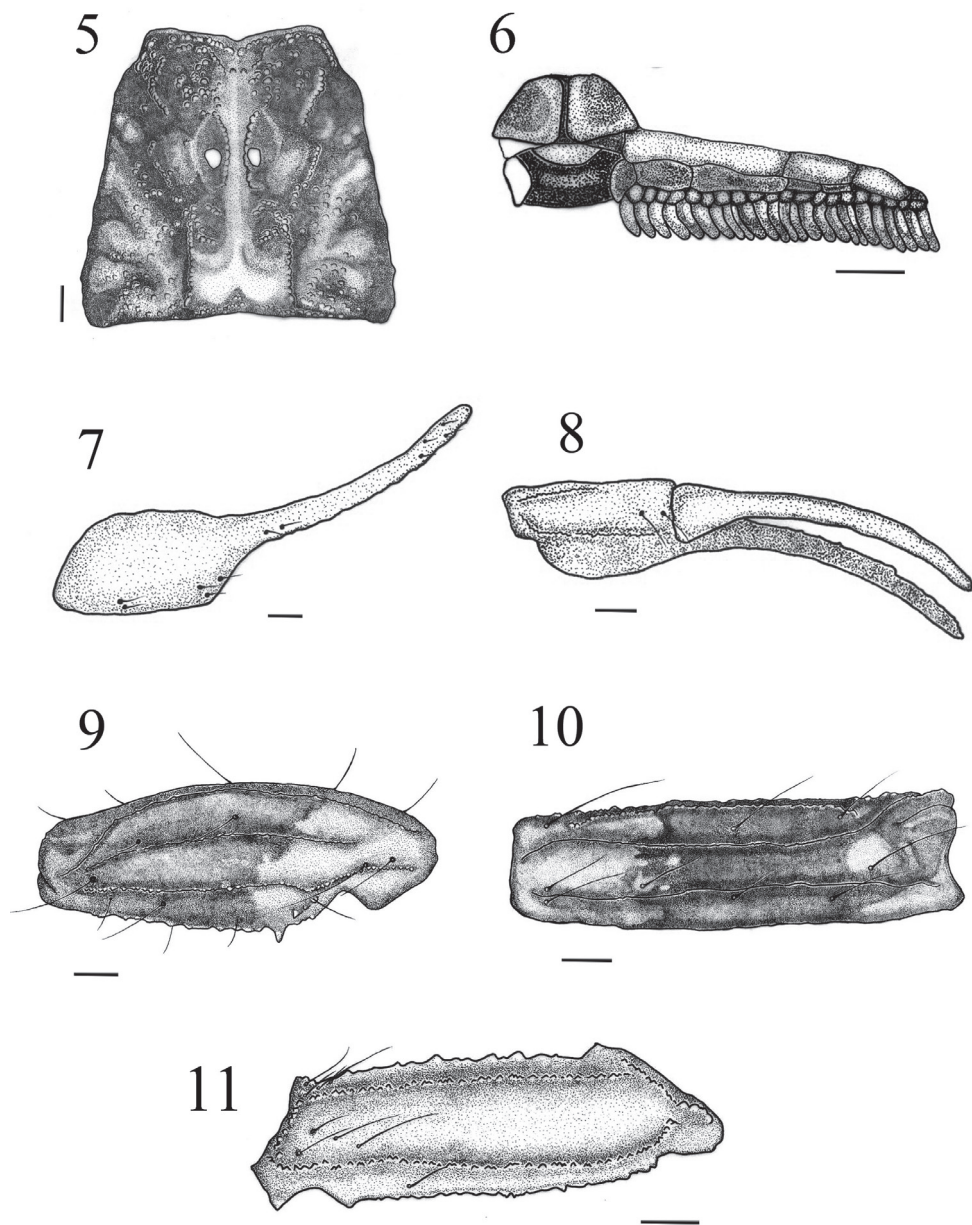
Morphology: Carapace: anterior margin with a weak median concavity (Fig. 5); median ocular tubercle situated anterior to the center of the carapace and median eyes

Table 1. Measurements (in mm) of two males and seven females used to investigate the sexual dimorphism in *Tityus kuryi*.

	Males		Females						
MZUFBA number	2569	2570	2451	2505	2529	2572	1000	1602	2166
Total Length	72.9	72.9	60.2	59.2	58.5	60.8	67.6	71.5	78.1
Carapace									
Length	8.6	8.5	8.0	6.7	7.2	8.1	8.2	8.1	8.3
Anterior width	5.5	5.9	5.0	5.0	5.2	5.2	4.3	4.6	4.6
Posterior width	7.8	9.1	7.7	6.7	7.4	7.1	9.0	8.8	8.8
Metasoma									
Segment I (length)	7.0	7.9	5.9	4.4	5.4	5.2	5.8	5.5	6.0
Segment I (width)	6.9	6.3	4.6	4.1	4.4	4.3	5.0	5.0	4.8
Segment II (length)	9.5	9.1	6.9	6.2	6.5	6.6	6.8	7.1	7.0
Segment II (width)	7.0	6.8	4.6	4.2	4.4	4.5	5.0	5.1	4.8
Segment III (length)	10.2	10.1	7.7	6.8	7.0	8.2	7.5	7.6	7.6
Segment III (width)	7.0	6.	4.9	4.4	4.3	4.7	5.1	5.1	5.0
Segment IV (length)	10.8	10.7	8.7	7.7	7.9	4.6	8.2	8.3	8.1
Segment IV (width)	6.5	6.7	4.6	4.2	4.3	8.2	5.5	5.1	5.0
Segment V (length)	10.6	10.4	8.7	8.4	8.3	9.1	9.5	8.8	9.1
Segment V (width)	5.7	5.8	4.2	4.0	4.1	4.2	4.6	4.1	4.5
Vesicle									
Length	8.5	8.7	8.0	5.9	7.3	6.9	6.8	8.2	8.3
Depth	2.5	2.4	2.7	1.5	1.1	2.6	2.7	2.7	2.7
Pedipalp									
Femur (length)	8.1	8.4	7.5	6.5	7.6	6.6	8.2	7.6	7.6
Femur (width)	2.2	2.2	2.0	1.8	1.9	1.8	2.2	2.5	2.3
Patella (length)	9.2	9.0	8.5	7.8	7.5	8.4	8.2	8.0	8.2
Patella (width)	2.8	2.9	2.8	2.4	2.8	2.9	3.2	3.2	3.2
Chela (length)	16.2	16.0	14.5	13.4	13.5	14.3	14.3	14.3	14.3
Chela (width)	3.0	3.0	2.9	2.7	2.7	2.9	3.1	3.1	3.1
Movable finger (length)	10.5	9.6	9.6	8.5	8.7	9.2	9.7	9.7	9.7

separated by more than one ocular diameter. Three pairs of lateral eyes; median ocular carina moderate with medium granules (Fig. 5); anterior median furrow moderately deep. Moderately granular.

Mesosoma: Tergites moderately granular with larger granules in the posterior region; presence of median carinae in all tergites. Tergites I–II with reduced carinae; in the tergites III–IV the carinae occupy the distal half and begin bifurcated and finish merged; tergite VII pentacarinate; transversal carinae present in all tergites. Pectines: pectinal teeth 24–25, basal middle lamellae of pectines not dilated (Fig. 6). Sternites weakly granular; a clear triangular zone in the posterior region of the sternite III and a reduced smooth and shiny slightly expanded triangular zone in the posterior region of the sternite V (Fig. 3). Sternite VI with two short median carinae occupying the distal half. Sternite VII with five carinae, two parallel submedian, occupying the entire sternite with a small carinae between them, and two lateral carinae restricted to the central region.



Figures 5–11. *Tityus kuryi* (male). **5** Carapace **6** Pectines **7–8** Chela, dorsal external and ventral views **9–10** Patella, dorsal and external views **11** Femur, dorsal view. Scale bars= 1 mm.

Metasoma: Metasomal segments: I with ten complete paired carinae (ventral submedian, ventral lateral, lateral inframedian, lateral supramedian and dorsal lateral with adjacent granules, the dorsal lateral has one spinoid posterior granule) (Fig.12); II with eight complete paired carinae (inframedian lateral carinae incomplete on anterior

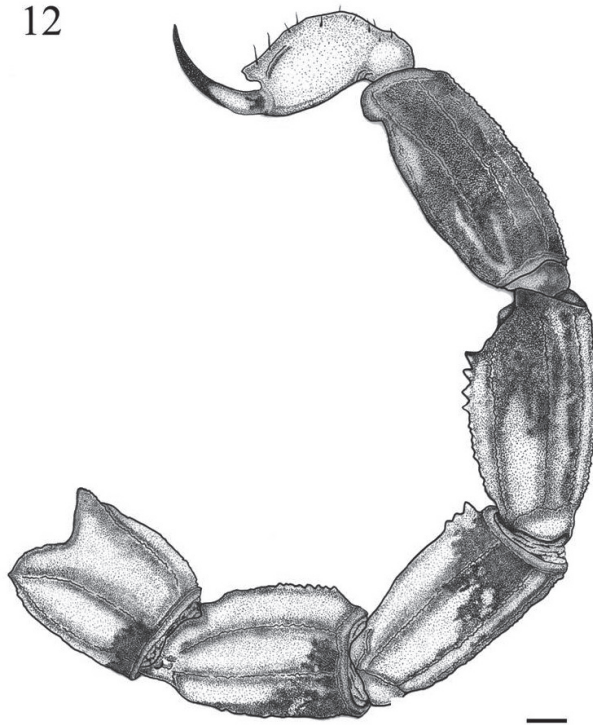
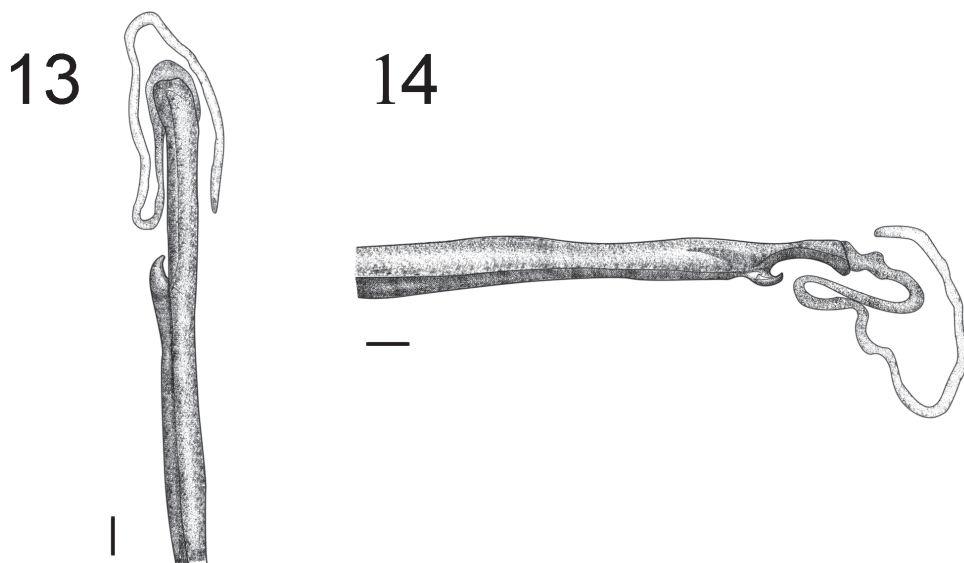


Figure 12. *Tityus kuryi* (male): Lateral views of the metasoma and telson. Scale bars= 1 mm.

third and present sparse granules; others are complete with adjacent granules; dorsal lateral with one spinoid granule) (Fig.12); III with eight complete paired carinae (inframedian lateral carinae absent; others complete with adjacent granules, the dorsal lateral with three spinoid posterior granules) (Fig.12); IV with eight complete paired carinae (inframedian lateral carinae absent; others are complete with adjacent granules; dorsal lateral with four spinoid posterior granules) (Fig.12) ; V with five complete carinae with uniform and adjacent granules (inframedian lateral carinae and dorsal lateral carinae absent; two complete paired carinae: ventral submedian and ventral lateral; one ventral median carina); intercarinal surface moderately granular (Fig.12). Telson: vesicle with five carinae (four of which vestigial and only the ventral well defined); aculeus long and strongly curved; subaculear tooth strong and romboid with two small dorsal teeth (Fig. 12).

Chelicerae: Dentition as defined by Vachon (1963) for the family Buthidae.

Pedipalp: (Figs 9–11) femur with 5 carinae, the dorsointernal, dorsoexternal and externomedian carinae present median granules; ventrointernal with smaller granules and internomedian with larger granules; patella with 7 carinae, the dorsoexternal, internomedian, ventrointernal and dorsomedian carinae present median and adjacent granules; internomedian with a proximal spinoid granule (Fig. 9); dorsoexternal, externomedian and ventroexternal with small and continuous granules; chela with 9



Figures 13–14. Hemispermaphore of *Tityus kuryi* (male MZUFBA 2570; Palmeiras, Bahia, Brazil): dorsal (1) and lateral (2) views. Scale bars= 1 mm

carinae of which the dorsoexternal, dorsal secondary, dorsointernal, ventrointernal, internomedian, ventroexternal, digital, subdigital and ventromedian, all with small and continuous granules; all pedipalp surfaces moderate to weakly granular. Movable fingers with 17–17 oblique lines of granules. Trichobothriotaxy: ortobothriotaxy A– α (Vachon 1974, 1975).

Hemispermaphore: Flagelliform, long and narrow, measuring approximately 13.5 mm, general color light brown; the trunk is trough-shaped; the flagellum is half the width of the trunk and approximately the same length (Fig. 13). Presence of three distal lobes: basal lobe, internal lobe and external lobe. The basal lobe is hook-shaped, protruding internally or externally; the internal lobe extends up to the base of the basal lobe flagellum, the external lobe extends from the medial basal lobe to the posterior third of the internal lobe (Fig. 14). The basal and external lobes are blackened.

Sexual dimorphism: Despite being similar to the females with regard to the coloration pattern and morphological details of the species (Figs 1–4), the male of *T. kuryi* presents metasomal segments 1.5 time more robust than those of the females (Figs 1–4; Table 1).

Distribution. Known only from the Chapada Diamantina region, Bahia State, Brazil.

Variation. The male of *T. kuryi* is usually larger than the female (male: 72.93–72.95 mm; female: 58.54–78.03mm) and pectinal tooth counts varied as follows: 24–25 teeth in males and 23–26 in females. The number of principal rows of granules varied from 16–17 in both sexes. The spinoid granules on the posterior end of the dorsal lateral carinae of metasomal segments III and IV are greater in number, is larger

and sharper on the left than on the right, and the counts varied as follows: 1–3 in metasomal segment III and 2–4 in metasomal segment IV.

Ecology. *Tityus kuryi* occurs in a restricted environment of montane savannas biome named “Campos Rupestres” of the Espinhaço Range (Cadeia do Espinhaço), in rocky areas of high altitudes in the Chapada Diamantina, Bahia State. The annual average temperature there is 22–24 °C, with 36–38 °C as absolute maximum and 4.8 °C as absolute minimum. It is found at altitudes above 840 m. They can also be found near to residential areas, but always near to natural fragments hidden in debris under or between stones.

Distribution of *Tityus serrulatus* and *T. stigmurus* males

In an attempt to explain the strategies of the life history in populations of scorpions, Vandel (1928 *apud* Lourenço 2008) was the first to use the term “geographical parthenogenetics” to name the features that various authors had already observed: the parthenogenetics and sexual populations of the same species tend to occur in different habitats.

The sexual populations of *Tityus serrulatus* and *T. stigmurus* have a highly restricted geographic distribution, while asexual populations (parthenogenetic) of both species have a wide geographic distribution, occupying urban areas across the Country (Lourenço 2008). This reproductive strategy is advantageous, it allows rapid colonization and wider dispersion in disturbed environments (Lourenço and Cuellar 1995, Lourenço 2002). Thus, it allows these scorpions to occupy areas where sexual populations have difficulties in establishing colonies (Lynch 1984, Cuellar 1994). This can increase the species reproductive capacity by about twofold, as parthenogenesis is of the thelytoky type (production of all-female progeny) (Glesener and Tilman 1978).

Although *Tityus serrulatus* has been known as parthenogenetic since 1962 (Matthiesen 1962), this not occur with *T. stigmurus*, whose confirmation of reproductive strategy came much later when Ross (2010) reported the occurrence of thelytokous parthenogenesis in this species. In both, parthenogenesis is not a mandatory feature, as shown in last review of the *Tityus stigmurus* complex that describes males for both species (Souza et al. 2009). The new records that we present in this study (Table 2) indicate the occurrence of sexual populations of *T. stigmurus* in eight municipalities of Bahia, in addition to those already known, Camaçari and Paulo Afonso (Souza et al. 2009) and one record in Pernambuco State (see Table 2). These records improve the knowledge on the distribution of the sexual populations of this species.

The male specimen of *T. serrulatus* used in this study is deposited in MZUFBA and came from the municipality of São Desiderio, Bahia. We can say now that sexual population of this species, previously restricted to the State of Minas Gerais (municipality Espinosa) and Southeastern Brazil (Lourenço and Cloudsley-Thompson 1999, Souza et al. 2009), can also be found in the Northeast of the Country (Fig. 15).

In spite of the new records of sexual populations of *Tityus serrulatus* and *T. stigmurus* to previously unknown areas, parthenogenesis seems to be the main reproductive strategy of these species. This assertion is primarily based on the low frequency of

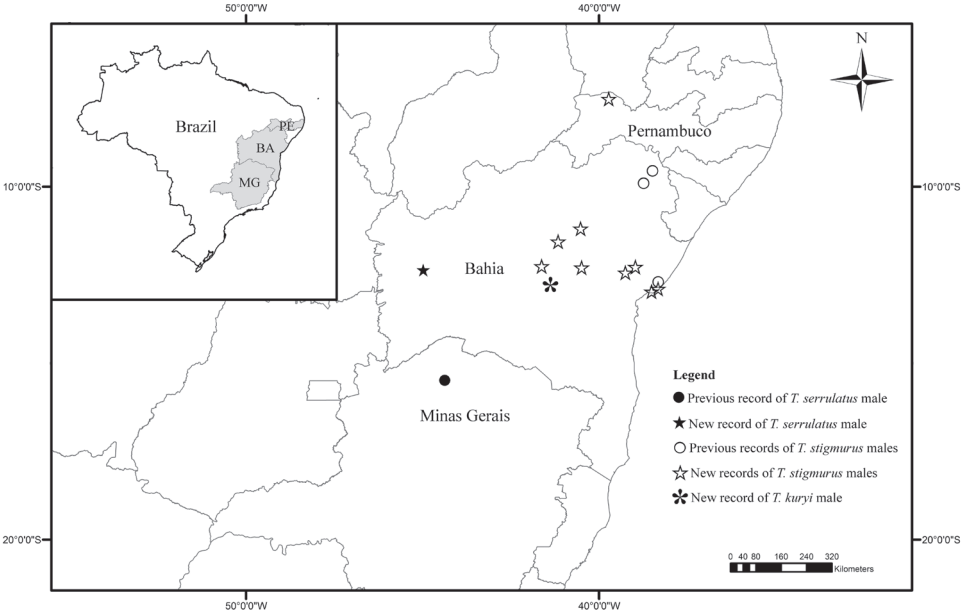


Figure 15. Map showing the previous and new records of males of *Tityus kuryi*, *T. serrulatus* and *T. stigmurus*.

Table 2. New records of males of *Tityus kuryi*, *T. serrulatus* and *T. stigmurus*.

Species	Registration number	Municipality and state of Brazil	Latitude (DMS)	Longitude (DMS)
<i>Tityus kuryi</i>	MZUFBA 2569	Palmeiras, Bahia	12°31'44"S	41°33'32"W
	MZUFBA 2570	Palmeiras, Bahia	12°31'44"S	41°33'32"W
<i>Tityus serrulatus</i>	MZUFBA 2573	São Desedério, Bahia	12°35'21"S	44°98'42"W
<i>Tityus stigmurus</i>	MZUFBA 2339	Exú, Pernambuco	07°30'43"S	39°43'26"W
	MZUFBA 166	Santo Estevão, Bahia	12°25'49"S	39°15'05"W
	MZUFBA 168	Santo Estevão, Bahia	12°25'49"S	39°15'05"W
	MZUFBA 270	Ruy Barbosa, Bahia	12°17'02"S	40°29'38"W
	MZUFBA 2104	Iraquara, Bahia	12°14'56"S	41°37'08"W
	MZUFBA 2297	Morro do Chapéu, Bahia	11°33'00"S	41°09'21"W
	MZUFBA 763	Feira de Santana, Bahia	12°16'00"S	38°58'00"W
	CIAVE 41	Jacobina, Bahia	11°10'50"S	40°31'06"W
	CIAVE 23	Lauro de Freitas, Bahia	12°53'38"S	38°19'37"W
	CIAVE 617	Salvador, Bahia	12°58'16"S	38°30'39"W
	CIAVE 923	Salvador, Bahia	12°58'16"S	38°30'39"W

males of these species in three of the largest scorpion collections in Brazil (Instituto Butantan-SP, Museu Nacional-RJ and MZUFBA) and on our field experience collecting with a UV flashlight. Unlike other parthenogenetic scorpions, *T. serrulatus* and *T. stigmurus* are actually the two species better adapted to urban environments. They are regarded as a public health problem due to their rapid expansion in urban ar-

eas, their proliferation and the toxic effects of their poison (Lourenço and Cloudsley-Thompson 1999, Brasil 2009).

We can emphasize here the large number of individuals analyzed as opposed to the few males found, providing evidence of the rarity of males, both in nature and in scientific collections.

Acknowledgments

The authors are grateful to Claudio Augusto Ribeiro de Souza for the help with confirmation of the dimorphism of the species. We are grateful to Silvanir Pereira Souza, Lucas Menezes Silva and Bruno Oliveira Cova for their help with the production of figures. We thank to Sonia Maria Christophe and Rafael Burguer for the permission to collect scorpions in their property. We acknowledge Leonardo Carvalho for his important suggestions and Nelson Silva for the help with English language. The authors thank the “Laboratório Central de Saúde Pública da Bahia Professor Gonçalves Moniz (LACEN-BA)”, “Laboratorio de Biomonitoramento e Ecologia de Bentos (LAMEB)”, “Laboratorio de Biomonitoramento e Ecologia de Abelhas (LABEA)” and “Laboratório de Geoecologia de Sedimentos Marinhos (GEOECO)” for providing infrastructure and equipment; and the “Fundação de Amparo e Pesquisa do Estado da Bahia (FAPESB)” for granting the financial support of two Scientific Initiation scholarships to the first author, which generated the results of this study.

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Three new species of the millipede genus *Tylopus* Jeekel, 1968 from Thailand, with additional notes on the species described by Attems (Diplopoda, Polydesmida, Paradoxosomatidae)

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Academic editor: Robert Mesibov | Received 16 July 2014 | Accepted 6 August 2014 | Published 18 August 2014

<http://zoobank.org/1840AA15-2D44-491F-AE26-B644D7EC88A1>

Citation: Likhitrakarn N, Golovatch SI, Panha S (2014) Three new species of the millipede genus *Tylopus* Jeekel, 1968 from Thailand, with additional notes on the species described by Attems (Diplopoda, Polydesmida, Paradoxosomatidae). ZooKeys 435: 63–91. doi: 10.3897/zookeys.435.8286

Abstract

Tylopus currently comprises 55 species, including three new from Thailand: *T. corrugatus* **sp. n.**, *T. trigonum* **sp. n.** and *T. parahilaroides* **sp. n.** A new distribution map and an updated key to all 29 species of *Tylopus* presently known to occur in Thailand are given. Illustrated redescrptions of all four Indochinese *Tylopus* species described by Carl Attems are also provided, based on type material.

Keywords

Millipede, *Tylopus*, taxonomy, new species, key, Thailand

Introduction

The Southeast Asian millipede genus *Tylopus* Jeekel, 1968 is one of the most speciose not only in the mainly Asian tribe Sulciferini, but also in the whole family Paradoxosomatidae. The latter is probably the largest in the entire class Diplopoda, dominating the millipede fauna of Indo-Australia (Jeekel 1968) and currently comprising nearly 200 genera and over 1,000 species (Nguyen and Sierwald 2013; authors' records). At the moment, all 52 constituent species of *Tylopus* range from southern China, through Laos, to Myanmar, western Thailand and southern Vietnam. Since the thorough reviews of the genus by Golovatch and Enghoff (1993) and Likhitrakarn et al. (2010), both of which focused on the fauna of Thailand, Nguyen (2012) provided a synopsis of and a key to all 18 species of *Tylopus* occurring in Vietnam, while Golovatch (2013, 2014) summarized all six congeners recorded in southern China.

The present paper is an updated review of all 29 *Tylopus* currently known from Thailand (Table 1), including three new congeners. In addition, all four Indochinese *Tylopus* species described by Carl Attems are redescribed and illustrated, based on the types kept in the collection of the Naturhistorisches Museum Wien, Austria.

Material and methods

New material was collected in northern Thailand and southern Laos from 2011 to 2013 by SP and members of the Animal Systematics Research Unit, Chulalongkorn University. Live animals were photographed in the laboratory shortly before fixing. Specimens were preserved in 75% ethanol, and morphological investigations were carried out in the laboratory using an Olympus stereomicroscope. Scanning electron micrographs (SEM) of gonopods coated with gold were taken using a JEOL, JSM–5410 LV microscope, and the gonopods removed from stubs and returned to alcohol after examination. Digital images of preserved specimens were taken in the laboratory and assembled using the “Cell^D” automontage software of the Olympus Soft Imaging Solution GmbH package. In addition, line drawings of gonopod characters were also prepared. Type material of the Attemsian congeners housed in the Vienna Museum was photographed with a Dino-Eye Eyepiece USB Camera AM423X, the digital images assembled using the automontage software technique, and the gonopods redrawn. Holotypes of the three new species, as well as most of the paratypes are housed in the Museum of Zoology, Chulalongkorn University (CUMZ), Bangkok, Thailand, a single duplicate paratype being donated to the collection of the Naturhistorisches Museum Wien, Austria (NHMW), as indicated in the text.

Collecting site positions and elevations were determined by GPS using the WGS84 datum.

In the catalogue sections, D stands for the original description, subsequent descriptive notes or appearance in a key, R for a subsequent record or records, and M for a mere mention.

Table 1. *Tylopus* species recorded in Thailand (Pocock 1895, Hoffman 1973, Golovatch and Enghoff 1993, Likhitrakarn et al. 2010).

No.	Species	Locality
1	<i>Tylopus affinis</i> Golovatch & Enghoff, 1993	Doi Pui, summit (1,650 m), Doi Suthep National Park; Mae Chaem road (1,700 m); main road (1,900 m), Doi Inthanon National Park, Chiang Mai Province.
2	<i>Tylopus allorugosus</i> Golovatch & Enghoff, 1993	Siripum Waterfall (1,300–1,400 m); Mae Chaem road (1,694–1,700 m); main road (2,200–2,500 m); Doi Inthanon National Park; Doi Pui, summit (1,650 m), Doi Suthep National Park, Chiang Mai Province.
3	<i>Tylopus amicus</i> Golovatch & Enghoff, 1993	northwestern Fang District (1,550–1,750 m), Doi Pha Hom Pok National Park, Chiang Mai Province.
4	<i>Tylopus asper</i> Golovatch & Enghoff, 1993	Doi Inthanon National Park (1,500 m), Chiang Mai Province.
5	<i>Tylopus baenzigeri</i> Golovatch & Enghoff, 1993	near stream (1,100 m); Doi Pui-Chang Khian (1,400–1,500 m), Doi Suthep National Park, Chiang Mai Province.
6	<i>Tylopus bispinosus</i> Likhitrakarn, Golovatch, Prateepasen & Panha, 2010	near Umphang City (492 m); Doi Hua Mod (900 m), Umphang District, Tak Province.
7	<i>Tylopus coriaceus</i> Golovatch & Enghoff, 1993	Phu Kheio (1,000 m), Chaiyapum Province.
8	<i>Tylopus corrugatus</i> sp. n.	Doi Inthanon National Park (1,700 m), Chiang Mai Province.
9	<i>Tylopus degerboelae</i> Golovatch & Enghoff, 1993	forest near stream (1,000 m); Doi Pui road (1,000–1,100 m); Siripum Waterfall (1,298 m); evergreen forest (1,300–1,500 m), Doi Suthep National Park; main road (1,500–1,600), Doi Inthanon National Park; limestone area, Doi Chiang Dao; Doi Phatang, Wiang Kaen District, Chiang Mai Province.
10	<i>Tylopus doriae</i> (Pocock, 1895)	Doi Suthep National Park (1,400–1,500 m), Chiang Mai Province.
11	<i>Tylopus extremus</i> Likhitrakarn, Golovatch, Prateepasen & Panha, 2010	Doi Phahom Pok National Park, Fang District, Chiang Mai Province.
12	<i>Tylopus grandis</i> Likhitrakarn, Golovatch, Prateepasen & Panha, 2010	near Pha Mon Cave; Mae Lana crossroad, Pangmapha District, Mae Hong Son Province.
13	<i>Tylopus haplorugosus</i> Golovatch & Enghoff, 1993	main road (1,694–1,900 m), Doi Inthanon National Park, Chiang Mai Province.
14	<i>Tylopus hoffmani</i> Golovatch & Enghoff, 1993	summit (1,600 m), Doi Suthep National Park, Chiang Mai Province.
15	<i>Tylopus jeekeli</i> Golovatch & Enghoff, 1993	Siripum Waterfall (1,200–1,300 m), Doi Inthanon National Park; Doi Suthep National Park (1,298 m), Chiang Mai Province.
16	<i>Tylopus pallidus</i> Golovatch & Enghoff, 1993	northwest of Fang (1,550–1,750 m); Doi Pha Hom Pok, Chiang Mai Province.
17	<i>Tylopus panajeekei</i> Likhitrakarn, Golovatch, Prateepasen & Panha, 2010	summit (2,520 m), Doi Inthanon National Park, Chiang Mai Province.
18	<i>Tylopus perarmatus</i> Hoffman, 1973	east slope (1,000–1,275 m); Mahidol Waterfall (1,250–1,500 m), Doi Suthep National Park; Siripum Waterfall (1,300–1,400 m); Vajirathan Waterfall (750 m), Doi Inthanon National Park; Doi Phatang, Wiang Kaen District; limestone cave (500 m), Doi Chiang Dao, Chiang Mai Province. sandy bank of stream (900 m), ca 8 km east of Ban Huai Kaeo, Thoen District; Thum Pha Thai, Ngao District, Lampang Province. Ban Pang Rim Kon, Mueang Chiang Rai District; Phuchee Fah, Thoeng District; Doi Pha Tang, Wiang Kaen District, Chiang Rai Province. Nam Min Waterfall, Chiang Kham District, Phayao Province. Tham Pha Nang Khoi (275 m), Rong Kwang District, Phrae Province. Ton Tong waterfall, Pua District, Nan Province.
19	<i>Tylopus perplexus</i> Golovatch & Enghoff, 1993	northwest of Fang (1,550–1,750 m); Doi Pha Hom Pok, Chiang Mai Province.

No.	Species	Locality
20	<i>Tylopus poolpermorum</i> Golovatch & Enghoff, 1993	northwest of Fang (1,550–1,750 m); Doi Pha Hom Pok, Chiang Mai Province.
21	<i>Tylopus prosperus</i> Golovatch & Enghoff, 1993	main road (2,200 m); summit (2,500 m), Doi Inthanon National Park, Chiang Mai Province.
22	<i>Tylopus pulvinipes</i> Golovatch & Enghoff, 1993	Tong Kamang Noi, forest (1,000 m); Phu Kheio, Chaiyaphum Province.
23	<i>Tylopus rugosus</i> Golovatch & Enghoff, 1993	Chiang Dao (1,800 m); Buathong Waterfall Forest Park (510 m), Phrao District, Chiang Mai Province.
24	<i>Tylopus semirugosus</i> Golovatch & Enghoff, 1993	Ban Mussoe, Mae Sot District, Tak Province.
25	<i>Tylopus similirugosus</i> Golovatch & Enghoff, 1993	Doi Suthep National Park (1,000 m); same locality (1,400–1,500 m), Chiang Mai Province.
26	<i>Tylopus parahilaroides</i> sp. n.	Phuluang Wildlife Sanctuary (1,486 m), Phuluang District, Loei Province.
27	<i>Tylopus subcoriaceus</i> Golovatch & Enghoff, 1993	near stream (1,000 m); evergreen forest (1,100 m), Doi Suthep National Park, Chiang Mai Province.
28	<i>Tylopus trigonum</i> sp. n.	Pa Wai Waterfall (804 m), Umphang District, Tak Province.
29	<i>Tylopus veliger</i> Likhitrakarn, Golovatch, Prateepasen & Panha, 2010	Ton Tong Waterfall (1,128 m), Pua District, Nan Province.

Taxonomy

Family Paradoxosomatidae Daday, 1889

Subfamily Paradoxosomatidae Daday, 1889

Tribe Sulciferini Attems, 1898

Genus *Tylopus* Jeekel, 1968

Tylopus corrugatus sp. n.

<http://zoobank.org/BF1AF28F-1392-44B1-A117-7C8F47BDF77A>

Figs 1–3

Holotype. ♂ (CUMZ), Thailand, Chiang Mai Province, Chom Thong District, Doi Inthanon National Park, 1,700 m a.s.l., 18°31'55"N, 98°29'30"E, 20.12.2013, leg. N. Likhitrakarn & S. Chaiwong.

Paratypes. 2 ♂, 6 ♀, 2 juveniles (CUMZ), 1 ♂ (NHMW), same locality, together with holotype. 1 ♂, 1 ♀ (CUMZ), same locality, 25.01.2013, leg. N. Likhitrakarn.

Name. To emphasize the clearly wrinkled postcollum metaterga.

Diagnosis. Differs from congeners mainly in the very strongly developed paraterga with evident oblong ridges. Gonopod process **h** prominent, hook-shape, much longer than solenophore.

Description. Length 15.5–18.2 (♂) or 16.5–21.0 mm (♀), width of midbody pro- and metazonae 1.50–1.70 and 1.95–2.15 mm (♂) or 1.55–2.0 and 2.0–2.5 mm (♀), respectively.

Coloration of live animals blackish-brown (Fig. 1A) with a pattern of contrasting light brown paraterga and posterior halves of midbody metaterga and epiproct, dark brown to light brown head, legs and antennae; coloration in alcohol faded after two months of preservation, paraterga, legs and epiproct being light brown to whitish;

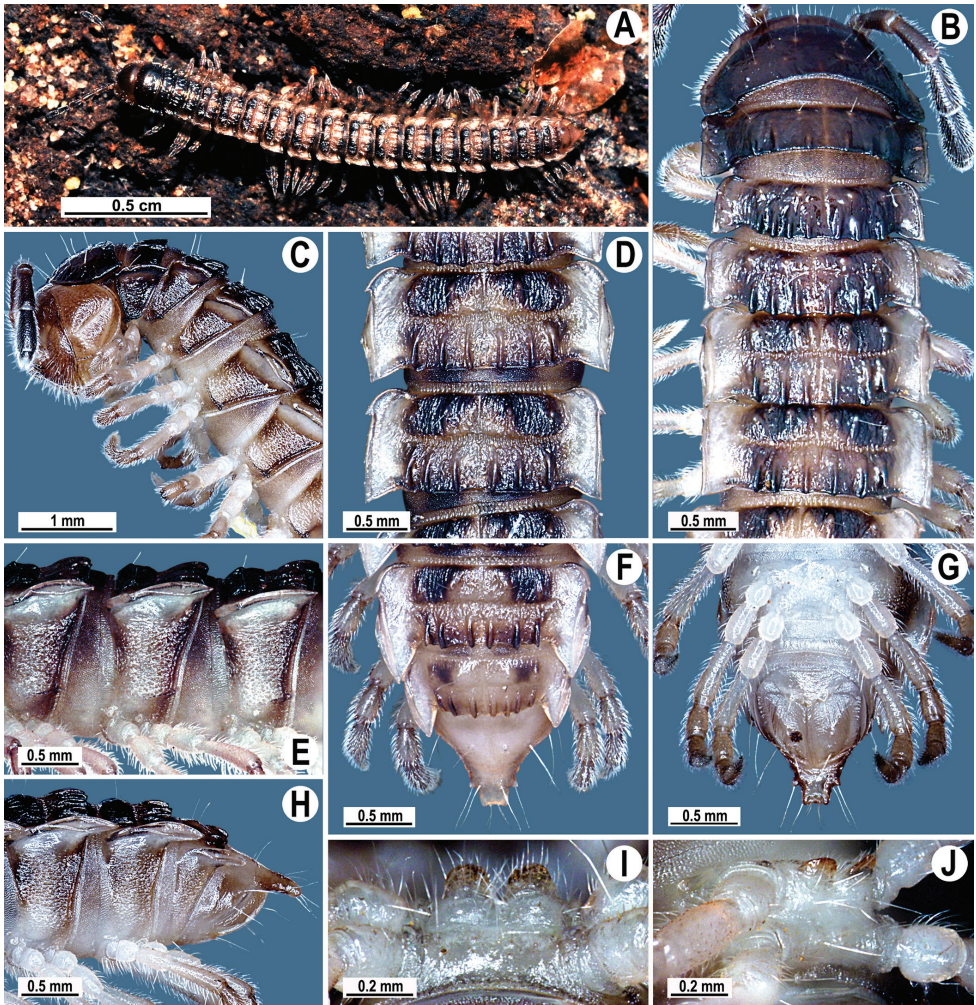


Figure 1. *Tylopus corrugatus* sp. n., ♂ holotype; **A** habitus, live coloration **B, C** anterior part of body, dorsal and lateral views, respectively **D, E** segments 10 and 11, dorsal and lateral views, respectively **F–H** posterior part of body, dorsal, ventral and lateral views, respectively **I, J** sternal cones between coxae 4, subcaudal and sublateral views, respectively.

head to metazonae 3 blackish, thereafter metazonae with a light brown to whitish cross (Fig. 1B, D, F); venter and a few basal podomeres light brown to yellow-brown, legs increasingly darker brown distally (Fig. 1B–J).

Clypeolabral region and vertex sparsely setose, epicranial suture distinct. Antennae moderately long (Fig. 1A–C), reaching body segment 3 (♂) or 2 (♀) when stretched dorsally. In width, head < segment 3 = 4 < collum < 2 < 5–17 (♂, ♀); thereafter body gently and gradually tapering. Collum with three transverse rows of setae: 4+4 anterior, 3+3 intermediate and 5+5 posterior; a small incision laterally in posterior half;

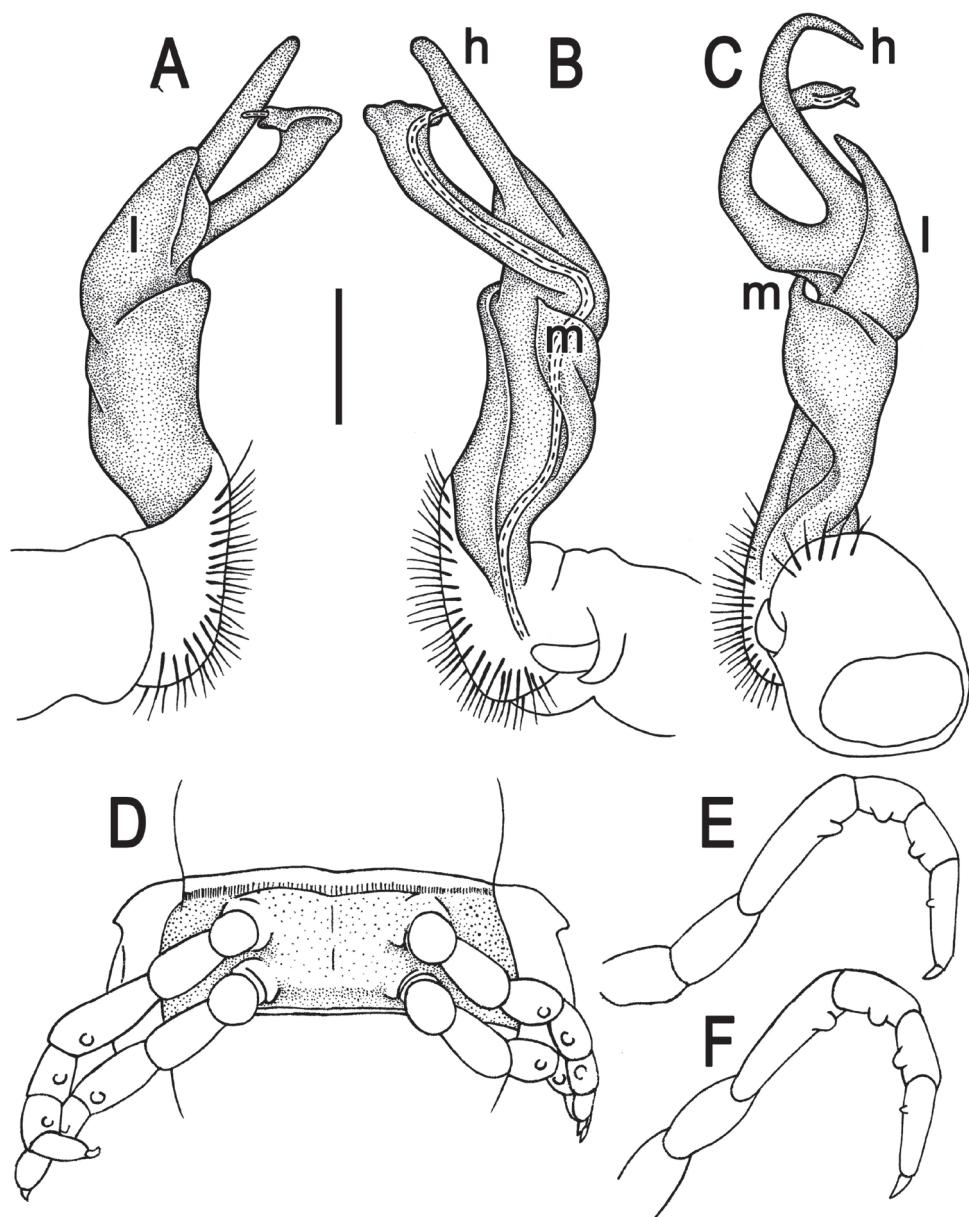


Figure 2. *Tylopus corrugatus* sp. n., ♂ holotype; **A–C** right gonopod, lateral, mesal and anteromesal views, respectively, scale bar: 0.2 mm **D** sternum of segment 10. **E, F** leg of segment 10, depicted not to scale.

caudal corner of paraterga rounded, slightly declined ventrad, produced behind rear tergal margin (Fig. 1B, C).

Tegument leathery and shining, prozonae very finely shagreened, metaterga leathery, finely microgranulate and delicately rugulose; surface below paraterga finely mi-

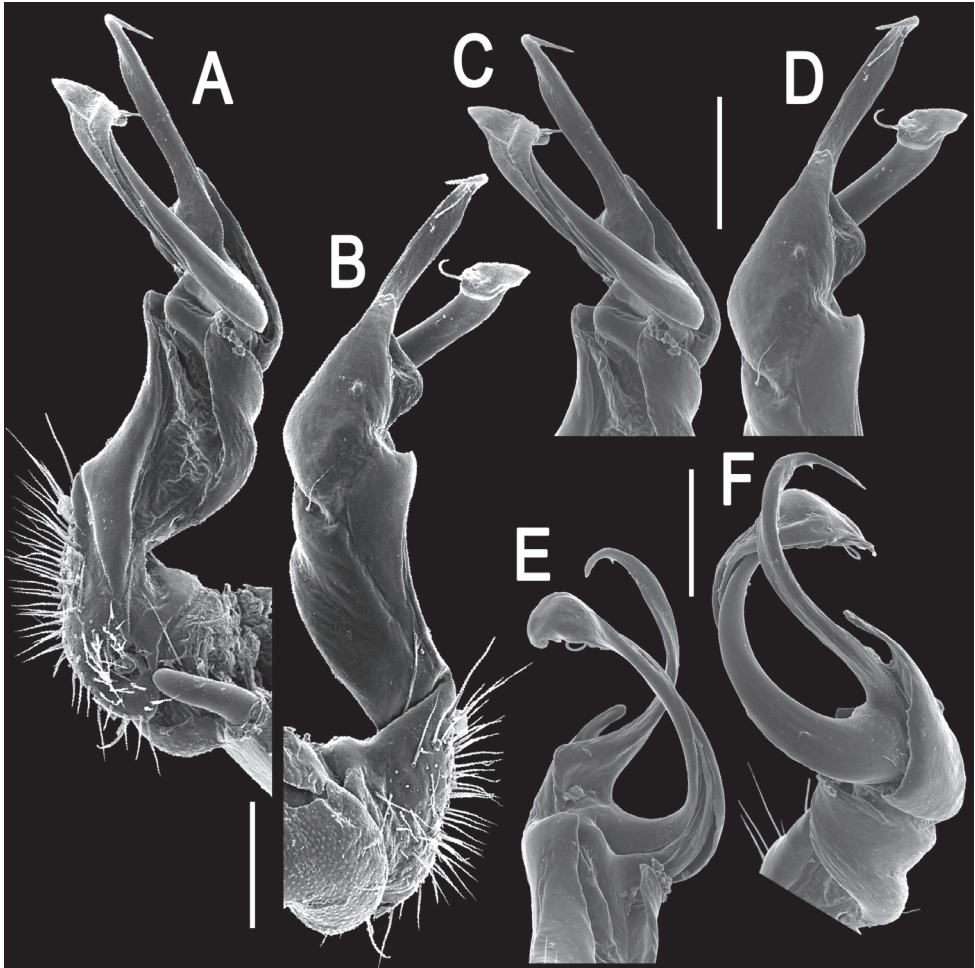


Figure 3. *Tylopus corrugatus* sp. n., ♂ paratype, right gonopod; **A, B** mesal and lateral views, respectively **C–F** distal part, mesal, lateral, posterior and anterior views, respectively. Scale bars: 0.2 mm.

crogranulate. Postcollum metaterga with two transverse rows of setae on evident oblong ridges: 2+2 in anterior (pre-sulcus) and 3+3 in posterior (post-sulcus) row, caudal row being more strongly developed than anterior one (Fig. 1B–F, H); behind segment 10, metaterga with: 2+2 in anterior and 3(4)+3(4) in posterior row. Tergal setae long, strong, slender, about 1/3 of metatergal length. Axial line visible on metaterga. Paraterga very strongly developed (Fig. 1B–F, H), especially well so in ♂, set at about 1/4 midbody height, mostly upturned, all lying high, but always below dorsum; shoulders well-developed, mostly rounded; caudal corner almost completely to fully pointed, extending increasingly beyond tergal margin, posterior edge mostly oblique, especially strongly so on segments 16–19 (Fig. 1F, H); paraterga very thin blunt blades in lateral view, a little thicker only on pore-bearing segments. Calluses on paraterga delimited by

a sulcus only dorsally. Paraterga 2 broad, anterior edge angular, lateral edge with two evident incisions in anterior half; posterior edge slightly concave (Fig. 1B, C). Lateral edge of paraterga with evident incisions, one in anterior 1/3, the other at midway, caudal incision being smaller in pore-bearing segments. Ozopores evident, lateral, lying in an ovoid groove at about 1/3 in front of caudal corner. Transverse sulcus usually distinct (Fig. 1B, D, F), slightly incomplete on segment 19, complete on metaterga 4–18, deep, reaching bases of paraterga, clearly beaded at bottom. Stricture between pro- and metazonae wide, clearly ribbed at bottom down to base of paraterga (Fig. 1B–E). Pleurosternal carinae complete crests with a sharp caudal tooth on segment 7 (♂, ♀), a small, caudal, mostly sharp tooth until segment 17 (♂) or 16 (♀), thereafter missing (Fig. 1C, E, H). Epiproct (Fig. 1F, G) conical, flattened dorsoventrally, with two strong apical papillae; tip subtruncate; pre-apical papillae evident, lying close to tip. Hypoproct roundly subtrapeziform (Fig. 1G), setiferous knobs at caudal edge well-separated and evident.

Sterna very densely setose, with a small cone caudally near each coxa, rear cones being a bit better developed than front ones (Fig. 2D); a deeply notched sternal lobe between ♂ coxae 4 (Fig. 1I, J). Legs moderately long and slender, midbody ones ca 1.0–1.2 (♂) or 0.9–1.1 times (♀) as long as body height, ♂ legs of segments 5–16 with an evident adenostyle (tubercle) on femur, postfemur, tibia and tarsus (Fig. 2D–F); tarsal brushes present until ♂ legs 7.

Gonopods (Figs 2A–C, 3) simple; coxa a little curved caudad, sparsely setose distoventrally. Prefemur densely setose, about 1/3 as long as femurite + “postfemoral” part. Femurite rather stout, expanded distad, slightly curved, showing a mesal groove; lobe **l** simple; process **m** apicoventral and spiniform; solenophore long and slender, typically coiled, tip subtruncate; process **h** strongly developed, curved and acute, longer than solenophore.

***Tylopus parahilaroides* sp. n.**

<http://zoobank.org/0E564999-E51A-4D50-9099-8857FF80E9D6>

Figs 4, 5

Holotype. ♂ (CUMZ), Thailand, Loei Province, Phuluang District, Phuluang Wildlife Sanctuary, 1,486 m a.s.l., 17°16'44.9"N, 101°31'10.2"E, 20.07.2011, leg. Sira Noommeechai.

Paratype. 1 ♀ (CUMZ), same data, together with holotype.

Name. To emphasize the close resemblance to *T. hilaroides* Golovatch, 1984.

Diagnosis. Very similar to *T. hilaroides*, especially as regards its gonopod conformation, but differs in the presence of two rows of setae on metaterga 3–18 (an anterior transverse row of 2+2 setae and a posterior row of 4+4 insertion points versus solely an anterior transverse row of 2+2 setae), by the transverse sulcus visible starting already from metatergum 4 (versus metatergum 5), as well as in gonopod process **z** with two evident spines along distal margin (versus three spines) and process **h** being smaller (versus stouter).

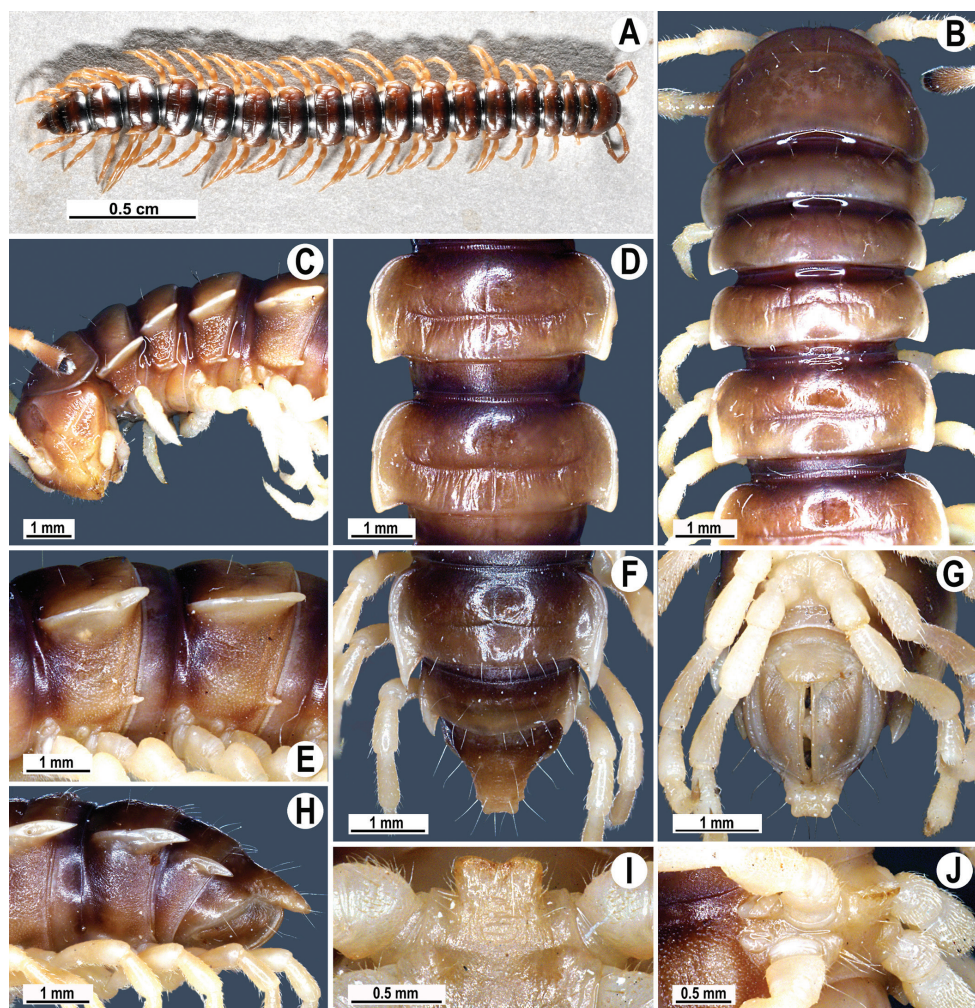


Figure 4. *Tylopus parahilaroides* sp. n., ♂ holotype; **A** habitus, live coloration **B, C** anterior part of body, dorsal and lateral views, respectively **D, E** segments 10 and 11, dorsal and lateral views, respectively **F–H** posterior part of body, dorsal, ventral and lateral views, respectively **I, J** sternal cones between coxae 4, caudal and lateral views, respectively.

Description. Length 34 (♂) or 33 mm (♀), width of midbody pro- and metazonae 3.1 and 4.3 mm (♂) or 3.2 and 4.1 mm (♀), respectively.

Coloration of live animals dark castaneous brown (Fig. 4A); legs red-brown, venter and a few basal podomeres light brown to yellow-brown; coloration of alcohol material after a half year preservation faded to dark brown; antennae and epiproct light brown to pallid, venter and a few basal podomeres light brown to pallid (Fig. 4B–H).

Clypeolabral region and vertex sparsely setose, epicranial suture distinct. Antennae moderately long (Fig. 4A), reaching behind body segment 3 (♂, ♀) when stretched

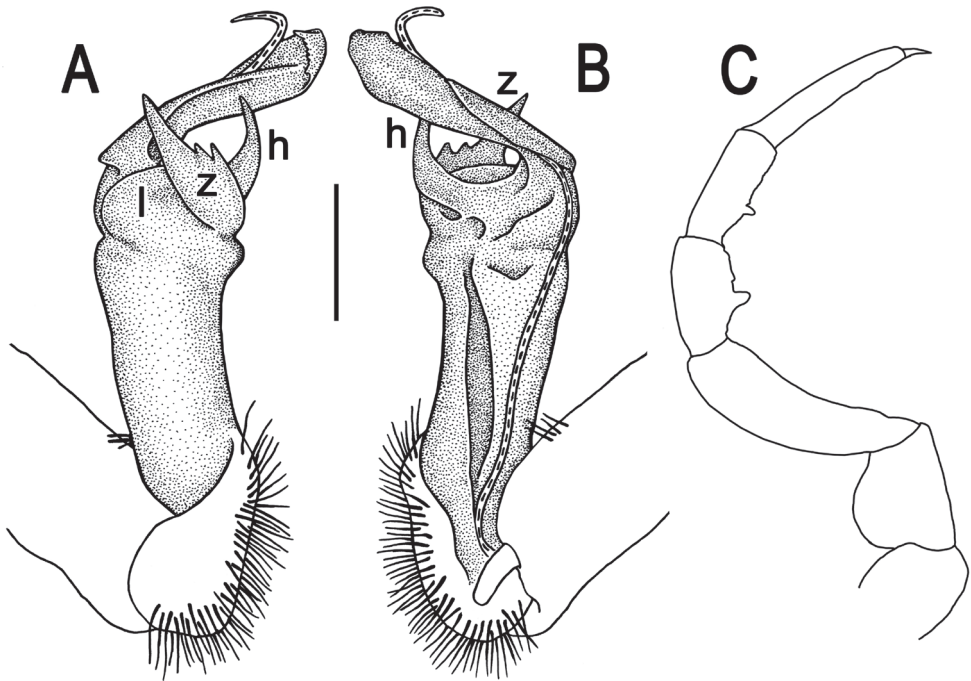


Figure 5. *Tylopus parahilaroides* sp. n., ♂ holotype; **A, B** right gonopod, lateral and mesal views, respectively, scale bar: 0.2 mm **C** leg of segment 10, depicted not to scale.

dorsally. In width, head < segment 3 < 4 < 5 < collum < segment 2 < 6–17 (♂) or head < segment 3 < 4 < collum < segment 2 < 5–17 (♀); thereafter body gently and gradually tapering. Collum with three transverse rows of setae: 4+4 anterior, 3+3 intermediate, and 4+4 posterior; a setigerous incision laterally in posterior 1/3; caudal corner of paraterga very narrowly rounded, not drawn behind rear tergal margin (Fig. 4B, C).

Tegument rather smooth and shining, prozonae finely shagreened, metaterga often rugose (Fig. 4A–F); surface below paraterga finely microgranular (Fig. 4C, E, H). Postcollum metaterga with an anterior transverse row of 2+2 setae visible at least as insertion points, and a posterior row of 4+4 insertion points. Tergal setae long, strong, slender, about 1/3 of metatergal length. Axial line clearly visible both on pro- and metazonae. Paraterga strongly developed (Fig. 4B–H), especially so in ♂, lying rather high (at 1/3 of midbody height), slightly upturned, but lying below dorsum; anterior edge rounded, caudal corner very narrowly rounded, starting from segment 13 extending increasingly beyond rear tergal margin, pointed, on segments 15–19 tips strongly curved mesad (Fig. 4F, H); lateral edge on poreless segments with two evident (anterior larger, posterior one smaller) setigerous incisions in anterior 1/3, but with only one strong (anterior) incision on pore-bearing segments (Fig. 4B, D, F); posterior edge oblique. Calluses on paraterga narrow, delimited by a sulcus only dorsally in segments 2–3, but both dorsally and ventrally in following segments. Paraterga 2 broad, posterior edge clearly oblique. Paraterga 2 and 3 broadly angular anteriorly, following

segments with rounded anterior edges (Fig. 4B). Ozopores evident, lateral, lying in an ovoid groove at about 1/3 in front of posterior edge of metaterga. Transverse sulcus usually distinct (Fig. 4B, D, H), slightly incomplete on segments 4 and 19, complete on metaterga 5–18 (♂, ♀), narrow, wavy, rather deep, not reaching bases of paraterga, at most faintly ribbed at bottom. Stricture between pro- and metazonae broad and deep, beaded at bottom down to well below base of paraterga (Fig. 4B, D, H). Pleurosternal carinae complete crests with a sharp caudal tooth on segments 2–4, thereafter split into a sharp front and a sharp caudal tooth, the former gradually turning into a bulge, the latter tooth gradually reduced until segment 17 (♂, ♀). Epiproct (Fig. 4F, G) conical, flattened dorsoventrally, with two evident apical papillae; tip subtruncate; pre-apical papillae small, lying rather close to tip. Hypoproct roundly subtrapeziform, setiferous knobs at caudal edge small and well-separated (Fig. 4G).

Sterna densely setose, without modifications; a single, linguiform, sternal lobe between ♂ coxae 4 (Fig. 4I, J). Legs rather long and slender, midbody ones ca 1.2–1.3 (♂) or 1.1–1.4 times (♀) as long as body height; appressed setation ventrally on coxa, prefemur and femur, but tarsal brushes absent; ♂ prefemora distinctly bulged laterally (Fig. 5C), ♂ postfemora and tibiae on segments 7–17 with an evident adenostyle at midway on ventral side (Fig. 5C).

Gonopods (Fig. 5A, B) simple; coxa a little curved caudad, sparsely setose distoventrally. Prefemur densely setose, about 1/3 as long as femorite + “postfemoral” part. Femorite rather stout, expanded distad, slightly curved, showing a mesal groove; lobe **I** simple; process **z** with two evident spines along dorsal margin; process **h** short and slender, curved, with an acute tip; solenophore long and slender, typically coiled, tip subtruncate.

Tylopus trigonum sp. n.

<http://zoobank.org/7B4546E1-7163-433F-816D-6DCB8E010BAF>

Figs 6, 7

Holotype. ♂ (CUMZ), Thailand, Tak Province, Umphang District, Pa Wai Waterfall, 804 m a.s.l., 16°34'29.6"N, 98°50'3.2"E, 20.01.2011, leg. C. Sutcharit & N. Likhitrakarn.

Paratypes. 1 ♂ (CUMZ), same data, together with holotype. 3 ♀ (CUMZ), same district, Thee Lor Sue Waterfall, 591 m a.s.l., 15°55'38.1"N, 98°45'12.8"E, 19.01.2011, leg. N. Likhitrakarn.

Name. To emphasize the light brown triangle on terga; noun in apposition.

Diagnosis. This new species shows a peculiar colour pattern, much like that observed in *T. schawalleri* Golovatch, 2013, but differs in gonopod process **h** being rather short and coiled (versus high and strongly twisted), as well as by the presence of a process **m** (versus absent).

Description. Length 21.2–27.8 (♂) or 22.1–24.0 mm (♀), width of midbody pro- and metazona 1.97–1.83 and 2.65–2.78 mm (♂) or 2.43–2.58 and 3.05–3.14 mm (♀), respectively.

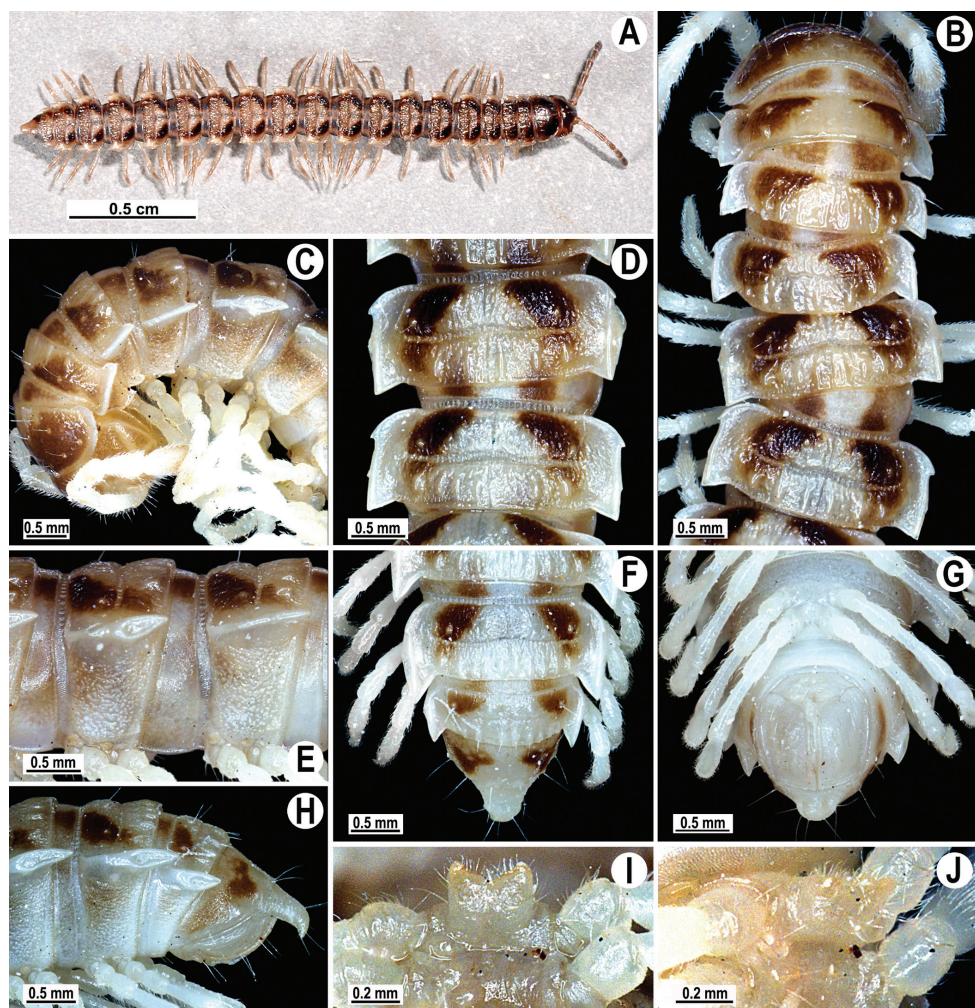


Figure 6. *Tylopus trigonum* sp. n., ♂ holotype; **A** habitus, live coloration **B, C** anterior part of body, dorsal and lateral views, respectively **D, E** segments 10 and 11, dorsal and lateral views, respectively **F–H** posterior part of body, dorsal, ventral and lateral views, respectively **I, J** sternal cones between coxae 4, subcaudal and sublateral views, respectively.

Coloration of live animals light brown (Fig. 6A); paraterga, legs and epiproct light brown, head and collum blackish, following terga with a light brown triangle and blackish collar covering both pro- and metazonae; coloration of alcohol material after three years of preservation faded to whitish with a pattern of a contrasting dark brown inverted triangle at anterior edge of metazonae and a light brown triangle at posterior edge of prozonae (Fig. 6B–H).

Clypeolabral region and vertex sparsely setose, epicranial suture distinct. Antennae very short (Fig. 6A, B), reaching only behind body segment 2 (♂) or collum (♀) when

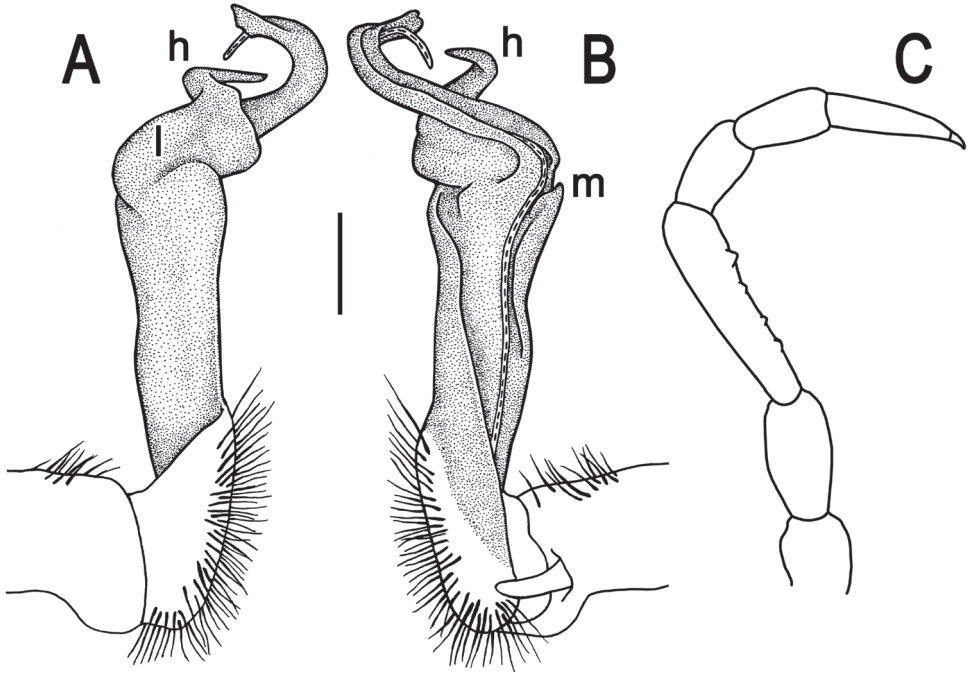


Figure 7. *Tylopus trigonum* sp. n., ♂ holotype; **A, B** right gonopod, lateral and mesal views, respectively, scale bar: 0.2 mm **C** leg of segment 10, depicted not to scale.

stretched dorsally. In width, head < segment 3 < 4 < collum < segment 2 < 5–17 (♂, ♀); thereafter body gently and gradually tapering. Collum with three transverse rows of strong setae: 4+4 anterior, 2+2 intermediate, and 4+4 posterior; a rounded incision laterally in posterior half; caudal corner of paraterga rounded, slightly declined ventrad, produced behind rear tergal margin (Fig. 6B, C).

Tegument rather smooth and shining, prozonae very finely shagreened, metaterga smooth and finely rugulose, leathery; surface below paraterga finely microgranulate (Fig. 6B–H). Postcollum metaterga with two transverse rows of setae on small knobs on oblong ridges: 2+2 in anterior (pre-sulcus), 3+3 in posterior (post-sulcus) row, caudal row more strongly developed than anterior one, starting from metaterga 11 with 2+2 in anterior and 4(3)+4(3) in posterior row. Tergal setae long, strong, slender, about 1/3 of metatergal length. Axial line visible. Paraterga very strongly developed (Fig. 6B–F, H), especially well in ♂, set high, at about 1/3 of midbody height, slightly upturned, always lying high, but below dorsum; shoulders well-developed, mostly regularly rounded and narrowly bordered, fused to callus; caudal corner narrowly rounded to fully pointed, extending increasingly beyond rear tergal margin, posterior edge clearly oblique (Fig. 6B, D, F); paraterga very thin blunt blades in lateral view, a little thicker only on pore-bearing segments. Calluses on paraterga delimited by a sulcus both dorsally and ventrally. Paraterga 2 broad, anterior edge angular, lateral edge with three evident incisions in anterior half (Fig. 6B, C). Lateral edge of following paraterga with two clear

incisions, one in anterior 1/3, the other at midway, front one being particularly evident. Ozopores evident, lateral, lying in an ovoid groove at about 1/3 in front of caudal corner. Transverse sulcus usually distinct (Fig. 6B, D, H), slightly incomplete on segments 4 and 19, complete on metaterga 5–18, deep, reaching bases of paraterga, clearly ribbed at bottom. Stricture between pro- and metazonae very wide, clearly beaded at bottom down to base of paraterga (Fig. 6B, D, H). Pleurosternal carinae complete crests with a sharp caudal tooth on segment 12 (♂) or 7 (♀), thereafter increasingly well reduced in size and sharpness until segment 17 (♂) or 14 (♀), onward missing (Fig. 6C, E, H). Epiproct (Fig. 6F–H) conical, flattened dorsoventrally, subtruncate, with two evident apical papillae directed caudally, both pointed at tip; pre-apical papillae evident, lying close to tip. Hypoproct roundly subtrapeziform (Fig. 6G), small setiferous knobs at caudal edge well-separated and evident.

Sterna very densely setose, with a small cone caudally near each coxa; a single, linguiform, deeply medially notched sternal lobe between ♂ coxae 4 (Fig. 9I, J). Legs moderately long and slender, midbody ones ca 1.1–1.2 (♂) or 1.0–1.1 times (♀) as long as body height, ♂ femora with 2–4 small adenostyles on ventral side (Fig. 7C); tarsal brushes present until ♂ leg 7.

Gonopods (Fig. 7A, B) very simple; coxa a little curved caudad, sparsely setose distoventrally. Prefemur densely setose, about 1/3 as long as femorite + “postfemoral” part. Femorite rather slender, expanded distad, slightly curved, showing a mesal groove; lobe **l** simple; solenophore long and slender, typically coiled, tip subtruncate; process **m** evident, but not spiniform; process **h** prominent, coiled, acute at tip.

Remark. The ♂ paratype on metatergum 19 shows 3+3 and 6+6 setae without knobs in the anterior and posterior rows, respectively.

Tylopus nodulipes (Attems, 1953)

Figs 8, 9

Agnesia nodulipes Attems, 1953: 174 (D).

Agnesia nodulipes – Jeekel 1965: 98 (R).

Tylopus nodulipes – Jeekel 1968: 60 (M); Hoffman 1973: 371 (M, D); Golovatch 1983: 182 (M); 1984: 69 (M, D); Golovatch and Enghoff 1993: 90 (M, D); Enghoff et al. 2004: 40 (R); Likhitrakarn et al. 2010: 25 (R, D); Nguyen 2012: 301 (R, D).

Lectotype ♂ (here designated) of *Agnesia nodulipes* (NHMW-3986), Laos, Luang Prabang, 1938–1939, leg. C. Dawydoff.

Lectotype designation proposed herewith is necessary to ensure the species is based on a complete ♂ coming from a certain locality, because (1) Attems (1953) provided no information on the number and sex of syntypes, and (2) he stated their provenance to have been both from Luang Prabang, Laos and Mount Fan-Si-Pan, Lao Cai Province, Vietnam. No paralectotype material could be traced in the Vienna Museum.

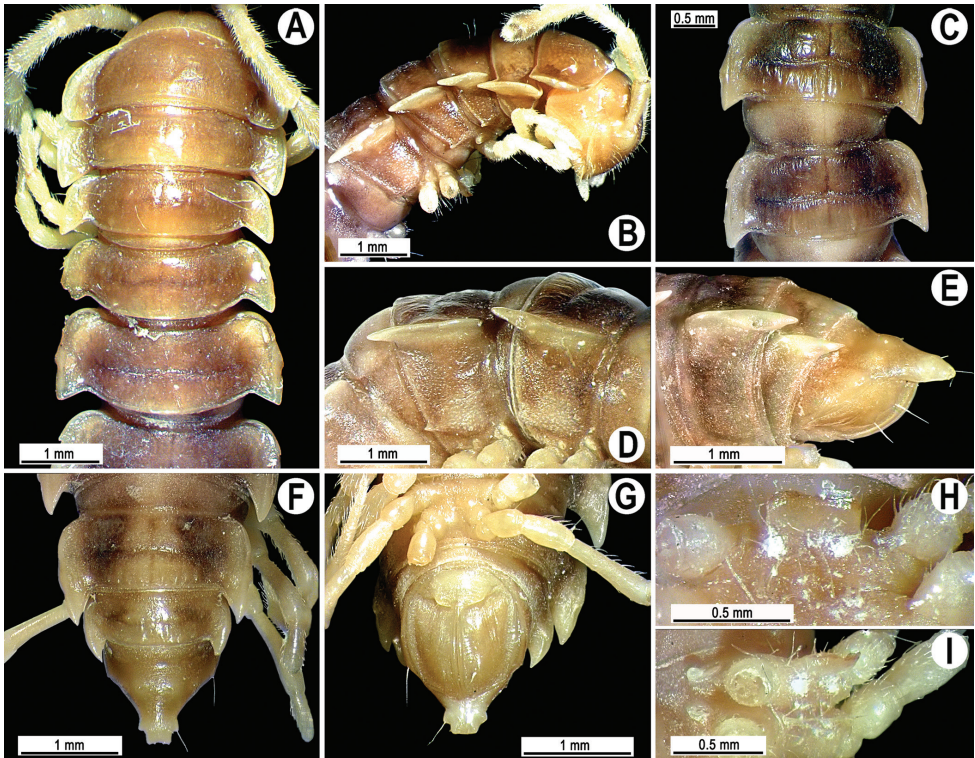


Figure 8. *Tylopus nodulipes* (Attems, 1953), ♂ lectotype; **A, B** anterior part of body, dorsal and lateral views, respectively **C** segments 10 and 11, dorsal view **D** segments 9–11, lateral view **E–G** posterior part of body, lateral, dorsal and ventral views, respectively **H, I** sternal cones between coxae 4, caudal and lateral views, respectively.

Redescription. Lectotype ca 24 mm long, width of midbody pro- and metazonae 2.1 and 2.9 mm (vs 3.0 in width, as given in the available description (Attems 1953)). Coloration of alcohol material after long preservation rather uniformly light reddish brown (Fig. 8A–G) with light yellow antennae, paraterga, epiproct and legs (versus dark maroon with light yellowish brown mid-dorsal parts of prozonae, paraterga a little lighter, antennae light chestnut brown and legs yellow brown, as given in the original description (Attems 1953)).

Clypeolabral region densely setose; vertex rather smooth, only faintly rugulose; epicranial suture distinct. Antennae rather long and slender (Fig. 8A, B), reaching behind body segment 3 when stretched dorsally. In width, head < segments 3 and 4 < collum < 2 < 5–16, gently and gradually tapering thereafter. Collum smooth, with three transverse rows of setae, 4+4 anterior, 2+2 intermediate, and 4+4 posterior; caudal corner of paraterga subrectangular, narrowly rounded (Fig. 8A, B), drawn behind rear tergal margin.

Tegument smooth and shining; metaterga rugulose, prozonae finely shagreened, surface below paraterga finely microgranulate. Metaterga 2–17 with two transverse

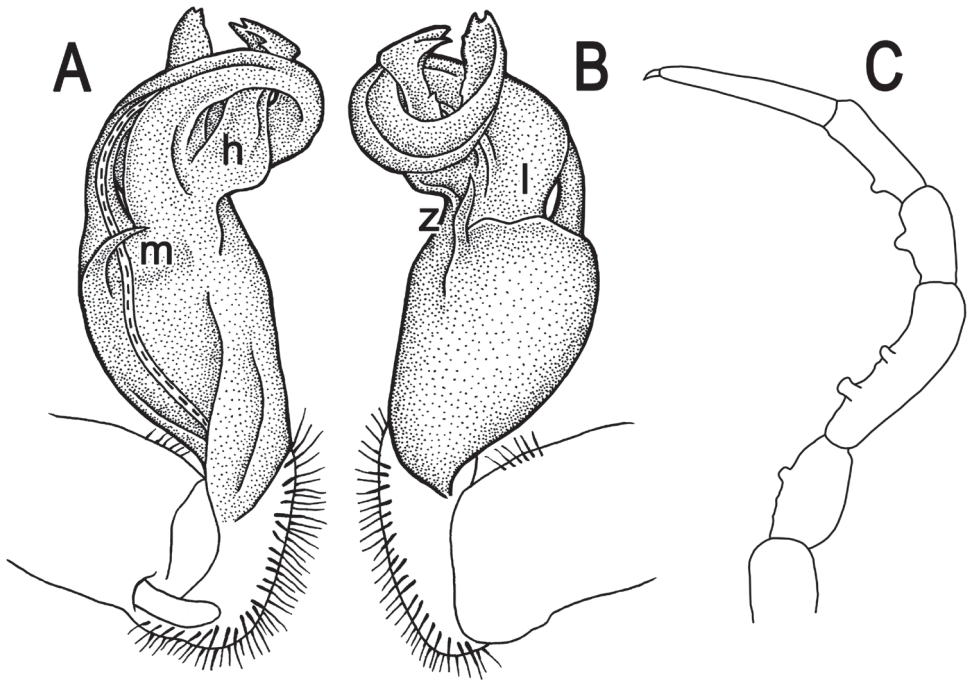


Figure 9. *Tylopus nodulipes* (Attems, 1953), ♂ lectotype; **A, B** left gonopod, mesal and lateral views, respectively **C** leg of segment 10, depicted not to scale.

rows of setae: 2+2 in anterior (pre-sulcus) row and 3(2)+3(2) in posterior (post-sulcus) row, setae being borne on very small tubercles growing a little larger laterally, metaterga 18 and 19 with two transverse rows of setae: 2+2 in anterior and 4+4 in posterior row. Tergal setae long, strong, slender, about 1/3 of metatergal length. Axial line visible. Paraterga very strongly developed (Fig. 8A–G), subhorizontal, lying below dorsum, thin blunt blades in lateral view, a little thicker only on pore-bearing segments, on postcollum segments extending increasingly beyond rear tergal margin, nearly pointed to pointed, caudal tip on paraterga 18–19 clearly curved mesad. Calluses delimited by a sulcus only dorsally, rather narrow. Paraterga 2 broad, slightly upturned, anterior edge rounded, lateral edge with three small incisions in anterior half; posterior edge oblique (Fig. 8A, B). Anterior edge of postcollum metaterga broadly rounded, bordered and fused to callus, lateral edge with two small incisions in anterior half on poreless segments, with only one incision near front 1/3 on pore-bearing ones. Ozopores evident, lateral, lying inside an ovoid groove at about 1/3 of metazonal length. Transverse sulcus complete on metaterga 5–18, incomplete on metatergum 19, rather wide, reaching bases of paraterga, faintly beaded at bottom (Fig. 8A, C, F). Stricture between pro- and metazonae very wide, shallow, faintly beaded at bottom down to base of paraterga. Pleurosternal carinae complete crests only on segment 2 (Fig. 8B), with anteriorly bulged crests and a sharp denticle caudally on segments 3–8, thereafter only a small sharp caudal tooth on segments 9–15, onward missing (Fig. 8B & D).

Epiproct (Fig. 8F, G) conical, flattened dorsoventrally, apical papillae evident; tip subtruncate; pre-apical papillae rather large, lying close to tip. Hypoproct (Fig. 8G) roundly subtrapeziform, setigerous knobs at caudal margin evident and well-separated.

Sterna sparsely setose, starting from segment 6 with a small cone caudally near each coxa, rear cones being a little larger than front ones; a rather large, linguiform, densely setose, sternal lobe between ♂ coxae 4 (Fig. 8H, I). Legs moderately long and slender, midbody ones ca 1.2–1.3 times as long as body height, legs of segments 8–18 with an evident adenostyle on each prefemur, postfemur and tibia, with two adenostyles on each femur (Fig. 9C); tarsal brushes present only until ♂ legs 4.

Gonopods (Fig. 9A, B) rather simple; prefemur densely setose, about 1/3 as long as femorite + “postfemoral” part. Femorite stout, expanded distad, slightly curved, showing a mesal groove; lobe **l** simple; solenophore long and slender, typically coiled, tip subtruncate; process **h** high, strongly twisted, tip bifid; process **m** rather long and spiniform, process **z** knife-shaped.

Remarks. This is the type species of *Tylopus* Jeekel, 1968, originally recorded from two localities: Luang Prabang Province, Laos and Mount Fan-Si-Pan, Lao Cai Province, Vietnam (Attems 1953). Golovatch (1984) redescribed and illustrated only a gonopod, but the locality remained unclear. So the lectotype is herewith selected for the sole type specimen still kept in the Vienna Museum.

This species has recently been reported from Nam Xay Commune (22°05'N, 104°05'E), 1,000 m a.s.l., Van Ban District, Lao Cai Province; Son Tay Commune, 600 m a.s.l., Huong Son District, Ha Tinh Province; and Chem Waterfall, 430 m a.s.l., Pu Mat National Park (18°46'–19°12'N, 104°01'–104°56'E), Nghe An Province, Vietnam (Nguyen 2012).

Tylopus hilaris (Attems, 1937)

Figs 10, 11

Anoplodesmus hilaris Attems, 1937: 105 (D).

Anoplodesmus hilaris – Attems 1938: 215 (D).

Agnesia hilaris – Jeekel 1965: 97 (M, D).

Tylopus hilaris – Jeekel 1968: 60 (M); Hoffman 1973: 371 (M, D); Golovatch 1983: 182 (M); 1984: 69 (M, D); Golovatch and Enghoff 1993: 90 (M, D); Enghoff et al. 2004: 40 (R); Likhitrakarn et al. 2010: 25 (R, D); Nguyen 2012: 301 (R, D).

Holotype ♂ of *Anoplodesmus hilaris* (NHMW-4248), Vietnam, Danang Prov., Mount Bana, 1,500 m, 28.09.1931, leg. C. Dawydoff.

Redescription. Length ca 38 mm, width of midbody pro- and metazonae 3.7 and 5.1 mm, respectively (vs 3.4 and 5.0 mm in width, as given in the available descriptions (Attems 1937, 1938)). Coloration of alcohol material after long preservation brown (Fig. 10A–G) with light yellow antennae, paraterga, epiproct and legs (versus dark brown with prozonae and posterior halves of metazonae blackish brown; edge

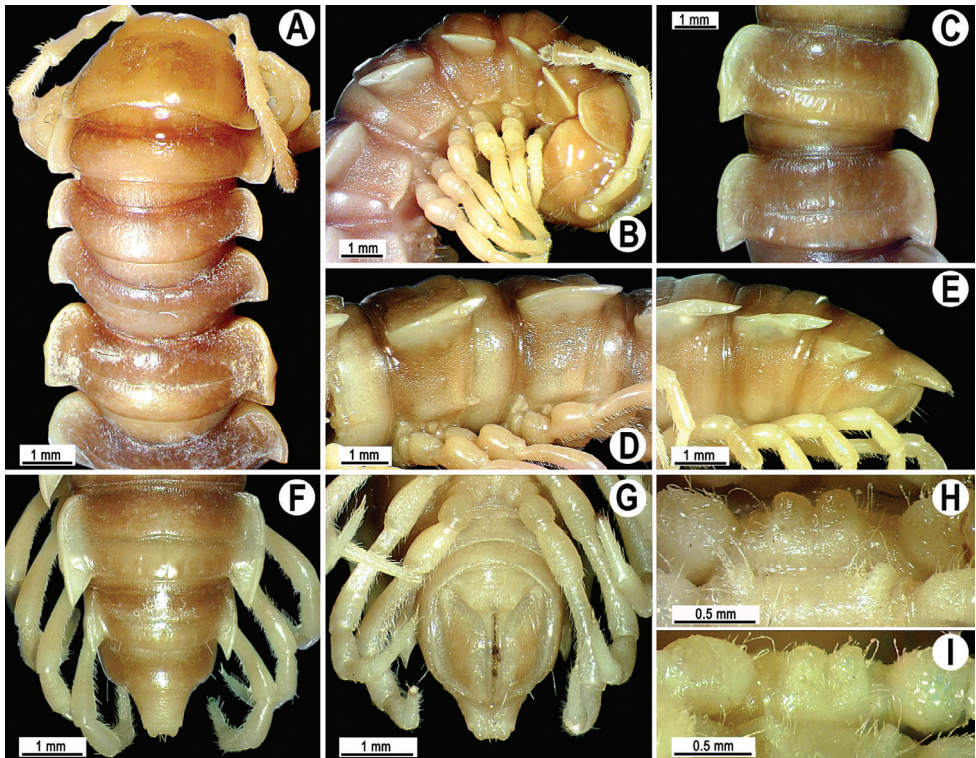


Figure 10. *Tylopus hilaris* (Attems, 1937), ♂ holotype; **A, B** anterior part of body, dorsal and lateral views, respectively **C** segments 10 and 11, dorsal view **D** segments 9–11, lateral view **E–G** posterior part of body, lateral, dorsal and ventral views, respectively **H, I** sternal cones between coxae 4, subcaudal and sublateral views, respectively.

of paraterga, antennae and legs yellowish brown, as given in the descriptions (Attems 1937, 1938)).

Clypeolabral region densely setose, vertex smooth, epicranial suture distinct. Antennae rather long (Fig. 10A, B), reaching behind body segment 3 when stretched dorsally. In width, head < segments 3 and 4 < collum < 2 < 5–16, gently and gradually tapering thereafter. Collum smooth, with three transverse rows of setae, 4+4 anterior, 2+2 intermediate, and 3+3 posterior; caudal corner of paraterga subrectangular, narrowly rounded (Fig. 10A, B). Tegument smooth and shining; metaterga faintly rugulose, prozonae finely shagreened, surface below paraterga finely microgranulate. Postcollum metaterga with an anterior transverse row (pre-sulcus) of 2+2, mostly abraded setae; caudal (post-sulcus) row barely traceable as 3+3 insertion points. Tergal setae short, simple, slender, about 1/5 metatergal length. Axial line barely visible, starting from collum. Paraterga very strongly developed (Fig. 10A–F), all subhorizontal and lying below dorsum, thin blunt blades in lateral view, a little thicker only on pore-bearing segments, on post-collum segments extending increasingly beyond rear tergal margin, nearly pointed to pointed, caudal tips on paraterga 17–19 evidently curved mesad. Calluses delimited

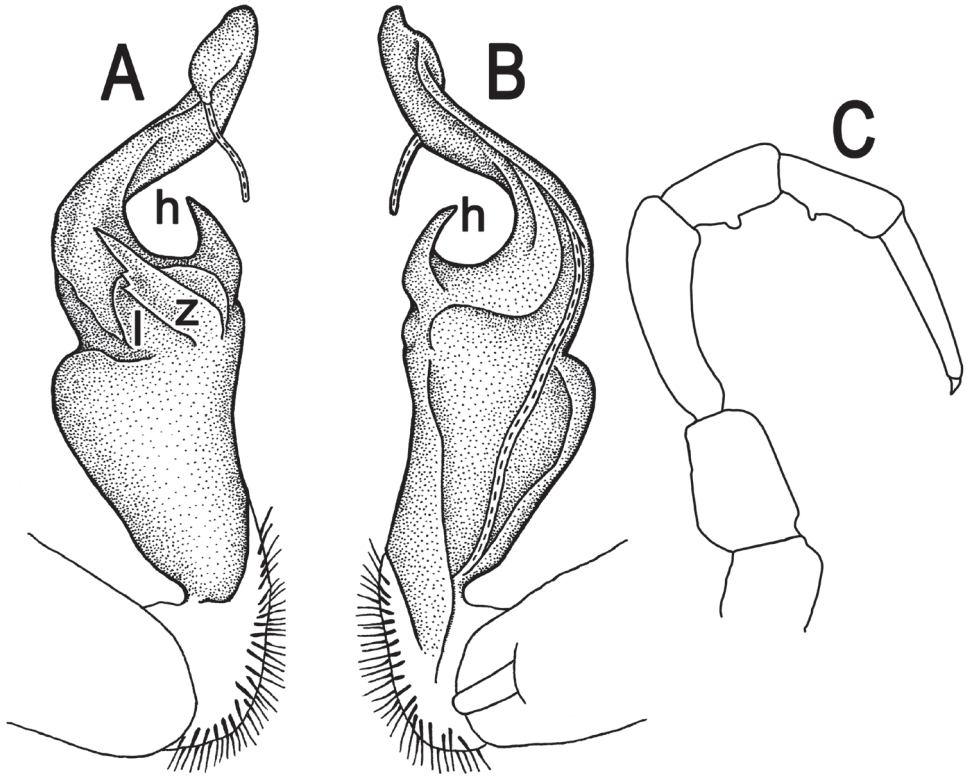


Figure 11. *Tylopus hilaris* (Attems, 1937), ♂ holotype; **A, B** right gonopod, lateral and mesal views, respectively **C** leg of segment 10, depicted not to scale.

by a sulcus only dorsally, rather narrow. Paraterga 2 broad, anterior edge rounded, lateral edge with three small incisions in anterior half; posterior edge concave (Fig. 10A). Anterior edge of postcollum segments broadly rounded, bordered and fused to callus, lateral edge with two small incisions in anterior half on poreless segments, with only one incision near front 1/3 on pore-bearing ones; posterior edge oblique. Ozopores evident, lateral, lying inside an ovoid groove at about 1/4 metazonal length in front of caudal corner. Transverse sulcus complete on metaterga 5–18, incomplete on metaterga 4 and 19, rather deep, wide, line-shaped, reaching bases of paraterga, ribbed at bottom (Fig. 10A, C, F). Stricture between pro- and metazonae shallow, broad, beaded at bottom down to base of paraterga. Pleurosternal carinae complete crests only on segment 2 (Fig. 10B), with a sharp tooth caudally on segments 3–7, only a small sharp caudal tooth on segments 8–16, onward missing (Fig. 10A, D, E). Epiproct (Fig. 10E–G) conical, flattened dorsoventrally, apical papillae very small; tip subtruncate; pre-apical papillae very small, lying close to tip. Hypoproct (Fig. 10G) roundly subtriangular, setiferous knobs at caudal margin small and well-separated.

Sterna sparsely setose, until segment 6 with an evident cone caudally near coxae; on segment 4 with an evident, central cone between coxae; on segment 5 with a small

central lobe with a paramedian pair of evident, sparsely setose, apical cones between coxae (Fig. 10H, I). Legs long and slender, midbody ones ca 1.2–1.3 (♂) or 0.8–0.9 (♀) times as long as midbody height, all legs until segment 17 with an evident adeno-style on each postfemur and tibia (Fig. 11C); tarsal brushes absent.

Gonopods (Fig. 11A, B) simple; coxa a little curved caudad, sparsely setose distoventrally. Prefemur densely setose, about 1/3 as long as femorite + “postfemoral” part. Femorite rather stout, expanded distad, slightly curved, showing a mesal groove; lobe **I** simple; process **z** with two small spines along ventral margin; process **h** short and stout, curved, tip acute; solenophore long and slender, typically coiled, tip subtruncate.

Remark. Endemic to Vietnam, *T. hilaris* is currently known from Mount Bana, 1,500 m a.s.l., Danang Province (Attems, 1937); Bach Ma National Park (16°05'–16°05'N, 107°43'–107°53'E), Thua Thein Hue Province; Mount Ngoc Linh (15°00'–15°18'N, 107°41'–108°01'E), Kon Tum Province, central Vietnam (Nguyen 2012).

Tylopus sigma (Attems, 1953)

Figs 12–13

Sundanina sigma Attems, 1953: 171 (D).

Sundanina sigma – Jeekel 1968: 60 (M).

Tylopus sigma – Golovatch 1983: 182 (M); 1984: 69 (M, D); Golovatch and Enghoff 1993: 90 (M, D); Enghoff et al. 2004: 40 (R); Likhitrakarn et al. 2010: 26 (R, D).

Lectotype ♂ (here designated) of *Sundanina sigma* (NHMW-3987), Vietnam, Lao Cai Prov., Sapa (= Chapa), 1938–1939, leg. C. Dawydoff.

Paralectotypes. 2 ♂ of *Sundanina sigma* (NHMW-3987), same data, together with lectotype.

Lectotype designation proposed herewith is necessary to ensure the species is based on a complete ♂, because Attems (1953) provided no information on the number and sex of syntypes.

Redescription. Length 18–19 mm (♂), width of midbody pro- and metazonae 1.0–1.1 and 1.5–1.7 mm (♂), respectively (versus length 25 mm and width of midbody metazonae 1.6 mm, as given in the original description (Attems 1953)). Lectotype 18 mm long, 1.0 and 1.5 mm wide on midbody pro- and metazonae, respectively. Coloration of alcohol material after long preservation rather uniformly brown (Fig. 12A–G) (versus blackish brown with edges of paraterga and legs yellowish brown, as given in the description (Attems 1953)).

Clypeolabral region sparsely setose, vertex smooth, epicranial suture distinct. Antennae long and slender (Fig. 12B), extending behind body segment 5 (♂) dorsally. In width, head < segments 2–4 < collum < 5–17 (♂), gently and gradually tapering thereafter. Collum smooth, with three transverse rows of setae, 4+4 anterior, 2+2 intermediate, and 3+3 posterior; caudal corner of paraterga subrectangular, narrowly rounded (Fig. 12A). Tegument smooth and shining; metaterga and prozonae finely shagreened;

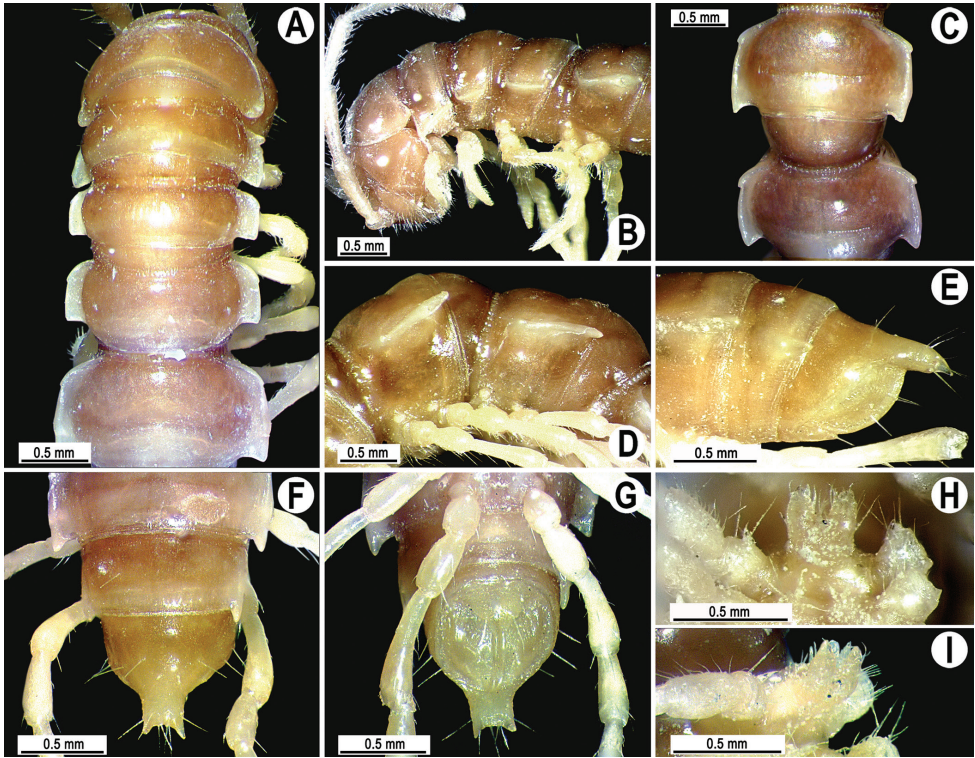


Figure 12. *Tylopus sigma* (Attems, 1953), ♂ paralectotype; **A, B** anterior part of body, dorsal and lateral views, respectively **C** segments 10 and 11, dorsal view **D** segments 9–11, lateral view **E–G** posterior part of body, lateral, dorsal and ventral views, respectively **H, I** sternal cones between coxae 4, caudal and lateral views, respectively.

surface below paraterga finely microgranulate. Postcollum with an anterior (pre-sulcus) transverse row of 2+2, mostly abraded setae; caudal (post-sulcus) row barely traceable as 3+3 insertion points. Tergal setae short, simple, slender, about 1/3 of metatergal length. Axial line barely visible, starting from collum. Paraterga very strongly developed (Fig. 12A, C, F, G), mostly subhorizontal and lying below dorsum, thin blunt blades in lateral view, a little thicker only on pore-bearing segments, posterior edge concave, caudal tip narrowly rounded. Calluses delimited by a sulcus only dorsally, rather narrow. Paraterga 2 broad, slightly upturned, anterior edge nearly straight, lateral edge with three more or less evident incisions; posterior edge clearly concave (Fig. 12A, B). Anterior edge of postcollum segments oblique, bordered and fused to callus, lateral edge with a strong incision near front 1/3; posterior edge oblique. Ozopores evident, lateral, lying inside an ovoid groove at about 1/4 metazonal length before caudal corner. Transverse sulcus complete on metaterga 5–18, shallow, not reaching bases of paraterga, faintly beaded at bottom (Fig. 12A, C, F). Stricture between pro- and metazonae broad, shallow, ribbed at bottom down to base of paraterga. Pleurosternal carinae complete crests only on segment 2, with a small sharp caudal tooth on seg-

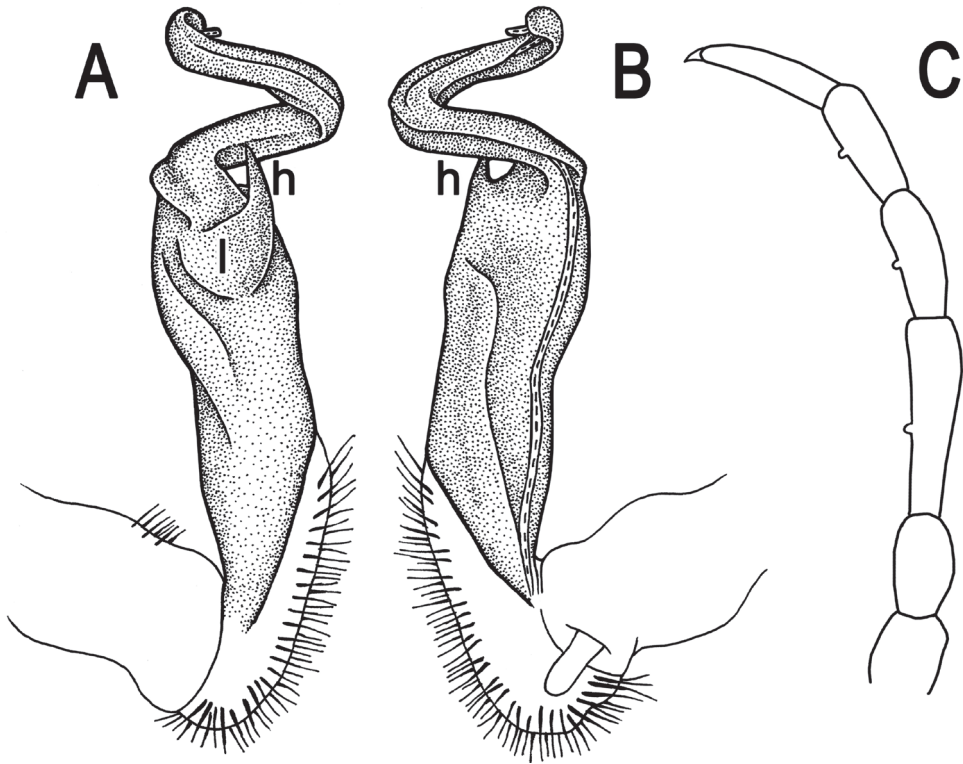


Figure 13. *Tylopus sigma* (Attems, 1953), ♂ lectotype; **A, B** right gonopod, lateral and mesal views, respectively **C** leg of segment 10, depicted not to scale.

ments 3–7, onward missing (Fig. 12B, D, E). Epiproct (Fig. 12E–G) conical, flattened dorsoventrally, apical papillae evident and large; tip subtruncate; pre-apical papillae small, but visible, lying close to tip. Hypoproct (Fig. 12G) roundly subtrapeziform, setiferous knobs at caudal margin small and well-separated.

Sterna sparsely setose, with a large central cone between coxae 3 and a small central lobe with a paramedian pair of evident, sparsely setose, apical cones between coxae 4 (♂) (Fig. 12H, I); segments 8–16 with a strong cone caudally near each coxa. Legs long and slender, midbody ones ca 1.4–1.5 (♂) as long as body height, legs on segments 8–18 with a small adenostyle on each prefemur, femur and postfemur (Fig. 13C); tarsal brushes absent.

Gonopods (Fig. 13A, B) very simple; coxa a little curved caudad, sparsely setose distoventrally. Prefemur densely setose, about 1/3 as long as femorite + “postfemoral” part. Femorite rather slender, expanded distad, slightly curved, showing a mesal groove; lobe **l** simple; solenophore long and slender, typically coiled, tip subtruncate; process **h** short, rather curved, tip acute.

Remark. Endemic to Vietnam, *T. sigma* is only known from Sapa (= Chapa), Lao Cai Province, Vietnam (Attems 1953).

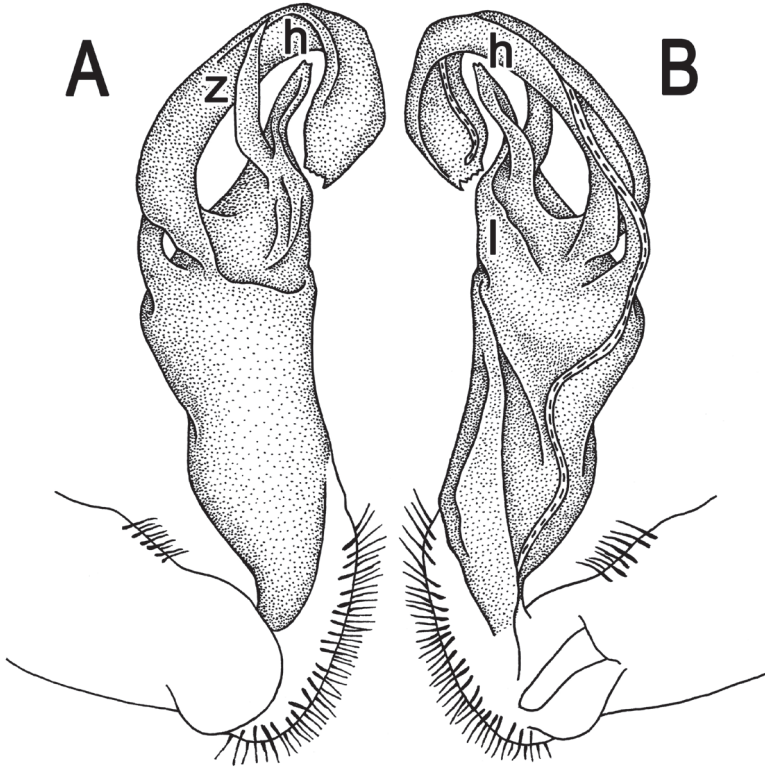


Figure 14. *Tylopus mutilatus* (Attems, 1953), ♂ syntype; **A, B** right gonopod, lateral and mesal views, respectively. Depicted not to scale.

***Tylopus mutilatus* (Attems, 1953)**

Fig. 14

Anoplodesmus mutilatus Attems, 1953: 163 (D).

Agnesia mutilata – Jeekel 1965: 98 (R).

Tylopus nodulipes – Jeekel 1968: 60 (M); Hoffman 1973: 371 (M, D); Golovatch 1983: 182 (M); 1984: 69 (M, D); Golovatch and Enghoff 1993: 90 (M, D); Enghoff et al. 2004: 40 (R); Likhitrakarn et al. 2010: 25 (R, D).

Syntype ♂ of *Anoplodesmus mutilatus* (NHMW-4245), locality unknown; a slide with mounted gonopod.

Gonopod (Fig. 14) rather simple. Coxa long and slender, with several setae distodorsally. Prefemur densely setose, nearly 1/3 as long as femorite + “postfemoral” part. Femorite stout, slightly curved, slightly enlarged distad, showing a mesal groove, “postfemoral” part demarcated by an oblique lateral sulcus; lobe **I** simple; process **h** long, rather simple, slightly curved, tip small and bifid; process **z** high, slightly curved, tip acute; solenophore long and slender, typically coiled, tip microdenticulate.

Remark. This species was described both from Luang Prabang, Xieng Kuang, Laos and Pic de Langbiang (Mount Langbian), Lamdong Province, Vietnam (Attems 1953). Golovatch (1984) redescribed and illustrated only a gonopod, but the locality remained unclear. As all our attempts at locating a torso of *T. sigma* in the collection of the Naturhistorisches Museum Wien, Austria had failed, we could only revise the very same right gonopod mounted on a slide. Fortunately, the gonopod is easily distinguished from congeners.

Key to the species of *Tylopus* currently known to occur in Thailand, chiefly based on ♂ characters:

- 1 Most ♂ prefemora clearly swollen laterally (Fig. 5C) **2**
- All ♂ prefemora normal, not bulged laterally (Figs 2E, F, 7C) **9**
- 2 Sternal lamina between ♂ coxae 4 divided into two cones (Fig. 1I, J) **5**
- Sternal lamina between ♂ coxae 4 single, not divided (Figs 4I, J, 6I, J) **3**
- 3 Gonopod processes **z**, **r** and **m** present ***T. coriaceus***
- Gonopod processes **z**, **r** and **m** absent **4**
- 4 Tarsal bushes on ♂ legs present, from legs pair 3 with tubercles on tarsi, tibiae and femora ***T. degerboelae***
- Tarsal bushes on ♂ legs absent, starting from legs 9 with tubercles on femora and following podomeres ***T. pallidus***
- 5 Smaller species: body width less than 2.5 mm. Metaterga with evident oblong ridges on both anterior and posterior halves ***T. corrugatus* sp. n.**
- Larger species: body width more than 2.5 mm. Metaterga with small oblong ridges to faint knobs only on posterior half **6**
- 6 Sternal lamina between ♂ coxae 4 fully divided into paramedian knobs (Fig. 1I, J) **7**
- Sternal lamina between ♂ coxae 4 with a deep median notch (Fig. 4I, J) **8**
- 7 Gonopod process **h** high, stout and strongly helicoid. Pleurosternal carinae missing on segments 18–19 ***T. asper***
- Gonopod process **h** rather small, slender and subdentiform. Pleurosternal carinae missing on segments 15–19 ***T. pulvinipes***
- 8 Coloration with a pattern of a contrasting dark brown inverted triangle at anterior edge of metaterga. Gonopod process **z** absent. Legs of ♂ segment 10 multituberculate ventrally only on femora ***T. trigonum* sp. n.**
- Coloration uniformly pale. Gonopod process **z** present. Legs of ♂ segment 10 multituberculate ventrally on femora, postfemora, tibiae and tarsi ***T. subcoriaceus***
- 9 Metaterga without evident setiferous tubercles, only sometimes with very small, rudimentary wrinkles or knobs **10**
- Metaterga with evident setiferous tubercles **16**
- 10 Midbody metaterga more than 4.1 mm wide **11**
- Midbody metaterga less than 3.9 mm wide **12**

- 11 Gonopods (Fig. 5A, B) with process **z** prominent and serrate along distal margin, whereas process **h** a strong hook *T. parahilaroides* sp. n.
- Gonopod with a short lobe **z**, whereas process **h** very small..... *T. grandis*
- 12 Both processes **h** and **z** of gonopod spiniform *T. bispinosus*
- Gonopod different..... 13
- 13 Gonopod process **h** subflagelliform, process **m** extremely long and prominent *T. extremus*
- Gonopod different..... 14
- 14 Gonopod process **h** a strong hook with a distally serrate process **z**; process **m** extremely long and prominent *T. similirugosus*
- Gonopod different..... 15
- 15 ♂ legs shorter, ca 1.2–1.3 times as long as body height. Gonopod lobe **l** velum-shaped and supplied with two denticles; process **z** short and knife-shaped while process **h** rudimentary..... *T. veliger*
- ♂ legs longer, ca 1.6–1.7 times as long as midbody height. Gonopod process **z** small, placed closer to base of process **h**..... *T. parajeekeli*
- 16 Most metaterga with a pattern of 2+2 and 2+2 setiferous tubercles in two rows, rear row somewhat less strongly developed than fore one..... *T. doriae*
- Most metaterga with rear row of setiferous tubercles or wrinkles more strongly developed than fore row, the latter (next to) wanting..... 17
- 17 Transverse sulcus on metaterga starting from segment 4, either fully or almost fully developed there, always fully developed starting from segment 5 18
- Transverse sulcus on metaterga starting only from segment 5 20
- 18 Paraterga 2 rather broadly rounded caudolaterally. Gonopod relatively simple, process **h** poorly developed, no additional outgrowths near base..... *T. affinis*
- Paraterga 2 pointed caudally. Gonopods more complex..... 19
- 19 Coloration dark brown, without cingulate pattern. Sternal lamina between ♂ coxae 4 low and distinctly bimodal. Gonopods with tooth **z** prominent and serrate along distal margin *T. rugosus*
- Coloration pale, with a cingulate pattern. Sternal lamina between ♂ coxae 4 high, subquadrate. Gonopod tooth **z** smaller and spiniform... *T. semirugosus*
- 20 Pattern of tergal setation on segments 18 and/or 19: 2+2 and 5+5 in two rows..... 21
- Pattern of tergal setation at least on segments 5–19: 2+2 and 4+4 in two rows..... 24
- 21 Pattern of tergal setation 2+2 and 5+5 on both segments 18 and 19. Paraterga 2 pointed caudally. Epiproct with pre-apical incisions very close to apical knobs. Sternal lamina between ♂ coxae 4 an unusually low and even ridge. Adenostyles on midbody ♂ postfemora and, to a lesser extent, tibiae exceptionally prominent..... *T. poolpermorum*
- Pattern of tergal setation 2+2 and 5+5 only on segment 19. Paraterga 2 more or less narrowly rounded. Pre-apical incisions on epiproct better removed from tip. Sternal lamina between ♂ coxae 4 concave medially. Ventral adenostyles on ♂ legs less prominent..... 22

- 22 Body smaller: width ca 2.0 mm. Sternal lamina between ♂ coxae 4 as a pair of separate, setiferous tubercles. Ventral adenostyles on ♂ legs almost missing. Gonopods without any outgrowth near base of process **h** ... *T. haplorugosus*
- Body larger: width over 3.0 mm. Sternal lamina between ♂ coxae 4 single. Ventral adenostyles on ♂ legs more prominent. Gonopod with a spine near base of process **h** **23**
- 23 Sternal lamina between ♂ coxae 4 high, emarginate. Adenostyles on ♂ post-femora and tibiae well-developed. Gonopods rather simple, process **z** inconspicuous..... *T. allorugosus*
- Sternal lamina between ♂ coxae lower, slightly concave. Adenostyles on ♂ postfemora and tibiae less strongly developed. Gonopods more complex, process **z** long and large..... *T. perarmatus*
- 24 Paraterga 2 pointed caudally. Sternal lamina between ♂ coxae 4 exceptionally densely setose, low, concave ventrally. Gonopods with a medium-sized process **h** and a smaller lobular **z** at base of **h** *T. jeekeli*
- Paraterga 2 more or less narrowly rounded caudally. Sternal lamina between ♂ coxae 4 higher and less strongly setose. Gonopod outgrowths **h** and **z** either almost wanting or very large..... **25**
- 25 Sternal lamina between ♂ coxae 4 with a straight ventral margin. Pleurosternal carinae poorly developed, in ♂ slightly projecting caudad beyond rear margin only until segments 8–10 **26**
- Sternal lamina between ♂ coxae 4 slightly concave ventrally. Pleurosternal carinae better developed, in ♂ slightly projecting caudad beyond rear margin at least until segment 15 **27**
- 26 Body smaller: width up to 3.1–3.2 mm. Mid-dorsal line very clear on both halves of metaterga. Gonopods relatively simple, with both **h** and **z** almost wanting..... *T. hoffmani*
- Body larger: width 4.0–5.3 mm. Mid-dorsal line not so well-developed at least on rear halves of metaterga. Gonopods more complex, with both **h** and **z** very conspicuous *T. baenzigeri*
- 27 Metatergum 19 slightly rugulose posteriorly. Calluses on segment 2 with three, on following paraterga with two, incisions. Gonopods extremely complex, with numerous spiniform outgrowths..... *T. perplexus*
- Metatergum 19 entirely smooth. Calluses with two or three incisions on poreless and poriferous paraterga, respectively. Gonopod less strongly differentiated..... *T. amicus*

Conclusions

Of a total of 55 species of *Tylopus* known now, Thailand supports as many as 29, followed by Vietnam (18 species), southern China (six species), Laos and Myanmar (two species each). The distributions of *Tylopus* spp. in Thailand, most of which are endemic to the country, are shown in Map 1.



Map I. Distribution of *Tylopus* species in Thailand (29 species): **1** Pha Mon Cave: *T. grandis* Likhitrakran et al., 2010 **2** Doi Inthanon: *T. affinis* Golovatch & Enghoff, 1993, *T. allorugosus* Golovatch & Enghoff, 1993, *T. asper* Golovatch & Enghoff, 1993, *T. degerboelae* Golovatch & Enghoff, 1993, *T. haplorugosus* Golovatch & Enghoff, 1993, *T. jeekeli* Golovatch & Enghoff, 1993, *T. perarmatus* Hoffman, 1973, *T. prosperus* Golovatch & Enghoff, 1993, *T. parajeekeli* Likhitrakran et al., 2010, *T. corrugatus* sp. n. **3** Ban Mussoe: *T. semirugosus* Golovatch & Enghoff, 1993 **4** Pa Wai Waterfall: *T. trigonum* sp. n. **5** Umphang District: *T. bispinosus* Likhitrakran et al., 2010 **6** Doi Suthep: *T. affinis* Golovatch & Enghoff, 1993, *T. allorugosus* Golovatch & Enghoff, 1993, *T. baenzigeri* Golovatch & Enghoff, 1993, *T. degerboelae* Golovatch & Enghoff, 1993, *T. doriae* (Pocock, 1895), *T. hoffmani* Golovatch & Enghoff, 1993, *T. jeekeli* Golovatch & Enghoff, 1993, *T. perarmatus* Hoffman, 1973, *T. similirugosus* Golovatch & Enghoff, 1993, *T. subcoriaceus* Golovatch & Enghoff, 1993 **7** Doi Chiang Dao: *T. degerboelae* Golovatch & Enghoff, 1993, *T. perarmatus* Hoffman, 1973, *T. rugosus* Golovatch & Enghoff, 1993 **8** Doi Pha Hom Pok: *T. amicus* Golovatch & Enghoff, 1993, *T. pallidus* Golovatch & Enghoff, 1993, *T. perplexus* Golovatch & Enghoff, 1993, *T. poolpermorum* Golovatch & Enghoff, 1993, *T. extremus* Likhitrakarn et al., 2010 **9** Buathong Waterfall: *T. rugosus* Golovatch & Enghoff, 1993 **10** Doi Phatang: *T. degerboelae* Golovatch & Enghoff, 1993, *T. perarmatus* Hoffman, 1973 **11** Ban Pang Rim Kon: *T. perarmatus* Hoffman, 1973 **12** Thum Pha Thai: *T. perarmatus* Hoffman, 1973 **13** Phucheefah: *T. perarmatus* Hoffman, 1973 **14** Nam Min Waterfall: *T. perarmatus* Hoffman, 1973 **15** Tham Pha Nang Khoi: *T. perarmatus* Hoffman, 1973 **16** Ton Tong Waterfall: *T. veliger* Likhitrakarn et al., 2010 **17** Phuluang Wildlife Sanctuary: *T. parahilaroides* sp. n. **18** Phu Kheoi: *T. coriaceus* Golovatch & Enghoff, 1993, *T. pulvinipes* Golovatch & Enghoff, 1993.

Almost all *Tylopus* species appear to be confined to montane forest habitats. In Thailand, *Tylopus* have only been taken from localities exceeding 500 m in elevation, except for Tham Pha Nang Khoi (275 m a.s.l) which solely supports the especially widespread *T. perarmatus*. In contrast, Doi Inthanon and Doi Suthep mountains each harbour as many as 10 species (Table 1), one of the highest values for congeners per local faunule among all Diplopoda, following perhaps the *madeirae*-group of *Cylindroiulus* endemic to Madeira, Portugal (29 spp., Enghoff 1982, Read 1989) or *Dolichoiulus* on Teneriffe, Canary Islands, Spain (21 spp., Enghoff 1992, 2012).

There is no doubt that more species of *Tylopus* will be found in the future, as at least the faunas of southern China, Myanmar, Laos and even Vietnam seem to be quite underrepresented compared to Thailand, while Cambodia is a completely blank area.

Acknowledgements

This project was partly funded by Chulalongkorn University Graduate School Post-doctoral Project to NL, while most of the financial support was received from The Thailand Research Fund, The TRF Senior Research Scholar RTA 5580001 (2012–2015) to SP. We thank the members of the Animal Systematics Research Unit for their invaluable assistance in the field. Special thanks go to Robert E. Mesibov, Penguin, Tasmania, Australia and William A. Shear, Hampden-Sydney, Virginia, U.S.A. for their thorough reviews of an advanced draft of the paper.

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The description of a new species of the Neotropical land crab genus *Gecarcinus* Leach, 1814 (Crustacea, Decapoda, Brachyura, Gecarcinidae)

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Academic editor: Joanne Taylor | Received 16 February 2014 | Accepted 29 July 2014 | Published 18 August 2014

<http://zoobank.org/9C499399-E236-4886-BC5A-AB9C8799066C>

Citation: Perger R, Wall A (2014) The description of a new species of the Neotropical land crab genus *Gecarcinus* Leach, 1814 (Crustacea, Decapoda, Brachyura, Gecarcinidae). ZooKeys 435: 93–109. doi: 10.3897/zookeys.435.7271

Abstract

In this contribution a new species of the land crab genus *Gecarcinus* Leach, 1814, from the Neotropical Pacific coast of South America is described and illustrated. In addition to its unique body color, *Gecarcinus nobilii* **sp. n.** is distinguished from congeners by a distinctly wider carapace front and differences in the shape of the infraorbital margin. The new species is not isolated from *Gecarcinus* populations from the Pacific coast of Central America by an insurmountable geographic barrier. Considering the closure of the Panamanian Isthmus as a calibration point for morphological divergence between the trans-isthmian mainland populations of *Gecarcinus*, the virtual lack of morphological differentiation (other than color) between them and the distinctness of *G. nobilii* **sp. n.** suggests that *G. nobilii* **sp. n.** evolved from a common ancestor before the Isthmus closed.

Keywords

Brachyura, Colombia, Ecuador, Gecarcinidae, *Gecarcinus*, Isthmus of Panama, Pacific, new species

Introduction

Land crabs of the genera *Gecarcinus* Leach, 1814, *Johngarthia* Türkay, 1970, and *Gecarcoidea* H. Milne Edwards, 1837, play an important ecological role on many tropical islands (see Lindquist et al. 2009 for a review). On some islands their biomass may exceed the total mass of animals reported in tropical rain forests in Costa Rica and the central Amazon (Lindquist et al. 2009) and they may occupy the top of the energy pyramid (Burggren and McMahon 1988). Nevertheless, despite their success on islands and the possibility of dispersal of their marine larvae via ocean currents, most species of these genera are absent from continental mainland habitats (Türkay 1987; see also Perger 2014 for a short review). Only *Johngarthia planata* (Stimpson, 1860) (see Perger 2014) and two populations of the Neotropical genus *Gecarcinus* are successfully established on the continental mainland. The Atlantic population, known as *Gecarcinus lateralis* (Fréminville, 1835), occurs along mainland beaches from Florida to Venezuela (Türkay 1970) and is partially sympatric with *G. ruricola* (Linnaeus, 1758), which is restricted to Western Atlantic islands. The distribution of the Pacific population, originally described as *G. quadratus* Saussure, 1853, extends along Pacific shorelines from Mexico to Peru (Türkay 1970).

Although both mainland populations of *Gecarcinus* have been separated by the definite closure of the Isthmus of Panama some three million years ago, the morphology of Pacific and Atlantic forms is so similar that Türkay (1970) treated *G. quadratus* as a subspecies of *G. lateralis*. As Türkay could not find any differences in the supplemental material he examined, he synonymized *G. lateralis quadratus* with *G. lateralis* (see Türkay 1973). The taxonomy of *Gecarcinus* has not been revised since Türkay's (1970, 1973) works: subsequent contributions on the ecology and general aspects of both trans-isthmian populations have followed Türkay's classification (e.g. Hartnoll 1988; Boyko 2000; Capistran-Barrados et al. 2003), while others maintained *G. quadratus* as a valid species without further justification (e.g. Abele and Kim 1986; Tavares 1991; Ng et al. 2008).

As in trans-isthmian *Gecarcinus*, the taxonomical status of the South American Pacific population has been uncertain. Whereas Nobili (1901) described specimens from the Ecuadorian coast as *G. ruricola*, following works do not distinguish between *Gecarcinus* from the Pacific coast of Central and South America and specimens from the latter have been referred to as *G. quadratus* (see Rathbun 1918), *G. lateralis quadratus* (see Türkay 1970; Prahll and Manjarres 1984) and *G. lateralis* (see Türkay 1987). To add further complexity, Prahll and Manjarres (1984) and Türkay (1987: Fig. 7) reported white forms of *Gecarcinus* from the Pacific coast of Colombia. However, such color forms have not been observed in other areas (see Bright 1966; Chace and Hobbs 1969; Martinez and Bliss 1989), nor were such color forms observed in a field sample of 678 individuals (carapace width 20–66 mm) from the Pacific and Atlantic coastline of Central America (Table 1; Fig. 1) that was examined by one of us (RP).

An Internet search revealed additional photographs of *Gecarcinus* individuals from the Pacific coast of South America with a body color different from the specimens that were collected on the Central American coasts. Further examination of

Table. 1. Locations, date, coordinates of conducted sampling and number of examined individuals of *Gecarcinus lateralis* (Fremenville, 1835) (*sensu* Türkay 1973) (carapace width 20–66 mm) (these crabs were subsequently used for analyses of stomach contents, dry weight, etc.).

Location	Date	Coordinates	N
Pacific coast			
Nicaragua, San Juan del Sur	15–17 July 2011	11°15' 39N; 85°52' 52W	54
Costa Rica, Pochote Beach	5–6 June 2011	9°44' 51N; 85°00' 01W	75
Costa Rica, Hermosa Beach	6–8 Nov. 2011	9°10' 07N; 83°45' 39W	69
Costa Rica, Drake Bay	16–18 Mar. 2011	8°41' 33N; 83°39' 42W	57
Panama, Santa Catalina	25–27 Oct. 2011	7°37' 39N; 81°14' 50W	60
Atlantic coast			
Costa Rica, Parismina	12–14 Nov. 2011	10°18' 34N; 83°20' 85W	56
Costa Rica, Puerto Viejo	26–28 May 2011	9°39' 20N; 82°44' 28W	68
Costa Rica, Manzanillo	20–22 Nov. 2011	9°37' 53N; 82°39' 47W	73
Costa Rica, Punta Mona	16–18 Nov. 2011	9°37' 24N; 82°37' 11W	123
Panama, Bocas del Toro, Bluff beach	10–12 Oct. 2011	9°23' 25N; 82°14' 14W	23
Panama, Maria Chiquita	20–22 Oct. 2011	9°26' 42N; 79°45' 44W	19

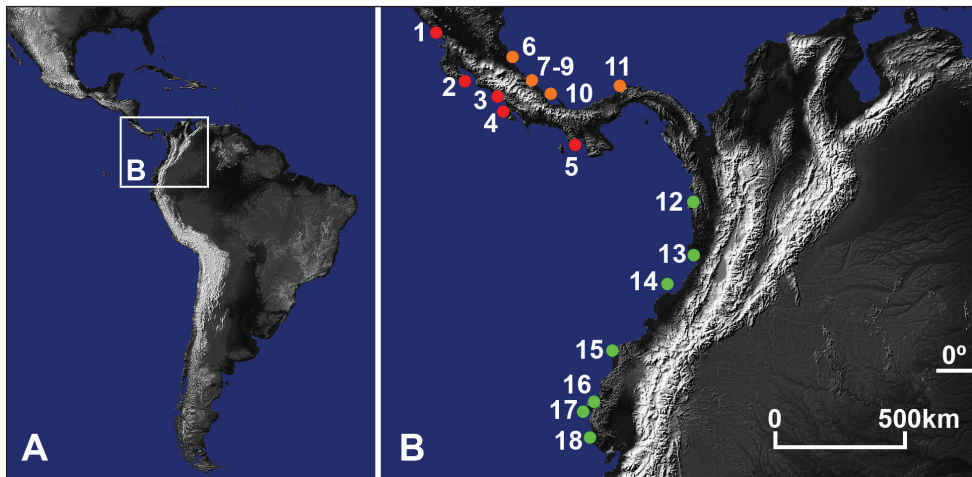


Figure 1. **A** Central and South America **B** Study area with locations of examined Pacific (red) and Atlantic (orange) *Gecarcinus lateralis* (Fremenville, 1835) (*sensu* Türkay 1973) and *G. nobilii* sp. n. (green). Nicaragua, Pacific coast: (1) Rivas, San Juan del Sur. Costa Rica, Pacific coast, Puntarenas dept.: (2) Pochote Beach; (3) Hermosa Beach; (4) Drake Bay. Panama, Pacific coast: (5) Veraguas, Santa Catalina. Costa Rica, Atlantic coast, Limón dept.: (6) Parismina; (7) Puerto Viejo; (8) Manzanillo; (9) Punta Mona. Panama, Atlantic coast: (10) Bocas del Toro, Bluff Beach; (11) Colón, Maria Chiquita. *G. nobilii* sp. n.: Colombia, Pacific coast: (12) Choco, Nuquí; (13) Buenaventura, Chucheros Beach; (14) Gorgona Island. Ecuador: (15) Esmeraldas, Punta Galera (type location); (16) Manabí, Ayampe; (17) Plata Island; (18) Santa Elena.

museum specimens and re-examination of the freshly collected specimens from Central America has revealed that the color differences are accompanied by differences in morphological structures as well. In accordance with these differences, a new species of *Gecarcinus* is herein proposed.

Specimens from the following institutions were examined: Academy of Natural Sciences of Drexel University, Philadelphia, USA (ANSP); Natural History Museum of Los Angeles County, Los Angeles, USA (LACM); Muséum National d'Histoire Naturelle, Paris, France (MNHN); Museo de Zoología, Universidad de Costa Rica, San José, Costa Rica (MZUCR); Naturhistorisches Museum, Basel, Switzerland (NHMB) and National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM).

Taxonomy

Gecarcinus Leach, 1814

Gecarcinus Leach, 1814:430.

Type species. *Cancer ruricola* Linnaeus, 1758 (original combination).

Diagnosis. Exopod not projecting beyond third maxilliped ischium-merus articulation, without flagellum; palp concealed by third maxilliped merus margin. Mesial segment of first male gonopod distally reduced and terminal segment basally exposed, terminal segment projecting beyond apical setae.

Remarks. Because further evidence challenging Türkay's (1973) synonymization of *G. quadratus* with *G. lateralis* has not been presented to date, we follow his taxonomy and treat *G. quadratus*, described from the Pacific mainland, as a junior synonym of *G. lateralis*.

Key to the species of *Gecarcinus* Leach, 1814

- 1 Mesial lobe of infraorbital margin curved around ventrolateral edge of carapace front. Third maxilliped merus covers epistome and can reach carapace front. Spines on lateral carina of dactylus and carpus of ambulatory legs prominently developed in adults..... ***G. ruricola* (Linnaeus)**
- Contact between carapace front and mesial lobe of infraorbital margin straight (Fig. 2B, C). Third maxilliped merus at the farthest reaching epistome. Spines on lateral carina of dactylus and carpus of ambulatory legs weakly developed to absent..... **2**
- 2 Carapace front wider than distance between mesial ends of suborbital cristae (Figs 2C; 3B). Width of mesial lobe of infraorbital margin at point of contact with carapace front longer than shortest distance between carapace front and mesial end of suborbital crista (Figs 2C; 3B). Light lateral margin on dorsal carapace without lighter anterolateral and posterior patches (Figs 4C; 5D) ...
..... ***G. nobilii* sp. n.**
- Carapace front about as wide as distance between mesial ends of suborbital cristae (Figs 2B; 6B, E). Width of mesial lobe of infraorbital margin at

point of contact with carapace front shorter than shortest distance between carapace front and mesial end of suborbital crista (Figs 2B; 6B, E). Without light lateral margin on dorsal carapace (Pacific, Fig. 5A; Atlantic, Fig. 5C) or with light lateral margin with anterior and posterior yellow to orange patches (Atlantic, Fig. 5B) *G. lateralis* (Fréminville)

***Gecarcinus nobilii* sp. n.**

<http://zoobank.org/F3BA2617-49DF-4C26-ACB5-5407122301FF>

Figs 2C–E; 3; 4; 5D

Gecarcinus ruricola. – Nobili 1901: 46.

Gecarcinus (*Gecarcinus*) *lateralis quadratus*. – Türkay 1970: 338. – Prahel and Manjarres 1984: 155.

Gecarcinus lateralis. – Türkay 1987: 147, fig. 7.

Material examined. Holotype: male, carapace width (CW) 31 mm, Ecuador, Punta Galera, 0°50'N, 80°6'W, shore, collected near a pile of fairly fresh cow manure, Te Vega Expeditions, Sta. NO. XVIII-6, 22 April 1968. Coll. E. Ball (LACM CR 1968-477). Paratypes: 1 male, CW 26 mm, same location data as holotype (LACM CR 1968-478); 1 female, Ecuador, St. Elena (MNHN- B12314); 3 females, CW 28, 23, 23.5 mm, Ecuador, Esmeraldas (NHMB-NMB1010b). (Note: The female paratype (MNHN-B12314) (Fig. 3D–F) of *G. nobilii* sp. n. was labeled as "*Gecarcinus festae* Nobili/(co-type)/St. Helena/Festa/Museum Paris/Ecuador/Nobili 1901" without information about the label author. Nobili never published a description of a species by this name. In 1901 he described *Sesarma festae* and *Uca festae* and in the same contribution referred to specimens of *Gecarcinus* collected in Ecuador as *Gecarcinus ruricola*, which is restricted to West Atlantic Islands (Türkay 1970; Bright and Hogue 1972).

Additionally, high resolution photographs of 14 captive individuals with unknown origin and 17 individuals taken at the following locations (confirmed by the photographers): Gorgona Island (Colombia) (Fig. 4A–C), Chucheros Beach (Buenaventura, Colombia) (Fig. 4D), Canangucho Forest Reserve (Nuquí, Chocó, Colombia) (Fig. 4E), Ayampe (Manabí, Ecuador) (Fig. 4F), and Isla de la Plata (Ecuador), were examined.

Comparative material. *Gecarcinus lateralis* (Fréminville, 1835): lectotype male, CW 47.2 mm, Guadeloupe, M. Beaupertius leg. (MNHN-3758). Paralectotypes: 1 male, CW 50 mm, Guadeloupe, M. Beaupertius leg. (MNHN-3757); 1 female, CW 28 mm, same data as preceding specimen. 1 male, CW 32 mm, Martinique, M. Bellanger leg. (MNHN-3756); 1 female, CW 37 mm, Martinique, Bellanger leg., 24.09.1964 (MNHN-3755). *Gecarcinus quadratus* Saussure, 1853: syntype male, CW 39.7 mm, Mexico, Mazatlan (ANSP-CA3741). Pacific *G. lateralis* (*sensu* Türkay 1973): 1 male, Mexico, Sinaloa, Estero el Verde (MNHN-B20900). 1 male, Costa Rica, Guanacaste, Playa del Coco, 5.8.1967, W. McCaul leg. (MZUCR13-01). 1 male, 1 female, Costa

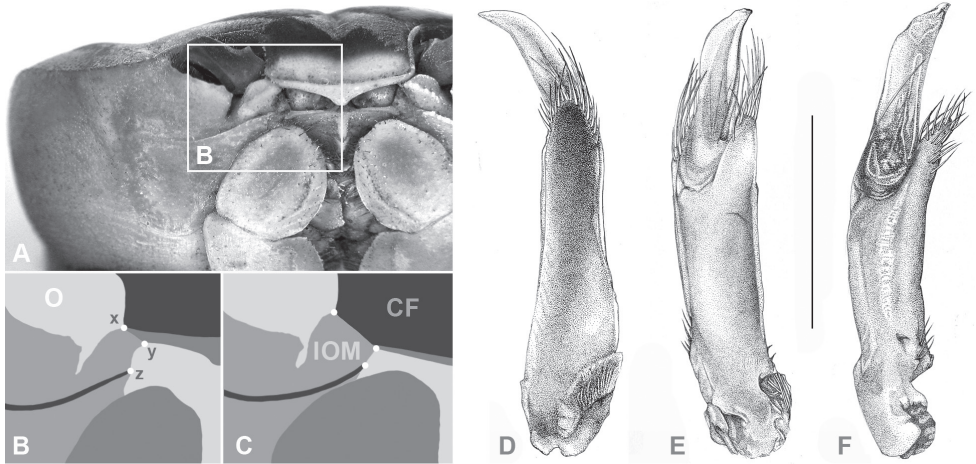


Figure 2. (CF) Carapace front; (O) orbit; (IOM) mesial lobe of infraorbital margin; (x) widest width of CF; (z) mesial end of suborbital crista; (x–y) width of IOM at point of contact with CF; (y–z) shortest distance between CF and mesial end of suborbital crista; **A, B** Atlantic *Gecarcinus lateralalis* (Fremenville 1835), male, carapace width (CW) 31 mm, Costa Rica, Puerto Viejo **C** *G. nobilii* sp. n., holotype, male, CW 31 mm, Ecuador, Punta Galera (LACM CR 1968–477). First male gonopod: *G. nobilii* sp. n., holotype: **D** mesial view **E** lateral view **F** Pacific *G. lateralalis* (*sensu* Türkay 1973), CW 31 mm, Costa Rica, Hermosa Beach, lateral view; Scale bar = 5 mm.

Rica, Puntarenas, Parque Nacional Manuel Antonio, 4.2.1995, J. Cortés leg. (MZU-CR-2016). 1 male, Panama, Canas Island, Los Santos, Turtle Hatchery on S Beach, J. Frazier leg. (USNM-190711). Additional comparative material is cited in Table 1.

Derivation of specific epithet. The species is named in honor of Giuseppe Nobili, who provided important contributions on the knowledge of crustaceans and built the crustacean collection in the Turin Museum (Italy). The species name is a noun in the genitive case.

Diagnosis. Frontal width distinctly wider than the distance between the mesial ends of the suborbital cristae (Figs 2C; 3B, E). Width of mesial lobe of infraorbital margin at point of contact with carapace front longer than shortest distance between carapace front and mesial end of suborbital crista (Figs 2C; 3B, E). Light lateral margin on dorsal carapace without lighter anterolateral and posterior patches (Figs 4C; 5D); cheliped carpus and palm homogeneously red or white (Fig. 4).

Description. Carapace transversely ovate, widest in anterior half, dorsal surface smooth. Cardiac, gastric and branchial chambers moderately swollen (Fig. 3B, E). Median groove distinct, cervical and urogastric grooves weakly developed; three relatively small pits anterior (close to orbit), median and posterior of cervical groove, one in urogastric groove (Fig. 3A). Supraorbital margin gently sinuous, with small granules, confluent with anterolateral margin; exorbital tooth weakly developed, tip not over-reaching orbit (Fig. 3B, D, E); granules along anterolateral and orbital margins weakly developed. Eyes well developed, filling orbital cavity; eyestalks short

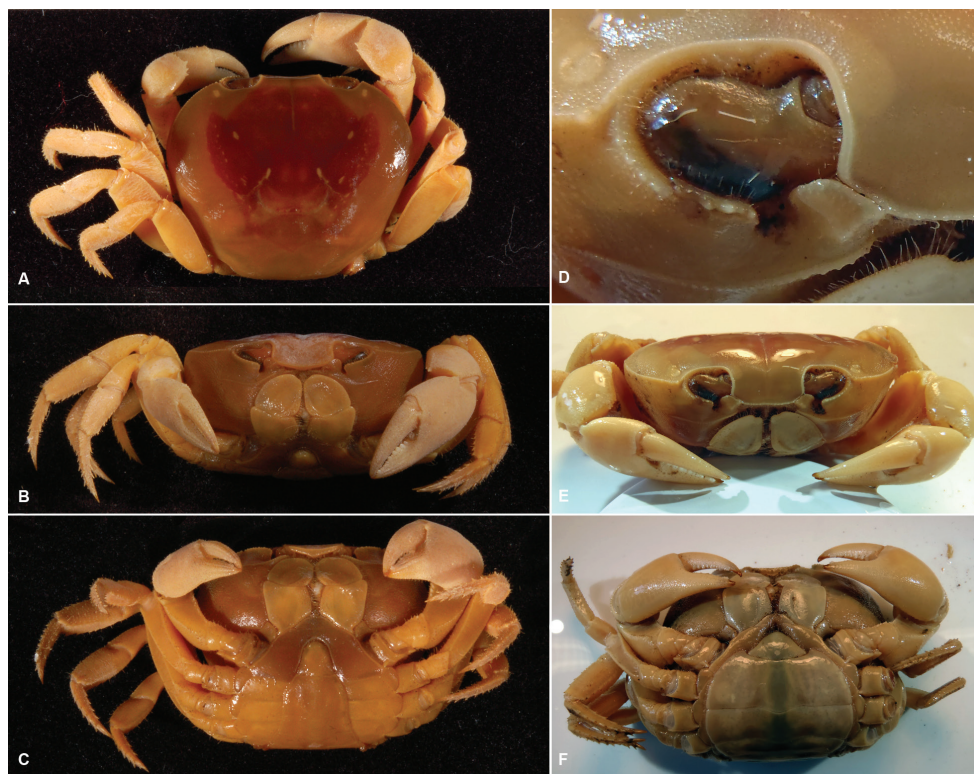


Figure 3. *Gecarcinus nobilii* sp. n., holotype, male, carapace width 31 mm, Ecuador, Punta Galera (LACM CR 1968-477), preserved in alcohol (color faded): **A** dorsal view **B** frontal view **C** ventral view. Paratype, female, Ecuador, St. Elena (MNHN, B12314), preserved in alcohol (color faded): **D** carapace front **E** frontal view **F** ventral view.

(Fig. 3B, E). Carapace front distinctly wider than the distance between mesial ends of the suborbital cristae (Figs 2C; 3B, E), deflexed downwards, concealing basal segments of antennules. Width of mesial lobe of infraorbital margin at point of contact with carapace front longer than shortest distance between carapace front and mesial end of suborbital crista (Figs 2C; 3B, D; 4H). Suborbital, pterygostomial regions sparsely granular laterally. Subhepatic region with rounded postero-lateral margins, with rows of small granules. Epistom linear, sunken.

Third maxilliped merus and outer ventral orbital border furnished with long setae (Fig. 3D); third maxilliped merus enlarged, reaching mesial border of suborbital crista, triangular, apex straight or moderately convex (Figs 3B, 4I); exopodit short, not protruding beyond third maxilliped ischium-merus joint, without flagellum; palpus concealed by external border of third maxilliped merus.

Chelipeds subequal; in large males larger with respect to the carapace width, surfaces relatively smooth, weakly granulate. Merus with transversal rows of small tubercles; dorsal margin rugose or with moderately developed, obtuse granules; ventral

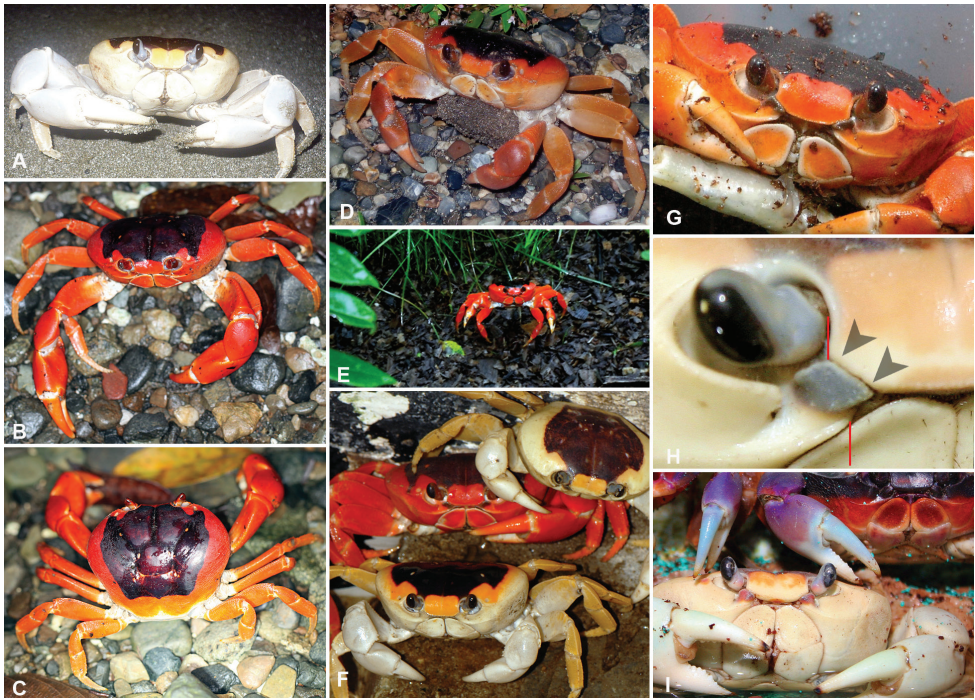


Figure 4. *Gecarcinus nobilii* sp. n., color in life; Colombia: Gorgona Island **A** male, photo by Karla Garcia Burneo (Peru) **B**, **C** male, photos by Rhett A. Butler (USA) **D** female, Buenaventura dept., Chucheros Beach, photo by Elena Gómez **E** sex unknown, Chocó dept., Nuquí prov., Canangucho Forest Reserve. Ecuador: **F** sex unknown, Manabí prov., Ayampe, photo by David Liebman (USA). Captive individuals from the pet trade, origin unknown: **G** sex unknown, photo by Oliver Mengedocht (Germany) **H**, **I** females, photos by John Beatty (USA) (the individual shown above in Fig. **I** belongs to the Pacific population of *G. lateralis* (sensu Türkay 1973), please note the differences in the mesial lobe of the infraorbital margin).

margin lined with weakly developed granules, otherwise smooth. Carpus with 2–5 well developed triangular inner subdistal tooth (Fig. 3A, B, E). Merus and carpus margins smooth in large individuals. Chela large, length not exceeding carapace width, surfaces smooth; lower margin gently sinuous. Fingers slightly shorter or as long as palm, tapering, gently curved, drop-shaped in cross-section, proximal half with irregular arranged pores and low, pectinated teeth; teeth on distal portion of finger arranged on well defined, subparallel longitudinal ridges, longitudinally separated by grooves with pores. Cutting margins with distinct triangular teeth along length; fingers without or with small gap between them when closed, ending in sharp, pectinated tips.

Ambulatory legs with second pair longest, last pair shortest; surfaces smooth to slightly rugose. Merus dorso-laterally flattened, cross-section triangular, stout; with transversal rows of small tubercles, dorsal margin distinct, granulated, with separate, short setae. Carpus stout, subtriangular in cross-section; dorsal surface with three carinae, median carina distinct, serrated or granular; dorso-lateral carinae weakly developed or absent; margins and carinae lined with separate, short setae. Propodus sub-

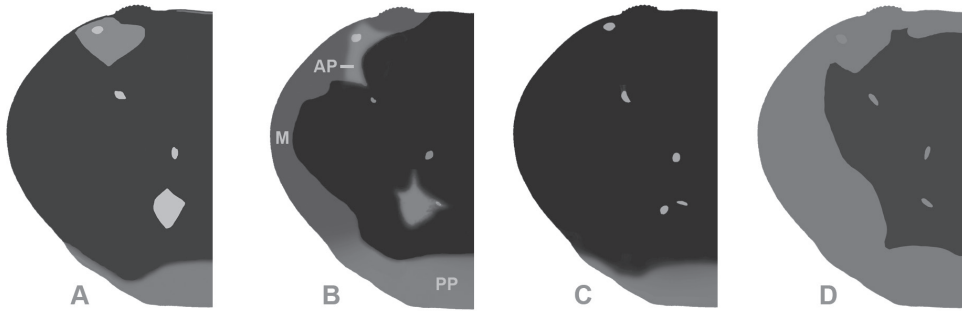


Figure 5. Dorsal carapace pattern (shape of light patches could vary slightly): *Gecarcinus lateralis* (Frem-inville 1835) (*sensu* Türkay 1973): **A** Pacific coast of Central America. Atlantic coast of Central America: **B** form with lateral margin (**M**) on dorsal carapace and orange patches at anterolateral (**AP**) and posterior (**PP**) carapace border; **C** form without lateral margin on dorsal carapace **D** *Gecarcinus nobilii* sp. n.

rectangular in cross-section; lateral margins subparallel, lined with low, obtuse spines and separate, short setae (Fig. 3A–C). Dactylus elongate, styliform, gently curving, subquadrate in cross-section, margins lined with distinct spines and separate, short setae; apical half of spines and dactylus tip corneous; lateral carina of dactylus weakly developed or absent (Fig. 3A–C).

Male abdomen relatively broad (Fig. 3C), all abdominal somites and telson distinct, freely articulating. Somite 1 filling space between last pair of ambulatory legs, longitudinally very narrow. Shape of somite 2 similar to somite 1 but narrower. Somites 3–5 increasingly trapezoidal in shape, lateral margins relatively straight. Somite 6 longest, longer than telson, distinctly wider than long, with lateral margin strongly convex. Telson sub-triangular, narrowest abdominal segment; as long as wide, lateral margins gently concave to almost straight, tip rounded (Fig. 3C).

First male gonopod with basal and terminal segment (Fig. 2E). Basal segment stout, straight, with digiform projection on distomesial end, projection directed in same manner with distal segment, fringed with long setae. Terminal segment about one-third of first gonopod (when seen from lateral view, Fig. 2E), folded longitudinally, compressed dorsoventrally, tapering and curved distally, slightly projecting over distal setae, laterally with narrow, longitudinal furrow.

Sex independent color dimorphism: red and white males and females (Fig. 4). Both forms with dark median pattern and contrasting light lateral margin on dorsal carapace without lighter anterior and posterior patches (Fig. 5D), margin of same color as lateral carapace; dark dorsal carapace pattern with pointed anterolateral edges anteriorly reaching the orbits (Fig. 5D). Mesial lobe of infraorbital margin mostly grey (Fig. 4). Red form with red lateral margin on dorsal carapace. Carapace pits white to orange. Legs and chelipeds uniformly red, inner sides of fingers cream to white, margin of the third maxilliped merus, coxa, basis and ischium of chelipeds and ambulatory legs whitish. In white form, lateral margin on dorsal carapace orange/white or completely white. Ventral carapace and chelipeds white, legs and carapace pits light orange to white (Fig. 4).

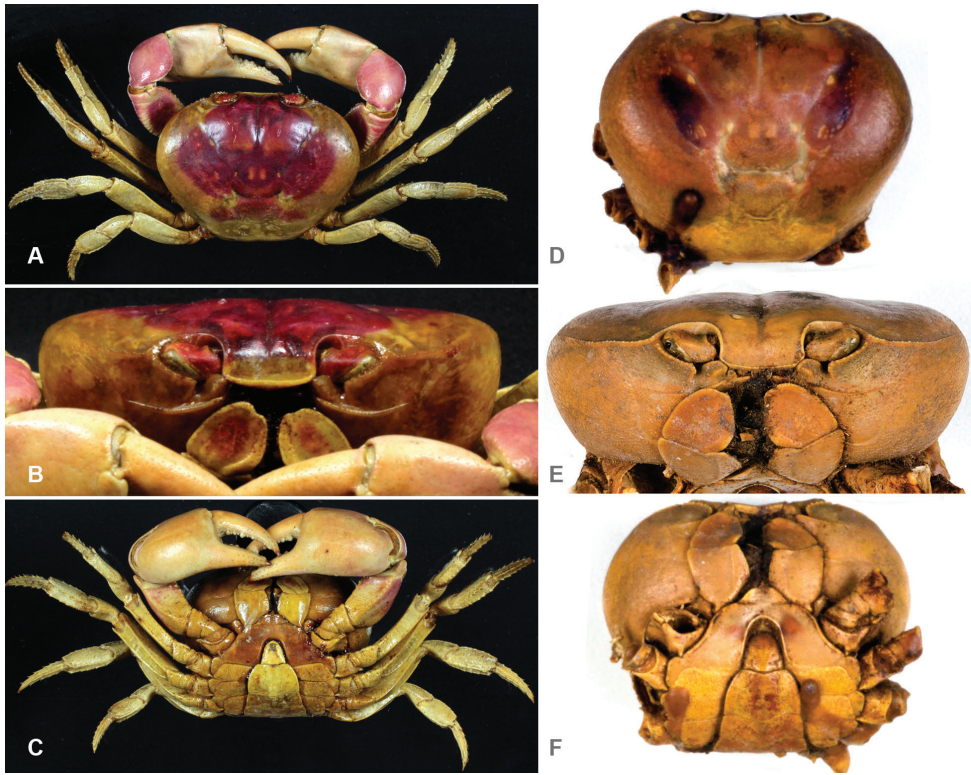


Figure 6. **A–C** lectotype of *Gecarcinus lateralis* (Fremenville, 1835), male, carapace width 47.2 mm, Guadeloupe (MNHN-3758) (dried specimen, color faded) **D–F** syntype of *G. quadratus* Saussure, 1853, male, carapace width 39.7 mm, Mexico, Mazatlan (ANSP-CA3741) (dried specimen, color faded) (photos by Paul Callomon, Academy of Natural Sciences of Drexel University, Philadelphia).

Geographic distribution. *G. nobilii* sp. n. is currently known to occur from Punta Galera and St. Elena (Ecuador). It is also documented in photographs taken at Gorgona Island (Colombia) (Fig. 4A–C), Chucheros Beach (Buenaventura, Colombia) (Fig. 4D), Canangucho Forest Reserve (Nuquí, Chocó, Colombia) (Fig. 4E), Ayampe (Manabí, Ecuador) (Fig. 4F), and Isla de la Plata (Ecuador). Individuals of *Gecarcinus* previously reported from Peru (Türkay 1970) may also refer to *G. nobilii* sp. n.

Available data and the photographs found during the Internet search suggest that *G. nobilii* sp. n. replaces Pacific *G. lateralis* between the Darien province (Panama) and the Choco dept. (Colombia). In addition to the individuals of Pacific *G. lateralis* found during fieldwork (Table 1), the Internet search revealed numerous photographs of Pacific *G. lateralis* from Central America. However, there are no photographs of Pacific *G. lateralis* from within the distributional area of *G. nobilii* sp. n.

Remarks. The resemblance of the general habitus, the shape and the surface structure of carapace, chelipeds, ambulatory legs (Figs 3; 6–8) and the first male gonopod (Fig. 2E, F) indicate a close relationship between all mainland *Gecarcinus* populations.

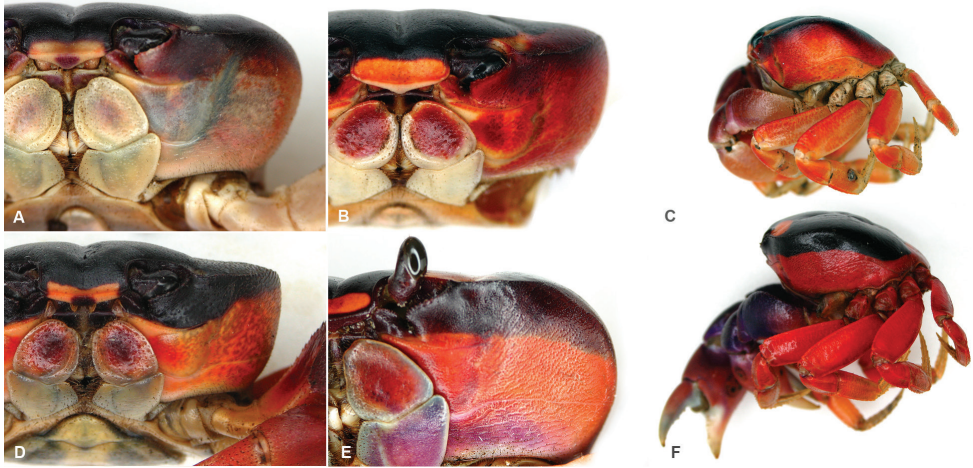


Figure 7. *Gecarcinus lateralis* (Fremenville, 1835) (*sensu* Türkay 1973), frontal and lateral views, color in life, in hard-shell condition. Atlantic coast: Costa Rica, Puerto Viejo: **A** male, carapace width (CW) 44 mm **B**, **C** male, CW 29 mm **D** female with contrasting dorso- and ventrolateral color, CW 32 mm. Pacific coast: Costa Rica, Playa Hermosa: **E** male, CW 58 mm **F** male, CW 38 mm.

However, the trans-isthmian populations of *G. lateralis* differ from *G. nobilii* sp. n. by having a carapace front approximately as wide as the distance between the mesial ends of the suborbital cristae, and the width of the mesial lobe of the infraorbital margin at the point of contact with the carapace front is shorter than the shortest distance between the carapace front and the mesial end of the suborbital crista (Figs 2B; 6B, E; 7A, B).

A character commonly used to distinguish between species of the Gecarcinidae is the shape of the third maxilliped merus margin (e.g. Rathbun 1918; Türkay 1970; Perger et al. 2011). According to Rathbun (1918), the Atlantic population of *G. lateralis* has an emarginated margin and the Pacific population a continuous margin. However, Bott (1955) and Türkay (1970, 1973) recognized the presence of both character states in trans-isthmian populations from Central America, South America and the Antilles, which we also observed in our sample from Central America. In contrast, all examined specimens of *G. nobilii* sp. n. have a relatively continuous third maxilliped margin.

In addition to observed differences in morphological structures, the body color of Pacific *G. lateralis* (*sensu* Türkay 1973) differs from *G. nobilii* sp. n. in the following manner: Dorsal carapace without light lateral margin (Fig. 5A), dark dorsal carapace pattern extending laterally over anterolateral carapace border (Fig. 7E, F); orange patch at anterolateral and posterior carapace border (Figs 5A; 8G, H). Cheliped carpus and palm violet, rarely purplish (Fig. 8G, H). Atlantic *G. lateralis* are distinguished from *G. nobilii* sp. n. by following color differences: Light lateral margin on dorsal carapace with lighter (yellow to orange) patch at anterolateral and posterior carapace border (Figs 5B; 8A, B) or margin and anterolateral patch absent (Figs 5C; 8D–F). Ventrolateral carapace color heterogeneous (Fig. 7A–C). Cheliped carpus and palm heterogeneously purple, red, orange and/or whitish (Fig. 8A–F).



Figure 8. *Gecarcinus lateralis* (Freminville, 1835) (*sensu* Türkay 1973), dorsal view, color in life, in hard-shell condition. Atlantic coast, Costa Rica, Puerto Viejo, showing the forms limiting the range of color variability: **A** male, carapace width (CW) 39 mm **B** male, CW 29 mm **C** female, CW 32 mm **D** male, CW 44 mm **E** male, CW 47 mm **F** female, CW 33 mm. Pacific coast: Costa Rica, Playa Hermosa: **G** male, CW 58 mm **H** male, CW 38 mm.

Apart from the consistent color differences between *G. nobilii* sp. n. and the other mainland populations of *Gecarcinus*, which provided the starting point for this contribution, the color differences between the trans-isthmian populations of *Gecarcinus* (Table 2; Figs 5A–C; 7; 8) also drew our attention. According to Bright (1966), *Gecarcinus* from the Pacific coast of Central America has a brownish-red carapace and chelipeds with a purple tinge, while *G. lateralis* from the Atlantic coast of Central America has a dark red carapace pattern and reddish-gray chelipeds. Chace and Hobbs (1969) provided the first color description of *G. lateralis* from the West Indies, which widely agreed with the brief description of the *Gecarcinus* specimens from the Pacific coast of Central America by Bright (1966). Martinez and Bliss (1989) later described and illustrated the color of *G. lateralis* from Bermuda and Bimini Islands in detail. The authors observed a remarkable variability in color and even color changes in single individuals, leaving open the possibility that Pacific *G. lateralis* might also approach the range of variability observed in Atlantic *G. lateralis*.

Table 2. Comparison of color in life for mainland *Gecarcinus* spp. (carapace width of *G. lateralis* (Freminville, 1835) (*sensu* Türkay 1973) 20–66 mm); (IOM) mesial lobe of infraorbital margin; (SUB) suborbital crista; (ACB) anterolateral carapace border.

	Atlantic <i>G. lateralis</i> (n=362)	Pacific <i>G. lateralis</i> (n=316)	<i>G. nobilii</i> sp. n. (n=19)
Color polymorphism	Morphs with transitional forms	-	Red and white forms
Light lateral margin on dorsal carapace	Present or absent, when absent, dark median pattern laterally extending over ACB with smooth transition to color of ventrolateral carapace	Absent, dark median pattern laterally extending over ACB, anteriorly mostly reaching SUB, with sharp contrast to color of ventrolateral carapace	Present, contrasting to dark median pattern, same color as lateral carapace, in some white forms with orange tinge
Orange patch at anterolateral carapace border	In forms with lateral margin on dorsal carapace, patch with smooth transition to bordering color, only posteriorly bordered by dark carapace pattern; patch absent in forms without light lateral margin on carapace	Always present, encircled by dark, sharply contrasting dorsal carapace color	Absent
Patch at posterior lateral urogastric groove	In forms with lateral margin on dorsal carapace heterogeneously yellowish, grayish, cream, sometimes with smooth transition to lateral margin; weakly developed to absent in forms without lateral margin	Homogeneously whitish, subtriangular to rhomboid, well defined, sharply contrasting with surrounding dark carapace color	Absent
Ventro-lateral carapace color	Heterogeneous, transition between dorsal and ventral carapace color	Uniformly bright deep orange to red, sharply contrasting to dorsolateral carapace color	Homogeneously red or white
Cheliped palm color	Orange to red, often with purple tinge anteriorly, or orange-purplish-whitish	Deep violet, sometimes with purplish tinge	Uniformly red or white
Cheliped dactylus color	Light orange, orange to light red, cutting edges cream	Completely white or base light violet, purplish, becoming white distally	Red or white, cutting edges cream or white
IOM color	As suborbital area		Mostly grey

While the color of examined *G. lateralis* from the Atlantic coast (n= 362) varied within the range described by Martinez and Bliss (1989) (see Fig. 8A–F), the color of individuals of Pacific *G. lateralis* examined in this study (n= 316) showed little variation (Fig. 8G, H) and did not approach the range of variability found in *G. lateralis* from the Atlantic coast of Central America (Table 2) and Bermuda and Bimini Islands (see Martinez and Bliss 1989). In a sample totaling 678 individuals, only a single female from the Atlantic coast (Fig. 7D) did not clearly match with each of the color characters attributed to either the Atlantic and Pacific population (Table 2). This individual had a dark dorsal carapace color expanding laterally over the dorsolateral carapace border and sharply contrasting with the ventrolateral carapace color. However, the remaining characters (Table 2) agreed with the other individuals of Atlantic *G. lateralis*. Within several groups of decapod crustaceans, color and color pattern reli-

ably distinguish a number of species that differ little in morphology (e.g. Bruce 1975; Knowlton 1986). Color pattern-level and genetic differentiation between cryptic species has been observed in hermit crabs (e.g. Malay and Paulay 2009), spiny lobsters (Ravago and Juinio-Menez 2003), porcelain crabs (Hiller et al. 2006) and in the Gecarcinidae genus *Discoplax* A. Milne-Edwards, 1867 (Ng and Davie 2012).

Studies of genetic divergence and reproductive isolation are needed to evaluate whether *G. quadratus* should be retained as a synonym of *G. lateralis*, or alternatively, the trans-isthmian populations of *G. lateralis* represent allopatric sister species.

Evolutionary relationships. When we consider the closure of the Panamanian Isthmus as a calibration point for morphological divergence between the trans-isthmian populations of *G. lateralis*, the virtual lack of morphological differentiation (other than color) between them and the distinctness of *G. nobilii* sp. n. suggests that *G. nobilii* sp. n. evolved from a common ancestor before the Isthmus closed. The common ancestor of the trans-isthmian *G. lateralis* may have been restricted to North America and/or the emerging Isthmus, which is assumed to have been a peninsula of North America (Kirby et al. 2008), and the ancestor of *G. nobilii* sp. n. to South America. Nevertheless, the distribution of the gecarcinid *Johngarthia planata* Stimpson, 1860, from Gorgona Island to Mexico (reviewed by Perger et al. 2013) and *Cardisoma crasum* Smith, 1870, from Peru to Mexico (Türkay 1970) as well as the absence of *G. nobilii* sp. n. from the Atlantic coast of South America suggests a more complex pattern. A promising approach to further investigation of the speciation processes in Neotropical Gecarcinidae may be the evaluation of how the connection between the habitats of the adults via sea currents may have changed during the formation of the Isthmus (see Schneider and Schmittner 2006; Molnar 2008). Further studies should also take into account that even today, as indicated by the actual distribution, there appear to be mechanisms separating the *Gecarcinus* populations from the Central and South American Pacific coast.

Acknowledgments

We wish to extend a hearty thanks to Oliver Mengedoht (Germany), Elena Gómez, David Liebman, John Beatty, Rhett A. Butler (USA) and Karla Garcia Burneo (Peru) for granting us permission to publish their photographs. We are very grateful to Paula Martin-Lefevre (Muséum National d'Histoire Naturelle, Paris), Edgar Stöckli (Naturhistorisches Museum, Basel, Switzerland), Paul Callomon (Academy of Natural Sciences of Drexel University, Philadelphia), Karen Reed and Katie Ahlfeld (Smithsonian Institution, Washington, D.C.) for providing photographs and data of museum specimens. Martha Iserman (bigredsharks.com) is thanked for their drawings of the gonopods. RP thanks to Jorge Cortés, Cristian Pacheco, and Rita Vargas (Universidad de Costa Rica, San José, Costa Rica) for supporting this project and for providing an abundance of insight and information, and to David Wilcox (USA), Joanne Taylor

(Museum Victoria, Melbourne, Australia) and the anonymous reviewers for providing comments and suggestions on the manuscript.

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A new species of the *Boophis rappiodes* group (Anura, Mantellidae) from the Sahamalaza Peninsula, northwest Madagascar, with acoustic monitoring of its nocturnal calling activity

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Academic editor: Johannes Penner | Received 26 February 2014 | Accepted 5 August 2014 | Published 18 August 2014

<http://zoobank.org/75D14A2F-AC23-4EC7-B7C5-3F9F66AC0C52>

Citation: Penny SG, Andreone F, Crottini A, Holderied MW, Rakotozafy LS, Schwitzer C, Rosa GM (2014) A new species of the *Boophis rappiodes* group (Anura, Mantellidae) from the Sahamalaza Peninsula, northwest Madagascar, with acoustic monitoring of its nocturnal calling activity. ZooKeys 435: 111–132. doi: 10.3897/zookeys.435.7383

Abstract

A new species of treefrog of the *Boophis rappiodes* group (Anura, Mantellidae) is described from the Sahamalaza – Iles Radama National Park in northwest Madagascar. This new species is green in colour with bright red speckling across its head and dorsum; similar in morphology to other species of this group including: *B. bottae*, *B. rappiodes*, *B. erythrodactylus* and *B. tasymena*. The new species can be distinguished by its advertisement call and by a genetic divergence of more than 4.9% in the analysed mitochondrial

16S rRNA gene fragment. Its call consists of two note types: a trill and a click; although similar sounding to *B. bottae*, the trill note of the new species has a faster pulse rate while the click note is predominantly two-pulsed rather than three. All individuals were detected from the banks of two streams in Ankarafa Forest. The new species represents the only member of the *B. rappiodes* group endemic to Madagascar's western coast, with the majority of other members known from the eastern rainforest belt. Despite its conspicuous call, it has not been detected from other surveys of northwest Madagascar and it is likely to be a local endemic to the peninsula. The ranges of two other amphibian species also appear restricted to Sahamalaza, and so the area seems to support a high level of endemism. Although occurring inside a National Park, this species is highly threatened by the continuing decline in the quality and extent of its habitat. Due to these threats it is proposed that this species should be classified as Critically Endangered according to the IUCN Red List criteria.

Keywords

Amphibia, *Boophis ankarakensis* sp. n., Sahamalaza – Iles Radama National Park, advertisement call, conservation

Introduction

The genus *Boophis* is a monophyletic group of treefrogs belonging to the family Mantellidae. Endemic to Madagascar and the Comoros, the group comprises over 70 species, many of which have only recently been described (Köhler et al. 2007, 2008, 2011; Wollenberg et al. 2008; Glaw et al. 2010; Vallan et al. 2010; Vences et al. 2010, 2012). The genus is classified into two subgenera, *Boophis* and *Sahona*, which largely correlate with breeding habit; the nominal *Boophis* being predominantly stream-breeders, and the *Sahona* pond-breeders (Glaw and Vences 2006). Of the two subgenera, *Boophis* is the most speciose and can be further divided into eight groups, although at least some of these appear to be paraphyletic and await taxonomic revision (Glaw et al. 2010). Among these is the *rappiodes* group – small, green treefrogs with red pigment patches and partially translucent skin – an appearance shared with the neotropical glass frogs of the family Centrolenidae (Vences and Glaw 2002; Glaw and Vences 2007; Köhler et al. 2007). As with most Malagasy amphibian diversity, the majority of members of the *rappiodes* group can be found in the eastern rainforests, and until now there have been no documented species from the drier forests of the western coast (Vences and Glaw 2002; Glaw and Vences 2007).

The Sahamalaza Peninsula in north-western Madagascar has undergone only two previous amphibian surveys (Andreone et al. 2001; Raselimanana 2008); the most recent of which led to the discovery of *Boophis tsilomaro* and *Cophyla berara* (Vences et al. 2005, 2010). However, one site on the peninsula, the Ankarafa Forest, had never been surveyed before. From this forest we describe a new species of *Boophis*, molecularly assigned to the *rappiodes* group, vocally distinct and genetically different to all other known species of this monophyletic group.

Methods

Study sites and survey periods

The Sahamalaza Peninsula is in the province of Mahajanga, northwest Madagascar (Fig. 1). Parts of the peninsula were declared the Sahamalaza – Iles Radama National Park in July 2007 and have been included in UNESCO's network of Biosphere Reserves since 2001 (Schwitzer et al. 2007). The peninsula covers around 26,000 ha and is characterised by a number of low hills of about 300–350 m a.s.l. intersected by a few largely seasonal streams (Andreone et al. 2001). Located between 13°52'S and 14°27'S, and 45°38'E and 47°46'E, it is defined by the Sahamalaza Bay to the east, the Mozambique Channel to the west and the Loza River to the south (Volampeno 2009).

The climate is sub-humid and has two distinct seasons: a cooler, drier season from May to November; and a hotter, wetter season from December to April. Monthly mean maximum temperature ranges from 28.5 ± 3.61 °C in July to 39.1 ± 2.11 °C in February; and monthly mean minimum temperature ranges from 13.2 ± 0.81 °C in October to 21.8 ± 0.81 °C in January (Volampeno et al. 2011). Rainfall is highest during January and February and the mean annual precipitation rate is around 1,600 mm (Schwitzer et al. 2007).

Sahamalaza supports a unique type of transitional forest that harbours plant species from both the wetter Sambirano domain and drier western domain (Birkinshaw 2004; Schwitzer et al. 2006). This forest is concentrated in two separate blocks: Anabohazo in the northeast (14°18.56'S, 47°54.89'E) and Ankarafo in the west (14°22.82'S, 47°45.46'E) (Schwitzer et al. 2007). Until recently a third block existed, called Analavory Forest (14°23.30'S, 47°56.15'E), but it experienced near complete destruction following an uncontrolled man-made fire in 2004 (Volampeno 2009). The forest blocks are composed of a matrix of smaller fragments isolated by savannah with high levels of human disturbance (Schwitzer et al. 2007).

Fieldwork took place over two separate periods: a three month survey between October 2011 and January 2012, and an additional survey between January and February 2013. This ensured the coverage of most of the wet season when rain is more abundant and the individuals are expected to be more active. Surveys were conducted in Ankarafo Forest, Anabohazo Forest and around the villages of Antafiabe and Betsimpoaka.

Survey methods

Surveys were conducted by opportunistic searching and directed towards vocalising males using headlamps and torches. Transects were made across a range of habitats and degradation levels, covering the four previously mentioned areas of the peninsula. Searches were repeated during the day and night to account for any diel differences in activity, taking place in the morning and evening. Searching took place approximately

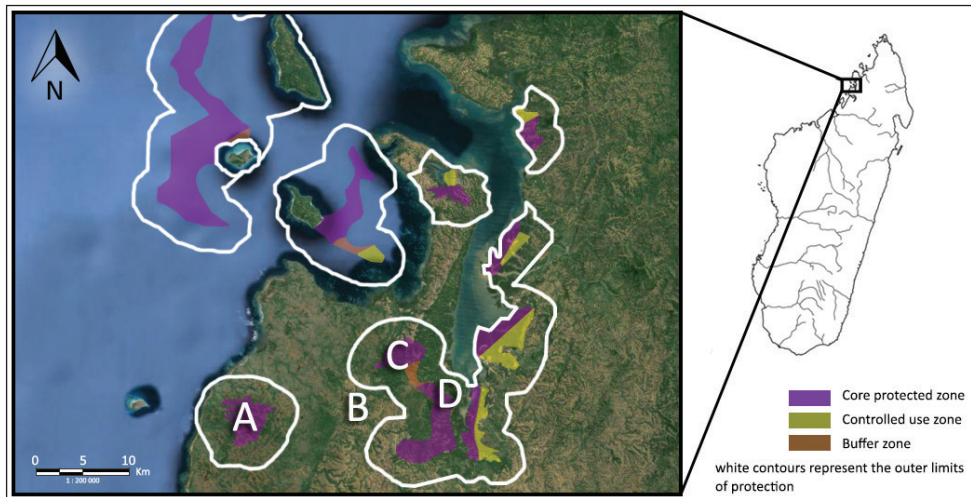


Figure 1. The Sahamalaza Peninsula in northwest Madagascar, indicating the study sites of (A) Ankarafa Forest, (B) Antafiabe Village, (C) Anabohazo Forest and (D) Betsimpoaka village. Source: Madagascar National Parks (MNP).

two metres either side of the transect and up to two metres in height. Most searches in Ankarafa were repeated at least once both in the dry and wet season (during the 2011–2012 period) following the same routes where possible. The sites in Anabohazo Forest, Antafiabe and Betsimpoaka village were sampled only once. Sites were sampled in a randomised order and all searches were conducted by the same two individuals to avoid systematic observer bias. The frogs' frequency of occurrence was estimated by dividing the total number of frogs encountered during each transect search by the respective length.

The vouchers were photographed to document life colouration and calls were recorded whenever possible. Acoustic description follows that outlined in the acoustic analysis methods below. The tissue samples (fourth digit of the left toe removed with scissors) were stored in 70% ethanol or 96% ethanol for genetic analysis. Location was logged using a handheld GPS receiver (Garmin eTrex Vista HCx; Garmin International Inc., Olathe, United States). Microhabitat was noted and vertical position from the ground measured using a tape measure.

Morphological measurements

Specimens were collected both day and night, euthanized in a chlorobutanol solution, fixed in 90% ethanol or 5% formalin, and preserved in 70% ethanol. Specimens are deposited in the collections of Museo Regionale di Scienze Naturali, Torino, Italy (MRSN; Table 1). Morphological measurements (in millimetres) were taken with a digital calliper (precision 0.01 mm) to the nearest 0.1 mm by F.A. Used abbreviations

are: SVL (snout-vent length), HW (greatest head width), HL (head length), ED (horizontal eye diameter), END (eye-nostril distance), NSD (nostril-snout tip distance), NND (nostril-nostril distance), TD (horizontal tympanum diameter), TL (tibia length), HAL (hand length), FOL (foot length), FOTL (foot length including tarsus), FORL (forelimb length), HIL (hindlimb length), RHL (reaching of tibiotarsal articulation when hindlimb is adpressed along body). Terminology and description follows Vences and Glaw (2002) and Glaw and Vences (1997) for eye colouration. Webbing formulae follow Blommers-Schlösser (1979).

DNA analysis

Tissue samples were available for four individuals. Total genomic DNA was extracted from the tissue samples using proteinase K digestion (10 mg/ml concentration) followed by a standard salt-extraction protocol (Bruford et al. 1992). We sequenced a fragment of ca. 550 bp of the 3' terminus of the mitochondrial 16S rRNA gene. For primers and cycling protocols see Crottini et al. (2011). The light strands were sequenced using an ABI3730XL by MacroGen Inc.

Sequences were checked by eye, edited and aligned using the BioEdit sequence alignment editor (version 7.0.5.3; Hall 1999). The alignment of the four processed samples and of the other species belonging to the *B. rappiodes* group taken from GenBank (12 homologous sequences of *B. bottae* from Ranomafana (8), Andasibe (2) and Betampona (2); 10 homologous sequences of *B. rappiodes*, from Ranomafana (5) and Andasibe (5); 1 homologous sequence of *B. erythrodactylus*, from Mandraka; 22 homologous sequences of *B. tasymena*, from Andasibe (1), An'Ala (5), Ranomafana (15) and Maharira (1); and 18 homologous sequences of *viridis*, from Ranomafana (1), Andasibe region (16) and Betampona (1)) required the inclusion of gaps to account for indels in only a few cases in some hypervariable regions. All newly determined sequences have been deposited in GenBank (KJ438141–KJ438144).

To assess genetic distinctness of the new species from all other Malagasy frogs and ascertain its belonging to the *Boophis rappiodes* group, sequences were compared using the BLAST algorithm with a database containing homologous sequences of reliably identified adult individuals of almost all Malagasy frog species (Vieites et al. 2009). Mean genetic distances matrix (uncorrected *p*-distance transformed into percent, using the complete deletion option) between and within individuals belonging to the type series of *B. ankarafensis* sp. n. (holotype and three paratypes) and of other species of the *B. rappiodes* group were computed using MEGA, version 6.06 (Tamura et al. 2013).

Acoustic monitoring and analysis

Most amphibian calls are species-specific and it is usually possible to identify syntopic calls to the species level. Sound recordings were taken to obtain detailed information

on the acoustic parameters of the species and investigate any intraspecific variability and overnight temporal patterns in activity. Acoustic recordings were made continuously from dusk until dawn on sixty nights between October 2011 and January 2012. Data were collected from 37 different locations; the majority of these locations were within Ankarafa Forest (29), followed by Anabohazo Forest (7) and a single location on the Vavan'aneno River near the village of Antafiabe. Nineteen locations had recordings made on two or more nights, separated between 9 and 79 days.

Calls were recorded in the field using a Song Meter SM2 digital recorder (Wildlife Acoustics Inc, Concord, United States) at a 16-bit resolution and 16 kHz sampling rate using two side-mounted SMX-II microphones. The digital recorder was placed one to two metres above the ground or water by securing it to deadwood or a protruding branch using bungee cords. Continuous recordings split into sections of 120 minutes each were saved in the standard uncompressed .WAV format. Preceding analysis, these were split using a custom-written MATLAB (The Mathworks, Natick, USA, v7.14.0.739) script into minute long segments to allow for more efficient analysis. Spectrograms were viewed individually as a dual channel output using Avisoft SASlab Pro (Berlin, Germany, v5.2.06); frequency resolution of 512 FFT, a 100% frame rate, Hamming window and an intensity threshold of 50%.

From each night-long recording where *B. ankarafensis* sp. n. was detected, five representative vocalisations for each identified call type were chosen. Calls with the highest recording quality were selected and where possible equally distributed over the entire recording period. This reduced the risk of selecting the same individual repeatedly (pseudoreplication) by maximising the time period between each of the selected vocalisations. From a subset of five trill notes, acoustic parameters were measured for ten sequential broadband pulses and ten sequential narrowband pulses per note.

From each of these notes spectral and temporal characteristics were measured, and the minimum, maximum and average values (with SD) calculated (Avisoft SASlab Pro; Berlin, Germany; v5.2.06). To remove interspecific and abiotic noise outside of the *B. ankarafensis* sp. n. bandwidth, and increase detection thresholds, sound files were band-pass filtered with a finite impulse response filter (Hamming) between 3.2 and 6 kHz using Avisoft SASlab Pro (Berlin, Germany, v5.2.06). The spectral measurements taken were peak frequency (= frequency of maximum energy) and bandwidth. These were calculated using averaged power spectra with peak interpolation over three data points (Hamming window, FFT width 512 points; bandwidth threshold -10dB; peak detection threshold -20 dB, hysteresis 10 dB). For the trill note (type 1) these were taken from each of the two pulse types present and also a section of 40–60 sequential pulses; measurements were taken from the click note (type 2) in its entirety. Durations were taken for the two notes types in their entirety and also for individual pulses. The pulse rate of the trill note was calculated by taking the inverse of the average time differences between pulses, calculated through pulse train analysis. All measurements are stated as the mean \pm standard deviation followed in parentheses by the maximum and minimum and number of analysed units (n).

Calls were then compared to an existing database of frog vocalisations (Vences et al. 2006; Rosa et al. 2011): comparisons were limited to notes recorded at similar ambient temperatures as, to a limited extent, some call parameters can be temperature dependent (Glaw and Vences 2007).

Minute by minute changes in activity were recorded for all detected species from dusk (sunset) until dawn (sunrise) for 60 nights. The activity index per minute was 1 for one caller and 2 for more than one. The time period between dusk and dawn was split into percentiles for each night; this controlled for the slight variations in night length experienced across the sampling period, enabling the summation of data across multiple nights for each analogous percentile. The number of minute periods containing calling activity within each percentile was calculated and the values for each analogous percentile across all nights summed. The totals for each percentile were then divided by the total activity to determine the proportional change in activity.

Results

Boophis ankarafensis sp. n.

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Etymology. The term *ankarafensis* is a specific epithet deriving from the species' *terra typica*, the Ankarafa Forest. The name is used as an adjective in the nominative singular.

Holotype. MRSN A6973, adult male (Fig. 2D and Fig. 3D) collected at Ankarafa Forest (Sahamalaza Peninsula, north-western Madagascar), 14°22.85'S, 47°45.52'E; ca 140 m a.s.l., transitional forest, 26 January 2013, leg. G. M. Rosa.

Paratypes. MRSN A6974 adult female (Fig. 3D), same data as holotype. MRSN A6975, adult male (Fig. 2A–B) collected at Ankarafa Forest (Sahamalaza Peninsula, north-western Madagascar), 14°22.83'S, 47°45.47'E; ca 130 m a.s.l.; transitional forest, 21 November 2011, leg. S. G. Penny. MRSN A6976, adult male (Fig. 3A) collected at Ankarafa Forest (Sahamalaza Peninsula, north-western Madagascar), 14°22.85'S, 47°45.51'E; ca 130 m a.s.l., transitional forest, 12 January 2012, leg. S. G. Penny.

Diagnosis. A treefrog assigned to the genus *Boophis* based on absence of femoral glands in males, the presence of an intercalary element between the ultimate and penultimate phalanges of fingers and toes (verified by external examination), presence of nuptial pads in males, general morphological resemblance to other *Boophis* species, and molecular evidence. Assigned to the *Boophis rappiodes* group based on small size (adult males 22.9–24.0 mm and one female 28.5 mm SVL), absence of lateral fringes along lower arm and tarsus, greenish and slightly translucent dorsal colouration and translucent venter (inner organs can be clearly seen through the skin in live specimens). *Boophis ankarafensis* sp. n. is distinguished from *B. erythrodactylus* by lack of reddish colour of fingertips, and from *B. erythrodactylus* and *B. tasymena* by lack of regular pattern of red dorsal spots. Distinguished from *B. viridis*

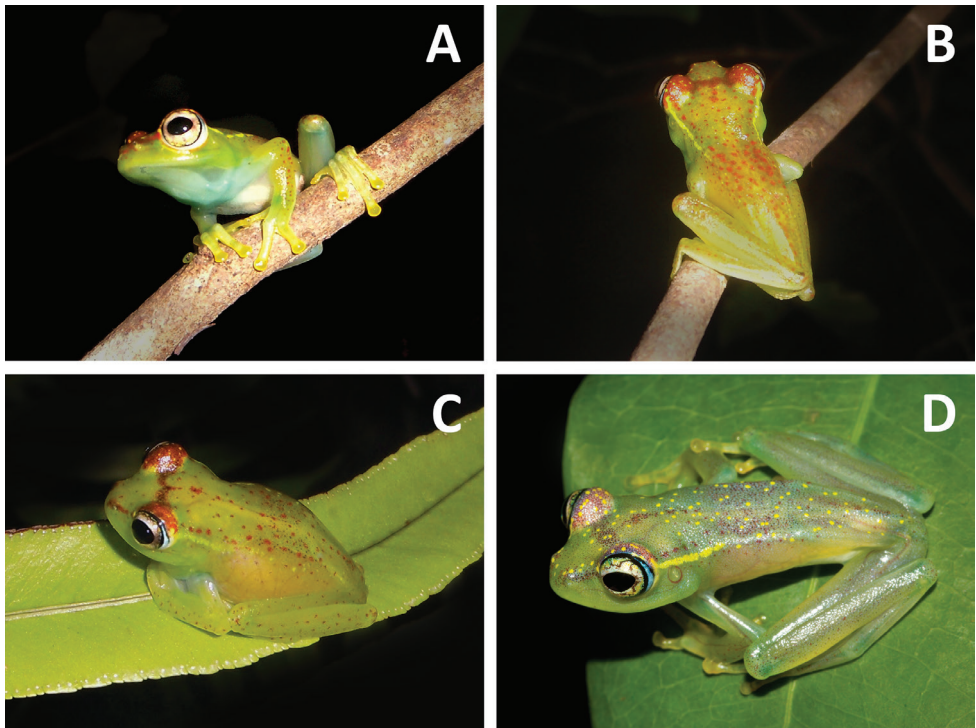


Figure 2. Life colouration of *Boophis ankarafensis* sp. n.: **A** Rostral view of a male paratype (MRSN A6975) **B** Dorsal view of the same male **C** Female specimen in resting position on a leaf (specimen not collected) **D** Dorso-lateral view of the holotype with day-time colouration (MRSN A6973).

by its smaller size (SVL up to 31 mm in males and 35 mm in females of *B. viridis*), iris colouration (*B. viridis* shows a distinctive brown inner-iris area and blue outer-iris area), and the presence (vs. absence) of yellowish dorsolateral stripes. Compared to *B. rappiodes*, the new species is distinguished by a more extensive darker pattern on the dorsum, which is most evident in living or freshly preserved specimens; while the dorsal pattern in *B. rappiodes* is intensely red, and remains red in preservative before it eventually fades, the pattern in *B. ankarafensis* sp. n. is reddish-brown in life and becomes persistently dark brown in preservative, often covering almost the entire dorsum. *B. ankarafensis* sp. n. is most similar in morphology to *Boophis bottae* and no apparent morphological feature distinguishes them. However, the new species can be distinguished by molecular analysis and by its advertisement calls (see below).

Description of the holotype. MRSN A6973, adult male in a good state of preservation. SVL 24.0 mm (see Table 1 for more detailed morphometric measurements). The body is slender with the head much wider than the body. Snout rounded in dorsal view, slightly truncate in lateral view, nostrils directed laterally, slightly nearer to tip of snout than to eye; canthus rostralis and loreal region both slightly concave; tympanum

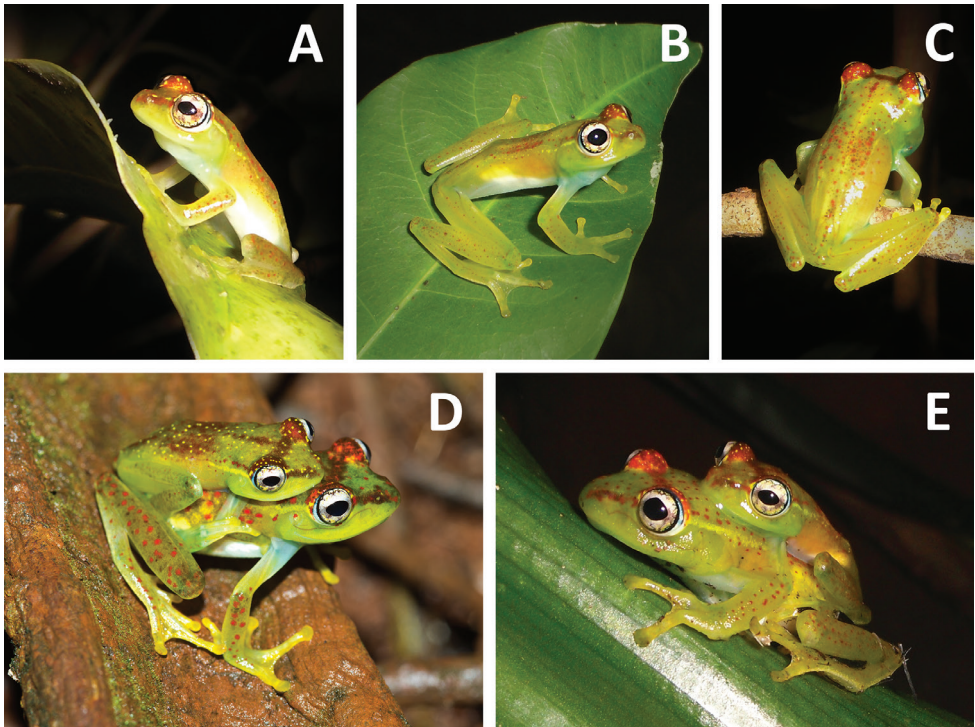


Figure 3. Breeding activity of *Boophis ankaraensis* sp. n.: **A** Paratype MRSN A6976 **B–C** Vocalising males sitting on leaves and on a branch (specimens not collected) **D** Male holotype MRSN A6973 and female A6974 **E** Couple in axillary amplexus.

distinct, rounded, 40% of eye diameter; supratympanic fold not recognizable; tongue ovoid, distinctly bifid, posteriorly half free; vomerine odontophores distinct; positioned posteromedian to choanae; choanae small, rounded. Arms slender, subarticular tubercles single, round; metacarpal tubercles unrecognizable; fingers with weak webbing; webbing formula 1(1), 2i(1.75), 2e(0.75), 3i(2.5), 3e(1.75), 4(1); relative length of fingers $1 < 2 < 4 < 3$ (finger 2 distinctly shorter than finger 4); finger disks moderately enlarged; small unpigmented nuptial pads faintly recognizable on inner side of first finger. Hindlimbs slender; tibiotarsal articulation reaches nostril when hindlimb is adpressed along body; lateral metatarsalia separated by webbing; inner metatarsal tubercle distinct, no outer metatarsal tubercle; webbing formula between toes 1(0), 2i(0.75), 2e(0), 3i(0.75), 3e(0), 4i(1), 4e(1.5), 5(0.25); relative length of toes $1 < 2 < 5 = 3 < 4$; toe disks slightly enlarged. Skin on dorsal surfaces and ventrally on throat smooth; ventral skin on belly and around cloacal opening glandular. The ground dorsal colour, including limbs, is light green. The webbing, finger and toe disks are green-yellow in colour. Speckles of reddish-brown and yellow pigment can be seen covering the dorsum and limbs. Thin yellow dorsolateral stripes run from behind the eye to the forelimb and then fade towards the mid-body. On the head a reddish-brown pigment

Table 1. Morphometric measurements (in mm) of preserved specimens of *Boophis ankaraensis* sp. n. For abbreviations of variables, see methods.

MRSN	A6973	A6974	A6975	A6976
STATUS	HOLOTYPE	PARATYPE	PARATYPE	PARATYPE
SEX	male	female	male	male
LIFE STAGE	adult	adult	adult	adult
SVL	24.0	28.5	23.7	22.9
HW	9.1	12.0	8.4	8.5
HL	7.8	11.5	8.2	8.1
ED	4.1	4.7	3.6	3.6
END	2.1	3.3	2.6	2.7
NSD	2.6	2.8	2.2	2.0
NND	3.0	3.8	2.7	2.3
TD	1.5	1.6	1.7	1.2
TL	12.7	17.2	12.0	10.8
HAL	8.1	9.2	7.5	6.1
FOL	11.2	14.1	10.2	9.6
FOTL	17.2	22.8	16.4	15.6
FORL	15.1	21.3	14.1	11.5
HIL	41.1	53.7	37.9	37.5

forms a band between the eyes and covers the supra-ocular area, interspersed with yellow speckling. This reddish-brown pigment also forms a faint rostral stripe between the eye and nose tip. The pupil is horizontal, with a beige iris containing darker brown patches and reticulations; the iris periphery is blue. The specimen has a white venter with some translucence exposing the inner organs, and a bluish throat. At day-time the green on the dorsum became pale and the red markings fade out to a pale brownish red colour (Fig. 2D). In preservative it is in good condition and comparatively more hydrated. The colouration, at about 4 months from the capture is vivid: the dorsum is pigmented and the dark bar between the eyes is contrasting and evident, as well as the pigmentation around the nostrils. The specimen has the last phalanx of the 4th toe of the left foot missing for genetic analysis.

Description of paratypes and variation. The paratypes (MRSN A6974-6976) closely match the holotype but with slightly different patterning of pigment patches. Finer regular black spots were observed on the dorsum and limbs (possibly single melanophores); a feature similarly observed in the related *B. bottae* (Vences and Glaw 2002). Based on other individuals photographed in nature, specimens matched the holotype and paratypes. However, pigment patterns vary in their distribution and intensity. The males MRSN A6975 and MRSN A6976 are in mediocre state of conservation and dehydrated due to fixation and preservation in ethanol. The colouration, after about 18 months from the capture, faded from green to whitish-yellowish except for

Table 2. Genetic divergence in the analysed 16S rRNA mitochondrial gene fragment of the *Boophis rappiodes* group (*p*-distance transformed into percent using the complete deletion option). Pairwise distances calculated for intra- (in bold) and inter-specific genetic divergence. n.c. (not calculated).

	<i>B. ankarafensis</i>	<i>B. bottae</i>	<i>B. rappiodes</i>	<i>B. erythrodactylus</i>	<i>B. tasymena</i>	<i>B. viridis</i>
<i>B. ankarafensis</i>	0					
<i>B. bottae</i>	4.9%	1.4%				
<i>B. rappiodes</i>	9.0%	8.0%	2.2%			
<i>B. erythrodactylus</i>	11.4%	11.6%	11.9%	n.c.		
<i>B. tasymena</i>	9.9%	9.6%	9.7%	9.1%	1.3%	
<i>B. viridis</i>	11.1%	10.2%	12.0%	13.0%	12.1%	1.2%

pigmentation on the upper eyelids and for the bar between the eyes. The dorsum and upper parts of legs are finely pigmented. Eyes are blackish, with whitish pupillae. The 5th toe of the left foot was removed and fixed in 96% ethanol for molecular analyses. The female specimen (SVL 28.5 mm) collected more recently (MRSN A6974) is in better condition, similar to the holotype. This specimen also has the last phalanx of the 4th toe of the left foot missing for molecular identification. See Table 1 for detailed morphometric measurements.

Mitochondrial variation and differentiation. The molecular data confirms the attribution of *B. ankarafensis* sp. n. to the *B. rappiodes* group (Glaw and Vences 2007). The four analysed specimens of *B. ankarafensis* are genetically uniform and did not show any intraspecific divergence, while the analysed specimens of *B. bottae*, *B. rappiodes*, *B. tasymena* and *B. viridis* are more heterogeneous and show intraspecific uncorrected divergence ranging from 1.2% (*B. viridis*) to 2.2% (*B. rappiodes*), in the 16S rRNA gene analysed fragment (Table 2). The species showing the highest values of intraspecific divergences is *B. rappiodes* (2.2%). This value of intraspecific divergence is computed based on the analyses of sequences coming from Andasibe and Ranomafana, two sites that are about 300 km far apart. The population of *B. ankarafensis* is about 400 km apart from the closest population of *B. bottae* (at Betampona) and their genetic distance is of 4.9%. As shown in Table 2, available values of intraspecific genetic divergence values never reach the minimum value of genetic divergence observed between different species of the *B. rappiodes* group (comparison *B. ankarafensis*/*B. bottae*).

The genetic distance between *B. ankarafensis* and the five other species of the *B. rappiodes* group ranges between 4.9% (comparison between *B. ankarafensis* and *B. bottae*) and 11.4% (comparison between *B. ankarafensis* and *B. erythrodactylus*). Among the species of the analysed species group the smallest genetic distance is observed between the newly described species and *B. bottae* (4.9%) and the highest value between *B. erythrodactylus* and *B. viridis* (13.0%). More details on genetic distances between species of the *B. rappiodes* group are provided in Table 2.

Advertisement call and acoustic monitoring. Vocalisations of *Boophis ankarafensis* sp. n. were recorded on thirteen occasions between October 2011 and Janu-

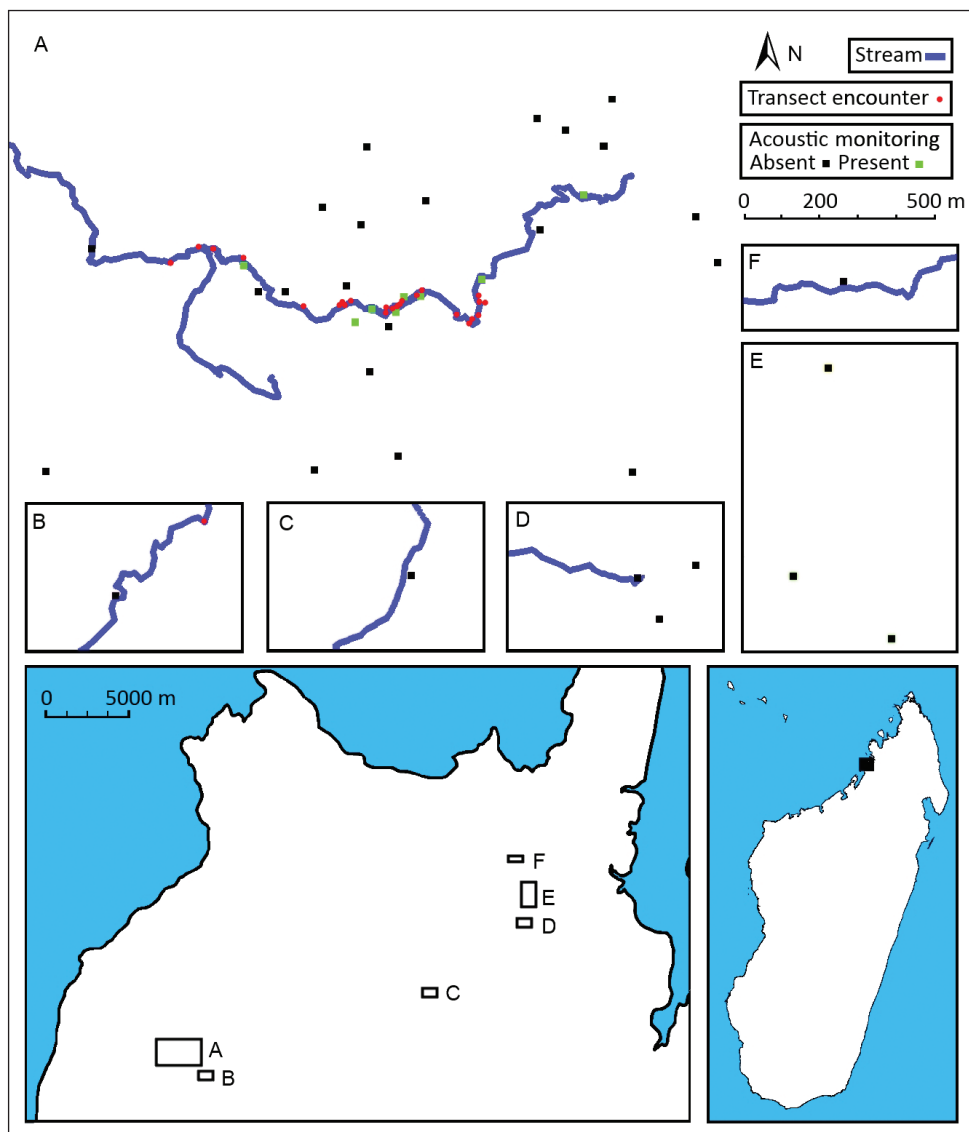


Figure 4. Detection of *Boophis ankaraensis* sp. n. Upper panel: Location of acoustic recording sites indicating presence (green) or absence (black) of vocal activity and transect encounters (red). Lower left: The Sahamalaza Peninsula: **A–B** Ankarafa Forest **C** Antafiabe Village **D–F** Anabohazo Forest. Lower right: location of the Sahamalaza Peninsula, in northwestern Madagascar.

ary 2012. No males were found in calling activity between January and February 2013 (later in the wet season). Calls were detected from just 8 of the 37 locations monitored on the peninsula (Fig. 4). All eight of these locations were along the banks of a single stream in Ankarafa Forest. Vocalisations were detected within 3978 minutes of acoustic recordings and averaged 306 ± 181 minutes per night ($n = 13$). A total of

Table 3. Acoustic measurements of two note types of *B. ankaraensis*. In note type two durations are shown for the final two pulses.

Note	Parameter	Section	Mean \pm SD	Range
Type 1. Trill	Duration	Entire Note (s)	4.29 \pm 1.29	1.61–8.09
		Broadband Pulse (ms)	3.47 \pm 0.485	2.50–5.06
		Narrowband Pulse (ms)	17.9 \pm 2.56	11.2–25.1
	Pulse Rate	20–30 Broadband Pulses (pulses/s)	15.0 \pm 1.19	11.7–17.3
	Peak Frequency	40–60 Pulses (kHz)	4.14 \pm 0.131	3.69–4.48
		Broadband Pulse (kHz)	4.19 \pm 0.122	3.91–4.34
		Narrowband Pulse (kHz)	4.15 \pm 0.108	4.00–4.31
Type 2. Click	Duration	Entire Note (ms)	50.9 \pm 5.20	40.0–68.7
		Pulse one (ms)	6.37 \pm 3.04	2.18–15.7
		Pulse two (ms)	6.61 \pm 2.99	1.75–15.9
		Interpulse Interval (ms)	37.9 \pm 6.28	20.0–50.7
	Peak Frequency	Entire Note (ms)	3.95 \pm 0.162	3.57–4.30

59.8% of these minutes contained vocalisations emitted by a single male caller, with the remainder emitted as a chorus of two or more callers. Total activity equalled 5576 minutes and average per night activity amounted to 429 ± 273 minutes ($n = 13$). Levels of calling fluctuated throughout the night (Fig. 5); there was a peak in activity just after dusk, followed by a slow decline until dawn, when the fewest vocalisations were detected ($y = 0.019e^{-0.015x}$; $R^2 = 0.582$).

The acoustic repertoire consists of two note types: a multi-pulsed trill (type 1; Fig. 6A) and a 1–3 pulsed click (type 2; Fig. 6B). Only 11 of the 13 occasions produced recordings of a sufficient audio quality to perform spectral analysis. Measurements were taken from five representative notes of each call type per night, thus a total of 55 trill notes and 55 click notes were measured (Table 3). From a subset of five trill notes, acoustic parameters were measured for ten sequential broadband pulses and ten sequential narrowband pulses per note. The environmental temperature of the recorded trill notes ranged between 25.2 and 30.3 °C (27.4 ± 1.08 °C, $n = 55$) and of the click notes between 22.9 and 29.7 °C (26.7 ± 1.41 °C, $n = 55$).

The trill note measured 4.29 ± 1.29 s (1.614–8.091 s, $n = 55$) and is composed of alternating broadband and narrowband pulses. These notes had a broadband pulse rate of 15.0 ± 1.19 pulses/s (11.7–17.3 pulses/s, $n = 25$) and peak frequency of 4.14 ± 0.131 kHz (3.69–4.48 kHz, $n = 55$). Broadband pulses measured 3.47 ± 0.485 ms (2.50–5.06 ms, $n = 50$) whereas narrowband pulses were slightly longer at 17.9 ± 2.56 ms (11.2–25.1 ms; $n = 50$). The broadband pulse had a peak frequency of 4.19 ± 0.122 kHz (3.91–4.34 kHz; $n = 50$), whereas the narrowband pulse measured 4.15 ± 0.108 kHz (4.00–4.31 kHz, $n = 50$). Bandwidths were 0.288 ± 0.169 kHz (0.120–0.780 kHz, $n = 50$) for the broadband pulse compared to just 0.155 ± 0.036 kHz (0.129–0.280 kHz, $n = 50$) for the narrowband pulse when measured at a -10 dB threshold. The majority of click notes consisted of two pulses, although singular and triple pulses were also observed. Click notes had a total duration of 52.9 ± 5.20 ms

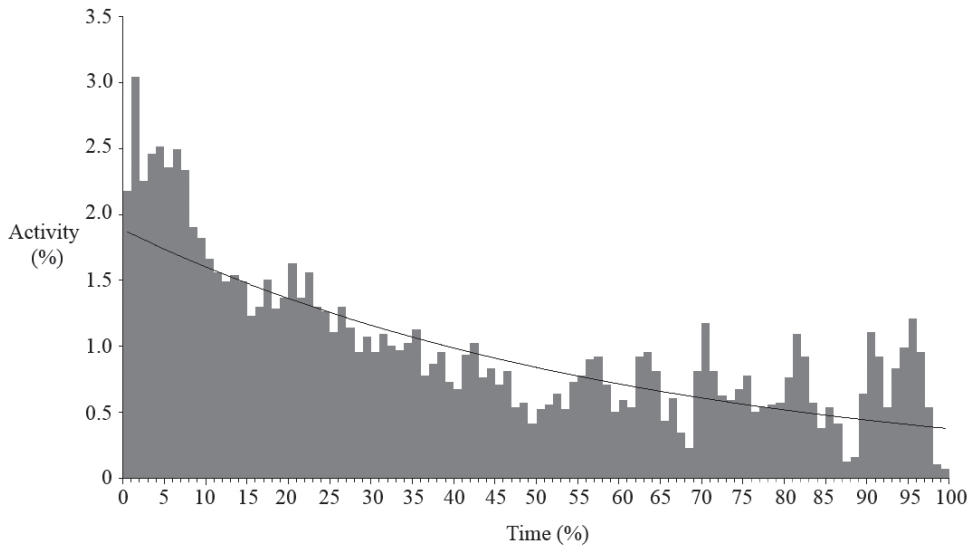


Figure 5. Nocturnal variation in calling activity of *Boophis ankaraensis* sp. n.; activity shown as a proportion of total calling activity and time shown as a proportion of night length from dusk [0%] until dawn [100%].

(40.0–68.7 ms; $n = 55$) and peak frequency of 3.95 ± 0.162 kHz (3.57–4.30 kHz; $n = 50$). Bandwidth of the click note measured 0.538 ± 0.234 kHz (0.120–0.143 kHz) at a -10 dB threshold.

The advertisement call of *B. ankaraensis* sp. n. sounds similar to that of the morphologically similar *B. bottae*; with both species possessing a trill note and a click note in their acoustic repertoires (Vences et al. 2006; Rosa et al. 2011). However, a number of differences can be used to distinguish them. In our comparison with *B. bottae* we selected only those notes recorded at a similar ambient temperature, and we have also distinguished the two pulse types of the trill by their relative differences in bandwidth, rather than duration as used by Vences and Glaw (2002); the broadband pulse and narrowband pulse of *B. ankaraensis* sp. n. are equivalent to the shorter and longer duration pulses of *B. bottae* respectively.

The trill note (type 1) of *B. ankaraensis* has a faster broadband pulse rate than the trill of *B. bottae* (13.4–13.5 pulses/s, 25.2 °C versus 8.12–11.6 pulses/s, 23.0 °C). The click note (type 2) of *B. ankaraensis* sp. n. usually contains just two pulses, and only rarely consists of three, in contrast the click notes of *B. bottae* are usually three-pulsed. Although only slightly divergent, it is discernable that the spectral frequency of the click note is lower in *B. ankaraensis* sp. n. than in *B. bottae* (3.75–3.84 kHz, 22.9 °C versus 4.23–4.42 kHz, 23 °C). The trill note of *B. ankaraensis* shows a slightly lower broadband pulse peak frequency (4.10–4.24 kHz, 25.2 °C versus 4.30–4.64 kHz, 23 °C) but a similar narrowband pulse peak frequency (4.18–4.31 kHz, 25.2 °C versus 4.23–4.42 kHz, 23 °C) in comparison to *B. bottae*.

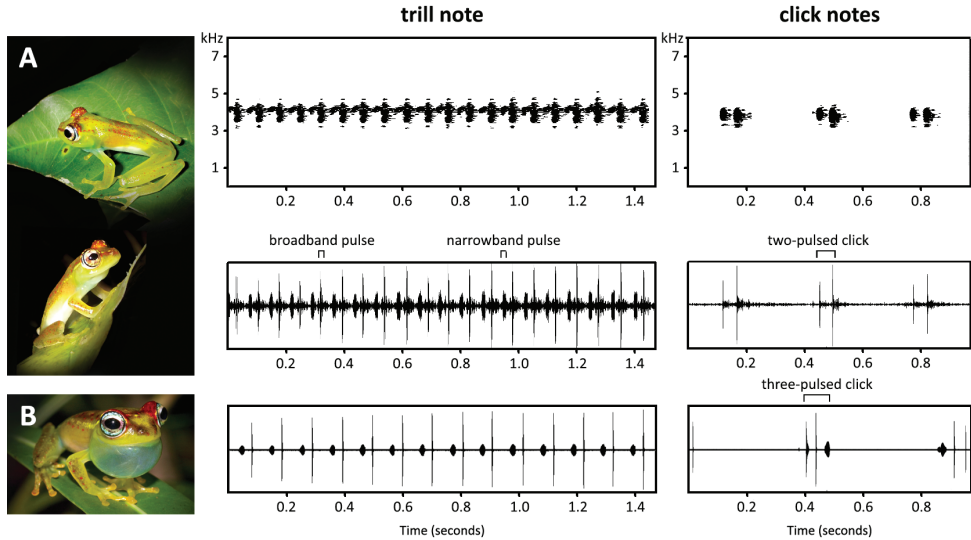


Figure 6. Representative call of *Boophis ankafensis* sp. n. and comparative call of *B. bottae* from Betampona (Rosa et al. 2011, track #08): **A** *B. ankafensis* sp. n. sonagrams (top) and oscillograms (bottom) referring to a section of trill note (type 1) constructed of alternating broad- and narrow-band pulses and click notes (type 2) (recorded at 25.2 °C, 13 October 2011) **B** *B. bottae* oscillograms of types 1 and 2 notes (recorded at 23.0 °C, 17 November 2007). Spectrogram parameters: FFT length 512, Hamming window.

Ecology and natural history. A total of 54 individuals of *B. ankafensis* sp. n. were encountered between 29 October 2011 and 05 January 2012. An additional amplexing couple was found on 26 January 2013. Individuals were found at night in Ankarafa Forest along the banks of two streams; these streams became fast flowing after heavy rains during the wet season. No individuals were detected from sections of stream in open habitat where vegetation was absent, and so it should be considered a forest species.

Of the 56 encounters, 48 frogs were male and 8 female. Males of this species were found calling from vegetation approximately 0.5 to 2 m high. Vocalising males were often within close proximity to one another, positioned on different leaves of the same plant. All but one of the eight females were found in axillary amplexus with males (Fig. 3D–E); mating pairs were positioned on leaves overhanging the stream bank, and in one instance on a rock. Calling and breeding activity were most intense during the first few months of the rainy season (Oct–Dec), decreasing later in the season (Jan–Feb). A lone female was found in a tree during the day approximately 3 m high and 30 m from a stream.

Distribution, conservation and proposed IUCN status. The suggested conservation status of this species was assessed using the criteria and guidelines of the IUCN Red List (IUCN Standards and Petitions Subcommittee 2011). This species is endemic to Madagascar and so far only recorded in a small forest fragment (Ankarafa Forest). Individuals were found along the vegetated banks of two streams, with forested sec-

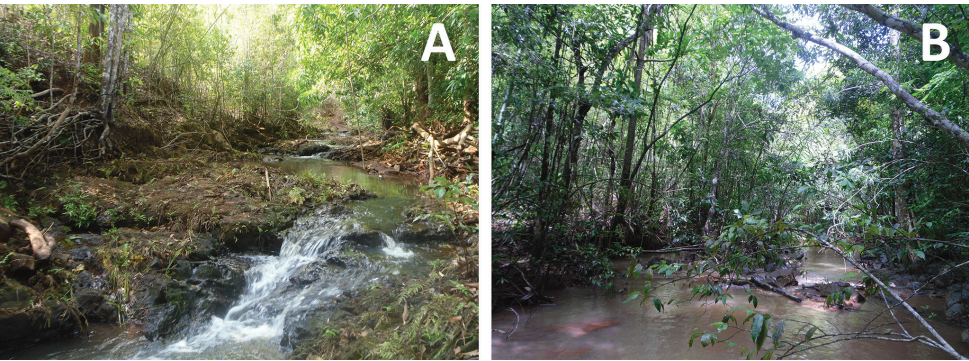


Figure 7. Habitat of *B. ankaraensis* sp. n. in Ankara Forest. **A** 21 November 2011; 14°23.39'S, 47°46.37'E; **B** 3 January 2012; 14°22.83'S, 47°45.57'E.

Table 4. Count and frequency of *Boophis ankaraensis* sp. n., along sections of stream in Ankara Forest.

Date	Transect Location	No. of frogs	Transect Length (m)	Frequency /100 m
29/10/2011	Ankara North 'upstream'	3	511	0.59
02/11/2011	Ankara North 'midstream'	5	350	1.43
25/11/2011	Ankara South	3	814	0.37
26/11/2011	Ankara North 'downstream'	7	609	1.15
15/12/2011	Ankara North 'upstream'	18	511	3.52
29/12/2011	Ankara North 'upstream'	11	511	2.15
05/01/2012	Ankara North 'midstream'	7	350	2
Total		54	3656	1.48

tions of these streams extending for approximately 2 km of the more northerly stream (Fig. 7B), and just 1 km for the stream south of this (Fig. 7A). No individuals were found upstream of these two locations, where the streams are replaced by *Raphia*-dominated swampland or downstream where the stream-banks are cleared of vegetation. An average occurrence of 3 specimens per 200 m of river was determined from those transect searches where the specimens were detected (Table 4). This species was not detected from Anabohazo Forest, which aside from Ankara represents the only other large area of intact forest remaining on the peninsula. A survey of the Vavan'ano River between Antafiabe and Ambinda villages, and a survey of Betsimpoaka village also failed to detect it.

If suitable habitat is considered to be all areas of Ankara Forest (likely an overestimate) then this area totals less than 5 km², giving an EOO (extent of occurrence) of less than 100 km². If plots with a scale of 2 km² are used to estimate AOO (area of occupancy), then this species occurs within 4 km² of habitat, resulting in an AOO of less than 10 km². Therefore the Critically Endangered thresholds for extent of occurrence and area of occupancy are both met (EOO < 100 km² and AOO < 10 km²) (CR B1+2). The most serious threat to the species is habitat destruction through *tavy* practice (slash and burn agriculture), small-scale logging and the uncontrolled burning of neighbouring

grasslands; a large out of control fire could easily affect the two subpopulations as they are separated by a distance of less than 2 km. Therefore, all individuals can be considered to occur within a single location only (CR B1a+2a). Given this on-going destruction of suitable habitat, population declines can be expected to continue unless some remedial action is taken (CR B1b(i, ii, iii, iv, v + B2b(i, ii, iii, iv, v)). Thus the species should qualify as Critically Endangered under criterion B (CR B1ab (i, ii, iii, iv, v)+2ab(i, ii, iii, iv, v) of the IUCN Red List (IUCN Standards and Petitions Subcommittee 2011).

Discussion

Boophis ankarafensis sp. n. appears to be restricted to Ankarafa Forest on the Sahamalaza Peninsula in northwest Madagascar. The species represents the only member of the *B. rappiodes* group known from West Madagascar, and the only member to occur within a transitional forest type. The other members of the *B. rappiodes* group (*B. bottae*, *B. rappiodes*, *B. erythrodactylus*, *B. tasymena* and *B. viridis*) are confined to the eastern rainforest belt of Madagascar (Glaw and Vences 2007) aside for a single population of *B. erythrodactylus* known from Mahajeby Forest on the western slopes of Madagascar's central plateau (Vences and Glaw 2002).

The closest relative of *B. ankarafensis* is *B. bottae*, known from over 400 km to the east of Sahamalaza. It can be possible that in the past *B. bottae* has spread along the southern slopes of Madagascar's northern massifs where it may have speciated and finally reached the transitional forest of the Sahamalaza Peninsula. Thus other populations of *B. ankarafensis* may be found here, although if they exist they will be isolated and fragmented due to habitat destruction. Other amphibian surveys in northwest Madagascar, e.g. in Sahamalaza, Manongarivo, Tsaratanana and Benavony, have failed to detect it, despite it possessing a conspicuous and distinctive advertisement call, (Vences and Glaw 2007, Raselimanana 2008) and so the species may be locally endemic to the peninsula. With this description, a total of three amphibian species are now known solely from Sahamalaza, with the species *B. tsilomaro* and *Cophyla berara* discovered during a previous survey in 2000 (Andreone et al. 2001; Vences et al. 2005, 2010). Thus, at just 26,000 ha, the peninsula appears to support a high level of amphibian endemism, although further surveys of northwest Madagascar should be undertaken to search for additional populations.

All breeding behaviour of *B. ankarafensis* sp. n. was observed during the wet season along the banks of fast-flowing streams, indicating that its spawn is most likely laid in or adjacent to bodies of lotic water; a feature in common with most members of the *Boophis* subgenus (Glaw and Vences 2007). The streams in Ankarafa Forest flow throughout the year, in comparison all streams in Anabohazo Forest are seasonal. The species' absence from this latter locality may be linked to the lack of perennial streams, for example its larval stage may not have enough time to complete development.

The frog was only found within intact forest and appears sensitive to anthropogenic disturbance. Intact forest is rare across the peninsula and aside from Anabohazo,

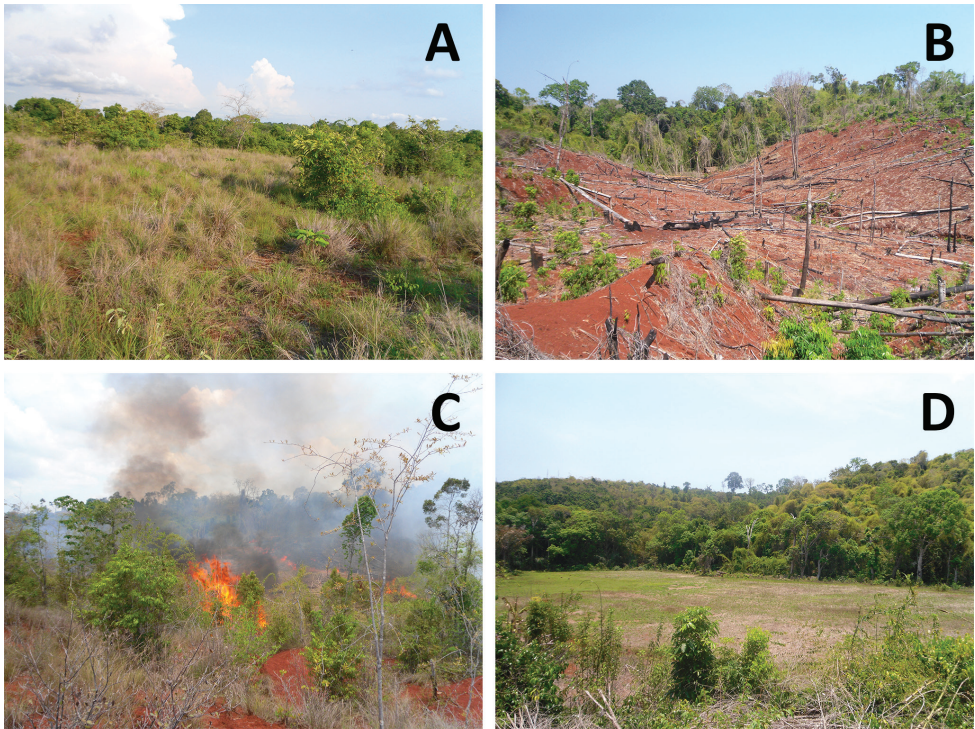


Figure 8. Anthropogenic disturbance within Ankarafa Forest: **A** Area of savannah, dividing Ankarafa Forest into many smaller fragments (14 December 2011; 14°22.77'S, 47°45.58'E) **B** Recent forest clearance (11 November 2011; 14°23.09'S, 47°44.92'E) **C** A fire lit to clear forest for agriculture (16 November 2011; 14°23.20'S, 47°44.80'E) **D** a Tavy field with intact forest in the background and the river acting as the boundary line (30 October 2011; 14°22.82'S, 47°45.28'E).

where the species was not found, Ankarafa represents the largest area of remaining forest. Isolated populations of *B. ankarafensis* sp. n. may survive in residual pockets of gallery forest elsewhere on the peninsula, but Ankarafa is likely to harbour the largest and most sustainable population of this species. Their habitat in Ankarafa is fragmented and the two streams it is known from are separated by savannah (Fig. 8A). As *B. ankarafensis* sp. n. is arboreal, this will most likely limit gene flow between the two populations, potentially reducing its long-term viability.

Despite its protected status, Ankarafa is experiencing widespread deforestation (Seiler et al. 2012), furthermore much of this destruction is concentrated on the streamside forests which this species relies upon (pers. obs.). *Boophis ankarafensis* sp. n. is highly threatened and we propose that it should be classified as Critically Endangered (CR) according to the IUCN Red List criteria. The other apparent endemics face similar threats; *C. berara* is already listed as CR (Andreone and Vences 2008), while *B. tsilomaro* most likely qualifies for CR status (Vences et al. 2010). A halt to all forest destruction and agricultural practices within the park must occur immediately to stop

any further decline of Sahamalaza's endemic amphibian fauna, or risk their possible extinction within the near future.

Acknowledgements

We would like to thank the staff of the AEECL research station in Ankarafa Forest for their help in the field including: Fan, Théophile, Régis, Falisara, Avitsara, Lauricia and Marlene. We would also like to thank Nicola Davies of Bristol Zoological Society for her help with the IUCN Red Listing and the anonymous reviewers for their valuable comments and suggestions towards the manuscript. We are grateful to the Ministère de l'Environnement et des Eaux et Forêts for providing the research permits, and MICET for logistical help. This work was financially supported by the European Association of Zoos and Aquaria (EAZA). A. Crottini was supported by a postdoctoral grant from the Portuguese 'Fundação para a Ciência e a Tecnologia' (FCT) (SFRH/BPD/72908/2010) under the Programa Operacional Potencial Humano – Quadro de Referência Estratégico Nacional funds from the European Social Fund and Portuguese Ministério da Educação e Ciência. G. M. Rosa is funded by the Doctoral Programme (SFRH/BD/69194/2010) of the FCT. We acknowledge the project 'Genomics and Evolutionary Biology' co-financed by north Portugal Regional Operational Programme 2007/2013 (ON.2 - O Novo Norte), under the National Strategic Reference Framework (NSRF), through the European Regional Development Fund (ERDF).

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Supplementary material I

Calls of *Boophis ankarafensis* sp. n. emitted from streamside vegetation in Ankarafa Forest.

Authors: Samuel Penny, Franco Andreone, Angelica Crottini, Marc Holderied, Lovasoa Rakotozafy, Christoph Schwitzer, Gonçalo Rosa

Data type: audio file

Explanation note: Calls of *Boophis ankarafensis* sp. n. emitted from streamside vegetation in Ankarafa Forest (Sahamalaza – Iles Radama National Park). Calls consist of multi-pulsed trill notes (type 1) and 1-3 pulsed click notes (type 2). Cut 1: chorus recorded on 13 October 2011, 18:34 h, 26.7 °C; Cut 2: chorus with background calls of *Cophyla berara* recorded on 30 December 2011 at 18:44 h, 28.4 °C.

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