

**Research Article** 

# A never-ending story: updated 3D cyber-taxonomic revision of the ant genus *Zasphinctus* Wheeler (Hymenoptera, Formicidae, Dorylinae) for the Afrotropical region

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#### Abstract

The ant genus Zasphinctus are fascinating ants due to their distinctive morphology, ecology, and rarity. In this study, a comprehensive revision of Zasphinctus in the Afrotropical region is presented, through a combination of morphological examination under the light microscope and three-dimensional (3D) cyber-taxonomy based on microtomography (micro-CT). Micro-CT based 3D surface models of all species were used for virtual morphological visualisation and examination. The 3D models were virtually visualised, rotated, scaled, and dissected in order to obtain the best shape data for whole specimens or individual body parts. This approach offered a greatly improved character evaluation, allowing the development of an updated taxonomic species delimitation system for the genus. Our revision recognises eight worker-based species, of which three were previously known and five are newly described in this study. Furthermore, based on distinctive morphological differences, two species groups are also proposed. The Z. obamai group includes the species Z. obamai Hita Garcia, 2017 (Kenya), Z. lumumbai Hita Garcia & Gómez, sp. nov. (Democratic Republic of Congo), and Z. wilsoni Hita Garcia, 2017 (Mozambique) while the Z. sarowiwai group contains Z. aprilia Hita Garcia & Gómez, sp. nov. (Democratic Republic of Congo, Uganda), Z. kouakoui Hita Garcia & Gómez, sp. nov. (Ivory Coast), Z. lolae Hita Garcia & Gómez sp. nov. (Ghana), Z. ndouri Hita Garcia & Gómez, sp. nov. (Senegal), and Z. sarowiwai Hita Garcia, 2017 (Cameroon). All species are easily distinguishable through a comprehensive character matrix illustrated by numerous diagnostic illustrations, as well as a traditional dichotomous identification key.

Key words: 3D-model, cybertype, micro-CT, morphology, new species, taxonomy

# Introduction

The Afrotropical region is of crucial importance for insect biodiversity due to its unique ecosystems, variety of bioregions, as well as high species richness and endemism. The region has also been recognised as a hotspot for ant diversity (Robertson 2000; Ward 2000; Fisher 2009; Guénard et al. 2012), but recent assessments concluded that Afrotropical ant diversity might be relatively less diverse compared to other regions (Kass et al. 2022). However, such findings might be due to a lack of comprehensive sampling compared to these other regions (Jimoh et al. 2024), which is supported by recent generic revisions that underline the view that the richness of the Afrotropical ant fauna has been vastly underestimated (Hita Garcia et al. 2019; Gómez 2022).

Afrotropical ant taxonomy lags behind our advances in biogeographic regions, such as the Malagasy or Neotropical for a variety of reasons, the most important ones being the lack of modern systematic sampling for most of the region, scarcity of qualified taxonomists, and lack of funding. The majority of the most species-rich genera have never been revised and their taxonomy remains at the level of the late 19<sup>th</sup> and first half of the 20<sup>th</sup> centuries (Robertson 2000; Hita Garcia et al. 2013). Diverse genera that have received one or more modern taxonomic revisions on a genus level were done mostly in the 70s or 80s of the last century, such as *Tetramorium* Mayr (Bolton 1976, 1980, 1985) or *Monomorium* by Bolton (1987). However, despite being excellently treated back then, their taxonomy is already outdated due to a constant stream of newly discovered undescribed species turning up in collections. The estimated number of ant species present in the Afrotropical region is expected to at least double its current numbers (Robertson 2000).

With currently 24 valid species, the ant genus Zasphinctus Wheeler is a rather moderately small Old-World genus, which can be found in the Afrotropical, Indomalayan, and Australasian regions (Antmaps, Janicki et al. 2016; Bolton 2024). Most species are known from the latter (17 spp. from Australia, New Guinea, and New Caledonia), whereas there is only one known from Southeast Asia (Jaitrong et al. 2016), another from India (Sadasivan and Kripakaran 2022), and five from the Afrotropics (Hita Garcia et al. 2017a). In general, specimens of Zasphinctus are somewhat rarely collected and the available material is restricted to few natural history collections. This rarity seems to be due to their rather cryptic subterranean biology. Based on current and limited knowledge of Australian Zasphinctus, these ants are myrmecophagous and prey on larvae and adults of a variety of other ant species captured during nest raids (Wilson 1958; Brown 1975; Buschinger et al. 1989). The morphological data on cuticle thickness, buccal mouthparts, musculature, and stinger laid out in Hita Garcia et al. (2017a) also supports this predatory lifestyle for the Afrotropical fauna.

Globally, the alpha taxonomy of the genus is in moderate condition. The largest known fauna in Australia has not been revised since Brown (1975) and would likely benefit from an updated revisionary treatment. The few Southeast Asian and Indian species were described very recently (Jaitrong et al. 2016; Sadasivan and Kripakaran 2022). The Afrotropical fauna was revised in Hita Garcia et al. (2017a) with three newly described species and a newly developed worker-based species delimitation system. However, since then the material of *Zasphinctus* available for taxonomic study has greatly increased, either by recent collections, such as in Senegal or Ghana by the second author, or by older material from natural history collections that became accessible to us, in particular from the natural history museums in London and Brussels.

The field of insect taxonomy has progressed at great pace within the last two decades through the implementation of novel computational, laboratory, and analytic tools and methods, such as DNA barcoding (e.g., Hebert and Gregory 2005; Miller 2007), molecular phylogenetics (e.g., Giribet 2010; Ward 2011), quantitative morphology (e.g., Csősz and Fisher 2016), or integrative approaches combining different lines of evidence (e.g., Schlick-Steiner et al. 2010). In recent years, an additional visualisation tool has entered the taxonomic stage: interactive three-dimensional (3D) imagery through x-ray microtomography (micro-CT). It is a state-of-the-art imaging technology that generates virtual, high-resolution, and interactive 3D reconstructions of whole specimens or particular body parts, thus allowing a maximum of morphological accuracy and fidelity (Faulwetter et al. 2013; Friedrich et al. 2014).

Within the last decade micro-CT started to be used for invertebrate taxonomy of myriapods (Stoev et al. 2013; Akkari et al. 2015, 2018), spiders (Michalik and Ramírez 2013), earthworms (Fernández et al. 2014), and flatworms (Carbayo et al. 2016). Even though the potential for insect taxonomy is enormous, micro-CT has so far mostly been used for lepidopterans (e.g., Simonsen and Kitching 2014; Moraes et al. 2023; Englund et al. 2024) and ants (e.g., Fischer et al. 2016; Sarnat et al. 2016, 2019; Agavekar et al. 2017; Hita Garcia et al. 2017b, 2019; Staab et al. 2018). The use of micro-CT provides the means for non-invasive and rapid generation of practically artefact-free morphological data for visualisation in 3D (Faulwetter et al. 2013; Friedrich et al. 2014). The non-destructive nature of the technique is of critical importance for taxonomic research since it permits the use of rare material from natural history collections, even type material (Hita Garcia et al. 2017a). Moreover, a crucial advantage of using 3D models based on micro-CT data is the option to include virtual 3D cybertypes in addition to the physical types. Based on some initial papers evaluating and pioneering the idea of openly available cybertype datasets linked to the original, physical type material (Faulwetter et al. 2013; Stoev et al. 2013; Akkari et al. 2015), it has been progressively extended and applied for ant taxonomy, with presently cybertype datasets of more than 40 species (Agavekar et al. 2017; Hita Garcia et al. 2017a, 2017b, 2019; Staab et al. 2018; Sarnat et al. 2019; Sharaf et al. 2019; Gómez et al. 2022). A detailed and critical assessment of the technology and its applications for ant taxonomy was provided by Hita Garcia et al. (2017a, 2017b, 2019).

In this study, we provide an updated taxonomic revision of the ant genus *Zasphinctus* for the Afrotropical region based on the worker caste. We describe five species as new to science and redescribe the three species treated in Hita Garcia et al. (2017a). As in the latter, our taxonomic decision-making is based on a thorough investigation of all available physical worker specimens in combination with virtual examinations of 3D surface reconstructions from high-resolution microtomography (micro-CT) scanning data from several specimens per species, if available. In Hita Garcia et al. (2017a) we presented a newly developed taxonomic discrimination system consisting of a synthesis of newly discovered and traditionally used morphological characters. Herein, we test that taxonomic system by expanding the number of worker-based species from three to eight, which led us to reassess the usefulness of some characters, but at

the same time we found some new characters of high diagnostic value used here for the first time in the genus. Furthermore, as in previous studies (e.g., Hita Garcia et al. 2017a, 2019; Gómez et al. 2022), we provide the complete datasets comprising the micro-CT raw data, 3D surface models, still images of shaded 3D surface models, and coloured stacked digital images, which have all been made available online as cybertype datasets for the new species.

# Materials and methods

## Abbreviations of depositories

Institutional museum collection abbreviations follow Evenhuis (2024). The material used in this study is located and/or was examined at the following institutions:

AFRC	AfriBugs, CC., Pretoria, Gauteng, South Africa
CASC	California Academy of Sciences, San Francisco, USA
KGAC	Kiko Gómez Abal Collection, Barcelona, Spain
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, USA
MNHNC	Museu Nacional de História Natural e da Ciência, Lisbon, Portugal
MRAC	Royal Museum for Central Africa, Tervuren, Belgium
NHMUK	The Natural History Museum, London, UK
NMKE	National Museums of Kenya, Nairobi, Kenya
RBINS	Royal Belgian Institute of Natural Sciences, Brussels, Belgium
SAMC	Iziko South African Museum, Cape Town, South Africa
ZMHB	Museum für Naturkunde, Berlin, Germany
ZFMK	Zoological Research Museum Alexander Koenig, Bonn, Germany

#### Material examined, data availability, and terminology

We gathered almost all currently available physical material of Afrotropical *Zas-phinctus* for this study from a variety of natural history collections (see above). All specimens used in this study have been databased and the data is freely accessible on AntWeb (http://www.antweb.org). Each specimen can be traced by a unique specimen identifier attached to its pin (i.e., CASENT#, KGCOL#, with # being a number).

In this study we focus exclusively on the worker caste in order to avoid confusion and contribute to two or even three parallel taxonomic systems based on worker vs queen vs male castes (Wilson 1964; Jaitrong and Yamane 2011; Hita Garcia et al. 2017a). The problematic starting situation for *Zasphinctus* prior to the previous revision was outlined in that study (Hita Garcia et al. 2017a) and the situation is still very similar with additional worker-based material from several new localities, whereas reproductives still remain scarce and completely unassociated with any workers. This situation will hopefully get resolved with future molecular sequencing, ideally some museomic approach to tackle old types and other dry mounted material in combination with multi-loci phylogenomic techniques for freshly collected specimens in ethanol.

The overall terminology for ant morphology follows Bolton (1990), Keller (2011), Borowiec (2016), and Hita Garcia et al (2017a). The terminology for the description of surface sculpturing follows Harris (1979).

#### Montage images and line drawings

For the previously known species already treated in Hita Garcia et al. (2017a) we used the colour montage images from that publication, which were taken with a Leica DFC450 camera attached to a Leica M205C microscope and the Leica Application Suite v, 4.1. The raw photo stacks were then processed to single montage images with Helicon Focus v. 6. The images of the five new species were taken with a Deimos System, containing Sony ILCE 7MK III Camera, Novoflex Tube with Mitutoyo M-Plan APO 10 × and 20 × lenses and Castel-Micro Stack Rail. Illumination was done with Profoto Flash System. The raw photo stacks were then also processed with Helicon Focus v. 6. All montage images used in this publication are available online and can be seen on AntWeb. Vector illustrations were created with Adobe Illustrator v. CS 6 by tracing specimen photographs. Compound plates of still images of 3D morphology and stacked colour images were processed and compiled in Adobe Photoshop and Illustrator v. CS 6.

#### **Measurements and indices**

We measured 50 workers with a Leica M165C stereo microscope equipped with an orthogonal pair of micrometres under magnifications of 80 × to 100 ×. Measurements and indices are presented as minimum and maximum values with arithmetic means in parentheses. In addition, measurements are expressed in mm to two decimal places. So far, all species of *Zasphinctus* possess eyeless workers, thus, as in Hita Garcia et al. (2017a), we omit any eye measurements and do not generate an ocular (or eye) index. Also, following that revision, we refrain from using total length since it is difficult to measure in already dry-mounted specimens that are not orientated in a straight line. The standard measurements HL and WL provide sufficient information about general body size dimensions. The following measurements and indices follow Hita Garcia et al. (2017a) (Fig. 1):

- **HL** Head Length: maximum distance from the midpoint of the anterior clypeal margin or from a line spanning the anterior-most points of the frontal lobes (depending on which projects farthest forward) to the midpoint of the posterior margin of head, measured in full-face view (Fig. 1C).
- **HW** Head Width: the maximum width of the head capsule, measured in full-face view (Fig. 1C).
- **SL** Scape Length: the maximum straight-line length of the scape, excluding the basal constriction or the neck (Fig. 1C).
- **PH** Pronotal Height: the maximum height of the pronotum in profile (Fig. 1A).
- **PW** Pronotal Width: the maximum width of the pronotum in dorsal view (Fig. 1B).
- **DML** Dorsal Mesosoma Length: maximum length of mesosomal dorsum from anterodorsal margin of pronotum to dorsal margin of propodeal declivity (Fig. 1B).
- WL Weber's Length of Mesosoma: the maximum diagonal length of the mesosoma in profile, from the angle at which the pronotum meets the cervix to the posterior basal angle of the metapleuron (Fig. 1A).

MFL	Metafemur Length: the maximum straight-line length of the metafe-
	mur, measured in dorsal view (Fig. 1D).
PTL	Abdominal Segment II (petiole) Length: the maximum length of ab-
	dominal segment II (petiole), measured in dorsal view (Fig. 1B).
PTH	Abdominal Segment II (petiole) Height: the maximum height of the
	petiolar tergum in profile view, including laterotergite, excluding pet-
	iolar sternum (Fig. 1A).
PTW	Abdominal Segment II (petiole) Width: the maximum width of ab-
	dominal segment II (petiole), measured in dorsal view (Fig. 1B).
A3L	Abdominal Segment III Length: the maximum length of abdominal
	segment III, measured in dorsal view (Fig. 1B).
A3W	Abdominal Segment III Width: the maximum width of abdominal
	segment III, measured in dorsal view (Fig. 1B).
A4L	Abdominal Segment IV Length: the maximum length of abdominal
	segment IV, measured in dorsal view (Fig. 1B).
A4W	Abdominal Segment IV Width: the maximum width of abdominal
	segment IV, measured in dorsal view (Fig. 1B).
A5L	Abdominal Segment V Length: the maximum length of abdominal
	segment V, measured in dorsal view (Fig. 1B).
A5W	Abdominal Segment V Width: the maximum width of abdominal
	segment V, measured in dorsal view (Fig. 1B).
A6L	Abdominal Segment VI Length: the maximum length of abdominal
	segment VI, measured in dorsal view (Fig. 1B).
A6W	Abdominal Segment VI Width: the maximum width of abdominal
	segment VI, measured in dorsal view (Fig. 1B).
CI	Cephalic Index: HW / HL × 100
SI	Scape Index: SL / HL × 100
DMI	Dorsal Mesosoma Index: PW / WL × 100
DMI2	Dorsal Mesosoma Index 2: DML / WL × 100
	Lateral Mesosoma Index: PH / WL × 100
MFI	Metafemur Index: MFL / HW × 100
LPI	Lateral Petiole Index: PTL / PTH × 100
DPI	Dorsal Petiole Index: PTW / PTL × 100
DA3I	Dorsal Abdominal Segment III Index: A3W / A3L × 100
DA4I	Dorsal Abdominal Segment IV Index: A4W / A4L × 100
DA5I	Dorsal Abdominal Segment V Index: A5W / A5L × 100
DA6I	Dorsal Abdominal Segment VI Index: A6W / A6L × 100

# Micro X-ray computed tomography, virtual reconstruction, and postprocessing of data

All micro-CT scans were performed at the Okinawa Institute of Science and Technology Graduate University (OIST), Japan, using a Zeiss Xradia 510 Versa 3D X-ray microscope operated with the Zeiss Scout-and-Scan Control System software v. 11.1.6411.17883 and saved in DICOM format. The scanned specimens were left attached to their paper point, which was clamped to a holding stage. Scan settings were selected according to yield optimum scan quality and followed protocols from previous studies (Hita Garcia et al. 2017a, 2017b, 2019).







**Figure 1.** Schematic line drawings illustrating the measurements used in this study **A** body in profile with measuring lines for PH, PTH, and WL **B** mesosoma and metasoma in dorsal view with measuring lines for A3L, A3W, A4L, A4W, A5L, A5W, A6L, A6W, DML, PW, PTL, and PTW **C** head in full-face view with measuring lines for HL, HW, and SL **D** metafemur in dorsal view with measuring line for MFL.

3D reconstructions of the resulting scan projection data were done with the Zeiss Scout-and-Scan Control System Reconstructor v. 11.1.6411.17883 and saved in DICOM file format. Postprocessing of DICOM raw data was performed with Amira software v. 6.3. 3D visualisations of the surface models were performed by using the 'volren' function. The desired volume renderings were generated by adjusting colour space range to a minimum so that the exterior surface of specimens remained visible at the highest available quality. The 3D models were then exported in PLY format to be uploaded to the online 3D model platform Sketchfab (https://sketchfab.com) and for virtual examination with Meshlab (Cignoni et al. 2008; https://www.meshlab.net). Images of shaded surface display volume renderings were made with the built-in "snapshot" function at the highest achievable resolution (1918 by 934 pixels).

#### Character recognition and virtual dissections

Following Hita Garcia et al. (2017a), we virtually examined external morphology of the treated species in addition to the traditional morphological examination of the physical specimens under a light microscope with magnifications up to 100 ×. Initially we used the 24 characters of high diagnostic value identified in Hita Garcia et al. (2017a) as a foundation to examine the morphology of all material. This was also a unique opportunity to test the robustness of that species delimitation system considering that the total number of specimens, locations, and species got significantly increased since its publication in 2017.

Meshlab allowed us a quick and efficient virtual examination and manipulation of all 3D models through rotation, scaling, dissection, and comparisons of entire specimens or particular body parts (Fig. 2). Every model was manipulated to show the desired angle in order to obtain a perfect view of the targeted morphological character. Once that was achieved, we took a still image with the "snapshot" function for further analysis and comparison among specimens and species. We took at least 21 still images of key diagnostic characters per species (one or two specimens per species) totalling more than 200 individual images used for illustrative purposes.

#### Cybertypes

The Cybertype datasets of the five new species provided in this study consist of the original micro-CT volumetric datasets (in DICOM format), 3D surface models (in PLY formats), still images of shaded 3D surface models, and all stacked digital colour images for each species. All cybertype datasets of the species described herein have been archived and are freely available from the Zenodo Digital Repository (https://doi.org/10.5281/zenodo.12593275). In addition to the cybertype data on Zenodo, we also provide freely accessible 3D surface models of all treated species on Sketchfab (https://skfb.ly/oXnuw). The cybertype datasets of the three previously described species were already published in Hita Garcia et al. (2017a) and are available online from the Dryad Digital Repository (Hita Garcia et al. 2017c). It should be noted that our cybertype approach has changed since the first revision of *Zasphinctus* (Hita Garcia et al. 2017a). We no longer include 3D PDFs or 3D rotation video files in order to avoid too much data redundancy. The 3D models in PLY format we provide



Figure 2. Representative screenshots of virtual dissection of exemplary 3D model, *Zasphinctus aprilia* sp. nov. holotype (CASENT0764763), in the software Meshlab **A** full body uncut **B** body after removal of antennae, legs, and AS III-VII **C** head and mesosoma after removal of remainder of body **D** head without antennae isolated **E** AS II (petiole) in isolated **F** AS III-VII isolated.

show the same (and more) visual data and offer much more usability since they can be freely downloaded and used with numerous types of software for multiple applications in 3D.

#### Species concept and species delimitation

Due to logistical and practical reasons this study does not include molecular data, even though we would have preferred that. The number of specimens available was rather low for almost all species. In addition, almost all the material used was on loan from several natural history museums or private collections that would not permit any destructive DNA extraction. Moreover, despite the possibilities to non-destructively extract DNA, many specimens of *Zasphinctus* are comparatively old and delicate, thus not easy to process in such a way without potentially harming pilosity, cuticle, or breaking of individual body parts. As a consequence, this taxonomic revision had to be based on external morphology alone.

The species delimitations presented here are based on detailed morphological examinations of the worker caste and the identification of discrete character sets for each taxonomic entity proposed as species. Furthermore, we considered habitat, microhabitat, elevation, and distributional data as additional evidence. We follow the Unified Species Concept of De Queiroz (2007) that defines a species as a separately evolving metapopulation lineage. In this framework, criteria laid out in other species concepts, such as the biological species concept and the morphological species concept, are integrated as independent lines of evidence reflecting progress through stages of the speciation process. The discrete gaps observed in morphological and distributional characteristics of *Zasphinctus* species are considered as evidence for long-standing divergence among such separately evolving lineages. Moreover, unlike many other groups of ants, every single *Zasphinctus* species delineated here is directly recognisable on the basis of numerous morphological differences and has its unique set of characters, which strongly support our species hypotheses.

## Results

#### Synoptic list of Zasphinctus species in the Afrotropics

Species known from workers and treated in this study:

#### Zasphinctus obamai group:

Zasphinctus lumumbai Hita Garcia & Gómez, sp. nov. [D.R. Congo] Zasphinctus obamai Hita Garcia, 2017 [Kenya] Zasphinctus wilsoni Hita Garcia, 2017 [Mozambique] Zasphinctus sarowiwai group: Zasphinctus aprilia Hita Garcia & Gómez, sp. nov. [D.R. Congo, Uganda] Zasphinctus kouakoui Hita Garcia & Gómez, sp. nov. [Ivory Coast] Zasphinctus lolae Hita Garcia & Gómez, sp. nov. [Ghana] Zasphinctus ndouri Hita Garcia & Gómez, sp. nov. [Senegal] Zasphinctus sarowiwai Hita Garcia, 2017 [Cameroon]

Species only known from males and excluded from this study:

Zasphinctus chariensis Santschi, 1915 [Chad] Zasphinctus rufiventris Santschi, 1915 [Benin, Mali]

#### **Distribution of species**

Despite that the genus is rather rarely collected compared to most other ant genera in the region, we were able to examine and revise the taxonomy of approximately 70 worker specimens that covered a wide area ranging from Senegal in the west to Kenya and Mozambique in the east and southeast, with most species and material being from Equatorial Africa. The distribution ranges of the species treated herein can be seen in Fig. 3.

Zasphinctus chariensis and Z. rufiventris are only known from males. Due to the non-existence of a taxonomic system for the male caste it is highly doubtful that males sampled throughout the region have been or can be correctly identified. As



Figure 3. Maps showing the known distribution ranges of Afrotropical Zasphinctus species.

a consequence, we only list the type locality countries for these two species and strongly recommend treating all other listings encountered in online databases as highly dubious or erroneous (Antmaps; AntWeb; AntWiki, https://antwiki.org).

#### **Diagnostic treatment**

The recent revision of Hita Garcia et al. (2017a) was based on a thorough examination of external morphology, both physically under the light microscope and virtually on the computer screen in 3D, which led to a novel way to evaluate characters and character states for species level taxonomy. Following the same approach, we used that taxonomic diagnostic system as a foundation for this study by examining the 24 diagnostic characters outlined in Hita Garcia et al. (2017a) for all our material. As a consequence, we had to exclude four characters from the list due to limited taxonomic usefulness or noticeable difficulty to visualise and apply. In particular we chose to omit the shape of the antennal scapes, the parafrontal ridges, the occiput in ventral view, and the subpetiolar process in ventral view. By contrast, we included six newly applied characters, such as the shape of the head in dorsal view, the torular-posttorular complex in profile, fusion of vertex and occiput, the postgenal sulcus running from the hypostoma to the postgenal bridge, the posterodorsal margin of the mesosoma separating the dorsum from the propodeal declivity, and surface sculpture on cephalic dorsum and genae. The complete list of diagnostic characters used for our newly developed species delimitation system, as well as the ones excluded, can be seen in Table 1.

In the following, we present compound diagnostic image plates displaying the morphological diversity observed during this study (Figs 4–18). Each body part was virtually sectioned, scaled, and dissected to allow a better examination in 3D. These diagnostic plates are intended to illustrate and aid the new identification key provided below. However, we believe that they also function as a general outline for the morphological characters of taxonomic importance and can be used by future taxonomists, parataxonomists, or ecologists to compare whole specimens or body parts in order to quickly gain a better understanding of the species studied. The full character matrix containing all morphological character states of diagnostic value is available as Suppl. material 1.

#### Head morphology

The head shape of all species is generally quite similar in being conspicuously much longer than wide, with a CI ranging from 78–86 (Fig. 4). However, there is some observable variation between species and groups. Measuring the head lengths of the *Z. sarowiwai* group species requires including either the clypeal tooth or its neighbouring basal projections of the parafrontal ridges. In contrast, the three species of the *Z. obamai* group do not have any clypeal teeth nor any conspicuous projections nearby. As a consequence, the values for head lengths of the *Z. obamai* group species are a bit shorter than their general head appearance, whereas the head lengths of the *Z. sarowiwai* group species are a bit longer. This means that, despite that the values of Cl 78–80 versus Cl 80–86 appear to be close and almost overlapping, the head shapes are very clearly different (Fig. 4D, F, H versus Fig. 4A, B, C, E, G). The head shape in lateral view is also overall

**Table 1.** List of all important characters examined in the previous study (Hita Garcia et al. 2017a) and used as foundation for this revision, with assessment of diagnostic potential and information on usage in this study (characters marked with \* were used for species delimitations in both revisions; characters marked with ± are newly used here).

Characters examined	Diagnostic assessment and usage
Head characters	
Shape of head in full-face view ±	high, <b>newly</b> used in this study
Shape of head in profile *	high, used in this study
Shape of mandibles	none, no significant interspecific variation observed, not used in this study
Mandibular dentition	none, no significant interspecific variation observed, not used in this study
Shape of clypeus	low, no significant interspecific variation observed, not used in this study
Presence of median clypeal tooth *	high, used in this study
Cuticular apron of clypeus	none, no significant interspecific variation observed, not used in this study
Torular-posttorular complex in dorsal view *	high, used in this study
Torular-posttorular complex in profile ±	high, <b>newly</b> used in this study
Antennal bulbus	none, no significant interspecific variation observed, not used in this study
Antennal pedicel and funiculus	none, no significant interspecific variation observed, not used in this study
Anterior tentorial pits	none, no significant interspecific variation observed, not used in this study
Eyes	none, absent in the worker caste
Vertex in posterodorsal and posterior view *	high, used in this study
Occipital margin in posterodorsal view *	high, used in this study
Fusion of vertex and occiput in posterior view $\pm$	high, <b>newly</b> used in this study
Occipital margin in posteroventral view *	high, used in this study
Hypostoma *	high, used in this study
Postgenal sulcus running through postgenal bridge $\pm$	high, <b>newly</b> used in this study
Mouthparts (maxillae, labium, labrum)	unclear, described in open condition for Z. lolae, but needs further investigation with better preserved alcohol material for $\mu$ CT scanning
Tentorium (internal)	unclear, tentatively examined in Hita Garcia et al. (2017a) and appears species–specific, but needs further investigation
Mesosoma characters	
Mesosoma in profile *	high, used in this study
Endosternum (internal)	unclear, tentatively examined in this study and appears species-specific, but needs further investigation with better preserved alcohol material for µCT scanning
Transverse mesopleural groove	moderately variable among species, not used in this study
Propleuron	none, no significant interspecific variation observed, not used in this study
Pleural endophragmal pit *	high, used in this study
Mesopleuron	moderately variable among species, not used in this study
Metapleuron	low, no significant interspecific variation observed, not used in this study
Mesosoma dorsal *	high, used in this study
Posterodorsal margin of mesosoma ±	high, <b>newly</b> used in this study
Probasitarsus	low, no significant interspecific variation observed, not used in this study
Calcar of strigil	low, no significant interspecific variation observed, not used in this study
Metasoma characters	
Levator of petiole	unclear, not examined in this study, very difficult to virtually dissect
Petiolar tergum in profile *	high, used in this study
Laterotergites	low, no significant interspecific variation observed, not used in this study
Subpetiolar process of petiole (AS II) in profile * *	high, used in this study
Petiolar (AS II) tergum in dorsal view *	high, used in this study
Disc of petiole (AS II)	none, no significant interspecific variation observed, not used in this study
Helcium	unclear, not examined in this study, very difficult to virtually dissect in some specimens
Abdominal segment III in dorsal view *	high, used in this study
Abdominal segment III in ventral view *	high, used in this study
Posterior end of abdominal segment III in ventral view *	high, used in this study
Prora in anteroventral view *	high, used in this study
Abdominal segment IV in dorsal view	moderate, relatively variable within species, not used in this study
Abdominal segment IV in ventral view	moderate, relatively variable within species, not used in this study
Abdominal segment V in dorsal view	low, no significant interspecific variation observed. not used in this study
Abdominal segment V in ventral view	low, no significant interspecific variation observed, not used in this study
Abdominal segment VI in dorsal view *	high, used in this study

Characters examined	Diagnostic assessment and usage				
Abdominal segment VI in ventral view	high, not used in this study				
Girdling constrictions abdominal segments IV, V, VI *	high, used in this study				
Pygidium	low, no significant interspecific variation observed, not used in this study				
Hypopygidium	high, not used in this study				
Spiracles abdominal segments II-VII	none, no significant interspecific variation observed, not used in this study				
General surface sculpture *	high, used in this study				
Cuticle thickness (internal)	unclear, examined in Hita Garcia et al. (2017a) but needs further investigation with more specimens				
Setation characters					
Pilosity and pubescence	moderate, but not used in this study due to varying degrees of preservation in many specimens and some observable intraspecific variability				
Characters used in Hita Garcia et al (2017a) but exclu	ded here				
Antennal scapes	moderate, but not used in this study due to difficulty in precisely measuring the scape				
Parafrontal ridges	high, but not used in this study due observed intraspecific variation and difficulty in describing shape and structure				
Occiput in ventral view	high, but not used in this study due to difficulty to virtually dissect in some specimens				
Subpetiolar process (AS II) in ventral view	high but not used in this study due to difficulty to virtually dissect in some specimens				



**Figure 4.** Diagnostic plate showing still images from surface volume renderings of the head in full-face view (the remainder of the body virtually removed) (torular-posttorular complex in semi-transparent red; anterior projections of parafrontal ridges in semi-transparent yellow) **A** *Z. aprilia* sp. nov. holotype (CASENT0764763) **B** *Z. kouakoui* sp. nov. paratype (CASENT0764653) **C** *Z. lolae* sp. nov. holotype (KGCOL02270) **D** *Z. lumumbai* sp. nov. holotype (MRACFOR0010007) **E** *Z. ndouri* sp. nov. holotype (KGCOL01883) **F** *Z. obamai* Hita Garcia, 2017 holotype (CASENT0764125) **G** *Z. sarowiwai* Hita Garcia, 2017 holotype (MCZ-ENT00512764).

quite similar but we observed some distinct variation between groups, in particular it appears that some species have a particularly swollen underside (Fig. 5). While we did not undertake any internal anatomical analysis, it appears that the ventral enlargement could be due to additional muscle mass in these species.



Figure 5. Diagnostic plate showing still images from surface volume renderings of the head in profile view (the remainder of the body virtually removed) (torular-posttorular complex in semi-transparent red) A Z. aprilia sp. nov. holotype (CASENT0764763) B Z. kouakoui sp. nov. paratype (CASENT0764653) C Z. lolae sp. nov. paratype (CASENT0764651) D Z. lumumbai sp. nov. holotype (KGCOL02270) E Z. ndouri sp. nov. holotype (KGCOL01883) F Z. obamai Hita Garcia, 2017 holotype (CASENT0764125) G Z. sarowiwai Hita Garcia, 2017 holotype (CASENT0764654) H Z. wilsoni Hita Garcia, 2017 holotype (MCZ-ENT00512764).

The anterior portion of the head bears several morphological structures of importance. Perhaps the most prominent when looking at a *Zasphinctus* head in full-face view is the vertical torular-posttorular complex (Keller 2011), which is typical for the genus in all species (Borowiec 2016). However, there are some pronounced differences in shape and size among species and groups. These differences are noticeable in dorsal (Fig. 4) and lateral view (Fig. 5). Another characteristic of dorylines is the presence of parafrontal ridges (Borowiec 2016), which are very well developed in all species of Afrotropical *Zasphinctus*. The shape seems to be somewhat species-specific but problematic as a diagnostic character (see below for further explanation). Despite the clypeus appearing similar among species, some species possess a conspicuous median tooth, or at least a denticle that is about the same size of the projections of the parafrontal ridges (Fig. 4A, C, E, G).

The posterior part of the head, usually overlooked in most dorylines, shows several interesting morphological structures of diagnostic significance. In particular the development of the vertexal margin (or posterodorsal margin of the head), the vertex itself, the occipital margin, and the occiput are of great importance (Figs 6, 7). In some species there is a very conspicuous and clearly demarcated vertexal margin that separates the frons (or dorsum of the head) from the vertex (posterior face of the head). This margin is clearly visible in posterodorsal and posterior view (Figs 6D, F, H, 7D, F, H). By contrast, the vertexal margin is either fully absent or only very weakly developed in other species (Figs 6A, B, C, E, G, 7A, B, C, E, G). The species with such strong vertexal margin also have the sides of the vertex clearly delimited and the whole vertex appears to be fused to the occiput (Fig. 7D, F, H). Furthermore, the shape and degree of development of the occipital and postoccipital margins shows diagnostic variation between species and groups (Fig. 8). However, despite using the anterior and posterior margins of the occiput, we omit



Figure 6. Diagnostic plate showing still images from surface volume renderings of the head in posterodorsal view (the remainder of the body virtually removed) (occipital margin in semi-transparent red; vertexal margin in semi-transparent yellow) **A** *Z. aprilia* sp. nov. holotype (CASENT0764763) **B** *Z. kouakoui* sp. nov. paratype (CASENT0764653) **C** *Z. lolae* sp. nov. holotype (KGCOL02270) **D** *Z. lumumbai* sp. nov. holotype (MRACFOR0010007) **E** *Z. ndouri* sp. nov. holotype (KGCOL01883) **F** *Z. obamai* Hita Garcia, 2017 holotype (CASENT0764125) **G** *Z. sarowiwai* Hita Garcia, 2017 holotype (CASENT0764654) **H** *Z. wilsoni* Hita Garcia, 2017 holotype (MCZ-ENT00512764).

the occiput itself from our diagnostic system. The reason is that it is somewhat difficult to dissect virtually, thus it will be almost impossible to be used by any regular taxonomists or ecologists that do not want to physically destroy their specimens.

As already mentioned above, we observed some conspicuous variability in some morphological structures of the head, not just between species but also within species. Perhaps the most variable is the shape of the parafrontal ridges (Fig. 9). Overall, it seems to be a rather irregular structure that even differs within the same specimen between the left and the right side (Fig. 9A) or among specimens of the same species in its general outline (Fig. 9A, B). But also, many structural details and the development of the anterior projections vary, especially the latter is of interest since it appears to be variable within the same species (Fig. 9A versus Fig. 9B; Fig. 9C versus Fig. 9D). As a consequence, we have omitted characters of the parafrontal ridges from our diagnostic system.

#### Mesosoma morphology

Overall, the mesosoma of all species is comparatively similar in most characters, except for proportions and few structural details. One important character of the genus is the presence of a pleural endophragmal pit concavity (Borowiec 2016),



**Figure 7.** Diagnostic plate showing still images from surface volume renderings of the head in posterior view (the remainder of the body virtually removed) (occipital margin in semi-transparent red; vertexal margin in semi-transparent yellow) **A** *Z. aprilia* sp. nov. holotype (CASENT0764763) **B** *Z. kouakoui* sp. nov. paratype (CASENT0764653) **C** *Z. lolae* sp. nov. holotype (KGCOL02270) **D** *Z. lumumbai* sp. nov. holotype (MRACFOR0010007) **E** *Z. ndouri* sp. nov. holotype (KGCOL01883) **F** *Z. obamai* Hita Garcia, 2017 holotype (CASENT0764125) **G** *Z. sarowiwai* Hita Garcia, 2017 holotype (CASENT0764654).

which was already recognised as having some diagnostic value in the previous revision (Hita Garcia et al. 2017a) (Fig. 10). Also in profile view, there is some noticeable variation in proportions, with some species having a bulkier and higher mesosoma compared to the more elongated one of the other species (Fig. 10). The same differences in proportions are also visible in dorsal view (Fig. 11).

One general characteristic of the genus is the presence of a distinct dorsal margin of the propodeal declivity that is also rectangular in posterior view (Borowiec 2016). This posterodorsal margin of the mesosoma shows some surprising variation since it is medially interrupted or much less strongly developed in several species (Figs 11A, D, F, H, 12A, D, F, H) compared to the others with an intact margin (Figs 11B, C, E, G, 12B, C, E, G).

#### Metasoma morphology

The tergum and laterotergite of AS II (petiole) are also generally quite similar among the studied species, except for their proportions, appearing lower and elongated in some species (Fig. 13D, F, H) and bulkier in others (Fig. 13A, B, C, E, G). The same phenomenon is also visible in dorsal view (Fig. 14). An important character for all studied species is the subpetiolar process of the petiole (AS



**Figure 8.** Diagnostic plate showing still images from surface volume renderings of the head in ventral view (the remainder of the body virtually removed) (hypostoma in semi-transparent red; postgenal sulcus in semi-transparent yellow; postoc-cipital carina in semi-transparent green) **A** *Z. aprilia* sp. nov. holotype (CASENT0764763) **B** *Z. kouakoui* sp. nov. paratype (CASENT0764653) **C** *Z. lolae* sp. nov. paratype (CASENT0764651) **D** *Z. lumumbai* sp. nov. holotype (MRACFOR0010007) **E** *Z. ndouri* sp. nov. holotype (KGCOL01883) **F** *Z. obamai* Hita Garcia, 2017 holotype (CASENT0764125) **G** *Z. sarowiwai* Hita Garcia, 2017 paratype (CASENT0764650) **H** *Z. wilsoni* Hita Garcia, 2017 holotype (MCZ-ENT00512764).

II), which is clearly visible in profile (Fig. 13). We observed some variation in the development of the anterior and ventral margins and the presence/absence of a differentiated fenestra. While there are some visible differences among species in ventral view (Hita Garcia et al. 2017a), we do not use the subpetiolar process in that particular perspective since it is often covered by legs, glue, or paper, thus challenging to examine in physical specimens and difficult for virtual dissections. Instead, we think it is useful to observe in profile view and use that perspective.

All species examined possess the typical *Zasphinctus* metasoma with conspicuous girdling constrictions between abdominal segments III, IV, V, and VI. The shape is overall relatively similar with differences only found in characters such as the proportions of some tergites/sternites, grooves at the posterior end of the sternites, the shape and development of the prora, and microsculpture on the constrictions. The metasomal segment of highest diagnostic value is certainly AS III. The tergum of AS III in dorsal view shows some distinct variation among groups by being more trapezoidal in some species (Fig. 15D, F, H) versus more rounded rectangular in others (Fig. 15A, B, C, E, G). The sternum of AS III provides several good diagnostic characters (Fig. 16). The shape of the sternum itself is variable among species and groups, as is the development of the



**Figure 9.** Diagnostic plate showing still images from surface volume renderings of the head in anterodorsal view focusing on the torular-posttorular complex (parafrontal ridges in semi-transparent yellow; anterior margin of parafrontal ridges in semi-transparent red) **A** *Z. sarowiwai* (CASENT0764654) **B** *Z. sarowiwai* (CASENT0764650) **C** *Z. lolae* sp. nov. (CASENT0764651) **D** *Z. lolae* sp. nov. (KGCOL02270).



Figure 10. Diagnostic plate showing still images from surface volume renderings of the mesosoma in profile view (the remainder of the body virtually removed) (pleural endophragmal pit concavity in semi-transparent yellow) **A** *Z. aprilia* sp. nov. holotype (CASENT0764763) **B** *Z. kouakoui* sp. nov. paratype (CASENT0764653) **C** *Z. lolae* sp. nov. holotype (KGCOL02270) **D** *Z. lumumbai* sp. nov. holotype (MRACFOR0010007) **E** *Z. ndouri* sp. nov. holotype (KGCOL01883) **F** *Z. obamai* Hita Garcia, 2017 holotype (CASENT0764125) **G** *Z. sarowiwai* Hita Garcia, 2017 paratype (CASENT0764650) **H** *Z. wilsoni* Hita Garcia, 2017 holotype (MCZ-ENT00512764).

prora, both well visible in ventral view (Fig. 16). In addition, another character is the groove at the posterior end of the sternite, which is highly variable ranging from a thick, deep, sharply, and irregularly outlined transverse groove (Fig. 16D, F), through a thinner, deep, sharply, and relatively regularly outlined transverse groove (Fig. 16A, G), to a weak or absent transverse groove (Fig. 16B, C, E, H).

As in Hita Garcia et al. (2017a), we also measured length and width of AS III to AS VI in order to assess differences in proportions among species. Our measurement data and observations showed little variation, except for AS VI (Fig. 17). The tergum of AS VI is clearly much broader than long in some species (Fig. 17A, B, C, G) contrasting with the less broad tergum seen in others (Fig. 17D, F, H), with one species being intermediate (Fig. 17E). Why only the tergum of AS VI shows such variability compared to AS IV, V, and VII is unknown.

An interesting observation is the presence/absence of the fine, cross-ribbed microsculpture within the girdling constrictions, both dorsally and ventrally,

even though usually much weaker dorsally. The species found in Senegal, Ivory Coast, Ghana, and Cameroon all display the cross-ribbed sculpture, whereas it is absent in the species from eastern Congo, Uganda, Kenya, and Mozambique



**Figure 11.** Diagnostic plate showing still images from surface volume renderings of the mesosoma in dorsal view (the remainder of the body virtually removed) **A** *Z. aprilia* sp. nov. holotype (CASENT0764763) **B** *Z. kouakoui* sp. nov. paratype (CASENT0764653) **C** *Z. lolae* sp. nov. holotype (KGCOL02270) **D** *Z. lumumbai* sp. nov. holotype (MRAC-FOR0010007) **E** *Z. ndouri* sp. nov. holotype (KGCOL01883) **F** *Z. obamai* Hita Garcia, 2017 holotype (CASENT0764125) **G** *Z. sarowiwai* Hita Garcia, 2017 paratype (CASENT0764650) **H** *Z. wilsoni* Hita Garcia, 2017 holotype (MCZ-ENT00512764).



Figure 12. Diagnostic plate showing still images from surface volume renderings of the mesosoma in posterior view focusing on propodeal declivity (outline of declivity in semi-transparent yellow) A Z. aprilia sp. nov. holotype (CASENT0764763) B Z. kouakoui sp. nov. paratype (CASENT0764653) C Z. lolae sp. nov. paratype (CASENT0764651)
D Z. lumumbai sp. nov. holotype (MRACFOR0010007) E Z. ndouri sp. nov. holotype (KGCOL01883) F Z. obamai Hita Garcia, 2017 holotype (CASENT0764125) G Z. sarowiwai Hita Garcia, 2017 paratype (CASENT0764650) H Z. wilsoni Hita Garcia, 2017 holotype (MCZ-ENT00512764).



**Figure 13.** Diagnostic plate showing still images from surface volume renderings of the tergum of AS II (petiole) in profile view (the remainder of the body virtually removed) (tergum in semi-transparent red, laterotergite in semi-transparent yellow) **A** *Z. aprilia* sp. nov. holotype (CASENT0764763) **B** *Z. kouakoui* sp. nov. paratype (CASENT0764653) **C** *Z. lolae* sp. nov. holotype (KGCOL02270) **D** *Z. lumumbai* sp. nov. holotype (MRACFOR0010007) **E** *Z. ndouri* sp. nov. holotype (KGCOL01883) **F** *Z. obamai* Hita Garcia, 2017 holotype (CASENT0764125) **G** *Z. sarowiwai* Hita Garcia, 2017 paratype (CASENT0764650) **H** *Z. wilsoni* Hita Garcia, 2017 holotype (MCZ-ENT00512764).



**Figure 14.** Diagnostic plate showing still images from surface volume renderings of the tergum of AS II (petiole) in dorsal view (the remainder of the body virtually removed) **A** *Z. aprilia* sp. nov. holotype (CASENT0764763) **B** *Z. kouakoui* sp. nov. holotype (KGCOL00589) **C** *Z. lolae* sp. nov. holotype (KGCOL02270) **D** *Z. lumumbai* sp. nov. holotype (MRACFOR0010007) **E** *Z. ndouri* sp. nov. holotype (KGCOL01883) **F** *Z. obamai* Hita Garcia, 2017 holotype (CASENT0764125) **G** *Z. sarowiwai* Hita Garcia, 2017 paratype (CASENT0764650) **H** *Z. wilsoni* Hita Garcia, 2017 holotype (MCZ-ENT00512764).

(Fig. 18). Since there are no character states supporting such a geographical division and it seems to be not correlated with the membership to any of the two species groups, we consider this more of a sporadic phenomenon.



**Figure 15.** Diagnostic plate showing still images from surface volume renderings of the tergum of AS III in dorsal view (the remainder of the body virtually removed) **A** *Z. aprilia* sp. nov. holotype (CASENT0764763) **B** *Z. kouakoui* sp. nov. paratype (CASENT0764653) **C** *Z. lolae* sp. nov. paratype (CASENT0764651) **D** *Z. lumumbai* sp. nov. holotype (MRAC-FOR0010007) **E** *Z. ndouri* sp. nov. holotype (KGCOL01883) **F** *Z. obamai* Hita Garcia, 2017 holotype (CASENT0764125) **G** *Z. sarowiwai* Hita Garcia, 2017 paratype (CASENT0764650) **H** *Z. wilsoni* Hita Garcia, 2017 holotype (MCZ-ENT00512764).



Figure 16. Diagnostic plate showing still images from surface volume renderings of the sternum of AS III in ventral view (the remainder of the body virtually removed) (Bum in semi-transparent yellow, prora in semi-transparent red) A Z. aprilia sp. nov. holotype (CASENT0764763) B Z. kouakoui sp. nov. paratype (CASENT0764653) C Z. lolae sp. nov. paratype (CASENT0764651) D Z. lumumbai sp. nov. holotype (MRACFOR0010007) E Z. ndouri sp. nov. holotype (KGCOL01883) F Z. obamai Hita Garcia, 2017 holotype (CASENT0764125) G Z. sarowiwai Hita Garcia, 2017 paratype (CASENT0764650) H Z. wilsoni Hita Garcia, 2017 holotype (MCZ-ENT00512764).



Figure 17. Diagnostic plate showing still images from surface volume renderings of the tergum of AS VI in dorsal view (the remainder of the body virtually removed) (outline of post-sclerite tergum in semi-transparent red) **A** *Z. aprilia* sp. nov. holotype (CASENT0764763) **B** *Z. kouakoui* sp. nov. paratype (CASENT0764653) **C** *Zasphinctus lolae* sp. nov. paratype (CASENT0764651) **D** *Z. lumumbai* sp. nov. holotype (MRACFOR0010007) **E** *Z. ndouri* sp. nov. holotype (KGCOL01883) **F** *Z. obamai* Hita Garcia, 2017 holotype (CASENT0764125) **G** *Z. sarowiwai* Hita Garcia, 2017 paratype (CASENT0764650) **H** *Z. wilsoni* Hita Garcia, 2017 holotype (MCZ-ENT00512764).



**Figure 18.** Diagnostic plate showing still images from surface volume renderings of the sternites of AS III-VII in ventral view (the remainder of the body virtually removed) (girdling constrictions with cross-ribbed sculpture are in semi-transparent red; unsculptured girdling constrictions are in semi-transparent yellow) **A** *Z. aprilia* sp. nov. holotype (CASENT0764763) **B** *Z. kouakoui* sp. nov. paratype (CASENT0764653) **C** *Z. lolae* sp. nov. paratype (CASENT0764651) **D** *Z. lumumbai* sp. nov. holotype (MRACFOR0010007) **E** *Z. ndouri* sp. nov. holotype (KGCOL01883) **F** *Z. obamai* Hita Garcia, 2017 holotype (CASENT0764125) **G** *Z. sarowiwai* Hita Garcia, 2017 paratype (CASENT0764650) **H** *Z. wilsoni* Hita Garcia, 2017 holotype (MCZ-ENT00512764).

#### Afrotropical species groups

The currently known species within the Afrotropical region can be roughly split into two species groups/complexes on the basis of qualitative and quantitative morphology: the *Z. obamai* group and the *Z. sarowiwai* group. We observed an astonishing number of robust differences (we list 18 clear-cut morphological characters in Suppl. material 1) between the members of these groups suggesting that they might very likely represent "genuine" monophyletic groups. However, there could be other explanations, thus without a molecular phylogenetic analysis these two groups are proposed as convenience groups for now. Furthermore, due to us focusing entirely on Afrotropical *Zasphinctus*, it remains to be tested if our groups work in other biogeographical regions.

#### Zasphinctus obamai group

Diagnosis. Body size significantly smaller (HL 0.54-0.60; WL 0.73-0.87); head in full-face view appearing thinner (CI 78-80); head in profile appearing conspicuously thinner, its underside only slightly curved; clypeal area always without conspicuous median tooth; torular-posttorular complex in dorsal view with sides more or less parallel; torular-posttorular complex in profile strongly arched anteriorly towards highest dorsal point and posterodorsally lobate; vertexal margin in posterodorsal view strongly developed delimiting posterior face of head; anterior outline of occipital margin in ventral view moderately or weakly and irregularly defined and with anterolateral projections angulate (in Z. obamai rounded); vertex with clear margin laterally and not appearing fused to the occiput; anterior outline of postoccipital margin in ventral view moderately or weakly and irregularly defined and with anterolateral projections angulate; mesosoma in profile relatively lower and elongate (LMI 34-37); pleural endophragmal pit strongly developed and deep; petiolar tergum in profile relatively lower (LPI 112-123); mesosoma in dorsal view appearing thinner and elongate (DMI 38-40; DMI2 49-53); petiolar tergum in profile relatively lower, ~ 0.8-0.9 × higher than long (LPI 112-123); petiolar tergum in dorsal view thinner, ~ 0.8-0.9 × broader than long (DPI 82-93); abdominal tergum III in dorsal view strongly trapezoidal with anterior margin more angulate; abdominal sternum III in ventral view rounded trapezoidal, comparatively thinner and higher, sides less rounded; usually with conspicuous surface sculpture somewhere on body (except for piliferous foveae), usually on cephalic dorsum and sides of mesosoma (Figs 19D, F, H, 20D, F, H).

The three species of the *Z. obamai* group appear to be rarer and are only known from Mozambique (*Z. wilsoni*), Kenya (*Z. obamai*) and D.R. of Congo (*Z. lumumbai*), with the latter two species only being found in their respective type localities.

#### Zasphinctus sarowiwai group

**Diagnosis.** Body size significantly larger (HL 0.73–0.98; WL 0.98–1.40); head in full-face view appearing thicker (CI 80–86); head in profile appearing conspicuously thicker, with a swollen underside; clypeal area usually with conspicuous median tooth (except for *Z. kouakoui*); torular-posttorular complex in dorsal



**Figure 19.** Diagnostic plate showing head in full-face view of all species treated herein (stacked colour images) **A** *Z. aprilia* sp. nov. holotype (CASENT0764763) **B** *Z. kouakoui* sp. nov. holotype (KGCOL00589) **C** *Z. lolae* sp. nov. holotype (KGCOL02270) **D** *Z. lumumbai* sp. nov. holotype (MRACFOR0010007) **E** *Z. ndouri* sp. nov. holotype (KGCOL01883) **F** *Z. obamai* Hita Garcia, 2017 holotype (CASENT0764125) **G** *Z. sarowiwai* Hita Garcia, 2017 paratype (CASENT0764650) **H** *Z. wilsoni* Hita Garcia, 2017 holotype (MCZ-ENT00512764).

view with sides converging posteriorly; torular-posttorular complex in profile funnel-shaped; vertexal margin either weakly developed or fully absent; outline of occipital margin in posterodorsal view sharp and very regularly defined; vertex not clearly demarcated and not appearing fused with the occiput; anterior outline of postoccipital margin in ventral view sharp and very regularly defined and with anterolateral projections rounded; mesosoma in profile relatively higher and compact (LMI 37-41); pleural endophragmal pit weakly developed, either shallow but visible or inconspicuous; mesosoma in dorsal view appearing thicker and more compact (DMI 41-45; DMI2 53-59); petiolar tergum in profile relatively higher, ~ 1.0-1.2 × higher than long (LPI 82–108); petiolar tergum in dorsal view thicker, ~ 1.0-1.3 × broader than long (DPI 102–131); abdominal tergum III in dorsal view weakly trapezoidal, more rounded rectangular with less angulate anterior margin; abdominal sternum III in ventral view campaniform, comparatively broader and shorter, sides strongly rounded; usually without any noticeable surface sculpture (except for piliferous foveae) (Figs 19A, B, C, E, G, 20A, B, C, E, G).

**Notes.** The *Z. sarowiwai* group appears to be more species-rich and better sampled since the vast majority of available specimens belong to this group. The distribution range is vast and stretches from Senegal in the west to western Uganda.



Figure 20. Diagnostic plate showing full body in profile view of all species treated herein (stacked colour images)
A Z. aprilia sp. nov. holotype (CASENT0764763) B Z. kouakoui sp. nov. holotype (KGCOL00589) C Z. lolae sp. nov. holotype (KGCOL02270) D Z. lumumbai sp. nov. holotype (MRACFOR0010007) E Z. ndouri sp. nov. holotype (KGCOL01883)
F Z. obamai Hita Garcia, 2017 holotype (CASENT0764125) G Z. sarowiwai Hita Garcia, 2017 holotype (CASENT0764654)
H Z. wilsoni Hita Garcia, 2017 holotype (MCZ-ENT00512764).



Figure 21. Diagnostic plate showing full body in dorsal view of all species treated herein (stacked colour images)
A Z. aprilia sp. nov. holotype (CASENT0764763) B Z. kouakoui sp. nov. holotype (KGCOL00589) C Z. lolae sp. nov. holotype (KGCOL02270) D Z. lumumbai sp. nov. holotype (MRACFOR0010007) E Z. ndouri sp. nov. holotype (KGCOL01883)
F Z. obamai Hita Garcia, 2017 holotype (CASENT0764125) G Z. sarowiwai Hita Garcia, 2017 holotype (CASENT0764654)
H Z. wilsoni Hita Garcia 2017 holotype (MCZ-ENT00512764).

#### Identification key to Afrotropical Zasphinctus species (workers)

The present work renders the key from Hita Garcia et al. (2017a) fully outdated and in need for revision. Below, we provide a newly developed identification key to the species groups/species of Afrotropical *Zasphinctus*.

- Body size significantly larger (HL 0.73–0.98; WL 0.98–1.40); in full-face view head appearing broader (CI 80–86) (Fig. 4A, B, C, E, G); vertexal margin weakly developed or absent (Fig. 6A, B, C, E, G); petiolar node 1.0–1.3 × wider than long (DPI 102–131) (Fig. 14A, B, C, E, G); ASIII in dorsal view appearing more rectangular and less trapezoidal (Fig. 15A, B, C, E, G) ..... 2 [Z. sarowiwai group]

- Significantly much larger species (HL 0.90–0.98; WL 1.29–1.40); sternite of AS III appearing very broad and short (Fig. 16C); tergite of AS VI appearing

shorter, ~  $1.9-2.0 \times$  broader than long (DA6I 189–200) (Fig. 17C); head, mesosoma and petiole always much darker in colour, very dark brown to black, AS III–VI ranging from light to very dark brown (Fig. 20C). [Ghana].....**Z. lolae** 

#### **Species accounts**

#### Zasphinctus obamai group

#### Zasphinctus lumumbai Hita Garcia & Gómez, sp. nov.

https://zoobank.org/083C169D-42ED-4A66-9D5A-32DAFF358DC1 Figs 3D, 4D, 5D, 6D, 7D, 8D, 10D, 11D, 12D, 13D, 14D, 15D, 16D, 17D, 18D, 19D, 20D, 21D, 22

**Type material examined.** *Holotype* • Pinned worker, DEMOCRATIC REPUBLIC OF CONGO, Equateur, Mabali, Tsuhapa River (Bikoro Terr.), Foret Inondée, Humus, collection code ANTC39356, IX.1959 (*N. Leleup*) (MRAC: MRACFOR0010007). [specimen re-mounted by KGA 2022]

**Cybertype** • Dataset of the holotype (MRACFOR0010007) consists of the volumetric raw data (in DICOM format), a 3D surface model (in PLY format), still images of multiple body parts from surface volume renderings of 3D models, stacked digital colour images illustrating head in full-face view, pro-file, and dorsal views of the body. The data is deposited at Zenodo (https://doi.org/10.5281/zenodo.12593275) and can be freely accessed as virtual representation of the physical holotype. In addition to the data at Zenodo, we also provide a freely accessible 3D surface model at Sketchfab (https://skfb.ly/p7M7p).



**Figure 22.** Shaded surface display volume renderings of 3D models of *Z. lumumbai* sp. nov. holotype (MRACFOR0010007) **A** full body in profile **B** full body in dorsal view **C** head in full-face view (with antennae) **D** head in full-face view (without antennae) **E** head in ventral view **F** abdominal segment II (petiole) in profile **G** abdominal segment II (petiole) in dorsal view **H** tergum of AS III in dorsal view I sternum of AS III in ventral view.

**Differential worker diagnosis.** With characters of the *Z. obamai* group plus the following: body size significantly much smaller (HL 0.54; WL 0.73); lateral arms of hypostomal carina less diverging, relatively thin, and angulate at widest points (Fig. 8D); postgenal sulcus restricted to area adjacent to hypostomal carina and only weakly impressed (Fig. 8D); postoccipital margin in ventral view with anterior outline moderately or weakly and irregularly defined; anterolateral projections angulate (Fig. 8D); pleural endophragmal pit weakly developed and shallow but visible (Fig. 10D); subpetiolar process of petiole (AS II) in profile with thickened anterior and ventral margins and weak concavity without differentiated fenestra (Fig. 13D); posterior end of abdominal segment III in ventral view with thick, deep, sharply and irregularly outlined transverse groove (Fig. 16D); prora in anteroventral view well-developed with thick, irregularly shaped and rounded lateroventral margins (Fig. 16D); surface sculpture on cephalic dorsum and genae mostly smooth and shiny with

abundant, relatively deep, and large piliferous foveae, except for reticulate-punctate anteromedian area (Figs 4D, 5D, 19D, 20D); general surface sculpture on mesosoma and metasoma seemingly smooth and shiny with varying degrees of scattered piliferous foveae, hypopygidium reticulate-rugose (Figs 20D, 21D). [general surface sculpture difficult to assess since larger areas are covered in glue and dirt]

**Measurements and indices.** Morphometric data is based on singleton holotype from the Democratic Republic of Congo and can be seen in Table 2, Suppl. material 3.

**Etymology.** The species epithet *lumumbai* is a Latinised noun in the genitive case, named in honour of Mr. Patrice Lumumba, first elected Prime Minister of the Democratic Republic of the Congo.

 Table 2. Comparative data of measurements and indices used for the eight species of Afrotropical Zasphinctus (raw data is available in Suppl. material 3).

	Z. aprilia (N = 6)	Z. kouakoui (N = 5)	Z. lolae (N = 6)	Z.lumumbai (N = 1)	Z.ndouri (N = 8)	Z.obamai (N = 7)	Z. sarowiwai (N = 4)	Z.wilsoni (N = 1)
HL	0.84-0.86	0.75-0.80	0.90-0.98	0.54	0.73-0.77	0.55-0.59	0.86-0.89	0.61
HW	0.69-0.73	0.63-0.66	0.77-0.83	0.42	0.59-0.62	0.44-0.47	0.73-0.75	0.49
SL	0.45-0.48	0.40-0.44	0.48-0.54	0.26	0.37-0.38	0.26-0.31	0.48-0.50	0.32
SW	0.17-0.19	0.15-0.18	0.20-0.23	0.12	0.14	0.12-0.14	0.19-0.21	0.12
PH	0.46-0.49	0.40-0.44	0.50-0.54	0.25	0.38-0.39	0.26-0.29	0.48-0.52	0.32
PW	0.50-0.54	0.42-0.46	0.55-0.63	0.29	0.42-0.45	0.28-0.33	0.50-0.53	0.35
DML	0.93-0.98	0.79-0.88	0.95-1.10	0.57	0.79-0.83	0.53-0.65	0.94-0.99	0.66
WL	1.18-1.26	1.03-1.10	1.29-1.40	0.73	0.98-1.05	0.73-0.81	1.20-1.30	0.87
MFL	0.61-0.64	0.55-0.58	0.69-0.75	0.31	0.46-0.51	0.33-0.37	0.62-0.67	0.49
PTL	0.36-0.42	0.33-0.35	0.38-0.44	0.26	0.31-0.34	0.27-0.29	0.44-0.47	0.29
PTH	0.36-0.42	0.36-0.43	0.43-0.48	0.23	0.34-0.35	0.22-0.24	0.42-0.45	0.26
PTW	0.41-0.46	0.36-0.40	0.49-0.53	0.23	0.38-0.40	0.23-0.26	0.45-0.49	0.27
A3L	0.50-0.56	0.45-0.49	0.59-0.68	0.32	0.43-0.46	0.33-0.39	0.53-0.59	0.43
A3W	0.58-0.66	0.50-0.56	0.67-0.75	0.38	0.51-0.55	0.38-0.43	0.62-0.67	0.48
A4L	0.44-0.47	0.39-0.43	0.51-0.57	0.27	0.40-0.43	0.26-0.29	0.50-0.56	0.31
A4W	0.68-0.77	0.66-0.71	0.83-0.90	0.43	0.63-0.67	0.46-0.52	0.77-0.82	0.54
A5L	0.41-0.43	0.35-0.40	0.47-0.51	0.26	0.36-0.38	0.25-0.29	0.44-0.47	0.32
A5W	0.76-0.78	0.68-0.71	0.85-0.92	0.45	0.64-0.67	0.47-0.52	0.78-0.84	0.55
A6L	0.37-0.39	0.33-0.38	0.41-0.44	0.26	0.34-0.37	0.26-0.30	0.37-0.40	0.32
A6W	0.69-0.72	0.66-0.68	0.78-0.84	0.44	0.61-0.64	0.45-0.49	0.73-0.76	0.51
CI	82-85	82-84	83-86	78	80-81	78-80	84-85	82
SI	54-57	53-55	53-55	48	49-51	47-53	56-57	53
SI2	253-282	243-267	239-246	217	264-271	215-242	238-253	267
DMI	42-44	41-43	43-45	40	42-44	38-40	41-42	40
DMI2	53-55	53-54	57-59	51	53-55	48-53	53-55	53
LMI	39-42	38-40	38-39	34	37-39	34-36	40	37
MFI	88-90	86-89	90-92	73	77-83	75-79	86-89	100
LPI	98-102	82-93	86-93	113	92-97	117-123	105-108	112
DPI	102-114	109-114	120-131	88	116-123	82-93	102-109	93
DA3I	113-118	111-116	109-114	119	113-120	108-115	114-117	112
DA4I	154-166	159-173	156-163	159	152-160	170-181	145-158	174
DA5I	178-191	178-200	181-192	173	168-178	174-188	177-179	172
DA6I	178-193	180-204	189-200	169	168-179	163-173	188-197	159

**Distribution and biology.** *Zasphinctus lumumbai* is so far only known from one specimen in the MRAC collection, so our knowledge is limited to it being found at the type locality in forest soil.

#### Zasphinctus obamai Hita Garcia, 2017

Figs 3F, 4F, 5F, 6F, 7F, 8F, 10F, 11F, 12F, 13F, 14F, 15F, 16F, 17F, 18F, 19F, 20F, 21F, 23

**Type material examined.** *Holotype* • Pinned worker, KENYA, Western Province, Kakamega Forest, Buyangu, 0.35222, 34.8647, 1640 m, secondary rainforest, leaf litter, collection code FHG00001, VII.–VIII.2004 (*F. Hita Garcia*) (NMKE: CASENT0764125). *Paratypes* • Seven pinned workers: two with same data as holotype (NHMUK: CASENT0764126; MCZC: CASENT0764127) • two from KENYA, Western Province, Kakamega Forest, Isecheno, equatorial rainforest, sifted litter and soil under *Morus mesozygia*, 0.34, 34.85, 1550 m, ANTC8506, 6.XI.2002 (*W. Okeka*) (LACM: CASENT0178218; ZFMK: CASENT0764648) • two from KENYA, Western Province, Kakamega Forest, Kisere Forest Fragment, 0.38505, 34.89378, 1650 m, rainforest, ex leaf litter, Transect 11, collection code FHG00036, 16.VII.2007 (*F. Hita Garcia*) (NMKE: CASENT0764128; NMKE: CASENT0764129) and • one from KENYA, Western Province, Kakamega Forest, Bunyala Forest Fragment, 0.37889, 34.69917, 1448 m, Winkler leaf litter extraction, collection code ANTC39476, VIII.2008 (*G. Fischer*) (ZFMK: CASENT0764647).

**Cybertype** • Dataset was published in Hita Garcia et al. (2017a) and consists of the volumetric raw data (in DICOM format), 3D PDFs, and 3D rotation videos of scans of head, mesosoma, metasoma, and the full body of the physical holotype (NMKE: CASENT0764125) and/or one paratype (MCZC: CASENT0764127) in addition to montage photos illustrating head in full-face view, profile, and dorsal views of the body of both specimens. The data was deposited at Dryad and can be freely accessed as virtual representation of both types (Hita Garcia et al. 2017c, http://dx.doi.org/10.5061/dryad.4s3v1). In addition to the cybertype data at Dryad, we also provided a freely accessible 3D surface model of the holotype at Sketchfab (https://skfb.ly/6sPvr).

**Non-type material examined.** • One worker from KENYA, Western Province, Kakamega Forest, Isecheno, equatorial rainforest, sifted litter and soil under *Morus mesozygia*, 0.24, 34.87, 1550 m, collection code ANTC8507, 6.XI.2002 (*W. Okeka*) (LACM: CASENT0178219).

**Differential worker diagnosis.** With characters of the *Z. obamai* group plus the following: body size significantly much smaller (HL 0.55–0.59; WL 0.73–0.81); lateral arms of hypostomal carina less diverging, relatively thin, and angulate at widest points (Fig. 8F); postgenal sulcus restricted to area adjacent to hypostomal carina and only weakly impressed (Fig. 8F); postoccipital margin in ventral view with anterior outline moderately or weakly and irregularly defined; anterolateral projections rounded (Fig. 8F); pleural endophragmal pit weakly developed and shallow but visible (Fig. 10F); subpetiolar process of petiole (AS II) in profile with extremely thickened anterior and ventral margins and well developed concavity with differentiated fenestra (Fig. 13F); posterior end of abdominal segment III in ventral view with thick, deep, sharply and irregularly outlined transverse groove (Fig. 16F); prora in anteroventral view well-developed with



**Figure 23.** Shaded surface display volume renderings of 3D models of *Z. obamai* Hita Garcia, 2017 holotype (CASENT0764125) **A** full body in profile **B** full body in dorsal view **C** head in full-face view (with antennae) **D** head in full-face view (without antennae) **E** head in ventral view **F** abdominal segment II (petiole) in profile **G** abdominal segment II (petiole) in dorsal view **H** tergum of AS III in dorsal view **I** sternum of AS III in ventral view.

thick, irregularly shaped and rounded lateroventral margins (Fig. 16F); surface sculpture on cephalic dorsum and genae mostly smooth and shiny, with abundant and small piliferous foveae, except for reticulate-punctate anteromedian area (Figs 4F, 5F, 19F, 20F); general surface sculpture on mesosoma and metasoma mostly smooth and shiny with abundant piliferous punctures, except for reticulate-punctate anterior pronotum, mesopleuron, lateral propodeum, most of lateral petiole, and hypopygidium (Figs 20F, 21F)).

**Measurements and indices.** Morphometric data is based on six workers from Kenya and can be seen in Table 2, Suppl. material 3.

**Distribution and biology.** Zasphinctus obamai is only known from the type locality in western Kenya. As noted in Hita Garcia et al. (2017a), despite a thorough ant inventory (Hita Garcia et al. 2009), it was only collected few times,

thus one of the rarest species in that forest system. It was only found in the leaf litter layer of primary or near-primary forest habitats. No new material was collected since its original description. Consequently, *Z. obamai* appears to be endemic to the Kakamega Forest.

#### Zasphinctus wilsoni Hita Garcia, 2017

Figs 3H, 4H, 5H, 6H, 7H, 8H, 10H, 11H, 12H, 13H, 14H, 15H, 16H, 17H, 18H, 19H, 20H, 21H, 24

**Type material examined.** *Holotype* • Pinned worker, Mozambique, Sofala, Gorongosa National Park, 2 km S Chitengo, -18.99472, 34.35769, 40 m, secondary forest, leaf litter, collection code ANTC37418, 30.V.2012 (*G.D. Alpert*) (MCZC: MCZ-ENT00512764).

*Cybertype* • Dataset was published in Hita Garcia et al. (2017a) and consists of the volumetric raw data (in DICOM format), as well as 3D PDFs and 3D rotation videos of scans of the head, mesosoma, metasoma, and the full body of the physical holotype (MCZC: MCZ-ENT00512764) in addition to montage photos illustrating head in full-face view, profile, and dorsal views of the body. The data was deposited at Dryad and can be freely accessed as virtual representation of the holotype (Hita Garcia et al. 2017c, http://dx.doi.org/10.5061/dryad.4s3v1). In addition to the cybertype data at Dryad, we also provided a freely accessible 3D surface model of the holotype at Sketchfab (https://skfb. ly/6sPwN).

**Non-type material examined.** • Five workers from: MOZAMBIQUE: Cabo Delgado, Parque Nacional Quirimbas, Mareja Reserve, miombo woodland, ex soil, -12.84778, 40.16542, 180 m, collection code BLF38248, 25.II.2016 (*B.L. Fisher; Arthropod Team*) (CASC: CASENT0779283, CASENT0779285) • Zambezia, Mount Mabu, rainforest, ex soil, -16.34888, 36.4081, 375 m, collection code BLF38954, 12.III.2016 (*B.L. Fisher; Arthropod Team*) (CASC: CASENT0779844) • Zambezia, Mount Mabu, rainforest, ex soil, -16.34888, 36.4081, 375 m, collection code BLF39161, 24.III.2016 (*B.L. Fisher; Arthropod Team*) (CASC: CASENT0781222) • Zambezia, Mount Mabu, rainforest, ex soil, -16.34888, 36.4081, 375 m, collection code BLF39209, 25.III.2016 (*B.L. Fisher; Arthropod Team*) (CASC: CASENT0781285).

**Differential worker diagnosis.** With characters of the *Z. obamai* group plus the following: body size significantly much smaller (HL 0.61; WL 0.87); lateral arms of hypostomal carina strongly diverging anteriorly, relatively thick, and strongly angulate at widest points (Fig. 8H); postgenal sulcus weakly impressed and running halfway to occipital margin (Fig. 8F); postoccipital margin in ventral view with anterior outline moderately or weakly and irregularly defined; anterolateral projections angulate (Fig. 8H); pleural endophragmal pit very weakly developed and inconspicuous (Fig. 10H); subpetiolar process of petiole (AS II) in profile with thickened anterior and ventral margins and weak concavity without differentiated fenestra (Fig. 13H); posterior end of abdominal segment III in ventral view with transverse groove weak to absent, instead with irregular groves and rugosity (Fig. 16H); prora in anteroventral view very weakly developed with almost absent lateroventral margins (Fig. 16H); surface sculpture on genae mostly smooth and shiny, on cephalic dorsum mostly retic-



**Figure 24**. Shaded surface display volume renderings of 3D models of *Z. wilsoni* Hita Garcia, 2017 holotype (MCZ-ENT00512764) **A** full body in profile **B** full body in dorsal view **C** head in full-face view (with antennae) **D** head in full-face view (without antennae) **E** head in ventral view **F** abdominal segment II (petiole) in profile **G** abdominal segment II (petiole) in dorsal view **H** tergum of AS III in dorsal view I sternum of AS III in ventral view.

ulate-rugose (Figs 4H, 5H, 19H, 20H); general surface sculpture on mesosoma and metasoma mostly smooth and shiny with abundant piliferous foveae, mesosoma and petiole laterally mostly reticulate-punctate, hypopygidium reticulate-rugose (Figs 20H, 21H).

**Measurements and indices.** Morphometric data is based on the singleton holotype from Mozambique and can be seen in Table 2, Suppl. material 3.

**Distribution and biology.** Fortunately, our knowledge of the distribution of *Z. wilsoni* has increased since its original description. Whereas in Hita Garcia et al. (2017a) it was only known from its type locality, the Gorongosa National Park, now it also known from two additional localities considerably further northeast, namely Quirimbas in Cabo Delgado and Mount Mabu in Zambezia. The species was collected in litter in Gorongosa and in soil in the other two lo-

calities. To our surprise it seems that *Z. wilsoni* is relatively flexible in its habitat requirements since it was collected in secondary dry forest, miombo woodland and rainforest.

#### Zasphinctus sarowiwai group

#### Zasphinctus aprilia Hita Garcia & Gómez, sp. nov.

https://zoobank.org/23504D6E-111E-4D62-B587-1AAFCDBB364B Figs 2, 3A, 4A, 5A, 6A, 7A, 8A, 10A, 11A, 12A, 13A, 14A, 15A, 16A, 17A, 18A, 19A, 20A, 21A, 25

**Type material examined.** *Holotype* • Pinned worker, UGANDA, Kabarole, Kibale National Park, Kanyawara Biological Station, rainforest, ex leaf litter, 0.56437, 30.36059, 1510 m, collection code FHG01047, 6.–16.VIII.2012 (*F. Hita Garcia*) (ZMHB: CASENT0764763). *Paratypes* • Three pinned workers from UGANDA, Kabarole, Kibale National Park, Kanyawara Biological Station, rainforest opening, field station clearing, hand collected, 0.55838, 30.35992, 1510 m, collection code PGH00079, 6.–16.VIII.2012 (*P.G. Hawkes*) (NHMUK: CASENT0790015; AFRC: CASENT0254676; SAMC: CASENT0254677) and • 2 pinned workers from UGANDA, Kabarole, Kibale National Park, Kanyawara Biological Station, moist evergreen forest, ground forager(s), 0.56437, 30.36059, 1520 m, collection codes BLF29378 and BLF29365, 8.VIII.2012 (*B.L. Fisher; F.A. Esteves; Malagasy Arthropod Team*) (CASC: CASENT0352810, CASENT0352813).

**Cybertype** • Dataset of the holotype (CASENT0764763) consists of the volumetric raw data (in DICOM format), a 3D surface model (in PLY format), still images of multiple body parts from surface volume renderings of 3D models, stacked digital colour images illustrating head in full-face view, profile and dorsal views of the body. The data is deposited at Zenodo (https://doi.org/10.5281/ zenodo.12593275) and can be freely accessed as virtual representation of the physical holotype. In addition to the data at Zenodo, we also provide a freely accessible 3D surface model at Sketchfab (https://skfb.ly/p7MpJ).

**Non-type material examined.** • Twenty workers from: DEMOCRATIC REPUBLIC OF CONGO: Ituri, Matenda, Label F.98, -1.15653, 27.41793, ca 600 m, 22.IX.1929 (*A. Collart*) (MRAC: MRACFOR000101, MRACFOR000102, MRACFOR000103, MRACFOR000104, MRACFOR000105, MRACFOR000106, MRACFOR000107, MRACFOR000108, MRACFOR000109, MRACFOR000110, MRACFOR000111, MRACFOR000112, MRACFOR000113, MRACFOR000114, MRACFOR000115, MRACFOR000116); Ituri, Madyu (La Moto), 1.77076, 30.29094, ca 1400 m (*L. Burgeon*) (MRAC: MRACFOR001000) • Haut Huelé, Abimva, 3.6452, 29.4306, ca 700 m, 19.–22.VI.1925 (*H. Schouteden*) (MRAC: MRACFOR001144) • UGAN-DA: Kabarole, Kibale National Park, Kanyawara Biological Station, moist evergreen forest, ground forager(s), 0.56437, 30.36059, 1520 m, collection code BLF29365, 8.VIII.2012 (*B.L. Fisher; F.A. Esteves; Malagasy Arthropod Team*) (CASC: CASENT0352811, CASENT0352812).

**Differential worker diagnosis.** With characters of the *Z. sarowiwai* group plus the following: body size significantly much larger (HL 0.84–0.86; WL 1.18–1.26); torular–posttorular complex in profile comparatively lower and funnel–shaped (Fig. 5A); vertexal margin very weak and dorsum smoothly rounding onto posterior face of head (Figs 6A, 7A); lateral arms of hypostomal carina


**Figure 25.** Shaded surface display volume renderings of 3D models of *Z. aprilia* sp. nov. holotype (CASENT0764763) **A** full body in profile **B** full body in dorsal view **C** head in full-face view (with antennae) **D** head in full-face view (without antennae) **E** head in ventral view **F** abdominal segment II (petiole) in profile **G** abdominal segment II (petiole) in dorsal view **H** tergum of AS III in dorsal view **I** sternum of AS III in ventral view.

strongly diverging anteriorly, relatively thick, and strongly angulate at widest points (Fig. 8A); postgenal sulcus weakly impressed and running less than half-way to occipital margin (Fig. 8A); posterodorsal margin of mesosoma interrupted medially (Figs 11A, 12A); subpetiolar process of petiole (AS II) in profile with thickened anterior and ventral margins and well developed concavity with differentiated fenestra (Fig. 13A); petiolar tergum in dorsal view relatively thicker: ~  $1.0-1.1 \times$  broader than long (DPI 102–114) (Fig. 14A); abdominal sternum III in ventral view campaniform, comparatively broad and short, sides strongly rounded (Fig. 16A); posterior end of abdominal segment III in ventral view with thinner, deep, sharply and relatively regularly outlined transverse groove (Fig. 16A); prora in anteroventral view well-developed with sharply and very regularly shaped lateroventral margins (Fig. 16A); abdominal segment VI in dorsal view

distinctly shorter: ~  $1.8-1.9 \times$  broader than long (DA6I 178-193) (Fig. 17A); girdling constrictions between abdominal segments IV, V, VI unsculptured (Fig. 18A); surface sculpture on cephalic dorsum and genae completely smooth and very shiny with moderately dense, deep, and moderately sized to large piliferous foveae (Figs 4A, 5A, 19A, 20A); general surface sculpture on mesosoma and metasoma almost completely smooth and very shiny with scattered, piliferous foveae (Figs 20A, 21A).

**Measurements and indices.** Morphometric data is based on seven workers from Uganda and the Democratic Republic of Congo and can be seen in Table 2, Suppl. material 3.

**Etymology.** This species is dedicated to Aprilia Selistiowati, the wonderful wife of the first author. The species epithet is to be treated as a noun in apposition.

**Distribution and biology.** Based on the current data, it seems that *Z. aprilia* has the widest distribution range of all its African congeners since it is known from its type locality in western Uganda, as well as from three additional ones in the eastern parts of the D.R. Congo.

#### Zasphinctus kouakoui Hita Garcia & Gómez, sp. nov.

https://zoobank.org/AB56303F-E461-42FB-8303-95CB04ECD0E7 Figs 3B, 4B, 5B, 6B, 7B, 8B, 10B, 11B, 12B, 13B, 14B, 15B, 16B, 17B, 18B, 19B, 20B, 21B, 26

**Type material examined.** *Holotype* • Pinned worker, IVORY COAST, Montagnes District, Taï National Park, Site 04, primary forest, hand collected, ex soil, 5.8309, -7.3440, 200 m, collection code KG04079, 10.XI.2019 (*K. Gómez and L. Kouakou*) (RBINS: KGC0L00589). *Paratypes* • Four pinned workers with same data as holotype (KGAC: KGC0L00586; MNHNC: KGC0L01321; RBINS: KGC0L02132; NHMUK: KGC0L01884) • 1 pinned worker fromIVORY COAST, Tai Forest, 5.83, -7.34, 18.V.77 (*T. Diomande*) (ZMHB: CASENT0764653).

**Cybertype** • Dataset includes data from the holotype (KGCOL00589) and one paratype (CASENT0764653), and consists of the volumetric raw data (in DI-COM format), 3D surface model (in PLY format), still images of multiple body parts from surface volume renderings of 3D models, and stacked digital colour images illustrating head in full-face view, profile, and dorsal views of the body. The data is deposited at Zenodo (https://doi.org/10.5281/zenodo.12593275) and can be freely accessed as virtual representation of the physical holotype and paratype. In addition to the data at Zenodo, we also provide a freely accessible 3D surface model at Sketchfab (https://skfb.ly/p7MpP and https://skfb.ly/p7MpQ).

**Differential worker diagnosis.** With characters of the *Z. sarowiwai* group plus the following: body size significantly larger (HL 0.75–0.80; WL 1.03–1.10); torular–posttorular complex in profile comparatively lower and funnel–shaped (Fig. 5B); vertexal margin very weak and dorsum smoothly rounding onto posterior face of head (Figs 6B, 7B); lateral arms of hypostomal carina strongly diverging anteriorly, relatively thick, and outline mostly rounded (Fig. 8B); postgenal sulcus deeply and conspicuously impressed but only running halfway to occipital margin (Fig. 8B); posterodorsal margin of mesosoma continuous across its entire length (Figs 11B, 12B); subpetiolar process of petiole (AS II)



Figure 26. Shaded surface display volume renderings of 3D models of *Z. kouakoui* sp. nov. paratype (CASENT0764653) **A** full body in profile **B** full body in dorsal view **C** head in full-face view (with antennae) **D** head in full-face view (without antennae) **E** head in ventral view **F** abdominal segment II (petiole) in profile **G** abdominal segment II (petiole) in dorsal view **H** tergum of AS III in dorsal view I sternum of AS III in ventral view.

in profile with thickened anterior and ventral margins and well developed concavity with differentiated fenestra (Fig. 13B); petiolar tergum in dorsal view relatively thicker: ~ 1.1 × broader than long (DPI 109–114) (Fig. 14B); abdominal sternum III in ventral view campaniform, comparatively broad and short, sides strongly rounded (Fig. 16B); posterior end of abdominal segment III in ventral view with transverse groove weak to absent, instead with irregular groves and rugosity (Fig. 16B); prora in anteroventral view well–developed with sharply and very regularly shaped lateroventral margins (Fig. 16B); abdominal segment VI in dorsal view distinctly shorter: ~  $1.8-2 \times$  broader than long (DA6I 180–204) (Fig. 17B); girdling constrictions between abdominal segments IV, V, VI crossribbed (Fig. 18B); surface sculpture on cephalic dorsum and genae completely smooth and very shiny with moderately dense, deep, and moderately sized to large piliferous foveae (Figs 4B, 5B, 19B, 20B); general surface sculpture on mesosoma and metasoma almost completely smooth and very shiny with scattered, piliferous foveae (Figs 20B, 21B).

**Measurements and indices.** Morphometric data is based on five workers from Ivory Coast and can be seen in Table 2, Suppl. material 3.

**Etymology.** The species name *kouakoui* is a Latinised noun in the genitive case, dedicated to our good friend and Ivorian myrmecologist Dr. Lombart Kouakou. May this serve as a recognition of his present and future endeavours in Afrotropical myrmecology.

**Distribution and biology.** Presently, *Z. kouakoui* is only known from two collection events from the type locality, the Tai National Park in Ivory Coast, which is the last remaining major intact block of primary forest in West Africa. It was declared a UNESCO World Heritage Site in 1982 due to exceptional richness in fauna and flora. Indeed, based on several criteria including species diversity, endemism, presence of rare species, and/or endangered and critical habitats, the Tai National Park is considered a priority for the conservation of mammals, birds, amphibians, and invertebrates in West Africa (Reizebos et al. 1994).

### Zasphinctus lolae Hita Garcia & Gómez, sp. nov.

https://zoobank.org/B9A5C45C-DE85-42BC-891E-785BC5C65EB3 Figs 3C, 4C, 5C, 6C, 7C, 8C, 9C, 9D, 10C, 11C, 12C, 13C, 14C, 15C, 16C, 17C, 18C, 19C, 20C, 21C, 27

**Type material examined**. *Holotype* • Pinned worker, GHANA, Bobiri Forest Reserve, primary unlogged forest, hand collected, ex soil, 6.69048, -1.33828, ca 260 m, collection code KG03946, 10.I.2019 (*K. Gómez*) (RBINS: KGCOL02270). *Para-types* • Three pinned workers with same data as holotype (KGAC: KGCOL02269; MNHNC: KGCOL00163; RBINS: CASENT0881885) • two pinned workers from GHANA, Wiawso, ant ecology sample, 6.915525, -2.03919, ca 300 m, collection code ANTC39479, 25.IV.1969 (*D. Leston*) (NHMUK: CASENT0764652; ZMHB: CASENT0764651).

**Cybertype** • Dataset includes data from the holotype (KGCOL02270) and one paratype (CASENT0764651), and consists of the volumetric raw data (in DI-COM format), 3D surface model (in PLY format), still images of multiple body parts from surface volume renderings of 3D models, and stacked digital colour images illustrating head in full-face view, profile and dorsal views of the body. The data is deposited at Zenodo (https://doi.org/10.5281/zenodo.12593275) and can be freely accessed as virtual representation of the physical holotype and paratype. In addition to the data at Zenodo, we also provide two freely accessible 3D surface models at Sketchfab (https://skfb.ly/p7MpV and https://skfb.ly/p7MpW).

**Differential worker diagnosis.** With characters of the *Z. sarowiwai* group plus the following: body size significantly much larger (HL 0.90–0.98; WL 1.29–1.40); torular-posttorular complex in profile comparatively lower and funnel-shaped (Fig. 5C); vertexal margin and posterior face of head weakly developed (Figs 6C, 7C); lateral arms of hypostomal carina strongly diverging anteriorly, relatively thick, and strongly angulate at widest points (Fig. 8C); postgenal sulcus deeply and conspicuously impressed and running almost to occipital



**Figure 27.** Shaded surface display volume renderings of 3D models of *Z. lolae* sp. nov. holotype (KGCOL02270) **A** full body in profile **B** full body in dorsal view **C** head in full-face view (with antennae) **D** head in full-face view (without antennae) **E** head in ventral view **F** abdominal segment II (petiole) in profile **G** abdominal segment II (petiole) in dorsal view **H** tergum of AS III in dorsal view I sternum of AS III in ventral view.

margin (Fig. 8C); posterodorsal margin of mesosoma continuous across its entire length (Figs 11C, 12C); subpetiolar process of petiole (AS II) in profile with thickened anterior and ventral margins and well developed concavity with differentiated fenestra (Fig. 13C); petiolar tergum in dorsal view relatively thicker: ~  $1.2-1.3 \times$  broader than long (DPI 120-131) (Fig. 14C); abdominal sternum III in ventral view campaniform, very broad and short, sides strongly rounded (Fig. 16C); posterior end of abdominal segment III in ventral view with transverse groove weak to absent, instead with irregular groves and rugosity (Fig. 16C); prora in anteroventral view well-developed with sharply and very regularly shaped lateroventral margins (Fig. 16C); abdominal segment VI in dorsal view distinctly shorter: ~  $1.9-2 \times$  broader than long (DA6I 189–200) (Fig. 17C); girdling constrictions between abdominal segments IV, V, VI cross-ribbed (Fig. 18C); surface sculpture on cephalic dorsum and genae completely smooth and very shiny with moderately dense, deep, and moderately sized to large piliferous foveae (Figs 4C, 5C, 19C, 20C); general surface sculpture on mesosoma and metasoma almost completely smooth and very shiny with scattered, piliferous foveae (Figs 20C, 21C).

**Measurements and indices.** Morphometric data is based on six workers from Ghana and can be seen in Table 2, Suppl. material 3.

**Etymology.** The species name *lolae* is a Latinised noun in the genitive case, dedicated to the mother of the second author Kiko Gomez. Thanks for everything.

**Distribution and biology.** Presently, *Z. lolae* is only known from two collection events from Ghana, from Wiawso and Bobiri Forest Reserve, both of which are/ were rainforest habitats.

[Note: the 3D model of the mouthparts presented in Hita Garcia et al. (2017a) is not *Z. sarowiwai*, but instead *Z. lolae* (CASENT0764652)]

### Zasphinctus ndouri Hita Garcia & Gómez, sp. nov.

https://zoobank.org/D714D293-666C-407D-AC7C-91C8C619F1E5 Figs 3E, 4E, 5E, 6E, 7E, 8E, 10E, 11E, 12E, 13E, 14E, 15E, 16E, 17E, 18E, 19E, 20E, 21E, 28

**Type material examined.** *Holotype* • Pinned worker, SENEGAL, Kedougou, Neménick, Niokolo Koba 10 Km W (Niokolo Koba NP), savannah, Winkler, 13.0764, -12.78196, collection code KG05413, 1.-30.IV.2018 (*A. Diallo*) (RBINS: KGCOL01883). *Paratypes* • Eight pinned workers with same data as holotype (CASC: KGCOL02264; KGAC: KGCOL02258; MNHNC: KGCOL02259; NHMUK: KGCOL02262; RBINS: KGCOL02260; SAMC: KGCOL02263; ZMHB: KG-COL02261).

**Cybertype** • Dataset of the holotype (KGCOL01883) consists of the volumetric raw data (in DICOM format), 3D surface model (in PLY format), still images of multiple body parts from surface volume renderings of 3D models, stacked digital colour images illustrating head in full-face view, profile and dorsal views of the body. The data is deposited at Zenodo (https://doi.org/10.5281/zenodo.12593275) and can be freely accessed as virtual representation of the physical holotype. In addition to the data on Zenodo, we also provide a freely accessible 3D surface model at Sketchfab (https://skfb.ly/p7MpY).

**Differential worker diagnosis.** With characters of the *Z. sarowiwai* group plus the following: body size significantly larger (HL 0.73–0.77; WL 0.98–1.05); torular–posttorular complex in profile comparatively lower and funnel–shaped (Fig. 5E); vertexal margin very weak and dorsum smoothly rounding onto posterior face of head (Figs 6E, 7E); lateral arms of hypostomal carina strongly diverging anteriorly, relatively thick, and strongly angulate at widest points (Fig. 8E); postgenal sulcus weakly impressed and running halfway to occipital margin (Fig. 8E); posterodorsal margin of mesosoma continuous across its entire length (Figs 11E, 12E); subpetiolar process of petiole (AS II) in profile only weakly thickened anterior and ventral margins, weak concavity and no conspicuous fenestra (Fig. 13E); petiolar tergum in dorsal view relatively thicker: ~ 1.2 × broader than long (DPI 116–123) (Fig. 14E); abdominal sternum III in ventral view campaniform, comparatively broad and

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**Figure 28.** Shaded surface display volume renderings of 3D models of *Z. ndouri* sp. nov. holotype (KGCOL01883) **A** full body in profile **B** full body in dorsal view **C** head in full-face view (with antennae) **D** head in full-face view (without antennae) **E** head in ventral view **F** abdominal segment II (petiole) in profile **G** abdominal segment II (petiole) in dorsal view **H** tergum of AS III in dorsal view I sternum of AS III in ventral view.

short, sides strongly rounded (Fig. 16E); posterior end of abdominal segment III in ventral view with transverse groove weak to absent, instead with irregular groves and rugosity (Fig. 16E); prora in anteroventral view well-developed with sharply and very regularly shaped lateroventral margins (Fig. 16E); abdominal segment VI in dorsal view moderately sized: around 1.7–1.8 × broader than long (DA6I 168–179) (Fig. 17E); girdling constrictions between abdominal segments IV, V, VI cross-ribbed (Fig. 18E); surface sculpture on cephalic dorsum and genae completely smooth and very shiny with moderately dense, deep, and moderately sized to large piliferous foveae (Figs 4E, 5E, 19E, 20E); general surface sculpture on mesosoma and metasoma almost completely smooth and very shiny with scattered, piliferous foveae (Figs 20E, 21E).

**Measurements and indices.** Morphometric data is based on eight workers from Senegal and can be seen in Table 2, Suppl. material 3.

**Etymology.** The species epithet is a Latinised noun in the genitive case, dedicated to the Senegalese activist, composer, and musician Youssou N'Dour.

**Distribution and biology.** Currently, *Z. ndouri* is only known from its type locality, the Niokolo Koba National Park in Senegal. Unlike the other species treated herein, *Z. ndouri* was found in a tropical savanna habitat.

#### Zasphinctus sarowiwai Hita Garcia, 2017

Figs 3G, 4G, 5G, 6G, 7G, 8G, 9A, 9B, 10G, 11G, 12G, 13G, 14G, 15G, 16G, 17G, 18G, 19G, 20G, 21G, 29

**Type material examined.** *Holotype* • Pinned worker, CAMEROON, Centre Province, Mbalmayo, 3.4597, 11.4714, ca 600 m, rainforest, collection code ANTC39478, XI.1993 (*N. Stork*) (NHMUK: CASENT0764654). *Paratypes* • three pinned workers with same data as holotype (NHMUK: CASENT0764646; CASENT0764649; CASENT0764650).

**Cybertype** • Dataset was published in Hita Garcia et al. (2017a) and consists of the volumetric raw data (in DICOM format), as well as 3D PDFs and 3D rotation videos of scans of the head, mesosoma, metasoma, and the full body of the physical holotype (CASENT0764654) and paratype (CASENT0764650) in addition to montage photos illustrating head in full-face view, and profile and dorsal views of the body. The data was deposited at Dryad and can be freely accessed as virtual representation of the holotype (Hita Garcia et al. 2017c; http://dx.doi. org/10.5061/dryad.4s3v1). In addition to the cybertype data at Dryad, we also provided two freely accessible 3D surface models of the holotype and paratype at Sketchfab (https://skfb.ly/6sQwn and https://skfb.ly/oX9VO).

**Non-type material examined.** • One worker from: CAMEROON, Centre Province, Mbalmayo, 3.4597, 11.4714, ca 600 m, rainforest, collection code ANTC39478, XI.1993 (*N. Stork*) (NHMUK: CASENT0900310).

Differential worker diagnosis. With characters of the Z. sarowiwai group plus the following: body size significantly much larger (HL 0.86-0.89; WL 1.20-1.30); torular-posttorular complex in profile comparatively much higher and funnel-shaped, funnel comparatively wider (Fig. 5G); vertexal margin and posterior face of head weakly developed (Figs 6G, 7G); lateral arms of hypostomal carina strongly diverging anteriorly, relatively thick, and outline mostly rounded (Fig. 8G); postgenal sulcus deeply impressed and running halfway to occipital margin (Fig. 8G); posterodorsal margin of mesosoma continuous across its entire length (Figs 11G, 12G); subpetiolar process of petiole (AS II) in profile with thickened anterior and ventral margins and well developed concavity with differentiated fenestra (Fig. 13G); petiolar tergum in dorsal view relatively thicker, ~  $1.0-1.1 \times$  broader than long (DPI 102-109) (Fig. 14G); abdominal sternum III in ventral view campaniform, comparatively broad and short, sides strongly rounded (Fig. 16G); posterior end of abdominal segment III in ventral view with thinner, deep, sharply and relatively regularly outlined transverse groove (Fig. 16G); prora in anteroventral view well-developed with sharply and very regularly shaped lateroventral margins (Fig. 16G); abdominal segment VI in dorsal view distinctly shorter: ~ 1.9-2 × broader than long (DA6I



**Figure 29.** Shaded surface display volume renderings of 3D models of *Z. sarowiwai* Hita Garcia, 2017 holotype (CASENT0764654) **A** full body in profile **B** full body in dorsal view **C** head in full-face view (with antennae) **D** head in full-face view (without antennae) **E** head in ventral view **F** abdominal segment II (petiole) in profile **G** abdominal segment II (petiole) in dorsal view **H** tergum of AS III in dorsal view **I** sternum of AS III in ventral view.

188–197) (Fig. 17G); girdling constrictions between abdominal segments IV, V, VI cross-ribbed (Fig. 18G); surface sculpture on cephalic dorsum and genae completely smooth and very shiny with widely scattered and small piliferous foveae (Figs 4G, 5G, 19G, 20G); general surface sculpture on mesosoma and metasoma almost completely smooth and very shiny with scattered, piliferous foveae (Figs 20G, 21G).

**Measurements and indices.** Morphometric data is based on four workers from Cameroon and can be seen in Table 2, Suppl. material 3.

**Distribution and biology.** Compared to its original description in Hita Garcia et al. (2017a), the distribution range of *Z. sarowiwai* appears to be significantly smaller. While initially thought to occur from Ivory Coast to Uganda, at present it is only known from Cameroon (see Discussion below for further details).

# Discussion

#### **Diversity of Afrotropical Zasphinctus**

Despite this current work in which we describe five new species, *Zasphinctus* still remains a rarely collected genus. The underlaying material for *Z. kouakoui*, *Z. lolae*, and *Z. ndouri* consists of just one or two collection events, and *Z. lumumbai* is even based on a singleton. The situation for the material of *Z. aprilia* is better since it is from three localities in the northeast of the D.R. Congo and one in western Uganda, but on a larger scale this is still rather limited. This scarcity of material limits our understanding of the genus regarding intraspecific and interspecific variability and geographic distribution.

Prior to this study, *Z. sarowiwai* was considered a single species with a relatively wide distribution, ranging through Equatorial Africa from Ivory Coast in the west to Uganda in the east. Our study with additional new material shows that it indeed consists of four species ("genuine" *Z. sarowiwai* plus *Z. aprilia, Z. kouakoui*, and *Z. lolae*), each of them more locally distributed. Thus, one might think that *Zasphinctus* species in general have more restricted geographic distributions than previously thought (Hita Garcia et al. 2017a), but that assessment could also be due to sampling bias. A good example is *Z. wilsoni*, which was only known from one locality in Mozambique, but is now known to occur also much further northeast in the country, thus not particularly endemic anymore. If this is the case for most other species that are currently only known from their type locality remains to be seen with further sampling in the region.

As noted above, the Afrotropical region is a centre for ant diversity (e.g., Guénard et al. 2012), but due to a severe lack of sampling and qualified taxonomists, our understanding of that diversity is fragmentary at best. The recent taxonomic history of *Zasphinctus* is a great example. Prior to Hita Garcia et al. (2017a) the genus was only known from two male-based species. The few known workers in collections were all wrongly identified as *Z. rufiventris*, and overall, there was no worker-based taxonomic system. Hita Garcia et al. (2017a) added three new worker-based species, which are very unlikely to be conspecific with the two previously known male-based forms, thus more than doubling the species count for the genus to five species. Just a few years later, we again double that number to a total of ten.

We believe this development for a comparatively small genus to be a symptom of severely underestimating Afrotropical ant diversity generally. Unlike other regional hotspots, such as the Neotropics or Madagascar, the Afrotropics remain vastly unknown, with vast regions, such as the Congo Basin (3.4 million square kilometres) virtually unsampled. Recent expeditions to few localities in Senegal, Ghana, and Ivory Coast that employed modern collection techniques, such as Winkler leaf litter sampling, have been one main source for most of the new specimens used in this study. As a consequence, we cannot emphasise enough the need for larger scale sampling efforts throughout the region.

Surprisingly the second source of crucial specimens for this study resulted to be the extensive historic material from the D.R. Congo housed in the natural history collections of the Royal Belgian Institute of Natural Sciences in Brussels and the Royal Museum for Central Africa in Tervuren, both in Belgium. Research in these collections unearthed the singleton of *Z. lumumbai* and all of the *Z. aprilia* specimens from the D.R. Congo. Many taxonomic studies are

done with material from very few sources of predominantly freshly collected material, and "old" museum collections are often overlooked or excluded. Reasons for this are manifold and involve funding and staff problems at natural history museums, time and funding constraints of taxonomists, and unawareness of the existence of such key material due to lack of public databases or other digitisation sources. Working with historic collections is especially relevant in our case since the northeastern provinces of the D.R. Congo are presently extremely dangerous rendering any field work activities challenging in the best cases. Therefore, we consider researching, funding, and making available the historic collections of natural history museums as imperative to improve our understanding of Afrotropical ant diversity.

# Virtual recovery of morphology

This study provides a degree of detail and resolution comparable to Hita Garcia et al. (2019), but falls short of the level of resolution of the first Zasphinctus revision that included higher resolution micro-CT scans of individual body parts (head, mesosoma, and metasoma) in addition to moderate resolution full-body scans (Hita Garcia et al. 2017a). Due to lower CT scanner availability, we only performed full-body scans for the five new species described herein. In order to avoid problems with comparability, we also only used the fullbody scans of the three previously described species. However, as already outlined in Hita Garcia et al. (2019), our approach has some disadvantages. While general morphology is quite accurate in our 3D models, surface sculpture, especially fine microsculpture, is less well recovered in some species. Still, surface sculpture is generally clearly visible in the stacked digital colour images provided. Another disadvantage encountered can be seen in the 3D models of Z. lumumbai, which is based on a singleton holotype that is particularly dirty and partly also covered in glue. As a consequence, it was not possible to clean the specimen beforehand and the surface quality of the 3D model is less detailed compared to the other species used in this study. Nonetheless, despite some disadvantages, the achieved resolution of our 3D models is fully acceptable for the comparison of morphological shape data among Zasphinctus species.

# Virtual character evaluation and presentation

One aim of our study was to evaluate the taxonomic delimitation system provided in Hita Garcia et al (2017a), test if its morphological characters still work against the background of many more species and material, and assess if some characters need to be omitted and others included. As noted above, overall, most characters from Hita Garcia et al (2017a) still performed rather well and provided their usefulness in either discriminating between species or species groups. However, we suggest some characters to be discarded, either because they are difficult to describe, visualise, or examine (e.g., antennal scape, occiput in ventral view), or exhibit some form of intraspecific variation (e.g., parafrontal ridges). Alternatively, we recommend the use of some characters previously not used to be of diagnostic importance, but we also discovered some never used before. Following previous studies (Hita Garcia et al. 2017a, 2019), our choice of characters targets diverse taxonomic audiences. We use many characters that can be easily observed under a microscope with moderate magnification (e.g., shapes of head, mesosoma, and petiole, as well as surface sculpture) for users with restricted microscopy resources or limited taxonomic background. For more taxonomically experienced users with better microscopy resources and deeper knowledge of ant morphology we also offer a plethora of additional, rarely used morphological characters located on the posterior or ventral faces of the head, or the ventral metasoma. The combination of both character sets presented in numerous high resolution diagnostic plates yields a high degree of illustrative power that will greatly enhance taxonomic identifications and future taxonomic revisions, but also serve as comparative data for future systematic studies.

In terms of above-species level characters, we provide almost 20 morphological differences that clearly separate the *Z. obamai* group from the *Z. sarowiwai* group (Suppl. material 1), which is a substantial degree of morphological divergence. Even though currently we do not have any molecular data available, based on such high number of diverging character states we predict that both species groups likely represent monophyletic entities. Considering species-level taxonomy, we used almost 20 morphological characters for species delimitations, thus permitting the generation of diagnoses that are limited to only diagnostically relevant data, but still provide a high level of morphological details.

# Cybertypes

As in previous studies (e.g., Agavekar et al. 2017; Hita Garcia et al. 2017a, 2017b, 2019; Staab et al. 2018; Sarnat et al. 2019; Sharaf et al. 2019; Gómez et al. 2022), we provide freely available cybertype datasets of all holotypes from all new species described herein (plus additional paratypes for some species), as well as from the previously described species (Hita Garcia et al. 2017c). However, as noted above and in contrast to the previous studies mentioned above, we no longer include 3D PDFs or 3D rotation video files in order to avoid too much data redundancy. The use of 3D videos has been rather prominent in taxonomic studies applying micro-CT data (e.g., Stoev et al. 2013; Akkari et al. 2015, 2018; Fischer et al. 2016; Hita Garcia et al. 2017a, 2019), and we still believe that from a visual point of view the 3D videos are an interesting addition. However, from the perspective of a taxonomist, the videos are of less use since they need to be constantly played back and forth and stopped in-between to examine morphological structures. We believe that the 3D surface models in PLY format provided in our cybertype datasets provide all necessary visual data and offer much more usability since they can be freely downloaded and used with numerous types of software for multiple applications in 3D.

Overall, the relatively high quality of the 3D models and the open availability of the cybertype datasets allow taxonomists, parataxonomists, or ecologists detailed and comprehensive examinations of Afrotropical *Zasphinctus*, hence alleviating the necessity to organise multiple loans or having to visit several natural history collections. By providing our 3D models available for download on online data repositories and as interactive models on Sketchfab we also target a wider audience. Interested users can download the models and open them in a free 3D model viewer software, such as Meshlab, on a regular computer with moderate computational power and perform any subsequent visualisation or manipulation in 3D. However, the 3D models on Sketchfab require much less computation and even be viewed on a mobile phone, thus targeting a different group of users that either do not have computational means or are away from such resources, for example in the field.

# Conclusions

Despite the fact that Afrotropical *Zasphinctus* were revised recently, herein we double the number of species from five to ten. Our new data is based on few recent collections in the Afrotropical region plus extra research in historical natural history collections in Europe. Thus, we would like to highlight the need for larger scale sampling efforts throughout sub-Saharan Africa, which will almost certainly yield additional new species of *Zasphinctus*, as well as from many other ant groups.

This study further emphasises the prospects of in-depth comparative morphology analyses for insect taxonomy that are based on our integrative approach of traditional examination of physical specimens under the light microscopy and the virtual study of 3D models on the computer screen. Our newly proposed taxonomic system is based on a wealth of morphological characters of high diagnostic value, which we would not have been able to study and visualise with traditional means alone. Moreover, taking into consideration the absence of a molecular phylogeny for Afrotropical *Zasphinctus*, our taxonomic revision with the species hypotheses proposed represents a great foundation for future molecular studies, for both the Afrotropics and globally.

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# Additional information

# **Conflict of interest**

The authors have declared that no competing interests exist.

#### **Ethical statement**

No ethical statement was reported.

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#### Author contributions

Conceptualization: KG, FHG. Data curation: KG, FHG. Formal analysis: FHG, KG. Funding acquisition: EPE, FHG. Investigation: FHG, KG, RAK. Resources: BS, EPE, FHG. Validation: EPE, RAK. Visualization: FHG. Writing - original draft: KG, FHG. Writing - review and editing: BS, FHG, RAK, EPE, KG.

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### Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

# References

- Agavekar G, Hita Garcia F, Economo EP (2017) Taxonomic overview of the hyperdiverse ant genus *Tetramorium* Mayr (Hymenoptera, Formicidae) in India with descriptions and X-ray microtomography of two new species from the Andaman Islands. PeerJ 5: e3800. https://doi.org/10.7717/peerj.3800
- Akkari N, Enghoff H, Metscher BD (2015) A new dimension in documenting new species: high-detail imaging for myriapod taxonomy and first 3D cybertype of a new millipede species (Diplopoda, Julida, Julidae). PLoS ONE 10: e0135243. https://doi. org/10.1371/journal.pone.0135243
- Akkari N, Ganske A-S, Komerički A, Metscher B (2018) New avatars for Myriapods: complete 3D morphology of type specimens transcends conventional species description (Myriapoda, Chilopoda). PLoS ONE 13: e0200158. https://doi.org/10.1371/ journal.pone.0200158
- Bolton B (1976) The ant tribe Tetramoriini (Hymenoptera: Formicidae). Constituent genera, review of smaller genera and revision of *Triglyphothrix* Forel. Bulletin of the British Museum (Natural History), Entomology 34: 281–379.

- Bolton B (1980) The ant tribe Tetramoriini (Hymenoptera: Formicidae). The genus *Te-tramorium* Mayr in the Ethiopian zoogeographical region. Bulletin of the British Museum (Natural History), Entomology 40: 193–384.
- Bolton B (1985) The ant genus *Triglyphothrix* Forel a synonym of *Tetramorium* Mayr (Hymenoptera: Formicidae). Journal of Natural History 19: 243–248. https://doi. org/10.1080/00222938500770191
- Bolton B (1987) A review of the *Solenopsis* genus-group and revision of Afrotropical *Monomorium* Mayr (Hymenoptera: Formicidae). Bulletin of the British Museum (Natural History). Entomology 54: 263–452.
- Bolton B (1990) Abdominal characters and status of the cerapachyine ants (Hymenoptera, Formicidae). Journal of Natural History 24: 53–68. https://doi. org/10.1080/00222939000770051
- Bolton B (2024) An online catalog of the ants of the world. http://antcat.org [accessed 12 June 2024]
- Borowiec ML (2016) Generic revision of the ant subfamily Dorylinae (Hymenoptera, Formicidae). Zookeys 608: 1–280. https://doi.org/10.3897/zookeys.608.9427
- Brown, WL (1975) Contributions toward a reclassification of the Formicidae. V. Ponerinae, tribes Platythyreini, Cerapachyini, Cylindromyrmecini, Acanthostichini, and Aenictogitini. Search Agriculture Entomology (Ithaca) 5: 1–115. https://doi.org/10.5281/ zenodo.26999
- Buschinger A, Peeters C, Crozier RH (1989) Life-pattern studies on an Australian *Sphinctomyrmex* (Formicidae: Ponerinae; Cerapachyini): functional polygyny, brood periodicity and raiding behavior. Psyche 96: 287–300. https://doi. org/10.1155/1989/13614
- Carbayo F, Francoy TM, Giribet G (2016) Non-destructive imaging to describe a new species of Obama land planarian (Platyhelminthes, Tricladida). Zoologica Scripta 45: 566–578. https://doi.org/10.1111/zsc.12175
- Cignoni P, Callieri M, Corsini M, Dellepiane M, Ganovelli F, Ranzuglia G (2008) MeshLab: an Open-Source Mesh Processing Tool. Sixth Eurographics Italian Chapter Conference, Salerno, Italy. 129–136.
- Csősz S, Fisher BL (2016) Toward objective, morphology-based taxonomy: a case study on the Malagasy *Nesomyrmex sikorai* species group (Hymenoptera: Formicidae). PLoS ONE 11: e0152454. https://doi.org/10.1371/journal.pone.0152454
- De Queiroz K (2007) Species concepts and species delimitation. Systematic Biology 56: 879–886. https://doi.org/10.1080/10635150701701083
- Englund M, Lee KM, Staude H, Duplouy A, Hausmann A, Laiho E, Söderholm M, Sihvonen P (2024) 130 years from discovery to description: micro-CT scanning applied to construct the integrative taxonomy of a forgotten moth from Southern Africa (Lepidoptera: Geometridae). Systematic Entomology 49: 507–525. https://doi.org/10.1111/syen.12627
- Evenhuis NL (2024) The insect and spider collections of the world website. http://hbs. bishopmuseum.org/codens [accessed 12 June 2024]
- Faulwetter S, Vasileiadou A, Kouratoras M, Dailianis T, Arvanitidis C (2013) Micro-computed tomography: Introducing new dimensions to taxonomy. ZooKeys 263: 1–45. https://doi.org/10.3897/zookeys.263.4261
- Fernández R, Kvist S, Lenihan J, Giribet G, Ziegler A (2014) Sine systemate chaos? A versatile tool for earthworm taxonomy: Non-destructive imaging of freshly fixed and museum specimens using micro-computed tomography. PLoS ONE 9: e96617. https:// doi.org/10.1371/journal.pone.0096617

- Fischer G, Sarnat E, Economo EP (2016) Revision and microtomography of the *Pheidole knowlesi* group, an endemic ant radiation in Fiji (Hymenoptera, Formicidae, Myrmicinae). PLoS ONE 11: e0158544. https://doi.org/10.1371/journal.pone.0158544
- Fisher BL (2009) Chapter 2 Biogeography. In: Lach L, Parr C, Abbott K (Eds) Ant Ecology Oxford Academic, Oxford, 18–37. https://doi.org/10.1093/acprof:oso/9780199544639.003.0002
- Friedrich F, Matsumura Y, Pohl H, Bai M, Hörnschemeyer T, Beutel RG (2014) Insect morphology in the age of phylogenomics: innovative techniques and its future role in systematics. Entomological Science 17: 1–24. https://doi.org/10.1111/ens.12053
- Giribet G (2010) A new dimension in combining data? The use of morphology and phylogenomic data in metazoan systematics. Acta Zoologica 91: 11–9. https://doi. org/10.1111/j.1463-6395.2009.00420.x
- Gómez K (2022) A revision of the Afrotropical species of the Dorylinae ant genus Aenictus (Hymenoptera: Formicidae) based on the worker caste. Belgian Journal of Entomology 124: 1–86.
- Gómez K, Kouakou LMM, Fischer G, Hita Garcia F, Katzke J, Economo EP (2022) *Pheidole klaman* sp. nov.: a new addition from Ivory Coast to the Afrotropical *pulchella* species group (Hymenoptera, Formicidae, Myrmicinae). ZooKeys 1104: 129–157 https://doi.org/10.3897/zookeys.1104.81562
- Guénard B, Weiser M, Dunn R (2012) Global models of ant diversity suggest regions where new discoveries are most likely are under disproportionate deforestation threat. Proceedings of the National Academy of Sciences of the United States of America 109: 7368–7373. https://doi.org/10.1073/pnas.1113867109
- Harris, RA (1979) A glossary of surface sculpturing. Occasional Papers in Entomology, State of California Department of Food and Agriculture 28: 1–31. https://doi. org/10.5281/zenodo.26215
- Hebert PDN, Gregory TR (2005) The promise of DNA barcoding for taxonomy. Systematic Biology 54, 852–859. https://doi.org/10.1080/10635150500354886
- Hita Garcia F, Fischer G, Peters MK, Snelling RR, Wägele JW (2009) A preliminary checklist of the ants (Hymenoptera: Formicidae) of Kakamega Forest (Kenya). Journal of East African Natural History 98: 147–165. https://doi.org/10.2982/028.098.0201
- Hita Garcia F, Wiesel E, Fischer G (2013) The ants of Kenya (Hymenoptera: Formicidae)
  Faunal overview, first species checklist, bibliography, accounts for all genera, and discussion on taxonomy and zoogeography. Journal of East African Natural History 101: 127–222. https://doi.org/10.2982/028.101.0201
- Hita Garcia F, Fischer G, Liu C, Audisio TL, Economo EP (2017a) Next-generation morphological character discovery and evaluation: an X-ray micro-CT enhanced revision of the ant genus *Zasphinctus* Wheeler (Hymenoptera, Formicidae, Dorylinae) in the Afrotropics. ZooKeys 693: 33–93. https://doi.org/10.3897/zookeys.693.13012
- Hita Garcia F, Fischer G, Liu C, Audisio TL, Alpert GD, Fisher BL, Economo EP (2017b) X-ray microtomography for ant taxonomy: an exploration and case study with two new *Terataner* (Hymenoptera, Formicidae, Myrmicinae) species from Madagascar. PLoS ONE 12: e0172641. https://doi.org/10.1371/journal.pone.0172641
- Hita Garcia F, Fischer G, Liu C, Audisio TL, Economo EP (2017c) Data from: Next-generation morphological character discovery and evaluation: an X-ray micro-CT enhanced revision of the ant genus *Zasphinctus* Wheeler (Hymenoptera, Formicidae, Dorylinae) in the Afrotropics [Dataset]. Dryad Digital Repository. https://doi.org/10.5061/dryad.4s3v1
- Hita-Garcia F, Lieberman Z, Audisio TL, Liu C, Economo EP (2019) Revision of the highly specialized ant genus *Discothyrea* (Hymenoptera: Formicidae) in the Afrotropics with

X-ray microtomography and 3D cybertaxonomy. Insect Systematics and Diversity 3(5): 1–84. https://doi.org/10.1093/isd/ixz015

- Jaitrong W, Yamane S (2011) Synopsis of *Aenictus* species groups and revision of the *A. currax* and *A. laeviceps* groups in the eastern Oriental, Indo-Australian, and Australasian regions (Hymenoptera: Formicidae: Aenictinae). Zootaxa 3128: 1–46. https:// doi.org/10.11646/zootaxa.3128.1.1
- Jaitrong W, Wiwatwitaya D, Sakchoowong W (2016) Review of the Thai species of the genus *Sphinctomyrmex* Mayr, 1866 (Hymenoptera: Formicidae, Dorylinae), with description of a new species. Far Eastern Entomologist 305: 1–9. https://doi.org/10.5281/zenodo.46404
- Janicki J, Narula N, Ziegler M, Guénard B, Economo EP (2016) Visualizing and interacting with large-volume biodiversity data using client-server web-mapping applications: The design and implementation of antmaps.org. Ecological Informatics 32: 185–193. https://doi.org/10.1016/j.ecoinf.2016.02.006
- Jimoh BO, Gómez K, Kemabonta KA, Wakanjuola WA, Phiri EE, Mothapo PN (2024) A checklist of Nigerian ants (Hymenoptera, Formicidae): a review, new records and exotic species. Biodiversity Data Journal 12: e99555. https://doi.org/10.3897/BDJ.12.e99555
- Kass JM, Guénard B, Dudley KL, Jenkins CN, Azuma F, Fisher BL, Parr CL, Gibb H, Longino JT, Ward PS, Chao A, Lubertazzi D, Weiser M, Jetz W, Guralnick R, Blatrix R, Lauriers JD, Donoso DA, Georgiadis C, Gomez K, Hawkes PG, Johnson RA, Lattke JE, MacGown JA, Mackay W, Robson S, Sanders NJ, Dunn RR, Economo EP (2022) The global distribution of known and undiscovered ant biodiversity. Science Advances 8: eabp9908. https://doi.org/10.1126/sciadv.abp9908
- Keller RA (2011) A phylogenetic analysis of ant morphology (Hymenoptera, Formicidae) with special reference to the poneromorph subfamilies. Bulletin of the American Museum of Natural History 355: 1–90. https://doi.org/10.1206/355.1
- Michalik P, Ramírez MJ (2013) First description of the male of *Thaida chepu* Platnick, 1987 (Araneae, Austrochilidae) with micro-computed tomography of the palpal organ. ZooKeys 352: 117–125. https://doi.org/10.3897/zookeys.352.6021
- Miller SE (2007) DNA barcoding and the renaissance of taxonomy. PNAS 104: 4775– 4776. https://doi.org/10.1073/pnas.0700466104
- Moraes SS, Söderholm MS, Aguiar TMC, Freitas AVL, Sihvonen P (2023) Micro-CT imaging in species description: exploring beyond sclerotized structures in lichen moths (Lepidoptera: Erebidae, Arctiinae, Lithosiini). PeerJ 11: e15505. https://doi.org/10.7717/peerj.15505
- Reizebos EP, Vooren AP, Guillaumet JL [Eds] (1994) The Taï National Park, Côte d'Ivoire.
  I: Synthesis of knowledge (Report). La Fondation Tropenbos, Horaplantsoen. [ISBN 90-5113-020-1]
- Robertson HG (2000) Afrotropical ants (Hymenoptera: Formicidae): taxonomic progress and estimation of species richness. Journal of Hymenoptera Research 9: 71–84.
- Sadasivan K, Kripakaran M (2022) First record of *Proceratium* Roger, 1863, *Zasphinc-tus* Wheeler, 1918, and *Vollenhovia* Mayr, 1865 (Hymenoptera: Formicidae) from the Western Ghats of peninsular India, description of three new species, and implications for Indian biogeography. Journal of Threatened Taxa 14: 21368–21387. https://doi.org/10.11609/jott.7682.14.7.21368-21387
- Sarnat E, Fischer G, Economo EP (2016) Inordinate spinescence: taxonomic revision and microtomography of the *Pheidole cervicornis* species group (Hymenoptera, Formicidae). PLoS ONE 11: e0156709. https://doi.org/10.1371/journal.pone.0156709
- Sarnat EM, Hita Garcia F, Dudley K, Liu C, Fischer G, Economo EP (2019) Ready species one: exploring the use of augmented reality to enhance systematic biology with a

revision of Fijian *Strumigenys* (Hymenoptera: Formicidae). Insect Systematics and Diversity 3(6): 1–43. https://doi.org/10.1093/isd/ixz005

- Schlick-Steiner BC, Steiner FM, Seifert B, Stauffer C, Christian E, Crozier RH (2010) Integrative taxonomy: a multisource approach to exploring biodiversity. Annual Review of Entomology 55: 421–438. https://doi.org/10.1146/annurev-ento-112408-085432
- Sharaf MR, Aldawood AS, Economo EP, Wachkoo AA, Hita Garcia F (2019) Taxonomy of Arabian *Temnothorax* Mayr (Formicidae: Myrmicinae) with description of a new species enhanced by x-ray microtomography. Scientific Reports 9: 11009 https://doi. org/10.1038/s41598-019-47260-y
- Simonsen TJ, Kitching IJ (2014) Virtual dissections through micro-CT scanning: a method for non-destructive genitalia 'dissections' of valuable Lepidoptera material. Systematic Entomology 39: 606–618. https://doi.org/10.1111/syen.12067
- Staab M, Hita Garcia F, Liu C, Xu Z-H, Economo EP (2018) Systematics of the ant genus Proceratium Roger (Hymenoptera, Formicidae, Proceratiinae) in China – with descriptions of three new species based on micro-CT enhanced next-generation-morphology. ZooKeys 770: 137–192. https://doi.org/10.3897/zookeys.770.24908
- Stoev P, Komerički A, Akkari N, Liu S, Zhou X, Weigand AM, Hostens J, Hunter CI, Edmunds SC, Porco D, Zapparoli M, Georgiev T, Mietchen D, Roberts D, Faulwetter S, Smith V, Penev L (2013) *Eupolybothrus cavernicolus* Komerički & Stoev sp. n. (Chilopoda: Lithobiomorpha: Lithobiidae): the first eukaryotic species description combining transcriptomic, DNA barcoding and micro-CT imaging data. Biodiversity Data Journal 1: e1013. https://doi.org/10.3897/BDJ.1.e1013
- Ward PS (2000) Broad-scale patterns of diversity in leaf litter ant communities. In: Agosti D, Majer J, Alonso L, Schultz TR (Eds) Ants: standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington, DC, 99–121. https://zenodo.org/record/11736
- Ward PS (2011) Integrating molecular phylogenetic results into ant taxonomy (Hymenoptera: Formicidae). Myrmecological News 15: 21–9. https://doi.org/10.25849/ myrmecol.news\_015:021
- Wilson EO (1958) Observations on the behavior of the cerapachyine ants. Insectes Sociaux 5: 129–140. https://doi.org/10.1007/BF02222432
- Wilson EO (1964) The true army ants of the Indo-Australian area (Hymenoptera: Formicidae: Dorylinae). Pacific Insects 6: 427–483.

# **Supplementary material 1**

# List of consistent morphological differences separating the Zasphinctus obamai group from the Zasphinctus sarowiwai group

Author: Francisco Hita Garcia

Data type: xlsx

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Link: https://doi.org/10.3897/zookeys.1223.131238.suppl1

# **Supplementary material 2**

# Character matrix showing all diagnostic characters used for worker-based species delimitation system of Afrotropical *Zasphinctus*

Author: Francisco Hita Garcia

Data type: xlsx

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Link: https://doi.org/10.3897/zookeys.1223.131238.suppl2

# **Supplementary material 3**

Measurement raw data used for the comparative data of measurements and indices of Afrotropical *Zasphinctus* (including unique specimen ID, species ID, and collection locality for each specimen)

Author: Francisco Hita Garcia

Data type: xlsx

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**Research Article** 

# Two new species of the genus *Sinonychus* (Coleoptera, Elmidae) from Guizhou, China

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#### Abstract

The riffle beetle genus *Sinonychus* Jäch & Boukal, 1995 (Elminae, Macronychini) includes only three species from East Asia. In this paper, two new species, *S. lipinae* **sp. nov.** and *S. luodianensis* **sp. nov.**, are described from Guizhou Province, China. Illustrations of the new species and a key to all five *Sinonychus* species are also provided.

**Key words:** China, Guizhou, identification key, Macronychini, new records, riffle beetles, taxonomy

# Introduction

The genus *Sinonychus* Jäch & Boukal, 1995 (Elmidae, Elminae, Macronychini) includes three species from East Asia (Jäch and Boukal 1995; Yoshitomi and Nakajima 2007, 2012). The genus was erected by monotypy with *Sinonychus lantau* Jäch & Boukal, 1995 from Hong Kong, China, the type species. Subsequently, two species from Japan, *S. satoi* Yoshitomi & Nakajima, 2007 and *S. tsujunensis* Yoshitomi & Nakajima, 2012 were added (Yoshitomi and Nakajima 2007, 2012). Kamite and Moriya (2011) recorded *S. satoi* from Amami-Ôshima, Japan. Hayashi (2019) described the minute structure of the body surface of *S. tsujunensis* adults. Moreover, Hayashi and Kamite (2020) described the immature stages of *S. tsujunensis*.

Members of the genus *Sinonychus* are characterized by the following: 1) body very small, usually less than 1.50 mm; 2) antenna 7-segmented; 3) pronotum wider than long; 4) sublateral grooves present on the pronotum; 5) longitudinal impression of the pronotum extending from its base almost to the anterior margin; 6) elytra obovate, disc more or less roof-like in cross-section; 7) elytral intervals 3, 5, 6, 7 or 5, 6, 7 with carinae; 8) hind wings absent; and 9) legs moderately long (Jäch and Boukal 1995; Yoshitomi and Nakajima 2007).

In this paper, two new species, *S. lipinae* sp. nov. and *S. luodianensis* sp. nov., are described and illustrated from Guizhou Province, China. A key to all five species of *Sinonychus* is provided.



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# **Material and methods**

Examined material is deposited in the Institute of Entomology, Guizhou University, Guiyang, China (**GUGC**).

Label data of the specimens is quoted verbatim. The Chinese translation of each locality below the provincial level is included in parentheses at the first appearance in the text. Each specimen from the type series bears one of the following labels: "HOLOTYPE (red) (or PARATYPE (yellow)),  $rightharpoonup (or \cite{appearance}), Sinony-chus + specific name sp. nov., Jiang & Chen, 2024."$ 

Habitus images were taken using a Canon 5D SR camera in conjunction with a Mitutoyo Plan NIR 5 lens. Images of the morphological details were taken using the same camera in conjunction with a Mitutoyo Plan NIR 10 lens or a Nikon DS-Ri2 camera with a Nikon SMZ25 stereoscopic microscope. Zerene Stacker (version 1.04) was used for image stacking. All images were modified and grouped into plates in Adobe Photoshop CS5 Extended.

The following abbreviations are used in the text: **HW**—width of head across eyes; **PL**—length of pronotum along midline; **PW**—maximum width of pronotum; **EL**—length of elytra along suture; **EW**—maximum width of elytra; **CL**—sum of PL + EL.

# Taxonomy

# Sinonychus Jäch & Boukal, 1995

(华溪泥甲属)

Sinonychus Jäch & Boukal, 1995: 306.

Type species. Sinonychus lantau Jäch & Boukal, 1995.

#### Sinonychus lipinae Jiang & Chen, sp. nov.

https://zoobank.org/26A5072B-6E7F-4EC1-B403-CD5189584B94 Figs 1A, C, 2A-F, 4A-G (李氏华溪泥甲)

**Type material.** 26 exs: 11 ♂♂, 5 ♀♀, 10 exs., sex undetermined. *Holotype*: • CHINA: ♂, labeled "China: Guizhou, Qiannan Buyi and Miao Autonomous Prefecture (黔南布依族苗族自治州), Longli (龙里县), Wantanhe Town (湾滩河镇), H: 1136.10±1.08m, 26°12'52"N 106°59'27"E, 31.VIII.2023, Jiang Ri-Xin, Hai-Tao Li, Pin Li, Yu-Hao Zhang, Yin-Lin Mu & Xiu-Dong Huang leg." (GUGC). *Paratypes*: • 10 ♂♂, 5 ♀♀, 10 exs., sex undetermined, with same label data as the holotype (GUGC).

**Diagnosis.** Body broadly oval, black; mouthparts, antennae, anterior margin of pronotum, trochanters and base of tibia and tarsi (including claws) light brown. Frons, pronotum and basal elytra finely granulate. Pronotum with anterolateral marginal band of silvery, sericeous tomentum. Elytral intervals 3, 5, 6, 7 with granulate carinae; carina of interval 3 short, less than half the length of elytron; other carinae longer than half length of elytron. Aedeagus slender, apex of median lobe acute; median lobe with a pair of long sclerotizations located at apical 1/2.



Figure 1. A dorsal habitus of *Sinonychus lipinae* sp. nov. B dorsal habitus of *S. luodianensis* sp. nov. C antenna of *S. lipinae* sp. nov. D antenna of *S. luodianensis* sp. nov. Scale bars: 0.5 mm (A, B); 0.05 mm (C, D).

**Description.** Body broadly oval (Fig. 1A); black, with mouthparts, antennae, anterior margin of pronotum, trochanters and base of tibia and tarsi (including claws) light brown. Plastron setae confined to the following areas: head (both dorsal and ventral surfaces, including clypeus); pronotum (anterolateral marginal areas); elytra (lateral areas, including epipleura); prosternum (except disc); mesoventrite, metaventrite and abdomen (lateral areas); and femora.

Head (Fig. 2A) wider than long, surface covered with plastron setae and mixed with sparse, long setae and granules. Clypeus anterior surface microreticulate; covered with sparse, long setae; without plastron setae. Labrum transverse, narrower than clypeus; surface microreticulate, apical 1/2 covered with sparse, long setae; apical margin nearly straight; lateral margins rounded and with long bristles. Antenna (Fig. 1C) 7-segmented with apical antennomere clubbed.

Pronotum (Fig. 2B) wider than long, widest at base, get narrowed from basal 1/3 to apex. Surface microreticulate and granulate except areas near apical



Figure 2. Diagnostic features of *Sinonychus lipinae* sp. nov. A head B pronotum C prosternal process D metaventrite E abdomen F elytron. Scale bars: 0.1 mm (A); 0.2 mm (B–F).

margin. Apicolateral margins covered with plastron setae. Anterior 1/2 of disc covered with sparse, long setae distinctly longer than setae on other parts of pronotum. Median longitudinal sulcus distinct and long, extending from base nearly to anterior margin, deep at basal 1/2, much shallower at apical 1/2. Sublateral grooves distinct and straight, parallel to each other. Anterior margin strongly curved, anterior angles not produced. Lateral margins nearly parallel at base, then evenly narrowed. Basal margin trisinuate, emarginate anterior to scutellum, posterior angles nearly orthogonal. Prosternal process (Fig. 2C) subtriangular, with rounded apex, surface distinctly microreticulate, covered with sparse, long setae.

Scutellum (Fig. 2B) cordate, longer than wide, widest at basal 1/3; surface shiny and glabrous. Anterior margin strongly curved, lateral margins weakly curved, apex acutangular.

Elytra (Fig. 2F) longer than wide, widest near middle. Surface granulate near base and apex; disc microreticulate. Strial punctures large in basal 2/3 of elytra, mostly separated by about twice a diameter; much smaller and widely separated in other parts of elytra. Elytral intervals 3, 5, 6, 7 with granulate carinae; carina of interval 3 shortest, about 1/3 length of elytra; carina of interval 5 about 2/3 length of elytra; other two carinae long, extending from base of elytra nearly to apex. Areas from interval 5 to lateral margins with plastron setae except for apical 2/3 between intervals 5 and 6. Hing wings reduced.

Metaventrite (Fig. 2D) with disc distinctly microreticulate and covered with sparse, long setae; lateral areas with plastron setae. Median sulcus shallow and indistinct, extending from posterior margin to anterior margin.

Abdominal surface finely granulate (Fig. 2E). Admedian carinae of ventrite 1 obscure, straight, extending from base to apex. Median areas of ventrites 1–4 and anterior middle part of ventrite 5 distinctly microreticulate; lateral areas of ventrites 1–5 covered with plastron setae and mixed with sparse long setae.

Legs simple, surface granulate (except tarsi). Surface of femora covered with sericeous tomentum; inner side of tibiae with cleaning fringes; tarsi slightly shorter tibiae; tarsal claws simple.

Aedeagus (Fig. 4A–D) slender and elongate. Parameres short, not obvious, weakly sclerotized, without setae. Median lobe symmetrical, distinctly narrowed near base; apex acute; with a pair of long sclerotizations at apical 1/2. Sternite IX (Fig. 4E) with apical margin curved, without setae, median strut with base distinctly curved. Phallobase short, about 1/6 length of median lobe.

Measurements: CL: 1.25–1.43 mm; PL: 0.42–0.50 mm, PW: 0.58–0.63 mm; EL: 0.81–0.93 mm, EW: 0.70–0.75 mm.

Female externally similar to the male, but averaging larger. Ovipositor as in Fig. 4F, G: valvifer about twice as long as coxite, distinctly expanded at base; coxite apex strongly expanded, broadly rounded at outer margin; stylus short, distinctly curved at middle.

Measurements: CL: 1.28–1.41 mm; PL: 0.43–0.48 mm, PW: 0.61–0.66 mm; EL: 0.85–0.93 mm, EW: 0.73–0.81 mm.

**Distribution.** China. Only known from the type locality in Longli County, Qiannan Buyi and Miao Autonomous Prefecture, Guizhou Province.

**Biology.** All adults were collected from gravel on the bottom of a small stream in a ravine (Fig. 5A-E).

**Etymology.** The species epithet *"lipinae"* honors our friend and colleague Dr Pin Li (Guizhou University), one of the collectors of this new species.

**Comparative diagnosis.** *Sinonychus lipinae* sp. nov. is highly similar to the Japanese species *S. tsujunensis* in appearance. The new species can be distinguished from the latter species by the following characters: 1) median longitudinal sulcus of pronotum narrower; basal 1/2 distinctly wider than apical 1/2 (vs. much wider; basal 1/2 weakly wider than apical 1/2); 2) male aedeagus with apex of median lobe acute (vs. apex rounded); 3) parameres without setae in basal parts (vs. bearing short setae in basal parts); and 4) median lobe about 6 times as long as phallobase (vs. about 5 times as long as phallobase).

# Sinonychus luodianensis Jiang & Chen, sp. nov.

https://zoobank.org/EC1B7D2E-24F8-4320-82A4-3F50B1E6D07C Figs 1B, D, 3A-F, 4H-N (罗甸华溪泥甲)

**Type material.** 41 exs: 11 ♂♂, 10 ♀♀, 20 exs., sex undetermined. *Holotype*: • CHINA: ♂, labeled "China: Guizhou, Qiannan Buyi and Miao Autonomous Prefecture (黔南布依族苗族自治州), Luodian County (罗甸县), Luokun Town (罗 悃镇), Xiangshui Village (响水村), 25°19'43"N 106°38'28"E, H: 666.10±6.40m, 09.XI.2022, Jiang Ri-Xin leg." (GUGC). *Paratypes*: • 10 ♂♂, 10 ♀♀, 20 exs., sex undetermined, with same label data as the holotype (GUGC).

**Diagnosis.** Body long-oval, mostly black; pronotum (except basal part), antennae, base of tibia and tarsi (including claws) light brown. Plastron setae



Figure 3. Diagnostic features of *Sinonychus luodianensis* sp. nov. A head B pronotum C prosternal process D metaventrite E abdomen F elytron. Scale bars: 0.1 mm (A); 0.2 mm (B–F).

scaly. Elytral intervals 5, 6 and 7 with granulate carinae. Aedeagus with apex of median lobe rounded; median lobe with two pairs of long, elongate sclerotizations located at basal 1/2; a very thin and long sclerotization extends from middle of median lobe to well beyond the apex, where it is curved.

**Description.** Body long-oval (Fig. 1B); black with pronotum (except basal part), antennae, base of tibia and tarsi (including claws) light brown. Plastron setae confined to following areas: head (both dorsal and ventral surfaces, including disc of clypeus); pronotum (lateral areas); elytra (lateral areas, including epipleura); prosternum, mesoventrite, metaventrite and abdomen (lateral areas); and femora.

Head (Fig. 3A), wider than long, surface covered with plastron setae and sparse, long setae and granules. Clypeus with disc covered with plastron setae; anterior and lateral areas without plastron setae, covered with sparse, long setae. Labrum transverse, narrower than clypeus, lateral margins with long bristles. Antenna (Fig. 1D) 7-segmented with apical antennomere clubbed.

Pronotum (Fig. 3B) slightly wider than long, widest at basal 2/5, gradually narrowed from basal 2/5 to apex. Surface finely punctate; covered with sparse, long setae and with plastron setae laterally. Median longitudinal sulcus distinct and long, extending from base nearly to anterior 1/4, with a pair of small round fovea near base. Sublateral grooves straight, short, less than 1/3 length of pronotum. Anterior margin distinctly curved, anterior angles not produced. Lateral margins gradually curved. Basal margin trisinuate, emarginate anterior to



Figure 4. Genital features of *Sinonychus* species: A–G *Sinonychus lipinae* sp. nov. H–N, *Sinonychus luodianensis* sp. nov. A, H aedeagus, dorsal view B, J ditto, ventral C, I ditto, median lobe D, K ditto lateral view E, L sternite IX F, M ovipositor G, N ditto, apical part. Scale bars: 0.05 mm (G, N); 0.1 mm (A–F, H–M).

scutellum, posterior angles nearly orthogonal. Prosternal process (Fig. 3C) very wide, with apex broadly rounded; surface distinctly microreticulate, glabrous.

Scutellum (Fig. 3B) cordate, longer than wide, widest at basal 1/4; surface microreticulate and glabrous. Anterior margin strongly curved, lateral margins weakly curved, apex acutangular.

Elytra (Fig. 3F) about 1.5 times as long as wide, widest near in median 1/3. Strial punctures large in basal 2/3 of elytra, separated by about twice a diameter; much smaller and more widely separated in other parts of elytra. Elytral intervals 5, 6, 7 with granulate carinae extending from base of elytra nearly to apex. Interval 5 to lateral margins covered with plastron setae. Hing wings reduced.

Metaventrite (Fig. 3D) with disc distinctly microreticulate and covered with sparse, long setae; lateral areas with plastron setae. Median sulcus shallow and indistinct, less than half the length of metaventrite.



Figure 5. Habitat of *Sinonychus lipinae* sp. nov. at the type locality **A** general environment **B** microenvironment **C** living adult **D** collectors, left: Miss Yu-Hao Zhang, right: Dr Yin-Lin Mu **E** collectors, left: Dr Hai-Tao Li, right: Dr Pin Li.

Admedian carinae of abdominal ventrite 1 indistinct, straight, extending from base to near apex. Median areas of ventrites 1-4 (Fig. 3E) and anteromedial area of ventrite 5 microreticulate, covered with sparse, long setae; remaining surface of ventrites 1-5 covered with plastron setae and mixed with sparse, long setae.

Legs simple, surface granulate (except tarsi). Surface of femora surface covered with plastron setae; inner side of tibia with cleaning fringes; tarsi slightly shorter than tibiae; tarsal claws simple.

Aedeagus (Fig. 4H–K) slender and elongate. Median lobe symmetrical, widest at base, weakly narrowed from base to apex; apex rounded; with two pairs of long, elongate sclerotizations located at basal 1/2; a very thin, very long



Figure 6. Habitat of *Sinonychus luodianensis* sp. nov. at the type locality **A** general environment **B** microenvironment **C** living adult.

sclerotization extends from middle of median lobe to well beyond the apex, where it is curved. Sternite IX (Fig. 4L) with apical margin weakly emarginate, without setae, median strut curved at middle with base curved.

Measurements: CL: 1.03–1.11 mm; PL: 0.33–0.35 mm, PW: 0.42–0.44 mm; EL: 0.70–0.78 mm, EW: 0.50–0.54 mm.

Female externally similar to the male, averaging larger. Ovipositor as in Fig. 4M, N: valvifer about twice as long as coxite, distinctly expanded at base; coxite apex strongly expanded, roundly broadened at outer margin; stylus short, weakly curved.

Measurements: CL: 1.04–1.17 mm; PL: 0.33–0.38 mm, PW: 0.39–0.44 mm; EL: 0.72–0.78 mm, EW: 0.49–0.57 mm.

**Distribution.** China. Only known from the type locality in Luodian County, Qiannan Buyi and Miao Autonomous Prefecture, Guizhou Province.

**Biology.** All adults were collected from gravel on the bottom of a small stream in a ravine (Fig. 6A-C).

**Etymology.** The specific epithet *"luodianensis"* refers to the type locality, Luodian County, Qiannan Buyi and Miao Autonomous Prefecture, Guizhou Province; the name is treated as an adjective.

**Comparative diagnosis.** The new species can be easily distinguished from other *Sinonychus* species by its scaly plastron setae, and males by the aedeagus with very long, thread-like sclerotization extending from the middle of the median lobe and exceeding its apex.

# Key to known species of the genus Sinonychus Jäch & Boukal, 1995

- Plastron setae scaly, median lobe of aedeagus with very long sclerotization extending from middle of median lobe and extending beyond its apex.......
   S. luodianensis sp. nov. (China)
- Plastron setae spiculate, sclerotizations of median lobe not as above .....2
- Elytral intervals 3 without granulate carina......4
- 3 Basal 1/2 of median longitudinal sulcus distinctly wider than apical 1/2; median lobe of aedeagus about 6 times as long as phallobase, base of sclerotizations of median lobe near middle of median lobe ..... *S. lipinae* sp. nov. (China)
- Basal 1/2 of median longitudinal sulcus not distinctly wider than apical 1/2; median lobe of aedeagus about 5 times as long as phallobase, base of sclerotizations of median lobe behind middle of median lobe
- 4 Mandible with two apical teeth; antennal segment 7 covered with short se-
- tae apically...... S. satoi Yoshitomi & Nakajima, 2007 (Japan) - Mandible with three apical teeth; antennal segment 7 covered with long
- setae apically......S. lantau Jäch & Boukal, 1995 (China)

# Discussion

Members of the tribe Macronychini are characterized by the reduced antennomeres and parameres of the aedeagus (Jäch and Boukal 1995). Members of this tribe usually possess a well-developed internal sac of the aedeagus; sclerotized structures of aedeagus can be observed and are usually seen as important characters to distinguish different species (Jäch and Boukal 1995; Hayashi and Yoshitomi 2015).

Sinonychus luodianensis sp. nov. shows a very special sclerotized structure that is quite rare in the tribe Macronychini, even in the family Elmidae: a very long and thin thread-like sclerotization extending from the middle of the median lobe and exceeding the apex of the median lobe. The functional significance of this structure is unknown. In our observations, the special long sclerotization appears to have the same origin as other shorter sclerotizations of the median lobe.

On the other hand, *Sinonychus luodianensis* sp. nov. has scaly plastron setae, which are quite different from those of other *Sinonychus* species. However, this species can be placed in *Sinonychus* under the current definition of the genus, while its true identity remains somewhat of a conundrum. The same situation is also present in other Macronychini members: e.g., Bian, Hu and Tong (2024) described *Cuspidevia pilosus* Bian, Hu & Tong, 2024, which could be placed in the genus *Cuspidevia*, but it also shows some unusual characters, such as the pronotum without any median impression. Those problems remind us that systematic work on the tribe Macronychini based on molecular data is still very incomplete.

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# Additional information

# **Conflict of interest**

The authors have declared that no competing interests exist.

# **Ethical statement**

No ethical statement was reported.

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# Author contributions

Xiang-Sheng Chen guide this workp Ri-Xin Jiang write the manuscript.

# **Data availability**

All of the data that support the findings of this study are available in the main text.

# References

- Bian DJ, Hu YQ, Tong YF (2024) A new species of *Cuspidevia* Jäch & Boukal, 1995. Biodiversity Data Journal 12: e117248. https://doi.org/10.3897/BDJ.12.e117248
- Hayashi M (2019) Observation of minute structure on body surface of elmid adults: *Sinonychus tsujunensis* Yoshitomi & Nakajima. Bulletin Hoshizaki Green Found 22: 109–118.
- Hayashi M, Kamite Y (2020) Description of larvae of Japanese Macronychini (Coleoptera: Elmidae: Elminae). Zootaxa 4859 (2): 195–227. https://doi.org/10.11646/zootaxa.4859.2.2
- Hayashi M, Yoshitomi H (2015) Endophallic Structure of the Genus *Zaitzeviaria* Nomura (Coleoptera, Elmidae, Elminae), with Review of Japanese Species. Elytra, Tokyo, New Series 5(1): 67–96.
- Jäch MA, Boukal DS (1995) ELMIDAE: 2. Notes on Macronychini, with descriptions of four new genera from China (Coleoptera). In: Jäch MA, Ji L-Z (Eds) Water Beetles of China, Vol. 1. Naturhistorisches Museum Wien, 299–323.
- Kamite Y, Moriya H (2011) New record of *Sinonychus satoi* (Coleoptera, Elmidae) from Amami-Ôshima, Japan. Elytra, Tokyo, New Series 1(1): 66.
- Yoshitomi H, Nakajima J (2007) A new species of the genus *Sinonychus* (Coleoptera, Elmidae) from Japan. Elytra, Tokyo 35: 96–101.
- Yoshitomi H, Nakajima J (2012) A new species of the genus *Sinonychus* (Coleoptera, Elmidae) from Kyushu, Japan. Elytra, Tokyo, New Series 2 (1): 53–60.



**Research Article** 

# A new species of *Cyrtodactylus* Gray, 1827 (Squamata, Gekkonidae) from Yunnan Nangunhe National Nature Reserve, China

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#### Abstract

A new forest-dwelling species of the *Cyrtodactylus chauquangensis* group is described from southwestern Yunnan Province, China. Phylogenetically, it was recovered as the sister species of *C. zhenkangensis*, with a genetic distance of 9.2% in the ND2 gene. Morphologically, the new species can be separated from *C. zhenkangensis* by the discontinuity of enlarged femoral scales and enlarged precloacal scales, the absence of femoral pores, and the difference in dorsal color pattern. In addition, although the new species and *C. zhenkangensis* are distributed relatively close, their habitats are clearly different. *Cyrtodactylus zhenkangensis* inhabits karst limestone, while the new species inhabits forest. The new species of the 29<sup>th</sup> species of the *C. chauquangensis* group and the third forest-dwelling species of this group.

**Key words:** Bent-toed gecko, Cangyuan, *Cyrtodactylus chauquangensis* group, mitochondrial DNA, systematics, taxonomy

# Introduction

The species diversity of the genus *Cyrtodactylus* Gray, 1827 had previously been severely underestimated, but currently the number of species in this genus has been rapidly increasing, and the number of species is now over 350 (Uetz et al. 2024). In China, only two species of this genus were recorded before 2010 (Zhao et al. 1999, 2000), namely *C. khasiensis* (Jerdon, 1870) from Yunnan Province and *C. tibetanus* (Boulenger, 1905) from Xizang Autonomous Region. Subsequently, *C. zhaoermii* Shi & Zhao, 2010 was described from Xizang, and *C. wayakonei* Nguyen, Kingsada, Rösler, Auer & Ziegler, 2010 was reported from Yunnan (Yuan and Rao 2011). Later, *C. khasiensis* was removed from the herpetofauna of China, and *C. khasiensis cayuensis* Li, 2007 was elevated to the level of species (Agarwal et al. 2018; Wang et al. 2020). Soon after, *C. dianxiensis* Liu & Rao, 2021, *C. zhenkangensis* Liu & Rao, 2021, *C. gulinqingensis* Liu, Li, Hou, Orlov & Ananjeva, 2021, *C. hekouensis* Zhang, Liu, Bernstein, Wang & Yuan, 2021, and *C. menglianensis* Liu & Rao, 2022 were described from Yunnan, and *C. arunachalensis* Mirza, Bhosale, Ansari, Phansalkar, Sawant, Gowete &



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**Copyright:** © Shuo Liu et al. This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0). Patel, 2021 and *C. kamengensis* Mirza, Bhosale, Thackeray, Phansalkar, Sawant, Gowande & Patel, 2022 were described from near the border between China and India. Recently, *C. caixitaoi* Liu, Rao, Hou, Wang & Ananjeva, 2023 was described from Yunnan, *C. wayakonei* was removed from the herpetofauna of China (Liu et al. 2023), *C. hekouensis* was treated as a junior synonym of *C. gulinqingensis* (Zhang et al. 2024), and *C. laevis* Ma, Wang & Jiang, 2024 was described from Xizang. So far, 11 species of this genus have been recorded in China, including six species from Xizang and five species from Yunnan (Ma et al. 2024).

Yunnan Nangunhe National Nature Reserve is located in southwestern Yunnan Province, China. This nature reserve has a total area of 508.87 km<sup>2</sup>, with the lowest and highest elevations at 510 m and 2,977 m, respectively. There are numerous high mountains and valleys and many rivers and streams, as well as multiple vegetation types, such as rainforest and seasonal rainforest, in this nature reserve. Its main protected species are rare and endangered wild animals such as elephants, tigers, gibbons, and monkeys (Yang and Du 2004; Tang et al. 2015).

During our fieldwork in southwestern Yunnan, China, in 2024, two specimens of *Cyrtodactylus* were collected in Yunnan Nangunhe National Nature Reserve. Both morphological and phylogenetic analyses support the recognition of the two specimens as belonging to an unnamed species of the *C. chauquangensis* group. Therefore, we describe them as a new species below.

# Materials and methods

# Sampling

The field survey in Yunnan Nangunhe National Nature Reserve was conducted under the permit from Yunnan Nangunhe National Nature Reserve Management and Protection Bureau. Specimens were collected by hand at night and photographed alive prior to preservation. Liver tissues were dissected and preserved in analytical pure ethanol. The specimens were stored in 75% ethanol and deposited at Kunming Natural History Museum of Zoology, Kunming Institute of Zoology, Chinese Academy of Sciences (**KIZ**).

# Morphological analyses

Measurements were taken with digital calipers to the nearest 0.1 mm. Bilateral scale counts are given as left/right. The methodology of measurements and meristic counts is the same as those in Liu et al. (2023):

- **AG** axilla to groin distance, measured from the posterior margin of the forelimb insertion to the anterior margin of the hindlimb insertion;
- **DTR** dorsal tubercle rows, the number of dorsal, longitudinal rows of the tubercles at midbody between ventrolateral folds;
- ED ear diameter, the greatest diameter of ear opening;
- **EE** eye to ear distance, measured from the posterior edge of the orbit to the anterior edge of the ear opening;
- **EFS** enlarged femoral scales, the number of the enlarged femoral scales beneath each thigh;

ForeaL forearm length, measured from the tip of the elbow to the wrist;FP femoral pores;

- GSDT granular scales surrounding dorsal midbody tubercles;
- **HH** maximum head height;
- **HL** head length, measured from the tip of the snout to the posterior margin of the retroarticular process of the lower jaw;
- HW maximum head width;
- I internasals, the number of the scales between the two supranasals;
- IFL infralabials, counted from the first labial scale to the corner of the mouth;
- IND internarial distance, the distance between nares;
- **IOD** interorbital distance, measured across the narrowest point of the frontal bone;
- **LF4** subdigital lamellae under the fourth finger, counted from the base of the digit where it contacts the body of the hand to the base of the claw, including the claw sheath;
- LT4 subdigital lamellae under the fourth toe, counted from the base of the digit where it contacts the body of the foot to the base of the claw, including the claw sheath;
- ML mental length, the maximum length of the mental;
- **MW** mental width, the maximum width of the mental;
- **OD** greatest diameter of orbit;
- **PAT** postcloacal tubercles, the number of the tubercles on each side of the postcloacal region;
- **PM** postmentals, the number of the scales bordering the mental shield, excluding infralabials;
- PP precloacal pores;
- **PVT** paravertebral tubercles, counted in a single paravertebral row from the level of the forelimb insertions to the level of the hind limb insertion;
- **RH** rostral height, the maximum height of the rostral;
- **RW** rostral width, the maximum width of the rostral;
- **SE** snout to eye distance, measured from the tip of the snout to the anterior edge of the orbit;
- SL shank length, measured from the base of the heel to the knee;
- SPL supralabials, counted from the first labial scale to the corner of the mouth;
- **SVL** snout-vent length, measured from the tip of the snout to the anterior margin of the cloaca;
- **TaL** tail length, measured from the posterior margin of the cloaca to the tip of the tail;
- V ventral scale rows, the number of longitudinal rows of ventral scales at midbody between ventrolateral folds.

Morphological comparisons were based on the original descriptions of each species of the *Cyrtodactylus chauquangensis* group (Hoang et al. 2007; Bauer et al. 2009, 2010; Ngo and Grismer 2010; Nguyen et al. 2010, 2014, 2015, 2017; Sumontha et al. 2010; Luu et al. 2011; Ngo 2011; Ngo and Chan 2011; Kunya et al. 2014; Nazarov et al. 2014; Pauwels et al. 2014; Schneider et al. 2014, 2020; Le et al. 2016; Pham et al. 2019; Liu and Rao 2021, 2022; Liu et al. 2021, 2023; Chomdej et al. 2022; Grismer et al. 2024; Tran et al. 2024).

#### **Molecular analyses**

Total genomic DNA was extracted from liver tissue samples. A fragment of the mitochondrial NADH dehydrogenase subunit 2 (ND2) gene was amplified and sequenced using the primers L4437b (5'-AAGCAGTTGGGCCCATACC-3') and H5540 (5'-TTTAGGGCTTTGAAGGC -3') (Macey et al. 2000) for the two newly collected specimens. Sequences were assembled and edited using SeqMan in Lasergene 7.1 (Burland 2000) and MEGA 11 (Tamura et al. 2021). New sequences have been deposited on GenBank and available sequences of the *C. chauquangensis* group were obtained from GenBank (Table 1). *Cyrtodactylus dammathetensis* Grismer, Wood, Thura, Zin, Quah, Murdoch, Grismer, Lin, Kyaw & Lwin, 2017 and *C. sinyineensis* Grismer, Wood, Thura, Zin, Quah, Murdoch, Grismer, Lin, Kyaw & Lwin, 2017 were used as outgroups following Grismer et al. (2024).

Sequences were aligned using MAFFT 7.471 (Katoh and Standley 2013) with default parameters. The best-fit substitution models (GTR+F+I+G4 for the first

Species	Locality	Catalog number	Accession number	
Cyrtodactylus nangunhe sp. nov.	China, Yunnan, Lincang, Cangyuan	KIZ 2024083	PQ670135	
Cyrtodactylus nangunhe sp. nov.	China, Yunnan, Lincang, Cangyuan	KIZ 2024084	PQ670136	
Cyrtodactylus auribalteatus	Thailand, Phitsanulok, Noen Maprang	AUP-01745	MZ439914	
Cyrtodactylus bichnganae	Vietnam, Son La, Son La Urban	UNS 0473	MF169953	
Cyrtodactylus bobrovi	Vietnam, Hoa Binh, Lac Son	IEBR A.2015.29	MT953471	
Cyrtodactylus chauquangensis	Vietnam, Nghe An, Quy Hop	NA 2016.1	MT953475	
Cyrtodactylus cucphuongensis	Vietnam, Ninh Binh, Cuc Phuong NP	CP 17.02	MT953477	
Cyrtodactylus doisuthep	Thailand, Chiang Mai, Doi Suthep	AUP-00777	MT497801	
Cyrtodactylus dumnuii	Thailand, Chiang Mai, Chiang Dao	AUP-00769	MT497802	
Cyrtodactylus dumnuii	Thailand, Chiang Mai, Chiang Dao	AUP-00770	MT497803	
Cyrtodactylus dumnuii	Thailand, Chiang Mai, Chiang Dao	AUP 00768	MW713972	
Cyrtodactylus erythrops	Thailand, Mae Hong Son, Pang Mapha	AUP-00771	MT497806	
Cyrtodactylus gulinqingensis	China, Yunnan, Maguan, Gulinqing	KIZ 061813	MZ782150	
Cyrtodactylus houaphanensis	Laos, Luang Houaphan	IEBR A.2013.109	MW792067	
Cyrtodactylus huongsonensis	Vietnam, Ha Noi, My Duc, Huong Son	IEBR A.2011.3A	MT953481	
Cyrtodactylus kunyai	Thailand, Loei, Nong Hin	AUP-01747	MZ439916	
Cyrtodactylus luci	Vietnam, Lao Cai, Bac Ha	IEBR R.5240	PP253960	
Cyrtodactylus menglianensis	China, Yunnan, Puer, Menglian	KIZ 20210713	OM296042	
Cyrtodactylus menglianensis	China, Yunnan, Puer, Menglian	KIZ 20210714	OM296043	
Cyrtodactylus menglianensis	China, Yunnan, Puer, Menglian	KIZ 20210716	OM296044	
Cyrtodactylus ngoiensis	Laos, Luang Prabang, Ngoi	IEBR A.2013.110	MW792066	
Cyrtodactylus otai	Vietnam, Son La, Van Ho, Na Bai	TBU 2017.2	MT953486	
Cyrtodactylus phamiensis	Thailand, Chiang Rai, Mae Sai, Pha Mi	ZMKU R 01074	PP430583	
Cyrtodactylus phukhaensis	Thailand, Nan, Pua, Doi Phu Kha	AUP-01823	MZ439912	
Cyrtodactylus phukhaensis	Thailand, Nan, Pua, Doi Phu Kha	AUP-01824	MZ439913	
Cyrtodactylus puhuensis	Vietnam, Thanh Hoa	ND 01.15	MT953489	
Cyrtodactylus solaensis	Vietnam, Son La, Phu Yen	IEBR A.2017.1	MT953492	
Cyrtodactylus soni	Vietnam, Ninh Binh, Gia Vien	IEBR R.2016.4	MT953491	
Cyrtodactylus spelaeus	Laos, Vientiane, Kasi	HLM 0315	MW713962	
Cyrtodactylus taybacensis	Vietnam, Son La, Quyun Nhai, Ca Nang	IEBR 4379	MT953495	
Cyrtodactylus vilaphongi	Laos, Luang Prabang, Luang Prabang	IEBR A.2013.103	MT953497	
Cyrtodactylus wayakonei	Laos, Luang Nam Tha, Vieng Phoukha	ZFMK 91016	MT953498	
Cyrtodactylus zhenkangensis	China, Yunnan, Lincang, Zhenkang	KIZ L2020047	MW792062	
Cyrtodactylus zhenkangensis	China, Yunnan, Lincang, Zhenkang	KIZ L2020048	PQ670137	
Cyrtodactylus dammathetensis	Myanmar, Mon State, Mawlamyine	LSUHC:12863	MF872277	
Cyrtodactylus sinyineensis	Myanmar, Kayin State, Hpa-an	LSUHC:12836	MF872355	

Table 1. Sequences (ND2) used in the phylogenetic analysis of this study.
and second codon positions and the tRNAs, and GTR+F+G4 for the third codon position) were chosen using the Akaike information criterion (AIC) in ModelFinder (Kalyaanamoorthy et al. 2017). The technical computation methods for genetic divergences calculation and Bayesian-inference and maximum-likelihood phylogenetic analyses were the same as those used by Liu and Rao (2022).

# Results

The phylogenetic topologies of Bayesian-inference and maximum-likelihood analysis were identical. The sequences of the newly collected specimens were nested within the *Cyrtodactylus chauquangensis* group and formed a strongly supported lineage sister to *C. zhenkangensis* (Fig. 1). The genetic distance between the sequences of the newly collected specimens and the sequences of *C. zhenkangensis* was 9.2%, and the genetic distances between the sequences of the newly collected specimens and the sequences of the newly collected specimens of the newly collected specimens of the newly collected specimens of the sequences of the newly collected specimens and the sequences of the newly collected specimens and the sequences of this group ranged from 11.4% to 18.3% (Table 2).



**Figure 1.** Bayesian phylogram of the *Cyrtodactylus chauquangensis* group based on the ND2 sequences. Numbers before slashes indicate Bayesian posterior probabilities and numbers after slashes indicate maximum-likelihood ultrafast bootstrap. The symbol "–" represents the value below 0.90/90.

Table 2. Uncorrected pairwi	se gen	etic d	istanc	es (%)	) amo	)ds bu	ecies	of the	Cyrto	Jactyl	us ché	uquan	igensi	s grou	p bas	ed on	the NI	J2 seq	Inence	ůS.					
	-	2	e	4	ß	9	7	8	6		11	2 1;	3 1/	15	16	17	18	19	20	21	22	23	24	25	26
1 Cyrtodactylus nangunhe sp. nov.																									
2 Cyrtodactylus auribalteatus	14.6																								
3 Cyrtodactylus bichnganae	18.3	18.0																							
4 Cyrtodactylus bobrovi	16.3	15.0	19.7																						
5 Cyrtodactylus chauquangensis	15.7	14.4	18.1	8.6																					
6 Cyrtodactylus cucphuongensis	16.8	15.7	19.9	7.9	8.5																				
7 Cyrtodactylus doisuthep	16.8	14.1	16.4	15.4	14.2	15.2																			
8 Cyrtodactylus dumnuii	13.6	13.3	16.9	13.7	12.2	14.2	14.0																		
9 Cyrtodactylus erythrops	15.9	14.7	16.7	14.8	13.7	15.1	10.9	13.7																	
10 Cyrtodactylus gulinqingensis	15.7	14.5	18.1	13.7	14.0	14.0	13.6	12.9 1	4.1																
11 Cyrtodactylus houaphanensis	16.3	15.6	19.4	6.5	9.0	7.5	15.1	14.2 1	5.1 1	4.0															
12 Cyrtodactylus huongsonensis	15.3	14.5	17.7	14.3	12.2	14.3	14.6	14.0 1	4.4 1	2.4 1	4.8														
13 Cyrtodactylus kunyai	16.5	12.5	17.8	15.5	14.4	17.1	14.9	13.8 1	5.7 1	4.4 1	6.3 14	4.7													
14 Cyrtodactylus luci	16.5	13.9	18.1	14.2	14.2	14.6	13.9	13.3 1	5.1	9.1 1.	4.4 12	2.4 14	.2												
15 Cyrtodactylus menglianensis	11.5	12.6	18.4	14.9	12.7	15.0	15.1	11.4	14.4	4.3 1	4.7 1.	4.4 15	.0 14.	0											
16 Cyrtodactylus ngoiensis	15.4	13.8	18.2	11.2	10.3	10.8	14.8	12.0	14.5 1	3.1 1	1.4 1	3.1 13	.8 13	.4 13.7	_										
17 Cyrtodactylus otai	15.9	14.1	19.1	3.6	9.1	8.4	16.2	15.6	16.4	5.6 6	5.8 14	4.7 15	.5 14	.8 15.2	2 12.1	~									
18 Cyrtodactylus phamiensis	17.0	16.0	16.4	16.0	14.8	16.4	14.1	14.9	15.1 1	5.6 1	6.0 14	4.4 16	.2 17.	.0 16.0	15.	5 16.9									
19 Cyrtodactylus phukhaensis	11.4	12.6	17.5	14.6	12.1	14.4	14.9	11.9	14.1	4.0 1	4.5 1;	3.8 14	.1 14	.4 7.0	11.	2 15.4	t 15.1								
20 Cyrtodactylus puhuensis	15.4	14.3	18.9	5.7	8.0	7.1	14.4	12.8	14.3	3.5	.8 1.	3.9 14	.9 14	.2 14.7	1 10.5	5 6.2	15.4	13.7							
21 Cyrtodactylus solaensis	16.9	16.5	19.4	17.5	16.9	18.2	16.4	16.7	17.3	4.8 1	8.0 1.	5.0 16	.2 15	.9 17.3	3 16.3	2 17.7	7 18.3	16.2	18.0						
22 Cyrtodactylus soni	15.5	14.0	18.2	14.6	13.3	14.7	13.9	13.4	14.1	3.4 1	5.4 7	.3 14	.1 12	.7 14.(	14.3	3 14.7	7 14.5	14.0	14.4	15.3					
23 Cyrtodactylus spelaeus	16.0	15.5	18.3	10.1	9.3	10.5	15.1	13.5	15.2 1	3.8 1	0.5 1,	4.3 15	.0 14	.5 14.6	5 11.	11.5	3 16.1	13.9	9.1	17.7	14.6				
24 Cyrtodactylus taybacensis	17.9	17.4	9.3	16.6	15.6	16.8	15.4	14.8	16.4 1	6.0 1	7.0 1.	5.8 17	.2 15	.6 16.6	5 16.4	4 18.5	3 16.8	16.8	16.3	18.9	15.6	16.1			
25 Cyrtodactylus vilaphongi	16.0	13.8	17.8	8.1	7.3	8.2	14.1	13.2	14.2 1	3.4 8	3.2 1.	4.2 14	.5 14	.4 14.0	0.4	9.1	15.0	13.8	7.0	16.9	13.7	9.6	16.3		
26 Cyrtodactylus wayakonei	12.1	13.5	18.0	15.5	13.1	15.5	16.2	12.5	15.6 1	5.3 1	4.7 1.	5.1 14	.2 15	.9 7.2	12.	2 15.4	15.5	5.0	14.2	16.5	14.0	15.2	17.5	13.7	
27 Cyrtodactylus zhenkangensis	9.2	12.8	18.3	14.3	13.2	13.8	14.9	11.8	4.3 1	2.9 1.	4.0 1	3.2 15.	.1 12.	.01 9.	7 13.3	3 15.5	15.7	10.2	13.3	17.3	13.9	14.1	15.3	13.7	1.9

#### Taxonomy

#### Cyrtodactylus nangunhe sp. nov.

https://zoobank.org/28F6B348-E2B0-4789-851B-55A9079DD67A Figs 2-5, 7

**Туре material.** *Holotype.* Сніла • ♂; Yunnan, Cangyuan; 23°13'19"N, 99°1'2"E; 950 m; 17 Aug. 2024; Shuo Liu leg.; KIZ 2024083. *Paratype.* Сніла • ♀; same locality; 24 Aug. 2024; Shuo Liu leg.; KIZ 2024084.

Diagnosis. Body size relatively large (SVL 89.5–97.0 mm); tail long (TaL/SVL 1.07-1.14); head relatively long (HL/SVL 0.27-0.28), moderately widened (HW/ HL 0.67-0.68); snout long (SE/HL 0.40); body slender (AG/SVL 0.43-0.44); 16-18 longitudinal rows of dorsal tubercles at midbody, 25-27 paravertebral tubercles; ventrolateral fold distinct, interspersed with tubercles; 29-31 longitudinal ventral scale rows at midbody; eight precloacal pores separated by one poreless scale in male; precloacal pores absent, three indistinct shallow pits on enlarged precloacal scales in female; 7-8 slightly enlarged femoral scales beneath each thigh in male, four slightly enlarged femoral scales beneath each thigh in female; enlarged femoral scales separated from enlarged precloacal scales by some smaller scales; femoral pores absent in both sexes; 3-4 shallow pits on enlarged femoral scales on each side in male, absent in female; 1-2 postcloacal tubercles on each side; 19-22 lamellae under finger IV, 24-25 lamellae under toe IV; two rows of subcaudals enlarged; dorsal ground color brownish-black; distinct reticulated pattern composed of thin, light-yellow stripes on dorsal head; six irregular, narrow, light-yellow, transverse bands on dorsum; 6–7 light bands on dorsal tail.

**Description of holotype.** Adult male, SVL 89.5 mm; head clearly distinguished from neck, relatively long (HL/SVL 0.28), moderately widened (HW/HL 0.67), depressed (HH/HL 0.44); nare oval, surrounded by supranasal dorsally, rostral anteriorly, first supralabial ventrally, and two postnasals posteriorly; snout long (SE/HL 0.40), round anteriorly, longer than diameter of orbit (SE/OD 1.29); snout scales much larger than those in frontal and parietal regions; eye large (OD/HL 0.31), pupils vertical; upper eyelid fringe with spinous scales; ear opening oval, much small in size (ED/HL 0.05); rostral large (RW/HL 0.17), wider than high (RW/RH 1.54), medially divided dorsally by a suture, reaching to approximately half down rostral, in contact with first supralabial laterally on each side and two supranasals and one internasal dorsally; mental triangular, wider than high (MW/ML 1.31), slightly narrower than rostral (MW/RW 0.88); two postmentals, enlarged, in contact posteriorly, bordered by mental anteromedially, first infralabial anterolaterally and one enlarged chin scale posterolaterally on each side, and small chin scales posteriorly; 8/8 supralabials; 8/8 infralabials.

Body slender (AG/SVL 0.42), ventrolateral fold distinct, interspersed with tubercles; dorsal scales granular; dorsal tubercles heterogeneous, conical, in approximately 18 longitudinal rows at midbody, largest ones approximately five times size of adjoining scales and surrounded by 10 granular scales, approximately 25 paravertebral tubercles; gular region with homogenous small smooth scales; ventral scales smooth, homogenous, larger than those of dorsum and in gular region, subimbricate, in approximately 29 longitudinal rows at midbody; precloacal groove absent; precloacal scales significantly enlarged; eight precloacal pores separated by one poreless scale in middle, round or oval; 8/7 slightly enlarged fem-



Figure 2. Type specimens of *Cyrtodactylus nangunhe* sp. nov. in preservative A dorsal view B ventral view.



**Figure 3.** Close-up views of the femoral and precloacal regions of *Cyrtodactylus nangunhe* sp. nov. in preservative **A** male holotype (KIZ 2024083) **B** female paratype (KIZ 2024084).

oral scales, separated from enlarged precloacal scales by some smaller scales; femoral pore absent, four indistinct shallow pits on enlarged femoral scales on left side, three distinct shallow pits on enlarged femoral scales on right side.

Limbs relatively long (ForeaL/SVL 0.16, SL/SVL 0.19), fore limbs slender, hind limbs robust; tubercles on dorsal surface of limbs heterogeneous, conical, ones on fore limbs smaller than most dorsal tubercles, ones on hind limbs approximately as large as most dorsal tubercles; interdigital webbing absent; lamellae under finger IV 21/22, under toe IV 24/24; relative length of fingers I<II≈V<III≈IV, relative length of toes I<II<IV.

Tail original, long (TaL/SVL 1.14); 2/2 postcloacal tubercles; dorsal tail base with tubercles; subcaudals smooth, two irregular rows enlarged.

**Color of holotype in life.** Dorsal ground color brownish-black; dorsal surface of head with distinct reticulated pattern composed of thin, light-yellow stripes; nape with irregular thin, light-yellow stripes; dorsum with six irregular, narrow,



Figure 4. Holotype (KIZ 2024083) of Cyrtodactylus nangunhe sp. nov. in life A dorsal view B lateral view C ventral view.

light-yellow, transverse bands and one longitudinal, continuous, thin, vertebral stripe; flanks scattered with some small light-yellow spots; dorsal surfaces of limbs with indistinct light-yellow bands; dorsal surface of tail black with seven light bands, first two yellowish-gray, last five grayish-white; ventral surface of head pinkish-white, ventral surfaces of body and limbs grayish-white, some light-yellow spots on ventral surfaces of limbs and on ventrolateral surfaces of head and body; ventral surface of tail base gray with some light-yellow spots, other region of ventral tail black; iris bronze.

**Variations.** Morphometric and meristic data for the type specimens are presented in Table 3. The female paratype (KIZ 2024084) resembles the holotype except that it has no precloacal pores but three indistinct shallow pits on the enlarged precloacal scales, fewer enlarged femoral scales, and no pits on the enlarged femoral scales. Color pattern of the female paratype (KIZ 2024084) also resembles the holotype except that it has no longitudinal vertebral stripe on dorsum and six light bands on the dorsal surface of the tail.



Figure 5. Paratype (KIZ 2024084) of Cyrtodactylus nangunhe sp. nov. in life A dorsal view B lateral view C ventral view.

**Distribution.** This species is currently known only from Yunnan Nangunhe National Nature Reserve in Cangyuan County, Yunnan Province, China (Fig. 6).

**Natural history.** There is no karst landform in the area where the type specimens were collected. This species was found on rocks or tree trunks in the virgin evergreen broadleaved forest at night. Individuals were slow and easy to catch. In addition, this species was found on the wall of an abandoned house near the collection site of the type specimens by locals (Fig. 7). The only female specimen did not carry eggs and no juveniles were found, so the reproductive season of this species is unknown. Other reptiles found at the type locality of the new species include *Acanthosaura rubrilabris* Liu, Rao, Hou, Orlov, Ananjeva & Zhang, 2022, *Boiga multomaculata* (Boie, 1827), *Calotes emma* Gray, 1845, *Hemidactylus garnotii* Duméril & Bibron, 1836, *Lycodon fasciatus* (Anderson, 1879), and *Ptyas korros* (Schlegel, 1837).

**Etymology.** The specific epithet *nangunhe* is a noun in apposition, and therefore invariable; it refers to Yunnan Nangunhe National Nature Reserve, where the new species was found.

	KIZ 2024083	KIZ 2024084		KIZ 2024083	KIZ 2024084
	Holotype	Paratype		Holotype	Paratype
	Male	Female		Male	Female
SVL	89.5	97.0	MW	3.8	3.4
TaL	102.2	103.8	ML	2.9	2.9
HH	11.1	11.3	SPL	8/8	9/8
HL	25.2	26.6	IFL	8/8	9/8
HW	17.0	18.2	I	1	1
OD	7.8	8.2	PM	2	2
SE	10.1	10.6	GSDT	10	9
EE	5.2	5.7	DTR	18	16
IND	3.3	3.5	PVT	25	27
IOD	3.2	3.6	V	29	31
ED	1.3	1.5	EFS	8/7	4/4
AG	37.5	42.6	PP	8	0 (3 pitted)
ForeaL	14.3	14.6	FP	0 (4/3 pitted)	0
SL	17.4	17.9	PAT	2/2	1/1
RW	4.3	4.3	LF4	21/22	19/20
RH	2.8	2.6	LT4	24/24	25/24

 Table 3. Measurements (in mm) and meristic data for the type specimens of the new species. Abbreviations defined in Materials and methods.



**Figure 6.** Map showing the distribution of species of the *Cyrtodactylus chauquangensis* group in China. Star, *Cyrtodactylus nangunhe* sp. nov.; dot, *C. zhenkangensis*; triangle, *C. menglianensis*; square, *Cyrtodactylus caixitaoi*; pentagon, *C. gulinqingensis*.

**Comparisons.** *Cyrtodactylus nangunhe* sp. nov. can be distinguished from all other members of the *C. chauquangensis* species group by a unique combination of morphological characters. *Cyrtodactylus nangunhe* sp. nov. differs from

*C. auribalteatus* Sumontha, Panitvong & Deein, 2010, *C. bichnganae* Ngo & Grismer, 2010, *C. doisuthep* Kunya, Panmongkol, Pauwels, Sumontha, Meewasana, Bunkhwamdi & Dangsri, 2014, *C. dumnuii* Bauer, Kunya, Sumontha, Niyomwan, Pauwels, Chanhome & Kunya, 2010, *C. erythrops* Bauer, Kunya, Sumontha, Niyomwan, Panitvong, Pauwels, Chanhome & Kunya, 2009, *C. gulinqingensis, C. huongsonensis* Luu, Nguyen, Do & Ziegler, 2011, *C. kunyai* Pauwels, Sumontha, Keeratikiat & Phanamphon, 2014, *C. luci* Tran, Do, Pham, Phan, Ngo, Le, Ziegler & Nguyen, 2024, *C. ngoiensis* Schneider, Luu, Sitthivong, Teynié, Le, Nguyen & Ziegler, 2020, *C. phamiensis* Grismer, Aowphol, Grismer, Aksornneam, Quah, Murdoch, Gregory, Nguyen, Kaatz, Bringsøe & Rujirawan, 2024, *C. phukhaensis* Chomdej, Pradit, Pawangkhanant, Naiduangchan & Suwannapoom, 2022, *C. soni* Le, Nguyen, Le & Ziegler, 2016, and *C. sonlaensis* Nguyen, Pham, Ziegler, Ngo & Le, 2017 by the absence of femoral pores (vs femoral pores present).

*Cyrtodactylus nangunhe* sp. nov. differs from *C. bobrovi* Nguyen, Le, Pham, Ngo, Hoang, Pham & Ziegler, 2015, *C. chauquangensis* Hoang, Orlov, Ananjeva, Johns, Hoang & Dau, 2007, *C. houaphanensis* Schneider, Luu, Sitthivong, Teynié, Le, Nguyen & Ziegler, 2020, *C. menglianensis*, *C. otai* Nguyen, Le, Van Pham, Ngo, Hoang, The Pham & Ziegler, 2015, *C. spelaeus* Nazarov, Poyarkov, Orlov, Nguyen, Milto, Martynov, Konstantinov & Chulisov, 2014, and *C. wayakonei* by having enlarged femoral scales (vs femoral scales not enlarged).

*Cyrtodactylus nangunhe* sp. nov. differs from *C. caixitaoi* by having different dorsal coloration (brownish-black ground color with thin stripes on head and narrow bands on dorsum vs orange brown or pinkish-brown ground color with thick stripes on head and wide bands on dorsum), more longitudinal rows of dorsal tubercles at midbody (16–18 vs 14–15), and more paravertebral tubercles (25–27 vs 20–21).

*Cyrtodactylus nangunhe* sp. nov. differs from *C. cucphuongensis* Ngo & Chan, 2011 by the different conditions of precloacal pores in males (present vs absent).

*Cyrtodactylus nangunhe* sp. nov. differs from *C. martini* Ngo, 2011 by having more precloacal pores in males (eight vs four), fewer longitudinal ventral scale rows (29–31 vs 39–43), and enlarged femoral scales separated from enlarged precloacal scales by smaller scales (vs enlarged femoral scales continuous with enlarged precloacal scales).

*Cyrtodactylus nangunhe* sp. nov. differs from *C. puhuensis* Nguyen, Yang, Le, Nguyen, Orlov, Hoang, Nguyen, Jin, Rao, Hoang, Che, Murphy & Zhang, 2014 by having more precloacal pores in males (eight vs five), enlarged femoral scales separated from enlarged precloacal scales by smaller scales (vs enlarged femoral scales continuous with enlarged precloacal scales), and two rows of subcaudals enlarged under original tail (vs one row).

*Cyrtodactylus nangunhe* sp. nov. differs from *C. taybacensis* Pham, Le, Ngo, Ziegler, Nguyen, 2019 by having fewer precloacal pores in males (eight vs 11–13), ventrolateral fold with interspersed tubercles (vs without), and two rows of subcaudals enlarged under original tail (vs one row).

*Cyrtodactylus nangunhe* sp. nov. differs from *C. vilaphongi* Schneider, Nguyen, Duc Le, Nophaseud, Bonkowski & Ziegler, 2014 by being larger (SVL 89.5– 97.0 mm vs 60.9–86.1 mm), dorsal head with a distinct reticulated pattern (vs indistinct), and having enlarged subcaudals (vs not enlarged).

*Cyrtodactylus nangunhe* sp. nov. differs from its sister species *C. zhenkangensis* by enlarged femoral scales separated from enlarged precloacal scales by smaller scales (vs enlarged femoral scales continuous with enlarged precloacal scales),



Figure 7. Cyrtodactylus nangunhe sp. nov. from near the type locality.

femoral pores absent (vs femoral pores present), having fewer pitted precloacal scales in females (three vs 7–9), fewer longitudinal rows of dorsal tubercles at midbody (16–18 vs 20–24), more lamellae under toe IV (24–25 vs 21–23), thin stripes on head and narrow bands on dorsum (vs thick stripes on head and wide bands on dorsum), fewer light bands on tail (6–7 vs 8–10), and most light bands on tail not connected on ventral surface of tail (vs connected on ventral surface of tail).

# Discussion

Grismer et al. (2021) partitioned the species of *Cyrtodactylus* into 10 ecotypes according to their habitat preferences. The *C. chauquangensis* group is a karst ecotype group, and most species of this group are karst dwellers except for

*C. doisuthep* and *C. phukhaensis*, which inhabit the forests in northern Thailand (Kunya et al. 2014; Chomdej et al. 2022; Tran et al. 2024). *Cyrtodactylus nangunhe* sp. nov. represents the third forest-dwelling species of this group. Although Cangyuan County is rich in karst landforms, we have not found any individual of *Cyrtodactylus* in the karst habitats in this county. On the contrary, there is no karst landform in the area where *C. nangunhe* sp. nov. was discovered. The reason is unknown why this species does not live in karst areas but instead in the forest without karst habitat.

The straight-line distance between the type localities of *C. nangunhe* sp. nov. and its sister species C. zhenkangensis is only approximately 65 km. However, these two species inhabit very different habitats: C. zhenkangensis in an area of limestone and C. nangunhe sp. nov. in forest. Limestone is usually grayish-white and has many cracks and holes. Individuals of C. zhenkangensis have a light general color and relatively distinct stripes on the dorsal surface, which may be to better hide themselves in limestone environments. On the other hand, the rocks or tree trunks in forests are often of a single color, and living in forests often requires passing on the ground. Individuals of C. nangunhe sp. nov. have a dark general color and relatively indistinct stripes on the dorsal surface, which may make them less visible to predators in the forest. Perhaps it is the differentiation of habitats that has led to the genetic divergence between C. zhenkangensis and C. nangunhe sp. nov. Although most species of this genus tend to inhabit karst habitats, some of them can adapt to other habitats such as forests. The discovery of the new species reminds us that the diversity of forest-dwelling species of this genus is still greatly underestimated.

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# **Additional information**

#### **Conflict of interest**

The authors have declared that no competing interests exist.

# **Ethical statement**

No ethical statement was reported.

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# Author contributions

Conceptualization: DR, ZL, WD. Formal analysis: SL, DR. Investigation: SL, ZL, WD. Writing - original draft: SL. Writing - review and editing: SL, MH, DR.

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#### Data availability

All of the data that support the findings of this study are available in the main text.

# Reference

- Agarwal I, Mahony S, Giri VB, Chaitanya R, Bauer AM (2018) Two new species of bent toed geckos, *Cyrtodactylus* Gray, 1827 (Squamata: Gekkonidae) from Northeast India with comments on name-bearing types from the region. Zootaxa 4420: 334–356. https://doi.org/10.11646/zootaxa.4420.3.2
- Bauer AM, Kunya K, Sumontha M, Niyomwan P, Panitvong N, Pauwels OSG, Chanhome L, Kunya T (2009) *Cyrtodactylus erythrops* (Squamata: Gekkonidae), a new cave-dwelling gecko from Mae Hong Son Province, Thailand. Zootaxa 2142: 51–62. https://doi. org/10.11646/zootaxa.2124.1.4
- Bauer AM, Kunya K, Sumontha M, Niyomwan P, Panitvong N, Pauwels OSG, Chanhome L, Kunya T (2010) *Cyrtodactylus dumnuii* (Squamata: Gekkonidae), a new cave-dwelling gecko from Chiang Mai Province, Thailand. Zootaxa 2570: 41–50. https://doi. org/10.11646/zootaxa.2570.1.2
- Burland TG (2000) DNASTAR's Lasergene sequence analysis software. Methods in Molecular Biology 132: 71–91. https://doi.org/10.1385/1-59259-192-2:71
- Chomdej S, Pradit W, Pawangkhanant P, Kuensaen C, Phupanbai A, Naiduangchan M, Piboon P, Nganvongpanit K, Yuan ZY, Zhang YP, Che J, Sucharitakul P, Suwannapoom C (2022) A new *Cyrtodactylus* species (Reptila: Gekkonidae) from Nan Province, northern Thailand. Asian Herpetological Research 13: 96–108. https://doi.org/10.16373/j. cnki.ahr.210055
- Grismer LL, Wood PLJr, Poyarkov NA, Le MD, Karunarathna S, Chomdej S, Suwannapoom C, Qi S, Liu S, Che J, Quah ESH, Kraus F, Oliver PM, Riyanto A, Pauwels OSG, Grismer JL (2021) Karstic landscapes are foci of species diversity in the world's third-largest vertebrate genus *Cyrtodactylus* Gray, 1827 (Reptilia: Squamata; Gekkonidae). Diversity 13: 183. https://doi.org/10.3390/d13050183
- Grismer LL, Aowphol A, Grismer JL, Aksornneam A, Quah ESH, Murdoch ML, Gregory JJ, Nguyen E, Kaatz A, Bringsøe H, Rujirawan A (2024) A new species of the *Cyr*todactylus chauquangensis group (Squamata, Gekkonidae) from the borderlands of extreme northern Thailand. ZooKeys 1203: 211–238. https://doi.org/10.3897/zookeys.1203.122758
- Hoang XQ, Orlov NL, Ananjeva NB, Johns AG, Hoang NT, Dau QV (2007) Description of a new species of the genus *Cyrtodactylus* Gray, 1827 (Squamata: Sauria: Gekkonidae) from the Karst of north central Vietnam. Russian Journal of Herpetology 14: 98–106. https://doi.org/10.30906/1026-2296-2007-14-2-98-106
- Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. Nature Methods 14: 587–589. https://doi.org/10.1038/nmeth.4285
- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology and Evolution 30: 772–780. https://doi.org/10.1093/molbev/mst010

- Kunya K, Panmongkol A, Pauwels OGS, Sumontha M, Meewasana J, Bunkhwamdi W, Dangsri S (2014) A new forest-dwelling bent-toed gecko (Squamata: Gekkonidae: *Cyrtodactylus*) from Doi Suthep, Chiang Mai Province, northern Thailand. Zootaxa 3811: 251–261. https://doi.org/10.11646/zootaxa.3811.2.6
- Le DT, Nguyen TQ, Le MD, Ziegler T (2016) A new species of *Cyrtodactylus* (Squamata: Gekkonidae) from Ninh Binh Province, Vietnam. Zootaxa 4162: 268–282. https://doi. org/10.11646/zootaxa.4162.2.4
- Liu S, Rao DQ (2021) A new species of *Cyrtodactylus* Gray, 1827 (Squamata, Gekkonidae) from Yunnan, China. ZooKeys 1021: 109–126. https://doi.org/10.3897/ zookeys.1021.60402
- Liu S, Rao DQ (2022) A new species of *Cyrtodactylus* Gray, 1827 (Squamata, Gekkonidae) from southwestern Yunnan, China. ZooKeys 1084: 83–100. https://doi.org/10.3897/zookeys.1084.72868
- Liu S, Li QS, Hou M, Orlov NL, Ananjeva NB (2021) A new species of *Cyrtodactylus* Gray, 1827 (Squamata, Gekkonidae) from southern Yunnan, China. Russian Journal of Herpetology 28: 185–196. https://doi.org/10.30906/1026-2296-2021-28-4-185-196
- Liu S, Rao DQ, Hou M, Wang QY, Ananjeva NB (2023) A new species of *Cyrtodactylus* Gray, 1827 (Squamata, Gekkonidae), previously confused with *C. wayakonei* Nguyen, Kingsada, Rösler, Auer et Ziegler, 2010. Russian Journal of Herpetology 30: 529–538. https://doi.org/10.30906/1026-2296-2023-30-6-529-538
- Luu VQ, Nguyen TQ, Do HQ, Ziegler T (2011) A new *Cyrtodactylus* (Squamata: Gekkonidae) from Huong Son limestone forest, Hanoi, northern Vietnam. Zootaxa 3129: 39– 50. https://doi.org/10.11646/zootaxa.3129.1.3
- Ma S, Shi SC, Qian TY, Sui LL, Wang B, Jiang JP (2024) A new species of *Cyrtodactylus tibetanus* group (Reptilia: Squamata: Gekkonidae) from Xizang Autonomous Region, China. Animals 14: 2384. https://doi.org/10.3390/ani14162384
- Macey JR, Schulte 2<sup>nd</sup> JA, Larson A, Ananjeva NB, Wang Y, Pethiyagoda R, Rastegar-Pouyani N, Papenfuss TJ (2000) Evaluating trans-Tethys migration: an example using acrodont lizard phylogenetics. Systematic Biology 49: 233–256. https://doi.org/10.1093/ sysbio/49.2.233
- Nazarov RA, Poyarkov NA, Orlov NL, Nguyen SN, Milto KD, Martynov AA, Konstantinov EL, Chulisov AS (2014) A review of genus *Cyrtodactylus* (Reptilia: Sauria: Gekkonidae) in fauna of Laos with description of four new species. Proceedings of the Zoological Institute RAS 318: 391–423. https://doi.org/10.31610/trudyzin/2014.318.4.391
- Ngo VT (2011) *Cyrtodactylus martini*, another new karst-dwelling *Cyrtodactylus* Gray, 1827 (Squamata: Gekkonidae) from northwestern Vietnam. Zootaxa 2834: 33–46. https://doi.org/10.11646/zootaxa.2834.1.3
- Ngo VT, Chan KO (2011) A new karstic cave-dwelling *Cyrtodactylus* Gray (Squamata: Gekkonidae) from northern Vietnam. Zootaxa 3125: 51–63. https://doi.org/10.11646/ zootaxa.3125.1.4
- Ngo VT, Grismer LL (2010) A new karst dwelling *Cyrtodactylus* (Squamata: Gekkonidae) from Son La Province, northwestern Vietnam. Hamadryad 35: 84–95.
- Nguyen TQ, Kingsada P, Rösler H, Auer M, Ziegler T (2010) A new species of *Cyrtodactylus* (Squamata: Gekkonidae) from northern Laos. Zootaxa 2652: 1–16. https://doi. org/10.11646/zootaxa.2652.1.1
- Nguyen SN, Yang JX, Le TNT, Nguyen LT, Orlov NL, Hoang CV, Nguyen TQ, Jin JQ, Rao DQ, Hoang TN, Che J, Murphy RW, Zhang YP (2014) DNA barcoding of Vietnamese benttoed geckos (Squamata: Gekkonidae: *Cyrtodactylus*) and the description of a new species. Zootaxa 3784: 48–66. https://doi.org/10.11646/zootaxa.3784.1.2.

- Nguyen TQ, Le MD, Pham AV, Ngo HN, Hoang CV, Pham CT, Ziegler T (2015) Two new species of *Cyrtodactylus* (Squamata: Gekkonidae) from the karst forest of Hoa Binh Province, Vietnam. Zootaxa 3985: 375–390. https://doi.org/10.11646/zootaxa.3985.3.3
- Nguyen TQ, Pham AV, Ziegler T, Ngo HT, Le MD (2017) A new species of *Cyrtodactylus* (Squamata: Gekkonidae) and the first record of *C. otai* from Son La Province, Vietnam. Zootaxa 4341: 25–40. https://doi.org/10.11646/zootaxa.4341.1.2
- Pauwels OSG, Sumontha M, Keeratikiat K, Phanamphon E (2014) *Cyrtodactylus kunyai* (Squamata: Gekkonidae), a new cave-dwelling bent-toed gecko from Loei Province, northeastern Thailand. Zootaxa 3821: 253–264. https://doi.org/10.11646/zootaxa.3821.2.5
- Pham AV, Le MD, Ziegler T, Nguyen TQ (2019) A new species of *Cyrtodactylus* (Squamata: Gekkonidae) from northwestern Vietnam. Zootaxa 4544: 360–380. https://doi. org/10.11646/zootaxa.4544.3.3
- Schneider N, Nguyen TQ, Le MD, Nophaseud L, Bonkowski M, Ziegler T (2014) A new species of *Cyrtodactylus* (Squamata: Gekkonidae) from the karst forest of northern Laos. Zootaxa 3835: 80–96. https://doi.org/10.11646/zootaxa.3835.1.4
- Schneider N, Luu VQ, Sitthivong S, Teynié A, Le MD, Nguyen TQ, Ziegler T (2020) Two new species of *Cyrtodactylus* (Squamata: Gekkonidae) from northern Laos, including new finding and expanded diagnosis of *C. bansocensis*. Zootaxa 4822: 503–530. https:// doi.org/10.11646/zootaxa.4822.4.3
- Sumontha M, Panitvong N, Deein G (2010) *Cyrtodactylus auribalteatus* (Squamata: Gekkonidae), a new cave-dwelling gecko from Phitsanulok Province, Thailand. Zootaxa 2370: 53–64. https://doi.org/10.11646/zootaxa.2370.1.3
- Tamura K, Stecher G, Kumar S (2021) MEGA11: Molecular Evolutionary Genetics Analysis version 11. Molecular Biology and Evolution 38: 3022–3027. https://doi. org/10.1093/molbev/msab120
- Tang FL, Du F, Sun GZ (2015) National Nature Reserve of Nangunhe, Yunnan Province Comprehensive Scientific Investigation Research. China Forestry Publishing House, Beijing, 1009 pp.
- Tran TT, Do QH, Pham CT, Phan TQ, Ngo HT, Le MD, Ziegler T, Nguyen TQ (2024) A new species of the *Cyrtodactylus chauquangensis* species group (Squamata, Gekkonidae) from Lao Cai Province, Vietnam. ZooKeys 1192: 83–102. https://doi.org/10.3897/zookeys.1192.117135
- Uetz P, Freed P, Aguilar R, Reyes F, Kudera J, Hošek, J (2024) The Reptile Database. http://www.reptile-database.org [Accessed on: 2024-9-14]
- Wang K, Ren JL, Chen HM, Lyu ZT, Guo XG, Jiang K, Chen JM, Li JT, Guo P, Wang YY, Che J (2020) The updated checklists of amphibians and reptiles of China. Biodiversity Science 28: 189–218. https://doi.org/10.17520/biods.2019238
- Yang YM, Du F (2004) Nangun River National Nature Reserve Of China. Yunnan Science and Technology Press, Kunming, 386 pp.
- Yuan SQ, Rao DQ (2011) A new record of a gekkonid (*Cyrtodactylus wayakonei*) from Yunnan, China. Zoological Research 32: 684–688. https://doi.org/10.3724/ SP.J.1141.2011.06684
- Zhang DR, Shen WJ, Liu S (2024) *Cyrtodactylus hekouensis* is the junior synonym of *Cyrtodactylus gulinqingensis*. Chinese Journal of Wildlife 45: 683–690. https://doi. org/10.12375/ysdwxb.20240329
- Zhao EM, Jiang YM, Huang QY, Zhao H, Zhao KT, Zhou KY, Liu YZ, Liu MY, Li DJ, Zhang YX (1999) Fauna Sinica (Reptilia 2): Squamata (Lacertilia). Science Press, Beijing, 394 pp.
- Zhao EM, Zhang XW, Zhao H, Adler K (2000) Revised checklist of Chinese amphibia & reptilia. Sichuan Journal of Zoology 19: 196–207.



Research Article

# Revision of the Oriental and Australasian diving beetle genus Sandracottus Sharp, 1882 (Coleoptera, Dytiscidae, Dytiscinae)

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#### Abstract

A comprehensive revision is presented of the Oriental and Australasian diving beetle genus Sandracottus Sharp, 1882 (Coleoptera: Dytiscidae: Dytiscinae: Aciliini) and seven junior subjective synonyms are proposed. Sandracottus guerini Balfour-Browne, 1939, syn. nov. is a junior subjective synonym of S. femoralis Heller, 1934; S. manipurensis Vazirani, 1969, syn. nov. of S. hunteri (Crotch, 1872); S. mixtus Blanchard, 1843, syn. nov. of S. chevrolati (Aubé, 1838); and S. angulifer Heller, 1934, syn. nov., S. nauticus Sharp, 1882, syn. nov., and S. palawanensis Satô, 1978, syn. nov. of S. maculatus (Wehncke, 1876). Finally, S. vijayakumari Anand et al., 2021, syn. nov. is a new synonym of S. dejeanii (Aubé, 1838). New status is assigned to S. bakewellii guttatus (Sharp, 1882), stat. nov. as well as S. hunteri (Crotch, 1872), stat. rev. Lectotypes are designated for the following taxa: Dytiscus flavocinctus Guérin-Méneville, 1830, Hydaticus chevrolati Aubé, 1838, Hydaticus insignis Wehncke, 1876, Sandracottus baeri Régimbart, 1899, Sandracottus bizonatus Régimbart, 1899, and Sandracottus ornatus Sharp, 1882. A neotype is designated for Hydaticus maculatus Wehncke, 1876. In total, three Oriental species, two of which also occur in the East Palaearctic, six Southeast Asian species, one species from New Guinea and the Moluccas, and one from Australia with an endemic subspecies in Central Australia (S. bakewellii guttatus) are recognised. Each taxon is presented with a diagnosis, habitat preferences, conservation assessments, distribution data, and a comprehensive bibliography. Important characters (habitus, dorsal colouration, median lobes and parameres) are illustrated. All currently valid taxa are redescribed. Sandracottus jaechi Wewalka & Vazirani, 1975 from Sri Lanka, S. bizonatus from Borneo, S. insignis from the Philippines and S. rotundus Sharp, 1882 from Sulawesi are recommended to be listed in the next IUCN red data book. A key to all species is provided.

**Key words:** Australasia, conservation, Indomalayan region, lectotype designation, neotype designation, new status, new synonymies, systematics, zoogeography

# Introduction

The genus *Sandracottus* Sharp, 1882 belonging to the subfamily Dytiscinae and tribe Aciliini is revised. Most of the species occur in the Indian and Indomalayan regions where the genus represents, together with some members of the genus *Hydaticus*, the most colourful larger predaceous water beetles of the local fauna.



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† Deceased.

To date, 17 species and one subspecies have been recognised from Asia and Australia (see Anand et al. 2021; Nilsson and Hájek 2024).

Sandracottus has not been subjected previously to a comprehensive revision. In this paper each species is presented with a diagnosis and redescription, habitat preferences, conservation assessment, distribution data and a comprehensive bibliography. Important species characters [habitus, dorsal colouration, median lobes and parameres] are illustrated, and finally a key to all species is provided.

The material dealt with in this paper was mainly collected during several field trips between the years 1990 and 2020 by Lars Hendrich and Michael Balke (Munich, Germany), Michel Brancucci † (Basel, Switzerland), Jan Haft (Dorfen, Germany), Andre Skale (Hof/Saale, Germany), Manfred Jäch, Günther Wewal-ka, Helena Shaverdo, Harald Schillhammer (Vienna, Austria), Wisrutta Atthakor (Bangkok, Thailand), Hendrik Freitag (Manila, Philippines), the staff of the Zoological Reference Collection in Singapore (e.g., Yang Chan Man), Paolo Mazzoldi (Brescia, Italy), and Jaroslav Šťastný and Jiří Hájek (Czech Republic) to Iran, India, China, Southeast Asia, New Guinea, and Australia. Furthermore, all historical specimens of *Sandracottus* deposited in the relevant museum and private collections of the world, including most of the type material, were studied for this revision.

The species of *Sandracottus* are lentic and inhabit temporary or semipermanent pools and ponds, often rich in decaying leaves and twigs. Particularly the Indomalayan and New Guinean species are restricted to shaded forest pools or shallow rest pools of intermittent forest streams and springs (e.g., Hendrich 1995; Hendrich and Balke 1995; Balke et al. 2004; Suprayitno et al. 2017; Atthakor et al. 2018; Alarie et al. 2023).

In freshwater management world-wide, the family Dytiscidae proved to be an important biomonitoring group. Many *Sandracottus* species, especially in Southeast Asia, are restricted to lentic habitats in primary or at least old second growth forests. Due to their habitat requirements and limited number of species they represent an ideal target group for environmental impact assessments (EIAs), conservation assessments and biodiversity studies in a wider sense, especially of freshwater habitats at rainforest sites.

# Materials and methods

# Material

This study is based on the examination on the adult stage of 1649 specimens, deposited in institutional and private collections listed below. Type specimens were re-examined for most species. New synonyms were based on comparisons of types.

# Descriptions

Beetles were studied with a Leica MZ 12.5 dissecting microscope at  $10-100\times$ . Male genitalia were studied and figured in dry condition. The terminology to denote the orientation of the genitalia follows Miller and Nilsson (2003).

# Abbreviations used in the text are TL = total length, measurements of length from head to apex of elytra; TL-h = total length minus head length, measurement of length from anterior margin of pronotum to apex of elytra; and TW = maximum width of body measured at right angle to TL. Label data of type material are cited between quotation marks.

# Photographs and illustrations

Images were taken with a Canon EOS 550D camera fitted with either a 65 mm or MPE65 macro lens, attached to a Stackmaster macrorail (Stonemaster: www. stonemaster-onlineshop.de). Illumination was with two Canon Speedlite 430EX III-RT flashlights and translucent paper diffusors or 3 Stonemaster LED-Segments SN-1. Image stacks were assembled using Helicon Focus software (method A) and cleaned using Adobe Photoshop CS6 software.

Coordinates are given in decimal notation unless cited verbatim from labels. Besides various Australian road maps, we also used Google Earth (http://earth. google.com) to locate several localities; our maps are based on "MICROSOFT ENCARTA World-Atlas 2000".

#### Codens

The material used for this study is deposited in the following 34 institutional and private collections:

AM	Australian Museum, Sydney, New South Wales, Australia (C. Reid)			
ANIC	Australian National Insect Collection, Canberra, Australia (T. Weir)			
NHMUK	Natural History Museum, London, England (M. Barclay)			
CAS	Collection André Skale, Gera, Germany			
CGW	Collection Günther Wewalka, Vienna, Austria			
СНН	Collection Hans Hebauer, Rain/Ndb., Germany			
CHF	Collection Hans Fery, Berlin, Germany (property of NMW)			
CJS	Collection Jaroslav Šťastný, Liberec, Czech Republic			
CLH	Collection Lars Hendrich, Berlin, Germany (property of the NMW)			
CLJW	Collection Liang-Jong Wang Taipei, Taiwan			
CLW	Collection Leopold Wendlandt, Greifswald, Germany			
СРМ	Collection Paolo Mazzoldi, Brescia, Italy			
CSUT	Collection Srinakharinwirot University, Thailand (W. Atthakor)			
DEI	Deutsches Entomologisches Institut, Müncheberg, Germany (V. Ferreira)			
HMUG	Hunterian Museum, University of Glasgow, Scotland (G. Hancock)			
NMPC	Národní muzeum, Praha, Czech Republic (J. Hájek)			
MNHN	Muséum national d´Histoire naturelle, Paris, France (H. Perrin)			
MZB	Museum Zoologicum Bogoriense, Cibinong, Indonesia			
NTM	Northern Territory Museum, Darwin, Northern Territories, Australia			
	(G. Dally)			
NMB	Naturhistorisches Museum Basel, Schweiz (M. Borer)			
NMST	National Museum of Nature and Science, Tokyo, Japan (S. Nomura)			
NMV	Museum of Victoria, Melbourne, Victoria, Australia (K. Walker)			
NMW	Naturhistorisches Museum Wien, Vienna, Austria (M.A. Jäch)			

- **QDPIB** Queensland Department of Primary Industries, Brisbane, Queensland, Australia (C. Burwell)
- **RMNH** Nationaal Natuurhistorisch Museum, Leiden, The Netherlands (M. Diekman)
- **QM** Queensland Museum, Brisbane, Queensland, Australia (G. Monteith)
- **SAMA** South Australian Museum, Adelaide, South Australia, Australia (C.H.S. Watts)
- SMTD Staatliches Museum für Tierkunde, Dresden, Germany (O. Jäger)
- **USNM** United States National Museum of Natural History, Smithsonian Institution, Washington, USA (W.E. Steiner)
- TDMB Természettudományi Múzeum, Budapest, Hungary (O. Merkl †)
- WADA Department of Agriculture, Western Australia, Perth, Australia (A. Szito)
- **ZHMB** Museum für Naturkunde, Berlin, Germany (J. Frisch)
- **ZSI** Zoological Survey of India, Kolkata, India (S. Sheela)
- **ZSM** Zoologische Staatssammlung, München, Munich, Germany (M. Balke)
- **ZRC** Zoological Reference Collection, Lee Kong Chian Natural History Museum National University of Singapore, Singapore (W.F. Hwang)

#### **Collecting procedures**

Most of the *Sandracottus* obtained by the authors were collected using heavy aquatic dip nets or kitchen strainers. Diameters of meshes varied from 500 to 1000 mm. Leaf litter, rotten twigs or wood, and aquatic vegetation were swept heavily; the material obtained was then placed on a white nylon sheet (2 m<sup>2</sup>) or in a white plastic box. Specimens were sorted by hand. Referring to the label data, a few specimens of *Sandracottus bakewellii bakewellii* (Clark, 1864), *S. festivus* (Illiger, 1802), *S. femoralis* Heller, 1934, *S. hunteri* (Crotch, 1872) and *S. rotundus* Sharp, 1882 were obtained by operating light traps.

# Taxonomy and systematics

#### Genus Sandracottus Sharp, 1882

**Notes.** Medium-sized (11.9–16.6 mm) oval beetles, black or with contrasting black and yellow markings. Outer margin of metaventral wings arcuate not straight as in *Hydaticus* Leach, 1817. Metacoxal lines obliterated so that no supra-articular border present; mesofemur with longer ventral setae, at least some as long as half width of mesofemur. Spur on metatibia blunt, minutely emarginate at apex. A small genus of 11 species and one subspecies distributed in the Oriental and Australasian realms. The larvae of *S. dejeanii* (Aubé, 1898) was described by Vazirani (1971). All larval instars of *S. hunteri* and *S. femoralis* were described in detail by Alarie et al. (2023).

#### World check list of Sandracottus

Sandracottus bakewellii bakewellii (Clark, 1864) Northern and coastal eastern Australia

#### Sandracottus bakewellii guttatus (Sharp, 1882) Central Australia

= Sandracottus rotundus ab. reductus Zimmermann, 1926

Sandracottus bizonatus Régimbart, 1899 Malaysia: Sabah, Sarawak, Indonesia: Kalimantan

*Sandracottus chevrolati* (Aubé, 1838) Indonesia: Lesser Sunda Islands, Timor, Tanimbar, Central and Southern Sulawesi

= Sandracottus mixtus (Blanchard, 1853) (syn. nov.)

Sandracottus dejeanii (Aubé, 1838) India, Nepal, Pakistan, Myanmar, E Iran

= Sandracottus vijayakumari Anand et al. 2021 (syn. nov.)

*Sandracottus femoralis* Heller, 1934 Indonesia: Moluccas, Irian Jaya; Papua New Guinea, Solomon Islands

= Sandracottus flavocinctus (Guérin-Méneville, 1830)

= Sandracottus guerini Balfour-Browne, 1939 (syn. nov.)

Sandracottus festivus (Illiger, 1802) China (?), India, Bhutan, Sri Lanka, Pakistan

*Sandracottus hunteri* (Crotch, 1872) India, Nepal, China, Korea, Vietnam, Laos, Myanmar, Thailand, Cambodia, West Malaysia, Indonesia: Sumatra, Java, Bali

- = Sandracottus fasciatus (Fabricius, 1775)
- = Sandracottus fasciatus var. crucialis Régimbart, 1899
- = Sandracottus manipurenis Vazirani, 1969 (syn. nov.)

*Sandracottus insignis* (Wehncke, 1876) Philippines: Palawan, Luzon, Mindanao, Malaysia: Sabah (?)

- = Sandracottus baeri (Régimbart, 1877)
- = Sandracottus insignis ornatus Sharp, 1882) (syn. nov.)

Sandracottus jaechi Wewalka & Vazirani, 1975 Sri Lanka: Nuwara Eliya

*Sandracottus maculatus* (Wehncke, 1876) Thailand, Vietnam, Laos, Cambodia, Malaysia: Sabah; Indonesia: Sumatra, Java, Kalimantan; Philippines: Mindanao

- = Sandracottus wehnckei J. Balfour-Browne, 1944
- = Sandracottus angulifer Heller, 1934 (syn. nov.)
- = Sandracottus palawanensis Sato, 1978 (syn. nov.)
- = Sandracottus nauticus Sharp, 1882 (syn. nov.)

#### Sandracottus rotundus Sharp, 1882 Indonesia: Sulawesi

#### Descriptions

Sandracottus bakewellii bakewellii (Clark, 1864) Figs 1, 12, 23, 31, 32, 46

- *Hydaticus bakewellii* Clark, 1864: 210 (type locality Moreton Bay, Queensland, Australia).
- Sandracottus bakewellii (Clark, 1864): Sharp 1882: 687 (descr.); Régimbart 1899: 336 (descr.); Zimmermann 1920: 234 (cat.); Watts 1978: 148 (descr.); Watts 1985: 26 (cat.); Lawrence et al. 1987: 356 (cat.); Larson 1993: 59 (faun., ecol.); Larson 1997: 273 (faun., ecol.); Hendrich et al. 2019: 46 (faun., ecol., tax.); Hájek and Nilsson 2024: 91 (cat.).

**Type material.** *Lectotype*: Male, "Lectotype", "Type, 6756", "Bakewelliii", "Hydaticus bakewellii Clk. Det. C. Watts 1979" (NHMUK). *Paralectotypes*: 1 female, "Moreton Bay", "Sandracottus bakewellii Clk", "Bakewellii Clark Moreton Bay", "Syntype" (NHMUK); 1 male, "Moreton Bay", "Bowring 6347\*", "Syntype" (NHMUK); 1 male, "Nova Holland.", "Syntype" (NHMUK). Examined.

Additional material. (183 specimens): AUSTRALIA. • Northern Territory: 1 ex., "N. Queensland Bloomfield River" (ZHMB); 2 ex., "Moreton Bay" (NHMUK) 1 ex., "Darwin, N.T., 1930" (MNHN); 1 ex., "Northern Austr." (MNHN); 1 ex., "Northern Territory, F.E.Wilson coll." (without further data) (VIC); 1 ex., "Tindal, 7.XI.1967, W.J.M. Vestjens leg." (ANIC); 1 ex., "Northern Territory, A.H. Elston collection" (AM); 1 ex., "Burrells Creek, 17 miles S Adelaide River, 7.IV.1971, T. Weir leg." (NTM); 1 ex., "Edith Falls, in pool, 23.VIII.1982, G. Allen & B. Russell leg." (NTM); 1 ex., "Adelaide River Hills, 24 km N Robin Falls turn off, in pool, 17.X.1982, G. Husband leg." (NTM); 3 exs., "Australia, Northern Territory, Katherine Gorge, Butterfly Gorge Walk, 150 m, 4.VII.1999, Hendrich leg., Loc. 33/133" (CLH); 1 ex., "Northern Territory, Burnside Stn., Brocks Crk., 25.VIII.1932, 25-018562, S 13.46.667 E 131.41.67, T.G. Campbell leg." (ANIC); 1 ex., "Australia NT, 23 km S Adelaide River, permanent creek at Scenic Route, 137 m, 22.VIII.2006, 13.26.593S 131.11.012E, L. & E. Hendrich leg." (NT 9) (ZSM). • Queensland: 1 ex., "Toowong District N. Queensland OE Janson sons" (USNM); 1 ex., "Rockhampton Sub. Distr. S.F.R. 5 Cpt. L.A. 17. VIII.1976 R.A. Yule Dept. For. Qld/ Acc. 1241/15", "QFIC specimen incorporated into QDPC March 2010" (QDPIB); 1 ex., "Gayndah QLD 17.II.1963 H.A.Rose" (QM); 1 ex., "Mt. Glorious Q. 7.III.1959 K. Korboot" (QM); 1 ex., "Brisbane 6.X.1963 I.R. Bock" (QM); 7 exs., "Moolyamba Creek 9.V.1948 J.L.Wassell" (QM); 1 ex., "N Queensland, Cooktown, Eichhorn" (MNHN); 4 exs., "Rockhampton (Australie), Thoret 1870" (MNHN); 2 exs., "Dawson district, Barnard coll." (MNHN, NMB); 2 exs., "Coll. French Queensland" (MNHN, RMNH); 2 exs., "Hydaticus bakewellii Clk Type mihi D.S. [David Sharp] Queensland 983" (NHMUK); 1 ex., "Bagot Creek" [SE Queensland, West of Dalby] (AUS); 1 ex., "Nova Holland Moreton Bay" (NHMUK); 1 ex., "Brisbane" (AM); 1 ex., "Brisbane Mt. Cootha 14.XI.1939 D 714" (QDPIB); 1 ex., "Brisbane" (NHMUK); 1 ex., "Rockhampton" (NHMUK); 2 exs., "Townsville" (MNHN); 2 exs., "Carnavon Gorge 26.I.1982 J.Sedlacek leg." (NMB); 1 ex., "North Queensland Mutchilba A.D. Selby leg., F.E. Wilson coll." (VIC); 1 ex., "Emu Creek pot hole 19.X.1940 J.Dewaney leg." (VIC); 2 exs., "Rollingstone S.R.E. Brock Collection" (ANIC); 12 exs., "Bouldercome, 14.V.1966", "A.N. C.G.L.Gooding Collection



Figures 1–3. Habitus of 1 Sandracottus bakewellii bakewellii (Northern Territory, Australia) 2 S. bizonatus (Borneo, Sabah, Kinabalu) 3 S. chevrolati (Sumba Island, Indonesia).

donated to ANIC 1979" (ANIC); 6 exs., "NW Queensland 28 N by E of Musselbrook Mining Camp Amphitheatre Springs S 18.21 E 138.11 12.V.1995 T. Weir leg." (ANIC); 1 ex., "North Queensland Eungella NP Broken River 31.VIII.-8. IX.1998 Neave Edwards Powell Sutrisno & Hebbard leg." (ANIC); 1 ex., "North Queensland 45 km N Aurukun 25.II.1981 M.Robinson leg." (AM); 1 ex., "Mt. Carbine T.W.Gamble leg." (AUS); 1 ex., "Queensland Carmila North coast Lancel. 1928 N. McArthur leg." (AM); 2 exs., "Blackall River F. Witteron leg." (QDPIB); 1 ex., "Highlands 4 km S Emmet, S 24°57'E 144°26′, 19.IV.2002, ex spring, sandstone gully, R.J.Felsham leg. (8951)" (QM); 4 exs., "N Queensland W. Cape York Peninsula Brown Creek pond VI.1982 P.Saenger leg." (QM); 1 ex., "near Mt. Molloy, Rifle Creek 3.I.1990 ANZSES Expedition" (QM); 1 ex., "ME Queensland, Blackdown Tableland Stoney Creek via Dingo at light 17–19.XII.1985 S.Hamlet leg." (QM); 1 ex., "N Queensland, White Mts. NP 2 km NE of RGSQ/AG Base Camp S 20.26 E 144.51 5–7.IV.2000, deep rocky pool, cloudy, sandy bottom,

vegetation, half shade, T.Weir leg." (ANIC); 2 exs., "N Queensland White Mts. NP, 53 km NE Prairie IX.1995, D.J.Cook leg." (QM); 2 exs., "C Queensland Mt. Abbott summit area S 20°06', E 147°45', 750-1000 m, 8-10.XII.1996, G.Monteith & D.J.Cook leg." (QM); 2 exs., "Watsonville 10 km W Herberton 9.XII.1990 D.J. Larson leg." (ANIC, QM); 2 exs., "Brisbane 30.IV.1912 H. Hacker" (QM); 3 exs., "Sutton Collection, donation December 1964" (QM); 1 ex., "Queensland", "coll. Felsche Geschenk 1907", "Sandracottus bakewellii det. Gschwendtner" (SMTD); 1 ex., "near Collins, Catherine Creek, 20.XI.1990, T.Weir leg." (ANIC); 1 ex., "Lake Mitchell 40 km N Mareeba 21.IX.1990 D.J.Larson leg." (ANIC); 1 ex., "SE Mt. Carbine Saddle Bag Creek 15.XI.1990 D.J.Larson leg." (ANIC); 3 exs., "Australia Queensland Atherton Tableland 30 km NNW Mareeba near Mitchell lake 9.XI.1996 Hendrich leg." (CLH); 1 ex., "Julatten 11.IV.1984 at light, K.& E. Carnaby leg." (ANIC); 1 ex., "North Queensland Julatten 2.IV.1977 Walford-Huggins leg." (CLH); 1 ex., "Queensland Brisbane I. 1931" (CLH); 1 ex., "Mareeba Road, Clohesy River Road, I.1974, A. & M. Walford-Huggins" (CLH); 1 ex., "Hell Hole Gorge NP, S 25.34 E 144.11, X.1997, at light in open forest T.Weir leg." (ANIC); 1 ex., "N Queensland, Coen River 1 km E of Rokeby Mungkan Kandju River, at light, S 13.39 E 142.41, 22.VII.1998, A.A.Calder leg." (ANIC); 9 exs., "North Queensland, Cape Tribulation 26.-27.XII.1969 leg. G. Hangay" (CLH, TDMB); 1 ex., "Queensland", "Coll. Franklin Müller", "Sandracottus bakewellii det. A. Zimmermann" (DEI); 1 ex., "Queensland, Wallaroo, 17.I.1968, G. Hangay" (CLH); 12 exs., "Northern Queensland, Silver Valley, Samml. A. Zimmermann (ZSM); 1 ex., "Silver Valley N. Queensl. III", "Coll. Gärtner", "Sandracottus bakewellii Clark" (DEI); 2 exs., "Queensland", "Coll. Franklin Müller" (ZSM); 1 ex., "Queensland Archer River 28.VII.1992 S 13.55 E 143.05 Zborowski, P. & Nielsen, E.S." (ANIC); 1 ex., "Queensland, Brisbane (general), I.1931, S 25.01.856 E 27.46.667, 153.0333, A Misko, S. leg." (ANIC); 2 exs., "Queensland, Mary Creek, S 16.33 E 145.12.5 at light 4.XII.1968 E.B.Britton & S.Misko leg." (ANIC); 1 ex., "Queensland Calliope River 23 km SE of Gladstone [approx. 23 km SW of Gladstone] 23.I.1970, at light, S 23.83.333 E 151.21.67 S.Misko leg." (ANIC); 5 exs., "S QLD, 40 km E Bundaberg, Tusky Creek, 9 m, 26.IX.2006, 24.39.139S 152.01.477E, L. & E. Hendrich leg. (QLD 52)"; 5 exs., "S QLD, Winfield, Winfield Road, forest pool, 21 m, 26.IX.2006, 24.34.084S 152.00.513E, L. & E. Hendrich leg. (QLD 54)" (ZSM, CLH); 3 exs., "NH [= Neuholland] Coll. Plason" (NMW); 2 historical specimens leg. Bauer! [beginning of 19th century, without any detailed locality data, Jäch pers. comm. 2010]. • Western Australia: 1 ex., "Kununurra, Cave Springs, ex. pool 9.X.1966" (WADA); 3 exs., "Kimberely Research Station, 16.II.1959, K.T.Richards leg." (WADA); 3 exs., "130 miles SE of Broome, 15.IX.1924, A.S.Cudmore leg." (VIC); 2 exs., "Kimberley district N.V. Mjöberg", "Samml. A. Zimmermann" (ZSM); 1 ex., "Australia occ." [= Western Australia] Lea leg.", "Sandracottus bakewellii Clark Dr. F. Guignot det." (TDMB); 3 exs., "Western Australia, 163 km SE by E Broome 5.VIII.1976 Common I.F.B. leg." (ANIC); 2 exs., "Western Australia, King Sd" [King Sound, area around Derby] (ANIC). • Unknown states: 1 ex., "Australia", "Coll'n J.D. Sherman Jr. 1926" (USNM); 2 exs., "Australie" (MNHN); 1 ex., "Australia 7642" (NHMUK); 2 exs., "Australia Blackburns Collection", "Sandracottus guttatus identified by L.A. Lea" (AUS); 4 exs., "Mootwingie 15.IX.195" (AUS). • Doubtfull records: 1 ex., "Victoria" (MNHN); 1 ex., "S. West Australia" (MNHN); 2 exs., "Museum Paris Tasmanie Verreaux 3-47" (MNHN).



Figures 4–7. Habitus of 4 Sandracottus dejeanii (South India) 5 S. festivus (Sri Lanka) 6 S. femoralis (Papua New Guinea, Rigo) 7 S. hunteri (Thailand).

Redescription. Body broad oval, shiny testaceous with dark brown markings.
Ventral side completely ferrugineus brown except testaceous fore and mid legs. Head testaceous with posterior part broadly black; black part prolonged along eyes and protruding on frons. Surface shiny, very superficially shagreened.
Punctation consisting of dense punctures, irregular in size and of larger and much sparser ones; these more numerous on frons. Clypeal grooves and punctures alongside eyes present, punctures medium-sized and coalescent. Antennae testaceous; antennomeres slender, antennomere V 5× as long as broad.

Pronotum testaceous with median black marking reaching from posterior to anterior margin; long and broad on posterior, distinctly shorter and narrower on anterior margin and strongly constricted in middle. Surface very slightly and superficially shagreened, with very dense punctation; punctures medium-sized not constant in size, distance 2–3× that of their diameter. Anterior rows of punctures interrupted in middle, punctures large and coalescent. Posterior row of punctures medially with large and coarsely impressed punctures in middle.

Elytra shiny, black, with larger basal, subbasal and apical elytral markings (Fig. 1). Epipleura ferrugineus brown. Surface distinctly shagreened and covered with small and dense punctures and with larger and much sparser ones.





Puncture lines with groups of medium-sized punctures mostly grouped by five or six punctures; discal row almost complete. Sutural puncture line marked only by few punctures.

Ventral side dark brown. Fore and mid legs testaceous, hind legs ferrugineus brown to dark brown. Prosternal process short and broad, 1.6× longer than broad, finely but distinctly sculptured; posterior margin broadly rounded. Metatibia with sparse medium-sized to large punctures on outer proximal part. Ventrites II–VI very superficially shagreened, distinctly longitudinally wrinkled on whole lateral parts, densely covered with very small punctures and larger and sparser ones. Posterior margins rounded, deeply bordered with a row of large and coalescent punctures in middle of each side alongside margin.

Measurements: TL = 13.5-14.5 mm, TL-h = 12.5-13.5 mm, TW = 8.0-9.0 mm.  $\bigcirc$ . Protarsomeres I–III strongly enlarged with three larger suckers and numerous smaller one. Mesotarsomeres I–III with two rows of small suckers. Median lobe of aedeagus in ventral view broadened in apical third, then tapering towards apex (Fig. 12a). Parameres elongate and pointed at apex (Fig. 12b).

 $\mathbb{Q}.$  Similar to male. Tarsomeres not enlarged. Microsculpture on ventrite VI as in male.

**Differential diagnosis.** Colour of dorsal surface and shape of the median lobe distinguish *S. bakewellii* from all other species of the genus. It is the only





species which occurs in Australia. The subspecies *S. bakewellii bakewellii* can be separated from *S. bakewellii guttatus* by the broader and not interrupted yellowish anteromedian, posteromedian and preapical markings (Figs 46, 47).

**Distribution.** Northern Australia, east coast from Northern Queensland south to Brisbane (Fig. 23). Specimens were collected from near sealevel to 1000 m a.s.l.

**Habitat.** Sandracottus bakewellii inhabits large (0.5 m depths or more) pools of seasonal streams and creeks, spring fed pools often with dark or gloomy water. The adults are generally found amongst tangles of roots and in places where the water is shaded. Habitats are often enriched with dead leaves and twigs (Figs 31, 32).

# Sandracottus bakewellii guttatus Sharp, 1882, stat. nov.

Figs 23, 33, 47

- Sandracottus guttatus Sharp, 1882: 688 (type locality: Adelaide (?) [most probably mislabelled], South Australia, Australia); Régimbart 1899: 337 (descr.); Zimmermann 1920: 234 (cat.); Watts 1978: 148 (syn.); Hájek and Nilsson 2024: 91 (cat.).
- Sandracottus rotundus ab. reductus Zimmermann, 1926: 97 (misidentification, infrasubspecific name).

**Type material.** *Lectotype*: Male, "Australia ? Adelaide 984 guttatus", "Lectotype", "Sharp Coll. 1905-313.", "Sandracottus guttatus Sharp Det. C.Watts 1979" (NHMUK). *Paralectotype*: Female, "Carpentaria 984", "Paralectotype", "Sharp Coll. 1905-313.", "Sandracottus guttatus Sharp Det. C.Watts 1979" (NHMUK). Examined.

Sandracottus rotundus ab. reductus Zimmermann, 1926: 1 female, "Burg Station I 10.II.-16.III.1921, L.J.Toxopeus", "Type", "ab. reductus Zimmerm" [handwritten by Zimmermann] (ZSM). This specimen clearly belongs to *S. bakewellii* guttatus. Toxopeus has collected it at a cattle station [Burg Station], somewhere in Central Australia. Examined.

Additional material. (63 specimens): AUSTRALIA. • Northern Territory: 1 ex., "N. Territory, S. Aust.", "Coll. Kraatz" "Zimmermann det." (DEI); 2 exs., "Moreton Bay" [doubtful record] (NHMUK); 1 exs., "Moreton Bay", "guttatus Shp" [handwritten label by Régimbart but doubtful record] (MNHN); 2 exs., "Ormiston Gorge, X.1972, M. Baehr leg." (ZSM, CLH); 6 exs., "Tallipatta Gorge, 20.VII.1947, C.W. Brazenov leg." (VIC); 2 exs., "Hart Range C. Barrett leg., F.E. Wilson coll." (VIC); 3 exs., "Central Australia Collection Horn Expedition, VII.1897" (VIC); 3 exs., "Illamurta Springs Conservation Reserve, small temporary rock pool, sandy bottom, S 24.19 E 132.41, 16.III.1995, T. Weir leg." (ANIC); 1 ex., "Finke Gorge NP, temporary pools above old Ranger Station, 12.III.1995, T. Weir leg." (ANIC); 2 exs., "Finke Gorge NP, gorge W of Finke River, permanent and temporary rock pools, algal growth and detritus, S 24.08 E 132.51, 15.III.1995, T. Weir leg." (ANIC); 2 exs., "Finke Gorge NP, Palm Valley, small temp. pools, rocky, some sandy base, algal growth, detritus, S 24.03 E 132.43, 14.III.1995, T.Weir leg." (ANIC); 3 exs., "45 km W of Alice Springs, Standley Chasm S 23.43 E 133.28 5.XI.1979, T.Weir leg." (ANIC); 6 exs., "38 km SSE of Alice Springs S 24.01 E 134.01 7.XI.1979, T.Weir leg." (ANIC); 1 ex., "60 km S of Alice Springs Ooraminna rockhole S 24.05 E 134.00 9.IV.1981 M. Malipatil & J. Hawkins leg." (NTM); 1 ex., "60 km S of Alice Springs, Ooraminna rockhole, 24.05 S 134.00 E, 25.VII.1976, G. Griffin leg." (NTM); 2 exs., "80 E of Alice Springs, Standley Chasm 26.III.1979 G. Griffin leg." (NTM); 5 exs., "Alice Springs Old Huckitta Homestead, 20.VII.1970, D. Nelson leg." (NTM); 2 exs., "Alice Springs, Valley of the Eagles, 14.II.1971 N.T.M.B. D. Nelson leg." (NTM); 1 ex., "Tallaputta Gorge, 7.IX.1958" (NTM); 1 ex., "Kings Canyon George Gill Range 25.-26.III.1983 at light I. Archibald leg." (NTM); 3 exs., "Kings Canyon, George Gill Range 24.V.2006 C.H.S. Watts leg." (ZSM, SAMA); 2 exs., "Northern Territory, nr. Reedy Rockhole Amadeus Basin 12.IX.1962 25-018565, -24.33333,131.5833, P. Ranford leg." (ANIC); 5 exs., "Northern Territory Standley Chasm 43 km W by S of Alice Springs, 11.X.1972, 25-018569,-23.71667, 133.4667 M.S. Upton leg." (ANIC). • Western Australia: 12 exs., "Rawlinson Range 22.VII.1967 K.J. Richards leg." (WADA).



Figures 16–19. Median lobe of aedeagus in ventral view (a), and right paramere in lateral view (b): 16 Sandracottus festivus 17 S. femoralis 18 S. hunteri and 19 S. insignis.

**Comments on classification.** Specimens with reduced yellow basal, subbasal and apical elytral markings or almost completely black elytra and pronotum (Fig. 47) have been described as *Sandracottus guttatus* Sharp, 1882 but were later synonymised with *S. bakewellii* by Watts (1978). Despite the fact that they are genetically (cox 1) and morphologically identical with specimens from coastal northern and eastern Australia, they have a very restricted distribution in the ranges and gorges of Central Australia, and no intermediate forms are known so far. We propose subspecific rank for the population from Central Australia.

The form described by Zimmermann as "ab. *reductus*" also refers to such a dark specimen with reduced yellow elytral markings.

**Distribution.** Central Australia (e.g., Macdonnell Ranges, Finke Gorge, Rawlinson Range) (Fig. 23).

**Differential diagnosis.** The subspecies *S. bakewellii guttatus* can be separated from *S. bakewellii bakewellii* by less expanded and interrupted yellowish antemedian, postmedian and preapical yellow markings on elytra (Figs 46, 47).

**Habitat.** Sandracottus bakewellii guttatus inhabit more or less permanent pools of seasonal streams and creeks, and spring fed pools. The adults are generally found in places where the water is shaded. Habitats are often enriched with dead leaves and twigs (Fig. 33).

**Conservation.** An isolated subspecies with a very small range which needs special conservation attention as surface water in this area is very limited.

#### Sandracottus bizonatus Régimbart, 1899

Figs 2, 13, 24, 48

Sandracottus bizonatus Régimbart, 1899a: 336 (type locality Malaysia, Sabah); Zimmermann 1920: 234 (cat.); Hájek and Nilsson 2024: 91 (cat.).

**Type material.** *Lectotype* (herewith designated): Male, "Borneo Sandakan Windrath" [white printed label], "bizonatus Reg." [handwritten label by Régimbart], "Lectotype Sandracottus bizonatus Régimbart Hendrich & Brancucci des." [red printed label] (MNHN). Examined.

Additional material. (45 specimens): MALAYSIA. · Sabah: 1 ex., "Borneo, Sabah Ranau, 4.v.2006 Steven Chew NHMUK 2006-36" (NHMUK); 1 ex., "E. Malaysia, Sabah Borneo, Mt. Trus March-April 2010 Local leg.", "coll. A. Skale Hof/ Germany" (CAS); 5 exs., "Nord Borneo Mt. Kina-Balu 5.VIII.1903 John Waterstradth" (MNHN); 2 ex., "Kinabalu Borneo" (MNHN); 1 ex., "N. Borneo, Kinabalu" (MNHN); 8 exs., "v.d. Does de Beye, Malakka" (RMNH); 1 ex., "Borneo, H.E. Andrewes Bequest. B.M. 1922-221" (NHMUK); 1 ex., "Kina Balu" (MNHN); 2 exs., "N. Borneo Mt. Kina Balu 5. VIII. 1903 J. Waterstradt leg." (MNHN); 1 ex., "Borneo, Sabah Mt. Kinabalu 3000f, 21.IV.1929 ex H.M. Pendlbury Collection" (CGW); 1 ex., "Borneo Kinabalu 1500 m H.Bolle Berlin SW11" (MNHN); 1 ex., "Borneo, Sabah, Tibow, 45 km NE of Sapulut, 600-900 m, 7.-15.IV.2000, Bolm leg." (NMB); 1 ex., "Borneo, Sabah, Kampung Pisang, Pisang env., tributary of Kuamut river, 29.VI.1998, J.Kodada & F.Ciampor leg." (NMW); 1 ex., "Sabah, Borneo env. Keningau V.1993" (CLH); 2 exs., "Nord Borneo", "Samml. A. Zimmermann" (ZSM); 2 exs., "Kinabalu Nord Borneo", "Samml. A. Zimmermann" (ZSM); 5 exs., "Kinabalu Borneo 1500 m", "Samml. A. Zimmermann" (ZSM); 1 ex., "Nordost Borneo Gebrüder W. Müller Vermächtnis 1909" (SMTD); 1 ex., without locality label, "Sandracottus bizonatus Gschwendtner det." (SMTD). • Sarawak: 1 ex., "Sarawak, Kapit distr., Rumah Ugap vill., Sut river, 3.-9.III.1994, J.Horák leg." (NMW); 4 exs., "Sarawak, Bario env., Pa Ukat, 24.VI. 2003, J. Šťastný lgt." (CJS); 2 exs., "Sarawak, Kelabit, Bario env. 21.-25.VI.2003, J. Šťastný lgt." (CJS).

**Redescription.** Body broad oval, shiny, reddish brown with broad black markings on elytra (Figs 2, 48). Ventral side completely dark brown to black, legs testaceous, hind legs somewhat darker.





Figures 20–22. Median lobe of aedeagus in ventral view (a), and right paramere in lateral view (b): 20 Sandracottus jaechi 21 S. maculatus and 22 S. rotundus.

Head ferrugineus with posterior part broadly black, shiny. Black band protruding forwards to frons. Surface almost smooth consisting of dense and very numerous punctures of different sizes and of larger, much sparser ones, particularly numerous on frons. Clypeal grooves, punctures alongside eyes and transverse depressions beside eyes distinctly impressed, punctures large and coalescent. Antennae ferrugineus; antennomeres slender, fifth 4× as long as broad. Pronotum ferrugineus with large median black marking reaching from posterior to anterior margins (Figs 2, 48). Surface shagreened, with dense punctation; punctures medium-sized mixed with smaller ones. Anterior and lateral puncture rows dense and coalescent, punctures becoming sparse towards middle and lacking in very middle of anterior margin. Posterior row of punctures with coarse and coalescent punctures in middle of each side, distinctly smaller and spaced on disc.

Elytra ferrugineus brown with black and broad markings consisting of three transverse bands (Figs 2, 48); an antemedian one, a postmedian one and a preapical one. Epipleura ferrugineus brown. Surface of elytra very slightly and superficially shagreened and with double punctation, a smaller and dense punctation as well as a larger one much more sparsely distributed. Row of punctures with groups of medium-sized punctures mostly grouped in five or six punctures, groups closer together on discal row.

Ventral side dark brown. Fore and mid legs particularly testaceous, hind legs ferrugineus brown to dark brown. Prosternal process short and broad, 1.5× longer than broad, flattened finely but distinctly sculptured; posterior margin broadly rounded. Whole surface very superficially shagreened and finely punctured. Metatibia with sparse medium-sized punctures on outer half. Ventrites II–VI very superficially shagreened, slightly and longitudinally wrinkled on lateral parts, on whole surface densely covered with very small punctures and larger and sparser ones. Posterior margins rounded, bordered with some large and coalescent punctures in middle of each side.

Measurements: TL = 12.5-13.0 mm, TL-h = 11.4-12.2 mm, TW = 8.5-9.0 mm.  $\bigcirc$ . Protarsomeres I–III strongly enlarged with three larger suckers and numerous smaller one. Mesotarsomeres I–III with two rows of small suckers. Median lobe of aedeagus, in ventral view, broad, parallel-sided up to apex where



Figure 23. Distribution of Sandracottus bakewellii bakewellii [black dots] and S. bakewellii guttatus [red squares] in Australia.



Figure 24. Distribution of Sandracottus bizonatus [red squares] and S. maculatus [black dots] in Southeast Asia.

it is slightly broadened and broadly rounded (Fig. 13a). Parameres broad, same length as median lobe, and pointed at apex (Fig. 13b).

 $\mathbb{Q}.$  Similar to male, tarsi not enlarged. Microsculpture on ventrite VI as in male.

**Differential diagnosis.** The combination of dorsal colour pattern (Figs 2, 48) and shape of median lobe of aedeagus and parameres (Fig. 13a, b) separates *S. bizonatus* from all other species of the genus. The species is endemic to Borneo and co-occurs with *S. maculatus*.

**Distribution.** Malaysia (Sabah, Sarawak) (Fig. 24). The eight specimens deposited in RMNH from Malacca are most probably mislabelled. According to a photo on a website from an insect dealer in Indonesia, the species was also collected in Kalimantan (https://www.giradis-insect.com/ 27.9.2024). Specimens were collected between 300 and 1.500 m a.s.l.

**Habitat.** Muddy and shaded forest pools, rich in rotten leaves and more permanent side pools of larger forest streams in primary rainforests, partly shaded and enriched with rotten leaves and twigs (J. Kodada and J. Šťastný, pers. comm. March 2013).

**Conservation.** A rare and highly endemic species of Borneo, probably associated with the declining primary lowland and hilly rainforests on the island (see Southeast Asian species S. *femoralis*, S. *insignis*, S. *maculatus* and S. *rotundus*). Most records are from the end of the 19<sup>th</sup> and the beginning of the 20<sup>th</sup> century. According to present knowledge it is an endangered species. It is recommended to be listed in the next IUCN red list.

#### Sandracottus chevrolati (Aubé, 1838)

Figs 3, 14, 25, 49

Hydaticus chevrolati Aubé, 1838: 164 (type locality Timor, Indonesia).

Sandracottus chevrolati (Aubé, 1838): Régimbart 1899: 334 (descr.); Zimmermann 1920: 234 (cat.); Hájek and Nilsson 2024: 91 (cat.).

*Hydaticus mixtus* Blanchard, 1843: plate 4, fig. 2 (type locality Timor, Indonesia) (syn. nov.).

**Comments on classification.** The verbal description of *H. mixtus* was published by Blanchard (1853). However, before the publication of the text, the colour plates to this book were published separately during the years 1842–1854 (see Clark and Crosnier 2000). Therefore, the plates must be considered as the original description (ICZN 1999: Article 12.2.7). *Sandracottus mixtus* was regarded as a junior subjective synonym of *Dytiscus fasciatus* Fabricius, 1775 (= primary homonym of *Dytiscus fasciatus* DeGeer, 1774) by Vazirani (1969). However, Vazirani mentioned that he had no possibility to see the type or the original description of that species. Although we did not see the type specimen of *H. mixtus*, the figure which serves as the original description is very accurate and refers without any doubt to the species described by Aubé (1838) under the name *H. chevrolati*. In addition, the type locality of both species is the same (Timor), and we are not aware of any records of *Sandracottus fasciatus* [= hunteri] east of the Wallace's line. Therefore, we consider *Hydaticus mixtus* as a junior subjective synonym of *H. chevrolati*.

**Type material of** *Hydaticus chevrolati. Lectotype* (herewith designated): Male, "Timor" [handwritten label], "typus" [handwritten label] "Lectotype Hydaticus chevrolati Aubé des. L. Hendrich & M. Brancucci 2010" [red printed label] (MNHN). *Paralectotype*: Female, "Timor" [handwritten label], "Paralectotype Hydaticus chevrolati Aubé des. L. Hendrich & M. Brancucci 2010" [red printed label] (MNHN). Examined.

Type material of S. mixtus. Not examined.

Additional material. (157 specimens): INDONESIA: · Lombok: 1 ex., "Indonesia: N Lombok, Senaru waterfall, alt. m. 0470, 13.x.1991, Huijbregts, Krikken" (RMNH). · Pantar: 2 exs., "Indonesia, Lesser Sundas, Pantar Isl, east coast, Tanah Labnag env., 350 m, S.Jakl leg. 9.-21.iii.2006" (NMPC). • Sumba: 7 exs., "O. Sumba Prai Jawang Rende Wai 14.7.1949 Dr. Bühler Dr. Sutter" (NMB); 1 ex., "W. Sumba Mata Kori Waimangura 23.8.1949 Dr. Bühler Dr. Sutter" (NMB); 1 ex., "W. Sumba Baing 30.6.1949 Dr. Bühler Dr. Sutter" (NMB); 1 ex., "O. Sumba Mau Maru 18.7.1943 Dr. Bühler Dr. Sutter" (NMB); 1 ex., "O. Sumba Kodi 8.8.1949 Dr. Bühler Dr. Sutter" (NMB); 1 ex., "O. Sumba Melolo 28.Mai 1949 Dr. Bühler-Dr. Sutter" (NMB); 1 ex., "Indonesia, Lesser Sundas Sumba East, 10-20.6.2006, Luku Melolo N.R., 300-500 m, S. Jakl leg." (CLH); 2 exs., "Sumba East, Melolo env., Luku Melcio, 300-600 m, 7.-9.II.2001, P. Votruba leg." (CJS); 2 exs., "Sumba Island mer., Tarimbang env., 0-100 m, 2.II.-3.II.2001, S.Jákl leg." (NMPC); 2 exs., "East Sumba 550 m, Luku Melolo N.R. 1.-10.7.2005" (CLH); 1 ex., "Sumba Island or., Mt. Wangameti, Kanangar env., 600-800 m, 10.II.2001, S. Jákl leg." (NMPC); 11 exs., "Indonesia, East Sumba, 20 km S of Waingapu Wairinding, 300 m, 30.I.-2.II.2001, P.Votruba leg." (CLH, NMPC). · Sumbawa: 33 exs., "Sumbawa, Dompu-Empang, restpools, 90 m, 15.ix.2011, 08 35.563S 118 17.454E (SUMB06)"



Figure 25. Distribution of Sandracottus chevrolati in Indonesia.

(MZB, ZSM); 1 ex., "Sumbawa" (MNHN); 2 exs., "Savu I. [=Savu Island] Viii 96 Hvereti" (MNHN); 3 exs, "Museum Paris Coupang Hombron 1841" (MNHN); 7 exs., "Sumbawa Colffs.", "Ex. Musaeo Van Landsberge" (MNHN); 1 ex., "Sumbawa" (MNHN); 2 exs., "v.Lansb., Sumbawa" (RMNH); 1 ex., "Sumbawa, 56993, Fry Coll. 1905-100" (NHMUK); 2 exs., "Sumbawa" (MNHN); 1 ex., "Indonesia, W-Sumbawa, Batoe Doelang, 10.-15.V.1927, B.Rensch" (CGW). • Flores: 2 exs., "Indonesia, Flores, Rinca, V.1990, C.H.S. Watts leg." (CLH, SAMA). • Tanimbar: 6 exs., "Indonesia, Tanimbar Yamdema isl., Lorulun, 20 km NE of Saumlaki, 150 m, 26.11.-4.12.2006, M Oboril Igt." (CLH, ZSM); 2 exs., "Indonesia, Tanimbar-Yamdena, Mams, 21 km N of Saumlaki, 27.XI.-11.XII.2005, J.Horák leg." (NMPC); 13 exs., "Indonesia, Tanimbar isls, Lorulun, 20 km NE of Saumlaki, 150 m, 25.11.-24.12.2006, St Jakl lgt." (CLH, ZSM). • Timor: 1 ex., "Indonesia, West Timor Buraen env. 28 km S Kupang 400 m, 16.-21.12.2005 St. Jakl leg." (CLH); 1 ex., "TIMOR ISL Buraen env. 60 km SE Kupang 350 m, 10.-21.2.2006 St. Jakl leg." (CLH); 4 exs., "Timor, Naikliu area, restpools in dry forest, 130 m, 3.x.2011, 09 58.425S 123 41.439E (TIM11)" (MZB, ZSM); 1 ex., "Timor, alte Sammlung" (ZSM); 1 ex., "Timor" (RMNH); 6 exs., "Macklot, Timor" (RMNH); 3 exs., "Dr. H. ten Kate, Timor centr." (RMNH); 4 exs., "S.O.Celebes, J. Elbert, 1909" (RMNH); 1 ex., "W.P. de Roever, Nenas en omgeving, Moetisgebergte Timor, Sept. 1937" (RMNH); 6 exs., "Tim. [Timor] 6756" (NHMUK); 1 ex., "Tim. [Timor], Wallace, Celebis (Hydaticus) MS Clark" (NHMUK); 1 ex., "Timor 978 var., Sharp Coll. 1905-313" (NHMUK); 2 exs., "Timor, Lelogama, Mai 1911, Haniel", "Samml. A. Zimmermann" (ZSM); 1 ex., "Timor", "Coll. C. Felsche Geschenk 1907" (SMTD). · Sulawesi: 2 exs., "Manado, Celebes [Sulawesi] 2014" (NHMUK); 1 ex., "S.O. Celebes T. Elbert 1909", "Rambi bis Mengkoka", "ex Museum Buitenzorg",

"Sandracottus chevrolati Aubé det. A. Zimmermann" (DEI); 2 exs., "Celebes [Sulawesi] Posso [Poso] See Drs. Sarasin" (NMB, SMTD); 1 ex., "SO Sulawesi, I. Albert", "Samml. A. Zimmermann" (ZSM). • **Moluccas**: 1 ex., "Moluccas" (MNHN); 2 exs., "Moluccas Batchian [most probably mislabeled] J. Waterstradt 1902" (MNHN); 1 ex., "Rotti Carl Auriv.", "Samml. A. Zimmermann" (ZSM); 2 exs., "Kisser Inseln Mai 1901" [Pulau Kisar], "Samml. A. Zimmermann" (ZSM); 2 exs., "Molukken Ins. Roma" [Pulau Romang], "Samml. A. Zimmermann" (ZSM). • **Timor-Leste**: 1 ex., "Timor-Leste, 6.ii.2011, Ossu, Mundo Perdido Mts. 945 m, 8°42'47.6"S, 12°49'29"E" (NMPC).

**Redescription.** Body broad oval, shiny, testaceous with black markings. Ventral side completely dark brown to black, legs testaceous, hind legs somewhat darker (Figs 3, 49).

Head testaceous with posterior part and broadly so on posterior half alongside as well as two elongate spots on clypeus black, shiny (Figs 3, 49). Punctation consisting of dense and very numerous punctures of different sizes and of larger, much sparser ones, particularly numerous on frons. Clypeal grooves, punctures alongside eyes and a transverse depression beside eyes distinctly impressed, punctures large and coalescent. Antennae testaceous; antennomeres slender, antennomere V 4.5× as long as broad.

Pronotum testaceous with a median black marking reaching from posterior to anterior margins; long and broad on posterior, distinctly shorter and narrower on anterior margin and strongly constricted in middle (Figs 3, 49). Surface very superficially shagreened, almost not discernible, with dense punctation; punctures medium-sized mixed with smaller ones. Anterior and lateral puncture lines dense and coalescent, punctures becoming sparse towards middle and lacking in very middle of anterior margin. Posterior puncture line with coarse and coalescent punctures in middle of each side, distinctly smaller and spaced on disc.

Elytra testaceous to ferrugineus brown with black markings consisting of three transverse bands; particularly characterised by the presence of longitudinal testaceous subsutural spots (Figs 3, 49). Epipleura testaceous to ferrugineus brown. Surface very slightly and superficially shagreened and covered with a double punctation, a smaller and dense one as well as a larger one more sparse. Puncture lines with groups of medium-sized punctures mostly grouped in five or six punctures, groups closer together on discal row.

Ventral side dark brown. Legs, particularly fore and mid legs testaceous, hind legs ferrugineus brown to dark brown. Prosternal process short and broad, 1.5× longer than broad, flattened finely but distinctly sculptured; posterior margin broadly rounded. Whole surface very superficially shagreened and finely punctured. Metatibia with sparse medium-sized punctures on outer half. Ventrites II–VI very superficially shagreened, slightly and longitudinally wrinkled on lateral parts, whole surface densely covered with very small punctures, with sparser larger ones. Posterior margins rounded, bordered with some large and coalescent punctures on the middle of each side.

Measurements: TL = 13.0-13.5 mm, TL-h = 11.2-12.4 mm, TW = 8.0-8.5 mm.  $\bigcirc$ . Protarsomeres I–III strongly enlarged with three larger suckers and numerous smaller one. Mesotarsomeres I–III with two rows of small suckers. Median lobe of aedeagus, in ventral view, broadened on apical third, then tapered up to apex, here broadly rounded (Fig. 14a). Parameres basally broad and pointed at apex (Fig. 14b). Q. Similar to male, tarsi not enlarged. Microsculpture on ventrite VI as in male.

**Differential diagnosis.** The dorsal colour pattern of the Indonesian *S. chevrolati* is near to the Indian *S. festivus* but *S. chevrolati* can be easily separated by its smaller size (TL = 10-13.5 mm, *S. festivus*: TL = 14.7-15.5 mm) (Figs 3, 49), its distributional range (Figs 25, 29), and shape of median lobe and parameres (Figs 14a, b, 16a, b).

**Distribution.** Indonesia: Lesser Sunda Islands east of the Wallace Line (Lombok, Sumba, Sumbawa, Flores), Tanimbar, Timor, south-eastern Sulawesi, and southern Moluccas (Pulau Romang) (Fig. 25). Old records from northern Sulawesi and Bacan Island need to be confirmed. Specimens were collected between 90 and 800 m a.s.l.

**Habitat.** The specimens from Rinca (Flores) and Sumbawa were collected in rest pools of an almost dry stream bed, partly shaded by monsoonal rainforest. The bottom consisted of rocks and coarse sand, covered with rotten leaves (C.H.S. Watts and M. Balke pers. comm. 2010).

#### Sandracottus dejeanii (Aubé, 1838)

Figs 4, 15, 26, 34, 35, 50

Hydaticus dejeanii Aubé, 1838: 165 (type locality "Indes Orientales").

- Sandracottus dejeani (Aubé, 1838) (sic.): Sharp, 1882: 686 (comb. nov.); Régimbart 1899: 335 (descr.); Zimmermann 1920: 234 (cat.); Guéorguiev 1965: 111 (faun.); Vazirani 1969: 275 (descr., cat.); Vazirani 1971: 25 (cat.); Sonali et al. 2022: 339 (faun.).
- Sandracottus dejeanii (Aubé, 1838): Hájek 2006: 50 (faun.); Ghosh and Nilsson 2012: 18 (cat.); Ghosh 2015a: 81 (faun.); Ghosh 2015b: 77 (faun.); Shangar et al. 2023: 455 (faun.); Deb and Subramanian 2023: 14 (faun.); Hájek and Nilsson 2024: 91 (cat.); Shaverdo et al. 2024: 38 (check list, faun.); Sheth et al. 2024: 10, 20 (check list, faun., key).
- Sandracottus vijayakumari Anand et al., 2021: 17999–18003 (type locality Western Ghats, Kerala, India) (syn. nov.).

#### Type material of Hydaticus dejeanii. Not found (MNHN).

Type material of Sandracottus vijayakumari. Not examined.

Additional material. (143 specimens): • INDIA: 2 exs., "Mahableshnar W. Ghato, 5500ft India", "Coll'n J.D. Sherman Jr. 1926" (USNM); 2 exs., "Aug. 43 Dehra Dun" [Prov. Uttarakand, 1943, Dehradun, Central Internment Camp for British India near Premnagar, 30°20 N 78°3 E] (ZSM); 1 exs., "Okt. 43 Dehra Dun" (ZSM); 1 ex., "Inde méridionale M. Moingeon" (NMB); 4 exs., "India, Batate, Patnitop 1600– 2100 m 6.-8.8.1980 W. Heinz leg." (NMB); 1 ex., "India Hydarabad M. Halva leg." (NMB); 2 exs., "Chota Nagpore Nowatoli R.P.Cardon VII-IX.1888" (NMB, MNHN); 2 exs., "Puna", "Coll. Kraatz", "Zimmermann det." (DEI); 23 exs., "Inde Anglaise, Kalka, ex. Coll. Oberthür" (MNHN); 32 exs., "Chota-Nagpore Nowatoli R.P. Cardon VIII-IX.1896" (MNHN); 4 exs., "Chota Nagpore, Nowafoli, R.P.Cardon, VIII-IX 1898" (RMNH); 4 exs., "Chota-Nagpore Nowatoli, R.P. Cardon IX-X.1896" (MNHN); 1 ex., "Chota-Nagpore Nowatoli R.P. Cardon IV-V.1897" (MNHN); 5 exs., "Maissour Shinoga Mai 1897" (MNHN); 3 exs., "Val de Kangra [Himachal Pradesh] Dharamsala vers 1300 m, J. Berlioz, 1937" (NMB, MNHN); 1 ex., "Calcutta [Kolgata] Ex. Museo



Figure 26. Distribution of Sandracottus dejeanii in Asia.

E. Steinheil" (MNHN); 1 ex., "Ex. E. Wehncke Acqu. 1884" (MNHN); 1 ex., "India bor. 980 Dejeani, Sharp Coll. 1905-313" (NHMUK); 1 ex., "Western Ghats, Bombay [Mumbay], 2250 feet, Matheran, Charlotte Lake, 31.III.1908 & pres. 1908 by G.B.Longstaff" (NHMUK); 1 ex., "S. Bombay 1902.294." (NHMUK); 1 ex., "Matheran II.1919 P.H.", "Brit. Mus. 1978-16" (NHMUK); 3 exs., "India N.W. frontier, E.Y. Watson 98-142" (NHMUK); 1 ex., "India orient", "Fry Coll. 1905-100 (NHMUK); 1 ex., "India 980 Dejeani", "Sharp Coll. 1905-313" (NHMUK); 3 exs., "Khandesh, T.R. Bell, H.E. Andrewes Bequest.", "B.M. 1922-221" (NHMUK); 6 exs., "Khandesh, H.E. Andrewes Bequest. B.M. 1922-221" (NHMUK); 3 exs., "Belgaum, H.E. Andrewes Bequest. B.M. 1922-221" (NHMUK); 1 ex., "India" (NHMUK); 2 exs., "Nilghiri Hills, H.L. Andrewes" (NHMUK); 1 ex., "Achmednagar, Gebauer leg." (NMW); 2 exs., "Shimoga, Et. Myore, V.1936" (MNHN); 6 exs., "South India, Salem District, IX.1943, P.S.Nathan leg." (MNHN); 1 ex., "India" (MNHN); 2 exs., "India Sunderbunds" (MNHN); 6 exs., "India, Sundabunds" (MNHN); 1 ex., "India, Sundabunds", "coll. Gärtner" (DEI); 1 ex., "S-India, Salem Distr. IX.1934 Nathan leg." (NMB); 1 ex., "Orissa, Daitari, 31.XII.1966, collected on lamp, Gy Topal leg." (NMB); 4 exs., "Orissa, Jaipur Keonjahr, District Daitari, 29.XI.1967, netted from water, Gy Topal leg." (NMB); 1 ex., "Dehra Dun 1883 Dr.Warth leg." (CGW); 1 ex., "Madhya Pradesh, Jablpur Dagmaga, 18.IV.1968, V.S.Durve leg." (CGW); 1 ex., "Ostindien", "Samml. A. Zimmermann" (ZSM); 1 ex., "Madras, "Samml. A. Zimmermann" (ZSM); 2 exs., "India or., Behar, "Samml. A. Zimmermann" (ZSM); 2 exs., "Khandesh., 27.II.1902, in water, T.R. Bell", "Samml. A Zimmermann" (ZSM); 2 exs., "Coorg Hallery, Fletch-
er leg.", "Samml. A. Zimmermann" (ZSM); 1 ex., "India, Bombay Biro.902" (TDMB); 2 exs., "India, Orissa, Jajpur-Keonjahr, District Daitari, leg. Gy Topál, No. 975, netted from water, 29.XI.1967" (TDMB); 1 ex., "India or." (TDMB); 1 ex., "India, Madras" (TDMB); 2 exs., "Maharashtra, Igatpuri env. 120 km NE Mumbai, 600 m, 1.-12. VIII.2002, 19°42.17'N, 73°33.06'E, P. Šípek & M. Fikáček leg." (NMPC); 1 ex., "Tamil Nadu, 15 km SE Kotagiri, Nilgiris, Kunchappanai, 900 m, 7.-22.V.2000, 11°22'N, 76°56'E, Rolčík leg." (NMPC); 1 ex., "India S, Tamil Nadu, Nilgiris, 15 km SE of Kotagiri, Kunchappanai, 900 m, 11° 22' N 76° 56' E, 7.-22.V.2000, D. Hauck leg." (CJS); 2 exs., "Bhimtal 20.V. 1300-1500 m", "India U.P. 8.81 M. Brancucci" (NMB); 1 ex., "Southern Madhya Pradesh Dhobighat Nala [stream] (= Clematis Point Stream), Pachmarhi Wildlife Sanctuary, Satpura Mountain Range, ca 5 km SSE Panchmarhi, Hoshangabad District, 900 m a.s.l., 22°27'31"N/78°26'41"E, 27.II.2008, M. Jäch leg. (Loc. MP 7)" (NMW); 1 ex., "N27°08'22" E76°20'38", India bor. Occ., Rajasthan state, Alwar di., Naranimata env., 460 m, 20-30.7.2002, Igt.P. Šrámek" (NMPC). • IRAN: 1 ex., "Sistan va Baluchestan Prov., Bampur, 6.-16. VI.1997, M.Kafka leg." (NMPC); 1 ex., "Sistan va Baluchestan Prov., Pir Sohrab env., 100 m, pool in dried up Wadi, 11.-12.IV.2000, 25°44'N 60°50'E, J. Hájek & M. Mikát leg." (NMPC). • MYANMAR: 1 ex., "Mulmein [= Mawlamyaing], 1871, Fieber" (NMW). • NEPAL: 1 ex., "Nepal" (NHMUK). • PAKISTAN: 1 ex., "Pakistan 20.05.1998 Kashmir Himalaya Mts. 20 km S Muzaffarabad 73°29'E,34°01'N, Nara village Ronkay" (CHF); 1 ex., "Kawai, Khagan Valley 1450–1800 m, 15.6.1977, Wittmer & Brancucci" (NMB); 1 ex., "NW Pakistan, Swat Prov., Madyan, 1400 m, VII.1971, Holzschuh leg." (CGW); 1 ex., "West Pakistan, Rawalpindi surr., 18.X.1971, E. Heiss leg." (CGW); 1 ex., "West Pakistan, Rawalpindi surr., Basal, 16.-18.I.1956, Kala Chitta Range, C. Lindemann leg." (ZSM); 1 ex., "Pakistan, Northern Frontier Province, Tathabaya, 34°36'48 N, 73°27'01 E, 2300 m, at light, No 4–6, 7.-9. VII.1998, G. Csorba & L. Ronkay leg." (TDMB).

**Doubtfull record and probably mislabelled.** 1 ex., "Philippines Luzon Ch. Semper" (MNHN).

Locality unknown. 4 exs., "leg. Stolicka 1865" (NMW); 2 exs., "Megerley" [= coll. Megerle] (NMW).

**Remarks.** Sandracottus vijayakumari recently described by Anand et al. (2021) from the Western Ghats in Kerala, India is proposed as a junior synonym of *S. dejeanii*. The illustrated and described dorsal colouration of the head, the pronotum, and the elytra is within the range of variation of *S. dejeanii* which can have both separated and contiguous testaceous markings on the elytra. Furthermore, all 143 specimens of *S. dejeanii* examined by the authors, including the ones having largely separated testaceous patches on the elytra, have a fine microreticulation with numerous larger punctures on the head. No information was given in the original publication on any differences in genital structure of both taxa.

**Redescription.** Body oval, shiny, testaceous to ferrugineus brown with black markings (Fig. 50). Ventral side completely dark brown to black, legs testaceous to ferrugineus brown.

Head testaceous with posterior half broadly black: black band protruding forwards to frons, shiny (Figs 4, 50). Surface sculpture consisting of dense microreticulation and of larger, much sparser punctures, particularly numerous on frons. Clypeal grooves, punctures alongside eyes and a transverse depression beside eyes distinctly impressed, punctures large and coalescent. Antennae testaceous; antennomeres slender, antennomere V 4× as long as broad.

Pronotum testaceous with a median black marking reaching from posterior to anterior margins (Figs 4, 50); long and broad posteriorly, narrower and shorter anteriorly, and strongly constricted in middle. Surface shagreened with a dense punctation; punctures medium-sized. Anterior and lateral puncture lines with dense and coalescent punctures, becoming sparse towards middle and lacking in the very middle of anterior margin. Posterior puncture line distinctly visible only at sides, superficial medially and transformed in long and very superficial wrinkles.

Elytra black to dark brown with testaceous markings in form of a chessboard, the testaceous markings alternating with the black ones. Epipleura testaceous to ferrugineus brown (Figs 4, 50). Surface very slightly and superficially shagreened and covered with a double punctation, a smaller and denser one as well as a larger and much sparser one. Puncture lines with groups of medium-sized punctures.

Ventral side dark brown. Legs particularly fore and mid legs testaceous, hind legs ferrugineus brown to dark brown. Prosternal process very short and broad, 1,3× only longer than broad, flattened and superficially sculptured; posterior border broadly rounded. Whole surface very superficially shagreened and finely punctured. Metatibia with only a few small punctures on outer half. Ventrites II–VI shagreened, densely covered with very small punctures and a few larger sparser ones. Posterior margins rounded, bordered with a short row of coalescent punctures in middle.

Measurements: TL = 12.0–13.0 mm, TL-h = 11.1–12.1 mm, TW = 7.3–7.6 mm.

♂. Protarsomeres I–III strongly enlarged with three larger suckers and numerous smaller ones. Mesotarsomeres I–III with two rows of small suckers. Median lobe of aedeagus, in ventral view, narrow and elongate, slightly tapered towards apex (Fig. 15a). Parameres also narrow, same length as median lobe, only slightly tapered at apical part (Fig. 15b).

♀. Similar to male. Tarsi not enlarged.

**Differential diagnosis.** The combination of size and dorsal colour pattern (Figs 4, 50) separates *S. dejeanii* from all other species of the genus. Furthermore, the species can be separated from all other species of the genus by the shape of the median lobe and parameres (Fig. 15a, b).

**Distribution.** India: Andhra Pradesh, Arunachal Pradesh, Rajasthan, Assam, Himachal Pradesh, Jharkhand, Karnataka, Madhya Pradesh, Maharashtra, Orissa, Punjab, and Tamil Nadu (Ghosh and Nilsson 2012; Deb and Subramanian 2023; Sheth et al. 2024); Nepal, Pakistan, Myanmar, and Iranian Baluchistan (Hájek 2006; Shaverdo et al. 2024) (Fig. 26). Specimens were collected from near sea level to 2300 m.

**Habitat.** In India widespread in different ponds, rest pools of intermittent streams and artificial water tanks, often rich in aquatic vegetation. The single specimen in Pachmarhi Wildlife Sanctuary was obtained from a forest stream (ca 1–2 m wide) with rocky bottom (Fig. 35). In Kerala, Anand et al. (2021) collected the species in a partly shaded, shallow, ditch-like forest pool which was rich in decaying leaves and twigs; lentic habitat. In Iran it was collected in remnant pools in a wadi, in a semidesert area (Hájek 2006) (Fig. 34). Together with the Indian *S. festivus* and the two subspecies of the Australian *S. bakewelli*, this species is not restricted to forested areas as are many other species of the genus, especially in Southeast Asia. *Sandracottus dejeanii* is capable of flight and was attracted to light. The larvae have been described by Vazirani (1971).

#### Sandracottus femoralis Heller, 1934

Figs 6, 17, 27, 36, 52

- *Dytiscus flavocinctus* Guérin-Méneville, 1830: 61 (type locality Manokwari, West Papua, Indonesia); Boisduval, 1835: 49 (preoccupied by Hummel 1823 and objective synonym of *Sandracottus guerini*); Boisduval, 1835: 49 (descr.).
- Sandracottus flavocinctus (Guérin-Méneville, 1830): Régimbart 1899: 339 (descr.); Zimmermann 1920: 234 (cat.).
- Sandracottus femoralis Heller, 1934b: 3 (type locality: Buka, Solomon Islands); Alarie et al. 2023: 305 (larval descr.), idem: 320 (habitat); Hájek and Nilsson 2024: 91 (cat.).
- Sandracottus guerini J. Balfour-Browne, 1939: 114, replacement name for Sandracottus flavocinctus; Hájek and Nilsson 2024: 91 (cat.) (syn. nov.).

**Comments on classification.** Sandracottus femoralis was described from the Solomon Islands. We have studied Heller's type specimen of *S. femoralis*, Guérin-Meneville's type of *D. flavocinctus*, as well as numerous specimens of *S. guerini* over its complete range. There is no doubt that both taxa belong to the same species. Sandracottus guerini Balfour-Browne, 1939 is a replacement name for *S. flavocinctus* Guérin-Méneville but is more recent than Sandracottus femoralis, so the valid name for this species must be *S. femoralis*.

**Type material of Sandracottus femoralis. Holotype**: Female, "Buka Salomonen Juli 1930", "Coll. H. Hediger", "1933 8" [blue label], "S. femoralis Typus" [red label], "Staatl. Museum für Tierkunde, Dresden", "Sandracottus femoralis Heller, 1934 Hendrich & Brancucci det. 2006". Examined.

*Dytiscus flavocinctus: Lectotype* (herewith designated): Female, "Mus. Paris Nouv. Guninée Dumont d'Urv. 1841", "Dory [Manokwari] N. Guinee Duvelle Durville" [Dumont d'Urville], [round handwritten label], "Hidaticus [sic!] flavocinctus" [handwritten label], "Lectotypus Dytiscus flavocinctus Guérin-Men. des. M. Brancucci & L. Hendrich 2010" [red printed label], "Sandracottus guerini B.-Br. Det. M. Brancucci L. Hendrich 10" [white printed label] (MNHN). Examined.

Additional material. (118 specimens): • INDONESIA: 1 ex., "Indonesia: Halmahera Isl., Khao Dist., Camp 34 34 km inland from Pan-Tunggal Lumber Co. base camp at Tg. Loleo", "1-14 Feb. 1981 AC Messer & PM Taylor" (USNM); 1 ex., "Indonesia: Halmahera Isl., Jailolo Dist., Kampung Psir Putih 0°53'N 127°41'E", "1-14 Aug. 1981 PM Taylor" (USNM); 13 exs., "Indonesia: Halmahera Isl., Jailolo Dist., Kampung Psir Putih 0°53'N 127°41'E", "15-31 Jan. 1981 AC Messer & PM Taylor" (USNM); 18 exs., "Indonesia: Halmahera Isl., Jailolo Dist., Kampung Psir Putih 0°53'N 127°41'E", "1-14 May 1981 AC Messer & PM Taylor" (USNM); 2 exs., "Indonesia: Halmahera Isl., Jailolo Dist., Kampung Psir Putih 0°53'N 127°41'E", "14. Aug. 1981 PM Taylor" (USNM); 1 ex., "Batanta Island [Pulau Batanta], Arefi, 2004, A. Skale leg." (CAS); 1 ex., "Bernstein Morotai", "flavocinctus Aubé" (MNHN); 1 ex., "Aru Insel", "Samml. A. Zimmermann" (ZSM); 1 ex., "Rosenberg, Ins. Aru" (RMNH); 1 ex., "Key Insel", "Samml. A.Zimmermann" (ZSM); 2 exs., "Bernstein, Morotai" (RMNH); 1 ex., "N. Moluccas, Bacan Island, Mt. Sibela, 400 m, 14 km SE Labuha, primary forest, 2-13.II.1996, 0°38' S Lat. 127°32´ E, leg. V. Siniaev & E. Afonin leg." (CLH); 2 exs., "SE Moluccas Aru ISLS, WOKAM I. 17 km NE Wakua vill., 1-7-II.2022, St. Jakl leg." (CLH, NMPC); 8 exs., "N Moluccas: Bacan, Wayaua, alt. m. 0050, 05.-16.vii.1985, J. Huijbregts"



Figure 27. Distribution of *Sandracottus femoralis* [black dots] in New Guinea and the Moluccas, and S. rotundus [red squares] on Sulawesi.

(RMNH); 1 ex., "Indonesia, Maluku, Obi Isl., South coast, 22 km N of Tapaya vill., Seribu Mts., 1200-1500 m, S. Jákl leg., 20.xi-10.xii.2008" (NMPC); 3 exs., "Indonesia, Papua Dekai, upper Brazza, 273 m, 2./3.vi.2015, -4.74108472466468 139.654211075976, Sumoked (Pap044)" (MZB, ZSM); 2 exs., "Indonesia Papua Barat, Kebar, shaded deep sandy irrigation roadside ditches, 584 m, 6.xi.2013, -0.80775253 133.05923529, UNIPA (BH031)" (ZSM); 4 exs., "Irian Jaya, Nabire, Nabire-Ilaga track, km 62, 250 m, 24.VII.1991, M.Balke & L.Hendrich leg. (IR 22)" (CLH, NMW); 1 ex., "Tami River Hollandia 1930 R.Voorhoeve leg." (CLH); 1 ex., "Seram, E Wahai, 12.II.1989, M.Jäch" (NMW); 1 ex., "New Guinea, Wareo, 1933" (ZSM); 6 exs., "Dutch New Guinea: Humboldt Bay Dist. Pukusam Dist. West of Tami River vi.1937", "B.M. Nat. Hist. London" (CLH, NHMUK). • PAPUA New GUINEA: 1 ex., "Nouvelle Guinée" (MNHN); 1 ex., "New Guinea, NE Zenag-Lae, 200 m, 16.I.1979" (NMB); 10 exs., "N. Guinea mer. Rigo Lugio 1889 L. Loria" (MNHN, RMNH); 5 exs., "N. Guinea mer. Rigo VII.1889 L. Loria" (MNHN, NMW); 1 ex., "Morobe Prov. Wau, 1200 m 1.-15.V.1962 light trap J.Sedlacek leg." (NMW); 1 ex., "Morobe Prov. Bulolo 700 m 9.XI.1962 J.&M.Sedlacek leg." (NMW); 1 ex., "Morobe Kilolo Creek 7 km W Wau 1070 m 15.-21.I.1969 J.Sedlacek leg."(NMW); 1 ex., "Morobe Prov. Garaina 700 m 21.III.1998 A.Riedel leg." (NMW); 1 ex., "Morobe Prov. Wau 15.XII.1968 H.Ohlmus leg." (ANIC); 6 exs., "Madang Prov. Batabag village 50 m XI.-XII.2000 5°08'S 145°46'E L.Cizek leg." (NMB); 1 ex., "Madang Alexishafen, sago swamp, 22.V.1991, D.J.Larson leg." (ANIC); 6 exs., "Madang, Nagada River near Nobanob, 12.VI.1991, D.J.Larson leg." (ANIC, QM); 1 ex., "New Guinea Biro 96 Friedrich-Wilhelmshafen" (TDMB). · SOLOMON ISLANDS: 1 ex., "Solomon Islands: New Georgia, 2 mls. W. Of Lamberte 1.IX.65. Roy. Soc. Exped. B.M. 1966-1", "bomb crater pool, coast road" (NHMUK); 3 exs. (+ numerous larvae), "SOLOMON ISLANDS, GUADALCANAL,



Figure 28. Distribution of Sandracottus insignis in the Philippines.

ca. 3.5 km SE of BARANA vill., (drying up stream in shaded gorge), 09°29.8'S, 159°59.5'E; 190 m, 24.xi.-14.xii.2013, Jiří Hájek leg." (NMPC); 3 exs., "South Pacific, Solomon Is. GUADALCANAL I., 500–650 m Koso vill. Env., ca. 15–18 km SSE of Honiara, 1–18.XII.2016 St. Jakl leg." (CLH).

**Redescription.** Body broadly oval, submatt /slightly shiny, black with ferrugineus brown markings. Ventral side completely dark brown to black, legs testaceous, hind legs somewhat darker.

Head testaceous with posterior part broadly black leaving free two small testaceous spots on vertex (Figs 6, 52). Surface submatt, shagreened, consisting of dense and minute punctures not very uniform in size and of larger and much sparser ones, more numerous on frons. Clypeal grooves and punctures alongside eyes marked, punctures medium-sized but coalescent. Antennae testaceous; antennomeres slender, antennomere V 4× as long as broad.

Pronotum black with lateral margins ferrugineus brown, and narrow, testaceous, horizontal band, interrupted medially (Figs 6, 52). Surface submatt, distinctly shagreened, with very dense punctation; punctures medium-sized and distant of only  $1-2\times$  their own diameter. Anterior puncture line interrupted in middle; punctures relatively small but coalescent, forming wrinkles and becoming sparse medially and lacking in mid-length of anterior margin. Posterior puncture line with coarse and coalescent punctures in middle of each side, forming distinct wrinkles, distinctly smaller and spaced on disc.

Elytra black with small testaceous markings consisting of basal band sometimes reduced to different small spots at base, one postmedian spot, one preapical short and reduced band, and an apical spot (Figs 6, 52), submatt. Epipleura ferrugineus brown. Surface distinctly shagreened and covered with small and dense punctures as well as with larger and much sparser ones. Puncture lines with groups of medium-sized punctures mostly grouped in five or six punctures, groups closer together on discal line. Sutural puncture line marked only by few punctures on apical part.

Ventral side dark brown. Legs, particularly fore and mid legs testaceous, hind legs ferrugineus brown to dark brown. Prosternal process short and broad, 1.3× longer than broad, flattened, finely but distinctly sculptured; posterior margin broadly rounded. Metatibia with sparse medium-sized punctures on whole surface. Ventrites II–VI very superficially shagreened, slightly and longitudinally wrinkled on lateral parts, densely covered with very small punctures and larger sparser ones. Posterior margins rounded, deeply bordered with some large and coalescent punctures in middle of each side along margin.

Measurements: TL = 11.9–12.6 mm, TL-h = 11.0–12.8 mm, TW = 7.0–7.5 mm.

♂. Protarsomeres I–III strongly enlarged with three larger suckers and numerous smaller ones. Mesotarsomeres I–III with two rows of small suckers. Median lobe of aedeagus, in ventral view, broad, parallel-sided up to apex, here slightly broadened and broadly rounded (Fig. 17a). Parameres broad and pointed at apex (Fig. 17b).

 $\mathbb{Q}$ . Similar to male, tarsi not enlarged. Microsculpture on ventrite VI as in male.

**Differential diagnosis.** The combination of size and dorsal colour pattern (Figs 6, 52) separates *S. femoralis* from all other species of the genus. The very similarly coloured *S. maculatus* is always larger (TL = 14.0-16.1 mm) and more broadly oval than *S. femoralis* (TL = 11.9-12.6 mm). Furthermore, *S. femoralis* can be separated from all other species of the genus by the shape of the median lobe and parameres (Fig. 17a, b). All instar larvae were described by Alarie et al. (2023).

**Distribution.** Indonesia: Moluccas (Bacan, Batanta, Halmahera, Obi, Seram, Morotai), Key and Aru Islands, and West Papua; Papua New Guinea up to the Solomon Islands (Fig. 27).

**Habitat.** In West Papua specimens were collected in small but mainly exposed primary rainforest pools and puddles, always enriched with decaying leaves (Fig. 36). On Bacan Island also collected at light. On the Solomon Islands found in an old water-filled bomb crater near a coastal road (New Georgia), and a pool formed by the drying up of a stream on a clay bed, covered with decaying leaves and twigs (Guadalcanal; Alarie et al. 2023: 320). *Sandracottus femoralis* is distributed from lowland forest up to hilly mountain rain forests at ~ 1200 m altitude.

## Sandracottus festivus (Illiger, 1801)

Figs 5, 16, 29, 35, 51

- *Dytiscus festivus* Illiger, 1802: 166. (type locality: "Ostindien ["East India" = India and the Malayan Archipelago]".
- Sandracottus festivus (Illiger, 1801): Sharp 1882: 686 (comb. nov.); Régimbart 1899: 334 (descr.); Zimmermann 1920: 234 (cat.); Vazirani 1969: 273 (descr., cat.); Ninje Gowda and Vijayan 1992: 29–32 (ecol.); Ghosh and Nilsson 2012: 18 (cat.); Ghosh and Hegde 2015: 73 (faun.); Sonali et al. 2022: 339 (faun.); Hájek and Nilsson 2024: 91; Sheth et al. 2024: 8, 20 (check list, faun., key).
- Sandracottus mixtus (non Blanchard, 1843): Shankar et al. 2023: 455 (faun., misidentified, photo shows *S. festivus*); Deb and Subramanian 2023: 10–15 (faun., misidentified, photo shows *S. festivus*).

### Type material. Not examined.

Additional material. (202 specimens): • CHINA: 1 ex., "Chine", "Samml. A. Zimmermann" (ZSM).• INDIA: 1 ex., "Panjab and U Provinces VI-X India", "RL Woglum coll." (USNM); 2 exs., "Mahableshnar W. Ghato [Ghatol, Rajastan], 5500ft India", "Coll'n J.D. Sherman Jr. 1926" (USNM); 2 exs., "INDIA - Tamil Nadu Road Salem - Yercaud Pond at 8-9 km from Yercaud - 1000 m 4.I.1995 Mazzoldi P. leg." (CPM); 9 exs., "INDIA - Kerala m 700 - Road Thekkadi - Kottayam at 13 km from Thekkadi - Muddy pool 2.I.1995 Mazzoldi P. leg." (CPM); 6 exs., "Aug. 43 Dehra Dun" [Prov. Uttarakand, October 1943, Dehradun, Central Internment Camp for British India near Premnagar, 30°20 N 78°3 E] (ZSM); 6 exs., "Montagnes du Wynaad", "Museum Paris ex Coll. R. Oberthur" (MNHN); 3 exs., "Solan près Simla Lakhat 1896" (NMB); 3 exs., "Pulney Hills R.P. Castets 1898" (MNHN); 4 exs., "Maissour, Shinoga, Mai 1897" (MNHN); 2 exs., "Himalaya Simla", "Coll. Franklin Müller" (DEI); 1 ex., "Simla, IV-VII.96", "Ex. Musaeo W. Rothschild 1899" (MNHN); 3 exs., "Bangalore, Silvepoore, G. Tabourel 1899" (MNHN); 3 exs., "Val de Kangra [Himachal Pradesh], Dharamsala, vers 1300 m, J. Berlioz, 1937" (MNHN); 1 ex., "Inde, Mont Abu, Tajputana, 1938, J. Berlioz Ex Musaeo Thorey" (MNHN); 1 ex., "Calcutta, Ex. Museo E. Steinheil" (MNHN); 4 exs., "Punjab, Simla, E.C. Ansorge B.M. 1922-455" (NHMUK); 1 ex., "Bangalore, Mysore 95-28" (NHMUK); 5 exs., "N.W. India 8438" (NHMUK); 1 ex., "Simla, Coll. Plason" (NMW); 1 ex., "South India, Salem District, IX.1943, P.S.Nathan leg." (MNHN); 1 ex., "South India, Coimbatore, 24.VIII.1937, P.S.Nathan leg." (MNHN); 1 ex., "India (M.P.) Jabalpur district Lamhetghat village 28.III.1962, R.G. Sharna leg.", "Zoological Survey of India Central R.S. Lot No. 29/63 F.C. No. 362" (NMB); 1 ex., "Parasnath Hills& Panchi Survey", "IV.1918 Sinha & Nath" (NMB); 1 ex., "India" (MNHN); 1 ex., "Coimbatore Inde merid. IX.1933" (MNHN); 3 exs., "Wagrar-Karur env. de Bellary, 1883, Chaper & de Morgan" (MNHN); 6 exs., "Mahé Malabar" (MNHN); 3 exs., "Côte de Malabar, T. Deschamps 1900" (NMB); 1 ex., "Orissa, Jaipur-Keonjahn Distr. Daitari, 29.XI.1967, collected from water, Gy Topal" (NMB); 1 ex., "Madhya Pradesh, Jablpur Dagmaga, 31.V.1965, H.P.Agywal leg." (CGW); 1 ex., "India or." (CGW); 1 ex., "Karnataka, Western Ghats Mts., 30 km SEE Bhatkal, Kollur env., 26.-28.V.2006, V.Ryjacek" (NMPC); 1 ex., "Tamil Nadu, Nilgiri Hills, Kunchappanai, 15 km SE Kotagiri, 900 m, 11°2'N 76°56'E, 13.-20.V.1994, Z.Kejval leg." (NMPC); 2 exs., "Rajasthan, Mt. Abu env., 100 km W Udaipur, 1150 m, 24°35.35'N 72°42.72'E, 24.-27.VIII.2002, P.Sipek & M. Fikacek leg." (NMPC); 1 ex., "Ostindien Coll. C. Felsche Geschenk 1907" (SMTD); 1 ex., "India or. post.", "Coll. Maerkel" (SMTD); 1 ex., "Madras, Coimbatore, 1400 feet, X.1964, P.S. Nathan leg." (ZSM); 2 exs., "India or." (ZSM); 1 ex., "Indien, Tanguelar" (ZSM); 2 exs., "Sammlung Cl. Müller" (ZSM); 2 exs., "S-India, Kerala, Theimala nr. Shenkottah (70 km N Trivandrum) 150 m, 8°57'N 77°01'E, 5.IV.1997, Schintlmeister & Siniaev leg." (CLH); 1 ex., "S India Rippon coll." (CLH); 2 exs., "Khasi Hills" (NHMUK); 1 ex., "Ranikhet, Kumaon, H.G.C., H.G. Champion Coll. B.M. 1953-156" (NHMUK); 10 exs., "W.Almora Division, Kumaon, U.P. H.G.C., H.G. Champion Coll. B.M. 1953-156" (NHMUK); 2 exs., "W.Almora Division, Kumaon, U.P., I.1920", "H.G. Champion Coll. B.M. 1953-156" (NHMUK); 2 exs., "W.Almora Division, Kumaon, U.P., IV.1917", "H.G. Champion Coll. B.M. 1953-156" (NHMUK); 8 exs., "India, Orissa, Jajpur-Keonjahr, District Daitari, No. 975, netted from water, 29.XI.1967, leg. Gy Topál" (TDMB); 1 ex., "Rhimtal, 25.IX.1979, Smetacek" (NMB); 1 ex., "Rhimtal, 2.VIII.1973, Smetacek" (NMB); 1 ex., "S-India, Kerala, 15 km SW Munnar, Kallar Valley, 9.V.1997,



Figure 29. Distribution of Sandracottus festivus [black dots] and S. jaechi [red square] in the Indian subcontinent.

1250 m, 10°02'N 76°58'E, Dembicky & Pacholatko leg." (NMB); 1 ex., "Tamil Nadu, Nilgiris, 15 km SE of Kotagiri, Kunchappanai, 900 m, 11° 22' N 76° 56' E, 7.-22.V.2000, leg. D. Hauck" (CJS); 1 ex., "Tamil Nadu, Nilgiri Hills, 11 km SE Kotagiri, 1100 m, E Kunchappanai, 11°24'N 76° 56'E, 3.-15.V.2002, P.Pacholatko leg." (NMB); 1 ex., "Southern Madhya Pradesh Hoshangabad District Pagara -Panchmarhi road, ca. 5 km NNE Panchmarhi, Panar Pani [stream], 850 m a.s.l. 22°30'25"N/78°26'43"E, 26.+27.II.2008 M. Jäch leg. (Loc. MP 6)" (NMW); 2 exs., "Nilghiri", "Coll. Kraatz Régimbart det.", "Sandracottus festivus Illiger", "Zimmermann det." (DEI); 1 ex., "Calcutta" (NHMUK). • NEPAL: 1 ex., "Nepal 02.08.1981 Khare 1600 Beron" (CHF); 1 ex., "Dhading distr., Thorpu bis Kordunje, 1300-1400 m, 24. VII. 1983, Martens & Schawaller leg." (NMB); 2 exs., "W Nepal, Kali Gandaki Khola Bhakta B. Tatopani 1100-1400 m, 12.-14.V.1984" (NMB); 1 ex., "Himalaya" (RMNH); 3 exs., "S Dhaulagiri, W Beni Darbang, 1150 m, 1.XII.2000, G.Riepl leg." (NMW). • BHUTAN: 2 exs., "Bhakta B., Beguna, 2730 m, 24.VIII.1976" (NMB). · SRI LANKA: 3 exs., "Belihul-Oya Ceylon 2 de trim. 89 I.Z. Kannegieter", "Muséum Paris, Coll. R. Oberthür" (MNHN, CLH); 1 ex., "Ceylon", "W Robinson bequest 1929" (USNM); 2 exs., "Ceylon N.P. Madugoda 15.IX.1953, F. Keiser" (NMB); 1 ex., "Museum Paris Inde Bellary du Ceylan de Morgan 1896" (MNHN); 1 ex., "Kandy, Ceylon H. Rolle, Berlin, SW", "coll. Gärtner" (DEI); 1 ex., "Süd Ceylon Mai 1889 H. Fruhstorfer", "Coll. Kraatz Régimbart det.", "Hydat. festivus", "Zimmermann det." (DEI); 15 exs., "Nalanda Ceylon W.Horn 1899", "Zimmermann det." (DEI); 3 exs., "Paradna W.Horn 1899", "Sandracottus festivus Illig, Zimmermann det." (DEI); 11 exs., "Ceylon Kannegieter 1889" (MNHN); 3 exs., "Ceylon Nalanda 2e trim. 89 I.Z. Kannegieter" (MNHN); 1 ex., "Ceylon, Belihul-Oya, 2e trim. 89, I.Z. Kannegieter" (MNHN); 1 ex., "Ceylan, Deschamps, 1889" (MNHN); 4 exs., "Kandy, IX-XII.1897, E.E. Green, 1917-54" (NHMUK); 2 exs., "Kelani Valley nr. Colombo W. Braine 1910-283" (NHMUK); 4 exs., "Ceylon G. Lewis 1910-320" (NHMUK); 1 ex., "Ceylon, 1891 Heuser leg." (NMW); 1 ex., "Kandy X.1907 H.E. Andrewes Bequest B.M. 1922-221" (NHMUK); 1 ex., "Kandy, 20.II.1902 Dr.Uzel leg." (NMW); 6 exs., "Haputale env., Beragala, 9.XII.1980, M.Jäch leg." (CGW, NMW); 2 exs., "Dambulla env. 300 m 19.IV.-9.V.1991 J.Kolibac leg." (NMB); 1 ex., "Habarana 10.XI.1982 G.Duranton leg." (NMB); 1 ex., "Sigiriya 10.XI.1982 G.Duranton leg." (NMB); 1 ex., "Anuradkapura 3.XI.1982 G.Duranton" (NMB); 1 ex., "Paradina 1899 W. Horn" (ZSM); 1 ex. "Matale Ceylon 1899 leg. W. Horn" (ZSM); 1 ex., "Ceylon Madarász Madatugama 21.II.1896", "Sandracottus festivus Illiger Guignot det. 1956" (TDMB); 9 exs., "Sri Lanka Moneragala Kumaradola group X.1997 M.M. Bahir & S.V. Nanayakkara leg." (CLH); 1 ex., "Sri Lanka, Ratnapura Sincharaja rain forest, 17.-19.II.1997, Udovichenko leg." (CLH). · PAKISTAN: 1 ex., "Hazara, Balakot 900-1100 m, 3.-7.VI.1983, leg. Eckweiler" (NMB); 1 ex., "Islamabad, 1 km S Hotel Adventure Inn, 500 m, 3.VII.1998, leg. Gy. Fábian & B. Herczig" (TDMB); 1 ex., "Pakistan, Kashmir, Himalaya Mts., 20 km S Muzaffarabad, Nara village, 73°29'E, 34°01'N, 750 m, 12.IX.1997, leg. Gy. Fábian & G. Ronkay" (TDMB).

Country unknown. 1 ex., "Novara Reise, 1857-1859" (NMW).

**Redescription.** Body broad oval, shiny, testaceous with black markings. Ventral side completely dark brown to black, legs testaceous, hind legs somewhat darker.

Head testaceous with posterior part and broadly so on posterior half alongside as well as two elongate spots on clypeus black, shiny (Figs 5, 51). Surface almost smooth consisting of dense and very numerous punctures of different size and of larger, much sparser ones, particularly numerous on frons. Clypeal grooves, punctures alongside eyes and transverse depression beside eyes distinctly impressed, punctures large and coalescent. Antennae testaceous; antennomeres slender, antennomere V 4.5× as long as broad.

Pronotum testaceous with median black marking reaching from posterior to anterior margins; long and broad on posterior, distinctly shorter and narrower on anterior margin and strongly constricted on middle (Figs 5, 51). Surface very superficially shagreened, almost not discernible, with dense punctation; punctures medium-sized mixed with smaller ones. Anterior and lateral puncture lines dense and coalescent, punctures becoming sparse towards middle and lacking in very middle of anterior margin. Posterior puncture line with coarse and coalescent punctures on middle of each side, distinctly smaller and spaced on disc.

Elytra testaceous to ferrugineus brown with black markings consisting of three transverse bands (Figs 5, 51); particularly characterised by presence of a longitudinal testaceous subsutural spot on anterior third. Epipleura testaceous to ferrugineus brown. Surface very slightly and superficially shagreened and covered with double punctation, a smaller and denser one as well as a larger one that is more sparsely distributed. Puncture lines with groups of medium-sized punctures mostly grouped by 5–6 punctures; groups closer together on discal row.

Ventral side dark brown. Legs, particularly fore and mid legs testaceous, hind legs ferrugineus brown to dark brown. Prosternal process short and broad, 1.5× longer than broad, flattened finely but distinctly sculptured; posterior margin broadly rounded. Whole surface very superficially shagreened and finely punctured. Metatibia with sparse medium-sized punctures on outer half. Ventrites II–VI very superficially shagreened, slightly and longitudinally wrinkled on lateral parts, whole surface densely covered with very small punctures and larger

sparser ones. Posterior margins rounded, bordered with some large and coalescent punctures on middle of each side.

Measurements: TL = 14.7–15.5 mm, TL-h = 13.5–14.4 mm, TW = 8.0–8.8 mm.  $\bigcirc$ . Protarsomeres I–III strongly enlarged with three larger suckers and numerous smaller one. Mesotarsomeres I–III with two rows of small suckers. Median lobe of aedeagus, in ventral view, broad, parallel-sided up to apex here slightly broadened and broadly rounded (Fig. 16a). Parameres broad and pointed at apex (Fig. 16b).

 $\mathcal{Q}$ . Similar to male, tarsi not enlarged. Microsculpture on ventrite VI as in male.

**Distribution.** India: Andhra Pradesh, Arunachal Pradesh, Assam, Himachal Pradesh, Jharkhand, Madhya Pradesh, Maharashtra, Orissa, Punjab, and Tamil Nadu (Ghosh and Nilsson 2012; Deb and Subramanian 2023; Sheth et al. 2024); Pakistan, Nepal, Bhutan, Sri Lanka (Fig. 29). Specimens were collected between 150 and 2700 m above sea level. Zeng (1989) in his doctoral thesis recorded *S. festivus* from numerous provinces in southern China (see also Nilsson 1995). However, revision of Zeng's specimens revealed that he misidentified *S. festivus* and *S. mixtus* [= *hunteri*] (S. Zhao, in litt. 2020). The single historical specimen from China deposited in ZSM is probably mislabelled. For now, we consider *S. festivus* as not occurring in China.

**Differential diagnosis.** The dorsal colour pattern of the Indian *S. festivus* is near to the Indonesian *S. chevrolati* but can be easily separated by its consistently larger size (TL = 14.7-15.5 mm, *S. chevrolati*: TL = 10.0-13.5 mm) (Figs 5, 51), its distributional range (Figs 25, 29), and shape of median lobe and parameres (Figs 14a, b, 16a, b).

**Habitat.** In India, Pakistan, and Sri Lanka the species is collected from protected embayments of slow flowing forest streams, ponds, swamps, and artificial water tanks, often rich in aquatic vegetation. At Panar Pani [stream] in broad but slow flowing forest stream (ca 3–5 m wide), with its bottom consisting of gravel and rocks (Fig. 35). Together with the Indian *S. dejeanii* and the two subspecies of the Australian *S. bakewellii*, this species is not restricted to densely forested areas as many other species of the genus, especially in SE Asia. Ninje Gowda and Vijayan (1992) have published their research results on the predatory behaviour of the species on mosquito larvae in sewage tanks. The species is capable to flight and was attracted to light.

## Sandracottus hunteri (Crotch, 1872), stat. rev.

Figs 7, 18, 30, 37, 38, 40, 41, 53

Dytiscus fasciatus Fabricius, 1775: 825 (type locality India).

- *Hydaticus hunteri* Crotch, 1872: 205 (type locality China) (replacement name for *Dytiscus fasciatus* Fabricius).
- Sandracottus fasciatus (Fabricius, 1775): Régimbart 1899: 333 (descr.); Zimmermann 1920: 234 (cat.); Hendrich and Balke 1995: 47 (ecol., cat.).
- Sandracottus mixtus (non Blanchard, 1843): Hendrich 1995: 48 (ecol.); Park et al. 2009: 47 (check list); Ghosh and Nilsson 2012: 19 (cat.); Lee et al. 2014: 36. (faun.); Suprayitno et al. 2022: 135 (check list, faun.); Atthakor et al. 2018: 93 (faun.); Ghosh and Gupta 2012: 110 (faun.); Alarie et al. 2023: 307 (larval descrip.); Hájek and Nilsson 2024: 91 (cat.).

- Sandracottus fasciatus var. crucialis Régimbart, 1899: 333 (type locality Vietnam, Myanmar); Vazirani 1977: 85 (syn.).
- Sandracottus manipurensis Vazirani, 1969: 277 (type locality Manipur, Assam, India); Mukhopadhyay and Ghosh 2004: 368 (cat.); Ghosh and Nilsson 2012: 19 (cat.); Hájek and Nilsson 2024: 91 (cat.) (syn. nov.).
- Sandracottus hunteri (Crotch, 1872): Sharp 1884: 447 (faun., check list); Jäch et al. 2012 (faun.); Suprayitno et al. 2017: 35 (faun., ecology).

**Type material of** *Dytiscus fasciatus. Holotype*, 1 male: "Dyt. Fasciatus Fabr. Pag. [page] 293 No 7" [handwritten label], "Compared with modern examples in Brit. Mus. R.A.G. March 1926" [printed label with red letters], "Hunter Coll. ZIHU 2199" [printed label, museum no.], "Type" [printed label with red frame], "139881" [catalogue number GLAHM 139881], "*Dytiscus fasciatus* Fab. Sandracottus fasciatus Fab." [printed label with red frame] (HMUG). Examined.

**Type material of** *Sandracottus manipurensis. Holotype* not examined (ZSI). *Paratype*, 1 male: "India Assam, Manipur 5000 ft. Phaiphenigaum 30.VIII.60 F. Schmid" [handwritten label], "Z.S.I. Lot No 61 1960" [printed label], "PARATYPE" [printed label], "*Sandracottus manipurensis* n.sp. T.G. Vazirani, det." [handwritten and printed label], "5147 H4A", "*Sandracottus hunteri* (Crotch) det.M.Brancucci & L.Hendrich 10" (ZSI). Examined.

Additional material. (473 specimens): • NEPAL: 7 exs., "E-Nepal, Dhankuta-Hills, Thamur Valley, 1150–2000 m, 23.-25V.1983, M.Brancucci leg." (NMB). · INDIA: 2 exs., "NE India, Assam Bhalukpong, 150 m, 27°02'N 92°36'E, 26.V.-3.VI.2005, Dembicky leg." (NMB); 2 exs., "NE India, Arunachal Prov., 8 km S Jamiri Sessa vicinity, 27°07'N 92°34'E, 26.V.-4.VI.2005, 350 m, P. Pacholatko leg." (NMB); 1 ex., "Darjeeling Distr., Alghera, 2900 m, 25.IV.1982, Ch.J.Rai leg." (NMB); 3 exs., "Darjeeling Distr., Kalimpong env., III.-IV.1989, Ch. J. Rai leg." (NMB). · CHINA: 1 ex., "China Kouy-Tcheou [= Guizhou] Kouy-Tcheou, Reg. de Pin-Fa, 1909 Cavalerie" (CHF); 1 ex., "China Yunnan-See, 1898 Excoiffier" (CHF); 1 ex., "Chengtu 1933" [Chengdu], "Szechwan China DC Graham XI-27-1700ft" (USNM); 1 ex., "Mu Dong Szechwan China DC Graham 6-15-33 Alt 1100ft" (USNM); 7 exs., "Spirit Valley", "Nanking Kiangsu Province", "China H.F. Loomis Oct. 25, 1919" (USNM); 2 exs., "China 1942 Yun Hsien March WL Jellison" (USNM); 17 exs., "Suifu Sz. China", "June 1928", "DCGraham Collector" (USNM); 1 ex., "Suifu Szchuen China 1923", "DCGraham Collector" (USNM); 1 ex., "Suifu 1000-2000ft Szchuen China 23' DCGraham Collector" (USNM); 8 exs., "Suifu Szchuen", "DCGraham Collector" (USNM); 1 ex., "China, Hayan Isl. Wuzhi Shan Mt. [Hainan, Wuzhi Shan Nature Reserve], 1500 m 18°53'N 109°43'E 20.02.-10.04.2001 local collector", "coll. H. Hebauer" (CHH); 2 exs., "Chine A. David" (MNHN); 1 ex., "Su Tschuen Siao Lou 1897" (MNHN); 1 ex., "Guanxi, 350 m a.s.l. 10 km S Yangshuo, muddy pools, fields, pasture 3.XI.1999 leg. J. Šťastný" (CJS); 5 exs., "Pingshiang [Pingxiang, Jiangxi] Süd-China Dr. Kreyenberg, Coll. Kraatz", "Zimmermann det." (DEI); 3 exs., "Kiukiang [Jiujiang] June 1887 AE Pratt", "Coll. Kraatz Régimbart det." (DEI); 2 exs., "Kiukiang July 1887 AE Pratt", "Coll. Kraatz Régimbart det." (DEI); 2 exs., "Kiangsi [Jiangxi] China", "Coll. Kraatz Régimbart det.", "Zimmermann det." (DEI); 1 ex., "China, coll. Gärtner" (DEI); 2 exs., "China Prov. Hupeh [Hubei] Mts. Wu-schan" (DEI); 2 exs., "Su Tschuen, Siàn-Lou 1897" (MNHN); 1 ex., "China, Kouang-si, P. Barrière 1909 ex. Coll. Oberthür" (MNHN); 33 exs., "Su Tschuen Chasseurs Indigènes 1903" (MNHN);



Figure 30. Distribution of Sandracottus hunteri, the most widespread species of the genus.

20 exs., "Sian-Lou Chasseurs du P. Dejean 1904" (MNHN); 1 ex., "China Kouangsi Rég. de Nanning 1931" (MNHN); 1 ex., "Foochau [Fuzhou, Fujian] April 1886 Leech" (MNHN); 4 exs., "Kiukiang [=Jiujiang] June 1887 A.E Pratt" (MNHN); 4 exs., "Su-Tchuen, Chasseurs Indigènes 1907" (MNHN); 2 exs., "Su-Tchuen, Siàn-Lou 1897" (MNHN); 1 ex., "Bas-Yunnan A. Salvat 1904" (MNHN); 2 exs., "Chine, A. David" (MNHN); 2 exs., "Kiang-Si A. David" (MNHN); 3 exs., "Kouy Tchéou Abbé Largeteau" (MNHN); 6 exs., "Kouy Tchéou Rég. De Pin-Fa Père Cavalerie 1908" (NMB, MNHN); 1 ex., "Chine Shanghai" (MNHN); 1 ex., "China bor. Ex Musaeo Thorey" (MNHN); 4 exs., "China" (NHMUK); 1 ex., "Danes Island [Changzhou Island, Guangdong] 6756" (NHMUK); 4 exs., "Canton [Guangzhou, Guangdong], C.W. Howard, B.M. 1922-22" (NHMUK); 5 exs., "Da-laen-saen near Nongpo [village near Ningpo, Zhejang] Walker Coll. 93.-18." (NHMUK); 3 exs., "Hong Kong, J.J.Walker", "G.C.Champion Coll. B.M.1927-409" (NHMUK); 19 ex., "China, Da-Iaen-saen [village near Ningbo, Zhejang], J.J.W.", "G.C.Champion Coll. B.M.1927-409" (NHMUK); 16 exs., "Western China Suiling W.A. Maw. 1909-38" (NHMUK); 1 ex., "Prov. Hunan, Huitong, 550 m, 9.-16.VII.1992, Ji Lanzhou leg." (NMW); 1 ex., "Yunnansen", "From R. Oberthür", "Coll'n J.D. Sherman Jr. 1926" (USNM); 1 ex., "Yünnan, Xishuangbanna ca. 10 km NW Menglun, ca. 700-800 m, 7.XI.1999, leg. Jäch et al. (CWBS360)" (NMW); 1 ex., "SE-Guangxi, District Yulin, Liuwan Mts. SW Yulin, 350-400 m, 16.XI.1993, Schillhammer leg. (20)"

(NMW); 1 ex., "Kiu Kiang [=Jiujiang] 1889", "Coll. Kraatz" (NMW); 2 exs., "Nanking, Dr.Jettmar" (NMW); 1 ex., "China, Dr.Stoltz BH" (NMW); 1 ex., "Kiukiang [=Jiujiang] VII.1887 A.E.Pratt" (NMW); 1 ex., "Chekiang, Chusan, 17.VII.1931, O.Piel leg." (MNHN); 2 exs., "China" (MNHN); 2 exs., "Prov. Hupeh" (MNHN); 1 ex., "Kiangsi, Staudinger & Bang Haas" (MNHN); 1 ex., "Szechuan, Chungking, E.Reitter" (MNHN); 1 ex., "Kuong Si" (MNHN); 2 exs., "China Yunnan" (MNHN); 1 ex., "S-China Canton S.W.Howard", "BM 1922-22" (CGW); 3 exs., "Central China", "Nonfried Coll." (CGW); 5 exs., "W-Guizhou Prov., Leigongshan, Xijiang, 1200-1900 m, 29.V.-2.VI.1997, Bolm leg." (NMB); 2 exs., "Hainan (217) 6 km W Dongxing, 50 m, 25.I.1996, Jäch leg." (NMW); 37 exs., "Chine Tchékiang [Ningpo] Coll. David" (MNHN); 1 ex., "Ou Hou", "Gebrüder W. Müller, Vermächt. 1909" (SMTD); 2 exs., "Kiangsi [Jiangxi]" (SMTD); 2 exs., "Kiautschau" (SMTD); 3 exs., "Shanghai", "Coll. C. Felsche Geschenk 1907" (SMTD); 3 exs., "Kiukiang [Jiujang] June 1887 A.E. Pratt", "Samml. A. Zimmermann" (ZSM); 3 exs., "China, "Samml. A. Zimmermann" (ZSM); 4 exs., "China, Kiautschou", "Samml. A. Zimmermann" (ZSM); 2 exs., "China, Pingshiang", "Samml. A. Zimmermann" (ZSM); 2 exs., "China, Kiaugsi", "Samml. A. Zimmermann" (ZSM); 1 ex., "China Su-Tchuen chasseurs indigènes 1903" (CLH); 2 exs., "China, Central Sichuan Baoguo Emet Co, 27.VII.-3.VIII.1994, Benes leg." (CLH); 4 exs., "Sechuan, Pingwu, 32°15'N 104°16'E, 3.- 9.VI.1997, E. Kucera leg." (CLH); 1 ex., "China, Shanghai", "Coll. E. Csiki", "Sandracottus fasciatus v. hunteri Crotch" (TDMB). • MYANMAR: 6 exs., "Taunggyi, Burma 2'27 Miss Northup" (USNM); 1 ex., "Myanmar Catcin Cauri Birranta Fea Ag. Nov. 1886" (MNHN); 1 ex., "Myanmar Sagaing Division, Alaungdaw Katthapa NP, Khaung Din stream, ca. 450 m, 11.V.2003, Boukal et al. leg. (119)" (NMW); 1 ex., "Myanmar Sagaing Division, Alaungdaw Katthapa NP, Khaung Din stream, ca. 360 m, 7.V.2003, Boukal et al. leg. (119)" (NMW); 4 exs., "Myanmar, Sagaing Division, Chatthin Wildlife Sanctuary, 23°31.481 N 95°38.804 E, ca. 260 m, 9.X.1998, Schillhammer leg. (9)"; 4 exs., "Myanmar Shan State, NE Mintaingbin Forest Camp [ca. 35 km N Aungban] above (150), pool, 22.VIII.2004, Shaverdo leg. (152)" (NMW); 6 exs., "Myanmar Shan State, NE Mintaingbin Forest Camp above (150), ca. 1200 m, puddles, 14.-20.VIII.2004, Shaverdo leg." (NMW); 6 exs., "Myanmar Shan State, NE Mintaingbin Forest Camp above (150A), ca. 1200 m, pond, 14.-20.VIII.2004, Shaverdo leg." (NMW); 1 ex., "Myanmar Shan State, Shwedaung Wildlife Sanctuary, 23°05.129 N 96°13.527 S, 360 m, 19.VII.2002, M.Hlaing & A.Moa leg." (NMW); 9 exs., "Myanmar SW Shan-State, 70 km W Taungguyi, 10.-11.VI.1997, J. Rejsek leg." (CJS, NMPC); 1 ex., "SW Shan state, Inle lake Nyaungshwe, 7.-16.VI.1997, J. Rejsek" (CJS); 1 ex., "Myanmar Shan State Kalaw env. 1356 m N 20.63200" E 96.56197" 8.-20.6.2015 Walter Grosser lgt." (CLH); 10 exs., "Myanmar, Shan-State, near Kalaw, 20°36'48''N 96°34'46''E, 1400 m, 15.XI.2003, M. Hornburg leg." (CLH). · CAMBODIA: 1 ex., "Cambodscha Schmidt" (MNHN); 5 exs., "Pnom Penh V.de Salvara" (MNHN); 1 ex., "Cambodia sept. or., Stung Treng 18.-22.IV.1998, 13°32'N 105°58'E, J. Mlíkovský leg." (NMPC). • LAOS: 1 ex., "NE Laos Huaphanne Prov. Mt. Phu Pane, 1220-1900 m Ban Saluei v.env., 18.V.-2.VI.2012 20°12'N 103°59'E, St. Jakl + Lao collector leg. Coll. Hendrich" (CLH);1 ex., "Khammouan Prov., Nakai env., 500-600 m, 22.V.-8.VI.2001, 17°43'N 105°09'E, E. Jendek & O. Šauša leg." (CHH); 8 exs., "Laos Attapeu prov., Ban Vang Tat Noi env. 900 m, 15°03-04'N / 107°24'E, 10.-25.V.2011", "NHMB Basel 2011 Expedition, M. Brancucci, M. Geiser, D. Hauck, Z. Kraus, A. Phantala & E. Vongphachan" (CLH, NMB);

2 exs., "Laos Svannakhet prov., Phou Xang He NBCA, ca. 5 km SW Ban Pa Phaknau, 250-400 m 17°00'N / 105°38'E, 31.V.-6.VI.2011", "NHMB Basel 2011 Expedition, M. Brancucci, M. Geiser, D. Hauck, Z. Kraus, A. Phantala & E. Vongphachan" (NMB); 2 exs., "Laos Bolikhamsay prov., Nam Kading NPA research training center near Ban Phon Kham, 18°20'N / 104°08'E, 250 m, 23.-29.V.2011", "NHMB Basel 2011 Expedition, M. Brancucci, M. Geiser, D. Hauck, Z. Kraus, A. Phantala & E. Vongphachan" (NMB); 2 exs., "Xayaboury Prov., Xayaboury env., 19°13'N, 101°42E, 300 m, 27.-30.VI.2010, leg. D. Hauck" (NMB); 1 ex., "Laos Umg. Vientiane III.-VI.1963" (NMB); 20 exs., "ATTAPEU prov., Annam Highlands Mts., Dong Amphan NBCA, ca. 1160 m, NONG FA [crater lake] env., 15°05.9'N, 107°25.6'E, 30.iv-6.V.2010, J. Hájek leg." (NMPC); 1 ex., "Pak Lag, 13.VIII.1918 V.de Salvara leg." (MNHN); 1 ex., "Luang Prabang I.1917 V.de Salvara" (MNHN); 3 exs., "Ban Mong 15.XII.1917 V.de Salvara" (MNHN); 2 exs., "Phongsaly Prov., Phongsaly env., 1500 m, 21°41'N 102°06'E, 28.V.-20.VI.2003, M. Brancucci leg." (NMB); 4 exs., "Phongsaly Prov. Ban Hatsa, 550 m, 21°44'N 102°12'E, 9.V.+17. VI.2004, M. Brancucci leg." (NMB); 8 exs., "Phongsaly Prov., Ban Sano Mai, 1150 m, 21°44'N 102°12'E, 19.V.-26.V.2004, M. Brancucci leg." (NMB); 3 exs., "NE Laos, Houa Phan prov., 20°13'N 104°00'E, Phou Pane Mt., 1.-16.VI.2009, 1350-1500 m, M. Brancucci leg." (NMB); 2 exs., "Xieng Khouang prov., 19°03'N 103°24'E, Ban Thaviang env., muddy puddle, 500-600 m, 19.V.2010, M. Geiser leg." (NMB); 1 ex., "N-Laos, Louangphrabang Prov., 19°53'N 102°09'E, Khan river, 300 m, V.Kuban leg." (NMB); 1 ex., "N-Laos, Louangphrabang Prov., 21°09'N 101°19'E, Namtha, 900-1200 m, 5.-31.V.1997, V.Kuban leg." (NMB); 1 ex., "Boloikhamxai Prov., 70 km NEE Vientiane, 150 m, 18°16'N 103°11'E, 27.-30. IV.1997, V.Kuban leg." (NMB); 1 ex., "Vientiane Prov., Lao Pako env. 55 km NE Vientiane, 1.-4.V.2004, J. Bezděek leg." (NMPC); 1 ex., "C-Laos, Bolikhamsai Province, Ban Nape - Kaew Nua Pass, 18.IV-1.V.1998, alt. 600 m, 18°22.3 N 105°09.1 E, M. Strba & R. Hergovits leg." (CLH); 1 ex., "N Laos, Vientiane Prov., Vang Vieng, 300 m, 18°55'23'N 102°26'55'E, 1.-15.V. & 1.-6.VII.2001, J.Koubac leg." (NMB); 1 ex., "CE Laos, Boli Khan Xai prov., 18°21'N 105°08'E, 8 km NE Ban Nape, 600 m, 1.-18.V.2001, V. Kuban leg." (NMB); 20 exs., "Annam Laos", "Sandracottus mixtus ab. crucialis Rég. Dr. Guignot det. 1956" (TDMB). • THAILAND: 2 exs., "Siam Kra Ding 12 III 56 RE Elbel" (USNM); 7 exs., "Siam 17 V 53 RE Elbel", "Pek-chong Sikiu-kerat Nong Min" (USNM); 7 exs., "Thailand 27 VI 54 REElbel", "Sakon Nakhon, Muang Sakon Nakhon, Phu Phan" (USNM); 24 exs., "Nakhon Ratchasima Province, Sakaerat Biosphere Reserve, King Cobra Cave, Thailand Coords: 14° 30.536' N, 101° 55.921' E, 362 m a.s.l., 27 Oct 2013, W. Atthakor leg., Sakaerat Expedition, lead by Professor Somsak Panha of Chulalongkorn University" (CSUT); 6 exs., "THAILAND Kanchanaburi Prov. Sai Yok N.P. - Pools on road, 23.VII.1996 leg. P. Mazzoldi" (CPM); 17 exs., "Thailand, Mukdahan LL 2000, Phu Pha Thoep N.P. Small pools on dry stream bed, Mazzoldi P. leg. (23)" (CPM); 1 ex., "Chiang Mai prov. 35 km NW of Muang Ngai, 18° 40' N 98° 42' E, 10.I.2006, S. Bečvář S. & R. Fouque leg." (CJS); 2 exs., "NE Thain Nan district, Ban Pha Khap, 15.-20.V.1992, Pacholatko leg." (NMW); 2 exs., "NW-Thailand, Chiang Mai, Soppong-Pai, 1800 m, 1.-8.V.1993, Pacholatko & Dembicky leg." (NMW); 4 exs., "NW-Thailand, Chiang Mai (Zoo), 9.-16.V.1988, at light, Malicky leg." (NMW); 1 ex., "NW-Thailand, Chiang Mai, 10.-17.V.1989, Malicky leg." (NMW); 2 exs., "Pang, 300 m, 19°55'N 99°12'E, D.Král leg." (NMB); 4 exs., "NW-Thailand, Mae Hong Son, Ban Huai Po, 1500 m, 8.-17.V.1992, S.Bily

leg." (NMB); 16 exs., "NW-Thailand, Mae Hong Son, Ban Huai Po, 1600-2000 m, 9.-16.V.1991, J.Horák leg." (NMB, NMW); 1 ex., "NW-Thailand, Mae Hong Son, Ban Huai Po, 1700 m, 24.-30.VI.1993, Schneider leg." (NMW); 1 ex., "NW-Thailand, Mae Hong Son, Ban Huai Po, 1600-2000 m, 9.-16.V.1991, Pacholatko leg." (NMB); 1 ex., "Lansang n.g., Thanon Thong Chai, 500 m, 18.-24.IV.1991, 16°48'N 98°57'E, D.Kral & V.Kuban leg." (NMB); 1 ex., "Thanon Thong Chai, Chiangdao, 19°24'N 98°55'E, 600 m, 10.-16.V.1991, D.Kral & V.Kuban leg." (NMB); 1 ex., "Lansang NP, 18.-24.IV.1991, 500 m, 16°48'N 98°57'E, D. Král leg." (NMPC); 1 ex., "Siam", "Gebrüder W. Müller Vermächt. 1909" (SMTD). • MALAYSIA: 1 ex., "West Malaysia, Kuala Lipis, small forest pool in rubber plantation, 15.IV.1997, Balke & Hendrich leg." (CLH); 3 exs., "Kedah Peak, 3200 feet, XII.1915", "ex. F.M.S. Museum B.M. 1955-354" (NHMUK); 2 exs., "West Malaysia, Penang, Botanical Garden, 27.I.1992, M.Jäch leg." (9) (NMW). • VIETNAM: 1 ex., "Vietnam 19.05.2007 Quang Tri Da Krong NP near headquarter lux Csorba leg." (CHF); 2 exs., "Vietnam N, Quang Binh prov. 1 km N of Cha Lo, 400 m Vitenam-Laos border area 17°41'22´´N 105° 45'45´´E, L. Dembicky leg., 11.-24.iv.2010" (NMB); 4 exs., "Pakha 4914", "Indochine Coll. Dussault" (NMB); 5 exs., "N Vietnam, Sa Pa, 1530 m, 25.-9.VI.1991, J. Strnad leg." (NMB); 1 ex., "S Vietnam, Saigon, jardin botanique [botanical garden], octobre 1870, A. Krempf leg." (MNHN); 3 exs., "Cuc Phuong (170 m) Ninh Bin Prov. (N-Vietnam) 10. vii.1997, S. Nomura leg." (NMST); 1 ex., "Tonkin Occ. Rég. De Hoa Binh R.P. A de Cooman 1919" (MNHN); 1 ex., "Sikkim, Kurseong, R.P. Bretaudeau 1894" (MNHN); 1 ex., "Chasseurs indigènes de ta-Tsién-Loù R.P. Dejean, 1901" (MNHN); 4 exs., "Tonkin Backan P. Lemée 1907-08" (MNHN); 8 exs., "Tonkin Backan P. Lemée, 1908" (MNHN); 1 ex., "Tonkin Occ., Env. de Hoa Binh, R.P. A. de Coomann, 1919" (MNHN); 5 exs., "S-Vietnam, 12 km N Dalat, Lang Bian, 28.-30.IV.1994, Pacholatko & Dembicky leg." (NMW); 1 ex., "S Vietnam, 16 km N Dalat-Ankroat, 1400 m, 12°05 N 108°24 E, 15.IV.1995, Pacholatko & Dembicky leg." (NMW); 1 ex., "Tonkin, Chaba, 27.VII.1917, Jeanvoine leg." (MNHN); 8 exs., "Hoa Binh Tonkin A.deCooman leg." (MNHN); 10 exs., "Lac Tho Tonkin, A.deCooman leg." (MNHN); 1 ex., "Hanoi 29.III.1917 V.de Salvara" (MNHN); 1 ex., "Hoa Binh I.1917 V.deSalvara" (MNHN); 1 ex., "N-Vietnam, Shonla [Son La], 9.X.1991, Murzin leg." (NMW); 1 ex., "N-Vietnam, Ma Da, 27.XII.1990, Murzin leg." (NMW); 1 ex., "Hoang Lien Son Prov., Sa Pa, 11.-19. VI.1990, M. Dvorák leg." (NMPC); 2 exs., "S Vietnam, Lao Cai Prov., Sa Pa district, 22°20'48.1 ... N, 103°47'45.2 ... E, 1690 m, at light, 24.-25. VIII.1998, leg. A. Kun" (TDMB); 1 ex., "S Vietnam, Sa-Pa, Hoang Lien Son, 11.-19. VI.1990, Mir. Dvořák leg." (CJS); 1 ex., "N-Vietnam, Tam Dao, V.-VI.1990, Pich Richard leg." (NMB); 1 ex., "N-Vietnam, Tam Dao, 20.-28.VI.1990, S.Brantlova leg." (NMB); 1 ex., "Tam Dao, 8.V.1990, M.Dudycha leg." (CJS). • Indonesia: 1 ex., "Java" (NMB); 1 ex., "Java Cote Sud Salatri" (MNHN); 1 ex., "Java", "Zimmermann det." (DEI); 9 exs., "Java", "Prov. Pasuruan, Kalipari, 300-500 met., W. Doherty, 1891" (MNHN); 3 exs., "Java occidental, Mons. Tjikorai, 4000 1852", "H. Fruhstorfer" (MNHN); 2 exs., "Java occ. Toegoë 1902" (MNHN); 1 ex., "Jav. Occ. G. Lamboreth, 1902" (MNHN); 1 ex., "Java Occ., Preanger [Parahyangan or Priangan] Tac Prau Ex. Musaeo van Lansberge" (MNHN); 1 ex., "Java Mts Kawie J.B. Lediou 1898" (MNHN); 2 exs., "Java Ex Museo Thorey" (MNHN); 1 ex., "Java Occ, G. Lambreth, 1908" (MNHN); 2 exs., "Java Schaum" (MNHN); 1 ex., "Java Coll. Le Moult" (MNHN); 6 exs., "E Java 50 km S Surabaya, Tretes, Kekek Bodo WF, 20.IX.1995, Schillhammer leg. (1)" (NMW); 1 ex., "Java Japara I.1933" (MNHN);

1 ex., "Karanggandoel Banjoemas K. Benner 1922 Muzeum Buitenzorg" (DEI); 1 ex., "Java" (NMW); 1 ex., "E Java, Bajoekidoel b. Banjoawangi 1930 Lucht leg." (MNHN); 1 ex., "Java Coll. Boucard" (MNHN); 2 exs., "NE Java Baluran NP 600 m 16.-19.IV.1996 R.Zajicek leg." (NMB); 2 exs., "Java Gebrüder W. Müller, Vermächt. 1909" (SMTD); 1 ex., "East Java Pare 10.III.1949 W.J.M.Vestjens leg." (ANIC); 1 ex., "Bali, Bedugul 3 km NE Candi Kuning, 1320 m, 11.VII.1991, Balke & Hendrich leg. (BA 8)" (CLH); 1 ex., "Holländisch Indien", "Zimmermann det." (DEI); 1 ex., "Sumatra", "Sandracottus hunteri Zimmermann det." (ZSM); 1 ex., "Sumatra, Balighe, X.90-III.91, E. Modiglioni" (MNHN); 1 ex., "Sumatra, Fort de Kock II.1925, native collector" (MNHN); 1 ex., "Sumatra 1873" (MNHN); 1 ex., "Sumatra Medan" (MNHN); 4 exs., "Sumatra, Dolog Merangir, 8.V.-10.VI.1983, E.W.Diehl leg." (NMB); 1 ex., "Sumatra, Dolog Merangir, 10.-12.V.1981, E.W.Diehl leg." (NMB); 3 exs., "NE Sumatra, Medan, Dr. Marx leg." (ZSM); 4 exs., "Sumatra O.K Medan 19.9.1921 J.B. Corporaal", "Museum Paris 1902 J.B. Corporaal" (NMB); 3 exs., "Sumatra Medan J.B. Corporaal", "Coll. A. Zimmermann" (ZSM); 1 ex., "Sumatra Palembang" (ZSM); 1 ex., "Sumatra, coll. Martin" (ZSM); 3 exs., "Sumatra Padang Fandjang, 800 m, 1.trim. 1896, Kannegieter" (ZSM); 2 exs., "Höllandisch Indien" [Indonesia] (ZSM); 4 exs., "Sumatra Palembang, Knappert leg." (NMW); 1 ex., "Sumatra Monte Battak [Bukit Batak] ex. coll. Fruhstorfer" (MNHN).

**Remarks.** Specimens with an absent subapical transverse band were described as var. *crucialis* Régimbart, 1899. Vazirani (1969) described his *S. manipurensis* from Assam based on specimens with more extensive black markings of the elytra. When studying the only male paratype of *S. manipurensis* available to us, we were not able to detect any morphological differences in the structure of the median lobes of *S. manipurensis* and *S. hunteri*. The colour pattern of the elytra of the paratype can also be found within the range of variation in *S. hunteri*. We therefore consider *S. manipurensis* synonymous with *S. hunteri*.

**Redescription.** Body broad oval, shiny, testaceous with black markings. Ventral side completely dark brown to black, legs ferrugineus brown to testaceous.

Head testaceous with posterior part and eye margin black, shiny (Fig. 7). Surface sculpture consisting of very small dense punctures and of larger, much sparser ones, particularly numerous on frons. Clypeal grooves, punctures alongside eyes and transverse depression beside eyes distinctly impressed, punctures large and coalescent. Antennae testaceous; antennomeres slender, antennomere V 3.5× as long as broad.

Pronotum testaceous with median black marking reaching from posterior to anterior margins (Figs 7, 53); broad on posterior, distinctly narrower on anterior margin. Surface shagreened with dense punctation; punctures medium-sized. Anterior and lateral puncture lines with dense coalescent punctures, becoming sparse towards middle, and lacking in middle of anterior margin. Posterior puncture line distinctly visible only at sides, towards middle punctures become superficial and transformed into long wrinkles.

Elytra testaceous to ferrugineus brown with black markings consisting of three transverse bands: broad antemedian, subapical, and apical; suture with narrow black frame, and puncture lines marked by black spots (Figs 9, 53). Epipleura testaceous to ferrugineus brown. Surface very slightly and superficially shagreened and covered with double punctation; denser smaller punctures and much sparser larger ones. Puncture lines with isolated groups of five



Figures 31–36. Habitats of Sandracottus 31 Australia, Northern Territory, 50 km S Adelaide River, creek at Scenic Route (NT 9) and 32 South Queensland, Winfield, Winfield Road, rest pool (QLD 54), habitats of *S. bakewellii bakewellii* (photos: L. Hendrich) 33 Northern Territory, Ormiston Gorge, habitat of *S. bakewellii guttatus* (photo: M. Baehr) 34 Pakistan, Sistan va Baluchestan Prov., Pir Sohrab env., rest pool in wadi, habitat of *S. dejeanii* (photo: J. Hájek) 35 India, southern Madhya Pradesh, Hoshangabad District, Pagara–Pachmarhi road, ca 5 km NNE Panchmarhi, Panar Pani, habitat of *S. dejeanii* and *S. festivus* (photo: M. Jäch) 36 Indonesia, Irian Jaya, Nabire, Nabire-Ilaga track, km 62, habitat of *S. femoralis* (photo: L. Hendrich).

or six medium-sized punctures; discal row almost complete and strongly impressed. Sutural puncture line marked only by few punctures along suture.

Ventral side dark brown. Legs, particularly fore and mid legs testaceous, hind legs ferrugineus brown to dark brown (Figs 9, 53). Prosternal process short and broad, 1.7× longer than broad, rounded apically, and finely but distinctly sculptured. Posterior border triangular, narrowly ended. Whole surface very



Figures 37–42. Habitats of *Sandracottus* 37, 38 Laos, Attapeu prov., Annam Highlands Mts., Dong Amphan NBCA, Nong Fa [puddles near lake shore] and lake, habitat of *S. hunteri* 39 Laos, Katamtok, rest pools along a rocky river bed, habitat of *S. maculatus* (photos: J. Hájek) 40 Thailand, near Salawin NP, open and muddy puddle made by elephants (photo: J. Šťastný), and 41 Sakaerat Biosphere Reserve, rocky pool in an otherwise dry stream bed, habitats of *S. hunteri* and *S. maculatus* (photo: W. Atthakor) 42 Philippines, Luzon, Pampanga Prov., Bano San Juan, Mt. Arayat NP, spring creek, habitat of *S. insignis* (photo: H. Freitag).

superficially shagreened and finely punctured. Metatibia with numerous and dense small punctures on basal half. Ventrites II–VI shagreened, longitudinally wrinkled on lateral parts, densely covered with very small punctures and larger sparser ones. Posterior margins rounded, bordered with some large and co-alescent punctures along margin.

Measurements: TL = 12.5-15.0 mm, TL-h = 11.4-14.0 mm, TW = 8.3-8.8 mm.  $\bigcirc$ . Protarsomeres I–III strongly enlarged with three larger suckers and numerous smaller one. Mesotarsomeres I–III with two rows of small suckers. Median lobe of aedeagus, in ventral view, broad, nearly parallel-sided on whole length, lobes narrowly rounded at apex (Fig. 18a). Parameres slightly longer than median lobe, broad and pointed at apex (Fig. 18b).

 $\mathbb{Q}.$  Similar to male, tarsi not enlarged. Microsculpture of ventrite VI as in male.

**Differential diagnosis.** The species is clearly distinguished from most other Indomalayan species of the genus by its characteristic colouration. From the dorsal colouration *S. hunteri* is near to *S. chevrolati* from the Lesser Sunda Islands which is generally smaller and more elongated. Furthermore, both species can be separated by the shapes of their median lobes.

**Distribution.** The most widespread and common species of the genus. India: Andhra Pradesh, Nagaland, Tamil Nadu, Uttarakhand, Uttar Pradesh, West Bengal, and Andaman and Nicobar Islands (Ghosh and Nilsson 2012; Ghosh and Gupta 2012); Nepal, China (Jäch et al. 2012), South Korea (Jeju-do Island) (Park et al. 2009; Lee et al. 2014), Japan (old record from Higo Province, Sharp 1884), Myanmar, Cambodia, Laos, Vietnam, West Malaysia, Indonesia (Sumatra, Java, Bali) (Fig. 30). The recent Indian records from the states Kerala, Karnataka, Maharashtra, and Tamil Nadu seems doubtful as the photograph in Deb and Subramanian (2023) clearly shows *S. festivus* and its median lobe, not *S. hunteri*. Specimens were collected from near sea level to 2900 m a.s.l.

**Habitat.** Sandracottus hunteri inhabits a broad variety of pools, puddles, ditches, and swamps of different sizes, shaded and exposed (Alarie et al. 2023). In Laos numerous specimens were collected by local collectors in pools in the littoral zone of a lake (Figs 37, 38). In Thailand, near Salawin NP, *S. hunteri* was found in open and muddy puddles made by elephants (Fig. 40) and near the King Cobra Cave at Sakaerat Biosphere Reserve, in a large rest pool of a rocky stream bed enriched with decaying leaves and twigs (Fig. 41). In Myanmar *S. hunteri* was collected from roadside pools on a muddy limestone bed with decomposing leaves (Alarie et al. 2023). *Sandracottus hunteri* also occurs in cultivated areas and is not restricted to forested sites. On Bali the species was collected several times in smaller pools of intermittent streams with decomposing leaves (Suprayitno et al. 2017). The species was attracted to light. All instar larvae were recently described by Alarie et al. (2023).

### Sandracottus insignis (Wehncke, 1876)

Figs 8, 19, 28, 42, 55

*Hydaticus insignis* Wehncke, 1876: 194 (type locality Philippines, "Insel Luzon"); Sharp 1882: 687 (descr.).

Sandracottus insignis (Wehncke, 1876); Régimbart 1899: 338 (tax., descr.); Freitag et al. 2016: 8 (check list); Hájek and Nilsson 2024: 91 (cat.).

- *Hydaticus baeri* Régimbart, 1877: 99 (type locality Philippines, "Manille"); Zimmermann 1920: 234 (syn., cat.).
- Sandracottus ornatus Sharp, 1882: 689 (type locality Borneo); Vazirani 1977: 84 (stat. nov.).
- Sandracottus insignis ssp. ornatus Sharp, 1882; Vazirani 1977: 84 (cat.); Hájek and Nilsson 2024: 91 (cat.) (syn. nov.).

**Type material of** *Sandracottus insignis. Lectotype* (herewith designated): Female: "Semper" [white handwritten label with black fram]; "Luzon" [handwritten yellowish label], Ex. Coll. E. WEHNCKE Acq. 1884" [printed white label], "Lectotype Hydaticus insignis Wehncke Hendrich & Brancucci des. 2010" [red printed label] (MNHN). Examined.

Type material of Sandracottus baeri. Lectotype (herewith designated): Male: "Manille Baer", "Typus", "Type", "Sandracottus baeri Rég.", "Lectotypus Hydaticus baeri Brancucci & Hendrich07" [red printed label], "Sandracottus insignis (Wehncke) det. M.Brancucci & L.Hendrich07" [white printed label] (MNHN). *Paralectotypes*: 2 males, "Manille Baer", "Typus", "Type", "Sandracottus baeri Rég.", "Paralectotypus Hydaticus baeri Brancucci & Hendrich07" [red printed label], "Sandracottus insignis (Wehncke) det. M.Brancucci & L.Hendrich07" [white printed label] (MNHN). Examined.

**Type material of Sandracottus ornatus. Holotype**: Female: "Borneo 986 ornatus", "Type H.T.", "Sharp coll. 1905-313", "Sandracottus insignis (Wehncke) Hendrich det. 2008" (NHMUK). **Paratype**: Female: "Borneo 986 1905-313", "Sandracottus insignis (Wehncke) Hendrich det. 2008" (NHMUK). Examined.

**Remarks.** The type locality of *S. ornatus*, "Borneo", needs to be confirmed. *Sand-racottus insignis/ornatus* has never been reported from Borneo again. However, it cannot be ruled out that the species occurs there, as some dytiscids that occur in the south of the Philippines have also been reported from the north of Borneo. From what is known so far, *S. insignis* appears to be endemic to the Philippines.

Additional material. (10 specimens): • PHILIPPINES: 1 ex., "Balabac" [handwritten label], "ornatus Shrp" [handwritten label] (MNHN); 1 ex., "Montalban" [Luzon], "Nr. 6 Fld.-H." [printed label], "baeri Régb. Insignis Sharp" [handwritten label by Régimbart] (MNHN), 2 exs., "Mindanao" (MNHN); 2 exs., "Luzon, Los Banos, Mt. Makiling [above the Botanical Garden, 180 m] (3), 13.XI.1992, H. Schillhammer leg." (NMW); 1 ex., "Luzon, Pampanga Province, Bano San Juan, Mt. Arayat NP, spring creek, bolders, root packs, riffle, 37 m, 15°10'21.62"N, 120°45'47.78"E, 31.X.2009, H. Freitag leg." (ZSM); 1 ex., "Polillo [Polillo Islands, Luzon], Taylor" (ZSM); 1 ex., "Palawan, Taytay [10°50'N 119°30'E], W. Schultze leg." (SMTD).

**Redescription.** Body broadly oval, shiny, testaceous with black markings. Ventral side completely dark brown to black, fore and mid legs testaceous, hind legs ferrugineus brown.

Head testaceous with posterior part dark brown as well as two dark brown, oblique, elongated patches on frons (Figs 8, 55). Surface finely microreticulate, particularly on anterior half, just shagreened on rest of surface. Punctation consisting of dense and very small punctures and of larger, much sparser ones, the latter particularly numerous on frons. Clypeal grooves, punctures alongside eyes and transverse depression beside eyes distinctly impressed, punctures large and coalescent. Antennae testaceous; antennomeres slender, antennomere V 4× as long as broad.

Pronotum testaceous with long and broad dark brown band posteriorly and narrow dark brown band anteriorly (Figs 8, 55). Surface sculpture shagreened with dense punctation; punctures medium-sized. Anterior rows of punctures with dense, strong, and coalescent punctures, shortly interrupted in middle. Lateral puncture lines broad; punctures medium-sized and coalescent. Posterior row limited to few punctures at latero-basal quarter.

Elytra testaceous with black markings leaving four angulous basal testaceous spots, two large postmedian as well as a preapical and an apical testaceous patch (Figs 8, 55). Epipleura testaceous. Surface microreticulate, meshes very small but strongly impressed. Punctation consisting of numerous minute punctures mostly in intersection of meshes and of large sparse punctures regularly spread on whole surface. Puncture lines with groups of medium-sized punctures, discal row almost complete. Sutural puncture line with few small punctures along suture.

Ventral side dark brown. Legs particularly fore and mid legs testaceous, hind legs ferrugineus brown to dark brown. Prosternal process very short and broad, only 1.4× longer than broad, flattened and superficially sculptured; posterior border broadly rounded. Metacoxa very superficially shagreened and finely punctured; punctures small and sparse; Metatibia with numerous medium-sized punctures on whole outer half, somewhat larger proximally. Ventrites II–VI shagreened, densely covered with very small punctures and larger sparser ones. Posterior margins rounded, bordered with short row of coalescent punctures each side of middle.

Measurements: TL = 12.5-13.1 mm, TL-h = 11.4-12.2 mm, TW = 7.8-8.1 mm.

♂. Protarsomeres I–III strongly enlarged with three larger suckers and numerous smaller ones. Mesotarsomeres I–III with two rows of small suckers. Median lobe of aedeagus, in ventral view, broad, apical half more or less parallel-sided, each part narrowly rounded apically (Fig. 19a). Parameres also narrow, slightly longer than median lobe, and gently tapered on apical half (Fig. 19b).

♀. Similar to male. Tarsi not enlarged. Microsculpture on ventrite VI as in male.

**Differential diagnosis.** The species is clearly distinguished from most other Oriental species of the genus by its characteristic colouration. From the dorsal colouration *S. insignis* is near to the Indian *S. festivus* which is generally larger and more elongated. Furthermore, both species can be separated by the shapes of their median lobes.

**Distribution.** Philippines: Palawan, Mindanao, Luzon. The record from Borneo seems to be doubtful (Fig. 28). Specimens were collected between 40 and 200 m above sea level.

**Habitat.** The three specimens at Mt. Makiling were collected in an exposed roadside ditch surrounded by mature second growth lowland rainforest (H. Schillhammer pers. comm. 2005). The single specimen from Bano San Juan at Mt. Arayat NP was collected among root packs in a shallow bay of a slow flowing creek, partly shaded by second growth vegetation (Freitag pers. comm. 2012) (Fig. 42). The larvae are still unknown.

**Conservation.** A rare species, probably associated with the declining primary lowland rainforests in the Philippines (see Indomalayan species *S. bizonatus*, *S. femoralis*, *S. maculatus*, and *S. rotundus*). According to the present knowledge it is an endangered species (Freitag et al. 2016). It is recommended to be listed in the next IUCN red list.

# Sandracottus jaechi Wewalka & Vazirani, 1975

Figs 9, 20, 29, 54

Sandracottus jaechi Wewalka & Vazirani, 1975: 114 (Ceylon [Sri Lanka], Nuwara Eliya); Ghosh and Nilsson 2012: 18 (cat.); Hájek and Nilsson 2024: 91(cat.).

**Type material.** *Holotype*: Male: "Nuwara Eliya, 1800 m, leg. Kruse [ca 1930, Wewalka and Vazirani 1975] Ceylon (Sri Lanka)", "TYPUS Sandracottus jaechi n. sp. Wewalka & Vazirani 82" [red label] (CGW, later in NMW). *Paratypes*: 1 female: "Nuwara Eliya, leg. Kruse 1800 m Ceylon [Sri Lanka]", "Paratypus Sandracottus jaechi n.sp. Wewalka & Vazirani 82" [red label] (NMW); 1 female: "Nuwara Eliya, leg. Kruse 1800 m Ceylon [Sri Lanka]", "Paratypus Sandracottus jaechi n. sp. Wewalka & Vazirani 82" [red label] (NMW); 1 female: "Nuwara Eliya, leg. Kruse 1800 m Ceylon [Sri Lanka]", "Paratypus Sandracottus jaechi n. sp. Wewalka & Vazirani 82" [red label] (NHMUK). Examined.

**Redescription.** Body oval, somewhat broadened posteriorly, completely black and shiny. Ventral side and legs completely black (Figs 9, 54).

Head black. Surface shiny, very superficially shagreened, covered with small and very dense punctures and of larger much sparser ones, the latter more numerous on frons. Clypeal grooves and punctures alongside eyes marked, punctures medium-size and coalescent. Both antennae lacking in holotype.

Pronotum black, sides not margined. Surface very slightly but distinctly shagreened, with very dense punctation; punctures small, less impressed than on head. Anterior puncture line broadly interrupted in middle, punctures large and strongly coalescent. Posterior puncture line with large and coarsely impressed punctures on middle of each side, building distinct wrinkles.

Elytra black, shiny. Epipleura black. Surface distinctly shagreened and covered with double punctation; smaller punctures with very small and dense punctures, larger one with much more sparser ones. Puncture lines with groups of medium-sized punctures mostly grouped by five or six punctures; discal row almost complete and strongly impressed. Sutural puncture line incomplete, marked only by few punctures along suture.

Ventral side black. Legs black. Prosternal process almost flat, short and broad, lanceolate, 1.4× longer than broad, flattened and finely but distinctly sculptured; posterior margin broadly rounded. Metatibial spurs bifid. Metatibia with sparse medium-sized punctures on whole surface. Setae along posterior margin of middle femora sparse and ~ 2/3 of the width of mesofemora at the base. Ventrites II– VI very superficially shagreened, distinctly longitudinally wrinkled on whole lateral parts, densely covered with very small punctures and with very large sparser ones. Posterior margins rounded, deeply bordered with a row of large and coalescent punctures on the middle of each side along the margin. Outer margin of metaventral wings curved. Metacoxal lines short, not reaching apices of metacoxal processes.

Measurements: TL = 14.4–15.0 mm, TL-h = 13.5–13.6 mm, TW = 8.35–8.8 mm.  $\bigcirc$ . Protarsomeres I–III strongly enlarged with three larger suckers and ten numerous smaller ones. Mesotarsomeres I–III with two rows of small suckers. Median lobe of aedeagus, in ventral view, broad, flattened parallel-sided on whole length, lobes broadly rounded at apex (Fig. 20a). Parameres slightly longer than median lobe, broad and pointed at apex (Fig. 20b).

 $\mathbb{Q}.$  Similar to male. Microsculpture on ventrite VI as in male.

**Differential diagnosis.** This species can be easily separated from all other species by its completely black dorsal surface and the shape of the median lobe.

Distribution. Sri Lanka, only known from the type locality (Fig. 29).

**Habitat.** The only three specimens were collected at Nuwara Eliya, a hill resort in the mountains of central Sri Lanka. From German and British botanists of the last century the area was well-known for tropical peatland habitats with many unique and endemic plants (e.g., Keilhack 1915a). Impressive black and white photographs of such peatland pools in central Sri Lanka can be seen in Keilhack (1915b). Today the area is mostly cultivated and drained. The completely black dorsal surface and venter of *S. jaechi* may be an adaptation for woodland or peatland ponds and puddles with dark bottoms, decaying leaves, or sedges but no vegetation.

**Conservation.** This is a highly endangered if not extinct species. It is by far the rarest species of the genus with a very limited distribution. It is recommended to be listed in the next IUCN red list.

#### Sandracottus maculatus (Wehncke, 1876)

Figs 10, 21, 24, 39, 41, 43, 44, 56

Hydaticus maculatus Wehncke, 1876: 196 (type locality "Siam" [Thailand]).

- Sandracottus wehnckei J. Balfour-Browne, 1944: 355, replacement name for Hydaticus maculatus Wehncke, 1876 (objective synonym of Hydaticus maculatus); Vazirani 1969: 277 (descr., syst.); 1977: 86 (cat.); Nilsson 2001: 84 (cat.).
- Sandracottus maculatus (Wehncke, 1876): Sharp 1882: 686 (comb. nov.); Régimbart 1899: 338 (descr.); Zimmermann 1920: 235 (cat.); Ghosh and Nilsson 2012: 18 (cat.); Balke et al. 2017: 146 (faun., habitat); Atthakor et al. 2018: 93 (faunistics, habitat); Hájek and Nilsson 2024: 91 (cat.).
- Sandracottus angulifer Heller, 1934a: 280 (type locality Davao, Mindanao, Philippines); Hájek and Nilsson 2024: 91 (cat.) (syn. nov.).
- Sandracottus palawanensis Satô, 1978: 41 (type locality Sabang, Palawan, Philippines); Hájek and Nilsson 2024: 91 (cat.) (syn. nov.).
- Sandracottus nauticus Sharp, 1882: 690 (type locality Borneo); Régimbart 1899: 339; Zimmermann 1920: 235 (cat.); Hájek and Nilsson 2024: 91 (cat.) (syn. nov.).

**Type material of** *Sandracottus maculatus. Neotype* (herein designated): Male, "Schoenich" [?], "Cambodscha" [yellowish handwritten label], "Ex. Coll. E. WEHNCKE Acq 1884" [white printed label], "NEOTYPUS Hydaticus maculatus L. Hendrich & M. Brancucci des. 2010" [red printed label] (MNHN). Examined.

**Comments on classification.** It was impossible to find any type material labelled "Siam" among the historical specimens in the NHMUK, MNHN, and ZHMB, so we decided to designate a neotype from Cambodia found in Wehncke's collection and deposited in MNHN. The neotype is designated to support taxonomic stability, as there are several morphological similar *Sandracottus* species described from the Indomalayan region, and it is paramount for present and future investigations to possess unambiguously characterised name-bearing specimens for all Indomalayan species of the genus.

**Type material of Sandracottus angulifer. Holotype**: Male, "Davao Mindanao Baker", "7251", "S. angulifer Typus" [red label], "1932 12", "Staatl. Museum für Tierkunde, Dresden", "Sandracottus maculatus (Wehncke, 1876) Hendrich & Brancucci det. 2006" (SMTD). Examined.

**Type material of** *Sandracottus palawanensis. Holotype*: Male, "Sabang, Palawan Philippines July 13, 1977 M. Sâto leg." [handwritten], "HOLOTYPE Sandracottus palawanensis M. Satô DET. M. SATÔ 1978" [red label], "Sandracottus maculatus (Wehncke, 1876) Hendrich & Brancucci det. 2010" (NMST). Examined.

**Type material of** *Sandracottus nauticus. Holotype*: Male, "Borneo 987 nauticus", "Type H.T.", "Sharp Coll. 1905-313" (NHMUK). "*Sandracottus maculatus* (Wehncke, 1876) Hendrich & Brancucci det. 2006". Examined.

Additional material. (150 specimens): · CAMBODIA: 1 ex., "Cambodia Pailin 200 m 11.-16.VI.2008 S. Murzin leg. Coll. Hendrich" (CLH). • LAOS: 7 exs., "LAOS centr., Kham Mouan Prov. Nakai vill. env. ca 70 km NNE Muang Khammouan, 500-600 m 17°43'N, 105°09'E, 7.-25.V.2002 M. Strba leg./Coll. HEN-DRICH" (CLH); 1 ex., "LAOS south, Attapeu prov. Bolaven Plateau 18.-30.IV.1999, 15 km SE of Ban Houaykong, NONG LOM (lake) env., N 15°02' E 106°35', alt. 800 m, E. Jendek & O. Sausa leg." (CLH); 1 ex., "Champasak Prov., Ban Nam Touad env. (near Xe Katamtok), village, agricultural lands, old secundary and degraded primary forest, light trapping, 500-800 m, 15°06'N, 106°35-38'E, 8.-10.VI.2010, leg. M. Geiser & D. Hauck" (NHB); 1 ex., "Northern Vientiane Prov. Vang-Vieng, 300 m, N 18°55.23 E 102°26.55, 10.-15.V. & 1.-6.VI.2001, J. Kolibac leg." (NMB); 1 ex., "Umg. Vientiane, III.-IV.1963, coll. M. Brancucci" (NMB); 2 exs., "Khammouan Prov., Ban Khoun Ngeun, 200 m, 18°07'N 104°29'E, 24.-29. IV.2001, V. Kuban leg." (NMB); 8 exs., "Khammouan Prov., Nakai env., 500-600 m, 22.V.-8.VI.2001, 17°43'N 105°09'E, E.Jendek & O.Sausa leg." (CHH, NMPC); 1 ex., "CHAMPASAK prov., Bolavens Plateau, waterfall ca., 2 km E TAD KATA-MTOK, 15°08.1'N, 106°38.8'E, 415 m, 10-12.V.2010, J. Hájek leg." (NMPC). • THAILAND: 1 ex., "N-Thailand, Khon Kaen Prov., Si Chom Phu, 220 m, 16°8531N, 102°2526E R. Ohnesorge, IX.2012", "coll. A. Skale Hof/Germany" (CAS); 1 ex., "Thailand 25 V 52 REElbel", "Kanchanaburi" (USNM), 14 exs., "Nakhon Ratchasima Province, Sakaerat Biosphere Reserve, King Cobra Cave, Thailand Coords: 14°30.536' N, 101°55.921' E, 362 m a.s.l., 27 Oct 2013, W. Atthakor leg., Sakaerat Expedition, led by Professor Somsak Panha of Chulalongkorn University" (CSUT); 1 ex., "N Thailand, Doi Pho Ka N.P. Road from Pua 1 km after Park Hq. m 1400, small pools on rock (24) 2.I.1999 P. Mazzoldi leg." (CPM); 2 exs., "Siam: MeSong Forest IV.1919 E.J.Godfrey 1920-244" (NHMUK); 2 exs., "E Thailand, Ko Chang White Sands Beach, 10.XII.1990, M.Jäch leg. (12)" (NMW); 1 ex., "Prov. Rayong, Khao Chamao NP, 12. &13.XII.1990, M.Jäch leg. (14)" (NMW); 1 ex., "Tham Sakoen NP, No. 21, 29.-30.XI.2003, 19°23'N 100°38'E, Peregovits, Foldvari, Korosi, Szappanos & Maklari-Kis leg." (TDMB); 2 exs., "Pak Lag, 14.VIII.1918, Jeanvoine" (MNHN); 17 exs., "Pak Lag 13.VIII.1918 V. de Salvaza" (MNHN); 6 exs., "Pak Lag, 13.VIII.1918 V. De S.", "Samml. A. Zimmermann" (ZSM); 3 exs., "Pak Lag 18.VII. 1918 no. 2119 V. de S." (MNHN, ZSM). 2 exs., "Thailand, E Bangkok, Nakhon Nayok: Khlong Maduea, 14°21'17"N, 101°16'22"E, 16.03.2017, leg. H. Shaverdo" (NMW); 3 exs., "Thailand, Phetchabun Province, near Nam Nao National Park, Route 2216 then small road off, in village Khlong Choen, 16°40'29"N, 101°44'01"E 21.03.2017, leg. H. Shaverdo" (NMW). • VIET-NAM: 1 ex., "VietnamN, Quang Binh prov. 1 km N of Cha Lo, 400 m Vietnam-Laos border area 17°41'22''N 105° 45'45''E, L. Dembicky leg., 11.-24.iv.2010" (NMB); 1 ex., "Tonkin Env. De Hoa Binh J. Laisi 1902", "S. maculatus Wke", "Dr. Régimbart vidit 1905" (MNHN); 1 ex., "Museum Paris Cochinchine" (MNHN); 3 exs., "Hoa Binh Tonkin" (MNHN); 3 exs., "Lactho Tonkin A.de Cooman" (MNHN); 1



**Figures 43–45.** Habitats of *Sandracottus* **43, 44** Malaysia, Sabah, Kinabatangan riv. 8.-15.VI.2003, Uncle Tan's camp, habitat of *S. maculatus* (photos: J. Šťastný) **45** Indonesia, Sulawesi, Togian Islands, Kaldidiri Island near Paradise Island Resort, Babirusa puddles (on the left), habitat of *S. rotundus* (photo: J. Haft).

ex., "S Vietnam, Saigon, jardin botanique [botanical garden], octobre 1870, A. Krempf leg." (MNHN); 1 ex., "Hoa Binh (Tonkin) A. de Cooman" (MNHN); 3 exs., "Hoa Binh (Tonkin) A. de Cooman" (MNHN); 2 exs., "Tonkin occ. env. de Hoa Binh 1919 A. de Cooman" (MNHN); 4 exs., "S-Vietnam, Nam Cat Tien NP, 1.-15.V.1994, Pacholatko & Dembicky leg." (NMW); 1 ex., "Vietnam, Dong NAI, Nam Cat Tien NP, 120 m, 18-IX-1998, leg. L. J. Wang" (CLJW). • MALAYSIA: "E-Malaysia, Sabah Borneo, Mt. Trus [= Trusmadi or Trus Madi] March-April 2010 Local leg.", "coll. A. Skale Hof/Germany" (CAS); 1 ex., "NE Borneo Sandakan, Coll. Guignot" (MNHN); 1 ex., "Hydaticus sp.? Pinang" [West Malaysia, Penang], "maculatus Wehncke" [handwritten label by Régimbart] (MNHN); 1 ex., "Borneo

Sandakan Windrath", "nauticus Shp" (MNHN), 1 ex., "Borneo, Kinabalu [Sabah], Whitehead, Fry Coll. 1905-100" (NHMUK); 1 ex., "Borneo 987, Sharp Coll. 1905-313" (NHMUK); 3 exs., "Borneo, Sabah, Kampung Pisang, Pisang env., tributary of Kuamut river, 29.VI.1998, J.Kodada & F.Ciampor leg." (NMW); 1 ex., "Borneo Sabah, Hot Springs, 26.V.1999, Bacovský leg." (NMPC); 20 exs., "Borneo, Sabah, Sungai Kinabatangan, stream near Danau Blandung Besar, 11.IV.1994, H.K. Lua leg." (CLH, ZRC); 2 exs., "Sabah, Kinabatangan riv. 8.-15.VI.2003, Uncle Tan's camp, J.Šťastný leg." (CJS); 1 ex., "Dindings 96-85" [Malaysia, Perak, Manjung District], "Determined by Dr Régimbart Sandracottus maculatus v. nauticus Sharp"; 1 ex., "Ex. Coll. E.Wehncke Acq 1864" (MNHN); 3 exs., "West Malaysia, Penang 988, Sharp Coll. 1905-313" (NHMUK); 5 exs., "West Malaysia, Penang, Pascoe Coll. 93-60" (NHMUK). • INDONESIA: 1 ex., "Ned. Indie Leg. A. Koller", "Coll. F.C. Drescher" (RMNH); 5 exs., "Sumatra Palembang M. Knappert" (RMNH); 7 exs., "East Kalimantan, Distr. Damai 12.VII.1995 Ngelung Stream Mazzoldi P. leg." (CPM); 1 ex., "East Kalimantan 12. VII. 1995, Distr. Tingai stream near Sembuan, opening in forest - leg. P Mazzoldi" (CPM); 1 ex., "Java Occ. Toeroe 1902", "Museum Paris ex. Coll. Oberthür 1952" (MNHN); 1 ex., "Java ex. J. Waterstradt 1904" (NMHN); 1 ex., "Java", "maculatus Wehncke (MNHN); 1 ex., "Malang Java" (MNHN); 1 ex., "Java, Prov. Pasuruan Kalipari, 300–500 m, 1891, W.Doherty leg." (MNHN); 1 ex., "Java, Blume leg." (RMNH); 1 ex., "Java, Muller leg." (RMNH); 4 exs., "Z.-Sumatra, Ranau, 500-700 m, Juli 35" (RMNH); 1 ex., "SW Java, Gautang Bay, III.1937, M.A.Lieftinck leg." (MNHN); 3 exs., "Sumatra, Palembang" (MNHN); 1 ex., "Sumatra, Dolok Merangir, 8.V.-10.VI.1983, E.W.Diehl leg." (NMB); 1 ex., "Mentawai Islands, Siberut, 5-50 m, 3.IV.2005, S.Jákl leg." (NMPC); 2 exs., "Sumatra, Palembang Coll. Peschet" (MNHN); 2 exs., "Sumatra Palembang", "Samml. A. Zimmermann" (ZSM); 1 ex., "Sumatra Medan Hayek leg. (ZSM). • PHILIPPINES: 1 ex., "Mindanao Davao XII.1932, Baker leg." (SMTD); 1 ex., "Mindanao" (MNHN); 1 ex., "Philippines: Luzon, Bicol, Camarines Sur, Lagonoy ca. 13°44'15.7"N, 123°31'16.1"E 09.2019 leg. local collector" (CLW).

**Remarks.** Specimens from Borneo and Sumatra with reduced yellow basal markings on elytra (habitus near *femoralis*) were described as *S. nauticus* Sharp. In the shape of the median lobe of aedeagus, some specimens from Borneo lies between *S. femoralis* and *S. maculatus* from mainland Asia. Furthermore, we do not have any molecular data for either form, so we here list *S. nauticus* as an objective junior synonym of *S. maculatus*.

**Redescription.** Body large, broad oval, submatt, only slightly shiny, black with ferrugineus brown markings. Ventral side completely dark brown to black, legs testaceous, hind legs somewhat darker.

Head testaceous with posterior part broadly black leaving free two small testaceous spots on vertex (Figs 10, 56). Surface submatt, shagreened, consisting of dense and minute punctures but not very uniform in size and of larger and much sparser ones, more numerous on frons. Clypeal grooves and punctures alongside eyes marked, punctures medium-sized but coalescent. Antennae testaceous; antennomeres slender, antennomere V 4× as long as broad.

Pronotum black with margins broadly testaceous, submatt (Figs 10, 56). Surface distinctly shagreened, with very dense punctation; punctures medium-sized and distant of only  $1-2\times$  their own diameter. Anterior puncture line interrupted in middle; punctures relatively small but coalescent, building wrinkles and becoming sparse towards middle and lacking in very middle of anterior margin. Posterior puncture line with coarse and coalescent punctures in middle of each sides building distinct wrinkles, distinctly smaller and spaced on disc.

Elytra black with testaceous markings consisting of one basal band sometimes reduced to different spots at base, one postmedian band, one preapical short and reduced band, and an apical spot (Figs 10, 56), submatt. Epipleura ferrugineus brown. Surface distinctly shagreened and covered with small and dense punctures as well as with larger and much more sparser ones. Puncture lines with groups of medium-sized punctures mostly grouped by five or six punctures; groups closer together on discal row. Sutural puncture line marked only by few punctures on apical part.

Ventral side dark brown. Legs particularly fore and mid legs testaceous, hind legs ferrugineus brown to dark brown. Prosternal process short and broad, 1.4× longer than broad, flattened finely but distinctly sculptured; posterior margin broadly rounded. Metatibia with sparse medium-sized punctures on whole surface. Ventrites II–VI very superficially shagreened, slightly and longitudinally wrinkled on lateral parts, densely covered with very small punctures and larger sparser ones. Posterior margins rounded, deeply bordered with some large coalescent punctures on middle of each side along margin.

Measurements: TL = 13.4-16.6 mm, TL-h = 13.1-15.2 mm, TW = 8.5-10 mm.  $\bigcirc$ . Protarsomeres I–III strongly enlarged with three larger suckers and numerous smaller one. Mesotarsomeres I–III with two rows of small suckers. Median lobe of aedeagus, in ventral view, elongate, parallel-sided on complete length, lobes narrowly rounded at apex (Fig. 21a). Parameres narrow and elongate, and slightly longer than median lobe (Fig. 21b).

 $\mathbb{Q}.$  Similar to male. Pro- and mesotarsi not enlarged. Microsculpture on ventrite VI as in male.

**Differential diagnosis.** The species is clearly distinguished from all other Indomalayan species of the genus by its colouration and larger size. It is the largest species of the genus. From the dorsal colouration *S. maculatus* is near to *S. femoralis* which is generally smaller in size (see *S. femoralis*). Furthermore, both species can be separated by the shapes of their median lobes.

**Distribution.** Cambodia, Laos, Thailand, Vietnam, Malaysia (Sabah), Indonesia (Kalimantan, Sumatra, Java, Siberut) and Philippines (Luzon, Mindanao, Palawan) (Fig. 24). Specimens were collected from approximately sea level to 800 m a.s.l.

**Habitat.** A widespread but rare species. According to various collectors all recent records are from well vegetated pools, forest pools, or rest pools of intermittent streams and rivers, mainly located in primary rainforest (Fig. 43). At least most habitats are partly shaded and enriched with decaying leaves and twigs (Fig. 44). In Thailand (Sakaerat Biosphere Reserve) the species was collected at the end of the dry season in a rest pond of a rocky stream, with very dark water and accumulated leaf litter. The pond was more or less permanent but with a high fluctuation of water level (Fig. 41). The species was collected in shallow water made by a passing jeep on a path. Syntopically occurring dytiscid species include *Leiodytes kualalipis* Balke, Wang, Bergsten & Hendrich, 2017, *L. nicobaricus* (Redtenbacher, 1867), and *Hydroglyphus orientalis* (Clark, 1863) (Balke et al. 2017). In Laos, *S. maculatus* was collected in a residual pool near the river (Fig. 39). The pool had a diameter of nearly 1 m, depth was ~ 40 cm, bottom with a thick layer of decaying leaves (Hájek pers. comm. 2023).

### Sandracottus rotundus Sharp, 1882

Figs 11, 22, 27, 45, 57

Sandracottus rotundus Sharp, 1882: 688 (type locality "Celebes" [Indonesia, Sulawesi]); Régimbart 1899: 337 (descr.); Zimmermann 1920: 235 (cat.); Hájek and Nilsson 2024: 91 (cat.).

**Type material.** *Holotype*: Male, "Type H.T.", "Celebes 985 rotundus", "Sharp Coll. 1905-313" (NHMUK). Examined.

Additional material. (80 specimens): • INDONESIA: 1 ex., "INDONESIA, N-Sulawesi vic. Raja Basar b. Moutong, 15 m N 0°29'78" E 121°12'99", 28.II.2009, river valley (\*016\*), A. Skale leg." (CAS); 2 exs., "Minahassa, Celebes" [Minahasa, Sulawesi] (RMNH); 5 exs., "Rosenberg, Toelabollo, Celebes" [Tulabalo, Sulawesi] (MNHN, RMNH); 1 ex., "Indonesia, Celebes" [Sulawesi] (NHMUK); 1 ex., "Indonesia, C-Sulawesi, 45 km SE Palu, 1994, 01°11'S 120°08'E, J. Haft leg. (5)" (NMW); 1 ex., "Indonesia, Sulawesi Utara, Dumoga Bone N.P., XI.1985, Rothamsted light trap, site 1, 200 m, H.Barlov leg." (NHMUK); 1 ex., "Indonesia, Sulawesi Utara, Dumoga Bone N.P., 17.I.1985, Iowland forest 200-300 m", "R. Ent. Soc. London Project Walace B.M. 1985-10" (NHMUK); 1 ex., "Indonesia, Sulawesi Utara, Dumoga Bone N.P., 6.II.1985, site 5, Tumpah transect, 300 m, J.D. Holloway leg." (NHMUK); 1 ex., "Indonesia, Sulawesi Togian Islands, Pulau Togian, river in forest south of Wakai, 5.-17.VIII.1987, D.T. Bilton leg." (CLH); 16 exs., "Sulawesi Togean Islands, Kadidiri Island interior, 30 m, 28.viii.2011, 00 21.531S 121 50.959E (SUL005)" (MZB, ZSM); 50 exs., "Indonesia, C-Sulawesi, Togian Islands, Kaldidiri Island near Paradise Island Resort, 50 m, S 00°21 E 121°50, 12.-15.II.1997, J. Haft leg." (CLH, CJS, NMB, NMPC).

**Redescription.** Body broad oval, shiny, testaceous with black markings. Ventral side completely dark brown to black, legs testaceous, hind legs somewhat darker.

Head testaceous with posterior part and broadly so on posterior half alongside as well as two elongate spots on clypeus black, shiny (Figs 11, 57). Surface almost smooth consisting of dense and very numerous punctures of different size and of larger, much sparser ones, particularly numerous on frons. Clypeal grooves, punctures alongside eyes and transverse depression beside eyes distinctly impressed, punctures large and coalescent. Antennae testaceous; antennomeres slender, antennomere V 4.5× as long as broad.

Pronotum black with broad lateral testaceous markings (Figs 11, 57). Surface very superficially shagreened, almost not visible, with dense punctation; punctures medium-sized mixed with smaller ones. Anterior and lateral puncture lines dense and coalescent, punctures becoming sparse towards middle and lacking in very middle of anterior margin. Posterior puncture line with coarse and coalescent punctures on middle of each side, distinctly smaller and spaced out on disc.

Elytra black with five testaceous markings, consisting of one basal, two lateral, one just behind middle, and one posterior apical one (Figs 11, 57). Epipleura testaceous to ferrugineus brown. Surface very slightly and superficially shagreened and covered with double punctation, smaller and denser ones as well as larger much sparser ones. Puncture lines with groups of medium-sized punctures mostly grouped by five or six punctures; groups closer together on discal line.



**Figures 46–49.** Colouration and habitus of **46** *Sandracottus bakewellii bakewellii* (Australia, Northern Queensland, Atherton Tableland, Mareeba) **47** *S. bakewellii guttatus* (Australia, Northern Territory, Ormiston Gorge) **48** *S. bizonatus* (Borneo, Sabah, Keningau) **49** *S. chevrolati* (Indonesia, Sumba Island, Waingapu).

Ventral side dark brown. Legs particularly fore and mid legs testaceous, hind legs ferrugineus brown to dark brown. Prosternal process short and broad, 1.3× longer than broad, flattened finely but distinctly sculptured. Posterior margin broadly rounded. Whole surface very superficially shagreened and finely punctured. Metatibia with sparse medium-sized punctures on outer half. Ventrites II–VI very superficially shagreened, slightly and longitudinally wrinkled on lateral parts, complete surface densely covered with very small punctures and larger sparser ones. Posterior margins rounded, bordered with some large and coalescent punctures on middle of each side.



Figures 50–53. Habitus of 50 Sandracottus dejeanii (India, Himachal Pradesh, Kangra Valley, Dharamsala) 51 S. festivus (Sri Lanka, Ratnapura, Sincharaja 52 S. femoralis (Indonesia, West Papua, Kapupaten Paniai, Nabire) 53 S. hunteri (China, Central Sichuan).

Measurements: TL = 12.4-12.8 mm, TL-h = 11.4-11.9 mm, TW = 7.6-7.9 mm.  $\bigcirc$ . Protarsomeres I–III strongly enlarged with three larger suckers and numerous smaller ones. Mesotarsomeres I–III with two rows of smaller suckers. Median lobe of aedeagus in ventral view broad, constricted medially, parallel-sided in apical part up to apex, here slightly broadened and broadly rounded (Fig. 22a). Parameres broad and strongly pointed at apex, slightly longer than median lobe (Fig. 22b).



Figures 54–57. Habitus of 54 Sandracottus jaechi (holotype, Sri Lanka, Nuwara Eliya) 55 Sandracottus insignis (Philippines; Luzon, Los Banos) 56 S. maculatus (Borneo, Sabah, Sungai Kinabatangan) 57 S. rotundus (Indonesia, Sulawesi, Togian Islands, Kaldidiri Island).

♀. Similar to male, tarsi not enlarged. Microsculpture on ventrite VI as in male. Differential diagnosis. The species is well distinguished from all other Oriental species of the genus by its colouration and roundish oval body. From the dorsal colouration *S. rotundus* is near to the Australian *S. bakewellii bakewellii* (Figs 1, 46) which is generally more elongated. Furthermore, both species can be separated by the shapes of their median lobes (Figs 12a, b, 22a, b).

**Distribution.** Indonesia: northern and central Sulawesi including Togian Islands (Fig. 27). Specimens were collected between 30 and 300 m a.s.l.

**Habitat.** Sandracottus rotundus seems to be restricted to stagnant water bodies in primary lowland forests of northern and central Sulawesi and their adjacent islands. All specimens on Kaldiri Island were obtained from muddy forest pools (depths up to 30 cm) and from shallow water of a forest lake not far from the sea. According to Jan Haft (pers. comm. 1998) those pools were frequently used and probably created by Babirusas [*Babyrousa togeanensis* (Sody, 1949)] (Fig. 45). Co-occurring species include the rare *Cybister aterrimus* Régimbart, 1899, *Hydaticus* species of the *pacificus* group, and some unidentified *Copelatus*.

**Conservation.** A rare species recorded from a very restricted area in Indonesia. Most probably the species is associated with the declining primary lowland rainforests on the island Sulawesi. It is recommended to be listed in the next IUCN red list.

# Key to all species of genus Sandracottus

1	Dorsal and ventral side completely black, without any yellowish markings
	of Sri Lanka Sizechi Wewalka & Vazirani 1975
_	Dorsal surface with vellowish markings ventral side black to reddish-brown
	and appendages dark brown to reddish brown
2	Pronotum mainly black laterally testaceous
_	Pronotum mainly vellowish, with black margins anteriorly and posteriorly 6
3	Pronotum with narrow, testaceous, lateral margins, and/or testaceous,
	horizontal band, interrupted medially. Elytron black, with several smaller
	testaceous markings and spots4
-	Pronotum with broad, testaceous, lateral margins. Elytron black, with large
	testaceous markings5
4	Larger species, TL = 13.4-16.6 mm. Horizontal testaceous band on pro-
	notum vague and almost invisible (Figs 10, 56). Thailand, Laos, Vietnam,
	Cambodia, Malaysia, Indonesia to the Philippines
	S. maculatus (Wehncke, 1876)
-	Smaller species, $TL = 11.9 - 12.6$ mm. Horizontal testaceous band on pro-
	notum well developed (Figs 6, 52). Moluccas, New Guinea, Solomon Is-
-	lands
5	Elytron with three large testaceous markings (Figs 2, 48). Endemic to Bor-
_	Elutron with five lorger testessource markings (Figs 11, 57), Endemis to Su
-	Lawosi S rotundus Sharp 1992
6	Elytron mainly testaceous with black markings consisting of three trans-
0	verse bands: a broad antermedian, a subanical and an anical one (Figs 7
	53). Larger species, $TL = 12.5-15$ mm. Widespread in India, China, and
	Southeast Asia (Fig. 53)
_	Elytron mainly black with testaceous markings
7	Species distributed in Australia
-	Species distributed in India and Southeast Asia9
8	Elytron black, with large basal, subbasal and apical band testaceous (Figs
	1, 46). Northern and eastern coastal Australia
	S. bakewellii bakewellii (Clark, 1864)
-	Elytron black, with small basal, subbasal and apical dots testaceous (Fig.
	47). Central AustraliaS. bakewellii guttatus (Sharp, 1882)

- Smaller species, TL = 12.0–13.5 mm ......10
- 10 Anterior and posterior black band of pronotum not connected medially. Species with one connected (Fig. 55) or two separated broad testaceous subbasal markings on elytron (Fig. 8), TL = 12.5–13.1 mm. Philippines ......
   S. insignis (Wehncke, 1876)
   Anterior and posterior black band of pronotum connected medially ......11
- 11 Elytron particularly characterised by the presence of several longitudinal testaceous subsutural spots (Figs 3, 49). TL = 13.0–13.5 mm. Indonesia, Lesser Sunda Islands east of Wallace Line, Tanimbar, Timor, SE Sulawesi.
  S. chevrolati (Aubé, 1838)
- Elytron black to dark brown with testaceous markings in form of a chessboard, the testaceous markings alternating with the black ones (Figs 4, 50).
   TL = 12.0–13.0 mm. India, Pakistan, Nepal, SE Iran....S. dejeanii (Aubé, 1838)

# Discussion

### Habitats

Just 30 years ago, almost nothing was known about the habitat requirements of these attractive and large diving beetles. Most of the Oriental species were only known from old dusty museum specimens without any habitat information. From time to time, single specimens of *S. hunteri*, *S. chevrolati*, and *S. dejeanii* were offered for sale at insect fairs, collected by anonymous local collectors most probably with light traps. Occasionally, living specimens of *S. hunteri* were offered in aquarist and pet shops via the internet.

The Oriental Sandracottus, except S. hunteri and S. chevrolati, are typical inhabitants of primary or very old secondary growth rain forests which are not, or only slightly, disturbed by human influences, whereas the two subspecies of the Australian S. bakewellii and the Indian S. dejeanii and S. festivus can be found mainly in side-pools or shaded rest pools of intermittent creeks and streams. On the Indian subcontinent single specimens of S. dejeanii and S. festivus are recorded from all kinds of lentic habitats. The bottom of the water bodies may be stony if it is a residual pool on a rocky riverbed, or sandy or gravelly if it is a rest pool or a sheltered inlet in a small stream, or muddy if it is a forest or woodland pool. In general, the bottom is enriched with a fine detritus of rotten, decaying leaves, twigs, or smaller logs.

It is supposed that the completely black-coloured *S. jaechi* from the highlands of Sri Lanka is restricted to high altitude peatland ponds and mires with dark bottom. The most eurytopic species is *S. hunteri*, inhabiting woodland pools, puddles, and ditches, often rich in emerged and submerged vegetation (Myanmar, west Malaysia, and Thailand), forested and swampy lake margins (Laos), rest pools of intermittent streams (India, Indonesia), and irrigation channels of paddy fields and open flooded meadows (Thailand, Vietnam, China).

For the Southeast Asian species (*S. bizonatus*, *S. insignis*, and *S. maculatus*) the population density seems to be quite low as only small numbers of beetles have been found at one spot. Only in *S. chevrolati*, *S. hunteri*, and *S. rotundus* are aggregations of a dozen or more specimens known (Balke, Hornburg, and

Hájek pers. comm. 2015). It is noteworthy that at many localities immature specimens were observed but no larvae. The larvae of most species, except *S. dejeanii* (Vazirani 1971), *S. hunteri*, and *S. femoralis* (Alarie et al. 2023), remain unknown. Some species may be sympatric and sometimes syntopic: In India *S. dejeanii* and *S. festivus* often co-occur, and in Laos, Thailand, and Indonesia *S. hunteri* and *S. maculatus* were collected in the same pools. Co-occurring dytiscid species mainly include various *Hydaticus* sp. of the *pacificus* group and the *fabricii* group, *Copelatus* sp., *Hyphydrus* sp., *Laccophilus* sp., different Bidessini, and occasionally *Cybister* species.

All species are capable to flight. Referring to the label data specimens of *Sandracottus bakewellii bakewellii*, *S. festivus*, *S. femoralis*, *S. hunteri*, and *S. rotundus* were obtained by operating light traps.

## Zoogeographic conclusions

A total of 1,649 specimens were studied for this revision, including all the available material from relevant museums in Europe and Australia. Thanks to this large amount of old and freshly collected material, it is now possible to draw some zoogeographic conclusions. The genus Sandracottus is distributed throughout the Oriental and Australasian realms, and occurs in the north from east Nepal, throughout central and southern China, South Korea, the Philippines to Borneo, Sumatra, Java, and Australia in the south. In the east, the distribution of two probably sister species S. hunteri and S. chevrolati are strictly defined by the Wallace line as S. hunteri is replaced on Sulawesi, from the Sunda Islands east of Bali, Timor, and Tanimbar by S. chevrolati. In the west S. dejeanii can be found in some wadis of Baluchistan, south-eastern Iran. Only one species, S. femoralis, is widespread in New Guinea and on the Moluccas. Sandracottus bakewellii is endemic to Australia with one subspecies in the north and along the east coast south to Brisbane (S. b. bakewellii), and a separated subspecies with a limited distribution in the red center of the continent (S. b. guttatus). Sandracottus hunteri is the most widespread species of the genus and is distributed from India, central and southern China, to southern Korea and the whole Southeast Asian region, excluding Borneo, west of the Wallace line. The four remaining species have very restricted distributions. One species is restricted to the Philippines (S. insignis), one to Borneo (S. bizonatus), and another to Sulawesi and some adjacent islands (S. rotundus). The species with the most restricted distribution is S. jaechi, known only from Nuwara Eliya, a mountain region (1300 m a.s.l.) in central Sri Lanka. In Malaysia, Indonesia, Thailand, and Vietnam the genus can be found at altitudes from around sea level (S. hunteri, S. chevrolati, S. insignis, S. rotundus, and S. maculatus) to 700 and 800 m a.s.l. (S. femoralis, S. maculatus). In India, China, and Pakistan S. dejeanii, S. festivus, and S. hunteri can be found from 100 to more than 2000 m. The altitudinal record is held by a single S. hunteri collected at 2900 m in Darjeeling District in northeastern India. The maps (Figs 23-30) show that more than half of the species occur in the central part of the Oriental region: in Myanmar, Thailand, Laos, Vietnam, Malaysia, Indonesia, and Philippines. This region can certainly be considered as a center of speciation of the genus Sandracottus.

### **Conservation aspects**

The Southeast Asian species *S. bizonatus*, *S. insignis*, and *S. rotundus* are associated with lentic or slow flowing habitats (pools, puddles, smaller lakes, and ditches) situated in the declining primary lowland rainforests on the islands Sulawesi, Borneo, and the Philippines. Based on the number of old specimens of *S. bizonatus* and *S. insignis* found in museum collections, it seems that both species were more common at the end of the 19<sup>th</sup> and the beginning of the 20<sup>th</sup> century than they are today. The highly endangered if not extinct *S. jaechi*, only known from three historical specimens collected at least more than one hundred years ago, is associated with the almost destroyed peatland habitats in the mountains of Sri Lanka. All four mentioned species are strongly recommended to be listed in the next IUCN red data book. Further investigations, especially on Sri Lanka, Borneo, Sulawesi, and the Philippines are needed to clarify their actual conservation status.

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# **Additional information**

## **Conflict of interest**

The authors have declared that no competing interests exist.

# **Ethical statement**

No ethical statement was reported.

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## **Author contributions**

Writing - original draft: Lars Hendrich & Michel Brancucci have written the manuscript.

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### **Data availability**

All of the data that support the findings of this study are available in the main text.

# References

- Alarie Y, Michat M, Shaverdo H, Hájek J (2023) Morphology of the larvae of *Sandracottus femoralis* Heller, 1934, and *S. mixtus* (Blanchard, 1843) and phylogenetic comparison with other known Aciliini (Coleoptera: Dytiscidae, Dytiscinae). Zootaxa 5263: 301–334. https://doi.org/10.11646/zootaxa.5263.3.1
- Anand PP, Ashiq PP, Smitha M, Adhithya M, Tibin T, Suresh V (2021) *Sandracottus vijaya-kumari* (Coleoptera: Dytiscidae), a new aquatic beetle species from landslide hit area of Nelliyampathy Forest Range, Western Ghats, Kerala, India. Journal of Threatened Taxa 13(3): 17999–18003. https://doi.org/10.11609/jott.6193.13.3.17999-18003
- Atthakor W, Hendrich L, Sangpradub N, Balke M (2018) Diving beetles of the Sakaerat Biosphere Reserve, Nakhon Ratchasima Province, with four new records for Thailand (Coleoptera, Dytiscidae). Spixiana 41(1): 91–98.
- Aubé C (1838) Hydrocanthares et gyriniens. In: Dejean P.F. Species géneral des coléoptères de la collection de M. le Comte Dejean. Vol. 6. Paris: Méquignon Père et Fils, xvi + 804 pp.
- Balke M, Jäch M, Hendrich L (2004) Insecta: Coleoptera, pp. 555–609. In: Yule, C. & Yong, L. (eds.): Freshwater invertebrates of the Malaysian Region. Academy of Sciences Malaysia, Kuala Lumpur, 868 pp.
- Balke M, Bergsten J, Wang L-J, Hendrich L (2017) A new genus and two new species of Southeast Asian Bidessini as well as new synonyms for Oceanian species (Coleoptera, Dytiscidae). ZooKeys 647: 137–151. https://doi.org/10.3897/zookeys.647.11231
- Blanchard É (1843) Insectes. In: Hombron J.B. & Jacquinot H. (eds): Atlas d'histoire naturelle zoologie. In: Voyage au pôle Sud et dans l'Océanie sur les corvettes l'Astrolabe et la Zélée, exécuté par ordre du roi pendant les année 1837-1838-1839-1840 sous le commandement de M.J. Dumont-d'Urville, capitaine de vaisseau, publié sous les auspices du département de la marine et sous la direction superieure de M. Jacquinot, capitaine de vaisseau commandant de la Zélée. Septième Livrasion. Oiseaux pls 4, 5, 6; Poissons pl. 5; Insectes coléoptères pl. 4. Paris: Gide.
- Blanchard É (1853) Description des insectes. In: Hombron J.B. & Jacquinot H. (eds): Voyage au pôle Sud et dans l'Océanie sur les corvettes l'Astrolabe et la Zélée, exécuté par ordre du Roi pendant les années 1837-1838-1839-1840, sous le commandement de M. J. Dumont-d'Urville, capitaine de vaisseau, publié par ordre du gouvernement, sous la direction superieure de M. Jacquinot capitaine de vaisseau commandant de la Zélée. Zoologie, Tome quatrième. Paris: Gide et J. Baudry, 422 pp.
- Boisduval JBA (1835) Faune entomologique de l'Océan Pacifique, avec l'illustration des insectes nouveaux recueillis pendant le voyage. 2. Coléoptères et autres ordres. Voyage de découvertes de l'Astrolabe exécuté par ordre du Roi, pendant les années 1826-1827-1828-1829, sous le commandement de M. J. Dumont d'Urville. Paris: J. Tastu, vii + 716 pp.
- Clark H (1864) Notes on the genus *Hydaticus* (Leach), with descriptions of new species. Transactions of the Royal Entomological Society of London (3) 2: 209–222 + pl. XIV. https://doi.org/10.1111/j.1365-2311.1864.tb00102.x
- Clark PF, Crosnier A (2000) The zoology of the voyage au pôle sud et dans l'Océanie sur les corvettes l'Astrolabe et la Zélée exécuté par ordre du roi pendant les années 1837-1838-1839-1840 sous le commendement de M. Dumont-d'Urville (1842–1854):
titles, volumes, plates, text, contents, proposed dates and anecdotal history of the publication. Archives of Natural History 27: 407–435. https://doi.org/10.3366/anh.2000.27.3.407

- Deb R, Subramanian KA (2023) New Records of *Sandracottus* species (Coleoptera: Dytiscidae) from Western Ghats of India. Uttar Pradesh Journal of Zoology 44(21): 10–15. https://doi.org/10.56557/upjoz/2023/v44i213663
- Freitag H, Jäch MA, Wewalka G (2016) Diversity of aquatic and riparian Coleoptera of the Philippines: checklist, state of knowledge, priorities for future research and conservation. Aquatic Insects 37(3): 177–213. https://doi.org/10.1080/01650424.2016 .1210814
- Ghosh SK (2015a) Diving beetles of Govind Sagar Wildlife Sanctuary, Himachal Pradesh, India (Coleoptera: Adephaga: Dytiscidae. Records of the Zoological Survey of India 115(1): 77–80. https://doi.org/10.26515/rzsi/v115/i1/2015/121525
- Ghosh SK (2015b) Further contribution on diving beetles from Maharashtra, India (Coleoptera: Dytiscidae). Records of the Zoological Survey of India 115(1): 81–84. https:// doi.org/10.26515/rzsi/v115/i1/2015/121526
- Ghosh SK, Gupta D (2012) Aquatic beetles of the the Great Nicobar Biosphere Reserve (Coleoptera: Noteridae, Dytiscidae and Hydrophilidae), pp. 107–120. In: Sivaperuman C, Baneryee D, Tripathy, B, Chandra K (Eds) Faunal Ecology and Conservation of the Great Nicobar. Springer Nature Singapore Pte Ltd., 666 pp. https://doi. org/10.1007/978-981-19-5158-9\_5
- Ghosh SK, Hegde VD (2015) Diving beetles of Karnala Bird Sanctuary, Himachal Pradesh, India (Coleoptera: Adephaga: Dytiscidae. Records of the Zoological Survey of India 115(1): 73–75. https://doi.org/10.26515/rzsi/v115/i1/2015/121523
- Ghosh SK, Nilsson AN (2012) Catalogue of the diving beetles of India and adjacent countries (Coleoptera: Dytiscidae). Skörvnöpparn, Umea, Supplement 3: 1–77.
- Guéorguiev VB (1965) Sur la faune des coléoptères hydrocanthares d'Iran. Bulletin de l'Institut de Zoologie et Musée, Académie Bulgare des Sciences 19: 101–117. [In Bulgarian]
- Hájek J (2006) The westernmost record of *Neptosternus circumductus*, and a review of Dytiscidae (Coleoptera) of Baluchistan (Iran, Pakistan). Acta Entomologica Musei Nationalis Pragae 46: 43–56.
- Heller KM (1934a) New and little-known Philippine Coleoptera. The Philippine Journal of Sciences 54: 279–307.
- Heller KM (1934b) Käfer aus dem Bismarck- und Salomo Archipel. Verhandlungen der Naturforschenden Gesellschaft in Basel 45: 1–34.
- Hendrich L (1995) Malaysia's predaceous water beetles. Nature Malaysiana 20(2): 46-50.
- Hendrich L, Balke M (1995) Die Schwimmkäfer der Sundainsel Bali. Faunistik, Taxonomie, Ökologie, Besiedlungsgeschichte und Beschreibung von vier neuen Arten (Coleoptera: Dytiscidae). Faunistische Abhandlungen des Museums für Tierkunde in Dresden 20(5): 29–56.
- Hendrich L, Lemann C & Weir TA (2019) 11. Dytiscidae Leach, 1815, pp. 34–60. In: Slipinski A, Lawrence J (Eds) Australian Beetles, Volume 2 – Archostemata, Myxophaga, Adephaga, Polyphaga (part). CSIRO Publishing, 784 pp.
- Hummel AD (1823) Observations sur les insectes de 1823. Monographia pelophilarum.
   Novae species. In: Hummel AD (Ed.) Essais entomologiques. Vol. 1. Nr. 3. St. Pétersbourg: Imprimerie de la Chancellerie Privée du Ministère de l'Intérieur, 48 pp. [+ 1 pl.]
- ICZN (1999) International Code of Zoological Nomenclature: adopted by the International Union of Biological Sciences. Fourth Edition. The International Trust for Zoological Nomenclature. https://www.iczn.org/the-code/the-code-online/

- Jäch MA, Li J, Zhang X, Gao M (2012) A remarkable collection of aquatic and riparian beetles from Xiachayu, Zayü County, southeastern Tibet (Gyrinidae, Noteridae, Dytiscidae, Spercheidae, Hydrophilidae, Heteroceridae, Limnichidae). Koleopterologische Rundschau 82: 65–69.
- Keilhack K (1915a) Tropische und subtropische Torfmoore auf Ceylon und ihre Flora. Vorträge aus dem Gesamtgebiet der Botanik herausgegeben von der Deutschen Botanischen Gesellschaft, Heft 2, Borntraeger, Berlin, 25 pp.
- Keilhack K (1915b) Über tropische und subtropische Torfmoore auf der Insel Ceylon. Jahrbücher der Königlich Preußischen Geologischen Landesanstalt 1905, II (1): 102–143. [+ 26 tables]
- Larson DJ (1993) Ecology of tropical Australian Hydradephaga (Insecta: Coleoptera). Part 1. Natural history and distribution of northern Queensland species. Proceedings of the Royal Society of Queensland 103: 47–63.
- Larson DJ (1997) Habitat and community patterns of tropical Australian hydradephagan water beetles (Coleoptera: Dytiscidae, Gyrinidae, Noteridae). Australian Journal of Entomology 36: 269–285. https://doi.org/10.1111/j.1440-60555.1997.tb01469.x
- Lawrence JF, Weir TA, Pyke JE (1987) Haliplidae, Hygrobiidae, Noteridae, Dytiscidae and Gyrinidae. In: Walton DW (ed.) Zoological Catalogue of Australia, Volume 4, Coleoptera: Archostemata, Myxophaga and Adephaga ed by Bureau of Flora and Fauna, Canberra. Australian Government Publishing Service, Canberra, viii + 444 pp.
- Lee D-H, Lee SH, Ahn K-J (2014) Hyphydrus falkenstromi Gschwendtner and Sandracottus mixtus (Blanchard) (Coleoptera: Dytiscidae) new to Korea. Korean Journal of Applied Entomology 53 (1): 35–38. https://doi.org/10.5656/KSAE.2013.09.0.041
- Miller KB, Nilsson AN (2003) Homology and terminology: communicating information about rotated structures in water beetles. Latissimus 17: 1–4.
- Mukhopadhyay P, Ghosh SK (2004) Insecta: Coleoptera: Adephaga (Fam. Haliplidae, Fam. Gyrinidae and Dytiscidae). Zoological Survey of India, State Fauna Series 10: Fauna of Manipur, 359–370.
- Nilsson AN (1995) Noteridae and Dytiscidae: Annotated check list of the Noteridae and Dytiscidae of China (Coleoptera). Pp. 35–96. In: Jäch MA, Ji L (Eds) Water beetles of China, Vol. 1. Wien: Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein, 410 pp.
- Nilsson A, Hájek J (2024) A world catalogue of the family Dytiscidae, or the diving beetles (Coleoptera, Adephaga). Version 1. I. 2024. Distributed as a PDF file via Internet, 323 pp. http://www.waterbeetles.eu/documents/W\_CAT\_Dytiscidae\_2024.pdf
- Ninje Gowda N, Vijayan VA (1992) Predatory behaviour of *Sandracottus festivus* on mosquito larvae and temporal changes in the density of prey and predator sewage tanks. Annals of Entomology 10: 29–32.
- Park HC, Lee HE, Lee YB, Han M-J (2009) Taxonomic review of the subfamily Dytiscinae Leech, 1815 of Korea (Coleoptera: Dytiscidae). International Symposium for the 11<sup>th</sup> Hampyeong Butterfly Festival, Hampyeong-gun Apr. 24–25, 2009. Program and Abstracts, 47 pp.
- Régimbart M (1877) Description de douze nouvelles espèces d'hydrocanthares recueillis à Manille par M. Baër [sic!]. Bulletin Bimensuel des Séances de la Société Entomologique de France 1877 (8) (Séance du 25 Avril): 99–100.
- Régimbart M (1899) Révision des Dytiscidae de la région Indo-Sino-Malaise. Annales de la Société Entomologique de France 68: 186–367. https://doi.org/10.1080/2168635 1.1899.12279737

- Satô M (1978) Two new dytiscid beetles from Palawan, the Philippines. Bulletin of the National Science Museum (A, Zoology) 5: 39–42.
- Shankar S, Kumar D, Deepa J, Madasamy K, Jadhav S, Kunte KB (2023) Aquatic beetles (Insecta, Coleoptera) of Koundinya Wildlife Sanctuary, Andhra Pradesh, India. Journal of Insect Biodiversity and Systematics 9(3): 449–467. https://doi.org/10.52547/jibs.9.3.449
- Sharp D (1882) On aquatic carnivorous Coleoptera or Dytiscidae. The Scientific Transactions of the Royal Dublin Society (2) 2: 179–1003. [+ pls. 7–18] https://doi. org/10.5962/bhl.title.9530
- Sharp D (1884) The water-beetles of Japan. The Transactions of the Entomological Society of London 1884: 439–464.
- Shaverdo H, Nasserzadeh H, Esfandiaric M, Wewalka G, Hájek J (2024) Diving beetles (Coleoptera: Dytiscidae) of Iran with province distribution based on literature records and new faunistic data. Aquatic Insects 45(2): 126–259. https://doi.org/10.1080/01 650424.2023.2280271
- Sheth SD, Padhye AD, Ghate HV (2024) Faunal inventory and illustrated taxonomic keys to aquatic Coleoptera (Arthropoda: Insecta) of the northern Western Ghats of Maharashtra, India. Journal of Threatened Taxa 16(3): 24854–24880. https://doi. org/10.11609/jott.5821.16.3.24854-24880
- Sonali S, Ghosh SK, Basu P, Gupta D (2022) Water beetles (Coleoptera: Dytiscidae. Noteridae and Hydrophilidae) of Hazaribagh Wildlife Sanctuary, Jharkhand, India. Records of the Zoological Survey of India 122(3): 337–343.
- Suprayitno N, Narakusumo RP, Sarino, Budi AS, Hendrich L, Hájek J, Balke M (2022) A citizen science case study to chart Indonesian biodiversity: Updating the diving beetle fauna of Bali (Coleoptera: Dytiscidae). Treubia 49(2): 115–136. https://doi. org/10.14203/treubia.v49i2.4411
- Suprayitno N, Narakusumo R, von Rintelen T, Hendrich L, Balke M (2017) Taxonomy and biogeography without frontiers–WhatsApp, Facebook and smartphone digital photography let citizen scientists in more remote localities step out of the dark. Biodiversity Data Journal 5: e19938. https://doi.org/10.3897/BDJ.5.e19938
- Vazirani TG (1969) A review of the subfamilies Noterinae, Laccophilinae, Dytiscinae and Hydroporinae (in part) from India. Oriental Insects 2 (1968): 221–341. https://doi.org /10.1080/00305316.1968.10433885
- Vazirani TG (1971) Description of the larva of the aquatic beetle Sandracottus dejeani (Aubé). Proceedings of the Zoological Society of Calcutta 24: 25–28.
- Vazirani TG (1977) Catalogue of Oriental Dytiscidae. Records of the Zoological Survey of India Miscellaneous Publication Occasional Paper 6 (1976): 1–111.
- Watts CHS (1978) A revision of the Australian Dytiscidae (Coleoptera). Australian Journal of Zoology, Supplement Series 57: 1–166. https://doi.org/10.1071/AJZS057
- Watts CHS (1985) A faunal assessment of Australian Hydradephaga. Proceedings of the Academy of Natural Sciences of Philadelphia 137: 22–28.
- Wehncke E (1876) Neue Dytisciden. Stettiner Entomologische Zeitung 37: 194–197, 356–360.

Wewalka G, Vazirani TG (1975) Two new species of Dytiscidae (Coleoptera) from Sri Lanka. Zeitschrift der Arbeitsgemeinschaft Österreichischer Entomologen 36(1984): 113–115.

- Zeng H (1989) Taxonomy of Chinese Dytiscidae in the museums of China. Abstract of Ph.D.-thesis. Guangzhou: Department of Biology, Zhongshan University, 8 pp.
- Zimmermann A (1920) Dytiscidae. In: Junk W, Schenkling S (Eds) Berlin, Coleopterorum Catalogus 4, pars 71, 326 pp.

Zimmermann A (1926) Fauna Buruana. Coleoptera, Fam. Dytiscidae. Treubia 7(2): 97-99.



**Research Article** 

## Descriptions of four species of Polyxenida Verhoeff, 1934 (Diplopoda, Penicillata) from China, including one new species and one new record

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#### Abstract

This study describes a new species of Polyxenida from China, *Lophoturus sineprocessus* **sp. nov.**, along with a species newly recorded from China: *Eudigraphis nigricans* (Miyosi, 1947), and provides additional descriptions of *Eudigraphis sinensis* Ishii & Liang, 1990 and *Polyxenus hangzhoensis* Ishii & Liang, 1990. The study conducted mitochondrial cytochrome *c* oxidase subunit I (COI) sequencing for all four species and constructed a phylogenetic tree based on the molecular data. The comprehensive morphological descriptions and molecular analyses confirm the addition of one new species and one newly recorded species for the Polyxenida fauna of China, elevating the total number of known Polyxenida species in the country from 10 to 12. The study also includes an identification key for Polyxenida species in China.

**Key words:** China, COI, *Eudigraphis*, identification key, *Lophoturus*, molecular phylogeny, millipede, *Polyxenus*, taxonomy

## Introduction

The order Polyxenida Verhoeff, 1934 belongs to the class Diplopoda, subclass Penicillata, and is the sole extant order within the subclass (Short and Vahtera 2017). Polyxenida possess elongated bodies typically ranging from 1.2 to 6 millimeters, with a soft, non-calcified cuticle (Enghoff et al. 2015). Members of this group inhabit diverse environments, with most species found under bark, in moist leaf litter, and decaying wood. Some specialized species reside in coastal environments (Huynh and Veenstra 2018a) or caves (Nguyen Duy-Jacquemin 2014). Polyxenida primarily feed on humus, algal films, lichens, and fungal hyphae (Vohland and Hamer 2013; Karasawa et al. 2020), and are preyed upon by predators such as spiders, ants, and centipedes. Currently, there are 3 families, 32 genera, and approximately 190 species of Polyxenida known worldwide, constituting approximately 1.5% of all known millipede species.



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Research on the order Polyxenida in China began relatively late. In 1990, Japanese scholar Ishii first reported *Eudigraphis taiwaniensis* Ishii, 1990 and *Lophoturus okinawai* (Nguyen Duy-Jacquemin & Condé, 1982), which are distributed in southern Taiwan (Ishii 1990). In the same year, Ishii collaborated with Liang to describe two new species from Hangzhou, Zhejiang: *Polyxenus hangzhoensis* Ishii & Liang, 1990, and *Eudigraphis sinensis* Ishii & Liang, 1990 (Ishii and Liang 1990). In 2000, Ishii and Yin reported six new species and one yet unnamed species from the northwest of Yunnan, Southwest China: *Lophoturus jianshuiensis* Ishii & Yin, 2000, *Monographis yunnanensis* Ishii & Yin, 2000, *Monographis xishuangbanna* Ishii & Yin, 2000, *Polyxenus anophthalius* Ishii & Yin, 2000, *Polyxenus triocellatus* Ishii & Yin, 2000, and *Polyxenus* sp. (Ishii and Yin 2000). Since then, there have been no further records of new Polyxenida from China.

China boasts a diverse array of climates and terrains, along with abundant natural vegetation, supporting a wide variety of animal species (Yang and Bu 2021). However, only 10 species of Polyxenida, belonging to 2 families and 4 genera, have been reported from China. Consequently, the understanding of Polyxenida species diversity in China remains limited, significantly lagging behind other arthropod groups.

In this study, the authors collected four Polyxenida species from four regions in China: *Eudigraphis nigricans* (Miyosi, 1947), *Eudigraphis sinensis* Ishii & Liang, 1990, *Polyxenus hangzhoensis* Ishii & Liang, 1990, and *Lophoturus sineprocessus* sp. nov. (Fig. 1), including one new species and one new record for China. The authors provided detailed morphological descriptions for these four



**Figure 1. A** *Eudigraphis nigricans* (Miyosi, 1947) **B** *Eudigraphis sinensis* Ishii & Liang, 1990 **C** *Polyxenus hangzhoensis* Ishii & Liang, 1990 **D** *Lophoturus sineprocessus* sp. nov. All Polyxenida photographed by Y. D. Wang.

species. Furthermore, by using DNA sequence data, we constructed a molecular phylogenetic tree to supplement the morphological analysis and compiled a key to the species of Polyxenida from China. This study represents the first report of a new species and a newly recorded species in China since Ishii's 2000 publication, increasing the known Polyxenida species in China from ten to twelve.

## Material and methods

## Specimen collection and morphological observations

Y. D. Wang collected the Polyxenida specimens and preserved them in 75% ethanol. Table 1 presents the specimen collection time and location information. The authors selected specimens for measurement, clearing, and mounting on slides using Hoyer's medium. They examined the mounted specimens using a ZEISS Axioscope 5 microscope (Germany). The Animal Collection of Chuzhou University will receive all specimens used for morphological observation, except for those severely damaged during dissection. Table 1 lists the corresponding voucher numbers.

The naming of leg segments follows the convention established by Manton (1956).

 Table 1. Specimen information including morphological identification, voucher number, collection details, and GenBank accession numbers.

Species	Voucher	Sampling sites	Sampling time	Accession No.
Eudigraphis nigricans	CZHZS3	Su Causeway, West Lake, Hangzhou, Zhejiang Province, China	April 23, 2024	PQ141065
Eudigraphis sinensis	CZHZS1	Su Causeway, West Lake, Hangzhou, Zhejiang Province, China	April 23, 2024	PQ142931
	CZNJS1	Zhongshan Mountain National Park, Nanjing City, Jiangsu Province, China	April 12, 2024	PQ142932
Polyxenus hangzhoensis	CZCZS1	Langya Mountain, Chuzhou City, Anhui Province, China	March 12, 2024	PQ142930
Lophoturus sineprocessus	CZYNS1	Menglai Rainforest Health Theme Park, Jinghong City, Xishuangbanna Dai Autonomous Prefecture, Yunnan Province, China	August 20, 2023	PQ142933

## DNA extraction and polymerase chain reaction (PCR) amplification

Through meticulous morphological examination, a total of five individuals (corresponding to five voucher numbers) were selected for DNA extraction. Total genomic DNA was extracted from each specimen using a QIAamp® DNA Micro Kit (Qiagen, Germany), following the manufacturer's protocol. A partial region of the mitochondrial cytochrome *c* oxidase subunit I (COI) was amplified by PCR using the following primers: CO1CF and CO1CR (Wang et al. 2022). PCRs were carried out in 12.5  $\mu$ I Taq PCR Master Mix (2X, Blue Dye) (Sangon Biotech, Shanghai), 0.5  $\mu$ I of each primer pair, 9.5  $\mu$ I distilled water, and 2  $\mu$ I sample DNA. The PCR cycle program included an initial denaturation at 94 °C for 3 min, 34 cycles of denaturation at 94 °C for 30 sec, annealing at 50 °C for 30 sec, elongation at 72 °C for 1 min, and a final extension at 72 °C for 10 min, with storage at 4 °C. The PCR products were directly sent to General Biology (Anhui) for purification and sequencing. New sequences were deposited in GenBank. The accession numbers are listed in Table 1.

## **Phylogenetic analysis**

In the phylogenetic analyses, we selected all COI sequences from the ingroup genera *Polyxenus (P. argentifer,* MN073978; *P. fasciculatus,* MN073933; *P. lagurus,* MN073968; *P.* sp., MN073971), *Lophoturus (L. boondallus,* MG204536; *L. queenslandicus,* MG204535; *L.* sp., MT679994), and *Eudigraphis (E. nigricans,* LC010896; *E.* sp., LC010908) available on the National Center for Biotechnology Information (NCBI); each sequence was at least 600 base pairs (bp) in length. Two species from closely related families, *Glomeris balcanica* (PP475128) and *Rhopalomeris sauda* (MT749404), were used as outgroups.

Sequence alignment was performed using MAFFT 7 (Katoh and Standley 2013), resulting in a COI alignment containing no gaps. Unrooted phylogenetic trees were constructed using maximum likelihood (ML) and Bayesian inference (BI) methods. The ML analysis was conducted using IQ-TREE 2 software (Minh et al. 2020), employing the General time reversible (GTR) model for COI sequence evolution. Bootstrap proportions (BP) for the ML analysis were assessed using 1000 replicates. Bayesian analyses were performed in MrBayes v. 3.2.7, implemented in the CIPRES Science Gateway (Miller et al. 2010 https://www.phylo.org). The BI analysis utilized the HKY85+I+G model and consisted of running four simultaneous chains for 100,000 generations, with tree sampling every 1000 generations and a 25% burn-in. Convergence of the runs was verified by an average standard deviation of <0.01.

## Taxonomy

Class Diplopoda de Blainville in Gervais, 1844 Subclass Penicillata Latreille, 1831 Order Polyxenida Verhoeff, 1934 Family Polyxenidae Lucas, 1840 Subfamily Monographinae Condé, 2008

Genus Eudigraphis Silvestri, 1948

## Type species. Eudigraphis japonica Silvestri, 1948.

**Genus diagnosis.** Adults with 13 pairs of legs and 8 ommatidia on each side. Dorso-medial (ornamental) barbate trichomes in one or two rows arranged transversely dorsal and anterior to the penicil of the telson. A small setiform hair with a round base is present on Tarsus II. *Eudigraphis* can be recognized by the presence of tergal trichomes in two lateral clusters plus an uninterrupted single posterior transverse row (Silvestri 1948).

Included species. Eudigraphis takakuwai (Miyosi, 1947), E. nigricans (Miyosi, 1947), E. kinutensis (Haga, 1950), E. sinensis Ishii & Liang, 1990, E. taiwanensis Ishii, 1990, E. xishuangbanna Ishii & Yin, 2000.

## Eudigraphis nigricans (Miyosi, 1947)

Fig. 2

*Monographis takakuwai nigricans* Miyoshi, 1947: 7; Takashima and Haga 1950: 23, fig. 2.

- *Eudigraphis takakuwai nigricans*: Ishii 1988: 957, figs 10, 11; Nguyen Duy-Jacquemin and Geoffroy 2003: 99; Mimizu Club and Minagoshi 2013: 44, 3 photos; Kawano 2017: 14, figs 1–12.
- *Eudigraphis nigricans*: Ishii and Tamura (1995) described this species on page 233; Ishii (1999) further discussed it on page 212; Ishii (2002) provided additional information on page 289; Karasawa et al. (2020) recently reviewed the species on page 94 and presented an illustration in figure 4D.

**Material examined.** Снима • 4♂2♀; Zhejiang, Hangzhou, West Lake; 30°23'58"N, 120°14'04"E; 23 April 2024; Y. D. Wang leg.; GenBank: PQ141065; CBF CZHZS3.

**Diagnosis.** Ground color of body pale yellowish-brown in dorsal view, but head black. Body dorsally with a pair of belt-like dark brown markings that run slightly off from both of the rims of each segment of body. Antennal article VI has 3 thick basiconic sensilla, and article VII has 2 thick basiconic sensilla.

**Description. Female.** With 13 pairs of legs. Measurements: Body length 3.4 mm, caudal bundle 0.5 mm.

**Head** (Fig. 2A): Eyes comprising 8 ommatidia. The posterior vertex possesses one pair of tufts each arranged in two rows; each anterior row consists of 13 trichomes, and the posterior row consists of 4 (Fig. 2A). Trichomes are depicted in Fig. 2J. Trichobothria are equal in size and arranged in an isosceles triangle formation (Fig. 2A). The gnathochilarium's lateral palps are twice the length of the medial palp. Lateral palps with 13 sensilla, medial palp with 20 sensilla (Fig. 2F). The labrum's anterior margin is granulated and armed with 3+3 lamellar teeth, and the clypeo-labrum with 6+6 setae (Fig. 2E).

**Antennae:** Long antennae with proportions of antennal articles as depicted in Fig. 2G. Antennal article VIII with 4 sensory cones, while article VI with 3 thick basiconic sensilla (Fig. 2I); article VII with 2 thick basiconic sensilla (Fig. 2H).

**Trunk:** Collum with one pair of tufts, each consisting of 44 trichomes, lateral protuberance of collum with 5 trichomes in a row (Fig. 2B). Tergite II, with one pair of tufts each consisting of 45 trichomes (Fig. 2C) connected by a continuous posterior row of trichomes. Tergite III, with one pair of tufts each composed of 52 trichomes (Fig. 2D) and connected by a continuous posterior row of trichomes. Tergites II–X have the same pattern of trichome insertions.

Legs (Fig. 2K): Trochanter, post-femur, tibia, and tarsus I lack setae. Prefemur and femur each with 1 seta (Fig. 2L), coxa I with 1 seta, coxae II–XII with 3–4 setae, coxa XIII with 2 setae, small setiform hair on tarsus II shorter than telotarsus (Fig. 2M). Telotarus is composed of a posterior process, almost as long as the claw, lamella process and a setiform process are present (Fig. 2N).

**Telson:** Dorso-medial trichomes on each side consist of 5 sockets of trichome  $a^{1-5}$ , a single trichome *b*, and three large protruding base sockets of trichome  $c^{1-3}$  (Fig. 2P). Beneath these, there are two bundles of caudal trichomes separated by a very narrow gap. The telson trichomes exist in two forms: those with hooks and those without hooks. The hooked trichomes most commonly with 2–4 hooks (Fig. 20).

**Male.** With 13 pairs of legs. Measurements: Body length 3.2 mm, caudal bundle 0.47 mm. Lateral palps with 13 sensilla, medial palp with 21 sensilla. The anterior margin of the labrum is granulated; the clypeo-labrum with 6+6 setae. The collum features one pair of tufts consisting of 41 trichomes each. Tergites II and III with one pair of tufts comprised of 42 or 50 trichomes. Coxa I with 1 seta, coxae



Figure 2. Eudigraphis nigricans (Miyosi, 1947) adult female A head B collum C and D tergites showcasing the pattern of trichome insertions C tergite II D tergite III E clypeo-labrum F gnathochilarium G antenna H sensilla on articles VII I sensilla on articles VI J anterior vertex trichome K left  $13^{th}$  leg L typical setae of coxa, prefemur, and femur M small setiform hair on tarsus II N telotarsus structure with processes indicated: c: claw, l: lamella, p: posterior process, s: setiform process O hooked caudal trichome P pattern of insertions of dorso-medial trichomes on telson. Scale bars: 200 µm (A, C, D); 100 µm (B, G, K, O); 50 µm (J, P); 40 µm (E); 20 µm (F); 10 µm (H, I, L, M, N).

II–X with 3–4 setae, coxae XI–XII with 2 setae, and coxa XIII with 1 seta. The dorso-medial trichomes on each side are composed of trichomes  $a^{1-4}$ , b, and  $c^{1-3}$ . **Distribution.** China (Zhejiang), Japan.

**Remarks.** This species closely resembles *Eudigraphis takakuwai* Miyosi, 1947, but differs in possessing a black head.

#### Eudigraphis sinensis Ishii & Liang, 1990

Fig. 3

Material examined. CHINA • 3♂5♀; Zhejiang, Hangzhou, West Lake; 30°24'60"N, 120°13'72"E; 23 April 2024; Y. D. Wang leg.; GenBank: PQ142931; CBF CZHZS1; • 4♂3♀; Jiangsu, Nanjing, Zhongshan Mountain National Park; 32°08'47"N, 118°84'38"E; 12 April 2024; leg. Y. D. Wang leg.; GenBank: PQ142932; CBF CZNJS1.

**Diagnosis.** Anterior margin of the labrum is not granulated and is equipped with 3+3 lamellar teeth on the anterior margin. Oval bases of setae on coxa, prefemur, and femur of each leg with some long spines at apex. Antennal article VI with 3 thick basiconic sensilla, 1 setiform sensillum, and 1 conical sensillum; article VII with 2 thick basiconic sensilla, 1 setiform sensillum, and 1 conical sensillum.

**Description. Female.** With 13 pairs of legs. Measurements: Body length 2.8 mm, caudal bundle 0.45 mm.

*Head* (Fig. 3A): Eyes comprising 8 ommatidia. The posterior vertex possesses es one pair of tufts each arranged in two rows: each anterior row comprises 12 trichomes, while the posterior row contains 10 (Fig. 3A). The trichomes are depicted in Fig. 3J. The trichobothria are equal in size and arranged in an isosceles triangle configuration (Fig. 3A). The gnathochilarium's lateral palps are twice the length of the medial palp. Lateral palps with 13 sensilla, medial palp with 22 sensilla (Fig. 3F). The anterior margin of the labrum is not granulated and is equipped with 3+3 lamellar teeth on the anterior margin. The clypeo-labrum with 6+6 setae (Fig. 3E).

**Antennae:** Long antennae with proportions of antennal articles as depicted in Fig. 3G. Antennal article VIII with 4 sensory cones, antennal article VI with 3 thick basiconic sensilla (a, i, and p), 1 setiform sensillum (s) situated between a and i, and 1 conical sensillum (c) behind p (Fig. 3I); article VII with 2 thick basiconic sensilla of a and p, 1 setiform sensillum (s) located between a and p, and 1 conical sensillum (c) behind p (Fig. 3H).

**Trunk**: Collum with one pair of tufts, each consisting of 35 trichomes, lateral protuberance of collum with 6 trichomes in a row (Fig. 3B). Tergites II, with one pair of tufts each consisting of 45 trichomes (Fig. 3C) connected by a continuous posterior row of trichomes. Tergites III, with one pair of tufts each composed of 40 trichomes (Fig. 3D) and connected by a continuous posterior row of trichomes. Tergites II–X exhibit a consistent pattern of trichome insertions.

Legs (Fig. 3K): Trochanter, post-femur, tibia, and tarsus I lack setae. Prefemur and femur each with 1 seta, coxa I with 1 seta, coxa II with 2 or 3 setae, coxae III–XII with 3 setae, coxa XIII with 1 seta (Fig. 3L), oval bases of setae on coxa, prefemur, and femur of each leg with some long spines at apex. Small setiform hair on tarsus II shorter than telotarsus (Fig. 3M). Telotarsus is composed of an anterior process, with an enlarged base, almost as long as the claw. Lamella process and a posterior process are present (Fig. 3N).



Figure 3. Eudigraphis sinensis Ishii & Liang, 1990, adult female A head B collum C and D tergites showcasing the pattern of trichome insertions C tergite II D tergite III E clypeo-labrum F gnathochilarium G antenna H sensilla on articles VII I sensilla on articles VI J anterior vertex trichome K left  $13^{th}$  leg L typical setae of coxa, prefemur, and femur M small setiform hair on tarsus II N telotarsus structure with processes indicated: a: anterior process, c: claw, l: lamella, p: posterior process O hooked caudal trichome P pattern of insertions of dorso-medial trichomes on telson. Scale bars: 200 µm (A, C, D); 100 µm (B, G, K, O); 50 µm (J, P); 40 µm (E); 20 µm (F); 10 µm (H, I, L, M, N).

**Telson:** Dorso-medial trichomes on each side consist of 10 sockets of trichome  $a^{1-10}$ , a single trichome *b*, and three large protruding base sockets of trichome  $c^{1-3}$  (Fig. 3P). Two bundles of caudal trichomes are located beneath with a very narrow gap. The telson trichomes are of two types: those with hooks and those without hooks. The hooked trichomes of the caudal bundles most commonly possess 1–5 hooks (Fig. 30).

**Male.** With 13 pairs of legs. Measurements: Body length 2.5 mm, caudal bundle 0.4 mm. Lateral palps with 13 sensilla, medial palp with 21 sensilla. The anterior margin of the labrum is not granulated and is armed with 3+3 lamellar teeth on the anterior margin. Clypeo-labrum with 6+6 setae. Collum each with one pair of tufts consisting of 32 trichomes; tergites II and III with one pair of tufts comprised of 42 or 39 trichomes. Coxa I with 1 seta, coxa II with 2 or 3 setae, coxae III–X with 3 setae, coxae XI–XII with 2 setae, coxa XIII with 1 seta.

Distribution. China (Zhejiang, Jiangsu).

**Remarks.** This species closely resembles *Eudigraphis kinutensis* Haga, 1950, but can be easily distinguished from the latter by the presence of 3+3 lamellar teeth on the anterior margin of the labrum (2+2 in *E. kinutensis*).

#### Subfamily Polyxeninae Lucas, 1840

#### Genus Polyxenus Latreille, 1802

#### Type species. Polyxenus lagurus Linnaeus, 1758.

**Genus diagnosis.** Adults with 13 pairs of legs, ommatidia are typically present, although they may be absent in certain species. A fan of barbate trichomes is situated dorso-medially, anterior to the penicil. The two bundles of trichomes that form the caudal penicil are widely separated. *Polyxenus* can be recognized by the presence of two rows of trichomes on each tergite.

Included species. Polyxenus albus Pocock, 1894, P. anacapensis Pierce, 1940, P. anophthalius Ishii & Yin, 2000, P. caudatus Menge, 1854, P. chalcidicus Condé & Nguyen Duy-Jacquemin, 1971, P. chilensis Silvestri, 1903, P. colurus Menge, 1854, P. conformis Koch & Berendt, 1854, P. fasciculatus Say, 1821, P. hangzhoensis Ishii & Liang, 1990, P. hawaiiensis Silvestri, 1904, P. koreanus Ishii & Choi, 1988, P. lagurus (Linnaeus, 1758), P. lapidicola Silvestri, 1903, P. lankaranensis Short, 2020, P. lepagei Mello-Leitão, 1925, P. lophurus Menge, 1854, P. macedonicus Verhoeff, 1952, P. miocenica Srivastava, 2006, P. oromii Nguyen Duy-Jacquemin, 1996, P. ovalis Koch & Berendt, 1854, P. paraguayensis Silvestri, 1903, P. platensis Silvestri, 1903, P. pugetensis Kincaid, 1898, P. rossi Chamberlin, 1957, P. senex Mello-Leitão, 1925, P. shinoharai Ishii, 1983, P. superbus Silvestri, 1903, P. triocellatus Ishii & Yin, 2000, P. tuberculatus Pierce, 1940.

## Polyxenus hangzhoensis Ishii & Liang, 1990

Fig. 4

**Material examined.** CHINA • 3♂4♀; Anhui, Chuzhou, Langya Mountain; 32°27'67"N, 118°30'01"E; 12 Mar. 2024; Y. D. Wang leg.; GenBank: PQ142930; CBF CZCZS1.

**Diagnosis.** Five ommatidia in each eye. Number of trichomes: posterior vertex, 47–48; collum, 54–55; collum's lateral protuberance, 4–5; tergite II, 56–62;

tergite III, 60–64. Four dorso-medial trichomes on the head, posterior vertex comprising 2 complete rows of trichomes with no medial gap. Antennal article VI with 2 thick basiconic sensilla, 1 setiform sensillum, and 6 thin basiconic sensilla. Antennal article VII with 2 thick basiconic sensilla, 1 setiform sensilla, 2 thick basiconic s

**Description. Female.** With 13 pairs of legs. Measurements: Body length 2.08 mm, caudal bundle 0.25 mm.

*Head* (Fig. 4A): Eye consisting of 5 ommatidia. Trichomes on the posterior vertex are arranged in 2 rows with no medial gap: the anterior row consists of 26 trichomes, and the posterior row comprises 20 trichomes. Additionally, 4 trichomes are arranged transversely in a dorso-medial position (Fig. 4A). The head features two types of trichomes (Fig. 4J). Three trichobothria are positioned in an equilateral triangle, with the trichobothrium furthest from the ommatidia being slightly smaller than the other two (Fig. 4A). The gnathochilarium possesses lateral palps that are 2.2 times the length of the medial palp. Lateral palps with 9 sensilla, medial palp with 17 sensilla (Fig. 4F). The anterior margin of the labrum is granulated and armed with 5+5 lamellar teeth. The clypeo-labrum is equipped with 8 setae (Fig. 4E).

**Antennae:** Long antennae with proportions of antennal articles as depicted in Fig. 4G. Antennal article VIII with 4 sensory cones, antennal article VI with 2 thick basiconic sensilla (anterior, a, and posterior, p); 1 setiform sensillum (s) between a and p, 6 thin basiconic sensilla behind p (Fig. 4I). Antennal article VII with 2 thick basiconic sensilla (a and p), 1 setiform sensillum (s) between a and p, 4 thin basiconic sensilla in front of p, and 1 conical sensillum (c) behind a (Fig. 4H).

**Trunk:** Tergal trichomes, including those on the collum, are arranged in a circular pattern. Collum with 54 trichomes, lateral protuberance of collum with 5 trichomes in a row (Fig. 4B). Tergite II with 56 trichomes (Fig. 4C). Tergite III with 60 trichomes (Fig. 4D). Tergites II–X have the same pattern of trichome insertions.

**Legs** (Fig. 4K): Coxa I with no seta, coxa II with 2 setae, coxae III–XIII with no seta, prefemur and femur with one seta (Fig. 4M), trochanter, post-femur, and tarsus I with no seta. The spine on tarsus II is far shorter than the setae on the prefemur and femur (Fig. 4L). There is a very small seta on the tibia (Fig. 4N). The telotarsus consists of an anterior process with an enlarged base, nearly equaling the length of the claw. Both a lamella process and a small posterior process are present (Fig. 4O).

**Telson:** The telson possesses 54 (27+27) dorso-medial trichomes in the caudal penicil (Fig. 4Q), arranged in two bundles separated by a gap. The caudal bundles consist of two types of trichomes, with the hooked trichomes having an apical lobed hook typical of *Polyxenus* (Fig. 4P).

**Male.** With 13 pairs of legs. Measurements: body length 1.9 mm, caudal bundle 0.22 mm. Posterior vertex with 48 trichomes, Collum with 55 trichomes, and tergites II and III with 62 and 64 trichomes. Coxa I with 1 seta, coxa II with 2 setae, coxae III–XIII with no seta. The caudal penicil comprises 48 (24+24) dorso-medial trichomes.

Distribution. China (Zhejiang, Anhui).

**Remarks.** This species closely resembles *Polyxenus shinoharai* Ishii, 1983 but differs in the number of trichomes present: the posterior vertex has 47 or 48 (40 or 41 in *P. shinoharai*), the collum with 54 or 55 (41 or 42), the lateral



Figure 4. *Polyxenus hangzhoensis* Ishii & Liang, 1990 adult female **A** head **B** collum **C** and **D** tergites showcasing the pattern of trichome insertions **C** tergite II **D** tergite III **E** clypeo-labrum **F** gnathochilarium **G** antenna **H** sensilla on articles VII I sensilla on articles VI J anterior vertex trichome **K** left 13<sup>th</sup> leg **L** spine on tarsus II **M** typical setae of prefemur and femur **N** seta on tibia **O** telotarsus structure with processes indicated: a: anterior process, c: claw, l: lamella, p: posterior process **P** hooked caudal trichome **Q** pattern of insertions of dorso-medial trichomes on telson. Scale bars: 200 μm (**A**, **C**, **D**); 100 μm (**B**, **G**); 50 μm (**J**, **K**, **P**); 40 μm (**E**); 20 μm (**F**, **Q**); 10 μm (**H**, **I**, **M**, **O**); 5 μm (**L**, **N**).

protuberance of the collum bears 4 or 5 (3), tergite II exhibits 56-62 (41 or 43), and tergite III displays 60-64 (42 or 46), antennal article VI with 6 thin basiconic sensilla (7 in *P. shinoharai*).

#### Family Lophoproctidae Silvestri, 1897

#### Genus Lophoturus Brolemann, 1931

### Type species. Lophoturus obscurus Brolemann, 1931.

**Genus diagnosis.** Ommatidia absent. Antennal segment VIII is equal to segment VII. It is characterized by 0 to 4 pairs of linguiform processes on each side of median cleft of labrum and antennal article VI with 3 thick sensilla (Ishii et al. 1999).

Included species. Lophoturus adisi Ishii, Nguyen Duy-Jacquemin & Condé, 1999, L. aequatus (Loomis, 1936), L. anisorhabdus (Condé & Terver, 1964), L. boondallus Huynh & Veenstra, 2018, L. crassipes Condé & Terver, 1979, L. danhomenou (Brolemann, 1926), L. difficilis (Condé & Jacquemin, 1963), L. drifti (Condé & Terver, 1964), L. fluctuans (Condé & Terver, 1964), L. guineensis (Silvestri, 1948), L. hesperius (Condé & Terver, 1963), L. humphreysi Nguyen Duy-Jacquemin, 2014, L. jianshuiensis Ishii & Yin, 2000, L. judsoni Nguyen Duy-Jacquemin, 2002, L. longisetis (Pocock, 1894), L. scopiger Condé & Terver, 1979, L. madecassus (Marquet & Condé, 1950), L. monserratensis Nguyen Duy-Jacquemin, 2002, L. molloyensis Huynh & Veenstra, 2018, L. niveus (Loomis, 1934), L. obscurus (Brolemann, 1931), L. catalai (Condé & Nguyen Duy-Jacquemin, 1977), L. O. kurtchevae Nguyen Duy-Jacquemin & Condé, 1982, L. tongae (Nguyen Duy-Jacquemin & Condé, 1982), L. okinawai (Nguyen Duy-Jacquemin & Condé, 1982), L. peruanus (Silvestri, 1949), L. quebradanus (Chamberlin, 1955), L. porchi Huynh & Veenstra, 2020, L. queenslandicus (Verhoeff, 1924), L. speophilus Nguyen Duy-Jacquemin, 2014, L. sturmi Nguyen Duy-Jacquemin, 2002, L. sineprocessus sp. nov., L. vicarius Condé & Terver, 1979.

#### Lophoturus sineprocessus sp. nov.

https://zoobank.org/CDFBBBC5-8162-4CBA-BC54-DD1EA23B3E65 Fig. 5

**Type material.** *Holotype*: CHINA • ♀; Yunnan, Xishuangbanna Dai Autonomous Prefecture, Jinghong, Menglai Rainforest Health Theme Park; 21°96'63"N, 100°80'55"E; 20 August 2023; Y. D. Wang leg.; GenBank: PQ142933. CBF CZYNS1. *Paratype*: • 1♂, same data as the holotype.

**Diagnosis.** Number of trichomes: posterior vertex: 28-36, collum: 76-84, lateral protuberance of collum: 6, tergite II: 82-88, tergite III: 80-84. Antennal article VI with 3 thick basiconic sensilla and 1 conical sensillum; article VII with 2 thick basiconic sensilla. Dorso-medial trichomes on each side consist of 6 sockets of trichome *a*, a single trichome *b*, and two large protruding base sockets of trichome *c*:  $c^1$  and  $c^3$ . No linguiform processes on the labrum.

**Description. Female.** With 13 pairs of legs. Measurements: Body length 2.0 mm, caudal bundle 0.38 mm.

*Head* (Fig. 5A): Ommatidia absent. The posterior vertex has one pair of tufts arranged in two rows, with the anterior row consisting of 14 trichomes and the



Figure 5. Lophoturus sineprocessus sp. nov. adult female A head B collum C and D tergites showcasing the pattern of trichome insertions C tergite II D tergite III E clypeo-labrum F gnathochilarium G antenna H sensilla on articles VII I sensilla on articles VI J anterior vertex trichome K left  $13^{th}$  leg L typical setae of coxa, prefemur, and femur M spine on tarsus II N telotarsus structure with processes indicated: ldd: latero-dorsal denticles, c: claw, smd: small denticle O hooked caudal trichome P pattern of insertions of dorso-medial trichomes on telson. Scale bars: 200 µm (A, C, D); 100 µm (B, G, K, O); 50 µm (J, P); 40 µm (E); 20 µm (F); 10 µm (H, I, L, M, N).

posterior row of 4 (Fig. 5A). Trichomes are depicted in Fig. 5J. Three trichobothria are arranged in an isosceles triangle, trichobothria *a* and *b* have typically thin sensory hairs with narrow cylindrical funicles compared to trichobothrium *c*, with a claviform funicle (Fig. 5A). The gnathochilarium is typical of Lophoproctidae, featuring a single medial palp with 18 sensilla (Fig. 5F). The clypeo-labrum possesses 4+1+4 setae and lacks linguiform processes on each side of the median cleft of the labrum (Fig. 5E).

**Antennae:** Long antennae with proportions of antennal articles as depicted in Fig. 5G. Antennal article VIII with 4 sensory cones; antennal article VI with 3 thick basiconic sensilla (a, i, and p) and 1 conical sensillum (c) (Fig. 5I); article VII with 2 thick basiconic sensilla (Fig. 5H).

**Trunk:** Collum, each with one pair of tufts consisting of 42 trichomes, lateral protuberance of collum with 6 trichomes in a row (Fig. 5B). Tergite II, each with one pair of tufts consisting of 44 trichomes (Fig. 5C). Tergite III, each with one pair of tufts consisting of 42 trichomes (Fig. 5D). Tergites II–X exhibit consistent patterns of trichome insertions.

**Legs** (Fig. 5K): Trochanter, post-femur, tibia, and tarsus I lack setae. Prefemur and femur each with 1 seta, coxa I with 1–2 setae, coxae II–XIII with 3–4 setae (Fig. 5L), spine on tarsus II slightly shorter than telotarsus (Fig. 5M). The telotarsus with two latero-dorsal denticles, a claw, and a small denticle (Fig. 5N).

**Telson:** Dorso-medial trichomes on each side with 6 sockets of trichome *a*, a single trichome *b*, and two large protruding base sockets of trichome *c*:  $c^1$  and  $c^3$  (Fig. 5P, the absence of  $c^2$  is characteristic of Lophoproctidae species). Two bundles of caudal trichomes are unseparated. The telson trichomes are of two types, both exhibiting barbs (Fig. 50).

**Male.** With 13 pairs of legs. Measurements: Body length 1.8 mm, caudal bundle 0.3 mm. The posterior vertex possesses one pair of tufts arranged in two rows, with the anterior row consisting of 12 trichomes and the posterior row containing 2 trichomes. The gnathochilarium features 32 sensilla. The collum exhibits one pair of tufts, each consisting of 38 trichomes. Tergites II and III each bear one pair of tufts comprising 41 or 40 trichomes, respectively. Coxa I with 2 setae, coxa II with 3 setae, coxae III–VII with 4 setae, coxae VIII–XII with 2–3 setae, coxa XIII with no seta.

Distribution. China (Yunnan).

**Etymology.** The species name is derived from the absence of linguiform processes on each side of the median cleft of the labrum, a distinctive characteristic of the species.

**Remarks.** The new species resembles *Lophoturus jianshuiensis* Ishii & Yin, 2000 but differs in the following aspects: absence of linguiform processes on each side of the median cleft of the labrum (*L. jianshuiensis* has 1 pair of linguiform processes), female gnathochilarium with 18 sensilla (30 or 31 sensilla), dorso-medial trichomes on each side with 6 sockets of trichome *a* (5 sockets of trichome *a*).

## **Phylogenetic results**

ML and BI trees have been constructed (Fig. 6). Most nodes exhibit strong support. The ML and BI tree topologies were identical, supporting *Polyxenus*, *Lophoturus*, and *Eudigraphis* as monophyletic groups. The newly sequenced



## 0.03

**Figure 6.** Unrooted phylogenetic tree based on cytochrome *c* oxidase subunit I (COI) sequence data. Bootstrap proportions of ML and Bayesian posterior probability (BPP) are shown at each node (BP/BPP). The species sequenced in this study are indicated in red.

species: *Eudigraphis nigricans* (Miyosi, 1947), *Eudigraphis sinensis* Ishii & Liang, 1990, *Polyxenus hangzhoensis* Ishii & Liang, 1990, and *Lophoturus sineprocessus* sp. nov., clustered within their respective genera.

## Discussion

Since Linnaeus first recorded Polyxenida in 1758 (Linnaeus 1758), this group has garnered significant attention from taxonomists worldwide due to their unique morphological characteristics and systematic position. However, research has been more substantial in Europe, the Americas, and Australia compared to Asia and Africa. Currently, there are 32 described species in the genus *Lophoturus* worldwide (Huynh and Veenstra 2018b; Huynh and Veenstra 2020), with China having two species. The genus *Monographis* comprises 16 described species worldwide (Huynh and Veenstra 2013; Huynh and Veenstra 2022; Huynh et al. 2023), with China having two species. The genus *Eudigraphis* includes six described species worldwide (Karasawa et al. 2020), with China having three species. The genus *Polyxenus* consists of 30 described species worldwide (Enghoff et al. 2015; Short et al. 2020), with China having three

species. The understanding of Polyxenida species diversity in China remains limited, and there is a pressing need for in-depth and systematic investigations.

This study collected four Polyxenida species from four regions in China. Comprehensive morphological descriptions and molecular phylogenetic tree construction corroborated the inclusion of one new species and one newly recorded species, increasing the known Polyxenida species in China from 10 to 12. However, the increasing scarcity of classical taxonomists, coupled with factors such as phenotypic plasticity and genetic variation, presents objective difficulties and confusion in the accurate identification of biological samples. Molecular markers, such as cytochrome COI, have been widely used in other groups to assist in species identification. Therefore, it is imperative to integrate classical taxonomy with molecular identification techniques and to standardize their application in the classification of Polyxenida and other soil fauna.

## Key to the species of Penicillata from China

1	Antennal segment VIII equal to segment VII (Fig. 5G)2
-	Antennal segment VIII shorter than segment VII (Figs 2G, 3G, 4G)
2	Two pairs of linguiform processes on each side of the median cleft of
	labrumLophoturus okinawai (Nguyen Duy-Jacquemin & Condé, 1982)
-	One pair of linguiform processes on each side of the median cleft of la-
	brum Lophoturus jianshuiensis Ishii & Yin, 2000
-	No linguiform processes on each side of the median cleft of labrum
	(Fig. 5E)Lophoturus sineprocessus sp. nov.
3	Fan of barbate trichomes present dorso-medially, anterior to penicil, with
	the two bundles of trichomes forming the caudal penicil being widely sep-
	arated4
-	Dorso-medial fan of barbate trichomes absent, two bundles of caudal
	penicil closely aligned, giving the appearance of a single bundle6
4	Ommatidia present5
-	Ommatidia absent Polyxenus anophthalius Ishii & Yin, 2000
5	Three ommatidia Polyxenus triocellatus Ishii & Yin, 2000
5 -	Three ommatidia <i>Polyxenus triocellatus</i> Ishii & Yin, 2000 Five ommatidia (Fig. 4A) <i>Polyxenus hangzhoensis</i> Ishii & Liang, 1990
5 - 6	Three ommatidia
5 - 6 -	Three ommatidia
5 - 6 - 7	Three ommatidia
5 - 6 - 7	Three ommatidia
5  6  7	Three ommatidia
5 - 6 - 7	Three ommatidia
5 - 6 - 7	Three ommatidia
5 - 6 - 7 -	Three ommatidia
5  7  8	Three ommatidia
5  7  8 	Three ommatidia
5  7  8 	Three ommatidia
5  7 - 8  8	Three ommatidia
5  6  7  8  9	Three ommatidia
5  7  8  9 	Three ommatidia       Polyxenus triocellatus Ishii & Yin, 2000         Five ommatidia (Fig. 4A)       Polyxenus hangzhoensis Ishii & Liang, 1990         The spine of the tarsus is thick and conical in shape.       7         Tarsal spine absent, small setiform hair with round base present       8         Antennal segment VI with short thick basiconic sensilla, anterior margin of labrum with a line of marginal setae       8         Monographis baihualingensis Ishii & Yin, 2000       9         Antennal segment VI without short thick basiconic sensilla, anterior margin of labrum without a line of marginal setae       9         Labrum with 3 + 3 lamellar teeth (Fig. 3E)       9         Labrum with 4 + 4 lamellar teeth       9         Labrum with 2 + 2 lamellar teeth       Eudigraphis taiwaniensis Ishii, 1990         Head black       Eudigraphis nigricans (Miyosi, 1947)         Head pale brown with cream yellow       1000

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## **Additional information**

## **Conflict of interest**

The authors have declared that no competing interests exist.

## **Ethical statement**

No ethical statement was reported.

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## **Author contributions**

Conceptualization: YDW, AJ, SCG, JJW, YD. Data curation: YDW, AJ. Formal analysis: YDW, AJ, SCG. Methodology: YDW, AJ. Investigation: YDW, AJ, SCG. Visualization: YDW. Supervision: AJ, SCG, JJW, YD. Writing—original draft preparation: YDW. Writing—review and editing: YDW, AJ, SCG, JJW, YD. All authors have read and agreed to the published version of the manuscript.

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## **Data availability**

All data supporting the findings of this study are available in the main text or the National Center for Biotechnology Information (NCBI) GenBank database (https://www.ncbi. nlm.nih.gov/Genbank) under accession numbers PQ141065, PQ142930, PQ142931, PQ142932, and PQ142933.

## References

Enghoff H, Golovatch SI, Short M, Stoev O, Wesener T (2015) Diplopoda-taxonomic overview. In: Minelli A (Ed.) Treatise on Zoology-Anatomy, Taxonomy, Biology. The Myriapoda. Volume 2. Brill, Leiden and Boston, 363-453. https://doi. org/10.1163/9789004188273\_017 Huynh C, Veenstra A (2013) Taxonomy and biology of a new species of Pincushion Millipede of the genus *Monographis* (Diplopoda: Polyxenidae) from Australia. Zootaxa 3721: 573–588. https://doi.org/10.11646/zootaxa.3721.6.4

- Huynh C, Veenstra AA (2018a) Two new species of penicillate millipedes (Diplopoda, Polyxenidae) from Phu Quoc Island in southern Vietnam. Zootaxa 4402(2): 283–302. https://doi.org/10.11646/zootaxa.4402.2.3
- Huynh C, Veenstra AA (2018b) Two new Lophoturus species (Diplopoda, Polyxenida, Lophoproctidae) from Queensland, Australia. In: Stoev P, Edgecombe GD (Eds) Proceedings of the 17<sup>th</sup> International Congress of Myriapodology, Krabi, Thailand. ZooKeys 741: 133–154. https://doi.org/10.3897/zookeys.741.21814
- Huynh C, Veenstra AA (2020) A new Lophoturus species (Diplopoda, Polyxenida, Lophoproctidae) from Rodrigues Island, the Republic of Mauritius: morphological and molecular evidence. Royal Society of Victoria 132: 65–77. https://doi.org/10.1071/RS20005
- Huynh C, Veenstra AA (2022) Four new species of *Monographis* Attems, 1907 (Diplopoda, Polyxenida, Polyxenidae) from Vietnam. Zootaxa 5214(3): 393–420. https://doi. org/10.11646/zootaxa.5214.3.4
- Huynh C, Veenstra AA, Likhitrakarn N (2023) First records of penicillate millipedes (Diplopoda, Polyxenidae) from Thailand, with descriptions of two new species. Zootaxa 5383(4): 514–536. https://doi.org/10.11646/zootaxa.5383.4.5
- Ishii K (1988) On the significance of the mandible as a diagnostic character in the taxonomy of penicillate diplopods (Diplopoda: Polyxenidae). The Canadian Entomologist 120: 955–963. https://doi.org/10.4039/Ent120955-11
- Ishii K (1990) Penicillate diplopods (Diplopoda: Polyxenidae) from Taiwan. Edaphologia 42: 1–20.
- Ishii K (1999) A list of myriapod species in Chiba Prefecture with general remarks on the fauna. In: Chiba Zoological Society (Ed.) Natural History of Animals in Chiba Prefecture, Japan. Bun-ichi Sogo Publishing, Tokyo, 206–218. [In Japanese]
- Ishii K (2002) Diplopoda. In: Research Foundation of History of Chiba Prefecture (Ed.) Natural History of Chiba Prefecture. Vol. 6. Animals of Chiba Prefecture 1. Land and Fresh Water Animals. Chiba Prefecture, Chiba, 287–296. [In Japanese]
- Ishii K, Liang LR (1990) Two new species of penicillate diplopods of the family Polyxenidae (Diplopoda: Penicillata) from China. Canadian Entomologist 122: 1239–1246. https://doi.org/10.4039/Ent1221239-11
- Ishii K, Tamura H (1995) The mandibular structure as a diagnostic character in taxonomy of diplopods. Acta Zoologica Fennica 196: 232–235.
- Ishii K, Yin WY (2000) New species of Penicillata (Diplopoda) from Yunnan, Southwest China. In: Aoki J, Yin WY, Imadate G (Eds) Taxonomical studies on the soil fauna of Yunnan Province in Southwest China. Tokai University Press, Tokai, 91–116.
- Ishii K, Nguyen Duy-Jacquemin M, Condé B (1999) The first penicillate millipedes from the vicinity of Manaus, Central Amazonia, Brazil (Diplopoda: Polyxenida). Amazoniana 15(3-4): 239-267.
- Karasawa S, Kawano K, Fukaya S, Tsurusaki N (2020) Upgrading of Three Subspecies of *Eudigraphis takakuwai* to the Species Rank (Diplopoda: Penicillata: Polyxenida: Polyxenidae). Species Diversity 25(1): 89–102. https://doi.org/10.12782/specdiv.25.89
- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology and Evolution 30(4): 772–780. https://doi.org/10.1093/molbev/mst010
- Kawano K (2017) Millipeds of Shimonoseki City. The Firefly Museum of Toyota Town, Shimonoseki, 30 pp. [In Japanese]

- Linnaeus C (1758) Systema Naturae per Regna tria Naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus 1, Editio Decima. Holmiae, Laurentii Salvii, 1–823. https://doi.org/10.5962/bhl.title.542
- Manton SM (1956) The evolution of arthropodan locomotory mechanisms. Part 5. The structure, habits and evolution of the Pselaphognatha (Diplopoda). Journal of the Linnean Society of London 43: 153–187. https://doi.org/10.1111/j.1096-3642.1957. tb02516.x
- Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES science gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE), IEEE, New Orleans, LA, USA, 1–8. https://doi.org/10.1109/ GCE.2010.5676129
- Mimizu Club, Minagoshi Y (2013) Field Guide to Small Animals under Fallen Leaves. Gijutsu-Hyoron-sha Publishing, Tokyo, 127 pp. [In Japanese]
- Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, von Haeseler A, Lanfear R (2020) IQ-TREE 2: New Models and Efficient Methods for Phylogenetic Inference in the Genomic Era. Molecular Biology and Evolution 37(5): 1530–1534. https:// doi.org/10.1093/molbev/msaa015
- Miyosi Y (1947) Eine neue Art von Monographis aus Japan. Acta Arachnologica 10: 1–8. [In Japanese] https://doi.org/10.2476/asjaa.10.1
- Nguyen Duy-Jacquemin M (2014) Two new species of *Lophoturus* (Diplopoda, Penicillata, Lophoproctidae) from caves in Christmas Island, Australia, including the second troglomorph in Penicillata. Zoosystema 36(1): 29–39. https://doi.org/10.5252/ z2014n1a2
- Nguyen Duy-Jacquemin M, Geoffroy JJ (2003) A revised comprehensive checklist, relational database, and taxonomic system of reference for the bristly millipedes of the world (Diplopoda, Polyxenida). African Invertebrates 44: 89–101.
- Short M, Vahtera V (2017) Phylogenetic relationships of millipedes in the subclass Penicillata (Diplopoda) with a key to the genera. Journal of Natural History 51: 2443– 2461. https://doi.org/10.1080/00222933.2017.1380241
- Short M, Vahtera V, Wesener T, Golovatch SI (2020) The millipede family Polyxenidae (Diplopoda, Polyxenida) in the faunas of the Crimean Peninsula and Caucasus, with notes on other European Polyxenidae. Zootaxa 4772(2): 306–332. https://doi.org/10.11646/zootaxa.4772.2.4
- Silvestri F (1948) Tavola sinottica dei generi dei Diplopoda Penicillata. Bollettino del Laboratoriodi Entomologia Agraria, Portici 8: 214–220.
- Takashima H, Haga A (1950) Notes on Polyxenidae of Japan. Acta Arachnologica 11: 21–26. [In Japanese] https://doi.org/10.2476/asjaa.12.21
- Vohland K, Hamer M (2013) A Review of the Millipedes (Diplopoda) of Namibia, with Identification Keys and Descriptions of Two New Genera and Five New Species. African Invertebrates 54(1): 251–304.
- Wang JJ, Bai Y, Dong Y (2022) A rearrangement of the mitochondrial genes of centipedes (Arthropoda, Myriapoda) with a phylogenetic analysis. Genes 13: 1787. https:// doi.org/10.3390/genes13101787
- Yang SQ, Bu Y (2021) Progress in systematic research of Polyxenida Verhoeff, 1934. Life Sciences 33(5): 546–556. [In Chinese]



**Research Article** 

# Revision of the orb-weaving spider genus *Yaginumia* Archer, 1960 (Araneae, Araneidae) from China

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#### Abstract

The orb-weaver spider genus *Yaginumia* Archer, 1960 from China is revised, and three species, including two new species, are recognized: *Y. medog* Mi & Wang, **sp. nov.** ( $\mathscr{J} Q$ ) from Xizang and *Y. qiong* Mi & Wang, **sp. nov.** ( $\mathscr{J} Q$ ) from Hainan; the type species, *Y. sia* (Strand, 1906) ( $\mathscr{J} Q$ ), is redescribed based on specimens from Guizhou and Hubei. A distributional map of the studied specimens is also provided.

Key words: Arachnida, diagnosis, identification key, morphology, new species, taxonomy

## Introduction

The orb-weaver spider genus *Yaginumia* Archer, 1960 was established by Archer (1960) to accommodate the type species *Y. sia* (Strand, 1906). This species was first described as a member of the genus *Araneus* Clerck, 1757 under the subgenus *Zilla* C.L. Koch, 1834 (Bösenberg and Strand 1906); then it was transferred to the genus *Zygiella* F.O. Pickard-Cambridge, 1902 by Roewer (1942) without any justification; Saitō (1959) returned it to the genus *Zilla*, again without justification. Levi (1974) treated it in *Zygiella*, but pointed to two characters that are unusual for typical *Zygiella* species, such as the wider spacing of the eyes and the cap on the embolus. Consequently, most subsequent taxonomic studies placed this species in the genus *Yaginumia* (WSC 2024). Several studies using traditional Sanger sequencing revealed that this genus was closely related to the genus *Guizygiella* Zhu, Kim & Song, 1997 (Gregorič et al. 2015; Kallal and Hormiga 2018; Kallal et al. 2020).

*Yaginumia sia* (Strand, 1906) always lives close to humans in and around houses, other buildings, rice fields and cotton fields. It is widely distributed in China (Lee 1966; Yin 1978; Song 1980; Hu 1984; Guo 1985; Zhang 1987; Chen and Gao 1990; Feng 1990; Chen and Zhang 1991; Zhao 1993, 1995; Yin et al. 1997, 2012; Song et al. 1999; Zhu and Zhang 2011), Japan (Bösenberg and Strand 1906; Roewer 1942; Saitō 1959; Archer 1960; Yaginuma 1960, 1971, 1986; Levi 1974; Ishinoda 1989; Baba and Tanikawa 2015; Tanikawa 2007;



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**Copyright:** <sup>©</sup> Xiaoqi Mi et al. This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0). 2009) and Korea (Namkung et al. 1972; Chikuni 1989; Namkung 2002, 2003; Kim and Cho 2002; Kim and Kim 2002; Kim and Lee 2012).

*Yaginumia* specimens deposited in the Museum of Tongren University were examined, and three species, including two new species, were identified. They are described in this paper, and a key to the species is provided.

## Material and methods

All specimens were collected by beating shrubs during the daytime or direct searching at night and are preserved in 75% ethanol. The specimens are deposited in the Museum of Tongren University, China (**TRU**). Methods follow Mi et al. (2023).

All measurements are given in millimeters. Leg measurements are given as total length (femur, patella + tibia, metatarsus, tarsus). Abbreviations used in the text and figures are as follows: **ALE** anterior lateral eye; **AME** anterior median eye; **C** conductor; **CD** copulatory duct; **CO** copulatory opening; **E** embolus; **FD** fertilization duct; **MA** median apophysis; **MOA** median ocular area; **Pc** paracymbium; **PLE** posterior lateral eye; **PME** posterior median eye; **Sp** spermatheca; **TA** terminal apophysis; **TP** tegular projection.

## Taxonomy

## Key to species of the genus Yaginumia

1	Male
-	Female4
2	Median apophysis with projection on middle part (Fig. 6A) Yaginumia sia
-	Median apophysis lacking projection on middle part (Figs 2A, 4A)3
3	Median apophysis curled about 90° in ventral view (Fig. 2A)
	Y. medog Mi & Wang, sp. nov.
-	Median apophysis curled about 45° in ventral view (Fig. 4A)
	Y. qiong Mi & Wang, sp. nov.
4	Copulatory openings arcuate (Fig. 1A) Y. medog Mi & Wang, sp. nov.
-	Copulatory openings almost rounded (Figs 3A, 5A)5
5	Scape heart-shaped (Fig. 5B) Y. sia
-	Scape tongue-shaped (Fig. 3B) Y. qiong Mi & Wang, sp. nov.

## Family Araneidae Clerck, 1757

#### Genus Yaginumia Archer, 1960

Yaginumia Archer, 1960: 14.

## Type species. Aranea sia Strand, 1906.

**Diagnosis.** Yaginumia resembles Guizygiella and Zygiella in having a dorsoventrally flattened elliptical abdomen with almost symmetrical dorsal folium, and, in males, an enlarged paracymbium. It can be distinguished from Guizygiella by: 1) with triangular, toothed tegular projection (Figs 2A-E, 4A-E, 6A-E) vs absent (Zhu et al. 2003: fig. 20I, J); 2) tibia of pedipalp at least  $1.5 \times$  longer than wide in ventral view (Figs 2C, 4C, 6C) vs about equal in length and width (Zhu et al. 2003: fig. 201); 3) epigyne with a scape (Figs 1A–D, 3A–D, 5A–D) vs lacking (Zhu et al. 2003: fig. 20F); and 4) abdomen bearing dense setae (Figs 1E–J, 3E–J, 5E–J) vs sparse setae (Zhu et al. 2003: fig. 20A). It differs from *Zygiella* by: 1) pedipalp of male with two patellar bristles (2A, B, 4A, B, 6A, B) vs only one patellar bristle (Levi 1974: 271); 2) long axis of tegulum in "horizontal" position in ventral view (Figs 2C, 4C, 6C) vs in "vertical" position (Levi 1974: figs 28, 29); 3) distance of PME–PLE is at least 3.6 × to that of PME–PME (Figs 1E, H, 3E, H, 5E, H) vs posterior eyes almost equal separated (Levi 1974: figs 26, 57); 4) abdomen bearing dense setae (Figs 1E–J, 3E–J, 5E–J) vs sparse setae (Levi 1974: fig. 26); and 5) web complete vs with a vacant sector.

**Description.** Medium spiders with female total length of 4.25–13.10 and male total length of 3.15–8.20. Carapace pear-shaped, yellow to dark brown, darker in cephalic region than in thoracic region, fovea transverse. Endites wider than long. Labium triangular, swollen. Sternum cordiform. Legs yellow, always with dark annuli (except *Y. medog* sp. nov.). Abdomen elliptical, dorsum bearing dense setae, with dark median longitudinal folium. Ventral abdomen yellow to yellowish-gray with pale line on each side.

Pedipalp of male with two patellar bristles; tibia at least 1.5 × longer than wide; paracybium enlarged at base with small distal lobe; tegular projection almost triangular in ventral view, with toothed inner edge; median apophysis tapered distally; embolus short and slightly curved, almost totally covered by terminal apophysis; conductor membranous or weakly sclerotized; terminal apophysis prominent, weakly sclerotized, curved distally in ventral view.

Epigyne heavily sclerotized, wider than long in ventral view, with scape, the scape always torn off; copulatory openings situated on ventral surface; copulatory ducts twisted, about equal length to spermathecal diameter; spermathecae rounded, touching or nearly touching.

**Composition.** *Yaginumia medog* Mi & Wang, sp. nov., *Y. qiong* Mi & Wang, sp. nov. and *Y. sia* (Strand, 1906) (type species).

Distribution. East Asia (China, Japan, Korea).

## Yaginumia medog Mi & Wang, sp. nov.

https://zoobank.org/5c95f73b-85c3-4919-8ffa-0231534a89ef Figs 1, 2, 7

**Type material.** *Holotype*: CHINA • ♂; Xizang Autonomous Region, Medog County, Beibeng Township, De'ergong Village; 29°10.84'N, 95°8.67'E; ca 1670 m elev.; 25.V.2024; X.Q. Mi et al. leg.; TRU-Araneidae-326. *Paratypes*: 2♀♀; same data as for holotype; TRU-Araneidae-327–328.

**Etymology.** The species name is a noun derived from the type locality: Medog County.

**Diagnosis.** The new species resembles *Y. qiong* sp. nov. in appearance and genitalia structures, but it can be distinguished as follows: 1) median apophysis strongly curled about 90° in ventral view (Fig. 2C) vs slightly curled about 45° (Fig. 4C); 2) basal part of paracybium ~2.1 × wider than distal part in retrolateral view (Fig. 2B) vs ~3.4 × wider (Fig. 4B); 3) copulatory openings arcuate (Fig. 1A) vs almost rounded (Fig. 3A); 4) spermathecae touching to each other (Fig. 1C, D) vs separated (Fig. 3C, D); and 5) legs with annuli (Fig. 1E, H) vs lacking (Fig. 3E, H).



**Figure 1.** *Yaginumia medog* Mi & Wang, sp. nov. **A–G** female paratype TRU-Araneidae-327 **H–J** male holotype **A** epigyne, ventral view **B** ibid., posterior view **C** vulva, posterior view **D** ibid., dorsal view **E**, **H** habitus, dorsal view **F**, **I** ibid., ventral view **G**, **J** ibid., lateral view. Abbreviations: CD copulatory duct, CO copulatory opening, FD fertilization duct, Sp spermatheca. Scale bars: 0.1 mm (**A–D**); 1.0 mm (**E–J**).

**Description. Male** (holotype, Figs 1H–J, 2). Total length 3.20. Carapace 1.85 long, 1.35 wide. Abdomen 2.10 long, 1.45 wide. Clypeus 0.05 high. Eye sizes and interdistances: AME 0.13, ALE 0.08, PME 0.10, PLE 0.08, AME–AME 0.10, AME–ALE 0.10, PME–PME 0.05, PME–PLE 0.18, MOA length 0.30, anterior



**Figure 2**. *Yaginumia medog* Mi & Wang, sp. nov. male holotype **A** pedipalp, prolateral view **B** ibid., retrolateral view **C** ibid., ventral view **D** ibid., apical view **E** part of expanded bulb. Scale bars: 0.1 mm. Abbreviations: C conductor, E embolus, MA median apophysis, Pc paracymbium, TA terminal apophysis, TP tegular projection.

width 0.33, posterior width 0.25. Leg measurements: I 6.65 (1.85, 2.40, 1.70, 0.70), II 5.70 (1.60, 2.05, 1.40, 0.65), III 3.50 (1.10, 1.10, 0.75, 0.55), IV 4.55 (1.40, 1.55, 1.10, 0.50). Carapace dark brown in cephalic region and yellowish-brown in thoracic region. Cervical groove conspicuous. Chelicerae dark brown, with four promarginal and three retromarginal teeth. Endites and labium dark brown at base, with paler tip. Sternum dark brown. Legs yellow with brown annuli. Abdomen ~1.45 × longer than wide, dorsal folium extended from anterior to posterior, grayish-brown with white spots anteriorly. Venter abdomen yellow to yellowish-brown.

**Pedipalp** (Fig. 2): tibia ~1.78 × longer than wide in ventral view; paracybium enlarged at base and lobe-like distally; tegular projection triangular, with toothed inner edge; median apophysis tapered and curled about 90° distally in ventral view; embolus almost straight, shorter than conductor; conductor membranous; terminal apophysis weakly sclerotized, covering embolus.

**Female** (paratype TRU-Araneidae-327, Fig. 1A–G). Total length 4.55. Carapace 2.10 long, 1.55 wide. Abdomen 2.90 long, 2.30 wide. Clypeus 0.05 high. Eye sizes and interdistances: AME 0.13, ALE 0.08, PME 0.13, PLE 0.08, AME–AME 0.13, AME–ALE 0.08, PME–PME 0.05, PME–PLE 0.20, MOA length 0.33, anterior width 0.35, posterior width 0.28. Leg measurements: I 6.75 (2.00, 2.45, 1.55, 0.75), II 5.80 (1.75, 2.05, 1.30, 0.70), III 3.85 (1.25, 1.30, 0.75, 0.55), IV 5.30 (1.70, 1.85, 1.15, 0.60). Habitus similar to that of male.

**Epigyne** (Fig. 1A–D):  $\sim$ 1.57 × wider than long in ventral view; copulatory openings arcuate, situated on ventral surface; copulatory ducts twisted, about equal length to spermathecal diameter; spermathecae rounded, touching.

**Variation.** Total length:  $\bigcirc \bigcirc 3.15 - 3.30$  (*N* = 2).

**Distribution.** China (Xizang).

**Comment.** Judging from the broken vestige, we conclude it must have an epigynal scape.

#### Yaginumia qiong Mi & Wang, sp. nov.

https://zoobank.org/FC336132-DB32-4363-BB2D-D6F5851CEA47 Figs 3, 4, 7

**Type material.** *Holotype*: CHINA – Hainan Province, • 3; Lingshui Li Autonomous County, Diaoluoshan National Nature Reserve, Popular Science Base; 18°40.25'N, 109°53.66'E; ca 260 m elev.; 26.VII.2023; C. Wang et al. leg.; TRU-Araneidae-329. *Paratypes*: 1022; same data as for holotype; TRU-Araneidae-330–339 • 13; Ledong Li Autonomous County, Jianfeng Township, Jianfengling National Nature Reserve, Tianchi; 18°44.45'N, 108°51.49'E; ca 860 m elev.; 11.IV.2019; C. Wang & Y.F. Yang leg.; TRU-Araneidae-340 • 12; Ledong Li Autonomous County, Jianfeng Township, Jianfengling National Nature Reserve, Yulingu; 18°44.79'N, 108°55.76'E; ca 630 m elev.; 15.IV.2019; C. Wang & Y.F. Yang leg.; TRU-Araneidae-341 • 2222; Ledong Li Autonomous County, Jianfeng Township, Jianfengling National Nature Reserve, Tianchi; 18°44.82'N, 108°51.64'E; ca 810 m elev.; 15.IV.2019; C. Wang & Y.F. Yang leg.; TRU-Araneidae-342–343.

**Etymology.** The species name is a noun in apposition derived from Chinese pinyin giong, short name of the type locality, Hainan.



**Figure 3.** *Yaginumia qiong* Mi & Wang, sp. nov. **A** female paratype TRU-Araneidae-330 **B**–**G** female paratype TRU-Araneidae-341 **H**–**J** male holotype **A** epigyne (scape torn off), ventral view **B** ibid, ventral view **C** vulva, posterior view **D** ibid, dorsal view **E**, **H** habitus, dorsal view **F**, **I** ibid., ventral view **G**, **J** ibid., lateral view. Abbreviations: CD copulatory duct, CO copulatory opening, FD fertilization duct, Sc scape, Sp spermatheca. Scale bars: 0.1 mm (A–D); 1.0 mm (E–J).

Diagnosis. See diagnosis of Y. medog Mi & Wang, sp. nov.

**Description. Male** (holotype, Figs 3H–J, 4). Total length 3.95. Carapace 2.00 long, 1.50 wide. Abdomen 2.25 long, 1.80 wide. Clypeus 0.05 high. Eye sizes and interdistances: AME 0.13, ALE 0.08, PME 0.10, PLE 0.08, AME–AME 0.13, AME–ALE 0.10, PME–PME 0.04, PME–PLE 0.23, MOA length 0.33, anterior width 0.38, posterior width 0.24. Leg measurements: I 6.70 (1.90, 2.45, 1.60,



**Figure 4**. *Yaginumia qiong* Mi & Wang, sp. nov. male holotype **A** pedipalp, prolateral view **B** ibid., retrolateral view **C** ibid., ventral view **D** ibid., apical view **E** part of expanded bulb. Abbreviations: C conductor, E embolus, MA median apophysis, Pc paracymbium, TA terminal apophysis, TP tegular projection. Scale bars: 0.1 mm.

0.75), II 5.90 (1.75, 2.05, 1.40, 0.70), III 3.60 (1.15, 1.15, 0.80, 0.50), IV 4.65 (1.40, 1.60, 1.10, 0.55). Carapace red brown in cephalic region and yellow in thoracic region. Cervical groove conspicuous. Chelicerae yellowish-brown, with five promarginal and three retromarginal teeth. Endites and sternum yellow. Labium yellow at base, with paler tip. Legs yellow to grayish-yellow, without annuli. Abdomen ~1.25 × longer than wide, dorsum grayish-brown with paler middle patch. Venter abdomen grayish-yellow. Spinnerets grayish-yellow.

**Pedipalp** (Fig. 4): tibia ~1.5 × longer than wide; paracybium extremely enlarged into disc, lobe-like distally; tegular projection triangular, with toothed inner edge; median apophysis rounded at base, tapered and curled distally; embolus almost straight, shorter than conductor; conductor weakly sclerotized, rounded distally; terminal apophysis longer than tegular projection, curved to C-shape in apical view.

**Female** (paratype TRU-Araneidae-330, Fig. 3A, paratype TRU-Araneidae-341, Fig. 3B–G). Total length 4.55. Carapace 2.20 long, 1.75 wide. Abdomen 3.20 long, 2.40 wide. Clypeus 0.08 high. Eye sizes and interdistances: AME 0.13, ALE 0.08, PME 0.10, PLE 0.08, AME–AME 0.13, AME–ALE 0.13, PME–PME 0.05, PME–PLE 0.25, MOA length 0.30, anterior width 0.38, posterior width 0.25. Leg measurements: I 6.50 (1.90, 2.40, 1.55, 0.65), II 5.75 (1.70, 2.10, 1.35, 0.60), III 3.70 (1.15, 1.25, 0.80, 0.50), IV 5.05 (1.65, 1.80, 1.10, 0.50). Habitus similar to that of male.

**Epigyne** (Fig. 3A–D): ~1.71 × wider than long in ventral view, with short, tongue-shaped scape; copulatory openings rounded in ventral view, situated on ventral surface; copulatory ducts twisted, about equal length to spermathecal diameter; spermathecae rounded, nearly touching.

**Variation.** Total length: ♂♂ 3.85–3.95 (*N* = 2); ♀♀ 4.25–5.70 (*N* = 13). **Distribution.** China (Hainan).

## Yaginumia sia (Strand, 1906)

Figs 5-7

- Aranea sia Strand, in Bösenberg and Strand 1906: 237, pl. 4, fig. 24 (♀); Song 1980: 94, fig. 40a−d (♂♀) (type material in Senckenberg Museum, Frankfurt am Main (SMF), Germany, not examined).
- Araneus sia Yaginuma, 1960: 115, fig. 50.1–3; Lee 1966: 40, fig. 10m–o; Yaginuma 1971: 54, fig. 50.1–3 (♂♀); Yin 1978: 2, fig. 3A–D (♂♀); Hu 1984: 97, fig. 92.1–2 (♂♀); Zhao 1993: 233, fig. 107a–b (♂♀); Zhao 1995: 950, fig. 446a–b (♂♀).
- Yaginumia sia Archer, 1960: 14, figs 1-4 (♂♀); Namkung et al. 1972: 93, fig. 11

   (♀); Guo 1985: 75, fig. 2-27.1-3 (♂♀); Yaginuma 1986: 109, fig. 57.6 (♂♀);

   Zhang 1987: 89, fig. 73.1-4 (♂♀); Ishinoda 1989: 21, figs 12, 13 (♂♀); Chikuni

   1989: 75, fig. 39 (♂♀); Feng 1990: 101, fig. 76.1-3 (♂♀); Chen and Gao 1990:

   73, fig. 92a-c (♂♀); Chen and Zhang 1991: 91, fig. 82.1-3 (♂♀); Zhao 1993:

   262, fig. 123a, b (♂♀); Zhao 1995: 979, fig. 462a, b (♂♀); Yin et al. 1997: 395,

   fig. 286a-d (♂♀); Song et al. 1999: 309, figs 184G-l, 185L (♂♀); Namkung

   2002: 303, fig. 19.64a, b (♂♀); Kim and Kim 2002: 225, figs 69, 155, 288, 289

   (♂♀); Kim and Cho 2002: 270, figs 685-690 (♀); Namkung 2003: 305, fig.

   19.64a, b (♂♀); Tanikawa 2007: 93, figs 299, 300, 760-763 (♂♀); Tanikawa

   2009: 463, figs 331-334 (♂♀); Zhu and Zhang 2011: 248, fig. 179A-D (♂♀);

   Yin et al. 2012: 762, fig. 381a-e (♂♀); Kim and Lee 2012: 109, fig. 81A-C,

   plate 24 (♂♀); Baba and Tanikawa 2015: 69, 4 fig. (♂♀).

**Material examined.** CHINA – Guizhou Province • 2334, 2334, 25; Tongren City, Shiqian County, Pingshan Township, Fodingshan Village, Yaoshang; 27°20.54'N, 108°9.50'E; ca 640 m elev.; 11.VII.2017; X.Q. Mi et al. leg.; TRU-Araneidae-344–349 • 23324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324, 25324

**Diagnosis.** This species resembles *Y. medog* Mi & Wang, sp. nov. in appearance and genitalia structures, but it can be distinguished as follows: 1) median apophysis with a projection on middle part (Fig. 6A, C–E) vs lacking (Fig. 2A, C–E); 2) median apophysis curled about 45° in ventral view (Fig. 6C) vs about 90° (Fig. 2C); 3) copulatory openings almost rounded in ventral view (Fig. 5A, B) vs arcuate (Fig. 1A); and 4) diameter of spermathecae about 1/4 width of epigynal base (Fig. 5D) vs about 2/5 width of epigynal base (Fig. 1D).

**Description. Male** (TRU-Araneidae-350, Figs 5H–J, 6). Total length 6.30. Carapace 3.30 long, 2.50 wide. Abdomen 3.70 long, 2.60 wide. Clypeus 0.08 high. Eye sizes and interdistances: AME 0.18, ALE 0.10, PME 0.13, PLE 0.10, AME–AME 0.15, AME–ALE 0.28, PME–PME 0.05, PME–PLE 0.45, MOA length 0.48, anterior width 0.48, posterior width 0.30. Leg measurements: I 13.30 (3.70, 5.10, 3.20, 1.30), II 11.60 (3.20, 4.20, 3.00, 1.20), III 6.50 (2.10, 2.10, 1.50, 0.80), IV 9.10 (2.70, 3.30, 2.20, 0.90). Carapace dark brown in cephalic region and yellowish-brown in thoracic region. Cervical groove conspicuous. Chelicerae dark brown, with four promarginal and three retromarginal teeth. Endites and labium dark brown at base, with paler tip. Sternum yellowish-brown. Legs yellow with brown annuli. Abdomen ~1.42 × longer than wide, dorsal grayish-brown with paler edges. Venter abdomen grayish-yellow with pair of lateral white patches. Spinnerets grayish-yellow.

**Pedipalp** (Fig. 6): tibia ~1.96 × longer than wide in ventral view; paracybium enlarged at base, lobe-like distally; tegular projection triangular, with serrated edge; median apophysis wide at base, with projection at middle part, tapered and curled distally; embolus slightly curled, shorter than conductor; conductor membranous, longer than wide; terminal apophysis with weakly sclerotized distal portion, about equal length to tegular projection.

**Female** (TRU-Araneidae-351, Fig. 5A, TRU-Araneidae-352, Fig. 5B–G). Total length 7.00. Carapace 3.00 long, 2.80 wide. Abdomen 4.30 long, 3.30 wide. Clypeus 0.08 high. Eye sizes and interdistances: AME 0.18, ALE 0.10, PME 0.13, PLE 0.10, AME–AME 0.15, AME–ALE 0.25, PME–PME 0.05, PME–PLE 0.45, MOA length 0.45, anterior width 0.45, posterior width 0.30. Leg measurements: I 11.90 (3.40, 4.40, 3.00, 1.10), II 10.30 (3.00, 3.80, 2.50, 1.00), III 6.20 (2.00, 2.20, 1.30, 0.70), IV 8.90 (2.80, 3.20, 1.90, 1.00). Habitus similar to that of male.

**Epigyne** (Fig. 5A–D): ~1.55 × wider than long in ventral view, with heartshaped scape; copulatory openings rounded, situated on ventral surface; copulatory ducts twisted, a bit longer than spermathecal diameter; spermathecae rounded, touching.



**Figure 5.** *Yaginumia sia* (Strand, 1906) **A** TRU-Araneidae-351 **B–G** TRU-Araneidae-352 **H–J** TRU-Araneidae-350 **A** epigyne (scape torn off), ventral view **B** ibid, ventral view **C** ibid., posterior view **D** vulva, posterior view **E**, **H** habitus, dorsal view **F**, **I** ibid., ventral view **G**, **J** ibid., lateral view. Abbreviations: CD copulatory duct, CO copulatory opening, FD fertilization duct, Sc scape, Sp spermatheca. Scale bars: 0.1 mm (**A–D**); 1.0 mm (**E–J**).



**Figure 6.** *Yaginumia sia* (Strand, 1906) TRU-Araneidae-350 **A** pedipalp, prolateral view **B** ibid., retrolateral view **C** ibid., ventral view **D** ibid., apical view **E** part of expanded bulb. Abbreviations: C conductor, E embolus, MA median apophysis, Pc paracymbium, TA terminal apophysis, TP tegular projection. Scale bars: 0.5 mm (**A–C**), 0.1 mm (**D**, **E**).


**Variation.** Total length: 33 5.60-8.20 (*N* = 15); 99 5.80-13.10 (*N* = 52). Scape torn off in most individuals.

**Distribution.** China (Anhui, Fujian, Guangdong, Guangxi, Guizhou, Henan, Hubei, Hunan, Jiangsu, Shaanxi, Shandong, Sichuan, Taiwan, Xinjiang, Zhejiang), Korea, Japan.

## Discussion

According to the literature and our fieldwork experience, *Y. sia* shows a high propensity to live close to humans; the specimens were collected in houses, under the eaves, around bridges, rice fields and cotton fields; it is widely distributed in eastern Asia, human activities may influence its distribution. However, the two new *Yaginumia* species were collected from low shrubs and didn't show the propensity to live close to humans.

The edges of the pedipalpal tegulum of most araneids are rounded and almost smooth, or with low ridges in some species; a long tegular process is rarely found in araneids. Levi (1974) introduced the term "projection of tegulum" for *Y. sia* for the first time; although the long tegular projection looks like a conductor, it is an extension of the tegulum, and the conductor is a structure of the outer bulb close to the tegulum. A long tegular projection was also described in some Chinese araneids species, such as *Hypsosinga alboria* Yin, Wang, Xie & Peng, 1990, *H. sanguinea* (C. L. Koch, 1844), *Larinia astrigera* Yin, Wang, Xie & Peng, 1990, *L. cyclera* Yin, Wang, Xie & Peng, 1990, *L. dinanea* Yin, Wang, Xie & Peng, 1990, *L. elegans* Spassky, 1939, *L. nolabelia* Yin, Wang, Xie & Peng, 1990, *L. phthisica* (L. Koch, 1871), *L. wenshanensis* Yin & Yan, 1994, and *Lariniaria argiopiformis* (Bösenberg & Strand, 1906).

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# **Additional information**

# **Conflict of interest**

The authors have declared that no competing interests exist.

# **Ethical statement**

No ethical statement was reported.

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## **Data availability**

All of the data that support the findings of this study are available in the main text.

# References

Archer A (1960) A new genus of Argiopidae from Japan. Acta Arachnologica 17(1): 13– 14. https://doi.org/10.2476/asjaa.17.13

Baba Y, Tanikawa A (2015) The handbook of spiders. Bun-ichi Sogo Shuppan, Tokyo, 112 pp.

- Bösenberg W, Strand E (1906) Japanische Spinnen. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 30: 93–422.
- Chen X, Gao J (1990) The Sichuan farmland spiders in China. Sichuan Science and Technology Publishing House, Chengdu, 226 pp.
- Chen Z, Zhang Z (1991) Fauna of Zhejiang: Araneida. Zhejiang Science and Technology Publishing House, Hangzhou, 356 pp.
- Chikuni Y (1989) Pictorial encyclopedia of spiders in Japan. Kaisei-sha Publishing Co., Tokyo, 310 pp.
- Feng Z (1990) Spiders of China in colour. Hunan Science and Technology Publishing House, 256 pp.
- Gregorič M, Agnarsson I, Blackledge T, Kuntner M (2015) Phylogenetic position and composition of Zygiellinae and *Caerostris*, with new insight into the orb-web evolution and gigantism. Zoological Journal of the Linnean Society 175: 225–243. https://doi.org/10.1111/zoj.12281
- Guo J [Ed.] (1985) Farm spiders from Shaanxi Province. Shaanxi Science and Technology Press, 227 pp.
- Hu J (1984) The Chinese spiders collected from the fields and the forests. Tianjin Science and Technology Press, 482 pp.
- Ishinoda T (1989) Studies on the ecology, distribution of the Japanese spider (Zuguro-onigumo): *Yaginumia sia* (Strand, 1906). Heptathela 4: 21–30.
- Kallal R, Hormiga G (2018) Systematics, phylogeny and biogeography of the Australasian leaf-curling orb-weaving spiders (Araneae: Araneidae: Zygiellinae), with comparative analysis of retreat evolution. Zoological Journal of the Linnean Society 184: 1055–1141. https://doi.org/10.1093/zoolinnean/zly014
- Kallal R, Dimitrov D, Arnedo M, Giribet G, Hormiga G (2020) Monophyly, taxon sampling, and the nature of ranks in the classification of orb-weaving spiders (Araneae: Araneoidea). Systematic Biology 69(2): 401–411. https://doi.org/10.1093/sysbio/syz043
- Kim J, Cho J (2002) Spider: Natural Enemy & Resources. Korea Research Institute of Bioscience and Biotechnology (KRIBB), 424 pp.
- Kim J, Kim, J (2002) A revisional study of family Araneidae Dahl, 1912 (Arachnida, Araneae) from Korea. Korean Arachnology 18: 171–266.
- Kim S, Lee S (2012) Arthropoda: Arachnida: Araneae: Araneidae. Araneid spiders. Invertebrate Fauna of Korea 21(16): 1–146.
- Lee C (1966) Spiders of Formosa (Taiwan). Taichung Junior Teachers College Publisher, 84 pp.
- Levi H (1974) The orb-weaver genus *Zygiella* (Araneae: Araneidae). Bulletin of the Museum of Comparative Zoology 146(5): 267–290.
- Mi X, Wang C, Gan J (2023) Six new species of the orb-weaver spider genus Araneus Clerck, 1757 (Araneae, Araneidae) and a redescription of A. colubrinus Song & Zhu, 1992 from Fanjingshan National Nature Reserve, Guizhou, China. ZooKeys 1173: 243–273. https://doi.org/10.3897/zookeys.1173.106315
- Namkung J (2002) The spiders of Korea. Kyo-Hak Publishing Co., Seoul, 648 pp. [2001 in the book, but publ. in 2002 per Platnick]

Namkung J (2003) The Spiders of Korea, 2<sup>nd</sup> edn. Kyo-Hak Publishing Co., Seoul, 648 pp.

- Namkung J, Paik W, Yoon K (1972) The spider fauna of Mt. Jiri, Cholla-namdo, Korea. Korean Journal of Plant Protection 11: 91–99.
- Roewer C (1942) Katalog der Araneae von 1758 bis 1940. 1. Band (Mesothelae, Orthognatha, Labidognatha: Dysderaeformia, Scytodiformia, Pholciformia, Zodariiformia, Hersiliaeformia, Argyopiformia). Natura, Buchhandlung für Naturkunde und exakte Wissenschaften Paul Budy, Bremen, 1040 pp.
- Saitō S (1959) The Spider Book Illustrated in Colours. Hokuryukan, Tokyo, 194 pp.
- Song D [Ed.] (1980) Farm Spiders. Science Press, Beijing, 247 pp.
- Song D, Zhu M, Chen J (1999) The spiders of China. Hebei Science and Technology Publishing House, Shijiazhuang, 640 pp.
- Tanikawa A (2007) An identification guide to the Japanese spiders of the families Araneidae, Nephilidae and Tetragnathidae. Arachnological Society of Japan, 121 pp.
- Tanikawa A (2009) Hersiliidae. Nephilidae, Tetragnathidae, Araneidae. In: Ono H (Ed.) The spiders of Japan with keys to the families and genera and illustrations of the species. Tokai University Press, Kanagawa, 149, 403–463.
- WSC (2024) World Spider Catalog, version 25.5. Natural History Museum Bern. [accessed on 2024-10-15] https://doi.org/10.24436/2
- Yaginuma T (1960) Spiders of Japan in colour. Hoikusha, Osaka, 186 pp.
- Yaginuma T (1971) Spiders of Japan in colour (enlarged and revised edition). Hoikusha, Osaka (for 1969), 197 pp.
- Yaginuma T (1986) Spiders of Japan in color (new ed.). Hoikusha Publishing Co., Osaka, 305 pp., 64 plates.
- Yin C (1978) A study on the general orb-weaver spiders and wolf-spiders (Araneae: Araneidae, Lycosidae) from rice fields. Journal of Hunan Teachers College [nat. Sci. Ed.] 1978(10): 1−21.
- Yin C, Wang J, Zhu M, Xie L, Peng X, Bao Y (1997) Fauna Sinica: Arachnida: Araneae: Araneidae. Science Press, Beijing, 460 pp.
- Yin C, Peng X, Yan H, Bao Y, Xu X, Tang G, Zhou Q, Liu P (2012) Fauna Hunan: Araneae in Hunan, China. Hunan Science and Technology Press, Changsha, 1590 pp.
- Zhang W [Ed.] (1987) Farm spiders from Hebei Province. Hebei University of Science and Technology Press, 299 pp.
- Zhao J (1993) Spiders in the cotton fields in China. Wuhan Publishing House, Wuhan, China, 552 pp.
- Zhao J (1995) Araneida. In: Natural enemies of cotton pests in China. Wuhan Publishing House, Wuhan, China, 762–1155.
- Zhu M, Zhang B (2011) Spider Fauna of Henan: Arachnida: Araneae. Science Press, Beijing, 558 pp.
- Zhu M, Song D, Zhang J (2003) Fauna Sinica: Invertebrata Vol. 35: Arachnida: Araneae: Tetragnathidae. Science Press, Beijing, 418 pp.



Research Article

# Revision of the millipede family Dalodesmidae in Madagascar, with descriptions of two new Malagasy species of *Dalodesmus* Cook, 1896 (Diplopoda, Polydesmida)

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#### Abstract

The family Dalodesmidae Cook, 1896 in the fauna of Madagascar is reviewed and shown to presently encompass eight species in three genera: Dalodesmus Cook, 1896 (six species), Eutubercularium Brölemann, 1916 (one species), and Phymatodesmus de Saussure & Zehntner, 1897 (one species). These genera are diagnosed, and their respective species keyed, all being endemic to Madagascar proper and/or the immediately adjacent islets of Nosy Be and/or Nosy Sakatia. Dalodesmus currently contains six species, including two new, all supplied either with brief descriptive notes and available iconography or extensive descriptions and new illustrations, as follows: D. hamatus (Brandt, 1841), from an unspecified locality in Madagascar, now redescribed from a male specimen from Makira, northeastern Madagascar; D. odontopezus (Attems, 1898), from Nosy Be Isle; D. orator Hoffman, 1974, from Ambohimitombo, central Madagascar; D. tectus Cook, 1896 (= D. hova (de Saussure & Zehntner, 1897), syn. nov.), originally described from an unspecified locality in central Madagascar, with a male type and additional males identified as D. hova recorded from the Andasibe National Park (= Périnet) in east-central Madagascar. Additionally, two new species are described, D. speophilus sp. nov., from Grotte de Anjohibe, northwestern Madagascar, and D. kompantsevi sp. nov., from Montagne d'Ambre, northern Madagascar. Both the type species of Dalodesmus and its synonym Tubercularium Attems, 1898, D. tectus and D. odontopezus, respectively, are partly revised and illustrated based on holotypes, while D. hamatus is duly described and illustrated based on the first discovery of a male. Both Eutubercularium and Phymatodesmus are still monospecific, comprising only E. voeltzkowi (Mesibov, Wesener & Hollier, 2018), from Nosy Be Isle, and P. sakalava (de Saussure & Zehntner, 1901), from Andasibe, respectively. The latter species is fully redescribed and illustrated for the first time from male material.

Key words: Endemism, key, Madagascar, map, new synonymies, taxonomy

# Introduction

The basically austral millipede family Dalodesmidae Cook, 1896 currently contains approximately 55 genera and more than 250 described species. The distribution pattern of the family is highly disjunct, ranging across the Southern Hemisphere: New Caledonia, New Zealand, Australia, southern Africa and Madagascar, and southern South America (Enghoff et al. 2015). Mesibov (2017) has since summarised the dalodesmid fauna of southern South America (Chile with the adjacent parts of Argentina and Brazil), recording 12 accepted genera and 52 species.

Madagascar, despite its huge size and outstanding biogeographic importance, is especially species-poor in indigenous members of the largest diplopod order Polydesmida. All species are contained in two endemic genera of Dalodesmidae (Wesener and Enghoff 2022). *Dalodesmus* Cook, 1896, the type genus of the family, is known to currently comprise six species, whereas *Phymatodesmus* de Saussure & Zehntner, 1902 is monospecific (Wesener and Enghoff 2022). Sometimes a third and also monospecific genus of the Dalodesmidae, *Eutubercularium* Brölemann, 1916, has occasionally been added to the list (Hoffman 1980).

The history of taxonomic research on Malagasy dalodesmids is unusually convoluted (e.g., Mesibov et al. 2018). Prompted by the recent discovery of two new species of *Dalodesmus* in northern Madagascar, we present a modern revision of the family and an illustrated identification key based on freshly collected and historical specimens. The present paper includes the record and first description of the male of *D. hamatus*, a partial revision of the holotypes of both *D. tectus* Cook, 1896, the type species of *Dalodesmus*, and *D. odontopezus* (Attems, 1898), and the description and the first illustration of somatic characters in the former two species.

## Materials and methods

The material underpinning the present contribution is based on the holotypes of *D. tectus* and *Phymatodesmus sakalava*, as well as four fresh collections (by Taiti and Bartolozzi from the MZUF, by Telnov from the NHML, by the late Kompantsev, and by Spelzhausen during her ecological study (see Spelzhausen et al. 2020), each containing a new species or the first male specimen needed for a proper redescription.

The images of *D. kompantsevi* sp. nov. were taken with a Canon EOS 5D digital camera and stacked using Zerene Stacker software. Final image processing was performed with Adobe Photoshop CC. The pictures of *D. hova* from Fort Dauphin and the holotype slide containing the gonopods of *D. odontopezus* were taken with a Nikon DS-Ri2 camera mounted on a Nikon SMZ25 stereo microscope, using NIS-Elements Microscope Imaging Software with an Extended Depth of Focus (EDF) patch. The photographs of *Phymatodesmus sakalava*, *D. tectus*, *D. hamatus*, and *D. speophilus* sp. nov. were obtained using a Leica Z6 Imaging System with the software AutoMontage.

For scanning electron microscopy (SEM), the samples were dehydrated via ethanol baths with ascending concentrations, mounted on stubs, and dried overnight. The stubs were sputter-coated with 100 nm of gold in a Hummer VI (Anatech, USA) sputtering system and observed under a Zeiss Sigma 300 VP scanning electron microscope.

The distribution map was generated using QGIS 3.38.3 'Grenoble' and processed applying Photoshop CS6.

In the synonymy section, D stands for a description or descriptive notes, K for the appearance in a key, N for nomenclatural issues, R for a new record or new records, and L for merely a listing.

List of museum acronyms:

MHNG	Muséum d'histoire naturelle de la Ville de Genève, Geneva, Switzerland
MZUF	Museum «La Specola», Florence, Italy
NHMW	Naturhistorisches Museum Wien, Austria
SMF	Senckenberg Museum of Natural History, Frankfurt/M., Germany
ZFMK	Zoologisches Forschungsinstitut und Museum Alexander Koenig,
	Germany
ZISP	Zoological Institute, Russian Academy of Sciences, StPetersburg,
	Russia
ZMB	Zoological Museum of the Humboldt University in Berlin, Germany
ZMUM	Zoological Museum, State University of Moscow, Russia

# Results

#### Taxonomy

## Order Polydesmida Leach, 1815 Family Dalodesmidae Cook, 1896

**Note.** Following Jeekel (1965, 1971), Hoffman (1980), and Wesener and Enghoff (2022), the Malagasy dalodesmid fauna comprises only three genera: *Dalodesmus* Cook, 1896; *Eutubercularium* Brölemann, 1916, and *Phymatodesmus* de Saussure & Zehntner, 1902.

## Genus Phymatodesmus de Saussure & Zehntner, 1902

*Phymatodesmus* de Saussure & Zehntner, 1902; type species *Polydesmus sakalava* de Saussure & Zehntner, 1897, by monotypy. See Mesibov et al. (2018) for the convoluted taxonomic history of this generic name.

**Diagnosis.** Body pale reddish, subcylindrical, much shorter than those of *Dalodesmus* and *Eutubercularium*, only ca 10 mm long, 1.0–1.05 mm wide. Paraterga very narrow, declivous and subrectangular, unlike in *Dalodesmus* and *Eutubercularium* where the paraterga are conspicuous and greatly expanded. *Phymatodesmus* differs from both *Eutubercularium* and *Dalodesmus* in the presence of circular cones/tuberculations (vs large, oval to polygonal, often irregular, piligerous tuberculations or areations), and in the 2+2 setae on the paraprocts borne on distinct knobs (not being borne on distinct knobs in *Eutubercularium* and *Dalodesmus*).

**Remark.** Hoffman (1980) tentatively listed this genus in the family Vaalogonopodidae, vs Dalodesmidae in recent species lists (Enghoff 2003; Wesener and Enghoff 2022), a placement we can confirm with the first description of the male.

#### Phymatodesmus sakalava (de Saussure & Zehntner, 1897)

Figs 1-3

- *Polydesmus sakalava* de Saussure & Zehntner, 1897: plate 5, fig. 22 (figure and caption only).
- Polydesmus (Phymatodesmus) sakalava de Saussure and Zehntner 1902: 95 (D).
- Eutubercularium sakalava Brölemann 1916: 605 (D); Hollier and Wesener 2017: 62 (L).
- Dalodesmus sakalava Jeekel 1965: 238 (L); Hoffman 1974: 230 (L); Golovatch and Hoffman 1989: 162 (L).
- Phymatodesmus sakalava Attems 1940: 490 (L); Enghoff 2003: 623 (L);Mesibov et al. 2018: 389 (N); Wesener and Enghoff 2022: 926 (L).

Dalodesmidae sp. - Spelzhausen et al., 2020: 4 (L).

**Note.** As iterated above, the confusion de Saussure and Zehntner (1897, 1901, 1902) created by the initial usage of the specific epithet *sakalava* for two species of *Polydesmus* Latreille, 1761 has been resolved only recently (Mesibov et al. 2018). While the original type locality of the species is unknown, Franz Sikora is known to have collected mainly around the capital, Antananarivo. The freshly collected male specimen comes from Andasibe (Spelzhausen et al. 2020), one of the largest remaining blocks of natural vegetation, on the old way from the coast to the capital.

Material examined. • ♀ holotype, fragmented (MHNG), 'Madagascar', coll. Sikora • 1 ♂, ZFMK MYR 12217; MADAGASCAR, Moramanga District, Andasibe National Park (= Périnet), Analamazaotra Forest Station, secondary forest, *Eucalyptus* 1909 plantation, sifted leaf litter, IV.2017, L. Spelzhausen and G. Rakotonirina leg.

**Brief description.** (After de Saussure and Zehntner 1897, 1902.) A single line drawing (Fig. 1G) and its caption reading "*Polydesmus sakalava*" in de Saussure and Zehntner (1897) serve as the original description. Combined with a later verbal description of the adult Q holotype, by de Saussure and Zehntner (1902), the following relevant information can be obtained: body pale reddish, subcylindrical, 10 mm long, 1 mm wide, with a strongly convex dorsum and very narrow, declivous, and subrectangular paraterga.

*Phymatodesmus* sakalava can be readily distinguished from other known Malagasy Dalodesmidae: the small size, a subcylindrical body, the mostly small, conical, and sharp tuberculations on midbody metaterga arranged in four unusually regular transverse rows, and strikingly small, narrow, and rectangular paraterga.

**First description of the male.** Length ca 10 mm, width of midbody pro- and metazona 0.75 and 1.05 mm, respectively.

Colouration (freshly preserved in ethanol) brown; prozona, basal parts of legs, mandibles, and paraprocts paler. Epicranium grey, antennae and apical parts of legs faded grey.

Body with 20 rings. Tegument mainly dull (Fig. 1A-F), microgranulate to microtuberculate throughout (Fig. 1G, H), even surfaces of prozona and of metazona below paraterga finely microgranulate, sterna granulate.

Head also densely microtuberculate or granulate throughout, micropilose; epicranial suture thin, but distinct; genae squarish, set off ventrally from gnathochilarial stipes by a small, but evident ridge. Interantennal isthmus  $\sim 2 \times$  diameter of antennal socket (Fig. 1C).



Figure 1. *Phymatodesmus sakalava* (de Saussure & Zehntner, 1897),  $\bigcirc$  holotype MHNG (G, H),  $\bigcirc$  specimen (ZFMK MYR12217). Multi-layer photographs and drawings **A** habitus, dorsal view **B** habitus, lateral view **C** habitus, ventral view **D** detail of midbody rings, dorsal view **E** detail of anterior body rings and gonopod, lateral view **F** detail of anterior rings and gonopods, ventral view **G** drawing from the original description in de Saussure and Zehntner (1897) **H** detail of body ring,  $\bigcirc$  holotype **I** gonopod still attached, ventral view. Abbreviations: lb = lateral branch; mb = mesal branch; sl = solenomere branch. Scale bar: 0.3 mm (**H**).

Antennae very short and rather clavate, in situ reaching back past ring 2 when stretched dorsally, very densely setose and microgranulate. In length, antennomere 6 > 5 = 3 > 4 > 2 > 1 = 7; antennomere 6 the largest and the highest, antennomeres 5 and 6 each with a small, round, distodorsal knob, most likely beset with sensory cones.



Figure 2. *Phymatodesmus sakalava* (de Saussure & Zehntner, 1897), 3 specimen (ZFMK MYR12217). SEM micrographs **A** midbody ring with pro- and metazonite, dorsal view **B** midbody ring, lateral view **C** midbody ring, paranota with ozopore **D** details of surface structures, dorsal view **E** detail of surface structures of prozonite and metazonite **F** endotergum. Scale bars: 100 µm (**A**–**C**); 10 µm (**D**); 20 µm (**F**).

In width, collum = head < ring 2 > 3 = 4-16; thereafter body gradually tapering towards telson (Fig. 1A–C). Collum transversely suboval, regularly and broadly rounded laterally, densely tuberculate, most tuberculations being circular, evident, equipped with very short, mostly subclavate setae and arranged in 15–17 lateral, 8–9 transverse, rather irregular, arcuated rows. Metaterga 2–4 narrow, each with four, similar, transverse, arcuated, circular rows of setigerous tubercles, following metaterga each largely with five such rows (Fig. 2A, B). Paraterga short, rectangular, strongly declivous, posterior margin straight (Fig. 2B, C). Lateral margin of paraterga beset with 5–6 similarly circular, setigerous (Fig. 2D) tubercles/lobulations. Ozopores inconspicuous, opening laterally near penultimate lateral lobulation on pore-bearing rings 5, 7, 9, 10, 12, 13, 15–19. Strictures between pro- and metazona narrow and rather deep, nearly smooth (Fig. 2E).

Telson: Epiproct small, conical, and subtruncate at tip. Hypoproct trapeziform, with 1+1 setae borne on distinct oblong knobs at caudal margin. Paraprocts with 2+2 setae on triangular and projecting knobs (Fig. 2C).

Limbus very thin, small, and entire. Neither an axial line nor pleurosternal carinae (Fig. 1A–C). Posterior margin of metazona a row of dense, elongate, apically microdenticulate (with 6–9 indentations (Fig. 2F), subrectangular projections (Fig. 2F)).

Gonopodal aperture roundly pentagonal, large, taking up  $\sim 2/3$  width of metazonum 7, clearly open and drawn into metazonum 6 (Fig. 11).

First two leg pairs shorter and thicker than other legs. Midbody legs incrassate, medium in length, as long as body height, with small, stout, abundant,



Figure 3. *Phymatodesmus sakalava* (de Saussure & Zehntner, 1897),  $\Im$  specimen (ZFMK MYR12217). Multi-layered photographs and drawings, gonopod **A** posterior view **B** lateral and mesal view **C** lateral view **D** posterior view **E** anterior view **F** lateral view. Abbreviations: fe = femorite; lb = lateral branch; mb = mesal branch; sl = solenomere branch.

and usually curved setae with admixture of sphaerotrichomes ventrally on all podomeres; gonopores on coxae 2 inconspicuous, prefemora not bulged laterally; claws simple, very small; in length, tarsus > femur > prefemur > coxa > tibia = postfemur.

Gonopods (Figs 1I, 3A–F) relatively simple. Both coxite and prefemorite very short, fused medially, prefemorite setose. Femorites (fe) contiguous medially, densely setose both ventrally and laterally, rather stout (~ 2 × as long as acropodites), suberect and clearly flattened dorsoventrally. Acropodite tripartite, divided into a dorsomedial, long, simple and subsecuriform solenomere (sl), a simple and subspiniform lateral branch (lb), both sl and lb being subequal in length, but clearly shorter than the longest, simple, rather finger-shaped, apically roundly and irregularly trifid, mesal branch (mb).

**Remarks.** Aside from the very obvious differences between *Phymatodesmus* and *Dalodesmus* in the development and shape of paraterga, clear-cut discrepancies also concern leg lengths (in *Phymatodesmus*, the whole legs, especially both postfemora and tibiae are shorter), the antennae are also shorter, the collum is as wide as the head, the head is completely micropilose, including the epicranium (vs glabrous in *Dalodesmus*), the paraprocts of the telson lack triangular setiferous knobs/projections (vs 2+2 setae borne on knobs on the paraprocts), and the 1+1 setae on the hypoproct are borne on prominent knobs and better separated (vs placed closer to one another in *Dalodesmus*).

#### Genus Eutubercularium Brölemann, 1916

Eutubercularium Brölemann, 1916; type species Pterodesmus sakalava de Sausure & Zehntner, 1901 (currently Dalodesmus voeltzkowi Mesibov, Wesener & Hollier, 2018), by original designation, synonymised with Dalodesmus by Jeekel (1965), resurrected from synonymy following Hoffman (1980).

**Diagnosis.** 26 mm long, 4.5 mm wide, habitus identical to that of *Dalodesmus*, with five rows of transverse, often rather irregular rows of piligerous tuberculations or obliterated areations between always strongly developed and laterally similarly piligerous and crenulate/tuberculate paraterga.

The basic differences from *Dalodesmus* lie only in gonopodal conformation: femorites densely setose all over ventral and lateral sides, relatively stout, only ~ 2 × as long as acropodites and, much like in *Phymatodesmus*, clearly flattened dorsoventrally (vs less strongly setose to nearly bare, much longer, slender and subcylindrical); solenomere (sl) lateral, long, flagelliform, and non-sigmoid (vs medial, short, usually simple and rather rod- or lobe-shaped, often sigmoid), lateral branch (lb) remarkably tripartite and complex (vs lb unipartite and usually simple to rather simple).

**Remarks.** Brölemann (1916) described *Eutubercularium* based on gonopod differences derived only from the drawings of the species published by de Saussure and Zehntner (1901: figs 8–10) for *Polydesmus sakalava* (now *Dalodesmus voeltzkowi* Mesibov, Wesener & Hollier, 2018). Apparently, the type specimens can no longer be located. Jeekel (1965) hesitantly decided to synonymise *Eutubercularium* with *Dalodesmus*, as the observed differences could be a simple drawing error. Hoffman (1980) listed *Eutubercularium* again as a valid genus, but without explanation, a move not followed in recent species lists (Enghoff 2003; Wesener and Enghoff 2022). Here, we resurrect *Eutubercularium* from synonymy with *Dalodesmus* following Hoffman (1980).

## *Eutubercularium voeltzkowi* (Mesibov, Wesener & Hollier, 2018), comb. nov. Fig. 4

Polydesmus (Pterodesmus) sakalava – de Saussure & Zehntner, 1901: 437, figs 8–10 (D).

Polydesmus (Tubercularium) sakalava - de Saussure and Zehntner 1902: 93 (D).

Eutubercularium sakalava – Brölemann 1916: 605 (D); nec Hollier and Wesener 2017: 62 (L, N).

Non Tubercularium sakalava – Attems 1940: 435, fig. 619 (D, K).

Nec Dalodesmus sakalava – Hoffman 1974: 230 (D); nec Golovatch and Hoffman 1989: 162 (L); nec Enghoff 2003: 623 (L).

*Dalodesmus voeltzkowi* Mesibov, Wesener & Hollier, 2018: 389 (N), nom. nov. *Dalodesmus voeltzkowi* – Wesener and Enghoff 2022: 926 (L).

**Note.** The new name *voeltzkowi* was proposed to dispose of the homonymy within *Polydesmus* Latreille, 1761, that had been created by de Saussure and Zehntner (1902), i.e., to correctly conserve *P. sakalava* de Saussure & Zehntner, 1897 as the older, and therefore valid, name (see below), and to replace *P. sakalava* de Saussure & Zehntner, 1901 as a later and invalid name (Mesibov et al. 2018). No material of *Polydesmus sakalava* could be traced at the SMF (P. Jäger, pers. comm. April 2024) and the type locality is Nosy Be (de Saussure and Zehntner 1901)

**Brief description.** (After de Saussure and Zehntner 1901, 1902.) First described in a short text with three drawings (de Saussure and Zehntner 1901: 8–10). Combined with a later verbal description of the adult ♂ holotype, by de Saussure and Zehntner (1902), the following relevant information can be derived: colouration brick red, metaterga castaneous brown, ends of paraterga brick red. Length 26 mm, width 4.5 mm. Paraterga strong, clearly rounded and crenulate laterally, acute caudolaterally. Metaterga with five, transverse rows of conical tuberculations (Fig. 4A).

Gonopods highly elaborate and complex, with coxites and densely setose prefemorites short and fused medially; femorites strongly flattened dorsoventrally, contiguous medially and fused in about basal half, without a sternal rudiment visible ventrally, each femorite setose until acropodite, this latter highly complex, basically 3-branched: (1) what seems to be a long and flagelliform solenomere branch (sl) lying lateral to and supported by (2) the highest solenophore branch (sph), unequally bifid apically, sl and sph both slightly and regularly curved ventrad; and (3), more basally, at apical ~ 1/3, a very complex lateral branch (lb) consisting of an ear-shaped lateral outgrowth (e) with a shelf ventrobasally, a strong, subacuminate, distomesal uncus, regularly curved mesad and lying just distal to (e) shelf, and a twisted mesal lobe (m), directed distally, originating near lb base and with its tip curved ventrad (Fig. 4B, C).

**Remarks.** It is only the unusually complex gonopodal conformation of *E. voeltzkowi* that allows us to clearly distinguish the genus *Eutubercularium* from the superficially very similar *Dalodesmus*: femorites densely setose all over the



**Figure 4**. *Eutubercularium voeltzkowi* (Mesibov, Wesener & Hollier, 2018),  $\Im$  or  $\square$ . Redrawn original drawings from de Saussure and Zehntner (1901) **A** midbody tergites, dorsal view **B** gonopod, posterior view **C** gonopod, lateral view of acropodite. Abbreviations: fe = femorite; lb = lateral branch; sl = solenomere branch; sph = highest solenophore branch.

ventral and lateral sides, relatively stout, only ~ 2 × as long as acropodites and, much like *Phymatodesmus*, clearly flattened dorsoventrally (vs much longer, slender, and subcylindrical, less strongly setose to nearly bare); solenomere (sl) lateral, long, flagelliform and non-sigmoid (vs medial, short, usually simple and rather rod- or lobe-shaped, often sigmoid), lateral branch (lb) remarkably tripartite and complex (vs lb unipartite and usually simple).

#### Genus Dalodesmus Cook, 1896

Dalodesmus Cook, 1896; type species D. tectus Cook, 1896, by monotypy.

- *Tubercularium* Attems, 1898; type species: *T. odontopezum* Attems, 1898, by monotypy, synonymised by Jeekel (1965).
- *Pterodesmus* de Saussure & Zehntner, 1901; invalidly proposed without a type species, also preoccupied by *Pterodesmus* Cook, 1896; synonymised by Jeekel (1965).

Note. Species included: 6 (including two new described below).

**Diagnosis.** Body medium-sized, 17–28 mm long and 3.7–5.3 mm wide. Midbody metaterga with 4–6 transverse, often rather irregular rows of piligerous tuberculations or obliterated areations between always strongly developed and laterally similarly piligerous crenulate/tuberculate paraterga, these being sub-horizontal to upturned. Gonopods less elaborate and more simple than in the other genera, both coxites and densely setose prefemorites equally short and fused medially; femorites (fe) mostly slender, subcylindrical, at most only insignificantly flattened sagittally, contiguous medially and fused in basal 1/3, with a sternal rudiment visible ventrally at the very base, bare to sometimes sparsely setose until acropodite, the latter (= acropodite) basically tripartite, a mostly distinct, occasionally branching and only rarely missing solenomere branch (sl) lying between and typically flanked by two or three branches of a rather simple to elaborate solenophore: one medial (mb), this only rarely subdivided into an apical (ab) and a subapical branch (sb), and the other lateral (lb).

*Dalodesmus* differs from *Phymatodesmus* in the much larger size (> 20 mm, vs ~ 10 mm), the strongly developed, apically pointed paratergites (vs short and rectangular in *Phymatodesmus*), the presence of large, oval to polygonal, often irregular, piligerous tuberculations or areations (vs circular cones/tuberculations in *Phymatodesmus*), and the 2+2 setae on the paraprocts not being borne on distinct knobs (vs borne on distinct knobs in *Phymatodesmus*).

In gonopodal structure, the genus *Dalodesmus* differs from both *Phyma-todesmus* and *Eutubercularium* in the femorites being long and slender, > 2 × as long as acropodites, subcylindrical, diverging in distal 2/3 to 1/2, bare to only poorly setose ventrally and/or laterally (vs femorites stout, only ~ 2 × as long as acropodites, clearly flattened dorsoventrally, contiguous all along or nearly so, and densely setose on both ventral and lateral sides).

Dalodesmus hamatus (Brandt, 1841) Figs 5–8

*Polydesmus hamatus* Brandt, 1841a: 10–11 (D); Brandt 1841b: 140 (D); Gervais 1847: 114 (D); Attems 1940: 493 (L); Golovatch and Hoffman 2000: 237 (L).

Non Polydesmus (Tubercularium) sakalava – de Saussure and Zehntner 1902: 93 (N).

Dalodesmus hamatus – Golovatch and Hoffman 1989: 160, figs 1–6 (D); 2000: 237 (L); Enghoff 2003: 623 (L); Wesener and Enghoff 2022: 926 (L).

**Note.** The  $\bigcirc$  holotype, currently housed in the ZISP collection and coming from an unspecified locality, presumably in Madagascar, has been revised, properly redescribed, and illustrated (Golovatch and Hoffman 1989).

**New material examined.** •  $\bigcirc$  (ZFMK MYR13631), MADAGASCAR, Toamasina Province, Analanjirofo, Makira Natural Park, ca 44.5 km NW of Maroantsetra, Antainambalana River tributary, 1 km around coordinates, 15°4'15"S, 49°34'48"E, 240–670 m, primary lowland rainforest on basalt, 30.VIII.–08.IX.2023, D. Telnov leg. • 2  $\bigcirc$  (ZFMK MYR13629), same data as previous • 2  $\bigcirc$  (ZFMK MYR13630), with eggs, same data as male • 1  $\bigcirc$  (NHML), same data as male.

**Diagnosis.** Tips of paraterga mostly sharp and projecting past posterior tergal margin, as in *D. odontopezus*, *D. orator*, vs wider and not projecting past rear tergal margin in *D. speophilus* sp. nov., *D. tectus*, and *D. kompantsevi* sp. nov. Colour uniformly dark grey to blackish, paraterga not yellow as opposed to *D. odontopezus* and *D. orator*. Both latter species with a male body length of 26–28 mm that is larger than *D. hamatus* with 20 mm male and 22–24 mm females. See also the key below.

Identity of the new material of *D. hamatus*. The  $\bigcirc$  holotype (after Golovatch and Hoffman 1989) has a similar size (length ~ 22 mm, width 2.9 mm) to the newly discovered material. Its colouration is rusty brown (dry specimen, probably faded). The habitus with the paraterga clearly upturned above the dorsum (Fig. 5A–D), dorsal surface between midbody paraterga largely areate, polygonal bosses mostly being clearly obliterated (Fig. 5B), this being identical to the new material. While the type locality of *D. hamatus* is just "Madagascar", the newly discovered locality in Makira Natural Park also included specimens of the very large (> 200 mm) spirostreptid *Analacostreptus sculptus* (de Saussure & Zehntner, 1902), another species otherwise known only from "Madagascar".

**Redescription.** (Based on fresh material from Makira.) Length ~ 20 mm (n = 1), width of midbody pro- and metazona 1.7 and 3.9 mm (n = 1), respectively ( $\Diamond$ ),  $\bigcirc \bigcirc 22-24$  mm long (n = 3), width of prozona 1.9–2.3 mm (n = 1), of metazona 4.1–4.3 mm (n = 4).

Colouration, after less than 6 months of preservation in alcohol, dark grey to blackish, collum faded brown, head brown, epicranium grey, legs pale grey; antennae dark brown (Fig. 6A–C).

Body with 20 rings. Tegument mainly dull, microgranulate to microtuberculate throughout (Figs 5A–D, 6A–C, 7A–D), even surfaces of prozona and of metazona below paraterga finely microgranulate, sterna granulate. Head also densely microtuberculate or granulate throughout, micropilose up to level of antennae; epicranial suture thin, but distinct; genae squarish, set off ventrally from gnathochilarial stipes by a small, but evident ridge. Interantennal isthmus ~ 2 × diameter of antennal socket. Antennae short and rather clavate, in situ reaching in both sexes back past ring 4 when stretched dorsally, very densely setose and microgranulate. In length, antennomere 6 > 3 > 5 > 4 = 2 > 1 = 7; antennomere 6 the largest and the highest, antennomeres 5 and 6 each with a small, round, distodorsal knob, most likely beset with sensory cones. In width, collum ≤ head < ring 2 =3 < 4–16; thereafter body gradually tapering towards telson (Fig. 6A–C). Collum transversely suboval, regularly and broadly rounded laterally, densely tuberculate, most tubercles slightly oblong-oval, evident,



**Figure 5.** *Dalodesmus hamatus* (Brandt, 1841),  $\bigcirc$  holotype **A** anterior part of body, dorsal view **B** right half of metazonum 10, dorsal view **C** posterior end of body, dorsal view **D** body ring 9, oral view **E** leg 2 and epigynal lobe, ventral view **F** midbody leg, lateral view. Scale bars: 1000 µm (after Golovatch and Hoffman 1989).



**Figure 6.** *Dalodesmus hamatus* (Brandt, 1841),  $\delta$  from Makira (ZFMK MYR13631). Multi-layer photographs **A** anterior body, dorsal view **B** midbody, dorsal view **C** telson, dorsal view **E** gonopods, posterior view **E** gonopods, anterior view **F** gonopods, lateral view **G** right gonopod, mesal view. Abbreviations: Ib = lateral branch; mb = mesal branch; sl = solenomere branch. Scale bars: 1000 µm.

equipped with very short, mostly subclavate setae and arranged in 16–17 lateral, 6 transverse, rather irregular, arcuated rows. Metaterga 2–4 narrow, each with 3–4 similar transverse arcuated rows of setigerous tubercles, following metaterga each largely with 4–5 such rows (Fig. 7A, B). Paraterga well-developed, set high (mostly at upper ¼ body), upturned to subhorizontal, thus leaving the dorsum only faintly convex (Fig. 7B); anterior and posterior margins of paraterga 2 and 3 clearly drawn forward and caudad, respectively, following paraterga drawn increasingly only caudad (Fig. 6A–C); caudal corners sharp, produced past rear tergal margin; caudal margins of paraterga with five oblong projections (Fig. 7B). Lateral margins of paraterga beset with numerous, similarly oblong and usually subequal, setigerous tubercles/lobulations. Ozopores inconspicuous, opening dorsally near penultimate lateral lobulation on pore-baring rings 5, 7, 9, 10, 12, 13, 15–19. Strictures between pro- and metazona narrow and rather deep, nearly smooth.



Figure 7. Dalodesmus hamatus (Brandt, 1841),  $\bigcirc$  from Makira (ZFMK MYR13631). SEM micrographs **A** midbody ring with pro- and metazonite, dorsal view **B** midbody ring, lateral view **C** details of surface structures of prozonite and metazonite **D** details of surface structures, dorsal view **E** tarsus of midbody leg **F** endotergum. Scale bars: 1000 µm (**A**); 200 µm (**B**); 100 µm (**C**, **E**); 30 µm (**D**); 0 µm (**F**).

Telson: Epiproct small, conical and subtruncate at tip. Paraprocts with 2+2 setae on triangular, projections/knobs (Figs 5C, 6C). Hypoproct trapeziform, with 1+1 setae borne on distinct oblong knobs at caudal margin.

Limbus very thin, small, and entire. Neither an axial line nor pleurosternal carinae (Fig. 7A–C). Endotergum inconspicuous, posterior margin of metazona projecting into long, sharp, apically microdenticulate, triangular projections (Fig. 7F).

Gonopodal aperture roundly pentagonal, relatively small, taking up  $\sim 1/2$  width of metazonum 7, clearly open and drawn into metazonum 6.

Midbody legs incrassate, rather long.  $1.4-1.5 \times as long as body height, with small, stout, abundant and usually curved setae with admixture of sphaerotrichomes ventrally on all podomeres (<math>\Im$ , Fig. 7E); gonopores on  $\Im$  coxae 2 inconspicuous, each borne on a very small swelling ( $\Im$ ); prefemora not bulged laterally; claws simple and very small; in length, tarsus > femur > prefemur > tibia > postfemur > coxa.

Gonopods (Figs 6D–G, 8A–I) very slender and long, tips in situ reaching anteriorly until coxae 5. Both coxites and prefemorites (= densely setose parts of telopodites) equally very short and stout, fused medially, the former fully and the latter mostly hidden inside gonopodal aperture. Femorites (fe) contiguous medially in basal 1/3, setose almost all along, both slightly diverging distad



Figure 8. Dalodesmus hamatus (Brandt, 1841),  $\overset{\circ}{\circ}$  from Makira (ZFMK MYR13631). SEM micrographs. Gonopod, **A** = right **B**-I = left. **A** Right, anterior view **B** left, anterior view **C** lateral view **D** posteromesal view **E** posterior view **F** acropodite, anterior view **G** acropodite, lateral view **H** acropodite, posteromesal view **I** acropodite, mesal view. Abbreviations: fe = femorite; lb = lateral branch; mb = mesal branch; sl = solenomere branch. Scale bars: 100 µm.

towards acropodites. Apical portions of each telopodite (= acropodites) clearly diverging, rather simple and compact, curved ventrad and clearly divided into three unequal branches: a short, slightly curved, submesal, tubiform, simple and non-sigmoid solenomere (sl) flanked by a rather simple, 2-branched solenophore, this latter being represented by a flagelliform, slightly barbed, short and acuminate lateral branch (lb), and a particularly large, lobe-shaped, acuminate and membranous mesal branch (mb) with a tooth near base.

#### Dalodesmus odontopezus (Attems, 1898)

Fig. 9

*Tubercularium odontopezum* Attems, 1898: 360, plate 7, figs 158–161 (D). *Polydesmus (Tubercularium) odontopezum* (sic!) – de Saussure and Zehntner

1902: 89 (D). Tubercularium odontopezum – Attems 1940: 435, fig. 618 (D, K).

Dalodesmus odontopezum (sic!) – Hoffman 1974: 230 (L).

Dalodesmus odontopezus – Jeekel 1965: 238 (L); Golovatch and Hoffman 1989: 161 (L); Enghoff 2003: 623 (L); Wesener and Enghoff 2022: 926 (L).

**Note.** This species was described from a single ♂ holotype, from Nosy Be Islet (Attems 1898), slide NHMW MY4429 containing its two legs and gonopods (Fig. 9C), labelled *Tubercularium odontopezum* (Attems, 1898), revised, in the NHMW collection. The torso seems to be misplaced.

**Brief description.** (After Attems 1898, 1940.)  $\stackrel{<}{\supset}$  holotype 28 mm long and 2.0 and 3.5 mm wide on pro- and metazona, respectively. Colouration of metaterga more intense brown in posterior halves, lighter in anterior ones; sides of paraterga yellowish, venter light yellowish brown, antennae and legs dirty yellow. Paraterga horizontal, not upturned above dorsum, sharpened caudally; dorsal tuberculations between paraterga mostly round (Fig. 9A).

Gonopods (Fig. 9B, C) showing setose femorites (fe), each with a small roundish, pulvillus-like field (p) of particularly dense setae ventrally near apex, coupled with complex acropodites: a slightly sigmoid and apically bifid solenomere (sl) lying between the highest, erect and subspiniform mesal branch (mb) and a much shorter, but prominent, roughly laciniate and fimbriate lateral branch (lb) directed ventrad.

#### Dalodesmus orator Hoffman, 1974

Fig. 10

*Dalodesmus orator* Hoffman, 1974: 225, figs 1–9 (D); Golovatch and Hoffman 1989: 162 (L); Enghoff 2003: 623 (L); Wesener and Enghoff 2022: 926 (L).

**Remark.** This species was described from a  $\Im$  holotype, two  $\Im$  and two  $\bigcirc$  paratypes, all coming from Ambohimitombo, central Madagascar (Hoffman 1974), in the collection of the Natural History Museum in London, United Kingdom.

**Brief description.** (After Hoffman 1974.)  $\bigcirc$  holotype ~ 26.5 mm long and up to 2.3 and 5.3 mm wide on pro- and metazona, respectively;  $\bigcirc$  up to 4.5 mm wide.



**Figure 9**. *Dalodesmus odontopezus* (Attems, 1898), ♂ holotype **A** right paratergum 14, dorsal view (after Attems 1898) **B** slide of holotype **C** both gonopods, ventral view (after Attems 1940) **D** both gonopods, ventral view (slide NHMW MY4429, photograph by 0. Macek) **E** midbody leg. Abbreviations: lb = lateral branch; mb = mesal branch; pfe = prefemorite; sl = solenomere branch. Scale bars: 500 µm.

Colouration light reddish brown with yellow paratergal apices and legs. Paraterga largely clearly upturned above dorsum and directed more laterad than caudad, at ca 45°, tips elongate and sharpened caudally; dorsal surface between paraterga mostly vaguely areate (Fig. 10A).

Gonopods (Fig. 10B–D) showing bare femorites (fe), coupled with rather complex acropodites: an unusually short and small solenomere (sl) directed ventrad, lying between the highest, suberect, distally unequally bifid mesal branch (mb) and a much shorter and strongly folded lateral branch (lb) directed ventrad.



**Figure 10**. *Dalodesmus orator* Hoffman, 1974,  $\mathcal{J}$  holotype, modified from Hoffman 1974 **A** midbody tergite, dorsal view **B** gonopod, posterior view **C** acropodite, mesal view **D** gonopod, lateral view. Abbreviations: Ib = lateral branch; mb = mesal branch; pfe = postfemorite; sl = solenomere branch. Not to scale.

## Dalodesmus tectus Cook, 1896 Figs 11, 12

Dalodesmus tectus Cook, 1896: 26 (D); Attems 1940: 489 (L); Jeekel 1965: 238, figs 1, 2 (D); Hoffman 1974: 230 (D); Golovatch and Hoffman 1989: 161 (L); Enghoff 2003: 623 (L); Wesener and Enghoff 2022: 926 (L).

Polydesmus hova de Saussure & Zehntner, 1897: plate 5, figs 23–23c (D), syn. nov. Pterodesmus hova – de Saussure and Zehntner 1901: 436 (D).

Polydesmus (Tubercularium) hova - de Saussure and Zehntner 1902: 91 (D).

Tubercularium hova – Attems 1940: 434, figs 619, 620 (D, K).

Dalodesmus hova – Jeekel 1965: 238 (L); Hoffman 1974: 230, figs 10, 11 (D); Golovatch and Hoffman 1989: 162, figs 7–9 (D); Enghoff 2003: 623 (L); Hollier and Wesener 2017: 58 (L, N); Wesener and Enghoff 2022: 926 (L).

**Note.** This species was described from a  $3^{\circ}$  holotype coming from an unspecified locality in central Madagascar (Cook 1896), in the ZMB collection, revised. The type series, ZMB MYR2110, actually contains two  $3^{\circ}$  syntypes, one with dissected and missing gonopods, apparently the one depicted by Jeekel (1965), the second  $3^{\circ}$  with still intact gonopods (Fig. 11A–F). Originally, *D. hova* was verbally described from an uncertain number of syntypes of both sexes (de Saussure and Zehntner 1901, 1902), with males from 'Madagascar' (coll. Sikora), as well as females and juveniles from Nosy Be Isle. Franz Sikora collected in Madagascar around the capital city Antananarivo and briefly in the southeast around Fort Dauphin. Hoffman (1974) recorded and illustrated the gonopods of *D. hova* from a  $3^{\circ}$  taken as far away from part of the type locality (Nosy Be) as the Andasibe National Park (= Périnet) in eastern Madagascar, questioning such a vast and disjunct distribution. An incomplete  $3^{\circ}$  syntype (with missing gonopods) from Nosy Be and 2  $9^{\circ}$  non-types from Nosy Sakatia Isle, all in the



Figure 11. *Dalodesmus tectus* Cook, 1896, 3 syntypes (ZMB MYR2110). Multi-layer photographs (A–F), drawings (after Hoffman 1974) (G, H). A Anterior body, dorsal view B both syntypes, fragmented mix C ventral view with gonopod D anterior body, lateral view with gonopod E telson, ventral view F telson, lateral view G gonopod, posterior view; gonopod, mesal view of acropodite. Abbreviations: fe = femorite; lb = lateral branch; mb = mesal branch. Not to scale.



Figure 12. *Dalodesmus tectus* Cook, 1896, syntypes of *D. hova* (de Saussure & Zehntner, 1897) syn. nov.,  $\bigcirc$  syntype (A) and  $\bigcirc$  syntype (E, F) (after de Saussure and Zehntner 1902),  $\bigcirc$  syntype (B–D) (after Golovatch and Hoffman 1989), all from Nosy Be, and  $\bigcirc$  from Andasibe National Park (E–H) (after Hoffman 1974). A Anterior part of body, dorsal view B right half of metazonum 10, dorsal view C posterior end of body, dorsal view D body ring 9, oral view E right gonopod, ventral view F left gonopod, lateral view G, H left gonopod, ventral and lateral views, respectively. Abbreviations: cx = coxite, fe = femorite, lb = lateral branch, mb = mesal branch, sl = solenomere. Scale bar: 1000 µm (B–D).

SMF collection, were later revised and partly depicted (Golovatch and Hoffman 1989). An additional six syntypes, collected by Franz Sikora, including the male on which the illustration of the gonopod was based in the original description, are in the MHNG collection (Hollier and Wesener 2017), as well as a non-type tube labeled *"Tubercularium hova"*, "Madag. Fort Dauphin, S2 Remy 49; leg. Remy, det. Attems 1951", in the NHMW collection.

Hoffman (1974) listed the type locality as Nosy Be, overlooking that the only male specimens used for the first description by de Saussure and Zehntner had come in fact from Franz Sikora (so either central Madagascar or Fort Dauphin in the southeast). We discovered another Malagasy Dalodesmidae species (see *Phymatodesmus sakalava* above) collected by Franz Sikora that had actually come from Andasibe, exactly the same locality whence Hoffman briefly redescribed the species and finely illustrated its gonopodal structure. Thus, based on the female-based records of "*D. hova*", *D. tectus* could be a congener particularly widely distributed across Madagascar, ranging from the isles of Nosy Be and Nosy Sakatia in the very north to Fort Dauphin (Tolagnaro) in the very southeast. If true, this seems to be the most widespread native millipede in Madagascar. The populations from Nosy Be and Fort Dauphin, from which the gonopods are currently unknown, should be carefully checked in the future to clarify their taxonomic status. Nosy Be is the type locality of another two Dalodesmidae, *D. odontopezus* and *Eutubercularium voeltzkowi*.

**Brief description.** (After Cook 1896 and Jeekel 1965.) Body of 3 syntypes ~ 21 mm long and 2.8 mm wide. Colouration uniformly dark brown. Paraterga largely subhorizontal, lying below dorsum; tips sharpened caudally, but not projecting past posterior margin; dorsal surface between paraterga mostly tuberculate, tuberculations being rounded to subconical (Fig. 11A).

Gonopods (Fig. 11C, D, G, H) showing nearly bare femorites (fe), both only basally with 2+2 lateral setae, coupled with rather simple acropodite: an untraceable, apparently rudimentary solenomere lying between both branches of a distinct solenophore: the highest, suberect, at midlength unequally bifid mesal branch (mb) and a much shorter, strongly folded and lamelliform lateral branch (lb).

Based on a restudy of the gonopods of the type series of *D. tectus*, no meaningful differences to the gonopodal structure of *D. hova* as illustrated by de Saussure and Zehntner (1897) and redescribed by Hoffman (1974) could be found (Fig. 12A–H). The potential type locality of *D. tectus* (central Madagascar) fits very well to the type locality of *D. hova* (Andasibe).

#### **Descriptions of new species**

#### Dalodesmus kompantsevi sp. nov.

https://zoobank.org/B8043509-6990-4E62-99B8-CDFE90E3B656 Figs 13, 14

**Type material.** *Holotype* • ♂ (ZMUM), Northern MADAGASCAR, Antsiranana Prov., 4 km SW of Joffreville (= Ambohitra), Parc National Montagne d'Ambre, 12.51358°S, 49.183001°E, 900–1000 m a.s.l., tropical forest, 16–18.XII.2018, A. Kompantsev leg.

**Other material.** • 1 ♀, (MZUF Fi-30A), MADAGASCAR, Montagne d'Ambre, 900 m, c/o grande cascade, leg. 26 Sept. 1989, L. Bartolozzi & S. Taiti.



**Figure 13.** *Dalodesmus kompantsevi* sp. nov.,  $\circlearrowleft$  holotype: **A–C** habitus, dorsal, lateral, and ventral views, respectively **D** body ring 7 with gonopods in situ, ventral view **E**, **F** gonopods, dorsal and ventral views, respectively. Abbreviations: fe femorite, lb lateral branch, mb mesal branch, sl solenomere. Photographs by K. Makarov, taken not to scale.

**Diagnosis.** Tips of paraterga not projecting past posterior tergal margin (Fig. 13A–C), like in *D. hova, D. tectus* and *D. speophilus* sp. nov., vs sharper and projecting beyond margin in *D. hamatus, D. odontopezus* and *D. orator*. Differs from all other species of the genus primarily by the light colouration, coupled with the unusually compact, short, and clearly trifid acropodite, this being divided into three subequally long and upright branches: a middle, subacuminate and non-sigmoid solenomere (sl) flanked by a securiform, axe-shaped mesal branch (mb) and a nearly finger-shaped lateral branch (lb) of the solenophore (Fig. 13E, F). See also Key below.

Etymology. To honour the late Aleksandr Kompantsev (Russia), the collector.

**Description.** Length of holotype ~ 23 mm, width of midbody pro- and metazona 1.5 and 2.9 mm, respectively. Width of prozona 2.2 mm, of metazona 4.2 mm in  $\mathcal{Q}$  non-type.

Colouration in alcohol uniformly pale brown to beige, axial stripe on prozona thin, vague, and grey, antennae somewhat infuscate, increasingly brown distad (Fig. 13A–C).

Body with 20 rings. Tegument mainly dull to only slightly shining, microgranulate to microtuberculate throughout, even surfaces of prozona and of metazona below paraterga finely microgranulate, sterna granulate. Head also densely microtuberculate or granulate throughout, micropilose up to level of antennae; epicranial suture thin, but distinct; genae squarish, set off ventrally from gnathochilarial stipes by a small, but evident ridge (Fig. 13A–C). Interantennal isthmus ~ 2 × diameter of antennal socket (Fig. 13C). Antennae short and rather clavate, in situ reaching back past ring 3 when stretched dorsally, very densely setose and microgranulate. In length, antennomere 6 > 5 > 3 > 4 > 2 > 1 = 7; antennomere 6 the largest and the highest, antennomeres 5 and 6 each with a small, round, distodorsal knob. In width, collum < head < ring 3 < 2 = 4-16; thereafter body gradually tapering towards telson (Fig. 13A). Collum transversely suboval, regularly and broadly rounded laterally, densely tuberculate, most tuberculations being slightly oblong-oval, evident, equipped with very short, mostly subclavate setae and arranged in 7–8 transverse, rather irregular, arcuate rows. Metaterga 2 and 3 each with four similar transverse arcuated rows of setiferous tubercles, following metaterga each largely with 5-6 such rows (Figs 13A, 14A, B). Paraterga well-developed, set high (mostly at upper <sup>1</sup>/<sub>4</sub> body), largely slightly upturned to subhorizontal, thus leaving the dorsum only faintly convex (Figs 13B, 14B); anterior and posterior margins of paraterga 2 and 3 clearly drawn both forward and caudad, following paraterga drawn increasingly only caudad, but caudal corners produced past rear tergal margin only on rings 17-19; posterior margins clearly bisinuate, well concave behind paraterga (Fig. 13A-C). Lateral and caudal margins of paraterga beset with numerous, similarly oblong, and usually subequal, setigerous tubercles/lobulations, caudolateral lobulation nearly sharp. Ozopores (Fig. 14B, D) inconspicuous, opening dorsally near penultimate lateral lobulation on pore-baring rings 5, 7, 9, 10, 12, 13, 15-19. Strictures between pro- and metazona narrow and rather deep, nearly smooth (Fig. 14C). Epiproct small, conical and subtruncate at tip. Hypoproct trapeziform, with 1+1 setae borne on distinct oblong knobs at caudal margin. Limbus very thin, small, and entire. Neither an axial line nor pleurosternal carinae (Fig. 13A-C). Endotergum inconspicuous, posterior margin of metazona projecting into long, sharp, apically microdenticulate, triangular projections (Fig. 14E).



Figure 14. Dalodesmus kompantsevi sp. nov.,  $\bigcirc$  (MZUF Fi30A). SEM micrographs **A** midbody ring with pro- and metazonite, dorsal view **B** midbody ring, paranotum with ozopore **C** detail of surface structures of prozonite and metazonite **D** ozopore **E** endotergum **F** midbody legs. Scale bars: 1000 µm (**A**); 100 µm (**B**, **C**); 10 µm (**D**, **E**); 200 µm (**F**).

Sterna mostly densely setose, deep, and narrow between coxae 1–3, increasingly broad thereafter, clearly excavate between coxae 5 and 6 ( $\mathcal{J}$ ); postgonopodal sterna rather flat, devoid of modifications, cross-impressions faint (Fig. 13C). Gonopodal aperture roundly pentagonal, relatively small, taking up ~ 1/3 width of metazonum 7, clearly open and drawn into metazonum 6 (Fig. 13D). Legs incrassate, rather long.  $1.4-1.5 \times as$  long as body height, with small, stout, abundant and usual curved setae (Fig. 14F) with admixture of sphaerotrichomes ventrally on all podomeres ( $\mathcal{J}$ ); gonopores on coxae 2 inconspicuous, each borne on a very small swelling ( $\mathcal{J}$ ); prefemora not bulged laterally; claws very small; in length, tarsus > femur > prefemur > tibia > postfemur > coxa.

Gonopods (Fig. 13D–F) very slender and long, tips in situ reaching anteriorly beyond coxae 6 (Fig. 13C, D). Both coxites and clearly prefemoral (= densely setose) parts of telopodites equally very short and stout, fused medially, the former fully and the latter mostly hidden inside gonopodal aperture. Femorites

(fe) contiguous medially in basal 1/3, basically bare and only one at base with a distinct lateral seta, both very faintly attenuating and diverging distad. Acropodites of both telopodites clearly diverging, but unusually compact, short, and clearly trifid, being divided into three subequally short and upright branches: a middle, subacuminate and non-sigmoid solenomere (sl) flanked by a solenophore represented by a securiform, axe-shaped mesal branch (mb) and a nearly finger-shaped lateral branch (lb) with a mesal knob parabasally.

#### Dalodesmus speophilus sp. nov.

https://zoobank.org/F72BC885-741B-4E04-B34D-4C0DDD286655 Figs 15-18

**Type material.** *Holotype* • ♂ (MZUF), MADAGASCAR, Grotta di Anjohibe, 15°32'33.08"S, 46°53'5.99"E, 12.ix.1989, L. Bartolozzi & S. Taiti leg.; *Paratypes:* 6 ♂, 12 ♀, 12 juv. (MZUF); 1 M, 1 F (ZFMK), same data as holotype.

**Diagnosis.** Length < 20 mm in both sexes, the smallest species of the genus (all other species with males > 21 mm). Tips of paraterga not projecting past posterior tergal margin, like in *D. hova, D. tectus, D. kompantsevi* sp. nov., vs sharper and projecting beyond margin in *D. hamatus, D. odontopezus* and *D. orator.* Differs from *D. hova, D. tectus,* and *D. kompantsevi* sp. nov. in the contrasting yellow paratergal tips (uniformly brown in the other species). Gonopods unique for the genus *Dalodesmus* in the main branch being subdivided into an apical and a subapical branch. See also Key below.

**Etymology.** From *speophilus*, a noun in apposition, after the type locality, a gigantic cave.

**Description.** Length in male ~ 16.5–17.5 mm (n = 3), width of midbody proand metazona 1.5 and 2.8–2.9 mm (n = 3), respectively, female length 16.5– 19 mm (n = 4), width of prozona 1.6 mm (n = 1), of metazona 3.7–4.1 mm (n = 4).

Colouration in alcohol light brown to beige, paraterga light, head brown, epicranium grey, legs light, except for a few tarsi pale grey; antennae dark brown (Fig. 15A–F). A live photograph of a potential *D. speophilus* sp. nov., 70 km away from the type locality, shows dull, dark brown to blackish tergites with pale white to almost yellow paratergal tips, legs white to pale grey (Fig. 16D).

Body with 20 rings. Tegument mainly dull, microgranulate to microtuberculate throughout, even surfaces of prozona and of metazona below paraterga finely microgranulate, sterna granulate. Head also densely microtuberculate or granulate throughout, micropilose up to level of antennae; epicranial suture thin, but distinct; genae squarish, set off ventrally from gnathochilarial stipes by a small, but evident ridge (Figs 15D, 16A). Interantennal isthmus ~ 2 × diameter of antennal socket (Fig. 15D). Antennae short and rather clavate, in situ reaching in both sexes back past ring 3 when stretched dorsally, very densely setose and microgranulate. In length, antennomere 6 > 2 > 5 > 4 > 2 > 1 = 7; antennomere 6 the largest and the highest, antennomeres 5 and 6 each with a small, round, distodorsal knob, most likely beset with sensory cones. In width, collum ≤ head < ring 3 < 2 < 4-16; thereafter body gradually tapering towards telson (Fig. 15A). Collum transversely suboval, regularly and broadly rounded laterally, densely tuberculate, most tuberculations being slightly oblong-oval, evident, equipped with very short, mostly subclavate setae and arranged in 20-22 lat-



Figure 15. *Dalodesmus speophilus* sp. nov., ♂ holotype (MZUF), multi-layer photographs **A** habitus, dorsal view **B** midbody rings, dorsal view **C** posterior body rings, dorsal view **D** head, ventral view **E** posterior body rings with telson, dorsal view **F** telson, ventral view. Not to scale.

eral, 7–8 transverse, rather irregular, arcuated rows. Metaterga 2 and 3 narrow, each with four similar, transverse, arcuated rows of setigerous tubercles (Fig. 17C), following metaterga each largely with 5–6 such rows (Fig. 15A). Paraterga well-developed, set high (mostly at upper ¼ body), largely slightly upturned to subhorizontal, thus leaving the dorsum only faintly convex (Fig. 15A–C); anterior and posterior margins of paraterga 2 and 3 clearly drawn both forward and caudad, following paraterga drawn increasingly only caudad, but caudal corners produced past rear tergal margin only on rings 15–19; posterior margins clearly bisinuate, well concave behind paraterga (Fig. 15E). Lateral and caudal margins of paraterga beset with numerous, similarly oblong and usually subequal, setigerous tubercles/lobulations, caudolateral lobulation being nearly sharp (Fig. 17A, B). Ozopores inconspicuous (Fig. 17E, F), opening dorsally near penulti-



Figure 16. Dalodesmus speophilus sp. nov., A–C, E ♂ holotype (MZUF), multi-layer photographs D photograph of live specimen of Dalodesmus cf. speophilus, courtesy Justin Gerlach. A Anterior part of body with gonopods, ventral view B gonopods, posterior view C gonopods, lateral view D live specimen E habitus, lateral view. Not to scale.

mate lateral lobulation on pore-baring rings 5, 7, 9, 10, 12, 13, 15–19. Strictures between pro- and metazona narrow and rather deep, nearly smooth (Fig. 17A).

Telson: Epiproct small, conical and subtruncate at tip. Hypoproct trapeziform, with 1+1 setae borne on distinct oblong knobs at caudal margin. Paraprocts with 2+2 setae on triangular, projecting knobs (Figs 15E, F, 16E).

Limbus very thin, small, and entire. Neither an axial line nor pleurosternal carinae (Fig. 15A–C). Endotergum inconspicuous, posterior margin of metazona projecting into dense, long sharp, apically microdenticulate, triangular projections (Fig. 15D, I).

Gonopodal aperture roundly pentagonal, relatively small, taking up  $\sim 1/2$  width of metazonum 7, clearly open and drawn into metazonum 6 (Fig. 16A).

First  $\bigcirc$  leg-pair shorter and wider than other legs, with long coxae, large; size of its podomeres: tarsus > coxa > prefemur = femur > postfemur = tibia (Fig. 17J), tarsus with sharp claw, ventral spines, and numerous long setae (Fig. 17K). Midbody legs incrassate, rather long. 1.4–1.5 × as long as body height (Fig. 17L), with small, stout, abundant, and usually curved setae with admixture of sphaerotrichomes ventrally on all podomeres ( $\bigcirc$ ); gonopores on  $\bigcirc$  coxae 2 inconspicuous, each borne on a very small swelling ( $\bigcirc$ ); prefemora not bulged laterally; claws very small; in length, tarsus > femur > prefemur > tibia > postfemur > coxa.

 $\bigcirc$  vulva setose, symmetrical, lateral and inner plates of same width. Operculum large, each side with three or four very long setae, longest reaching the apical margin of vulva (Fig. 17H).

Gonopods (Figs 16B, C, 17G, 18A–L) very slender and long, tips in situ reaching anteriorly until coxae 5 (Fig. 16A, B). Both coxites and prefemoral (= densely setose parts) of telopodites equally very short and stout, fused medially, the former fully and the latter mostly hidden inside gonopodal aperture. Femorites (fe) contiguous medially in basal 1/3, sparsely setose almost all along, both slightly flattened dorsoventrally and diverging distad towards acropodites. Apical portions of telopodite (= acropodites) clearly diverging, rather complex and compact, curved ventrad and clearly divided into four unequal branches: a short, submesal, tubiform, simple and non-sigmoid solenomere (sl) flanked by a rather elaborate, tri-branched solenophore, this latter being represented by an



Figure 17. Dalodesmus speophilus sp. nov.,  $\circlearrowleft$  holotype (MZUF),  $\bigcirc$  paratype (ZFMK), SEM micrographs **A** midbody ring with pro- and metazonite, dorsal view **B** surface of metazonite **C** detail of surface structures of metazonite **D** endotergum **E** paratergum with ozopore **F** ozopore **G** gonopod, apical view **H** female vulva; **I** endotergum, ventral view **J** male leg pair 1, posterior view **K** tarsus 1 **L** midbody legs. Scale bars: 200 mm (**A**, **L**); 100 µm (**B**, **E**, **G**, **H**, **J**, **K**); 10 µm (**C**; **D**, **I**); 20 µm (**F**).

immediately adjacent, short, lobe-shaped, lateral branch (lb), a large, subacuminate, slender, twisted, and membranous medial branch (mb) with a denticle near base, and an apical (ab) and a subapical branch (sb), both latter membranous, curved/bent ventrad and ragged/irregular in shape.

## Unidentified Dalodesmidae from Madagascar

In order to provide a better overview of the distribution, permitting future collection efforts to be more successful, all unidentified but available material of the family Dalodesmidae is listed below. The morphological description of these samples is beyond the scope of this study.



Figure 18. *Dalodesmus speophilus* sp. nov.,  $\bigcirc$  holotype (MZUF), SEM micrographs, right gonopod **A** anterior view **B** postero-mesal view **C** mesal view **D** posterior view **E** lateral view **F** lateral view **G** acropodite, anterior view **H** acropodite, postero-mesal view **I** acropodite, mesal view **J** acropodite, posterior view **K** acropodite, lateral view **L** acropodite, lateral view. Abbreviations: ab = apical branch; fe = femorite; lb = lateral branch; mb = mesal branch; sb = subapical branch; sl = solenomere branch. Scale bars: 100 µm.

#### Dalodesmus spp.

1 F, CAS DSD006, Madagascar, Toamasina, Prov., Parc National Masoala, Ambohitsitondroina Mt., Ambanizana, rainforest, 650 m, 15°34'10"S, 050°00'12"E, coll. 26 Feb - 06 Mar 2003, Andriamalala, Silva et al. general collecting day, at campsite; 1 F, CAS DSD0016, same data as previous, but raking tree trunks; 1 M, CAS DSD0023, Madagascar, Toamasina, Prov., Parc National Masoala, Ambohitsitondroina Mt., Ambanizana, rainforest, 900-9502 m, 15°34'20"S, 050°00'25"E, coll. 5 March, 2003, Andriamalala, Silva et al., sweeping low herbs; 1 M, CAS DSD0027, Madagascar, Toamasina Prov., Parc National Masoala, Ambohitsitondroina Mt., Ambanizana, montane rainforest, 1010 m, 15°34'27"S, 050°00'39"E, coll. 6 March, 2003, Andriamalala, Silva et al., beating low vegetation; 2 F, CAS DSD0037, Madagascar, Antananarivo, Prov., R. S. d'Ambohitantely, Forêt d'Ambohitantely, ca. 20.9 km 72° NE, Ankazobe, primary forest, 1574 m, 18°13'30"S, 047°16'44"E, coll. 19 March 2003, Andriamalala, Silva et al., raking tree trunks; 3 ?, CAS DSD0045, Madagascar, Antananarivo, Prov., R. S. d'Ambohitantely, Forêt d'Ambohitantely, 20 km NE Ankazobe, forest fragment, montane rainforest, 1638 m, 18°12'30"S, 047°17'08"E, coll. 20 March 2003, Andriamalala, Silva et al., raking tree trunks; 1 M, 1 F, 1 juvenile, CAS BLF7917, Madagascar, Toliara Province, Fôret Classée d'Analavelona, 33.2 km 344° NNW Mahaboboka, montane rainforest, 1300 m, 22°38'34"S, 044°10'16"E, coll 22-26 Feb 2003, Fisher, Griswold et al., beating low vegetation; 8 M & F, CAS BLF8151, Toamasina, Montagne d'Anjanaharibe, 19.5 km 27° NNE Ambinanitelo, montane rainforest, 1100 m, 15°10'42"S, 049°38'06"E, coll. 12-16 Mar 2003, Fisher, Griswold et al., beating low vegetation; 1 M, CAS BLF9558, Madagascar, Antsiranana, Forêt de Binara, 7.5 km 230°, SW Daraina, tropical semi-dry forest, 375 m, 13°15'8"S, 049°37'00"E, coll. 1 December 2003, B.L. Fisher, pitfall trap; 1 F, MZUF Fi24, Mag1107, Madagascar, RNI Andohahela, particella 1, versante E, forest pluviale, lettiera vagliata, 300 m, [24°57'S, 46°43'N] coll. 24.-26.v.1991, L. Bartolozzi, S. Taiti, C. Raharimina; 1 immature specimen, "Mg5" NHMW, Madagascar, "Forststation Manjakatompo bei Ambatolampy, Ankaratra- Massiv, [19°22'S, 47°18'E] Gesiebe aus morschem Holz und Strauch am Fuße großer Bäume u. a. Weinmannia spec., 12.04.1969", Franz leg; 1 immature specimen, "Mg42" NHMW, Madagascar, "Galeriewald von Berenty [25°00'S, 46°18'E], Gesiebe aus morschem Holz und Fomes, Gesiebe aus schimmelnder Laubstreu, 02.05.1969", Franz leg.; 1immature specimen, "Mg43" NHMW, Madagascar, "Straße nach Ft. Dauphin, 44 km von dort, [25°00'5.85"S, 46°36'28"E] Gesiebe aus Laubstreu neben Bach und Bachdetritus, 02.05.1969", Franz leg.; 2 immature specimens, "Mg62" NHMW, "Madagascar, Montagne d'Ambre, unterhalb der Forststation, [12°30'S, 49°11'E], Gesiebe unter faulenden Baumstämmen, und aus Laubstreu, 20.05.1969", Franz leg.

Dalodesmidae, unidentified genus (Phymatodesmus?):

1 F, **ZFMK MYR13919**, Madagascar, Toliara Prov., Ambatotsirongorongo Mountain, Grande Lavasoa, rainforest, 500 m, 25°5'10.23"S, 46°44'55.93"E, coll. 14.vi.2007, T. Wesener & K. Schütte.



#### Key to Dalodesmidae species of Madagascar

- Body length ~ 10 mm. Paraterga short, rectangular (Fig. 1A, D, H). Metatergal surface with regular, circular piligerous tuberculations (Figs 1H, 2A-E), at low magnification appearing to be pointed posteriorly due to the setae (Fig. 1G). Antennae short, protruding back to beginning of ring 2 (Fig. 1C).
|   | Paraprocts with 2+2 setae located on knobs Genus Phymatodesmus,<br>one species: P. sakalava (Central, Eastern Madagascar: Andasibe) |
|---|-------------------------------------------------------------------------------------------------------------------------------------|
| 2 | Gonopodal femorites long and slender, > 2 × as long as acropodites (Fig.                                                            |
|   | 5D-G). Femorites diverging in distal half (Fig. 5D). Femorites bare or poor-                                                        |
|   | ly setose ventrally and laterally (Fig. 5D-G)                                                                                       |
|   | Genus Dalodesmus (6 species) (3)                                                                                                    |
| - | Gonopodal femorites stout, twice as long as acropodites (Fig. 4B). Femo-                                                            |
|   | rites parallel dorsoventrally (Fig. 4B). Femorites densely setose both ven-                                                         |
|   | trally and laterally (Fig. 4B, C)                                                                                                   |
|   | Genus Eutubercularium, single species: E. voeltzkowi (Nosy Be)                                                                      |
| 3 | Paratergal tips rather sharp and narrow, projecting past posterior tergal                                                           |
|   | margin (Fig. 5B)4                                                                                                                   |
| - | Paratergal tips blunt and wide, not projecting past posterior tergal margin                                                         |
|   | (Fig. 11A)6                                                                                                                         |
| 4 | Body dark, paratergal tips contrasting yellow. Males > 25 mm5                                                                       |
| - | Body uniformly brown or black (Fig. 6A–C), paratergal tips of same colour.                                                          |
|   | Males 20–23 mm long. Tegument either as usual, strongly calcified, and body                                                         |
|   | rigid, or poorly calcified, and body unusually fragile. Gonopodal femorites se-                                                     |
|   | tose (Fig. 6D-F), main branch broad apically, single-tipped; lateral branch bi-                                                     |
|   | fid, narrow (Fig. 8A–I) Dalodesmus hamatus ('Madagascar', Makira).                                                                  |
| 5 | Paraterga not upturned. Gonopodal femorites setose (Fig. 9B), soleno-                                                               |
|   | mere branch (sl) lying between single-tipped mesal branch (mb) and later-                                                           |
|   | al branch (lb), lateral branch laciniate and fimbriate (Fig. 9B)                                                                    |
|   | Dalodesmus odontopezus (Nosy Be).                                                                                                   |
| - | Paraterga upturned. Gonopod femorites bare (Fig. 10B), solenomere                                                                   |
|   | branch (sl) lying between bifid mesal branch (mb) and lateral branch (lb),                                                          |
|   | lateral branch strongly folded (Fig. 10C, D)                                                                                        |
|   | Dalodesmus orator (Ambohimitombo).                                                                                                  |
| 6 | Paratergal tips same colour as terga, pale to chocolate brown (Fig. 13A).                                                           |
|   | Both sexes > 20 mm long (males 21-23 mm). Gonopod without a subdi-                                                                  |
|   | vided medial branch7                                                                                                                |
| - | Paratergal tips contrasting yellow (Fig. 16D). Both sexes < 20 mm long                                                              |
|   | (16.5–19 mm). Gonopod with a medial branch (mb) carrying a basal den-                                                               |
|   | ticle and subdivided into an apical (ab) and a subapical (sb) branch (Fig.                                                          |
|   | 18A-L) Dalodesmus speophilus sp. nov. (NE Madagascar)                                                                               |
| 7 | Dark brown or chocolate brown (Fig. 11A). Solenomere branch (sl) very                                                               |
|   | short (Fig. 11G, H) or even rudimentary (Fig. 12G, H). Medial branch bifid,                                                         |
|   | lateral branch folded Dalodesmus                                                                                                    |
|   | tectus (Andasibe, "Central Madagascar", Nosy Be?, Fort Dauphin?)                                                                    |
| - | Pale brown (Fig. 13A). Solenomere branch (sl) as long as lateral branch                                                             |
|   | (lb) and medial branch (mb). Gonopod uniquely trifid (Fig. 13E, F)                                                                  |
|   | Dalodesmus kompantsevi sp. nov. (Montagne d'Ambre).                                                                                 |

# Conclusions

Dalodesmidae seem to be rarely encountered on Madagascar. There are very few photographic posts on iNaturalist of the group, especially compared to other large millipedes. A leaf litter sifting project (Spelzhausen et al. 2020) only captured one specimen, and in fact most of the collection samples exam-

ined by us only have few individuals (1 or 2, rarely 3), with the sole exception of the Grotte d'Anjohibe (*D. speophilus* sp. nov.), which is a very special habitat (a cave in a dry forest during the dry season). On a positive note, Malagasy Dalodesmidae millipedes seem to be capable of survival in old secondary forests next to natural woodlands (the *Eucalyptus* plantation planted in 1909 with many indigenous species in Andasibe, as well as the Manjakatompo forest). From the hundreds of Madagascar samples at the CAS and Field Museum (pitfall traps and Winkler extractions for ants), we only have nine collection events of Dalodesmidae.

All encounters of Dalodesmidae on Madagascar, including unidentified samples, mapped in Fig. 19, show that the family occurs virtually all over the island except for dry spiny forests. Yet it seems especially characteristic of woodlands, this being true of most Diplopoda of Madagascar and elsewhere. In millipedes, both the generic and, especially, the specific diversity seems to be higher in the northern part of Madagascar, gradually being reduced to the south. As a result of the absence of adult male material, numerous samples still remain unidentified to species, or even genus-level. Further taxonomic research on Malagasy Dalodesmidae may well reveal not only new records, but even new species. In addition, molecular studies would be very helpful to refine the picture in terms of both fauna and distribution.

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# **Additional information**

## **Conflict of interest**

The authors have declared that no competing interests exist.

## **Ethical statement**

No ethical statement was reported.

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#### Author contributions

Conceptualization: SIG, NA. Data curation: NA. Formal analysis: TW, SIG. Investigation: TW, SIG. Project administration: TW. Resources: TW. Visualization: SIG, NA. Writing – original draft: NA, SIG, TW. Writing – review and editing: TW, SIG, NA.

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## Data availability

All of the data that support the findings of this study are available in the main text.

## References

- Attems C (1898) System der Polydesmiden. I. Theil. Denkschriften der Kaiserlichen Akademie der Wissenschaften zu Wien, Mathematisch-Naturwissenschaftliche Classe 67: 221–482.
- Attems C (1940) Myriapoda 3. Polydesmoidea III. Fam. Polydesmidae, Vanhoeffeniidae, Cryptodesmidae, Oniscodesmidae, Sphaerotrichopidae, Peridontodesmidae, Rhachidesmidae, Macellolophidae, Pandirodesmidae. Das Tierreich 70, i– xvii+1–577. https://doi.org/10.1515/9783111609645.1
- Brandt JF (1841a) Note supplémentaire sur les espèces qui composent le genre *Polydesmus*, suivie d'une caractéristique de deux espèces nouvelles. Bulletin scientifique publié par l'Académie Impériale des Sciences de St.-Pétersbourg 9(1): 9–11.
- Brandt JF (1841b) Recueil de mémoires relatifs à l'ordre des Insectes Myriapodes et lus à l'Académie Impériale des Sciences de St.-Pétersbourg. Leipsik, 189 pp.
- Brölemann HW (1916) Essai de classification des polydesmiens (Myriapodes). Annales de la Société Entomologique de France 84(4): 523–617. https://doi.org/10.1080/21 686351.1915.12279415
- Cook OF (1896) Cryptodesmus and its allies. Brandtia 5: 19-28.
- de Saussure H, Zehntner L (1897) Atlas de l'histoire naturelle des Myriapodes. In: Grandidier A (Ed.) Histoire physique, naturelle et politique de Madagascar. Paris: Imprimérie nationale, PI 1–15.
- de Saussure H, Zehntner L (1901) Myriopoden aus Madagaskar und Zanzibar, gesammelt von Dr. A. Voeltzkow. Abhandlungen der Senckenbergischen naturforschenden Gesellschaft 26(4): 429–460.
- de Saussure H, Zehntner L (1902) Myriapodes de Madagascar. In: Grandidier A (Ed.) Histoire physique, naturelle et politique de Madagascar. Imprimérie nationale, Paris, 1–356.
- Enghoff H (2003) Diplopoda, millipedes. In: Goodman SM, Benstead JP (Eds) The Natural History of Madagascar. University of Chicago Press, Chicago and London, 617–627.
- Enghoff H, Golovatch SI, Short M, Stoev PE, Wesener T (2015) Diplopoda taxonomic overview. In: Minelli A (Ed.) Treatise on Zoology – Anatomy, Taxonomy, Biology. The Myriapoda. Volume 2. Brill, Leiden, 363–453. https://doi.org/10.1163/9789004188273\_017
- Golovatch SI, Hoffman RL (1989) Identity of *Polydesmus hamatus* Brandt 1841, a Malagasy milliped (Diplopoda Polydesmida Dalodesmidae). Tropical Zoology 2: 159–164. https://doi.org/10.1080/03946975.1989.10539436
- Golovatch SI, Hoffman RL (2000) On the diplopod taxa and type material of J. F. Brandt, with some new descriptions and identities (Diplopoda). Fragmenta Faunistica 43(Supplement): 229–249.

- Hoffman RL (1974) Short studies on dalodesmid millipeds from South Africa and Madagascar. Wasmann Journal of Biology 32(2): 221–246.
- Hoffman RL (1980) Classification of the Diplopoda. Muséum d'histoire naturelle, Geneva, 237 pp.
- Hollier J, Wesener T (2017) The Diplopoda (Myriapoda) of Madagascar described by Henri de Saussure and Leo Zehntner. Revue suisse de Zoologie 124(1): 53–65. https://doi.org/10.5281/zenodo.322665
- Jeekel CAW (1965) The identity of *Dalodesmus tectus* Cook, 1896, and the status of the family names Dalodesmidae Cook, 1896, Vanhoeffeniidae Attems, 1914 and Sphaeriotrichopodidae Attems, 1914 (Diplopoda, Polydesmida). Entomologische Berichten 25: 236–239.
- Jeekel CAW (1971) Nomenclator generum et familiarum Diplopodorum: A list of the family and genus-group names in the Class Diplopoda from the 10<sup>th</sup> edition of Linnaeus, 1758, to the end of 1957. Monografieën van de Nederlandse Entomologische Vereniging 5: 1–412.
- Mesibov R (2017) Annotated catalogue of South American Dalodesmidae (Diplopoda, Polydesmida). Zootaxa 4338(3): 507–525. https://doi.org/10.11646/zootaxa.4338.3.6
- Mesibov R, Wesener T, Hollier J (2018) A replacement name for *Dalodesmus sakalava* (de Saussure & Zehntner, 1901) (Diplopoda: Polydesmida: Dalodesmidae). Zootaxa 4413 (2): 389–391. https://doi.org/10.11646/zootaxa.4413.2.11
- Spelzhausen L, Wesener T, Schütte K (2020) Vegetation thresholds for the occurrence of millipedes (Diplopoda) in different tropical forest types in Andasibe, Madagascar. Madagascar Conservation and Development 15 (1): 1–8. http://doi.org/10.4314/ mcd.v15i1.3
- Wesener T, Enghoff H (2022) Diplopoda, millipedes, Menavetraka, Ankodabitra, Ankodiavitry, Marotanana, Sakolavitsy. In: Fisher BL, Goodman SM (Eds) The New Natural History of Madagascar. Princeton University Press USA, 918–933. https://doi. org/10.2307/j.ctv2ks6tbb.118



**Research Article** 

# Taxonomic study of the genus *Campylomyza* Meigen (Diptera, Cecidomyiidae) in Korea with descriptions of seven new species

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Abstract

The genus *Campylomyza* Meigen, 1818, belongs to the subfamily Micromyinae (Diptera, Cecidomyiidae). The genus, comprising 40 species, is best known in the Palearctic Region. To date, four species are recorded in Korea: *Campylomyza appendiculata*, *C. flavipes, C. furva*, and *C. spinata*. Based on our field investigations from 2017 to 2020, five species are newly recorded from Korea (*C. abjecta, C. aborigena, C. cornuta, C. cavitata*, and *C. cingulata*) and seven new species are described (*C. ambulata* **sp. nov.**, *C. angusta* **sp. nov.**, *C. convexa* **sp. nov.**, *C. cornigera* **sp. nov.**, *C. hori* **sp. nov.**, *C. odae* **sp. nov.**, and *C. salicia* **sp. nov.**), based on morphological identification and molecular analyses. Detailed morphological and molecular data, including mitochondrial *COI* sequences are provided, with species diagnosis, descriptions, and keys for identification of those species.

**Key words:** Distributional new records, Korea, Micromyinae, Mycophagous cecidomyiids, new species

## Introduction

Cecidomyiidae, a family within the order Diptera, is known for its diverse ecological roles and is considered part of the "Dark Taxa" with other Dipteran families such as Chironomidae, Phoridae, and Sciaridae, owing to their high species diversity (Chimeno et al. 2022). The term "Dark Taxa" refers to groups with a high number of undescribed species, reflecting their status as significantly understudied, which in turn limits our understanding of their taxonomy. Ecological traits of Cecidomyiidae vary among species, and can be categorized into three groups based on their larval feeding behavior: fungivorous, phytophagous, and predatory (Yukawa 2005). Additionally, Cecidomyiidae can be further classified into six subfamilies based on morphological traits: Catotrichinae, Lestremiinae, Micromyinae, Winnertziinae, Porricondylinae, and Cecidomyiinae (Gagné and Jaschhof 2021). The genus *Campylomyza*, belonging to the fungivorous group within the Micromyinae subfamily, typically inhabits decaying plant roots, leaves, and fungal fruiting bodies in soil (Mamaev and Krivosheina 1993). These small flies, measuring between 1.0 and 1.8 mm, are known for their swarming



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**Copyright:** © Daseul Ham & Yeon Jae Bae. This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0). behavior, mainly observed for mating purposes during the cooler months (early April, May, and October), particularly when temperatures range from 16 °C to 24 °C (Kanmiya 1985, 1996, 1999; Kanmiya and Yukawa 2020).

Taxonomic studies of Campylomyza began in 1818 with Meigen's description of four species (C. aceris Meigen, 1818, C. atra Meigen, 1818, C. bicolor Meigen, 1818, and C. flavipes Meigen, 1818) (Meigen 1818). Westwood (1840) provided a concise description of Campylomyza with a catalog-like list of insects, designating C. flavipes as the type species. However, the original descriptions were insufficient for accurate identification. Subsequently, Edwards and Jaschhof provided revised characters and detailed descriptions of Campylomyza species (Edwards 1938a, b; Jaschhof 1998a; Jaschhof and Jaschhof 2009). Mamaev (1963, 1998), Jaschhof (1998a, 2015), and Jaschhof and Jaschhof (2009) made significant contributions to the taxonomy, describing the majority of known species. Campylomyza species exhibit remarkably high morphological similarities and display complex diversity with potentially numerous cryptic species (Jaschhof 2015). Jaschhof and Jaschhof (2009) subdivided Campylomyza into seven groups (alpina, bicolor, cornuta, flavipes, ormerodi, serrata, and incertae sedis group) based on male genitalia morphology. This reclassification revealed distinct species within putatively highly variable species, such as C. flavipes, C. ormerodi (Kieffer, 1913), and C. serrata Jaschhof, 1998. For instance, the C. flavipes complex was split into five species, C. ormerodi into six species, and C. serrata into five species (Jaschhof and Jaschhof 2009; Jaschhof 2015).

Cecidomyiidae is recognized as one of the most species-rich taxa, with an estimated 1.8 million species worldwide, yet only 6,651 species have been recorded to date (Gagné and Jaschhof 2021; Hebert et al. 2016). In South Korea, only 117 species have been documented, including 68 mycophagous cecidomyiids (Han 2021). The genus Campylomyza has been primarily studied within the Palearctic region, with limited research conducted in other biogeographic regions, including the Nearctic. To date, 40 Campylomyza species are recognized globally, comprising 39 species from the Palearctic region, two from the Nearctic region, and one from the Oriental region. Two species occur in both the Nearctic and Palearctic regions: C. dilatata Felt, 1907 and C. flavipes. Among them, five species are known from the Russian Far East, four species from Japan, and one species from China (Mamaev 1998; Gagné and Jaschhof 2021; Jaschhof 1998a, 2015; Jaschhof and Jaschhof 2009). In Korea, only four Campylomyza species have been previously recorded (Ham et al. 2019, 2020). In this study, we report five species newly recorded in South Korea and describe seven species new to science. Consequently, the global total of described Campylomyza species has increased to 47, with South Korea accounting for 16 of these, as determined through morphological analysis and mitochondrial Cytochrome Oxidase subunit I (mtCOI) sequencing. Detailed descriptions, diagnoses, and illustrations are provided for both the new and redescribed species. Our study aims to enhance our knowledge of the Campylomyza fauna in South Korea and contribute to various scientific fields, including forest ecology and the study of invasive species (Kang et al. 2023). Given the ongoing rapid climate change, it is crucial to thoroughly study organisms in their existing habitats to predict and understand potential environmental changes.

# Materials and methods

## Taxon sampling and morphological identification

All samples were collected between 2017 and 2020 using Malaise traps (Fig. 1A) located in Gyeonggi-do, Gangwon-do, Gyeongsangbuk-do, and Jeollanam-do, Korea. The locations where Malaise traps were installed are indicated by abbreviations (Fig. 1B, Table 1, Suppl. material 1: table S1), and the corresponding habitat information is provided as follows:

- **Gariwang** A deciduous forest composed of medium-aged trees of the 6<sup>th</sup> class. The Malaise trap was placed beside a hiking trail on slightly sloped terrain. The forest floor consisted of broadleaf litter mixed with stones larger than 30 cm in diameter. The surrounding area was highly humid, with abundant organic matter and a high presence of spiders and flies observed between the stones.
- **GP** The Malaise trap was installed along a valley near oak and Korean pine trees, classified as 5<sup>th</sup> class or higher in maturity. This location was situated close to residential areas.
- **GW** An urban-managed forest. The Malaise trap was placed near a trail that occasionally becomes a stream during heavy rainfall. The forest is mainly composed of medium-sized deciduous trees of the 5<sup>th</sup> class or higher.
- **HN** Located in the southern part of the Korean Peninsula near the coastline. The Malaise trap was installed close to farmland in a coniferous forest composed of small trees (2<sup>nd</sup> class black pine).
- **KUF** The Malaise trap was placed in the experimental farm of Korea University, surrounded by pine trees.
- **NERC** The Malaise trap was installed at the National Ecology Research Center in Yeongyang, next to a large river and reed field.
- **Odae1** Situated in Mt. Odae National Park, a protected area. The Malaise trap was placed next to a valley in a deciduous forest with medium-aged trees classified as 5<sup>th</sup> class or higher.
- **Odae2** Located at an altitude of more than 1,200 meters, the site features a deciduous forest with medium-sized trees (5<sup>th</sup> class). Due to the high elevation, the trees were relatively shorter, and the area was comparatively less humid.
- **SJ1, SJ2** The Malaise traps were placed next to farmland near Mt. Sokri National Park.
- **Sobaek** A protected area within Mt. Sobaek National Park. The forest consists of medium-sized deciduous trees, classified as 4<sup>th</sup> class or higher.

Specimens were dissected, with one or two legs removed, and preserved in 100% alcohol for molecular analysis. The samples were cleared in Creosote reagent and subsequently mounted in Canada balsam under a stereomicroscope (Olympus SZ51, Tokyo, Japan) following the methods described in relevant literature (Jaschhof and Jaschhof 2009, 2013). The specimens were examined using a bright-field and optical microscopy (Olympus BX50, Tokyo, Japan). Microscopic images of the specimens were captured using a Nikon D750 camera (Tokyo, Japan) attached to an optical microscopy (Olympus BX50).



**Figure 1. A** Malaise trap in Odae mountain (17 Sept. 2019) **B** map of sampling sites for specimens collected in the present study. For abbreviations of locations, see Table 1. The map was prepared using QGIS 3.28.1 (https://www.qgis.org/ko/site/) **C** male adult habitus of *Campylomyza aborigena* excluding genitalia and two legs. Scale bar = 0.5 mm. Abbreviations: AntC: anterior cubitus,  $R_1$ : anterior branch of radius, Apic $R_1$ : apical part of  $R_1$ ,  $R_{4+5}$ : third branch of radius,  $M_{1+2}$ : combined form of the first and second branches of the media, CuA: anterior branch of cubitus.

The images were taken at different focal planes and stacked using Helicon Focus software® (Helicon Soft, Ltd). Drawings were created using a drawing tube (Olympus U-DA). The terminology used in this study generally follows Jaschhof and Jaschhof (2009) and Jaschhof and Fitzgerald (2016). We list species in alphabetical order. The illustrations and photographs include arrows to indicate the diagnostic features. The body length was measured as the horizontal length of the head, thorax, and abdomen, excluding the antenna.

Voucher material is deposited in the collections of the Korean Entomological Institute, Korea University (**KU**), and the National Institute of Biological Resources, Incheon, Korea (**NIBR**).

In a previous abstract presented at '2024 Spring conference of KSAE & ESK (Korean Society of Applied Entomology & The Entomological Society of Korea)', the species names (*C. angusta* sp. nov., *C. ambulata* sp. nov., *C. convexa* sp. nov., *C. cornigera* sp. nov., *C. hori* sp. nov., and *C. odae* sp. nov.) were mentioned but not formally described (Ham et al. 2024; https://db.koreascholar.com/Article/ Detail/433436). According to the International Code of Zoological Nomenclature (ICZN), those names were considered nomina nuda, as no formal description was provided at that time. This manuscript provides the first formal descriptions of these species, fulfilling the requirements of valid publication and nomenclature.

## DNA extraction, sequencing, and alignment

Total genomic DNA was extracted from typically two or three legs of adult male specimens of *Campylomyza* using the DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) according to the manufacturer's instructions. For PCR amplification of the mitochondrial cytochrome oxidase subunit I (mtCOI, ~ 676 bp), we utilized the primer set: Forward: LCO1490 (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3'; Folmer et al. 1994) and Reverse: COIA (5'-CCC GGT AAA ATT AAA ATA TAA ACT TC-3'; Funk et al. 1995). Amplification was performed using AccuPower PCR Premix (Bioneer, Daejeon, Republic of Korea) following standard protocols.

Abbreviation	Location	Species
Gariwang	Gangwon-do, Jeongseon-gun, Jeongseon-eup, Hoedong-ri, 870, Gariwangsan Recreational Forest	C. hori sp. nov.
GP	Gyeonggi-do, Gapyeong-gun, Buk-myeon, Garimgyo (bridge name)	C. ambulata sp. nov.
GW	Seoul, Seongbuk-gu, Bugaksan-ro, Mt. Gaewun	C. ambulata sp. nov.
HN	Jeollanam-do, Haenam-gun, Hwangsan-myeon, Oeip-gil	C. cornuta
KUF	Gyeonggi-do, Namyangju-si, Wabu-eup, Dosim-gil, Korea University's farm to practice	C. abjecta
		C. appendiculata
		C. cornigera sp. nov.
		C. convexa sp. nov.
		C. furva
NERC	Gyeongsangbuk-do, Yeongyang-gun, Yeongyang-eup, Gowol-gil, 23, National Endangered Species Restoration Center	C. abjecta
		C. ambulata sp. nov.
		C. cornigera sp. nov.
		C. flavipes
		C. furva
		C. furva
		C. salicia sp. nov.
		C. spinata
Odae 1	Gangwon-do, Pyeongchang-gun, Jinbu-myeon, Odaesan-ro, Mt. Odae, small valley before So-Myeong valley	C. angusta sp. nov.
		C. cavitata
		C. cornigera
		C. cingulata
Odae 2	Gangwon-do, Pyeongchang-gun, Jinbu-myeon, Odaesan-ro, Mt. Odae, the road before temple (Buk-Dae-Mi-Reuk-Am)	C. aborigena
		C. ambulata
		C. flavipes
		C. flavipes
		C. odae sp. nov.
SJ 1	Gyeongsangbuk-do, Sangju-si, Hwabuk-myeon, Ipseok-ri	C. abjecta
		C. appendiculata
		C. spinata
SJ 2	Gyeongsangbuk-do, Sangju-si, Hwabuk-myeon, Ipseok-ri	C. abjecta
		C. ambulata sp. nov.
		C. appendiculata
Sobaek	Gyeongsangbuk-do, Yeongju-si, Punggi-eup, Sucheol-ri, Mt. Sobaek	C. aborigena
		C. hori sp. nov.

Table 1. Location data of collected Korean Campylomyza species and species occurrence by region.

The PCR conditions consisted of an initial denaturation at 95 °C for 3 min, followed by 35 cycles of denaturation at 95 °C for 30 s, annealing at 50 °C for 30 s, extension at 72 °C for 1 min, and a final extension at 72 °C for 10 min. Successfully amplified PCR products were checked on 1.2% Agarose gels and were purified and sequenced at BIONICS, Inc. (Seongdong-gu, Seoul, Republic of Korea). The sequences obtained were compared using Geneious Prime v. 2023.1.1 and deposited in the NIBR (National Institute of Biological Resources; https://species.nibr.go.kr/index. do) and GenBank (https://www.ncbi.nlm.nih.gov/) with accession numbers.

## DNA barcode sequence analysis and delimitation

A total of 33 *COI* sequences were analyzed as DNA barcodes in this study (Suppl. material 1: table S2). These include 31 sequences from 15 *Campylomyza* species found in Korea, one sequence of *C. flavipes* from GenBank, and one sequence from the outgroup species, *Peromyia trifida* Jaschhof, 2001. For phylogenetic analyses, we constructed the neighbor-joining (NJ) under the Kimura-2-parameter (K2P) model (Kimura 1980) with 1,000 bootstrap replicates using MEGA X (Kumar et al. 2018). Pairwise comparison of uncorrected genetic distances (*p*-distances) was used to estimate sequence divergence, and the complete deletion option was applied in MEGA X. Also, we used Automatic Barcode Gap Discovery (ABGD) as species delimitation method for estimating the number of Molecular Operational Taxonomic Units (MOTUs) (Puillandre et al. 2012). The ABGD assessment was conducted online using the provided website (https://bioinfo.mnhn.fr/abi/public/abgd/), utilizing the Jukes-Cantor (JC69), Kimura 2-parameter (K2P), and uncorrected distance (p-distance) models, with a relative gap width set at X = 1.5 (Oh et al. 2022).

## **Taxonomic accounts**

Family Cecidomyiidae Subfamily Micromyinae

Genus Campylomyza Meigen, 1818 Fig. 1C

Campylomyza Meigen, 1818: 101; Westwood 1840: 126; Jaschhof 1998b: 136; Jaschhof and Jaschhof 2009: 89.

**Type species.** *Campylomyza flavipes* Meigen, 1818 (original designation by Westwood 1840). Type locality Germany.

**Diagnosis.** The adult males of the South Korean genus *Campylomyza* can be distinguished from other mycophagous cecidomyiid taxa based on the following combination of characters [adapted from Jaschhof and Jaschhof 2009]: 1) Antenna with 12 flagellomeres; 2) Node of fourth antennal flagellomere featuring one complete and two incomplete crenulate whorls with sensory hairs with two incompletely collar-shaped sensilla distally; 3) Apical part of the R<sub>1</sub> vein, located near wing tip (ApicR<sub>1</sub>) elongated, approximately 4–6 times the length of Rs; 4) Gonostyli strongly convex posteriorly without apical spines; 5) Aedeagal apodeme equipped with typical head-like structure; 6) Tegmen with transverse brace (i.e., H-shaped), various processes on apex.

## Campylomyza abjecta Mamaev, 1998

*Campylomyza abjecta* Mamaev 1998: 6. *Campylomyza abjecta* Jaschhof and Jaschhof 2017: 5, fig. 2A–C (redescription).

Distribution. Russia (Primorsky), Sweden, new record for South Korea.

Specimens examined. KOREA • 3♂♂ (slides no. 19AY-3, 7, 19AYa-9, 10); NERC; 10-17 Apr. 2019; Y. J. Choi, H. G. Kim leg.; deposited in KU • 1♂ (slide no. NIBRIN0000857557); KUF; 2-8 Apr. 2017; D. Ham leg.; deposited in NIBR • 1♂ (slide no. NIBRIN0000992636); SJ 1; 13 Apr. - 4 May 2019; W. G. Kim leg.; deposited in NIBR • 1♂ (slide no. NIBRIN0000992634); SJ 2; 8-24 Apr. 2020; W. G. Kim leg.; deposited in NIBR.

## Campylomyza aborigena Mamaev, 1998

Fig. 1C, 2A-C

Campylomyza aborigena Mamaev, 1998: 6.

**Specimens examined.** KOREA • 1♂ (slide no. NIBRIN0000992639); **Sobaek**; 6 May – 6 Jun. 2019; D. Ham, S. Park leg.; deposited in NIBR • 2♂♂ (slides no. NIBRIN0000992638, 19-38); **Odae 2**; 23 Apr. – 11 May 2019; D. Ham, S. Park leg.; deposited in NIBR.

**Diagnosis.** *Campylomyza aborigena* closely resembles *C. aemula* Mamaev, 1998 (inferred from the illustration in Jaschhof and Jaschhof 2009) and shares the following characteristics: 1) Tegmen with lamellate (Fig. 2C,  $\downarrow_5$ ), tapering apical points that are rounded and strongly sclerotized anteriorly, and weakly sclerotized posteriorly; 2) Large foliate dorsal processes (Fig. 2C,  $\downarrow_6$ ) with narrower, sharp points; 3) Gonostyli tapering apically and curved anteroventrally with convex apex margins (Fig. 2B). However, *C. aborigena* can be distinguished from *C. aemula* by the following characteristics: tegmen with parallel-sided apical points (Fig. 2C,  $\downarrow_5$ ); dorsal processes large, broad basally, pointed apically with strongly sclerotized margin (Fig. 2C,  $\downarrow_6$ ).

**Measurements.** Male adult (Slide no. NIBRIN0000992639): Body length 1.454 mm. Wing length 1.484 mm. Hind leg coxa 0.170 mm; femur 0.547 mm; tibia 0.551 mm; tarsomere I 0.307 mm; tarsomere II 0.164 mm; tarsomere III 0.130 mm; tarsomere IV 0.067 mm; tarsomere V 0.062 mm.

Redescription. Male adult. Head. Postocular bristles four or five. Antenna with 12 flagellomeres. Neck of fourth antennal flagellomeres as long as node. Node with one complete and two incomplete crenulate whorls with sensory hairs, two incompletely collar-shaped sensilla distally. Palpus 4-segmented; fourth segment longest. Thorax. Preepisternum with eight setae. Wing length to width ratio 2.44, AntC ending beyond  $R_{4+5}$  but before reaching  $M_{4}$ ; Apic  $R_{1}$ 3.23× length of Rs; CuA separated (Fig. 1C). Tarsomere I longer than tarsomere II. Claws sickle-shaped, toothed; empodia longer than claws; pubescent. *Terminalia*. Tg9 slightly tapered towards apex (Fig. 2A,  $\downarrow_1$ ). Gonocoxites emarginated broad U-shaped ventrally. (Fig. 2A,  $\downarrow_2$ ); ventromedial portion swollen, pronounced (Fig. 2A,  $\downarrow_3$ ); dorsal transverse bridge narrower to apex, extending far beyond ventrobasal margin (Fig. 2A,  $\downarrow_{a}$ ). Gonostyli curved anteroventrally; apical margin strongly convex; medial portion excavated; setae becoming denser towards apex. On tegmen, apical points long, lamellate, rounded apically (Fig. 2C,  $\downarrow_{c}$ ); dorsal processes spoon-shaped with hollow in the center and strongly sclerotized apex; directed anteriorly (Fig. 2C,  $\downarrow_6$ ). Mesal processes short, sclerotized (Fig. 2C,  $\downarrow_7$ ). Tegmen shoulders inconspicuous.

Distribution. Russia (Primorsky), new to South Korea.

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**Figure 2.** Male morphology of *Campylomyza aborigena* Mamaev, 1998 (**A–C**) and *Campylomyza ambulata* sp. nov. (**D–G**) **A** gonocoxites, ventral view, slide no. NIBRIN0000992639 **B** gonostylus, dorsal view, slide no. NIBRIN0000992639 **C** tegmen, dorsal view, slide no. 19–38 **D** gonocoxites, ventral veiw, holotype **E–G** tegmen, dorsal view **E** holotype **F** paratype (slide no. NIBRIN0000919403) **G** paratype (slide no. 19AY-9). Scale bars: 0.05 mm.

**Remarks.** *Campylomyza aborigena* Mamaev, 1998 was originally described based on a single specimen collected in Far East Russia in 1964. Mamaev's description was limited to just seven lines of text, without any accompanying drawings or photographs. However, thanks to the observations made by Dr. Mathias Jaschhof on the holotype specimen of *C. aborigena* in the Zoological Museum of Moscow State University in 2006, we now know that the Korean species is the same as the Russian *C. aborigena*. This is significant because it provides further evidence supporting the existence of *C. aborigena*, with the Korean finding being only the second record except for the holotype. Mamaev often described species based on a single specimen without proper illustration or depiction. Therefore, the discovery of this species in Korea and the possibility of obtaining additional specimens are of great importance for further supporting Mamaev's species concept and advancing the taxonomy of mycophagous cecidomyiids.

## Campylomyza ambulata sp. nov.

https://zoobank.org/EFD8D1BC-5BE8-4C74-AF49-5B7B59531A0D Fig. 2D-G

**Type material examined.** *Holotype*: KOREA • 1♂ (slide no. 19AYa-11); Gyeongsangbuk-do, Yeongyang-gun, Yeongyang-eup, Gowol-gil, 23, National Endangered Species Restoration Center (**NERC**); 10–17 Apr. 2019; Y. J. Choi, H. G. Kim leg.; deposited in KU. *Paratypes*: KOREA • 6♂♂ (slides no. 19AY-4, 8, 9, 11, 12, 14, 19AYa-6, 12); same data and deposition as holotype • 1♂ (slide no. 19AZ-10); **NERC**; 3–10 Apr. 2019; Y. J. Choi, H. G. Kim leg.; deposited in KU • 1♂ (slide no. NIBRIN0000919403); **NERC**; same data as for preceding; deposited in NIBR.

**Other material examined.** KOREA • 2♂♂ (slides no. NIBRIN0000992627, NI-BRIN0000992628); **Odae 2**; 23 Apr. – 11 May 2019; D. Ham, S. Park leg.; deposited in NIBR • 1♂ (slide no. HDS-674); **GW**; 8 Nov. 2017; D. Ham leg.; deposited in KU • 1♂ (21AE-2-2); **GP**; 28 Apr. – 5 May 2019; Y. J. Bae leg.; deposited in KU • 1♂ (21AG-1-5); **SJ 2**; 8–24 Apr. 2020; W. G. Kim leg.; deposited in KU.

**Diagnosis.** *Campylomyza ambulata* sp. nov. can be distinguished from other species in the *flavipes* group found in Korea through the following characteristics: 1) gonostyli curved anteroventrally, excavated ventromesally with denser setae towards the apex; 2) apical point small, short subtriangular (Fig. 2E,  $\downarrow_{10}$ ); 3) dorsal processes strongly tapering anteriorly, moveable depending on the pressure (Fig. 2E,  $\downarrow_{11}$ ); 4) shoulders of tegmen conspicuous (Fig. 2E,  $\downarrow_{12}$ ); 5) parameral apodeme short.

**Measurements.** Male adult (holotype): Body length 1.187 mm. Wing length 1.364 mm. Hind leg coxa 0.134 mm; femur 0.480 mm; tibia 0.500 mm; tarsomere I 0.290 mm; tarsomere II 0.133 mm; tarsomere III 0.112 mm; tarsomere IV 0.071 mm; tarsomere V 0.058 mm.

Description. Male adult (holotype). Head. Postocular bristles 3-5. Antenna with 12 flagellomeres. Neck of fourth antennal flagellomeres as long as node. Node with one complete and two incomplete crenulate whorls with sensory hairs, two incompletely collar-shaped sensilla distally. Palpus 4-segmented; fourth segment longest. Thorax. Preepisternum with eight setae. Wing length to width ratio 2.28, AntC ending beyond  $R_{4+5}$  but before reaching  $M_{4}$ ; Apic  $R_{1}$ 3.46× length of Rs; CuA separated. Tarsomere I longer than tarsomere II. Claws sickle-shaped, toothed; empodia longer than claws, pubescent. Terminalia. Tg9 tapering towards apex with five fine setae apically. Ventral emargination U-shaped; ventromedial portion of gonocoxites slightly pronounced (Fig. 2D, L<sub>s</sub>). Gonostyli with moderately convex apical margins, excavated ventromedially, narrowly rounded apically. Dorsal transverse bridge broadly rounded apically, extending beyond ventrobasal margin (Fig. 2D,  $\downarrow_q$ ). On tegmen, apical points small, subtriangular, lamellate (Fig. 2E,  $\downarrow_{10}$ ), dorsal processes long, strongly tapering towards apex beyond midlength, blunt apically (Fig. 2E,  $\downarrow_{11}$ ). Tegmen shoulders well-developed (Fig. 2E,  $\downarrow_{12}$ ), Parameral apodeme short (Fig. 2E,  $\downarrow_{15}$ ).

**Variation.** We observed significant variation concerning apical points and tegmen shoulders (Fig. 2F–G). Apical points bulged with round serrated surfaces (Fig. 2G,  $\downarrow_{13}$ ); Shoulders inconspicuous, when almost in the same position or lower than apical points of tegmen (Fig. 2G,  $\downarrow_{14}$ ). Dorsal processes moveable apically.

**Etymology.** The species epithet *ambulata* is derived from the Latin word *ambulātus*, which means ambulatory, referring to the movable nature of the dorsal processes.

#### Campylomyza angusta sp. nov.

https://zoobank.org/69317C2B-444C-466F-98FE-F7B9100AE181 Fig. 3A-C

**Type material examined.** *Holotype*: KOREA • 1♂ (slide no. NIBRIN0000941947); Gangwon-do, Pyeongchang-gun, Jinbu-myeon, Odaesan-ro, Mt. Odae, small valley before So-Myeong valley **(Odae 1)**; 18 Apr. – 1 May 2020; D. Ham, S. Park leg.; deposited in NIBR.

**Diagnosis.** *Campylomyza angusta* sp. nov. belongs to the *ormerodi* group of species where it is reminiscent of *C. pubescens* (Jaschhof and Jaschhof 2009) mainly due to cerci bearing strikingly large pubescence and short dorsal transverse bridge, which is almost not protruding beyond the ventrobasal margin. *Campylomyza angusta* sp. nov. is distinguished as follows. Gonostyli moderately convex posteriorly with narrowly rounded apex (Fig. 3A,  $\downarrow_6$ ). Gonocoxites strongly protruding dorsomedially, ventral bridge short. The tegmen lacks shoulders (Fig. 3C,  $\downarrow_4$ ), parameral apodemes long (Fig. 3C,  $\downarrow_5$ ), apical points directed slightly laterally, mesal points short, weakly sclerotized, rounded apically (Fig. 3C,  $\downarrow_2$ ).

**Measurements.** Male adult (holotype): Body length 1.329 mm. Wing length 1.569 mm. Hind leg coxa 0.160 mm; femur 0.571 mm; tibia 0.567 mm; tarsomere I 0.330 mm; tarsomere II 0.153 mm; tarsomere III 0.109 mm; tarsomere IV 0.078 mm; tarsomere V 0.061 mm.

Description. Male adult (holotype). Head. Postocular bristles seven. Antenna with 12 flagellomeres. Neck of fourth antennal flagellomeres shorter than node. Node with one complete and two incomplete crenulate whorls with sensory hairs, two incompletely collar-shaped sensilla distally. Palpus 4-segmented; fourth segment longest. Thorax. Preepisternum with eight setae. Wing length to width ratio 2.53. AntC ending beyond  $R_{4+5}$  but before reaching  $M_{4}$ ; Apic  $R_{1}$  4.18× length of Rs. CuA separated. Tarsomere I longer than tarsomere II. Claws sickle-shaped, fine toothed; empodia shorter than claws; pubescent. Terminalia. Tg9 tapered towards apex with 13 setae apically. Ventral bridge of gonocoxites short, dorsal transverse bridge protruding only slightly beyond the ventrobasal margin. Ventral emargination deep, U-shaped. Ventromedial portion broad rounded, not protruding medially (Fig. 3A,  $\downarrow_1$ ). Gonostyli rounded apically with semi-circular apical margin; excavated ventromedially, plump dorsally; setae denser towards apex. On tegmen, apical points not lamellate, pointed apically, directed slightly posterolaterally (Fig. 3C,  $\downarrow_2$ ); mesal points weakly sclerotized, short, tapered basally, broadened at apical third, rounded apically (Fig. 3C,  $\downarrow_3$ ). Tegmen shoulders indistinct (Fig. 3C,  $\downarrow_4$ ). Parameral apodemes long, more than half-length of tegmen (Fig. 3C,  $\downarrow_{c}$ ).

**Etymology.** The specific epithet *angusta* in Latin means narrow, referring to the narrowness of the shoulder region of the tegmen in this species.

#### Campylomyza cavitata Mamaev, 1998

*Campylomyza cavitata* Mamaev, 1998: 7; Jaschhof and Jaschhof 2009: 112–113, fig. 37A–C.

**Specimens examined.** KOREA • 13 (slide no. NIBR0000919409); **Odae 1**; 11–26 May 2019; D. Ham, S. Park leg.; deposited in NIBR.



Figure 3. Male morphology of *Campylomyza angusta* sp. nov., holotype **A–C** and *Campylomyza convexa* sp. nov., holotype **D–F**: **A** gonocoxites, ventral veiw **B** gonostylus, dorsal view **C** tegmen, dorsal view **D** gonocoxites, ventral veiw **E** gonostylus, dorsal view. Scale bars: 0.05 mm.

Distribution. Sweden, Finland, Germany, Russia, new record for South Korea.

Campylomyza cingulata Jaschhof, 2009

Campylomyza cingulata Jaschhof, 2009: 119, fig. 41A-E.

Specimens examined. KOREA • 1♂ (slide no. NIBRIN0000941946); Odae 1; 18 Apr. – 1 May 2020; D. Ham, S. Park leg.; deposited in NIBR.

Distribution. Fennoscandia, Germany, new record for South Korea.

#### Campylomyza convexa sp. nov.

https://zoobank.org/2A011D80-C1EE-4EB4-BCB1-787C972052F8 Fig. 3D-F

**Type material examined.** KOREA • 1♂ (slide no. HDS-505); Gyeonggi-do, Namyangju-si, Wabu-eup, Dosim-gil, Korea University's farm to practice **(KUF)**; 2–8 Apr. 2017; D. Ham leg.; deposited in KU. *Paratypes*: KOREA • 1♂ (slide no. HDS-504); same data and deposition as holotype • 2♂♂ (slides no. NIBRIN0000857555, NIBRIN0000919405) **KUF**; 2–8 Apr. 2017; D. Ham leg.; deposited in NIBR.

**Other material examined.** KOREA • 4♂♂ (slides no. NIBRIN0000992649 – NI-BRIN0000992652); **KUF**; 2–8 Apr. 2017; Y. J. Bae leg.; deposited in NIBR.

**Diagnosis.** *Campylomyza convexa* sp. nov. is most similar to *C. aemula* (cf. Jaschhof and Jaschhof 2009: fig. 29A–D), especially in having the rounded apical points on the tegmen, tapering posteriorly, the dorsal processes are broad basally, directed dorsolaterally with a strongly sclerotized triangular apex. However, *C. convexa* sp. nov. can be distinguished from *C. aemula* by following characteristics: 1) Gonostyli moderately convex apically, not excavated medially, broadly rounded apically, with small dorsomedial lobe (Fig. 3E,  $\downarrow_8$ ); 2) Apical points of tegmen parallel-sided to rounded apically, longer than *C. aemula* (Jaschhof and Jaschhof 2009: 102); 3) Mesal points of tegmen longer and narrower than in *C. aemula* (Fig. 3E,  $\downarrow_{11}$ ); 4) Dorsal processes lacking sclerotized ridge, strongly sclerotized apically (Fig. 3E,  $\downarrow_{10}$ ).

**Measurements.** Male adult (holotype): Body length 1.417 mm. Wing length 1.639 mm. Hind leg coxa 0.105 mm; femur 0.555 mm; tibia 0.574 mm; tarsomere I 0.333 mm; tarsomere II 0.170 mm; tarsomere III 0.138 mm; tarsomere IV 0.082 mm; tarsomere V 0.065 mm.

Description. Male adult (holotype). Head. Postocular bristles seven. Antenna with 12 flagellomeres. Neck of fourth antennal flagellomeres shorter than node. Node with one complete and two incomplete crenulate whorls with sensory hairs, two incompletely collar-shaped sensilla distally. Palpus 4-segmented; fourth segment longest. Thorax. Preepisternum with nine setae. Wing length to width ratio 2.24. AntC ending beyond  $R_{4+5}$  but before reaching  $M_{4}$ ; Apic  $R_{1}$  3.82× length of Rs. CuA separated. Tarsomere I longer than tarsomere II. Tarsomere I longer than tarsomere II. Claws sickle-shaped, slightly toothed; empodia as long as claws, slightly broaden apically; pubescent. Terminalia. Tg9 tapered towards apex with eight fine setae. Ventral bridge of gonocoxites long, ventral emargination relatively short and broad, U-shaped, dorsal transverse bridge broad, extending far beyond ventrobasal margin. Ventromedial portion of gonocoxites broad, slightly pronounced (Fig. 3D,  $\downarrow_7$ ). Gonostyli curved anteroventrally, rounded apically, moderately convex apically with small dorsomedial lobe (Fig. 3E,  $\downarrow_{R}$ ); setae distributed evenly in ventral view, denser towards apex in dorsal view. On tegmen, apical points long, parallel-sided to rounded apically, not lamellate, sclerotized (Fig. 3F,  $\downarrow_{o}$ ); dorsal processes strongly sclerotized apically, directed dorsolaterally (Fig. 3F,  $\downarrow_{10}$ ); mesal points weakly sclerotized, faint apically, directed anteriorly (Fig. 3F,  $\downarrow_{11}$ ). Shoulders of tegmen inconspicuous. Transverse brace rib-shaped without extension (Fig. 3F,  $\downarrow_{12}$ ). Parameral apodeme sclerotized, long, slightly shorter than half of tegmen (Fig. 3F,  $\downarrow_{12}$ ). Ejaculatory apodeme of typical Campylomyza outline.

**Etymology.** From the Latin word *convexus*, meaning 'a surface with rounded edges', which refers to the rounded outline of the apex of the apical points on the tegmen.

#### Campylomyza cornigera sp. nov.

https://zoobank.org/52110DC2-AC64-4EAC-AC9A-639CBFD1C1AF Fig. 4A-C

**Type material examined.** *Holotype*: KOREA • 1♂ (slide no. 19Aya-8); Gyeongsangbuk-do, Yeongyang-gun, Yeongyang-eup, Gowol-gil, 23, National Endangered Species Restoration Center (**NERC**); 10–17 Apr. 2019; Y. J. Choi, H. G. Kim leg.; deposited in KU. *Paratype*: KOREA • 1♂ (slide no. NIBRIN0000857558); **KUF**; 2–8 Apr. 2017; D. Ham leg.; deposited in NIBR.

**Other material examined.** KOREA • 1♂ (slide no. NIBRIN0000992637); **Odae 1**; 18 Apr. – 1 May 2020; D. Ham, S. Park leg.; deposited in NIBR.

**Diagnosis.** *Campylomyza cornigera* sp. nov. is most similar to *C. nigroliminata* Mamaev, 1998 (cf. Jaschhof and Jaschhof 2021: fig. 30A, B), especially in having lamellate apical points of the tegmen that are rounded apically and pointed processes directed anterolaterad (Fis. 4C,  $\downarrow_{5, 6}$ ), and mesal processes es are directed anteriorly (Fig. 4C,  $\downarrow_7$ ). However, *C. cornigera* sp. nov. can be distinguished from *C. nigroliminata* by the following characteristics: 1) Pointed processes directed anterolaterally of apical points slightly curved; 2) Dorsal processes missing; 3) Tegmen shoulders indistinct.

**Measurements.** Male adult (holotype): Body length 1.315 mm. Wing length 1.574 mm. Hind leg coxa 0.141 mm; femur 0.539 mm; tibia 0.515 mm; tarsomere I 0.302 mm; tarsomere II 0.142 mm; tarsomere III 0.105 mm; tarsomere IV 0.062 mm; tarsomere V 0.056 mm.

Description. Male adult (holotype). Head. Postocular bristles seven. Antenna with 12 flagellomeres. Neck of fourth antennal flagellomeres as long as node. Node with one complete and two incomplete crenulate whorls with sensory hairs, two incompletely collar-shaped sensilla distally. Palpus 4-segmented; fourth segment longest. Thorax. Preepisternum with 1-9 setae. Wing length to width ratio 2.58. AntC ending beyond  $R_{4+5}$  but before reaching M<sub>4</sub>; ApicR<sub>1</sub> 3.08× length of Rs. CuA separated. Tarsomere I longer than tarsomere II. Claws sickle-shaped, toothed; empodia longer than claws, slightly broaden apically; pubescent. Terminalia. Tg9 tapered towards apex with seven or eight fine setae apically. Ventral bridge of gonocoxites long (Fig. 4A,  $\downarrow_1$ ), with U-shaped emargination; dorsal transverse bridge narrowly tapering, extending far beyond basal margin (Fig. 4A,  $\downarrow_2$ ). Ventromedial portion of gonocoxites almost angular (Fig. 4A,  $\downarrow_3$ ). Gonostyli narrowly rounded to pointed apically (Fig. 4A,  $\downarrow_{a}$ ), moderately convex posteriorly, and slightly excavated medially, plump dorsally; setae denser towards apex. Tegmen long and narrow, apical points sclerotized, short, stout, and broadly rounded apically (Fig. 4C,  $\downarrow_s$ ); a pair of strongly sclerotized processes directed dorsolaterally (Fig. 4C,  $\downarrow_6$ ); true dorsal processes missing. Mesal points of tegmen slightly sclerotized, narrowly long, directed anteriorly (Fig. 4C,  $\downarrow_{\gamma}$ ). Shoulders of tegmen inconspicuous; width between apices of shoulders narrower than processes directed dorsolaterally. Transverse brace rib-shaped (Fig. 4C,  $\downarrow_{s}$ ). Parameral apodemes long (Fig. 4C,  $\downarrow_{a}$ ). Ejaculatory apodeme of typical Campylomyza outline.

**Etymology.** The species epithet cornigera, derived from Latin meaning 'having horns,' refers to the horn-shaped processes on the tegmen that are directed dorsolaterally.

#### Campylomyza cornuta Jaschhof, 1998

Campylomyza cornuta Jaschhof 1998b: 260-261, Abb. 1a-e.

Specimens examined. KOREA • 2♂♂ (slides no. NIBRIN0000941945, NI-BRIN0000992653); HN; 3 Mar. – 12 Apr. 2019; H. S. Ahn leg.; deposited in NIBR. Distribution. Sweden, Lithuania, Germany, and new to South Korea.

## Campylomyza hori sp. nov.

https://zoobank.org/8D43A3F5-2FF5-4E08-BDD6-85A776E46646 Fig. 4D-F

**Type material examined.** *Holotype*: KOREA • 1♂ (slide no. 19I-5); Gangwon-do, Jeongseon-gun, Jeongseon-eup, Hoedong-ri, 870, Gariwangsan Recreational Forest (**Gariwang**); 13 Apr. – 12 May 2019; D. Ham, S. Park leg.; deposited in KU. *Paratype*: KOREA • 1♂ (slide no. NIBRIN0000919401); same data as holotype and deposited in NIBR.

**Other material examined.** KOREA • 233 (slides no. NIBRIN0000992654, NI-BRIN0000992655); **Sobaek**; 6 May – 6 Jun. 2019; D. Ham, S. Park leg.; deposited in NIBR.

**Diagnosis.** *Campylomyza hori* sp. nov. is most similar to *C. mohrigi* Jaschhof, 2009, especially in having the apical points divided, and the dorsal processes with sclerotized ridge, subtriangular apex on tegmen. However, *C. hori* sp. nov. can be distinguished from *C. mohrigi* by the following characteristics: 1) Necks of antennal flagellomeres longer than nodes; 2) Gonostyli slightly longer and narrower (Fig. 4E); 3) Dorsal processes wider, margin sclerotized, with subtriangular apex, center membranous (Fig. 4F,  $\downarrow_{13}$ ) vs. narrower, leaf-shaped with sclerotized ridge and points apically in *C. mohrigi*.

**Measurements.** Male adult (holotype). Body length 1.441 mm, wing length 1.645 mm. Hind leg coxa 0.156 mm; femur 0.607 mm; tibia 0.647 mm; tarsomere I 0.351 mm; tarsomere II 0.180 mm; tarsomere III 0.141 mm; tarsomere IV 0.088 mm; tarsomere V 0.070 mm.

**Description.** Male adult (holotype). *Head.* Postocular bristles three. Antenna with 12 flagellomeres. Neck of fourth antennal flagellomere longer than node. Node with one complete and two incomplete crenulate whorls with sensory hairs, two incompletely collar-shaped sensilla distally. Palpus 4-segmented; fourth segment longest. **Thorax.** Preepisternum with five fine setae anteriorly. Wing length to width ratio 2.47. AntC ending beyond  $R_{4+5}$  but before reaching; ApicR<sub>1</sub> 2.77× length of Rs. CuA separated. Tarsomere I longer than tarsomere II. Claws sickle-shaped, weakly toothed; empodia as long as claws; pubescent. *Terminalia.* Tg9 tapering towards apex with six fine setae apically. Ventral emargination deep, U-shaped, ventral bridge short. Dorsal transverse bridge broadly rounded apically, slightly extended beyond ventrobasal margin (Fig. 4D,  $\downarrow_{10}$ ). Gonostyli elongated apically, curved anteroventrally, constricted ventrosubapically (Fig. 4D,  $\downarrow_{11}$ ) with fine setae denser towards apex; incised dorsomesally. On tegmen, apical points pointed, directed posteriorly (Fig. 4F,  $\downarrow_{12}$ ); dorsal processes broad basally, constricted medially, pointed apically (Fig. 4F,  $\downarrow_{13}$ ),



Figure 4. Male morphology of *Campylomyza cornigera* sp. nov., holotype **A–C** and *Campylomyza hori* sp. nov., holotype **D–F**: **A** gonocoxites, ventral view **B** gonostylus, dorsal view **C** tegmen, dorsal view **D** gonocoxites, ventral view **E** gonostylus, dorsal view, dorsal view **F** tegmen, dorsal view. Scale bars: 0.05 mm.

directed anterodorsally, with strongly sclerotized margin basally; mesal points faint, short, pointed (Fig. 4F,  $\downarrow_{14}$ ). Tegmen shoulders almost angular, equipped with several small bumps laterally (Fig. 4F,  $\downarrow_{15}$ ). Transverse brace with lobe-like dorsal extensions. Ejaculatory apodeme swelling medially (Fig. 4D,  $\downarrow_{16}$ ), narrow basally.

**Etymology.** The species epithet *hori* originates from the Korean native term, pronounced 'hori-hori-hada', an adjective describing a slender or tapered part. This name specifically denotes the narrowed part of the gonostyli.

#### Campylomyza odae sp. nov.

https://zoobank.org/4901DF68-5CC0-4023-A8C6-5D29649014E0 Fig. 5A-D

**Type material examined.** *Holotype*: KOREA • 1♂ (slide no. NIBRIN0000992641) Gangwon-do, Pyeongchang-gun, Jinbu-myeon, Odaesan-ro, Mt. Odae, the road before temple (Buk-Dae-Mi-Reuk-Am) **(Odae 2)**; 11–26 May 2019; D. Ham, S. Park leg.; deposited in NIBR. *Paratype*: KOREA • 1♂ (slide no. NIBRIN0000919408); same data and deposition as holotype.

**Diagnosis.** *Campylomyza odae* sp. nov. is distinguishable from other *Campylomyza* species by the following combination of characteristics: 1) Apical margin of gonostyli rounded (Fig. 5A,  $\downarrow_3$ ); 2) Dorsal processes on tegmen with inconspicuous pair of subtriangular processes anterolaterally; 3) Dorsal processes constricted medially, forming mesal cleft (Fig. 5C,  $\downarrow_6$ ); 4) Cerci visible (Fig. 5D).

**Measurements.** Male adult (Holotype): Body length 1.737 mm. Wing length 1.870 mm. Hind leg coxa 0.221 mm; femur 0.713 mm; tibia 0.624 mm; tarsomere I 0.369 mm; tarsomere II 0.193 mm; tarsomere III 0.134 mm; tarsomere IV 0.089 mm; tarsomere V 0.072 mm.

**Description.** Male adult. Slightly larger than other *Campylomyza* species. *Head*. Postocular bristles four. Antenna with 12 flagellomeres. Neck of fourth antennal flagellomere slightly shorter than node. Node with one complete and two incomplete crenulate whorls with sensory hairs, two incompletely collar-shaped sensilla distally. Palpus 4-segmented; fourth segment longest. Thorax. Wing length to width ratio 2.39, AntC ending beyond  $R_{4+5}$  but before reaching  $M_4$ ; Apic $R_1$  4.31× length of Rs; CuA separated. Tarsomere I longer than tarsomere II. Claws sickle-shaped, toothed; empodia small, shorter than claws. Terminalia. Tg9 broadly tapered towards apex with eight fine setae. Ventral emargiantion U-shaped; ventral bridge long; dorsal transverse bridge extending far beyond ventrobasal margin (Fig. 5A,  $\downarrow_1$ ); ventromedial portion of gonocoxites relatively narrow, not pronounced (Fig. 5A,  $\downarrow_2$ ). Gonostyli short, stout, strongly convex posteriorly, truncated apically (Fig. 5A,  $\downarrow_3$ ), directed ventrally, bearing dorsoapically numerous straight setae of various length, with denser stiff setae as it goes to apex. Tegmen narrow, shoulders inconspicuous. Parameral apodemes short. Apical points lamellated, triangular-shaped, directed posteriorly (Fig. 5C,  $\downarrow_{a}$ ), separated by wide cleft mesally; dorsal processes subtriangular shaped, directed dorsomedially, apices crossed with spreading subtriangular extensions (Fig. 5C,  $\downarrow_{s}$ ); each dorsal process constricted at midlength, forming mesal cleft (Fig. 5C,  $\downarrow_{c}$ ). Cerci visible.

**Etymology.** The species name *odae* is a noun in apposition to the collection locality, Mt. Odae in Gangwon province.

#### Campylomyza salicia sp. nov.

https://zoobank.org/53F03A9D-EBE9-4D6A-9599-65617BADF8FC Fig. 5E-G

**Type material examined.** *Holotype*: KOREA • 1♂ (slide no.19Aya-2); Gyeongsangbuk-do, Yeongyang-gun, Yeongyang-eup, Gowol-gil, 23, National Endangered Species Restoration Center (**NERC**); 10–17 Apr. 2019; Y. J. Choi, H. G. Kim leg.; deposited in KU. **Paratypes:** KOREA • 5♂♂ (slides no. 19AY-5, 10,



Figure 5. Male morphology of *Campylomyza odae* sp. nov., holotype **A**–**D** and *Campylomyza salicia* sp. nov., holotype **E**–**G**: **A** gonocoxites, ventral view **B** gonostylus, dorsal view **C** tegmen, dorsal view **D** cerci, ventral view **E** gonocoxites, ventral view **F** gonostylus, dorsal view. Scale bar: 0.05 mm.

13, 17, 19AYa-13); same data and deposition as holotype  $\cdot$  13 (slide no. NI-BRIN0000919404); same data as holotype, deposited in NIBR.

**Other material examined.** KOREA • 2♂♂ (slides no. 19AZ-6, 9); **NERC**; 3–10 Apr. 2019; Y. J. Choi, H. G. Kim leg.; deposited in KU • 1♂ (slide no. 19AX-4); **NERC**; 20–27 Mar. 2019; Y. J. Choi, H. G. Kim leg.; deposited in KU • 1♂ (slide no. NIBRIN0000992640); **NERC**; 27 Mar. – 3 Apr. 2019; Y. J. Choi, H. G. Kim leg.; deposited in NIBR.

**Diagnosis.** *Campylomyza salicia* sp. nov. is most similar to *C. mohrigi* (cf. illustration of Jaschhof and Jaschhof 2009: 109), especially having the elongated, tapering Gonostyli ventrally, not lamellate apical points and foliate

dorsal processes which reaching to transverse brace on tegmen. However, *C. salicia* sp. nov. can be distinguished from *C. mohrigi* by following characteristics: 1) dorsal processes of tegmen sclerotized margin without sclerotized ridge (Fig. 5G,  $\downarrow_9$ ); 2) the dorsal processes are directed dorsolaterally with a strongly sclerotized triangular apex; 3) parameral apodeme shorter than that of *C. mohrigi* (Fig. 5G,  $\downarrow_{10}$ ).

**Measurements.** Male adult (holotype): Body length 0.944 mm. Wing length 1.266 mm. Hind leg coxa 0.142 mm; femur 0.441 mm; tibia 0.463 mm; tarsomere I 0.275 mm; tarsomere II 0.123 mm; tarsomere III 0.103 mm; tarsomere IV 0.072 mm; tarsomere V 0.057 mm.

Description. Male adult (holotype). Slightly smaller than other Campylomyza species. Head. Postocular bristles five. Antenna with 12 flagellomeres. Neck of fourth antennal flagellomere longer than node. Node with one complete and two incomplete crenulate whorls with sensory hairs, two incompletely collar-shaped sensilla distally. Palpus 4-segmented; fourth segment longest. Thorax. Preepisternum with six fine setae anteriorly. Wing length to width ratio 2.70. AntC ending beyond  $R_{4+5}$  but before reaching  $M_{a}$ ; Apic  $R_1$  3.23× length of Rs; CuA separated. Tarsomere I longer than tarsomere II. Claws slightly toothed; empodia small, narrow. Terminalia. Tg9 tapered towards apex with 8 setae apically. Ventral bridge of gonocoxites half-length of gonocoxites; dorsal transverse bridge tapering, extending beyond ventrobasal margin. Ventral emargination U-shaped. Gonostyli elongated, blunt to slightly pointed apically, moderately convex apically; ventrosubapically constricted (Fig. 5E,  $\downarrow_{\gamma}$ ); excavated ventromesally; setae denser towards apex. On tegmen, apical points triangular shaped, not lamellate, pointed apically, directed posterolaterally (Fig. 5G,  $\downarrow_{g}$ ); dorsal processes leaf-shaped, elongated slightly beyond transverse brace, with strongly sclerotized apex (Fig. 5G, ↓<sub>o</sub>). Shoulders of tegmen well developed, thick. Transverse brace slightly extended, lobe shaped. Parameral apodemes short (Fig. 5G,  $\downarrow_{10}$ ).

**Etymology.** The species name *salicia* is derived from the Latin word *salici*, meaning 'willow,' in reference to the dorsal processes of the tegmen, which resembles the shape of a willow leaf.

## Key to the Species of Korean Campylomyza

Ejaculatory apodeme without apical extension. Tegmen without dorsal
processes C. cornuta Jaschhof, 1998
Ejaculatory apodeme with apical extension. Tegmen bearing apical points
and processes
On tegmen, dorsal processes forming mesal cleft with expended subtrian-
gular processes laterally
On tegmen, dorsal processes elongated without mesal cleft or absent, or
dorsomesal processes present3
On tegmen, apical points present; dorsal processes elongated, foliate or
dorsolaterad processes horn-shaped at apex; shoulders well developed
On tegmen, dorsal processes absent or single pair of small dorsomesal
processes present12
Gonostyli short, ovoid-shaped; not pointed C. abjecta Mamaev, 1998
Gonostyli elongated, curved inwardly5

5	Gonostyli elongated, strongly curved inwardly; constricted ventrosubapi-
	cally with dense setae apically. On tegmen, apical points sharp apically .6

Gonostyli blunt, rounded apically; slightly curved inwardly ......7

- 7 On tegmen, apical points rounded apically, parallel-sided......8
- 8 Gonocoxites with swollen, pronounced ventromedial portion. On tegmen, dorsal processes spoon-shaped; elongated with subtriangular narrow tips apically, directed anteriorly ....... C. aborigena Mamaev, 1998 (Fig. 2A–C)
- 9 On tegmen, apical points rounded, short, slightly curved anterolaterally.... C. cornigera sp. nov. (Fig. 4A–C)
- Gonostyli with small dorsomedial lobe. On tegmen, apical points long, parallel-sided to rounded apically; dorsal processes strongly sclerotized, straightened, directed dorsolaterally with triangular apex .....
  - ..... C. convexa sp. nov. (Fig. 3D-F)
- 10 On tegmen, apical points pointed or broadly rounded apically with serrated surfaces; dorsal processes elongated, directed anteriorly...... C. ambulata sp. nov. (Fig. 2D-G)
- On tegmen, dorsal processes with subtriangular apex, directed anterolaterally......11
- 11 Gonostyli slightly excavated mesally, flattened dorsally, narrowly rounded apically with convex apical margins; Tegmen apical points lamellate; dorsal processes foliate, directed anterolaterally..... *C. flavipes Meigen*, **1818**
- 12 On tegmen, apical points tapering; dorsal processes absent; mesal processes es rounded at apex; shoulders indistinct or missing ....... *ormerodi* group, 13
- Tegmen with 1 pair of small dorsomesal processes which are serrated or extended ......14

- 15 Gonostyli with lobe dorsally. Serrated processes on tegmen situated subapically dorsomedially in longitudinal direction. Aedeagal head small...... *C. appendiculata* Jaschhof, 2015

## DNA barcode analysis and MOTU estimation

The 658-bp *COI* sequences were analyzed, revealing 234 variable sites, of which 63 were parsimony informative. Within the genus *Campylomyza*, the interspecific divergences (*p*-distances) ranged from 6.18% to 15.28%. The mean distance across the entire dataset was 10.72% (Suppl. material 1: table S3). Intraspecific genetic distances varied from 0% to 0.92%. The species delimitation using the ABGD method delineated 17 Molecular Operational Taxonomic Units (MOTUs), including the outgroup. These MOTUs are illustrated by the color bars on the Neighbor Joining (NJ) tree in Fig. 6, corresponding with the delineations observed in the same NJ tree. All 17 MOTUs correspond to groups distinguished by their morphological characteristics.

## Discussion

The discovery of C. abjecta and C. aborigena in Korea is particularly significant due to the inherent challenges in studying fungivorous cecidomyiids. This finding underscores the need to expand research on species previously known only from single specimens in Russia. Initially, the type specimens of these species were based on solitary samples that lacked adequate descriptions and illustrations, limiting precise identification. Given the geographic proximity between Korea and Russia, it is crucial to broaden research efforts on these species. In 2006, Dr. Mathias Jaschhof visited the Russian Zoological Museum and sketched the type specimens, which greatly aided in their identification in Korea (M. Jaschhof pers. comm. Oct. 2019). Notably, C. abjecta has also been recorded in Europe, particularly in Sweden (Jaschhof and Jaschhof 2017), while the finding of C. aborigena in Korea marks only the second confirmed sighting since its original description in Russia. Considering Russia's vast size, the presence of these species in both European and Far Eastern regions complicates our understanding of their biogeography. This situation highlights the importance of thoroughly studying all previously described species, as some, like those discussed here, may be more widespread than previously thought. The discovery of C. aborigena in Korea is especially significant because it not only confirms the species' presence in a new region but also emphasizes its ecological and taxonomic relevance, contributing to a more comprehensive understanding of this group.

This study extends the application of DNA barcoding for species delimitation within the genus *Campylomyza*, beyond the initial barcoding of individual species such as *C. flavipes* for subfamily relationship analysis within the Cecidomyiidae (Sikora et al. 2019). Comprehensive mitochondrial Cytochrome Oxidase subunit I (mtCOI) data is provided for all 16 documented species, encompassing seven that are newly described and five that are newly reported in Korea. The analyses of the Neighbor Joining (NJ) tree and genetic divergence have effectively dif-

ferentiated all species by their interspecific variations, with interspecific divergences noted to be between 6.18% and 15.28% (Suppl. material 1: table S3). The maximum intraspecific genetic distance (0.92%) was significantly smaller than the minimum interspecific one (6.18%). The NJ tree (Fig. 6) strongly supported the monophyly of each new species and the overall monophyly of the genus *Campylomyza*. Moreover, the species identifications are in agreement with the Automated Barcode Gap Discovery (ABGD) results, as depicted in Fig. 6.



**Figure 6.** Neighbor-joining (NJ) Kimura-2-parameter tree derived from the *COI* analysis of sixteen Korean *Campylomyza* species, with *Peromyia trifida* as the outgroup. Numbers at the nodes represent NJ bootstrap support values. The vertical purple color bar on the right represents results from the ABGD delimitation method.

The genus *Campylomyza* encompasses a diverse range of species occurring across different continents, including the Holarctic, Neotropical, Oriental, and Australasian/Oceanian regions (Gagné and Jaschhof 2021). *Campylomyza* are characterized by their small size, typically measuring around 1.0–1.8 mm and exhibit distinctive behaviors such as clustering and swarming during the mating season, which typically occurring in cooler weather such as April or November (Kanmiya and Yukawa 2020). Our study utilized Malaise traps to collect this aggregation and provide insights into their geographical distribution and species occurrence patterns. Notably, some species occur in large numbers in the *Campylomyza* population, but only a few individuals of some species can be identified. For example, *C. convexa, C. appendiculata*, and *C. furva* occurred collectively, but only a small number of individuals of *C. odae* and *C. angusta* were found to have occurred. In addition, our findings revealed instances of sympatric occurrence, where multiple species coexisted within the same sampling sites. In the National Endangered Species Restoration Center in Yeongyang, (Table 1, Suppl. material 1: table S1)

region, we observed up to eight species occurring together at a single location, highlighting the coexistence and potential ecological interactions among these species. Furthermore, our investigations unveiled cases of wide distribution for certain species. For instance, *C. abjecta* was found in Namyangju in Gyeonggi-do, as well as Yeongyang and Sangju in Gyeongsangbuk-do. *Campylomyza cornigera* sp. nov. was documented in Namyangju in Gyeonggi-do, Yeongyang and Pyeong-chang in Gangwon-do (Table 1, Suppl. material 1: table S1). These finding emphasize the complexity of species assemblages within the genus *Campylomyza* and shed light on their ecological dynamics. By studying the microhabitat preferences and geographic distributions, we contribute to the understanding of species diversity and their spatial patterns. Such knowledge is crucial for comprehensive biodiversity assessments and conservation efforts.

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# **Additional information**

# **Conflict of interest**

The authors have declared that no competing interests exist.

## **Ethical statement**

No ethical statement was reported.

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## Author contributions

Conceptualization: DH. Data curation: DH. Formal analysis: DH. Funding acquisition: YJB. Investigation: YJB, DH. Methodology: DH. Resources: YJB. Supervision: YJB. Validation: DH. Visualization: DH. Writing - original draft: DH. Writing - review and editing: DH, YJB.

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### Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

## References

- Chimeno C, Hausmann A, Schmidt S, Raupach MJ, Doczkal D, Baranov V, Hübner J, Höcherl A, Albrecht R, Jaschhof M, Haszprunar G, Hebert PD (2022) Peering into the Darkness: DNA Barcoding Reveals Surprisingly High Diversity of Unknown Species of Diptera (Insecta) in Germany. Insects 13(1): 82. https://doi.org/10.3390/insects13010082
- Edwards FW (1938a) A re-definition of the genus *Campylomyza* Meigen, with notes of Meigen's types (Diptera, Cecidomyiidae). Encyclopédie Entomologique, Série B. Mémoires et Notes. II. Diptera 9: 47–52.
- Edwards FW (1938b) On the British Lestremiinae, with notes on exotic species. 4. (Diptera, Cecidomyiidae). Proceedings of the Royal Entomological Society of London 7: 173–182. https://doi.org/10.1111/j.1365-3113.1938.tb01273.x
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3(5): 294–299.
- Funk DJ, Futuyama DJ, Orti G, Meyer A (1995) Mitochondrial DNA sequences and multiple data sets: a phylogenetic study of phytophagous beetles (Chrysomelidae: Ophraella). Molecular Biology and Evolution 12: 627–640. https://academic.oup. com/mbe/article/12/4/627/951590
- Gagné RJ, Jaschhof M (2021) A Catolog of the Cecidomyiidae (Diptera) of the World. Fifth Ed. Digital, 816 pp. https://www.ars.usda.gov/ARSUserFiles/80420580/Gagne\_ Jaschhof\_2021\_World\_Cat\_5th\_Ed.pdf
- Ham D, Jaschhof M, Bae YJ (2019) Twenty new records of mycophagous gall midges (Diptera: Cecidomyiidae) from Korea. Journal of Species Research 8(2): 238–246. https://doi.org/10.12651/JSR.2019.8.2.238
- Ham D, Jaschhof M, Bae YJ (2020) Mycophagous Gall Midges (Diptera: Cecidomyiidae) in Korea: Newly Recorded Species with Discussion on Four Years of Taxonomic Inventory. Animal Systematics, Evolution and Diversity 36(1): 60–77. https://doi. org/10.5635/ASED.2020.36.1.055
- Ham D, Jaschhof M, Bae YJ (2024) Taxonomic review of the genus *Campylomyza* Meigen (Diptera: Cecidomyiidae) in Korea with description of seven new species. In: Park JK, Lee YS (Eds) Threat to Insect Biodiversity by Humas & Threat to Human Health by Insects. 2024 Spring conference of KSAE & ESK (Korean Society of Applied Entomology & The Entomological Society of Korea), Cheongju (Korea), April 2024. KSAE & ESK, Suwon-Seoul, 161 pp. https://entomology.or.kr/down/pdf\_202404/file.pdf
- Han HY (2021) Diptera. In: Check List of Insects from Korea. Korean Society of Applied Entomology & The Entomological Society of Korea. Paper and Pencil, Daegu, 390 pp.
- Hebert PDN, Ratnasingham S, Zakharov EV, Telfer AC, Levesque-Beaudin V, Milton MA, Pedersen S, Jannetta P, deWaard JR (2016) Counting animal species with DNA barcodes: Canadian insects. Philosophical Transactions of the Royal Society B: Biological Sciences 371(1702): 20150333. https://doi.org/10.1098/rstb.2015.0333
- Jaschhof M (1998a) Revision der "Lestremiinae" (Diptera, Cecidomyiidae) der Holarktis. Studia Dipterologica Supplement 4: 1–552.

- Jaschhof M (1998b) Neue Gallmücken-Arten aus der Paläarktis (Diptera, Cecidomyiidae, Lestremiinae). 3. Beitrag: Gattungen *Campylomyza*, *Bryomyia*, *Heterogenella*, *Xylopriona* und *Polyardis*. Studia Dipterologica 4: 259–274.
- Jaschhof M (2009) *In* Jaschhof M, Jaschhof C. The wood midges (Diptera: Cecidomyiidae: Lestremiinae) of Fennoscandia and Denmark. Studia Dipterological Supplement 18 (2009): 1–333.
- Jaschhof M (2015) Morphological re-examination reveals that *Campylomyza* serrata Jaschhof, 1998 is a complex of five cryptic species (Diptera: Cecidomyiidae, Micromyinae). Beiträge zur Entomologie (Contributions to Entomology) 65(2): 373–381. https://doi.org/10.21248/contrib.entomol.65.2.373-381
- Jaschhof M, Fitzgerald SJ (2016) *Trichoceromyia oregonensis* gen. et. spec. nov., a third Catotrichinae (Diptera: Cecidomyiidae) from the Nearctic Region. Studia Dipterologica 22: 59–66.
- Jaschhof M, Jaschhof C (2009) The wood midges (Diptera: Cecidomyiidae: Lestremiinae) of Fennoscandia and Denmark. Studia Dipterologica Supplement 18: 1–333.
- Jaschhof M, Jaschhof C (2013) The Porricondylinae (Diptera: Cecidomyiidae) of Sweden, with notes on extralimital species. Studia Dipterologica Supplement 20: 1–392.
- Jaschhof M, Jaschhof C (2017) Mycophagous gall midges (Diptera, Cecidomyiidae: Lestremiinae, Micromyinae, Winnertziinae, Porricondylinae): first records in Sweden and descriptions of closely related new species from elsewhere. Zootaxa 4226(4): 546–570. https://doi.org/10.11646/zootaxa.4226.4.6
- Jaschhof M, Jaschhof C (2021) Mycophagous gall midges (Diptera: Cecidomyiidae excl. Cecidomyiinae) in Sweden: status report after 15 years of taxonomic inventory, annotated taxonomic checklist, and description of *Campylomyia alstromi* sp. nov. Entomologisk Tidskrift 142: 105–184. http://www.et-online.nu/index.php/contents/article/view/84
- Kang JH, Ham D, Park SH, Hwang JM, Park SJ, Baek MJ, Bae YJ (2023) Population genetic structure of a recent insect invasion: a gall midge, *Asynapta groverae* (Diptera: Cecidomyiidae) in South Korea since the first outbreak in 2008. Scientific Reports 13(1): 2812. https://doi.org/10.1038/s41598-023-29782-8
- Kanmiya K (1985) Record of courtship sound in a phorid species, *Puliciphora tokyoensis* Kinoshita, with notes on its acoustic properties. Acta Dipterologica 13: 1–7.
- Kanmiya K (1996) Mating behavior of *Tinearia alternata* (Say), and acoustic signals by wing fanning (Diptera, Psychodidae). Makunagi/Acta Dipterologica 19: 40–49. [in Japanese with English summary]
- Kanmiya K (1999) Behavior, Physiology and Chemical Ecology. In: Hidaka T, Matsumoto Y, editors. Acoustic communication. University of Tokyo Press, Japan, 495–509. [in Japanese]
- Kanmiya K, Yukawa J (2020) Observation on swarming and mating behavior of Campylomyza flavipes Meigen (Diptera: Cecidomyiidae: Micromyiinae). まくなぎ(Acta dipterology) 31: 4–9.
- Kimura M (1980) A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution 16(2): 111–120. https://doi.org/10.1007/BF01731581
- Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. Molecular Biology and Evolution 35(6): 1547–1549. https://doi.org/10.1093/molbev/msy096
- Mamaev BM (1963) [Gall midges of the USSR. 2. The tribe Micromyini (Diptera, Itonididae).] Entomologicheskoe Obozrenie 42: 436–454. Translated in Entomological Review (1964) 42(2): 239–247.

- Mamaev BM (1998) [New species of gall midges of the subfamily Lestremiinae (Diptera, Cecidomyiidae).] All-Russian Institute of Continuous Education in Forestry, Pushkino, Moscow Region 10: 1–10.
- Mamaev BM, Krivosheina NP (1993) The Larvae of the Gall Midges (Diptera, Cecidomyiidae): Comparative Morphology, Biology, Keys. A.A. Balkema, Rotterdam, The Netherlands, Brookfield, Vermon, ix + 293 pp.
- Meigen JW (1818) Systematische Beschreibung der bekannten europäischen zweiflügeligen Insekten. Vol. 1, xxxvi + 333 pp. [pls 1–11] https://doi.org/10.5962/bhl. title.12464
- Oh JH, Kim S, Lee S (2022) DNA barcodes reveal population-dependent cryptic diversity and various cases of sympatry of Korean leptonetid spiders (Araneae: Leptonetidae). Scientific Reports 12(1): 15528. https://www.nature.com/articles/s41598-022-18666-y
- Puillandre N, Lambert A, Brouillet S, Achaz G (2012) ABGD, automatic barcode gap discovery for primary species delimitation. Molecular Ecology 21: 1864–1877. https:// doi.org/10.1111/j.1365-294X.2011.05239.x
- Sikora T, Jaschhof M, Mantič M, Kaspřák D, ševčík J (2019) Considerable congruence, enlightening conflict: molecular analysis largely supports morphology-based hypotheses on Cecidomyiidae (Diptera) phylogeny. Zoological Journal of the Linnean Society 185(1): 98–110. https://doi.org/10.1093/zoolinnean/zly029
- Westwood JO (1840) An Introduction to the Modern Classification of Insects. Synopsis of the genera of British Insects. London 2: 126–127. https://www.biodiversitylibrary. org/item/45812#page/7/mode/1up
- Yukawa J (2005) Biology and ecology of gall-inducing Cecidomyiidae (Diptera). Biology, Ecology, and Evolution of Gall-Inducing Arthropods 1: 273–304.

## Supplementary material 1

#### Additional information

Authors: Daseul Ham, Yeon Jae Bae

- Data type: xlsx
- Explanation note: **table S1**. Detailed location data for collected *Campylomyza* species in Korea and species occurrence by region; **table S2**. Accession numbers of *Campylomyza* species deposited in NIBR and NCBI for *COI* sequence data; **table S3**. The percentage of genetic divergence between sequences was estimated, and the number of base differences per site between sequences is presented (Cells with values below 3% are shaded in gray; important values are highlighted in red). Standard errors, expressed as percentages, are provided above the diagonal and were calculated using a bootstrap procedure with 1,000 replicates. Positions with gaps and missing data were excluded from the analysis (complete delete option).
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**Research Article** 

# Mountainous millipedes in Vietnam. III. Two new dragon millipedes from limestone mountains in northern Vietnam (Polydesmida, Paradoxosomatidae, *Hylomus*), with an identification key to Vietnamese *Hylomus* species

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## Abstract

Two new species of the dragon millipede genus *Hylomus* Cook & Loomis, 1924 are described from mountainous areas in northern Vietnam, namely *Hylomus piccolo* **sp. nov.** and *Hylomus borealis* **sp. nov.** The COI barcodes are provided for these species, and an identification key is presented to all Vietnamese *Hylomus* species.

Key words: Biodiversity, COI barcode, mountainous fauna, Southeast Asia, taxonomy

# Introduction

The term "dragon millipedes" refers to species from seven genera: *Desmoxytes* Chamberlin, 1923; *Hylomus* Cook & Loomis, 1924; *Gigaxytes* Srisonchai, Enghoff & Panha, 2018; *Nagaxytes* Srisonchai, Enghoff & Panha, 2018; *Spinaxytes* Srisonchai, Enghoff & Panha, 2018; *Burmaxytes* Srisonchai, Lin & Panha, 2020 and *Siamaxytes* Srisonchai & Panha, 2024 (Srisonchai et al. 2018a, 2018b, 2018c, 2018d, 2020, 2024). While *Burmaxytes* is currently exclusively known in Myanmar, four of these genera – *Gigaxytes*, *Nagaxytes*, *Spinaxytes*, and *Siamaxytes* – are endemic to Thailand; and *Desmoxytes* is known from both Thailand and Malaysia (Srisonchai et al. 2018a). The remaining genus, *Hylomus*, comprises 38 species distributed in southern China (19 species), Vietnam (16), Laos (3), and Thailand (1) (Srisonchai et al. 2018a, Golovatch 2019, Nguyen et al. 2019).

In Vietnam, *Hylomus* is the only known group of dragon millipedes, with 16 species described to date, including three considered troglobiotic (Attems 1938, 1953; Golovatch 2019; Nguyen et al. 2019, 2021). All species, except the post 2018 described species, were originally placed in *Desmoxytes* but have recently been reallocated under *Hylomus* (Srisonchai et al. 2018a). The Vietnamese species are listed in alphabetical order below.



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- 1. Hylomus asper (Attems, 1937) from Da Nang and Ninh Thuan provinces.
- 2. *Hylomus cattienensis* (Nguyen, Golovatch & Anichkin, 2005) from Cat Tien National Park, Dong Nai Province.
- 3. Hylomus cervarius (Attems, 1953) from Sa Pa, Lao Cai Province.
- Hylomus enghoffi (Nguyen, Golovatch & Anichkin, 2005) from Phong Nha
  Ke Bang National Park, Dong Nai Province.
- 5. *Hylomus grandis* (Golovatch, VandenSpiegel & Semenyuk, 2016) from Kon Chu Rang Nature Reserve, Gia Lai Province.
- 6. *Hylomus hostilis* (Golovatch & Enghoff, 1994) from Tam Dao National Park, Vinh Phuc Province.
- 7. *Hylomus namek* Nguyen, Nguyen, Nguyen & Phung, 2019 from Duc Xuan commune, Ha Giang Province.
- 8. *Hylomus pilosus* (Attems, 1937) from Cat Tien National Park, Dong Nai Province and Hon Ba Mountain, Khanh Hoa Province.
- 9. *Hylomus propinquus* Golovatch, 2019, troglobiotic, from Ba Be National Park, Bac Kan Province.
- 10. *Hylomus proximus* (Nguyen, Golovatch & Anichkin, 2005) from Van Ban commune, Lao Cai Province.
- 11. *Hylomus saiyans* Nguyen, Nguyen, Nguyen & Phung, 2019 from Cuc Phuong National Park, Ninh Binh Province and Tam Dao NP, Vinh Phuc Province.
- 12. *Hylomus solenophorus* Nguyen, Nguyen & Eguchi, 2021 from Hoang Lien National Park, Lao Cai Province.
- 13. *Hylomus songoku* Nguyen, Nguyen, Nguyen & Phung, 2019, troglobiotic, from Xuan Son National Park, Phu Tho Province.
- 14. *Hylomus specialis* (Nguyen, Golovatch & Anichkin, 2005) from Ngoc Linh Mountain, Kon Tum Province.
- 15. *Hylomus spectabilis* (Attems, 1937) from Ba Na Nui Chua National Park, Da Nang City.
- 16. *Hylomus srisonchai* Golovatch, 2019, troglobiotic, from Tra Linh District, Cao Bang Province.

This work is devoted to a better understanding of *Hylomus* diversity through the descriptions of two new species from limestone areas of northern Vietnam.

# Material and methods

Millipede specimens were collected from limestone areas in northern Vietnam during expeditions organized by the Institute of Ecology and Biological Resources (IEBR), Vietnam Academy of Science and Technology.

Morphological characters were investigated under an Olympus SZX16 stereomicroscope. Gonopods were dissected for morphological examination and photographed. Color images were taken at various focal planes using a Sony A6000 camera coupled to a SMZ800N Nikon stereomicroscope. UV images were taken using the aforementioned camera-microscope in combination with illumination from a Nichia Convoy UV flashlight. Images were then stacked using Helicon Focus version 7.0 and assembled in Adobe Photoshop CS6.

For the scanning electron microscope (SEM), gonopods were dissected from the body, dehydrated using a series of ethanol concentrations, 90%, 95%,

and 99%, for 24 hours, mounted on an aluminum stub, and then sputter coated with gold. SEM images were taken using the Prisma E system (ThermoFisher Scientific) at IEBR.

Total genomic DNA was extracted from the legs of midbody rings using a Qiagen DNeasy Blood and Tissue Kit. A 680 base pairs fragment of the mitochondrial gene, cytochrome c oxidase subunit I (COI), was amplified using a pair of universal primers, LCO1490 and HCO2198 (Folmer et al. 1994). Polymerase chain reaction (PCR) conditions for amplification of the COI gene follow those of Nguyen et al. (2017) as follows: an initial denaturation at 95 °C for 2 min followed by 36 cycles of 95 °C for 20 s, 42 °C for 45 s and 72 °C for 1 min, and a final extension at 72 °C for 5 min. The successfully amplified PCR products were submitted to GenLab (Vietnam) for purification and sequencing. COI sequences were checked and confirmed using BLASTN 2.6.0+ search (Zhang et al. 2000) and registered into GenBank with accession numbers.

Holotypes and paratypes are deposited in the myriapod collection, Institute of Ecology and Biological Resources (IEBR).

## Abbreviation

IEBR-Myr Institute of Ecology and Biological Resources, Myriapod collection.

## Results

#### Taxonomy

Class Diplopoda de Blainville in Gervais, 1844 Order Polydesmida Pocock, 1887 Family Paradoxosomatidae Daday, 1889 Genus *Hylomus* Cook & Loomis, 1924

#### Hylomus piccolo sp. nov.

https://zoobank.org/7B27F484-2BBB-47DF-81E4-86A671ED853E Figs 1-4

**Material examined.** *Holotype.* VIETNAM • 1 male; Cao Bang Province, Pia Oac -Pia Den National Park; 22.5943°N, 105.8846°E; 1200 m a.s.l.; 9 May 2021; Anh D. Nguyen leg.; bushes; IEBR-Myr 904H. *Paratypes.* VIETNAM • 10 males, 5 females; same data as for holotype; EBR-Myr 904P • 1 male, 1 female; same data as for holotype; IEBR-Myr 901.

**Diagnosis.** The species can be discriminated from the congeners by the presence of long spiniform paraterga, midbody metaterga with only two rows of 1+1 small setiferous spines in the middle and 2+2 longer setiferous spines near posterior margin; male femora 6 with a large tubercle ventrally; sternite 5 with a large, sparsely setose, bifid, trapeziform lamina between male coxae 4; epiproct without conspicuous setiferous knobs near tip; gonopod lamina lateralis broadly rounded, partly folded to sheathe distal part of solenomere; gonopod lamina medialis with a small rounded lobe at middle.

The new species is similar to *Hylomus namek* Nguyen et al., 2019 but differs from this species by the following characters: the ventral side of male femora



Figure 1. *Hylomus piccolo* sp. nov., holotype (IEBR-Myr 904H) **A**, **B** anterior-most body part, lateral view (**A**), ventral view (**B**) **C** head, anterior view **D** body rings 8–10, dorsal view. Scale bars: 1 mm.

6 with a big, robust tubercle in the middle (vs. femora 6 and 7 with large tubercles); longer spiniform paraterga; and gonopod lamina medialis with a small rounded lobe in the middle (vs. without processes).

**Etymology.** The name refers to "*piccolo*", a main character of the Japanese manga "Dragon balls" by Toriyama Akira (Japan). Noun in apposition.

**Description.** Length c. 11.6–12.8 mm (male), 13.9–15.2 mm (female); width of midbody pro- and metazona (distance between two paratergal tips) 0.6–0.8 mm (male), 1.12–1.25 mm (female) and 3.1–3.3 mm (male), 3.4–3.6 mm (female), respectively. Holotype length c. 11.8 mm, width of midbody pro- and metazona 0.74 mm and 3.2 mm, respectively.

**Coloration:** Generally darkish-red to darkish-brown except paraterga, sterna, legs whitish-yellow; distal part of main branch pinkish.



**Figure 2**. *Hylomus piccolo* sp. nov., holotype (IEBR-Myr 904H) **A** body rings 8–10, lateral view **B** body ring 10, dorsal view (under UV light) **C** body rings 8–10, ventral view **D** posterior-most body part, dorsal view. Scale bars: 1 mm.

*Head* (Fig. 1A–C): Clypeolabral region densely setose, vertex sparsely setose. Epicranial suture distinct, dividing frons into two equal parts; with setae along the suture. Antenna slender, extremely long, reaching back to body ring 7 if stretched along the body axis; antennomere 1 < 7 < 6 < 2 < 3 = 4 = 5 in length.

**Collum** (Fig. 1C): Slightly narrower than head; surface dull, coarsely microgranulate; with two rows of spines: 3+3 spines in anterior row and 2+2 spines in posterior row. Paraterga of collum well developed, spiniform; directed dorsad; highly elevated above dorsal surface; with two conspicuous teeth on anterior side.

**Body rings:** Ring 3 < 4 < 2 = 5-16 in width, thereafter gradually tapering towards telson. Prozona finely shagreened; metazona and pleura with microgranulations. Transverse sulcus present, but inconspicuous on metaterga 5-18. Axial line missing. Metaterga with two rows of 1+1 smaller setiferous spines in middle and 2+2 longer setiferous spines near posterior margin (Fig. 2B). Suture between pro- and metazona broad, very shallow. Pleurosternal carinae present as a complete keel on body rings 2-3, then missing on subsequent body rings.

**Paraterga** (Figs 1, 2): Very well developed; directed dorsad; long and spiniform with a large branch and 2–3 tiny teeth on anterior side (2 on poreless body rings and 3 on pore-bearing rings) and with 1 larger spine on posterior side. Paratergum on ring 19 directed caudad. Ozopore located between the second tooth and main branch of paraterga, visible in dorsal view.

**Telson** (Fig. 3A, B): Epiproct without conspicuous setiferous knobs near tip, but broadly truncated; tip with four spinnerets; lateral tubercles well developed





(Fig. 3A). Hypoproct subtrapeziform, with two distolateral, completely separated, setiferous knobs (Fig. 3B).

**Legs:** Extremely long, slender and thin, c. 1.8–2.0 times as long as midbody height. Prefemora not swollen. Male femora 6 each ventrally with a large, robust tubercle in middle (Figs 1A, 3C).

**Sterna:** With distinct cross-impressions, no modification – except a large, sparsely setose, bifid, trapeziform lamina between male coxae 4 (Figs 1A, 3D).

**Gonopod** (Fig. 4): Suberect. Coxite (**co**) cylindrical, larger than femorite, sparsely setose distodorsally. Prefemorite (**pref**) densely setose, equal to femorite as well. Femorite (**fe**) slightly enlarged distad (from ventral view); without a demarcation with postfemoral region. Postfemoral region inconspicuous. Solenophore (**sph**) well developed; lamina lateralis (**II**) broadly rounded, partly folded to sheathe distal part of solenomere; lamina medialis (**Im**) with a small rounded lobe at about midway. Seminal groove running entirely on mesal side, then entering a flagelliform solenomere (**sl**), solenomere partly sheathed by solenophore. Tip of solenophore rounded.

**DNA barcoding.** (Appendix 1) A fragment of the COI gene is accessioned at NCBI GenBank with the following accession number PQ676351. The new species exhibits a COI gene similarity of 86.22% and 86.57% (OR765910 and MG669370, respectively) identity with *Hylomus cervarius* (Attems, 1953).


Figure 4. *Hylomus piccolo* sp. nov., holotype (IEBR-Myr 904H), SEM A–D left gonopod, lateral view (A), dorsal view (B), ventral view (C), mesal view (D) E–H distal part of left gonopod, lateral view (E), dorsal view (F), ventral view (G), mesal view (H). Abbreviations: co = coxite; pref = prefemorite; fe = femorite; ca = canula; Im = lamina medialis; II = lamina lateralis; sI = solenomere. Scale bars: 200 µm (A–D); 100 µm (E–G); 50 µm (H).

#### Hylomus borealis sp. nov.

https://zoobank.org/0459DB77-C98E-4DC6-B79F-E13950DAED19 Figs 5-7

**Material examined.** *Holotype*. VIETNAM • 1 male; Cao Bang Province, Pia Oac - Pia Den National Park, on the way to Hang Ong; 22.5540°N, 105.8622°E; 850m a.s.l.; 8 May 2021; Anh D. Nguyen leg.; bushes; IEBR-Myr 908H. *Paratypes*. VIETNAM • 2 females; same data as for holotype; IEBR-Myr 908P • 2 females; same data as for holotype; IEBR-Myr 908P • 2 females; same data as for holotype; IEBR-Myr 908P • 2 females; same data as for holotype; IEBR-Myr 851 • 1 female; same data as for sample IEBR-Myr 851; IEBR-Myr 854.

**Diagnosis.** The species can be discriminated from the congeners by the presence of spiniform paraterga; metaterga densely covered with microgranulations; midbody metaterga with two rows of setiferous spines: 2+2 in anterior row and 2+2 near posterior margin, the anterior row hardly seen, the posterior row more distinct; male femora 6 each with a large tubercle ventrally; sternite 5 with a large, sparsely setose, bifid, trapeziform lamina between male coxae 4; epiproct with several evident setiferous knobs near tip; gonopod solenophore partly folded to sheathe distal part of solenomere; tip of solenophore consisting of seven overlapping laminae.



**Figure 5.** *Hylomus borealis* sp. nov., holotype (IEBR-Myr 908H) **A** anterior-most body part, lateral view **B** frons and collum, anterior view (under UV light) **C** body rings 8–12, dorsal view **D** body rings 8–10, lateral view. Scale bars: 1 mm.

The new species is similar to *H. proximus* in body size and shape, but the two species are distinguished by the number of metatergal posterior spines (2+2 vs 3+3), male femoral modifications (femur 6 vs femora 5 & 6), and go-nopod conformation. The new species has a well-developed gonopod solenophore (sph); a broadly rounded lamina medialis, partly folded to sheathe distal part of solenomere; and gonopod tip consisting of seven overlapping laminae while *H. proximus* has a gonopod femorite that is subequal to the postfemoral region in length; both solenophore and solenomere long; and a serrated solenophore tip.

*Hylomus borealis* sp. nov. is also similar to *H. jeekeli* (Golovatch & Enghoff, 1994) from northern Thailand in terms of general body and gonopod shape. However, the new species can be distinguished from it by the combination of these characters: smaller in size with 10.4 mm in males and 12.3–13.4 mm in females (vs 15–16 mm in males and 18–20 mm in females); metaterga with 2+2 spines in posterior rows (vs 3+3 spines); modification in only femur 6 (vs femora 6 and 7); tip of solenophore consisting of seven overlapping laminae and not serrate (vs serrated solenophore).

**Etymology.** An adjective epithet "*borealis*" refers to the northern-most province (Cao Bang) of Vietnam, the type locality.

**Description.** Holotype length 10.4 mm, width of mid pro- and metazona 0.6 mm and 1.8 mm (distance between two paratergal tips), respectively.



**Figure 6**. *Hylomus borealis* sp. nov., holotype (IEBR-Myr 908H) **A** body rings 8–10, ventral view **B** body rings 8–10, dorsal view (under UV light) **C** telson, dorsal view (under UV light) **D** sternum 5, subposterior view. Scale bars: 1 mm.

Female length 12.3–13.4 mm, width of mid pro- and metazona 0.9–1.0 mm and 1.7–1.8 mm, respectively.

**Coloration:** Generally dark to castaneous brown except paratergal bases, sterna, leg coxae and prefemora whitish-yellow.

*Head* (Fig. 5A, B): Clypeolabral region densely setose, vertex sparsely setose. Epicranial suture distinct, dividing frons into two equal parts; with setae along suture. Antenna slender, extremely long, reaching to body ring 5 if stretched along the body axis; antennomere 1 < 7 < 6 < 2 < 3 = 4 = 5 in length.

**Collum** (Fig. 5B): Subequal to head in width; surface dull, coarsely and densely microgranulate, with three rows of spines: 3+3 spines in anterior row, 1+1 spines in intermediate row, and 2+2 spines in posterior row; all spines equal in size. Paratergum well developed; directed dorsad; highly elevated above dorsal surface; with two conspicuous teeth on anterior side.

**Body rings:** Rings 3 < 4 < 2 = 5-16 in width, thereafter gradually tapering towards telson. Prozona finely shagreened; metazona and pleura with microgranulations. Transverse sulcus present, but inconspicuous on metaterga 5-18. Axial line missing. Metaterga with two rows of setiferous spines: 2+2 spines in anterior row and 2+2 spines near posterior margin (Figs 5C, 6B), the anterior row hardly visible, the posterior row more distinct (Fig. 6B). Suture between pro- and metazona broad, very shallow. Pleurosternal carinae present as a complete keel on body rings 2–3, then missing on subsequent body rings.



Figure 7. *Hylomus borealis* sp. nov., holotype (IEBR-Myr 908H), SEM A-D left gonopod, lateral view (A), ventral view (B), dorsal view (C), mesal view (D) E-G distal part of left gonopod, ventral view (E), dorsal view (F) G tip of left gonopod, ventral view. Abbreviations: **co** = coxite; **pref** = prefemorite; **fe** = femorite; **ca** = canula; **Im** = lamina medialis; **II** = lamina lateralis; **sI** = solenomere. Scale bars: 200 µm (A-D); 100 µm (E), 50 µm (F), 30 µm (G).

**Paraterga** (Fig. 5): Very well developed; directed laterodorsad; antler-shaped with a large branch and 2 small teeth on anterior side and 1 smaller spine on posterior side. Ozopore located between the first tooth and main branch of paraterga, visible in dorsal view.

**Telson** (Fig. 6C): Epiproct with several evident setiferous knobs near tip; tip with four spinnerets; lateral tubercles well developed. Hypoproct sub-trapeziform, with two distolateral, completely separated, setiferous knobs.

*Legs:* Extremely long, slender and thin, c. 1.5-1.6 times as long as midbody height. Prefemora not swollen. Male femora 6 each ventrally with a large, robust tubercle in middle.

**Sterna:** with distinct cross-impression, no modification – except a large, sparsely setose, trapeziform lamina carrying two distal, separated lobes between male coxae 4 (Fig. 6D).

**Gonopod** (Fig. 7): Suberect. Coxite (**co**) cylindrical, much shorter than femorite, sparsely setose distodorsally. Prefemorite (**pref**) densely setose, shorter than femorite as well. Femorite (**fe**) slightly enlarged distad, without a demarcation with postfemoral region. Postfemoral region slightly twisted mesad. Solenophore (**sph**) well developed; lamina medialis (**Im**) broadly rounded, partly folded to sheathe distal part of solenomere, lamina lateralis (**II**) well developed. Seminal groove running entirely on mesal side, then entering a flagelliform solenomere (sl) which is partly sheathed by solenophore. Tip of gonopod consisting of seven overlapping laminae (Fig. 7G).

**DNA barcoding.** (Appendix 1) A fragment of the COI gene is accessioned at NCBI GenBank with the following accession number PQ676352. The new species exhibits a COI gene similarity of 85.29% identity with *Hylomus proximus* Nguyen, Golovatch & Anichkin, 2005 (MG669371) and 83.11% identity with *Desmoxytes takensis* Srisonchai, Enghoff, Likhitrakarn & Panha, 2016 (OR765894).

# Key to Hylomus species in Vietnam

(based on male characters)

1	Body unpigmented. Troglobiotic2
-	Body pigmented. Non-troglobiotic4
2	Paraterga well developed, spiniform. Metaterga with 56 + 56 setiferous
	spines in posterior row of midbody ring. Lamina lateralis of gonopod sole-
	nophore with dense setal region
_	Paraterga small, poorly developed. Metaterga with less than 4 + 4 setifer-
	ous knobs in posterior row of midbody ring. Lamina lateralis of gonopod
	solenophore without dense setal region3
3	Metaterga with 2 + 2 setiferous knobs in posterior row of midbody ring.
	Gonopod lamina lateralis with a small, but evident, slender, slightly twist-
	ed, apicomesal process, about half as long as a slender, distally conspic-
	uously rugged and denticulate lamina medialis
-	Metaterga with 3-4 + 3-4 setiferous knobs in posterior row of midbody
	ring. Gonopod lamina lateralis a simple rounded lobe, while lamina medi-
	alis deeply split into a long distal spine and a strongly bifid basal ribbon,
	both slightly spinulate H. propinquus
4	Paraterga wing-shaped
-	Paraterga antler- or spine-shaped5
5	Paraterga antler-shaped6
-	Paraterga spine-shaped15
6	Epiproct without conspicuous setiferous knobs near tip7
-	Epiproct with several evident setiferous knobs near tip12
7	Metaterga smooth, more or less shining. Male femora 5–9 unmodified
	H. asper
_	Metaterga rough, dull, granular. Male femora 5/6/7/9 modified, inflated8
8	Metaterga with 3 + 3 setiferous spines in posterior row. Male femora 6,
	/ and 9 humped ventrally. Fifth sternum with a pair of tubercles between
	male coxae 4
_	Metaterga with 2 + 2 setiferous spines in posterior row. Male femora 6
	and 7, sometimes temur 5 modified, each with a large nump on ventral
	side. Fifth sternum with either a rectangular process or a bifid, trapeziform
0	amina between male coxae 4
9	Body light or darkish-brown. Fifth sternum with a bifid, trapeziform lamina
	Detween male coxae 4
_	body requisit or prinkish. Firth stemum with four round tubercles on a
	prominent, elevated, rectangular lamina between male coxae 4
	н. епдпоті

10	Only male femur 6 with a big, robust ventral tubercle in middle
-	Male femora 6, 7, sometimes 5 humped ventrally11
11	Male femora 6, 7 humped ventrally. Tip of solenophore lobuliform, broadly
	rounded
-	Male femora 6, 7, sometimes 5, humped ventrally. Tip of solenophore
	acute
12	Metaterga with at least 3 + 3 spines in posterior row13
-	Metaterga with only 1 + 1 setae in posterior row
13	Body pink to red. Metaterga with numerous microsetae, and 4 + 4 spines
	in posterior row
_	Body dark to castaneous brown. Metaterga with microganulations, and
	with less 4+4 spines in posterior row14
14	Metaterga with 3 + 3 spines in posterior row. Male femora 5 and 6 with a
	large ventral tubercle
-	Metaterga with 2 + 2 spines in posterior row. Male femur 6 with a large
	ventral hump
15	Metaterga with 1 + 1 spines in posterior row. Gonopod subfalcate, femo-
	rite slightly curved; solenophore long H. specialis
-	Metaterga with 2 + 2 tubercles/spines in posterior row. Gonopod falcate;
	solenophore short, pointed terminally16
16	Fifth sternum with two setiferous tubercles between male coxae 4, clearly
	separated. Antenna long and slender
-	Fifth sternum with a bifid setiferous trapeziform lamina between male
	coxae 4. Antenna short and stout

### Discussion

The genus Hylomus is widely distributed from southern China to northern Thailand, all parts of Laos, and all regions of Vietnam, with Srisonchai et al. (2024) suggesting that the Tenasserim mountain range, located between Thailand and Myanmar, may serve as the center of origin for dragon millipedes, including another six genera. While Hylomus appears to be primarily confined to the north and south Annamite Mountain ranges as indicated by Srisonchai et al. (2024), a comprehensive phylogenetic analysis of the genus remains lacking. Preliminary studies, such as those by Nguyen et al. (2019), which used a short fragment of the 16S rRNA gene, and Srisonchai et al. (2024), which conducted a broader phylogenetic assessment of dragon millipedes, have yielded different results: Hylomus was found to be monophyletic in Nguyen et al. (2019) but non-monophyletic in Srisonchai et al. (2024). Additionally, most Hylomus species exhibit a diverse range of paratergal morphologies, including winglike (H. spectabilis), spinelike (H. hostilis), subspiniform (H. piccolo), and antlerlike (H. pilosus) forms, as categorized by Golovatch and Enghoff (1994) and Srisonchai et al. (2024). The evolutionary relationships and diversification of paratergal morphology within Hylomus remain unclear, highlighting the need for more comprehensive phylogenetic studies using additional gene markers.

With an area exceeding 60,000 km<sup>2</sup>, Vietnam is renowned for its rich karst ecosystem, and is heavily reliant on its limestone karst regions, known for their

extraordinary species diversity (Tuyet 2001). Composed primarily of calcium carbonate, these karsts have developed over millions of years, hosting a wide variety of plant and animal species. According to Tuyet (2001), the phylum Chordata alone includes 541 species across 80 families, 40 orders, and 5 classes, with several rare and endangered species. Recent discoveries of new millipede species, such as *Paracortina kyrang* (Nguyen et al., 2023), *Hyleoglomeris halang* (Kuroda et al., 2022), *Hyleoglomeris alba* (Kuroda et al., 2022), and *Pacidesmus tuachua* (Nguyen et al., 2024), in limestone caves further highlight the rich yet underexplored biodiversity of the region. Positioned at the center of diversity for *Hylomus*, Vietnam may contain many undiscovered species, awaiting identification through comprehensive surveys.

# Conclusion

The number of *Hylomus* species in Vietnam has increased to 16, with the addition of two new species, *H. piccolo* sp. nov. and *H. borealis* sp. nov., from limestone forests in northern Vietnam. More extensive surveys and additional DNA data are needed to fully clarify the diversity, biogeography and phylogenetics of the genus *Hylomus* in Vietnam and Southeast Asia.

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# Additional information

## **Conflict of interest**

The authors have declared that no competing interests exist.

## **Ethical statement**

No ethical statement was reported.

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#### Author contributions

Conceptualization: ADN. Data curation: TATN, ADN. Funding acquisition: TTTV, ADN. Investigation: ADN. Visualization: TATN. Writing – original draft: TTTV, ADN. Writing – review and editing: TTTV, TATN, ADN.

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#### Data availability

All of the data that support the findings of this study are available in the main text.

## References

- Attems C (1938) Die von Dr. C. Dawydoff in französisch Indochina gesammelten Myriopoden. Mémoires du Muséum national d'histoire naturelle, N. S. 6: 187–353.
- Attems C (1953) Myriopoden von Indochina. Expedition von Dr. C. Dawydoff (1938– 1939). Mémoires du Muséum national d'Histoire naturelle, N. S., série A 5: 133–230.
- Cook OF, Loomis HF (1924) A new family of spined millipeds from Central China. Journal of the Washington Academy of Sciences 14(5): 103–108. https://www.biodiversitylibrary.org/partpdf/50532
- Daday J (1889) Myriopoda Regni Hungariae. e commisione regiae societatis Hungaricae scientiarum naturalium. Myriopoda Regni Hungariae: 1–125.
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3: 294–299.
- Golovatch SI (2019) On several new or poorly-known Oriental Paradoxosomatidae (Diplopoda: Polydesmida), XXVII. Arthropoda Selecta 28: 459–478. https://doi. org/10.15298/arthsel.28.4.01
- Golovatch SI, Enghoff H (1994) Review of the dragon millipede, genus *Desmoxytes* Chamberlin, 1923 (Diplopoda, Polydesmida, Paradoxosomatidae). Steenstrupia 20(2): 1–71.
- Kuroda M, Eguchi K, Oguri E, Nguyen AD (2022) Two new cave Hyleoglomeris species (Glomerida, Glomeridae) from northern Vietnam. ZooKeys 1108: 161–174. https:// doi.org/10.3897/zookeys.1108.85423
- Nguyen AD, Sierwald P (2019) On the paradoxosomatid collection in the field museum of natural history: Dragon millipedes from Laos (Polydesmida: Paradoxosomatidae: *Hylomus*). Raffles Bulletin of Zoology 67: 119–128. https://doi.org/10.26107/RBZ-2019-0009
- Nguyen DA, Golovatch SI, Anichkin AE (2005) The dragon millipedes in Vietnam (Polydesmida: Paradoxosomatidae, genus *Desmoxytes* Chamberlin, 1923). Arthropoda Selecta 14(3): 251–257.
- Nguyen AD, Korsós Z, Jang K-H, Hwang U-W (2017) A revision and phylogenetic analysis of the millipede genus *Oxidus* Cook, 1911 (Polydesmida, Paradoxosomatidae). European Journal of Taxonomy 293: 1–22. https://doi.org/10.5852/ejt.2017.293
- Nguyen AD, Nguyen M-H, Nguyen T-AT, Phung H-LT (2019) Review of dragon millipedes (Diplopoda, Polydesmida, Paradoxosomatidae) in the fauna of Vietnam, with descriptions of three new species. Zoological Studies 58(14): 1–31. https://doi.org/10.6620/ ZS.2019.58-14
- Nguyen AD, Nguyen DD, Eguchi K (2021) Mountainous millipedes in Vietnam. I. Two new species of the family Paradoxosomatidae from Mount Fansipan (Diplopoda, Polydesmida). ZooKeys 1032: 1–15. https://doi.org/10.3897/zookeys.1032.64917

- Nguyen AD, Stoev P, Nguyen LTP, Vu TT (2023) A new species of *Paracortina* from a Vietnamese cave, with remarkable secondary sexual characters in males (Callipodida, Paracortinidae). ZooKeys 1149: 181–195. https://doi.org/10.3897/zookeys.1149.99651
- Nguyen AD, Vu TTT, Eguchi K (2024) The millipede family Polydesmidae Leach, 1816 (Diplopoda, Polydesmida) from Vietnam, with a description of a new cavernicolous species. ZooKeys 1190: 259–280. https://doi.org/10.3897/zookeys.1190.114958
- Pocock RI (1887) On the classification of the Diplopoda. The Annals and Magazine of Natural History, including Zoology. Botany and Geology, ser. 5, 20(118): 283–295. https://doi.org/10.1080/00222938709460057
- Srisonchai R, Enghoff H, Likhitrakarn N, Panha S (2016) Four colorful new species of dragon millipedes, genus *Desmoxytes* Chamberlin, 1923, from northern Thailand (Diplopoda: Polydesmida: Paradoxosomatidae). Zootaxa. 4170(1): 93–113. https:// doi.org/10.11646/zootaxa.4170.1.4
- Srisonchai R, Enghoff H, Likhitrakarn N, Panha S (2018a) A revision of dragon millipedes I: genus *Desmoxytes* Chamberlin, 1923, with the description of eight new species (Diplopoda, Polydesmida, Paradoxosomatidae). ZooKeys 761: 1–177. https://doi. org/10.3897/zookeys.761.24214
- Srisonchai R, Enghoff H, Likhitrakarn N, Panha S (2018b) A revision of dragon millipedes II: the new genus *Nagaxytes* gen. nov., with the description of three new species (Diplopoda, Polydesmida, Paradoxosomatidae). European Journal of Taxonomy 462: 1–44. https://doi.org/10.5852/ejt.2018.462
- Srisonchai R, Enghoff H, Likhitrakarn N, Panha S (2018c) A revision of dragon millipedes III: the new genus *Gigaxytes* gen. nov., with the description of three new species (Diplopoda, Polydesmida, Paradoxosomatidae). European Journal of Taxonomy 463: 1–43. https://doi.org/10.5852/ejt.2018.463
- Srisonchai R, Enghoff H, Likhitrakarn N, Panha S (2018d) A revision of dragon millipedes IV: the new genus *Spinaxytes*, with the description of nine new species (Diplopoda, Polydesmida, Paradoxosomatidae). ZooKeys 797: 19–69. https://doi.org/10.3897/ zookeys.797.29510
- Srisonchai R, Lin A, Panha S (2020) A revision of dragon millipedes. V. The new genus *Burmaxytes* for two new species from Myanmar (Diplopoda: Polydesmida: Paradoxosomatidae). Raffles Bulletin of Zoology 35: 88–100.
- Srisonchai R, Enghoff H, Likhitrakarn N, Jeratthitikul E, Jirapatrasilp P, Panha S, Sutcharit C (2024) Molecular phylogeny of dragon millipedes (Diplopoda: Polydesmida: Paradoxosomatidae) from mainland South-East Asia, with description of a new genus and species. Zoological Journal of the Linnean Society 202: 1–33. https://doi. org/10.1093/zoolinnean/zlad164
- Tuyet D (2001) Characteristics of Karst Ecosystems of Vietnam and Their Vulnerability to Human Impact. Acta Geologica Sinica English Edition 75: 325–329. https://doi. org/10.1111/j.1755-6724.2001.tb00539.x
- Zhang Z, Schwartz S, Wagner L, Miller W (2000) A Greedy Algorithm for Aligning DNA Sequences. Journal of Computational Biology 7: 203–214. https://doi. org/10.1089/10665270050081478

# Appendix 1

>IEBR\_Myr\_904 [organism = Hylomus piccolo sp.nov.]

>IEBR\_Myr\_908 [organism = Hylomus borealis sp.nov.]



**Research Article** 

# From surface to caves: new species of *Diploexochus* Brandt, 1833 (Oniscidea, Armadillidae) from Colombia, with the description of the first troglobitic species

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## Abstract

Two new species of *Diploexochus* are described, *Diploexochus cacique* **sp. nov.** from Cerro Bañaderos in Hatonuevo, La Guajira, and *Diploexochus troglobius* **sp. nov.** from Roca Madre Cave, Toluviejo, Sucre, both from the Tropical Dry Forest (TDF) areas of the Colombian Caribbean. The latter represent the first troglobitic species of the genus. Moreover, based on specimens from Sierra Nevada de Santa Marta, Magdalena (type locality), *Venezillo brevispinis* is placed into *Diploexochus* and an identification key for all species of the genus is given. The present work describes the first troglobitic species of the genus, and expand the knowledge of its distribution in northern South America.

**Key words:** Cave-dwelling, Colombian Caribbean, Neotropical, subterranean systems, terrestrial isopods, Tropical Dry Forest

## Introduction

Terrestrial isopods (Oniscidea) are considered one of the most diverse groups of crustaceans, comprising approximately 4,000 species in more than 500 genera in 38 or 39 families, distributed in almost all terrestrial habitats, including caves (Schmalfuss 2003; Hornung 2011; Sfenthourakis and Taiti 2015; Campos-Filho et al. 2017a, 2018, 2023a, 2023b; Taiti 2017; Dimitriou et al. 2019; Campos-Filho and Taiti 2021). Within Oniscidea, the family Armadillidae Brandt, 1831 is the most diverse, including more than 600 species in 81 genera and distributed in Neotropical, Afrotropical, Oriental, and Australian regions (Taiti et al. 1998; Schmalfuss 2003; Sfenthourakis and Taiti 2015; Rodríguez-Cabrera and Armas 2023). In Colombia, 13 species of the family are known: *Ctenorillo binomio* Carpio-Díaz, Bichuette & Campos-Filho, 2023, *C. dazai* Carpio-Díaz, López-Orozco & Campos-Filho, 2018, *C. humboldti* Carpio-Díaz, López-Orozco & Campos-Filho,

2023, C. mincaensis López-Orozco, Carpio-Díaz & Campos-Filho, 2023, C. orientalis Carpio-Díaz, Taiti & López-Orozco, 2023, C. papagayoensis Carpio-Díaz, Borja-Arrieta & Campos-Filho, 2023, C. tayrona López-Orozco, Borja-Arrieta & Campos-Filho, 2023, C. tuberosus (Budde-Lund, 1904), Synarmadillo ruthveni (Pearse, 1915), Venezillo brevispinis (Pearse, 1915), V. gigas (Miers, 1877), V. grenadensis (Budde-Lund, 1893), and V. vincentis (Budde-Lund, 1904) (Richardson 1912; Pearse 1915; Carpio-Díaz et al. 2018, 2023a; López-Orozco et al. 2022).

The genus *Diploexochus* Brandt, 1833 comprises five species exclusively distributed in South America, i.e., *D. echinatus* Brandt, 1833 from Brazil, French Guiana, Guyana, and Trinidad, *D. obscurus* Cardoso, Bastos-Pereira & Ferreira, 2022, *D. spinatus* Cardoso, Bastos-Pereira & Ferreira, 2022, *D. carrapicho* Campos-Filho, López-Orozco & Taiti, 2023, and *D. exu* Campos-Filho, Sfenthourakis & Bichuette, 2023 from Brazil (Schmalfuss 2003; Campos-Filho et al. 2023a; Cardoso et al. 2023). The genus is characterized by the shape and direction of the pereonites 1–7 epimera and pleonites 3–5 epimera, large schisma of the pereonite 1 epimera, frontal shield surpassing the vertex of the cephalon, and the presence of well-developed dorsal tubercles (see Campos-Filho et al. 2017a).

According to the Sector Technical Standard NTS-AV012 of 2008, a cavern is defined as any subterranean space within rocks large enough for human entry; it may have been formed in rocks or ice and may be filled with water, sediments, blocks, lava, and sometimes it may be impenetrable. The environmental conditions in these habitats are stable and support the establishment of various forms of life, including troglobitic organisms. These organisms are characterized by completing their entire life cycle within caves and exhibit high degree of troglomorphism (Galán and Herrera 1998). Various subterranean systems have been reported in Colombia, especially for the department of Santander, where most of the studies are concentrated (Muñoz-Saba et al. 1998a, 1998b; 2013; Castellanos-Morales et al. 2015; Barriga et al. 2019; Valdivieso 2022). Despite this, the associated diversity for most caves is still only estimated, particularly in the Caribbean region, where the number of subterranean systems remains unknown.

The diversity of Oniscidea from Colombia has increased considerably in the last years (López-Orozco et al. 2014, 2016, 2017, 2022; Carpio-Díaz et al. 2016, 2018, 2021, 2023a, 2023b; Campos-Filho et al. 2020). However, this knowledge is far from complete, considering the territorial extension of the country which difficult extensive surveys. In this study, two new species of *Diploexochus* are described for the department of La Guajira and Sucre. Moreover, the examination of specimens of *V. brevispinis* from Sierra Nevada de Santa Marta, Magdalena Department (type locality), allowed the placement of the species into the genus *Diploexochus*. Additionally, an identification key for the species and ecological and conservation remarks are provided.

# Materials and methods

The specimens were preserved in 70% ethanol. Identifications were based on morphological characters using micropreparations in Hoyer's medium (Anderson 1954). Illustrations were made with aid of a camera lucida mounted on Wild M3 and M20 microscopes. The images of the species were obtained using a stereomicroscope SteREO Discovery.V12 ZEISS with an adapted camera

Axiocam ERc 5s. The final illustrations were created using GIMP software (v. 2.8) following the method proposed by Montesanto (2015, 2016). Respiratory structures were classified according to Paoli et al. (2002). The examined material is deposited in the Collection of the University of Cartagena, Cartagena, Colombia (CBUDC-CRU).

### **Results**

#### **Systematics**

Suborder Oniscidea Latreille, 1802 Family Armadillidae Brandt, 1831

Genus Diploexochus Brandt, 1833

**Type species.** *Diploexochus echinatus* Brandt, 1833, by monotypy (see Schmidt and Leistikow 2004).

#### Diploexochus brevispinis (Pearse, 1915), comb. nov.

Figs 1-4, 8A, 13A

Cubaris brevispinis Pearse, 1915: 543, fig. 5. Cubaris brevispinis: Van Name 1936: 382, fig. 232. Venezillo (Vandelillo) brevispinis: Arcangeli 1957: 121. Venezillo brevispinis: Leistikow and Wägele 1999: 47; Schmalfuss 2003: 286.

**Material examined.** COLOMBIA • 1♂, 1♀ (parts in micropreparations), Hacienda Cafetera Cincinati, Sierra Nevada de Santa Marta, Santa Marta, Magdalena, 11°6'34.14"N, 74°5'30.84"W, leg. CM López-Orozco, YM Carpio-Díaz, 13.VIII. 2018, CBUDC-CRU 344 • 3♂, 4♀, same locality and collectors as for preceding, CBUDC-CRU 343.

Redescription. Maximum body length: male 7 mm, female 7.5 mm. Color dark brown, cephalon, pereon, pleon, and telson strongly pigmented, pleonites 3-5 epimera less pigmented (Fig. 8A); upper portion of tubercles, pereonite 1 epimera anterior and posterior corners, pereonites 2, 3, and 6 epimera weakly pigmented, sometimes depigmented. Color pattern preserved in ethanol (Figs 2A, 13A). Body in lateral view as in Fig. 2A. Endoantennal conglobation (Figs 2A, 13A). Dorsum covered with large triangular tubercles, arranged as follows (Fig. 2A, B): vertex of cephalon with 10 tubercles in three rows; pereonite 1 with 25–29 tubercles; pereonites 2–6 with 17 tubercles; pereonite 7 with 15 tubercles; pleonites 3-5 with one tubercle on median portion, and telson with two paramedian tubercles. Pereonites 1-7 epimera with one line of noduli laterales per side inserted on outer surface of second tubercle of posterior row (Fig. 2A). Dorsal surface with short semi-circular scale-setae (Fig. 2C). Cephalon (Fig. 2D-F) with frontal shield prominent, distinctly protruding above vertex; eyes of 16 ommatidia. Pereonites 1-7 epimera flattened and directed outwards; pereonite 1 strongly grooved on lateral margin, inner lobe of schisma rounded, not extending beyond posterior margin of outer lobe (Fig. 2G-H), pereonite 2 with triangular ventral lobe obliquely directed backwards; pereonites 3-7 with



**Figure 1.** Distribution map of the *Diploexochus* species from Colombia. Green areas: Tropical Dry Forest (TDF) from Colombia (García et al. 2014).

oblique ventral ridge (Fig. 2A–G). Pleonites 3–5 (Fig. 2I, J) with epimera well developed, rectangular, and directed outwards. Telson (Fig. 2I) with proximal part slightly broader than distal part, dorsum slightly depressed, distal margin straight. Antennula (Fig. 2K) of three articles, proximal article longest, distal article with five aesthetascs inserted apically. Antenna (Fig. 2L) short, not surpassing posterior margin of pereonite 1 when extended backwards; flagellum of two articles, distal article about three times as long as first bearing one row of two lateral aesthetascs. Mandibles with molar penicil dichotomized; left mandible (Fig. 3A) with 2+1 penicils, right mandible (Fig. 3B) with 1+1 penicils. Maxillula (Fig. 3C) inner endite with two stout penicils; outer endite with 4+6 simple teeth. Maxilla (Fig. 3D) inner lobe rounded and covered with thin setae; outer lobe rounded, twice as wide as inner lobe, covered with thin setae. Maxilliped (Fig. 3E) basis rectangular bearing sparse setae; palp with two distinct setae on basal article; endite subrectangular, medial seta overpassing distal margin, distal margin.



Figure 2. Diploexochus brevispinis (Pearse, 1915), comb. nov. ( $\bigcirc$  CBUDC-CRU 344) **A** habitus, lateral view **B** dorsal tubercles scheme **C** dorsal scale-seta **D** cephalon, dorsal view **E** cephalon, posterior view **F** cephalon and pereonites 1 and 2, frontal view **G** pereonites 1–7 epimera, ventral view **H** pereonites 1 and 2 epimera, ventral view **I** pleonites 4 and 5, telson, and uropods, dorsal view **J** pleonites 4 and 5, telson, and uropods, ventral view **K** antennula **L** antenna.





gin with one short seta. Pereopods 1–7 merus and carpus with sparse setae on sternal margin; carpus 1 with distal setae cleft at apex; ungual seta and dactylar organ simple. Uropod (Fig. 3F) protopod flattened, enlarged on basal part, distal part subrectangular, medial margin slightly concave; exopod short, inserted dorsally near medial margin below distinct lobe, lobe not extending beyond medial margin. Pleopod exopods 1–5 with monospiracular respiratory structures.

**Male.** Pereopods 1–7 (Fig. 4A, B) without particular modifications. Genital papilla as in Fig. 5C. Pleopod 1 (Fig. 4D) exopod triangular, wider than long, outer and inner margin bearing many small setae, distal part triangular, proximal



**Figure 4.** *Diploexochus brevispinis* (Pearse, 1915), comb. nov. male (♂ CBUDC-CRU 344) **A** pereopod 1 **B** pereopod 7 **C** genital papilla **D** pleopod 1 **E** pleopod 2 **F** pleopod 3 exopod **G** pleopod 4 exopod **H** pleopod 5 exopod.

outer part quadrangular; endopod about twice as long as exopod, distal portion slightly directed outwards. Pleopod 2 (Fig. 4E) exopod triangular, outer margin strongly concave bearing many setae; endopod longer than exopod. Pleopod 3–5 exopods as in Fig. 4F–H.

**Remarks.** Pearse (1915) described *Cubaris brevispinis* from Minca, Sierra Nevada de Santa Marta, Colombia. Vandel (1952) proposed new morphological characters for the genus *Venezillo*, such as the shape of the epimera and ventral lobes of pereonites 1 and 2. Arcangeli (1957), based on the previous characters, transferred *C. brevispinis* to the genus *Venezillo*, at that time within the subgenus *Vandelillo*.

Among the characteristics mentioned by Pearse (1915), the number and arrangement of the dorsal tubercles of the cephalon, pereonites 2–7, pleon, and telson, the shape and direction of the pereonites 1–7 epimera, and the number of ommatidia were confirmed here. The only distinct characteristic contrasting with the original description was the number of tubercles on pereonite 1. Pearse reported 29 tubercles, while 25 were observed in the present study. Probably, this difference is related with the size of the specimens. Additionally, in the drawings of Pearse, the lateral schisma of the pereonite 1 epimera reached about half of its length, which was also confirmed here [see Fig. 2F–H for comparison with Pearse (1915)]. Thus, based on the generic diagnostic characters mentioned previously, *V. brevispinis* is placed into the genus *Diploexochus*.

Diploexochus brevispinis comb. nov. easily differs from *D. carrapicho*, *D. echinatus*, *D. exu*, *D. obscurus*, and *D. spinatus* in the number and arrangement of the dorsal tubercles of the cephalon, pereon, and pleon. Moreover, it differs in having the antennula with five distal aesthetascs (vs six in *D. exu* and *D. carrapicho*, 10 in *D. echinatus*, seven in *D. obscurus*, and nine in *D. spinatus*), mandibles with dichotomized molar penicil (vs simple in all species), and uropod protopod with median lobe not protruding beyond the medial margin (vs protruding in all species) (see Campos-Filho et al. 2017a, 2023a; Cardoso et al. 2023).

**Natural history.** Specimens of *Diploexochus brevispinis* comb. nov. were collected under fallen logs in a sub-Andean forest close to the road at the Cincinnati farm in the Sierra Nevada de Santa Marta, Magdalena, Colombia (Fig. 8A).

**Distribution.** This species is known only from its type locality in Tropical Dry Forest (TDF) and Andean forest of Sierra Nevada de Santa Marta (Fig. 1).

*Diploexochus cacique* López-Orozco, Carpio-Díaz & Campos-Filho, sp. nov. https://zoobank.org/3BD3757B-7DFF-4554-B456-09AFC7AF3E2E Figs 1, 5–7, 8B, 13B

**Type material.** COLOMBIA • 1♂, *holotype*, Cerro Bañaderos, Hatonuevo, La Guajira, 11°7'33.3"N, 72°47'6.9"W, 12.1.2016, leg. M Gutierrez-Estrada, CBUC-CRU 350 • 1♂,1♀ (parts in micropreparations), *paratypes*, same data as holotype, CBUDC-CRU 413 • 1♀, *paratypes*, same data as holotype, CBUDC-CRU 413.

**Description.** Maximum body length: male 8 mm, female 9 mm. Body outline as in Fig. 5A. Color dark brown with typical muscular insertions (Figs 8B, 13B); upper portion of tubercles randomly depigmented; pereonite 1 epimera anterior corner, pereonites 2–7 paramedian portions, pereonites 3 and 4



Figure 5. Diploexochus cacique López-Orozco, Carpio-Díaz & Campos-Filho, sp. nov. ( $\bigcirc$  paratype, CBUDC-CRU 413) A habitus, lateral view B dorsal tubercles scheme C dorsal scale-seta D cephalon, dorsal view E cephalon, posterior view F cephalon and pereonites 1–3, frontal view G pereonites 1–7 epimera, ventral view H pereonites 1 and 2 epimera, ventral view I peonites 3–5, telson, and uropods, dorsal view J pleonites 3–5, telson, and uropods, ventral view K antennula L antenna.



Figure 6. *Diploexochus cacique* López-Orozco, Carpio-Díaz & Campos-Filho, sp. nov. (♀ paratype, CBUDC-CRU 413) A right mandible B left mandible C maxillula D maxilla E maxilliped F uropod.

epimera, and pleonites 3–5 epimera randomly depigmented. Endoantennal conglobation (Figs 5A, 8B, 13B). Dorsum covered with large triangular tubercles, arranged as follows (Fig. 5A, B): vertex of cephalon with 12 tubercles in three rows; pereonite 1 with 20 tubercles; pereonites 2–6 with 16 tubercles; pereonite 7 with 15 tubercles; pleonites 3–5 and telson with two paramedian tubercles. Pereonites 1–7 epimera with one line of **noduli laterales** per side inserted on outer surface of second tubercle of posterior row (Fig. 5A). Dorsal surface with short and narrow semi-circular scale-setae (Fig. 5C). Cephalon (Fig. 5D–F) with frontal shield prominent, distinctly protruding above vertex; eyes with 20–21 ommatidia. Pereonites 1–7 epimera flattened and slightly directed outwards; pereonite 1 strongly grooved on lateral margin, inner lobe of schisma rounded, extending beyond posterior margin of outer lobe (Fig. 5G, H), pereonite 2 with triangular and narrow ventral lobe directed outwards, not extending beyond posterior margin of epimera; pereonites 4–7 with oblique ventral ridge (Fig. 5F–H). Pleonites 3–5 (Fig. 5I, J) with epimera well devel-



**Figure 7**. *Diploexochus cacique* López-Orozco, Carpio-Díaz & Campos-Filho, sp. nov. (*d* paratype, CBUDC-CRU 413) **A** pereopod 1 **B** pereopod 7 **C** pleopod 1 and genital papilla **D** pleopod 2 **E** pleopod 3 exopod **F** pleopod 4 exopod **G** pleopod 5 exopod.



**Figure 8.** A *Diploexochus brevispinis* (Pearse, 1915), comb. nov. under fallen tree in the Sierra Nevada de Santa Marta, Magdalena **B** *Diploexochus cacique* López-Orozco, Carpio-Díaz & Campos-Filho, sp. nov. on the tree bark, Cerro Bañaderos, Hatonuevo, La Guajira.

oped, rectangular and slightly directed outwards. Telson (Fig. 5I) with proximal part slightly broader than distal part, dorsum slightly depressed, distal margin straight. Antennula (Fig. 5K) of three articles, proximal and distal articles subequal in length, distal article with four aesthetascs inserted sub-apically. Antenna (Fig. 5L) short, not surpassing posterior margin of pereonite 1 when extended backwards; flagellum of two articles, distal article about twice as long as first bearing one row of two lateral aesthetascs. Mandibles with molar penicil semi-dichotomized; left mandible (Fig. 6A) with 2+1 penicils, right mandible (Fig. 6B) with 1+1 penicils. Maxillula (Fig. 6C) inner endite with two stout penicils, distal margin bearing fringe of thin setae; outer endite of 4+6 teeth simple. Maxilla (Fig. 6D) inner lobe rounded covered with thick setae; outer lobe rounded, three times as wide as inner lobe, covered with thin setae. Maxilliped (Fig. 6E) basis rectangular bearing sparse setae; palp with two distinct setae on basal article; endite subrectangular, medial seta overpassing distal margin, distal margin bearing two setae. Pereopods 1-7 merus and carpus bearing setae on sternal margin, not sparse appearance; carpus 1 with distal setae cleft at apex; ungual seta and dactylar organ simple, both surpassing outer claw. Uropod (Fig. 6F) protopod flattened, enlarged on basal part, distal part subrectangular, medial margin concave; exopod short inserted dorsally near medial margin bellow distinct lobe, lobe not extending beyond medial margin; endopod club-shaped bearing many short setae on distal part. Pleopods 1-5 exopods with monospiracular respiratory structures.

**Male.** Pereopods 1–7 (Fig. 7A, B) without particular modifications. Genital papilla as in Fig. 9C. Pleopod 1 (Fig. 7C) exopod triangular, as wide as long, outer and inner margin bearing many small setae, distal and proximal outer parts triangular; endopod about twice as long as exopod. Pleopod 2 (Fig. 7D) exopod triangular, outer margin strongly concave bearing many setae; endopod slightly longer than exopod. Pleopod 3–5 exopods as in Fig. 7E–G.

**Etymology.** The new species is named after the Vallenato music singer Diomedes Díaz Maestre, also known as "El Cacique de la Junta".

**Remarks.** *Diploexochus cacique* sp. nov. easily differs from the previously mentioned species in the pattern of the dorsal tubercles of the pleon and telson, the pereonites 1 and 2 epimera with ventral lobes surpassing the posterior margin of the epimera, and the club-shaped uropod endopod.

**Natural history.** Specimens of *Diploexochus cacique* sp. nov. were collected on tree bark around the Luis Pablo Ojeda Cave (Bañaderos cave), Cerro Bañaderos, Hatonuevo, La Guajira (Fig. 8B). The area where the *D. cacique* sp. nov. species is found is composed of TDF and is part of the Sierra de Bañadero integrated management district (DMI), a mountain system in the upper basin of the Camarones River in the department of La Guajira, which is connected to the Sierra Nevada de Santa Marta.

**Distribution.** This species is known only from the type locality at Cerro Bañaderos, Hatonuevo, La Guajira, which is included into a TDF area (Fig. 1).

*Diploexochus troglobius* López-Orozco, Borja-Arrieta & Campos-Filho, sp. nov. https://zoobank.org/0EB8C9FC-F2AD-4D8F-963F-412AE50B7586 Figs 1, 9–13C

**Type material.** COLOMBIA • 1♂, *holotype*, Roca madre Cave, Campo Aventura Roca Madre, La Piche, Toluviejo, Sucre, 9°30'50.2"N, 75°23'36.6"W, 12.VII.2018, leg. CM López-Orozco, R Borja-Arrieta, CBUDC-CRU 393 • 1♂, *paratypes*, same data as holotype, CBUDC-CRU 394 • 1♂, 1♀ (parts in micro-preparations), *paratypes*, same data as holotype, CBUDC-CRU 396.

**Description.** Maximum body length: male 2.7 mm, female 4.2 mm. Body outline as in Fig. 9A. Color faintly brown; body pigments not discernible in vivo (Fig. 12D). Endoantennal conglobation (Figs 9A, 12D, 13C). Dorsum covered with large triangular tubercles, arranged as follows (Fig. 9A, B): vertex of cephalon with 10 tubercles in two rows; pereonite 1 with 19 tubercles; pereonites 2-6 with 13 tubercles; pereonite 7 with 11 tubercles; pleonites 3, 4, and telson with two median tubercles. Pereonites 1-7 epimera with one line of noduli laterales per side inserted on outer surface of second tubercle of posterior row (Fig. 9A). Dorsal surface densely covered with elongated semi-circular scale-setae, conferring pilous aspect (Fig. 9C). Cephalon (Fig. 9D-F) with prominent frontal shield, distinctly protruding above vertex; eyes with four ommatidia. Pereonites 1-7 epimera flattened and slightly directed outwards; pereonite 1 grooved on posterior lateral margin, inner lobe of schisma rounded and extending beyond posterior margin of outer lobe. Pereonite 2 with triangular ventral lobe rounded at apex, extending beyond posterior margin of epimera; pereonites 3 and 5-7 with well-marked ventral ridge (Fig. 9A, F, G). Pleonites 3-5 epimera (Fig. 9H, I) well developed, sub-rectangular, and directed outwards, distal margins rounded. Telson (Fig. 9H) with proximal part broader than distal part, dorsum slightly depressed, distal margin sinuous. Antennula (Fig. 9J) of three articles, proximal and distal subequal in length, distal article with five stout aesthetascs inserted sub-apically. Antenna (Fig. 9K) short, not surpassing posterior margin of pereonite 1 when extended backward; flagellum of two articles, the distal about three times as long as first, bearing one row of two lateral aesthetascs. Mandibles with molar penicil semi-dichotomized; left mandible (Fig. 10A) with 2+1 penicils, right mandible (Fig. 10B) with 1+1 penicils. Maxillula (Fig. 10C) inner endite with two stout penicils, distal margin bearing thin setae; outer endite with 4+6 teeth simple. Maxilla (Fig. 10D) inner lobe rounded covered with thick setae; outer lobe rounded three times as wide as inner lobe covered with thin setae.



Figure 9. Diploexochus troglobius López-Orozco, Borja-Arrieta & Campos-Filho, sp. nov. ( $\bigcirc$  paratype, CBUDC-CRU 396) A habitus, lateral view B dorsal tubercles scheme C dorsal scale-seta D cephalon and pereonite 1, dorsal view E cephalon and pereonite 1, posterior view F cephalon and pereonites 1–4, frontal view G pereonites 1–7 epimera, ventral view H pleotelson and uropods, dorsal view I pereonite 7, pleonites 3–5, telson, and uropods, ventral view J antennula K antenna.



Figure 10. *Diploexochus troglobius* López-Orozco, Borja-Arrieta & Campos-Filho, sp. nov. (♀ paratype, CBUDC-CRU 396) A left mandible B right mandible C maxillula D maxilla E maxilliped F uropod.

Maxilliped basis (Fig. 10E) rectangular, bearing sparse setae; palp with two distinct setae on basal article; endite subrectangular, medial seta surpassing distal margin, distal margin bearing one seta. Pereopods 1–7 merus and carpus with sparse setae on sternal margin; carpus 1 with distal seta cleft at apex; ungual seta and dactylar organ simple not surpassing outer claw. Uropod (Fig. 10F) protopod flattened, enlarged on basal part, distal part elongated and sub-rectangular, distal margin rounded, medial margin concave with L-shaped appearance; exopod as long as endopod inserted dorsally near medial margin bellow distinct lobe, lobe not extending beyond medial margin; endopod short bearing many short setae. Pleopods 1–5 exopods with monospiracular respiratory structures.

**Male.** Pereopods 1–7 (Fig. 11A, B) without particular modifications. Genital papilla as in Fig. 11C. Pleopod 1 (Fig. 11D) exopod hour-glass shaped, twice as



**Figure 11**. *Diploexochus troglobius* López-Orozco, Borja-Arrieta & Campos-Filho, sp. nov. (♂ paratype, CBUDC-CRU 396) **A** pereopod 1 **B** pereopod 7 **C** genital papilla **D** pleopod 1 **E** pleopod 2 **F** pleopod 3 exopod **G** pleopod 4 exopod **H** pleopod 5 exopod.



**Figure 12. A** Tropical Dry Forest around Roca Madre Adventure Park, Sucre **B** livestock around Roca Madre Adventure Park **C** Roca Madre Cave Gallery **D** *Diploexochus troglobius* López-Orozco, Borja-Arrieta & Campos-Filho, sp. nov. under limestone rocks.

wide as long, inner portion rounded, outer portion triangular, distal and proximal margins narrow on middle; endopod about three times as long as exopod. Pleopod 2 (Fig. 11E) exopod triangular, outer margin strongly concave; endopod slightly longer than exopod. Pleopod 3–5 exopods as in Fig. 11F–H.

**Etymology.** Latin: *troglo* + *bio* = cave-dwelling. The new name of the species is an adjective that refers to the troglobitic category of the species.

**Remarks.** *Diploexochus troglobius* sp. nov. is easily distinguishable from the congeners in the arrangement of the dorsal tubercles of the pleon, dorsal surface with pilose aspect, eyes of four ommatidia, and the shape of the male pleopod 1 exopod.

**Natural history.** Specimens of *D. troglobius* sp. nov. were collected in the aphotic zone of the Roca Madre Cave, beneath limestone rocks (Fig. 12D). This species is considered troglobitic due to the reduction of body pigments and reduction in the number of ommatidia. In addition, several surveys were conducted outside the cave and other subterranean ecosystems to confirm its restricted distribution. This species is considered endemic to the study area.

**Distribution.** This species is known only from the type locality at Roca Madre Cave, Sucre, inserted on TDF area (Fig. 1).



**Figure 13.** Habitus of the species of the genus *Diploexochus* Brandt, 1833 of Colombia: **A** *Diploexochus brevispinis* (Pearse, 1915), comb. nov. **B** *Diploexochus cacique* López-Orozco, Carpio-Díaz & Campos-Filho, sp. nov. **C** *Diploexochus troglobius* López-Orozco, Borja-Arrieta & Campos-Filho, sp. nov. Scale bars: 1 mm.

# Key to species of Diploexochus

n with 10 tubercles	2
n with < 10 tubercles	3
triangular, and acute tubercles	
D. echinatus Brandt, 18	33
and rectangular tubercles	
curus Cardoso, Bastos-Pereira & Ferreira, 20	)22
percles	4
tubercles	5
bercles distributed in two rows; pleonites 3 a	and
cles	
cho Campos-Filho, López-Orozco & Taiti, 20	)23
percles distributed in a single row; pleonites	s 3
tubercles	
ampos-Filho, Sfenthourakis & Bichuette, 20	)23
natidia	6
natidia	7
l aesthetascs; pereonites 2-6 with 13 tuberc	les
oinatus Cardoso, Bastos-Pereira & Ferreira, 20	)22
ally inserted aesthetascs; pereonites 2-6 w	/ith
2 rows <b>D. cacique sp. n</b>	ov.

# Discussion

The genus *Diploexochus* is distributed in the Neotropical region and is distinguished by the shape and direction of the epimera and pleonites, the frontal shield of the cephalon, and the arrangement of dorsal tubercles (Campos-Filho et al. 2017a, 2023a; Cardoso et al. 2023). In the illustrations of *D. obscurus* provided by Cardoso et al. (2023), pleonite 4 appears to have four tubercles. However, the description mentions that it has two paramedian tubercles, a pattern shared with the species *D. echinatus*. Therefore, a reanalysis of this species is necessary for its correct description and comparison.

The Colombian species of *Diploexochus* are distributed in TDF areas (Fig. 1), considered to host a high level of diversity and endemism, where the species are adapted to extreme environmental conditions, such as drought and extreme temperatures (Alcázar et al. 2021). However, TDF is currently one of the most threatened and least protected tropical biomes on the planet (Murphy and Lugo 1986; Janzen 1988). In Colombia, it is estimated that ~ 720,000 hectares of the original 8 million hectares of TDF remain, and only 5% are under the protection of the National System of Protected Areas (García et al. 2014; Pizano and García 2014). This reduction in vegetation cover is mainly due to various anthropogenic pressures, leading to a loss of biodiversity (Hoekstra et al. 2005; Portillo-Quintero and Sánchez-Azofeifa 2010). Therefore, studies regarding dynamics of populations, including oniscidean species, are necessary to better understand the ecological relations between species and area. Moreover, as in other parts of the world, these organisms could act model to improve conservation and sustainable programs (Solomou et al. 2019; Reboleira et al. 2022).

Subterranean systems are considered biodiversity refuges (Muñoz-Saba et al. 1998a; Culver and Sket 2000; Pipan et al. 2020). The species diversity contained in these habitats mainly depends on strict climatic conditions and energy flow (Ardila 2006; Castellanos-Morales 2018). However, this emerging biodiversity is primarily threatened by the alteration of surrounding natural habitats, anthropogenic pressure, uncontrolled tourism, and mining, among other factors (Restrepo 2007, 2011; Manco et al. 2017; Angarita 2018; Zafra 2021). In Colombia, more than 500 subterranean systems located in 12 biospeleological provinces are known (Muñoz-Saba et al. 1998a, 1998b; Valdivieso 2022). Despite this number, biodiversity research is scarce and isolated for some areas or departments of the country (Muñoz-Saba et al. 1998b, 2013; Vides-Navarro et al. 2015; Angarita 2018; Barriga et al. 2019). Furthermore, most of the country's caves are distributed along transformed agro-ecosystems without any protection (Muñoz-Saba et al. 1998a, 2013). Recently, the National Government enacted the Law number 2237 of 2022, assuring the protection of the Colombian speleological heritage, where environmental authorities will declare protected areas that include speleological biodiversity. However, efforts to conserve these fragile ecosystems are not sufficient, since the number of subterranean ecosystems is still under estimation and the biotic composition, which are sensitive to anthropogenic disturbances, is mostly unknown. It is worth mentioning that this component probably hosts a high degree of endemic species and specific microhabitats or substrates as observed in other studies (Campos-Filho et al. 2017a, 2017b, 2018; López-Orozco et al. 2024a, 2024b). Thus, more studies are needed to assess the conservation status of these ecosystem and quantify and identify its diversity for better conservation efforts.

Regarding the knowledge of oniscideans in Colombian caves, only the species Ctenorillo papagayoensis Carpio-Díaz, Borja Arrieta & Campos-Filho, 2023, has been described from the Cueva de Los Papagayos in the department of Santander; Ctenorillo binomio Carpio-Díaz, Bichuette & Campos-Filho, 2023, for the Cueva de San Miguel in the department of Bolívar; Pulmoniscus turbanaensis López-Orozco, Carpio-Díaz & Campos-Filho, 2017; and Porcellionides pruinosus (Brandt, 1833) for the Cueva La Mojana in the department of Atlántico (Carpio-Díaz et al. 2023a, 2023b). Additionally, the genera Colomboniscus Vandel, 1972, Colomboscia Vandel, 1972, Sphaeroniscus Gerstäcker, 1854, Neosanfilippia Brian, 1957 (Scleropactidae Verhoeff, 1938), and Ischioscia Verhoeff, 1928 (Philosciidae Kinahan, 1857) have been reported from the Cueva de los Papagayos in Santander. The data from the study also include Cueva de Los Indios and Hoyo del Aire in the department of Santander (Sket 1988; Castellanos-Morales et al. 2015; Barriga et al. 2019), although these records do not include species formal descriptions. Regarding other taxa, five studies related to arachnids and a biological inventory of some orders in the Caribbean region have been published (Armas et al. 2015; Cala-Riquelme et al. 2015; Torres-Contreras et al. 2015; Vides-Navarro et al. 2015; García et al. 2022; Moreno-González et al. 2023). This work represents the first record of a troglobitic terrestrial isopod for both the genus and the country, increasing the number of species in the national inventory.

The species *Diploexochus troglobius* sp. nov. is recorded only from Roca Madre cave and has a low population density, supporting both the cave and the species suitable for conservation. Similarly, species such as *Charinus rocamadre* Torres-Contreras, Álvarez García & De Armas, 2015 and *Heterophrynus caribensis* De Armas, Torres-Contreras & Álvarez García, 2015 (Amblypygi, Charinidae) are under ecological stress due to cattle (Fig. 12B), deforestation, mining, and uncontrolled ecotourism (vandalism). This demonstrates the need to formulate and implement conservation strategies by governmental entities including the scientific community and the general public in decision-making processes.

In the last years, the study of the oniscofauna from Colombia has increased, of which more than 30 epigean species have been described, consolidating a total of 73 species distributed throughout the territory (e.g. López-Orozco et al. 2014, 2016, 2017, 2022; Carpio-Díaz et al. 2016, 2018, 2021, 2023a, 2023b; Campos-Filho et al. 2020; Bravo-Rodríguez et al. 2024). However, the biodiversity of the cave-dwelling isopod species is a new topic and considering the number of caves, this diversity is far from complete.

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# Additional information

## **Conflict of interest**

The authors have declared that no competing interests exist.

## **Ethical statement**

No ethical statement was reported.

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## **Author contributions**

Conceptualization: RLBA. Data curation: RLBA, GRNS, MGE. Formal analysis: CMLO, RLBA, ISCF, YMCD, MEB. Funding acquisition: RLBA, GRNS. Investigation: ISCF, RLBA, CMLO. Methodology: MGE, RLBA. Software: YMCD. Supervision: MEB, ISCF. Visualization: RLBA. Writing – original draft: YMCD, ISCF, MGE, CMLO, MEB, RLBA, GRNS. Writing – review and editing: YMCD, CMLO, MGE, MEB, GRNS, ISCF, RLBA.

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## **Data availability**

All of the data that support the findings of this study are available in the main text.

## References

- Alcázar C, Avella EA, Norden N, García DH, García H, Castellanos C, González-M R (2021) Programa Nacional para la Conservación y Restauración del Bosque Seco Tropical en Colombia-PNCBST, Plan de Acción 2020–2030, Bogotá, Colombia, Ministerio de Ambiente y Desarrollo, 78 pp.
- Anderson LE (1954) Hoyer's solution as a rapid permanent mounting medium for bryophytes. The Bryologist 57(3): e242. https://doi.org/10.1639/0007-2745(1954)57[242:H-SAARP]2.0.CO;2
- Angarita T (2018) Breve historia de la bioespleología en Colombia: perspectivas y oportunidades. I Congreso Colombiano de Espeleología y VIII Congreso Espeleológico de América Latina y el Caribe, 40–58.
- Arcangeli A (1957) I generi *Diploexochus*, *Venezillo*, *Paramardillo* [sic] (crostacei isopodi terrestri). Bollettino dell'Istituto e Museo di Zoologia dell'Università di Torino 5: 101–142.
- Ardila CA (2006) *Trichomycterus sandovali*, (Siluriformes, Trichomycteridae) una nueva especie de pez cavernícola para el departamento de Santander, Colombia. Peces del departamento de Santander 2: 1–16.
- Armas LF De, Torres-Contreras R, Álvarez DM (2015) Nueva especie de *Heterophrynus* (Amblypygi: Phrynidae) del Caribe Colombiano. Revista Ibérica de Aracnología 26: 69–73.
- Barriga JC, Martínez-Torres D, López-Orozco CM, Villarreal O, Murcia MA (2019) Artrópodos terrestres de las cuevas y cavernas de El Peñón (Andes), Santander, Colombia.
  In: Lasso CA, Barriga JC, Fernández-Auderset J (Eds) Biodiversidad subterránea y epigea de los sistemas cársticos de El Peñon (Andes), Santander, Colombia. Serie Fauna Silvestre Neotropical VII. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, D. C., Colombia, 99–155. https://doi.org/10.21068/c2020SFSNVII01
- Bravo-Rodríguez AE, López-Orozco CM, Nisperuza-Pérez CA, Quirós-Rodríguez JA, Campos-Campos NH (2024) Ampliación del ámbito geográfico de isópodos terrestres (Oniscidea) para el Caribe colombiano y primer registro de Nagurus nanus (Trachelipodidae) para Colombia. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 48(188): 606–622. https://doi.org/10.18257/raccefyn.2630
- Cala-Riquelme F, Gutiérrez-Estrada MA, Flórez E (2015) The genus *Loxosceles* Heineken & Lowe 1832 (Araneae: Sicariidae) in Colombia, with description of new cave-dwelling species. Zootaxa 4012(2): 396–400. https://doi.org/10.11646/zootaxa.4012.2.12
- Campos-Filho IS, Taiti S (2021) Oniscidea taxonomy: present and future. Abstract book of the 11<sup>th</sup> International Symposium on Terrestrial Isopod Biology. Spinicornis, Ghent, 9.
- Campos-Filho IS, Montesanto G, Araujo PB, Taiti S (2017a) New species and new records of terrestrial isopods (Crustacea, Isopoda, Oniscidea) from Brazil. Iheringia. Série Zoologia 107: e2017034. https://doi.org/10.1590/1678-4766e2017034
- Campos-Filho IS, Bichuette ME, Montesanto G, Araujo PB, Taiti S (2017b) The first troglobiotic species of the family Pudeoniscidae (Crustacea, Isopoda, Oniscidea) with descriptions of a new genus and two new species. Subterranean Biology 23: 69–84. https://doi.org/10.3897/subtbiol.23.20963
- Campos-Filho IS, Cardoso GM, Aguiar JO (2018) Catalogue of terrestrial isopods (Crustacea, Isopoda, Oniscidea) from Brazil: an update with some considerations. Nauplius 26: 2018038. https://doi.org/10.1590/2358-2936e2018038

- Campos-Filho IS, López-Orozco CM, Carpio-Díaz YM, Águiar JO, Navas-S GR (2020) Three new species of *Ischioscia* Verhoeff, 1928 (Isopoda, Oniscidea, Philosciidae) from Serrania de Perijá, Andean Cordillera, Colombia Caribbean. Zoosystema 42(8): 115–130. https://doi.org/10.5252/zoosystema2020v42a8
- Campos-Filho IS, Sfenthourakis S, Gallo JS, Gallão JE, Torres DF, Chagas-Jr A, Horta J, Carpio-Díaz YM, López-Orozco CM, Borja-Arrieta R, Araujo PB, Taiti S, Bichuette ME (2023a) Shedding light into Brazilian subterranean isopods (Isopoda, Oniscidea): expanding distribution data and describing new taxa. Zoosystema 45(19): 531–599. https://doi.org/10.5252/zoosystema2023v45a19
- Campos-Filho IS, López-Orozco CM, Carpio-Díaz YM, Borja-Arrieta R, Gallão JE, Taiti S, Sfenthourakis S, Bichuette ME (2023b) Everything is similar, everything is different! *Trichorhina* Budde-Lund, 1908 (Oniscidea, Platyarthridae) from Brazilian caves, with descriptions of 11 new species. Biota Neotropica 23(4): e20231545. https://doi.org/10.1590/1676-0611-bn-2023-1545
- Cardoso GM, Bastos-Pereira R, Ferreira RL (2023) Cave-dwellers *Diploexochus* (Oniscidea, Armadillidae): new species and new records of the genus for Brazil. Nauplius 31: e2023008. https://doi.org/10.1590/2358-2936e2023008
- Carpio-Díaz YM, López-Orozco CM, Herrera-Medina Y, Navas-S GR, Bermúdez A (2016) Primer registro de *Tylos niveus* y nuevo reporte de *Porcellionides pruinosus* (Oniscidea: Tylidae y Porcellionidae) para Colombia. Revista de la Academia Colombiana de Ciencias Exactas Físicas y Naturales 40(156): 4233–4437. https://doi.org/10.18257/raccefyn.343
- Carpio-Díaz YM, López-Orozco CM, Campos-Filho IS, Navas GR (2018) Terrestrial isopods (Isopoda: Oniscidea) of the Botanical Garden of Cartagena "Guillermo Piñeres", Colombia, with the description of three new species. Arthropoda Selecta 27(4): 301– 318. https://doi.org/10.15298/arthsel.27.4.05
- Carpio-Díaz YM, López-Orozco CM, Borja-Arrieta R, Campos-Filho IS (2021) A new species and first record of *Trichorhina* Budde-Lund, 1908 (Isopoda, Oniscidea, Platyarthridae) from the Department of Norte de Santander, Colombia. Nauplius (29): e2021028. https://doi.org/10.1590/2358-2936e2021028
- Carpio-Díaz YM, López-Orozco CM, Borja-Arrieta R, Gutierrez-Estrada M, Campos-Filho IS, Sfenthourakis S, Taiti S, Neita JC, Bermúdez A, Navas-S GR, Bichuette ME (2023a) The genus *Ctenorillo* Verhoeff, 1942 (Oniscidea, Armadillidae) from Colombia: new records, new species, and conservation comments. Tropical Zoology 36(3–4): 53– 84. https://doi.org/10.4081/tz.2023.141
- Carpio-Díaz YM, López-Orozco CM, Borja-Arrieta R, Navas-S GR, Bermúdez A, Neita-Moreno JC, Campos-Filho IS (2023b) New records of terrestrial isopods (Crustacea: Isopoda: Oniscidea) from Colombia. Arthropoda Selecta 32(4): 399–408. https://doi. org/10.15298/arthsel.32.4.04
- Castellanos-Morales CA (2018) A new species of cave catfish, genus *Trichomycterus* (Siluriformes: Trichomycteridae), from the Magdalena River system, Cordillera Oriental, Colombia. Biota Colombiana 19(Sup. 1): 117–130. https://doi.org/10.21068/c2018.v19s1a10
- Castellanos-Morales CA, Moreno F, Malagón LM, Arango ÁJ, Pardo DD, Méndez MA (2015) Aportes al conocimiento y uso de los Ecosistemas Subterráneos del Municipio de la Paz (Santander). Boletín Científico Centro de Museos, Museo de Historia Natural 19(2): 173–185. https://doi.org/10.17151/bccm.2015.19.2.10
- Culver DC, Sket B (2000) Hotspots of Subterranean Biodiversity in Caves and Wells. Journal of Cave and Karst Studies 62(1): 11–17.

- Dimitriou AC, Taiti S, Sfenthourakis S (2019) Genetic evidence against monophyly of Oniscidea implies a need to revise scenarios for the origin of terrestrial isopods. Scientific Reports 9: 18508. https://doi.org/10.1038/s41598-019-55071-4
- Galán C, Herrera FF (1998) Fauna cavernícola: Ambiente, especiación y evolución. Boletín de la Sociedad Venezolana de Espeleología 32: 13–43.
- García H, Corzo G, Isaacs P, Etter A (2014) Distribución y estado actual de los remanentes del Bioma de Bosque Seco Tropical en Colombia: insumos para su gestión. In: Pizano C, García H (Eds) El Bosque Seco Tropical en Colombia. Instituto de Investigación de Recursos Biológicos Alexander von Humbolt, Bogotá, D. C., Colombia, 229–251 pp.
- García AF, González A, Gutiérrez M (2022) New records and a new cave-dwelling species of Agoristenidae (Arachnida, Opiliones) from Colombia. Zoosystematics and Evolution 98(1): 55–63. https://doi.org/10.3897/zse.98.78202
- Hoekstra JM, Boucher TM, Ricketts TH, Roberts C (2005) Confronting a biome crisis: global disparities of habitat loss and protection. Ecology Letters 8: 23–29. https:// doi.org/10.1111/j.1461-0248.2004.00686.x
- Hornung E (2011) Evolutionary adaptation of oniscidean isopods to terrestrial life: Structure, physiology and behavior. Terrestrial Arthropod Reviews 4: 95–130. https://doi. org/10.1163/187498311X576262
- Janzen DH (1988) Tropical dry forest: the most endangered major tropical ecosystem. In: Wilson EO (Ed.) Biodiversity. Washington D.C.: National Academy Press, 130–137 pp.
- Leistikow A, Wägele JW (1999) Checklist of the terrestrial isopods of the new world (Crustacea, Isopoda, Oniscidea). Revista brasileira de Zoologia 16(1): 1–72. https://doi.org/10.1590/S0101-81751999000100001
- López-Orozco CM, Bermúdez A, Navas GR (2014) Primer registro de Ligia baudiniana (Crustacea: Isopoda: Oniscidea) para el Caribe colombiano. Boletín de Investigaciones Marinas y Costeras 43(1): 195–200. https://doi.org/10.25268/bimc.invemar.2014.43.1.41
- López-Orozco CM, Carpio-Díaz YM, Navas GR, Campos-Filho IS (2016) A new species and first record of *Androdeloscia* (Oniscidea: Philosciidae) from Colombia. Studies on Neotropical Fauna and Environment 52(1): 18–24. https://doi.org/10.1080/0165 0521.2016.1254861
- López-Orozco CM, Carpio-Díaz YM, Navas GR, Campos-Filho IS (2017) A new species and first record of *Pulmoniscus* Leistikow, 2001 (Isopoda, Oniscidea, Philosciidae) from Colombia. Nauplius 25: e2017014. https://doi.org/10.1590/2358-2936e2017014
- López-Orozco CM, Carpio-Díaz YM, Borja-Arrieta R, Navas-S GR, Campos-Filho IS, Taiti S, Mateos M, Olazaran A, Caballero IC, Jotty K, Gómez-Estrada H, Hurtado LA (2022) A glimpse into a remarkable unknown diversity of oniscideans along the Caribbean coasts revealed on a tiny island. European Journal of Taxonomy 793: 1–50. https://doi.org/10.5852/ejt.2022.793.1643
- López-Orozco CM, Campos-Filho IS, Gallo JS, Gallão JE, Carpio-Díaz YM, Borja-Arrieta R, Bichuette ME (2024a) Iron-isopods: new records and new species of terrestrial isopods (Isopoda, Oniscidea) from Brazilian Amazon iron ore caves. European Journal of Taxonomy 921: 116–135. https://doi.org/10.5852/ejt.2024.921.2421
- López-Orozco CM, Campos-Filho IS, Cordeiro LM, Gallão JE, Carpio-Díaz YM, Borja-Arrieta R, Bichuette ME (2024b) First amphibius Crinocheta (Isopoda, Oniscidea) from Neotropics with a troglobitic status: a relictual distribution. Zookeys 1192: 9–27. https://doi.org/10.3897/zookeys.1192.114230

- Manco DC, Robles CA, Rojas EE (2017) Descripción de los impactos ambientales causados por el inadecuado manejo en la caverna Sabana de León y cueva Coco Loco, municipio de Manaure, serranía de Perijá, departamento del Cesar – Colombia. Ingeniare (23): 25–34. https://doi.org/10.18041/1909-2458/ingeniare.2.2880
- Montesanto G (2015) A fast GNU method to draw accurate scientific illustrations for taxonomy. ZooKeys 515: 191–206. https://doi.org/10.3897/zookeys.515.9459
- Montesanto G (2016) Drawing setae: A GNU way for digital scientific illustrations. Nauplius 24(0): e2016017. https://doi.org/10.1590/2358-2936e2016017
- Moreno-González JA, Gutierrez-Estrada M, Prendini L (2023) Systematic revision of the whip spider family Paracharontidae (Arachnida: Amblypygi) with description of a new troglobitic genus and species from Colombia. American Museum Novitates (4000): 1–36. https://doi.org/10.1206/4000.1
- Muñoz-Saba Y, Andrade-Pérez GI, Baptiste-Ballera BLG, Salas D, Villarreal H, Armenteras D (1998a) Conservación de los Ecosistemas Subterráneos en Colombia. Biosíntesis, 10: 1–4.
- Muñoz-Saba Y, Andrade GI, Baptiste LG (1998b) Cuevas y Cavernas. Tomo I. In: Chávez ME, Arango N (Eds) Informe Nacional sobre el Estado de la Biodiversidad (1997) Colombia. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, PNUMA, Ministerio del Medio Ambiente, Bogotá, D. C., Colombia, 164–175 pp.
- Muñoz-Saba Y, González-Sánchez I, Calvo-Roa N (2013) Cavernas de Santander, Colombia: Guía de campo. Serie de Guías de campo del Instituto de Ciencias Naturales, Bogotá, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, 325 pp.
- Murphy PG, Lugo AE (1986) Ecology of tropical dry forest. Annual Review of Ecology and Systematics 17: 67–68. https://doi.org/10.1146/annurev.es.17.110186.000435
- Paoli P, Ferrara F, Taiti S. 2002. Morphology and evolution of the respiratory apparatus in the family Eubelidae (Crustacea, Isopoda, Oniscidea). Journal of Morphology 253(3): 272–289. https://doi.org/10.1002/jmor.10008
- Pearse A (1915) An account of the Crustacea collected by the Walker Expedition to Santa Marta, Colombia. Proceedings of the United States National Museum 49: 531–556. https://doi.org/10.5479/si.00963801.49-2123.531
- Pipan T, Deharveng L, Culver DC (2020) Hotspots of subterranean biodiversity. Diversity 12(5): 209. https://doi.org/10.3390/d12050209
- Pizano C, García H (2014) El Bosque Seco Tropical en Colombia, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH). Bogotá, DC, Colombia, 353 pp.
- Portillo-Quintero CA, Sánchez-Azofeifa GA (2010) Extent and Conservation of tropical dry forests in the Americas. Biological Conservation 143: 144–155. https://doi.org/10.1016/j.biocon.2009.09.020
- Reboleira ASP, Eusébio RP, Taiti S (2022) Species conservation profiles of cave-adapted terrestrial isopods from Portugal. Biodiversity data journal 10: e78796. https://doi. org/10.3897/BDJ.10.e78796
- Restrepo C (2007) El deterioro del sistema kárstico de la Danta (Sonsón-Antioquia). In: Património Geológico, Arqueológico e Mineiro em Regioes Cársicas. Batalha, 47–53.
- Restrepo C (2011) El sistema kárstico de la Danta (Sonsón Antioquia) Colombia. Dyna 78(169): 239–246.
- Richardson H (1912) Terrestrial isopods of Colombia. Mémoires de la Société des Sciences Naturelles de Neuchâtel 5: 29–32.
- Rodríguez-Cabrera TM, Armas LF De (2023) Taxonomy of the enigmatic genus Acanthoniscus Gosse, 1851 (Isopoda: Oniscidea: Armadillidae), from Jamaica, with the

description of a new species. Nauplius 31: e2023006. https://doi.org/10.1590/2358-2936e2023006

- Schmalfuss H (2003) World catalog of terrestrial isopods (Isopoda: Oniscidea). Stuttg Beitr Naturkd 654: 1–341.
- Schmidt C, Leistikow A (2004) Catalogue of genera of the terrestrial Isopoda (Crustacea: Isopoda: Oniscidea). Steenstrupia 28 (1): 1–118.
- Sfenthourakis S, Taiti S (2015) Patterns of taxonomic diversity among terrestrial isopods. ZooKeys 515: 13–25. https://doi.org/10.3897/zookeys.515.9332
- Sket B (1988) Speleobiological investigation in the Colombian Andes 1984. Biolosky. Vestnik 36(2): 52–62.
- Solomou AD, Sfougaris AI, Sfenthourakis S (2019) Terrestrial isopods as bioindicators for environmental monitoring in olive groves and natural ecosystems. Journal of Natural History 53(27–28): 1721–1735. https://doi.org/10.1080/00222933.2019.1658821
- Taiti S (2017) Biologia e biogeografia degli isopodi terrestri (Crustacea, Isopoda, Oniscidea). Atti Accademia Nazionale Italiana di Entomologia, Anno 65: 83–90.
- Taiti S, Paoli P, Ferrara F (1998) Morphology, biogeography, and ecology of the family Armadillidae (Crustacea, Oniscidea). Israel Journal of Zoology 44(3-4): 291-301.
- Torres-Contreras R, Álvarez DM, Armas LF De (2015) Una nueva especie de *Charinus* Simon, 1892 (Amblypygi: Charinidae) del Caribe Colombiano. Revista Ibérica de Aracnología 27: 145–148.
- Valdivieso GE (2022) Parámetros espeleométricos para levantamientos espeleológicos de cavidades colombianas. Mundo Subterráneo 8: 2–22.
- Van Name WG (1936) The American land and freshwater isopod Crustacea. Bulletin of the American Museum of Natural History 71: 1–535.
- Vandel A (1952) Étude des isopodes terrestres récoltés au Vénézuela par le Dr. G. Marcuzzi. Memorie del Museo Cívico di Storia Naturale di Verona 3: 59–203.
- Vides-Navarro F, Montes-Calderón A, Fernández-Cuello G, Rojas-Martínez E (2015) Caracterización espeleológica e inventario biológico de la Caverna del Diablo en el municipio de Becerril, Departamento del Cesar. Respuestas 20(2): 93–104. https:// doi.org/10.22463/0122820X.356
- Zafra D (2021) Propuesta para la conservación de cuevas y cavernas en la Región Andina de Colombia. Tesis de especialización, Universidad Pontificia Bolivariana, Bucaramanga, Colombia, 89 pp.


Research Article

# A new species of supergiant *Bathynomus* A. Milne-Edwards, 1879 (Crustacea, Isopoda, Cirolanidae) from Vietnam, with notes on the taxonomy of *Bathynomus jamesi* Kou, Chen & Li, 2017

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# Abstract

A new supergiant species of *Bathynomus* A. Milne-Edwards, 1879 from Vietnam is described. *Bathynomus vaderi* **sp. nov.** is characterised by its wide, rectangular clypeal region with parallel lateral margins, concave distal margin, and narrowly acute apex; the distally narrowing and posteriorly curved coxa of pereopod 7; and the presence of 11 upwardly curved pleotelson spines. The new *Bathynomus* is the fourth species with upwardly curved pleotelson spines and the second supergiant in the South China Sea. The taxonomy of *B. jamesi* Kou, Chen & Li, 2017 from the South China Sea is also discussed based on a large series of specimens. Previously reported differences in body form and pleotelson spines, which suggest that there may be two forms or species, are regarded as intraspecific variation for the time being. The contemporary culinary trend and fishing of *Bathynomus* in Vietnam, which have contributed to this discovery, are also discussed.

Key words: Deep sea, fisheries, morphology, new taxon, taxonomy, seafood

# Introduction

Four species of giant isopods of the genus *Bathynomus* A. Milne-Edwards, 1879 (Cirolanidae) are currently known from the South China Sea: *B. affinis* Richardson, 1910, *B. decemspinosus* Shih, 1972 (from southernmost Taiwan), *B. doederleini* Ortmann, 1894 (from eastern and southwestern Taiwan), and *B. jamesi* Kou, Chen & Li, 2017 (from the northern part of the South China Sea) (Shih 1972; Tso and Mok 1991; Soong and Mok 1994; Kou et al. 2017; Huang et al. 2022). The material identified as *"Bathynomus kensleyi* Lowry & Dempsey, 2006" from the South China Sea, Philippines and Hong Kong (Lowry and Dempsey 2006) and Vietnam (Truong 2015) have since been shown to be *B. jamesi*, and two individuals from near the Sulu Islands (AM P42711, AM P42712; Lowry and Dempsey 2006) appear to belong to an undescribed species (Huang et al. 2022; Huang and Bruce 2024).



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**Copyright:** © Peter K. L. Ng et al. This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0). Over the last seven years, *Bathynomus* has become increasingly popular in Vietnam as a delicacy in contemporary culinary culture, and it has even been compared to lobsters for the quality of the flesh (Bang 2017). The demand has resulted in increased fishing efforts to collect *Bathynomus* for the live-seafood market, and specimens have been sold alive in eateries (out of water in chilled boxes) or in cold-water tanks in large restaurants (personal observations).

As a result of the seafood trade, we managed to obtain a large series of specimens collected by the Vietnamese fishermen in Quy Nhon City, all of which have been obtained in the South China Sea. While most of the material can be referred to *Bathynomus jamesi*, six specimens were distinct in having a differently shaped clypeal region and pleotelson structure, with the appendix masculina distinctly shorter. They are here recognised as a new species, *B. vaderi* sp. nov. and described in this paper.

# Materials and methods

Material from Vietnam were all purchased from the restaurants and local fishermen in Quy Nhơn City, Đà Nẵng City, and Hanoi. The terminology used in the description follows Bruce (1986) and Lowry and Dempsey (2006). Measurements are made of the maximum total length (TL) (in a straight line) from the base of the rostrum to the base of the pleotelson spines. Some of the drawings for description were inked electronically from a series of photographs using Adobe Illustrator v. 28.71. Specimens examined are deposited in the following institutions (with their acronyms indicated): **MNHN** – Muséum National d'Histoire Naturelle, Paris, France; **MZB** – Museum Zoologicum Bogoriense, BRIN, Cibinong, Indonesia; **RUMF** – Ryukyu University Museum, Fujukan, University of the Ryukyus, Japan; **TMCD** – Taiwan National Museum, Taipei, Taiwan; **ZVNU** – Zoology Collection of the Biological Museum, VNU University of Science, Hanoi, Vietnam; **ZRC** – Zoological Reference Collection of the Lee Kong Chian Natural History Museum, National University of Singapore.

# Taxonomy

Suborder Cymothoida Wägele, 1989 Family Cirolanidae Dana, 1852

Genus Bathynomus A. Milne-Edwards, 1879

**Restricted synonymy.** A. Milne-Edwards, 1879: 21–Bruce 1986: 126; Kensley and Schotte 1989: 129; Magalhães and Young 2003: 222; Lowry and Dempsey 2006: 168.

**Type species.** *Bathynomus giganteus* A. Milne-Edwards 1879; by monotypy. **Remarks.** Bruce (1986) reviewed the taxonomic history of *Bathynomus* and diagnosed the genus. Lowry and Dempsey (2006) provided the most recent comprehensive worldwide review of the *Bathynomus* species, along with their global distribution. Over the last decade, four more species have been added (Shipley et al. 2016; Kou et al. 2017; Sidabalok et al. 2020; and Huang et al. 2022), and the distributions of some have also been extended (e.g., Huang et al. 2022).

al. 2022; Dueñas et al. 2024). To date, Bathynomus has 11 "supergiant" and

nine "giant" extant species (Boyko et al. 2024), but there are still several species of *Bathynomus* that remain undescribed (see Sidabalok et al. 2020; Huang et al. 2022). Molecular methods (using COI and 16S rRNA sequences) have proved to be useful to help identify species as in the case of *B. jamesi*, which is morphologically similar to *B. kensleyi*, and to distinguish *B. yucatanensis* from *B. giganteus* s. str., with support from morphology (Huang et al. 2022; Huang and Bruce 2024). *Bathynomus* fossil species have been recently reviewed by Hyžný et al. (2019), with a new species described later by Hyžný et al. (2020).

#### Bathynomus jamesi Kou, Chen & Li, 2017

Figs 1-3, 9E-H, 10B-D

- Bathynomus kensleyi–Lowry and Dempsey 2006: 184; Truong 2015: 80. (Not Bathynomus kensleyi Lowry & Dempsey, 2006).
- Bathynomus jamesi Kou, Chen & Li, 2017: 285, figs 1–5–Huang et al. 2022: 890, figs 3–8, 9a.
- Bathynomus sp.-Huang et al. 2022: 902, fig. 9b.

**Material examined.** VIETNAM • 1 3; 300 mm; 1 2; 280 mm; collected by trawlers operating off Quảng Ngãi, Bình Định, Khánh Hòa and/or Phú Yên Provinces, central Vietnam; purchased by Nguyen Thanh Son from seafood markets in Hanoi; April 2024; ZRC 2024.0088 • 1 ♀; 285 mm; same collection data as for preceding; MZB. Cru. Iso 118 • 4 3; 415 mm, 407 mm, 380 mm, 313 mm; 1 2; 303 mm; same collection data as for preceding; ZRC 2024.0118 • 1 ♀; 293 mm; same collection data as for preceding; ZRC 2024.0119 • 1 ♂; 325 mm; 1  $\bigcirc$ ; 305 mm; same collection data as for preceding; RUMF-ZC-8375 • 1  $\bigcirc$ ; 410 mm; same collection data as for preceding; ZRC 2024.0179. TAIWAN • 1 2; 303 mm; TMCD 3326; north part of South China Sea between North Vereker Bank (21.061°N, 116.109°E) and Pratas Island (20.717°N, 116.700°E); coll. bottom trawl, Keelung-based fishing vessel Jin Ruiyi 37; 17 June 2019 • 1 3; 369 mm; same collection data as for preceding; TMCD 3327 • 1 ♂; 314 mm; same collection data as for preceding; TMCD 3328 • 1 2; 288 mm; same collection data as for preceding; TMCD 3329 • 1 3; 342 mm; same collection data as for preceding; TMCD 3330 • 1 ♀; 260 mm; about 300 km south-west of Pratas Island (19.084°N, 115.250°E); coll. bottom trawl, Keelung-based fishing vessel Jing Yang; 12 May 2020; TMCD 3331 • 1 2; 267 mm; same collection data as for preceding; TMCD 3332 • 1 d; 296 mm; same collection data as for preceding; TMCD 3333 • 1 3; 330 mm; same collection data as for preceding; TMCD 3334. PHILIPPINES • 1 d; 320 mm; MUSORSTOM 2 station CP75, 13°51'N, 120°30'E, off Manila, Luzon Island 300-330 m; 25 March 1976; MNHN IS.2290.

**Remarks.** The species was originally described from a subadult female and three juveniles by Kou et al. (2017) from off Hainan Island in the northern part of the South China Sea. Huang et al. (2022) subsequently obtained a series of specimens from Pratas (= Tungsha) Islands in the South China Sea and redescribed the species at length. Huang et al. (2022: 903) observed that there appeared to be two forms of *B. jamesi*, a slender type (with the body having the lateral edge of the pereon relatively straight; Huang et al. 2022: fig. 9b) and a stout type (with the pereonal lateral edge convex; Huang et al. 2022: fig. 9a).



Figure 1. *Bathynomus jamesi* Kou, Chen & Li, 2017, colour in life, dorsal views **A** ♂ (300 mm) (ZRC 2024.0088), Vietnam **B** ♀ (280 mm) (ZRC 2024.0088), Vietnam **C** ♂ (410 mm) (ZRC 2024.0179), Vietnam.

Huang et al. (2022) also observed that compared to the stout type, the pleotelson of the slender type was relatively longer (0.70 times as long as wide) (vs 0.42–0.56) and its pleotelson spines are flat and proximally broad (vs round and proximally narrow).

Huang et al. (2022: table 1) reported four males (TMCD 3327, 3328, 3330, 3333) and three females (TMCD 3329, 3331, 3332) of the stout type which they regarded as *B. jamesi* s. str., and one male (TMCD 3334) and one female (TMCD 3326) of the slender type which they considered as either a morphological variation of *B. jamesi* or possibly a separate species. In their photograph of the two forms, however, these authors depicted specimen TMCD 3329 as the slender type (Huang et al. 2022: fig. 9b) and TMCD 3326 as the stout type (Huang et al. 2022: fig. 9b) (sexes not stated). Their photograph of the slender type showed a proportionately longer pleotelson with the spines relatively broader and flatter while that of the stout type has a proportionately wider pleotelson with acute spines; these observations contradict what was discussed in Huang et al. (2022: 903).

We examined the specimens of Huang et al. (2022) in TMCD and found that the character states of the pereon and pleotelson discussed by them, including the associated body types in their table with codes TMCD 3326 and 3329, are indeed reversed. The slender type (based on their figured female specimen TMCD 3329) has the lateral edge of the pereon gently or distinctly convex and



**Figure 2**. Dorsal views. *Bathynomus jamesi* Kou, Chen & Li, 2017 A ♂ (320 mm) (MNHN IS.2290), Philippines B ♂ (296 mm) (TMCD 3333), Taiwan C ♂ (330 mm) (TMCD 3334), Taiwan D, E ♀ (288 mm) (TMCD 3329), Taiwan F ♀ (303 mm) (TMCD 3326), Taiwan.

a proportionately wider pleotelson with the spines relatively wider and somewhat flatter (Figs 2D, E, 3A); while the stout type (based on their figured female specimen TMCD 3326) has the lateral edge of the pereon gently convex to almost straight posteriorly and a narrower pleotelson with the spines acute and more cylindrical (Figs 2F, 3B). The relative shape or convexity of the pereon and its lateral edge is not a reliable character as they are somewhat flexible; depending on how they are positioned or flexed, it can appear more slender or stout. For example, the female specimen (288 mm, TMCD 3329) figured as the slender type by Huang et al. (2022: fig. 1b) has the lateral edge of the pereon appears gently or strongly convex depending on how they are stretched and photographed (Fig. 2D, E). Other specimens from Taiwan regarded by Huang et al. (2022) as the stout type (e.g., TMCD 3327, 3333) or slender type (e.g., TMCD 3334) show varying forms of the pereon (Fig. 2B, C).

There is some variation in the kind of pleotelson spines present. Huang et al. (2022) noted that the spines may be more acute or are flattened and broader. We did not detect any pattern with the kind of spines present. The pleotelson spines do tend to be more slender, with a rounder cross-section and are usually longer in smaller specimens (ca 300 mm TL or less) (e.g., Fig. 3B, D), but we also have smaller specimens with more flattened spines as well (Fig. 3A, F). The largest specimens (exceeding 350 mm TL), however, invariably have shorter spines which are more flattened (Fig. 3C, E). We also note that the form of the median pleotelson spine also varies; in some specimens, the lateral margins have an additional tubercle, and its base may have an additional small spine or sharp tubercle (Fig. 3A, E).

For the adult specimens from Taiwan and Vietnam, the shape and proportions of the pleotelson appears to vary rather considerably, from proportionately wider and subrectangular in shape to narrower and more rounded, with length-to-width ratios ranging from 0.57–0.72 (Fig. 3). This is unexpectedly substantial for one species. As the shape of the pleotelson is a critically important and usually highly consistent species character in cirolanid taxonomy (as is the number of robust setae on the appendages), this was rather surprising. For the Taiwanese specimens examined by Huang et al. (2022), the pleotelson ratios are 0.57 and 0.71 for the two specimens of the "slender type" they reported (Fig. 3A), with the rest of the specimens (the "stout type") ranging from 0.58-0.72 (Fig. 3B–D). As discussed above, we cannot differentiate their two types for the specimens from Taiwan and Vietnam we examined. There is, however, some correlation with size as the specimens below 300 mm TL tend to have relatively longer pleotelsons, with the ratios 0.70-0.73 (Fig. 3A, D, F). That being said, while most specimens above 300 mm TL have pleotelson ratios ranging from 0.63-0.68, the largest specimens from Vietnam exceeding 400 mm TL (ZRC 2024.0118, ZRC 2024.0179) have ratios of 0.72 as well (Fig. 3E). There is no correlation of pleotelson shape with sex. We also could not correlate pleotelson proportions with the kind of spines present along the margin. Those with more spines that have a relatively flat cross-section (Fig. 3A, C, E, F) have ratios of 0.63-0.71, while those spines that have a more rounded cross-section (Fig. 3B, D) range from 0.63–0.72.

The degree of within species variation observed in pleotelson shape and setation is slight in the Cirolanidae, and for most species in most genera, pleotelson shape is a prime taxonomic character in distinguishing species. This may not be the case for some cryptic species groups where the pleotelson is similar in form, but that reinforces the point of pleotelson uniformity. For example, the *Cirolana 'parva*-group' is a well-known species group established by Bruce (1986) for 13 taxa, with seven characters used to differentiate species (including structures of the frontal lamina, pereopod 1, pleotelson and uropods). This species group currently contains 34 similar looking species worldwide (Rodcharoen et al.



**Figure 3**. Pleotelson, dorsal views. *Bathynomus jamesi* Kou, Chen & Li, 2017 **A** ♀ (288 mm) (TMCD 3329), Taiwan **B** ♀ (303 mm) (TMCD 3326), Taiwan **C** ♂ (369 mm) (TMCD 3327), Taiwan **D** ♀ (260 mm) (TMCD 3331), Taiwan **E** ♂ (407 mm) (ZRC 2024.0118), Vietnam **F** ♀ (293 mm) (ZRC 2024.0119), Vietnam.

2016; Sidabalok and Bruce 2017; Jennings et al. 2020), and there remain many undescribed species. The degree of variation observed in *B. jamesi* specimens suggests that it may well be a species complex. To ascertain this, a much larger series of specimens collected from a wider geographical area will be needed, with the associated morphological and genetic studies done.

*Bathynomus jamesi* was first reported from Vietnam by Truong (2015) as "*Bathynomus kensleyi*" (cf. Huang et al. 2022; Huang and Bruce 2024). Truong (2015) based this record on a single specimen (sex not stated) measuring 260 mm collected by fishermen from the "Trường Sa area" (the Spratly Islands) in the South China Sea. The repository for the specimen is not known. As his figures do not show the clypeal region in frontal view, form of the pereopod 7 coxa or convexity of the pleotelson, so we cannot be certain of its identity, and as such, we retain it under *B. jamesi* for the time being.

*Bathynomus jamesi* is one of the largest supergiants known. The largest is believed to be *B. giganteus*, with one specimen from Brazil supposedly reaching 500 mm in length (Lowry and Dempsey 2006: 166). The two largest males of *B. jamesi* we have seen (ZRC 2024.0118, ZRC 2024.0179) measure 415 mm and 410 mm in length, respectively and weigh more than 2.6 kg each (Fig. 1C). This makes *B. jamesi* the largest known supergiant species (and largest isopod) in the Indo-West Pacific.

One female specimen examined (TMCD 3329, 288 mm) had the oostegites developed forming a brood pouch. There were about a dozen eggs inside the pouch, but the number of eggs is an underestimate as many had fallen out during collection and preservation.

#### Bathynomus vaderi sp. nov.

https://zoobank.org/9021E442-A46D-45FA-A760-9F25F5A9B05F Figs 4-8, 9A-D, 10A

Material examined. *Holotype*, VIETNAM, ♂; 266 mm; offshore of Quy Nhơn City, Bình Định Province, south-central Vietnam, ca. 50 nautical miles from shore, from deep-water (depth not known); purchased by Tran Anh Duc from Eo Gió, Nhơn Lý commune; 27 March 2022; ZRC 2022.0621. *Paratypes*: 1 ♂; 270 mm; same data as holotype; ZRC 2024.0176 • 1 ♂; 258 mm; same data as holotype; ZVNU 110001 • 1 ♂; 257 mm; same data as holotype; ZVNU 110002 • 2 ♂; 325 mm, 295 mm; collected by trawlers operating off Quảng Ngãi, Bình Định, Khánh Hòa and/or Phú Yên Provinces, central Vietnam; purchased by Nguyen Thanh Son from seafood restaurant in Đà Nẵng City, Vietnam; September 2024; ZRC 2024.0180.

**Type locality.** Offshore of Quy Nhơn, ca 50 nautical miles from shore, south-central Vietnam, west of the Spratly Islands.

**Diagnosis.** Clypeal region with lateral margin parallel, distal margin concave, apex narrowly acute, transversely rectangular (Figs 4C, 5C, 6C, 9A). Coxa of pereopod 7 narrows distally, curved posteriorly (Figs 5D, 6D, E, 9B). Distinct row of setae present between pleotelson spines; 11 upwardly curved pleotelson spines; pleotelson 0.6 as long as wide (Figs 5A, 9D); pleotelson vaulted laterally (Figs 6E, 9C). Appendix masculina slightly shorter than or reaching to end of endopod of pleopod 2 (Fig. 10A).

**Description of male holotype.** Body (Figs 4A, B, 5A, 6A) 266 mm long, 135 mm wide at pereonite 5, length 1.9 times width, ovate in shape, coarsely punctate, without sculpture (Figs 4A, 5A, 6A). Head ridge above eyes discontinuous (Figs 4C, 5B, 6B). Clypeal region transversely rectangular, lateral margins parallel, distal margin slightly concave, apex narrowly subacute (Figs 4C, 5C, 6B, C, 9A).



Figure 4. Bathynomus vaderi sp. nov., paratype ♂ (258 mm) (ZVNU 110001), Vietnam, colour in life A dorsal view B body, ventral view C cephalon, anterior view.

Antennula (Fig. 6B); flagellum 1.2 longer than peduncle. Antenna peduncle article 4-articulate (Fig. 6B), article 4 about 1.4 times longer than article 3 (Fig. 6B), flagellum extending to within pereonite 2 (Fig. 6A, B).

Mandible (Fig. 7D) palp not reaching incisor, with setal fringe on lateral margin of distal half of article 2 and along article 3. Maxillula (Fig. 7E) mesial lobe with 4 robust setae, lateral lobe with 9 keratinised robust setae. Maxilla (Fig. 7C) lateral lobe with 9 keratinised robust setae, middle lobe with 7 keratinised robust setae, mesial lobe with fringe of long plumose setae. Maxilliped palp (Fig. 7A) typical of genus; maxilliped endite with 4 coupling hooks (Fig. 7B).



Figure 5. *Bathynomus vaderi* sp. nov., holotype ♂ (266 mm) (ZRC 2022.0621), Vietnam **A** dorsal view **B** cephalon, anterior view **C** clypeal region and buccal cavity **D** body, lateral view.

Pereopod 1 (Fig. 8A) ischium with 1 posteroproximal robust seta and 3 robust setae on posterodistal margin; merus with 6 robust setae on anterodistal angle, posterolateral margin with 4 robust setae in proximal row on and 3 robust setae in distal row; propodus 2.3 as long as wide, with 4 robust setae on posterior margin. Pereopod 2 (Fig. 8B) ischium with 3 robust setae on posterior margin and 4 robust setae on posterodistal margin; merus with 9 robust setae on anterodistal angle,



Figure 6. Bathynomus vaderi sp. nov., holotype ♂ (266 mm) (ZRC 2022.0621), Vietnam A dorsal view B cephalon, anterior view C clypeal region D body, lateral view E pereon, lateral view F pleotelson. Scale bars: 2.0 cm (A, D–F); 1.0 cm (B, C).

posteromedial margin with 3 robust setae in proximal row and 3 robust setae in distal row; propodus with 4 robust setae on posterior margin. Pereopod 7 (Fig. 8C) basis 3.5 times as long as greatest width, inferior margin convex; ischium 0.5 times as long as basis, inferior margin with 1 robust seta, superior distal angle with 6 robust setae, inferior distal angle with 6 robust setae; merus 0.6 as long as ischium, as long as wide, inferior margin with 1 robust seta, superior distal angle with 11 robust setae, inferior distal angle with 13 robust setae; carpus as long as ischium, 2 times as long as wide, inferior margin with 3 robust setae (as 1 + 2), superior distal angle with 13 robust setae, inferior distal angle with 10 robust setae; propodus 0.9 as long as ischium, 3.8 times as long as wide, inferior margin with 8 robust setae, inferior distal angle with 1 robust setae (as 2 clusters of 2), superior distal angle with 8 robust setae, inferior distal angle with 1 robust setae, inferior distal angle 0.5 as long as propodus. Coxa of pereopod 7 distally narrowed, gently curved posteriorly (Figs 5D, 6E, 9B).



**Figure 7**. *Bathynomus vaderi* sp. nov., holotype 3 (266 mm) (ZRC 2022.0621), Vietnam **A** right maxilliped palp, outer view **B** right maxilliped endite, inner view, setae omitted **C** right maxilla **D** left mandible and palp, outer view **E** lateral lobe of right maxilulla, outer view. Scale bars: 2.0 mm.

Pleonite 3 (Fig. 6E) not extending beyond pleonite 5. Pleonite 4 (Fig. 6E) reaching to end pleonite 5. Penial process flat lobes (Fig. 4B). Appendix masculina with parallel margins, not extending beyond endopod, distally narrowly rounded (appendix masculina absent on holotype male) (Fig. 10A).

Pleotelson (Figs 5A, 6F, 9C, D) 0.6 time as long as greatest width, smooth (minute pores), with inconspicuous longitudinal carina on dorsal surface; dorsal



**Figure 8.** *Bathynomus vaderi* sp. nov., holotype ♂ (266 mm) (ZRC 2022.0621), Vietnam **A** pereopod 1 **B** pereopod 2 **C** pereopod 7 **D** uropod, ventral view **E** uropod, dorsal view. Scale bars: 1.0 cm (**A**−**C**); 2.0 cm (**D**, **E**).

surface distinctly convex (Figs 5D, 6E, 9C, D); posterior margin with 11 long, prominent, upwardly curved spines and pair of small posterolateral spines, with setae between spines, central spine simple.

Uropods (Figs 4A, 6F, 8D, E) not extending beyond pleotelson. Peduncle with 3 short robust setae on caudolateral margin (Fig. 8D); exopod and endopod with smooth lateral and distal margins; exopod lateral margin convex with 12 left and 11 right robust setae along margin, setal fringe continuous length (83.3%), medial margin straight, distomedial corner rounded, distal margin convex with



**Figure 9. A–D** *Bathynomus vaderi* sp. nov., holotype ♂ (266 mm) (ZRC 2022.0621), Vietnam **E–H** *B. jamesi* Kou, Chen & Li, 2017, ♂ (320 mm) (MNHN IS.2290), Philippines **A, E** clypeal region **B, F** pereon lateral view **C, G** pleotelson, dorsal view **D, H** pleotelson, lateral view. Abbreviations: c6 = coxa of pereopod 6; c7 = coxa of pereopod 7.

5 left and 7 right robust setae, distolateral corner produced, acute; endopod lateral margin convex, distally straight, with 5 left and 6 right robust setae; medial margin posteriorly convex; distomedial corner rounded; distal margin straight with 12 left and 13 right robust setae; distolateral corner produced, acute. **Female.** Not known.



**Figure 10.** Appendix masculina **A** *Bathynomus vaderi* sp. nov., paratype ♂ (270 mm) (ZRC 2024.0176) **B** ♂ *B. jamesi* Kou, Chen & Li, 2017 (320 mm) (MNHN IS.2290), Philippines **C** *B. jamesi* Kou, Chen & Li, 2017 ♂ (296 mm) (TMCD 3333), Taiwan **D** *B. jamesi* Kou, Chen & Li, 2017 ♂ (314 mm) (TMCD 3328), Taiwan.

**Variation.** Paratype robust setae counts as follows exopodal lateral margin with 9–13 robust setae, distal margin with 4–6, endopodal lateral margin with 1, 4 and 5 and distal margin with 10–14; pleotelson with 11 upwardly curved spines and one paratype with addition 2 small posterolateral spines. The holotype lacks the appendix masculina, but it is present in the other type specimens (Fig. 10A). As discussed by Barradas-Ortiz et al. (2003), these structures may be lost and regrow at different moults throughout the life of the animal.

**Etymology.** The species named after the most famous Sith Lord in the *Star Wars* movie series, Darth Vader, whose helmet resembles the head of the new *Bathynomus* species.

**Distribution.** Known only from Vietnam. We are unable to determine the exact location where *B. vaderi* was trawled, as the dealers and fishermen would only say they were obtained from deep waters off Vietnam near the Spratly Islands.

**Remarks.** *Bathynomus vaderi* sp. nov. can be distinguished by the parallel margin of clypeal region, rectangular shape of clypeal region, the posteriorly curved coxa of pereopod 7, upwardly curved spines of the pleotelson, setae between pleotelson spines, and the laterally vaulted pleotelson. *Bathynomus vaderi* is the fourth species with upwardly curved pleotelson spines.

Bathynomus vaderi is very similar to the congeners with upwardly curved pleotelson spines, i.e., B. jamesi, B. kensleyi, and B. lowryi Bruce & Bussarawit, 2004. Other similarities with B. jamesi are in the length of antennae, which reaches pereonite 2, the number of pleotelson spines, pleonite 4 extending beyond pleonite 5, uropod endopod reaching the end of the pleotelson and beginning of central pleotelson spine, exopod and endopod distolateral angle is produced and subacute. Bathynomus vaderi, however, differs from B. jamesi in the following character states: the lateral margins of the clypeal region are parallel (Figs 4C, 5C, 9A) (vs gently converging distally in B. jamesi; Fig. 9E); the apex of the clypeal region is acute (Figs 4C, 5C, 9A) (vs obtusely rounded in B. jamesi; Fig. 9E); the clypeus is transversely rectangular in shape (Figs 4C, 5C, 9A) (vs square or subquadrate; Fig. 9E); the distolateral corners of the uropod endopod and exopod are acute (Fig. 8D, E) (vs subacute in B. jamesi; Huang et al. 2022: fig. 4d, e); the P7 coxa has the lateral margins more sinuous, with the posterior margin distinctly concave in form towards the tip (Figs 6E, 9B) (vs margins less sinuous with the posterior margin only slightly concave towards the tip in B. jamesi; Fig. 9F); the dorsal surface of the pleotelson is distinctly raised, being gently convex in lateral view (Figs 5D, 6D, 9D) (vs almost flat or only slightly convex in lateral view in B. jamesi; Fig. 9H); there are numerous short setae present between the pleotelson spines (Fig. 9C) (vs absent or only with scattered setae in B. jamesi; Figs 3, 9G); and the appendix masculina is shorter, just reaching to edge of endopod of pleopod 2 (Fig. 10A) (vs distinctly longer, reaching well beyond edge of endopod of pleopod 2 in B. jamesi; Fig. 10B-D). Bathynomus vaderi and B. jamesi are sympatric congeners in the South China Sea, a pattern of co-occurrence which has been discovered before in B. giganteus, B. yucatanensis, and B. maxeyorum from Gulf of Mexico (Huang et al. 2022).

The denser setation between the pleotelson spines is diagnostic for *B. vaderi* but may not be a reliable character once a larger series of specimens is collected. We note that, in *B. jamesi*, most of the specimens do not have setae or only a few scattered ones between the pleotelson spines. In a few specimens (from the recent material from Vietnam), however, the setae are slightly denser, although not to the same degree observed in *B. vaderi*.

*Bathynomus vaderi* is similar to *B. kensleyi* in the clypeal region characters, i.e., parallel margin, concave distal margin and rectangular shape; and uropod endopod characters, i.e. straight distal margin with produced acute distolateral corner. *Bathynomus vaderi* differs from *B. kensleyi* in having the clypeal region with a pointed apex (Figs 4C, 5C, 6C, 9A) (vs rounded in *B. kensleyi*; Lowry and Dempsey 2006: fig. 18E; Huang et al. 2022: fig. 2b), 11 spines on the pleotelson (Figs 4A, 5A, 6F, 9A) (vs 9 in *B. kensleyi*; Lowry and Dempsey 2006: fig. 18A, F; Huang et al. 2022:



Figure 11. Seafood market in Hanoi, Vietnam, selling *Bathynomus jamesi* **A**, **B** chilled water tanks keeping specimens alive for sale **C** three large specimens weighing 7.7 kg **D** Large specimens exceeding 2 kg in weight command premium prices.

fig. 2), the pleotelson broader than long (Figs 5A, 6F, 9A) (vs longer than broad in *B. kensleyi*; Lowry and Dempsey 2006: fig. 18A, F; Huang et al. 2022: fig. 2), the uropod exopod distolateral corner produced and acute (Fig. 8D, E) (vs not produced in *B. kensleyi*; Lowry and Dempsey 2006: fig. 19D, E), and the posterior end of pleonites 3 and 4 not reaching beyond the posterior end of pleonite 5 (Figs 5D, 6E) (vs pleonite 3 exceeds pleonites 4 and 5; pleonite 4 reaches the end of pleonite 5 in *B. kensleyi*; Lowry and Dempsey 2006: fig. 18B, C; Huang et al. 2022: fig. 2a).

Other than sharing the upwardly curved pleotelson spines, there are other similarities between *B. vaderi* and *B. lowryi*: the antenna flagellum extends within pereonite 2, the clypeus is rectangular, and the pleotelson is broader than long. Both species, however, differ in having the apex of the clypeal region pointed (Figs 4C, 5C, 6C, 9A) (vs truncated in *B. lowryi*; Bruce and Bussarawit 2004: fig. 1C), 11 spines on the pleotelson (Figs 4A, 5A, 6F, 9C) (vs seven in *B. lowryi*; Bruce and Bussarawit 2004: figs 1A, 4A, 5), setae between the pleotelson spines (Figs 5A, 9C) (vs absent in *B. lowryi*; Bruce and Bussarawit 2004: figs 1A, 5), an inconspicuous longitudinal carina on the dorsal surface of the pleotelson (Figs 5A, 9C) (vs conspicuous in *B. lowryi*; Bruce and Bussarawit 2004: figs 1A, 4A, 5), a continuous setal fringe on the exopod of the uropod, which covers 83% of the margin (Fig. 8D, E) (vs fringe of medium length, covering 67% of margin in *B. lowryi*; Bruce and Bussarawit 2004: fig. 4B, C), and a convex lateral margin of the uropod exopod (Fig. 8D, E) (vs strongly convex and expanded in *B. lowryi*; Bruce and Bussarawit 2004: fig. 4B, C).

Huang et al. (2022) excluded the material from Sulu Sea previously considered to be *B. kensleyi* by Lowry and Dempsey (2006) and treated it as an undescribed species based on the states of the pereon, pleonite, maxilliped, pleotelson spines, and other characters. Based on the above characters reported by Huang et al. (2022) (species was not figured), the Sulu material is similar to *B. vaderi* in possessing more slender pleotelson spines and pleonite 4 that does not extend beyond end of pleonite 5. The two taxa, however, are different, as the Sulu Sea individual has a strongly convex uropodal exopod lateral margin (vs convex in *B. vaderi*, Fig. 8D, E). Furthermore, Shane Ahyong (pers. comm.) has compared specimens of *B. vaderi* with the Sulu Sea material, which is in the Australian Museum, and he comments that they are different taxa.

# A note on the Bathynomus fishery

In Vietnam, Bathynomus, known locally as bo bien or "sea bugs", has been fished for food apparently since 2017. Specimens are caught in deep water by trawlers operating in various parts of Biển Đông (= East Sea, Vietnamese part of the South China Sea) and brought back to shore alive in ice boxes. The isopods are kept out of water and chilled, and in this state, can survive for many days if well insulated. They are then transported to restaurants for sale. Smaller eating establishments keep the isopods in ice boxes to be cooked when asked, while large restaurants have dedicated tanks with chilled water to keep and display the animals (Fig. 11). One local restaurant owner in Eo Gió in Nhơn Lý commune (Quy Nhơn City, Bình Định Province), who was selling these isopods, explained that Bình Định, which is a coastal province at south-central Vietnam, is the main area where the isopods are caught, and a number of fishermen target these animals. Once every few days, this restaurant receives the catch from the fishermen, usually about 10 individuals each time. He also knows that they are sent alive to restaurants in Hanoi, where there is a high demand for them (Tran Anh Duc pers. comm. 2022). In Hanoi, Bathynomus once was sold at high prices, but this has decreased over the years. In 2017, the price was up to 2 million Vietnamese Dong (ca USD \$80) per kilogram, with large individuals reaching 2 kg in weight (Bang 2017). As noted above, large specimens of B. jamesi can reach weights in excess of 2.5 kg. Because of these prices, fishermen started

to increase the supply, and by 2023 the price dropped to around 1.5 million Vietnamese Dong per kilogram (An 2023); by early 2024, it was about 1 million Vietnamese Dong (ca USD \$40) per kilogram for 1-2 kg individuals. In 2017, specimens had to be pre-ordered, and diners had to wait up to a month to collect their Bathynomus specimens in seafood outlets in Hanoi (Bang 2017). Today, some seafood markets in Hanoi, Hồ Chí Minh City, and Đà Nẵng City keep up to 30 individuals in their chilled water tanks for customers to buy. It is also common to see advertisements selling "sea bugs" on social network by some seafood stores. Once they are purchased online, the stores will immediately ship the alive animals in icebox to customers. Individuals weighing between 0.6-0.9 kg are the best sellers because the price is more affordable. Large specimens in excess of 2 kg are also sought after as they are less common, and their size makes for an impressive dish. In mid-2024, prices in some places in Hanoi have dropped and cost only 0.68 million Vietnamese Dong (ca USD \$27) per kilogram. The prices of these animals, however, do vary quite a bit due to supply and demand, and can cost substantially more in higher end restaurants.

It is noteworthy that four type specimens of *B. vaderi* were obtained from dealers in Quy Nhơn in south-central Vietnam, where the isopods are fished. In the restaurants in Hanoi where *Bathynomus* is also sold, we have only seen *B. jamesi* so far, although we were told the specimens are also from Quy Nhơn. It is possible *B. vaderi* has a slightly different habitat, depth range, or distribution than *B. jamesi*, and what is caught depends on where individual boats trawl. In the early 2020s, *Bathynomus* was also sold for high prices in Taiwan for food, often cooked with noodles in niche restaurants (Everington 2023), with fishermen collecting them from the Pratas Islands. Fishermen collecting *Bathynomus* for restaurants in Taiwan in these islands were also the source of the material reported by Huang et al. (2022) (Huang Ming-Chih pers. comm.). During the last year, however, *Bathynomus*, is no longer popular in Taiwan, and few places sell it now (Chan Tin-Yam pers. comm.). All the supergiant specimens we know of and/or have seen from Pratas and Taiwan belong to only one species, *B. jamesi*.

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# Additional information

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#### Author contributions

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#### Data availability

All of the data that support the findings of this study are available in the main text.

## References

- An T (2023) Bo biển 4 triệu đồng một con, dân sành ăn vẫn tranh nhau mua [Sea bug 4 million VND each, gourmets are still competing to buy]. Vietnamnet newspaper, 6 April 2023. [In Vietnamese] https://vietnamnet.vn/bo-bien-4-trieu-dong-mot-con-dansanh-an-van-tranh-nhau-mua-2128935.html [Accessed on: 2024-12-9]
- Bang N (2017) Bo biển khổng lồ 4 triệu/con: Món nhậu lạ của dân Hà thành [Giant sea bug 4 million VND each: a strange delicacy for the people of Hanoi]. Vietnamnet newspaper, 17 May 2017. [In Vietnamese] https://vietnamnet.vn/bo-bien-khong-lo-4trieucon-mon-nhau-la-cua-dan-ha-thanh-372986.html [Accessed on: 2024-12-9]
- Barradas-Ortiz C, Briones-Fourzán P, Lozano-Álvarez E (2003) Seasonal reproduction and feeding ecology of giant isopods *Bathynomus giganteus* from the continental slope of the Yucatan Peninsula. Deep Sea Research Part I: Oceanographic Research Papers 50: 495–513. https://doi.org/10.1016/S0967-0637(03)00036-0
- Boyko CB, Bruce NL, Hadfield KA, Merrin KL Ota Y, Poore GCB, Taiti S (Eds) (2024) World Marine, Freshwater and Terrestrial Isopod Crustaceans database. *Bathynomus* A. Milne-Edwards, 1879. World Register of Marine Species https://www.marinespecies. org/aphia.php?p=taxdetails&id=248508 [Accessed on 2024-11-06]
- Bruce NL (1986) Cirolanidae (Crustacea: Isopoda) of Australia. Records of the Australian Museum, Supplement 6: 1–239. https://doi.org/10.3853/j.0812-7387.6.1986.98
- Bruce NL, Bussarawit S (2004) *Bathynomus lowryi* sp. nov. (Crustacea: Isopoda: Cirolanidae), the first record of the 'giant' marine isopod genus, from Thailand waters. Phuket Marine Biological Center Research Bulletin 65: 1–8.

Dana JD (1852) On the classification of the Crustacea Choristopoda or Tetradecapoda. The American Journal of Science and Arts, Second Series 14(41): 297–316.

- Dueñas LF, Bolaños-Cubillos N, Abril-Howard A, Mayorga JS, Friedlander AM, Whitney G (2024) First record of *Bathynomus giganteus* A. Milne-Edwards, 1879 (Crustacea: Isopoda) in oceanic waters of the Western Colombian Caribbean. Caribbean Journal of Science 54: 185–188. https://doi.org/10.18475/cjos.v54i2.a1
- Everington K (2023) Taipei eatery features giant isopod ramen. Taiwan News, 23 May 2023.
- Huang M-C, Bruce NL (2024) DNA barcoding of the supergiant isopods from *Bathyno-mus kensleyi* Lowry & Dempsey, 2006 (Cirolanidae) and a molecular biology comparison of *B. jamesi* Kou, Chen & Li, 2017. Biodiversity Data Journal 12: e111046. https://doi.org/10.3897/BDJ.12.e111046
- Huang M-C, Kawai T, Bruce NL (2022) A new species of *Bathynomus* Milne-Edwards, 1879 (Isopoda: Cirolanidae) from the southern Gulf of Mexico with a redescription of *Bathynomus jamesi* Kou, Chen & Li, 2017 from off Pratas Island, Taiwan. Journal of Natural History 56(13–16): 885–921. https://doi.org/10.1080/00222933.2022. 2086835
- Hyžný M, Pasini G, Garassino A (2019) Supergiants in Europe: on the cirolanid isopod Bathynomus A. Milne Edwards, 1879 (Malacostraca, Peracarida) from the Plio-Pleistocene of Italy. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 291: 283–298. https://doi.org/10.1127/njgpa/2019/0802
- Hyžný M, Campos IB, Carretero JC (2020) A new species of *Bathynomus* A. Milne-Edwards, 1879 (Malacostraca: Peracarida: Isopoda: Cirolanidae) from the upper Miocene of the Guadalquivir Basin (Spain). Zootaxa 4819(1): 159–169. https://doi. org/10.11646/zootaxa.4819.1.8
- Jennings LA, Bojko J, Rotjan RD, Behringer DC (2020) *Cirolana westbyi* (Isopoda: Cirolanidae) a new species in the *'Cirolana parva*-group' from the Turneffe Atoll, Belize. Journal of Natural History 54(31–32): 2053–2069. https://doi.org/10.1080/002229 33.2020.1837273
- Kensley B, Schotte M (1989) Guide to the Marine Isopod Crustaceans of the Caribbean. Smithsonian Institution Press, Washington, D.C. & London, 308 pp. https://doi. org/10.5962/bhl.title.10375
- Kou Q, Chen J, Li X, He L, Wang Y (2017) New species of the giant deep-sea isopod genus *Bathynomus* (Crustacea, Isopoda, Cirolanidae) from Hainan Island, South China Sea. Integrative Zoology 12: 283–291. https://doi.org/10.1111/1749-4877.12256
- Lowry JK, Dempsey K (2006) The giant deep-sea scavenger genus *Bathynomus* (Crustacea, Isopoda, Cirolanidae) in the Indo-West Pacific. In: Richer De Forges B, Justine J-L (Eds) Tropical Deep-Sea Benthos, Volume 24. Mémoires du Muséum national d'Histoire naturelle 193: 163–192.
- Magalhães N, Young PS (2003) *Bathynomus* A. Milne Edwards, 1879 (Isopoda, Cirolanidae) from the Brazilian coast, with description of a new species. Arquivos do Museu Nacional, Rio de Janeiro 61: 221–239.
- Milne-Edwards A (1879) Sur un isopode gigantesque, des grandes profondeurs de la mer. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 88: 21–23.
- Richardson H (1910) Marine isopods collected in the Philippines by the U.S. Fisheries steamer Albatross in 1907–8. Department of Commerce and Labor, Bureau of Fisheries Document 736: 1–44. https://doi.org/10.5962/bhl.title.82673

- Rodcharoen E, Bruce NL, Pholpunthin P (2016) Description of four new species of the *Cirolana 'parva* group' (Crustacea: Isopoda: Cirolanidae) from Thailand, with supporting molecular (COI) data. Journal of Natural History 50(31–32): 1935–1981. https://doi.org/10.1080/00222933.2016.1180718
- Shih CT (1972) Note on the giant isopod genus *Bathynomus* Milne Edwards, 1979 with description of a new species. Publications of the Seto Marine Biological Laboratory 21: 31–42. https://doi.org/10.5134/175798
- Shipley ON, Bruce NL, Violich M, Baco A, Morgan N, Rawlins S, Brooks EJ (2016) A new species of *Bathynomus* Milne Edwards [*sic*], 1879 (Isopoda: Cirolanidae) from The Bahamas, Western Atlantic. Zootaxa 4147: 82–88. https://doi.org/10.11646/zoot-axa.4147.1.6
- Sidabalok CM, Bruce NL (2017) Review of the species of the *Cirolana 'parva*-group' (Cirolanidae: Isopoda: Crustacea) in Indonesian and Singaporean waters. Zootaxa 4317(3): 401–435. https://doi.org/10.11646/zootaxa.4317.3.1
- Sidabalok CM, Wong HPS, Ng PK (2020) Description of the supergiant isopod *Bathynomus raksasa* sp. nov. (Crustacea, Isopoda, Cirolanidae) from southern Java, the first record of the genus from Indonesia. ZooKeys 947: 39–52. https://doi.org/10.3897/ zookeys.947.53906
- Soong K, Mok HK (1994) Size and maturity stage observations of the deep-sea isopod *Bathynomus doederleini* Ortmann, 1894 (Flabellifera: Cirolanidae), in eastern Taiwan. Journal of Crustacean Biology 14: 72–79. https://doi.org/10.2307/1549056
- Truong SHT (2015) The first record of *Bathynomus kensleyi* Lowry & Dempsey, 2006 (Crustacea, Isopoda) in Vietnamese seawaters. Collection of Marine Research Works 21(1): 80–83. [in Vietnamese, abstract in English]
- Tso SF, Mok HK (1991) Development, reproduction and nutrition of the giant isopod *Bathynomus doederleini* Ortmann, 1894 (Isopoda, Flabellifera, Cirolanidae). Crustaceana 61: 141–154. https://doi.org/10.1163/156854091X00641
- Wägele J-W (1989) Evolution und phylogenetisches System der Isopoda. Stand der Forschung und neue Erkenntnisse. Zoologica 140: 1–262.



**Research Article** 

# A new species of the genus *Oiketicoides* Heylaerts, 1885 (Lepidoptera, Psychidae) from Korea with its natural parasitoid enemy

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#### Abstract

*Oiketicoides gohadoensis* Roh & Lee, **sp. nov.** is described as new to science. The morphology of male adult, including genitalia, is described, and DNA barcodes for precise identification of the species are provided. A parasitoid, *Neophryxe psychidis* Townsend, 1916 (Diptera, Tachinidae) of *O. gohadoensis* is also reported for the first time in Korea, together with its DNA barcode sequence.

Key words: Bagmoths, bagworms, DNA barcode, Psychidae, taxonomy



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# Introduction

The family Psychidae, so-called bagworms or bagmoths, consists of 241 genera with 1350 described species (van Nieukerken et al. 2011). Phylogenetically, Psychidae have been placed in the superfamily Tineoidea (Regier et al. 2015).

The genus *Oiketicoides* Heylaerts, 1885 is based on the type species *Psyche inquinata* Lederer, 1858, by subsequent designation by Hampson in 1892 (Sobczyk 2011). In total, 45 species of *Oiketicoides* are known, with 40 species distributed throughout the Palaearctic Region (Arnscheid and Sobczyk 2023). In East Asia, only one species, *Oiketicoides orophila* (Wehrli, 1928) is known from Xinjiang Province, China (Jia and Wu 2023). *Oiketicoides* species occur in dry habitats at high altitudes up to 3000 m. Almost all species of *Oiketicoides* are uniformly dark yellowish-brown or grey in colour and characterized by the following adult morphological characters: the decreasing length of the antennal pecten towards the antennal tip; a very long tibial epiphysis on the foreleg; and 11 veins on the forewing and seven veins on the hindwing (Arnscheid and Sobczyk 2023). The larvae live mostly hidden on the ground without showing any preference for particular food plants (Arnscheid and Sobczyk 2023).

In this study, *Oiketicoides gohadoensis* sp. nov. is described as new. All available information is presented, including the collection locations, microhabitats, and illustrations of male and its genitalia. DNA barcodes are provided for precise identification. A parasitoid dipteran, *Neophryxe psychidis* Townsend, 1916 (Tachinidae) of *O. gohadoensis* was reported for the first time in Korea.

# Material and methods

The material examined in this study is kept in the Insect Collection, Honam National Institute of Biological Resources (**HNIBRIN**), Mokpo, Korea. The male genitalia were dissected and examined after mounting on glass slides in 80% glycerol solution. The wing venations were examined in 70% alcohol solution. Photographs of adults were taken using a Canon MP-E 65 mm f/2.8 1–5 × macro lens attached to Canon 5D Mark IV digital camera (Canon, Tokyo, Japan). Photographs of the male genitalia were taken using a DFC 95 mm digital camera (Leica, Wetzlar, Germany) attached to a Leica M205A stereomicroscope (Leica, Wetzlar, Germany). Terminology and morphological characters of the adult, wing venation and genitalia follow Saigusa and Sugimoto (2014) and Arnscheid and Weidlich (2017).

Genomic DNA from three specimens of *Oiketicoides gohadoensis* sp. nov. and one specimen of *Neophryxe psychidis* was extracted from the legs of dried specimens of adults in 100% alcohol using a DNeasy Blood and Tissue kits (Qiagen, Inc, Hilden, Germany) according to the manufacturer's protocol. Specimens were sequenced and the DNA barcode, cytochrome *c* oxidase subunit I gene (COI), was amplified using the primers LCO1490 and HCO2198 (Folmer et al. 1994). Polymerase Chain Reaction (PCR) conditions for amplification followed the manufacturer's protocol (Platinum Taq, Invitrogen, Carlsbad City, CA, USA). The amplicons were purified using the QIAquick® PCR purification kit (QIAGEN, Inc, Hilden, Germany) and directly sequenced at Macrogen (Seoul, Korea). Contigs were assembled in Geneious Prime (Kearse et al. 2012). Successful sequences were uploaded to GenBank (*O. gohadoensis*: PP983255–PP983257 and *N. psychidis*: PP983258).

# Results

#### **Oiketicoides Heylaerts**, 1881

Acanthopsyche (Oiketicoides) Heylaerts, 1881. Annales de la Société entomologique de Belgique 25: 66.

**Type species.** *Psyche inquinata* Lederer, 1858. Wiener entomologische Monatschrift 2(5): 142.

# Oiketicoides gohadoensis Roh & Lee, sp. nov.

https://zoobank.org/B284172B-2DE9-4138-B308-A07E96EEB422

**Туре material.** *Holotype*: ♂, SOUTH KOREA • Mokpo, Gohado Island; 28.vi.2023; 34°46′01″N, 126°22′02″E; altitude 12 m; leg. J.W. Kim; HNIBRIN 16107.

*Paratypes*: 9♂; same label data as holotype; HNIBRIN 16104–16106, 16108–16113.

**Diagnosis.** The genus *Oiketicoides* has little difference in external morphological characters between the males of the species, making morphological diagnosis difficult (Arnscheid and Sobczyk 2023). This new species also appears to have typical characters (uniformly dark, yellowish-brown coloration), but it has a noticeably shorter wingspan (11–13 mm) compared to the other species. The male genitalia of *O. gohadoensis* are very similar to those of *O. elegantis* Arnscheid & Sobczyk, 2023, but the cucullus is wider and club-shaped. Moreover, the male genitalia differ in having a wide vinculum and a downwardly thick saccus.

**Description.** *Adult* (Fig. 1). Male. Head: vertex densely clothed with yellowish-brown hairs; ocelli absent; antennae less than length of 2/5 of forewing, scape roughly covered with hairs, bipectinate, with 14 flagellomeres. Thorax: notum covered with dark, yellowish-brown scales. Legs with femora, tibiae, and tarsi clothed in light-brown hairs; tarsi and apical and medial spurs covered by yellowish-brown scales; foreleg with a long and narrow tibial epiphysis. Wingspan 11–13 mm. Forewing dark brown, mostly covered with short, hair-like scales; accessory and intercalary cells absent; 10 separate veins originating at discal cell; Sc terminating at 3/5 of costa; R3 and R4 stalked at anterior part of cell to reach apex; M2 and M3 parallel; scales slightly narrowed; apical margin usually produced into 2–4 weak, rounded lacininations. Hindwing covered with dark-brown scales; 6 veins from discal cell; M2 + M3 fused; scales narrowed; apical margin usually produced into two or three weak, rounded lacininations. *Male genitalia* (Fig. 2). Tegumen wide, slightly folded; valva short and slen-

der; sacculus sclerotized with short setae; cucullus arched, club-shaped;



Figure 1. Adult *Oiketicoides gohadoensis* Roh & Lee, sp. nov. A male of adult B anterior view of head C anterior view of head and antennae D basic view of antenna E foreleg F tibial epiphysis of foreleg G midleg H hindleg I wing venation J forewing scales K hindwing scales.

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Figure 2. Male genitalia of *Oiketicoides gohadoensis* Roh & Lee, sp. nov. A dorso-ventral aspect B tegumen C valva D lateral aspect.

vinculum slightly narrow; saccus straight, slightly thick, and long; phallus thick and long, 0.87 times as long as genitalia.

**Distribution.** Korea (new species).

**DNA barcode.** DNA barcode sequences were generated from three specimens of *Oiketicoides gohadoensis* sp. nov. (PP983255, PP983256, and PP983257). Multiple alignments using the BLAST tool in the NCBI database showed *Clania ignobilis* Grote, 1873 to be the nearest neighbor at 86.49%. The maximum intraspecific genetic variation ranged from 1.09 to 0.62%, a little lower than interspecific distances.

**Etymology.** This species was discovered on a tree in the garden at Honam National Institute of Biological Resources, Mokpo, Korea (Fig. 3A). The specific name is derived from the type locality (Gohado Island) of the new species.

**Biology.** Larvae of the new species build their cases (8.1–10.3 mm in length) by adhering the tiny particles of bark to their case. In addition, they were found to live in dried conditions between the bark or leaves of trees (Fig. 3). Adults emerge from late June to mid-July in breeding condition. Of 11 larvae, 11 males emerged in the present study.

# Natural enemy of O. gohadoensis

#### Neophryxe psychidis Townsend, 1916 (Diptera, Tachinidae)

During the breeding of *O. gohadoensis* in this study, we discovered a parasitoid, *N. psychidis* (Fig. 4). This species is reported for the first time in Korea. According to the literature, this species is known to emerge from psychid cases and is distributed in China, Japan, and Russia (O'Hara et al. 2009). In the Palearctic region, 31 species of Tachinidae are known to be associated with at least 36 species of psychid moths, and at least seven species of psychid Dong-June Lee et al.: A new species of Oiketicoides from Korea, with its natural enemy



**Figure 3.** Microhabitat and larval case of *Oiketicoides gohadoensis* Roh & Lee, sp. nov. **A** microhabitat in my office garden (Korea: Honam National Institute of Biological Resource, Gohado Island, Mokpo-si, Jeollanam-do, 1.vi.2023, 34°.46'01"N, 126°22'02"E, altitude 12 m) **B** larval case.



**Figure 4**. *Neophryxe psychidis*, a natural enemy of *Oiketicoides gohadoensis*, sp. nov. **A** male of adult **B** parasitic view of larva **C** male genitalia of *N*. *psychidis*, lateral aspect **D** ditto, posterior aspect **E** ditto, 5<sup>th</sup> sternite.

moths are known to be associated with *N. psychidis* (Tschorsnig 2017). DNA barcode sequences were generated (NCBI accession number PP983258). Multiple alignments using the BLAST tool in the NCBI database showed *N. psychidis* as the nearest neighbor (locality of reference data from Japan; 100%).

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# Additional information

# **Conflict of interest**

The authors have declared that no competing interests exist.

# **Ethical statement**

No ethical statement was reported.

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# Data availability

All of the data that support the findings of this study are available in the main text.

# References

Arnscheid WR, Sobczyk T (2023) Taxonomic review of the Oiketicoides species (Lepidoptera: Psychidae: Oiketicinae: Acanthopsychini) from Anatolia, the Middle East and Central Asia. Zootaxa 5239 (3): 373–394. https://doi.org/10.11646/zootaxa.5239.3.3
Arnscheid WR, Weidlich M (2017) Microlepidoptera of Europe. Vol. 8. Brill, Leiden, 423 pp.

- Folmer O, Black M, Hoech W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3(5): 294–299.
- Heylaerts FJM (1881) Essai d'une monographie des psychides de la faune européene. Bulletin & Annales de la société entomologique de Belgique 25: 29–73.
- Heylaerts F (1885) Psychides nouvelles ou moins connues de l'Empire Russe. Mémoires sur les Lépidoptères (Romanoff), St. Petersburg 2: 176–194 [pls 9, 10].
- Jia QJ, Wu CS (2023) Catalogue of the family Psychidae in China (Lepidoptera: Tineoidea). SHILAP Revista de Lepidopterología 51(203): 549–560. https://doi. org/10.57065/shilap.540
- Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Meintjes P, Drummond A (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28 (12): 1647–1649. https://doi. org/10.1093/bioinformatics/bts199
- Lederer J (1858) Noch einige syrische Schmetterlinge. Wiener entomologische Monatsschrift 2 (5): 135–143.
- Nieukerken EJ van, Kaila L, Kitching IJ, Kristensen NP, Lees DC, Minet J, Mitter C, Mutanen M, Regier JC, Simonsen TJ, Wahlberg N, Yen S-H, Zahiri R, Adamski D, Baixeras J, Bartsch D, Bengtsson BÅ, Brown JW, Bucheli SR, Davis DR, De Prins J, De Prins W, Epstein ME, Gentili-Poole P, Gielis C, Hättenschwiler P, Hausmann A, Holloway JD, Kallies A, Karsholt O, Kawahara AY, Koster JC, Kozlov M, Lafontaine JD, Lamas G, Landry J-F, Lee S, Nuss M, Park K-T, Penz C, Rota J, Schintlmeister A, Schmidt BC, Sohn J-C, Solis MA, Tarmann GM, Warren AD, Weller S, Yakovlev RV, Zolotuhin VV, Zwick A (2011) Order Lepidoptera Linnaeus, 1758. In: Zhang Z-Q (Ed.) Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness. Zootaxa 3148: 212–221. https://doi.org/10.11646/zootaxa.3148.1.41
- O'Hara JE, Shima H, Zhang C (2009) Annotated catalogue of the Tachinidae (Insecta: Diptera) of China. Zootaxa 2190: 1–236. https://doi.org/10.11646/zootaxa.2190.1.1
- Regier J, Mitter C, Davis DR, Harrison T, Sohn J-C, Cummings M, Zwick A, Mitter K (2015) A molecular phylogeny and revised classification for the oldest ditrysian moth lineages (Lepidoptera: Tineoidea), with implications for ancestral feeding habits of the mega-diverse Ditrysia. Systematic Entomology 40(2): 409–432. https://doi. org/10.1111/syen.12110
- Saigusa T, Sugimoto M (2014) Japanese species of the genus *Proutia* Tutt, 1899(Lepidoptera: Psychidae). Zootaxa 3869: 143–152.
- Sobczyk T (2011) World Catalogue of Insects, Vol. 10 Psychidae (Lepidoptera). Apollo Books, Stenstrup, 467 pp. https://doi.org/10.1163/9789004261044
- Tschorsnig HP. (2017) Preliminary host catalogue of Palaearctic Tachinidae (Diptera). http://www.nadsdiptera.org/Tach/WorldTachs/CatPalHosts/Cat\_Pal\_tach\_hosts\_ Ver1.pdf [Accessed on: 2024-11-15]
- Wehrli E (1928) Neue Psychiden und Geometriden (Lep.). Internationale Entomologische Zeitschrift 21(47): 454–457. https://doi.org/10.1002/mmnd.48119280102



Data Paper

# Mammals in urban centers: a dataset from the perspective of the media in Brazil

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#### Abstract

The continuous growth of the urban population, coupled with habitat loss, has resulted in unanticipated interactions between animals and humans in urban centers. In this study, we investigated the presence of mammals in urban centers through newspaper reports on websites. Specifically, we examined: i) the frequency of photographic records, ii) the temporal trends (2001 to 2021) and spatial trends (Brazilian Federative regions and states) of the records, and iii) the orders, families, and species most frequently reported in urban centers. On the Google platform (http://www.google.com.br), we used combinations of the keywords "mammals in urban centers," "mammals found in the city", and "mammals found in the municipality" to survey mammal records. We excluded repeated news items, sites that experienced technical problems during the search period, and those that did not cover the topic. We compiled a total of 733 websites. The records spanned from 2002 to 2021, with 73% occurring in the last four years. The Southeast, South, and Midwest regions stood out. The animals recorded belonged to 55 mammal species (16 vulnerable and 3 endangered), distributed in 22 families and 10 orders. The data indicate that the majority of mammal sightings in urban areas occur on streets, with some conflictual interactions. This is the first study that utilizes websites for diagnosing the mammal fauna present in urban centers in Brazil. The dataset generated here could aid in understanding the occurrence of mammal species in the urban environment.

Key words: Carnivora, data paper, Ocelot, photographic records, São Paulo state, southeastern region

# Introduction

Cities emerged thousands of years ago, and urban sprawl has led to a disruption in human-environment interaction (Seto et al. 2017; Perry et al. 2020). Continuous population growth and the demand for more resources alter and transform natural habitats, resulting in negative consequences for biodiversity (McDonald et al. 2013; Schenk and Souza 2014; Start et al. 2020); these consequences include the reduction of genetic diversity, threats from pathogens, the spread of exotic and invasive species, air, noise, and light pollution, as well



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Copyright: © Carolina Alves & Wellington Hannibal. This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0). as the alteration of natural hydrological regimes and fires (Theodorou 2022). Furthermore, population growth has been identified as one of the main causes of species and population extinction at a global level (Ceballos and Ehrlich 2002; Ceballos et al. 2010, 2015).

Ever since humans began living in settlements, wildlife has visited these places and found resources, such as shelters, food scraps, and garbage for food (Ceballos and Ehrlich 2002). As a result, there is an increase in the frequency of contact and complexity of the human-fauna relationship (Aronson et al. 2014). Species that were previously not observed in urban areas have been reported, even in cities with high population densities (Prezoto and Vale 2019). However, when wild species pose a threat to people and their livelihoods, this relationship can become conflictual (Zimmermann et al. 2010). In Brazil, conflicts between animals and humans have increased due to the migration of fauna from natural and rural areas to suburban and urban areas (Marchini and Crawshaw 2015).

Encounters and interactions between humans and animals have consequences for both. People are susceptible to zoonoses and economic damage, while animals face risks such as vehicle collision, entanglement, and attacks by domestic animals (Taylor-Brown et al. 2019). The frequency of recording wild animals in urban centers can be associated with local physical factors or the urban landscape, such as the presence of green areas, parks, waterways, and the often-practiced urban tree planting (Bateman and Fleming 2012; Van Bommel et al. 2020). Identifying these factors is important for formulating public policies and mitigating conflicts (Basak et al. 2020).

In this study, we investigated the presence of mammals in urban centers through newspaper reports and other communication networks on websites. Specifically, we examined: i) the frequency of photographic records, ii) the temporal trends (2001 to 2021), and spatial trends (Brazilian Federative regions and states) of records, and iii) the orders, families, and species most frequently reported in urban centers.

# Metadata

#### **Data set identity**

**Title:** Mammals in urban centers: a dataset from the perspective of the media in Brazil.

**Data set identification code:** BRAZIL\_SM\_loc.csv, BRAZIL\_SM\_rec.csv, BRAZIL\_SM\_ref.csv, and BRAZIL\_SM\_int.csv.

#### Data set description

#### **Principal investigators:**

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#### **Overall project description**

**Identity:** Compilation of mammals' occurrence in urban centers, providing city, state and region of records, and richness, composition and threatened category data.

**Period of study:** The data presented were collected from 2002 to 2021, and the process of organizing and producing the current data set took place from 2021 to 2024.

**Objectives:** Our goal was to gather detailed information about mammal records in urban centers from Brazil, focusing on i) spatial trends of records (city, state and region); and ii) frequency in taxonomic records (orders, families and species) in urban centers of Brazil.

#### Specific subproject description

**Site description:** Brazil is a country of continental proportions, with a territorial extension of 8,510,345.540 km<sup>2</sup> (Instituto Brasileiro de Geografia e Estatística IBGE 2022), encompassing six climatic types: Equatorial, Semi-arid, Tropical, High-altitude Tropical, Atlantic Tropical, and Subtropical (Ministério do Meio Ambiente MMA 2022). Brazil is home to more than 100,000 animal species, encompassing mammals, birds, amphibians, fish, reptiles, insects, and invertebrates that inhabit forests, mangroves, savannahs, fields, rivers, and lakes across the following biomes: Amazon, Caatinga, Cerrado, Pantanal, Atlantic Forest, and Pampa (IBGE 2022, MMA 2022). The Brazilian mammal fauna consists of 778 species distributed across 11 orders, 51 families, and 247 genera (Abreu et al. 2022).

**Data collection:** The data were obtained from online media outlets, including news sites, videos, blogs, and government websites. We searched for potential studies in the following sources: (i) Google Search engine, (ii) social networks, (iii) newspapers, and (iv) government websites (city halls, state halls, and organizations such as the Fire Department and Military Police websites). We conducted a search for news stories using the following phrases: "mammals in urban centers", "mammals found in the city", "mammals seen in urban centers" and "mammals seen in the municipality" in Portuguese. Additionally, we employed a combination of keywords like the "common name of the species" (e.g., puma, capybara, monkey) along with the phrase "found in urban centers", also in Portuguese.

**Research criteria:** We included in this database only news items that specifically reported the appearance of wild mammals in urban centers. From these sites, we extracted the following information: i) presence of a photo or video, ii) date, iii) city and state of the record, iv) geographic coordinates of the record and/or city, v) scientific name and main taxonomic categories (genus, family, and order), vi) name of the species reported on the site, and vii) title of the news item.

Taxonomic nomenclature was based on the updated checklist of Brazilian mammals by the Taxonomic Committee of the Brazilian Society of Mammalogy (Abreu et al. 2022). We identified the species using field guides and books on mammals in Brazil, as well as the species' distribution areas according to the IUCN Red List. (Bonvicino et al. 2008; Reis et al. 2011; Nascimento and Feijó 2017; Faria et al. 2019; Azevedo et al. 2021; Menezes et al. 2021; Rumiz et al. 2022; IUCN 2022). We added a column with the current scientific name based on the aforementioned literature. However, due to the lack of a photo or video, the poor quality of the image or footage, and the existence of a species complex for the same genus at the cited site, some species were identified only at the genus level, followed by "sp." or "spp." In these cases, we filled in the cell in the 'Actual\_species\_name' column with the genus, followed by "sp.".

#### Data set status and accessibility

**Data verification:** All localities were checked for accuracy and precision. The taxonomic status of the species was verified by the authors. In the bibliographic records, the taxonomic update was made based on the most recent literature. Carolina Alves conducted the searches and analysis of websites for inclusion in this dataset, carefully evaluating which ones met the inclusion criteria. Wellington Hannibal analyzed the dataset and created the figures. The data were mostly derived from news websites and newspapers, and we sought to correct any errors in taxonomic information about the species.

#### Accessibility

**Storage location and medium:** Available as Supporting Information to this Ecology Data Paper in .csv format (https://figshare.com/articles/dataset/\_b\_MAM-MALS\_IN\_URBAN\_CENTERS\_a\_dataset\_for\_Brazil\_b\_/26616214).

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Copyright restrictions: None

**Proprietary restrictions:** Please cite this data paper when using it in publications. We also request that researchers and teachers inform us of how they are using the data.

Costs: None.

# Data set file

BRAZIL\_SM\_loc.csv BRAZIL\_SM\_rec.csv BRAZIL\_SM\_ref.csv BRAZIL\_SM\_int.csv

**Format and storage mode:** comma-separated values (.csv). **Header information:** See Table 1 in section B for column descriptions.

## **Tables and figures**

Table 1. Description of columns of .csv files;

Table 2. Systematic list of mammals' species in urban areas of Brazil.

Figure 1. Number of photographic, temporal and spatial records of mammalian species in urban areas of Brazil;

Figure 2. Geographic distribution of mammal occurrence records in Brazilian urban areas, categorized by federative regions;

Figure 3. Number of records by families of mammals in urban areas of Brazil;

BRAZIL_SM_loc.csv	
id	Code given to each locality
Municipality	Municipality of the locality
State	State of the locality
Lat	Decimal coordinates of the locality
Long	Decimal coordinates of the locality
Datum	Geodetic coordinate system
Coordinates Location	Reference from where the coordinates were obtained
Biomes	Biomes from where the coordinates were obtained
BRAZIL_SM_rec.csv	
id	Code given to each locality
Month	Month when the record was published
Year_Publication	Year when the record was published
Order	Order taxonomic classification
Family	Family taxonomic classification
Genus	Genus taxonomic classification
Species_name_on_site	Species name published on website
Actual_species_name	Species name according taxonomic classification
Species_origin	Origin of species
Record_Type	Type of record, photography, video
BRAZIL_SM_ref.csv	
id	Code given to each locality
Site_Name	Name of the site where record was published
Type_Site	Category of the site where the record was published
Link	Link to website
BRAZIL_SM_int.csv	
id	Code given to each locality
Location	Exact location where the animal was found
Rescueorganization	Agency responsible for the rescue
Destination	Release or sent for rehabilitation
Interactions	Whether there was human-wildlife interaction
Injuries	Whether there was an injury or not
Zone	Encounter in rural, urban, or peri-urban area
deceased	The animal died

Table 1. Description of columns of .csv files.

Figure 4. Number of records by species of mammals in urban areas of Brazil; Figure 5. Collector's curve showing species accumulation with increasing sampling effort across urban areas.

# **Results description**

This dataset comprises 733 records of 450 mammal locations found in urban centers across Brazil, as reported on various websites. Of the total number of records, 89% (N = 652) included an image or video, spanning the period between 2002 and 2021, with a noticeable increase in the number of records in the last five years (Fig. 1). The Southeast (41%, N = 302), South (25%, N = 182), and Midwest (18%, N = 129) regions had the highest number of records, particularly in the cities of São Paulo, Minas Gerais, Mato Grosso do Sul, Rio Grande do Sul, Rio de Janeiro, Santa Catarina and Paraná (Figs 1, 2).



Figure 1. Number of photographic (A), temporal (B) and spatial (C) records of mammalian species in urban areas of Brazil.



Figure 2. Geographic distribution of mammal occurrence records in Brazilian urban areas, categorized by federative regions.
Our data demonstrate a geographic bias in media reports on human-mammal encounters in urban areas (Figs 1, 2). The regions showing the highest number of records are economically more developed compared to other areas of the country (Saraiva, Souza, 2012). Consequently, these regions have greater media coverage. One recommendation to reduce this bias is to foster stronger communication between scientists and the media, along with more studies to investigate public perception of wildlife and interpretation of media events. Additionally, increased investment in communication, education, and public awareness programs could help rebalance both media and public perception (Bornatowski et al. 2019).

Of the total 733 records, we found 55 species, 22 families and 10 orders of mammals in urban areas of Brazil (Table 2). Carnivora (N = 399 records, 19 species) was the more representative order, followed by Rodentia (93, 11 spp.), Pilosa (92, 4 spp.), Cetartiodactyla (52, 4 spp.), Didelphimorphia (35, 4 spp.), Primates (29, 5 spp.), Cingulata (17, 6 spp.), Perissodactyla (13, 1 sp.), Lagomorpha (2, 1 sp.) and Chiroptera (1, 1 sp.). Felidae and Canidae comprised 48% of records (N = 353); Felidae occur in 96% of localities (Fig. 3).

The Ocelot, Puma, Southern Tamandua, Maned Wolf, Crab-eating Fox, Gray Brocket, and Capybara reach more than 30 records and represented 49% of mammalian fauna in urban areas from Brazil (Fig. 4). Of the total species recorded in urban areas, 32.7% are threatened according Brazilian Red List (MMA 2022), highlighted by the orders: Carnivora (Maned Wolf *Chrysocyon brachyurus*, Hoary Fox *Lycalopex vetulus*, Bush Dog *Speothos venaticus*, Margay *Leopardus wiedii*, Southern Tiger Cat *L. guttulus*, Jaguar *Panthera onca*, Jaguarundi *Herpailurus yagouaroundi* and Giant Otter *Pteronura brasiliensis*), Cingulata (Giant Armadillo *Priodontes maximus* and Brazilian Three-banded Armadillo *Tolypeutes tricinctus*), Pilosa (Giant Anteater *Myrmecophaga tridactyla* and Maned Three-toed Sloth *Bradypus torquatus*), Primates (Brown Howler Monkey *Alouatta guariba* and Buffy-tufted-ear Marmoset *Callithrix aurita*), Perissodactyla (Lowland Tapir *Tapirus terrestris*) and Cetartiodactyla (White-lipped Peccary *Tayassu pecari*) (Fig. 4)

The species accumulation curve (Fig. 5) provides validation for using this dataset to make inferences about mammal diversity in urban areas within the sampled context. The curve shows a gradual plateau, indicating that a sufficient sampling effort (in terms of the number of cities) has been reached to capture the diversity most frequently reported in the media. However, we acknowledge that the data carry an inherent media bias, favoring reports of mammals that capture public attention—typically emblematic, charismatic, and vulnerable species more likely to be impacted by human activities. This is because, for an event to become newsworthy, it must hold relevance from the media's perspective, drawing public attention (Freitas and Barszcz 2015; Shaw et al. 2022).

Thus, the media focus on these specific species is a reflection of journalistic trends rather than a methodological flaw in the study. Although this bias may prevent uniform records across all species, the accumulation curve suggests that the data collected still provide a legitimate basis for understanding broader trends. It serves as a valuable repository of information on the increasing frequency of human-wildlife interactions in urban areas, opening pathways for further discussions on how media coverage influences public perception of urban wildlife. While this dataset may not fully reflect the actual diversity or abundance of species in urban areas, it highlights patterns in human-wildlife relationships shaped by media representation, offering an opportunity for future analyses of these dynamics.

Table 2. Systematic list of mammal species in urban areas of Brazil. Brazilian states legend: Acre (AC), Alagoas (AL), Amapá (AP), Amazonas (AM), Bahia (BA), Ceará (CE), Distrito Federal (DF), Espírito Santo (ES), Goiás (GO), Maranhão (MA), Mato Grosso (MT), Mato Grosso do Sul (MS), Minas Gerais (MG), Pará (PA), Paraíba (PB), Paraná (PR), Pernambuco (PE), Piauí (PI), Rio de Janeiro (RJ), Rio Grande do Norte (RN), Rio Grande do Sul (RS), Rondônia (RO), Roraima (RR), Santa Catarina (SC), São Paulo (SP), Sergipe (SE), Tocantins (TO).

Taxon	Common Name	Federative Unit		
DIDELPHIMORPHIA GIII, 1872				
Didelphidae Gray, 1821				
Caluromys philander (Linnaeus, 1758)	Bare-tailed Woolly Opossum	ES		
Didelphis albiventris Lund, 1840	White-eared Opossum	DF, MG, MS, PR, RS, SC, SP		
Didelphis aurita (Wied-Neuwied, 1826)	Big-eared Opossum	ES, MG, RJ, RS, SC, SP		
Philander canus (Osgood, 1913)	Gray Four-eyed Opossum	GO		
Cingulata Illiger, 1811				
Chlamyphoridae Bonaparte, 1850				
Euphractus sexcinctus (Linnaeus, 1758)	Six-banded Armadillo	ES, MS, TO		
Cabassous tatouay (Desmarest, 1804)	Southern Naked-tailed Armadillo	RJ		
Priodontes maximus (Kerr, 1792)	Giant Armadillo	ТО		
Tolypeutes matacus (Desmarest, 1804)	Southern Three-banded Armadillo	MS		
Tolypeutes tricinctus (Linnaeus, 1758)	Brazilian Three-banded Armadillo	CE		
Dasypodidae Gray, 1821				
Dasypus novemcinctus Linnaeus, 1758	Nine-banded Armadillo	AC, MG, MS, PR, RJ, RS		
Pilosa Flower, 1883				
Bradypodidae Gray, 1821				
Bradypus (Scaeopus) crinitus Gray, 1850	Maned Three-toed Sloth	RJ		
Bradypus (Bradypus) variegatus Schinz, 1825	Brown-throated Three-toed Sloth	AM, BA, CE, MG, PE, RJ, SC, SP		
Myrmecophagidae Gray, 1825				
Myrmecophaga tridactyla Linnaeus, 1758	Giant Anteater	GO, MG, MS, MT, RR, SP, TO		
Tamandua tetradactyla (Linnaeus, 1758)	Southern Tamandua	AM, AP, BA, CE, ES, MG, MS, MT, PR, RJ, RN, RS, SC, SP, TO		
PRIMATES Linnaeus, 1758				
Atelidae Gray, 1825				
Alouatta caraya (Humboldt, 1812)	Black-and-gold Howler Monkey	GO, MS, RS		
Alouatta guariba (Humboldt, 1812)	Brown Howler Monkey	MG, PR, RJ, RS, SC, SP		
Cebidae Bonaparte, 1831				
Callithrix aurita (É. Geoffroy StHilaire, 1812)	Buffy-tufted-ear Marmoset	RJ		
Callithrix penicillata (É. Geoffroy StHilaire, 1812)	Black-pencilled Marmoset	MG, PR		
Saimiri collinsi Osgood, 1916	American Squirrel Monkey	МА		
RODENTIA Bowdich, 1821				
Caviidae Fischer, 1817				
Hydrochoerus hydrochaeris (Linnaeus, 1766)	Capybara	DF, ES, GO, MS, MT, PE, RJ, RN, RS, SC, SE, SP, TO		
Cuniculidae G. S. Miller & Gidley, 1918				
Cuniculus paca (Linnaeus, 1766)	Lowland Paca	GO, MG, PR		
Dasyproctidae Bonaparte, 1838				
Dasyprocta azarae Lichtenstein, 1823	Azara's Agouti	MS		
Myoprocta pratti Pocock, 1913	Green Acouchi	AM		

Taxon	Common Name	Federative Unit		
Dinomyidae Alston, 1876				
Dinomys branickii Peters, 1873	The Pacarana	AC		
Echimyidae Gray, 1825				
Myocastor coypus (Molina, 1782)	Coypu, Nutria, River rat. The Nutria	PR, RS		
Erethizontidae Bonaparte, 1845	1			
Chaetomys subspinosus (Olfers, 1818)	Bristle-spined Rat	ВА		
Coendou prehensilis (Linnaeus, 1758)	Brazilian Porcupine	CE, DF, MG, MS, PR, RJ, RO, RS, SC, SP, TO		
Coendou spinosus (Cuvier, 1823)	Paraguaian Hairy Dwarf Porcupine	ES, MG, RJ, RS, SP		
Sciuridae Fischer, 1817				
Guerlinguetus aestuans (Linnaeus, 1766)	Guianan Squirrel	RS		
Guerlinguetus brasiliensis (Gmelin, 1788)	Ingram's squirrel	BA, PR, RJ, SC		
CARNIVORA Bowdich, 1821				
Canidae Fischer, 1817				
Cerdocyon thous (Linnaeus, 1766)	Crab-eating Fox	BA, CE, DF, ES, MA, MG, MS, PR, RJ, RS, SC, SE, SP		
Chrysocyon brachyurus (Illiger, 1815)	Maned Wolf	GO, MG, MS, MT, PI, PR, RJ, SP, TO		
Lycalopex vetulus (Lund, 1842)	Hoary Fox	GO, MG, SP, TO		
Lycalopex gymnocercus (Fischer, 1814)	The Pampas Fox	RS		
Speothos venaticus (Lund, 1842)	Bush Dog	MS, MT		
Felidae Fischer, 1817				
Herpailurus yagouaroundi (É. Geoffroy Saint-Hilaire, 1803)	Jaguarundi	BA, CE, DF, MG, MS, MT, PA, PE, RS		
Leopardus guttulus (Hensel, 1872)	Southern Tiger Cat	ES, MG, PR, RS, SC, SP		
Leopardus pardalis (Linnaeus, 1758)	Ocelot	AC, AL, BA, CE, ES, GO, MG, MS, MT, PA, PB, PE, PI, PR, RJ, RS, SC, SE, SP, TO		
Leopardus tigrinus (Schreber, 1775)	Little Spotted Cat	CE, PB		
Leopardus wiedii (Schinz, 1821)	Margay	AL, AM, AP, MA, PR, RS, SC, SP		
Puma concolor (Linnaeus, 1771)	Puma	BA, ES, GO, MG, MS, MT, PA, PR, RJ, SC, SP, TO		
Panthera onca (Linnaeus, 1758)	Jaguar	AL, AM, GO, MG, MS, MT, PR, RR, SP, TO		
Mustelidae Fischer, 1817				
Eira barbara (Linnaeus, 1758)	Тауга	RS		
Galictis cuja (Molina, 1782)	Lesser Grison	MG, PR, RS, SC, SE, SP		
Pteronura brasiliensis (Zimmermann, 1780)	Giant Otter	AM, TO		
Lontra longicaudis (Olfers, 1818)	River Otter	AP, BA, MS		
Procyonidae Gray, 1825				
Nasua nasua (Linnaeus, 1766)	South American Coati	BA, ES, MG, MS, MT, PB, PE, PR, RJ, RS, SP		
Potos flavus (Schreber, 1774)	Kinkajou	RJ, RO		
Procyon cancrivorus (Cuvier, 1798)	Crab-eating Raccoon	MG, MT, RS, SC, SP		
Perissodactyla Owen, 1848				
Tapiriidae Gray, 1821				
Tapirus terrestris (Linnaeus, 1758)	Lowland Tapir	MG, MS, MT, SP		
CETARTIODACTYLA Montgelard, Catzeflis & Douzery, 1997				
Cervidae Goldfuss, 1820				
Mazama rufa (Erxleben, 1777)	Red Brocket	DF, ES, MG, MS, MT, SP, TO		
Subulo gouazoubira (Fischer, 1814)	Gray Brocket	BA, CE, ES, GO, MG, MS, MT, PR, RS, SC, SP, TO		
Tayassuidae Palmer, 1897				
Dicotyles tajacu (Linnaeus, 1758)	Collared Peccary	МТ, ТО		
Tayassu pecari (Link, 1795)	White-lipped Peccary	MS		



Figure 3. Number of records by orders (pie plot) and families (bar plot) of mammals in urban areas of Brazil.





Figure 5. Collector's curve showing species accumulation with increasing sampling effort across urban areas.

Based on reports gathered through the media, the locations with the highest number of mammal sightings in urban centers are streets (280 records), followed by residential properties (191), highways (116), parks (41), businesses (33), gated communities (19), vacant lots (9), schools (5), hospitals (5), airports (2), churches (2), rivers (2), hotels (1), banks (1), nursing homes (1), universities (1), and gardens (1). Other reports did not specify where the animals were sighted or found. After being located, 292 records indicate that the mammals were sent for rehabilitation, with 188 of these animals found injured and 99 fatalities recorded.

Regarding interactions, not all reports included information on conflicts or relationships beyond encounters between humans and wildlife. The recorded interactions include road accidents (108), conflicts with dogs (16), predation of domestic animals (10), retaliation (4), electric shocks (3), intentional feeding (3), poisoning (2), nuisance wildlife (2), mutilation (1), and crop damage (1). Interactions between humans and wild animals, particularly mammals, are diverse and complex, often resulting in conflicts. Both habitat loss due to urbanization and agricultural expansion, along with the presence of urban parks, contribute to these conflicts (Griffin et al. 2022; Adhikari et al. 2024). The majority of records (679) are from urban areas, as the database focuses on mammals in urban centers.

# **Final considerations**

Compiling information on all mammal species found in urban centers into a single document is particularly challenging for several reasons: i) sites with incomplete information, ii) incorrectly identified animals, iii) sites with technical problems, and iv) poor-quality photos and videos.

Even so, our dataset reflects the number of mammal records in urban centers in Brazil. This is the first study to utilize websites to diagnose the mammal fauna present in urban centers in Brazil. The dataset generated here could help us understand the occurrence of mammal species in urban environments and serve as a foundation for future studies related to urban landscape ecology and its implications for the distribution and conservation of mammals in these environments.

# **Additional information**

#### **Conflict of interest**

The authors have declared that no competing interests exist.

#### **Ethical statement**

No ethical statement was reported.

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#### Author contributions

WH – originally formulated the idea, performed descriptive analyses; CA – data collected. All authors added substantial contribution in the concept and design of the study. Contribution to critical revision, adding intellectual content.

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### Data availability

Data published through figshare: https://figshare.com/articles/dataset/\_b\_MAMMALS\_ IN\_URBAN\_CENTERS\_a\_dataset\_for\_Brazil\_b\_/26616214.

# References

- Abreu EF, Casali D, Costa-Araújo R, Garbino GST, Libardi GS, Loretto D, Loss AC, Marmontel M, Moras LM, Nascimento MC, Oliveira ML, Pavan SE, Tirelli FP (2022) Lista de Mamíferos do Brasil. https://doi.org/10.5281/ZENOD0.10428436
- Adhikari JN, Bhattarai BP, Thapa TB (2024) Correlates and impacts of human-mammal conflict in the central part of Chitwan Annapurna Landscape, Nepal. Heliyon 10(4): e26386. https://doi.org/10.1016/j.heliyon.2024.e26386
- Aronson MF, La Sorte FA, Nilon CH, Katti M, Goddard MA, Lepczyk CA, Warren PS, Williams NS, Cilliers S, Clarkson B, Dobbs C, Dolan R, Hedblom M, Klotz S, Kooijmans JL, Kühn I, Macgregor-Fors I, McDonnell M, Mörtberg U, Pysek P, Siebert S, Sushinsky J, Werner P, Winter M (2014) A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. Proceedings of the Royal Society B: Biological Sciences 281(1780): 20133330. https://doi.org/10.1098/rspb.2013.3330
- Azevedo N, Oliveira M, Duarte J (2021) Guia ilustrado dos cervídeos brasileiros. Sociedade Brasileira de Mastozoologia. https://doi.org/10.32673/9788563705037
- Basak, SM, Wierzbowska IA, Gajda A, Czarnoleski M, Lesiak M, Widera E (2020) Human-Wildlife Conflicts in Krakow City, Southern Poland. https://doi.org/10.3390/ ani10061014
- Bateman PW, Fleming PA (2012) Big city life: carnivores in urban environments. Journal of Zoology 287(1): 1–23. https://doi.org/10.1111/j.1469-7998.2011.00887.x

- Bonvicino CR, Oliveira JA, D'Andrea PS (2008) Guia dos roedores do Brasil, com chaves para gêneros baseadas em caracteres externos. https://iris.paho.org/handle/10665.2/49675 [June 25, 2024]
- Bornatowski H, Hussey NE, Sampaio CL, Barreto RR (2019). Geographic bias in the media reporting of aquatic versus terrestrial human predator conflicts and its conservation implications. Perspectives in Ecology and Conservation 17(1): 32–35. https://doi.org/10.1016/j.pecon.2018.12.004
- Ceballos G, Ehrlich PR (2002) Mammal population losses and the extinction crisis. Science (New York, N.Y.) 296: 904–907. https://doi.org/10.1126/science.1069349
- Ceballos G, Garcia A, Ehrlich P (2010) The sixth extinction crisis. Journal of Cosmology 2, 452: 180–185.
- Ceballos G, Ehrlich PR, Barnosky AD, Gacía A, Pringle RM, Palmer TM (2024) Accelerated modern human-induced species losses: Entering the sixth mass extinction | Science Advances. https://www.science.org/doi/full/10.1126/sciadv.1400253 [June 25, 2024]
- Faria MB, Lanes RO, Bonvicino CR (2019) Guia dos marsupiais no Brasil: guia de identificação com base em caracteres morfológicos externos e cranianos. Amélie Editorial.
- Freitas SD, Barszcz LB (2015) A perspectiva da mídia online sobre os acidentes entre veículos e animais em rodovias brasileiras: uma questão de segurança. Desenvolvimento e Meio Ambiente 33: 261–276. https://doi.org/10.5380/dma.v33i0.36910
- Griffin LL, Haigh A, Conteddu K, Andaloc M, McDonnell P, Ciuti S (2022) Reducing risky interactions: Identifying barriers to the successful management of human-wildlife conflict in an urban parkland. People and Nature 4(4): 918–930. https://doi.org/10.1002/ pan3.10338
- IBGE Áreas Territoriais (2022) IBGE. https://www.ibge.gov.br/geociencias/organizacao-do-territorio/estrutura-territorial/15761-areas-dos-municipios.html [June 25, 2024a]
- IBGE [Fauna Ameaçada de Extinção] (2022) IBGE. https://educa.ibge.gov.br/jovens/materias-especiais/22384-especies-ameacadas-de-extincao.html#:~:text=S%C3%A3o%20mais%20de%2050%20mil,no%20territ%C3%B3rio%20brasileiro%20at%C3%A9%202022 [June 25, 2024b]
- IUCN (2022) The IUCN Red List of Threatened Species. Version 2022. https://www. iucnredlist.org
- Marchini, S, Crawshaw Jr P (2015) Human-Wildlife Conflicts in Brazil: A Fast-Growing Issue. https://doi.org/10.1080/10871209.2015.1004145 [June 25, 2024]
- McDonald RI, Marcotullio PJ, Güneralp B (2013) Urbanization and global trends in biodiversity and ecosystem services. In: Elmqvist T, Fragkias M, Goodness J, Güneralp B, Macotullio PJ, McDonald RI, Panell S, Schewenius M, Sendstad M, Seto KC, Wilkinson C (Eds) Urbanization, biodiversity and ecosystem services: challenges and opportunities: a global assessment. Springer: Dordrecht, The Netherlands, 31–52. https://doi. org/10.1007/978-94-007-7088-1\_3
- Menezes FH, Feijó A, Fernandes-Ferreira H, Da Costa IR, Cordeiro-Estrela P (2021) Integrative systematics of Neotropical porcupines of *Coendou prehensilis* complex (Rodentia: Erethizontidae). Journal of Zoological Systematics and Evolutionary Research 59: 2410–2439. https://doi.org/10.1111/jzs.12529
- MMA (2022) Portaria MMA n° 148, de 7 de junho de 2022. https://www.icmbio.gov. br/cepsul/images/stories/legislacao/Portaria/2020/P\_mma\_148\_2022\_altera\_ anexos\_P\_mma\_443\_444\_445\_2014\_atualiza\_especies\_ameacadas\_extincao.pdf

- MMA Biomas (2024) Ministério do Meio Ambiente e Mudança do Clima. https://www. gov.br/mma/pt-br/assuntos/biodiversidade-e-ecossistemas/ecossistemas/biomas/biomas [June 25, 2024a]
- MMA Clima (2024) Ministério do Meio Ambiente e Mudança do Clima. https://www.gov.br/ mma/pt-br/assuntos/mudanca-do-clima/clima/mudancasclimaticas [June 25, 2024b]
- Nascimento FO do, Feijó A (2017) Taxonomic revision of the tigrina Leopardus tigrinus (Schreber, 1775) species group (Carnivora, Felidae). Papéis Avulsos de zoologia 57: 231–264. https://doi.org/10.11606/0031-1049.2017.57.19
- Perry G, Boal C, Verble R, Wallace M (2020) "Good" and "Bad" Urban Wildlife. Problematic Wildlife II, 141–170. https://doi.org/10.1007/978-3-030-42335-3\_5
- Prezoto F, Vale A (2019) Fauna Urbana: Quem Vive Aqui? 33: 119–146.
- Reis NR, Peracchi AL, Pedro WA, Lima IP (2011) Mamíferos do Brasil. 2a edição. Universidade Estadual de Londrina, Londrina, Brazil, 439 pp.
- Rumiz D, Boron V, Rivera-Brusatin A, Holzmann A, Payán-Garrido E, Gaspairini-Morato RL, Paula RC, Morato RG, Ferreira JM, Feliciani F, Foster VC, Reginato T, Kotz A, Oliveira TG, Barros YM (2022) Guia de identificação de partes de felinos, Brasil. ICMBio, 116 pp.
- Saraiva KR, Souza FS (2012) Estatísticas sobre irrigação nas regiões Sul e Sudeste do Brasil segundo o censo agropecuário 2005–2006. IRRIGA 17(2): 168–176. https://doi.org/10.15809/irriga.2012v17n2p168
- Schenk AN, Souza MJ (2014) Major anthropogenic causes for and outcomes of wild animal presentation to a wildlife clinic in East Tennessee, USA, 2000–2011. PLoS ONE 9: e93517. https://doi.org/10.1371/journal.pone.0093517
- Seto KC, Golden JS, Alberti M, Turner BL (2017) Sustainability in an urbanizing planet. Proceedings of the National Academy of Sciences 114: 8935–8938. https://doi. org/10.1073/pnas.1606037114
- Shaw MN, Borrie WT, McLeod EM, Miller KK (2022) Wildlife Photos on Social Media: A Quantitative Content Analysis of Conservation Organisations' Instagram Images. Animals 12(14):1787. https://doi.org/10.3390/ani12141787
- Start D, Barbour MA, Bonner C (2020) Urbanization reshapes a food web. In: Rodriguez-Cabal M (Ed.) Journal of Animal Ecology 89: 808–816. https://doi.org/10.1111/1365-2656.13136
- Taylor-Brown A, Booth R, Gillett A, Mealy E, Ogbourne SM, Polkinghorne A, Conroy GC (2019) The impact of human activities on Australian wildlife. PloS ONE 14: e0206958. https://doi.org/10.1371/journal.pone.0206958
- Theodorou P (2022) The effects of urbanisation on ecological interactions. Current Opinion in Insect Science 52: 100922. https://doi.org/10.1016/j.cois.2022.100922
- Van Bommel JK, Badry M, Ford AT, Golumbia T, Burton AC (2020) Predicting human-carnivore conflict at the urban-wildland interface. Global Ecology and Conservation 24: e01322. https://doi.org/10.1016/j.gecco.2020.e01322
- Zimmermann A, Baker N, Inskip C, Linnell JD, Marchini S, Odden J, Rasmussen G, Treves A (2010) Contemporary views of human-carnivore conflicts on wild rangelands. In: Du Toit JT, Kock R, Deutsch JC (Eds) Wild rangelands: Conserving wildlife while maintaining livestock in semi-arid ecosystems, Wiley-Blackwell, Oxford, 129–151. https://doi.org/10.1002/9781444317091.ch6



Research Article

# *Plectranthias raki* (Teleostei, Serranidae), a new species of perchlet from mesophotic coral ecosystems of the Maldives

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#### Abstract

Herein, we describe a new species of *Plectranthias* perchlet found at depths of 100-125 meters in mesophotic coral ecosystems of the Maldives in the Indian Ocean. *Plectranthias raki* **sp. nov.** is unique in both morphology and coloration. The following combination of characters distinguishes it from all known congeners: dorsal fin X, 15; anal-fin rays III, 7; pectoral-fin rays 13 | 13 (13 | 12), all unbranched; principal caudal-fin rays 9 + 8; lateral line complete with 30-32 tubed scales; gill rakers 5 + 12; circumpeduncular scales 11-12; and absence of antrorse or retrorse spines on ventral margin of preopercle. Coloration in life consists of a white to light pink body with two indistinct rows of irregularly shaped red-orange to yellow-orange patches along the dorsal two-thirds of the body, a golden-yellow opercle and maxilla, an indistinct yellow stripe on the dorsal fin, two yellow spots near the base of the anal fin, and two irregularly shaped yellow-orange spots located on either side of centermost caudal-fin rays. With this publication, the genus *Plectranthias* now comprises 67 valid species. This discovery adds to a strong body of research highlighting the novel biodiversity of mesophotic ecosystems, especially in locations like the Indian Ocean, where few prior ichthyological surveys have been conducted.

Key words: COI gene, deep reefs, ichthyology, Indian Ocean, rebreather diving, taxonomy

# Introduction

The anthiadine genus *Plectranthias* Bleeker, 1873, comprises 66 valid species found in tropical and temperate waters in the Atlantic, Pacific, and Indian oceans (Fricke et al. 2024). In general, they are small (20 cm maximum length, but most in the 5–10 cm range), benthic, feed on small mobile invertebrates, and hide in crevices and holes in relatively deep habitats (depths of 90–420 m) with complex rocky formations (Kuiter 2004; Allen and Walsh 2015). Due to their small size and cryptic habits, they are poorly represented in museum collections, and many species have been described based on a small number of specimens or single individuals (Randall 1980; Heemstra and Randall 2008; Wu et al. 2011; Bineesh et al. 2014; Allen and Walsh 2015; Gill et al. 2016;

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Shepherd et al. 2018; Gill and Roberts 2020; Shepherd et al. 2020; Wada et al. 2020; Fricke 2021; Koeda et al. 2022). The genus *Plectranthias* is distinguished from other genera in the subfamily Anthiadinae by the following characters: a dorsal fin with 10-12 spines and 13-20 rays, incised between the spinous and soft portions of the dorsal fin; anal fin III, 6-8; pelvic fin I, 5; pectoral fin with 12-18 rays; an absence of auxiliary scales on the head or body; teeth on the palatine and a V- or U-shaped vomer tooth patch, but no teeth on the tongue; 26 vertebrae (rarely 27); and 12-31 total gill rakers (Gill et al. 2021).

Mesophotic coral ecosystems (MCEs), coral reef habitats found at depths of 30–150 m commonly known as the coral reef "twilight zone," are home to a diversity of organisms that are largely distinct from their shallow-water counterparts (Rocha et al. 2018). While conducting ichthyological and ecological surveys of MCEs at various locations around the globe, our team has encountered many undescribed species, especially from the families Labridae, Pomacentridae and Serranidae (Arango et al. 2019; Shepherd et al. 2019; Tea et al. 2019; Pinheiro et al. 2019; Shepherd et al. 2021). Recent research expeditions in the Maldives have revealed a similar pattern of discovery. In this paper, we describe a new species of *Plectranthias* perchlet seen in MCEs at two atolls in the Maldives.

# Material and methods

All specimens were collected with hand nets while diving on a mixed-gas closed-circuit rebreather (Hollis Prism 2). Specimens were collected and immediately transported to a field laboratory, where they were photographed, tissues sampled, fixed in 10% formalin, and preserved in 75% ethanol. The preserved specimens were later measured and x-radiographed at the California Academy of Sciences. Measurements were taken with digital calipers to the nearest 0.01 mm and rounded to one decimal place, following the conventions described in Anderson and Heemstra (2012), Williams et al. (2013), and Gill and Roberts (2020). Diagrams in Gill et al. (2021) were especially useful to identify obscure characters. Principal caudal rays are those associated with hypurals. The lowermost principal caudal-fin ray is the ray articulating between the distal tips of the parahypural and the haemal spine of preural centrum 2 as described in Gill et al. (2021). Procurrent caudal-fin rays are those dorsal and ventral to the principal rays. Principal and procurrent caudal-fin ray counts are presented as upper + lower. Vertebral counts are presented as precaudal + caudal. The anterior-most vertebra with a haemal spine was counted as the first caudal vertebra, the urostylar complex the last. Gill raker counts are presented as upper (epibranchial) + lower (ceratobranchial) rakers on the anterior face of the first arch; the angle raker is included in the second count. The anterior supraneural-dorsal ray-pterygiophore-neural spine interdigitation pattern follows Ahlstrom et al. (1976), and is presented as a formula with "0" representing a supraneural, "/" a neural spine, and numerals indicating the number of spines borne by each pterygiophore. The elongated portions of dorsal-fin ray filaments were not included in the measurements, as they were damaged by preservation. Morphometric data for the holotype and paratype is presented in Table 1. Measurements in the text are proportions of standard length (SL) unless otherwise noted. Values in parentheses represent data from the paratype when different from the holotype.

The holotype was deposited at the California Academy of Sciences ichthyological collection (**CAS**), and the paratype was deposited at the Natural History Museum of Los Angeles County (**LACM**).

Mitochondrial cytochrome c oxidase subunit I (COI) DNA was sequenced and analyzed for the new species. DNA extraction and PCR amplification of the COI gene were performed following protocols detailed in Weigt et al. (2012). DNA sequences were compared to the 19 Plectranthias species available in GenBank (P. ahiahiata Shepherd, Phelps, Pinheiro, Perez-Matus & Rocha, 2018: MH025944; P. alleni Randall, 1980: FOA01479; P. bennetti Allen & Walsh, 2015: KT601636; P. bilaticlavia Paulin & Roberts, 1987: MN915262; P. flammeus Williams, Delrieu-Trottin & Planes, 2013: KC565477-KC565480; P. fourmanoiri Randall, 1980: KC567662, KC567663; P. inermis Randall, 1980: OQ386015; P. japonicus Steindachner, 1883: JQ681323, JQ681324; P. kamii Randall, 1980: KU943548; P. kelloggi Jordan & Evermann, 1903: KP267643; P. longimanus Weber, 1913: JF494178; P. maculicauda Regan, 1914: FNZ095; P. nanus Randall, 1980: JQ432001-JQ432004, KC565481, KC567661; P. polygonius Shepherd, Phelps, Pinheiro, Rocha & Rocha, 2020: MN922331; P. wheeleri Randall, 1980: LC730852; P. randalli Fourmanoir & Rivaton, 1980: KP267613; P. retrofasciatus Fourmanoir & Randall, 1979: JN313133; P. winniensis Tyler, 1966: KC565482, KC565483; P. yamakawai Yoshino, 1972: OP614925) and two in the Barcode of Life Database (P. ferrugineus Gill, Pogonoski, Moore & Johnson, 2021: FOA01382-18; P. mcgroutheri Gill, Pogonoski, Moore & Johnson, 2021: FOA02412-20). Alignments of DNA sequences were done using a standard Geneious global alignment with free end gaps and 65% similarity in the program Geneious Prime 2020.0.3 (Biomatters, Auckland; Kearse et al. 2012).

# Results

### Taxonomy

### Plectranthias raki sp. nov.

https://zoobank.org/9B0CEAD6-829B-4BE7-B82C-2AB8E3EBDE77 Figs 1, 2, Table 1 Dhivehi common name: Raki bureki English common name: Maldivian Perchlet

### Type locality. Maldives.

**Material examined.** *Holotype.* • CAS-ICH 248439 (Field number LAR2951) 66.2 mm SL, GenBank PQ416576. Location: Kuramathi Outer Reef, Rasdhoo Atoll, Maldives 4°15′22″N, 72°59′00″E, depth of collection 118 m, collected with hand nets by B Shepherd, HT Pinheiro, MV Bell, and LA Rocha, 9 December 2022. *Paratype.* • LACM 61827 (Field number LAR2952) 70.4 mm SL, GenBank PQ416577. Same collection data as holotype.

**Diagnosis.** *Plectranthias raki* sp. nov. is unique in both morphology and coloration. The following combination of characters distinguishes it from all known congeners: dorsal fin X, 15; anal-fin rays III, 7; pectoral-fin rays 13 | 13 (13 | 12), all unbranched; principal caudal-fin rays 9 + 8; lateral line complete with 30-32tubed scales; 3 supraneural bones, predorsal formula 0/0 + 0/2/1 + 1/1/1/;gill rakers 5 + 12; circumpeduncular scales 11-12; oblique rows of scales on



**Figure 1.** Holotype (left) and paratype (right) of *Plectranthias raki* sp. nov. Holotype CAS-ICH 248439 66.2 mm SL, shortly after collection (**A**), preserved specimen (**B**) and x-radiograph (**C**). Paratype LACM 61827, 70.4 mm SL, shortly after collection (**D**), preserved specimen (**E**) and x-radiograph (**F**). Photos: **A**, **D** by Luiz Rocha. **B**, **C**, **E**, **F** by Jon Fong.

cheek 8 (7); longest dorsal spine the 4<sup>th</sup> or 5<sup>th</sup>; no fleshy tips on the dorsal-fin spines; no antrorse serrations on preopercle. Live coloration consisting of a series of irregularly shaped patches of red-orange along dorsal two-thirds of body; patches divided into two indistinct rows by the lateral line; patches red-orange dorsally and posteriorly, becoming more yellow-orange anteriorly and ventrally, golden yellow on opercle and maxilla; anal fin pointed, mostly white proximally, yellow distally, with two yellow spots approximately one-third orbit diameter at base of third spine and fifth and sixth soft rays; two irregularly shaped yellow-orange spots, approximately one-third orbit diameter, located on either side of centermost caudal-fin rays; small orange spot, approximately one-half orbit diameter, at base of pelvic fin.

**Description.** Dorsal rays X, 15, all segmented rays branched; anal rays III, 7, all segmented rays branched; pectoral-fin rays 13 | 13 (13 | 12), all unbranched; pectoral fin moderately long, longest ray reaching to vertical above midpoint of anal fin; pelvic-fin I, 5; upper procurrent caudal-fin rays 6; lower procurrent caudal-fin rays 4; principal caudal-fin rays 9 + 8; branched caudal-fin rays 9 + 7



Figure 2. Living specimen (not retained) of *Plectranthias raki* sp. nov. photographed at 110 m depth at Dhaalu Atoll, Maldives. Photo by Luiz Rocha.

(8 + ?); lateral line complete with 32 (30) tubed scales on the left side; scales above lateral line to origin of dorsal fin 3; scales above lateral line to base of middle dorsal spine 2; scales below lateral line to origin of anal fin 10; oblique rows of scales on cheek 8 (7); circumpeduncular scales 11 (12); gill rakers 5 + 12, the upper 4 and lower 3 rudiments; pseudobranchial filaments 18 (15); branchiostegal rays 7. Vertebrae 10 + 16; supraneural (predorsal) bones 3; predorsal formula 0/0 + 0/2/1 + 1/1/1/; dorsal pterygiophores in interneural spaces 9-13 1/1/1+1/1+1/1; no trisegmental pterygiophores associated with dorsal fin; terminal dorsal pterygiophore in interneural space 18; no trisegmental pterygiophores associated with anal fin; terminal anal pterygiophore in interhaemal space 5; ribs present on vertebrae 3 through 10; epineurals present on vertebrae 1 through 12 (possibly 13); parhypural and hypurals autogenous; well-developed hypurapophysis on parhypural; epurals 3; single uroneural (posterior uroneural absent); ventral tip of cleithrum with well-developed posteroventral process; proximal tip of first anal-fin pterygiophore near distal tips of parapophyses on vertebra 10.

Body moderately deep, the depth 2.7 in SL, and compressed, the width 2.2 in depth; head fairly short, 2.2 (2.1) in SL; dorsal fin originates at a vertical line just above the third lateral line scale; dorsal fin continuous and notched between the spinous and soft portions to about half of the length of the first soft ray; dorsal-fin spines without fleshy tabs on the tips; dorsal-fin base length 3.2 (2.1) in SL; the fourth and fifth dorsal spines the longest and the same length in the holotype (the fourth the longest on the paratype); third dorsal-fin

soft ray the longest, with extended filament; anal-fin base length 6.0 (5.7) in SL; second anal-fin spine the longest; anal fin pointed with the third segmented ray the longest; pectoral fin moderately long and pointed, 2.9 (2.7) in SL; pelvic fin relatively short, 4.0 (4.2) in SL, and not reaching anus; caudal fin slightly emarginate, with several filaments on elongated ray branches (caudal fin in paratype damaged); caudal peduncle length 3.9 (5.1) in HL; caudal peduncle depth 3.7 (4.2) in HL.

Morphometric values are summarized in Table 1.

Plectranthias raki sp. nov. HOLOTYPE PARATYPE CAS-ICH 248439 LACM 61827 Standard length (mm) 66.15 70.41 Head length 44.9 47.7 Greatest body depth 37.4 36.9 Body width 17.1 16.7 Snout length 13.1 12.3 Postorbital of head 25.0 24.6 Bony interorbital width 6.6 6.2 Orbit diameter 9.8 10.0 Upper jaw length 20.0 19.0 Maxilla width 7.5 6.2 Caudal peduncle length 11.7 9.3 Caudal peduncle depth 12.2 11.5 Predorsal length 40.3 38.9 Preanal length 72.9 74.8 Prepelvic length 37.5 39.5 Dorsal fin base length 31.0 47.6 First dorsal spine 5.8 6.3 Longest dorsal spine (number) 16.8 (4th and 5th) 18.2 (4<sup>th</sup>) First segmented dorsal ray 14.7 damaged Longest segmented dorsal ray- without filament (number) 19.0 (3<sup>rd</sup>) 20.6 (3<sup>rd</sup>) Anal fin base length 16.8 17.6 First anal spine 8.8 8.6 Second anal spine 19.0 17.4 15.2 12.8 Third anal spine First segmented anal ray 19.2 18.8 Longest anal spine (number) 11.5 (2<sup>nd</sup>) 10.8 (2<sup>nd</sup>) Longest segmented anal ray (number) 10.5 (3rd) 9.9 (3rd) Caudal fin length 27.0 24.2 (damaged) 37.5 Pectoral fin length 34.8 Pelvic spine length 15.8 15.3 Pelvic fin length 24.8 24.1

 Table 1. Morphometric data for *Plectranthias raki* sp. nov., expressed as a percentage of standard length.

Head of moderate size, 2.2 (2.1) in SL; snout pointed, 3.4 (3.9) in HL; mouth relatively large, terminal and oblique, the posterior margin of maxilla reaching to vertical line almost directly beneath the center of pupil; upper jaw length 2.3 (2.5) in HL; maxilla expanded posteriorly; upper jaw with one large canine on each corner; 5 irregular rows of villiform teeth, largest in back, the teeth on the last row as big as the front canines; lower jaw with one small canine on either side of symphysis and 4–5 irregular rows of villiform teeth, the largest in the back; a pair of enlarged canines on each side of the dentary; teeth on the last row as big as the canines; palatine with 4 rows of small villiform teeth; vomer with 5 rows of villiform teeth.

Opercle with 3 spines, the middle one the largest, sharp and pointed, and terminating most posteriorly, the upper one obscured by scales; posterior margin of preopercle with 26 serrae; ventral margin of preopercle smooth and without conspicuous antrorse or retrorse spines; posterior margins of interopercle and subopercle smooth, obscured by scales; posttemporal with 3 small serrations; lower margin of infraorbital 1 smooth; anterior nostril located close to the anterior margin of orbit, with a small flap; posterior nostril located adjacent to anterior border of orbit, without flap.

Scales ctenoid with peripheral cteni; lateral line broadly arched over pectoral fin, following body contour beneath dorsal fin to caudal-fin base; scales between eyes; no scales on maxilla, chin, mandible, lower part of snout, or branchiostegal rays; scales on head starting above the center of the eyes; triangular shaped patch of 6 rows of scales on pectoral fin, extending approximately  $\frac{1}{4}-\frac{1}{3}$  length of fin, extending furthest on 7<sup>th</sup> and 8<sup>th</sup> rays; scales on basal fourth of caudal fin; anal fin with one row of scales along anterior half of base; all other fins without scales.

Coloration when fresh: (Figs 1A, C, 2) Body pinkish-white with a series of irregularly shaped patches of red-orange along dorsal two-thirds of body; patches red-orange dorsally and posteriorly, becoming more yellow-orange anteriorly and ventrally; patches are golden yellow on opercle, especially on maxilla; one indistinct yellow stripe crossing opercle diagonally from bottom edge of eye; indistinct orange-red stripe extending from anterior margin of eye to upper lip; orbit white with indistinct yellow stripe through pupil, a continuation of the red-orange stripe originating at the snout tip; sharp break in orange-colored body-patches along lateral line, forming two distinct rows; this is especially pronounced in living specimens; patches above lateral line smaller and associated with pairs or trios of dorsal-fin spines and rays, creating an alternating pattern of five orange spots interspersed with white areas along the base of dorsal fin; patches below the lateral line are larger and more irregular in shape and distribution anteriorly, more rectangular and uniform on posterior half of body; throat and belly white; dorsal fin white at base; interspinous membranes of dorsal fin mostly yellow, white proximally, hyaline distally; membranes of soft dorsal mostly white with yellow stripe roughly midway from body and following contour of body; dorsal spines yellow, rays with yellow tips; anal fin mostly white proximally, yellow distally, with two yellow spots approximately one-third orbit diameter at base of third spine and fifth and sixth soft rays; anal-fin spines white; pelvic fins white proximally, hyaline distally, with yellow-orange spot at base of spine; pectoral fin white to hyaline, with orange spot, approximately one-half diameter of orbit, at fin base; caudal fin white at origin, becoming pale

yellow distally, with two irregularly shaped yellow-orange spots, approximately one-third orbit diameter, located on either side of centermost fin rays; additional, smaller spots of similar coloration distally; tips of caudal-fin rays yellow; proximal half of dorsalmost and ventralmost caudal-fin rays yellow-orange.

**Color in alcohol:** Uniform pale golden-brown with no distinct markings. Scattered melanophores on the nape and along base of dorsal fin (denser on the nape).

**Etymology.** The species name, raki, means "feeling shy to confront people" in the Dhivehi language. This was chosen because *Plectranthias* are shy by nature and typically hide from us when we are conducting surveys. To be treated as a noun in apposition.

**Distribution and habitat.** *Plectranthias raki* sp. nov. is known only from the Maldives, where it is likely widespread. It was seen inhabiting small holes of reef walls at several locations between Rasdhoo (4°15'N, 72°57'E) and Dhaalu atolls (2°41'N, 72°51'E) at approximately 100 to 125 m depth.

# Discussion

The Maldives Archipelago shelters a rich biodiversity of reef fishes. However, only Plectranthias winniensis Tyler, 1966 was previously known for the region (Randall and Anderson 1993). Plectranthias raki is distinguished from P. winniensis by the number of pectoral-fin rays (12-13, versus 16-18), tubed lateral line scales (32, versus 8-27), and in coloration, especially in having a yellow stripe on the dorsal fin and lacking a white spot at the caudal peduncle, as in P. winniensis. Four species, Plectranthias garrupellus Robins & Starck, 1961, Plectranthias hinano Shepherd, Phelps, Pinheiro, Rocha & Rocha, 2020, Plectranthias kojiorum Koeda, Muto & Wada, 2021, and Plectranthias longimanus Weber, 1913, share the following diagnostic characters with Plectranthias raki: dorsal fin X, 15; anal fin III, 7; and pectoral-fin rays 12–13. In addition to the morphological differences that follow, P. raki is easily distinguished from these four species based on its living coloration. Plectranthias raki can be distinguished from Plectranthias garrupellus by having 30-32 tubed lateral-line scales, compared to 28-29 in P. garrupellus, and by lacking antrorse spines on the preopercle (versus 2 spines in P. garrupellus). Plectranthias raki has 5 gill rakers on the upper arch compared to 7-8 in P. hinano, a shorter dorsal-fin base length, 31% SL versus 48.5% in P. hinano, and lacks antrorse spines on the preopercle, whereas P. hinano has 3 antrorse spines. Plectranthias raki has 16 branched caudal-fin rays, while Plectranthias kojiorum has only 13. Plectranthias raki has 3 supraneural bones and lacks antrorse spines on the preopercle, while P. kojiorum has 2 predorsal bones and 2 antrorse spines. Plectranthias raki differs from P. longimanus by having a complete lateral line with 30-32 tubed scales, compared to the incomplete line of 12–15 tubed scales in P. longimanus.

Plectranthias raki is similar in many counts and measurements to Plectranthias klausewitzi Zajonz, 2006 from the Red Sea, but differs in having a longer snout length (13.1% SL versus 10.7% SL in *P. klausewitzi*, a smaller orbit diameter (9.8% SL in *P. raki* versus 13.9% in *P. klausewitzi*), and by having fewer pectoral-fin rays (12–13 in *P. raki* versus 14–15 in *P. klausewitzi*). The living coloration of *Plectranthias klausewitzi* is unknown at this time.

*Plectranthias raki* is distinct from the other Indian Ocean species, *Plectranthias alcocki* Bineesh, Gopalakrishnan & Jena, 2014, *Plectranthias alleni* Randall, 1980, and *Plectranthias morgansi* Smith, 1961 based on the following characteristics. *Plectranthias raki* has 12–13 pectoral-fin rays and 30–32 tubed lateral-line scales, and three scales above the lateral line to the origin of the dorsal fin, while *P. alcocki* has 14 pectoral-fin rays, 28 tubed lateral-line scales, and only one scale above the lateral line to the origin of the dorsal fin. *Plectranthias raki* differs from *P. alleni* in dorsal-fin counts (X, 15 versus X, 14), pectoral-fin rays (12–13, versus 15–17), the number of circumpeduncular scales (11–12 versus 14–15), and in coloration, by lacking the short narrow dark stripe in front of the eye and the faint dusky stripe from behind the eye across the upper side of the body that distinguishes *P. alleni*. *Plectranthias raki* differs from *Plectranthias morgansi* by having the 4<sup>th</sup> dorsal spine the longest (versus the 3<sup>rd</sup> in *P. morgansi*), pointed anal fin (versus rounded in *P. morgansi*) and an emarginate caudal fin (versus rounded in *P. morgansi*) (Smith 1961).

Our specimens also resemble an undescribed species of Plectranthias collected in the Andaman Sea on the Tanintharyi coast of Myanmar (Gill and Psomadakis 2018). However, there are key differences that distinguish them. Plectranthias raki has 12-13 pectoral-fin rays versus 14 on the Myanmar specimen, and lacks the two enlarged antrorse spines on the lower part of the preopercle seen on the specimen from Myanmar. In addition, there are several morphometric differences, including a smaller orbit diameter (9.8% SL in Plectranthias raki versus 14.9% SL in the specimen from Myanmar), a shorter caudal peduncle (11.7% SL versus 20.4% SL in the Myanmar specimen), shorter pectoral fins (34.8% SL in Plectranthias raki versus 42.9% SL in the Myanmar specimen), and the longest segmented dorsal ray being the 3rd in Plectranthias raki and the 7th in the specimen from Myanmar. A second undescribed species, also collected in Myanmar, is documented in the same publication (Gill and Psomadakis 2018). The specimen was subsequently lost, so there are limited details for comparison, but it is also distinguishable from Plectranthias raki morphologically and in coloration. Plectranthias raki has 12-13 pectoral fin rays, while the second specimen from Myanmar has 14. Plectranthias raki also has a predominately white caudal fin with two indistinct, but pronounced, yellow-orange spots, while the caudal fin on the second specimen from Myanmar is solid yellow, and Plectranthias raki lacks the red marking on the middle spines of the dorsal fin as seen in the photograph of the specimen from Myanmar.

The barcode fragment of the COI gene of *Plectranthias raki* is not within 10% distance to any COI sequences of *Plectranthias* available on GenBank and the Barcode of Life Database. Therefore, we couldn't identify a close genetic relative. However, the new species seems to form a group with other distantly related species (12–15% genetic divergence) that include *P. bennetti*, *P. hinano*, *P. ferrugineus*, and *P. kojiorum*. Since DNA sequences are available for just about 30% of the species in the genus, we prefer not to discuss their relationships here in detail because they will likely change with the addition of more species.

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# Additional information

# **Conflict of interest**

The authors have declared that no competing interests exist.

# **Ethical statement**

All specimens were collected following the California Academy of Sciences Institutional Animal Care and Use Committee guidelines under protocol number 2022-01.

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### **Author contributions**

B Shepherd, H Pinheiro, and L Rocha discovered and collected the new species. L Rocha and B Shepherd took specimen data and obtained all collecting permits. C Rocha did the DNA sequencing. All authors contributed to manuscript writing and editing.

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### **Data availability**

All of the data that support the findings of this study are available in the main text.

# References

- Ahlstrom EH, Butler JL, Sumida BY (1976) Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distributions, and early life histories and observations on five of these from the northwest Atlantic. Bulletin of Marine Science 26: 285–402.
- Allen GR, Walsh F (2015) *Plectranthias bennetti*, a new species of anthiine fish (Pisces: Serranidae) from the Coral Sea, Australia. Journal of the Ocean Science Foundation 16: 82–89. http://oceansciencefoundation.org/josf/josf16d.pdf
- Anderson WD, Heemstra PC (2012) Review of Atlantic and eastern Pacific Anthiine fishes (Teleostei: Perciformes: Serranidae), with descriptions of two new genera.

Transactions of the American Philosophical Society, New Series 102(2): 1–173. https://doi.org/10.70249/9798893983760

- Arango BG, Pinheiro HT, Rocha C, Greene BD, Pyle RL, Copus JM, Shepherd B, Rocha LA (2019) Three new species of *Chromis* from mesophotic coral ecosystems of the Philippines. ZooKeys 835: 1–15. https://doi.org/10.3897/zookeys.835.27528
- Bineesh KK, Akhilesh KV, Gopalakrishnan A, Jena JK (2014) *Plectranthias alcocki*, a new anthiine fish species (Perciformes: Serranidae) from the Arabian Sea, off southwest India. Zootaxa 3785: 490–496. https://doi.org/10.11646/zootaxa.3785.3.10
- Fricke R (2021) *Plectranthias normanby*, a new species of perchlet from Papua New Guinea, western Pacific (Teleostei: Serranidae). FishTaxa 20: 25–38.
- Fricke R, Eschmeyer WN, van der Laan R (Eds) (2024) Eschmeyer's Catalog of Fishes: Genera, Species, References. http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp
- Gill AC, Psomadakis PN (2018) *Pseudanthias emma* new species, with notes on a collection of anthiadine serranid fishes from off Myanmar (eastern Indian Ocean). Zootaxa 4455(3): 525–536. https://doi.org/10.11646/zootaxa.4455.3.8
- Gill AC, Roberts CD (2020) *Plectranthias cruentus*, a new species of anthiadine perchlet (Teleostei: Serranidae) from the Lord Howe Rise, Tasman Sea. Zootaxa 4750(4): 560–566. https://doi.org/10.11646/zootaxa.4750.4.6
- Gill AC, Tea YK, Senou H (2016) *Plectranthias takasei*, new species of anthiadine fish from southern Japan (Teleostei: Serranidae). Zootaxa 4205(4): 349–356. https://doi. org/10.11646/zootaxa.4205.4.3
- Gill AC, Pogonoski JJ, Moore GI, Johnson JW (2021) Review of Australian species of *Plectranthias* Bleeker and *Selenanthias* Tanaka (Teleostei: Serranidae: Anthiadinae), with descriptions of four new species. Zootaxa 4918(1): 1–116. https://doi.org/10.11646/zootaxa.4918.1.1
- Heemstra PC, Randall JE (2008) A review of the anthiine fish genus *Plectranthias* (Perciformes: Serranidae) of the Western Indian Ocean, with description of a new species, and a key to the species. Smithiana Bulletin 10: 3–17.
- Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Meintjes P, Drummond A (2012) Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28: 1647–1649. https://doi. org/10.1093/bioinformatics/bts199
- Koeda K, Muto N, Wada H (2022) *Plectranthias kojii* sp. nov., a new perchlet (Perciformes: Serranidae: Anthiinae) from Okinawa, Japan. Ichthyological Research (2022) 69: 352–360. https://doi.org/10.1007/s10228-021-00842-1
- Kuiter RH (2004) Serranidae & Plesiopidae: A Comprehensive Guide to Basslets, Hamlets, Longfins & relatives. Aquatic Photographics, Seaford, Australia, 108 pp.
- Pinheiro HT, Shepherd B, Castillo C, Abesamis RA, Copus JM, Pyle RL, Greene BD, Coleman RR, Whitton RK, Thillainath E, Bucol AA, Birt M, Catania D, Rocha LA (2019) Deep reef fishes in the world's epicenter of marine biodiversity. Coral Reefs 38: 985–995. https://doi.org/10.1007/s00338-019-01825-5
- Randall JE (1980) Revision of the genus *Plectranthias* (Serranidae: Anthiinae) with descriptions of 13 new species. Micronesica 16 (1): 101–187.
- Randall JE, Anderson C (1993) Annotated checklist of the epipelagic and shore fishes of the Maldives Islands. Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology (59): 1–47.

- Rocha LA, Pinheiro HT, Shepherd B, Papastamatiou YP, Luiz OJ, Pyle RL, Bongaerts P (2018) Mesophotic coral ecosystems are threatened and ecologically distinct from shallow water reefs. Science 361: 281–284. https://doi.org/10.1126/science. aaq1614
- Shepherd B, Phelps T, Pinheiro HT, Pérez-Matus A, Rocha LA (2018) *Plectranthias ahiahiata*, a new species of perchlet from a mesophotic ecosystem at Rapa Nui (Easter Island) (Teleostei, Serranidae, Anthiadinae). ZooKeys 762: 105–116. https://doi.org/10.3897/zookeys.762.24618
- Shepherd B, Pinheiro HT, Phelps T, Pérez-Matus A, Rocha LA (2019) Luzonichthys kiomeamea (Teleostei: Serranidae: Anthiadinae), a new species from a mesophotic coral ecosystem of Rapa Nui (Easter Island). Journal of the Ocean Science Foundation 33: 17–27. https://doi.org/10.5281/zenodo.3237914
- Shepherd B, Phelps TAY, Pinheiro HT, Rocha CR, Rocha LA (2020) Two new species of *Plectranthias* (Teleostei, Serranidae, Anthiadinae) from mesophotic coral ecosystems in the tropical Central Pacific. ZooKeys 941: 145–161. https://doi.org/10.3897/ zookeys.941.50243
- Shepherd B, Pinheiro HT, Phelps TAY, Pérez-Matus A, Rocha LA (2021) *Pseudanthias hangapiko*, a new anthiadine serranid (Teleostei, Serranidae, Anthiadinae) from Rapa Nui (Easter Island). ZooKeys 1054: 1–13. https://doi.org/10.3897/zookeys.1054.64508
- Smith JLB (1961) Fishes of the Family Anthiidae from the Western Indian Ocean and the Red Sea. Ichthyological Bulletin. 21: 359–369. http://hdl.handle.net/10962/ d1018951
- Tea YK, Pinheiro HT, Shepherd B, Rocha LA (2019) *Cirrhilabrus wakanda*, a new species of fairy wrasse from mesophotic ecosystems of Zanzibar, Tanzania, Africa (Teleostei, Labridae). ZooKeys 863: 85–96. https://doi.org/10.3897/zookeys.863.35580
- Wada H, Suzuki T, Senou H, Motomura H (2020) *Plectranthias ryukyuensis*, a new species of perchlet from the Ryukyu Islands, Japan, with a key to the Japanese species of *Plectranthias* (Serranidae: Anthiadinae). Ichthyological Research 67: 294–307. https://doi.org/10.1007/s10228-019-00725-6
- Weigt LA, Baldwin CC, Driskell A, Smith DG, Ormos A, Reyier EA (2012) Using DNA Barcoding to Assess Caribbean Reef Fish Biodiversity: Expanding Taxonomic and Geographic Coverage. PLoS ONE 7: e41059. https://doi.org/10.1371/journal.pone.0041059
- Williams JT, Delrieu-Trottin E, Planes S (2013) Two new fish species of the subfamily Anthiinae (Perciformes, Serranidae) from the Marquesas. Zootaxa 3647(1): 167–180. https://doi.org/10.11646/zootaxa.3647.1.8
- Wu KY, Randall JE, Chen JP (2011) Two new species of Anthiine fishes of the genus Plectranthias (Perciformes: Serranidae) from Taiwan. Zoological Studies 50(2): 247–253. http://zoolstud.sinica.edu.tw/Journals/50.2/247.pdf



**Short Communication** 

# Taxonomic notes on the genus *Spinosodus* Breuning & de Jong, 1941 (Coleoptera, Cerambycidae) with a generic and specific synonym

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#### Abstract

Taxonomic notes on the genus *Spinosodus* Breuning & de Jong, 1941 are presented. The genus *Bulbolmotega* Breuning, 1966 is synonymized with *Spinosodus*, and *Bulbolmotega* sumatrensis Breuning, 1966 is recognized as a junior synonym of *Spinosodus* spinicollis Breuning & de Jong, 1941. Additionally, *Spinosodus* is redescribed, and *S. rufomaculatus* Breuning, 1973 is formally reported from China, Vietnam, Thailand, and India for the first time.

Key words: Bulbolmotega, Lamiinae, new record, new synonym



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# Introduction

The genus Spinosodus Breuning & de Jong, 1941 (Coleoptera, Cerambycidae) was established for Spinosodus spinicollis Breuning & de Jong, 1941 from Java, Indonesia. Subsequently, both the genus and the species were redescribed by Breuning (1963) in a revision of the Asian Pteropliini. The second species of this genus, Spinosodus rufomaculatus Breuning, 1973 was described based on a single specimen from Pakson, Laos. Currently, the genus is recognized as comprising these two species: the insular S. spinicollis from Indonesia and the continental S. rufomaculatus from Laos (Tavakilian and Chevillotte 2024). The monotypic genus Bulbolmotega Breuning, 1966 was described for Bulbolmotega sumatrensis Breuning, 1966 from Sumatra (Indonesia), and no additional species are known to date. Recently, two intriguing individuals of these genera were collected in Guangxi Zhuang Autonomous Region, China. Initial identification suggested that these specimens belong to Spinosodus. However, further comparison revealed striking similarities to Bulbolmotega. This observation triggered us to discuss the relationship between these two genera. Therefore, we aim to verify whether the genus Bulbolmotega should be synonymized with Spinosodus, based on a comparison of the type material.

# Materials and methods

Specimens from the following collections were examined and/or photographed in this study. The place where the specimens were deposited is indicated in the text.

MNHN	Muséum National d'Histoire Naturelle, Paris, France;		
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden, Holland;		
SNSD	Senckenberg Naturhistorische Sammlungen Dresden, Dresden,		
	Germany;		
YZU	Yangtze University, Jingzhou, China;		
CXG	Collection of Xavier Gouverneur, Rennes, France.		

The photographs of the specimens from Guangxi were taken using a Canon 7D Mark II digital camera equipped with a Canon EF 100 mm f/2.8L IS USM. The photographs of the holotype of *S. spinicollis* were photographed by Oscar Vorst (RMNH). The photographs of the holotype of *S. rufomaculatus* were photographed by Antoine Mantilleri and Christophe Rivier (MNHN). The photographs of the holotype of *B. sumatrensis* were photographed by Olaf Jäger (SNSD). All photographs were edited using Adobe Photoshop 2020.

# Results

After examining photographs of the type specimens of both genera, it is clear that the genus *Bulbolmotega* should be considered a junior synonym of *Spinosodus*. Consequently, *B. sumatrensis* is recognized as a junior synonym of *S. spinicollis*. Additionally, *S. rufomaculatus* is formally reported here for the first time from China, Vietnam, Thailand, and India based on own observations and the data presented on the Cerambycoidea Forum (Vitali 2024), as well as the materials provided by Xavier Gouverneur.

#### Genus Spinosodus Breuning & de Jong, 1941

Chinese common name: 刺球腿天牛属

Spinosodus Breuning & de Jong, 1941: 96—Breuning 1961: 283; Breuning 1963: 509. Type species: S. spinicollis Breuning & de Jong, 1941.

*Bulbolmotega* Breuning, 1966: 124. Type species: *B. sumatrensis* Breuning, 1966. Syn. nov.

**Redescription.** Body relatively broad. Head retracted backwards, frons wider than long. Antennae shorter than body, with short setae beneath; antennal insertions flat, not obviously protruding upwards, widely separated from each other; scape short and stout, pedicel relatively long, antennomere 3 slightly longer than antennomere 4 or scape. Eyes slightly coarsely faceted, inner side deeply emarginate, lower lobe longer than broad, remarkably longer than gena. Pronotum transverse, with two transverse grooves on anterior and posterior margins, respectively, the second one on anterior margin strongly curved backwards at middle; each side provided a small but acute spine behind the middle, slightly directed backwards; disc uneven, with a large and blunt hump on each

side. Elytra wider than pronotum, rounded apically; each elytron with a longitudinal blunt median ridge at base. Prosternal process narrow, lower than procoxae; mesosternal process shortly vertical anteriorly; metasternum normal. Legs moderately long, femur slightly clavate.

**Comments.** Based on the comparison of the type species of *Spinosodus* and *Bulbolmotega* (images and original descriptions), we found no significant morphological differences between these genera. As a result, *Bulbolmotega* is considered a junior synonym of *Spinosodus*.

#### Spinosodus spinicollis Breuning & de Jong, 1941

Figs 1, 3a-d, 4a, b, e, f Chinese common name: 刺球腿天牛

- Spinosodus spinicollis Breuning & de Jong, 1941: 96–Breuning 1961: 283; Breuning 1963: 509. Type locality: Java, Indonesia.
- *Bulbolmotega sumatrensis* Breuning, 1966: 124. Type locality: Sumatra, Indonesia. Syn. nov.

**Type material examined.** *Holotype* of *S. spinicollis* (RNMH, INS. 1488475), label details are shown in Fig. 1b. *Holotype* of *B. sumatrensis* (SNSD), label details are shown in Fig. 1d.

Distribution. Indonesia.

**Comments.** Based on the comparison of *S. spinicollis* and *B. sumatrensis*, we found that there are no significant differences between the two species. For example, in both species, the body colour is predominantly pale reddish brown, the pronotum has a small, rounded, ochraceous pubescent patch on each side of the anterior margin, which is distinctly separated from the outer pubescent



Figure 1. Habitus of Spinosodus spinicollis Breuning & de Jong, 1941 **a**, **b** holotype of S. spinicollis **c**, **d** holotype of Bulbolmotega sumatrensis Breuning, 1966.

patch and the posterior large, rounded pubescent patch, and the elytra that are unevenly scattered with the yellowish brown pubescence. Therefore, we propose that *B. sumatrensis* Breuning, 1966 is a junior synonym of *S. spinicollis* Breuning & de Jong, 1941.

As *B. sumatrensis* is the type species of *Bulbolmotega*, this genus becomes a junior synonym of the genus *Spinosodus*.

#### Spinosodus rufomaculatus Breuning, 1973

Figs 2, 3e-h, 4c, d, g-i Chinese common name: 赭斑刺球腿天牛

Spinosodus rufomaculatus Breuning, 1973: 660.

**Type material examined.** *Holotype* (MNHN, EC36967), label details are shown in Fig. 2b.

**Non-type material examined. CHINA** • 2 females (YZU); Guangxi, Fengshan county, Fengcheng town; 24°23'56.78"N, 107°1'30.46"E; alt. 479 m; 24 Apr. 2024; Yitong Fu leg.; captured by light trap • **LAOS:** 1 male (CXG); Oudomxay province, Nam Kat; alt. 750 m; May 2024; Steeve Collard leg.; captured by UV light trap • **THAILAND:** 1 female (CXG); Phrae province, Wangchin, Punjen; alt. 436 m; 16 Apr. 2017; Xavier Gouverneur leg.; captured by UV light trap.

**Distribution.** Laos, China (new country record), Vietnam (new country record), Thailand (new country record), and India (new country record).

**Comments.** This species is very similar to the type species, *S. spinicollis* from Indonesia, with the main differences being in body coloration and the shape of pubescent patches on the pronotum. In *S. rufomaculatus*, the body color is darker, and the premedian pubescent patches on both sides of the pronotum are narrow, transverse, and uniformly ochre-colored, while in the type species, the body color is lighter, and the premedian pubescent patches on the pronotum are nonuniform in color, featuring a distinct, circular ochre spot on the inner side with noticeably lighter pubescence on the outer side.

Previously, S. *rufomaculatus* was known only from Laos. However, based on our own records presented in this study (Fig. 2d, e), data and images provided by Xavier Gouverneur (Fig. 2c, f), and the Cerambycoidea Forum (Vitali 2024), the range of this species has been extended to Guangxi and Yunnan in China, Cao Bang in Vietnam, Phrae in Thailand, and Kerala in India.

### Discussion

Breuning and de Jong (1941) described *Spinosodus spinicollis* based on the specimen from Java, Indonesia. Subsequently, the same author (Breuning 1966) described *Bulbolmotega sumatrensis* from Sumatra, Indonesia. Although Breuning stated in the original description of *B. sumatrensis* that the lower eye lobe is about five times as long as the gena, compared to four times in *S. spinicollis*, we found that the difference most likely due to a measurement error. In fact, there are no taxonomically significant differences between the two species.

*Spinosodus spinicollis* is highly similar to *S. rufomaculatus* in external habitus, differing primarily in body color and the shape and color of the premedian



**Figure 2.** Habitus of *Spinosodus rufomaculatus* Breuning, 1973 **a, b** holotype **c** the individual from Oudomxay, Laos **d, e** individuals from Guangxi, China **f** individual from Phrae, Thailand.

pubescent patches on the pronotum. However, the available material indicates that *S. rufomaculatus* shows some intraspecific variability in body color and pubescence distribution, which suggests that the coloration and pubescent patterns are not reliable characters for differentiation of these two taxa. Nevertheless, we treat them here as separate species due to their clearly different geographic ranges. The type species is insular, found in Java, Sumatra, and Borneo in Indonesia, while *S. rufomaculatus* is a typical continental species, recorded from Laos, China, Vietnam, Thailand, and India.

The genus *Spinosodus* was originally placed in tribe Pteropliini Thomson, 1860, while the genus *Bulbolmotega* was classified in the tribe Acanthocinini



Figure 3. Habitus of *Spinosodus* spp. **a**, **c** holotype of *S*. *spinicollis* Breuning & de Jong, 1941 **b**, **d** holotype of *Bulbolmotega* sumatrensis Breuning, 1966 **e**–**h** *Spinosodus* rufomaculatus Breuning, 1973 **e**, **g** holotype **f**, **h** individual from Guangxi, China.

Blanchard, 1845. However, we show that the mesotibia lacks an external oblique groove near the apex and the mesocoxal cavity opens laterally, which suggests that *Spinosodus* belongs to Pteropliini rather than Acanthocinini. Breuning and de Jong (1941) indicated that *Spinosodus* is closely related to *Sodus* Pascoe, 1865 (= *Similosodus* McKeown, 1945), but it differs from the latter in the antennae, which are distinctly shorter than the body, and in the pronotum, which is equipped with a short, small lateral spine located posterior to the middle of each side.





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### **Additional information**

#### **Conflict of interest**

The authors have declared that no competing interests exist.

#### **Ethical statement**

No ethical statement was reported.

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#### **Author contributions**

Investigation: GX. Project administration: TQ. Resources: WW. Writing - original draft: SZ. Writing - review and editing: GX, WW.

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#### Data availability

All of the data that support the findings of this study are available in the main text.

# References

- Breuning S (1961) Catalogue des Lamiaires du Monde (Col. Céramb.) 4. Lieferung. Museum G. Frey, Tutzing, 183–284.
- Breuning S (1963) Bestimmungstabelle der Lamiiden-Triben nebst Revision der Pteropliini der asiatischen Region (Col. Cerambycidae) III. Teil. Entomologische Arbeiten aus dem Museum G. Frey 14(1): 466–537.
- Breuning S (1966) Neue Lamiinae aus den Beständen des Museums für Tierkunde in Dresden (Coleoptera, Cerambycidae). Reichenbachia 6(14): 119–128.
- Breuning S (1973) Lamiaires nouveaux ou peu connus du muséum de Paris. Annales de la Société Entomologique de France (N. S.) 9(3): 647–665. https://doi.org/10.1080/21686351.1973.12278939
- Breuning S, de Jong C (1941) Neue und seltene Lamiinae (Coleoptera, Cerambycidae). Zoologische Mededelingen 23: 47–106.
- Tavakilian G, Chevillotte H (2024) Titan: base de données internationales sur les Cerambycidae ou Longicornes. Version 3.0. http://titan.gbif.fr/index.html [accessed 10 September 2024]
- Vitali F (2024) Cerambycoidea Forum. http://www.cerambycoidea.com/forum/default. asp [accessed 29 October 2024]