



Deutsche Entomologische Zeitschrift

65 (2) 2018



ISSN 1435-1951 (print), ISSN 1860-1324 (online)
Dtsch. Entomol. Z. 65 (2) 2018, 117–253



Deutsche Entomologische Zeitschrift

An International Journal of Systematic Entomology

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- Results
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Deutsche Entomologische

Zeitschrift

65 (2) 2018

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An International Journal of Systematic Entomology

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Deutsche Entomologische Zeitschrift

2018. Volume 65. Issue 2

ISSN: 1435-1951 (print), 1860-1324 (online)

Abbreviated keys title: Dtsch. Entomol. Z.

In Focus

The cover picture shows *Quedius fuliginosus* (Gravenhorst).

See paper of **Salnitska M & Solodovnikov A** Revision of the *Quedius* fauna of Middle Asia (Coleoptera, Staphylinidae, Staphylininae)

Cover design

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Abstract & Indexing Information

Biological Abstracts® (Thompson ISI)
BIOSIS Previews® (Thompson ISI)
Cambridge Scientific Abstracts (CSA/CIG)
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Revision of the *Quedius* fauna of Middle Asia (Coleoptera, Staphylinidae, Staphylininae)

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<http://zoobank.org/B1A8523C-A463-4FC4-A0C3-072C2E78BA02>

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Abstract

Received 29 May 2018

Accepted 6 July 2018

Published 31 July 2018

Academic editor:

James Liebherr

Key Words

Staphylininae

Staphylinini

Quedius

Middle Asia

taxonomy

synonymy

lectotype designation

key to species

Twenty eight species of the genus *Quedius* from Middle Asia comprising Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan and Uzbekistan, are revised. *Quedius altaicus* Korge, 1962, *Q. capitalis* Eppelsheim, 1892, *Q. fusicornis* Luze, 1904, *Q. solskyi* Luze, 1904 and *Q. cohaesus* Eppelsheim, 1888 are redescribed. The following new synonymies are established: *Q. solskyi* Luze, 1904 = *Q. asiaticus* Bernhauer, 1918, **syn. n.**; *Q. cohaesus* Eppelsheim, 1888 = *Q. turkmenicus* Coiffait, 1969, **syn. n.**, = *Q. afghanicus* Coiffait, 1977, **syn. n.**; *Q. hauseri* Bernhauer, 1918 = *Q. penneckei* Bernhauer, 1918, **syn. n.**, = *Q. ouzbekiscus* Coiffait, 1969, **syn. n.**; *Q. imitator* Luze, 1904 = *Q. tschinganensis* Coiffait, 1969, **syn. n.**; *Q. novus* Eppelsheim, 1892 = *Q. dzambulensis* Coiffait, 1967, **syn. n.**, *Q. pseudonigriceps* Reitter, 1909 = *Q. kirklarensis* Korge, 1971, **syn. n.** Lectotypes are designated for *Q. asiaticus* Bernhauer, 1918, *Q. fusicornis* Luze, 1904, *Q. hauseri* Bernhauer, 1918, *Q. imitator* Luze, 1904, *Q. novus* Eppelsheim, 1892 and *Q. solskyi* Luze, 1904. For all revised species, taxonomy, distribution and bionomics are summarized. *Quedius fuliginosus* (Gravenhorst, 1802), *Q. sundukovi* Smetana, 2003 and *Q. pseudonigriceps* Reitter, 1909 are recorded for Middle Asia for the first time. One species from the *Q. coloratus*-group, found to be new to science is not described due to shortage of material. Another possibly new species is tentatively identified as *Q. fulvicollis* Stephens, 1833 until the taxonomy of that widespread species is revised. An identification key to all species is provided.

Introduction

The rove beetle genus *Quedius* Stephens, 1829 is one of the largest in the family Staphylinidae. Even according to a recent phylogenetic study (Brunke et al. 2016) which restricted *Quedius* to a cluster of lineages confined mostly to the Holarctic region, it remains a very speciose taxon to deal with. The greatest diversity of *Quedius* in this restricted sense, ca. 700 species, is confined to the humid areas of the Palaearctic region (Herman 2001; Schülke and Smetana 2015). A satisfactory alpha-taxonomic knowledge of the mega-diverse Palaearctic fauna of *Quedius* is crucial for implementing a badly needed phylogenetic

study and reclassification of this genus. Such taxonomic work is also important for an overall inventory and understanding of the Palaearctic entomofauna. Unfortunately, our knowledge of the Palaearctic *Quedius* is uneven and in some places very limited. For example, hardly anything has been done on *Quedius* of North Africa, Middle Asia, or Near and Middle East.

This paper aims to fill one of these knowledge gaps and focuses on *Quedius* of Middle Asia in the sense of Cowan (2007), i.e. the area covering five countries: Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan and Uzbekistan (Fig. 1). These countries are indeed dominated by arid landscapes and their faunas have much in com-



Figure 1. Middle Asia, our study region comprising five countries according to Cowan (2007).

mon (Kryzhanovsky 1965). However, one must bear in mind the poor correspondence of this large territory to biogeography. Due to certain patterns of geography, landscape mosaic and biogeographic history, various areas of Middle Asia may show stronger faunal connections with other respective neighboring regions than to each other. Nevertheless, we limit our paper by the formal political borders of the listed countries for practical reasons. As the former republics of the Soviet Union, they often were (and often still are) studied together. As a result, legacy taxonomic and faunistic literature considers Middle Asia largely within these borders.

Where necessary, we have considered literature or material from areas outside Middle Asia. However, species known only from outside this region were not included in this paper. One rather specialized and distinct group of species related to *Quedius* (*Microsaurus*) *mutilatus*, which comprises endemic Middle Asian species with narrow montane distributions, has been revised in a separate publication (Salnitska and Solodovnikov 2018). However, species of the *Q. mutilatus* group are here included in the identification key to all species of *Quedius* currently known from Middle Asia. We hope that this taxonomic revision and the first specialized key of Middle Asian *Quedius* will stimulate further investigations of the genus in this and adjacent poorly known areas of the Palaearctic region.

Material and methods

Depositories of material

Material for this paper is deposited in the public institutions and private collections abbreviated as follows:

- FMNH Field Museum of Natural History, Chicago, USA (C. Mayer, M. Thayer, A. Newton)
- HNHM Hungarian Natural History Museum, Budapest, Hungary (G. Makranczy)
- MNHN National Museum of Natural History, Paris, France (A. Taghavian)
- NHMD Natural History Museum of Denmark (former ZMUC, Zoological Museum of the University of Copenhagen) (A. Solodovnikov, S. Selvantharan)
- NMW Natural History Museum, Vienna, Austria (H. Schillhammer)
- ZIN Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (B.A. Korotyaev)
- ZMLU Zoological Museum (part of the Biological Museum, Lund University), Sweden (C. Fägerström)
- ZMMU Zoological Museum of Moscow University, Moscow, Russia (N.B. Nikitsky)

- cAss Private collection of V. Assing, Hannover, Germany
- cKoc Private collection of M. Kocián, Praha, Czech Republic
- cKur Private collection of S.A. Kurbatov, Moscow, Russia
- cRyv Private collection of A.B. Ryvkin, Moscow, Russia
- cSch Private collection of M. Schülke, Berlin, Germany (to be deposited at the Museum of Natural History, Berlin, Germany)

Preparation, examination and illustration of specimens

Specimens were examined with Lomo MSP-2 ver. 2 and Leica M125 dissecting scopes. Habitus and genitalia photographs were obtained using a Nikon SMZ 1500 binocular microscope with a Nikon D700 digital SLR camera. Illustrations of the male genitalia were done from soft preparations of these structures in glycerin (after dissecting, maceration in 10% KOH, and rinsing in distilled water) using a drawing tube attached to a Nikon SMZ 1500 binocular microscope. All dissected aedeagi are kept in glycerin in genitalia microvials pinned under their respective specimens.

Measurements

Measurements were taken at X4.5 magnification using an ocular micrometer. They are abbreviated as follows: HL – head length (from base of labrum to neck constriction along the head midline); HW – head width (maximum, including eyes); PL – pronotum length (along midline); PW – pronotum width (maximum); EL – length of elytra (from humerus to the most distal part of the elytral posterior margin); EW – width of elytra (maximum, with elytra closed along suture). Overall body length was measured from apex of labrum to apex of abdomen.

Type material

Where possible type material was examined and supplied with our standard respective labels indicating the revised status or identity of the respective type specimens. All original labels of the type specimens are cited verbatim in the ‘Material examined’ sections and, where available, photographed.

Classification

We use conventional subdivision of the genus *Quedius* into subgenera as in e.g. Schülke and Smetana (2015). Within the subgenera we list species so that those we presume to be closely related appear close to each other. Except the recently defined *coloratus*-group (Assing 2017) and *mutilatus*-group (Salnitska and Solodovnikov 2018), we cannot use any of the hitherto proposed species groups in *Quedius*. Species groups of Coiffait (1978) for the West Palearctic fauna are very outdated, inconsistent and even lack any diagnoses. Among those of Smetana (1971,

1988, 1992, 1995b, 1996, 2001, 2015a, 2017), species groups proposed for the fauna of China (Smetana 2017) are worth consideration, especially given that the large Xinjiang province of the north-western China borders with Middle Asia via Tajikistan, Kyrgyzstan and Kazakhstan. However, that large province of China seems to be one of the least explored areas there, what can be seen for example, from the lacking records for any wide-spread Middle Asian species from that province. Therefore, placing Middle Asian species in the species groups of Smetana (2017) was not possible, at least without extensive direct comparisons with the material from China. We can only propose that among the Middle Asian species, *Q. hauseri* and a species tentatively identified here as *Q. fulvicollis* may be related to the Chinese *muscolola*-group. Also, it should be noted that Smetana (2017) placed *Q. koltzei* in its own monotypic species group. We should also point to our disagreement with Smetana (2017) who considers *Q. equus* a member of the *przewalskii*-group, while we place it in the *mutilatus*-group (Salnitska and Solodovnikov 2018, and here). These disagreements are not essential for the taxonomic purposes of this paper and they once again call for a necessity of a large-scale phylogenetic study of *Quedius*. All species treated in this revision are also listed alphabetically in Table 1.

Distribution maps

All distributions were mapped using QGIS 2.12.0 and geographical coordinates indicated on the original locality labels of the specimens. In the case of older, non-georeferenced labels, we used approximate geographic coordinates that we were able to find for the respective toponyms with the aid of various printed maps or online systems (Google Maps, Google Earth, Global Gazetteer version 2.3 and others). Ambiguously indicated localities are cited verbatim in the ‘Material examined’ sections and taken in quotation marks. All our interpretations for such localities are given in square brackets. Those of which that are mapped are also given with their approximate coordinates in Table 2.

Results

Borders and geography of Middle Asia

The term “Middle Asia” is somewhat fuzzy in the geographical or historical literature. For example, sometimes Kazakhstan is considered as a part of Middle Asia, sometimes an expression “Middle Asia and Kazakhstan” is used. Often the distinction between “Middle Asia” and “Central Asia” is not clear. English-language publications have used “Central Asia” to refer to areas of the former USSR, to areas of China and Mongolia and to areas that cross the former Soviet/Chinese border. To avoid this ambiguity we follow Cowan (2007) and use “Middle Asia” to refer to Kazakhstan, Turkmenistan, Uzbekistan, Tajikistan and Kyrgyzstan collectively. The geographic area covered by these five countries is a subject of this paper (Fig.1). In

the west, Middle Asia is bordered by the Caspian Sea and the state border between Russia and Kazakhstan, nearly coinciding with the Volga River. In the north, Middle Asia is outlined by the long administrative border between Kazakhstan and Russia. In the east, Middle Asia borders with north-western China through the eastern administrative borders of Kazakhstan, Kyrgyzstan and Tajikistan. In the south, it is outlined by the northern borders of Afghanistan and Iran. While large areas of Kazakhstan and Turkmenistan are covered by more or less flat, desert landscape, eastern and south-eastern Kazakhstan, as well as Kyrgyzstan and Tajikistan are mainly montane countries with complex relief and a diverse landscape mosaic. In north-eastern Kazakhstan, the Altai mountain chain stretches into Middle Asia from Russia. In eastern Kazakhstan, as well as in Kyrgyzstan and Tajikistan, the area is dominated by the vast mountain systems of Tien Shan and Pamir. Large lakes like the Aral Sea, Balkhash, Issyk-Kul, and rivers like Amu Darya or Syr Darya are significant elements in the geography of Middle Asia as well.

History of the study of *Quedius* of Middle Asia

Middle Asia is the region in the western Palaearctic where published data about *Quedius* remained the most fragmentary and confusing, limited to a number of scattered and mostly outdated species descriptions. Eppelsheim (1888, 1892) was the first who studied *Quedius* material collected in Middle Asia by the early explorers such as Hauser, Staudinger, Akinin and described four new species: *Q. (M.) mutilatus* Eppelsheim, 1888, *Q. (Raphirus) cohaesus* Eppelsheim, 1888, *Q. (M.) capitalis* Eppelsheim, 1892 and *Q. (R.) novus* Eppelsheim, 1892. Later, based on the material from Semenov and Hauser, Luze (1904) and Bernhauer (1918), respectively, described five more new species from Middle Asia: *Q. (M.) solskyi* Luze, 1904, *Q. (M.) rufilabris* Luze, 1904, *Q. (M.) fusicornis* Luze, 1904, *Q. (R.) imitator* Luze, 1904, *Q. (M.) asiaticus* Bernhauer, 1918, *Q. (M.) bucharensis* Bernhauer, 1918 and *Q. (R.) hauseri* Bernhauer, 1918. These species descriptions varied in quality and, in accordance with the time, were based exclusively on external morphology. Some of these species have been re-examined in the monograph by Gridelli (1924), while the first drawings of the aedeagi for some of them appeared in Wüsthoff (1938).

The next notable contribution to the study of Middle Asian *Quedius* was made in the papers by Coiffait (1954, 1955, 1963, 1967, 1969, 1970, 1975, 1978) devoted to the Western Palearctic fauna. Henry Coiffait added aedeagus illustrations for many Middle Asian species and integrated them in his identifications keys for the Western Palearctic *Quedius*. He also described *Q. (R.) dzambulensis* Coiffait, 1967, *Q. (R.) ouzbekiscus* Coiffait, 1969, *Q. (R.) tschinganensis* Coiffait, 1969, *Q. (R.) turkmenicus* Coiffait, 1969, and *Q. (M.) tadjikiscus* Coiffait, 1975, all from Middle Asia. Unfortunately, Coiffait's input was based on very limited material from Middle Asia and additionally suffered from inconsistent study of type material and omissions of the

earlier literature. For example, three species described from Middle Asia by Luze (1904), *Q. (M.) fusicornis*, *Q. (M.) rufilabris* and *Q. (M.) solskyi*, were entirely overlooked in the influential monograph of Coiffait (1978) and have not been studied since their original description. The most unfortunate flaw of Coiffait's taxonomy was an artificial and over-splitting approach to species. As a result, all species of *Quedius* from Middle Asia he described as new, except *Q. (M.) tadjikiscus*, turned out to be synonyms here.

Finally, some bionomic and distributional data on Middle Asian *Quedius* were published by local authors stationed in that region (Kascheev, 1984–2002; Kadyrov et al., 2014a, b; Gabdullina, 2016). With the scattered, confusing and then poorly accessible taxonomic literature on *Quedius*, no surprise that their local faunistic papers were greatly infested by incorrect species identifications. Examination of the material collected by Kascheev (1984–2002), now deposited at ZIN, largely helped to reveal such misidentifications summed up in the Table 1 here.

Overall, due to a hitherto lacking targeted contemporary taxonomic investigation of the Middle Asian *Quedius*, identity of the majority of species described from, or recorded for, that region remained highly ambiguous. Most of the species described from Middle Asia needed broader comparisons and a revision of the type material. At the same time, a number of widespread species from Middle Asia were misidentified or overlooked. A large amount of *Quedius* material from Middle Asia remained undetermined and scattered in some institutional and private collections. The revision of *Q. (M.) mutilatus* species group by Salnitska and Solodovnikov (2018) was the only recent taxonomic work that touched upon Middle Asian *Quedius*.

Taxonomic part

Genus *Quedius* Stephens, 1829

Type species. *Quedius levicollis* (Brullé, 1832).

According to the latest phylogenetic hypotheses (Solodovnikov, 2006; Chatzimanolis et al., 2010; Brunke et al., 2016) the genus *Quedius* as it stands now in the taxonomic literature (e.g., summaries in Herman, 2001 or Schülke and Smetana, 2015) is a polyphyletic assemblage of species belonging to several different subtribes of Staphylinini. Within the Palaearctic or Middle Asia, all species of *Quedius* are members of the subtribe *Quediina* in the restricted sense of Brunke et al. (2016). Because of the polyphyly, *Quedius* in the current composition lacks synapomorphies and clear diagnosis. However, genus descriptions and diagnostic combination of characters that can define any Palaearctic species as a member of the genus *Quedius* are available in Coiffait (1978), Smetana (1988), Assing and Schülke (2012) and other sources. The diagnosis of the genus *Quedius* and comparative notes we provide here are tuned for the fauna of Middle Asia.

Adults and larvae of *Quedius* seem to be predators hunting small invertebrates in various, sufficiently hu-

mid ground-based debris, mostly in forest leaf litter. In a largely arid region like Middle Asia, *Quedius* are mainly confined to humid open or forested habitats along creeks or rivers in the lowland or forests, meadows, snowfield margins and talus in the mountains. Some members of the subgenus *Microsaurus* are specialized inhabitants of mammal burrows. Overall, bionomics of the genus in Middle Asia remain largely unstudied.

Diagnosis. Medium to large size (body length 3.5–24.0 mm) rove beetles with glossy forebody, infraorbital ridges extended from neck to base of mandibles and pronotal hypomera strongly inflexed under pronotal disk (not visible in lateral view). First segment of antennae at most slightly longer than second and third segments together. Last segment of maxillary palps fusiform, not densely setose. Tarsal formula 5–5–5; anterior tarsi widened in both sexes, with pale adhesive setae ventrally, with pair of

empodial setae. Males always with distinct apical emargination on abdominal sternite VIII. Aedeagus varies in shape, paramere mostly with sensory peg setae.

Comparison. Among other Staphylinini in Middle Asia *Quedius* can be sometimes confused with *Philonthus* (subtribe Philonthina), a genus with somewhat similar habitus and very abundant in the region. Species of *Philonthus*, however, do not have long infraorbital ridges, they lack empodial setae and mostly have a pronotal hypomeron well visible in lateral view. Also, *Philonthus* mostly possess multiple setiferous punctures in dorsal rows of pronotum (usually at most three in *Quedius*). Smaller species of *Quedius* may be confused with the genus *Heterothops* (subtribe Amblyopinina), but the latter have very thin acicular apical segments of maxillary palps, and a very different aedeagus without sensory peg setae and reduced median lobe giving the appearance of an absent paramere).

Table 1. Alphabetical list of *Quedius* species recorded for Middle Asia, with new synonyms. Boldfaced species are those confirmed by material in our study; species in regular font not given in square brackets are those known from literature only, presumably absent in Middle Asia; species in regular font and given in square brackets are those previously recorded for the region in literature based on misidentifications and here excluded from the fauna.

Species	Subgenus	Records from Middle Asia	Notes	Page here
[<i>Q. acuminatus acuminatus</i> Hochhuth, 1849]	<i>Raphirus</i>	Kascheev 2001, 102; 2002, 181	Misidentification of <i>Q. hauseri</i>	150
<i>Q. altaicus</i> Korge, 1962	<i>Quedius</i> (s. str.)	Toleutaev 2014, 44		128
[<i>Q. auricomus</i> Kiesenwetter, 1850]	<i>Raphirus</i>	Kascheev 1989, 36	Based on misidentification; here not confirmed by material	–
<i>Q. balticus</i> Korge, 1960	<i>Quedius</i> (s. str.)	Klimenko 1996, 121		–
[<i>Q. boopoides</i> Munster, 1923]	<i>Raphirus</i>	Kascheev 2002, 181	Apparently misidentification of <i>Q. hauseri</i>	150
[<i>Q. boops boops</i> Gravenhorst, 1802]	<i>Raphirus</i>	Eppelsheim 1892, 332; Kascheev 2001, 102; Toleutaev 2014, 44	Apparently misidentification of <i>Q. hauseri</i>	150
<i>Q. brevis</i> Erichson, 1840	<i>Microsaurus</i>	Gabdullina 2016, 61		–
<i>Q. bucharensis</i> Bernhauer, 1918	<i>Microsaurus</i>	Bernhauer 1918, 93; Gridelli 1924, 56; Coiffait 1978, 186; Kadyrov et al. 2014a, 31; 2014b, 49		138
<i>Q. capitalis</i> Eppelsheim, 1892	<i>Microsaurus</i>	Eppelsheim 1892, 329; Gridelli 1924, 40; Coiffait 1978, 148; Kadyrov et al. 2014a, 31; 2014b, 49		132
[<i>Q. cincticollis cincticollis</i> Kraatz, 1857]	<i>Raphirus</i>	Toleutaev 2014, 44 (cited as <i>Q. cincticollis</i> Kr.)	Misidentification, likely of <i>Q. hauseri</i>	150
<i>Q. cohaesus</i> Eppelsheim, 1888	<i>Raphirus</i>	<i>Q. cohaesus</i> : Eppelsheim 1888, 60; Gridelli 1925, 126; Coiffait 1963, 393; 1978, 248; Toleutaev 2014, 44; <i>Q. turkmenicus</i> : Coiffait 1969, 49; <i>Q. afghanicus</i> : Coiffait 1977: 139; Coiffait 1978, 232		142
=<i>Q. turkmenicus</i> Coiffait, 1969, syn. n.				
=<i>Q. afghanicus</i> Coiffait, 1977, syn. n.				
<i>Q. sp. aff. Q. coloratus</i>	<i>Raphirus</i>			149
<i>Q. curtipennis</i> Bernhauer, 1908	<i>Quedius</i> (s. str.)	Bernhauer 1908, 335		125
<i>Q. equus</i> Smetana, 2004	<i>Microsaurus</i>	Salnitska and Solodovnikov 2018, 10		139
<i>Q. fulgidus fulgidus</i> Fabricius, 1792	<i>Microsaurus</i>	Kascheev 2002, 181 (cited as <i>Q. fulgidus</i> F.)		–
<i>Q. fuliginosus</i> Gravenhorst, 1802	<i>Quedius</i> (s. str.)		First record from Middle Asia	125
<i>Q. fulvicollis</i> Stephens, 1833 (tentative identification)	<i>Raphirus</i>	Klimenko 1996, 121 (based on uncertain reference)		155
[<i>Q. fumatus</i> Stephens, 1833]	<i>Raphirus</i>	Kascheev 2001, 102; Toleutaev 2014, 44; Gabdullina 2016, 61	Presumed misidentification	–
<i>Q. fusicornis</i> Luze, 1904	<i>Microsaurus</i>	Luze 1904, 101; Gridelli 1924, 40		134
<i>Q. hauseri</i> Bernhauer, 1918	<i>Raphirus</i>	<i>Q. hauseri</i> : Bernhauer 1918, 94; Tronquet 1981, 71; Klimenko 1996, 121; <i>Q. peneckeii</i> : Bernhauer 1918, 95; <i>Q. ouzbekiscus</i> : Coiffait 1969, 52; 1970, 143; 1978, 278; Kascheev 2001, 102	Records of <i>Q. acuminatus acuminatus</i> , <i>Q. boops</i> and <i>Q. boopoides</i> likely belong to this species	150
=<i>Q. peneckeii</i> Bernhauer, 1918, syn. n.				
=<i>Q. ouzbekiscus</i> Coiffait, 1969, syn. n.				

Species	Subgenus	Records from Middle Asia	Notes	Page here
<i>Q. humeralis</i> Stephens, 1832	<i>Raphirus</i>	Eppelsheim 1892, 332; Gridelli 1922, 130, 134	Presumed misidentification	–
<i>Q. imitator</i> Luze, 1904 = <i>Q. tschinganensis</i> Coiffait, 1969, syn. n.	<i>Raphirus</i>	<i>Q. imitator</i> : Luze 1904, 102; Coiffait 1967, 406; 1978, 237; Boháč 1988, 556; Kadyrov et al. 2014a, 31; 2014b, 49; <i>Q. tschinganensis</i> : Coiffait 1969, 50; 1970, 143; 1978, 237; Klimenko 1996, 121; Kascheev 2001, 102		143
<i>Q. infuscatus</i> Erichson, 1840	<i>Microsaurus</i>	Kascheev 1984, 28; 1985, 46		–
<i>Q. limbatus</i> Heer, 1839	<i>Raphirus</i>	Eppelsheim 1892, 332; Smetana 1962, 146; Horion 1965, 284; 32; Kascheev 2001, 102; 2002, 181		139
[<i>Q. longicornis</i> Kraatz, 1857]	<i>Microsaurus</i>	Kascheev 2002, 181	Presumed misidentification	–
[<i>Q. maurorufus</i> Gravenhorst, 1806]	<i>Raphirus</i>	Toleutaev 2014, 44	Presumed misidentification of <i>Q. pseudonigriceps</i>	140
<i>Q. meridiocarpaticus</i> Smetana, 1958	<i>Quedius</i> (s. str.)	Klimenko 1996, 121 (based on uncertain reference)		–
<i>Q. mutilatus</i> Eppelsheim, 1888	<i>Microsaurus</i>	Eppelsheim 1888, 58; Gridelli 1924, 23; Coiffait 1978, 161; Klimenko 1996, 121; Smetana 1998, 118; Solodovnikov and Hansen 2016, 3–8; Salnitska and Solodovnikov 2018, 4		139
<i>Q. kalabi</i> Smetana, 1995	<i>Microsaurus</i>	Smetana 1995a, 77; 1998, 119; Salnitska and Solodovnikov 2018, 9		139
<i>Q. koltzei</i> Eppelsheim, 1892	<i>Microsaurus</i>	Coiffait 1978, 164		137
<i>Q. molochinus</i> Gravenhorst, 1806	<i>Quedius</i> (s. str.)	Protopoyan 1967, 168 (cited as <i>Q. 'nittidipennis</i> Steph. [sic!])		–
<i>Q. kungeicus</i> Solodovnikov & Salnitska	<i>Microsaurus</i>	Salnitska and Solodovnikov 2018, 13		139
[<i>Q. nigriceps</i> Kraatz, 1857]	<i>Raphirus</i>	Kascheev 2001, 102; 2002, 181; Kadyrov et al. 2014a, 31; 2014b, 49	Presumed misidentification	–
[<i>Q. nigrocaeruleus</i> Fauvel, 1876]	<i>Microsaurus</i>	Gabdullina 2016, 61	Presumed misidentification	–
<i>Q. novus</i> Eppelsheim, 1892 = <i>Q. dzambulensis</i> Coiffait, 1967, syn. n.	<i>Raphirus</i>	<i>Q. novus</i> : Eppelsheim 1892, 331; Gridelli 1925, 125; Coiffait 1963, 389; 1970, 143; 1978, 228; Boháč 1988, 556; Smetana 1995a, 84; Klimenko 1996, 121; Kadyrov et al. 2014a, 31; 2014b, 49; <i>Q. dzambulensis</i> : Coiffait 1967, 403; Coiffait 1978, 229; Boháč 1988, 556; Kascheev 2001, 102		146
<i>Q. ochripennis</i> Ménetries, 1832	<i>Microsaurus</i>	Gridelli 1929, 21; Klimenko 1996, 121; Kascheev 2001, 102; Kadyrov et al. 2014a, 31; 2014b, 49		131
[<i>Q. persimilis</i> Mulsant & Rey, 1876]	<i>Raphirus</i>	Kascheev 2001, 102; 2002, 181 (cited as <i>Q. joyi</i> Fagel)	Presumed misidentification of <i>Q. hauseri</i>	–
<i>Q. pseudonigriceps</i> Reitter, 1909 = <i>Q. kirklarensis</i> Korge, 1971, syn. n.	<i>Raphirus</i>		First record for Middle Asia	140
[<i>Q. picipes</i> Mannerheim, 1830]	<i>Microsaurus</i>	Kascheev 2001, 102	Presumed misidentification	–
<i>Q. puncticollis</i> Thomson, 1867	<i>Microsaurus</i>	Kascheev 2001, 102		132
<i>Q. rufilabris</i> Luze, 1904	<i>Microsaurus</i>	Luze 1904, 100; Gridelli 1924, 72; Kadyrov et al. 2014a, 31; 2014b, 49	Type material not found	138
<i>Q. scintillans</i> Gravenhorst, 1806	<i>Raphirus</i>	Eppelsheim 1892, 332;		155
[<i>Q. scitus</i> Gravenhorst, 1806]	<i>Microsaurus</i>	Kascheev 2001, 102	Presumed misidentification	–
<i>Q. solskyi</i> Luze, 1904 = <i>Q. asiaticus</i> Bernhauer, 1918, syn. n.	<i>Microsaurus</i>	<i>Q. solskyi</i> : Luze 1904, 99; Gridelli 1924, 72; <i>Q. asiaticus</i> : Bernhauer 1918, 92; Gridelli 1924, 57; Coiffait 1978, 183; Kascheev 2002, 181		135
<i>Q. sundukovi</i> Smetana, 2003	<i>Quedius</i> (s. str.)		First record for Middle Asia	130
<i>Q. tadjikiscus</i> Coiffait, 1975	<i>Microsaurus</i>	Coiffait 1975, 32; 1978, 149; Kadyrov et al. 2014a, 31; 2014b, 49		138
<i>Q. umbrinus</i> Erichson, 1839	<i>Raphirus</i>	Kascheev 1989, 36		149
<i>Q. vicinus</i> Ménetries, 1832	<i>Quedius</i> (s. str.)	Boháč 1988, 554		131

Table 2. Suggested georeferencing for ambiguous toponyms from old labels.

Label data verbatim	Locality	Long	Lat	Country
“ISKANDER-KUL ISKANDER-DARIA Glasunov 1892”	Iskanderkul Lake, Iskander Darya river, Ayni Distr.	[39°4.2’]	[68°22.2’]	Tajikistan
“Seravschan Kumar Glasunov 1892”	Kumar River valley, Ayni Distr.	[68°31.8’]	[39°16.2’]	Tajikistan
“JAGNOB KARSANU Glasunov 1892”	Yaghnob River valley, Sughd Distr.	[68°32.4’]	[39°11.4’]	Tajikistan
“JAGNOB CHISHARTOB Glasunov 1892”	Yaghnob River valley, Sughd Distr.	[68°32.4’]	[39°11.4’]	Tajikistan
“Trkst. Jagnob Kol Schach-Sara Glasunov 1892”	Yaghnob River valley, Sughd Distr.	[68°32.4’]	[39°11.4’]	Tajikistan
“SERAVSCHAN DARCH Glasunov 1892”	Darg, Sughd Distr.	[68°58.8’]	[39°21’]	Tajikistan
“Seravschan Kschtut. Artutsch. Glasunov 1982”	Kylali, Sughd Distr.	[68°2.4’]	[39°21.6’]	Tajikistan
“Seravschan Fl. Magian Glasunov 1892”	Seravschan Mt. Ridge, Mogiyon, Panjakent Distr.	[67°39.6’]	[39°15’]	Tajikistan
“SERAVSCHAN OBBURDEN Glasunov 1892”	Obburdon, Mastchoh Distr.	[69°18’]	[40°25.8’]	Tajikistan
“Mts. Karateghin Baldschuan 924 m. F. Hauser 1898”	Karateghin Mts, Baljuvon, Baljuvon Distr.	[69°40.2’]	[38°18’]	Tajikistan
“Mt. Karateghin Sary-pul 1482 m. F. Hauser 1898”	Karateghin Mts, Saripul, Khatlon Distr.	[70°7.8’]	[38°25.2’]	Tajikistan
“PROV. KULIAB, Ak-sou-Tal, F. Hauser 1898/ Gift from Nat. Mus. Praha. 2009”	Ak-Su, Khatlon Distr.	[68°34.8’]	[38°7.2’]	Tajikistan
“Gaudan, Transcaspien reg., 15.I.1898, E. Fimyanovich”	Gaudan, Ashgabat Distr.	[58°24’]	[37°39’]	Turkmenistan
“Trkst. Mnt. Nurata UCHUN Glasunov 1892”	Nurata Mt., Nurata Distr.	[65°41.4’]	[40°32.4’]	Uzbekistan
“Fergana valley, tract Aral, Achinsk, L. Arnoldi”	Aral, Namangan Distr.	[71°55.2’]	[41°00’]	Uzbekistan

Key to species of *Quedius* of Middle Asia

- 1 Anterior margin of labrum entire so that labrum never bilobed or notched in the middle. Large species with body length 9.0–15.0 mm (fig. 187a in Assing and Schülke 2012) 2 (Subgenus *Quedius* s. str.)
- Anterior margin of labrum either with distinct notch in the middle, or with deep emargination so that labrum looks bilobed. Mostly smaller species with body length 5.0–12.0 mm (fig. 187b–d in Assing and Schülke 2012) 6
- 2 Scutellum without setiferous punctures, glabrous. Frons with additional setiferous punctures (that only occasionally maybe lost) between anterior frontal punctures 3
- Scutellum with setiferous punctures, setose. Frons without additional setiferous punctures between anterior frontal punctures 4
- 3 Aedeagus (in parameral view): apical portion of paramere lanceolate, wider than its sinuate middle part; rows of sensory peg setae on the parameral underside, in their basal half, extended more medially from parameral lateral margins (fig. 188c in Assing and Schülke 2012); lateral contours of apical part of median lobe not visible from under paramere (fig. 188a in Assing and Schülke 2012)..... *Q. fuliginosus* (Habitus Fig. 2A).
- Aedeagus (in parameral view): apical portion of paramere gradually narrowing apicad, medially not sinuate and not narrower than its more apical part; rows of sensory peg setae on the parameral underside, in their basal half, extended more laterally, closer to parameral lateral margins (fig. 188f in Assing and Schülke 2012); lateral contours of median lobe apically visible from under paramere (fig. 188d in Assing and Schülke 2012) *Q. curtipennis*
- 4 Body dark brown, with paler (sometimes reddish) elytra (Habitus as in Fig. 2C). Aedeagus (in lateral view): apex of paramere protruding beyond median lobe in the form of a distinct hook (fig. 1 in Hachikov 2003) *Q. vicinus*
- Body and elytra black, or at most dark brown. Aedeagus (in lateral view): apex of paramere straight, not pointing out from median lobe as a distinct hook 5
- 5 Elytra shortened, distinctly shorter than pronotum. Obviously brachypterous species, without whitish apical seam on abdominal tergite VII. Smaller: body length 7.50–9.00 mm (Habitus Fig. 2B). Aedeagus as in figs 4–6 in Smetana 2002.....
..... *Q. sundukovi*
- Elytra normal, about as long as pronotum. Species with whitish apical seam on abdominal tergite VII. Larger: body length 8.6–12.5 mm. Habitus and aedeagus as in Fig. 5E–G *Q. altaicus*
- 6 Eyes small or moderate in size, always distinctly shorter than temples (fig. 187d in Assing and Schülke 2012). Vertex (at least one side) with two basal punctures postero-medially from posterior frontal puncture (fig. 186b in Assing and Schülke 2012). Postero-lateral areas of pronotum somewhat explanate 7 (Subgenus *Microsaurus*)
- Eyes large and convex, always longer than temples (fig. 187b, c in Assing and Schülke 2012). Vertex with one basal puncture postero-medially from posterior frontal puncture (fig. 186a in Assing and Schülke 2012). Postero-lateral areas of pronotum not explanate 18 (Subgenus *Raphirus*)
- 7 Elytra brownish, of about same or very similar coloration as the rest of the body. Eyes very small, 2.5–2.7 times as long as temples. Elytra shorter than pronotum. Distinctly brachypterous species without whitish apical seam on abdominal tergite VII (Fig. 2E) 8
- Elytra reddish, always different in coloration from the rest of the body, which is black or at most dark brown. Eyes larger, ca. 0.5–1 times as long as temples. Elytra longer than, or as long as pronotum. Apical seam on abdominal tergite VII always distinct 11

- 8 Aedeagus (fig. 4G–N in Salnitska & Solodovnikov 2018), in parameral view: paramere apically deeply incised, appearing bilobed *Q. equus*
- Aedeagus (in parameral view): paramere apically at most slightly incised..... 9
- 9 Aedeagus (fig. 4E, F Salnitska & Solodovnikov 2018), parameral view: apical portion of paramere ovoid (lanceolate), not rhomboid..... *Q. kungeicus*
- Aedeagus, in parameral view: apical portion of paramere somewhat rhomboid (fig. 4B, D in Salnitska & Solodovnikov 2018) 10
- 10 Aedeagus (fig. 4C, D in Salnitska & Solodovnikov 2018), in lateral view: apical portion of median lobe relatively narrower and acute) *Q. kalabi*
- Aedeagus (fig. 4A, B in Salnitska & Solodovnikov 2018), in lateral view: apical portion of median lobe relatively broader and blunt *Q. mutilatus*
- 11 Smaller species: body length around 6.0–9.3 mm. Aedeagus, underside of the paramere: peg setae arranged in rows with maximum 6–8 pegs in each row extending basad from pairs of lateral setae (Figs 7D, 8D)..... 12
- Larger species: body length around 8.0–11.0 mm. Aedeagus, underside of the paramere: peg setae located at the apex of paramere only (*Q. solskyi*, Fig. 9C) or arranged in groups extending basad from the parameral apical margin, beyond the pairs of lateral setae (fig. 191j–k, t–v in Assing and Schülke 2012)..... 13
- 12 Aedeagus: underside of the paramere (Fig. 7D): with ca. 4–8 sensory peg setae in each of two rows curved along lateral sides of paramere *Q. capitalis*
- Aedeagus: underside of paramere (Fig. 8D): with ca. 3 sensory peg setae in each of two linear rows..... *Q. fusicornis*
- 13 Aedeagus, paramere (Fig. 9C) parallel-sided along most of its length, not lanceolate, with only 1–2 peg setae at apical margin on each side of the mid-apical incision 14
- Aedeagus, paramere not parallel-sided, with more or less lanceolate or rhomboid apical portion (fig. 191j, l in Assing and Schülke 2012); peg setae on parameral underside more numerous and arranged in irregular rows or groups. 15
- 14 Larger species with body length 8.9–9.7 mm; head distinctly wider than long (HL/HW ratio 0.7–0.8) with posterior frontal puncture situated in the middle of distance between posterior margin of eye and nuchal ridge. (Habitus and aedeagus as in Fig. 9A–D) *Q. solskyi*
- Smaller species with body length 8.5–9.4 mm; head from nearly as long as wide to longer than wide (HL/HW ratio 0.9–1.1) and posterior frontal puncture situated closer to posterior margin of eye than to nuchal ridge. Structure of the aedeagus unknown (for details see below) *Q. bucharensis*
- 15 Pronotum with basalmost setiferous puncture of sublateral group (sometimes may be lost at one side) situated distinctly behind the level of large lateral puncture (fig. 186a in Assing and Schülke 2012)..... 16
- Pronotum with punctures of sublateral group always situated before or at most at the same level as large lateral puncture (fig. 186b in Assing and Schülke 2012) 17
- 16 Aedeagus, in parameral view: apical portion of the paramere lanceolate with bluntly pointed apical contour (fig. 191j, l in Assing and Schülke 2012) *Q. ochripennis*
- Aedeagus, in parameral view: apical portion of the paramere not lanceolate, with broad and shallow apical emargination (fig. 191t, v in Assing and Schülke 2012)..... *Q. puncticollis*
- 17 Pronotum with dorsal rows each with only two punctures. Aedeagus, underside of the paramere: peg setae arranged in four irregular groups: a pair of apical groups and a pair of subapical groups (fig. 11C in Coiffait, 1978)..... *Q. koltzei* (externally *Q. rufilabris*, an ambiguous species described from ‘Zeravshan’ also fits here; for details see the section on this species)
- Pronotum with dorsal rows each with three punctures. Aedeagus, underside of the paramere: peg setae arranged only in two subapical groups, the pair of apical groups absent (fig. 7K–M in Coiffait 1978)..... *Q. tadjikiscus*
- 18 Scutellum with setiferous punctation; eyes large and convex, occupying almost entire lateral side of head; rather small species. Body not longer than 6.0 mm. Aedeagus as in (Figs 19B–D, 21B, C)..... 19
- Scutellum glabrous, without setiferous punctation; eyes smaller and more flat; temples more distinct. Body length varies but includes larger species. Aedeagus different..... 20
- 19 Aedeagus: paramere almost parallel-sided, only slightly narrowing in the middle portion, rows of peg setae long and regular (Fig. 19C) Habitus and aedeagus as in Fig. 19A–D *Q. hauseri*
- Aedeagus: paramere not parallel-sided, strongly narrowing in the middle portion, rows of peg setae shorter and irregular (Fig. 23C). Habitus and aedeagus as in Fig. 23A–C *Q. fulvicollis*
- 20 Frons with two additional punctures between anterior frontal punctures. Rather small species, body not longer than 6.0 mm *Q. scintillans*
- Frons without punctures between anterior frontal punctures. Species varying in size 21
- 21 Elytra shortened, slightly shorter than, or at maximum, as long as pronotum. Brachypterous species without whitish apical seam on abdominal tergite VII (Fig. 3F). Aedeagus as in Fig. 11 *Q. pseudonigriceps*
- Elytra longer than, or at minimum, as long as pronotum. Species with whitish apical seam on abdominal tergite VII (Fig. 3C). Aedeagus different 22

- 22 Relatively large species, body length 8.1–11.7 mm. Aedeagus: paramere shorter, its apex far from reaching apex of median lobe (in lateral view) with subapical tooth located far basad from its apex (Fig. 18B). Habitus and aedeagus as in Fig. 18A–C..... *Q.* sp. aff. *Q. coloratus*
- Mostly smaller species, body length 5.0–7.5 mm. Aedeagus different..... 23
- 23 Aedeagus: median lobe (in lateral view) distinctly curved; multiple sensory peg setae on the underside of the paramere arranged in one or two irregular longitudinal groups, never in clear straight rows along parameral margins (e.g., Fig. 17). Larger species 6.0–8.0 mm..... 24
- Aedeagus, in lateral view: median lobe straight, not curved dorso-ventrally (fig. 193r–t in Assing and Schülke 2012). Smaller species, body not longer than 6.5 mm..... 25
- 24 Body brown to dark brown, sometimes elytra paler or reddish. Larger (body length 6.0–8.0 mm) and more robust species (Fig. 4B). Aedeagus (fig. 194j–l in Assing and Schülke 2012): median lobe in lateral view with subapical tooth situated close to its apex (fig. 194k in Assing and Schülke 2012); underside of paramere with sensory peg setae arranged in wide irregular rows diverging from each other basad..... *Q. umbrinus*
- Body light-brown to brown, but never black, elytra brownish; larger (body length 6.0–7.0 mm) and more slender species (Figs 3E, 16A). Aedeagus (Figs 16B, C, 17): median lobe in lateral view with subapical tooth situated far basad from its apex; underside of paramere with ca. 40–50 peg setae arranged in one irregular median row..... *Q. novus*
- 25 Aedeagus (fig. 193r–t in Assing and Schülke 2012): underside of paramere with ca. 4–5 sensory peg setae in each of two rows along its lateral margins. Habitus as in Fig. 3D..... *Q. limbatus*
- Aedeagus (Figs 12C, D, 15): underside of paramere with many more (ca. 8–18) sensory peg setae in each of two rows along its lateral margins..... 26
- 26 Aedeagus (Figs 15, 14B, C, F, G): median lobe in lateral view with subapical tooth located distinctly more basad from its apex (Figs 14B, F; 15); underside of paramere with sensory peg arranged in two regular rows very close to each other (Figs 14C, G, 15)..... *Q. imitator*
- Aedeagus (Figs 12C, D, 13B, C): median lobe in lateral view with subapical tooth located close to its apex (Figs 12C, 13B); underside of paramere with sensory peg setae arranged in two irregular rows more remote from each other (Figs 12D, 13C)..... *Q. cohaesus*

Subgenus *Quedius* Stephens, 1829

Quedius (s. str.) *curtipennis* Bernhauer, 1908

Quedius fuliginosus var. *curtipennis* Bernhauer, 1908, 335 (original description)

Quedius curtipennis: Herman 2001, 3134 (summary of literature); Assing and Schülke 2012, 457, 458 (diagnosis, distribution and bionomics, aedeagus illustration).

Type material examined. Syntypes (all in FMNH): Faroe Islands: 1 ♂, “Suderö Faroer Ins./ Dr. Cornu 1907/ v. curtipennis Brh. Typus [handwritten]/fuliginosus Grav. Scheerp. [handwritten]/ Chicago NHMus M. Bernhauer Collection [printed]/ D. Drugmand det. 1994 *Quedius* (s. str.) *curtipennis* Brnh. [preprinted handwritten]”; 1 ♂, “Nördl. Faroer Ins./ Dr. Cornu 1907/ v. curtipennis Brh. Typus [handwritten]/ fuliginosus Scheerp. [sic!] det. [illegible] [handwritten]/ Chicago NHMus M. Bernhauer Collection [printed]/ D. Drugmand det. 1994 *Quedius* (s. str.) *curtipennis* Brnh. [preprinted handwritten]”; Uzbekistan: 1 ♂, “v. curtipennis Buchara Bang Haas det. Bernh. [preprinted handwritten]/ Chicago NHMus M. Bernhauer Collection [printed]”.

Comments on taxonomy, distribution and bionomics. Bernhauer (1908) described *Q. curtipennis* as a variety of *Q. fuliginosus* without clear information on the type material. In addition to the morphological diagnosis of a new variety Bernhauer (1908) mentioned that it is common on the Faroe Islands and also occurs in “Vorarlberg, Buchara and Böhmen (Wrana. Moldau)”. Interestingly, revision of the type material has never been published for this com-

mon widespread species since its original description. We have examined three male syntypes of *Q. curtipennis* kept at the FMNH, two from Faroe Islands and one from ‘Buchara’ in Uzbekistan, all listed above. Our examination of the syntypes confirms that they are conspecific and matching current interpretation of this species (e.g. in Assing and Schülke 2012). *Quedius curtipennis* is a common species widely distributed in the forests and humid microhabitats of the open landscapes of the Western Palaearctic (Herman 2001; Assing and Schülke 2012). Because of the strong morphological similarity, *Q. curtipennis* can be easily confused with *Q. fuliginosus*. As a result, current broad distributions for both species as recently summarized in Assing and Schülke (2012), especially outside Europe, need revision. A male syntype of *Q. curtipennis* from “Buchara” (Uzbekistan) collected more than a century ago (see below) and overlooked in the subsequent literature is the only specimen of this species known from Middle Asia. Since the original description *Q. curtipennis* has not been recorded from any of the countries of Middle Asia.

Quedius (s. str.) *fuliginosus* Gravenhorst, 1802

Fig. 2A

Quedius fuliginosus: Herman 2001, 3155 (summary of literature); Assing and Schülke 2012, 457, 458 (diagnosis, distribution and bionomics, aedeagus illustration).

Material examined. Kazakhstan: 1 ♂, Akshatau Mt., NW Ayaguz, Semipalat, forest leaf litter, 17.VII.1962,

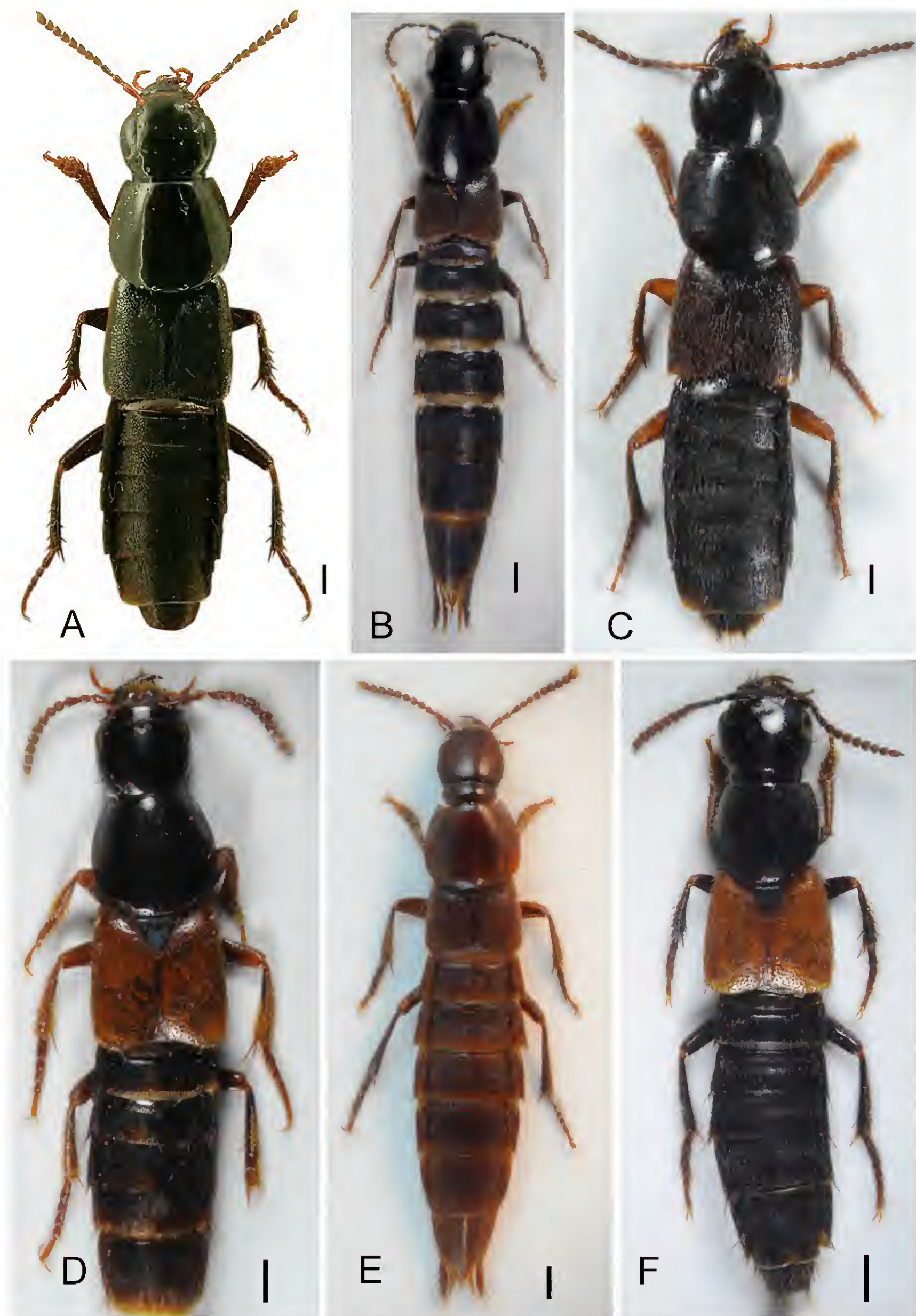


Figure 2. Habitus of *Quedius* recorded in Middle Asia. **A** *Q. fuliginosus* (photo Lech Borowiec) **B** *Q. sundukovi* **C** *Q. vicinus* **D** *Q. koltzei* **E** *Q. mutilatus* **F** *Q. ochripennis*. Scale bars: 1 mm.

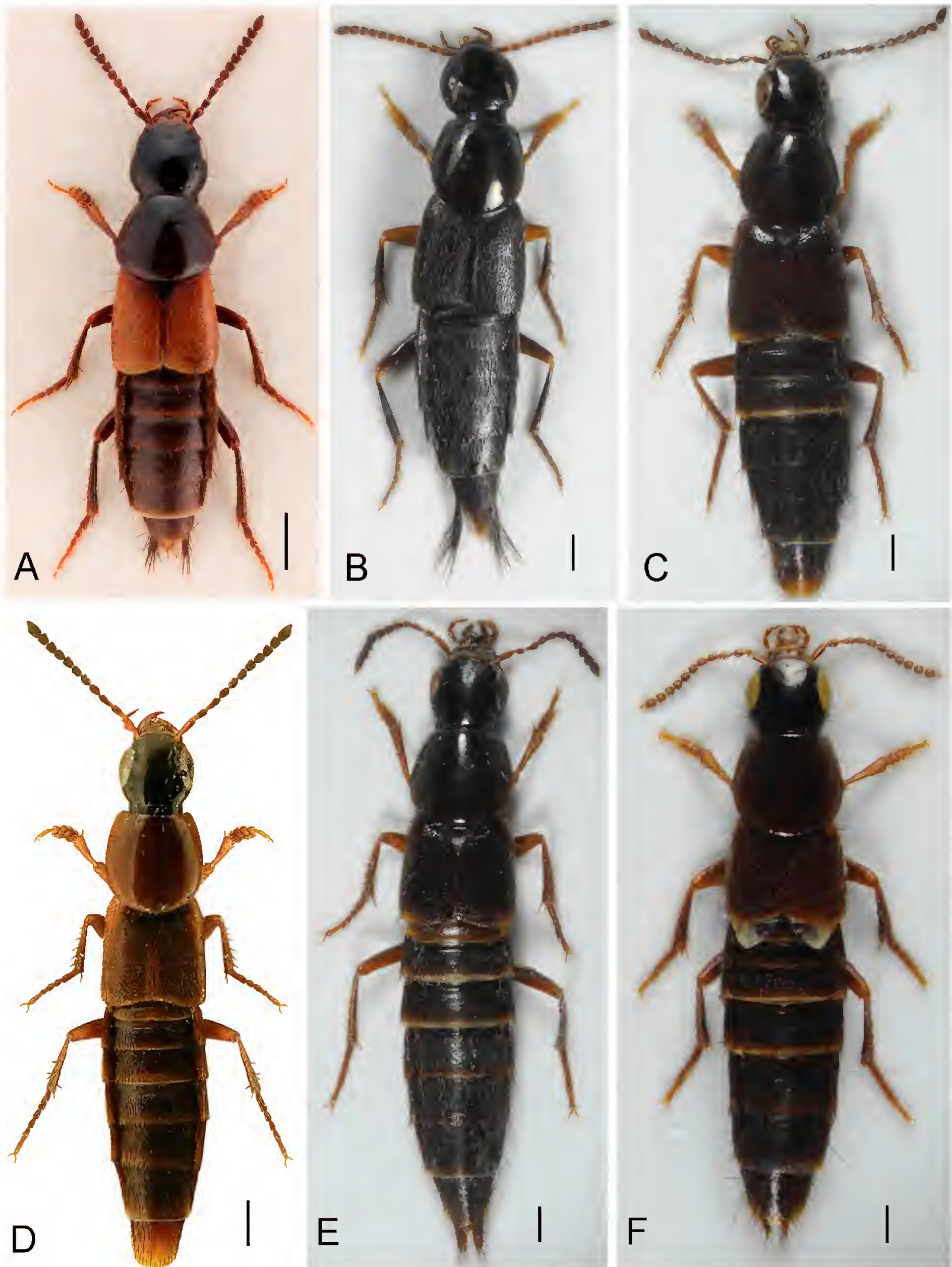


Figure 3. Habitus of *Quedius* recorded in Middle Asia. A *Q. puncticollis* (photo <http://danbillier.dk>) B *Q. hauseri* C *Q. imitator* D *Q. limbatus* (photo Lech Borowiec) E *Q. novus* F *Q. pseudonigriceps*. Scale bars: 1 mm.



Figure 4. Habitus of *Quedius* recorded in Middle Asia. **A**, *Q. scintillans*; **B**, *Q. umbrinus* (Lech Borowiec). Scale bars: 1 mm.

L.V. Arnoldi leg. (ZIN); 2 ♂ Stepnyak, Zhukey Lake, 10.VII.2002, V.A. Kastcheev leg.; 1 ♂, Ivanovsky Mt. Ridge, 32 km S Leninogorsk, 1300 m a.s.l. 14.VIII.1986, I.I. Kabak leg. (ZIN); **Uzbekistan:** 1 ♂, 1 ♀, Tashkent, near railway station, plant residues, 24.V.1986, S.A. Kurbatov leg. (cKur).

Comments on taxonomy, distribution and bionomics. Similarly to *Q. curtipennis* (see above), *Q. fuliginosus* is a widespread and common species in the Western Palearctic, and subject of numerous publications. The most recent summary of its diagnostic characters, bionomics and distribution can be found in Assing and Schülke (2012). For the same reasons as *Q. curtipennis* above, the exact distribution of *Q. fuliginosus* needs careful revision. Limited material from Kazakhstan and Uzbekistan examined here represents the first records of this species from Middle Asia.

Quedius (s. str.) *altaicus* Korge, 1962

Figs 5, 6

Quedius altaicus Korge, 1962, 152 (original description); Coiffait 1978 (characters), 194; Toleutaev 2014, 44 (distribution records).

Material examined. Holotype: *Russia:* female, “Zentral-Altai, lg. Leder, det. Bang-Haag [handwritten]/ unicolor Kies. det. Bernhauer [handwritten]/ ♀ Holotypus *Quedius* s. str. *altaicus* H. Korge [printed]/ Chicago NHMus M. Bernhauer Collection/ Holotype teste D.J. Clarke 2014 GDI Imaging Project [printed]/ Photo-

graphed Kelsey Keaton 2014 Emu Catalog/ FMNHINS 2819427 Field Museum [printed]” (FMNH);

Additional material. Kazakhstan: 1 ♂, West Altai, Ivanovsky Mt. Ridge, 32 km Leninogorsk [Ridder], 14.VIII.1986, 1300 m a.s.l., I.I. Kabak leg. (ZIN); 1 ♂, SW Altai, E Narymsky Mt. Ridge, upper reaches of Shurshutsu River [Forpostnaya], lower forest zone, 21.VII.1997, 1300 m a.s.l., R.Yu. Dudko, V.K. Zinchenko leg.; 2 ♂, 1 ♀, SW Altai, E of Markakol Lake, Urunhayka, ground traps, 21.VI–07.VII.1997, 1500 m a.s.l., R.Yu. Dudko, V.K. Zinchenko leg.; 1 ♂, same locality and collectors, but 8 km ESE Matabai, north slope of Matabai Mt. Ridge, forest, 10.VII.1997, 1600–2000 m a.s.l. (NHMD); 1 ♂, Manrak Mt. Ridge, 12 km Priozerny [Tugil], 16.VII.1986, I.I. Kabak leg. (ZIN); **Russia:** 1 ♂, Altai, Listvyaga Mt. Ridge, 10 km SSE Tesninskiy Belok Mt., Seredchiha River, forest, 27.VII.1997, 1200–1500 m a.s.l., R.Yu. Dudko, V.K. Zinchenko leg. (NHMD).

Comparative material on *Quedius subunicolor*. **Type material: Paratypes:** *Sweden:* 1 ♂, “Häggenäs s-n Jtl. T. Palm 4–8, 8 1945 [printed]/ det. H. Korge *Quedius subunicolor* Korge [printed]/ Paratypus *subunicolor* Korge [pre-printed]/ *Quedius subunicolor* Korge [handwritten]/ Type no. 1202:2 MZLU [printed]/ 2016 189 MZLU [printed]” (ZMLU); 3 ♀, same data, but two last labels as “Type no: 1202:3 MZLU/ 2016 190 MZLU [printed]” (Fig. 5D) (ZMLU); **Additional material:** *Norway:* 3 ♀, Fn. Nesseby h:d, Nyborg, 35483, 04–09.VI.1963, Gom. Israelson leg.; *Sweden:* 1 ♀, Nb. [Norbotten] Kihlangi, 10–17.VI.1947, T. Palm leg.; 1 ♀, Vittangi, 02–14.VIII.1963, Th. Palm leg.; 1 ♀, L. Lpm, Vittanger, 08.VI.1968, S. Lundberg leg.; 1 ♂, Lu. Lpm. Messaure, 09–16.VII.1973, K. Muller leg.; 2 ♂, 1 ♀, Jokkmokk, 21.V.1965, T.B. Engelmark leg. (ZMLU).

Comments on taxonomy and type material. The original description of *Quedius altaicus* was based on two female specimens (a holotype and a paratype) from “Central-Altai” without precise record of the type locality (Korge, 1962). Such ambiguity was stressed by Korge who noted that the status of *Q. altaicus*, which externally appeared very similar to *Q. unicolor* and *Q. subunicolor*, should be confirmed by the examination of male genitalia. Toleutaev (2014) recorded *Q. altaicus* from Saur Mountains (Eastern Kazakhstan), but that record needs verification.

In spite of the ambiguous original description of *Q. altaicus*, new material from Altai including males examined here for the first time can be safely attributed to that species. This material perfectly matches Korge’s original description, and the information together with high quality photos of the holotype available from the Field Museum online beetle type database (FMNH, 2018). Besides, there are no other species in the Altai region that could be misidentified as *Q. altaicus*. *Quedius sundukovi*, the only other similar species distributed from the Russian Far East to the South-Western Altai is distinctly different (for details see below).



Figure 5. *Quedius subunicolor* (paratype, male): A–D; *Quedius altaicus* (male): E–G. A, E, habitus; B, C, F, G, aedeagus. D, labels. B, F, median lobe, lateral view. C, G, paramere, underside; H, sclerite of internal sac. Scale bars: 1 mm.

The aedeagus of *Q. altaicus* (Fig. 5F, G) here examined for the first time is nearly identical with the aedeagus of the northern European *Q. subunicolor* (Fig. 5B, C). Both species slightly differ from each other in the shape of a large sclerite in the internal sac (labeled as H in Fig. 5B, F) and the degree of development of the subapical teeth of the median lobe (less pronounced in *Q. altaicus*, compare Fig. 5B, F). Comparison of the external morphology of the multiple specimens of *Q. altaicus* to each other and with the available specimens of *Q. subunicolor*, including its paratypes, demonstrates that the external characters provided by Korge (1962) as unique for *Q. altaicus* (microstructure of the head, proportions of the pronotum, chaetotaxy of the head and pronotum) do not hold. Given a subtle morphological difference between both species and poorly sampled areas of Russia, there remains a possibility that *Q. subunicolor* may be a polytypic species continuously distributed from the Northern Europe to Altai. Or, *Q. subunicolor* and *Q. altaicus* may be a hitherto unrecorded case of the boreo-montane distribution. Both species should be subject to further sampling in the area which seems as a distribution gap between them. Also, a DNA-based phylogeographic investigation would be interesting. Below we provide a redescription of *Q. altaicus*.

Redescription. Measurements and ratios (range, arithmetic mean; $n = 8$): HL: 1.4–1.5 (1.5); HW: 1.4–1.5 (1.5); PL: 1.7–1.8 (1.8); PW: 1.9–2.0 (2.0); EL: 1.7–1.8 (1.8); EW: 1.8–2.0 (1.9); FB: 5.0–5.2 (5.1); TL: 8.6–11.4 (10.0); HL/HW: 0.9–1.0 (1.00); PL/PW: 0.9–1.0 (1.0); EL/EW: 0.9–1.1 (1.0).

Body piceous black, only sometimes dark brownish; apical margin of abdominal segments vaguely paler; maxillary, labial palpi, and antennae dark-reddish; legs dark with paler brownish tarsi (Fig. 5E).

Head with broadly rounded, but distinct hind angles with microsculpture consisting of transverse waves; eyes as a long as or slightly longer than tempora; posterior frontal puncture situated closer to posterior margin of head than to posteromedial margin of eye; two to four additional punctures present along medial margin of eye between anterior and posterior frontal punctures; temporal puncture situated close to posterior margin of eye at distance nearly equal to diameter of puncture.

Antennae moderately long, segment 3 somewhat longer than 2, segments 4–8 longer than wide, each gradually becoming shorter towards apex, segments 7–11 about as long as wide.

Pronotum wider than long PL/PW: 0.9–1.0 (1.0), widest at posterior third, narrowed anteriorly; hind angles broadly rounded, but distinct; dorsal rows each with three punctures; sublateral rows each with two to three punctures; waves of microsculpture transverse, similar to that on head. Scutellum finely punctured in its posterior half, with transverse or slightly isodiametric microsculpture.

Elytra parallel-sided, as long as pronotum, at base narrower than pronotum at widest point; shiny, punctation moderately dense and shallow, interspaces larger than diameter of punctures, pubescence yellowish-grey.

Abdomen with tergite VII (5th visible) with fine distinct whitish apical seam of palisade fringe; punctation dense and fine gradually becoming sparser towards apex



Figure 6. Distribution of sister species *Quedius altaicus* (Altai Mts. in Kazakhstan and Russia) and *Q. subunicolor* (Northern Europe). Dots indicate material examined in this paper, colored areas summarise literature data. Black dots indicate type localities.

of abdomen, surface between punctures with very superficial transverse irregularities, pubescence as on elytra.

Male: aedeagus: median lobe with acute apex and small teeth on its parameral side near apex (Fig. 5B, F); paramere distinctly protruding over apex of median lobe, with two pairs of setae apically and two pairs of longer setae laterally below apex, its underside with numerous sensory peg setae forming two subapical longitudinal rows connected near apex (Fig. 5C, G). Internal sac (examined in situ) with two pairs of strongly sclerotized microstructures positioned laterally and one characteristically shaped medial sclerite (Fig. 5H) with rounded apex.

Comparison. Based on the structure of the aedeagus, especially the characteristic armature of the internal sac with the large middle sclerite ‘H’ (Fig. 5B, F; fig 189 in Assing and Schülke, 2012), *Q. altaicus* can be placed in the group with *Q. subunicolor*, *Q. balticus*, *Q. molochinus* and *Q. meridiocarpaticus*. *Quedius altaicus* differs from *Q. meridiocarpaticus* in the unicolorous black coloration of the body (brown reddish with paler elytra in *Q. meridiocarpaticus*) and in the shape of the medial sclerite of the internal sac that has rounded apex. Some authors stressed a strong similarity of *Q. subunicolor* (from which *Q. altaicus* is hardly distinct) with *Q. unicolor*, and the latter mainly Central European montane species was incorrectly cited as *Q. subunicolor* in a number of the faunistic papers (e.g., Ciceroni and Zanetti 1995; Geiser et al. 2003; Boháč et al. 2004, 2005; Wojas 2006). *Quedius subunicolor* (and *Q. altaicus*), however, can be easily distinguished from *Q. unicolor* by transversal (not

isodimetric) microsculpture of the frons and the structure of the aedeagus, especially by the internal sac with the obvious medial sclerite. From similar species that occur in Middle Asia *Q. altaicus* can be easily distinguished by the following characters: from *Q. fuliginosus* by the punctured (setose) scutellum and absence of additional punctures between anterior frontal punctures; from *Q. sundukovi* by normally developed elytra (very short in distinctly brachypterous in *Q. sundukovi*), presence of fine whitish apical seam of palisade fringe on VII tergite (5th visible), and distinctly larger body.

Distribution. *Quedius altaicus* is known from “central” (Korge, 1962) and southwestern Altai. Records from the southwestern Altai stretching across the border between Russia and Kazakhstan, provided here, are the first exact distributional data for this subspecies. We were not able to examine the material on which Toleutaev (2014) recorded this species from Saur Mountains, the latter records remains ambiguous.

Bionomics. All clearly georeferenced specimens of *Q. altaicus* have been collected at the elevations between 1200 and 2000 m.

Quedius (s. str.) *sundukovi* Smetana, 2003

Fig. 2B

Quedius sundukovi Smetana, 2003, 189

Material examined. Kazakhstan: 1 ♂, SW Altai, East of Narymskij Mt. Ridge, upper course of Ozernaja River,

subalpine zone, 1900–2300 m a.s.l., 18.VII.1997, R.Yu. Dudko and V.K. Zinchenko leg. (NHMD); 3 ♂, 3 ♀, Stanovoe nagorje [highland], S part of Kodar Mt. Ridge, upper course of Chara River, 50 km WSW of village Novaja Chara, 1700–2000 m a.s.l., 26–27.VII.1995, A.Yu. and R.Yu. Dudko, and D.E. Lomakin leg (NHMD, ZIN); 1 ♀, same locality and collectors, but environs of lake Bolshoe Leprindo, 1000 m a.s.l., 23.VII.1995 (ZIN).

Comments on taxonomy, distribution and bionomics. *Quedius sundukovi* was known from the Russian Far East (Smetana, 2003) and from Irkutsk Province and Zabaikalsky Territory (Smetana and Shavrin 2018). From the newly examined material it has become clear that *Q. sundukovi* is distributed even wider: from the Russian Far East through southern Siberia to Altai Mountains in Northeastern Kazakhstan. In the material examined we here provide only new records for Middle Asia, because the detailed documentation of its entire distribution will be published elsewhere.

Detailed description and illustration of the species is available in Smetana (2003). *Quedius sundukovi* is one of the smallest species in the nominative subgenus *Quedius* s. str. and the smallest in this subgenus in the fauna of Middle Asia. Additionally, it stands out from all other *Quedius* s. str. species in Middle Asia as the only distinctly brachypterous species, with very short elytra and lacking whitish apical seam on abdominal tergite VII.

All hitherto known specimens of *Q. sundukovi* were collected by pitfall traps (Smetana 2003). Based on the newly examined material here, *Q. sundukovi* inhabits talus-associated debris. Also it is found in regular leaf litter and moss on the ground.

Quedius (s. str.) *vicinus* Ménétriés, 1832

Fig. 2C

Quedius vicinus Ménétriés, 1832, 144 (original description); Faldermann 1835, 129 (distribution records); Gusarov 1993, 73 (lectotype designation, = *Q. libanicus* Coiffait); Assing and Wunderle 2001, 37 (distribution records); Hachikov 2003, 46 (illustration of aedeagus); Ghahari 2009, 2012, 5; Assing and Feldmann 2012; Özgen et al. 2016, 621.

Quedius libanicus Coiffait, 1954, 160 (original description); 1955, 427 (notes); 1978, 195 (characters); Jarriège 1971, 497; Korge 1971, 11; Boháč 1988, 554 [= 1989: 38] (characters, distribution records).

Material examined. Kazakhstan: 1 ♂, 1 ♀, Karatau Mts, Khantagi River, 570 m a.s.l., 43°33'32.4N, 68°40'52.7E, 25.VI.2011, V.A. Kastcheev leg. (ZIN); **Turkmenistan:** 2 ♀, N Kopetdag, Firjusa-Cleft near Aschabad, 07.V.1989, D.W. Wrase leg. (cSch); 4 ♂, Firjusa, 25.V.1903, K.O. Anger, A. Jakovleva leg. (ZIN); 4 ♂, 2 ♀, Kopetdag, Chili River valley, 23–24.VIII.1935, L.V. Arnoldi leg.; 1 ♂, W Kopetdag, Kara-Kala [Garrygala], canyon Porchai, to light, village of the Nature Reserve, 05.IX.1986, A.L.

Lobanov leg.; 3 ♂, Kopetdag, Firjusa, 07.V.1968, G.S. Medvedev leg. (ZIN); 1 ♂, Kara-Kala, 29.IV–03.V.1989, S. Bečvář leg. (cSch).

Comments on taxonomy, distribution and bionomics. Gusarov (1993) clarified the identity and synonymy of *Q. vicinus*. A description and the illustrations of the aedeagus for this species can be found, for example, in Coiffait (1954, 1978, as *Q. libanicus*), Boháč (1988, as *Q. libanicus*), and Hachikov (2003). By the brown body with reddish elytra, frons without additional setiferous punctures between anterior frontal punctures and by punctate scutellum, *Q. vicinus* can be distinguished from all other Middle Asian species of the nominal subgenus *Quedius* s. str. based on the external characters alone. The aedeagus of this species, with the parameral apex pointing outwards from the median lobe, is also very characteristic.

Based on literature data it is a common species in Western Asia. In Middle Asia it was known only from Turkmenistan (Boháč 1988, as *Q. libanicus*). Based on the newly examined material *Q. vicinus* is recorded for the first time from southern Kazakhstan (Karatau Mountains). The species prefers ground based debris and leaf litter, but also was found (Coiffait 1955, as *Q. libanicus*) in caves. Specimens from Middle Asia were collected along rivers, in ground traps and at light.

Subgenus *Microsaurus* Dejean, 1833

Quedius (*Microsaurus*) *ochripennis* Ménétriés, 1832

Fig. 2F

Herman 2001, 3227 (summary of literature); Kascheev 2001, 102 (records); Assing and Schülke 2012, 466, 467 (diagnosis, distribution and bionomics, aedeagus illustration).

Material examined. Kazakhstan: 1 ♂, Karatau Mts, Byzhi River, Rynagus stream, 24.VII.2010, V.A. Kastcheev leg.; 1 ♂, Karatau Mts, near stream, 11.VII.2010, 42°53'41.42N, 70°42'56.6E, 600 m a.s.l., V.A. Kastcheev leg.; 1 ♂, 1 ♀, Aksu-Dzhabagly, Taldy-Bulak River, 10–20.IV.1979, B.V. Isakov leg.; 2 ♂, same locality and collector, but, 04.V.1986; 1 ♂, 1 ♀, Aksu-Dzhabagly, Ulken-Kaindy, near water in moss, 18.VII.1986, B.V. Isakov leg.; 1 ♂, S Kazakhstan, Boralday, 12–15.VI.1983, B.V. Isakov leg.; 1 ♂, Zalatayskiy Alatau Mts, Krasnogorka [Sulutor], near stream, under tree, 75°13'50.4N, 43°23'45.7E, 28.VII.2010, V.A. Kastcheev leg.; **Uzbekistan:** 1 ♂, 1 ♀, Aruk-Tau Mt. Ridge, 25 km W Kyzyl-Kala, 04.IV.1966, O.L. Kryzhanovsky leg. (ZIN); 1 ♂, 1 ♀, Tashkent, near railway station, plant debris, 24.V.1986, S.A. Kurbatov leg. (cKur); 1 ♂, Samarkand, Agalyk, 18.X.1935, Y.D. Kirschenblat leg.; 4 ♂, 4 ♀, Aman Kutan, 12.VI–06.VII.1932, V.V. Gussakovsky leg. (ZIN); 1 ♂, Yakkabag, *Convulvulus* sp. and thorny bushes, 02.XII.1941, K.V. Arnoldi leg. (cRyv); 1 ♂, 1 ♀, Yakkabag, hills S of the town, ravine in forest, cave, 30.XI.1941, K.V.

Arnoldi leg. (cRyv); 1 ♂, Ishkent, Kashkadarya River, 24.X.1947, K.V. Arnoldi leg. (ZMMU); **Kyrgyzstan:** 1 ♂, Kyrgyz-Alatoo Mts, 09.VII.2010, 72°28'38.6N, 42°48'49.2E, V.A. Kastcheev leg.; 1 ♂, 2 ♀, S Fergak-skiy Mt. Ridge, Ak-Terek, 31.VIII–20.IX.1937, A.N. Kirichenko leg. (ZIN); 1 ♂, Kara-Alma, Ferganskiy Mt. Ridge, 26.VI.1945, K.V. Arnoldi leg. (ZMMU); **Turkmenistan:** 2 ♂, 3 ♀, Kopetdag Mts, 22.VI.1953, Ployvanova leg.; 5 ♂, 4 ♀, E Kopetdag Mts, Sunt Mt., in *Ulmus* sp. leaves rolled by aphids, 22–24.VI.1953, O.L. Kryzhanovsky leg.; same locality, but 1 ♂, *Ulmus* sp., Odyncova leg. (ZIN); 1 ♀, N Kopetdag Mts, Firjusa-Cleft, near Ashchabad, 07.V.1989, D.W. Wrase leg. (cSch); 3 ♂, 3 ♀, W Kopetdag Mts, N Karakala, 28.IX.1989, A.V. Puchkov (cSch); **Tajikistan:** 3 ♂, 2 ♀, 20 km S Danghara, 08.V.1962, Guryeva leg.; 1 ♂, Vakhsh Mt. Ridge, 10 km N Kangurt, 08.V.1970, G.S. Medvedev leg. (ZIN); 1 ♂, Pamir-Alai, Hisaar Mts, Adshuk-Cleft, near Warsob, 1200 m a.s.l., 01–03.VII.1990, M. Schülke & D.W. Wrase leg. (cSch); 1 ♂, 2 ♀, Gazimalyk Mt. Ridge, 15 km W Ganjin, 2000 m a.s.l., 17.V.1970, G.S. Medvedev leg. (ZIN); 2 ♂, Mountains near Kuljab, 1500–2000 m a.s.l., 20.VI.1963, A.V. Bogachev leg. (ZMMU).

Comments on taxonomy, distribution and bionomics. The diagnostic characters including illustrations of the aedeagus and the most recent summary of the bionomic and distribution data of this widespread and rather common Western Palaearctic species can be found in Assing and Schülke (2012). From similar Middle Asian species *Q. capitalis* and *Q. fusicornis*, *Q. ochripennis* is distinguished by the larger body and shape of the aedeagus. From the larger *Q. solskyi* it can be safely distinguished by the characters of aedeagus.

Quedius ochripennis is widely distributed in Europe and in the Mediterranean region. It is also known from Simla Hills in Himalaya, India (Smetana, 1988) and from Middle Asia where, based on earlier records (Table 1) and material examined here, it occurs in southwestern Turkmenistan, entire territory of Tajikistan, and southern Uzbekistan.

Quedius ochripennis inhabits various ground based debris, often associated with decaying wood, also in nests of mammals, ants and wasps (Assing and Schülke 2012). Based on the material examined here, in Middle Asia *Q. ochripennis* prefers humid plant debris usually near water bodies, also it was found in caves and in tree foliage in an aphid nest. In the mountains it was recorded at elevations up to 2000 m.

Quedius (Microsaurus) puncticollis Thomson, 1867

Fig. 3A

Herman 2001, 3249 (summary of literature); Kascheev 2001, 102 (distribution records); Assing and Schülke 2012, 466, 467 (diagnosis, distribution and bionomics, aedeagus illustration).

Material examined. Tajikistan: 3 ♂, 1 ♀, Pamir-Alai, Hisaar Mts, Adshuk-Cleft near Warsob, Bachufer, 01–03.VII.1990, M. Schülke leg. (cSch).

Comments on taxonomy, distribution and bionomics. *Quedius puncticollis* is widely distributed in Northern, Central and Eastern Europe for which the latest summary of diagnostic characters, distribution and biology can be found in Assing and Schülke (2012). It is most similar to *Q. ochripennis* from which it can be easily distinguished by the apically not lanceolate paramere with a broad and shallow apical emargination.

Quedius puncticollis is commonly found in the burrows of small mammals, especially moles, also in bee and wasp nests (Assing and Schülke 2012). Based on literature data (Table 1) and material examined here, there are only few records of *Q. puncticollis* in Middle Asia: from southern Kazakhstan and southern Tajikistan.

Quedius (Microsaurus) capitalis Eppelsheim, 1892

Fig. 7

Quedius capitalis Eppelsheim 1892, 329 (original description); Gridelli 1924, 40 (characters); Coiffait 1978, 148 (characters and illustration of aedeagus); Kadyrov et al. 2014a, 31 and 2014b, 49 (distributional records).

Material examined. Type material. Uzbekistan: Syntypes: 1 ♂, “♂/ c.Eppelsh. Steind. d. [printed]/ Qu. capitalis Epp. Type Taschkent, Leder [handwritten]/ Typus”; 1 ♂, “♂/ capitalis Epp. Taschkent Leder. [handwritten]/ Typus” (Fig. 7E, F) (NMW).

Additional material. Uzbekistan: 2 ♀, Tien Shan, Aktasch, near Taschkent, 2000 m a.s.l., 13.VII.1984, D.W. Wrase leg. (cSch); **Kazakhstan:** 3 ♂, Karatau Mts, Khantagi River, 570 m a.s.l., 43°33'32.4N, 68°40'52.7E, 25.VI.2011, V.A. Kastcheev leg. (ZIN); **Tajikistan:** 3 ♂, Mountains near Kuljab, 1500–2000 m a.s.l., 20.VI.1963, A.V. Bogachev leg. (ZMMU).

Comments on taxonomy and type material. In the original description, Eppelsheim (1892) mentioned morphological characters of both males and females and stated that the species was known to him from a few specimens from “Tashkent”. As we learn from the introduction in his paper, specimens were collected by Hans Leder. Both male specimens from NMW labeled as “types” of *Q. capitalis* originally come from Eppelsheim’s collection and their morphology and label information fit the original description; therefore they are syntypes.

We have examined aedeagi of both syntypes and confirm they are conspecific. Eppelsheim (1892) compared *Q. capitalis* with *Q. ragusai* Eppelsheim, 1889. Gridelli (1924), based on the examination of a syntype, provided additional morphological details for the species including verbal description of its aedeagus (but no illustration) and placed it near *Q. ochripennis*. Based on a syntype male, Coiffait (1978) again redescribed this species and

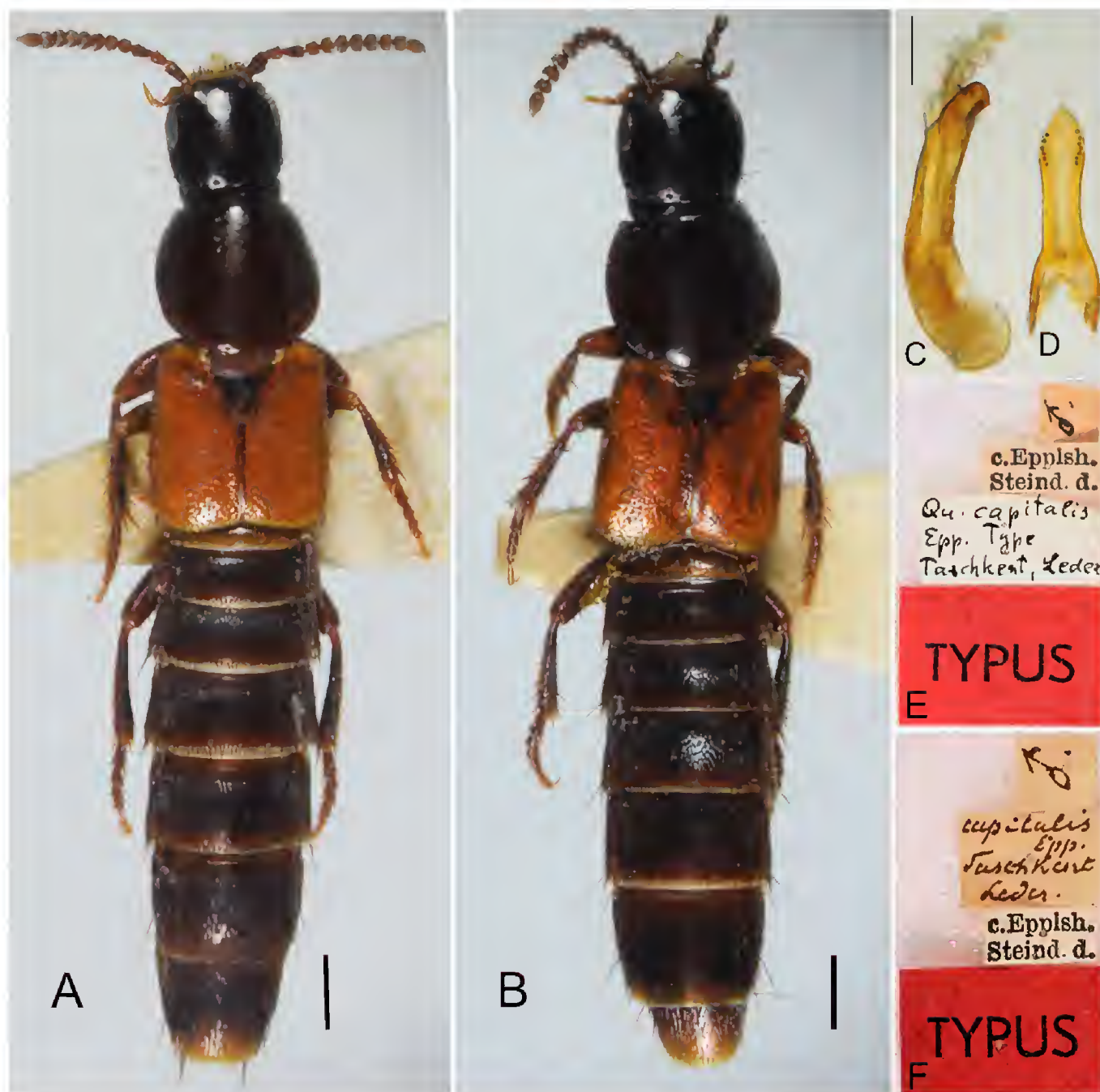


Figure 7. *Quedius capitalis*, syntypes, males. **A, B**, habitus; **C, D**, aedeagus of the syntype in the photo **A**. **E** (of the syntype in the photo **A**), **F** (of the syntype in the photo **B**), labels. **C**, median lobe, lateral view; **D**, paramere, underside. Scale bars: **A, B** = 1 mm; **C** = 0.5 mm.

provided its first and hitherto the only available illustration of the aedeagus. Our examination of the syntypes of *Q. capitalis* confirms the correct identification of this species by both Gridelli (1924) and Coiffait (1978). In Schülke and Smetana (2015) *Q. capitalis* was erroneously placed in the subgenus *Raphirus*. Here we redescribe this poorly known species and provide further data on its distribution.

Redescription. Measurements and ratios (range, arithmetic mean; $n = 10$): HL: 0.8–1.3 (1.0); HW: 0.8–1.5 (1.1); PL: 0.9–1.6 (1.3); PW: 1.1–1.8 (1.4); EL: 1.2–2.0 (1.6); EW: 1.2–1.9 (1.5); FB: 2.9–4.7 (3.9); TL: 6.5–9.3 (7.8); HL/HW: 0.8–1.1 (1.0); PL/PW: 0.8–1.0 (0.9); EL/EW: 1.0–1.2 (1.1).

Body black to dark brown, hind margins of abdominal tergites slightly paler; elytra reddish; palpi and other appendages slightly lighter; body glossy (Fig. 7A, B).

Head approximately as wide as long or slightly longer; eyes small, not convex; temples as long as longitudinal diameter of eye; posterior frontal puncture closer to posterior margin of head than to anterior frontal puncture; temporal puncture closer to posterior margin of head than to posterior margin of eye; two vertical punctures behind posterior frontal puncture arranged as slightly oblique line between posterior margin of eye and dorsal part of neck; microsculpture of head with transverse distinct wavelines.

Antennae moderately long, antennal segments: 3rd longer than 2nd, 4th–10th gradually widening towards apex of antenna.

Pronotum slightly wider than long, widest at about middle to posterior third; hind angles rounded but distinct; dorsal and sublateral rows each with three punctures; microsculpture with transverse waves as on posterior part of head. Scutellum impunctate with microsculpture slightly coarser than on pronotum. Elytra parallel-sided, slightly longer than wide, longer than pronotum, their punctation dense, interspaces shiny with distinct minute irregularities.

Abdomen: punctation fine and dense; interspaces with minute irregularities; posterior margin of tergite VII with palisade fringe.

Male: protarsi with tarsomeres 1–4 dilated stronger than in females. Sternite VIII with weak triangular medio-apical emargination; tergite X triangular with setae; sternite IX elongate, gradually narrowed apically, with moderately wide and long basal portion and obtusely rounded apical margin with numerous setae. Aedeagus (Fig. 7C, D): median lobe parallel-sided with broad and obtuse apex and tooth located near apex (Fig. 7C). Paramere rhomboid sharply narrowing apicad; its apex almost reaching apex of median lobe, with two pairs of apical setae and two pairs of lateral setae below apex;

paramere (underside) with ca. 4–8 sensory peg setae in each of two sinuate lateral rows that extend basad over pairs of lateral setae (Fig. 7D).

Comparison. *Quedius capitalis* seems to be closely related to *Q. fusicornis* and *Q. ochripennis* from which it can be easily distinguished externally by smaller body size and proportions, and by the structure of paramere with two sinuate lateral rows of peg setae (ca. 4–8 in each row) extending basad over pairs of lateral setae.

Distribution. Based on the literature data (Table 1) and newly examined material, *Q. capitalis* is known from several localities near Tashkent (Uzbekistan), Karatau Mountains (southwestern Kazakhstan) and Hazratisho Mountains (southern Tajikistan).

Bionomics. Unknown.

Quedius (Microsaurus) fusicornis Luze, 1904

Fig. 8

Quedius fusicornis Luze, 1904, 28 (original description);
Gridelli 1924, 69 (characters, notes)

Material examined. Type material: Tajikistan or Uzbekistan: Lectotype (here designated): ♂, “♂/ Seravchan Putschin Pass. Glasunov 1892 [printed]/ Type fusicornis Luze [handwritten]/ ex. coll. Luze [printed]/ ex. coll. Scheerpeltz [printed]/ Typus *Quedius fusicornis* Luze [pre-printed]”; Paralectotypes: 1 ♀, “Seravchan Putschin Pass. Glasunov 1892 [printed]/ Type fusicornis Luze [handwritten]/ *Quedius fusicornis* Luze [handwritten]/ [square orange piece of paper]”; 1 ♀, “Seravchan Boschara Glasunow 1892 [printed]/ Type fusicornis Luze [handwritten]/ *Quedius fusicornis* Luze [pre-printed]” (Fig. 8F, G) (NMW).

Additional material. Uzbekistan: 1 ♂, Samarqand Region, Aman Kutan, 04.VII.1932, V.V. Gussakovsky leg.; **Kyrgyzstan:** 1 ♂, Kyrgyz-Alatoo Mts, 09.VII.2010, 72°28'38.6N, 42°48'49.2E, V.A. Kastcheev leg. (ZIN).

Comments on taxonomy and type material. In the original description, Luze (1904) provided no information on the type material, but he indicated 7.7–8.5 mm body size range for the species. This suggests that he must have had more than one specimen to base a description on. He also indicated “Seravschan: Putschin-Pass, Boschara” as a locality that his material was from. Finally, we know from the introduction in Luze’s paper that the material he examined was collected by Glasunov. Therefore, a single male (NMW) and two females (ZIN) that we examined and that match the original description morphologically and in the label data, are syntypes. Luze (1904) compared *Quedius fusicornis* with his *Q. solskyi* and the widespread *Q. cruentus* Ol. Gridelli (1924) apparently based his short notes about this species exclusively on Luze’s description, without seeing any material. Similarly to other species of *Quedius* described by Luze (1904), *Q. fusicornis* is missing in the monograph by Coiffait (1978) who apparently overlooked Luze’s publication. Here we provide a redescription and first illustrations of this poorly known species, including its aedeagus.

Redescription. Measurements and ratios (range, arithmetic mean; n = 6): HL: 1.0–1.2 (1.1); HW: 1.0–1.4 (1.1); PL: 1.1–1.5 (1.3); PW: 1.3–1.6 (1.4); EL: 1.5–1.7 (1.6); EW: 1.3–1.6 (1.5); FB: 3.7–4.4 (4.0); TL: 6.0–8.6 (7.3); HL/HW: 0.9–1.1 (1.0); PL/PW: 0.8–0.9 (0.9); EL/EW: 1.00–1.2 (1.1).

Body length: 6.0–8.6 (7.3); head, scutellum and abdomen blackish, pronotum and hind margins of abdominal tergites slightly paler; elytra light red or orange; palpi, antennae and legs brown; body glossy (Fig. 8A, B).

Head approximately as wide as long HL/HW: 0.9–1.1 (1.0); eyes small, not convex; temples slightly longer or as long as longitudinal diameter of eye; posterior frontal puncture closer to posterior margin of head than to anterior frontal puncture; temporal puncture closer to posterior margin of head than to posterior margin of eye; two vertical punctures behind posterior frontal puncture arranged as slightly oblique line between posterior margin of eye and dorsal part of neck; microsculpture of entire surface of head with transverse waves.

Antennae moderately long, antennal segments: 3rd longer than 2nd, 4th–10th gradually widening towards apex of antenna.

Pronotum slightly wider than long PL/PW: 0.8–0.9 (0.9), widest at about posterior third, gradually narrowing anteriorly; hind angles rounded but distinct; dorsal and sublateral rows each with three punctures; microsculpture with transverse waves similar to that on posterior part of head. Scutellum impunctate with microsculpture as on pronotum. Elytra parallel-sided, slightly longer than wide, as long as or slightly longer than pronotum and narrower than maximum width of pronotum; punctation dense; setation gray; interspaces shiny, with distinct minute irregularities.

Abdomen: punctation fine and moderately dense; interspaces with vaguely distinct minute irregularities; posterior margin of tergite VII with palisade fringe.

Male: protarsi with tarsomeres 1–4 dilated stronger than in females. Aedeagus (Fig. 8C–E: median lobe parallel-sided along most of its length with broad and obtuse apex and tooth located near apex (Fig. 8C). Paramere parallel-sided, narrowing only in rhomboid apical portion; its apex almost reaching apex of median lobe, with two pairs of apical setae and two pairs of lateral setae below apex, with 6 peg setae arranged in two regular longitudinal rows apically extending basad over pairs of lateral setae (Fig. 8D).

Comparison. *Quedius fusicornis* is similar to *Q. capitalis*. For comparison, see the latter species above. From other similar species such as *Q. solskyi*, *Q. cruentus* and *Q. ochripennis*, it can be easily distinguished by the structure of the apical part of the paramere with two medially situated short rows of peg setae (3 in each row) extending basad the pairs of lateral setae.

Distribution. We were not able to locate the type locality “Putschin Pass” situated somewhere along Zeravchan River that is extended from eastern Uzbekistan to western Tajikistan. Additional material was studied from eastern Uzbekistan (near Aman-Kutan) and north-west-

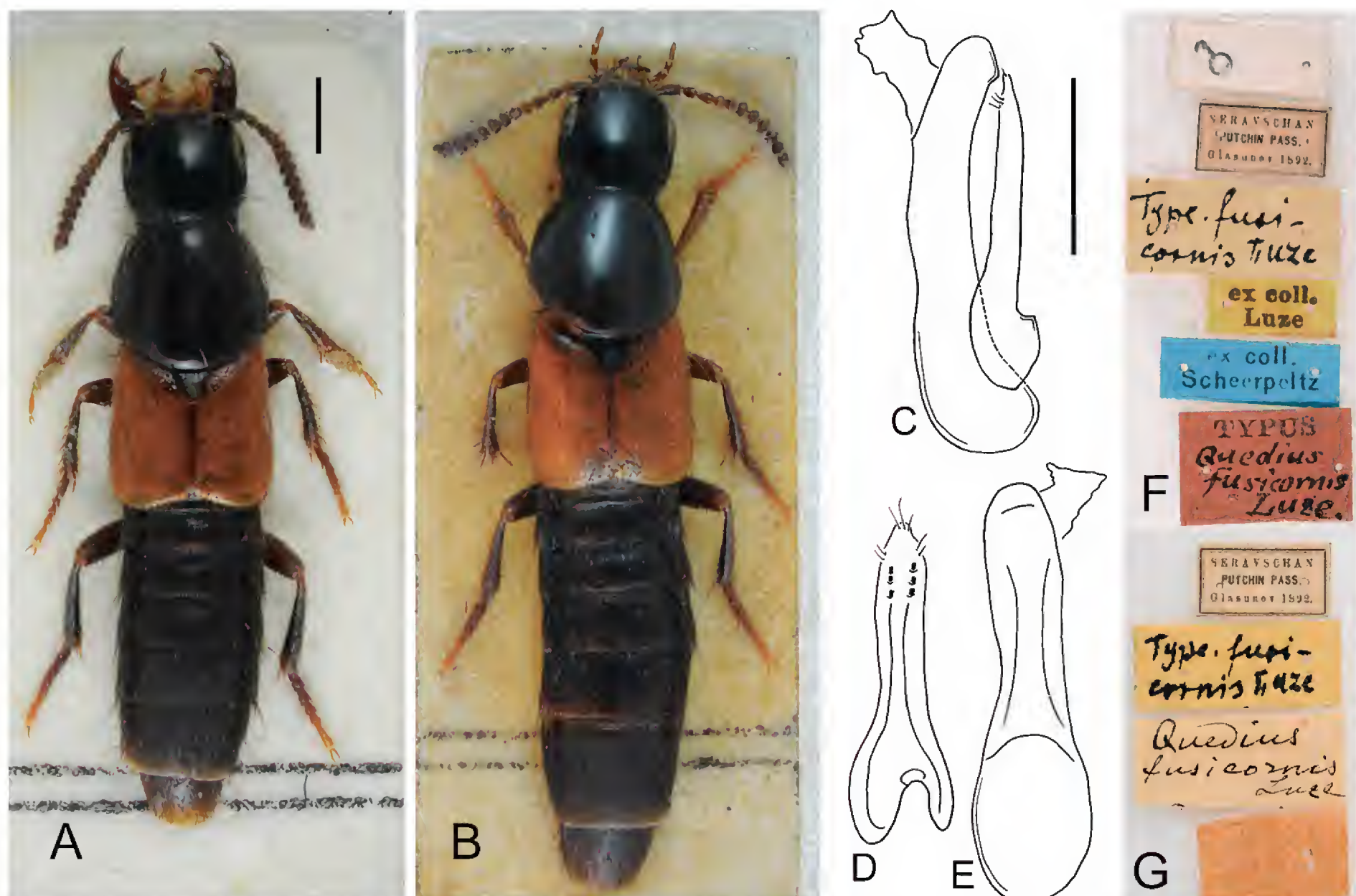


Figure 8. *Quedius fusicornis*, types. **A**, lectotype, male, habitus; **B**, paralectotype, female, habitus. **C–E**, aedeagus of the lectotype: **C**, lateral view; **D**, paramere, underside; **E**, median lobe, ventral view. **F** (lectotype), **G**, (paralectotype), labels. Scale bars: 1 mm.

ern Kyrgyzstan (Kyrgyz-Alatoo). Finally, one specimen was from ‘Tangi-Gharuh’, a toponym in Afghanistan that we could not locate.

Bionomics. Unknown.

Quedius (Microsaurus) solskyi Luze, 1904

Figs 9, 10

Quedius asiaticus Bernhauer, 1918, **syn. n.**

Quedius solskyi Luze, 1904, 99 (original description); Gridelli 1924, 72 (characteres, notes);

Quedius asiaticus Bernhauer, 1918, 92 (original description); Gridelli 1924, 57 (characters); Coiffait 1978, 183 (characters); Kascheev 2002, 181 (distribution records).

Material examined. Type material: *Quedius solskyi*: **Tajikistan:** Lectotype (here designated): ♂, “♂/ Trkst. Jagnob Schach-Sara, Glasunov 1892 [printed]/ Type solskyi Luze [handwritten]/ ex. coll. Luze/ ex. coll. Scheerpeltz [printed]/ Typus Quedius solskyi Luze [pre-printed]” (Fig. 9E) (NMW);

Quedius asiaticus: **Tajikistan or Uzbekistan:** Lectotype (here designated): ♂ “Ost. Buchara Rickmers. [handwritten] / Mus. Bremen [handwritten]/ asiaticus Bernh. Typus [handwritten]/ Chicago NHMus M. Bernhauer Collection [printed]”; paralectotype: 1 ♂ “abietum

[illegible word] [handwritten]/ asiaticus Bernh. Cotypus. [handwritten]/ Chicago NHMus M. Bernhauer Collection [printed]” (Fig. 10G, H) (FMHN),

Additional material. Tajikistan: 1 ♂, Ramid [Ramit], Kafirnigan River, 27.VII.1939, A. Romanov leg. (ZMMU).

Comments on taxonomy, lectotype designation and new synonymy. In the original description of *Q. solskyi*, Luze (1904) did not specify the number of specimens he studied, but provided characters for both sexes and the locality “Jagnob: Kol, Schach-Sara” [Tajikistan, Yagnob river, Sughd Distr.]. Therefore, a male from NMW with the locality label “Trkst. Jagnob Schach-Sara” is considered a syntype. We could not locate other syntypes. Gridelli (1924), similarly to the case with *Q. fusicornis*, based his notes about *Q. solskyi* only on Luze’s description, without checking type material. And as with other species of *Quedius* described by Luze (1904), *Q. solskyi* is missing in the monograph of Coiffait (1978). Under the circumstances of uncertain identity of other syntypes, we designate the only available male syntype as a lectotype to unambiguously fix the identity of *Q. solskyi*.

Bernhauer (1918) described *Q. asiaticus* from “Ost. Buchara” and compared it with *Q. abietum* distributed in southern Europe. Bernhauer (1918) did not even mention Luze’s *Q. solskyi*, even though his description matches the latter species. Both examined syntypes of *Q. asiaticus* are clearly conspecific in morphology. In order to fix the identity of the species, we designate here one better

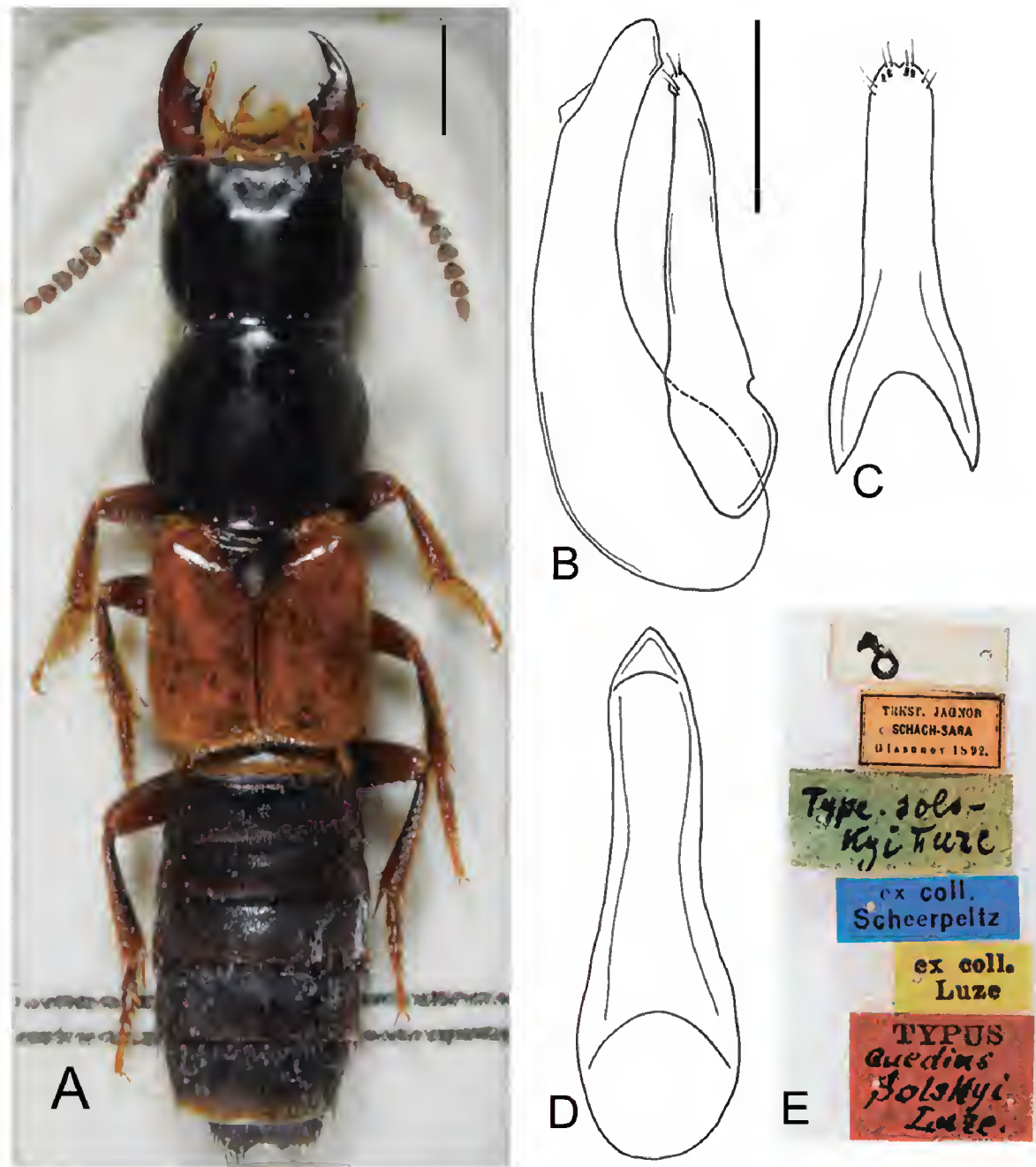


Figure 9. *Quedius solskyi*, lectotype. A, habitus. B–D, aedeagus: B, lateral view; C, paramere, underside. D, median lobe, ventral view. E, labels. Scale bars: 1 mm.



Figure 10. *Quedius asiaticus* (new synonym of *Q. solskyi*), syntypes. A, B, habitus. C–F, aedeagus. C, E, median lobe, lateral view; D, F, paramere, underside. G, H, labels. Scale bars: 1 mm.

preserved male syntype (Fig. 10A, B) with the locality label “Ost. Buchara” exactly matching the data from the original description and the identification label “asiaticus Bernh. Typus” hand written by Bernhauer as a lectotype.

Our examination of the mentioned types of both *Q. solskyi* and *Q. asiaticus* undoubtedly reveal they are conspecific. Thus we place *Q. asiaticus* Bernhauer, 1918 in synonymy with *Q. solskyi* Luze, 1904 and provide a redescription with the first illustration of the aedeagus of this poorly known species.

Redescription. Measurements and ratios (arithmetic mean = 4): HL: 1.4–1.6 (1.5); HW: 1.7–1.9 (1.9); PL: 1.6–1.8 (1.7); PW: 1.9–2.1 (2.1); EL: 2.0–2.2 (2.1); EW: 1.9–2.1 (2.0); FB: 5.1–5.6 (5.3); TL: 8.1–9.7 (9.1); HL/HW: 0.7–0.8 (0.8); PL/PW: 0.8–0.9 (0.9); EL/EW: 1.0–1.1 (1.1).

Body dark brown to brown; apical margin of abdominal tergites vaguely paler; elytra reddish; maxillary and labial palpi, as well as antennae dark-brownish; body glossy (Figs 9A, 10A–B).

Head wider than long HL/HW: 0.7–0.8 (0.8), eyes very small, not convex; temples more than two times as long as longitudinal diameter of eye; posterior frontal puncture in the middle between anterior puncture and posterior margin of head; temporal puncture closer to posterior margin of head than to posterior margin of eye; two vertical punctures arranged in almost straight line between posterior frontal puncture and neck; microsculpture with transverse waves. Antennae long; antennal segments: 3rd longer than 2nd; 4th–10th slightly widening towards apex of antenna.

Pronotum slightly wider than long PL/PW: 0.8–0.9 (0.9), widest at its middle, slightly narrowing anteriorly; hind angles rounded, barely distinct; dorsal and sublateral rows each with three punctures; microsculpture with transverse waves similar to that on posterior part of head. Scutellum impunctate, with microsculpture as on pronotum. Elytra parallel-sided, as long as or longer than wide, narrower and longer than pronotum; punctation dense, setation brownish, interspaces shiny and with distinct minute irregularities.

Abdomen: punctation fine and moderately dense; interspaces with vaguely distinct minute irregularities; posterior margin of tergite VII with palisade fringe.

Male: head wider than long, larger than in females and with longer temples (Luze 1904). Aedeagus (Figs 9B–D, 10C, D, E, F): Median lobe (in parameral view) parallel-sided along most of its length with obtusely pointed apex, with tooth located near apex (Figs 9B, 10C, E). Paramere parallel-sided, its apex almost reaching apex of median lobe; with two pairs of apical setae and two pairs of lateral setae below apex; underside with pair of peg setae close to apical margin on each side of medial emargination (Figs 9C, 10D, F).

Comparison. *Quedius solskyi* is similar to *Q. fuscicornis* and *Q. ochripennis*, but it can be externally distinguished from both by the larger body size, distinctly elongated elytra and smaller eyes with their diameter two

times as short as tempora. In the structure of the aedeagus *Q. solskyi* is more similar to *Q. fuscicornis* but differs from the latter by the paramere with incised apex and two pairs of sensory peg setae. The aedeagi of *Q. solskyi* and *Q. ochripennis* differ in many ways.

Distribution. Vaguely recorded type localities for *Q. solskyi* and *Q. asiaticus* are located somewhere in northern Tajikistan and in eastern Uzbekistan or western Tajikistan. The only additional and better georeferenced specimen examined here comes from western Tajikistan: Ramid, Kafirnigan River.

Bionomics. Unknown.

Quedius (Microsaurus) koltzei Eppelsheim, 1887

Fig. 2D

Quedius koltzei Eppelsheim, 1887, 420 (original description); Bernhauer and Schubert 1916, 425 (catalog); Gridelli 1924, 24 (characters, new records); Scheerpeltz 1933, 1445 (catalog); Coiffait 1978, 164 (new records, characters, first illustration of the aedeagus); Smetana 1998, 115 (study of the holotype, redescription, comments); Smetana 2015b, (new records, characters).

Material examined. Kazakhstan: 2 ♂, 1 ♀, Dzhungarskiy Alatau, Keskenterek River, 10–20.VII.1988, V.A. Kastcheev leg.; 3 ♂, same locality and collector, but 20–30.VIII.1988 (ZIN); 1 ♂, Aksu-Dzhabagly, Taldy-Bulak River, 10–20.IV.1979, B.V. Iskakov leg. (ZIN); 3 ♂, Terskey-Alatau, VI.1957, Skopin leg. (MNHN).

Comments on taxonomy, type material and distribution. *Quedius koltzei* was described by Eppelsheim (1887) from “Chabarovka” [Khabarovsk, Far East, Russia] based on a single female specimen. Gridelli (1924) basically repeated the original description. Coiffait (1978) interpreted a few males as that species from Terskey-Alatau, a mountain range in Kazakhstan very far from the type locality of *Q. koltzei*. Based on that material, he redescribed *Q. koltzei* again and provided the illustration of the aedeagus for the first time. Smetana (1998) also redescribed *Q. koltzei*, but based on the holotype. Later, Smetana (2015b) determined one male and one female from Heilongjiang province of China as *Q. koltzei* and illustrated their genital structures. Smetana’s comparison of the Chinese specimens with the type material and geographic proximity of Heilongjiang province to the type locality of *Q. koltzei* corroborate his identification. Our examination of the male specimens from Terskey-Alatau from Henry Coiffait’s collection that he identified as *Q. koltzei* revealed that they match as far as we can observe, with the illustrations of *Q. koltzei* from China in Smetana (2015b). But since Smetana (2015b) did not illustrate the lateral view of the aedeagus, only the re-examination of Chinese and, preferably, additional material may help to clarify the status of Middle Asian specimens from Terskey-Alatau. In the absence of neg-

ative evidence, we consider *Q. koltzei* as a potentially widespread Asian species. It is also possible that *Q. rufilabris*, whose identity currently remains ambiguous, is conspecific with *Q. koltzei* (for details see the former species below).

Quedius koltzei differs from other similar Middle Asian *Microsaurus* as follows: from *Q. fusicornis*, *Q. capitalis* and *Q. solskyi* in peg setae on paramere arranged in irregular lines or groups; from *Q. ochripennis*, *Q. puncticollis* and *Q. tadjikiscus* in median lobe (in lateral view) narrowing into a blunt, but clear apex and peg setae on paramere arranged in four irregular groups. From *Q. bucharensis*, a species whose identity remains ambiguous (for details see that species below) *Q. koltzei* differs in the chaetotaxy of head (posterior frontal puncture situated closer to nuchal ridge than to posterior margin of eye) and pronotum (two punctures in dorsal row and sublateral group always situated before or at most at the same level as large lateral puncture).

Based on the material examined here, we have additional records for *Q. koltzei* from Kazakhstan. Bionomics remains unknown.

Quedius (Microsaurus) rufilabris Luze, 1904

Quedius rufilabris Luze, 1904, 100 (original description); Gridelli 1924, 72 (characters, notes).

Comments on taxonomy. Luze (1904) described *Quedius rufilabris* from “Seravschan: Putschin Pass” [Mountain Range or river Zeravshan in Tajikistan or Uzbekistan]. The description was based on a single female specimen. Gridelli (1924) based his knowledge of this species on Solsky’s original description only and placed *Q. rufilabris* near *Q. solskyi*. Similarly to Luze’s other species, Coiffait (1978) overlooked this species in his monograph. Unfortunately, we were unable to find the holotype of *Q. rufilabris*, but based on its original description all diagnostic characters, especially chaetotaxy of the head and pronotum, match *Q. koltzei*. Since the presumed type locality of *Q. rufilabris* is rather remote from the distribution of *Q. koltzei*, if the latter even occurs in Middle Asia (see above), we treat the former species as different from *Q. koltzei*, at least until more material from relevant geographic areas will be studied.

Quedius (Microsaurus) tadjikiscus Coiffait, 1975

Quedius tadjikiscus Coiffait, 1975, 32 (original description); 1978, 149 (notes).

Comments on taxonomy. We could not locate and examine the type material of *Q. tadjikiscus* described from “Tadjikabad, Daran-Nazaran” in Tajikistan, and did not come across any material that could be identified as that species. The description and the illustrations of the aedeagus of *Q. tadjikiscus* available from Coiffait (1975,

1978) suggest that this may be a species very similar to *Q. koltzei*. But *Quedius tadjikiscus* differs from *Q. koltzei* in the presence of three punctures in the dorsal row of pronotum and the absence of apical groups of peg setae on the paramere.

Quedius (Microsaurus) bucharensis Bernhauer, 1918

Quedius bucharensis Bernhauer, 1918, 93 (original description); Gridelli 1924, 56 (characters, distribution); Scheerpeltz 1933, 1435 (catalog); Coiffait 1978, 186 (external characters).

Type material examined. Syntypes: Tajikistan: 1 ♂, “Mts. Karateghin Balldschan 924 m. F. Hauser 1898 [printed]/ bucharicus Bern. det. Bernh. det. Bernh. [handwritten]/ bucharensis Bernh. Typus [handwritten]/ Chicago NHmus M. Bernhauer Collection [printed]”; 1 ♀, “Buchara Handiger [handwritten]/ ochripennis Asia centr. Handiger [handwritten]/ bucharensis Bernh. Cotypus [handwritten]/ bucharensis Bernh. [handwritten]/ Chicago NHmus M. Bernhauer Collection [printed]” (FMNH); **Turkmenistan:** 1 ♀, “♀/ Pers. Kopet-Dagh. Siaret 1160 m 5.99. Coll. Hauser [printed]/ *Quedius persicus* Brh. [handwritten]/ solskyi Luze [handwritten]/ ex. coll. Moczarski [printed]/ ex. coll. Scheerpeltz [printed]”; 1 ♀, “♀/ Pers. Kopet-Dagh. Siaret 1160 m 6.99. Coll. Hauser [printed]/ solskyi ? [sic!] Luze [handwritten]/ ex. coll. Moczarski [printed]/ ex. coll. Scheerpeltz [printed]” (NMW).

Comments on taxonomy. *Quedius bucharensis* was described from an unspecified number of specimens of both sexes coming from localities in Uzbekistan, Turkmenistan and Tajikistan indicated as “Karateghingebirge (Balldschan, 924 m, Hauser), Buchara (ohne nähere Fundortangabe, Bang-Haas) und Persien (Kopet-Dagh, Siaret, 1160 m, V. 1899, Hauser)” (Bernhauer 1918).

We have examined one male and one female from the FMNH which are clearly syntypes of *Q. bucharensis*. Of them, a male specimen was earlier dissected and its aedeagus must have been glued on the card point beside the specimen, but was obviously lost. Since there were no publications with the structure of *Q. bucharensis* aedeagus, the identity of this species remains ambiguous. An additional two females from NHMW with the same locality labels as in the original description but without Bernhauer’s handwritten type labels, seem conspecific with both mentioned syntypes even though they are somewhat smaller than the latter. Their earlier identifications as *Q. solskyi*, evident from the labels, are wrong because of the following characters: chaetotaxy of head with posterior frontal puncture closer to posterior margin of eye than to nuchal ridge, larger eyes, head longer than wide and as long and as wide as elytra.

The material used by Bernhauer (1918) in the original description of *Q. bucharensis* comes from localities rather remote from each other. Given that and the body size

variation among the examined specimens from different localities, it is possible that they are not conspecific. On the other hand, significant intraspecific variability in body size and proportions is usual in some *Microsaurus* species. More extensive material including males is needed to clarify the case.

Quedius (Microsaurus) mutilatus-group

Fig. 2E

Comments. We have proposed the *mutilatus*-group for several Middle Asian species in Salnitska and Solodovnikov (2018), where we revised all available material. Thus only brief information for each of these species is provided with reference to the revision for details.

Diagnosis. The *mutilatus*-group is characterized by the following: brown to dark brown dorso-ventrally flattened body, notably small eyes, short elytra, absence of palisade fringe on abdominal tergite VII; aedeagus robust, with apical portion of median lobe slightly curved towards paramere with characteristic tooth near apex (in lateral view), with paramere widest shortly before apex (in parameral view) having four distinct groups of sensory peg setae on the underside: two apical and two lateral.

Distribution and biology. The *mutilatus*-group is restricted to the Tien-Shan Mountains where all species of the group are confined to high elevations, up to 3600 m. Based on the morphology and limited bionomic data, all species of the group are hypogean and are mostly found under stones or deep in leaf litter.

Quedius (Microsaurus) mutilatus Eppelsheim, 1888

figs 1–2, 4A–B in Salnitska and Solodovnikov 2018

Diagnosis. *Quedius mutilatus* is most similar to *Q. kungeicus* from which it can be distinguished by the rhomboid shape of the paramere with slight apical incision; by the less curved apical portion of the median lobe (lateral view) with more stronger ventral sub-apical tooth. From *Q. kalabi* and *Q. equus* it differs by the not so deeply incised apex of paramere and distinctly larger number of sensory peg setae in lateral groups on the paramere.

Distribution. *Quedius mutilatus* is restricted to the central part of Terskey-Alatoo Mountains south from Issyk-Kul lake in Kyrgyzstan.

Quedius (Microsaurus) kalabi Smetana, 1995

figs 1, 3, 4C–D in Salnitska and Solodovnikov 2018

Diagnosis. *Quedius kalabi* differs from all other species of the *mutilatus*-group by its narrower and somewhat curved apical portion of the median lobe of the aedeagus with relatively short blade of its subapical tooth (aedeagus in lateral view). In shape of the apical portion of the

paramere and degree of its incision *Q. kalabi* displays a transition between *Q. mutilatus* having lesser incised paramere with more peg setae in lateral groups, and *Q. equus* having deeper incised paramere with lesser peg setae in lateral groups.

Distribution. *Quedius kalabi* replaces *Q. mutilatus* in the eastern part of Terskey-Alatoo Mountains in Kyrgyzstan.

Quedius (Microsaurus) equus Smetana, 2014

figs 1, 4G–N in Salnitska and Solodovnikov 2018

Diagnosis. *Quedius equus* distinctly differs from all other species of the *mutilatus*-group by the deep apical incision of the paramere and by low number (1–3) of sensory peg setae on its underside arranged in lateral longitudinal rows.

Distribution. *Quedius equus* is known from north-east Terskey-Alatoo Mountains in Kazakhstan and from Xinjiang province of China. Presumably it has a broader continuous distribution in this area.

Quedius (Microsaurus) kungeicus Solodovnikov & Salnitska, 2018

figs 1, 4E–F, 5 in Salnitska and Solodovnikov 2018

Diagnosis. Among all species of the group, *Quedius kungeicus* can be distinguished by the ovoid apical part of the paramere without a distinct apical incision (in parameral view) and by the distinctly curved apical portion of the median lobe (in lateral view) with longer tip and without distinct sub-apical tooth.

Distribution. *Quedius kungeicus* is known only from the holotype collected in the Kungey-Alatoo Mountains of Kazakhstan.

Subgenus *Raphirus* Stephens, 1829

Quedius (Raphirus) limbatus Heer, 1839

Fig. 3D

Herman 2001, 3187 (summary of literature); Kascheev 2001, 102; 2002, 181 (distribution records); Assing and Schülke 2012, 473, 474 (diagnosis, distribution and bionomics, aedeagus illustration).

Material examined. Kazakhstan: 2 ♂, 1 ♀, 7 Almaty area, Dzhungarskiy Alatau, 7 km E Lepsinsk, Chornaya River canyon, 1200–1400 m a.s.l., *Betula* sp., *Malus*, *Populus* etc. forest, 45°31'N, 80°43'E, 13–15.VI.2001, S.I. Golovatch leg. (cRyv); 3 ♂, 6 km SE Rudnichnyi, Koxu River canyon, 1300–1400 m a.s.l., 44°41'N, 78°58'E, *Betula* sp., *Populus*, *Picea* etc. forest, 09–10.VI.2001, S.I. Golovatch leg. (cRyv); 2 ♂, 3 km SSE Lepsinsk, Bulinka River canyon, 1100–1800 m a.s.l., 45°30'N, 80°38'E, 16–17.VI.2001, S.I. Golovatch leg.

(cRyv); 1 ♂, Zailiysky Alatau Mts, ca. 20 km Turgen, Turgen River canyon, near Batan, 1750 m a.s.l., *Picea*, *Betula* sp., *Salix* etc. forest, 25.V.2001, 43°14'N, 77°46'E, S.I. Golovatch leg. (cRyv); 1 ♂, Urjar Distr., Tarbagatay River valley, ca. 1000 m a.s.l., highly disturbed *Populus* forest with *Salix*, *Rosa*, *Lonicera*, *Crataegus*, 47°17'N, 81°34'E, 24–25.VI.2001, S.I. Golovatch leg. (cRyv); 3 ♂, Makanchi Distr., Tarbagatay Mts, 4 km NE Petrovskoe (=Kyzylbulak), Kyzylbulak River valley, 1100–1200 m a.s.l., riverine, *Populus*, *Malus*, *Salix* forest, 22.VI.2001, 47°03'N, 82°18'E, S.I. Golovatch leg. (cRyv).

Comments on taxonomy, distribution and bionomics. The latest summary of diagnostic characters, bionomics and distribution of *Q. limbatus*, a common Western Palearctic species can be found in Assing and Schülke (2012). Based on earlier records (Table 1) and newly examined material in Middle Asia it is known from southern Kazakhstan and Turkmenistan.

Among all Middle Asian species *Q. limbatus* is more similar to *Q. cohaesus* from which it can be easily distinguished by the structure of aedeagus with a sharper apex of the median lobe (in lateral view) and sensory peg setae of the paramere (underside) arranged in short regular rows, slightly diverging from each other basally.

Usually this species occurs in lowlands up to the subalpine zone, but is mostly confined to forests and humid ground-based debris, often near streams (Assing and Schülke 2012). In Middle Asia *Q. limbatus* was collected at elevations up to 1750 m near rivers in forested landscapes.

Quedius (Raphirus) pseudonigriceps Reitter, 1909

Fig. 3F, 11

Quedius kirklarensis Korge, 1971, **syn. n.**

Quedius pseudonigriceps: Herman 2001, 3247 (summary of literature); Assing and Schülke 2012, 473, 474 (diagnosis, distribution and bionomics, aedeagus illustration); Solodovnikov 2004, 223 (characters, synonymy, notes).

Quedius kirklarensis Korge, 1971, 52 (original description); Coiffait 1978, 257 (notes, distribution records).

Material examined. Kazakhstan: 1 ♀, Altai, Bukhtarma River, Uryl-Chingistai, 13.VI.1987, V.A. Kastcheev leg. (ZIN); 3 ♂, 1 ♀, Saur Mt. Ridge, 15 km S Kindirlik, 2000 m a.s.l., 10.VII.1962, L.V. Arnoldi leg. (ZIN); 1 ♂, Almaty Area, Dzhungarskiy Alatau Mts, 7 km E Lepsinsk, Chyornaya River canyon, 1200–1400 m a.s.l., 45°31'N, 80°43'E, *Betula* sp., *Malus*, *Populus* etc. forest, 13–15.VI.2001, S.I. Golovatch leg. (cRyv); 1 ♂, Dzhungarskiy Alatau Mts, upper reaches of Sarydzhaz River, 3500 m a.s.l., 13.VII.1991, V.A. Kastcheev leg. (cRyv); 1 ♂, 1 ♀, W part of Dzhungarskiy Alatau Mts, N slope, upper reaches of Aktau River S of Glinovka, 2500–2800 m, 06.VIII.1991, A.V. Tishechkin leg. (cRyv); 1 ♂, Dzhungarskiy Alatau Mts, E slope of Sandyktas Mt., right side

of Mynteke River, leaf litter, 2100 m a.s.l., 11.VIII.1991, A.V. Tishechkin leg. (cRyv); 2 ♂, Lle-Alatau NP Talgar env., SW slope, leaf litter sifting, 2745 m a.s.l., 43.24846N, 77.40380E, 10–11.V.2014, M. Kocián leg. (cKoc); 1 ♂, Almaty Area, Talgar district, Ak-Bulak, 2700 m a.s.l., 43.1454N, 77.2404E, 24.V.2014, O. Nاكلadal leg. (cKoc); 3 ♂, Zailiyskiy Alatau Mts, 2300 m a.s.l., Levyi Talgar River, 22.VIII.2009, V.A. Kastcheev leg. (cRyv); 2 ♂, Almaty Area, Zailiyskiy Alatau Mts, ca. 20 km Turgen, Turgen River canyon, near Batun, 1750 m a.s.l., 43°14'N, 77°46'E, *Picea*, *Betula*, *Salix*, etc. forest, 25.V.2001, S.I. Golovatch leg. (cRyv); 1 ♂, Almaty Area, Uygurskiy District, Ketmen Mts, 5 km SE Kyrghyzsay (=Podgornoye), 1500–1900 m a.s.l., 43°17'N, 79°31'E, *Picea*, *Betula*, *Populus*, etc. forest, 01–02.VI.2001, S.I. Golovatch leg. (cRyv); 1 ♂, Tastau, 2–3 km up-stream of river mouth, leaf litter, 09.VIII.1991, A.V. Tishechkin leg. (cRyv); 1 ♂, 1 ♀, Ketmen Mts, near Ketmen, 2500 m a.s.l., 28.VII.1991, S.V. Saluk leg. (cRyv); 1 ♂, E Zailiyskiy Alatau Mts., Belshabdar River, 2600 m a.s.l., 26.VI.2002, A.V. Puchkov leg. (cSch); 2 ♂, Zailiyskiy Alatau, Semirechye, Kargalinka valley, 2000–2350 m a.s.l., 01–07.VI.1907, A. [sic!] Jacobson leg.; same locality and collector, but 1 ♀, 1800–2350 m a.s.l., 05.VI.1907 (ZIN); 1 ♂, Kungey-Alatau Mts, Kulbastau canyon, 20–27.VII.1988, V.A. Kastcheev leg. (ZIN); 2 ♂, Kungey-Alatau, Chilik River, Sarybastau, 12–15.VI.1988, V.A. Kastcheev leg. (ZIN); **Kyrgyzstan:** 2 ♂, 2 ♀, Kungey-Alatau Mts, upper reaches of Tschon-Kemin River, 2200–2500 m a.s.l., VII.1999, J. Frisch leg. (cKoc); 1 ♂, Kungey-Alatau, Kurmenti River, 09–11.VII.1987, V.A. Kastcheev leg. (ZIN); 2 ♂, Issyk-Kul' Area, Kungey-Alatau Mts, valley of left confluent of Chon-Uryukty River, leaf litter in slope forest with *Picea schrenkiana*, *Sorbus tianschanica*, etc, 10.IX.1983, A.B. Ryvkin leg. (cRyv); 1 ♂, Issyk-Kul' Area, Terskey-Alatau Mts, Chon-Kyzyl-Suu River valley near Geographical Field Research Station, 2500 m a.s.l., moss in forest with *Picea schrenkiana* (He+Hm+C), 02.IX.1983, A.B. Ryvkin leg.; 1 ♂, Terskey-Alatau Mts, Barskoon Valley, Chuli River, 15.VII.1983, S.K. Alekseev leg. (cRyv); 1 ♂, Terskey Alatau Mts, Kochevnikov field research station, meadow, 19.VI.1984, N. Turtseva leg. (cRyv).

Comments on taxonomy, distribution and bionomics. The latest summary about *Quedius pseudonigriceps* can be found in Solodovnikov (2004) and Assing and Schülke (2012). *Quedius pseudonigriceps* is widespread in Southern Europe and Western Asia. We here record it for the first time from Middle Asia: from southern Kazakhstan and northern Kyrgyzstan. It can be easily distinguished from all similar Middle Asian species by the shortened elytra and absence of fine whitish apical seam of palisade fringe on tergite VII.

In Middle Asia *Q. pseudonigriceps* is brachypterous (Fig. 3F) and characterized by the significant variability in the structure of aedeagus which nevertheless has no geographical pattern and leaves no doubt about species identity (Fig. 11). Solodovnikov (2004) noted that *Que-*



Figure 11. *Quedius pseudonigriceps*, distribution, median lobe of the aedeagus laterally, and variability of the paramere (as examples specimens from various localities numbered respectively on the map). Scale bars: 0.5 mm.

Quedius kirkclarensis from Turkey is almost identical with *Q. pseudonigriceps* from South Europe and Western Asia except for the absence of palisade fringe on abdominal tergite VII in the former. Therefore he suggested that *Q. kirkclarensis* may be a brachypterous form of *Q. pseudonigriceps*. A new synonymy could not be established back then because of the limited material and also due to the similar species *Quedius cohaesus* and *Quedius turkmenicus* from Middle Asia. With more material available here for all relevant taxa we can undoubtedly place *Quedius kirkclarensis* Korge, 1971 in synonymy to *Q. pseudonigriceps* Reitter, 1909. For details on *Quedius cohaesus* and *Quedius turkmenicus*, see below.

In Middle Asia *Q. pseudonigriceps* usually inhabits moist leaf litter in deciduous and mixed forests and wet ground debris near streams in the mountains at the altitudes up to 2800 m.

Quedius (Raphirus) cohaesus Eppelsheim, 1888

Fig. 12

Q. afghanicus Coiffait, 1977, **syn. n.** (Fig. 13)

Q. turkmenicus Coiffait, 1969, **syn. n.**

Quedius cohaesus Eppelsheim, 1888, 60 (original description); Bernhauer and Schubert 1916, 421 (catalog); Gridelli 1925, 26 (characters, distribution records); Coiffait 1963, 393 (characters); Korge 1964, 122 (distribution records); Smetana 1967, 558 (distribution records); Coiffait 1978, 248 (characters, distribution records); Solodovnikov 2004, 227 (= *Q. meurguesae*

Coiff., notes, distribution records); Toleutaev 2014, 44 (distribution records).

Quedius afghanicus Coiffait, 1977, 139 (original description).

Quedius turkmenicus Coiffait, 1969, 49 (original description); Coiffait 1978, 245 (characters, notes).

Type material examined. *Quedius cohaesus*: Lectotype, ♂, “Turcmenia Leder. Reitter [printed]/ c. Eppelsh. Steind. d. [printed]/ ♂ [handwritten]/ *cohaesus* mihi [handwritten]/ Lectotype *Quedius cohaesus* Eppelsheim, 1888 A. Solodovnikov des. 2003 [printed]” (NMW); Paralectotype, ♀, “Turcmenia Leder. Reitter [printed]/ c. Eppelsh. Steind. d. [printed]/ *cohaesus* mihi/ ♀ [handwritten]/ Paralectotypus *Quedius cohaesus* Eppelsheim, 1888 A. Solodovnikov des. 2013 [printed]” (Fig. 12E, F) (NMW).

Quedius afghanicus: Holotype, ♂, “Khat Chaï 2600 m. 22.VIII.74 [handwritten]/ Paktui Afghan. [handwritten]/ G.M.uG.L. [handwritten]/ Type [printed]/ Museum Paris Coll. H. Coiffait [printed]/ *Q. (Sauridus) afghanicus* H. Coiffait 1977 [pre-printed]” (Fig. 13D) (MNHN).

Additional material. Turkmenistan: 1 ♂, Asia. centr., N-Kopet-Dagh, Firjusa-Cleft, near Ashchabad, 07.V.1989, D.W. Wrase leg. (cSch); 1 ♂, Kopetdag Mts, Karakala env., 28.IX.1989, A.V. Puchkov leg. (cSch); **Tajikistan:** 1 ♂, Gazimalyk Mt. Ridge, 15 km NW Ganjin, 2000 m a.s.l, 14.V.1970, G.S. Medvedev leg. (ZIN).

Comments on taxonomy and new synonymy. Coiffait (1969, 1977) described *Q. turkmenicus* and *Q. afghanicus* from Turkmenistan and Afghanistan, respectively.

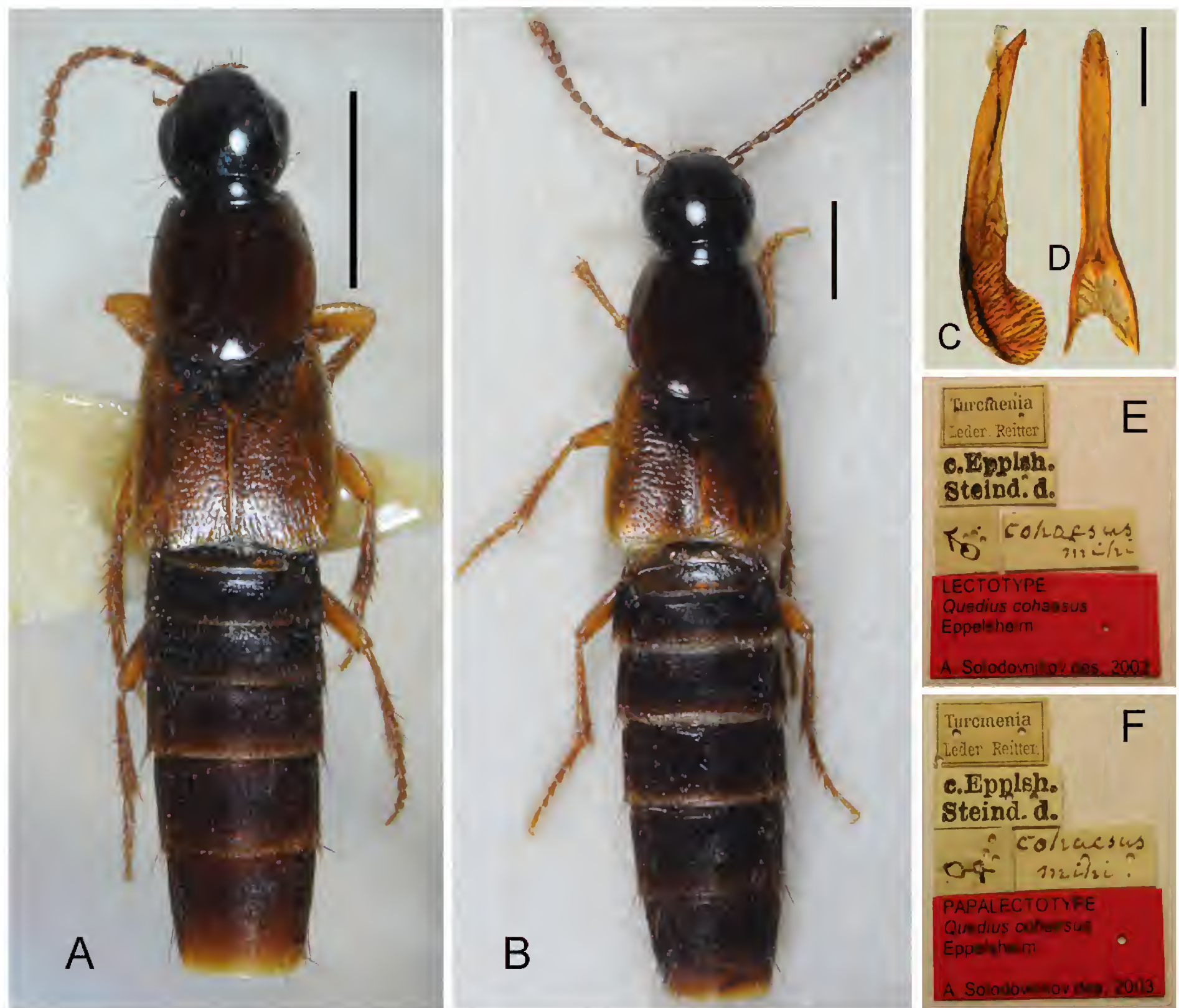


Figure 12. *Quedius cohaesus*, types: **A** (lectotype, male), **B** (paralectotype, female), habitus. **C**, **D**, aedeagus of the lectotype: **C**, median lobe, lateral view; **D**, paramere, underside. **E**, **F**, labels. Scale bars: **A**, **B** = 1 mm; **C**, **D** = 0.3 mm.

We were able to study the type material for *Q. afghanicus* only (Fig. 13), which turns out to be conspecific with *Q. cohaesus* and therefore is placed here into synonymy with the latter. Unfortunately, we were unable to examine the type material of *Q. turkmenicus* which, according to Coiffait (1969) is deposited in the collection of the Paul Sabatier University at Toulouse, France. Nevertheless, because it is obvious from the original descriptions and illustrations that *Q. turkmenicus* is conspecific with *Q. cohaesus*, the former is also placed into synonymy with the latter. These new synonymies are consistent with the earlier revealed synonymy of *Q. cohaesus* with *Q. meurguesae* Coiffait, 1977 from Iran (Solodovnikov 2004). Below we redescribe this insufficiently known widespread species and provide data on its distribution and bionomics.

Redescription. Measurements and ratios (range, arithmetic mean; $n = 3$): HL: 0.7–0.9 (0.8); HW: 0.8–0.9 (0.9); PL: 0.9–1.2 (1.0); PW: 0.9–1.1 (1.0); EL: 1.2–1.5 (1.4); EW: 1.2–1.3 (1.3); FB: 2.9–3.6 (3.2); TL: 5.6–6.7 (6.2); HL/HW: 0.9–1.1 (1.0); PL/PW: 0.9–1.1 (1.0); EL/EW: 1.0–1.2 (1.1).

Body light to dark brownish; head black, pronotum dark brown to brown; elytra brownish with hind angles paler; abdomen dark brown with posterior margins distinctly lighter; hind legs yellowish, antennae, maxillary and labial palps darker, body glossy (Figs 12A; 13A).

Head slightly wider than long HL/HW: 0.9–1.1 (1.0), eyes large and convex; temples distinctly shorter than eyes (ratio 0.2–0.3 (0.3)); with shallow, but dense transverse microsculpture; punctation: one puncture at anterior margin near antennal pit, anterior frontal puncture at posterior margin of antennal pit, posterior frontal and temporal punctures closer to posterior margin of eye than to posterior margin of head; vertical punctures (ca. 1–2) closer to neck than to posterior margin of eye.

Antennae long: antennal segments: 3rd longer than 2nd; 4th–10th distinctly widening towards apex of antennae.

Pronotum slightly wider than long or transverse PL/PW: 0.9–1.1 (1.0), widest at its posterior half, vaguely narrowing anteriad, wider and longer than head; hind angles rounded barely distinct; dorsal rows each with three

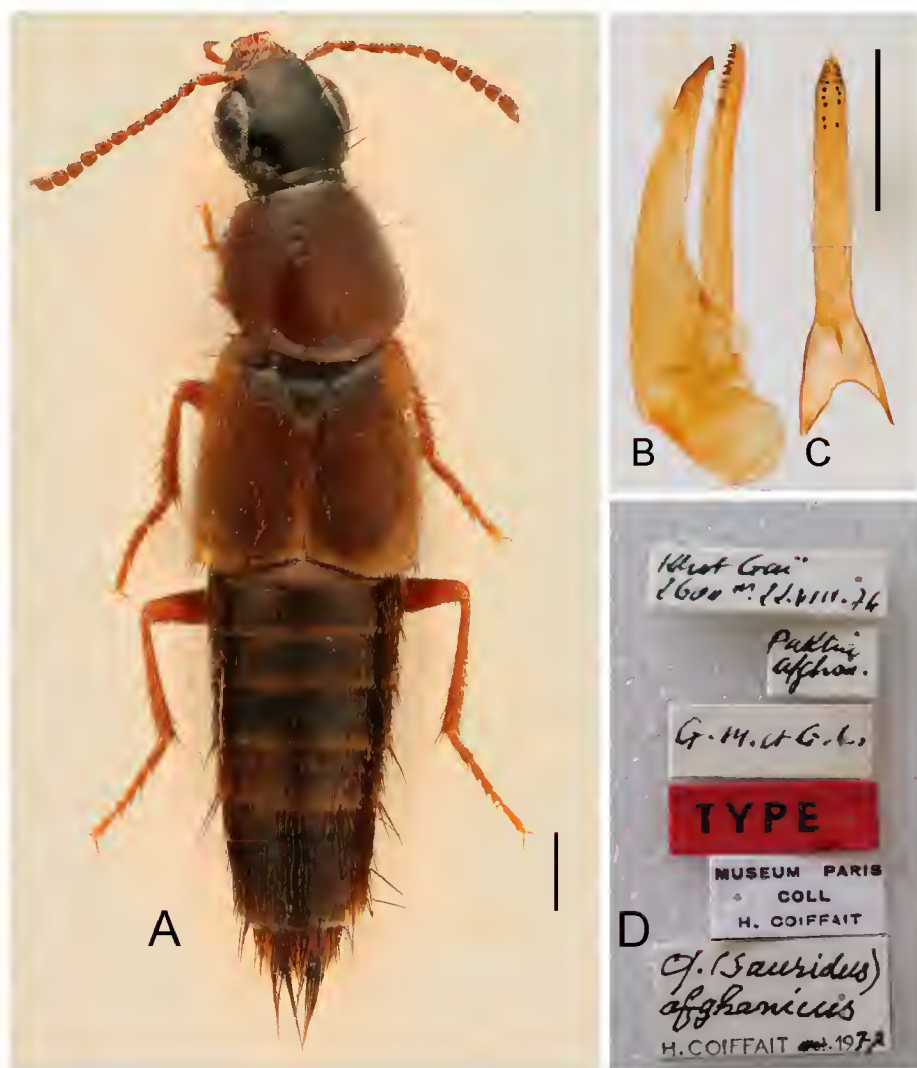


Figure 13. *Quedius afghanicus* (new synonym of *Q. cohaesus*), holotype, male. **A**, habitus. **B**, aedeagus, lateral view; **C**, paramere, underside. **D**, labels. Scale bars: 0.5 mm.

punctures; sublateral rows each with two punctures; microsculpture with shallow hardly visible transverse waves.

Scutellum punctate with microsculpture distinctly denser as on pronotum.

Elytra parallel-sided, hardly narrowing anteriorly, as long as wide or slightly longer than wide EL/EW: 1.0–1.2 (1.1); wider and slightly longer than pronotum; punctation dense with interspaces wider than diameter of punctures, interspaces shiny, with distinct minute irregularities; setation brownish.

Abdomen: punctation fine and dense; interspaces with minute irregularities; posterior margin of tergite VII with palisade fringe.

Male: protarsi with tarsomeres 1–4 dilated stronger than in females. Aedeagus (Figs 12C, D; 13B, C): Median lobe parallel-sided with moderately acute apex, tooth situated close to its apex (Figs 12C, 13B). Paramere parallel-sided, slightly narrowing basally; its apex almost reaching apex of median lobe; sensory peg setae arranged in two irregular and wide longitudinal rows along each lateral margin of apical portion extending over pairs of lateral setae below apex (Figs 12D, 13C).

Comparison. Among other *Raphirus* that occurs in Middle Asia, *Q. cohaesus* is most similar to *Q. pseudonigriceps* from which it can be easily distinguished by the presence of an apical seam of palisade fringe VII and normally developed elytra, as well as by the characters of the aedeagus.

Distribution. *Quedius cohaesus* was described from “Turkmenia” which is not necessarily Turkmenistan in the

modern sense, but certainly some locality in Middle Asia (Eppelsheim, 1888). Based on the literature (Table 1) and material examined here, *Q. cohaesus* is known from Iran (material not recorded here), Turkmenistan, Tajikistan and Afghanistan (most of the material not recorded here).

Bionomics. It is only known that *Q. cohaesus* can be found at rather high elevations, up to 2600 m (Coiffait, 1977).

Quedius (Raphirus) imitator Luze, 1904

Figs 3C, 15

Quedius tschinganensis Coiffait, 1969, **syn. n.** (Fig. 14)

Quedius imitator Luze, 1904, 102 (original description); Bernhauer 1905, 596 (notes); Bernhauer and Schubert 1916, 429 (list with synonyms); Gridelli 1924, 135 (characters, notes); Coiffait 1967, 406 (characters); Coiffait 1978, 237 (characters, distribution records); Boháč 1988, 556 (distribution records); Klimenko 1996, 121;

Quedius tschinganensis Coiffait, 1969, 50 (original description); Coiffait 1970, 143 (list); Coiffait 1978, 237 (characters); Kascheev 2001, 102 (distribution records); *Quedius tschinganensis* var. *gracilicornis* Coiffait, 1977, 139 (original description);

Quedius tschinganensis var. *debilicornis* Coiffait, 1978, 237 (replacement name for *gracilicornis*).

Type material examined. *Quedius imitator*: Tajikistan or Uzbekistan:

Lectotype (here designated): 1 ♂, “Seravschan Darch Glasunov 1892 [printed]/ *Q. imitator* Luze J. Boháč det. 1983 [pre-printed]”; paralectotypes: 1 ♂, “[square orange piece of paper]/ Seravschan Putschin Pass. Glasunov, 1892 [printed]/ *Quedius imitator* Luze [handwritten]/ *Q. imitator* Luze J. Boháč det. 1983 [pre-printed]”; paralectotypes: 1 ♂, “Seravschan Putschin Pass. Glasunov, 1892 [printed]/ *Quedius imitator* Luze [handwritten]/ *Q. imitator* Luze J. Boháč det. 1983 [pre-printed]/ *Quedius* sp.1. cf. *suturalis* Ksw. A. Solodovnikov 1997 [handwritten]”; 3 ♂, “Seravschan Putschin Pass. Glasunov 1892 [printed]/ *Q. imitator* Luze J. Boháč det. 1983 [pre-printed]/ *Quedius* sp.1. cf. *suturalis* Ksw. A. Solodovnikov 1997 [handwritten]”; 2 ♀, “Seravschan Putschin Pass. Glasunov 1892 [printed]”; 2 ♂, “Seravschan Obburden Glasunov, 1892 [printed]/ *Q. imitator* Luze J. Boháč det. 1983 [pre-printed]/ *Quedius* sp.1. cf. *suturalis* Ksw. A. Solodovnikov 1997 [handwritten]”; 1 ♀, “Iskander-Kul Iskander-Darja Glasunov 1892 [printed]/ *Q. imitator* Luze J. Boháč det. 1983 [pre-printed]” (ZIN).

***Quedius tschinganensis*: Uzbekistan:** Holotype: ♂, “Ouzbekistan 8-68 Mts Tschingan 1500 m. H.C. [printed]/ *Q. (Sauridus) tschinganus* [sic!] Coiff. H. Coiffait det. 1968 [pre-printed]/ Holotype [printed]”; 5 ♂, 1 ♀, “Ouzbekistan 8-68 Mts Tschingan 1500 m. H.C. [printed]/ Paralectotype [printed]” (Fig. 14D, H) (MNHN).

***Quedius tschinganensis gracilicornis*: Tajikistan:** ♂, “Karatak Buchara [printed]/ Type [printed]/ *Q. (Sau-*

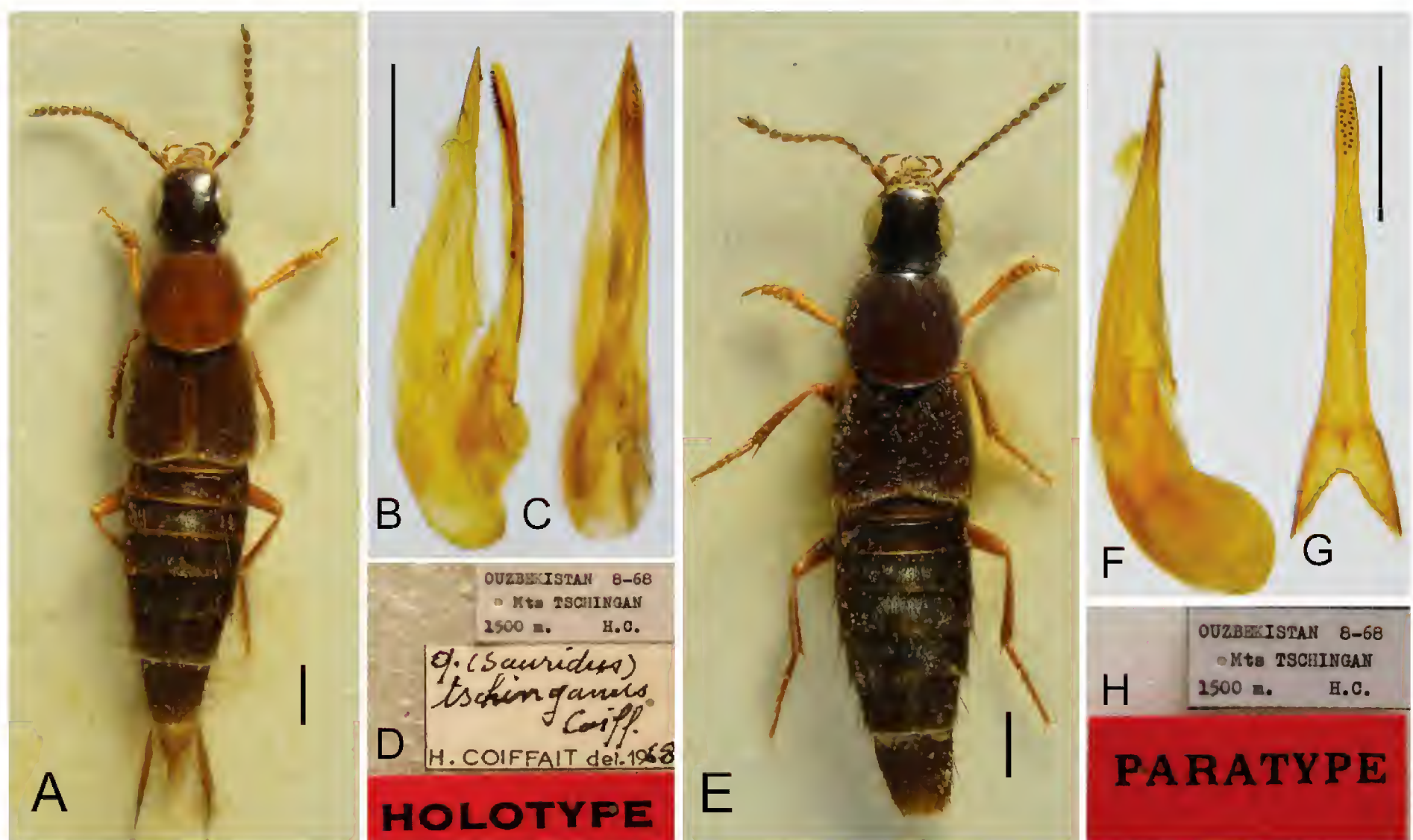


Figure 14. *Quedius tschinganensis* (new synonym of *Q. imitator*), types. A–D, holotype; E–H, paratype. A, E, habitus. B, C, F, G, aedeagus: B, lateral view; C, dorsal view; F, median lobe, lateral view; G, paramare, underside. D, H, labels. Scale bars: A, E = 1 mm; B, C, F, G = 0.5 mm.

ridus) *tschinganensis* v. *gracilicornis* H. Coiffait det. [sic!] 1977 [pre-printed]" (MNHN).

Additional material. Tajikistan: 3 ♂, Zeravshan Mt. Ridge, Chap-Dara River valley, 2500 m a.s.l., 26.VI.1983, S.K. Alekseev leg. (cRyv); 1 ♂, Pamir-Alai, Zeravshan Mt Ridge, Zavron valley, 2100–3000 m a.s.l., 12–13.VII.1990, M. Schülke & D.W. Wrase leg (cSch); 1 ♂, Zeravshan Mt. Ridge, near Mazor, 14.VIII.1989, K.G. Michailov leg. (NHMD); **Kazakhstan:** 1 ♂, Makanchi District, Tarbagatay Mts, 6 km NE Kirovka (=Karatum), Sholakterek River valley, ca. 1200 m a.s.l., 47°10'N, 82°06'E, highly disturbed *Populus* forest with *Salix*, *Rosa*, *Lonicera*, *Crataegus*, etc., 23–24.VI.2001, S.I. Golovatch leg. (cRyv); 1 ♂, Dzhungarskiy Alatau, S Koktuma, Alakol Lake, 05.VI.1962, L.V. Arnoldi leg. (ZIN); 2 ♂, Almaty Area, Dzhungarskiy Alatau Mts, 6 km NE Rudnichnyi, Koksus River canyon, 1300–1400 m a.s.l., 44°41'N, 78°58'E, *Betula* sp., *Populus*, *Picea* etc. forest, 09–10.VI.2001, S.I. Golovatch leg. (cRyv); 2 ♂, Zalataysky Alatau, Krasnogorka [Sulutor], stream beach under tree, 75.13504E, 43.23457N, 28.VII.2010, V.A. Kastcheev leg. (ZIN); 2 ♂, 1 ♀, Lle-Alatau NP Talgar env., Ak-Bulak Resort horse and cow dung, 1750 m a.s.l., 43.26897N, 77.37145E, 08.V.2014, M. Kocián leg. (cKoc); 2 ♀, Lle-Alatau NP Talgar env., Ak-Bulak Resort, horse and cow dung, 1690 m a.s.l., 43.27039N, 77.37137E, 12–15.V.2014, M. Kocián leg. (cKoc); 1 ♂, Almaty Area, Zailiyskiy Alatau Mts, Medeo near Almaty, 1500–1600 m a.s.l., 43°10'N, 77°04'E, *Picea*, *Betula*, etc. forest, 27.V.2001, S.I. Golovatch leg. (cRyv); 3 ♂, Almaty Area, Zailiyskiy Alatau Mts, ca. 20 km SE Turgen, Turgen

River canyon, near Batun, 1750 m a.s.l., 43°14'N, 77°46'E, *Picea*, *Betula* sp., *Salix*, etc. forest, 25.V.2001, S.I. Golovatch leg. (cRyv); 1 ♂, Zailiyskiy Alatau, Chilik River, Sarybastau, 15.VI.1988, V.A. Kastcheev leg. (ZIN); 4 ♂, 1 ♀, Almaty Area, Uygurskiy Distr., Ketmen Mts, 5 km SE Kyrghyzsay (=Podgornoye), 1500–1900 m a.s.l., 43°17'N, 79°31'E, *Picea*, *Betula* sp., *Populus*, etc. forest, 01–02.VI.2001, S.I. Golovatch leg. (cRyv); 1 ♂, Ketmen Mts, Malyy Kyrgisai, 28.VII.1987, V.A. Kastcheev leg., (ZIN); 3 ♂, Karatau Mts, 660 m a.s.l., 42°53'41.42N, 70°42'56.6E, leaf litter along stream, 11.VII.2010, V.A. Kastcheev leg. (ZIN); 8 ♂, 1 ♀, Karatau Mts, Byzhi River, Rynagus stream, 757 m a.s.l., 43°57'08.7N, 68°12'04.2E, 24–25.VII.2010, V.A. Kastcheev leg. (ZIN); 2 ♂, 1, Karatau Mts, Aktobe River, grove, 25.VII.2010, V.A. Kastcheev leg. (ZIN); 6 ♂, 1 ♀, Karatau Mts, Khantagi River, 570 m a.s.l., 43°33'32.4N, 68°40'52.7E, 25.VI.2011, V.A. Kastcheev leg. (ZIN); same locality and collector, but 1 ♂, leaf litter under *Salix* sp., 536 m a.s.l., 43°32'46.5N, 68°39'50.6E, 21.VII.2010 (ZIN); ♂, 1 ♀, 27 km S Chulak-Kurgan, 04.VI.1983, B.V. Isakov leg. (ZIN); 1 ♂, 1, Chimkent, Aksukent, Aksu River, 29.VI.1983, V.A. Kastcheev leg. (ZIN); 2 ♂, Aksu-Zhabagly Nature Reserve, Tokmak River, near border, under stones, 1600 m a.s.l., 30.V.1974, E.V. Ishkov leg. (ZIN); 1 ♂, 2 ♀, Aksu-Dzhabagly, Taldy-Bulak River, 15–25.VI.1983, B.V. Isakov leg. (ZIN); 1 ♂, Aksu-Dzhabagly, Isbala River, 18.VII.1986, (ZIN); 1 ♂, Aksu-Dzhabagly, Djabagly River, tract Ulken-Kaindy, IV.1986, B.V. Isakov leg. (ZIN); same locality and collector, but 1 ♂, Kshi-Kaindy River, 01.V.1986 (ZIN); **Uzbekistan:** 1 ♂, Kitab, 30.VII.1933, V.V.



Figure 15. *Quedius imitator*, distribution, median lobe of the aedeagus laterally, and variability of the paramere (as an example specimens from one locality, indicated by black dot). Scale bars: 1 mm.

Gussakovskiy leg. (ZIN); **Kyrgyzstan:** 1 ♂, Terskey Ala-too Mts, Barskoon Valley, Chuli River, 15.VII.1983, S.K. Alekseev leg. (cRyv); 1 ♂, 1 ♀, Osh Area, Sary-Chelek Biosphere Reserve, near Arkit, Bakay-say Tract, 14.VII.1983, K.G. Mikhailov leg. (cRyv); 1 ♂, Chatkal Mt. Ridge, near Arkit, nut-fruit forest, 16.V.1961, V.A. Zaslavsky leg. (ZIN); 2 ♂, Tien Shan, Kichik-Alai Mt. Ridge, upper reaches of Kyrghyz-Ata River, Kara-Goy, 2400–2850 m a.s.l., *Juniperus* stand, 21–23.V.1993, S.I. Golovatch leg. (cRyv); 1 ♂, Osh Area, environs of Sary-Chelek Biosphere Reserve, confluent of Aflatun River, Batrakhon (=Baltyrkan) Tract, moss and leaf litter in birch forest & under *Picea schrenki-*

ana at stream bank, 31.VII.1983, A.B. Ryvkin leg. (cRyv); 3 ♂, Tien Shan, Chatkal Mt. Ridge, Sary-Chelek Biosphere Reserve, 1550–2200 m a.s.l., forests, 29–31.V.1993, S.I. Golovatch leg. (cRyv); 2 ♂, 1 ♀, Osh Area, W Tien Shan, Ferganskiy Mt. Ridge, near Yarodar, 1100–1200 m a.s.l., *Juglans* forest, in leaf litter, 27–28.IX.1983, K. Yu. Eskov leg. (cRyv); 1 ♂, Osh Area, W Tien Shan, Ferganskiy Mt. Ridge, Yarodar, 1300 m a.s.l., rill bank, in leaf litter and under stones, 24–25.IX.1983, K. Yu. Eskov leg. (cRyv); 3 ♂, Tien Shan, Baubash-Ata Mt. Ridge, near Arslanbob, 1800–1900 m a.s.l., scrub, litter & under stones. 19.V.1993. S.I. Golovatch leg. (cRyv); 10 ♂, 1 ♀, Tien Shan, Baubash-Ata

Mt. Ridge, near Yarodar, 1400–1700 m a.s.l., *Juglans* forest, litter & under bark. 16–17.V.1993. S.I. Golovatch leg. (cRyv); 4 ♂, 1 ♀, Ferganskiy Mt. Ridge, Kara-Alma, 1800 m a.s.l., 22–24.VI.1945, K.V. Arnoldi leg. (ZMMU); ♂ 1 ♂, 3 ♀, Gava, Fergana Valley, Jalal-Abad Region, near station of Forest Institute of Russian Academy of Sciences, 04.IX.1950, L.V. Arnoldi leg. (ZIN); 1 ♂, Fergana Valley, Kulun Lake, 3000 m a.s.l., 07.V.1993, I.I. Kabak leg. (ZIN); 2 ♂, 1 ♀, S Fergana Valley, Ak-Terek, 25.IX.1937, A.N. Kirichenko leg. (ZIN).

Comments on the lectotype designation. In the original description of *Q. imitator*, Luze (1904) did not specify the number of syntypes but provided geographical data that indicated multiple syntypes collected in the localities “Seravschan, Putchin-Pass, Darch, Obburden, Urmitan, Kumar; Jagnob, Varsaut; Iskander-Kul, Iskander-Darja” (approximate coordinates as we interpret these localities are given in the Table. 2). Also, the syntype series must have included both sexes because male characters were specified separately in the description. In the ZIN collection we found 11 specimens from several localities along Zeravchan and Iskander Darya Rivers matching those in the original description (for details see ‘Material examined’ above). Based on that and additional information from the specimen labels, there is no doubt that they are syntypes. Earlier they were identified by Boháč (1988) as *Q. imitator* without recognizing them as syntypes. In order to fix the identity of the species, we designate here one male syntype with more precise locality “Seravschan Darch Glasunov 1892” (Darg, Sughd Distr.) as the lectotype. Bernhauer (1905) considered *Q. imitator* as a “rough form” of *Q. oblitteratus* (now synonym of *Q. humeralis* Stephens, 1832). Gridelli (1924) not seeing types or any other material of *Q. imitator* was not sure about the status of this species. Based on the non-type material, Coiffait (1967, 1978) illustrated its aedeagus for the first time that here is shown to be the correct species interpretation. Boháč (1988) provided new records for the species from Uzbekistan and Turkmenistan that are reliable because he examined syntypes.

Comments on the new synonym. Coiffait (1969) described *Quedius tschinganensis* (Fig. 14) from Uzbekistan and separated it from *Q. imitator* by darker body coloration, antennal segment 3 longer than 2, presence of ‘lateral’ puncture on pronotum, denser punctation of the elytra and more elongated median lobe. Additionally Coiffait (1977) described *Q. tschinganensis gracilicornis*, a variety of *Q. tschinganensis* from Tajikistan based on some differences in coloration of the body and the proportions of antennae. Later (1977), he replaced the preoccupied name *gracilicornis* by the new name *debilicornis*. Both are unavailable names due to ICZN Article 15.2 as already noted in Herman (2001).

Our examination of the material from Middle Asia, including types, showed continuous variability in the external morphology and aedeagus that connects the states of *Q. imitator* and *Q. tschinganensis*. The shape of the paramere varies from the state with narrow and sharp apex with lesser number of sensory peg setae arranged in regular rows away

from the apex, to the state with obtuse apex and with more sensory peg setae arranged denser and closer to the apex (Figs 14C, G; 15). Shape of the median lobe is more stable and varies only slightly in length and degree of sharpness of its apex (Figs 14B, F; 15). Mapping of this variability across the species distribution does not show any geographical patterns. Externally all specimens including females, also show no traits that would correspond to variants different in the shape of the paramere. Thus we place *Q. tschinganensis* Coiffait, 1969 in synonymy with *Q. imitator* Luze, 1904. Our study of the type specimen of *Q. tschinganensis debilicornis* also shows it to be conspecific with *Q. imitator*.

Comments on taxonomy, distribution and bionomics. *Quedius imitator* can be diagnosed by the following character combination: body dark brown with darker head and abdomen; elytra with slightly yellowish anterior angles; antennae usually pale; scutellum without setiferous punctation; aedeagus with ventral tooth of median lobe located remotely from its apex, with median lobe and paramere very narrow, apex of paramere obtusely sharpened and sensory peg setae arranged in two regular rows convergent to each other. Among other *Raphirus* that occur in Middle Asia, *Q. imitator* is most similar to *Q. cohaesus* from which it can be easily distinguished by the mentioned diagnostic characters of the aedeagus.

Based on the examined material and literature (Table 1), *Q. imitator* is widely distributed in all countries of Middle Asia (Fig. 15). According to the label data of the examined material, *Q. imitator* inhabits ground based debris and leaf litter of mainly deciduous forests along rivers and streams at various elevations, up to 3000 m. Also it can be found in dung or under stones.

Quedius (Raphirus) novus Eppelsheim, 1892

Figs 3E, 17

Quedius dzambulensis Coiffait, 1967, **syn. n.** (Fig. 16)

Quedius novus Eppelsheim, 1892, 331 (original description); Gridelli 1925, 125; Wüsthoff 1938 (illustration of aedeagus); Coiffait 1963, 389 (characters); Coiffait 1970, 143 (distribution records); Coiffait 1978, 228 (notes); Boháč 1988, 556 (distribution records; notes); Smetana 1995a, 84 (distribution records); Klimenko 1996, 121 (distribution records); Kadyrov et al. 2014a, 31; 2014b, 49 (distribution records).

Quedius dzambulensis Coiffait, 1967, 403 (original description); Coiffait 1978, 229 (characters, distribution records); Boháč 1988, 556 (notes); Kascheev 2001, 102 (distribution records).

Material examined.

Type material examined. *Quedius novus*: **Uzbekistan:** Lectotype (here designated), ♂, “novus Epp. Taschkent Leder. [handwritten]/ c. Eppsh. Steind. d. [printed]/ Typus [printed]” (NMW); Paralectotypes, 2 ♀, same data as in lectotype; 2 ♂, 2 ♀, same data as in lectotype, but without “novus Epp. Taschkent Leder.”; 1 ♂, same data as in lectotype,

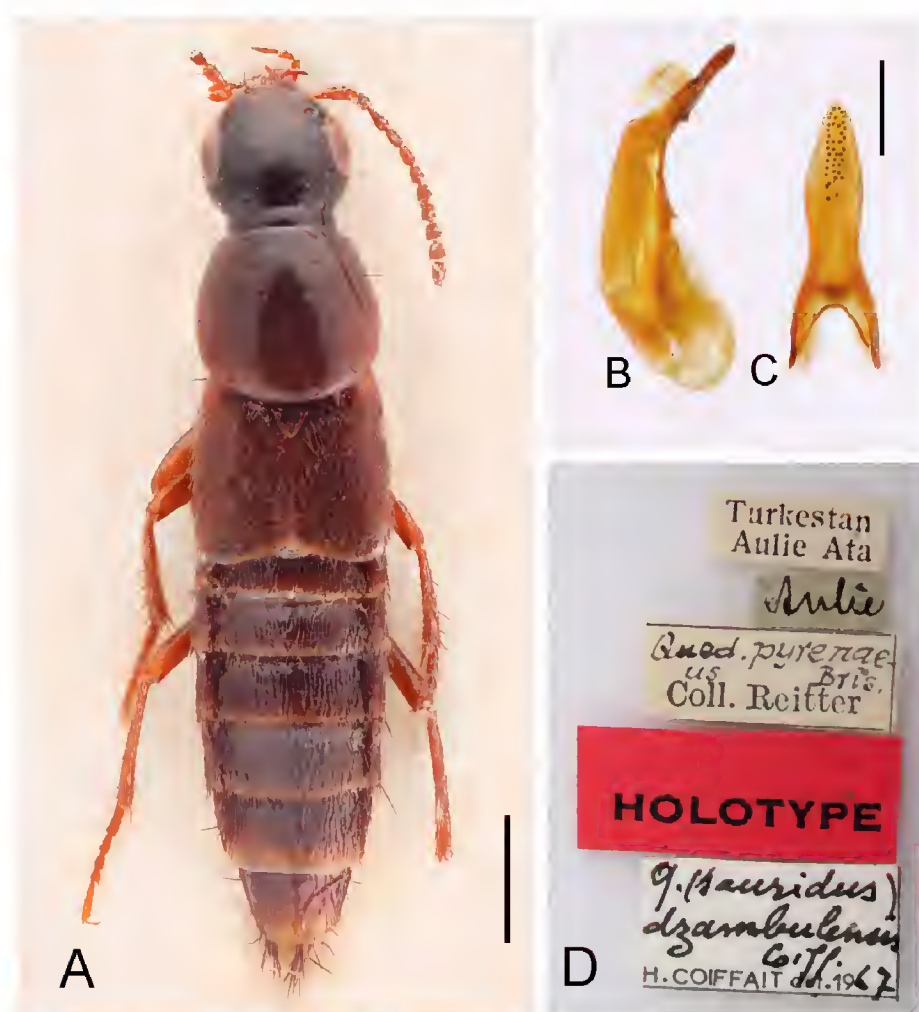


Figure 16. *Quedius dzambulensis* (new synonym of *Q. novus*), holotype, male. **A**, habitus. **B**, median lobe, lateral view; **C**, paramere, underside. **D**, labels. Scale bars: 1 mm.

but “♂/ novus Epp. Deutsch. ent. Zeit. 1892. P. 331 [handwritten]”; 1 ♀, “Taschkent Leder.Reitter. [printed]/ *Quedius novus* Epph. n.sp. [handwritten]/ 95”; 1 ♀, “Taschkend [sic!] Reitter. [printed]/ Collect. Hauser [printed]”; 1 ♀, “Taschkend Leder. Reitter. [printed]” (NMW); 1 ♂, “Tashkent, Leder, Reitter [printed]/ *Q. novus* Epp. J. Boháč det. 1983 [handwritten]” (ZIN); 1 ♀, “Tashkent, Leder, Reitter [printed]/ *Q. novus* Epp. [handwritten]/ *Q. novus* Epp. J. Boháč det. 1983 [handwritten]/ *Quedius dzambulensis* Coiff. A. Solodovnikov det. 1997 [handwritten]” (ZIN)

Quedius dzambulensis: Holotype, “Turkestan Aulie Ata [printed]/ Aulie [handwritten]/ *Quedius pyrenaeus* Coll. Reitter [pre-printed]/ Holotype [printed]/ *Q. (Sauridus) dzambulensis* Coiff. H. Coiffait det. 1967” (Fig. 16D) (HNHM).

Additional material examined. Uzbekistan: 2 ♂, 1 ♀, Chatkal Mt. Ridge, Ters River bank up-stream of Yangibazar, 27.IV.1986, I.A. Belousov leg. (cRyv); 1 ♂, Chatkal Nature Reserve, bank of small rill, wet ground, *Poaceae* gen. sp., *Equisetum* sp., moss, 19.IX.1983, K.Yu. Eskov leg. (cRyv); 1 ♂, 60 km W Jizzakh, near Asmansay, by the stream, 15.V.1986, B.V. Iskakov leg. (ZIN); 1 ♂, 2 ♀, 60 km W Jizzakh, by the stream, Nuratau Mt., 14.V.1986, B.V. Iskakov leg. (ZIN); 1 ♂, “Trkst., Mnt. Nurata, UCHUN Glasunov 1892” [Nurata Distr., Nurata] (ZIN); 3 ♂, 1 ♀, Aman Kutan River 12.VI.1932, V.V. Gussakovsky leg. (ZIN); same locality and collector, but 1 ♀, 05.VII.1932 (ZIN); 4 ♂, 3 ♀, Agalyk, Samarkand, 22–23.X.1935, Y.D. Kirschenblat leg. (ZIN); 4 ♂, 2 ♂, Kugitangtau Mts, near Kampyrtepa, Kampyrtepa say, under stones near stream, 1400 m a.s.l., 10.V.1984, A.V. Tanasevitch leg. (cRyv);

same locality and collector, leaf litter near stream, 1600–1700 m a.s.l., 17–19.V.1984 (cRyv); **Kazakhstan:** 1 ♂, Almaty Area, Dzhungarskiy Alatau Mts, 6 km NE Rudnichnyi, Koxsu River canyon, 1300–1400 m a.s.l., 44°41’N, 78°58’E, *Betula* sp., *Populus*, *Picea* etc. forest, 09–10.VI.2001, S.I. Golovatch leg. (cRyv); 1 ♂, Dzhungarskiy Alatau Mts, S slope, E ridge, middle reaches of Ispul River, 1900 m a.s.l., litter in *Abies* forest, 14.VIII.1991, A.V. Tishechkin leg. (cRyv); 1 ♂, Almaty Area, Talgar District, Ak-Bulak, 2700 m a.s.l., 43.1613N, 77.2404E, 24.V.2014, O. Nakladal leg. (cKoc); 3 ♂, 1 ♀, Aksu-Dzhabagly, Isbala River, 15–25.VI.1983, B.V. Iskakov leg. (ZIN); 2 ♂, 1 ♀, Aksu-Dzhabagly, Taldy-Bulak River, 10–20.IV.1979, B.V. Iskakov leg. (ZIN); 1 ♂, Aksu-Dzhabagly, Ulken-Kaindy River, 15.VI.1991, V.A. Kastcheev leg. (ZIN); 1 ♂, SW slopes of Ugamskiy Range, Silbili River, 18.VI.2004, A.V. Matalin leg. (cSch); 2 ♂, 1 ♀, Karzhantau, Kaskasu River, 10–12.VII.1983, B.V. Iskakov leg. (ZIN); 2 ♂, 2 ♀, Karzhantau, 30 km E Leninskoe, Karabau River valley, 01–05.VII.1983, B.V. Iskakov leg. (ZIN); 1 ♂, Urochishe Shilikti, 05.VI.2010, K.V. Makarov, A.V. Matalin leg. (cSch); **Kyrgyzstan:** 1 ♂, Kyrgyz Alatau, under *Salix* sp., 09.VII.2010, 72°28’38.6N, 42°48’49.2E, V.A. Kastcheev leg. (ZIN); 3 ♂, Osh Area, Sary-Chelek Biosphere Reserve, “head” of Sary-Chelek Lake, 1940–1945 m a.s.l., lake shore and bottom of partly dried rill with *Carex* spp., *Equisetum* sp., *Juncus* sp., *Phragmites australis*, etc., 12.VIII.1983, A.B. Ryvkin leg. (cRyv); 1 ♂, Tien Shan, Baubash-Ata Mt. Ridge, near Arslanbob, 1800–1900 m a.s.l., scrub, litter & under stones, 19.V.1993, S.I. Golovatch leg. (cRyv); 1 ♂, Aruktau 25 km Kyzyl-Kiya, IV.1966, O.L. Kryzhanovsky leg. (ZIN); **Tajikistan:** 1 ♀, “Seravshan Kumar Glasunov 1892/ *Q. dzambulensis* J.Boháč det. 1983” (ZIN); 1 ♂, “Seravshan Kshtut. Artutsch. Glasunov 1892/ *Q. dzambulensis* J.Boháč det. 1983/ *Quedius dzambulensis* Coiff. A. Solodovnikov det. 1997” (ZIN); 1 ♀, “Seravshan Fl. Magian Glasunov 1892/ *Q. dzambulen sis* J. Boháč det. 1983/ *Quedius dzambulensis* Coiff. A. Solodovnikov det. 1997” (ZIN); 1 ♂, “Trkst. Jagnob Kol Glasunov 1892/ *Q. dzambulensis* Epp. J. Boháč det. 1983” (ZIN); 3 ♂, Zeravshan Mt. Ridge, Chap-Dara River valley, 2500 m a.s.l., 26.VI.1983, S.K. Alekseev leg. (cRyv); 1 ♂, Kondarra, under stones near aryk, 03.VI.1973, V.V. Yanushev leg. (cRyv); 1 ♂, Warsob, 03.V.1988, S.V. Saluk leg. (cRyv); 1 ♂, Pamir-Alai, Hisaar Mts, Adshuk-Cleft near Warsob, 1200 m a.s.l., 01–03.VII.1990, M. Schülke & D.W. Wrase leg. (CSch); 1 ♂, 2 ♀, “♀ or ♂/ Mts Karateghin Baldschuan 924 m. F. Hauser 1898/ novus/ ex. coll. Scheerpleltz” (NMW); 2 ♂, 1 ♀, “♀ or ♂/ Mts. Karateghin Baldschuan 924 m. F. Hauser 1898/ novus Epp./ ex. coll. Breit/ ex. coll. Scheerpleltz” (NMW); 1 ♂, “♀/ Mts. Karateghin Baldschuan 924 m. F. Hauser 1898/ *Quedius novus* Epp. det. Bernhauer/ ex. coll. Scheerpleltz” (NMW); 2 ♂, 1 ♀, “♀/ Mts. Karateghin Baldschuan 924 m. F. Hauser 1898/ Collect. Hauser /*Q. novus* Epp. Bernh.d.” (NMW); 3 ♀, “♀/ Mts. Karateghin Baldschuan 924 m. F. Hauser 1898/ Collect. Hauser” (NMW); 3 ♀, “♀/ Mt. Karateghin Sary-pul 1482 m. F. Hauser 1898/ Collect. Hauser” (NMW); 1 ♂,



Figure 17. *Quedius novus*, distribution, median lobe of the aedeagus laterally, and variability of the paramere (as examples specimens from various localities numbered respectively on the map). Scale bars: 0.5 mm.

2 ♀, “Collect. Hauser” (NMW); 1 ♀, near Muminobod, 1300 m a.s.l., 15.V.1962, O.L. Kryzhanovsky leg. (ZIN); **Tajikistan or Uzbekistan:** 1 ♂, “Seravshan Boschara Glasunov 1892/ *Q. dzambulensis* J. Boháč det. 1983” (ZIN); 4 ♂, 2 ♀, “Seravshan Putschin pass. Glasunov 1892/ *Q. dzambulensis* J. Boháč det. 1983” (ZIN).

Comments on taxonomy and lectotype designation. In the original description of *Q. novus*, Eppelsheim (1892) stated that he had examined numerous specimens from Tashkent and one from Margelan [Margilan in Uzbekistan]. He also stated in the introduction of that study that he received material from ‘Turkestan’ from multiple collections of Hauser, Staudinger and Reitter. In particular, he mentioned that the material from Tashkent from Reitter’s collection was collected by Leder. In NMW altogether we found 11 conspecific specimens, all originally from Eppelsheim’s collection (with printed label “c.Epplsh. Steind.”), whose morphology and label data match with the original description. We consider all of them to be syntypes. Of them, 8 specimens (on 5 pins) were earlier supplied with the curatorial printed red labels “types”; only two specimens have what we consider Eppelsheim’s hand written labels “novus Epp. Taschkent Leder.” and one specimen having “novus Epp. Deutsch. ent. Zeit. 1892. P. 331” label in a different handwriting probably attached by somebody later, after the species description was published. Also in the ZIN collection we found two more specimens conspecific with the syntypes at NMW and with the label

“Taschkent Leder. Reitter” indicating that they are likely to be syntypes as well. Examination of all syntypes confirms that previous authors correctly interpreted this species. In order to fix its identity, here we designate one male syntype from NMW as the lectotype. Due to the intraspecific variability (Figs 16, 17) and resulting new synonymy *Q. novus* = *Q. dzambulensis* (see below), we chose a syntype for lectotypification which has a more narrow longitudinal row of sensory peg setae on the paramere, best matching Coiffait’s (1967) illustration for *Q. novus*.

Comments on the new synonym. The aedeagus of *Q. novus* was first illustrated by Wüsthoff (1938) based on non-type material. Coiffait (1963, 1970, 1978) redescribed the species, also illustrated the aedeagus and provided more records for *Q. novus* from Uzbekistan. Our examination of syntypes proved both Wüsthoff’s and Coiffait’s interpretation of this species was correct. Also Coiffait (1967) described *Q. dzambulensis* from Dzambul (Kazakhstan) (Fig. 16), a species which seemed to be very similar to *Q. novus* even from the illustrations of the aedeagi for both species.

Later, Boháč (1988) examined material from the ZIN collection and provided new records from Uzbekistan, Tajikistan, Kyrgyzstan of *Q. dzambulensis* and only one record from Uzbekistan for *Q. novus*. He also stated that *Q. novus* is very closely related to *Q. dzambulensis* with which it can be easily confused. We checked all material from ZIN studied by Boháč (1988) and found that, without knowing it, the only specimens he identified as *Q. no-*

novus were the syntypes of that species. All other specimens he identified as *Q. dzambulensis*.

Our examination of a broader sample from Middle Asia, including types of both species, showed continuous variability in the structure of the aedeagus connecting the state of *Q. novus* with the state of *Q. dzambulensis*. Sensory peg setae on the paramere vary in arrangement, from denser (as in Coiffait's illustration for *Q. novus*) to sparser (as in Coiffait's illustration for *Q. dzambulensis*) within a longitudinal group (Fig. 17). The mentioned variability has no geographic pattern. Therefore, we consider *Q. dzambulensis* Coiffait, 1967 to be a junior synonym of *Q. novus* Epp.

Diagnosis. Body dark brown; elytra with lighter colored humeri and shallow micropunctuation between punctures; antennae slightly paler; scutellum without setiferous punctation. (Figs 3E, 16A) Aedeagus (Figs 16B, C, 17): ventral tooth of median lobe located remotely from its apex; median lobe and paramere very broad (Figs 16B, 17); apex of paramere obtusely pointed and sensory peg setae arranged in long wide band in the middle of paramere (Figs 16C, 17). *Quedius novus* can be easily distinguished from the similar Middle Asian species *Quedius umbrinus* by the coloration and micropunctuation of elytra and also by the mentioned above aedeagal characters.

Distribution. Based on the literature data (Table 1) that proved to be reliable for this species and the material examined here, *Q. novus* is widely distributed in Middle Asia and appears the most common in southern Kazakhstan, eastern Uzbekistan, western Kyrgyzstan and north-eastern Tajikistan (Fig. 17).

Bionomics. *Quedius novus* prefers various wet ground based plant debris or moss usually near water bodies. It seems to occur both in forested and open habitats, up to 2700 m. Occasionally it was also found under stones and in dung.

Quedius (Raphirus) umbrinus Erichson, 1839

Fig. 4B

Quedius umbrinus: Herman 2001, 3287 (summary of literature); Kascheev 1989, 36 (records); Assing and Schülke 2012, 475, 477 (diagnosis, distribution and bionomics, aedeagus illustration).

Material examined. Kazakhstan: 1 ♂, Almaty Area, Dzhungarskiy Alatau Mts, 3 km SSE Lepsinsk, Bulinka River canyon, 1100–1800 m a.s.l., 45°30'N, 80°38'E, *Betula* sp., *Malus*, *Populus* etc. forest, 16–17.VI.2001, S.I. Golovatch leg. (cRyv); 1 ♂, Almaty Area, Talgar District., Ak-Bulak, 43.1613N, 77.2214E, 10–15.V.2014, O. Nakladal leg. (cKoc); 1 ♂, Lle-Alatau NP Talgar env., Ak-Bulak Resort, horse and cow dung, 1690 m a.s.l., 43.27039N, 77.37137E, 12–15.V.2014, M. Kocián leg. (cKoc); 1 ♂, 1 ♀, Lle-Alatau NP Talgar env., SW slope, leaf litter sifting, 1845 m a.s.l., 43.25851N, 77.38501E, 09.V.2014, M. Kocián leg. (cKoc).

Comments on taxonomy, distribution and bionomics. Among all Middle Asian *Raphirus*, *Q. umbrinus*

is most similar to *Q. novus* from which it can be distinguished by the structure of aedeagus: median lobe with distinct ventral tooth near its apex and apical portion slightly curved dorso-ventrally (in lateral view); paramere (underside) with sensory peg setae arranged in wide lateral rows merging at parameral anterior margin.

As a common and widespread species in Europe, *Q. umbrinus* was noted and illustrated in numerous papers. The latest summary can be found in Assing & Schülke (2012). Based on Kascheev (1989) and material examined here, *Q. umbrinus* occurs in the mountains of southern Kazakhstan where it can be found in leaf litter and dung at elevations up to 1845 m.

Quedius (Raphirus) sp. aff. Q. coloratus Fauvel, 1875

Fig. 18

Quedius coloratus: Herman 2001, 3129 (summary of literature); Assing 2017, 207 (characters, distribution records, bionomics).



Figure 18. *Quedius* sp. aff. *Q. coloratus* (specimen from Kyrgyzstan). A, habitus. B, median lobe, lateral view; C, paramere, underside. Scale bars: A = 1 mm; B, C = 0.5 mm.

Material examined. Kyrgyzstan: 1 ♂, N Tien-Shan, Kyrgyz Alatau Mts, S Tokmak, near Kegety Pass, left tributary of Tuyuk River, 3000 m a.s.l., 42°24'43"N, 75°00'52"E, 13.V.1986, I.A. Belousov leg. (cRyv).

Comments on taxonomy, distribution and bionomics. Externally and by the structure of the aedeagus, a single male specimen from Kyrgyzstan (Fig.18) examined here seems to be a new species from the *coloratus*-group, recently revised by Assing (2017). *Quedius coloratus* and allied species forming that group are regional Mediterranean endemics with allopatric distributions, altogether extending from Greece, through Turkey to Jordan. Our specimen differs from all known species of the *coloratus*-group in the structure of aedeagus (sharp apex of median lobe, subapical tooth located much further away from the apex, peg setae of the paramere less distinctly arranged in longitudinal rows and situated more medially (Fig. 18B, C).

This specimen from the high elevations of Kyrgyz Alatau, far from the Mediterranean region, is a noteworthy finding for the *coloratus*-group. More material is needed for a clearer understanding of its identity and formal description.

Quedius (Raphirus) hauseri Bernhauer, 1918

Figs 19, 22

Quedius penecke Bernhauer, 1918, **syn. n.** (Fig. 20)

Quedius ouzbekiscus Coiffait, 1969, **syn. n.** (Fig. 21)

Quedius hauseri Bernhauer, 1918, 94 (original description); Gridelli 1925, 154 (characters); Scheerpeltz 1933, 1443 14 (= *Q. penecke* Bern.); Wüsthoff 1938, 221 (illustration of aedeagus); Coiffait 1978, 264 (characters, distribution records); Tronquet 1981, 71 (distribution records); Klimenko 1996, 121 (distribution records).

Quedius penecke Bernhauer, 1918, 95 (original description); Gridelli 1925, 154 (variety of *Q. hauseri*); Scheerpeltz 1933, 1443 (variety of *Q. hauseri*); Coiffait 1978, 264 (variety of *Q. hauseri*, characters).

Quedius ouzbekiscus Coiffait, 1969, 52 (original description); Coiffait 1970, 143 (list); Coiffait 1978, 278 (characters, notes); Kascheev 2001, 102 (distribution records).

Type material examined. *Quedius hauseri*: Lectotype (here designated): Tajikistan: 1 ♂, "Mts. Karateghin Baldschuan 924 m. F. Hauser 1898. [printed]/ *hauseri* Bern. Typus [handwritten]/ Chicago NHMus M. Bernhauer [printed]/ Syntype teste D.J. Clarke 2014 GDI Imaging Project [printed]/ Photographed Kelsey Keaton 2014 Emu Catalog [printed]/ FMNHINS 2819454 Field Museum [printed]" (Fig. 19E) (FMNH).

***Quedius penecke*: Syntype: Kyrgyzstan:** 1 ♀, "Tien-schan. [sic!] Przewalsk. Karakolthal [printed]/ *picipennis* Hr. Turkest. Penecke det. Bernhauer [pre-handwritten]/ *acuminatus* Hoch. var. *elytris brevibus* det. Bernh. [pre-printed]/ var. *Penecke* Bern. Typus. [handwritten]/ Chicago NHMus M. Bernhauer Collection [printed]/

Syntype teste D.J. Clarke 2014 GDI Imaging Project [printed]/ Photographed Kelsey Keaton 2014 Emu Catalog [printed]/ FMNHINS 2819453 Field Museum [printed]" (Fig. 20B) (FMNH).

***Quedius ouzbekiscus*: Holotype: Uzbekistan:** ♂: "Uzbekistan 8-68 Mts Tschingan 1500 m. H.C. [printed]/ *Q. (Raphirus) ouzbekiscus* Coiff. H. Coiffait det. 1968 [pre-printed]/ Holotype [printed]" (Fig. 21D); paratypes, 3 ♂, 35 ♀: same data, but "paratype [printed]" (MNHN) (one of the male paratypes is *Q. fulvicollis*, see that species below).

Additional material examined. Kazakhstan: 1 ♂, Almaty Area, Dzhungarskiy Alatau Mts, 6 km NE Rudnichnyi, Koxsu River canyon, 1300–1400 m a.s.l., 44°41'N, 78°58'E, *Betula* sp., *Populus*, *Picea* etc. forest, 09–10.VI.2001, S.I. Golovatch leg. (cRyv.); 1 ♂, Kolbas-tau, under bark in *Abies* forest, spruce logs, 04.VI.1988, V.A. Kastcheev leg. (ZIN); 5 ♂, Karatau Mts, Byzhi River, Rynagus stream, 757 m a.s.l., 43°57'08.7N, 68°12'04.2E, 24–25.VII.2010, V.A. Kastcheev leg. (ZIN); 1 ♂, 2 ♀, NW Karatau, 15 km NW Babai kurgan, 09.VI.1983, B.V. Iskakov leg. (ZIN); 1 ♂, Karatau Mts, 660 m a.s.l., 42°53'41.42N, 70°42'56.6E, 11.VII.2010, V.A. Kastcheev leg. (ZIN); 1 ♂, Karatau Mts, Khantagi River, 570 m a.s.l., 43°33'32.4N, 68°40'52.7E, 25.VI.2011, V.A. Kastcheev leg. (ZIN); 1 ♂, S Kazakhstan, near Merke, 10–15.VI.1988, B.V. Iskakov leg. (ZIN); 2 ♂, near Almaty, Zailiyskiy Alatau Mts, 2500–2800 m a.s.l., 29.VIII–03.IX.1992, K.Yu. Eskov leg.; 1 ♂, Almaty Area, Zailiyskiy Alatau Mts, Medeo near Almaty, *Picea*, *Betula* etc. forest, 1500–1600 m a.s.l., 43°10'N, 77°04'E, 27.V.2001, S.I. Golovatch leg.; 2 ♂, 2 ♀, S of Alma-Ata, upper reaches of Bolshaya Almatinka River, 2300–2500 m a.s.l., *Picea schrenkiana* forest, 06.VI.1993, S.I. Golovatch leg. (cRyv); 2 ♂, Almaty Area, Talgar district, Ak-Bulak, 2700 m a.s.l., 43.1454N, 77.2404E, 10.V.2014, O. Nakladal leg. (cKoc); 1 ♂, Lle-Alatau, NP Talgar env., Ak-Bulak, resort horse and cow dung, 1750 m a.s.l., 12–15.V.2014, 77.37145N, 43.26897 E.M. Kocián leg. (cKoc); 4 ♂, 1 ♀, Zailiyskiy Alatau, Sarybastau Valley, Chilik River, 12–15.VI.1988, V.A. Kastcheev leg. (ZIN); 5 ♂, 1 ♀, Ketmen Mts, Dolayty Valley, 15.VII.1988, V.A. Kastcheev leg. (ZIN); 2 ♂, same locality and collector, but 24.VIII.1987 (ZIN); 1 ♂, Kyrgyz Alatau, 42°48'49.2E, 72°28'38.6N, 09.VII.2010, V.A. Kastcheev leg. (ZIN); 1 ♂, Aksu-Dzhabagly Nature Reserve, 27.VI.2004, A.V. Matalin leg. (ZIN); 1 ♂, Aksu-Dzhabagly Nature Reserve, Kish-Koyandy-Tau, meadow-steppe belt, 17.VII.1986, B.V. Iskakov leg.; 2 ♂, same locality and data, but in moss, 17.VII.1988, (ZIN); 1 ♂, 4 ♀, Aksu-Dzhabagly Nature Reserve, Taldy-Bulak River, 10–20.IV.1979, B.V. Iskakov leg.; 1 ♂, 2 ♀, same locality and collector, but same locality and collector, but 10–20.V.1979; 3 ♂, same locality and collector, but 04.V.1986 (ZIN); 2 ♂, Aksu-Dzhabagly Nature Reserve, Dzhatanskoi River., 18.V.1985, V.A. Kastcheev leg. (ZIN); 1 ♀, NW slopes of Ugamskiy Mt. Ridge, left tributary of Boldabrek River, 18.VI.2004, A.V. Matalin leg. (ZIN); 1

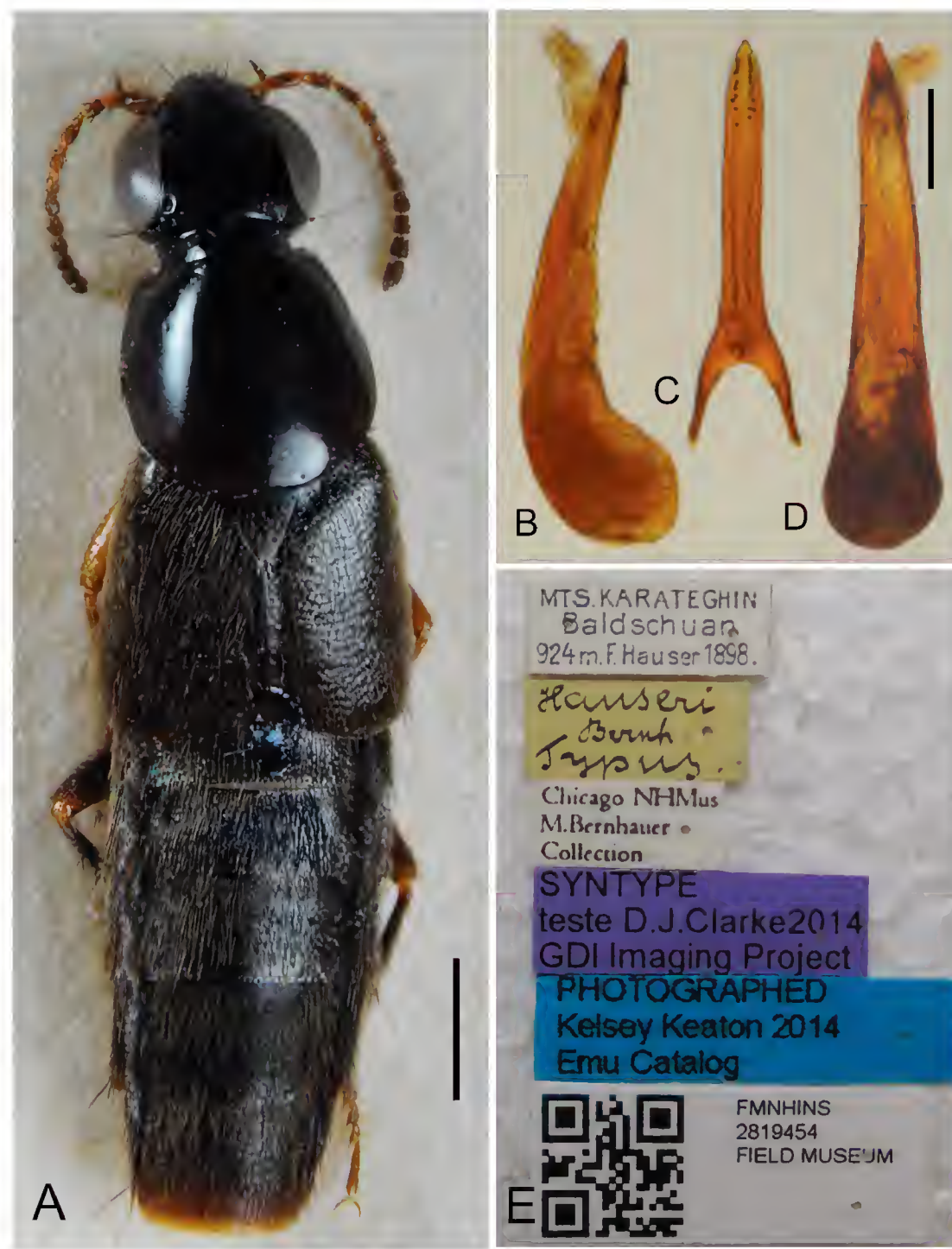


Figure 19. *Quedius hauseri*, lectotype, male. **A**, habitus. **B–D**, aedeagus: **B**, median lobe, lateral view; **C**, paramere, underside, **D**, median lobe, ventral view. **E**, labels. Scale bars: **A** = 1 mm; **B–D** = 0.2 mm.

♂, 2 ♀, Karzhantau, Kaskasu River, 10–12.VII.1983, B.V. Iskakov leg. (ZIN); **Uzbekistan**: 1 ♂, Chimgan Valley, bank of stream with *Equisetum* sp., 1984, A.V. Tanasevitch leg. (cRyv); 1 ♂, Tien Shan, Aktasch, Taschkent, 2000 m a.s.l., 13.VII.1984, D.W. Wrase leg. (cSch); 1 ♂, 2 ♀, Samarkand, Agalik, 23.X.1935, Y.D. Kirschenblat leg. (ZIN); 1 ♂, 1 ♀, Aman Kutan, 12.VI.1932, leg. V.V. Gussakovsky (ZIN); 1 ♂, same locality, but in dung, 29.V.1965, Guryeva leg. (ZIN); 1 ♂, "789[.] 24.5.62. Région de Boukhara. Ouest de Zeravchan [.] pris d'un ruisseau' [=789. 24.V.1962. Bukhara Area, Eastwards of Zeravshan, captured from a rill]/ '24.5.62. Китабский перевал [.] У ручья [.] пр [.] 121-124 [.]' [=24.V.1962. Kitab Pass. Near rill. Samples 121–124.] " (ZMMU); 5 ♂, 1 ♀, "797 [.] 11.5.62. Région de Boukhara. Ouest de Zeravchan. Pente marécageuse." [=797. 11.V.1962. Bukhara Area. Eastwards of Zeravshan. Swampy slope.] (ZMMU); 1 ♂, Shahrizabz, near city wall, 14.XII.1941, K.V. Arnoldi leg.; 1 ♂, 1 ♀, same locality and collector, gardens along road to Kitab, 27.XI.1941 (cRyv); 1 ♂, Kugitangtau Mts, near Kampyrtepa, Kampyrtepa say, under stones along stream, 1400 m a.s.l., 15.V.1984, A.V. Tanasevitch leg.; 3 ♂, same locality and collector, but in litter along stream, 1600–1700 m a.s.l., 17–19.V.1984

(cRyv); **Kyrgyzstan**: 1 ♂, Chuy Region, S Bishkek, SE Kashkasu, Kyzyl-Beles, 2010 m a.s.l., 74.3226N, 42.3904E, 05.VII.2011, J. Frisch leg. (cKoc); 1 ♂, Tien Shan, Ala Archa, 2000 m a.s.l., 09.VII.1984, D.W. Wrase leg. (cSch); 4 ♂, 1 ♀, Kungey-Alatoo, Chilik River, tract Sarybastau, 12–15.VI.1988, V.A. Kastcheev leg. (ZIN); 1 ♂, Issyk-Kul' Area, Tyupskiy District, Kungey-Alatoo Mts, valley 3–4 km N of Shaty, banks of river and rill: under stones, in moss, and among sedges, 30.VIII.1983, A.B. Ryvkin leg. (cRyv); 1 ♂, 1 ♀, Issyk-Kul', Kyzyl-Tuu-Kyzyl-Suu, Barskoon Barskaun Pass, *Picea schrenkiana*-forest, 2200 m a.s.l., 77.3551N, 42.0242E, 23.VI.2011, J. Frisch leg. (cKoc); 3 ♂, Issyk-Kul' Area, Terskey-Alatoo Mts, Chon-Kyzyl-Suu River basin, Kashkator River canyon near Geographical Field Research Station, 2900 m a.s.l., in moss & under stones near swampy rill in slope forest with *Picea schrenkiana* & *Juniperus turcomanica*, 25.VIII.1983, A.B. Ryvkin leg. (cRyv); 2 ♂, 1 ♀, Terskey-Alatoo Mts, Chon-Kyzyl-Suu River, spruce litter, motley grass, 2150 m a.s.l., 08.VII.1988, V.V. Yanushev leg. (cRyv); 1 ♂, Terskey-Alatoo, Chon-Kyzyl-Suu River, 2500 m a.s.l., 28.VI.1959, Panfilov leg. (ZIN); 1 ♂, 1 ♀, Terskey-Alatoo, Lahol River, 3300 m a.s.l., 25.VII.1992, D. Milko leg. (cSch); 1 ♂, East



Figure 20. *Quedius peneckeii* (new synonym of *Q. hauseri*), syntype, female. **A**, habitus. **B**, labels. Scale bar: 1 mm.

Tien Shan, Turgen valley, Tshon Ashu Pass, 2900–3500 m a.s.l., VII.2001, V.G. Dolin & S. Andreeva leg. (cSch); 1 ♂, 1 ♀, Osh Area, Sary-Chelek Biosphere Reserve, shore of Iri-Kyol Lake, mosses and peat among *Carex* sp., *Juncus* sp., and *Phragmites australis*, 04–05. VIII.1983, A.B. Ryvkin leg.; 1 ♂, Osh Area, Sary-Chelek Biosphere Reserve, combe under pass from Khodzha-Ata River to the “head” of Sary-Chelek Lake, 2000 m a.s.l., at slope with *Carex* spp., *Brachypodium* sp., *Poa* sp., etc., 11.VIII.1983, A.B. Ryvkin leg.; 1 ♂, Osh Area, Sary-Chelek Biosphere Reserve, “head” of Sary-Chelek Lake, 1940–1945 m a.s.l., lake shore and bottom of partly dried rill with *Carex* spp., *Equisetum* sp., *Juncus* sp., *Phragmites australis*, etc., 12.VIII.1983, A.B. Ryvkin leg.; 2 ♂, 1 ♀, Sary-Chelek Biosphere Reserve, 04–10. VII.1983, S.K. Alekseev leg.; 1 ♂, Tien Shan, Chatkal Mt. Ridge, Sary-Chelek Biosphere Reserve, 1550–2200 m a.s.l., forests, 29–31.V.1993, S.I. Golovatch leg. (cRyv); 2 ♂, Osh Area, Sary-Chelek Biosphere Reserve, Keltesay stream valley, leaf litter in slope *Juglans* forest, 28.VI.1983, A.B. Ryvkin leg. (cRyv); 1 ♂, Ala Kul Pass, Kara Kol, 3860 m a.s.l., VII.1998, C. Reuter leg. (cSch); 1 ♀, Bajduly Mt., Dolon Pass, 1600 m a.s.l., 15–18. VII.2001, V.G. Dolin & S. Andreeva leg. (cSch); 1 ♂, Tien Shan, Dolon Pass, 2500–3200 m, 23–25.VII.1991, J. Turna leg. (cSch); 1 ♂, Naryn Area, 50 km W Naryn

City, Karatoo Mts, Ala-Myshik Tract, leaf litter in birch forest at river bank, 22.VIII.1983, A.B. Ryvkin leg.; 2 ♂, Ferganskiy Mt. Ridge, near Arslanbob, dry subalpine meadow, under stones, 2200 m a.s.l., 1.X.1983, K. Yu. Eskov leg. (cRyv); 2 ♂, Osh Area, W Tien Shan, Ferganskiy Mt. Ridge, Yarodar, 1300 m a.s.l., rill bank, in leaf litter and under stones, 24–25.IX.1983, K. Yu. Eskov leg. (cRyv); 1 ♂, Tien Shan, E slope Ferghanskiy Mt. Ridge, upper reaches of Urumbash River 2000 m a.s.l., 19.VII.2001, A.V. Puchkov leg. (cSch); 1 ♂, Tien Shan, Ferghanskiy Mt. Ridge, Burgut Pass, 3200 m a.s.l., 20. VII.2001, A.V. Puchkov leg. (cSch); 1 ♂, Ferganskiy Mt. Ridge, Kara-Unkur valley, 2150 m, 22–24.VII.2001, V.G. Dolin & S. Andreeva leg. (cSch); 1 ♂, Alay valley, Nyra, 19.VII.1960, Lopatin leg. (ZIN); **Tajikistan:** 1 ♂, 2 ♀, “Seravshan Kshtut. Artutsch. Glasunov 1892” (ZIN); 1 ♀, “Jagnob Karsau Glasunov 1892” (ZIN); 3 ♂, “Jagnob Chishartob Glasunov 1892” (ZIN); 1 ♂, 1 ♀, “Iskander-Kul/ Glasunov 1892”; 1 ♂, same collector, but “Iskander-Daria” (ZIN); 1 ♀, Pamir-Alai, Seravshan Valley, near Navobod, 10–01.VII.1990, M. Schülke & D.W. Wrase leg. (cSch); 3 ♂, 1 ♀, Pamir-Alai, Hisaar Mts, Adshuk-Cleft near Warsob, 1200 m a.s.l., 01–03.VII.1990, M. Schülke & D.W. Wrase leg. (cSch); 1 ♂, same locality and collectors, but snowfiled edge at km 55, 1800 m a.s.l., 28.VI.1990 (cSch); 8 ♂, 1 ♀, same locality and



Figure 21. *Quedius ouzbekiscus* (new synonym of *Q. hauseri*), holotype, male. **A**, habitus; **B**, median lobe, lateral view; **C**, paramere, underside; **D**, labels. Scale bars: **A** = 1 mm; **B**, **C** = 0.2 mm.

collectors, but Bachufer, 01–03.VII.1990 (cSch); 2 ♀, “Gissaar: Karatag. (stgr.) E. Willberg” (ZIN); 5 ♂, 1 ♀, Dushanbe, Charangon River, 03.VI.1934, V.V. Gussakovky leg. (ZIN); 1 ♂, Dushanbe, foothills, 16.V.1963, A.V.Bogachev leg. (ZMMU); 1 ♂, “Prov. Kuliab, Ak-sou-Tal, F.Hauser 1898/ Gift from Nat. Mus. Praha. 2009” (ZMMU); 1 ♀, Schugnan, Sardym, Gunt River, 16.VII.1897, A. Kaznakov leg. (ZIN); **Uzbekistan or Tajikistan:** 1 ♂, “Buchara./ Staudinger./ 825./ boops/ *Quedius (Raphirus) acuminatus*” (ZMMU); 1 ♂, “Putchin Pass Glasunov 1892” (ZIN).

Comments on taxonomy, lectotype designation and new synonymy. In the original description of *Q. hauseri*, Bernhauer (1918) did not specify the type material but he mentioned localities “Baldschuan [Baljuvon], 924 m, Sary-pul, 1482 m” [Tadjikistan: Karateghin Mts.] (Fig.19E) and “Ost-Buchara: Tschitschantan, Karatag und Repetek, vor.” [Tadjikistan: Vorukh jamoat, according to Frisch 2015] where his material came from. Also it is clear from the original description that he studied both sexes. All this suggests multiple syntypes. Bernhauer (1918) compared *Q. hauseri* with *Q. boops* and *Q. acuminatus*. Wüsthoff (1938) illustrated the structure of the aedeagus for *Q. hauseri* for the first time based on some material “aus Buchara” [from Buchara]. Next, the aedeagus for *Q. hauseri* was illustrated by Coiffait (1978), also based on some non-type material.

We were able to study a male specimen from the FMNH (for details see above) which is clearly a syntype and which we designate as the lectotype to fix the identity of that species. Our examination of the type specimen of *Q. hauseri* confirms the correct identification of this species by both Wüsthoff (1938) and Coiffait (1978).

In the same paper, Bernhauer (1918) described *Quedius peneckeii* as a brachypterous variation of *Q. hauseri* from ‘Tien-Shan, Przewalsk, Karakoltal’ [now Karakol, Issyk-Kul region, Kyrgyzstan], also not specifying either a number or sex of the material he studied. He only stated that *Q. peneckeii* was similar to *Q. fulvicollis* from which it could be distinguished by the elongate pronotum and more densely punctured abdomen. Gridelli (1924) and Coiffait (1978) also considered *Q. peneckeii* as a variation of *Q. hauseri*. Of them, Gridelli (1924) stated that he had studied the type material but without details on sex or number of specimens. In catalogs *Q. peneckeii* is given as a variation (Scheerpeltz, 1933; Hermann, 2001) or synonym (Schülke & Smetana, 2015) of *Q. hauseri*. There was not a single illustration of *Q. peneckeii* ever published. We were able to study one female specimen from the FMNH which is clearly a syntype of *Q. peneckeii*. It is conspecific with *Q. hauseri* and does not look to be distinctly brachypterous. Based on that and the fact that there is only one species of this type in Middle Asia,



Figure 22. *Quedius hauseri*, distribution and variability of the paramere (as an example specimens from one locality, indicated by black dot). Scale bar: 1 mm.

which is rather common and widespread (Fig. 22), we place *Q. peneckeii* in synonymy with *Q. hauseri*.

Coiffait (1969) described *Q. ouzbekiscus* from Uzbekistan based on the male holotype (Fig. 21) and 40 paratypes (4 males and 36 females). He considered it similar to the species from the *boops*-group and stated that *Q. ouzbekiscus* can be distinguished from other members of the group by the structure of aedeagus and proportions of the body. Also he noticed that *Q. ouzbekiscus* is especially similar to *Q. fulvicollis*. Our examination of the type material of *Q. ouzbekiscus* reveals that this species is conspecific with *Q. hauseri* and therefore we place the former in synonymy with the latter.

Diagnosis. Head and abdomen usually black, pronotum, elytra and appendages pale-brown to brown; scutellum punctate (Figs 19A, 20A, 21A). Aedeagus (in lateral view) (Figs 19B, 21B): ventral contour of median lobe apically and basally from subapical tooth form one line, so that the tooth is protruding and median lobe apically from that does not look like an axe blade. Among all Middle Asian *Raphirus*, only *Q. hauseri* and *Q. fulvicollis* (see below) have the punctate scutellum. *Quedius hauseri* differs from *Q. fulvicollis* by the shape of the paramere (Figs 19C, 21C, 23C, respectively).

Distribution. *Quedius hauseri* is common and widely distributed in Middle Asia where it occurs from south-

eastern Kazakstan (southern border through Dzhungaskiy Alatau) to southern Tajikistan (Pamir Mountains, Schugnan) (Fig. 22). It was also recorded from Afghanistan (Schülke and Smetana, 2015).

Bionomics. Based on the material examined here *Q. hauseri* usually inhabits various humid ground based plant debris or moss near water bodies. It occurs both in forested and open habitats. It also can be found under stones, bark and in dung, mostly at the medium to high elevations up to 3300 m.

Quedius (Raphirus) fulvicollis Stephens, 1833

Fig. 23

Quedius fulvicollis: Herman 2001, 3159 (summary of literature); Assing and Schülke 2012, 481, 482 (diagnosis, distribution and bionomics, aedeagus illustration); Klimenko 1960, 121 (distribution records)

Material examined. One of the male paratypes of *Q. ouzbekiscus* (new synonym of *Q. hauseri*, see above), for details see material examined for *Q. hauseri* and Fig. 23

Comments on taxonomy, distribution and bionomics.

One of the male paratypes of *Q. ouzbekiscus* (new synonym of *Q. hauseri*) was in fact a different species that we tentatively identify as *Q. fulvicollis*. It can be easily distinguished from *Q. hauseri* by the shape of the paramere (compare Fig. 23C and Figs 19C, 21C, respectively). *Quedius fulvicollis* is considered a widely distributed Holarctic species, in Asia confined to Siberia and Russian Far East (Schülke and Smetana, 2015). The specimen from Chatkal Mountains in Uzbekistan examined here would be a distinct southernmost record for this species in the Palaearctic region and the first record for Middle Asia. In this respect it is noteworthy that it comes from ca. 1500 m of elevation. Also it is remarkable that this specimen from Middle Asia stands out from the variability range of *Q. fulvicollis* by the very narrow middle portion of the paramere and shorter and more irregular rows of peg setae. It well may be that our specimen represents a species new to science. Given the poorly studied variation of *Q. fulvicollis*, which itself maybe a complex of species and very limited material from Middle Asia, a decision on this matter is pending further study.

In general *Q. fulvicollis* prefers forest landscapes and usually can be found in wet ground-based debris, at banks of ponds, forest lakes and in swampy areas. Apart from the elevation, no bionomic data is available for the Middle Asian specimen. An earlier record of *Q. fulvicollis* from Tajikistan in Klimenko (1996) was based on uncertain material and needs verification.

Quedius (Raphirus) scintillans Gravenhorst, 1806

Fig. 4A

Quedius scintillans: Herman 2001, 3260 (summary of literature); Assing and Schülke 2012, 471, 473 (diagnosis, distribution and bionomics, aedeagus illustration)

Material examined.

Additional material. Kazakhstan: 3 ♂, Karatau Mts, 660 m a.s.l., 42°53'41.42N, 70°42'56.6E, 11.VII.2010, V.A. Kastcheev leg. (ZIN); **Uzbekistan:** 1 ♂, Chatkal Nature Reserve, bank of small rill, wet ground, *Poaceae* gen. sp., *Equisetum* sp., moss, 19.IX.1983, K. Yu. Eskov leg. (cRyv); 1 ♂, Golodnaya Step [Sirdaryo Reg., Guliston], 17.V.1903, G.G. Jacobson (ZIN); 1 ♂, “Trkst. Mnt. Nurata UCHUN Glasunov 1892” (ZIN); 1 ♂, Samarkand Reg., Kattakurgan, 18.V.1932, V.V. Gussakovsky leg. (ZIN); 1 ♂, Aman Kutan, shady wet say, near forestry building, 31.V.1942, K.V. Arnoldi leg. (ZMMU); 2 ♂, Qashqadaryo Reg., Kitab, 30.VII.1933, V.V. Gussakovsky leg. (ZIN); **Turkmenistan:** 1 ♂, Kov-Ata [Bacharden] 110 km NW Ashchabad, 10.V.1989, D.W. Wrase leg. (cSch); 2 ♂, 5 ♂, N Kopetdag, Firjusa-Cleft, near Ashchabad, 07.V.1989, D.W. Wrase leg. (cSch); 1 ♂, Kugitangtau Mts, near Svintsovyi Rudnik, 1300 m a.s.l., under stones, 11.V.1984, A.V. Tanasevitch leg. (cRyv); **Tajikistan:** 3 ♂, Warsobob, 03.VI.1988, S.V. Saluk leg. (cRyv); 1 ♂, Dushabe, Kharangon River, 03.VI.1934, V.V. Gussakovsky leg. (ZIN); 2 ♂, 15 km SE Shaahrtuz, Tuyntau Mt., 02–03.VI.1982, G.S. Medvedev



Figure 23. *Quedius 'fulvicollis'* (specimen from Uzbekistan). **A**, habitus. **B**, median lobe, lateral view; **C**, paramere, underside. Scale bars: **A** = 1 mm; **B**, **C** = 0.2 mm.

leg. (ZIN); 4 ♂, 1 ♀, Pyandj District, in hay, 28.IV.1988, S.V. Saluk leg. (cRyv); **Uzbekistan or Tajikistan:** 2 ♂, “Uzbekistan Buchara./ Staudinger. 823.” (ZMMU).

Comments on taxonomy, distribution and bionomics. *Quedius scintillans* is widely distributed in Europe, Western and Middle Asia, and its diagnostic characters, distribution and biology were recently summarized in Assing and Schülke (2012). In Middle Asia, from the newly examined material here, the species is recorded in southern and eastern Turkmenistan and southwestern Tajikistan for the first time.

From all Middle Asian *Raphirus* species it can be easily distinguished by the presence of two additional punctures between anterior frontal punctures on the head.

Quedius scintillans prefers various wet ground-based debris mostly in lowland forests or open landscapes. In the mountains it can be found up to 1300 m elevation.

Discussion

This revision is the first focused summary on *Quedius* of Middle Asia. It clarifies the taxonomy of many poorly or very poorly known species such as *Q.* (s. str.) *subunicolor*, *Q.* (M.) *capitalis*, *Q.* (M.) *fusicornis*, *Q.* (M.) *solskyi* and *Q.* (R.) *cohaesus*, and it records from Middle Asia a few widely distributed species such as *Q.* (s. str.) *fuliginosus*, *Q.* (s. str.) *sundukovi* and *Q.* (R.) *pseudonigriceps* for the first time. It shows how confusing and incomplete the taxonomy was of the species that constitute the core of this fauna. In the course of this revision (including Salnitska and Solodovnikov 2018) the rate of new species discovery was negligible compared to the rate of revealed misidentifications and synonymies. Many “endemic” species described from various regions of Middle Asia, mainly by H. Coiffait, turned out to be synonyms of the species described from this region at the border between XIX and XX centuries (Table 1). These species, with the newly examined material, expectedly turned out to be more widespread than they were previously thought. Several species, especially in the subgenus *Microsaurus*, remain very poorly known (e.g., *Q.* (M.) *bucharensis*, *Q.* (M.) *fusicornis*, *Q.* (M.) *solskyi*, *Q.* (M.) *koltzei* and *Q.* (M.) *tajikiscus*). Here they are represented by fragmentary, poorly georeferenced type material (often females only) and, at most, a few additional specimens. For *Q.* (s. str.) *subunicolor* and *Q.* (s. str.) *sundukovi* and *Q.* (M.) *koltzei*, new distributional records from Middle Asia change our idea of their distribution patterns and calls for their more thorough exploration. In general this revision made it obvious that, apart from a handful of species such as *Q.* (s. str.) *fuliginosus*, *Q.* (s. str.) *vicinus*, *Q.* (M.) *ochripennis*, *Q.* (R.) *hauseri*, *Q.* (R.) *imitator*, *Q.* (R.) *limbatus*, *Q.* (R.) *novus*, *Q.* (R.) *pseudonigriceps* and *Q.* (R.) *scintillans*, well represented in the examined material, the Middle Asian species are known from very scarce sampling. Because Middle Asia is mainly a warm and arid region that is not well suited to such a distinctly temperate and mesophilous genus, the fauna of *Quedius* is relatively poor. For example, the *Quedius* fauna

of Denmark, a much smaller, geographically uniform and flat area, contains 41 species (<http://danbiller.dk>) as opposed to 28 species recorded from Middle Asia. It is not expected that the Middle Asian *Quedius* fauna will significantly grow with more explorations. But some increase of this number is likely, due to widespread species to be found there and new species for science to be discovered, especially from the mountain areas of Middle Asia. We hope that our work will encourage further field exploration of this diverse region by using collecting techniques targeting Staphylinidae, especially sifting.

Acknowledgements

We are very thankful to all curators and colleagues listed in the “Material and methods” section who provided the material under their care for this paper. Our special thanks are due to Alexander Ryvkin (Moscow, Russia) for his valuable help in decoding and editing the label data and also to Boris Korotyaev, Igor Belousov, Ilya Kabak and Sergey Sinev (Saint-Petersburg, Russia) for their further help in georeferencing some of the labels. We are grateful to Lech Borowiec (Wroclaw, Poland), Aslak Kappel Hansen (Copenhagen, Denmark), Andre Nel (Paris, France) all colleagues who provided or helped us to obtain some illustrations. We sincerely thank Michael Schülke for providing some difficult-to-obtain references, and Volker Assing (Hannover, Germany) for his critical and important comments on the content of the manuscript. And we are very grateful to both reviewers Aleš Smetana and Adam Brunke (Ottawa, Canada) for their thoughtful comments and suggestions that significantly improved the quality of this paper. This study was conducted using equipment of the Center for Molecular and Cell Technologies and the Resource Center ‘Chromas’ of the Research Park at St. Petersburg State University. Support for this research partly was provided by the Saint-Petersburg State University foundation (Saint-Petersburg, Russia) under the programm “Meropriyatie № 5”.

References

- Assing V (2017) On *Quedius coloratus* Fauvel, 1875 and allied species, with an appendix on *Quedius* species collected in Greece with subterranean pitfall traps, and a new synonymy (Coleoptera: Staphylinidae: Staphylininae). *Linzer Biologische Beiträge* 49(1): 207–228. https://www.zobodat.at/pdf/LBB_0049_1_0207-0228.pdf
- Assing V, Feldmann B (2012) On the Staphylinidae of Israel (Insecta: Coleoptera). *Linzer biologische Beiträge* 44(1): 351–363. http://www.zobodat.at/web4beta/pdf/LBB_0044_1_0351-0363.pdf
- Assing V, Schülke M (2012) Freude–Harde–Lohse–Klausnitzer – Die Käfer Mitteleuropas. Band 4. Staphylinidae I. Zweite neubearbeitete Auflage. Spektrum Akademischer Verlag, Heidelberg.
- Assing V, Wunderle P (2001) On the Staphylinidae of Cyprus (Coleoptera). *Entomologische Zeitschrift* 111(2): 34–41.
- Bernhauer M (1905) 13. Folge neuer Staphyliniden der paläarktischen Fauna, nebst Bemerkungen. *Verhandlungen der k. k. zoologisch-bot-*

- anischen Gesellschaft in Wien 55: 580–596. http://www.zobodat.at/pdf/VZBG_55_0580-0596.pdf
- Bernhauer M (1908) Beiträge zur Kenntnis der paläarktischen Staphyliniden-Fauna. Münchner Koleopterologische Zeitschrift 3: 320–335.
- Bernhauer M (1918) Neue *Quedius* Arten der paläarktischen Fauna. Verhandlungen der k. k. zoologisch-botanischen Gesellschaft in Wien 68: 92–96. http://www.zobodat.at/pdf/VZBG_68_0092-0096.pdf
- Bernhauer M, Schubert K (1916) Staphylinidae V. In: Schenkling S (Ed.) Coleopterorum Catalogus Pars 67. Junk, Berlin, 409–498
- Boháč J (1988) Novye i maloizvestnye zhuki-stafilinidy podsemeistva Staphylininae (Coleoptera, Staphylinidae). Entomologicheskoe Obozrenie 67(3): 549–558.
- Boháč J, Matějček J (2004) Biodiversity of staphylinid beetles (Coleoptera, Staphylinidae). Aktuality Šumavského Výzkumu II, Srní 4–7: 218–220.
- Boháč J, Matějček J, Rous R (Eds) (2005) Staphylinidae (drabčíkovití). In: Farkač J, Král D, Škorpík M (Eds) Červený seznam ohrožených druhů České republiky. Bezobratlí. Red list of threatened species in the Czech Republic. Invertebrates. Agentura ochrany přírody a krajiny ČR, Praha, 435–449.
- Brunke AJ, Chazimanolis S, Schillhammer H, Solodovnikov A (2016) Early evolution of the hyperdiverse rove beetle tribe Staphylinini (Coleoptera: Staphylinidae: Staphylininae) and a revision of its higher classification. Cladistics: 1–25. <https://doi.org/10.1111/cla.12139>
- Chazimanolis S, Cohen IM, Schomann A, Solodovnikov A (2010) Molecular phylogeny of the mega-diverse rove beetle tribe Staphylinini (Insecta, Coleoptera, Staphylinidae). Zoologica Scripta 39(5): 436–449. <https://doi.org/10.1111/j.1463-6409.2010.00438.x>
- Ciceroni A, Zanetti A (1995) [Genera 47–61, 79–147]. In: Ciceroni A, Puthz V, Zanetti A (Eds) Fascicolo 48. Coleoptera Polyphaga III. (Staphylinidae). Edizioni Calderini, Bologna, 10–14, 19–33.
- Coiffait H (1954) Contribution à la connaissance de la faune cavernicole et endogée du Liban. (Mission H. Coiffait au Liban, 1951). II. Staphylinidés nouveaux. Notes et Mémoires sur le Moyen-Orient 5: 155–162.
- Coiffait H (1955) Biospeologica. LXXV. (Mission H. Coiffait au Liban, 1951). Coléoptères cavernicoles et endogés. Archives de Zoologie Expérimentale et Générale 91(4): 423–436.
- Coiffait H (1963) Les *Quedius* du sous-genre *Sauridus* de la région Paléarctique occidentale (avec description de formes nouvelles). Bulletin de la Société d'Histoire Naturelle de Toulouse 98: 372–420.
- Coiffait H (1967) *Quedius* nouveaux ou mal connus. Bulletin de la Société d'Histoire Naturelle de Toulouse 103: 391–424.
- Coiffait H (1969) *Quedius* nouveaux. 5e note sur le genre *Quedius*. Bulletin de la Société d'Histoire Naturelle de Toulouse 105: 44–54.
- Coiffait H (1970) Staphylinidae d'Ouzbekistan. L'Entomologiste 26: 142–148.
- Coiffait H (1975) Staphylinides nouveaux d'U.R.S.S. récoltés par S.M. Khnzorian-Iablokoff. Nouvelle Revue d'Entomologie 5(1): 31–37.
- Coiffait H (1977) Note sur quelques *Quedius* et *Heterothops* nouveaux ou mal connus (Coleoptera: Staphylinidae). Nouvelle Revue d'Entomologie 7(2): 133–143.
- Coiffait H (1978) Coléoptères Staphylinidae de la région paléarctique occidentale. III. Sous famille Staphylininae, tribu Quediini; sous famille Paederinae, tribu Pinophilini. Nouvelle Revue d'Entomologie, Supplement 8(4).
- Cowan PJ (2007) Geographic usage of the terms Middle Asia and Central Asia. Journal of Arid Environments 69(2): 359–363. <https://doi.org/10.1016/j.jaridenv.2006.09.013>
- Eppelsheim E (1887) Neue Staphylinen vom Amur. Deutsche Entomologische Zeitschrift 31: 419–430.
- Eppelsheim E (1888) Neue Staphylinen Central-Asiens. Deutsche Entomologische Zeitschrift 32(1): 49–67.
- Eppelsheim E (1892) Zur Staphylinenfauna Turkestan's. Deutsche Entomologische Zeitschrift 1892: 321–346. <https://doi.org/10.1002/mmnd.48018920111>
- Faldermann F (1835) Additamenta entomologica and faunam rossicam in itineribus jussu imperatoris augustissimi annis 1827–1831 a Cl. Ménériés et Szovitz susceptis collecta, in lucem edita. Nouveaux Mémoires de la Société Impériale des Naturalistes de Moscou 4: 1–310.
- Frisch J (2015) On the taxonomy and phylogeography of the *Scopaeus obscuripes* species group from Central Asia and the Middle East (Coleoptera: Staphylinidae: Paederinae). Stuttgarter Beiträge zur Naturkunde A, Neue Serie 8: 137–163.
- Gabdullina AU (2016) The beetles (Insecta, Coleoptera) fauna of Kanton-Karagay state national nature park (South-Western Altay, East Kazakhstan). Acta Biologica Sibirica 2(1): 41–91. <http://dx.doi.org/10.14258/abs.v2i1-4.923>
- Ghahari H, Anlas S, Sakenin H, Ostovan H, Tabari M (2009) A contribution to the rove beetles (Coleoptera: Staphylinidae: Staphylininae) of Iranian rice fields and surrounding grasslands. Linzer biologische Beiträge 41(2): 1959–1968. http://www.zobodat.at/pdf/LBB_0041_2_1959-1968.pdf
- Ghahari H, Makhan D, Hawkeswood TJ (2012) A faunistic survey on some families of Coleoptera from cotton fields of northern Iran. Calodema 203: 1–7.
- Gridelli E (1924) Studi sul genere *Quedius* Steph. (Coleoptera: Staphylinidae). Secondo contributo. Specie della regione paleartica. Memorie della Società Entomologica Italiana 3(1): 5–180.
- Gridelli E (1925) Studi sul genere *Quedius* Steph. (Coleoptera: Staphylinidae) Secondo contributo. Specie della regione paleartica. Memorie della Società Entomologica Italiana 3(2): 113–180.
- Gusarov V (1993) New and little-known Palearctic Staphylinidae (Coleoptera). Zoosystematica Rossica 1: 65–74.
- Hachikov EA (2003) New and little known rove beetles (Coleoptera: Staphylinidae) of the Southern European Part of Russia and Northern Caucasus. The Kharkov Entomological Society Gazette 10(1–2): 44–50.
- Herman LH (2001) Catalog of the Staphylinidae (Insecta: Coleoptera). 1758 to the end of the second Millennium. VI. Staphylinina Group (Part 3). Staphylininae: Staphylinini (Quediina, Staphylinina, Tanygnathinina, Xanthopygina), Xantholinini. Staphylinidae: Incertae Sedis fossils, Protactinae. Bulletin of the American Museum of Natural History 265: 3021–3840.
- Isaksson D (2007) Inventering av träskammetslöpare i Gävleborgs län 2006. Länsstyrelsen i Gävleborgs län, 2007, rapport 13, 26.
- Jarrige J (1971) Contribution a la faune de L'Iran. 21. Coléoptères Brachelytra. Annales de la Société Entomologique de France 7(2): 483–502.
- Kadyrov AX, Yakubova DSh, Dadabaev XR (2014a) Systematic list of family Staphylinidae (Coleoptera) of the slope Southern Gissar Mountains. News of the Academy of Sciences of the Republic of Tajikistan. Department of Biological and Medical Sciences 2(186): 46–50.

- Kadyrov AX, Yakubova DSh, Dadabaev XR (2014b) Specific structure and distribution of bugs of Staphylinidae (Coleoptera) on biotopes. News of the Academy of Sciences of the Republic of Tajikistan. Department of Biological and Medical Sciences 3(187): 26–33.
- Kascheev VA (1984) K faune stafilinid (Coleoptera, Staphylinidae) doliny nizhnego techeniya r. Ili. Izvestiia Akademii Nauk Kazakhskoi SSR (Biologicheskaya) 1: 24–29.
- Kascheev VA (1985) Raspredelenie stafilinid (Coleoptera: Staphylinidae) v pojmennih biotopah srednego i nizhnego techeniya reki Ili. Izvestiia Akademii Nauk Kazakhskoi SSR (Biologicheskaya) 2: 42–47.
- Kascheev VA (2002) Naselenie stafilinid (Coleoptera: Staphylinidae) v agrocenozah yugo-vostoka Kazahstana. Tethys Entomological Research VII: 179–192.
- Kascheev VA, Ishkov EV (2001) List of beetles (Coleoptera) of Aksu-Dzhabagly Natural Reserve. Tethys Entomological Research III: 99–108.
- Kascheev VA, Zibnitskaia LV, Childebaev MK (1989) Materialy po faune mitsetobiontnykh stafilinid (Coleoptera, Staphylinidae) gornyx lesov severnogo Tian-Shania i Dzhungarskogo Alatau. Izvestiia Akademii Nauk Kazakhskoi SSR (Serii Biologicheskaya) 2: 35–38.
- Klimenko AA (1996) Staphylinidae. Genetical Fund Cadastre of Kyrgyz Republic, III, Supeclassis Hexapoda (Entognatha and Insects). Bishkek, 117–121.
- Korge H (1961) *Quedius subunicolor* n. sp. aus Nordeuropa (Coleoptera: Staphylinidae). Mitteilungen der Deutschen Entomologischen Gesellschaft 20: 81–83.
- Korge H (1962) Beiträge zur Kenntnis der palaearktischen Staphyliniden (Coleoptera). Reichenbachia 1: 149–154.
- Korge H (1964) Carabiden und Staphylinidenfunde in den Pontischen Gebirgen Kleinasien und in Mazedonien (Coleoptera). Reichenbachia 4(14): 105–126.
- Korge H (1971) Beiträge zur Kenntnis der Koleopterenfauna Kleinasien. Annotationes Zoologicae et Botanicae 67: 1–68.
- Kryzhanovsky OL (1965) Sostav i proishozhdenie nazemnoi fauni Srednei Azii. Moscow, Nauka, 430 pp.
- Lohse, GA, Lucht WH (1989) Die Käfer Mitteleuropas. Supplement band I mit Katalogteil. Goecke and Evers, Krefeld, 346 pp.
- Luze G (1904) Beitrag zur Staphyliniden Fauna von Russisch Central Asien (Coleoptera). Horae Societatis Entomologicae Rossicae 37: 74–115.
- Ménétriés E (1832) Catalogue raisonné des objets de zoologie recueillis dans un voyage au Caucase et jusqu'aux frontières actuelles de la Perse entrepris par ordre de S. M. L'Empereur. St. Pétersbourg: L'Académie Impériale des Sciences, 271.
- Munster T (1923) Quediini (Coleoptera). De norske arter. Norsk Entomologisk Tidsskrift 1(4): 183–204.
- Özgen İ, Hachikov EA, Örgel S (2016) Some additional notes on the genus *Quedius* Stephens, 1829 (Coleoptera: Staphylinidae: Staphylininae) fauna of Turkey. Munis Entomology & Zoology 1(2): 619–621.
- Palm T (1962) Bidrag till kännedomen om svenska skalbaggars biologi och systematik. 42–47. Entomologisk Tidsskrift 83: 185–198.
- Palm T (1963) Svensk Insekfauna. 9. Skalbaggar. Coleoptera. Kortvingar: Family Staphylinidae. Unterfam. Paederinae, Staphylininae. Häfte 3. Almquist and Wiksells, Uppsala, 168 pp.
- Salnitska M, Solodovnikov A (2018) Taxonomy of the poorly known *Quedius mutilatus* group of wingless montane species from Middle Asia (Coleoptera: Staphylinidae: Staphylinini). European Journal of Taxonomy 401: 1–17. <https://doi.org/10.5852/ejt.2018.401>
- Scheerpeltz O (1933) Staphylinidae VII. Pars 129. Supplementum 1, 989–1500.
- Shilov EF (1975) Korotkonadkrylye zhuki podsemeistva Staphylininae (Coleoptera, Staphylinidae) Komi ASSR. Entomologicheskoe Obozrenie 54(2): 374–377.
- Schülke M, Smetana A (2015) Staphylinidae, 304–1134. In: Löbl I, Löbl D (Eds) Catalogue of Palaearctic Coleoptera. Volume 2. Hydrophiloidea–Staphyliniidea, Revised and updated edition. Brill, Leiden, Boston, 1702 pp.
- Smetana A (1967) Wissenschaftliches Ergebnis der zoologischen Expedition des Nationalmuseum in Prag nach der Türkei. Coleoptera-Staphylinidae, Subfamily Staphylininae. Acta Entomologica Musei Nationalis Pragae 37: 551–564.
- Smetana A (1971) Revision of the tribe Quediini of America north of Mexico (Coleoptera: Staphylinidae). The Memoirs of the Entomological Society of Canada 103(79): 1–303.
- Smetana A (1988) Revision of the tribes Quediini and Atanygnathini, Part II. The Himalayan region (Coleoptera: Staphylinidae). Quaestiones Entomologicae 24: 163–464.
- Smetana A (1992) Revision of the tribes Quediini and Atanygnathini, Part II. The Himalayan Region. Supplement 2. (Coleoptera: Staphylinidae: Staphylininae). Stuttgarter Beiträge zur Naturkunde Serie A (Biologie) 487: 1–11.
- Smetana A (1995a) Taxonomic and faunistic contributions to the knowledge of Palaearctic Quediina (Coleoptera, Staphylinidae, Staphylinini). Elytra 23(1): 77–88.
- Smetana A (1995b) Revision of the tribes Quediini and Tanygnathini, Part III. Taiwan (Coleoptera: Staphylinidae). National Museum of Natural Sciences, Special Publication 6: 1–145.
- Smetana A (1996) Revision of the tribes Quediini and Atanygnathini, Part III. Taiwan. Supplementum 1. National Museum of Natural Sciences, Special Publication 8: 23–28.
- Smetana A (1998) Taxonomic and faunistic contributions to the knowledge of Palearctic Quediina (Coleoptera, Staphylinidae, Staphylinini). Part 2. Elytra 26(1): 115–128.
- Smetana A (2001) Revision of the subtribe Quediina and the tribe Tanygnathini. Part III. Taiwan. (Coleoptera: Staphylinidae). Supplement II. Special Publication of the Japan Coleopterological Society 1: 55–63.
- Smetana A (2003) *Quedius (Quedius) sundukovi* (Coleoptera, Staphylinidae, Staphylinini, Quediina), an Interesting New Species from the Russian Far East. Elytra, Tokyo 31(1): 189–193.
- Smetana A (2014) Contributions to the knowledge of the Quediina (Coleoptera, Staphylinidae, Staphylinini) of China. Part 44. Genus *Quedius* Stephens, 1829. Subgenus *Microsaurus* Dejean, 1833. Section 22. Folia Heyrovskyana, Series A 21(1–4): 1–39.
- Smetana A (2015a) Revision of the tribes Quediini and Atanygnathini. Part II. The Himalayan region (Coleoptera: Staphylinidae). Supplementum 3 (Coleoptera: Staphylinidae: Staphylininae). Verna 34: 239–251.
- Smetana A (2015b) Contributions to the knowledge of the Quediina (Coleoptera: Staphylinidae: Staphylinini) of China. Part 56. Genus *Quedius* Stephens, 1829 Subgenus *Microsaurus* Dejean, 1833. Section 23. Linzer biologische Beiträge 47: 1843–1854.
- Smetana A (2017) Taxonomic review of the 'quediine' subtribes of Staphylinini (Coleoptera: Staphylinidae: Staphylininae) of mainland China. Prague, Nakladatelství Jan Farkač, 434 pp.

- Smetana A, Shavrin AV (2018): Contribution to the knowledge of the genus *Quedius* Stephens, 1829 of Siberia and Russian Far East (Coleoptera: Staphylinidae: Staphylinini: Quediina). Linzer biologische Beiträge, 0050_1: 825–836.
- Solodovnikov A (2004) Taxonomy and faunistics of some West Palearctic *Quedius* Stephens subgenus *Raphirus* Stephens (Coleoptera: Staphylinidae). Koleopterologische Rundschau 74: 221–243. https://www.zobodat.at/pdf/KOR_74_2004_0221-0243.pdf
- Solodovnikov A (2006) Revision and phylogenetic assessment of *Afroquedius* gen. nov. from South Africa: toward new concepts of the genus *Quedius*, subtribe Quediina and reclassification of the tribe Staphylinini (Coleoptera: Staphylinidae: Staphylininae). Annals of the Entomological Society of America 99(6): 1064–1084. [https://doi.org/10.1603/0013-8746\(2006\)99\[1064:RAPAOA\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2006)99[1064:RAPAOA]2.0.CO;2)
- Toleutaev SS, Kaman Ulipkan (2015) K faune stratobionnykh stafilinid (Coleoptera, Staphylinidae) oh the Saur Mountain Ridge (Eastern Kazakhstan). In Sbornik nauchnih trudov po materialam Mezhdunarodnoi nauchno-practicheskoi konferentsii 30 Dekabrya 2014 g: v 8 chastyah. Chyast I, Moscow, “AR-Consalt”: 41–45.
- Tronquet M (1981) Staphylinidae d’Afghanistan (Coleoptera). Revue Française d’Entomologie 3(3): 69–83.
- Wüsthoff W (1938) Die Forcipes der mir bisher bekannt gewordenen Arten der Gattung *Quedius*. Entomologist Tidskrift 59: 214–223.
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The tropical African genus *Morgenia* (Orthoptera, Tettigoniidae, Phaneropterinae) with emphasis on the spur at the mid tibia

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Abstract

Received 15 May 2018

Accepted 13 July 2018

Published 2 August 2018

Academic editor:

Susanne Randolph

Key Words

Taxonomy
new species
bioacoustics
cytogenetics

The authors revised the genus *Morgenia* Karsch, 1890 which now consists of eight species, of which three are here newly described (*Morgenia plurimaculata* Massa & Moulin, **sp. n.**, *M. angustipinnata* Massa, **sp. n.**, and *M. lehmannorum* Heller & Massa, **sp. n.**). Six of the eight species occur in the Tri National Sangha (TNS) comprising Dzanga-Sangha Special Reserve and Dzanga Ndoki National Park (Central African Republic), whose high biodiversity has been recently highlighted. In particular the genus is characterised by the presence of a more or less long spur at the inner mid tibia, different in each species; in *M. modulata*, it moved lower down into a new position at about ¼ of tibia, which has a hollow underneath where the rest of the spur remains hidden. This is a unique known case in Phaneropterinae. Morphological characters distinguishing males of different species are presented. Bioacoustics of the new species *M. lehmannorum* are described. The patterns of the chromosome evolution in *M. lehmannorum* differ from other investigated African Phaneropterinae in terms of chromosome number and morphology, reduced ancestral chromosome number (2n = 25) implying a more derived condition.

Introduction

The genus *Morgenia* was described by Karsch (1890a), together with the species *M. hamuligera* (type species of the genus). Later, Karsch (1893, 1896) described *M. melica* and *M. modulata*, Griffini (1908) described *M. spathulifera* and Sjöstedt (1913) *M. rubricornis* respectively. Apart from that of Griffini (1908), the descriptions are short and, in some cases, it is very difficult to understand differences between species without examination of the types. For this reason, Massa (2013) considered that very likely some of them were synonymously described. However, more recently Massa (2017a) has shown the differences that allow *M. spathulifera*, *M. hamuligera*, *M. rubricornis* and *M. melica* to be separated, highlighting that *M. spathulifera* has narrower tegmina than the other taxa. A long series of specimens belonging to this genus

were available in recent years from different countries of tropical Africa. This allowed a deeper study of their characters and the comparison with the types and photographs in Orthoptera Species File Online (Cigliano et al. 2018). In the present paper, the results of this study are reported, with the description of another three species.

Presently eight species of *Morgenia* are known in tropical Africa; six of them occur in the Tri National Sangha (TNS) comprising Dzanga-Sangha Special Reserve and Dzanga Ndoki National Park (Central African Republic). We should point out the remarkable importance of this area from the conservation and the biodiversity point of view. Recently different papers on insects of this area have been published, showing the high diversity of co-occurring species (Massa 2013, 2015, 2016, 2017b, Tortorici et al. 2016, Hemp and Massa 2017, Moulin et al. 2017).

Material and methods

Morphology

Some specimens were collected in the field during expeditions in tropical Africa. Most Orthoptera were collected at night with the aid of UV lamps, one installed above ground, the other placed under a canopy. Specimens were dried by smoke and preserved individually in paper bags each day. These bags were later sent to the Department of Agricultural, Food and Forest Sciences, Palermo University, Italy and were later mounted.

Central African Republic site: Dzanga-Ndoki National Park is part of the Sangha Trinational, a UNESCO World Heritage Site which covers an area of 4,520,000 ha and includes three national Parks: Lobokeye (Cameroon), Nouabale-Ndoki (Congo) and Dzanga-Ndoki (Central African Republic). Dzanga-Ndoki National Park is located in the Congo River basin, within an extensive tropical forest, approximately six days walk from the nearest inhabited village and constitutes a very rich sanctuary of biodiversity which is still poorly known. The park is bordered to the West by the Sangha River, which also borders with Cameroon and contains more than ten natural lakes of different size (from ca. 1 km by 400 m to 100 m by 150 m). Dzanga-Ndoki National Park is located in the extreme southwest of the Central African Republic, in a triangular-shaped part of the country. Established in 1990, it is divided into two non-continuous sectors: the northern Dzanga Park (49,500 ha) and the southern Ndoki Park (72,500 ha). The two are joined by the Dzanga-Sangha Rainforest Reserve (335,900 ha), where controlled hunting and other exploitation is allowed. The whole park is on alluvial sands; along streams, forest clearings can be found with marshy depressions. The Dzanga Bai (= the village of elephants) is a sandy salt lick that measures 250 m by 500 m. It is traversed through the middle by the Dzanga stream. There are three types of forest within Dzanga-Ndoki National Park: mainly dry-land, a semi-evergreen forest that contains swamp-forest areas along the rivers and a closed-canopy, mono-dominant *Gilbertiodendron dewevrei* forest. The dry-land forest is an open, mixed canopy that is dominated by Sterculiaceae and Ulmaceae; often associated with it is a dense understorey of Marantaceae and Zingiberaceae (Massa 2013).

Gabonese site: Research Station on Gorilla and Chimpanzee (SEGC-CIRMF, Station d'Etudes des Gorilles et Chimpanzés, gérée par le Centre International de Recherches Médicales de Franceville) is situated in the northern part of Lopé National Park, about 10 km south from Lopé village and the Dr Alphonse Mackanga Missandzou Training Center (CEDAMM, Wildlife Conservation Society; coordinates: 0°12'09.62"S, 11°36'05.19"E; altitude 265m). Vegetation comprises a mosaic of forest and shrub savannah. Shrub savannah is dominated by Poaceae and Cyperaceae like *Anadel-*

phia arrecta, *Andropogon pseudapricus*, *Schizachyrium platyphyllum*, *Hyparrhenia diplandra* or *Ctenium newtonii* and by a shrub layer with *Nauclea latifolia* and *Crossopteryx febrifuga* (White and Abernethy 1997). Forest patches are mainly secondary to mature okoumé rainforests, the dominant forest type in western Gabon, dominated by *Aucoumea klaineana* ("okoumé"), *Desbordesia glaucescens*, *Scyphocephalum ochochoa*, *Dacryodes buttneri*, *Santiria trimera*, *Sindoropsis letestui*, *Lophira alata* and *Uapaca guineensis* (Ben Yahmed and Pourtier 2004, White and Abernethy 1997).

Ivory Coast site: Research Station in the Taï Forest National Park. It is one of the last primary forests in western Africa, UNESCO Heritage, is bordered by the Sassandra river to the east, by Liberia to the west, by Peko and Saon Mts to the north and by Niéno Koué Mt. to the south. The park covers 3,300 km². Some entomological expeditions to Taï Forest were carried out in 2015–2017, managed by Philippe Moretto.

A series of specimens were examined from collections housed in the museums or collections cited below. Abbreviations used in this paper:

BMPC	Bruno Massa Collection, University of Palermo;
MfN	Museum für Naturkunde, Berlin;
MNHN	Museum national d'Histoire naturelle, Paris;
MRT	Museo Regionale di Storia Naturale, Terrasini (Palermo);
MSNG	Museo Civico di Storia Naturale 'G. Doria', Genoa;
NHMW	Naturhistorisches Museum, Vienna;
NHRS	Natural History Museum, Stockholm;
RBINS	Royal Belgian Institute Natural Sciences, Bruxelles.

Some specimens were photographed with a Nikon Coolpix 4500 digital camera, mounted on a Wild M5 Stereomicroscope or Leica MZ75 and photographs were integrated using the freeware CombineZP (Hadley 2008). Mounted specimens were measured with a digital calliper (precision 0.01 mm); the following measurements were taken (in mm): Body length: dorsal length from the head to the apex of the abdomen; Tegmina: length and maximum width of tegmina; Ovipositor: maximum length, subgenital plate included.

The shape of the stridulatory file under the male's left forewing and the number and arrangement of the teeth are useful characters that identify whether a species is bioacoustically separated from another one (Ragge 1980, Heller 2006). Therefore, the stridulatory file of each species was photographed and described.

Bioacoustics

Bioacoustical methods and terminology. The male calling songs of one specimen of a new species from Uganda (*Morgenia lehmannorum* Heller & Massa sp. n.) were

recorded in the laboratory using a digital bat detector (Pettersson D1000X; sampling rate 100 or 192 kHz). The sounds were analysed using the programmes Amadeus II (Martin Hairer; <http://www.hairersoft.com>) and Audacity (Audacity 2.1.0; <http://audacity.sourceforge.net>). For the frequency measurements, 8–12 ms sections were evaluated, using fast fourier transformation (FFT) analysis, hanning window, 512 points per frame, one or mean of several overlapping frames. Oscillograms of the songs were prepared using Turbolab (Bressner Technology, Germany). All recordings were made at temperatures between 20 and 21 °C. The singing insect was caged in a gauze cage with a microphone fixed at a distance of ca. 80 cm. Results are given as mean±standard deviation.

The following definitions describe the terminology used during this work:

Syllable: sound produced during one cycle of movements (opening and closing of the tegmina); syllable duration: time period measured from the first impulse to the last; impulse: a simple, undivided, transient train of sound waves (here: the damped sound impulse arising from the contact of one tooth of the stridulatory file with the scraper); pulse: undivided train of sound waves increasing in amplitude at the beginning and containing several similarly sized wave maxima and minima (cricket-like song structure).

Cytotaxonomic analysis

One male (CH7840) of *Morgenia lehmannorum* Heller & Massa sp. n. was used for cytotaxonomic analyses. The testes were incubated in a hypotonic solution (0.9% sodium citrate) and fixed in ethanol : acetic acid (3:1). The fixed material was stored in 70% ethanol at 2 °C until use. Subsequently, the testes were macerated in 45% acetic acid and squashed. The cover slips were removed using the dry ice procedure and the preparations were air dried. The C-banding examination was carried out according to Sumner (1972) and the silver staining method (with AgNO₃) for the nucleolar organiser region (NOR) was performed as previously reported (Warchalowska-Śliwa and Maryńska-Nadachowska 1992).

DNA barcoding

DNA barcoding, the analysis of a standardised segment of the mitochondrial cytochrome c oxidase subunit I (COI) gene, was performed on three specimens from Gabon in the project context: “ORGAA – Orthoptera of Gabon – Project 1 [ECOTROP 2014]” on Barcode of Life Data System (BOLD, Biodiversity Institute of Ontario, Canada; boldsystems.org). Tissues were sent to the Canadian Institute for DNA extraction, polymerase chain reaction (PCR) and sequencing. PCR was performed using the PCR primers C_LepFolF/C_LeFolR (Ratnasingham and Hebert 2007). Sequences were then analysed using BOLD 4.0 interface.

Results and discussion

Taxonomy

Characters of the genus *Morgenia* Karsch, 1890 (Tribe Poreuomenini Brunner von Wattenwyl, 1878)

Fastigium of vertex quite acuminate, not contiguous with fastigium of frons. Pronotum narrow, superiorly flat, anterior margin concave, posterior margin rounded, humeral sinus rounded, lateral lobes as wide as high, inferior margin rounded. Tegmina with rounded margins, wide mirror in the right tegmen. Wings exceeding tegmina a little. Legs slender, fore coxae armed, femurs inferiorly armed, fore tibiae with inner tympanum conchate, outer open; fore and mid tibiae superiorly sulcate, with spinules. Mid tibiae of males provided with an inner ventral moving spur before the apex, not exceeding the first tarsal article, longer or shorter depending on the species (with the exception of *M. modulata*, where it has a different shape); in the females, this spur is absent. Supra-anal plate nearly concave, cerci stout, curved and provided with an apical spine. Subgenital plate deeply concave, wide, without styli (Karsch 1890a, pers. obs.).

The species of the genus *Morgenia* have one of two types of cerci: a) club-shaped, with concave internal and rounded external part, armed at the apex; b) stout and incurved, with concave internal and rounded external part, armed at the apex. In addition, four lesser known facts have been highlighted: c) tegmina may be more or less wide and differences in the ratio length/width allow the separation of some species; d) costal area of tegmina may have a pattern with regularly spaced crossveins or a net of small cells; e) the inner ventral spur of the mid tibia has three different patterns; f) the stridulatory file is very characteristic for each species. Here the species are arranged by the type of cerci, according to their affinities.

The two final tables and relative photographs summarise the main characters of the species.

Annotated list of species

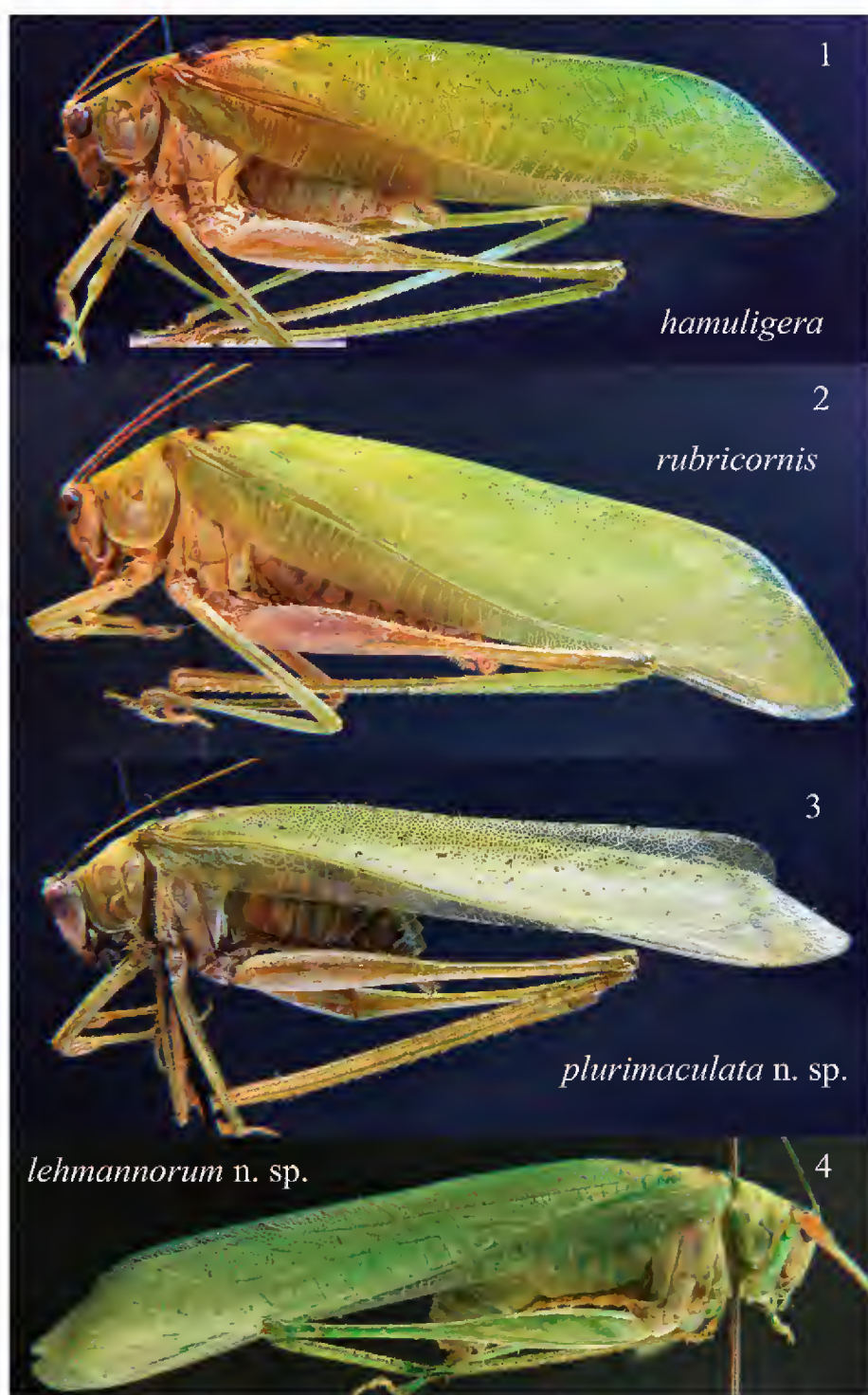
Morgenia hamuligera Karsch, 1890

Figs 1, 9, 13, 20, 27, 37, 38

Karsch, 1890a. Entom. Nachricht. 16: 263.

Type locality: Kribi (Cameroon) (MfN, Berlin).

Material examined. Cameroon, Kribi (holotype ♂) (MfN); Central African Republic, Sangha Special Reserve, Epiphyte 2008 Expedition, Camp 2, 22–23.X.2008 (light) (2♂), P. Annoyer; Central African Republic, Dzanga-Ndoki National Park, Ndoki, Lakes Region (light) 31.I.–23.II.2012 (10♂), Sangha2012 team; Mbo-ki, 24.I.2012 (3♂), Sangha2012 team; 35 km S Bangui, env. Salanga, 28–31.XII.2008, J. Halada (1♂); Gabon, Lope National Park, SEGC-CIRMF 12.III.2013 (light), N. Moulin (1♂); Ivory Coast, Taï Nat. Park, Res. Station



Figures 1–4. Habitus of the male of *Morgenia hamuligera* (1), *M. rubricornis* (2), *M. plurimaculata* sp. n. (3) and *M. lehmannorum* sp. n. (4) (left side for the first three species, right side for the fourth species).

16–20.III.2017 (light), B. Massa (5♂); Ivory Coast, Taï Nat. Park, Res. Station 22.III-4.IV.2017 (light) (7♂, 1♀), P. Moretto (BMPC).

Distribution. *M. hamuligera* was the first species described in the genus *Morgenia*, from Kribi (Cameroon) and later reported from Barombi Station (Cameroon) (Karsch 1890a, 1890b). Griffini (1906, 1908) recorded it from Fernando Poo (Equatorial Guinea) and Umangi (Democratic Republic of Congo), Ebner (1943) from Fernando Poo and Massa (2013) from Central African Republic. It is here reported from Gabon and Ivory Coast.

Remarks. The short description by Karsch (1890a) points out the presence of a blackish spot on the stridulatory area of the left tegmen; the shape of this spot is similar to that of *M. rubricornis* (see below), but its inner margin is more or less rectangular, not triangular, as in *rubricornis* (Figs 9, 10, 13, 14). The mirror of the right tegmen is wide (Fig. 9). Antennae may be yellowish or reddish. The pattern of the costal area of the tegmina has regularly spaced crossveins (Fig. 9). The stridulatory file is 3.5 mm long, arched and composed of ca. 80 dense

and evenly spaced teeth in the proximal part, followed by ca. 70 more or less widely spaced teeth in the distal part (Fig. 20). The inner ventral spur of the mid tibiae is long and does not exceed the first tarsal article; its length is about 18–20% of the tibia length. On the outer ventral margin of the mid tibiae, three close short spines are present (Fig. 27). Cerci are very stout, club-shaped, the ratio tegmina length/width is 4.0 (Figs 37–38, Table 1).

Morgenia rubricornis Sjöstedt, 1913

Figs 2, 10, 14, 20, 28, 35, 36

Sjöstedt, 1913. Ark. Zool. 8 (6): 4.

Type locality: Mukimbungu (Democratic Republic of the Congo) (NHRS Stockholm).

Material examined. **Central African Republic**, Dzanga-Ndoki National Park, (light) 22.X.2008 (light), P. Annoyer (1♂); same data 24.II.2012 (light), P. Annoyer (1♂); 31.I.–29.II.2012 (11♂, 1♀) (light), Sangha2012 team; **Gabon**, Lope National Park Res. Station, Ogooue-Ivindo 28–31.III.2014 (light), (2♂, BOLD LopeORT14-617 and -673) (light), ecotrop 2014 team; **Ivory Coast**, Korhogo, Kogo 21.VII.2014 (1♂) (light), P. Moretto; Man Mt. Tonkoui (1200 m) 28.VI-1.VII.2014, 18–20.VI.2015 (2♂) (light), P. Moretto; Touba, Biémasso 10–11.VII.2013 (1♂) (light), P. Moretto; Taï National Park, Res. Station 20.III.2017 (light), B. Massa (1♂) (BMPC).

Distribution. *M. rubricornis* was known only from the type locality; however, it has also been found in Central African Republic, Gabon and Ivory Coast (see material examined). Thus, its distribution probably covers central and western tropical Africa.

Remarks. According to Sjöstedt (1913), *M. rubricornis* was the largest species of the genus known at that time. He also reported measurements of the length and width of the tegmina (39.0 and 12.0) of the holotype; even if his values are much higher than those of specimens measured by us, the ratio length/width of the tegmina (3.25) lies within the variability observed in this taxon (Table 1). The male of this species is easily identifiable by its dark spot in the left tegmen; it has a larger base and a narrower tip than that of *M. hamuligera* (compare Figs 9, 10, 14). The mirror of the right tegmen is smaller than in *M. hamuligera* (Fig. 10). Antennal segments are generally reddish (from this character the name *rubricornis*). The pattern of the costal area of the tegmina has regularly spaced crossveins (Fig. 10). The inner ventral spur of the mid tibiae is short, more or less directed upwards and reaches the middle of the first tarsal article; its length is about 4.5–5.0% of the tibia length. On the outer ventral margin of the mid tibiae, three close short spines are present (Fig. 28). The stridulatory file is 2.2 mm long, arched and composed of ca. 60 dense and evenly spaced teeth in the proximal part, followed by ca. 50 widely spaced teeth in the distal part (Fig. 20). The subgenital plate of the male in ventral view is very similar to that of *M. hamuligera*, while, in the lateral view, it appears more upwards bent (compare Figs 35–36 with 37–38).

Table 1. Measurements of tegmina length and width and ratio of tegmina length/width of the eight species currently known in the genus *Morgenia*.

Species	Tegmina length	Tegmina width	Tegmina length/width
<i>Morgenia hamuligera</i> (n = 10) ¹	33.2±1.4 (30.3–34.9)	8.3±0.4 (8.0–9.2)	4.0±0.3 (3.5–4.2)
<i>Morgenia rubricornis</i> (n = 10)	29.4±1.1 (27.5–30.2)	7.5±0.5 (7.0–8.5)	3.9±0.2 (3.3–4.2)
<i>Morgenia spathulifera</i> (n = 5)	29.6±1.4 (27.9–31.4)	4.5±0.1 (4.3–4.6)	6.6±0.2 (6.4–6.8)
<i>Morgenia plurimaculata</i> sp. n. (n = 10)	34.1±0.9 (33.0–35.7)	8.0±0.2 (7.8–8.5)	4.2±0.1 (4.1–4.4)
<i>Morgenia lehmannorum</i> sp. n. (n = 1)	32.5	5.4	6.0
<i>Morgenia angustipinnata</i> sp. n. (n = 4)	32.0±1.7 (30.5–33.9)	5.0±0.4 (4.7–5.4)	6.4±0.1 (6.3–6.5)
<i>Morgenia melica</i> (n = 10)	34.3±2.2 (29.0–36.9)	7.6±0.3 (7.0–8.0)	4.5±0.2 (4.1–4.8)
<i>Morgenia modulata</i> (n = 10)	30.4±0.9 (29.1–31.4)	6.7±0.5 (6.0–7.6)	4.5±0.2 (4.1–4.9)

¹ Massa (2017a) reports 5.5–5.6 as ratio length/width of tegmina in *M. hamuligera* and *M. rubricornis*, but more accurate measurements allowed to change them to 4.0 and 3.9, respectively.

Morgenia spathulifera Griffini, 1908

Figs 5, 11, 23, 32, 43, 44

Griffini, 1908. Mem. Soc. entom. Belgique, Bruxelles 15: 209.

Type locality: Bussanga (Democratic Republic of Congo) (RBINS, Bruxelles).

Material examined. Democratic Republic of the Congo, Bussanga 14.XI.1905 (1♂ syntype); Ngowa 9.I.1939 (1♂), J. Mertens; **Cameroon,** Mukonje Farm, R. Rohde (1♀ syntype); Mt Koupe 31.I-8.II.1983 (1♂), J. van Stalle (RBINS); **Ivory Coast,** Tai Nat. Park, Res. Station 13.III.2017 (1♂) (light), B. Massa; Tai Nat. Park, Res. Station 22.III-4.IV.2017 (2♂) (light), P. Moretto (BMPC).

Distribution. *M. spathulifera* is presently known from Cameroon, Democratic Republic of the Congo and Ivory Coast (Griffini 1908, Massa 2017). We presume that it covers central and western tropical forests of Africa.

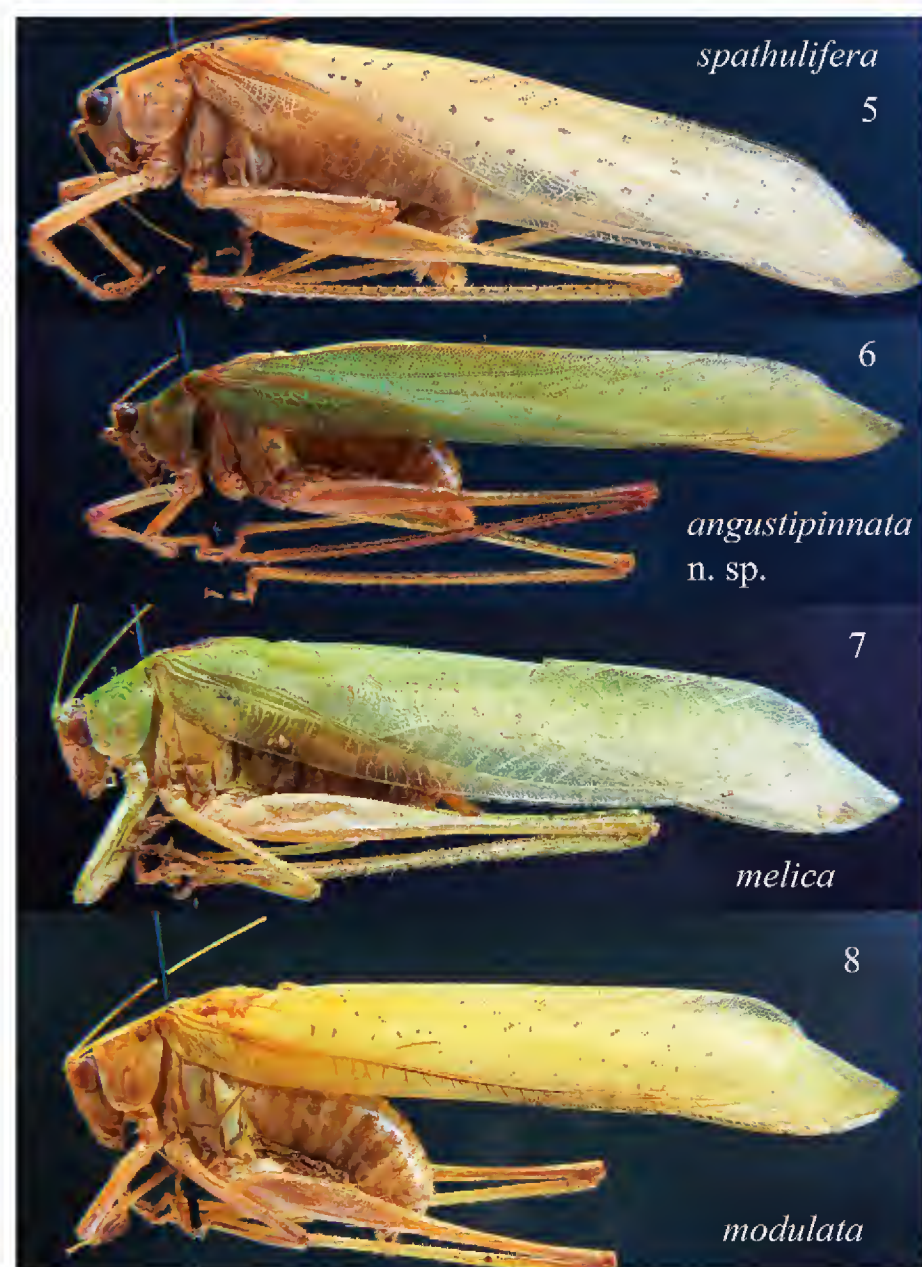
Remarks. *M. spathulifera* may be easily separated from other known species by the ratio length/width of the tegmina (6.4–6.8). It is also characterised by the presence of small grey dots on the tegmina and costal area of the tegmina with a net of small cells (Figs 5, 11). The stridulatory area of the left tegmen is protruding below its posterior margin and it is composed of the stridulatory file and has a raised parallel posterior bulge (Fig. 11). The mirror of the right tegmen is smaller than in *M. hamuligera* (Fig. 11). The stridulatory file is 1.2 mm long, arched and composed of ca. 60 densely spaced teeth (Fig. 23). The inner ventral spur of mid tibiae is more apical, short, up- and incurved and does not exceed the base of the first tarsal article; its length is about 2.5–3.0% the length of tibia. On the outer ventral margin of the mid tibiae, three close short spines are present (Fig. 32).

Morgenia plurimaculata Massa & Moulin, sp. n.

<http://zoobank.org/E89917DE-ECC8-4A48-A0E5-6BA932D95018>

Figs 3, 15, 21, 29, 41, 42

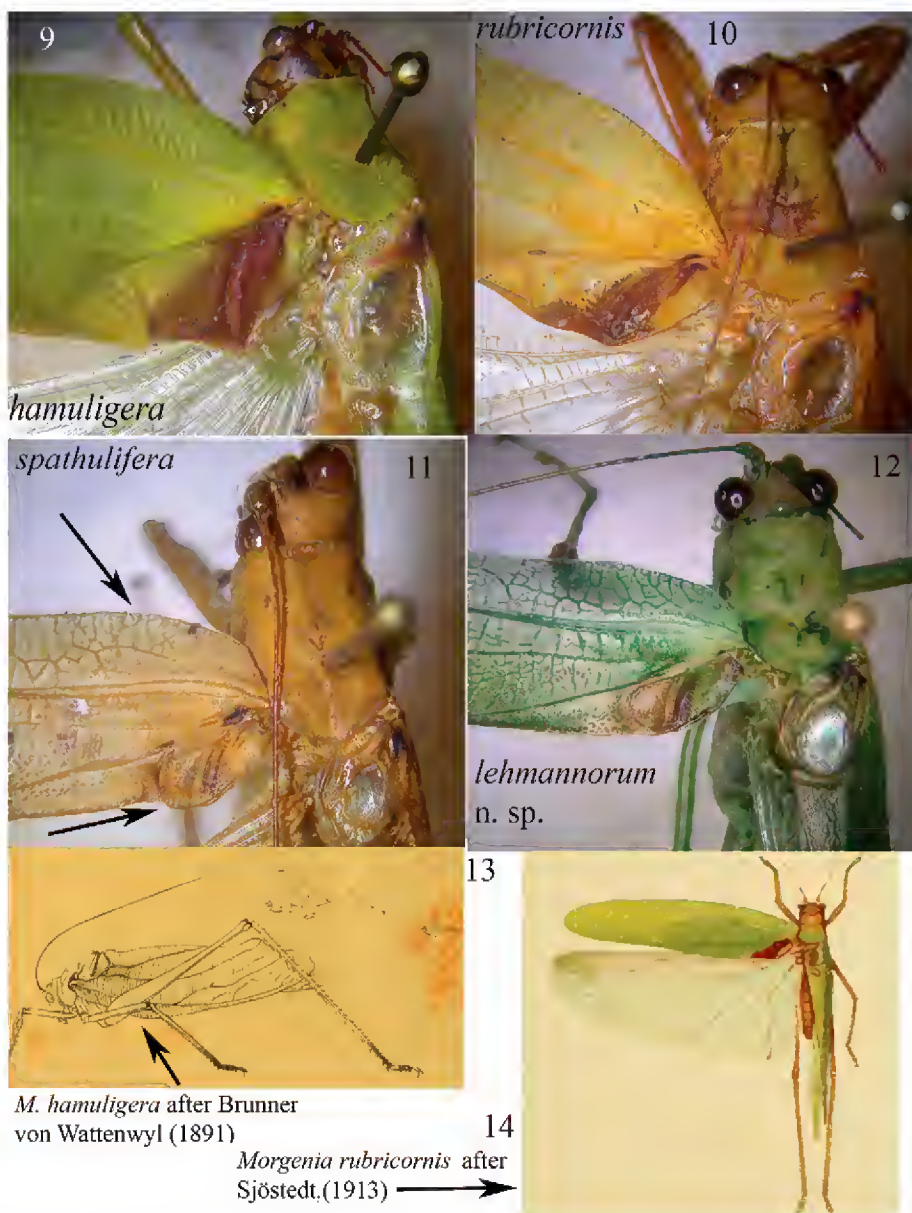
Material examined. Central African Republic, Dzanga-Ndoki National Park, Lakes Region (02°28'40.5"N, 16°13'02.6"E) 31.I.–29.II.2012 (light), Sangha2012



Figures 5–8. Habitus of the male of *Morgenia spathulifera* (5), *M. angustipinnata* sp. n. (6), *M. melica* (7) and *M. modulata* (8) (left side).

team (1♂ holotype, 19♂ and 3♀ paratypes); Mboki (5°18'31"N, 25°57'16"E) 24.I.2012 (2♂ paratypes) (♂ holotype and 1♀ paratype in the MSNG, other paratypes in BMPC); Sangha Special Reserve, Epiphyte 2008 Expedition, Camp 2, 21.X.2008 (light), P. Annoyer (1♂ paratype); 30.I-4.II.2012 (light), Sangha2012 team (2♂, 1♀ paratypes) (1♂ and 1♀ paratypes in the MNHN, other paratypes in BMPC). Some specimens here listed were erroneously identified by Massa (2013) as *M. hamuligera*.

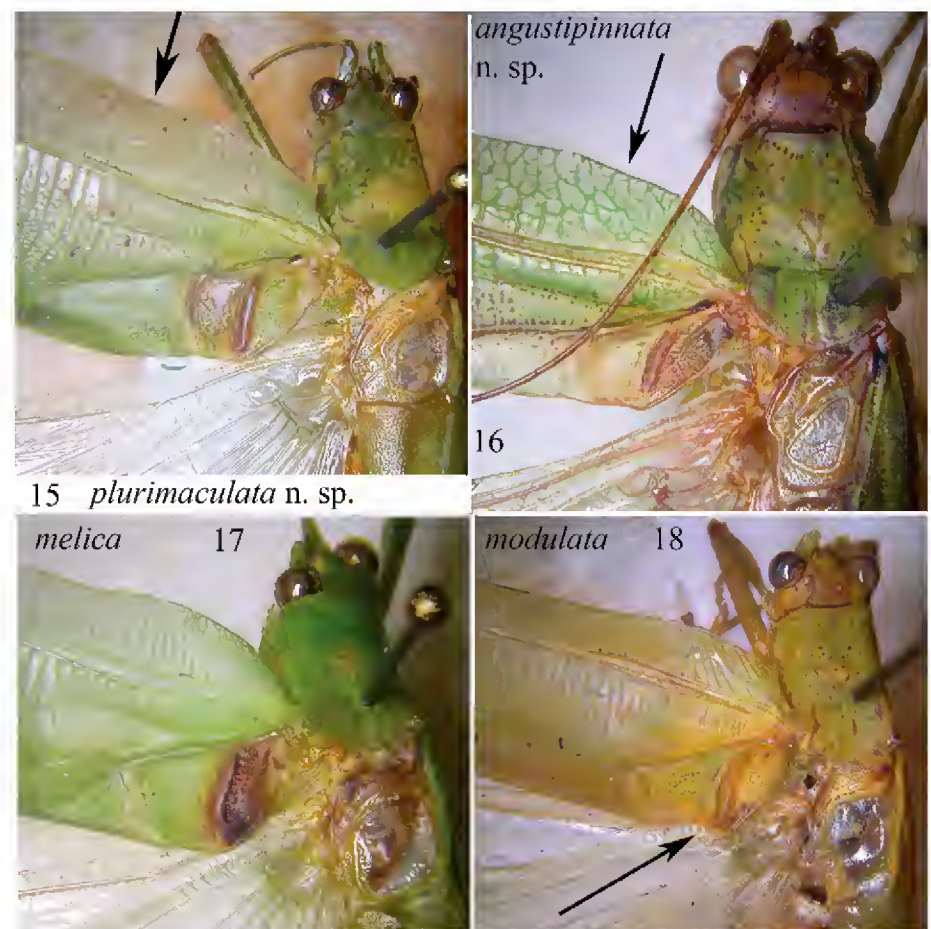
Distribution. At the present time, known only from the type locality, Dzanga-Ndoki National Park (Central African Republic).



Figures 9–14. Stridulatory area of left tegmen and mirror of right tegmen of the male of *Morgenia hamuligera* (9), *M. rubricornis* (10), *M. spathulifera* (11), *M. lehmannorum* sp. n. (12); habitus of *M. hamuligera* after Brunner von Wattenwyl (1878) (13) and of *M. rubricornis* after Sjöstedt (1913) (14). Arrow shows the particular net of small cells in the costal area of tegmina of *M. spathulifera*, present also in *M. lehmannorum* sp. n.

Colour. Head and pronotum yellow-green with scattered brown spots, antennae yellowish, abdomen yellow-brown, cerci yellow-blackish, tegmina with a black spot at their base, green with black stridulatory area and small brown spots between cells; in some specimens, the black area is lacking. One black spot between tympana of fore tibiae is found only in males.

Description. Males. Head and antennae. Fastigium of vertex narrow, sulcate above, not contiguous with fastigium of frons. Eyes rounded, well projecting. Antennae longer than body. Legs. Fore coxae armed with a fine spine. Fore tibiae furrowed on upper margin, distinctly widening above tympanum, conchate on inner, open on outer side. Fore femora armed on inner ventral side with 6 small spines, fore tibiae with 4 spines + 1 spur on inner side and 3 spines + 1 spur on outer ventral side, mid femora unarmed, mid tibiae with 4–5 outer and 2–3 inner ventral spines. The inner ventral spur of mid tibiae is short and does not exceed the first tarsal article; its length is about 5.0–5.5% the length of tibia. On the outer ventral margin of mid tibiae, three closely set short spines are present (Fig. 29). Hind femora armed with 3–4 small spines on outer and 2–3 on inner ventral sides, hind tibiae with many spines on ventral and dorsal sides + 3 spurs



Figures 15–18. Stridulatory area of left tegmen and mirror of right tegmen of the male of *Morgenia plurimaculata* sp. n. (15), *M. angustipinnata* sp. n. (16), *M. melica* (17) and *M. modulata* (18). Arrows in *M. plurimaculata* sp. n. and *M. angustipinnata* sp. n. show the net of small cells in costal area of their tegmina, while in *M. modulata* the protruding stridulatory area.

on each side. Thorax. Pronotum narrowing at the level of the humeral sinus, flat above, lateral margins rounded, anterior margin incurved, posterior rounded, humeral sinus well developed, lobes of pronotum rounded. Tegmina narrow with rounded apices (Figs 3, 15, measurements in Table 1), wings longer than tegmina. Stridulatory area of the left tegmen composed of the stridulatory file and of a raised parallel posterior bulge (Fig. 13). Mirror of the right tegmen smaller than in *M. hamuligera* (Fig. 15). Pattern of costal area of tegmina with a net of small cells; stridulatory file 2.8 mm long, arched and composed of ca. 90 widely spaced teeth (Fig. 21). Cerci club-shaped with an apical spine, the inner part is concave, the outer rounded. Subgenital plate widely concave in ventral view with tips downwards bent in lateral view (Figs 41, 42).

Females. Same characters of the males except for the following. The colour of fore legs is yellow without the black spot between tympana. Also, tegmina lack the black area but have small brown spots between cells. Interestingly, the costal area of tegmina differs from that of males by the regularly spaced crossveins. Ovipositor gently up-curved, 6.8–7.0 mm long, tips finely toothed. Cerci long and pointed, subgenital plate narrow and pointed.

Diagnosis. *M. plurimaculata* sp. n. is characterised by club-shaped cerci, a short spur on the mid tibia, the stridulatory area with a small dark spot, many small dark spots scattered on tegmina in most specimens, pattern of the costal area of tegmina with a net of small cells and a stridulatory file that is 2.8 mm long, arched and composed of ca. 90 widely spaced teeth. The stridulatory area is composed of the stridulatory file and of a raised parallel

posterior bulge. Differences to other species of the genus are summarised in Table 2.

Etymology. From Latin *plus pluris* = many and *maculata* = provided with spots.

***Morgenia lehmannorum* Heller & Massa, sp. n.**

<http://zoobank.org/D2D2EC20-466B-4F8C-A819-09FC9BEEA163>

Figs 4, 12, 22, 30, 39, 40

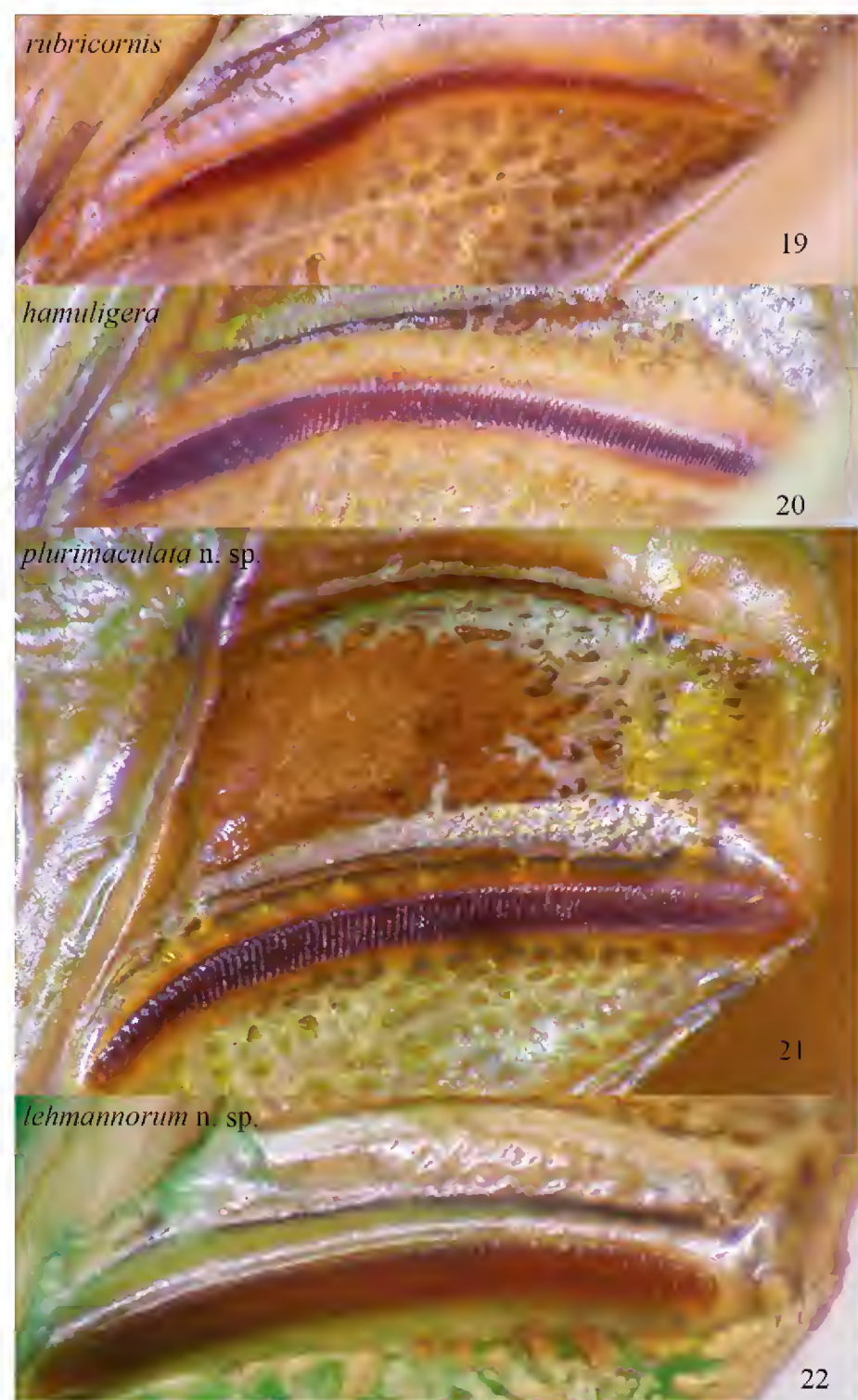
Material examined. Uganda, Semliki Forest National Park (00°49'30"N, 30°03'40"E) 1–31.VIII.2014, A. and G. Lehmann (♂ holotype) (MfN).

Distribution. Presently known only from the type locality, Semliki Forest (Uganda).

Colour. Green, with the exception of tympana of fore legs that are brown and one black spot between tympana. Stridulatory area brownish. Black spots at the base of tegmina.

Description. Males. Head and antennae. Fastigium of vertex narrow, sulcate above, not contiguous with fastigium of frons. Eyes rounded, well projecting. Legs. Fore coxae armed with a fine spine. Fore tibiae furrowed on upper margin, distinctly widening above tympanum, conchate on inner, open on outer side. Fore femora armed on inner ventral side with 4 small spines, fore tibiae with 2 spines + 1 spur on inner ventral side and 1 spine + 1 spur on outer ventral side, mid femora unarmed, mid tibiae with 2 outer and 2 inner ventral spines, inner ventral spur of mid tibiae long, up-curved, exceeding $\frac{3}{4}$ of the first tarsal article; its length is about 10% the length of tibia. On the outer ventral margin of mid tibiae, three close short spines are present (Fig. 30). Hind femora armed with 3 small spines on outer and 3 on inner ventral sides, hind tibiae with many spines on ventral and dorsal sides + 3 spurs on each side. Thorax. Pronotum narrowing at the level of the humeral sinus, flat above, lateral margins rounded, anterior margin straight, posterior rounded, humeral sinus well developed, lobes of pronotum rounded. Tegmina narrow with rounded apices (Figs 4, 12, measurements in Table 1), wings longer than tegmina. Stridulatory area of the left tegmen raised (Fig. 12). Mirror of the right tegmen smaller than in *M. hamuligera* (Fig. 12). Pattern of costal area of tegmina with a net of small cells; stridulatory file 1.8 mm long, arched and composed of ca. 100 teeth; the distal teeth of the stridulatory file are more widely spaced than the proximal ones, that are also more densely set together (Fig. 22). Cerci club-shaped with an apical spine, the inner part is concave, the outer rounded. Subgenital plate with a small apical concavity in ventral view with tips straight in lateral view (Figs 39, 40).

Diagnosis. *M. lehmannorum* sp. n. is characterised by narrow tegmina (Table 1), club-shaped cerci, a long and up-curved spur on the mid tibia, the stridulatory area brown, the costal area of tegmina with a net of small cells and the stridulatory file that is 1.8 mm long, arched and composed of ca. 100 teeth, the distal teeth are more widely, the proximal ones more closed set. Differences to other species of the genus are summarised in Table 2.



Figures 19–22. Stridulatory file of the left tegmen in the male of *Morgenia rubricornis* (19), *M. hamuligera* (20), *M. plurimaculata* sp. n. (21) and *M. lehmannorum* sp. n. (22).

Etymology. We have the pleasure to dedicate this species to the German orthopterologists Arne and Gerlind Lehmann, who collected the only known specimen.

***Morgenia angustipinnata* Massa, sp. n.**

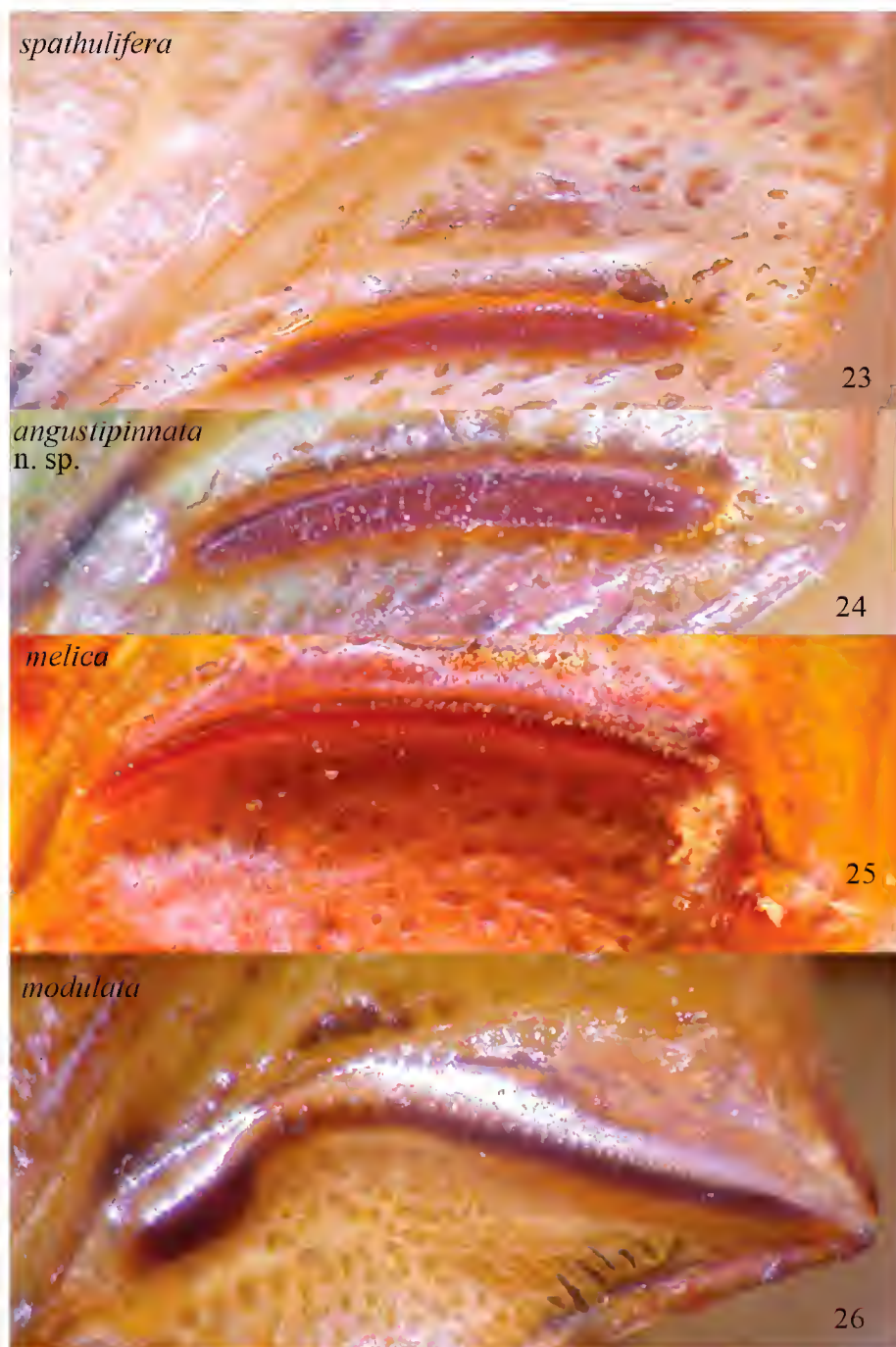
<http://zoobank.org/254C7B6A-00DD-4663-B44B-B0008D2587AF>

Figs 6, 16, 24, 31, 45, 46

Material examined. Central African Republic, Dzanga-Ndoki National Park, Mboki (5°18'31"N, 25°57'16"E), 24.I.2012 (light), Sangha2012 team (1♂ holotype, MSNG); Dzanga-Sangha Special Reserve at 35m on canopy of *Terminalia superba* (02°20'03.0"N, 16°08'11.2"E, 375m) 9.II.2005, P. Annoyer (1♂ paratype, BMPC); same locality 13–23.II.2012 (light), Sangha2012 team (2♂ paratypes, BMPC).

Distribution. At the present time, known only from the type locality, Dzanga-Ndoki National Park (Central African Republic).

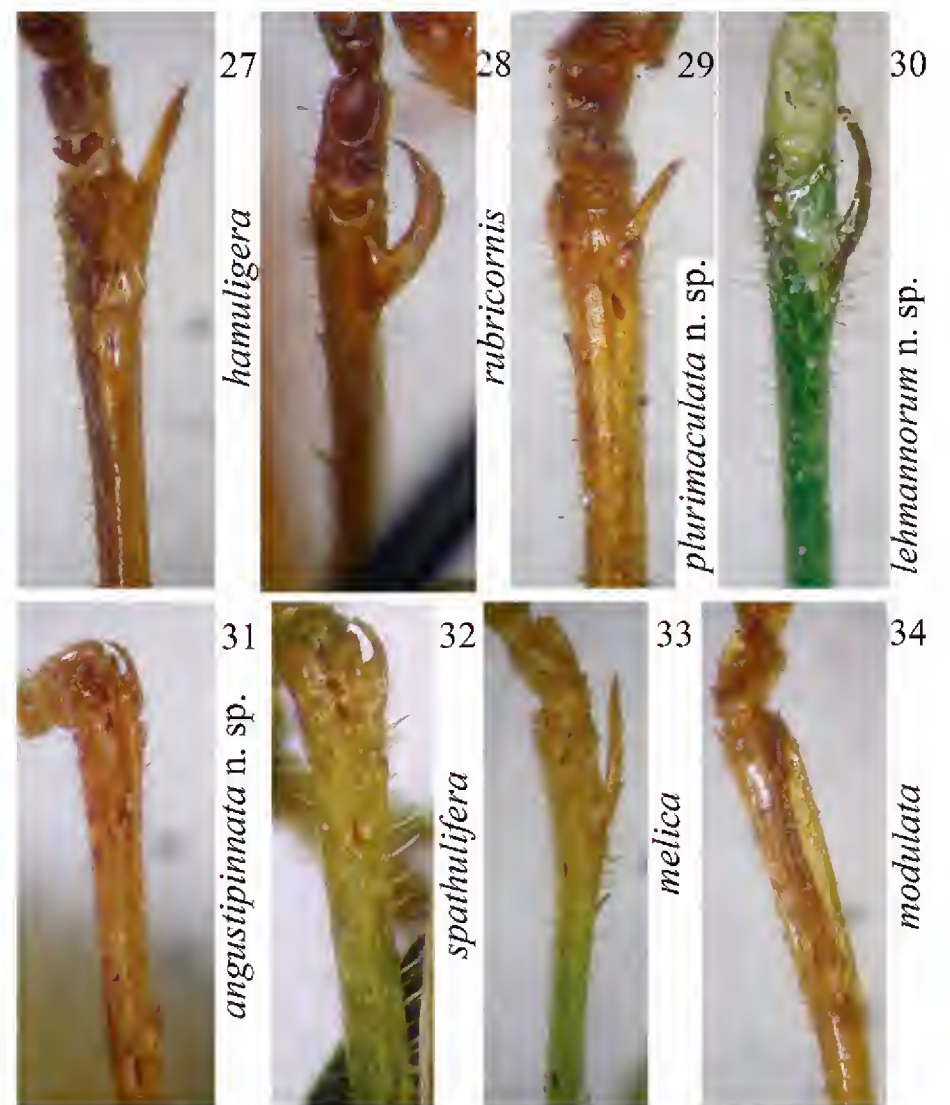
Colour. Head and pronotum yellow-green, antennae yellowish, abdomen yellow-brown, cerci yellow, tegmina



Figures 23–26. Stridulatory file of the left tegmen in the male of *Morgenia spathulifera* (23), *M. angustipinnata* sp. n. (24), *M. melica* (25) and *M. modulata* (26).

with a black line at base, green with brownish stridulatory area. One black spot between tympana of fore tibiae.

Description. Males. Head and antennae. Fastigium of vertex narrow, sulcate above, not contiguous with fastigium of frons. Eyes rounded, well projecting. Antennae longer than body. Legs. Fore coxae armed with a small spine. Fore tibiae furrowed on upper margin, distinctly widening above tympanum, conchate on inner, open on outer side. Fore femora armed on inner ventral side with 3–4 small spines, fore tibiae with 3 spines + 1 spur on inner side and 3 spines + 1 spur on outer ventral side, mid femora with 4–5 spines on outer ventral side, mid tibiae with 6–7 spines on outer and 3–4 on inner ventral sides. The inner ventral spur of mid tibiae is more apically located, short, up-curved and does not exceed the base of the first tarsal article; its length is about 2.5–3.0% the length of tibia. On the outer ventral margin of mid tibiae, three close short spines are present (Fig. 31). Hind femora armed with 3–4 small spines on outer and on inner ventral sides, hind tibiae with many spines on ventral and dorsal sides + 3 spurs on each side. Thorax. Pronotum narrowing at the level of the humeral sinus, flat above, lateral margins rounded, anterior margin incurved, posterior margin rounded, humeral sinus well developed, lobes of pronotum rounded. Tegmina very narrow with rounded



Figures 27–34. Mid tibia showing the inner spur in the male of *Morgenia hamuligera* (27), *M. rubricornis* (28), *M. plurimaculata* sp. n. (29), *M. lehmannorum* sp. n. (30), *M. angustipinnata* sp. n. (31), *M. spathulifera* (32), *M. melica* (33) and *M. modulata* (34).

apices (Figs 6, 16, measurements in Table 1), wings longer than tegmina. Stridulatory area of the left tegmen raised and stout. Mirror of the right tegmen smaller than in *M. hamuligera* (Fig. 14). Costal area of tegmina with a net of small cells (Fig. 16); stridulatory file 1.7 mm long, arched, composed of ca. 70 widely spaced teeth (Fig. 24). Cerci club-shaped with an apical spine, the inner part is concave, the outer rounded. Subgenital plate long and narrow, with a small concavity, interior margins undulate in ventral view with tips rather straight in lateral view (Figs 45, 46).

Diagnosis. Tegmina of *M. angustipinnata* sp. n. are very narrow (Table 1); their costal area has a net of small cells. The stridulatory file is 1.7 mm long, arched, composed of ca. 70 widely spaced teeth and the spur of the mid tibia is very short. Differences to other species of the genus are summarised in Table 2.

Etymology. From Latin *angusta* = narrow, and *pinnata* = winged.

Morgenia melica Karsch, 1893

Figs 7, 17, 25, 33, 47, 48

Karsch, 1893. Entom. Nachricht. 19 (13): 196.

Type locality: Victoria (Cameroon) (MfN, Berlin).

Material examined. Cameroon, Victoria (holotype ♂) (MfN); Gabon, Lope National Park Res. Station, Ogooue-Ivindo 28.III.2014, (1♂, BOLD LopeORT14-618)

Table 2. Main characters that allow the separation of males of the eight species of the genus *Morgenia*.

	Spot on stridulatory area	Costal area of tegmina	Stridulatory file	Cerci	Subgenital plate (ventral)	Subgenital plate (lateral)	Spur of mid tibia
<i>Morgenia hamuligera</i>	Blackish, rectangular (Figs 9, 54)	Spaced crossveins (Fig. 13)	3.5 mm long (80 dense + 70 widely spaced teeth) (Fig. 20)	Club-shaped (Fig. 37)	Widely concave (Fig. 37)	Rather straight (Fig. 38)	Long and pointed (Fig. 27)
<i>Morgenia rubricornis</i>	Blackish, triangular (Figs 10, 14)	Spaced crossveins (Fig. 10)	2.2 mm long (60 dense + 50 widely spaced teeth) (Fig. 20)	Club-shaped (Fig. 35)	Widely concave (Fig. 35)	Tips up-curved (Fig. 36)	Long and more or less up-curved (Fig. 28)
<i>Morgenia spathulifera</i>	Very few small spots on tegmina (Fig. 11)	Net of small cells (Fig. 11)	1.2 mm long (60 densely spaced teeth) (Fig. 23)	Club-shaped (Fig. 43)	Concave, interior margins undulate (Fig. 43)	Rather straight (Fig. 44)	Very short and up-curved (Fig. 32)
<i>Morgenia plurimaculata</i> sp. n.	Few scattered spots on tegmina in most specimens (Figs 15, 55)	Net of small cells (Fig. 15)	2.8 mm long (90 widely spaced teeth) (Fig. 21)	Club-shaped (Fig. 41)	Widely concave (Fig. 41)	Tips down-curved (Fig. 42)	Short and pointed (Fig. 29)
<i>Morgenia lehmannorum</i> sp. n.	Very few (Figs 12, 56)	Net of small cells (Fig. 12)	1.8 mm long (ca. 100 teeth, distal more widely spaced than proximal) (Fig. 22)	Club-shaped (Fig. 39)	Small apical concavity (Fig. 39)	Rather straight (Fig. 40)	Long and up-curved (Fig. 30)
<i>Morgenia angustipinnata</i> sp. n.	Very few, brownish (Fig. 16)	Net of small cells (Fig. 16)	1.7 mm long (70 widely spaced teeth) (Fig. 24)	Club-shaped (Fig. 45)	Long and narrow, small concavity, interior margins undulate (Fig. 45)	Rather straight (Fig. 46)	Very short and up-curved (Fig. 31)
<i>Morgenia melica</i>	Blackish, more or less square (Fig. 17)	Spaced crossveins (Fig. 17)	2.3 mm long (70 widely spaced teeth) (Fig. 25)	Slender, apically flattened (Fig. 47)	Widely concave, tips divergent (Fig. 47)	Tips up-curved (Fig. 48)	Long and pointed (Fig. 33)
<i>Morgenia modulata</i>	Very few, nearly absent (Fig. 18)	Spaced crossveins (Fig. 18)	3.0 mm long (100 dense, + ca. 20 widely and ca. 30 evenly spaced) (Fig. 26)	Slender, apically flattened (Fig. 49)	Widely concave with right base (Fig. 49)	Tips gently up-curved (Fig. 50)	Long but enclosed inside the tibia (Fig. 34)

(light), ecotrop 2014 team; **Central African Republic**, Dzanga-Ndoki National Park, 31.I.–29.II.2012 (light) (19♂), Sangha2012 team; Mboki 24.I.2012 (1♂), Sangha2012 team; **Ivory Coast**, Tâi National Park, Res. Station 16–20. III.2017 (light) (3♂, 1♀), B. Massa; 22.III–4.IV.2017 (light) (26♂), P. Moretto (BMPC); **Democratic Republic of the Congo**, Hombo 22.XII.1970, T. De Stefani (1♂) (MRT).

Distribution. *M. melica* is known from Cameroon, Democratic Republic of the Congo, Central African Republic, Uganda, Gabon and Ivory Coast (Karsch 1893, Massa 2013, Holstein 2015, present paper).

Remarks. The left tegmen of *M. melica* has a small brown spot covering only the stridulatory area, costal area of tegmina has regularly spaced crossveins (Fig. 17) and cerci are slender, apically flattened and end with a small inner spine (Figs 47, 48). The mirror of the right tegmen is as wide as in *M. hamuligera* (Fig. 17). The stridulatory file is 2.3 mm long, arched and composed of ca. 70 widely spaced teeth (Fig. 25). The inner ventral spur of mid tibiae is long and does not exceed the first tarsal article; its length is about 12–12.5% the length of the tibia. On the outer ventral margin of mid tibiae, three close short spines are present (Fig. 33).

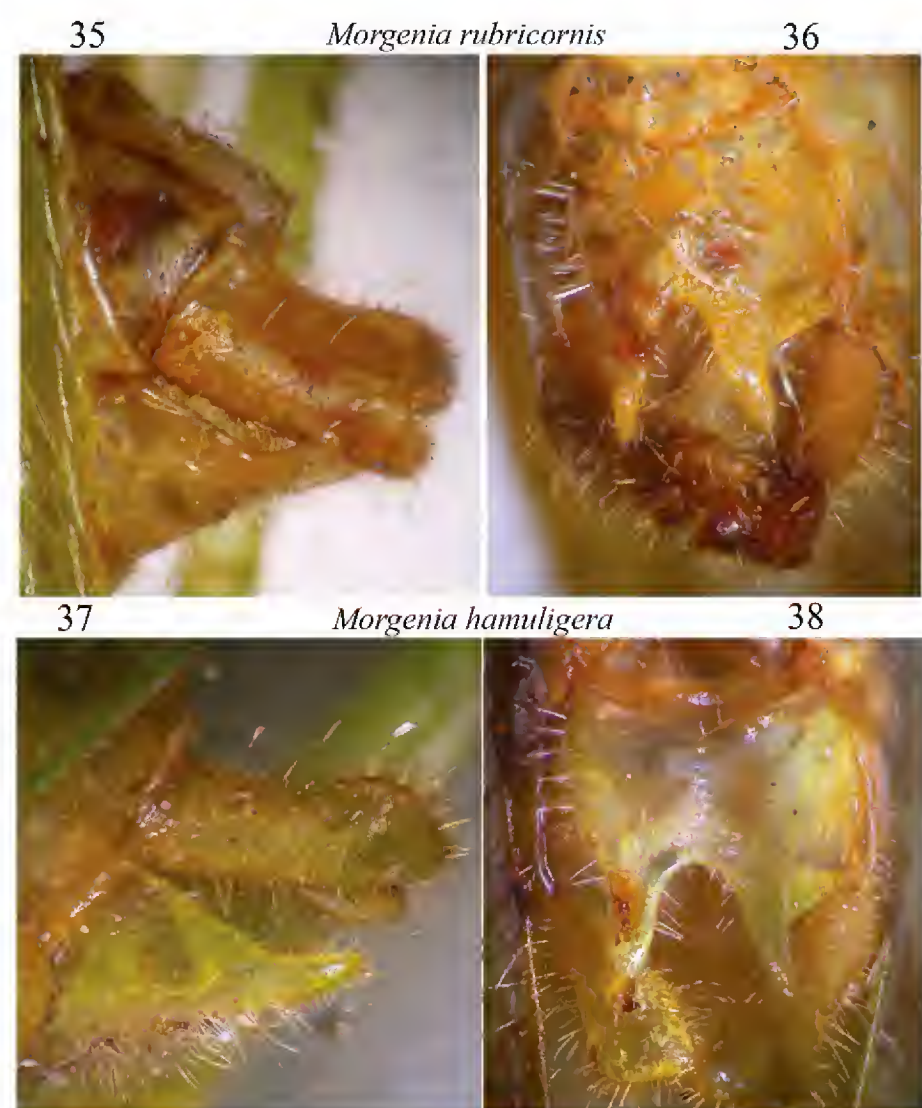
Morgenia modulata Karsch, 1896

Figs 8, 18, 26, 34, 49, 50

Karsch, 1896. Stett. Entomol. Z. 57: 340.

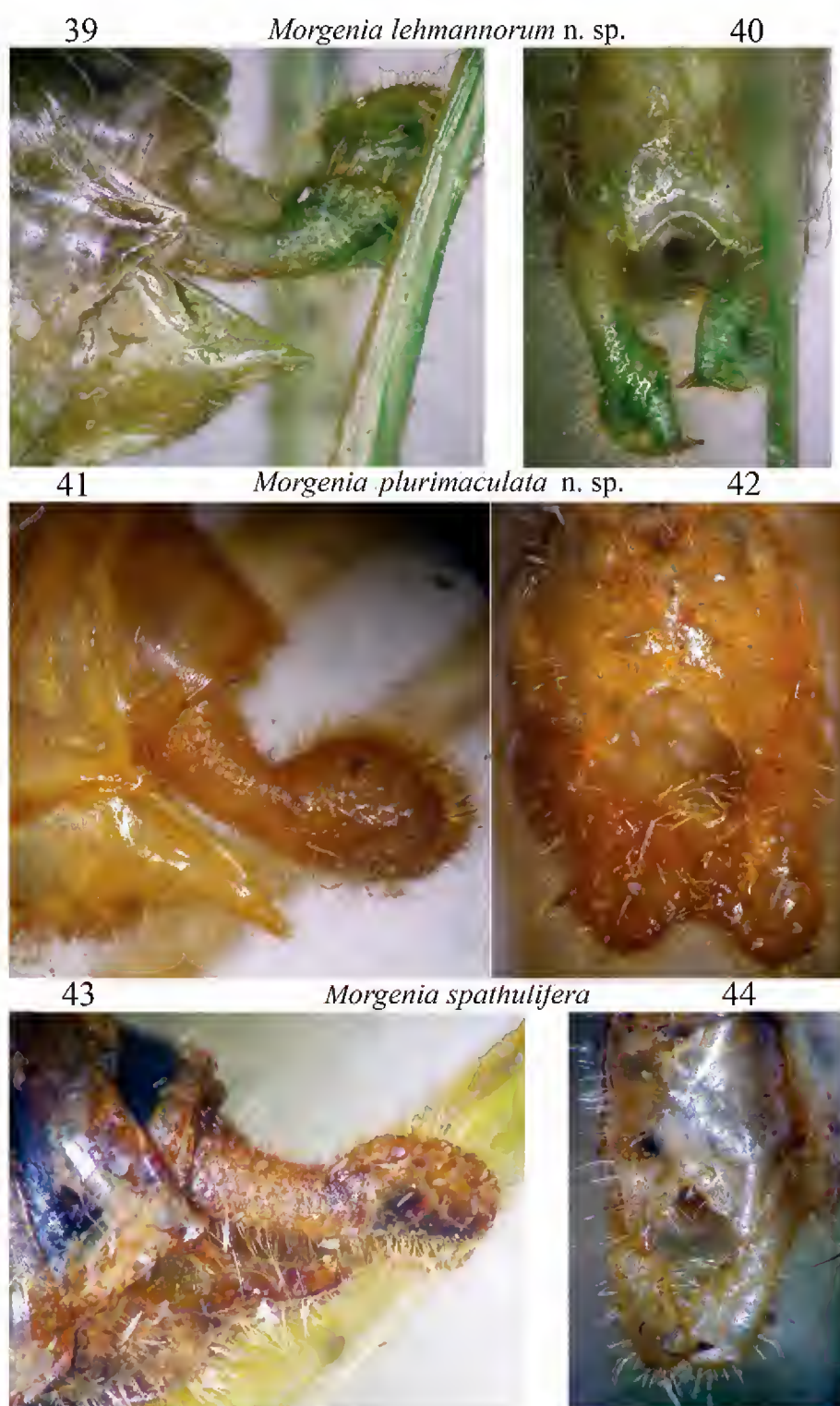
Type locality: Lolodorf (Cameroon) (MfN, Berlin).

Material examined. **Cameroon**, Lolodorf, L. Conradt (♂, ♀ syntypes, labeled as *Morgenia maculata*); Johann



Figures 35–38. Cerci and subgenital plate of male of *Morgenia rubricornis* (35 lateral, 36 ventral) and *M. hamuligera* (37 lateral, 38 ventral).

Albrechtshöhe, L. Conradt (♂, labeled as *M. maculata*) (MfN); **Central African Republic**, Sangha Special Reserve, Epiphyte 2008 Expedition, Camp 2, 22.X.2008 (light) (1♂), P. Annoyer; Dzanga-Ndoki National Park,



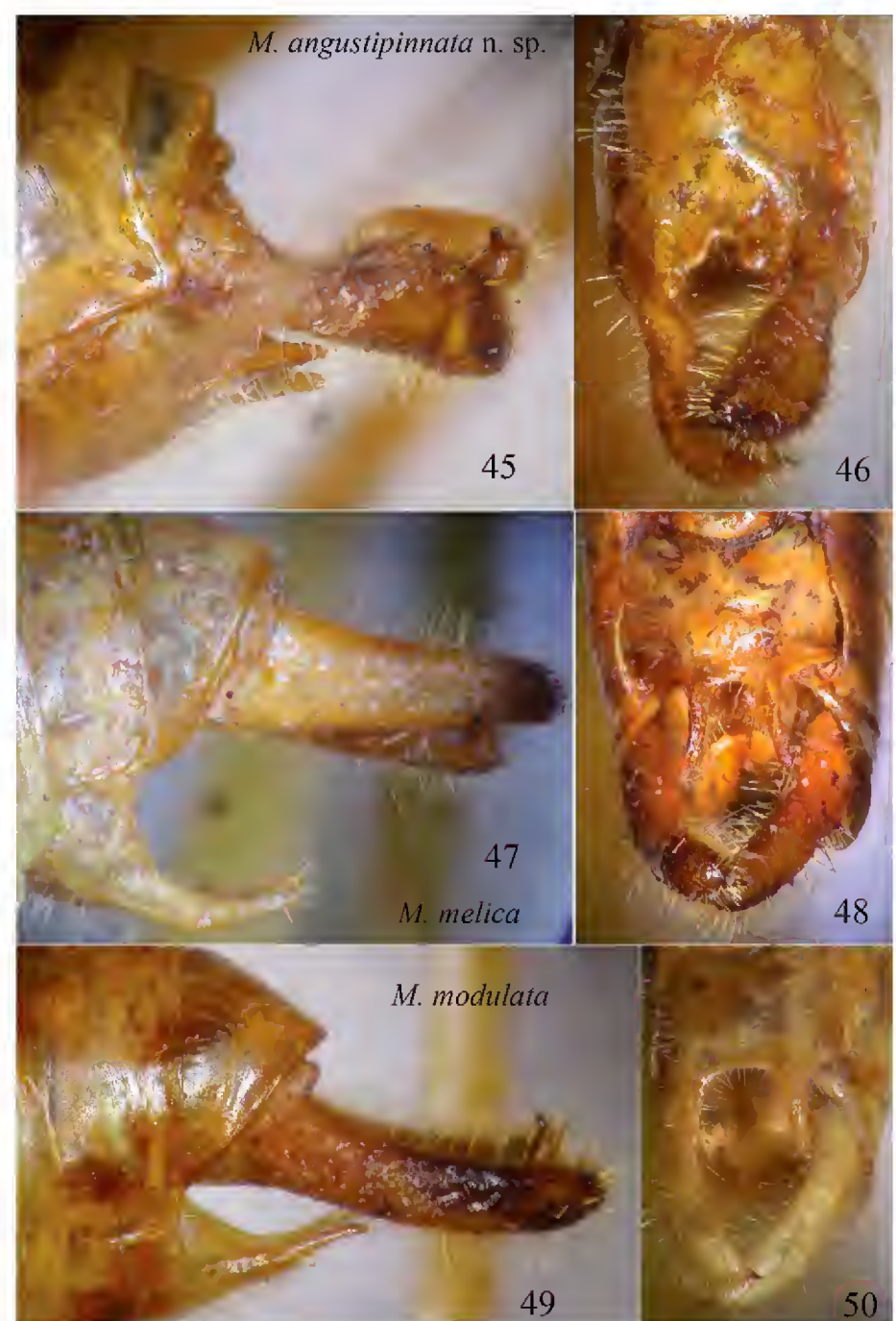
Figures 39–44. Cerci and subgenital plate of male of *Morgenia lehmannorum* sp. n. (39 lateral, 40 ventral), *M. plurimaculata* sp. n. (41 lateral, 42 ventral) and *M. spathulifera* (43 lateral, 44 ventral).

Ndoki 26.I.–23.II.2012 (light) (28♂); Mboki 24.I.2012 (5♂), Sangha2012 team; **Gabon**, Lope National Park Res. Station, 22.III.2012 (light) (1♂) (GAB12-05), Ecotrop2012 team; **Ivory Coast**, Tāi National Park, Res. Station 16–18. III.2017 (light) (2♂), B. Massa; 22.III–4.IV.2017 (light) (2♂), P. Moretto; **Togo**, Fazao Hotel 4.VIII.2013 (light), P. Moretto (1♂) (BMPC). Some specimens here listed were erroneously identified by Massa (2013) as *M. melica*.

Distribution. *M. modulata* is known from Gabon, Cameroon, Central African Republic, Ivory Coast and Togo (Karsch, 1896, Leroy 1970¹, present paper).

Remarks. Karsch (1896) described *M. modulata* very briefly, only highlighting its affinity with *M. melica*. Later Griffini (1908) also pointed out that the cerci of this species are not club-shaped, but similar to those of *M. melica*. Actually, the syntypes of *M. modulata* are labelled as *Morgenia maculata* (J. Deckert, pers. comm.), which probably

¹ Leroy (1970) cited *M. melica*, but the photograph of the stridulatory file reported by her corresponds to that of *M. modulata*.



Figures 45–50. Cerci and subgenital plate of male of *Morgenia angustipinnata* sp. n. (45 lateral, 46 ventral), *M. melica* (47 lateral, 48 ventral) and *M. modulata* (49 lateral, 50 ventral).

was the first name that Karsch wished to use. This name very probably derived from the high number of scattered brown spots on the body of most specimens of this species. The stridulatory area of the left tegmen is protruding below its posterior margin (Figs 18, 26), the mirror of the right tegmen is rather wide (Fig. 18). *M. modulata* is also characterised by the costal area of the tegmina that has regularly spaced crossveins (Fig. 18) and by a very atypical stridulatory file that is 3.0 mm long, strongly arched and composed of two parts, the proximal part that is composed of at least 100 dense and evenly spaced teeth, followed by the distal part, composed of ca. 50 teeth, the first 20–22 widely spaced, the others closely set (Fig. 26). The spur of the mid tibiae is very long and straight, its insertion is at about ¼ the length of the tibia from the tip (its length is ca. 22.5–23.0% the length of the tibia), which has a hollow underneath where the spur remains hidden; the spur does not exceed the apex of the tibia. On the outer ventral margin of the mid tibiae, three close short spines are present (Fig. 34).

Identification of females of the genus *Morgenia*

We know very little about morphological differences of the females of species of the genus *Morgenia*. However, according to Griffini (1908), the female of *M. hamuligera* has

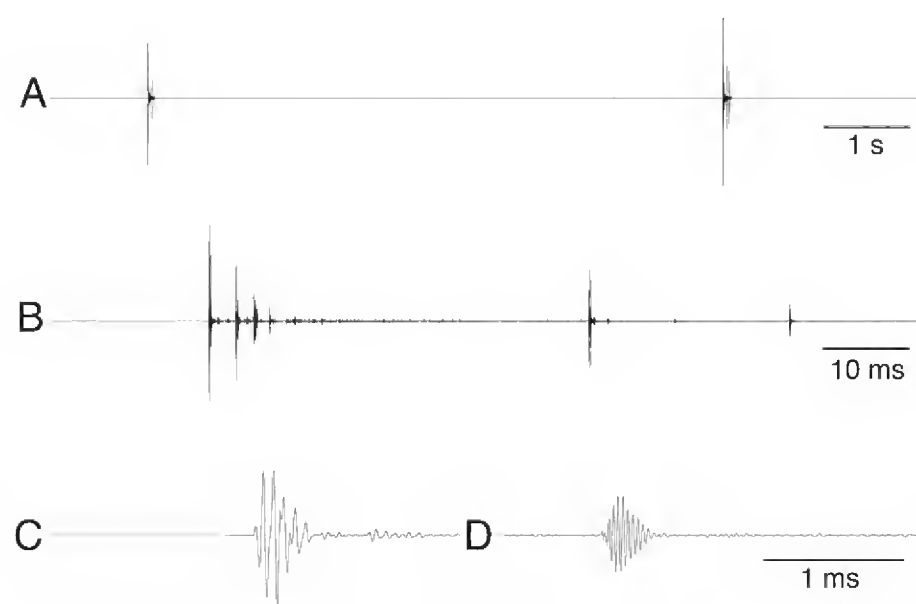


Figure 51. Oscillogram of the calling song of *Morgenia lehmannorum* sp. n. at different time scales. **A** two syllables with an unusually short inter-syllable interval **B** complete syllable **C** first impulse of syllable **D** pulse-like middle element.

a black spot between the tympana of the fore tibiae and we can confirm this character. In all other species, we were unable to find this black spot. In addition, females of *M. rubricornis*, *M. hamuligera*, *M. plurimaculata* sp. n., *M. spathulifera* and *M. melica* have regularly spaced crossveins in the costal area of the tegmina, while females of *M. modulata* have a net of cells in the costal area. No female specimens were available for *M. angustipinnata* sp. n. and *M. lehmannorum* sp. n. The subgenital plates of the examined females have more or less the same shape, triangular and apically rounded. However, the female of *M. plurimaculata* sp. n. has a more pointed subgenital plate. The females of *M. spathulifera*, *M. plurimaculata* sp. n. and *M. modulata* have brown spots scattered on the tegmina.

Generally, females are rarely collected; however, it may be the method of collecting these insects (by artificial light during the night) that attracts mainly males and only rarely some females are captured. Overall, both by means of studying material preserved in museums or by collecting in the field, males are always much more numerous than females.

The spur in the mid tibia of males

The presence of a spur on the mid tibia of males is already known in other genera of Phaneropterinae (in tropical Africa genera *Atlasacris* Rehn, 1914, *Monticolaria* Sjöstedt, 1909, *Odonturoides* Ragge, 1980 and *Meruterrana* Sjöstedt, 1912; in tropical America *Centrofera bimaculata* Brunner von Wattenwyl, 1878). Its origin could be a modified apical spur and probably it appeared several times independently. In the genus *Morgenia*, the spur may be an apical, very short and up-curved spur in *M. angustipinnata* sp. n. and *M. spathulifera* or a sub-apical spur, long and pointed or up-curved in *M. hamuligera*, *M. melica*, *M. rubricornis* and *M. lehmannorum* sp. n., and short and pointed in *M. plurimaculata* sp. n.; only in the case of *M. modulata*, it is very long, not sub-apical or apical located, but enclosed inside the mid tibia. The

remarkable difference, evolving in *M. modulata*, has not been previously noticed.

Where spurs are present on the forelegs of insects, these are generally used to clean antennal segments. Zaggatti and Castel (1987) have also noticed a sexual role for the spurs; they have highlighted the presence of male spurs on hind legs of a Lepidoptera Tortricidae (*Thaumatotibia leucotreta*) and that the insect places these spurs on the female's head during the courtship in such a way that the spurs fit the base of the female antennal segments. It is possible that the original role of spurs was to clean antennae, but secondary adaptations may have changed the original role and involved it during courtship and mating. In most species, it disappeared or never appeared, in others it remained only in the mid or hind legs. Thus, this peculiar structure of mid-leg in *Morgenia*, present only in males, possibly is used during the mating. It may be a case of a Darwinian sexual selection, a structure evolved by sexual factors.

A possible relation between the colour of the stridulatory area and the shape of the spur has been observed: four species with a blackish stridulatory area (*M. hamuligera*, *M. rubricornis*, *M. melica*, *M. plurimaculata* sp. n.) and only one with a less coloured stridulatory area (*M. lehmannorum* sp. n.) have a more or less long and pointed or up-curved, sub-apical spur, while the two species with less coloured stridulatory areas (*M. angustipinnata* sp. n., *M. spathulifera*) have a short and up-curved apical spur; the sole species with a nearly colourless stridulatory area (*M. modulata*) has a very modified spur at the mid tibiae. Within the tribe Poreuomenini, other genera may have a blackish coloured stridulatory area (e.g. *Cestromoecha* Karsch, 1893, *Poreuomena* Brunner von Wattenwyl, 1878); thus, we can consider that this pattern could be ancestral, even if it appeared independently at different times. If this interpretation is correct, the long and pointed spur at the mid tibiae in *Morgenia* species could be the ancestral character, while the short and up-curved spur could be a more recent adaptation, a sort of reduction of the character. The very singular shape of the spur in *M. modulata* remains seemingly inexplicable. It does not seem an adaptation; it changed very probably the original apical position of a modified spur and moved lower down into a new position, where probably it has maintained its function. We were unable to find this kind of modified spur in other genera of Phaneropterinae.

Bioacoustics of *Morgenia lehmannorum* Heller & Massa, sp. n.

The calling song of the male was recorded only during daytime, from 6 a.m. to 5 p.m. It consisted of isolated, very short syllables (less than 100 ms: 71 ± 6 ms; $n=12$) which were produced at intervals of about 10 s or longer (Fig. 51A). A syllable (ca. 150 recorded) starts with a short (3 to 5) series of impulses with mean intervals between of 2–4.5 ms (2.65 ± 0.7 ms; $n=12$) and decrescending in amplitude (Figs 51B, 51C). After a longer interval (37 ± 2 ms; $n=12$),

two (rarely one or three) sound elements follow which are pulse-like in structure (Fig. 51D) separated by an interval of 23 ± 7 ms ($n=12$). Interestingly, the carrier frequency of the impulses and the pulse-like sounds always distinctly differed. The impulses had a peak frequency of about 14 ± 1.5 kHz, while the pulses were around 28.6 ± 1.3 kHz (first pulse; in the second 28.5 ± 1.4 kHz; $n=12$) (Fig. 52).

Comparing the syllable structure with the stridulatory file (Fig. 22), it seems plausible that the impulse series (or at least the first sounds) is produced by contact of the scraper with the large teeth at the distal end of the file. The stridulatory movement would thus have similarities to that of *Ectadia fulva* (see Heller et al. 2015). The high frequency pulses may be produced by using the dense basal part of the file. Different carrier frequencies within one syllable are quite rare amongst tettigoniids (see discussion in Heller and Hemp 2017). It will be very interesting to study the song of other species of the genus to see if this characteristic is more widespread.

Cytogenetics of *Morgenia lehmannorum* Heller & Massa, sp. n.

Analysis of the standard karyotype of *Morgenia lehmannorum* Heller & Massa sp. n. revealed a diploid chromosome number ($2n$) of 25 for the male with the X0 sex determination system. Study of the mitotic metaphase showed one large and one small biarmed submetacentric pairs, four medium and six small acrocentric pairs; the X chromosome is metacentric and the largest element in the set. So, the FN (Fundamental Number, the number of chromosome arms including of the X chromosome) of this species = 30. The C-heterochromatin was characterised by paracentromeric C-bands of similar size (Figs 53a, 53b). Staining with AgNO_3 revealed the presence of one active NOR in the interstitial region of the large bivalent (Fig. 53c), probably in the secondary constriction region in the largest arm of the biarmed chromosome (Fig. 53b).

The modal karyotype of Phaneropterinae consists in the male of 31 acrocentric chromosomes, with the X0 sex determination system probably plesiomorphic for the whole

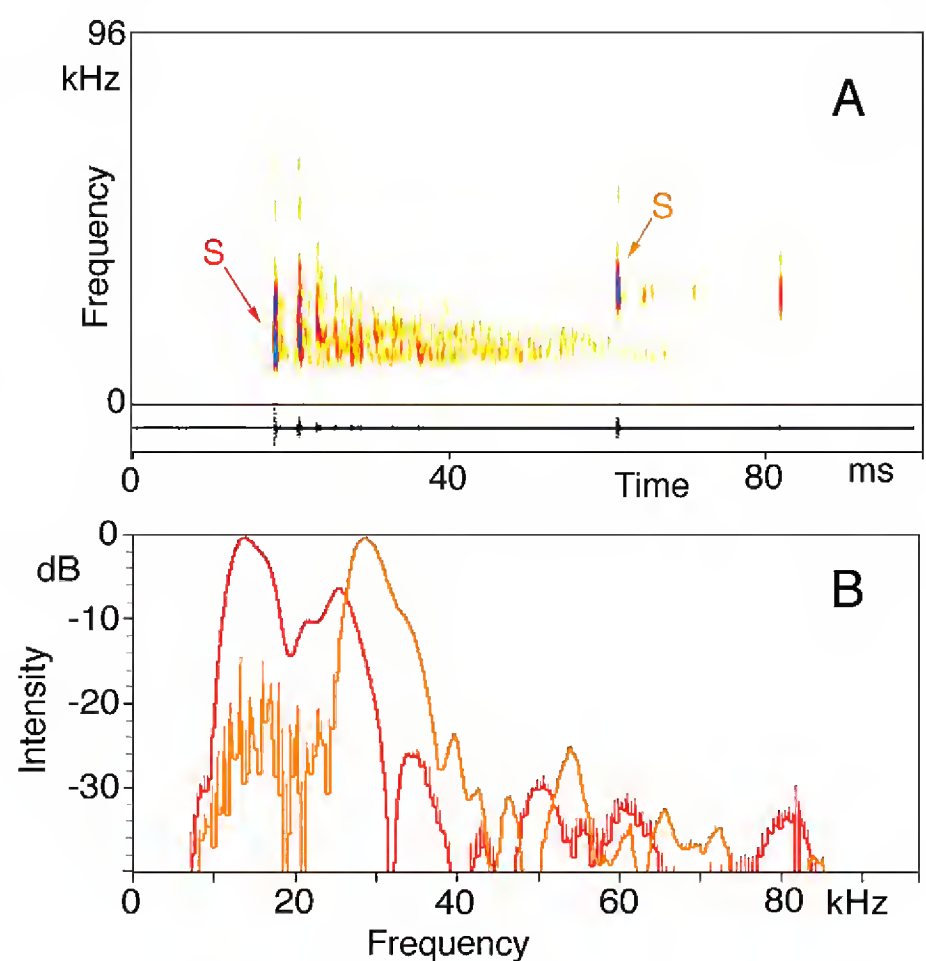
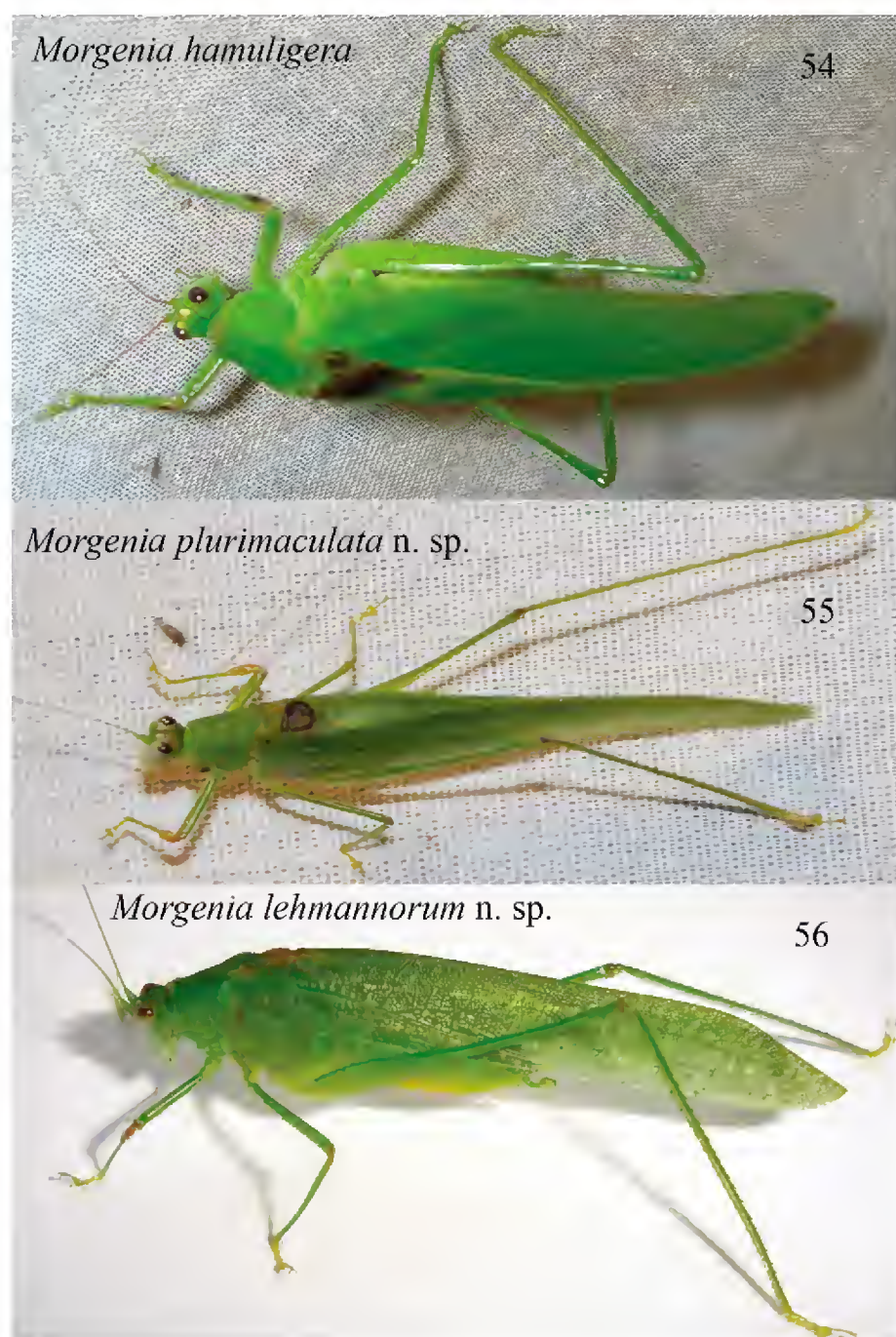


Figure 52. Sonogram of a syllable (A) and power spectra of song elements (B; see markings in A) in the calling song of *Morgenia lehmannorum* sp. n. (different colours mark the different sound elements; red: impulse, orange: pulse-like sound).

Tettigoniidae (e.g. Warchałowska-Śliwa 1998). Most hitherto African genera investigated up to now – *Altihoratosphaga*, *Horatosphaga*, *Monticolaria* (Hemp et al. 2010a), *Lunidia* (Hemp et al. 2010b), *Parapyrrhicia* (Hemp et al. 2017) *Tropidonotacris* (Hemp et al. 2014) possess this karyotype as well. The ancestral chromosome number is reduced to 29 chromosomes (X0) in the African genera *Eurycorypha*, *Plangia* and *Gonatoxia* (Hemp et al. 2013, 2015, 2016), implying a more derived condition. In *Morgenia*, presented in this paper, the chromosome set is reduced to $2n = 25$ (FN = 30). The patterns of the chromosome evolution in this species are interesting and differ from ancestral karyotypes in terms of chromosome number and morphology. Such a karyotype is probably the result of two Robertsonian fusions between the autosomes



Figure 53. Chromosomes of *Morgenia lehmannorum* sp. n.; C-banded mitotic metaphase (A) and diakinesis (B) as well as silver nitrate staining of diakinesis (C) of male complement. Arrows indicate secondary construction region in the largest arm of biarmed chromosome (b) which correspond to the presence of one active NOR (c). An asterisk indicates biarmed medium and small pairs. X, sex chromosome. Scale bars = 10 μm .



Figures 54–56. Living specimens of *Morgenia hamuligera* from Central African Republic, Dzanga-Ndoki National Park (54; photo by P. Annoyer), *M. plurimaculata* sp. n. from Central African Republic, Dzanga-Ndoki National Park (55; photo by S. Danflous) and *M. lehmannorum* sp. n. from Uganda, Semliki Forest National Park (56; photo by K-G Heller).

(leading to the formation of biarmed chromosomes) and one tandem fusion. Pericentric inversion modified the position of the centromere and changed the morphology of the ancestral acrocentric to the metacentric X chromosome in this species. Both pericentric inversion and tandem fusion constitute the common mode of karyotype evolution within Phaneropterinae; however, Robertsonian fusion is not typical for this subfamily (e.g. Warchałowska-Śliwa 1998, Warchałowska-Śliwa et al. 2011). The great majority of cytotaxonomic analyses in African phaneropterids are based on the conventional cytogenetic (C-banding, NOR Ag-staining) methods, which were established for a better understanding of chromosome organisation and evolution.

DNA barcoding

Barcoding diagnoses separate species from gabonese specimens. The male of *M. rubricornis* (LopeORT14-617) with BIN: BOLD: ACO0217 has a sequence different from the male of *M. melica* (LopeORT14-618) with BIN: BOLD: ACN9970. Sequencing of a specimen, LopeORT14-673

did not work but was identified as *M. rubricornis* by one of the authors (BM). There is not enough data in BOLD or public data for the sequences of *Morgenia* to be compared with each other. The construction of a neighbour-joining tree of DNA barcodes (COI) was not possible.

Acknowledgements

We wish to thank all persons of Sangha Expedition “SANGHA2012 Biodiversité en Terre Pygmée Expedition Team”, Philippe Moretto, who kindly allowed BM to study the material collected during 2012–2017 from central and western African countries, Philippe Annoyer, Président de l’Association Insectes du Monde, et Organisateur de l’expédition Sangha 2012, Matias Loubes, President of the Association Tout là-Haut, Jean-Louis Fijalkowski, for his logistic help in Bangui, the porters and guides who, from Bayanga, accompanied the expedition, the Central African population, partners and all persons who directly or indirectly supported the Sangha project team, *Biodiversité en Terre Pygmée*, Dieu béni Bongo-la Omonoma, local collector of insects within the forest during the expedition Sangha 2012 and Cyrille Perez, who participated to the expeditions Sangha in 2010 and 2012. BM very much thanks Philippe Annoyer, Samuel Danflous, Matias Loubes and Philippe Moretto for their collaboration and help during the collecting nights in the Taï National Park (Ivory Coast) in March 2017, both on the ground and at 40 m over a tree of *Klainedoxia gabunensis*. Philippe Moretto kindly allowed BM to study the material collected during 2012–2017 from central and western African countries. Our thanks also go to Gerlind and Arne Lehmann who collected and presented to K-GH the specimen of a new species from Uganda. For Gabon, fieldwork was supported by University of Rouen, French Embassy at Libreville, Gabon (“Service de Coopération et d’Action Culturelle”) and IRD. Logistical support was provided by WCS (Libreville, Gabon) and CEDAMM (La Lopé, Gabon), Research Station on Gorilla and Chimpanzee (La Lopé, Gabon), the Gabonese Agency for National Parks (Libreville, Gabon).

This research received support to BM from the Synthesis Project, which is financed by European Community Research Infrastructure Action under the FP7 “Capacities” Programme at the Museo Nacional de Ciencias Naturales, Madrid (CSIC) (2013: ES-TAF-2438), the Museum für Naturkunde, Berlin (2014: DE-TAF-4109), the Naturhistorisches Museum, Vienna (2016: AT-TAF-5324), the National Museum, Prague (2016: CZ-TAF-5559) and the Royal Belgian Institute of Natural Sciences, Bruxelles (2017: BE-TAF-6319). BM is especially indebted to Mercedes Paris (Museo Nacional de Ciencias Naturales of Madrid), Michael Ohl (Museum für Naturkunde of Berlin), Susanne Randolph and Harald Bruckner (Naturhistorisches Museum, Vienna), Jérôme Constant (Royal Belgian Institute of Natural Sciences, Bruxelles), Martin Fikáček (National Museum Natural

History, Prague), Roberto Poggi, Maria Luisa Tavano and Giuliano Doria (Museo Civico di Storia Naturale 'G. Doria' of Genoa), Emanuela Palmisano (Museo Regionale di Palazzo D'Aumale, Terrasini, Palermo), who facilitated the study of specimens preserved in their museums. We are especially indebted to Jürgen Deckert (Museum für Naturkunde, Berlin) for his advice about the types of *M. modulata*. We thank also Philippe Annoyer and Samuel Danflous, who provided photographs of live specimens.

Collecting authorisations were obtained as follows: 019/UB/DSV2012 of 16.I.2012 from Bangui University, Central African Republic; AE0001/14/MESRS/CENAREST/CG/CST/CSAR of 08.IV.2014 from the Ministère de l'Enseignement Supérieur et de la Recherche Scientifique of Gabon; 135/MESRS/DGRSIT/mo of 12.VI.2015, 238/MESRS/DGRSIT/mo of 13.X.2015, 040/MESRS/DGRSIT/mo of 8.III.2016 from the Ministère de l'Enseignement Supérieur et de la Recherche Scientifique of Ivory Coast; 0429/MINEDD/OIPR/DG of 14.VII.2016, 0505/MINEDD/OIPR/DG of 18.VIII.2016 from the Ministère de l'Environnement et du Développement Durable of Ivory Coast; 021/MESRS/DGRI of 15.II.2017 from the Ministère de l'Enseignement Supérieur et de la Recherche Scientifique of Ivory Coast.

References

- Ben Yahmed D, Pourtier R (2004) Atlas du Gabon. Editions J.A., Paris.
- Brunner von Wattenwyl C (1878) Monographie der Phaneropteriden. Vienna, 401 pp. <http://www.biodiversitylibrary.org/item/37136>
- Cigliano MM, Braun H, Eades DC, Otte D (2018) Orthoptera Species File Online. Version 2.0/4.0. <http://Orthoptera.SpeciesFile.org> [Accessed: March 2018]
- Ebner R (1943) Einige Orthoptera Saltatoria von Fernando Poo (Spanisch-Guinea). 28. Beitrag zu den wissenschaftlichen Ergebnissen der Westafrika-Expedition Eidmann 1939–40. Zoologischer Anzeiger 143: 259–274.
- Griffini A (1906) Ortoteri raccolti da Leonardo Fea nell'Africa occidentale. 1. Hetrodidi, Conocephalidi, Meconemidi, Pseudophyllidi, Mecopodidi e Fanerotteridi. Annali del Museo Civico di Storia Naturale di Genova 3(2): 358–397.
- Griffini A (1908) Phasgonuridae africane del R. Museo di Storia Naturale in Bruxelles. 6. Phaneropteridae pars 2a (reliquae species omnes). Mémoires de la Société entomologique Belgique 15: 201–226. <https://biodiversitylibrary.org/page/11121989>
- Hadley A (2008) Combine Z. <http://www.hadleyweb.pwp.blueyonder.co.uk> [Downloaded on February 2009]
- Heller K-G (2006) Song Evolution and Speciation in Bushcrickets. In: Drosopoulos S, Claridge MF (Eds) Insect Sounds and Communication. Taylor & Francis, Boca Raton, London, New York, 137–151.
- Heller K-G, Hemp C (2017) Context specific signaling with different frequencies – directed to different receivers? A case study in *Gonatoxia* katydids (Orthoptera, Phaneropteridae). Journal of Insect Behavior 30: 420–431. <http://link.springer.com/article/10.1007/s10905-017-9628-y>
- Heller K-G, Hemp C, Ingrisch S, Liu C (2015) Acoustic communication in Phaneropterinae (Tettigoniodea) – a global review with some new data. Journal of Orthoptera Research 24: 7–18. <http://www.bioone.org/doi/abs/10.1665/034.024.0103>
- Hemp C, Massa B (2017) Review of the African genera *Arantia* Stål and *Goetia* Karsch (Orthoptera: Tettigoniidae: Phaneropterinae). Zootaxa 4362(4): 451–498. <https://doi.org/10.11646/zootaxa.4362.4.1>
- Hemp C, Heller K, Warchałowska-Śliwa E, Hemp A (2016) Spotted males, uniform females and the lowest chromosome number in Tettigoniids recorded: Review of the genus *Gonatoxia* Karsch (Orthoptera, Phaneropterinae). Deutsche Entomologische Zeitschrift 63(2): 271–286. <https://doi.org/10.3897/dez.63.10799>
- Hemp C, Heller K-G, Warchałowska-Śliwa E, Hemp A (2010b) A new genus and species of African Phaneropterinae (Orthoptera: Tettigoniidae), with data on its ecology, bioacoustics and chromosomes. Organisms, Diversity and Evolution 10: 215–226. <https://doi.org/10.1007/s13127-010-0013-3>
- Hemp C, Heller K-G, Warchałowska-Śliwa E, Grzywacz B, Hemp A (2013) Biogeography, ecology, acoustics and chromosomes of East African *Eurycorypha* Stål species (Orthoptera, Phaneropterinae) with the description of new species. Organisms Diversity and Evolution 13: 373–395. <https://doi.org/10.1007/s13127-012-0123-1>
- Hemp C, Heller K-G, Warchałowska-Śliwa E, Hemp A (2014) Description of the female and notes on distribution, habitat, nymphal development, song and chromosomes of *Tropidonotacris grandis* Ragge (Orthoptera: Phaneropterinae). Zootaxa 3893(4): 569–578. <https://doi.org/10.11646/zootaxa.3893.4.6>
- Hemp C, Heller K-G, Warchałowska-Śliwa E, Grzywacz B, Hemp A (2015) Review of the *Plangia graminea* (Serville) complex and the description of new *Plangia* species from East Africa (Orthoptera: Phaneropteridae, Phaneropterinae) with data on habitat, bioacoustics, and chromosomes. Organisms Diversity and Evolution 15(3): 471–488. <https://doi.org/10.1007/s13127-015-0216-8>
- Hemp C, Heller K-G, Warchałowska-Śliwa E, Grzywacz B, Hemp A (2017) Review of the African species of the phaneropterine genus *Parapyrrhicia* Brunner von Wattenwyl, 1891 (Insecta: Orthoptera); secret communication of a forest-bound taxon. Organisms Diversity and Evolution 17: 231–250. <https://doi.org/10.1007/s13127-016-0303-5>
- Hemp C, Voje KL, Heller K-G, Warchałowska-Śliwa E, Hemp A (2010a) A new genus in African Acrometopini (Tettigoniidae: Phaneropterinae) based on morphology, chromosomes, acoustics, distribution, and molecular data, and the description of a new species. Zoological Journal of the Linnean Society 158: 66–82. <https://doi.org/10.1111/j.1096-3642.2009.00542.x>
- Holstein J (Ed) (2015) A Field Guide to insects and allies of the Kakamega Forest National Reserve. BIOTA Field Guide, Stuttgart, 292 pp.
- Karsch FAF (1890a) Neue westafrikanische durch Herrn Premierlieutenant Morgen von Kribi eingesendete Orthopteren. Entomologische Nachrichten 16: 257–276. <https://biodiversitylibrary.org/page/25409483>
- Karsch FAF (1890b) Verzeichnis der von Herrn Dr. Paul Preuss auf der Barombi-Station in Deutsch-Westafrika 1890 gesammelten Locustodeen aus den Familien der Phaneropteriden, Mekonemiden und Gryllakriden. Entomologische Nachrichten 16: 353–369. <https://biodiversitylibrary.org/page/25409579>
- Karsch FAF (1893) Locustodeen von Victoria in Kamerun, gesammelt von Herrn Dr. Paul Preuss. Entomologische Nachrichten 19(13): 195–199. <https://biodiversitylibrary.org/page/25410231>

- Karsch FAF (1896) Neue Orthopteren aus dem tropischen Afrika. *Stettiner Entomologische Zeitung* 57: 242–359. <https://biodiversitylibrary.org/page/9008659>
- Leroy Y (1970) Diversités d'aspects et évolution de la dissymétrie des râpes de stridulation des insectes orthoptères Phaneropterinae. *Comptes rendus hebdomadaires de l'Académie des Sciences* 270: 96–99.
- Massa B (2013) Diversity of leaf katydids (Orthoptera: Tettigoniidae: Phaneropterinae) of Dzanga-N'Doki National Park, Central African Republic, with selected records from other African countries. *Journal of Orthoptera Research* 22: 125–152. <https://doi.org/10.1665/034.022.0201>
- Massa B (2015) Taxonomy and distribution of some katydids (Orthoptera Tettigoniidae) from tropical Africa. *Zookeys* 524: 17–44. <https://doi.org/10.3897/zookeys.524.5990>
- Massa B (2016) On some interesting African katydids (Orthoptera Tettigoniidae). *Entomologia* 4(303): 1–15. <https://doi.org/10.4081/entomologia.2016.303>
- Massa B (2017a) New genera, species and records of Afrotropical Phaneropterinae (Orthoptera, Tettigoniidae) preserved at the Royal Belgian Institute of Natural Sciences, Bruxelles. *Zootaxa* 4358(3): 401–429. <https://doi.org/10.11646/zootaxa.4358.3.1>
- Massa B (2017b) Revision of the tropical African genus *Tetraconcha* (Orthoptera: Tettigoniidae: Phaneropterinae) with the description of ten new species. *Journal of Orthoptera Research* 26: 211–232. <https://doi.org/10.3897/jor.26.21469>
- Moulin N, Decaëns T, Annoyer P (2017) Diversity of mantids (Dictyoptera: Mantodea) of Sangha-Mbaere Region, Central African Republic, with some ecological data and DNA barcoding. *Journal of Orthoptera Research* 26: 117–141. <https://doi.org/10.3897/jor.26.19863>
- Ragge DR (1980) A review of the African Phaneropterinae with open tympana (Orthoptera: Tettigoniidae). *Bulletin British Museum (Natural History) Entomology* 40: 1–192. <http://www.archive.org/details/bulletinofbritis40entolond>
- Ratnasingham S, Hebert PDN (2007) BOLD: The Barcode of Life Data System (www.barcodinglife.org). *Molecular Ecology Notes* 7: 355–364. <https://doi.org/10.1111/j.1471-8286.2007.01678.x>
- Sjöstedt Y (1913) Neue Orthopteren aus Ost- und Westafrika nebst einigen anderen zugehörigen Formen. *Arkiv för Zoologi* 8(6): 1–26. <https://biodiversitylibrary.org/page/6425929>
- Sumner AT (1972) A simple technique for demonstrating centromere heterochromatin. *Experimental Cell Research* 75: 304–306. [https://doi.org/10.1016/0014-4827\(72\)90558-7](https://doi.org/10.1016/0014-4827(72)90558-7)
- Tortorici F, Caleca V, van Noort S, Masner L (2016) Revision of Afrotropical *Dyscritobaeus* Perkins, 1910 (Hymenoptera: Scelionidae). *Zootaxa* 4178(1): 1–59. <https://doi.org/10.11646/zootaxa.4178.1.1>
- Warchałowska-Śliwa E (1998) Karyotype characteristics of katydid orthopterans (Ensifera, Tettigoniidae) and remarks on their evolution at different taxonomic levels. *Folia Biologica Kraków* 46: 143–176.
- Warchałowska-Śliwa E, Maryńska-Nadachowska A (1992) Karyotypes, C-bands, NORs location in spermatogenesis of *Isophya brevipennis* Brunner (Orthoptera: Phaneropteridae). *Caryologia* 45: 83–89. <https://doi.org/10.1080/00087114.1992.10797213>
- Warchałowska-Śliwa E, Maryńska-Nadachowska A, Grzywacz B, Karamysheva T, Lehmann AW, Lehmann GUC, Heller K-G (2011) Changes in the numbers of chromosomes and sex determination system in bushcrickets of the genus *Odontura* (Orthoptera, Tettigoniidae, Phaneropterinae). *European Journal of Entomology* 108: 183–195. <https://doi.org/10.14411/eje.2011.025>
- White LJT, Abernethy KA (1997) A guide to the vegetation of the Lopé Reserve, Gabon. Wildlife Conservation Society, New York, USA.
- Zagatti P, Castel Y (1987) Courtship behaviour of the False Codling Moth, *Cryptophlebia leucotreta* (Meyrick): androconial display and mating success (Lepidoptera, Tortricidae). *Annales Société Entomologique de France* 23: 113–123.

Taxonomic review of Australian *Mecyclothorax* Sharp (Coleoptera, Carabidae, Moriomorphini) with special emphasis on the *M. lophoides* (Chaudoir) species complex

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Abstract

Received 13 June 2017

Accepted 24 July 2018

Published 13 August 2018

Academic editor:

Dominique Zimmermann

Key Words

biogeography

cladistics

cryptic species

insect

genitalia

sexual selection

speciation

The Australian fauna of *Mecyclothorax* Sharp (Coleoptera: Carabidae: Moriomorphini) is reviewed, with special focus on species assigned to the monophyletic subgenus *Eucyclothorax* Liebherr: *M. isolatus*, **sp. n.** from Western Australia, *M. moorei* Baehr, *M. punctatus* (Sloane), *M. curtus* (Sloane), *M. blackburni* (Sloane); *M. eyrensis* (Blackburn); *M. peryphoides* (Blackburn); *M. darlingtoni*, **sp. n.** from Queensland; *M. jameswalkeri*, **sp. n.** from Western Australia; *M. lophoides* (Chaudoir); and *M. cordicollis* (Sloane). The last six species listed above—the *M. lophoides* species complex—have been the source of long-term confusion for taxonomists, with male genitalic characters providing trouble-free species circumscription. One new subspecies, *M. lewisensis estriatus*, **subsp. n.** from Queensland is added to the seven previously described taxa of the monophyletic subgenus *Qecyclothorax* Liebherr. The balance of the fauna consists of four species in the subgenus *Mecyclothorax*: **1** and **2**, the sister-species pair *M. lateralis* (Castelnau) and *M. minutus* (Castelnau); **3**, *M. ambiguus* (Erichson); and **4**, *M. punctipennis* (MacLeay). *Mecyclothorax fortis* (Blackburn), **syn. n.**, is newly synonymized with *M. minutus*. *Mecyclothorax ovalis* Sloane is recombined as *Neonomius ovalis* (Sloane), **comb. n.**, and a neotype is designated to replace the destroyed holotype. Phylogenetic relationships for the Australian *Mecyclothorax* are proposed based on information from 68 terminal taxa and 139 morphological characters. The biogeographic history of Australian *Mecyclothorax* is deduced based the sister-group relationship between *Mecyclothorax* and the *Amblytelus*-related genera, with both groups hypothesized to have originated during the late Eocene. Diversification within *Mecyclothorax* has occurred since then in montane rainforests of tropical Queensland, temperate forest biomes of the southwest and southeast, and in grasslands and riparian habitats adjacent and inland from those forests. Several species presently occupy interior desert regions, though no sister species mutually occupy such climatically harsh habitats. The *M. lophoides* species complex exhibits profound male genitalic diversification within the context of conserved external anatomy. This disparity is investigated with regard to the functional interaction of the male internal sac flagellum and female spermathecal duct. Though limited association of flagellar and spermathecal duct configurations can be documented, several factors complicate proposing a general evolutionary mechanism for the observed data. These include: **1**, the occurrence of derived, elongate spermathecal ducts in three species, two of which exhibit very long male flagella, whereas males of the third exhibit a very short flagellum; and **2**, a highly derived and exaggerated male flagellar configuration shared across a sister-species pair even though the two species can be robustly diagnosed using external anatomical characters, other significant genitalic differences involving male parameral setation, and biogeographic allopatry associated with differential occupation of desert versus forest biomes.

Introduction

Although relatively few in number of species, the Australian *Mecyclothorax* have proved confusing throughout much of their taxonomic history. This is partly due to the description of species and associated deposition of type specimens by taxonomists working half a world away from Australia. Yet, the confusion has been also caused in part by the broad geographic distribution of the taxon across Australasia, Java, Borneo and Polynesia, with constituent radiations in islands and island continents distantly separated from each other. *Mecyclothorax* taxonomy started in mid-19th century Berlin with Erichson's (1842) study of the insect fauna of Vandiemensland, a treatise predominantly focusing on Coleoptera, but also treating some Orthoptera *s.l.*, Hymenoptera, Diptera, and Hemiptera. Among Carabidae, Erichson perceived and described as new the distinctive genera *Lestignathus*, *Amblytelus* and *Scopodes*, but he consigned one apparently unremarkable new species from Melbourne—*Anchomenus ambiguus* Erichson—to a Bonelli (1810) genus now recognized as a monophyletic, holarctically restricted taxon of tribe Platynini (Liebherr 1991, 1994a, Schmidt 2014). Throughout much of the mid-19th century, species were described in Bonelli's *Anchomenus* that are now known to be members of a broad array of phylogenetically distant, morphologically disparate, and geographically disjunct platynine taxa including, non-exhaustively: **1**, Neotropical *Glyptolemus* Bates (e.g. *Anchomenus chalybaeus* Dejean, 1831; Whitehead 1974); **2**, Hawaiian *Blackburnia* Sharp (e.g. *Anchomenus corruscus* Erichson, 1834; Liebherr and Zimmerman 2000); **3**, Asia-Pacific *Metacolpodes* Jeannel (e.g. *Anchomenus laetus* Erichson, 1834; Liebherr 2005); **4**, South American *Incagonum* Liebherr (e.g. *Anchomenus aeneum* Reiche, 1843; Liebherr 1994b, Moret 2005); **5** New Zealand *Ctenognathus* Fairmaire (e.g. *Anchomenus colenisonis* White, 1846; Larochelle and Larivière 2007); **6**, Australasian *Notagonum* Darlington (e.g. *Anchomenus lafertei* Montrouzier, 1860; Darlington 1952); **7**, Mediterranean and Macaronesian *Paranchus* Lindroth (e.g. *Anchomenus nicholsii* Wollaston, 1864; Machado 1992); **8**, Mexican *Elliptoleus* Bates (e.g. *Anchomenus vixstriatus* Bates, 1878; Bates 1882); and **9**, Holarctic *Agonum* Bonelli (e.g. *Anchomenus (Agonum) charillus* Bates, 1883; Habu 1978). Consistent with the use of *Anchomenus* as a catch-all genus, Chaudoir (1854) described the second *Mecyclothorax* from Australia as *Anchomenus lophoides*. As with Erichson, this description was done remotely, in the Ukraine (Ball and Erwin 1983), based on specimens from Melbourne sent to Chaudoir by the English entomologist André Melly. Then in 1867 Australia received its first home-grown descriptions for species of *Mecyclothorax*: *Phorticosomus lateralis* Castelnau and *P. minutus* Castelnau. Castelnau's confusion concerning placement of these species was evident in that he described the two species destined for future membership in *Mecyclothorax* within an assemblage of five new species he assigned to Schaum's (1863) genus

Phorticosomus; these also including one future *Simodontus*, as well as two currently recognized *Phorticosomus*. Castelnau's specimens of the two future *Mecyclothorax* species were deposited in the Museo Civico in Genoa after his death in 1880, not with the balance of his Australian collections deposited in Museums Victoria, Melbourne (Evenhuis 2012). It was not until Barry Moore visited Genoa in 1968 that these specimens were compared to those of other Australian taxa.

When William MacLeay (1871) described *Cyclothorax punctipennis* from Gayndah, N.S.W., Australia witnessed the beginning of a local network of taxonomists that would describe the bulk of Australian *Mecyclothorax*. However, at that early date MacLeay admitted his confusion regarding placement of his species, writing: "I am not at all sure of the position of this genus, the dilatation of the tibiae in the male is so slight as to be in most instances unnoticeable (MacLeay 1871: 105)." His placing the species after *Acupalpus* and before *Abacetus* suggests an ambiguous placement within generalized Harpalinae. The *Cyclothorax* name then traveled to the middle of the Pacific, at the eastern end of the generic distributional range, where Thomas Blackburn recognized the similarity between Hawaiian species he was collecting and MacLeay's species. Blackburn (1878a, 1878b, 1879, 1881, 1882) described 21 species that he placed in *Cyclothorax*, forever moving the center of diversity of the genus to Hawaii. Blackburn was able to continue his study of the genus when he was assigned in 1882 as rector to a church in Port Lincoln, South Australia (Lea 1912). During the remainder of his life he described several thousands of Australian beetle species, including four future *Mecyclothorax*: understandably including two junior synonyms of Castelnau names, the types for those specimens unavailable to him as they had sailed for Europe.

The closing of the 19th century saw Thomas G. Sloane take up description of *Mecyclothorax* from specimens he collected or received from colleagues (Sloane 1895, 1898, 1900). With Sloane the confusion concerning *Cyclothorax* began to dissipate: "I believe Dr. Sharp has placed *Cyclothorax* in the tribe Feronini, but it is evident this is not its true position, which cannot be far from *Amblytelus* ... (Sloane 1895: 447)." Nonetheless on that same page he also wrote: "A species of *Cyclothorax* is found everywhere in south-eastern Australia ... I believe it to be identical with *C. ambiguus*, Erichs., and that *C. lophoides*, Chaud., is also founded on it. I do not feel that *C. punctipennis*, Macl., is a distinct species from *C. ambiguus*, though it is quite likely that it is (Sloane 1895: 447)." Sloane was also the first taxonomist to look carefully at more than the dorsal surface of card-mounted specimens. Of *M. (Eucyclothorax) punctatus*, treated below, he wrote: "The episterna of the metasternum are punctate, and probably more of the undersurface as well, but not having detached the specimen before me from the card to which it is gummed, the episterna only have been seen (Sloane 1898: 473)." Of the last *Mecyclothorax* he described—*M. cordicollis* (Sloane) (Sloane 1900)—he wrote

of his confusion, but in fact he had deduced the specific differences between *M. cordicollis* and *M. peryphoides*, confirmed by results of this study completed 118 years later: “This is the species I formerly regarded as *C. peryphoides*, Blkb.* but Mr. Blackburn has informed me that it differs from that species. The only difference the description of *C. peryphoides* suggests to me is the darker colour of the legs in that species, a character that seems of little value, but probably *C. peryphoides* has the prothorax more strongly sinuate near the base, the basal angles more marked, and perhaps a coarser puncturation on the basal area” (Fig. 2H versus 2I). Sloane (1903) was also the first to point out homonymy of *Cyclothorax* MacLeay, 1871 with *Cyclothorax* Frauenfeld, 1868, solving that issue by nomenclaturally uniting *Cyclothorax* MacLeay with *Mecyclothorax* Sharp, 1903.

The beginning of the modern era of Australian *Mecyclothorax* taxonomic research is synonymous with Moore’s (1984) type examinations and associated male dissections, which clearly defined the species boundaries between the two most commonly encountered Australian species, *M. ambiguus* and *M. punctipennis*. Moore was able to examine the types of the long-mysterious *Anchomenus lophoides*, available at the Paris Museum after more than a century of seclusion in the Chaudoir and Oberthür private collections, and he established its independence from *M. ambiguus* while proposing its close relationships to *M. cordicollis*, *M. peryphoides*, and *M. eyrensis*. Moore also described the first two Queensland species of subgenus *Qecyclothorax* Liebherr, which laid the foundation for Baehr’s (2003) comprehensive revision.

Material and methods

This taxonomic review is based on 3273 specimens of Australian *Mecyclothorax* held in 21 institutional or personal collections (codens used in species treatments): American Museum of Natural History, New York (AMNH); Australian Museum, Sydney (AMS); Australian National Insect Collection, Canberra (ANIC); The Natural History Museum, London (BMNH); Bernice P. Bishop Museum, Honolulu (BPBM); California Academy of Sciences, San Francisco (CAS); Carnegie Museum of Natural History, Pittsburgh (CMNH); Cornell University Insect Collection, Ithaca (CUIC); Essig Museum of Entomology, University of California, Berkeley (EMEC); Field Museum of Natural History, Chicago (FMNH); Martin Baehr Collection, Munich (MBC); Museo Civico Storia Naturale, Genova (MCG); Museo Civico Storia Naturale, Milano (MCM); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Museum national d’Histoire naturelle, Paris (MNHN); Museums Victoria, Melbourne (MVM); Queensland Museum, Brisbane (QMB); South Australian Museum, Adelaide (SAMA); University of Alberta Strickland Museum, Edmonton, CA (UASM); Western Australian Museum, Welshpool (WAM); Zoological Museum, University of Copenhagen (ZMUC).

Laboratory methods follow Liebherr (2015, 2018). The qualitative configuration of various features of the beetles was quantified using a variety of ratios. Three ratios were used to assist in description of the eyes: **1**, the ocular ratio, or the maximum head width across the eyes divided by the minimum breadth of the frons between the eyes (MHW/mFW); **2**, ocular lobe ratio, or the length of the compound eye measured from above divided by length of the protruded ocular lobe measured from the anterior margin of the eye to the groove at the ocular lobe-genal juncture (EyL/OLL); and **3**, eye convexity, or eye length divided by the maximal depth of the eye measured with the internal margin vertical in the field of view (EyL/EyD). Pronotal configuration was assessed using three ratios: **1**, maximal pronotal width divided by median pronotal length (MPW/PL); **2**, relative basal constriction of the pronotum, or the maximal pronotal width divided by pronotal breadth across the hind angles (MPW/BPW); and **3**, relative apical and basal pronotal widths (APW/BPW). The elytral configuration was described using the ratio MEW/EL, or maximum elytral width (usually situated near midlength) divided by elytral length, measured from the basal margin of the flattened posterior surface of the scutellum to the apex of the longer elytron (if elytral lengths differ slightly side to side). Presence or absence of macrosetae at specific positions on the bodies of *Mecyclothorax* beetles prove diagnostic for several taxa within the Australian fauna. Information regarding setal configuration is summarized using a setal formula comprising presence (+) or absence (–) of: **1**, the anterior and posterior supraorbital setae; **2**, the lateral and basal pronotal setae; **3**, the parascutellar seta; **4**, the dorsal elytral setal number (in these taxa 1-2); **5**, the subapical and apical elytral setae, the former situated in stria 7 apicad the lateral elytral setae of interval 8, the latter between the apex of stria 2 and the elytral apex. For ease of visualization, the various somites or structures—head, pronotum, elytra—are demarked by a slash: “/.” Thus, +++/+++2++ is the setal formula for presence of both supraorbital setae, both pronotal setae, the parascutellar seta, two dorsal elytral setae, and both the subapical and apical elytral setae. Standardized body length is used to assess body size, and consists of the sum of three measurements: **1**, head length measured as the distance from the middle of the labrum to the cervical carina at the posterior margin of the vertex; **2**, median pronotal length; and **3**, elytral length measured from the basal margin of the flattened posterior surface of the scutellum to the apex of the longer elytron (if elytral lengths differ slightly side to side).

Sclerites associated with the male aedeagal sac flagellum proved essential for species diagnosis and circumscription within the *M. lophoides* assemblage of cryptic species. Dissected aedeagi were temporarily slide-mounted in glycerin, and viewed under phase contrast microscopy using an Olympus BH2 scope. At least one male specimen from each collecting series was dissected, with the cleared aedeagal median lobe assessed for the configuration of the flagellum and the flagellar sheath. These

two structures occur at the apex of the internal sac, with the flagellum near the gonopore, and the flagellar sheath situated to the right of the gonopore (Figs 7H, 14B, 14F, 14H). A broad sclerotized plate is situated to the left of the gonopore and flagellum; herein called the dorsal plate. The parameral configuration varies among the species treated, both in shape and setation (Figs 8, 13, 16). For diagnosis of the adelphotaxa *M. eyrensis* and *M. peryphoides*, the numbers of setae along the ventral margin of the right, or ventral paramere were assessed in 10 individuals of the former and 15 of the latter. The distributions of setal numbers were compared using the Wilcoxon rank-sum test for individual samples with unequal sample sizes (Snedecor and Cochran 1980).

Other structures of the male genitalia and female reproductive tract and gonocoxae are presented as in Liebherr (2018), with figured abbreviations presented in Table 1. Terminology of the female characters follows Liebherr and Will (1998). For presentation of male genitalic characters, and female reproductive tract characters, the numbers of individuals dissected, examined, and photographed are provided parenthetically ($n = X$) at the start of those sections. The numbers of individuals measured to calculate ratios of various external structures are presented at the beginning of each diagnosis. Specimens that were chosen for measurement included both the largest and smallest individuals, males and females, and representatives from multiple localities. Type label data are presented verbatim, including typeface.

Nomenclatural actions conform to The Code (I.C.Z.N. 1999). In order to clarify the ambiguous status of allotypes under the current version 4 of The Code (Santiago-Blay et al. 2008), the allotype for *M. darlingtoni*, sp. n. is designated as an allotypic paratype.

Cladistic methods are identical to those utilized in the earlier associated analysis of New Caledonian *Mecyclothorax* (Liebherr 2018), augmented with the following additional data. Two additional characters are reported, with these characters added to the end of the prior character matrix so as not to disturb the character numbering scheme presented in Liebherr (2018, pp. 6–11, Supplementary Material 1). These characters include:

137. Clypeus with: two setae, one each side (0); with four setae, two each side, the medial pair smaller (1).

138. Spermathecal duct: of equal width/sclerotization from base to spermatheca (0); sclerotized and broader basally, a narrow membrane at midlength (1, Fig. 9A–B).

Additional taxon-related information is also presented below, including the addition of the newly described species *M. isolatus* and *M. jameswalkeri*, the addition of male genitalic characters for *M. curtus* (characters 92–113) and both male genitalic and female reproductive tract characters for *M. punctatus* (characters 92–136). The previously mentioned *M. sp. n. D* (Liebherr 2018) is newly described as *M. darlingtoni*. Thus the present taxon-character matrix includes 68 terminals representing 67 species and 139 characters. The analysis is rooted at *Neonomius laevicolis* Sloane, a member of the subtribe Moriomorphina, and

Table 1. Key to abbreviations for morphological structures labelled in illustrations of male genitalia, female reproductive tracts, and female gonocoxae.

Abbreviation	Structure
af	apical face, male aedeagal median lobe
afs	apical fringe setae, basal gonocoxite
ams	apicomedial seta, basal gonocoxite
ans	apical nematiform setae, apical gonocoxite
bc	female bursa copulatrix
co	female common oviduct
des	dorsal ensiform seta, apical gonocoxite
dp	dorsal or left plate, male internal sac
fl	flagellum, male aedeagal internal sac
fp	flagellar plate, male aedeagal internal sac
fs	flagellar sheath, male aedeagal internal sac
gc1	basal gonocoxite, female
gc2	apical gonocoxite, female
gp	gonopore, male aedeagal internal sac
hg	hindgut
hs	helminthoid sclerite, female bursa
les	lateral ensiform setae, apical gonocoxite
ovo	ostial ventroapical operculum, male
r	ramus, female basal gonocoxite
sc	sagittal crest, male aedeagus
sd	spermathecal duct, female
sg	spermathecal gland, female
sp	spermatheca, female
ssd	sclerotized spermathecal duct, female
vss	ventrobasal spicular sclerite, male sac

thus outside the ingroup representatives of this analysis which are all members of the subtribe Amblytelina (Liebherr 2018). Within Amblytelina, the genera related to *Amblytelus* Erichson comprise the primary outgroup to the various representatives of *Mecyclothorax* (Liebherr 2018, table 1).

Cladistic data were compiled using WinClada (Nixon 2002) with the search for most-parsimonious cladograms using the parsimony ratchet (Nixon 1999) with tree searches run using NONA (Goloboff 1999). Tree searches were conducted using standard WinClada defaults for 1000 iterations of the ratchet. Once the shortest trees were found using NONA and the ratchet, the results were checked using TNT (Goloboff and Catalano 2016). The TNT analysis used sectorial search, the ratchet, tree fusing, with the minimum tree cache set at 50 trees.

Results

Cladistic analysis

The NONA/WinClada analysis found 2 shortest trees of 1232 steps in 1000 iterations of the ratchet (C.I. = 0.21, R.I. = 0.67), with the strict consensus collapsing 1 node and resulting in a consensus tree length of 1235 steps (Fig. 1A). The TNT search for 1000 minimum-length trees, using sectorial search and the ratchet, also resulted in 2 trees of 1232-step length (3,572,933,738 rearrange-

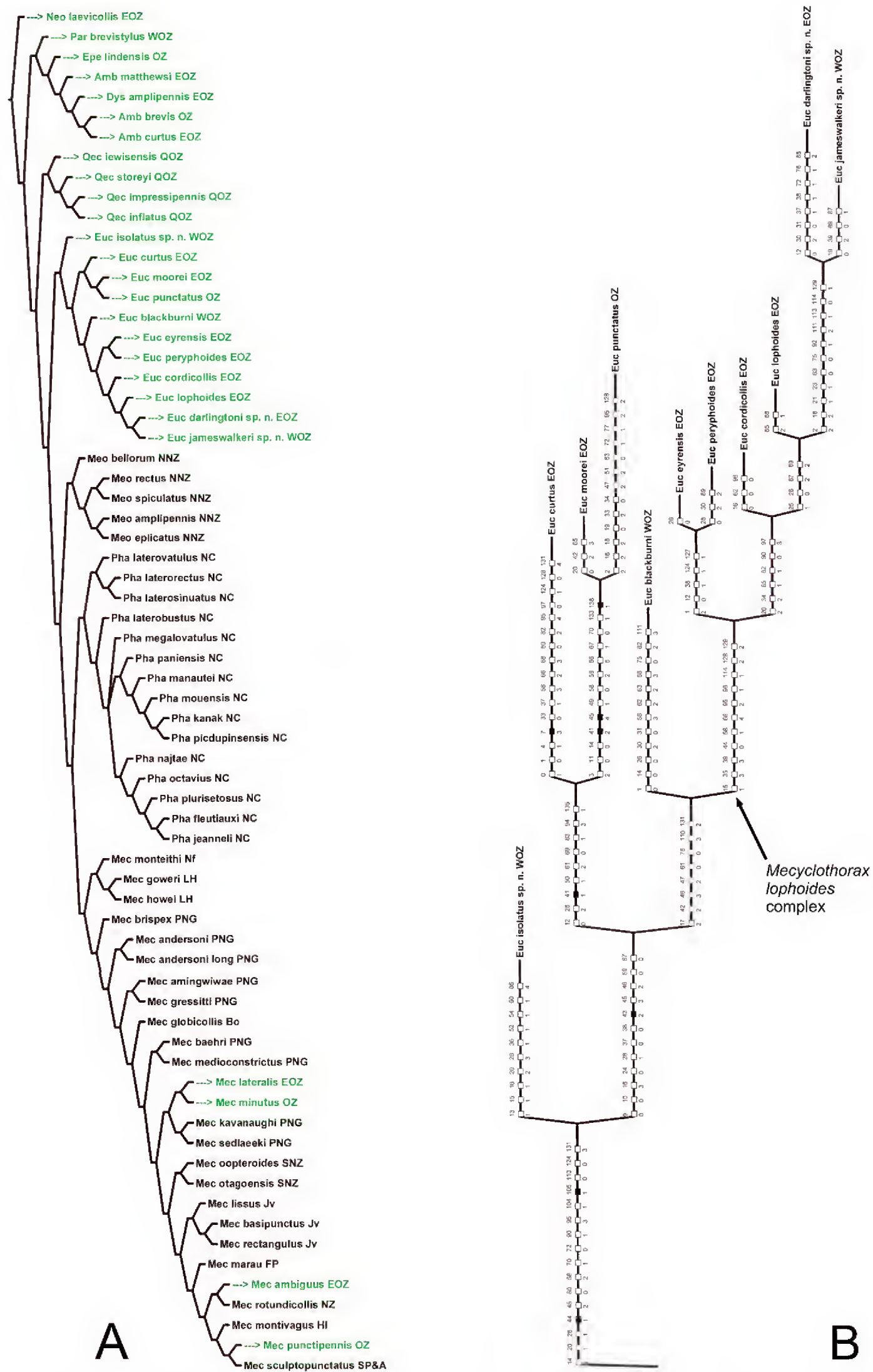


Figure 1. Cladograms resulting from cladistic analysis. Species terminals are labeled with species epithet and three-letter abbreviation of relevant generic or subgeneric name: Neo, *Neonomius* Moore; Par, *Paratrichothorax* Baehr; Epe, *Epeylyx* Blackburn; Amb, *Amblytelus* Blackburn; Dys, *Dystrichothorax* Baehr; Euc, *Eucyclothorax* Liebherr; Qec, *Qecyclothorax* Liebherr; Meo, *Meonochilus* Liebherr and Marris; Pha, *Phacothorax* Jeannel; Mec, *Mecyclothorax* Sharp. Areas occupied by the included taxa are indicated by abbreviations following species epithets: **Bo**, Borneo; **EOZ**, eastern Australia, i.e. restricted to east of the Nullarbor Plain; **FP**, French Polynesia, Tahiti; **HI**, Hawaiian Islands, Maui; **Jv**, Java; **LH**, Lord Howe Island; **NC**, New Caledonia; **Nf**, Norfolk Island; **NNZ**, North Island of New Zealand; **NZ**, generally distributed across New Zealand; **OZ**, generally distributed across Australia; **PNG**, Papua New Guinea; **QOZ**, restricted to Queensland, Australia; **SNZ**, South Island of New Zealand plus Chatham Islands; **SP&A**, St. Paul and Amsterdam Islands; **WOZ**, western Australia, i.e. restricted to west of the Nullarbor Plain. **A.** Strict consensus cladogram of 2 equally most-parsimonious trees. Green-colored terminals represent mainland Australian taxa. **B.** Resolved cladistic relationships of 11 *Mecyclothorax* (*Eucyclothorax*) spp. represented in all cladograms. Character numbers are shown to left of cladogram edges, character states to right. Filled boxes represent characters that change to the indicated state only once on cladogram.

ments tried). The consensus cladogram maintains monophyly of the five previously recognized *Mecyclothorax* subgenera (Liebherr 2018), although the subgenus *Qecyclothorax* is hypothesized to be the adelphotaxon of the other four subgenera. The four subgenera *Eucyclothorax*, *Meonochilus*, *Phacothorax*, and *Mecyclothorax s. s.* are hypothesized as successive sister groups (Fig. 1A). In all trees, relationships proposed for the Australian *Mecyclothorax* species are identical; e.g. Fig. 1B for the species of subgenus *Eucyclothorax*.

Cladistic analysis demonstrates the Australian *Mecyclothorax* fauna to be composed of several species or species assemblages interpolated among non-Australian taxa. The Queensland *Qecyclothorax* represent a the earliest divergent clade in Australia (Fig. 1A). Subgenus *Eucyclothorax*, a principal focus of this study, comprises the next divergent lineage (Fig. 1A–B). Subgenus *Mecyclothorax*, by far the most diverse component of the genus with over 350 species included (Liebherr 2013, 2015, 2017, 2018), is represented in mainland Australia by only four species; the adelphotaxa *M. lateralis* and *M. minutus*, and the more widespread species *M. ambiguus* and *M. punctipennis*. This subgenus diversified first in New Guinea, with species from Lord Howe and Norfolk Islands, and Borneo cladistically derived from that grade (Fig. 1A, Liebherr 2018). The Australian species pair *M. lateralis* plus *M. minutus* (Fig. 1A) are related to New Guinean taxa, whereas a third Australian species—*M. ambiguus*—is the adelphotaxon to *M. rotundicollis* of New Zealand. Most spectacularly, *M. punctipennis* is the most closely related species to not only *M. sculptopunctatus* of the St. Paul and Amsterdam Islands, but also to *M. montivagus*, the most generalized Hawaiian species that serves in this analysis as the surrogate representative for the 239 *Mecyclothorax* species that have radiated from a single ancestor in the Hawaiian Islands (Liebherr 2015).

Taxonomic treatment

At present, the best means to determine Australian *Mecyclothorax* beetles to genus is the key of Moore (1963), though the phylogenetic relationships of the Moore's recognized generic-level taxa are better represented in the analysis of Liebherr (2011a). It should be noted, however, that the relationships of the *Amblytelus*-related genera and *Mecyclothorax* should be assessed using the present analysis (Fig. 1A) as the enhanced taxonomic representation of Liebherr (2018) and this paper allow a more robust delineation of *Mecyclothorax* monophyly and its constituent subgenera.

Species treatments below follow one of three formats: **1**, a diagnosis and full description of external characters for all newly described taxa; **2**, an extended diagnosis presenting all salient external characters for previously described species of the *M. lophoides* species complex (see key below); and **3**, brief diagnostic combinations sufficient to allow determination of the balance of species in the subgenera *Eucyclothorax* and *Mecyclothorax*.

Genus *Mecyclothorax* Sharp

- Mecyclothorax* Sharp, 1903: 243 (type species *Cyclothorax montivagus* Blackburn by Andrewes 1939).
- Cyclothorax* MacLeay, 1871: 104 (not *Cyclothorax* Frauenfeld, 1868; type species *Cyclothorax punctipennis* MacLeay by monotypy; synonymy Sloane 1903).
- Thriscothorax* Sharp, 1903: 257 (type species *Cyclothorax unctus* Blackburn by original designation; synonymy Britton 1948).
- Atelothorax* Sharp, 1903: 269 (type species *Atelothorax optatus* Sharp by monotypy; synonymy Britton 1948).
- Metrothorax* Sharp, 1903: 269 (type species *Metrothorax molops* Sharp by Lorenz 1998; synonymy Britton 1948).
- Antagonaspis* Enderlein, 1909: 488 (type species *Antagonaspis sculptopunctata* Enderlein by original designation; synonymy Jeannel 1938).
- Loeffleria* Mandl, 1969: 54 (type species *Loeffleria globicollis* Mandl by monotypy; synonymy Baehr and Lorenz 1999).
- subgenus *Phacothorax* Jeannel, 1944: 84 (type species *Phacothorax fleutiauxi* Jeannel by original designation; synonymy Liebherr and Marris 2009).
- subgenus *Meonochilus* Liebherr & Marris, 2009: 10 (type species *Tarastethus amplipennis* Broun by original designation; synonymy Liebherr 2018).
- subgenus *Eucyclothorax* Liebherr, 2018: 12 (type species *Cyclothorax blackburni* Sloane by original designation).
- subgenus *Qecyclothorax* Liebherr, 2018: 14 (type species *Mecyclothorax storeyi* Moore by original designation).

Diagnosis. Moore (1963) diagnosed *Mecyclothorax* based on: **1**, apical palpomeres glabrous; **2**, pronotum cordate; **3**, male parameres narrowed apically. These characters were chosen to differentiate *Mecyclothorax* from *Neonomius* Moore, a genus now placed far from *Mecyclothorax* in the subtribe Moriomorphina. The first character works well for *Mecyclothorax*, with the rare occurrence of very short setae on the apical palpomeres, those setae about 0.10× the palp's maximal diameter. Since Moore's pioneering exposition, pronotal shape has been shown worthless for diagnosing *Mecyclothorax* given the great diversity in shape among the Tahitian (Perrault 1984, Liebherr 2013), Hawaiian (Liebherr 2015), and New Caledonian species (Liebherr 2018). The male parameres differ in configuration among the various subgenera of *Mecyclothorax*, but as Moore proposed, both right and left parameres are elongate and setose apically (Liebherr 2018, fig. 5). Other characters that diagnose *Mecyclothorax* from various other taxa in tribe Moriomorphini, both symplesiomorphically and synapomorphically (Liebherr 2011a), include: **1**, labrum truncate to moderately and broadly emarginate apically; **2**, ligula truncate medially between the 2 marginal setae, paraglossae elongate; **3**, pronotal base at least moderately punctate; **4**, elytral humeral margin smooth, without tooth at humeral angle; **5**, female apical ventrite with median patch of 4–5 smaller setae.

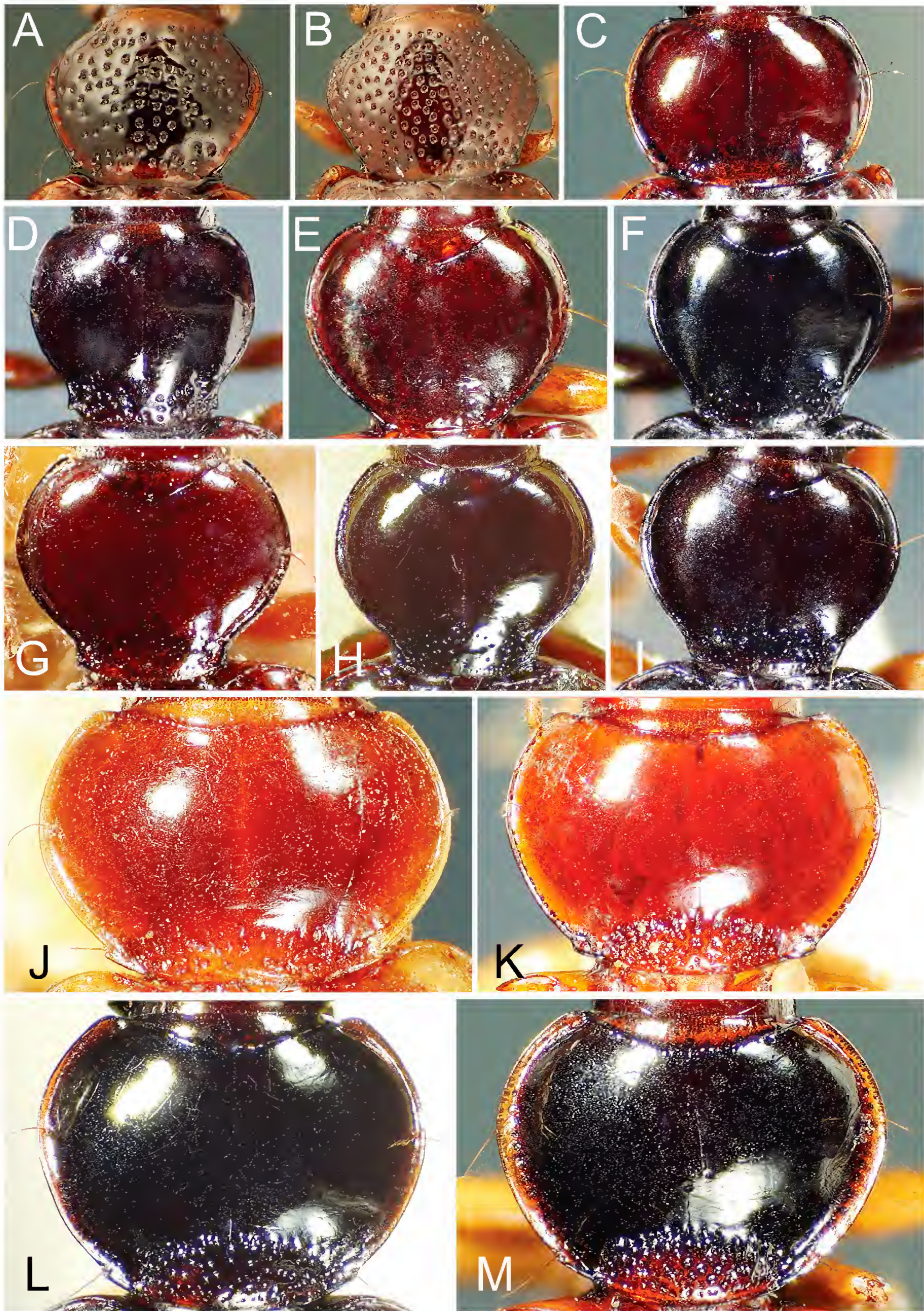


Figure 2. Pronota, dorsal view, of mainland Australian *Mecyclothorax* spp.: **A**, *M. (Eucyclothorax) moorei*; **B**, *M. (Eucyclothorax) punctatus*; **C**, *M. (Eucyclothorax) curtus*; **D**, *M. (Eucyclothorax) blackburni*; **E**, *M. (Eucyclothorax) darlingtoni*; **F**, *M. (Eucyclothorax) lophoides*; **G**, *M. (Eucyclothorax) eyrensis* lectotype; **H**, *M. (Eucyclothorax) peryphoides* holotype; **I**, *M. (Eucyclothorax) cordicollis*; **J**, *Mecyclothorax (s. s.) lateralis* paralectotype; **K**, *M. (s. s.) minutus* lectotype; **L**, *M. (s. s.) ambiguus*; **M**, *M. (s. s.) punctipennis*.

Nomenclatural note. Sloane (1915) described *Mecyclothorax ovalis* from Manjimup, WA, with label data (ANIC): Manjimup, W.A. / 31.12.13 T. G. S. // Mecyclothorax / ovalis Sl. Type // Holotype [pink label]. The pink holotype label is consistent with those used by P. J. Darlington, Jr. during his curation of the Sloane collection in 1957 (Darlington 1962: 328). The specimen is mostly destroyed, with only partial remnants of the legs remaining glued to the card. As such, because the holotype specimen can no longer be used to diagnose the species nor the species' generic placement, a neotype is designated. As this neotype designation is required to stabilize both the concept of this species and the species' new generic combination, such an action is valid under Article 75 of The Code (I.C.Z.N. 1999). Therefore a Neotype male (MCZ specimen deposited in ANIC) is hereby designated: Mullewa, W.A. / Sept. 19 1931 // Australia / Harvard Exp., / Darlington // MCZ // Neotype / Mecyclothorax / ovalis Sloane / det. J.K. Liebherr 2004 [black-margined red label]. These specimens, both neotype and others in the series (MCZ) exhibit densely setose apical palpomeres as well as the small ovoid body diagnostic for *Neonomius* Moore (1963). The male genitalia conform to the configuration observed in the subtribe Moriomorphina (Liebherr 2011a), with both parameres broad, parallel-sided with rounded apices, and the right

paramere ventrally setose, as observed in the generic type species *N. laevicollis* (Sloane) (Moore 1963, fig. 7). Based on these characters, Sloane's species is newly combined as *Neonomius ovalis* (Sloane), comb. n. Among species of *Neonomius*, *N. ovalis* is diagnosable from the sympatric *N. australis* (Sloane) by: **1**, the smaller body size, standardized body length 3.2–3.6 mm for the *N. ovalis* neotype series – agreeing with Sloane (1915; 451) – versus 5.0 mm for *N. australis* (Sloane 1915: 450); and **2**, the reddish-brown body color versus “black, nitid; legs piceous-red; antennae reddish (Sloane 1915, 450)” for *N. australis*. *Neonomius ovalis* can be diagnosed from the other two southeastern Australian species placed in the genus – *N. laevicollis* (Sloane) and *N. laticollis* (Sloane) – by the apically less convex elytral interval 8, versus the laterally compressed, subcarinate interval 8 characterizing those two species. The type locality for *M. ovalis* (Sloane) becomes Mullewa. That Moore et al. (1987) did not recognize Sloane's *Mecyclothorax ovalis* as a member taxon of *Neonomius* Moore is based on the lack of any other specimens in the ANIC beyond the destroyed holotype of *M. ovalis* Sloane, whereas Darlington made this nomenclatural connection, but only for specimens he deposited in the MCZ.

All other names placed under *Mecyclothorax* Sharp in Moore et al. (1987: 147–149) are treated below.

Key to the adults of the species of *Mecyclothorax* Sharp from mainland Australia

This key can be used to identify all mainland Australian species of *Mecyclothorax*. All previously recognized species of subgenus *Qecyclothorax* revised by Baehr (2003) are included, with his key couplets complemented by the addition of *M. lewisensis estriatus* subsp. n.

- 1 Prosternum punctate, either with punctures longitudinally oriented within a medial depression anterad procoxae, or more broadly distributed across the apical half of the prosternum (subgenus *Eucyclothorax* Liebherr) 2
- Prosternum smooth medially, though an impunctate depression may be present between procoxae 13
- 2 Proepisternum punctate either along the prosternal suture, or more broadly across apical half of entire sclerite 3
- Proepisternum impunctate near prosternal suture and on median surface, though punctures may be present in the proepimeral sutural groove 7
- 3 Pronotum densely punctate across entire surface, the punctures deep and round (Fig. 2A–B) 4
- Pronotal disc impunctate, punctures, if present, small and restricted to the pronotal base (Fig. 2D–I) 6
- 4 Elytral striae 1–5 present and evident on disc (Figs 3B–E, 4); elytra broad basally, lateral margins subparallel, humeri extended laterally so that the humeral angles lie laterad to the positions of pronotal hind angles 5
- Elytral striae 1–4 present on disc, though the punctures indicating the stria positions irregular and distant and stria 4 indicated by only a few very shallow punctures (Fig. 3A); elytra constricted basally, the lateral margins convexly divergent from humeral angles *M. moorei* Baehr
- 5 Dorsal punctation denser and finer, pronotal discal punctures separated from each other by distances equal to the punctural diameters (Fig. 2B) *M. punctatus* (Sloane)
- Dorsal punctures larger, less dense, pronotal discal punctures irregularly separated from each other by distances 1–2× setal diameters (see Baehr 2016a, fig. 1) *M. punctatus peckorum* Baehr
- 6 Pronotum transverse, MPW/PL = 1.39–1.47, lateral margins broadly convex with hind angle indicated by denticle on convex lateral margin (Fig. 2C); elytra broad, lateral margins convex posterad rounded humeri, MEW/EL = 0.71–0.76 *M. curtus* (Sloane)
- Pronotum narrow, distinctly cordate with narrow base, MPW/PL = 1.09–1.12, lateral margins constricted and parallel anterad projected hind angles (Fig. 2D); elytra quadrate, narrow, lateral margins parallel, MEW/EL = 0.62–0.66 *M. blackburni* (Sloane)
- 7 Pronotum constricted basally, the lateral margins straight to sinuate anterad the well-defined hind angles (Figs 4, 5A–C) (*M. lophoides* species complex) 8
- Pronotum broadly ovoid, hind angles only suggested as change of curvature of lateral margin at basal pronotal seta (Fig. 3E) *M. isolatus* Liebherr, sp. n.

- 8 Pronotum quadrisetose, both lateral and basal setae present, pronotal basal margin not beaded medially, though margin may be beaded for short distance mesad hind angle (Fig. 2F–I)..... 9
- Pronotum bisetose, hind angles glabrous, pronotal basal margin beaded medially (Fig. 2E, 4A–B) 10
- 9 Pronotum very narrow basally relative to transverse breadth at midlength, MPW/BPW = 2.23–2.32 (Fig. 2E); posterior margin of eye in dorsal view broadly margined by gena, ocular lobe ratio = 0.84–0.88; parascutellar striole consisting of 4–5 isolated punctures..... *M. darlingtoni* Liebherr, sp. n.
- Pronotum narrow basally but less transverse at midlength, MPW/BPW = 1.68 (Fig. 4B); eyes covering most of ocular lobe, EyL/OLL = 0.95; parascutellar striole consisting of 7–8 isolated punctures *M. jameswalkeri* Liebherr, sp. n.
- 10 Dorsal body surface rufopiceous to rufous, legs paler with femora, tibiae and tarsi flavous (Fig. 5A–C); male aedeagal internal sac either with flagellum much longer than flagellar sheath (Fig. 14D–F), or with sheath bifurcated apically (Fig. 14G–H) .. 11
- Dorsal body surface piceous, legs dark, femora fuscous, tibiae and tarsi paler, brunneous with piceous cast (Fig. 4C–D); male aedeagal internal sac with flagellum and flagellar sheath of moderate, equal length, the flagellar sheath unbranched (Fig. 14A–C)..... *M. lophoides* (Chaudoir)
- 11 Elytral disc dark brunneous to rufopiceous, suture and lateral margins concolorous with disc, though apex may be broadly paler, rufoflavous (Fig. 5B–C); surface of discal elytral intervals subiridescent due to dense transverse-line microsculpture, sutural stria smooth or irregularly punctate in apical half (Fig. 12D–E); pronotal lateral margins shallowly concave anterad obtuse or obtuse-rounded hind angles (Fig. 2H–I), basal pronotal seta set in expanded marginal bead that is only slightly broader at hind angle versus anterad in lateral concavity..... 12
- Elytral disc rufous, suture and lateral margins with piceous cast (Fig. 5A); surface of discal elytral intervals glossy, microsculpture obsolete, vaguely defined transverse lines visible at margins of reflected microscope illumination, sutural stria distinctly punctate in apical half (Fig. 12C); pronotal lateral margins deeply, distinctly concave anterad slightly obtuse, well-projected hind angles (Fig. 2G), basal pronotal seta set in middle of upraised triangle defined laterally and basally by pronotal margins..... *M. eyrensis* (Blackburn)
- 12 Pronotal lateral marginal depression broader, margin upraised in a bead, hind angles obtuse, with marginal depression continued mesoposteriorly for short distance beyond basal pronotal seta (Fig. 2H); elytral apex concolorous with disc, only the lateral marginal depression near subapical sinuation narrowly paler (Fig. 5B); standardized body length 4.3–5.0 mm..... *M. peryphoides* (Blackburn)
- Pronotal lateral marginal depression very narrow, margin not upraised in a bead, hind angles obtuse-rounded, with marginal depression terminated posteriorly at basal pronotal seta (Fig. 2I); elytral apex broadly, diffusely paler, rufoflavous, in contrast to the dark brunneous disc (Fig. 5C); standardized body length 4.0–4.7 mm..... *M. cordicollis* (Sloane)
- 13 Elytra with a single dorsal elytral seta in third interval, situated near elytral midlength (Fig. 5D); standardized body length 2.6–3.7 mm (subgenus *Qecyclothorax* Liebherr)..... 14
- Elytra with two dorsal elytral setae in third interval (Fig. 6); standardized body length 4.9–6.4 mm (subgenus *Mecyclothorax* Sharp) 21
- 14 Clypeus bisetose; base of pronotum coarsely punctate, basal angles without seta, anterior transverse impression deep; male aedeagus inverted from ground-plan condition so that it everts toward right side..... 15
- Clypeus quadrisetose; base of pronotum not or sparsely punctate, basal angles with seta, anterior transverse impression barely indicated; male aedeagus oriented in groundplan condition so that apex everts toward left side..... 16
- 15 Pronotum not sinuate in front of base; aedeagus larger, apex shorter and wider, internal sac with two small spinose areas in front (Baehr 2003, fig. 1A) (Bellender Ker Range, Massey Range, QLD)..... *M. storeyi storeyi* Moore
- Pronotum slightly sinuate in front of base (Baehr 2003, fig. 3A); aedeagus smaller, apex longer and narrower, internal sac without spinose areas in front (Baehr 2003, fig. 1B) (Bartle Frere Range, QLD) *M. storeyi frerei* Baehr
- 16 Lateral margins of pronotum not perceptibly sinuate posteriorly (Baehr 2003, fig. 3G); genital ring with broad, moderately elongate apex (Baehr 2003, fig. 1E) 17
- Lateral margins of pronotum perceptibly sinuate posteriorly (Baehr 2003, fig. 3C, E); genital ring, when known, with narrow elongate apex (Baehr 2003, fig. 1C–D) 18
- 17 Spinose fields with apex of aedeagal ostium smaller, situated at left and right sides (Baehr 2003, fig. 1E) (southwestern part of Atherton Tbl.: Mt. Fisher, Mt. Hugh Nelson, Mt. Father Clancy, Malaan Rd. nr. Palmerston Hwy., QLD)..... *M. inflatus inflatus* Baehr
- Spinose fields with apex of aedeagal ostium very large, situated only at the right side (Baehr 2003, fig. 1F) (Upper Boulder Creek at Water Hill Range, QLD) *M. inflatus spinifer* Baehr
- 18 Inner striae of elytra at most lightly impressed and finely punctate..... 19
- Four inner striae of elytra impressed and finely punctate (Baehr 2003, fig. 3F; Isley Hills, ne. Atherton Tbl., QLD)..... *M. impressipennis* Baehr
- 19 Inner four elytral striae evident on disc, consisting of distinct rounded punctures separated along the stria by 1–2 puncture diameters (Baehr 2003, fig. 3D)..... 20
- Only the sutural stria slightly impressed on elytral disc, striae 2–4 completely absent, the planar discal surface interrupted only by the puncture associated with the dorsal elytral seta (Fig. 5D; Brandy Creek nr. Conway N. P., QLD)..... *M. lewisensis estriatus* Liebherr, subsp. n.

- 20 Apex of aedeagus rounded off, genital ring with longer apex (Baehr 2003, fig. 1C); pronotum with comparatively wider base, ratio base/apex > 1.20 (Carbine Tbl., Thornton Peak, Mt. Pieter Botte, north of Thornton Peak, QLD)..... *M. lewisensis lewisensis* Moore
- Apex of aedeagus sharply spined, genital ring with considerably shorter apex (Baehr 2003, fig. 1D); pronotum with comparatively narrow base, ratio base/apex < 1.17 (Mt. Hemmant, Mt. Halcyon, Roaring Meg Ck., mountain tops nr. Cape Tribulation, all north of Thornton Peak, QLD)..... *M. lewisensis uncinatus* Baehr
- 21 Dorsal body coloration brunneous to rufous, legs concolorous or only slightly paler than lateral elytral intervals (Fig. 6A–B); parascutellar seta absent 22
- Dorsal body coloration rufopiceous to piceous, legs flavous, contrastingly paler than lateral elytral intervals (Fig. 6C–D); parascutellar seta present 23
- 22 Elytra bicolored, intervals 2–6 brunneous to rufopiceous, contrastedly darker than rufous sutural interval and flavous intervals 7–9 (Fig. 6A); elytra broad, MEW/EL = 0.78–0.81; body size larger, 5.2–6.4 mm *M. lateralis* (Castelnau)
- Elytral disc, suture and margins concolorous, rufoflavous to rufobrunneous (Fig. 6B); elytra narrower, MEW/EL = 0.68–0.75; body size smaller, 4.9–5.7 mm *M. minutus* (Castelnau)
- 23 Pronotal lateral marginal depression moderately broad, extended laterally as far as distance from lateral pronotal seta to marginal depression (Fig. 2L); elytral disc with well-developed transverse microsculpture, a mixture of transverse sculpticells 2–3× broad as long and loosely connected transverse lines, the surface with bluish iridescence; male aedeagal apex broadly subquadrate, the tip subangulate (Fig. 15C) *M. ambiguus* (Erichson)
- Pronotal lateral marginal depression broad, extended laterally 3–4× as far as distance from lateral pronotal seta to marginal depression, the extended margin translucent (Fig. 2M); elytral disc glossy, ill-defined transverse lines and elongate sculpticells present over portions of surface; male aedeagal apex narrowly rounded, the tip slightly downturned (Fig. 15D) *M. punctipennis* (MacLeay)

Subgenus *Eucyclothorax* Liebherr

Diagnosis. Beetles assigned to this subgenus have the prosternum punctate, with punctures either: **1**, distributed over the lateral reaches of the prosternum and medial reaches of the proepisternum; **2**, more generally distributed across both sclerites; **3**, lining a median depression anterad the prosternal process; **4**, lining the prosternal-proepisternal suture; or **5**, lining a transverse preapical depression (Liebherr 2018, fig. 2D–F). The pronotum may be distinctly punctate (Fig. 2A–B) or not (Fig. 2C–I), but in all species the median pronotal base is coplanar to only slightly depressed relative to the pronotal disc, not greatly depressed as in Australian species of subgenus *Mecyclothorax* (Fig. 2J–M). The vertex is transversely flat to convex, without a transverse dorsal impression, or neck. Generally the species conform to the full complement of standard setae; formula ++/++/2++. However the basal pronotal seta is absent in *M. darlingtoni* and *M. jameswalkeri*, the parascutellar seta is polymorphically present or absent within *M. punctatus*, and *M. isolatus* exhibits only a single dorsal elytral seta. Body size ranges from small to moderately large, with standardized body length 2.7–6.0 mm.

All *Eucyclothorax* spp. are characterized by male genitalia that possess a flagellum, flagellar sheath, and dorsal plate at the apex of the internal sac, as well as robust aedeagal median lobes, i.e. dorsoventrally broad (Figs 7, 14). The female reproductive tract is configured with the spermathecal duct joined ventrally to the juncture of the common oviduct and the bursa copulatrix (Fig. 9). A helminthoid sclerite is present on the bursal wall ventrad the juncture of the spermathecal duct and common oviduct. Like all other *Mecyclothorax*, the gonocoxae have setae along the apicolateral margin of the basal gonocoxite

(Fig. 10), and the apical gonocoxite has 1–3 (usually 2) lateral ensiform setae.

Mecyclothorax moorei Baehr

Figures 2A, 3A, 7A–B, 8A, 9A, 10A, 11A

Mecyclothorax moorei Baehr, 2009: 90.

Diagnosis (n = 2). This species is diagnosed by the broadly punctate pronotal disc (Fig. 2A), punctate head with a transverse line of about 5 large punctures between the posterior supraorbital setae, and convex, smooth elytra with only striae 1–4 in evidence, striae 2–4 only a series of small isolated punctures. The prosternum and proepisternum are also broadly punctate, the punctures large and separated from each other by a distance equal to the punctural diameters (Liebherr 2018, fig. 2F). The punctate pronotal disc, head, and prosternum + proepisternum are shared with *M. punctatus*, but the pronotal punctures are more numerous and less separated in *M. punctatus* (Fig. 2A–B), with about 30 punctures each side in *M. moorei*, and about 60 each side in *M. punctatus*. In addition, the elytral striae are more distinct in *M. punctatus*, with striae 1–5 present in the basal half of the elytra, though the punctures of stria 5 are smaller and shallower. The elytra of *M. moorei* are more ovoid, with the lateral margins more narrowly rounded behind the subangulate humeri (Fig. 3A–B). Whereas the parascutellar seta is present or absent in *M. punctatus*, and if present appearing short and narrow, this seta is well developed in *M. moorei*, with the setal articulatory socket set within a depression coincident with the base of the parascutellar striole, the seta as long as the breadth of 2–3 elytral intervals. The eyes of *M. moorei* are convex but they cover only the anterior 4/5

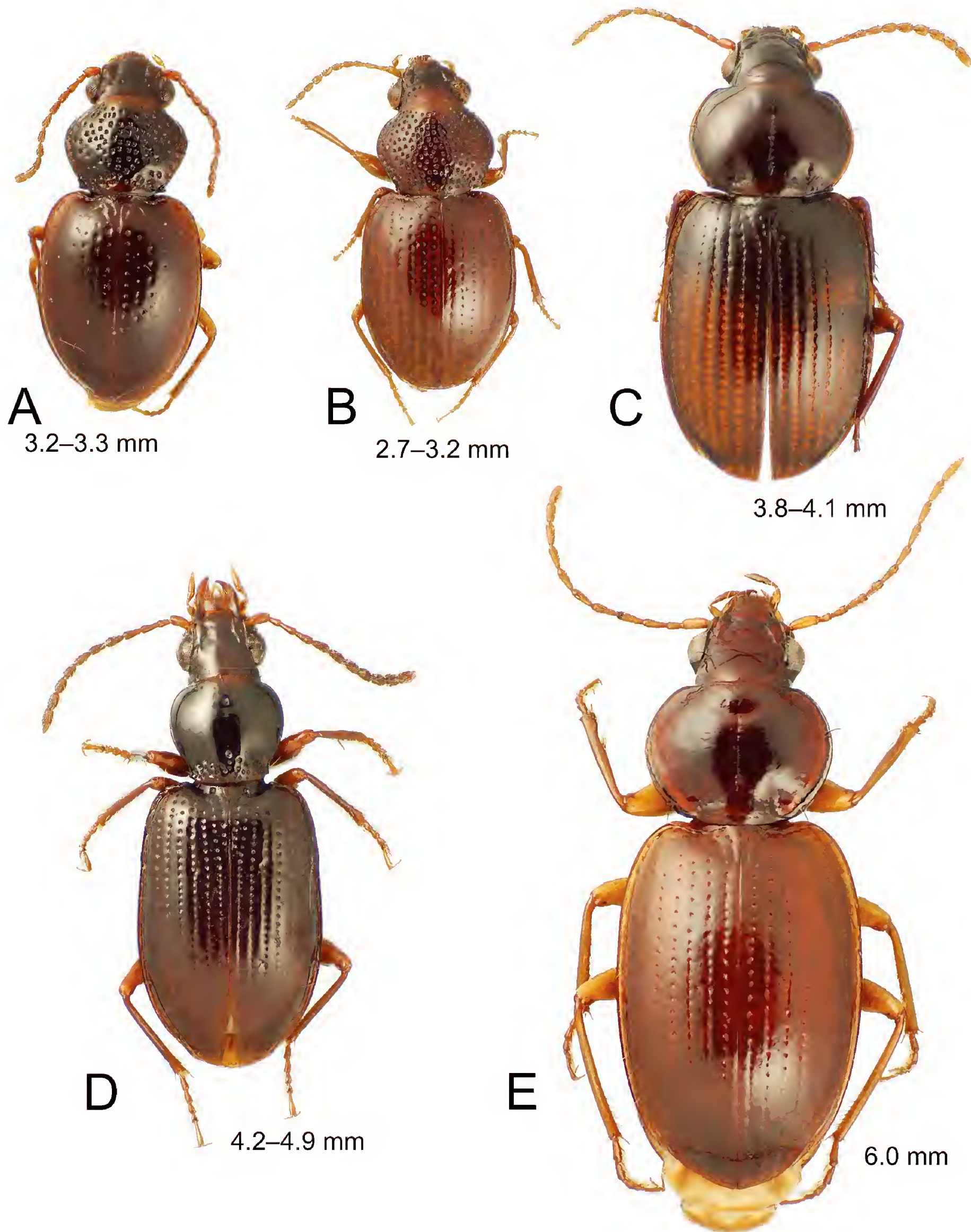


Figure 3. *Mecyclothorax* (*Eucyclothorax*) spp., dorsal view: **A**, *M. moorei*; **B**, *M. punctatus*, NSW; **C**, *M. curtus*; **D**, *M. blackburni*; **E**, *M. isolatus* holotype.

of the ocular lobe: $EyL/OLL = 0.83–0.86$. Finally, males of this species, *M. punctatus*, and *M. curtus* all exhibit 2 setae each side of the apical abdominal ventrite, an unusual character state within *Mecyclothorax*, and evidence

of their monophyletic relationship within subgenus *Eucyclothorax* (Fig. 1B, character 83). Standardized body length 3.2–3.3 mm. Setal formula ++/++/2++.

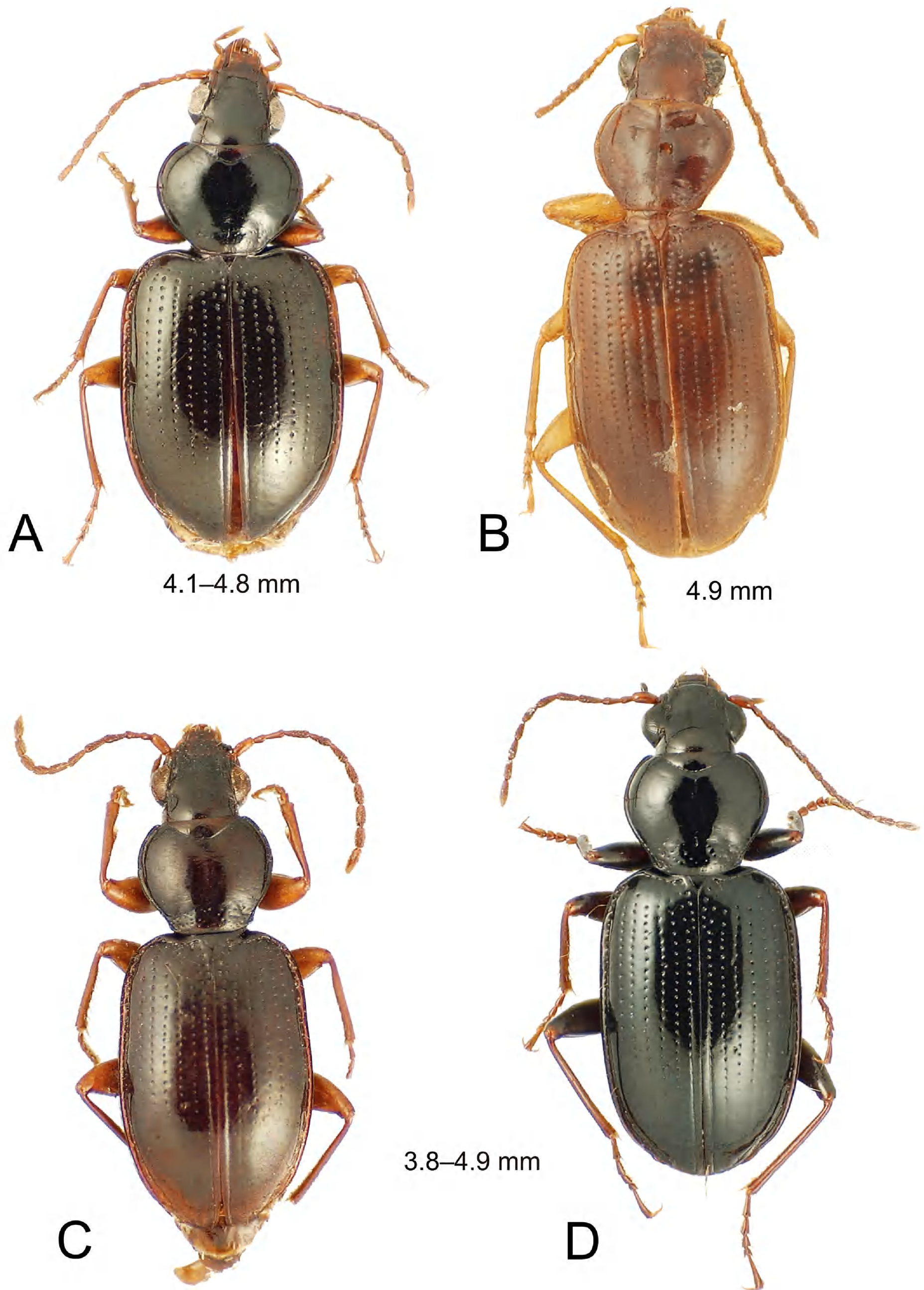


Figure 4. *Mecyclothorax* (*Eucyclothorax*) spp., dorsal view: **A**, *M. darlingtoni*; **B**, *M. jameswalkeri* holotype; **C**, *M. lophoides* lectotype, Melbourne; **D**, *M. lophoides*, ACT: Smoker's Gap.

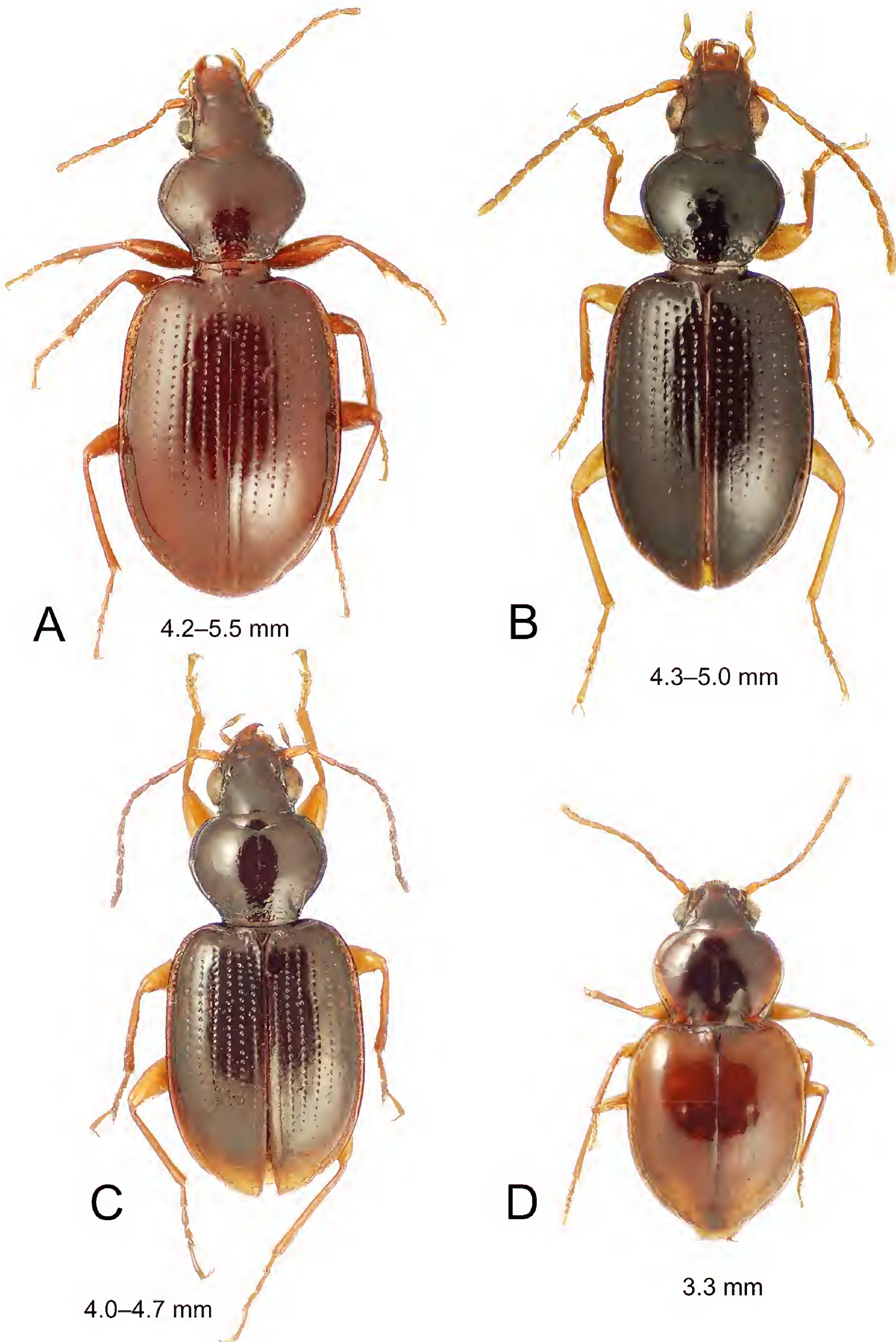


Figure 5. *Mecyclothorax* spp., dorsal view: **A**, *M. (Eucyclothorax) eyrensis*, paralectotype; **B**, *M. (Eucyclothorax) peryphoides*; **C**, *M. (Eucyclothorax) cordicollis*; **D**, *M. (Qecyclothorax) lewisensis estriatus* holotype.

Male genitalia (n = 2). Aedeagal median lobe apex narrowly rounded and only slightly projected beyond apical ostial margin (Fig. 7A); aedeagal internal sac elongate, membranous, with apical dorsal plate, flagellum, and flagellar sheath (Fig. 7B); right paramere narrow, elongate, with 6 setae along the ventral margin, 1–2 apical setae, and the dorsal margin glabrous except for a small apical seta (Fig. 8A); left paramere broadly quadrate basally, the apical 1/3 of length very narrow in contrast to broad base.

Female reproductive tract (n = 1). Bursa copulatrix elongate, columnar (Fig. 9A); helminthoid sclerite elongate; spermathecal duct basally expanded and sclerotized, the more apical portion of duct membranous and of lesser diameter; basal gonocoxite with 2 larger setae laterally along apical margin (Fig. 10A), a very small seta medially near margin; apical gonocoxite broad basally, breadth more than half length; lateral ensiform setae elongate, ~0.60× length of apical gonocoxite; apical nematiform setae in subbasal sensory furrow.

Type information. Holotype male (AMS): site 32AR NSW Banda Rd about 4.5 km E Hastings Forest Hwy 31°09'S 152°25'E Mount Boss State Forest 17 1100m (NPWS Survey) 4 Feb–9 Apr 1993 M. Gray, G. Cassis (AMS K241125) (Baehr 2009).

Distribution and habitat. *M. moorei* is restricted to northeastern New South Wales (Fig. 11A), with populations allopatrically distributed relative to eastern populations of the more southerly distributed *M. punctatus*. Recorded elevations of collecting localities range from 110 m near Ramornie and 1100 m in Mt. Boss State Forest (Baehr 2009). Philip Darlington collected this species in Bellangry Forest NW of Wauchope (MCZ). All specimens are vestigially winged.

Mecyclothorax punctatus (Sloane)

Figures 2B, 3B, 7C, 8B, 9B, 10B, 11A

Cyclothorax punctatus Sloane, 1895: 449.

Mecyclothorax punctatus, Sloane, 1903: 585; Moore 1984: 163, fig. 12.

Mecyclothorax punctatus peckorum Baehr, 2016a: 94.

Diagnosis (n = 5). This species is most similar to *M. moorei*, with several diagnostic characters differentiating the two listed there. The eyes are large and convex, largely covering the ocular lobes; EyL/OLL = 0.92–0.96. The elytra are broad, with broadly rounded humeri (Fig. 3B). The single available female specimen assignable to *M. p. peckorum* has the elytral base broad, slightly different from the nominate form. However the pronotal and elytral stria punctures are deeper and less dense in *M. p. peckorum*—as reported in Baehr (2016a)—resulting in recognition of the two forms here. In addition, the parascutellar seta is much less in evidence among individuals of this species. When present it is short and fine, and it is certainly absent from the majority of examined spec-

imens. Standardized body length 2.7–3.2 mm. Setal formula ++/++/±2++.

Male genitalia (n = 1). Aedeagal median lobe apex narrowly rounded and not projected beyond apical ostial margin (Fig. 7C); right paramere narrow, elongate, with ~10 setae along the ventral margin, 2 apical setae, and the dorsal margin with 3 small setae (Fig. 8B); left paramere broadly expanded basally, its dorsal margin convex, the apical 1/3 of length very narrow in contrast to broad base. Baehr (2016a, fig. 2) documents a short leftward expansion on the median lobe apex of *M. p. peckorum*. The parameral setation of the two subspecific forms is identical (Fig. 8B; Baehr 2016a, fig. 2).

Female reproductive tract (n = 1). Bursa copulatrix elongate, columnar (Fig. 9B); helminthoid sclerite elongate; spermathecal duct basally expanded and sclerotized, the more apical portion of duct membranous and of lesser diameter; basal gonocoxite with 3 larger setae laterally along apical margin (Fig. 10B); apical gonocoxite broad basally, breadth more than half length; lateral ensiform setae broad, elongate, length about 0.5× length of apical gonocoxite, setal surface longitudinal striate; apical nematiform setae in subbasal sensory furrow.

Type information. For *M. punctatus*, Lectotype female (SAMA) hereby designated: white card with “5104” and “N.S.W.” in red ink // N.S. Wales // *punctatus* Sloane // J. 7252 / *Mecyclothorax* / *punctatus* / M.S. Wales / Cotype [red ink] // Lectotype ♀ / *Cyclothorax* / *punctatus* Sloane / det. J.K. Liebherr 2004 [red label with black border]. For *M. punctatus peckorum*, Holotype male (ANIC, not seen): Pemberton Warren N.P. WA 12 Jul. 1980 S. & J. Peck SBP106 // Berlesate karri litter and moss (Baehr 2016a).

Distribution and habitat. Following Baehr's (2016a) circumscription of this species, it is distributed across an easterly set of populations in southern New South Wales and northern Victoria (Fig. 11A), plus a disjunct set of western localities in the southwest region of Western Australia. Sloane wrote of the type series, “I have found it in considerable numbers under logs and the leaves of saplings at a place about twenty-five miles north-west from the town of Urana. It is sluggish in its movements (Sloane, 1895: 449–450).” Thus the type locality is very close to one of the localities where he collected types of *M. cordicollis* (Sloane 1900). More recently, specimens from the western localities have been collected via litter sifting of jarrah forest litter (*Eucalyptus marginata* Donn ex Sm.). All specimens are vestigially winged.

Mecyclothorax curtus (Sloane)

Figures 2C, 3C, 7D, 8C, 9C, 10C, 11B

Cyclothorax curtus Sloane, 1895: 448.

Mecyclothorax curtus Sloane, 1903: 585.

Diagnosis (n = 4). The transverse pronotum—MPW/PL = 1.39–1.47 with nearly impunctate median base and broadly convex margins (Fig. 2C), and broad, subpar-

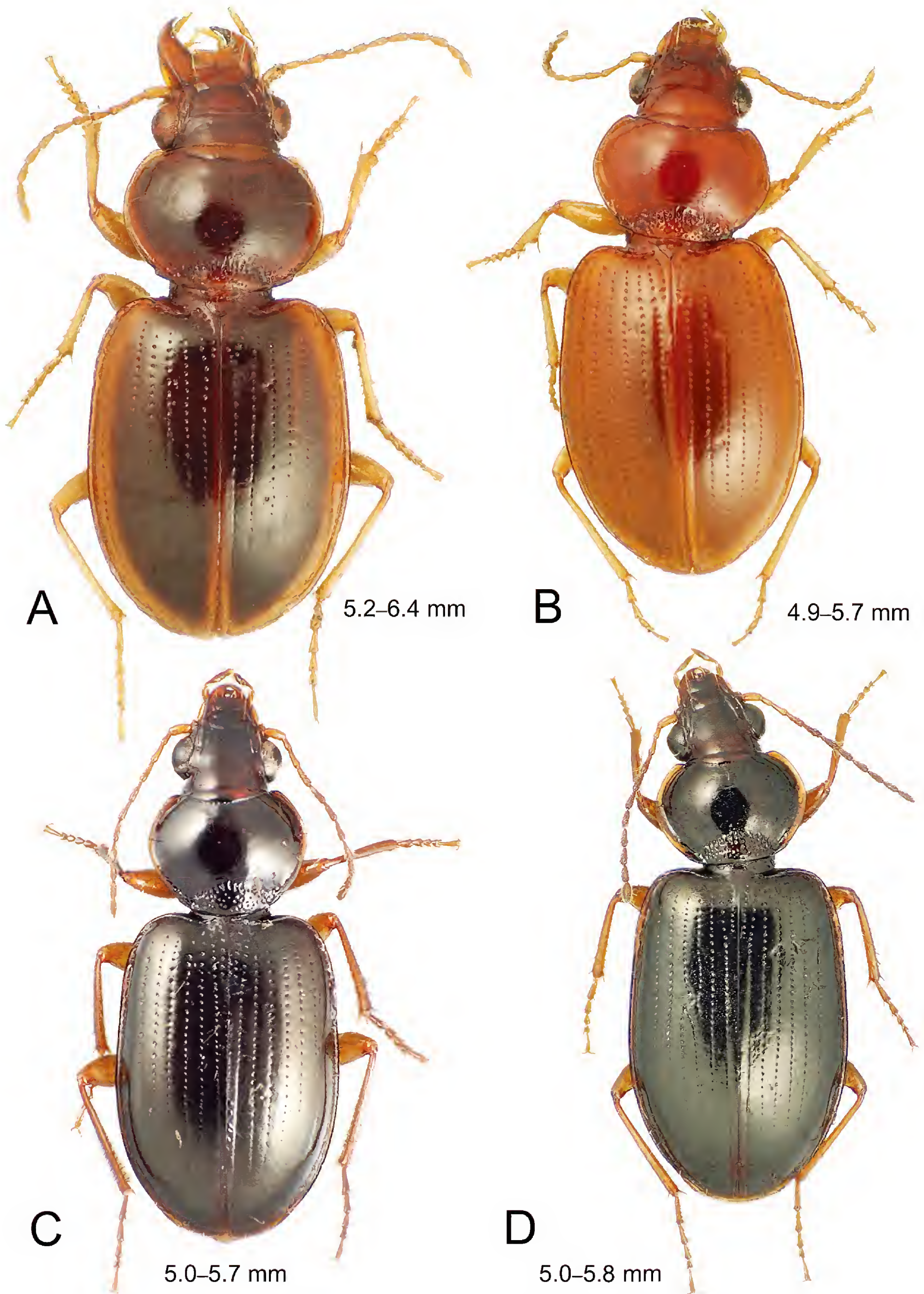


Figure 6. *Mecyclothorax* (s. s.) spp., dorsal view: **A**, *M. lateralis*; **B**, *M. minutus*; **C**, *M. ambiguus*; **D**, *M. punctipennis*.

allel elytra (Fig. 3C), are unique within *Mecyclothorax*, unmistakably diagnosing this very rarely collected species. The pronotal hind angles are defined by denticles on a more broadly convex margin, the basal pronotal setae associated with a broadened marginal bead at their point of insertion. There are 5–6 minute punctures each side on the median base inside the laterobasal depressions, which are marked by 2–3 oblique lines of larger punctures associated with the depression (Fig. 2C, left side). Ventral prothoracic punctation is restricted to the lateral reaches of the prosternum (Liebherr 2018, fig. 2D). The lateral margins of the abdominal ventrites are also distinctly punctate, the punctures distributed densely and irregularly enough to give the surface a dented look. As in the above two species, both males and females have 4 setae along the apical margin of the apical abdominal ventrite. As in *M. punctatus*, the eyes are large and convex, $EyL/OLL = 0.87–0.91$. However unlike *M. punctatus* and *M. moorei*, the elytral striae are fully developed, with all striae evident nearly to the elytral apex. There is a well-developed carina immediately laterad stria 7 that extends from the position of the posterior series of lateral elytral setae to the elytral margin distad the well-developed elytral plica, parsimoniously interpreted as a parallelism also observed in *M. blackburni* (Fig. 1B, Liebherr 2018, fig. 2L). The apical palpomeres bear a sparse pelage of very short setae, a character otherwise only observed within the genus in Norfolk Island's *M. monteithi*. Standardized body length 3.8–4.1 mm. Setal formula ++/++/2++.

Male genitalia ($n = 1$). Aedeagal median lobe apex narrowly rounded with broad dorsal expansion, the apical face of the lobe concave (Fig. 7D); flagellum short, associated with very elongate sclerotized saccal surface herein interpreted as flagellar sheath (single available male with sac uneverted); right paramere elongate but broad apically (Fig. 8C), the paramere more robust than in other *Eucyclothorax* (Figs 8, 13), and with ventral surface bearing only a single short seta complementing the 2 long apical setae, and the dorsal surface glabrous; left paramere broad basally (as in males of *M. moorei* and *M. punctatus*), but also broad apically, the apex more than half the breadth of base, a single longer seta present at apex.

Female reproductive tract ($n = 1$). Bursa copulatrix elongate, columnar (Fig. 9C); helminthoid sclerite with distal projection; spermathecal duct elongate, more than twice length of spermathecal reservoir, the duct moderately sclerotized, undulated along length; basal gonocoxite with a single large seta laterally along apical margin (Fig. 10C); apical gonocoxite very broad, the base extended and recurved basally so that lateral margin is distinctly concave; lateral ensiform setae broad, dorsal ensiform seta situated medially so that its apex extends beyond medial margin; apical nematiform setae in sub-basal sensory furrow.

Type information. Holotype (ANIC): specimen on white triangle, lacking head and prothorax // *C. curtus* Sl.

(type) / Bendigo. W.W.F. / 1176; “1176” is in Sloane's specimen list for 1893/94 (ANIC, unpubl. data).

Distribution and habitat. The lone holotype was collected by W.W. Froggatt at Bendigo, Victoria. Besides the holotype, I have had the opportunity to examine only a second specimen from Bendigo (MVM), two specimens from Sea Lake, Victoria (Fig. 11B; ANIC, MVM) and a single female from 27 km W Manangatan (ANIC). This last specimen is labeled “South Australia”, but based on the locality data it must be from Victoria. Nothing is recorded concerning this species' habits, though occupation of a terrestrial microhabitat associated with forest vegetation near water would be consistent with the habits of its adelphotaxon, the sister-species pair *M. moorei* and *M. punctatus* (Fig. 1B). All specimens are vestigially winged.

Mecyclothorax blackburni (Sloane)

Figures 2D, 3D, 7E, 8D, 9D, 10D, 11B

Cyclothorax blackburni Sloane, 1898: 472.

Mecyclothorax blackburni Csiki, 1929: 487 (see Nomenclatural note).

Diagnosis ($n = 5$). Beetles of this species are very narrow-bodied, with a narrow, cordate pronotum (Fig. 2D), and narrow, subparallel elytra and an elongate head (Fig. 3D). The pronotal median base is coplanar with the disc, but distinguished by the presence of about 14 large deep punctures each side. The right pronotal hind angles protrude both laterally and posteriorly in association with a broadened marginal bead at the articulatory socket of the basal pronotal seta. Otherwise the pronotal lateral margin is extremely narrow, defined only by a marginal bead. Basally the elytral striae consist of series of closely spaced punctures, their separations equal to their diameters. Puncture size decreases, and puncture distances increase laterally and apically on the elytra, with stria 7 represented by only a few small punctures at mid-length. Interval 8 is broadly convex apically, and the elytral plica is well developed and evident in dorsal view. Ventrally, the body punctation includes a punctate median depression anterad the prosternal process, punctures along the lateral reaches of the prosternum, and a punctate anteapical groove (Liebherr 2018, fig. 2E). The lateral reaches of the mesosternum, metasternum, and all of the metepisternum are also intensely punctate. The basal 3 abdominal ventrites are covered with numerous small punctures laterally, and the suture between visible ventrites 2 and 3 is traceable only as a shallow groove. The apical margin of the male apical abdominal ventrite bears the usual 2 setae, 1 each side, but also 4 small medial setae in the position observed in *Mecyclothorax* females. Standardized body length 4.2–4.9 mm. Setal formula ++/++/2++.

Male genitalia ($n = 2$). Aedeagal median lobe very broad and only slightly curved, the apex with subacuminate ventroapical projection and a broadly convex dor-

soapical expansion resulting in a broadly concave apical face (Fig. 7E); flagellum short, flagellar sheath robust, and dorsal plate lightly sclerotized, difficult to discern in single available unverted male; right paramere narrow, with 4 small setae ventrally and dorsal surface glabrous (Fig. 8D); left paramere broad basally, narrowly attenuate apically.

Female reproductive tract (n = 1). Bursa copulatrix elongate, extended dorsodistally beyond juncture of common oviduct and bursa (Fig. 9D); helminthoid sclerite robust, with distal projection; spermathecal duct straight and slightly longer than spermathecal reservoir, evenly, moderately sclerotized; basal gonocoxite with 1 larger seta apically, a smaller seta present or not (Fig. 10C); apical gonocoxite narrowly triangular, narrowed apically to acuminate apex; lateral ensiform setae narrow, moderately elongate; apical nematiform setae in apical sensory furrow.

Type information. Holotype male (SAMA): card mounted // TY Pinjarrah // Holotype *M. blackburni* / PJD Sl. [red label].

Nomenclatural note. Sloane (1903) proposed the replacement of *Cyclothorax* MacLeay (1871) (not Frauenfeld 1868) with Sharp's *Mecyclothorax* (1903), mentioning the new combinations of *M. lateralis* (Castelnau), *M. fortis* (Blackburn) = *M. minutus* (Castelnau) [NEW SYNONYMY herein], *M. punctatus* (Sloane), and *M. curtus* (Sloane). By not mentioning *M. blackburni*, nor also *M. eyrensis* (Blackburn), *M. peryphoides* (Blackburn), *M. cordicollis* (Sloane), *M. minutus* (Castelnau), and *M. punctipennis* (MacLeay), Csiki (1929) became the first to propose these combinations (see also below).

Distribution and habitat. *M. blackburni* is known only from coastal Western Australia (Fig. 11B) from Perth south to Harvey (ANIC, 2 specimens). The Perth locality is denoted as "Bridgel'a" (MVM, 1 specimen), which is here interpreted to be an abbreviation of Bridgeleigh, a remnant area of bush vegetation in Swan Valley, Wanneroo. Commander J.J. Walker, Royal Navy, collected a specimen at Fremantle in 1914 (BMNH). When Sloane (1898) described the species based on one specimen received from Arthur Lea he listed no biological information, and none accompanies the other four available specimens. Those four specimens are all macropterous.

Mecyclothorax isolatus, sp. n.

<http://zoobank.org/B41F0209-F1AF-4C25-BAED-3315A834227C>

Figures 3E, 11B

Diagnosis (n = 1). The larger body size, standardized body length 6.0 mm, ferruginous body color, and broadly transverse, ovoid pronotum (Fig. 3E) serve to diagnose this species from others of subgenus *Eucyclothorax*, except perhaps the smaller-bodied *M. curtus* (Fig. 3C). However the lateral margin of the pronotum is broadly rounded behind in this species, with the margin explanate in the region of the basal pronotal seta. The metathorax is remarkably abbreviated, more so than in any other Australian species of *Mecyclothorax*, with the metepis-

ternum transversely broader than its lateral length. The elytra exhibit a subcarinate ridge along the eighth interval dorsad the subapical sinuation, reminiscent of such a carinate ridge observed in *M. blackburni*. The carinate ridge lies dorsad a well-developed internal elytral plica, with the plica and elytral margin fitting into a corresponding invagination along the margin of the apical abdominal ventrite, thereby forming, in concert with the conjoining of the elytra at the suture, a very robust, shell-like hind-body. Finally, there is a single dorsal elytral seta on each elytron (Fig. 3E), situated near midlength as observed in species of subgenus *Qecyclothorax* (Fig. 5D). Setal formula +/+/+/+/+/1/+/+.

Description. Head capsule elongate, frons with medial depression but otherwise convex mesad the deep, sinuous frontal grooves; frontal grooves deeply and obliquely continued onto clypeus toward lateral clypeal margins; labrum slightly emarginate apically; antennae filiform, antennomere 9 length 2.36× breadth; mandibles moderately elongate, overall length 1.57× distance from anterior condyle to lateroapical labral margin; eyes well developed and moderately convex, ocular lobe broadly projected, outer eye surface of same curvature behind as posterior portion of lobe meeting gena, ocular ratio = 1.47, ocular lobe ratio = 0.79; mentum tooth with sides obtuse, apex broadly rounded; ligular apex moderately narrowed, 2 ligular setae separated by 3 setal diameters; paraglossae thin, extended 1/2× as far past ligular margin as distance from base to ligular margin; mentum broad, breadth/length across the lateral lobes = 3.25. Pronotum broadly ovoid, MPW/PL = 1.31, without any indication of hind angles save a slight change of curvature of the lateral margin at the hind seta; articulatory socket of lateral seta 1 setal diameter mesad deepest part of marginal depression; median base convex, unmarginated medially though broadly upraised mesad laterobasal depressions; base convex anterad basal margin, slightly depressed relative to convex disc, and separated from disc by broad, smooth oblique depressions that extend to laterobasal depressions; about 8 indistinct punctures each side from midline to mesal margins of laterobasal depressions, the depressions broadly extended to explanate lateral margin, with a low upraised tubercle in the middle of each depression; median longitudinal impression fine, well indicated, crossed by transverse wrinkles on disc; anterior transverse impression broad, shallow medially, not indicated laterally; anterior callosity slightly, broadly convex, a well-defined marginal bead along front of pronotum; front angle moderately protruded, tightly rounded; prosternal process broadly depressed between procoxae; prosternum smooth and convex medially, indistinctly punctate anterolaterally with an indistinct anteapical groove consisting of broad punctures that anastomose into a groove along lateral reaches; proepisternum impunctate, however prosternal-proepisternal suture lined with about 5 indistinct punctures; proepimeron with broadly raised posterior bead, the suture with proepisternum smooth. Mesepisternum punctate at its deepest portion, about

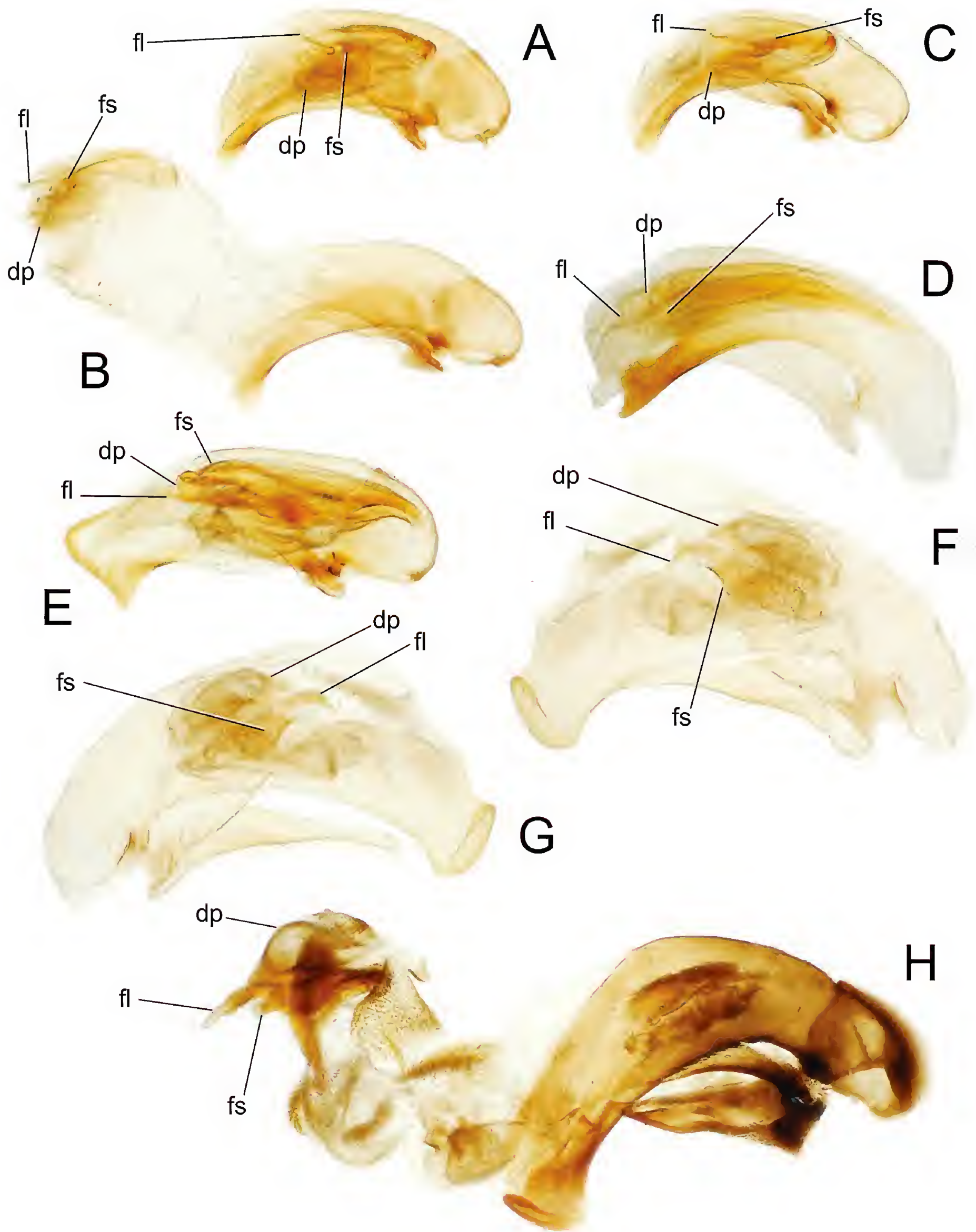


Figure 7. Male aedeagus, right view (unless stated otherwise), for *Mecyclothorax* (*Eucyclothorax*) spp.: **A**, *M. moorei*, NSW: Bellangry For.; **B**, *M. moorei*, NSW: Bellangry For.; **C**, *M. punctatus*, VIC: Sea Lake; **D**, *M. curtus*, VIC: Bendigo; **E**, *M. blackburni*, WA: Fremantle; **F**, *M. darlingtoni*, QLD: Woondom For. Res.; **G**, same specimen left view; **H**, *M. darlingtoni*, QLD: 30 mi. N Brisbane.

6 deep punctures in 1–2 dorsoventral rows. Elytra with striae 1–5 composed of isolated punctures in basal half, less punctate though traceable in apical 1/3 of length, stria 6 represented by small, isolated punctures at mid-

length, stria 7 absent except near apex mesad subcarinate eighth interval dorsad subapical situation; sutural stria broadly depressed in apical half in association with convex sutural interval, the elytra conjoined apically; stria 8

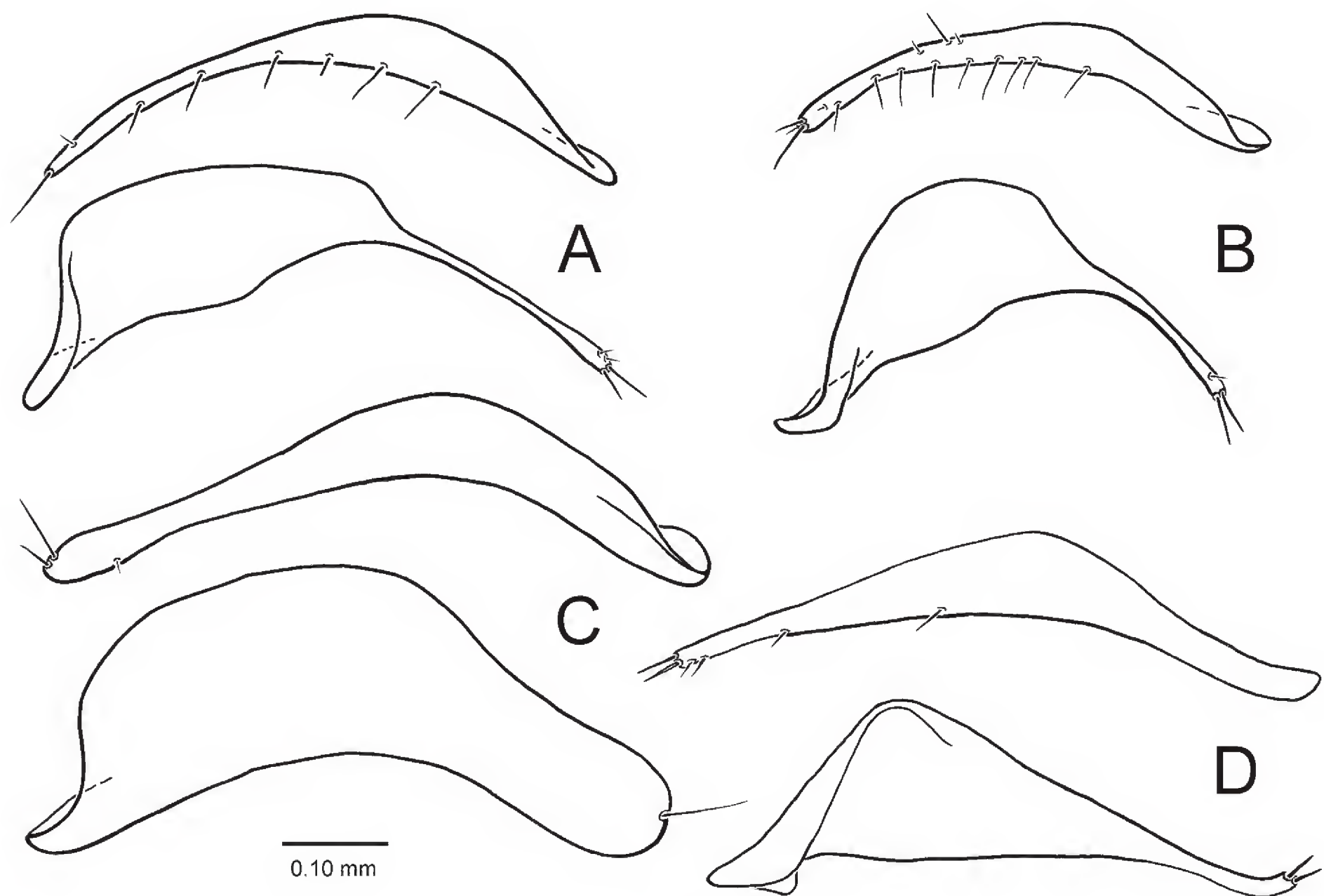


Figure 8. Male parameres of *Mecyclothorax* (*Eucyclothorax*) spp., ectal view, right paramere above in each pair, left paramere below: **A**, *M. moorei*, NSW: Bellangry For.; **B**, *M. punctatus*, VIC: Sea Lake; **C**, *M. curtus*, VIC: Bendigo; **D**, *M. blackburni*, WA: Fremantle.

a series of deep, interrupted punctures at midlength, deep and continuous mesad the posterior series of lateral elytral setae; lateral elytral setae arrayed in 7 + 6 (anterior series setae and posterior series setae), with the posterior seta of the anterior series slightly separated from the rest; subapical sinuation angulate, abruptly curved anteriorly, with well-developed internal elytral plica visible in quarter view, though obscured by the elytral margin in dorsal view. Metepisternum short, trapezoidal, maximum breadth $1.1 \times$ lateral length, metepimeron broadly convex posteriorly; metasternal process with sides acute, apex narrow, triangular with margin very broad medially in apex of process. Abdomen with broad linear depressions on lateral reaches of visible ventrites 3–6; suture between ventrites 1 and 2 deeply sinuous laterally, ventrite 2 depressed within sinuosity; female with 2 setae each side and a median patch of 4–5 smaller setae; apical margin of the female apical ventrite with deep emargination each side bordered laterally by a vertical, sclerotized border, these emarginations and lateral wall fitting into the elytral plica above. Microsculpture absent from frons, the surface glossy, micropunctures visible across the surface; pronotal disc and base with indistinct transverse microsculpture consisting of transverse lines and elongate meshes, these visible in surface irregularities such as wrinkles and depressions; elytral disc glossy with fine transverse lines faintly visible outside areas of reflection, elytral apex with

transverse sculpticells visible in irregularly depressed areas associated with striae; metasternum glossy with indistinct transverse sculpticells, their breadth $2\text{--}3 \times$ length; abdominal ventrites glossy with swirling transverse mesh and transverse lines. Coloration of head rufous; antennomere 1 flavous, antennomeres 2–3 rufoflavous, 4–11 with brunneous cast; pronotal disc dark rufous, margins rufoflavous; elytral disc rufobrunneous, sutural interval concolorous, interval 9 and marginal depression, and apex narrowly rufoflavous; proepipleural margin rufous, rufoflavous ventrally, proepisternum rufous; elytral epipleuron broadly flavous, margin darker, brunneous, metepisternum rufoflavous; abdominal ventrites rufoflavous with dark rufous posterior margins, apical ventrite with apical half rufoflavous; femora flavous; tibiae brunneous.

Female reproductive tract ($n = 1$). The unique female holotype was not dissected, however the gonocoxae are exerted from the specimen allowing the following characters to be assessed: basal gonocoxite with 2 stout apicolateral setae, medioapical surface glabrous (as in Fig. 10A); apical gonocoxite extended laterally at base, basal width about $0.7 \times$ length, 2 stout lateral ensiform setae along lateral margin of coxite and an elongate dorsal ensiform seta present; apical nematiform setae within fossa at about $0.8 \times$ gonocoxite length. Thus the gonocoxal configuration is most like that of *M. moorei* (Fig. 10A), another early divergent species within subgenus *Eucyclothorax* (Fig. 1).

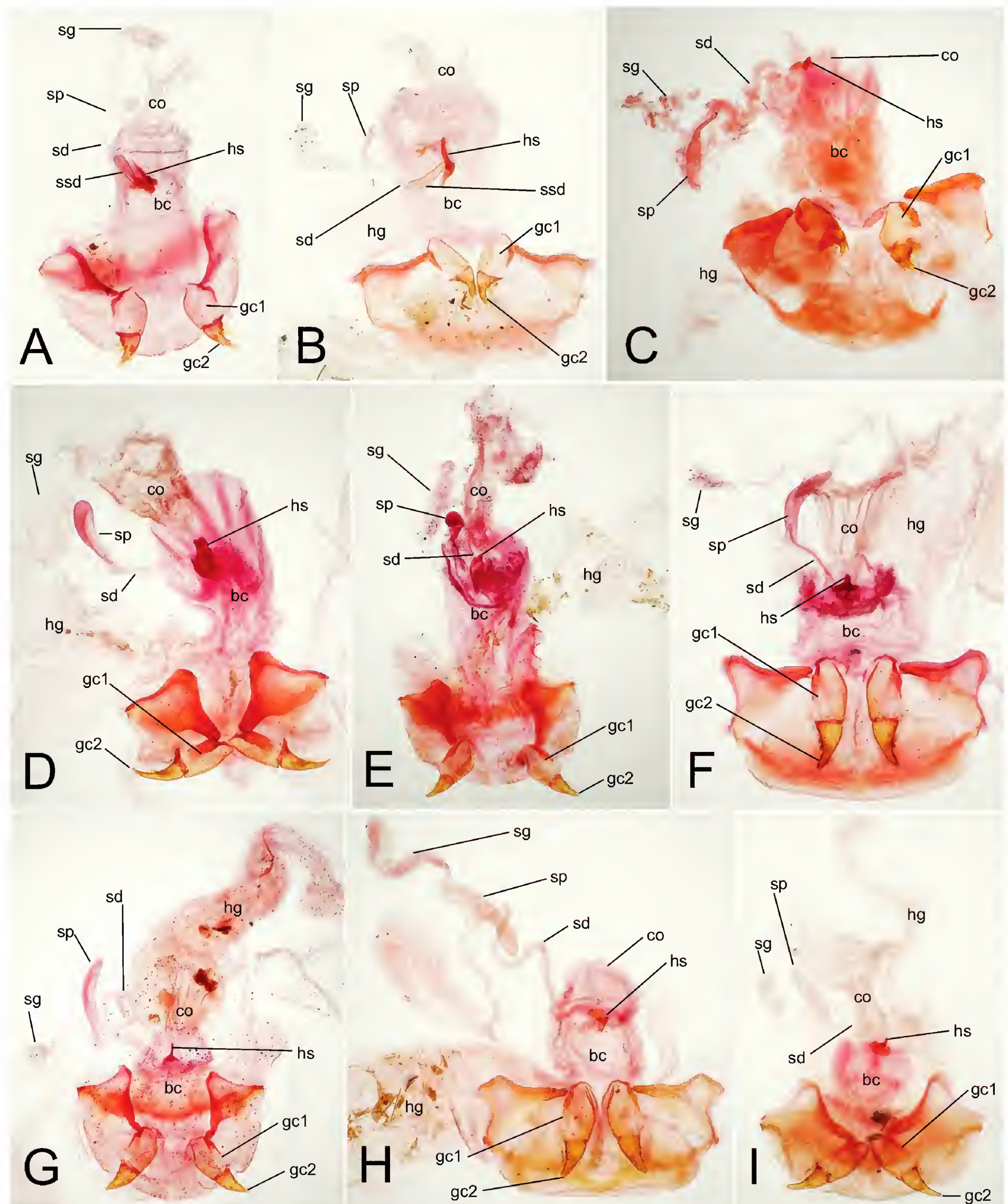


Figure 9. Female reproductive tract and gonocoxae of *Mecyclothorax* (*Eucyclothorax*) spp., ventral view: **A**, *M. moorei*, NSW: Werrikimbe N. P.; **B**, *M. punctatus*, VIC: Birchip; **C**, *M. curtus*, SA: Manangatan; **D**, *M. blackburni*, WA: Harvey; **E**, *M. darlingtoni*, QLD: Woondom For. Res; **F**, *M. lophoides*, ACT: Smoker's Gap; **G**, *M. eyrensis*, SA: Telowie Gorge; **H**, *M. peryphoides*, ACT: Black Mountain; **I**, *M. cordicollis*, NSW: Gosford.

Holotype female (ANIC): Walpole N.P. /Zig Zag Rd. WA / 20–27 June 1980 / S. & J. Peck SBP 70B // berlesate / rotted log / litter and / fungi // HOLOTYPE / *Mecyclothorax* / isolatus / J.K. Liebherr 2018 (black-margined red label).

Etymology. The adjectival species epithet *isolatus* signifies both the geographic isolation of this species that is distributed in the south coast region of Western Australia (Fig. 11B), as well as the phylogenetic isolation of this

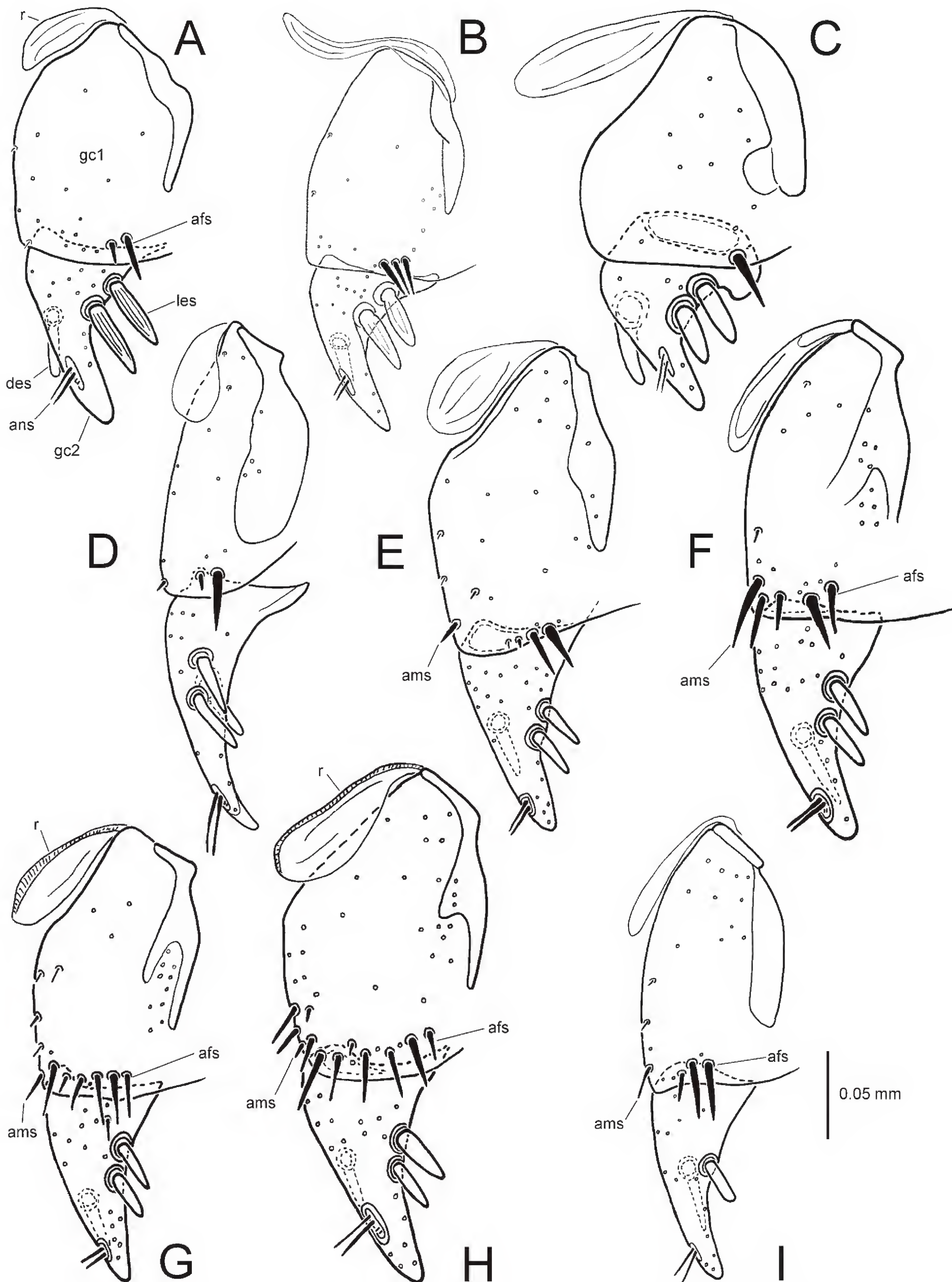


Figure 10. Left gonocoxa of *Mecyclothorax* (*Eucyclothorax*) spp., ventral view: **A**, *M. moorei*, NSW: Werrikimbe N. P.; **B**, *M. punctatus*, VIC: Birchip; **C**, *M. curtus*, SA: Manangatan; **D**, *M. blackburni*, WA: Harvey; **E**, *M. darlingtoni*, QLD: Woondom For. Res; **F**, *M. lophoides*, ACT: Smoker’s Gap; **G**, *M. eyrensis*, SA: Telowie Gorge; **H**, *M. peryphoides*, SA: Blackwood; **I**, *M. cordicollis*, NSW: Gosford.

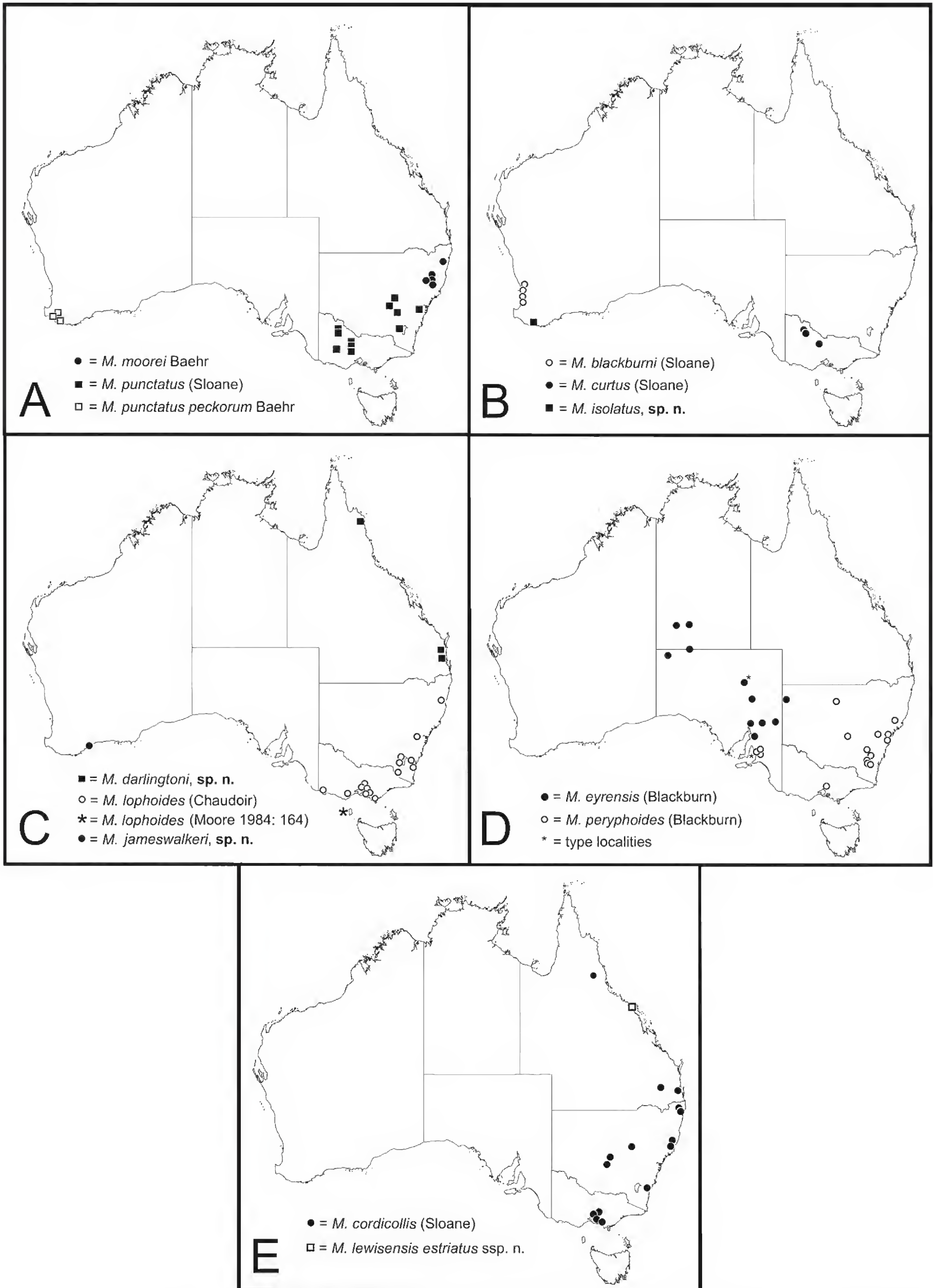


Figure 11. Distributional ranges of 11 *Mecyclothorax* spp. assigned to subgenus *Eucyclothorax*, plus newly described subspecies of *M. lewisensis*.

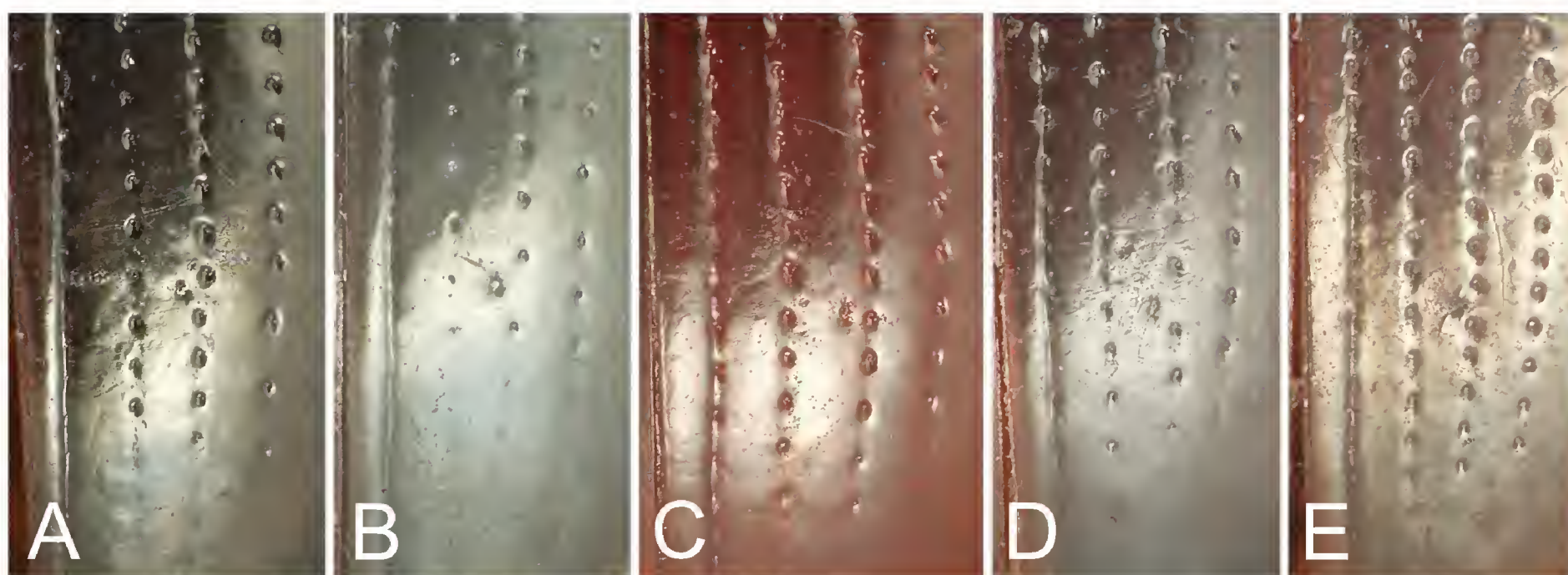


Figure 12. Distal portion of right elytron centered on apical dorsal elytral seta–sutural interval at left in view—showing differential punctuation of sutural stria and striae 2 to 4: **A**, *M. darlingtoni* female; **B**, *M. lophoides* male; **C**, *M. eyrensis* paralectotype female; **D**, *M. peryphoides* male; **E**, *M. cordicollis*, paralectotype male.

species, as it comprises the adelphotaxon to all other species of subgenus *Eucyclothorax* (Fig. 1)

Distribution and habitat. This species is known only from the tingle tree (*Eucalyptus jacksoni* Maiden) forest in the south coast region of Western Australia (Fig. 11B). The single individual was collected in berlesate moist enough to support growth of fungal hyphae (S. B. Peck, pers. comm.). The vestigialized flight wings occur in concert with an extremely abbreviated metathorax and a well-developed plical lock between the elytra and apical abdominal ventrite. This species' adelphotaxic relationship to the remainder of subgenus *Eucyclothorax* (Fig. 1) supports its long-term persistence in this region since the early diversification of all *Mecyclothorax*.

Mecyclothorax darlingtoni, sp. n.

<http://zoobank.org/1D1DDE5B-6CB1-4A6F-A5AD-C9586A3087AC>
Figures 2E, 4A, 7F–H, 9E, 10E, 11C, 12A, 13A

Mecyclothorax sp. n. D, Liebherr 2018: 3 (non-valid terminal in cladistic analysis).

Diagnosis (n = 5). This species and *M. jameswalkeri* are the only species of subgenus *Eucyclothorax* with glabrous hind pronotal angles (Fig. 2E). Of the two, *M. darlingtoni* is more broad-bodied (Fig. 4A–B), with: **1**, a more transverse and basally constricted pronotum, MPW/PL = 1.32–1.35, MPW/BPW = 2.21–2.32; and **2**, relatively broader elytra, MEW/EL = 0.70–0.75. Both species are characterized by large eyes, but the eyes of *M. darlingtoni* do not cover as much of the ocular lobe; EyL/OLL = 0.84–0.88. The parascutellar striole in this species is composed of 4–5 small, deep, isolated pits arcuately joining the basal groove. Standardized body length 4.1–4.8 mm. Setal formula ++/+–/+2++.

Description. Head capsule broad, vertex broadly convex between deep, sinuous frontal grooves, the grooves more shallowly continued onto clypeus; labrum broad-

ly, moderately concave; mandibles moderately elongate, overall length 1.64× distance from anterior condyle to lateroapical labral margin; ocular lobes convexly projected, outer eye surface slightly more convex than posterior portion of lobe meeting gena; mentum tooth with sides acute, apex rounded; ligular apex moderately narrowed, 2 ligular setae separated by 2 setal diameters; paraglossae thin, extended 2× as far past ligular margin as distance from base to ligular margin; mentum breadth/length across lateral lobes = 2.58. Pronotum with articulatory socket of lateral seta touching marginal depression; hind angles obtusely rounded, margin anterad angle slightly concave (Fig. 2E); median base completely margined, the marginal bead uniform and continuous across width (Fig. 4A), base convex anterad basal margin, nearly coplanar with disc though disc is convex and upraised anterad toward middle of pronotum; about 6 minute punctures on base each side of midline, laterobasal depression a shallow longitudinal depression immediately anterad hind angle; median longitudinal impression fine, well indicated, crossed by oblique transverse wrinkles anterad base; anterior transverse impression deep, punctate medially, fine and deep to front angle; anterior callosity slightly convex, defined posteriorly by deep transverse impression; front angle slightly protruded, tightly rounded; prosternal process with broad deep median depression with 4 indistinct pits along its length; prosternum with anteapical groove that is deep and distinctly punctate laterally, smoother and more irregular medially, marginal bead of procoxal cavity bordered anteriorly by distinct, close-set punctures; proepisternum impunctate; proepimeron with broadly raised posterior bead, punctures along suture with proepisternum and anterad posterior bead. Mesepisternum punctate at its deepest portion, about 6 deep punctures in 1–2 dorsoventral rows. Elytra with striae 1–6 composed of isolated punctures in basal half, striae 2–6 reduced to absence in apical 1/3 of length (Fig. 12A), stria 7 absent except near apex from position of subapical situation to apical margin; sutural stria deeper in apical half in association with convex sutural interval, the

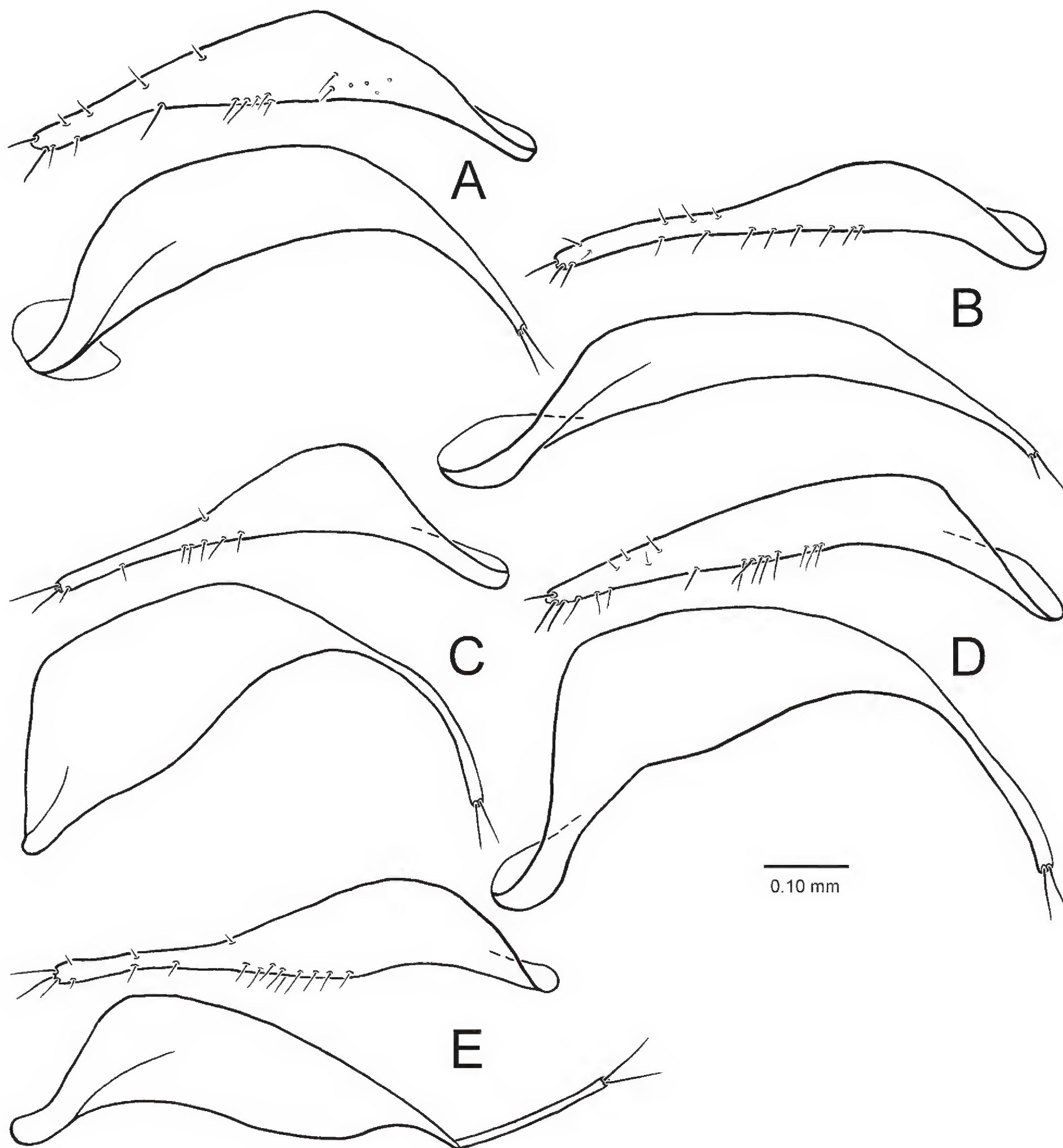


Figure 13. Male parameres of *Mecyclothorax* (*Eucyclothorax*) spp., ectal view, right paramere above in each pair, left paramere below: **A**, *M. darlingtoni*, QLD: Woondom For. Res.; **B**, *M. lophoides*, NSW: Blackheath; **C**, *M. eyrensis*, SA: Telowie Gorge; **D**, *M. peryphoides* holotype, SA: Woodville; **E**, *M. cordicollis*, NSW: Gosford.

suture smooth from near position of apical dorsal elytral seta to apex (Fig. 12A); stria 8 deep, punctate and bordering lateral marginal depression anteriorly, deeper, smooth and distinct mesad posterior series of lateral elytral setae; lateral elytral setae arrayed in 7 + 6 (anterior series setae and posterior series setae); subapical sinuation evident, abruptly curved anteriorly, but elytral plica covered by margin in dorsal view. Metepisternum moderately elongate, maximum width/lateral length = 0.63; metasternal process with sides acute, apex narrowly rounded, margin

very broad medially in apex of process. Abdomen with linear wrinkles on lateral reaches of visible ventrites 1–2, more rounded depressions laterally on ventrites 3–6; suture between ventrites 1 and 2 deeply sinuous laterally; males with 1 seta each side along margin of apical ventrite, females with 2 setae each side and a median patch of 4–5 smaller setae; apical margin of the female apical ventrite with small convex projection medially. Microsculpture absent from frons, the surface glossy, micropunctures visible across the surface; pronotal disc with shallow transverse

mesh, sculpticell breadth 3–4× length, pronotal base with evident, regular transverse mesh, sculpticell breadth 2–3× length; elytral disc glossy with fine transverse lines, loosely connected into a mesh and producing an iridescent reflection (Fig. 12A), elytral apex with elongate transverse mesh, surface iridescent; metasternum with distinct transverse mesh, sculpticell breadth 2–3× length; basal abdominal ventrites with swirling transverse mesh and transverse lines, surface iridescent. Coloration of vertex piceous, frons rufous near clypeus, clypeus rufoflavous; antennomeres 1–3 rufoflavous, 4–11 with piceous cast; pronotal disc piceous; margins concolorous; elytral disc dark rufous with iridescent reflection, sutural interval concolorous, interval 9 and marginal depression rufoflavous; elytral apex narrowly brunneous; proepipleuron margin piceous, dark rufous ventrally, proepisternum rufopiceous; elytral epipleura rufoflavous apically, dark rufous ventrally, metepisternum dark rufous; abdominal ventrites rufopiceous with amber posterior margins, apical ventrite with apical half rufobrunneous; femora flavous with brunneous cast; tibiae brunneous with piceous cast.

Male genitalia (n = 4). Male aedeagal median lobe robust, curved, with broad blunt apex, the apical margin curled toward right resulting in a dorsoventral crease (Fig. 7H); internal sac with a robust flagellar sheath, attenuate flagellum, and broad, well-sclerotized dorsal plate (Fig. 7G–H); right paramere elongate, broader basally, conchoid (Fig. 13A), ventral surface with ~9 setae along margin, dorsal margin with 4 setae; left paramere narrow basally, evenly narrowed to apex.

Female reproductive tract (n = 1). Bursa copulatrix elongate, columnar (Fig. 9E); helminthoid sclerite robust with distal projection; spermathecal duct straight, shorter than spermathecal reservoir, evenly sclerotized; basal gonocoxite with 3–4 setae along apical margin, 2 larger laterally and the balance small and positioned medially (Fig. 10E), an apicomedial seta present; apical gonocoxite subtriangular, apex narrowly rounded; lateral ensiform setae small relative to gonocoxite length; apical nematiform setae in apical sensory furrow.

Types. Holotype male (MCZ deposited in ANIC): c30 mi. N. of / Brisbane SQ / Mar. '58 / Darlingtons // HOLOTYPE / Mecyclothorax / darlingtoni / J.K. Liebherr 2018 (black-margined red label). Allotypic paratype female (MCZ deposited in ANIC): (same data as holotype, with black-margined red Allotype label).

Paratypes (61 specimens). AUSTRALIA: Queensland: Brisbane, 30 mi. N, iii-1958, Darlingtons (CUIC, 1; MCZ, 19); Mt. Webb, 3 km NE, 15. 03°S 145. 09°E, 03-v-1981, Calder (ANIC, 1); Woondom For. Res., Mothar Mtn. For. Dr., dry rainfor., palm gully, FMHD #2004-217, berl. wet litter along stream, Solidovnikov 1139, 26°15.77'S 152°49.48'E, 380-400 m, 09-xii-2004, Solidovnikov (CUIC, 2; FMNH, 24); FMHD #2004-218, berl. litter under palms, Thayer 1139, 26°15.77'S, 152°49.48'E, 09-xii-2004, Thayer (CUIC, 3; FMNH, 10); Thayer 1139, pyr. fog old logs, 26°15.77'S, 152°49.48'E, 380-400 m, 09-xii-2004, Thayer (FMNH, 1).

Etymology. The species commemorates Prof. Philip J. Darlington, who collected extensively across Australia during various expeditions undertaken throughout his career. He personally developed the most extensive collection of Australian Carabidae housed in North America, allowing American scientists the ability to work with the fauna. He also curated the Thomas G. Sloane collection after its receipt by C.S.I.R.O., stabilizing the specimens and thereby preserving their information for future researchers. Although he focused on the New Guinea carabid fauna (summarized in Darlington 1971), he rightfully viewed the New Guinean fauna as an extension of the Australian, making biogeographic connections underpinned by taxonomic relationships for much of the Australian Region (Wallace 1876).

Distribution and habitat. *M. darlingtoni* is broadly distributed along the Queensland coast, with recorded localities spanning the vicinity of Brisbane to Mt. Webb in northern Queensland (Fig. 11C). The extensive numbers of specimens collected in Woondom Forest Reserve (FMNH) were extracted from Berlese samples from mesic litter under palms, or from wet litter along a stream. The single specimen from the northerly and, based on present specimens, disjunct Mt. Webb locality is macropterous, as is one of the two specimens from Dalby, whereas all other specimens from southern Queensland are vestigially winged.

Mecyclothorax jameswalkeri, sp. n.

<http://zoobank.org/27A7A15F-B09B-4B59-9F8E-CB0AA17A78A2>

Figures 4B, 11C

Diagnosis (n = 1). This, the second of two Australian species of subgenus *Eucyclothorax*– with *M. darlingtoni*– characterized by the absence of basal pronotal setae, can be diagnosed by aspects of the narrow body, including: **1**, a narrow, basally constricted pronotum, MPW/PL = 1.28, MPW/BPW = 1.88; and **2**, narrow, subparallel elytra, MEW/EL = 0.64. Like *M. darlingtoni*, the prosternum of this species has a punctate medial depression anterad the prosternal process, in this instance lined with 7 punctures. The prosternal anteapical groove is continuous and distinctly punctate laterally, more irregular and smoother ventrally. The eyes are large and moderately convex, and they cover much of the ocular lobe; EyL/OLL = 0.95. The parascutellar striole is composed of 7–8 deep, isolated pits. Standardized body length 4.9 mm. Setal formula ++/+–/+2++.

Description. Head elongate with large eyes (Fig. 4B), vertex broadly convex between deep, sinuously convergent frontal grooves that continue anterolaterally onto clypeus, anterior supraorbital seta in deep depression behind frontolateral callous; labrum broadly, slightly emarginate; mandibles elongate, overall length 1.9× distance from anterior condyle to lateroapical labral margin; mentum tooth with obtuse side, apex shallowly bifid; mentum breadth/length across lateral lobes = 2.57. Pronotum with

lateral setal articulatory socket within associated expansion of lateral marginal depression, the lateral marginal depression otherwise broad enough to observe microsculpture at its deepest part, its margin beaded; hind angle obtusely rounded, the lateral margin slightly sinuate before angle; medial base unmargined inside marginal bead that extends only slightly inside hind angle, convex, with ~10 small punctures each side from midline to laterobasal depression; laterobasal depression a narrow oblique groove extended from mesad sinuate lateral margin toward middle of disc; median longitudinal impression very fine and shallow, occluded by broad, shallow transverse wrinkles, deepest between arms of anterior transverse impression; anterior transverse impression smooth, continuous from near midline to rounded, slightly protruded front angles; marginal bead of procoxal cavity lined anteriorly with 3 small isolated punctures: proepisternum impunctate. Mesepisternum punctate at its deepest portion, about 9 deep punctures in 2–3 dorsoventral rows. Elytra with serially punctate striae 1–6, stria 7 absent except near subapical seta; elytral punctures round with distinct center point, separated by their diameter on disc, smaller in stria 6 where separated by 2 punctural diameters; sutural stria distinctly punctate basally, becoming smoother toward apical 1/4 of length, but sutural interval slightly convex (teneral condition?), the transition from punctate to smooth as in Fig. 12A; stria 8 deep, punctate and bordering lateral marginal depression anteriorly, deeper, smooth and distinct mesad posterior series of lateral elytral setae; lateral elytral setae arrayed as 7 + 6 (anterior series setae and posterior series setae); subapical sinuation evident, abruptly curved anteriorly, but elytral plica covered by margin in dorsal view. Metepisternum moderately elongate, maximum width/lateral length = 0.44; metasternal process acute, apex knob-like, margins upraised, twice as broad at apex; metathoracic flight wing macropterous, veins evident in folded condition under teneral elytra, apex reflexed. Abdomen with linear wrinkles laterally on visible ventrites 1–3, shallow rounded depressions laterally on ventrites 3–6; suture between ventrites 1 and 2 slightly sinuate, deep midway along suture; female with 2 marginal setae each side of apical ventrite plus a trapezoidal patch of 4 smaller medial setae. Microsculpture of frons indistinct, surface glossy, vertex with indistinct transverse mesh in parts; pronotal disc and median base with shallow transverse mesh, sculpticell breadth 3–4× length, sculpticells irregularly swirling in laterobasal depressions; elytral disc with transverse lines loosely connected into mesh, the surface subiridescent; elytral apex with transverse lines in a loose mesh, the convex, estriate surface iridescent. Coloration (assessed on single teneral specimen) of vertex rufous with brunneous cast; antennomeres 1–3 rufoflavous, 4–11 with piceous cast; pronotal disc dark rufous, margins paler, flavobrunneous; elytral disc rufobrunneous, sutural interval concolorous, lateral marginal depression rufoflavous, translucent; elytral apex broadly flavobrunneous; proepipleuron rufoflavous, proepisternum rufobrunneous; abdomen rufobrunneous,

apical half of apical visible ventrite paler, rufoflavous; femora and tibiae flavous with brunneous cast.

Female reproductive tract (n = 1). The single teneral female specimen of this species was not dissected.

Holotype. Holotype female (BMNH): Albany / W. Australia / J.J. Walker // G. C. Champion Coll. / B. M. 1927–09 // HOLOTYPE / *Mecyclothorax* / *jameswalkeri* / J.K. Liebherr 2018 [black-bordered red label].

Etymology. This species commemorates James John Walker, Commander and Fleet Engineer, Royal Navy, active member and officer in many scientific societies—including President of the Linnean Society of New South Wales (Walker 1921)—and in retirement, an editor of the *Entomologist's Monthly Magazine* (Poulton 1939). Walker's collections from Australia and New Zealand were passed to George C. Champion, his brother-in-law, and then bequeathed by Champion to The Natural History Museum, London. Walker's collections were as far flung as the British Empire, with his naval duties taking him to places where he could collect. Among many other species, carabid beetles named after him include: *Protopaussus walkeri* Waterhouse (1897) from China; *Calosoma walkeri* Waterhouse (1898), junior synonym of *C. oceanicum* Perroud, from Australia; *Rhaebolestes walkeri* Sloane (1903) from New South Wales; *Duvaliomimus walkeri* (Broun 1903), *Megadromus walkeri* (Broun, 1903), and *Mecodema walkeri* Broun (1903), the last a junior synonym of *Mecodema howitti* (Castelnau 1867), all from South Island, New Zealand; and *Trirammatius walkeri* (Andrewes 1931) from Juan Fernandez Island. Walker's collecting acumen can be attested to by his discovery of this broad assortment of carabid diversity.

Distribution and habitat. The lone specimen of this species is from Albany, W.A. (Fig. 11C). We know nothing specific about the habitat in which this beetle was discovered. The specimen is macropterous with the wings bearing well-developed venation and a reflexed apex, the wing structures being visible through the very translucent elytra of the teneral specimen. Thus occupation of a riparian habitat requiring recolonization of habitat patches may be predicted (Darlington 1936, 1943).

Mecyclothorax lophoides (Chaudoir)

Figures 2F, 4C–D, 9F, 10F, 11C, 12B, 13B, 14A–C

Anchomenus lophoides Chaudoir, 1854: 135.

Platynus lophoides Gemminger & Harold, 1868: 373.

Cyclothorax lophoides Blackburn, 1892: 481.

Agonum lophoides Csiki, 1931: 848.

Mecyclothorax lophoides Moore, 1984: 164.

Cyclothorax punctipennis Blackburn, 1889: 1388 (mis-identification?, Blackburn 1892: 481).

Diagnosis (n = 5). This species is characterized by a narrow, moderately cordate pronotum, the lateral margins slightly sinuate anterad obtuse, moderately projected hind angles (Fig. 2F); MEW/BPW = 1.57–1.68, MPW/

PL = 1.18–1.22. The pronotal lateral marginal depression is very narrow, with only the narrowest indication of microsculpture between the convex disc and the marginal bead. The hind angle is obtuse, rounded at its apex, with the basal pronotal seta set slightly anterad the angle. The marginal depression continues for only a short distance mesad the hind angle. The median base is covered with ~10 erratically distributed small punctures each side of midline. The laterobasal depression is a longitudinal depression lined with 4–5 larger punctures, with the flat area between depression and the marginal bead also bearing several larger punctures. The prosternum is medially depressed from the prosternal process between the procoxae 1/2 the distance toward the anterior margin, the depression lined with 6–7 pits. The anteapical groove is shallowly punctate laterally, continuous and irregularly indented medially, and the marginal bead of the procoxal cavity is bordered anteriorly by about 3 very shallow punctures. The mesepisternum is punctate at its deepest portion, about 9 deep punctures in 2–3 dorsoventral rows. The elytra are narrowly subparallel (Fig. 4C–D), with the humeral angles distinctly obtuse; MEW/EL = 0.64–0.69. The parascutellar striole is composed of 4–6 small, deep, isolated punctures. Elytral striae 1–6 are present on the disc, though striae 2–6 are absent basally and from the apical quarter to half, the outer striae progressively shorter. The striae punctures are isolated, progressively so apically, and the sutural stria is smooth or only slightly punctate in the apical half (Fig. 12B). Body coloration varies from dark brunneous (Fig. 4C) to piceous (Fig. 4D), with the legs correspondingly brunneous to piceous; i.e. there is less contrast between leg and body color than in *M. peryphoides* (Fig. 5B) or *M. cordicollis* (Fig. 5C). The elytral apex may be slightly paler than the disc in the brunneous specimens, however any difference is gradual, not a distinct transition as in *M. cordicollis* (Fig. 5C). Elytral margins are concolorous with the disc in the darker specimens. Cuticular microsculpture is relatively less developed in this species than in *M. darlingtoni*, *M. james-walkeri*, *M. peryphoides*, or *M. cordicollis*, with: **1**, frons glossy, indistinct transverse lines visible over portions of the surface; **2**, pronotal disc glossy with shallow elongate transverse microsculpture visible outside the area of reflection; **3**, flat elytral intervals covered with dense transverse lines producing an iridescent reflection. Standardized body length 3.8–4.9 mm. Setal formula ++/++/+2++.

Male genitalia (n = 12). Aedeagal median lobe dorsoventrally broad, the apex broadly rounded and slightly projected beyond the apical margin of ostium (Fig. 14A, C); flagellum elongate and hooklike, the flagellar sheath of similar length, its surface scabrous (Fig. 14A–B), dorsal plate ovoid, lightly sclerotized (Fig. 14B); right paramere expanded basally, narrowed beyond midlength, the ventral surface with ~9 setae along margin, dorsal margin with 4 setae in apical half (Fig. 13B); left paramere narrow basally, evenly narrowed to apex.

Female reproductive tract (n = 2). Bursa copulatrix squat, as broad as long (Fig. 9F); helminthoid sclerite

broad basally, with distinct mediobasal projection; spermathecal duct straight, narrow, evenly sclerotized, as long as spermathecal reservoir; basal gonocoxite with 4–5 apical setae plus a large seta at the apicomedial angle (Fig. 10F); apical gonocoxite subtriangular, broadly rounded apically; lateral ensiform setae small, narrow; apical nematiform setae in apical sensory furrow.

Type information. Lectotype male (MNHN) hereby designated: pointed specimen // Musaeo Chaudoir [red typeface] // Lectotype [red label] // Museum Paris / ex. Coll. Oberthur // *Mecyclothorax* (Ch.) det. P. M. Johns. There are also a male paralectotype and a female paralectotype (MNHN).

Distribution and habitat. *M. lophoides* is allopatrically distributed to the south of its adelphotaxon *M. darlingtoni*, with localities ranging from northeastern New South Wales southward through eastern N.S.W. to Melbourne (Fig. 11C). Non-type material and repositories include: A.C.T.: Paddy's R. 1 mi. S Cotter Dam (ANIC, 1); Smoker's Gap 43 km SW Canberra (CAS, 10; CUIC, 2); NSW: Blackheath (MVM, 1); Braidwood (CUIC, 2; MCZ, 37); Mt. Kosciuszko (MCZ, 2); New England N. P., Thungutti Camp (ANIC, 3); VIC: Dandenong Ck. (MVM, 1); Gellibrand R., Otway Ranges (MCZ, 1); Oakleigh (MVM, 1); Portland to Pt. Fairy (CUIC, 1; MCZ, 21); Wilson's Promontory (ANIC, 1); Winchester (MCZ, 1).

Specimens of this species collected by John Nunn on King Island (Moore 1984: 164) were preceded temporally by beetles laid down from 143,000–75,000 years ago in subfossiliferous deposits at Yarra Creek, King Island, during the Pleistocene last interglacial (Porch et al. 2009). Long-term residence on King Island suggests the species can persist in communities ranging from the present more mesic, more seasonal forest types to the wetter, more aseasonal forests present on King Island during the Pleistocene. All specimens are vestigially winged.

Mecyclothorax eyrensis (Blackburn)

Figures 2G, 5A, 9G, 10G, 11D, 12C, 13C, 14D

Cyclothorax eyrensis Blackburn 1892: 480.

Mecyclothorax eyrensis Csiki, 1929: 488.

Diagnosis (n = 5). Among species of the *M. lophoides* complex this species stands out based on its rufous coloration (Fig. 5A), and distinctly cordate pronotum with projected, nearly right hind angles (Fig. 2G). In the most melanized specimens, the forebody–head and pronotum–may be rufopiceous, but the elytra retain rufous coloration, and the legs are pale, flavous, with a slightly smoky piceous cast. The eyes are moderately convex, MHW/mFW = 1.51–1.57, less convex than those of the other *M. lophoides* complex species (Figs 4, 5B–C). The pronotum is quite constricted basally, MEW/BPW = 1.76–1.82, and moderately transverse, MEW/PL = 1.22–1.28. The pronotal lateral marginal depression is moderately broad, with the marginal bead only slightly upraised. The me-

dian base is minutely punctate, with 5–8 isolated punctures each side from midline to the ill-defined laterobasal depressions, those defined mostly by a longitudinal line of larger punctures, with several larger punctures also present between that line and the marginal bead. The hind angle is right to slightly obtuse, with the posterior margin transverse and anterad the convex median basal margin, which is smooth not beaded. The prosternum is flat to depressed medially, the medial area bearing a longitudinal series of 7 distinct punctures. The anteapical groove is deep and distinctly punctate laterally, continuous and more shallowly punctate medially, and the marginal bead of the procoxal cavity is bordered anteriorly by 5–6 strigose punctulae. The mesepisternum is covered with punctures, about 13 deep punctures arrayed in 3–4 irregular rows. The elytra are relatively broad, MEW/EL = 0.67–0.73, and flat medially on disc. Elytral striae 1–4 bear large punctures, those serial punctures close set enough on the disc to depress the intervening cuticle. Strial punctation is more strongly developed in this species than in other species of the *M. lophoides* complex (Fig. 12), with the sutural stria distinctly punctate mesad the posterior dorsal elytral seta. In this species cuticular microsculpture is less well developed than in the other *M. lophoides* complex species, with: **1**, frons smooth, glossy, with micropunctures sporadically visible across surface; **2**, pronotal disc glossy with sporadic micropunctures visible, very transverse lines sporadically visible laterally and near concavities of median longitudinal impression and laterobasal depression; **3**, elytral discal intervals largely glossy, with shallow transverse lines sporadically visible over surface (Fig. 12C), transverse microsculpture more developed on elytral apex where it forms an elongate transverse mesh, sculpticells 3–4× broad as long. Body coloration varies from a bright rufous, mostly in desert inhabiting beetles from the northern part of the range including the type locality of Leigh's Creek (Fig. 11D), to darker with rufopiceous head and pronotum and rufous elytra at localities on the southern edge of the range; Mt. Remarkable and Telowie Gorge. Even in the darker specimens, the base of the pronotum is an amber rufous, the cuticle appearing translucent. Standardized body length 4.2–5.5 mm. Setal formula ++/++/+2++.

Male genitalia (n = 10). Aedeagal median lobe broadest near basal 1/3 of length, ventral margin distinctly and evenly curved (Fig. 14D); internal sac bearing a long sinuous flagellum, a large bean-shaped dorsal plate, and a well-sclerotized, smooth flagellar sheath, the sheath length less than 1/4 flagellar length (Fig. 14D, as in Fig. 14F); right paramere expanded dorsally in basal half, the dorsal margin convex, 7–11 setae along ventral margin and ~1 on dorsal margin (Fig. 13C); left paramere broadly quadrate basally, extended as a narrowly attenuated whip to apex. Comparing the dissected aedeagi of 10 *M. eyrensis* males (e.g. Fig. 14D) and 16 *M. peryphoides* males (e.g. Fig. 14E) resulted in no discernible differences in overall shape of the median lobe, in curvature or expanse of the apex, in the basal bulb or development of the sag-

ittal crest, nor in structures of the internal sac such as the flagellum, flagellar sheath, or dorsal plate (Fig. 14D–E). The only male genitalic differences noted between males of these two species involved the presence of fewer setae along the ventral margin of the right parameres of *M. eyrensis* versus *M. peryphoides* (e.g. Fig. 13C–D). To determine whether these differences could diagnose the species, the numbers of setae along the ventral margin of the right paramere in 10 individuals of *M. eyrensis* (setal numbers: 7, 7, 8, 8, 8, 8, 9, 11, 11, 11) were compared to those in 15 individuals of *M. peryphoides* (setal numbers: 9, 10, 10, 11, 11, 11, 12, 12, 13, 13, 13, 14, 15, 15, 17) using the Wilcoxon rank-sum test (Snedecor and Cochran 1980). The distribution of values resulted in a minimal $T_1 = 69$, below the threshold value of 84 for a $p = 0.01$ level of significance for difference between the two distributions (Supplementary material 2). Even though the values among individuals overlap slightly in the 9–11 setal counts, there is a statistically significant difference between the setal configurations of the two species. This significant difference augments the diagnostic differences found in the external characters.

Female reproductive tract (n = 3). Bursa copulatrix short, slightly longer than broad (Fig. 9G); helminthoid sclerite broad basally, with narrow, elongate mediobasal projection; spermathecal duct elongate, sclerotized enough to hold coiled configuration, length ~2× length of spermathecal reservoir; basal gonocoxite with 2–6 apical setae, 2–4 of those larger and the balance smaller, plus a similarly sized seta at the apicomedial angle (Fig. 10G); medial surface of basal gonocoxite with several smaller setae along length; apical gonocoxite subtriangular, narrowly rounded apically; lateral ensiform setae small, narrow; apical nematiform setae in apical sensory furrow.

Type information. Lectotype male (BMNH) hereby designated: platen mounted with “2710 T / L. C. (red ink) // Type (round, red-margined label) // Blackburn coll. 1910-236 // *Cyclothorax eyrensis* Blackb. // Lectotype *Cyclothorax eyrensis* Blackburn / J.K. Liebherr 2006 [black-margined red label]. The abbreviation “L. C.” stands for Leigh Creek based on the labels below. Paralectotype female (SAMA): platen mounted with L. C. 2710 in red ink // Leigh Ck. C.A. / Blackb's Coll. // *Cyclothorax eyrensis* Bl. / Co-type // *Mecyclothorax eyrensis* Blkn / S. Australia / Cotype [red ink] // Paralectotype ♀ / *Cyclothorax eyrensis* Blackburn / det. J.K. Liebherr 2004 [black-margined red label]. The type locality is Leigh Creek, South Australia.

Distribution and habitat. This species is distributed across the interior of southeastern Australia (Fig. 11D), in South Australia from Telowie Gorge to Mt. Remarkable (FMNH), eastward to western N.S.W., and northward into southern Northern Territory at Palm Valley and Stokes Creek in the Gill Range (FMNH). Localities and repositories for non-type material include: NSW: Silverton (ANIC, 1). NT: Gill Range, Stokes Ck. (CUIC, 1; FMNH, 2); Palm Valley (FMNH, 1). SA: Flinders Ranges, Bunyeroo Gorge (CUIC, 1; FMNH, 14), Telowie Gorge

(CUIC, 2; FMNH, 5); Mann Range, 0.5 km N Angatja Homestead (CUIC, 1; FMNH, 1); Musgrave Range, 13 km N Ernabella (CUIC, 1; FMNH, 10), 15 km W Officer Ck. (FMNH, 10), 17 km W Jacky Pass (CUIC, 1); Mt. Remarkable (CUIC, 6; FMNH, 94); Wilmington (MVM, 3); Yunta (FMNH, 3). The extensive collections made by L. Watrous (FMNH) were obtained from sieved litter or reed drift from along dry or running streams. Nonetheless, and going against Darlington's generalization for riparian species, all observed individuals are vestigially winged.

Mecyclothorax peryphoides (Blackburn)

Figures 2H, 5B, 9H, 10H, 11D, 12D, 13D, 14E–F

Cyclothorax peryphoides Blackburn 1889: 1392.

Cyclothorax peryphoides Sloane, 1895: 446.

Mecyclothorax peryphoides Csiki, 1929: 489.

Mecyclothorax cordicollis Jeannel, 1940: 100 (misidentification).

Mecyclothorax lophoides Liebherr, 2011a: 292, table 2 (misidentification).

Diagnosis (n = 5). Among the species of the *M. lophoides* complex characterized by darker bodies and contrastingly pale legs (Figs 4B, 5B–C), this species has an ellipsoid elytra with large stria punctures, a pronotum with distinct obtuse hind angles, and concolorous elytral disc and apex, i.e. without an apical flavous marginal band (Fig. 5B). The eyes are broadly convex, MHW/mFW = 1.60–1.66. The pronotal margins are sinuate anterad the well-defined hind angles, but the posterior margin behind the angle is at most slightly sinuate, and usually convex, smoothly meeting the curved median basal margin (Fig. 2H). Body coloration is dark, with the head, pronotum and elytra piceous. The pronotum is transverse and constricted basally—MEW/EL = 1.20–1.28, MPW/BPW = 1.63–1.71—though the basal constriction less than that observed in beetles of *M. eyrensis*; MEW/BPW = 1.76–1.82. The pronotal median base is covered with distinct punctures, about 20 punctulae each side from midline to the very shallow, poorly defined laterobasal depression (Fig. 2H). The pronotal lateral marginal depression is narrow, but broad enough for sculpticells to line the deepest part, and the margin is beaded. Like *M. eyrensis*: **1**, the prosternum is flat to depressed medially, the medial area bearing a longitudinal series of 4–7 distinct punctures; **2**, the anteapical groove is deep and distinctly punctate laterally, continuous and more shallowly punctate medially; **3**, the marginal bead of the procoxal cavity is bordered anteriorly by 5–6 strigose punctulae; and **4**, the concave mesepisternal surface is lined with 13 deep punctures arrayed in 3–4 irregular rows. The elytral striae are punctate on the disc, though the punctures are far enough apart that the cuticle is coplanar with the intervals between the punctures. Like *M. eyrensis*, the punctures of striae 1–6 are progressively more isolated laterally on the elytra, but the sutural stria is more shallowly and irreg-

ularly punctured mesad the posterior dorsal elytral seta in this species (Fig. 12C–D). Cuticular microsculpture is well developed in this species, with: **1**, frons covered with indistinct transverse lines, vertex with more well-developed sculpticells, transforming from transverse just behind posterior supraorbital setae to nearly isodiametric near pronotum; **2**, pronotal disc with indistinct transverse lines visible outside areas of direct reflection, irregular surface of pronotal base covered with irregular transverse mesh; **3**, elytral disc with transverse lines visible outside areas of direct reflection, apex covered with well-developed elongate transverse mesh. Standardized body length 4.3–5.0 mm. Setal formula ++/++/+2++.

Male genitalia (n = 16). As stated under *M. eyrensis*, the aedeagal median lobe and flagellar complex of that species and *M. peryphoides* show no differences (Fig. 14D–E). However the right paramere of this species bears significantly more setae (9–17) along its ventral margin.

Female reproductive tract (n = 3). Bursa copulatrix short, slightly longer than broad (Fig. 9H); helminthoid sclerite broad basally, with narrow mediobasal projection; spermathecal duct elongate, sclerotized enough to hold coiled configuration, length ~2× length of spermathecal reservoir; basal gonocoxite with 3–6 apical setae, 2–3 large and the balance smaller, plus a similarly sized seta at the apicomedial angle (Fig. 10H); medial surface of basal gonocoxite with larger setae apically; apical gonocoxite subtriangular, narrowly rounded apically; lateral ensiform setae small, narrow; apical nematiform setae in apical sensory furrow.

Type information. Holotype male (BMNH): platen mounted with “1614” in red ink and “T” in black ink on the obverse, with basal marginal black and red lines, the red crossed by an arrowhead // Type (round red-margined label) // Blackburn coll. 1910-236. // *Cyclothorax peryphoides* [sic.], Blackb. Blackburn states the type locality as “Woodville, near Adelaide; a single specimen (Blackburn 1889: 1393).”

Distribution and habitat. This species is distributed (Fig. 11D) to the south of its sister species, *M. eyrensis*, in South Australia. The type locality of Woodville is near recent collections made at Belair Recreation Park, 10 miles S of Adelaide (FMNH), Blackwood, Sturt Gorge Reserve (ZMUC), and Hale Conservation Park SE Williamstown (FMNH). To the east the species is recorded from the following localities: A.C.T.: Black Mountain (CUIC, 8; EMEC, 1); NSW: Belmore (AMS, 1); Bogan R. (AMS, 1); “Calosoma” via Gundaroo (ANIC, 4); Federal Hwy. (ANIC, 1); Jerrawa (AMCS, 2); Mt. Wilson (CUIC, 1; FMNH, 4); Narrabeen (AMS, 1); Queanbeyan (ANIC, 1); Tuglo Wldf. Ref. 48 km N Singleton (FMNH, 1); Weddin Mtns. N. P. (FMNH, 1); VIC: Lake Eildon N. P., Sebastopol Ck. (ZMUC, 1). Collections have been made via litter sifting along streams or in *Eucalyptus* (Myrtaceae) or mixed deciduous forest, or in rainforest on Mt. Wilson. As for *M. eyrensis*, even though this species occupies predominantly riparian situations, it appears to be vestigially winged.

***Mecyclothorax cordicollis* (Sloane)**

Figures 2I, 5C, 9I, 10I, 11E, 12E, 13E, 14G–H

Cyclothorax cordicollis Sloane 1900: 563.*Mecyclothorax cordicollis* Csiki, 1929: 488.

Diagnosis (n = 5). This species (Fig. 5C) and *M. lophoides* (Fig. 4C–D) include the smallest-bodied, most gracile beetles in the *M. lophoides* species complex, with standardized body length for this species = 4.0–4.7 mm. Individuals exhibit a flavous marginal band on the elytra, brunneous to rufobrunneous body, and pale, flavous legs. The pronotum is very similar to that of *M. lophoides* (Fig. 2F, I); moderately transverse, MPW/PL = 1.17–1.24, and basally constricted, MPW/BPW = 1.62–1.68, these values broadly overlapping those calculated from specimens of *M. lophoides*. The eyes are also similar in configuration in the two species: here MHW/mFW = 1.63–1.71, with the eyes covering most of the ocular lobe, EyL/OLL = 0.86–0.91. The pronotal lateral marginal depression is slightly broader in this species than in *M. lophoides*, with microsculpture evident in its deepest part. The pronotal hind angles are obtusely rounded, with the margin behind the angle smoothly curved onto median base. The marginal bead terminates at the laterobasal depression just mesad the hind angle, and the bead is only slightly broader at the setal insertion. The pronotal median base is covered with 10–13 large isolated punctures present each side of midline. The laterobasal depression is defined by a medially arcuate line of punctures commencing at the termination of the marginal bead mesad the basal seta. The prosternum is medially depressed from the prosternal process anterad slightly less than 1/2 the distance to the anterior margin, the depression broader anteriorly, and lined with ~8 pits. The anteapical groove is punctate laterally, continuous and indistinctly punctate medially, and the procoxal cavity marginal bead is bordered by 4–5 small punctures along its anterior margin. The mesepisternum is variously punctate, the deepest portion covered with about 9 shallow to deep punctures arranged in 2–3 dorsoventral rows. The elytra are broad basally, subparallel, and broad relative to their length (Fig. 5C), MEW/EL = 0.69–0.71, versus values of 0.64–0.69 for individuals of *M. lophoides* (Fig. 4C–D). The elytral disc is flat, with the sutural intervals apically raised into a callosity. Elytral striae 1–6 are distinctly punctate on the disc, with the punctures nearly contiguous on the inner striae, however the intervening intervals are nearly flat. As in the other *M. lophoides* complex species, stria punctures are smaller and therefore further apart along the lateral striae, though in this species stria 6 is indicated until posterad midlength. As in *M. peryphoides*, the sutural stria is indistinctly punctate mesad the posterior dorsal elytral seta (Fig. 12D–E), but the punctures in striae 2–4 are more well developed, agreeing with *M. eyrensis*, but not *M. lophoides* (Fig. 12 B–C). Coincident with the presence of a flavous marginal band on the darker elytra, other body coloration tends toward the polychromat-

ic: **1**, elytral epipleura dorsally flavous versus ventrally rufobrunneous adjacent to the metepisternum; **2**, coxae dark brunneous, trochanters rufous, femora flavous, and tibiae and tarsomeres brunneous with smoky cast. Cuticular microsculpture includes: **1**, vertex glossy with an indistinct transverse mesh in parts; **2**, pronotal disc glossy with an elongate transverse mesh restricted to transverse wrinkles, and a shallow elongate transverse mesh on the median base, sculpticells more irregular in the laterobasal depression; **3**, elytral disc with a shallow, elongate transverse mesh, sculpticell breadth 3–4× length, the convex apex covered with traceable transverse lines, the entire elytral surface subiridescent. Setal formula ++/++/2++.

Male genitalia (n = 13). Aedeagal median lobe of moderate dorsoventral breadth (Fig. 14G), evenly curved as in *M. lophoides* (Fig. 14A); flagellar complex including a very short, spine-like flagellum, a bifurcated flagellar sheath, and a lightly sclerotized, ovoid dorsal plate (Fig. 14H); right paramere broader basally, conchoid, with ~12 setae along ventral margin and 2–3 small setae on dorsal margin (Fig. 13E); left paramere broadest basally, but evenly narrowed to whiplike apex, the apex flexible and often twisted relative to base when aedeagus mounted on slide.

Female reproductive tract (n = 1). Bursa copulatrix squat, as broad as long (Fig. 9I); helminthoid sclerite broad basally, with narrow elongate mediobasal projection; spermathecal duct straight and narrow, evenly sclerotized, of similar length to spermathecal reservoir; basal gonocoxite with 2–3 apical setae, 2 larger setae laterally, and a moderately sized seta at the apicomedial angle (Fig. 10F); apical gonocoxite subtriangular, narrowly rounded apically; 1–2 small lateral ensiform setae present; apical nematiform setae in apical sensory furrow.

Type information. Lectotype male (ANIC) hereby designated: 2nd specimen from left on 6-specimen platen, specimen annotated “♂ -w”, male genitalia dissected and placed in polyethylene genitalia vial below labels // *Cyclothorax* Type / *cordicollis* Sl. MSS. / Colombo Plains 11/6/95 // *C. cordicollis* Sl. / Holotype / PJD not HT JKL 18 [pink label with Holotype crossed out] // ANIC Database / 25 014958 // ANIC Specimen [green label] / ANIC Image [orange label] // Lectotype / *Cyclothorax* / *cordicollis* / J.K. Liebherr 2017 [black-margined red label] / *Mecyclothorax* / *cordicollis* / (Sloane) ♂LT / det. J.K. Liebherr 2018. Although P.J. Darlington labelled these specimens as “Holotype”, a lectotype must be designated given Sloane’s description stating the multiple localities given as “Queensland–Brisbane (sent by Mr. Lea); N.S. Wales–Clarence River and Windsor (Lea), Grenfell, Junee, Urana, Mulwala (Sloane); Victoria–Ferntree Gully and Lilydale (Sloane) (Sloane 1900: 564).” Colombo Creek [Colombo Plains sic] is near and northwest of Lake Urana and the town of Urana, and so these specimens would correspond to the “Urana” locality of Sloane’s list. Moreover, Sloane wrote regarding the habits of these beetles; “Found in damp situations near water, usually rare, but on July 11th, 1895, I found it very plentifully under sticks along the edge of a swamp about 20 miles north

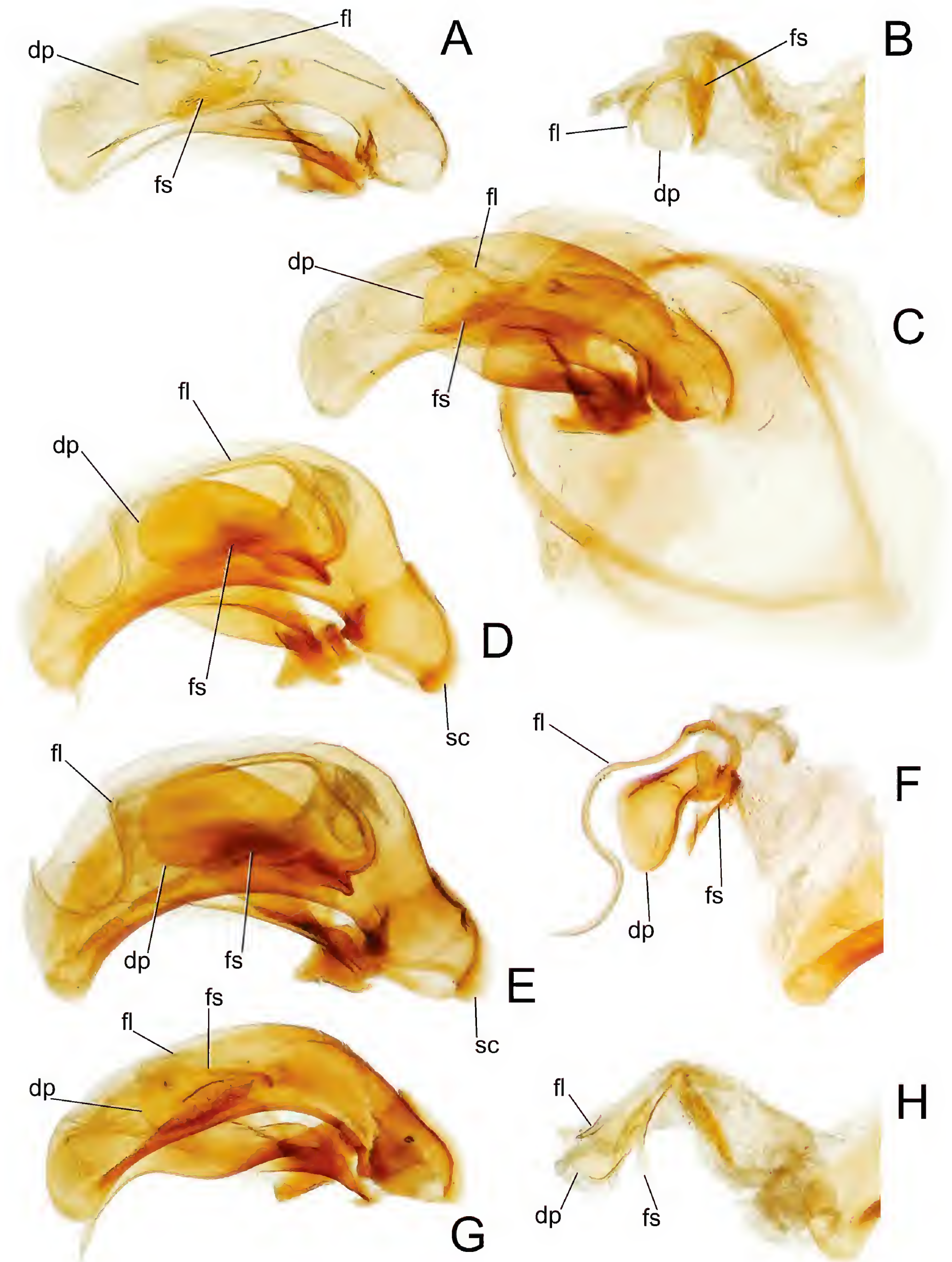


Figure 14. Male aedeagus, right view, for *Mecyclothorax (Eucyclothorax)* spp.: **A**, *M. lophoides*, ACT: Paddy's R.; **B**, *M. lophoides* everted internal sac, NSW: Braidwood.; **C**, *M. lophoides*, lectotype, aedeagus *in situ* with laterotergite IX, or ring sclerite, VIC: Melbourne; **D**, *M. eyrensis*, NSW: Silvertown; **E**, *M. peryphoides* holotype, SA: Woodville; **F**, *M. peryphoides* everted internal sac, ACT: Black Mountain; **G**, *M. cordicollis*, VIC: Melbourne; **H**, *M. cordicollis* everted internal sac, NSW: Bodalla.

from the town of Urana (Sloane 1900: 564).” As the label clearly reads “11/6/95” and Sloane wrote of “July 11th, 1895”, some ambiguity concerning the date of this collection remains [though the label data would hold precedence]. However no such ambiguity can be countenanced regarding this collecting locality.

Distribution and habitat. Sloane (1900) described this species from specimens representing much of the distributional range as now known augmented by more than another century of collections (Fig. 11E), with the single notable exception of two specimens collected by the Darlings, ii–1958, at Ravenshoe, W of the Atherton Tableland (MCZ, 2). Localities and repositories of other non-type specimens include: NSW: Bodalla (CUIC, 1; MCZ, 10); Gosford (MVM, 2); Narrandera (MCZ, 1); Sydney vic. (CUIC, 1; MCZ, 15); QLD: Blunder (ANIC, 1); Brisbane vic. (CUIC, 2; MCZ, 9); Dalby (ANIC, 2); VIC: Dandenong Vy. (ANIC, 2); Lilydale (ANIC, 1); Melbourne (ANIC, 1); Powlett R. (ANIC, 1).

Sloane’s perspicacity with regard to species boundaries is very evident in his sorting out this taxon from the very similar appearing beetles of *M. lophoides* and *M. peryphoides*. What we know about the habits of this species can be taken from Sloane’s description, quoted above. The species is uniformly represented by vestigially winged individuals with the exceptions of macropterous beetles from two Queensland localities: **1**, one of two beetles from Ravenshoe; and **2**, two of two specimens from Dalby.

Subgenus *Qecyclothorax* Liebherr

Diagnosis. These robust-bodied species (e.g. Fig. 5D) are geographically restricted to Queensland, Australia, and have been recently revised by Baehr (2003). The pronotum of species in this subgenus is broad, with obtuse or obtusely rounded hind angles. Each elytron bears a single dorsal elytral seta just before midlength (Fig. 5D). The prosternum is medially depressed both between and anterad the procoxal cavities, a condition shared with most member species of *Eucyclothorax*, although punctures are not present in the depression. The elytral striae are reduced; striae 1–3 to 1–4 shallow to evanescent, striae 4– or 5–7 obsolete. Striae 1, 7, or both may be present apically on the elytra, but striae 4–6 are consistently absent there. The elytra are broadly convex, with interval 8 not, or only slightly upraised (*M. lewisensis*) relative to the general curvature of the elytral surface. The suture between abdominal ventrites 1 and 2 is nearly straight, with the second ventrite hardly depressed relative to the first. Body size is small for the genus; standardized body length 2.6–3.7 mm.

The male aedeagal median lobe internal sac bears a flagellum (Liebherr 2018, fig. 4E), and the ventral paramere is elongate-conchoid in shape, broadly to narrowly subtriangular with ventral setae present (Liebherr 2018, fig. 5B; Baehr 2003, fig. 1). The female bursa copulatrix is relatively short (Liebherr 2018, fig. 6D). The spermathecal duct joins the bursa copulatrix-common oviduct juncture.

Member species. Baehr (2003) recognized four species, three of them represented by two subspecies each, for a total of seven specific and subspecific forms. The subspecies described below is added to the inventory of *M. lewisensis*, resulting in three subspecies; *M. lewisensis*, *M. lewisensis uncinatus*, plus the newly described subspecies.

Mecyclothorax lewisensis estriatus, subsp. n.

<http://zoobank.org/88C1027C-46AE-4BB2-975F-D327B10E55B7>

Figures 5D, 11E

Mecyclothorax lewisensis Moore, 1984: 165.

Mecyclothorax lewisensis uncinatus Baehr, 2003: 74.

Diagnosis (n = 1). This taxon is distinguished from all others of subgenus *Qecyclothorax* by the reduced elytral striation, with only the sutural stria evident, and the positions of all outer striae only traceable by the longitudinal tracks of trachea (Shelford 1915). As for all *Qecyclothorax*, the elytra exhibit only a single dorsal elytral seta positioned near midlength (Fig. 5D). Consistent with membership in *M. lewisensis*, this beetle exhibits a quadrisetose clypeus and a pronotum with explanate lateral margins that are indistinctly sinuate basally. The parascutellar seta are very short and fine, and they are set in shallow depressions, however careful examination allows their discernment along with the fine articulatory sockets from which they extend. Baehr used the comparative breadth of the pronotal base relative to its apex as one criterion to differentiate the two subspecies *M. lewisensis* and *M. l. uncinatus*: the former with a ratio APW/BPW < 0.83 (note inverted ratio herein versus Baehr 2003), the latter with APW/BPW > 0.85. In the single specimen of *M. l. estriatus*, APW/BPW = 0.85. Standardized body length for the type specimen below, 3.3 mm. Setal formula ++/++/+1++.

Description. Head broad, frontal groove deep, arcuately convergent toward clypeus, continued onto clypeus, terminated posteriorly midway between 2 supra-orbital setae; eyes moderately convex, MHW/mFW = 1.52, covering much of ocular lobe, EyL/OLL = 0.83; antennae elongate, long enough so that apex would extend to basal 1/4 of elytra, antennomere 9 length/maximal breadth = 1.89; mentum tooth with sides acute, apex broadly rounded; ligular apex narrowed, slightly concave between ligular setae, setae separated by 2 setal diameters; paraglossae extended as far beyond ligular apical margin as distance from base to ligular margin. Pronotum transverse, MPW/PL = 1.41, moderately constricted basally, MPW/BPW = 1.35; lateral pronotal seta placed 1 diameter mesad lateral margin depression, depression very narrow at front, gradually widened to explanate at hind angle; basal margin nearly straight, slightly convex between laterobasal depressions, margin flat and effaced behind laterobasal depressions, a convex roll medially; median base depressed relative to disc, smooth with ~3 small punctures each side mesad laterobasal depression; laterobasal depression a linear to slightly outwardly ar-

cuate line of 3–4 broad punctures, the area laterad line of punctures broadly convex to explanate lateral margin; median longitudinal impression fine, deep, adjacent depression covered with transverse wrinkles on disc; anterior transverse impression broad, evenly depressed fore and aft, the anterior callosity broadly, slightly convex to front margin; front angles slightly protruded, subangulate with marginal bead mesad angle that is continuous with transverse impression; prosternum depressed medially anterad procoxal cavities, the depression's surface irregular with 3 shallow irregularities disturbing the surface; anteapical groove very shallow laterally discontinuous, not present medially; lateral reaches of prosternum irregular, procoxal cavity with very fine marginal bead. Mesepisternum covered with 7 large, isolated pits on a smooth surface, the pits arranged in 2 dorsoventral rows; metepisternum nearly quadrate, lateral margin length $1.2 \times$ maximal width. Elytral broadly hemiovoid (Fig. 5D), convex laterally with sides nearly vertical, disc flattened; basal groove slightly curved laterad position of parascutellar striole, punctate near basal positions of striae 3 and 4 (indicated by tracheae; Shelford 1915), and straight laterally to obtusely angulate humeri; elytral striae obsolete, striae 1 and 2 traceable only by very small serial punctures on disc, stria 3 less easily traced as punctures are irregular and easily confused with micropunctures scattered over cuticle; dorsal elytral setae short, in depressions that span only $1/4$ – $1/2$ of third interval; only stria 7 evident on elytral apex as a broad shallow depression connecting the subapical and apical elytral setae; stria 8 deep, present from posterad anterior series of lateral elytral setae, slightly irregular along length behind anterior series of lateral elytral setae; lateral elytral setae arranged as 7 + 6–7 setae; subapical sinuation very broad and shallow, the elytral plica visible in dorsal view. Head capsule with reduced microsculpture, frons glossy and vertex covered with fine transverse lines; pronotal disc glossy, a transverse mesh present over parts, sculpticell breadth 2 – $3 \times$ length; pronotal base glossy, indistinct transverse mesh in laterobasal depression; elytral disc glossy, indistinct transverse lines outside area of reflection, apex glossy with indistinct transverse mesh in irregularly depressed areas. Coloration of head rufous on frons, darker on vertex; antennomeres 1 rufoflavous, 2–11 brunneous; Pronotal disc dark rufous, lateral margins broadly paler, rufoflavous, base a translucent amber; elytral disc rufobrunneous overall, but with a darker transverse field posterad dorsal elytral seta that continues along suture to apex leaving 2 paler lateroapical fields; sutural interval concolorous with adjacent intervals; proepipleuron rufoflavous with darker explanate margin; proepisternum dark rufous with subiridescent reflection; elytral epipleuron broadly rufoflavous, metepisternum rufobrunneous; abdomen rufobrunneous, apical $2/3$ of apical ventrite flavous; femora flavous, tibiae flavous with rufous cast.

Female reproductive tract ($n = 1$). The unique female holotype was not dissected. Nonetheless, the gonocoxae extend from the abdominal apex, allowing the following

characters to be assessed: basal gonocoxite with medio-apical margin glabrous; apical gonocoxite broad basally with 2 lateral ensiform setae; apical nematiform setae in subbasal sensory furrow. These characters conform to states previously scored for *M. lewisensis* (Liebherr 2018) though they are not definitive.

Holotype female (QMB): QLD: $20^{\circ}21'S$, $148^{\circ}43'E$ / Brandy Creek, 150 m / 20 Nov 1992 / Monteith, Thompson / & Janetzki, Pyrethrum // HOLOTYPE / Mecyclothorax / lewisensis / estriatus / J.K. Liebherr 2018 (black margined red label).

Distribution and habitat. The lone specimen of this subspecific taxon is from near the Queensland coast south of Cannonvale (Fig. 11E), approximately 600 km south of the localities near Mossman from where the other subspecies of *M. lewisensis* have been described (Baehr 2003, fig. 6).

Subgenus *Mecyclothorax* Sharp

Diagnosis. This subgenus comprises over 350 species (Liebherr 2018), and so morphological variation among the species is the most extreme observed among the various *Mecyclothorax* subgenera. However, throughout taxa of this subgenus, the labrum is emarginate apically, either distinctly and angularly as in *M. goweri* Moore of Lord Howe Island (Liebherr 2018, fig. 1A), or less so as in *M. aeneipennis* Liebherr of Haleakalā, Maui, Hawai'i (Liebherr 2015, fig. 7). The ligular margin is generally truncate with the ligular setae well separated (Liebherr 2018, fig. 1G), though as exceptions, the ligula is apically rounded in the Papuan taxa *M. brispex* and *M. andersoni* (Liebherr 2017, 2018, fig. 7). The prosternum exhibits a smooth to distinctly punctate anteapical groove, though never any other punctures, such as in the median depression observed among species of subgenus *Eucyclothorax*. The parascutellar striole is present, and may be smooth or punctate, with up to 8 punctures along its length (Fig. 6). Among the mainland Australian species, the pronotal median base is depressed relative to the disc, and punctate; a distinction noted by Blackburn (1889).

The male aedeagus has an internal sac with an apical flagellar plate surrounding the gonopore (Fig. 15E). The female reproductive tract most often has the spermathecal duct entering the bursa copulatrix mediodorsally (Fig. 17C–D), however the sister-species pair *M. lateralis* + *M. minutus* (Fig. 1A) revert to the plesiomorphic configuration wherein the spermathecal duct basally joins the juncture of the common oviduct and the bursa copulatrix (Fig. 17A–B).

Member species. This subgenus is represented by four species in mainland Australia. Numbers of taxa in the substantial radiations from Hawaii, the Society Islands, New Guinea, New Zealand, the Sundas, and Lord Howe, Norfolk, and St. Paul and Amsterdam Islands are summarized in Liebherr (2018: 15).

***Mecyclothorax lateralis* (Castelnau)**

Figures 2J, 6A, 15A, 16A, 17A, 18A, 19A

Phorticosomus lateralis Castelnau, 1867: 92 (as *Forticosomus*); Castelnau, 1868: 178.

Simodontus lateralis Chaudoir, 1873: 114 (see Nomenclatural note).

Cyclothorax lateralis Sloane, 1895: 448.

Mecyclothorax lateralis Sloane, 1903: 586.

Cyclothorax cinctipennis Blackburn, 1889: 1391 (synonymy Sloane 1895: 448).

Diagnosis (n = 5). This large-bodied species—standardized body length 5.2–6.4 mm—is further distinguished by the rufous to brunneous body with contrasting, flavous elytral margins (Fig. 6A). The labrum is broadly and distinctly emarginate apically. The ligula is truncate apically, with the 2 apical setae separated by 4 setal diameters, the ligular surface longitudinally depressed between the setal articulations. The paraglossae are elongate, apically extended beyond the ligular apical margin twice the distance from ligular margin to their base. The pronotum is robust, transverse, with a convex disc, and depressed and circularly punctate median base (Fig. 2J); MPW/BPW = 1.45–1.56, MPW/PL = 1.35–1.40. The prosternal process is broad, only slightly depressed between the coxae, and convex anterad the coxae. The prosternal anteapical groove is deep and narrow, with only slight irregularities along its length at its deepest part. As in its sister species *M. minutus*, the parascutellar seta is absent. The metepisternum is abbreviated, with lateral length about 2× maximum width, and the metathoracic wings are vestigial in examined material. The suture between visible ventrites 1 and 2 is sinuous, with the area behind markedly depressed. Microsculpture of the head is reduced, with frons glossy, vertex with indistinct transverse sculpticells; pronotal disc and median base glossy, indistinct transverse lines visible in places; elytral surface glossy with well-defined isodiametric sculpticells visible over entire surface, the apex with sculpticells more upraised; thoracic ventrites glossy, abdominal ventrites glossy medially but with isodiametric sculpticells visible in lateral depressions. Setal formula ++/++/-2++.

Male genitalia (n = 1). Aedeagal median lobe moderately broad dorsoventrally, apex narrowly rounded and slightly projected beyond ostium (Fig. 15A); flagellar plate large and lightly sclerotized; right paramere narrow and elongate (Fig. 16A), ventral margin setose, with >20 setae along margin, setae more densely distributed in basal half; left paramere broadly subquadrate basally, apically attenuated into a whip-like apex.

Female reproductive tract (n = 1). Bursa copulatrix broadest at midlength, its surface membranous and covered with pleat-like wrinkles, apex narrowed (Fig. 17A); spermathecal duct narrow, elongate, about twice length of spermathecal reservoir; basal gonocoxite broad, 2–4 setae along apical margin (Fig. 18A), several setae along

median margin; apical gonocoxite broadly rounded apically, mesal and lateral margins subparallel; a single broad lateral ensiform seta, its length about 1/3 length of apical gonocoxite; apical nematiform setae in large, apical positioned sensory furrow.

Type information. Lectotype female (MCG) designated by Straneo (1941): specimen glued to platen // Lateralis / Cast. / Paroo riv. // Australia / Paroo River / Coll. Castelnau // LECTOTYPUS / Forticosomus / lateralis / Castelnau, 1867 / des. S.L. Straneo, 1941 [orange label] // Forticosomus / lateralis // Mecyclothorax / lateralis Cast / holotypus / Det. B.P. Moore '68 // MUSEO GENOVA / Coll. Castelnau. A female paralectotype accompanies the lectotype. It bears only the newer “Australia / Paroo River / Coll. Castelnau” label and Straneo’s orange PARALECTOTYPUS label. As noted by Straneo (1941: 89), the paralectotype is teneral. For *C. cinctipennis* Blackburn, holotype (BMNH; label data not recorded): Torrens River, S.A. (Moore et al. 1987).

Nomenclatural note. In the paragraph within which Chaudoir (1873) combined *Phorticosomus minutus* Castelnau with *Simodontus* Chaudoir (pp. 113–114), Chaudoir writes “Je crois que son *Ph. lateralis* est encore une espèce de *Simodontus*, qui m’a semblé différente de *curtulus* (p. 114).” Such a statement falls short of a nomenclatural act proposing a valid new combination. Csiki (1929) interpreted Chaudoir (1873) to have officially combined *Ph. lateralis* with *Simodontus*, however his listing the page of that action as Chaudoir (1873: 113) suggests that he did not see the work personally, thus leading him to give Chaudoir credit for a nomenclatural act that Chaudoir did not commit. Sloane agreed that Chaudoir did not combine *Ph. lateralis* with *Simodontus*, writing: “*Ph. lateralis* is a species of *Mecyclothorax*. *Ph. minutus*, from the Paroo River, has been examined by Chaudoir, who referred it to *Simodontus* ... (Sloane, 1915, 462).” Moore’s labelling of the lectotype as holotype was corrected in Moore et al. (1987), where the presence of a paralectotype was also noted.

Distribution and habitat. This species is distributed in interior Victoria, western New South Wales and southeastern South Australia (Fig. 19A). Localities and repositories for non-type specimens I have examined include: SA: Lucindale (MCZ, 1); Pt. Lincoln (MVM, 1); VIC: Bendigo (MVM, 1); Birchip (MVM, 1); Evansford (BMNH, 15); Lake Hattah (MVM, 1); Maldon (MVM, 1); Wedderburn (MVM, 1). These records represent beetles collected between 1911 and 1950, none with any ecological data, and so nothing can be reported with confidence concerning the ecological preference of this species: but see *M. minutus* below. This species is polymorphic for flight-wing configuration, with 3 brachypterous individuals observed among the 27 beetles examined; 2 of the individuals from Evansford exhibit wings that are broad, slightly more than half as long as the elytra, and without a reflexed apex. Other examined individuals have vestigialized wings, with the wing stubs shorter than the metanotum.

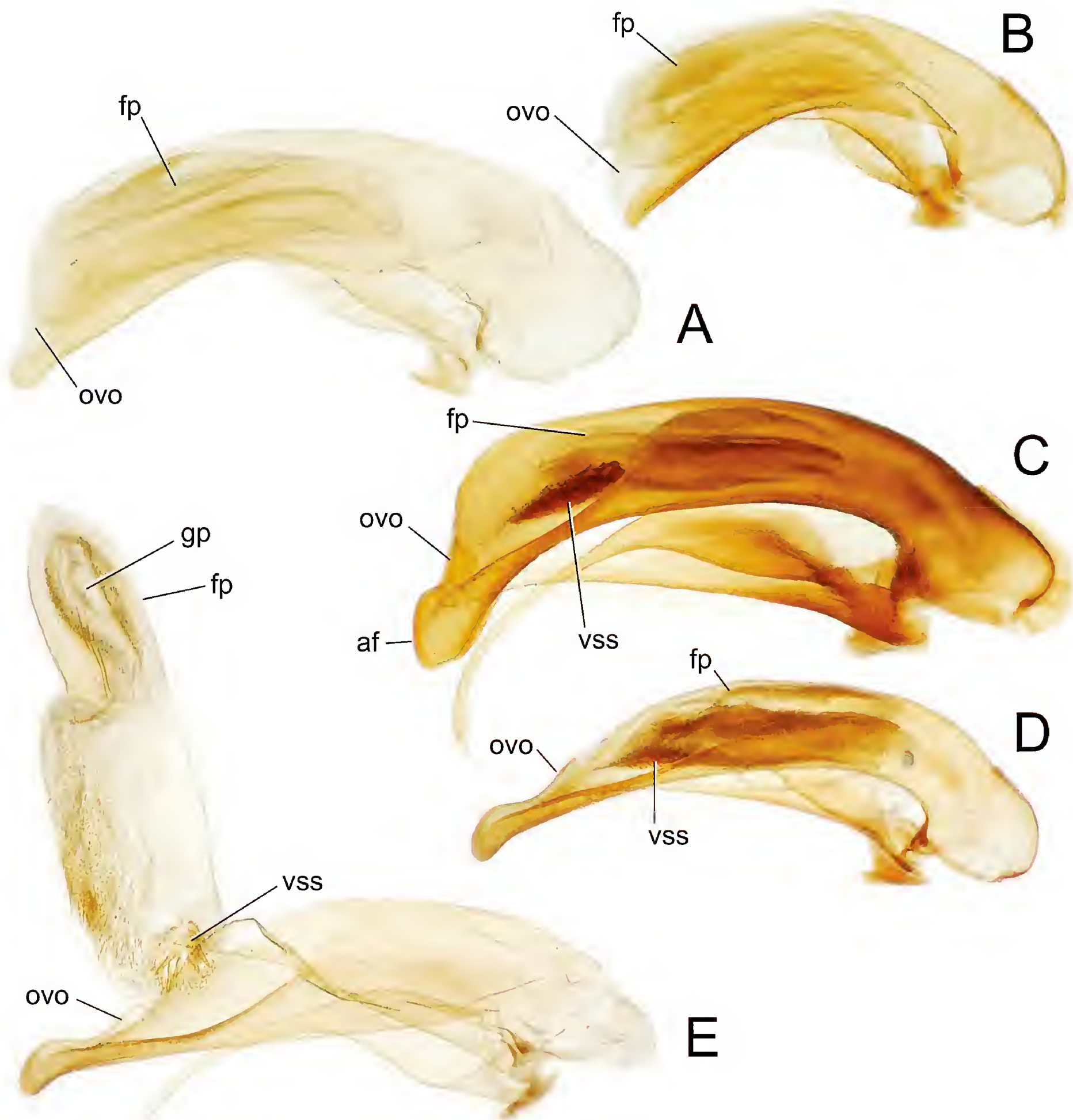


Figure 15. Male aedeagus, right view, for *Mecyclothorax* (*s. s.*) spp.: **A**, *M. lateralis*, VIC: Lake Hattah; **B**, *M. minutus*, WA: Merredin; **C**, *M. ambiguus*, VIC: Peshurst; **D**, *M. punctipennis*, ACT: Black Mountain; **E**, *M. punctipennis* internal sac everted, NSW: Kosciuszko N. P., Bullock Hill Tr.

***Mecyclothorax minutus* (Castelnau)**

Figures 2K, 6B, 15B, 16B, 17B, 18B, 19B

Phorticosomus minutus Castelnau, 1867: 92 (as *Forticosomus*); Castelnau, 1868: 178.

Simodontus minutus Chaudoir, 1873: 113.

Mecyclothorax minutus Csiki, 1929: 488.

Cyclothorax fortis Blackburn, 1889: 1390 (NEW SYNONYMY).

Mecyclothorax fortis Sloane, 1903: 486.

Diagnosis (n = 5). This species shares the rufous to brunneous body color (Fig. 6A–B) and lack of the parascutellar seta with *M. lateralis*, however the beetles are smaller—standardized body length 4.9–5.7 mm—and the elytral lateral and apical margins do not markedly contrast with the elytral disc. In teneral individuals the margins may appear somewhat paler, partly due to reflection of the underlying abdominal tergites through the cuticle, and partly due to a smoky infuscation of the median elytral disc. However, the difference in coloration from disc to

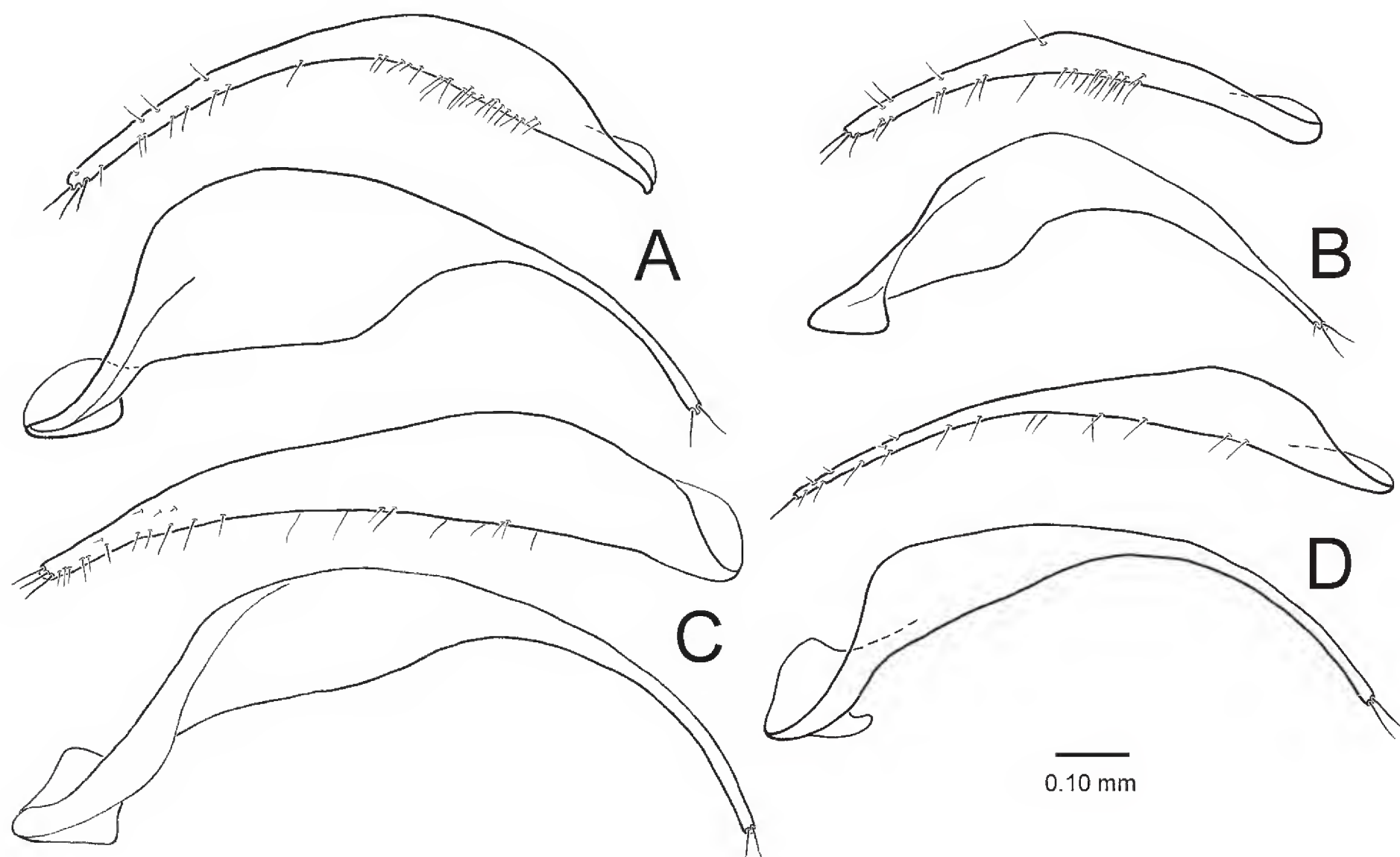


Figure 16. Male parameres of *Mecyclothorax* (s. s.) spp., ectal view, right paramere above in each pair, left paramere below: **A**, *M. lateralis*, VIC: Lake Hattah; **B**, *M. minutus*, WA: Merredin; **C**, *M. ambiguus*, VIC: Peshurst; **D**, *M. punctipennis*, ACT: Black Mountain.

margin is gradual, never marked. Males exhibit 2 setae each side of the apical ventrite margin, for a total of 4 apical setae, differing from *M. lateralis* which retains the plesiomorphic single seta per side: i.e. a total of 2 apical abdominal setae. The labrum is distinctly emarginate apically, the 2 sides subangulate medially. The ligula is truncate apically, with the 2 apical setae separated by 4 setal diameters, the ligular surface longitudinally depressed between the setal articulations. The paraglossae elongate, extending twice as far beyond the ligular apical margin as the distance from paraglossal base to ligular margin. The pronotum is transverse, with the depressed median base margined at the disc with strigose punctures (Fig. 2K); MPW/BPW = 1.47–1.56, MPW/PL = 1.42–1.51. The prosternal process is broad and only slightly depressed between the coxae, convex anterad the coxae. The prosternal anteapical groove is deep and narrow, smooth at depth. As in *M. lateralis*, the metepisternum is abbreviated, with lateral length about 2× maximum width, and the metathoracic wings are vestigial in examined material. The suture between visible ventrites 1 and 2 is sinuous, with a broad circular depressed area posterad the sinuosity. Microsculpture of the head is reduced, with frons and vertex glossy, the surface interrupted only by scattered micropunctures. Similarly the pronotal disc and median base are glossy, with indistinct transverse lines visible in places. The elytral surface is glossy with micropunctures covering the surface of the disc, the apex with margins of transverse sculpticells upraised. Ventrally, the thoracic

ventrites are glossy; abdominal ventrites glossy medially but with swirling transverse sculpticells visible in lateral depressions. Setal formula ++/++/-2++.

Male genitalia (n = 1). Aedeagal median lobe moderately broad dorsoventrally, apex narrowly rounded and not projected beyond ostium (Fig. 15B); flagellar plate large and lightly sclerotized; Right paramere narrow, elongate, >20 setae along ventral margin, setae more densely packed in basal half, dorsal margin with ~4 small setae (Fig. 16B); left paramere slightly broadened basally, evenly narrowed to apex.

Female reproductive tract (n = 1). Bursa copulatrix broadest at midlength, its surface membranous, apex narrowed into an elongate projection covered with pleat-like wrinkles (Fig. 17B); spermathecal duct moderately narrow, elongate, about twice length of spermathecal reservoir; basal gonocoxite broad, 2–4 setae along apical margin (Fig. 18B), 1 seta at apicomedial angle, and several setae along median margin; apical gonocoxite broadly rounded apically, mesal and lateral margins subparallel; a single narrow, acuminate lateral ensiform seta, its length about 1/4 length of apical gonocoxite; apical nematiform setae in large, apical positioned sensory furrow.

Type information. For *P. minutus*, lectotype female (MCG) designated by Straneo (1941): specimen glued onto elongate trapezoidal point // riv. N.H. / Murray [blue label] // minutus / Cast. // N(ova) Hollandia / Riv. Murray / Coll. Castelnau // Forticosomus / minutus / Cast. // LECTOTYPUS / Forticosomus / minutus / Castelnau, 1867 /

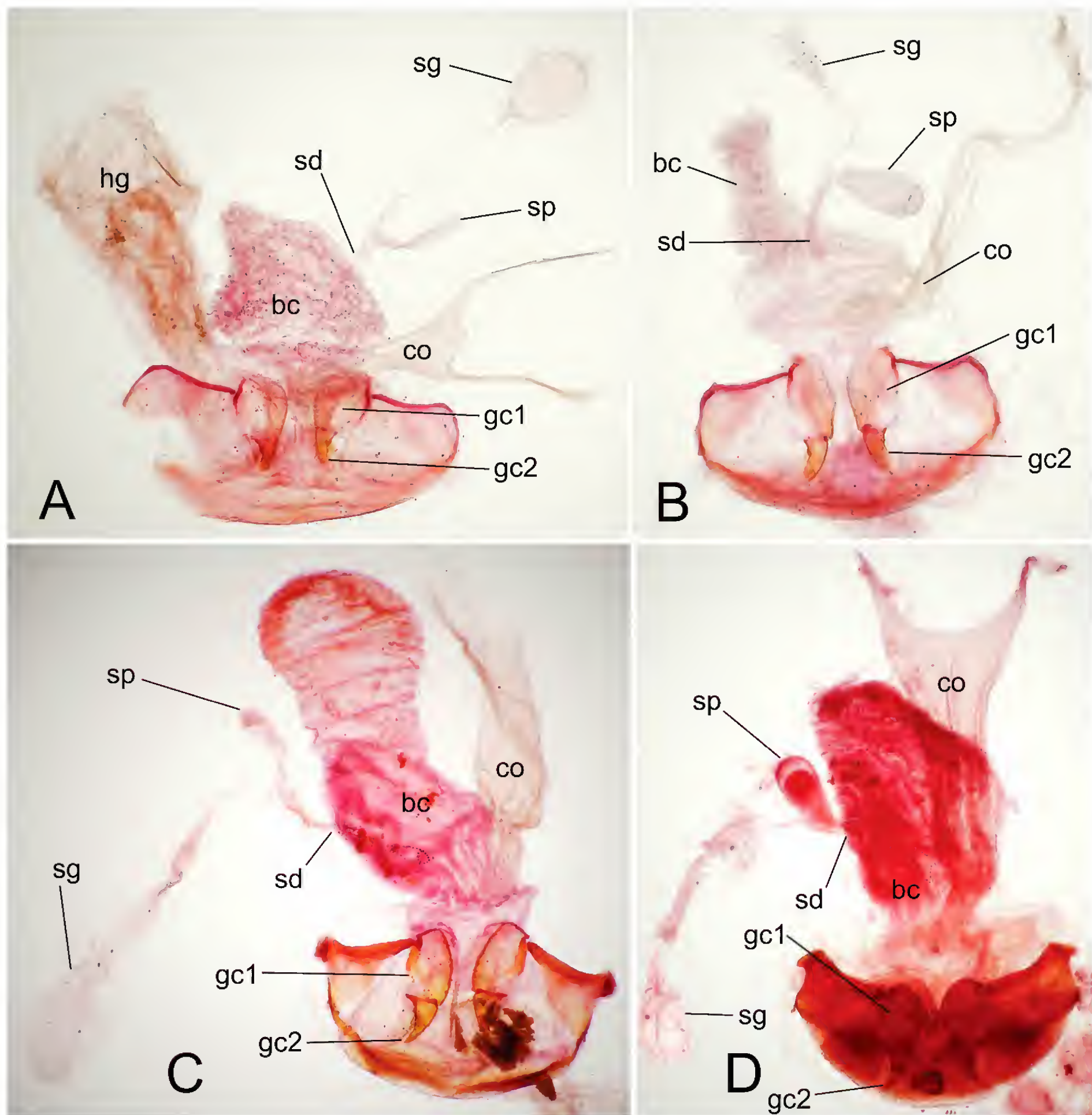


Figure 17. Female reproductive tract and gonocoxae of *Mecyclothorax* (*s. s.*) spp., ventral view: **A**, *M. lateralis*, VIC: Maldon; **B**, *M. minutus*, NSW: Lake Urana; **C**, *M. ambiguus*, NSW: Kosciuszko N. P., Thredbo R.; **D**, *M. punctipennis*, WA: Stirling Range N. P.

des. S.L. Straneo, 1941 // *Mecyclothorax* / *minutus* Cast / holotypus / Det. B.P. Moore '68 // MUSEO GENOVA / Coll. Castelnau. Moore's labelling of this specimen as holotype, as done for *M. lateralis* above, is corrected in Moore et al. (1987) to reflect Castelnau's lack of mention of how many specimens from Paroo River were before him at description. For *C. fortis* Blackburn, lectotype male (BMNH) hereby designated: specimen mounted on white card with "913 T" on obverse, black and red lines at base, the red crossed by two triangles // round, red-margined Type label // Blackburn Coll. / 1910-236 // *Cyclothorax fortis*, Blackb. // Lectotype / *Cyclothorax* / *fortis* / Blackburn / J.K. Liebherr 2006 (black-margined red label). Female paralectotype (SAMA): specimen card-mounted with

ventral surface upward, card with black and red line, "913" in red ink // S. Australia / Blackburn // *Cyclothorax* / *fortis*, Bl / Co-type // Paralectotype ♀ / *Cyclothorax* / *fortis* Blackburn / det. J.K. Liebherr 2004 [black margined, red label]. The lectotype (BMNH) was assigned based on its occupation of the first locality, Port Lincoln, mentioned in Blackburn's description (Blackburn 1889: 1391), with the paralectotype assigned to the second locality mentioned by Blackburn; "Yorke's Peninsula." Thus Port Lincoln becomes the type locality for the Blackburn name.

Distribution and habitat. This species exhibits a bi-centric distribution, occupying the interiors of Western Australia, and New South Wales, South Australia and Victoria (Fig. 19B). Distributional records and institu-

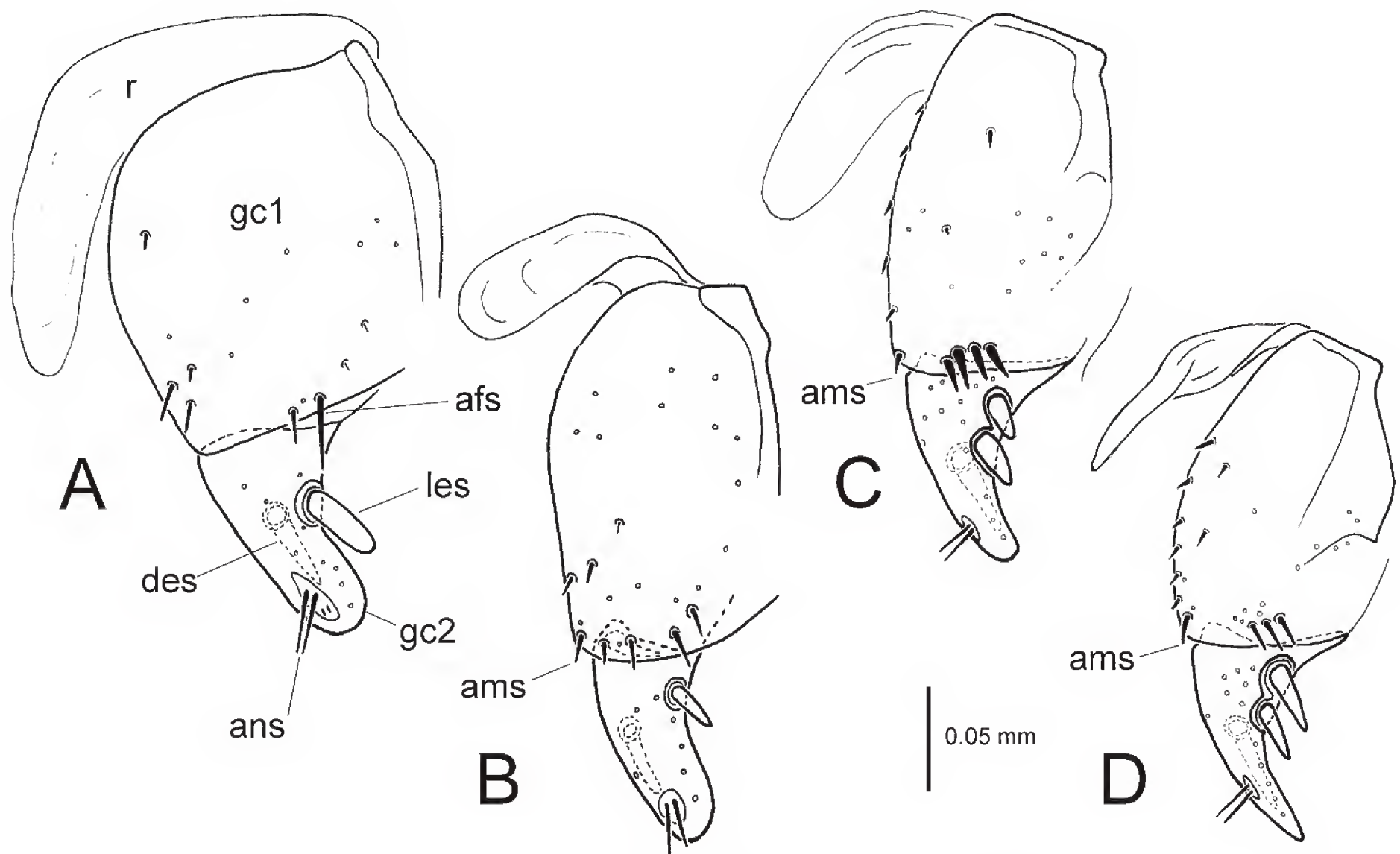


Figure 18. Left gonocoxa of *Mecyclothorax* (*s. s.*) spp., ventral view: **A**, *M. lateralis*, VIC: Maldon; **B**, *M. minutus*, NSW: Lake Urana; **C**, *M. ambiguus*, NSW: Kosciuszko N. P., Thredbo R; **D**, *M. punctipennis*, ACT: Black Mountain.

tional repositories for examined non-type specimens include: NSW: Bogan R. (MCZ, 1); Lake Urana Nat. Res. (EMEC, 17); SA: Koongawa, 4 mi. ESE (ANIC, 1); Pt. Augusta (BPBM, 7); Birchip (MVM, 1); Mallee Dist. (MVM, 3); Nyah (MVM, 1); WA: Burracoppin, 129 mi. S (WAM, 1); Coongardie, 85 km W (BPBM, 3); Hine's Hill, 10 mi. SW Merredin (CAS, 4); Hughden Rock (WAM, 2); Mullewa (MCM, 1; MCZ, 10); Newman Rock (ANIC, 1); Ravensthorpe, 50 mi. E (CAS, 1); Southern Cross, 14 mi. W (CAS, 1); Yellowdine, 18 km S (UASM, 2). Beetles constituting the sizable series collected by K.W. Will at Lake Urana Nature Reserve were found under rocks near pools of water in forest, by headlamp at night. As with most carabid beetles living in dry habitats, such nighttime entomological activity is a requisite for obtaining more than the odd specimen. Given the close, adelphotaxon relationship between *M. minutus* and *M. lateralis*, this type of habitat is suggested as the situation within which to find *M. lateralis* as well.

Mecyclothorax ambiguus (Erichson)

Figures 2L, 6C, 15C, 16C, 17C, 18C, 19C

Anchomenus ambiguus Erichson, 1842: 130.

Cyclothorax ambiguus Sloane, 1895: 447.

Mecyclothorax ambiguus Sloane, 1920: 153.

Cyclothorax lophoides Sloane, 1895: 447 (misidentification).

Diagnosis ($n = 5$). Moore (1984) deferred reliable diagnosis of this species from *M. punctipennis* based on the

configuration of the male aedeagus (e.g. Fig. 15C–D), however the pronotal lateral margins are reliably narrower in individuals of this species (Fig. 2L). Although variable melanization of the pronotal disc and marginal depressions may confuse the appearance of the width of the lateral depressions, other aspects of the pronotum may be used, including: **1**, punctation of the median base, with about 20–22 punctures each side in this species versus nearly 30 deeper punctures each side in *M. punctipennis* (Fig. 2L–M); **2**, median base juncture with pronotal disc lined with deep, nearly round to moderately elongate punctures in this species, versus distinctly strigose depressions with 1–2 punctures in each depression for *M. punctipennis*. Microsculpture also varies unambiguously between the two species: **1**, in *M. ambiguus* a transverse mesh visible over portions of the pronotal disc and median base, best viewed adjacent to areas of reflected microscope light, versus glossy pronotal disc and median base, with only indistinct transverse lines within irregularities of the cuticular surface in *M. punctipennis*; and **2**, discal elytral intervals with well-developed transverse mesh, sculpticell breadth 2–3× length, and surface subiridescent in *M. ambiguus*, versus discal elytral intervals glossy, with at most indistinct transverse sculpticells visible at margins of fields of reflected light, the surface without any iridescence in *M. punctipennis*. The depth of elytral striae varies on the elytral apex, however in *M. ambiguus*, interval 8 is broadly convex adjacent to the well-developed stria 7 between the subapical and apical elytral setae, whereas in *M. punctipennis*, interval 8 is internally subcarinate and angularly depressed laterally (Liebherr

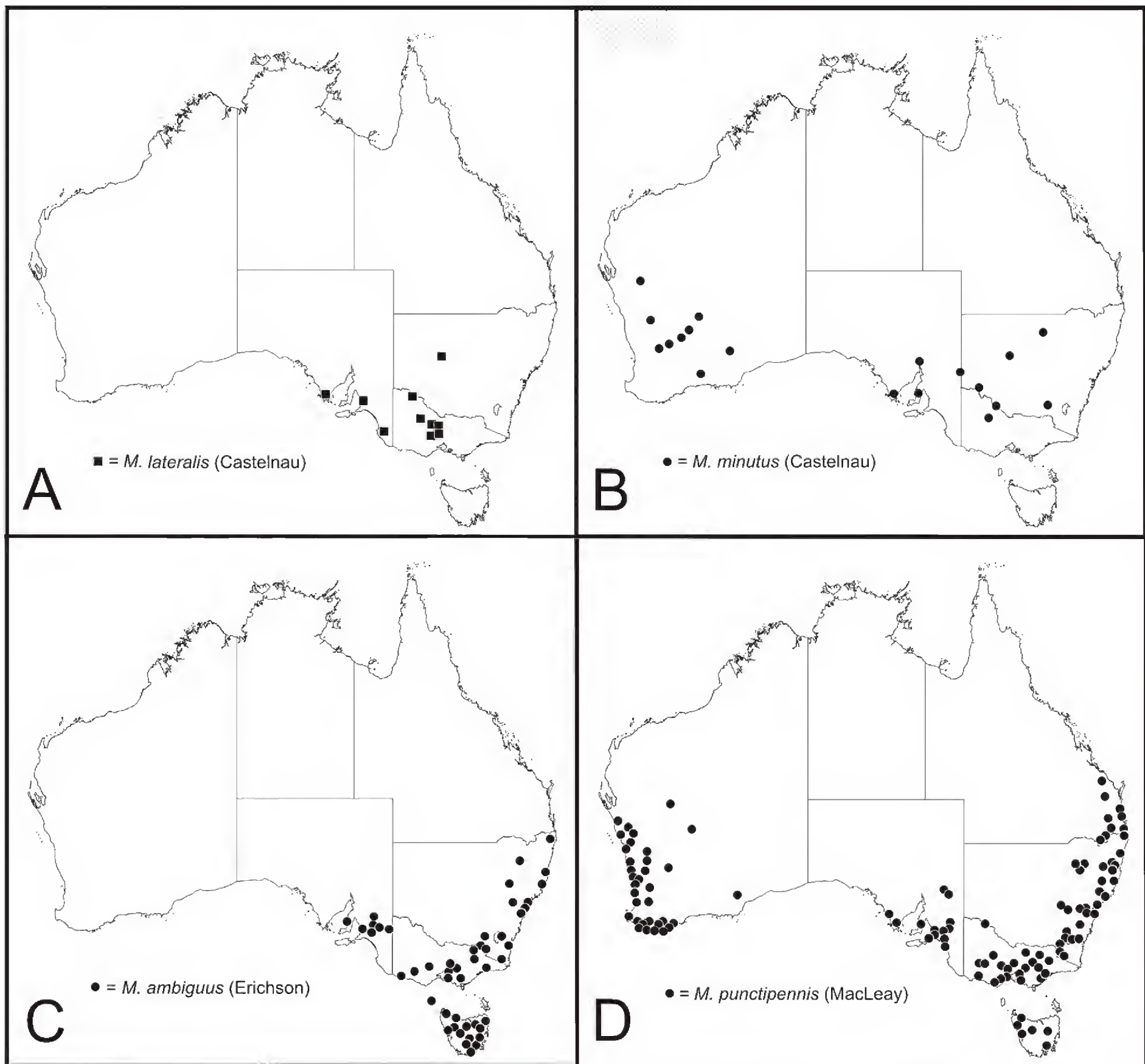


Figure 19. Distributional ranges of the four Mainland Australian *Mecyclothorax* (s. s.) spp.

2012a, fig. 7). For *M. ambiguus*, the mentum tooth has sides obtuse, the apex broadly rounded, whereas *M. punctipennis* is characterized by an acute mentum tooth with apex tightly rounded. The prosternal anteapical groove is deep and smooth here, but broader and distinctly punctate laterally, though smoother and slightly irregular medially, in *M. punctipennis*. In addition, the depressions surrounding the dorsal elytral setae span 1/4–1/2 of elytral interval 3 in this species, but up to 1/2–3/4 of the interval width in *M. punctipennis*. Standardized body length 5.0–5.7 mm. Setal formula ++/++/2++.

Male genitalia (n = 3). Aedeagal median lobe gracile, narrow dorsoventrally relative to length, apex broad, expanded both ventrally and dorsally resulting in a nearly straight apical face (Fig. 15C); ostial ventroapical operculum well developed as a broadly triangular sclerite; flagellar plate very large, well-sclerotized with longitudinal ridges; aedeagal internal sac bearing a ventral spicular sclerite; right paramere slightly broadened basally, even-

ly narrowed to apex, ventral surface with ~20 setae along margin, additional very small setae may be present near apex (Fig. 16C); left paramere slightly expanded in basal half, apically narrowed to whip-like apex.

Female reproductive tract (n = 2). Bursa copulatrix elongate, columnar, length about 3× diameter when pressed under cover slip, surface membranous, translucent, wrinkled (Fig. 17C); spermathecal duct entering bursa copulatrix mediodorsally, duct length about 2× length of spermathecal reservoir; spermathecal gland duct long, >3× length of spermathecal reservoir; basal gonocoxite apical margin with 4 setae, 1 setae at apico-medial angle, and several smaller setae along medial margin (Fig. 18C); apical gonocoxite broad basally with 2 short, stout lateral ensiform setae, apex narrowly rounded; apical nematiform setae in sensory furrow near apex of apical gonocoxite.

Type information. Dissected and pinned male Lectotype (ZMHU): 3294 // ring sclerite and aedeagus on card

// *ambiguus* / Er. / Van Diemens Land / Schayer [blue label] // LECTOYPE (red label) *Mecyclothorax* / “Anchomenus” / *ambiguus* / Erichson 1842 / designated by / B. P. Moore. An additional two male and one female paralectotypes (ZMUH) accompany the lectotype.

Distribution and habitat. This species is distributed throughout southeastern Australia including Tasmania and King Island (Fig. 19C). Localities and repositories for examined material include: NSW: Bodalla (MCZ, 4); Braidwood (MCZ, 41); Breakfast Ck. (MVM, 1); Cabramatta (BMNH, 1); Comboyne plateau (MCZ, 4); Cumberland (BMNH, 1); Greta (AMNH, 1); Kosciuszko N. P. (CUIC, 8; MCZ, 7); Mt. Wilson (FMNH, 1); Narrabeen Lagoon (FMNH, 5); Richmond R. vic. Wiangaree (MCZ, 8); Tallaganda St. For. (CAS, 1); Uralla (CAS, 3); SA: Adelaide (CAS, 1); Adelaide, 18 km E, Carey, 3 km SE (FMNH, 1); Adelaide, 8 km S, Waterfall Gully (FMNH, 1); Blackwood, Sturt Gorge Res. (ZMUC, 13); Goose Island (MVM, 3); Norton Summit, 10 km E Adelaide (FMNH, 2); Williamstown (FMNH, 1); Yorketown (CAS, 2; FMNH, 13); TAS: Burnie (MCZ, 8); Cockle Ck. (MCZ, 2); Florentine R. (MCZ, 3); Goulds Country (CMNH, 2); Hartz N. P. (MCZ, 2); Hastings (MCZ, 3); Hobart (MVM, 3); King Is. (MVM, 2); Launceston (FMNH, 1; MCZ, 1); Mersey R. Vy. (MCZ, 2); Mt. Ben Lomond (MCZ, 6); Mt. Field, base (MCZ, 7); Mt. Wellington (MCZ, 1); Parratah (MVM, 2); Queenstown (MCZ, 16); Smithton (CAS, 7); Tarraleah (MCZ, 3); Waldheim (MCZ, 1); Zeehan (CAS, 1); VIC: Ballarat (BMNH, 2); Bogong (MVM, 2); Dandenong (CAS, 2); Frankston (MVM, 1); Ferntree Gully (MVM, 1); Lakes Entrance (MVM, 1); Mt. Buller (MCZ, 1); Mt. Donna Buang (MCZ, 15); Mt. Hotham (MCZ, 3); Mt. Wogwog (EMEC, 1); Oakleigh (MVM, 2); Olinda (BMNH, 2); Penshurst (CUIC, 7); Port Melbourne (MVM, 2); Portland to Pt. Fairy (MCZ, 2); Pretty Vy. Dam (MVM, 1); Warburton (MVM, 6); Warrendyte (MVM, 1); Whiskey Ck. (MVM, 3); Yarra Glen (MVM, 1).

Mecyclothorax punctipennis (MacLeay)

Figures 2M, 6D, 15D–E, 16D, 17D, 18D, 19D

Cyclothorax punctipennis MacLeay, 1871: 105.

Mecyclothorax punctipennis Csiki, 1929: 487.

Cyclothorax obsoletus Blackburn, 1889: 1389 (synonymy Moore, 1984: 162).

Cyclothorax ambiguus Sloane 1898: 472 (misidentification).

Diagnosis (n = 5). For purposes of this review, all diagnostic external characters that distinguish this species from *M. ambiguus*—and therefore all other Australian species—are presented under *M. ambiguus*. Standardized body length 5.0–5.8 mm. Setal formula ++/++/+2++.

Male genitalia (n = 3). Aedeagal median lobe gracile, narrow dorsoventrally relative to length, the apex well extended beyond ostium, the tip downturned (Fig. 15D); ostial ventroapical operculum well developed, an elongate triangular sclerite; flagellar plate large, bearing

longitudinal sclerotic ridges (Fig. 15E); base of aedeagal internal sac bearing a ventral spicular sclerite; right paramere narrow, elongate, bearing >12 setae along the ventral margin, 4 small setae long dorsal margin (Fig. 16D); left paramere narrow basally, narrowed to elongate, attenuated whip-like apex.

Female reproductive tract (n = 2). Bursa copulatrix elongate, columnar, length about 2× diameter when pressed under cover slip, surface thickened, wrinkled, (Fig. 17D); spermathecal duct entering bursa copulatrix mediodorsally, duct length about 2× length of spermathecal reservoir; spermathecal gland duct long, ~1.5× length of spermathecal reservoir; basal gonocoxite apical margin with 3 setae, 1 seta at apicomedial angle, and several smaller setae along medial margin (Fig. 18D); apical gonocoxite broad basally with 2 acuminate lateral ensiform setae, apex acuminate; apical nematiform setae in subbasal sensory furrow.

Type information. For *M. punctipennis*, lectotype male (ANIC): Gayndah, Queensland (Moore 1984). For *C. obsoletus* Blackburn, two syntypes (SAMA): Port Lincoln, S.A. (Moore 1984, Moore et al. 1987).

Distribution and habitat. This species is broadly distributed in numerous habitats across Australia (Fig. 19D). Recorded collection localities range in elevation from sea level to over 2000 m near the summit of Mt. Kosciuszko. These beetles are at home in leaf litter on the floor of *Eucalyptus* forests, under dense mats of dead leaves surrounding the bases of *Xanthorrhoea* (Asphodelaceae) grass trees, in tussock grass clumps of high-elevation grasslands, under wrack on sea beaches, and in home gardens in urban settings. The species is monomorphically macropterous, with adults often collected at lights in great profusion.

Even given this species' catholic ecological preferences and propensity for winged flight, its geographic distribution is discontinuous across Australia (Fig. 19D). Moreover, the Western Australian populations of this bicentric species distribution interact little if at all with coastal populations east of the Great Australian Bight, based on geographic restriction of polymorphic male genitalic chiral antisymmetry to the populations inhabiting Western Australia (Liebherr and Will 2015). In contrast, all eastern populations monomorphically comprise males with plesiomorphic genitalic torsion, whereby the right side of the aedeagus is held ventrally when in repose. The Western Australian populations vary greatly in the proportions of left- and right-torsioned males, demonstrating that their mutual geographic isolation is great enough to preclude extensive homogenizing dispersal among populations.

Baehr (2000) reported a 1998 record for *M. punctipennis* from Rocky Cape N. P. as the first Tasmania record. However, Darlington material (MCZ) indicates *M. punctipennis* was present at Hobart in 1956–1957 (Liebherr and Will 2015). Tasmanian localities and repositories represented in material examined for this review (Fig. 19D) include: Corinna, West Tasmania (MCZ, 4); Hobart (MCZ, 8); Great Lake, north end (MCZ, 5); Waldheim nr. Cradle Mtn. (MCZ, 1); Zeehan, north (MCZ, 3).

Discussion

Biogeographic History. The adelphotaxon relationship (Liebherr 2011a) between *Mecyclothorax* and genera allied with and including *Amblytelus* Erichson – i.e. *Epeilyx* Blackburn, *Dystrichothorax* Baehr, *Paratrichothorax* Baehr, and *Trichoamblytelus* Baehr – requires both clades to be of equal age of origin. Baehr (2004) proposed an Eocene age of origin for the *Amblytelus* lineage, based on the restriction of *Paratrichothorax* and *Trichamblytelus* to coastal forests of southwest Australia. The late Eocene marine transgression would have isolated the ancestors of extant species in these genera from other lineages diversifying in eastern Australia, with subsequent aridification and periodic marine transgressions maintaining that isolation (Mast and Givnish 2002). Oligocene cooling allowed the evolution of rain forest communities, whereas Miocene drying (associated with the rise of Myrtaceae) resulted in the assembly of communities dominated by *Eucalyptus* (Crisp et al. 1999). The intense association of the tree-dwelling *Amblytelus* lineages with *Eucalyptus* forests allowed those taxa the opportunity to diversify over the past 20 Myr, with many of the more than 100 species evolving arboreal life styles (Baehr 2004, 2016b). *Mecyclothorax* spp., on the other hand, have been principally restricted to terrestrial microhabitats in southwest or southeast Australia, Queensland, New Caledonia, and especially New Guinea during the Miocene orogeny (Liebherr 2018). Species of the montane rainforest, Queensland *Qecyclothorax* have been principally collected in sieved litter from terrestrial situations, though some specimens have been collected via pyrethrin spray of mossy logs and trunk bases. The early divergence of *Qecyclothorax* in these rainforests is hypothesized to have occurred commencing in Oligocene when these communities were being assembled. Conversely, based on collecting records for Australian *Mecyclothorax* of the subgenus *Eucyclothorax*, we know that these species are distributed along waterways and in wetlands, often in association with open forest vegetation, fallen wood, and massed vegetation such as flood debris. Thus, like *Amblytelus*, this line could have diversified in the myrtaceous communities of southern Australia.

Though most of the diversification occurred in south-eastern Australia, multiple east-west vicariance events of different ages are mandated by the cladistic taxon-area relationships of the taxa (Rix et al. 2015). The earliest east-west vicariance event would have isolated *M. isolatus* in the forests of the south west coastal region. That *M. isolatus* has a remarkably reduced metathorax and well-developed plical lock between the abdominal ventrites and elytra points to prolonged occupation of stable, persistent forest habitats (Southwood 1977) now conserved within Walpole-Nornalup National Park. Subsequently *M. blackburni* was isolated in Western Australia (Figs 1B, 11B) prior to diversification of the six species in the *M. lophoides* complex (Fig. 1B). Later in the history of that same clade, *M. jameswalkeri* was derived as a Western Australian isolate related to *M. dar-*

lingtoni from Queensland and *M. lophoides* from south-east Australia (Figs 1B, 11C). The most recent east-west pattern involves widespread species with populations in both eastern and western Australia: **1**, *M. punctatus*, with the subspecific form *M. p. peckorum* described from the southwest Cape region; **2**, *M. minutus* (Fig. 19B); and **3**, *M. punctipennis* (Fig. 19D).

Within the subgenus *Mecyclothorax*, the vast majority of Australian Plate species evolved first in association with rainforest habitats in New Guinea (Fig. 1A; Baehr 2014, Liebherr 2017), and subsequently following over-water dispersal to locales such as Lord Howe and Norfolk Islands (Moore 1985, 1992), Borneo (Baehr and Lorenz 1999), Java (Andrewes 1933, Louwerens 1949, 1953), Timor Leste (Baehr and Reid 2017), New Zealand (Liebherr and Marris 2009), and most recently the Hawaiian and Society Islands. The colonizing taxon founding the very diverse Hawaiian radiation occupied terrestrial grassland, based on sharing of this habitat preference by the very close relatives *M. punctipennis* and *M. montivagus* (Fig. 1A, Liebherr 2015). The third species completing this triplet, *M. sculptopunctatus* of St. Paul and Amsterdam Islands, also occupies such an open habitat on these very small, windswept Indian Ocean islands (Jeanel 1940, plate IV, fig. 1), corroborating an open grassland habitat as the initial landing area for these island species. It is within the many Hawaiian species that have radiated from the common ancestor with *M. montivagus* that ecological diversification has reached its maximal range among known *Mecyclothorax*, with the evolution of alpine, riparian, and arboreal epiphyte-loving species (Liebherr 2015), as well as a cave-adapted troglomorphic species (Liebherr 2008a). Even within the estimated 10% of *Mecyclothorax* species predicted to be discovered in New Guinea (Liebherr 2017), species have evolved to occupy alpine habitats—*M. sedlaceki* Darlington, *M. toxopei* Darlington, and *M. kavanaughi* Liebherr (Liebherr 2008b)—as well as dense lowland rainforest; *M. amingwivae* Liebherr, *M. andersoni* Liebherr, and *M. gressitti* Liebherr (2017). Being highly complex geologically and largely unexplored, the New Guinea highlands on the active tectonic margin of the Australian plate are likely to provide further examples of ecological diversification within the genus.

Paleoecological research has resulted in the discovery of Australian subfossils assignable to *Mecyclothorax* (Sniderman et al. 2009). In deposits laid down ~1.84–1.56 Ma in the Stony Creek Basin, Victoria, subfossils determined as “*Mecyclothorax* ‘*punctatus*’ grp n. sp.” and “*Mecyclothorax* sp. 3 (*cordicollis* grp.)” were recovered. The site is within the present-day distributional range of *M. punctatus* (Fig. 11A), and so these subfossils presumably represent extant species or representatives of an ancestral population that evolved to become the extant species. Most parsimoniously then, the common ancestor of *M. punctatus* and its sister species *M. moorei* can be dated to the Pleistocene age of this assemblage (Fig. 1B). For the “*cordicollis* grp.” taxon, the site lies within the distributional ranges of *M. lophoides*, *M. peryphoides*,

and *M. cordicollis* (Fig. 11C–E). Given this contribution's sorting out of species in the *M. lophoides* species complex based on comprehensive use of external and male genitalic characters, more concise determination of these subfossils may allow more precise dating of cladogram nodes connecting these species (Fig. 1B). Regardless of the outcome of such a determination, the rate of speciation for these *Eucyclothorax* species is an order of magnitude lower than that observed in the Pacific Island radiations, where time between speciation is estimated to be 220,000 years for Hawaii (Liebherr 2015) and 300,000 years for the Society Islands (Liebherr 2013).

Genitalic Evolution. Confirmation of species assignment for specimens in the *M. lophoides* species complex is greatly assisted by examination of the male aedeagus, a finding in keeping with the utility of male genitalia for diagnosis of cryptic species in the Hawaiian *Mecyclothorax* fauna (Liebherr 2007, 2008a, 2011b, 2015), where numerous species may be sympatric across a limited portion of an island. In contrast, male genitalia vary infraspecifically within species of the New Caledonian *Mecyclothorax* subgenus *Phacothorax* on an island where often only two species occur sympatrically (Liebherr 2018). Even though the overall diversity of Australian *Mecyclothorax* is modest, the aggregate distributional patterns are more like those observed in Hawaii, as nine species are broadly sympatric across portions of New South Wales and Victoria (Figs 11, 19). Given the long duration of *Mecyclothorax* species in Australia (Sniderman et al. 2009), there has been abundant time for the evolution of discrete male genitalia, thereby assisting species recognition during the encounters of male and female beetles (Nagata et al. 2009, Okuzaki and Sota 2014). The only region of Australia where this pattern breaks down is Western Australia, where chiral antisymmetry occurs within populations of *Mecyclothorax punctipennis*. Here only that species and *M. minutus* share much of the region (Fig. 19), as the four *Eucyclothorax* species are allopatrically distributed within limited areas along the coast (Fig. 11A–C).

Species diagnosis within the *M. lophoides* complex (Fig. 1B) lies most specifically in differential characters of the internal sac flagellar complex (Figs 7F–H, 14). This is especially so for the sympatric species *M. lophoides*, *M. cordicollis*, and *M. peryphoides* (Figs 14B, F, H). A succession of taxonomists have routinely confused these closely related species (Fig. 1) because the external anatomical characters vary little among the species, and infraspecific variation blurs the subtle patterns of external character evolution. Yet the beetles' flagellar complexes differ very dramatically, with no possibility of misidentification given access to a male specimen. This disparity points to relative stasis in external anatomy during accelerated evolution of male genitalic characters. Two questions may be asked about this evolutionary disparity. Firstly, what are the functional ramifications for mating given the dramatic differences among species? Secondly, what are the evolutionary selection pressures that have resulted in accelerated genitalic evolution?

The internal sac flagellum of male tiger beetles functions during copulation as a semi-rigid structure that enters the female spermathecal duct (Schincariol and Freitag 1986). The *Cicindela* L. flagellum is elongate, sclerotized, and in cross-section U-shaped, with either the internal surface of the groove, or the convex outer surface of the flagellum bearing basally directed, micro-serrate teeth (tempers). These act to hold the flagellum in the duct when required, but can be detached from the duct's surface through flagellar flexion when removal of the flagellum is required (Freitag et al. 2001). The flagellum ranges from about half the length of the spermathecal duct to slightly longer than the duct in four species of *Cicindela* and *Pseudoxychila tarsalis* Bates (Freitag 1966, Freitag et al. 1980, Rodríguez 1999). In all instances, the flagellar diameter is similar to the diameter of the spermathecal duct, though the flagellar base is larger than the duct and presumably does not enter it. The flagellum cannot transfer sperm, as its base is closed, and it does not connect directly to the male gonopore. Its function includes opening of the spermathecal duct during the complicated multi-phase mating behavior of cicindelids (Schincariol and Freitag 1986), and possibly facilitating insertion of the spermatophore neck into the spermathecal duct (Rodríguez 1999), allowing sperm passage into the duct and to the spermatheca.

Aedeagal internal sac flagella occur throughout the Carabidae (Jeannel 1955, Maddison et al. 2013). In Hawaiian *Bembidion* Latreille beetles of the subgenus *Nesocidium* Sharp, the male flagellum length is subequal to the female spermathecal duct length, to 60–75% longer than the duct (Liebherr 2008c). Correspondence in length between male flagellum and female spermathecal duct was maximal in *Nesocidium* spp. with spermathecal ducts of uniformly narrow diameter, whereas species in which the male flagellum was longer than the duct included females with a basally broad duct, suggesting that the flagellum touches the walls of the duct, undergoing circular torsion and thus expanding the duct to its maximal diameter as it is pushed into the duct by the male. The presence of a short male flagellum is a groundplan character for the tribe Moriomorhini (Liebherr 2011a). Among species of *Mecyclothorax* subgenus *Eucyclothorax*, the flagellum ranges from a plesiomorphic shortened condition, as in *M. moorei*, *M. punctatus*, *M. curtus*, and *M. blackburni* (Fig. 7A–E), to the highly derived, elongate, and rigidly sinuous structure of *M. eyrensis* and *M. peryphoides* (Fig. 14D–F). The other species of the *M. lophoides* complex exhibit a flagellum of intermediate length; **1**, slightly longer than the associated flagellar sheath in *M. darlingtoni* (Fig. 7G–H); **2**, equal in length to the flagellar sheath in *M. lophoides* (Fig. 14B); and **3**, slightly shorter than the flagellar sheath in *M. cordicollis* (Fig. 14H). Among the females, most species have spermathecal ducts equal in length to the apical spermathecal reservoir, i.e. of moderate length (Fig. E–F, I). However, in females of *M. curtus*, *M. eyrensis*, and *M. peryphoides* the spermathecal duct is elongate, i.e. more than twice the length of the fusiform

apical reservoir (Fig. 9C, G–H). In the species pair *M. eyrensis* + *M. peryphoides*, insertion of the long, semi-rigid and sinuous flagellum would make the spermathecal duct conform to the flagellar configuration.

The species pair *M. eyrensis* and *M. peryphoides* are also unique within subgenus *Eucyclothorax* in that the highly derived structures of the male aedeagal median lobe and internal sac are identical among males of both species, apparently violating one of the precepts of modern taxonomy that associate species diagnosis with male genitalic differences (Huber 2003). However parameral setation varies significantly among males of these species. This finding begs the question of how the male parameres interact with the external surface of the female abdomen during intromission, at the same time providing a genitalic difference between the species to accompany diagnostic external characters that include differences in: **1**, pronotal shape, especially at the pronotal hind angles; **2**, cuticular microsculpture; and **3**, coloration. The two species also occupy very different ecological zones in Australia; with *M. eyrensis* residing in the arid interior of South Australia, Northern Territory and New South Wales, whereas *M. peryphoides* occupies the more temperate grass- and woodland habitats to the south and east (Fig. 11D). Both species occupy riparian habitats within their respective distributions, perhaps the reason that *M. eyrensis* can persist in the dry interior, as the larvae would be seriously impacted were the occupied habitat too xeric during the period of larval development. Though only a single datum, the genitalic situation in *M. eyrensis* and *M. peryphoides* parallels that reported by Huber and Dimitrov (2014) for a sister-species pair of Taiwanese pholcid spiders: two species sharing highly distinctive yet identical male genitalia (i.e. chelicerae), while differing in body coloration and proportions, and occupying discrete ecological situations across allopatric distributions. Molecular divergence is minimal between the two pholcid species, supporting very recent speciation between them.

The second question posited above concerning the evolutionary basis for male and female genitalic correlations can be addressed preliminarily by the distribution of differences among the species in subgenus *Eucyclothorax*. It seems likely that genitalic characters provide specific cues for mate recognition (e.g. Nagata et al. 2009). Can such differences be interpreted as the results of sexual selection (Eberhard 1985, 2004)? Males of *M. moorei*, *M. punctatus*, and *M. curtus* exhibit short flagella (Fig. 7A–D), whereas the females exhibit several derived characters of the reproductive tract. Females of the sister species *M. moorei* and *M. punctatus* exhibit a basally sclerotized and bulbously expanded spermathecal duct (Fig. 9A–B). Females of *M. curtus* deviate from that by having a spermathecal duct that is elongate and moderately sclerotized (and therefore coiled when at rest), as observed in females of *M. eyrensis* and *M. peryphoides*. If we invoke runaway sexual selection to explain the association of elongate male flagella and spermathecal ducts of *M. eyrensis* and *M. peryphoides*, then how do we explain the similarly elongate duct in *M.*

curtus, here in association with a short male flagellum? Moreover, given that we do not understand the function of the basally expanded and sclerotized spermathecal ducts in *M. moorei* and *M. punctatus* females, nor how the duct might interact with the male flagellum, currently we are best left to report the findings and introduce their use in phylogenetic inference. Finally, if we were to implicate the difference in parameral setation between *M. eyrensis* and *M. peryphoides* as the result of sexual selection, then we must posit the introduction of a novel focus of selection in the mating system at this point; a decidedly unparsimonious rescue attempt for a hypothesis compromised by the phylogenetic distribution of female spermathecal duct configurations.

Based on revisionary taxonomy for the *Mecyclothorax* faunas of the Hawaiian Islands (Liebherr 2006, 2007, 2008a, 2009a, 2009b, 2011b, 2015), the Society Islands (Liebherr 2012a, 2012b, 2013), New Zealand (Liebherr and Marris 2009), Papua New Guinea (Liebherr 2017), New Caledonia (Liebherr 2018) and now Australia, we have accrued information on genitalic correlates between the sexes for more than 350 species. Plucking from this cornucopia of genitalic riches, all manner of genitalic correlates among closely related species can be observed. The parapatric Moloka'i sister species *M. lissopterus* Liebherr and *M. arcuatus* Liebherr of the *M. ovipennis* species group are not distinguishable based on external anatomy. However, genitalia of both sexes are both diagnostic and concordant with regard to size: **1**, the male aedeagal median lobe of *M. arcuatus* has a much longer and broader apex (Liebherr 2007, figs 75–78); and **2**, the female bursa copulatrix of *M. arcuatus* is much broader and more elongate (Liebherr 2007, figs 157, 159). In this instance, an elongate male median lobe is associated with an elongate female bursa, with the structures functionally related because the former enters the latter during intromission, followed by eversion of the male internal sac and transfer of the spermatophore. A second pair of allopatric *M. ovipennis* group sister species from Moloka'i – *M. joni* Liebherr and *M. lisae* Liebherr – exhibit males with significantly different aedeagal median lobe lengths across species, but females with bursae of very similar lengths (Liebherr 2007 figs 71–74, 150, 152). A similar non-correlated pattern is observed among five sympatric species of Oahu's monophyletic *M. brevis* species complex, with the male aedeagal median lobes and internal sacs varying dramatically among the species, but the known female bursae differing little (Liebherr 2009a, figs 6A–K, 9A, C). If we wish to implicate sexual selection across just these three examples, each involving most-closely related species, the first example of concordant transgender-based association of dramatically larger male and female genitalia in *M. arcuatus* would better fit the model of antagonistic sexual selection, whereas the latter two examples involving dramatic changes in male genitalia along with female genitalic stasis would fit conditions of Eberhard's (2004) female choice model. Yet, the latter two examples consistent with observations of female choice also differ in that the former involves allo-

patric sister species, and the latter involves five sympatric species. Females could choose among sympatric males, but not among allopatric males. Alternatively species-specific male genitalia could have evolved during allopatric speciation, with secondary sympatry enhancing either or both pre-mating sexual discrimination and post-mating reproductive isolation (Malone et al. 2015). Character displacement operating on characters of either system could reinforce divergence among secondarily sympatric species or populations (Brown and Wilson 1956). These myriad options point to the requirement for hypothesis testing specific to singular or closely associated evolutionary events when studying sexual selection (Simmons 2014). They also suggest that it is inappropriate to consider sexual selection as a singular factor responsible for the accelerated speciation of Polynesian *Mecyclothorax* beetles.

Acknowledgements

This research depends absolutely on the supportive efforts of curators making taxonomic material available through their field collecting and curational efforts. I thank the following individuals for providing access to taxonomic material (parenthetical codens identify institutions cited in Material and methods): Lee Herman (AMNH); Chris Reid (AMS); Cate Lemann and Thomas Weir (ANIC); Beulah Garner and Max Barclay (BMNH); James Boone and Neal Evenhuis (BPBM); David H. Kavanaugh (CAS), Robert L. Davidson (CMNH); Kipling W. Will (EMEC); Margaret Thayer and Alfred F. Newton (FMNH); Martin Baehr (MBC); Roberto Poggi (MCG); Riccardo Sciaky (MCM); Philip D. Perkins (MCZ); Azadeh Taghavian and Thierry Deuve (MNH); Catriona MacPhee (MVM); Susan Wright and Geoff Monteith (QMB); Peter Hudson and Jan Forrest (SAMA); Danny Shpeley (UASM); Brian Hanich and Terry Houston (WAM); Sree Selvantharan and Alexey Solidovnikov (ZMUC). I thank Nick Porch, Deakin University, for advice about Australian subfossils, and Kip Will for providing access to Chaudoir (1873) and for collaborative museum work. I also sincerely thank Stewart B. Peck, Carleton University, for information on the habitat of *M. isolatus*, and for his encouraging suggestion that I should investigate the Hawaiian Carabidae. An American Philosophical Society grant and National Science Foundation awards (DEB-9208269, DEB-9806349, DEB-0315504) supported museum visits to London, Paris, Berlin, Adelaide, Canberra, Brisbane, Honolulu, and Cambridge, as I tracked the diaspora of *Mecyclothorax* types. I thank Achille Casale and David Seldon for extremely helpful reviews of the manuscript.

References

- Andrewes HE (1931) 56. Coleoptera-Carabidae of the Juan Fernandez Islands. In: Skottsberg C (Ed.) The Natural History of Juan Fernandez and Easter Island, 3 (Zoology). Almqvist and Wiksells Boktryckeri-A-B, Uppsala, 629–637.
- Andrewes HE (1933) On some new species of Carabidae, chiefly from Java. *Treubia* 14: 273–286.
- Andrewes HE (1939) Papers on Oriental Carabidae.—XXXV. On the types of some Indian genera. *Annals and Magazine of Natural History* (11th ser.) 3: 128–139.
- Baehr M (2000) A new species of the genus *Lestignathus* Erichson from Tasmania with a note on the Tasmanian species of *Mecyclothorax* Sharp (Insect: Coleoptera: Carabidae: Liciniinae, Psydrinae). *Records of the South Australian Museum* 33: 123–126.
- Baehr M (2003) Psydrine ground beetles (Coleoptera: Carabidae: Psydrinae), excluding Amblytelini, of eastern Queensland rainforests. *Memoirs of the Queensland Museum* 49: 65–109. <https://www.biodiversitylibrary.org/part/243680>
- Baehr M (2004) The Amblytelini. A tribe of corticolous ground beetles from Australia. Taxonomy, phylogeny, biogeography. (Coleoptera: Carabidae: Psydrinae). *Coleoptera* 8: 1–286.
- Baehr M (2009) A new species of the genus *Mecyclothorax* Sharp from New South Wales (Insecta: Carabidae: Psydrinae). *Records of the Australian Museum* 61: 89–92. <https://doi.org/10.3853/j.0067-1975.61.2009.1519>
- Baehr M (2014) A new species of the genus *Mecyclothorax* Sharp from New Guinea (Coleoptera, Carabidae, Psydrini, Mecyclothoracina). *Spixiana* 37: 123–129. http://www.zobodat.at/pdf/Spixiana_037_0123-0129.pdf
- Baehr M (2016a) A new subspecies of *Mecyclothorax punctatus* (Sloane) from south-western Australia. *Spixiana* 39: 93–97. http://www.zobodat.at/pdf/Spixiana_039_0093-0097.pdf
- Baehr M (2016b) New species of the genera *Amblytelus* Erichson, 1842 and *Dystrichothorax* Blackburn, 1892 from Queensland and New South Wales, Australia (Insecta: Coleoptera: Carabidae: Psydrini: Amblytelina). *Memoirs of the Queensland Museum – Nature* 60: 13–27. <https://doi.org/10.1082/j.2204-1478.60.2016.2016-01>
- Baehr M, Lorenz W (1999) A reevaluation of *Loeffleria globicollis* Mandl from Borneo (Insecta, Coleoptera, Carabidae, Psydrinae). *Spixiana* 22: 263–267.
- Baehr M, Reid CAM (2017) On a collection of Carabidae from Timor Leste, with descriptions of nine new species (Insecta: Coleoptera: Carabidae). *Records of the Australian Museum* 69: 421–450 (<https://doi.org/10.3853/j.2201-4349.69.2017.1660>).
- Ball GE, Erwin TL (1983 [1982]) The Baron Maximilien de Chaudoir: inheritance, associates, travels, work, and legacy. *Coleopterists Bulletin* 36: 475–501.
- Bates HW (1878) On new genera and species of geodephagous Coleoptera from Central America. *Proceedings of the Zoological Society of London* 1878: 587–609.
- Bates HW (1882) *Biologia centrali-americana*, Insecta, Coleoptera 1(1): 1–316.
- Bates HW (1883) Supplement to the geodephagous Coleoptera of Japan, chiefly from the collection of Mr. George Lewis, made during his second visit, from February, 1880, to September, 1881. *Transactions of the Entomological Society of London* 1883: 253–264. <https://doi.org/10.1111/j.1365-2311.1883.tb02947.x>
- Blackburn T (1878a) Characters of new genera and descriptions of new species of Geodephaga from the Hawaiian Islands II. *Entomologist's Monthly Magazine* 15: 119–123.
- Blackburn T (1878b). Characters of new genera and descriptions of new species of Geodephaga from the Hawaiian Islands II. *The Entomologist's Monthly Magazine* 15: 156–158.

- Blackburn T (1879) Characters of new genera and descriptions of new species of Geodephaga from the Hawaiian Islands III. *Entomologist's Monthly Magazine* 16: 104–109.
- Blackburn T (1881). Characters of new genera and descriptions of new species of Geodephaga from the Hawaiian Islands IV. *The Entomologist's Monthly Magazine* 17: 226–229.
- Blackburn T (1882) Characters of new genera and descriptions of new species of Geodephaga from the Hawaiian Islands V. *Entomologist's Monthly Magazine* 19: 62–64.
- Blackburn T (1889) Further notes on Australian Coleoptera, with descriptions of new genera and species. *Proceedings of the Linnean Society of New South Wales (2nd ser.)* 3: 1387–1506.
- Blackburn T (1892) Notes on Australian Coleoptera, with descriptions of new species. *Proceedings of the Linnean Society of New South Wales (2nd ser.)* 6: 479–550. <https://doi.org/10.5962/bhl.part.29903>
- Bonelli FA (1810) *Observations Entomologiques, première partie (cicindéletes et portion des carabiques)* [with the “*Tabula synoptica exhibens genera carabiorum in sectiones et stirpes disposita*”]. Turin, 58 pp.
- Britton EB (1948) A revision of the Hawaiian species of *Mecyclothorax* (Coleoptera: Carabidae). *Occasional Papers of the Bernice P. Bishop Museum* 19: 107–166.
- Broun T (1903) Descriptions of new genera and species of New Zealand Coleoptera. *Annals and Magazine of Natural History (7th ser.)* 11: 450–458.
- Brown WL, Wilson EO (1956) Character displacement. *Systematic Biology* 5: 49–64. <https://doi.org/10.2307/2411924>
- Castelnau FL Laporte de (1867) Notes on Australian Coleoptera. *Proceedings of the Royal Society of Victoria, Melbourne*, 139 pp.
- Castelnau FL Laporte de (1868) Art. XV.–Notes on Australian Coleoptera, part II. *Proceedings of the Royal Society of Victoria, Melbourne* 8: 95–225.
- Chaudoir M de (1854) Mémoire sur la famille de Carabiques. *Bulletin de la Société Impériale des Naturalistes de Moscou* 27(1): 112–144.
- Chaudoir M de (1873) Matériaux pour servir à l'étude des Féroniens. *Bulletin de la Société Impériale des Naturalistes de Moscou* 46(1): 85–116.
- Crisp MD, West JG, Linder HP (1999) Biogeography of the Terrestrial Flora. In: Orchard AE (Ed.) *Flora of Australia, Introduction 1*, 2nd ed. ABRS/CSIRO, Melbourne, 321–367.
- Csiki E (1929) Carabidae: Harpalinae III. In: Schenkling S (Ed.) *Coleopterorum Catalogus* 104. W. Junk Verlag, Berlin, 347–527.
- Csiki E (1931) Carabidae: Harpalinae V. In: Schenkling S (Ed.) *Coleopterorum Catalogus* 115. W. Junk Verlag, Berlin, 740–1022.
- Darlington PJ Jr (1936) Variation and atrophy of flying wings of some carabid beetles. *Annals of the Entomological Society of America* 29: 136–176.
- Darlington PJ Jr (1943) Carabidae of mountains and islands: data on the evolution of isolated faunas, and on atrophy of wings. *Ecological Monographs* 13: 37–61. <https://doi.org/10.2307/1943589>
- Darlington PJ Jr (1952) The carabid beetles of New Guinea, part 2, the Agonini. *Bulletin of the Museum of Comparative Zoology* 107: 89–252.
- Darlington PJ Jr (1962) The carabid beetles of New Guinea, part I. Cicindelinae, Carabinae, Harpalinae through Pterostichini. *Bulletin of the Museum of Comparative Zoology* 126: 321–564.
- Darlington PJ Jr (1971) The carabid beetles of New Guinea. Part IV. General considerations; analysis and history of fauna; taxonomic supplement. *Bulletin of the Museum of Comparative Zoology* 142: 129–337.
- Dejean PFMA (1831) *Spécies général des coléoptères de la collection de M de la Compte Dejean*. Mequignon-Marvis, Paris 5(2): 383–883.
- Eberhard WG (1985) *Sexual Selection and Animal Genitalia*. Harvard University Press, Cambridge, 256 pp. <https://doi.org/10.4159/harvard.9780674330702>
- Eberhard WG (2004) Rapid divergent evolution of sexual morphology: comparative tests of antagonistic coevolution and traditional female choice. *Evolution* 58: 1947–1970. <https://doi.org/10.1111/j.0014-3820.2004.tb00482.x>
- Enderlein G (1909) 9. Des Insektenfauna der Insel Neu-Amsterdam. In: Enderlein G (Ed.) *Die Insekten des Antarktischen Gebietes*, 10. Druck und Verlag von Georg Reimer, Berlin, 486–492.
- Erichson WF (1834) Coleoptera. In: Erichson WF, Burmeister H (Eds) *Beiträge zur Zoologie, gesammelt auf einer Reise um die Erde, von Dr FJF Meyen*, 6 (Insekten). *Nova Acta Physico-Medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum* 16(suppl.): 219–308.
- Erichson WF (1842) Beitrag zur Insecten-Fauna von Vandiemensland. *Archiv für Naturgeschichte* 8: 83–287.
- Evenhuis NL (2012) François-Louis Comte de Castelnau (1802–1880) and the mysterious disappearance of his original insect collection. *Zootaxa* 3168: 53–63.
- Frauenfeld GR von (1868) *Zoologische Miscellen, XV. Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gesellschaft in Wien* 18(6 Mai): 885–899.
- Freitag R (1966) The female genitalia of four species of tiger beetles. *Canadian Entomologist* 98: 942–952. <https://doi.org/10.4039/Ent98942-9>
- Freitag R, Hartwick A, Singh A (2001) Flagellar microstructures of male tiger beetles (Coleoptera: Cicindelidae): implications for systematics and functional morphology. *Canadian Entomologist* 133: 633–641. <https://doi.org/10.4039/Ent133633-5>
- Freitag R, Olynyk JE, Barnes BL (1980) Mating behavior and genitalic counterparts in tiger beetles (Carabidae: Cicindelinae). *International Journal of Invertebrate Reproduction* 2: 131–135. <https://doi.org/10.1080/01651269.1980.10553348>
- Gemminger M, Harold B de (1868) *Cicindelidae – Carabidae*. *Catalogus Coleopterorum* 1: 424 pp.
- Goloboff PA (1999) NONA (NO NAME). Tucumán, Argentina, Published by the author. <http://www.softpedia.com/get/Science-CAD/NONA.shtml> [accessed 6-ix-2016]
- Goloboff PA, Catalano SA (2016) TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* 32: 221–238. <https://doi.org/10.1111/cla.12160>
- Habu A (1978) *Carabidae: Platynini (Insecta: Coleoptera)*. Keigaku Publishing Co., Tokyo, 447 pp.
- Huber BA (2003) Rapid evolution and species-specificity of arthropod genitalia: fact or artifact? *Organisms Diversity and Evolution* 3: 63–71. <https://doi.org/10.1078/1439-6092-00059>
- Huber BA, Dimitrov D (2014) Slow genital and genetic but rapid non-genital and ecological differentiation in a pair of spider species (Araneae, Pholcidae). *Zoologischer Anzeiger* 253: 394–403. <https://doi.org/10.1016/j.jcz.2014.04.001>
- International Commission on Zoological Nomenclature (1999) *International Code of Zoological Nomenclature*. The International Trust for Zoological Nomenclature, London, UK, 306 pp. <http://iczn.org/iczn/index.jsp>, [accessed 26 June 2018]
- Jeannel R (1938) Les Migadopides (Coleoptera Adephegata), une lignée subantarctique. *Revue Française d'Entomologie* 5: 1–55.

- Jeannel R (1940) Coléoptères. In Jeannel R (Ed.) Croisière de Bougainville aux Iles Australes Françaises. Mémoires de Muséum national d'Histoire naturelle, Paris 14 (nouv. ser.): 63–201.
- Jeannel R (1944) Un carabique nouveau de la Nouvelle-Calédonie. *Revue Française d'Entomologie* 10: 84–86.
- Jeannel R (1955) L'Édage, initiation aux recherches sur la systématique des Coléoptères. Publications du Muséum national d'Histoire naturelle no. 16: 1–155.
- Larochelle A, Larivière M-C (2007) Carabidae (Insecta: Coleoptera): synopsis of supraspecific taxa. *Fauna of New Zealand / Ko te Aitanga Pepeke o Aotearoa* 60: 1–188.
- Lea AM (1912) The late Rev. Canon Thomas Blackburn, B.A., and his entomological work. *Transactions and Proceedings of the Royal Society of South Australia* 36: iii–xl.
- Liebherr JK (1991) Phylogeny and revision of the *Anchomenus* clade: the genera *Tetraleucus*, *Anchomenus*, *Sericoda*, and *Elliptoleus* (Coleoptera: Carabidae: Platynini). *Bulletin of the American Museum of Natural History* 202: 1–167. <http://hdl.handle.net/2246/895>
- Liebherr JK (1994a) Recognition of the West Asian *Anchomenus kurnakovi* and *A. punctibasis* (Coleoptera: Carabidae: Platynini) and Miocene evolution of the Mediterranean and Paratethys Seas. *Journal of the New York Entomological Society* 102: 127–141.
- Liebherr JK (1994b) Identification of New World *Agonum*, review of the Mexican fauna, and description of *Incagonum*, new genus, from South America (Coleoptera: Carabidae: Platynini). *Journal of the New York Entomological Society* 102: 1–55.
- Liebherr JK (2005) Platynini (Coleoptera: Carabidae) of Vanuatu: Miocene diversification on the Melanesian Arc. *Invertebrate Systematics* 19: 263–295. <https://doi.org/10.1071/IS04032>
- Liebherr JK (2006[2005]) New species of *Mecyclothorax* (Coleoptera: Carabidae, Psydrini) from Polipoli, Maui define an area of endemism on Haleakala Volcano, Hawaii. *Journal of the New York Entomological Society* 113: 97–128. [https://doi.org/10.1664/0028-7199\(2005\)113\[0097:NSOMCC\]2.0.CO;2](https://doi.org/10.1664/0028-7199(2005)113[0097:NSOMCC]2.0.CO;2)
- Liebherr JK (2007[2006]) Taxonomic revision of the *Mecyclothorax* beetles (Coleoptera: Carabidae, Psydrini) of Molokai, Hawaii and recognition of areas of endemism on Kamakou Volcano. *Journal of the New York Entomological Society* 114: 179–281. [https://doi.org/10.1664/0028-7199\(2007\)114\[179:TROTMB\]2.0.CO;2](https://doi.org/10.1664/0028-7199(2007)114[179:TROTMB]2.0.CO;2)
- Liebherr JK (2008a) Taxonomic revision of *Mecyclothorax* Sharp (Coleoptera, Carabidae) of Hawaii Island: abundant genitalic variation in a nascent island radiation. *Deutsche Entomologische Zeitschrift* 55: 19–78. <https://doi.org/10.1002/mmnd.200800004>
- Liebherr JK (2008b) ZIPFILE *Mecyclothorax kavanaughii* sp. n. (Coleoptera: Carabidae) from the Finisterre Range, Papua New Guinea. *Tijdschrift voor Entomologie* 151: 147–154. <https://doi.org/10.1163/22119434-900000260>
- Liebherr JK (2008c) Taxonomic revision of Hawaiian *Bembidion* Latreille (Coleoptera: Carabidae, Bembidiini) with a discussion of their reductive and derivative evolutionary specializations. *Annals of Carnegie Museum* 77: 31–78. <https://doi.org/10.1163/22119434-900000260>
- Liebherr JK (2009a) Taxonomic revision of the *Mecyclothorax* beetles (Coleoptera: Carabidae) of Oahu: epithets as epitaphs for an endangered fauna? *Systematic Entomology* 34: 649–687. <https://doi.org/10.1111/j.1365-3113.2009.00477.x>
- Liebherr JK (2009b) Native and alien Carabidae (Coleoptera) share Lanai, an ecologically devastated island. *Coleopterists Bulletin* 63: 383–411. <https://doi.org/10.1649/1176.1>
- Liebherr JK (2011a) Cladistic assessment of subtribal affinities within the tribe Moriormorphini with description of *Rossjoycea glacialis*, gen. n. and sp. n. from the South Island, and revision of *Meonochilus* Liebherr and Marris from the North Island, New Zealand (Coleoptera, Carabidae). *ZooKeys* 147: 277–335. <https://doi.org/10.3897/zookeys.147.1898>
- Liebherr JK (2011b) The *Mecyclothorax* beetles (Coleoptera: Carabidae: Moriormorphini) of West Maui, Hawaii: taxonomy, biogeography, and conservation. *Deutsche Entomologische Zeitschrift* 58: 15–76. <https://doi.org/10.1002/mmnd.201100005>
- Liebherr JK (2012a) The first precinctive Carabidae from Moorea, Society Islands: new *Mecyclothorax* spp. (Coleoptera) from the summit of Mont Tohiea. *ZooKeys* 224: 37–80. <https://doi.org/10.3897/zookeys.224.3675>
- Liebherr JK (2012b) New *Mecyclothorax* spp. (Coleoptera, Carabidae, Moriormorphini) define Mont Mauru, eastern Tahiti Nui, as a distinct area of endemism. *ZooKeys* 227: 63–99. <https://doi.org/10.3897/zookeys.227.3797>
- Liebherr JK (2013) The *Mecyclothorax* beetles (Coleoptera, Carabidae, Moriormorphini) of Tahiti, Society Islands. *ZooKeys* 322: 1–170. <https://doi.org/10.3897/zookeys.322.5492>
- Liebherr JK (2015) The *Mecyclothorax* beetles (Coleoptera, Carabidae, Moriormorphini) of Haleakalā, Maui: Keystone of a hyperdiverse Hawaiian radiation. *ZooKeys* 544: 1–407. <https://doi.org/10.3897/zookeys.544.6074>
- Liebherr JK (2017) Review of *Mecyclothorax* Sharp (Coleoptera: Carabidae: Moriormorphini) from Papua New Guinea with descriptions of five new species. *Coleopterists Bulletin* 71: 679–703. <https://doi.org/10.1649/0010-065X-71.4.679>
- Liebherr JK (2018) Cladistic classification of *Mecyclothorax* Sharp (Coleoptera, Carabidae, Moriormorphini) and taxonomic revision of the New Caledonian subgenus *Phacothorax* Jeannel. *Deutsche Entomologische Zeitschrift* 65: 1–63. <https://doi.org/10.3897/dez.65.21000>
- Liebherr JK, Marris JWM (2009) Revision of the New Zealand species of *Mecyclothorax* Sharp (Coleoptera: Carabidae: Psydrinae, Mecyclothoracini) and the consequent removal of several species to *Meonochilus* gen. n. (Psydrinae: Meonini). *New Zealand Entomologist* 32: 5–22. <https://doi.org/10.1080/00779962.2009.9722172>
- Liebherr JK, Will KW (1998) Inferring phylogenetic relationships within Carabidae (Insecta, Coleoptera) from characters of the female reproductive tract. In: Ball GE, Casale A, Vigna Taglianti V (Eds) *Atti Museo Regionale di Scienze Naturali, Museo Regionale di Scienze Naturali, Torino*, 107–170.
- Liebherr JK, Will KW (2015) Antisymmetric male genitalia in Western Australian populations of *Mecyclothorax punctipennis* (Coleoptera: Carabidae: Moriormorphini). *Insect Systematics & Evolution* 46: 393–409. <https://doi.org/10.1163/1876312X-45042124>
- Liebherr JK, Zimmerman EC (2000) Hawaiian Carabidae (Coleoptera), Part 1: Introduction and Tribe Platynini. *Insects of Hawaii* 16. University of Hawaii Press, Honolulu, 494 pp.
- Lorenz W (1998) *Nomina Carabidarum, A Directory of the Scientific Names of Ground Beetles*. Published by the author, Tutzing, 937 pp.
- Louwerens, CJ (1949) Some notes on the Carabidae, collected by Mr. P. H. van Doesburg in the Malay Archipelago with descriptions of new species. *Tijdschrift voor Entomologie* 90: 45–53.
- Louwerens, CJ (1953) Carabidae (Col.) from the Sunda Islands. *Verhandlungen der Naturforschenden Gesellschaft in Basel* 64: 303–327.

- Machado A (1992) Monografía de los Carábidos de las Islas Canaria (Insecta, Coleoptera). Instituto de estudios Canarios, La Laguna, 743 pp.
- MacLeay W (1871) Notes on a collection of insects from Gayndah. Transactions of the Entomological Society of New South Wales 2(2): 79–205.
- Maddison DR, Toledano L, Sallenave S, Roig-Juñent S (2013) Phylogenetic relationships of the South American ground beetle subgenus *Chilioperphus* Jeannel (Coleoptera: Carabidae: Trechinae: Bembidiini: *Bembidion* Latreille). Zootaxa 3636: 547–560. <http://dx.doi.org/10.11646/zootaxa.3636.4.3>
- Malone CD, Lehmann R, Teixeira FK (2015) The cellular basis of hybrid dysgenesis and stellate regulation in *Drosophila*. Current Opinion in Genetics & Development 34: 88–94. <http://dx.doi.org/10.1016/j.gde.2015.09.003>
- Mandl K (1969) Zwei neue *Heptodonta*-Arten und eine neue Carabidae-Gattung (Col.) aus Nord-Borneo. Zeitschrift der Arbeitsgemeinschaft Österreichs Entomologen 21: 51–54.
- Mast AR, Givnish TJ (2002) Historical biogeography and the origin of stomatal distributions in *Banksia* and *Dryandra* (Proteaceae) based on their CpDNA phylogeny. American Journal of Botany 89: 1311–1323. <https://doi.org/10.3732/ajb.89.8.1311>
- Montrouzier P (1860) Essai sur la faune entomologique de la Nouvelle-Calédonie (Balade) et des îles des Pins, Art, Lifui, etc. Annales de la Société Entomologique de France (3rd ser.) 8: 229–308.
- Moore BP (1963) Studies on Australian Carabidae (Coleoptera)–3. the Psydrinae. Transactions of the Royal Entomological Society of London 115: 277–290. <https://doi.org/10.1111/j.1365-2311.1963.tb00810.x>
- Moore BP (1984) Taxonomic notes on some Australasian *Mecyclothorax* Sharp (Coleoptera: Carabidae: Psydrinae) and descriptions of new species. Journal of the Australian Entomological Society 23: 161–166. <https://doi.org/10.1111/j.1440-6055.1984.tb01935.x>
- Moore BP (1985) The Carabidae of Norfolk Island. In: Ball GE (Ed.) Taxonomy, Phylogeny and Zoogeography of Beetles and Ants. Dr W Junk Publishers, Dordrecht, 237–256.
- Moore, BP (1992) 7. The Carabidae of Lord Howe Island. In Noonan GR, Ball GE, Stork NE (Eds) The Biogeography of Ground Beetles of Mountains and Islands. Intercept Ltd., Andover, Hampshire, 159–173.
- Moore BP, Weir TA, Pyke JE (1987) Coleoptera: Adephaga: Rhysodidae and Carabidae. In: Walton DW (Ed.) Zoological Catalogue of Australia 4, Australian Government Printing Service, Canberra, 17–320.
- Moret P (2005) Los coleópteros Carabidae del páramo en los Andes del Ecuador. Museo de Zoología, Centro de Biodiversidad y Ambiente, Escuela de Biología, Pontificado Universidad Católica del Ecuador, Monografía 2: 1–306.
- Nagata N, Kubota K, Takami Y, Sota T (2009) Historical divergence of mechanical isolation agents in the ground beetle *Carabus arrowianus* as revealed by phylogeographical analyses. Molecular Ecology 18: 1408–1421. <https://doi.org/10.1111/j.1365-294X.2009.04117.x>
- Nixon KC (1999) The parsimony ratchet, a new method for rapid parsimony analysis. Cladistics 15: 407–414. <https://doi.org/10.1111/j.1096-0031.1999.tb00277.x>
- Nixon KC (2002) WinClada. Ithaca, NY, Published by the author. <http://www.softpedia.com/get/Science-CAD/WinClada.shtml> [accessed 16-ix-2016]
- Okuzaki Y, Sota T (2014) How the length of genital parts affects copulation performance in a carabid beetle: implications for correlated evolution between the sexes. Journal of Evolutionary Biology 27: 565–574. <https://doi.org/10.1111/jeb.12323>
- Perrault GG (1984) La faune des Carabidae de Tahiti VI. révision du genre *Mecyclothorax* (Sharp) (Psydrini). 1. le groupe de *M. muri-auri* Perrault (Coleoptera). Nouvelle Revue d'Entomologie (nouv. ser.) 1: 19–31.
- Porch N, Jordan DJ, Price DM, Barnes RW, Macphail MK (2009) Last interglacial climates of south-eastern Australia: plant and beetle-based reconstructions from Yarra Creek, King Island, Tasmania. Quaternary Science Reviews 28: 3197–3210. <https://doi.org/10.1016/j.quascirev.2009.09.023>
- Poulton EB (1939) In Memoriam, James John Walker, MA, RN, FLS, FRES. The Entomologist's Monthly Magazine (3rd ser.) 75: 64–70.
- Rix MG, Edwards DL, Byrne M, Harvey MS, Joseph L, Roberts JD (2015) Biogeography and speciation of terrestrial fauna in the south-western Australian biodiversity hotspot. Biological Reviews 90: 762–793. <https://doi.org/10.1111/brv.12132>
- Rodríguez S, RL (1999) Spermatophore transfer and ejection in the beetle *Pseudoxychila tarsalis* (Coleoptera: Cicindelidae). Journal of the Kansas Entomological Society 72: 1–9.
- Santiago-Blay JA, Ratcliffe BC, Krell F-T, Anderson R (2008) Allotypes should be from the type series: a position paper for reinstating Recommendation 72A from the third edition of the Code that defines the term 'allotype'. Bulletin of Zoological Nomenclature 65: 260–264.
- Schaum HR (1863) Descriptions of four new genera of Carabidae. Journal of Entomology 2: 74–78.
- Schincariol LA, Freitag R (1986) Copulatory locus, structure and function of the flagellum of *Cicindela tranquebarica* Herbst (Coleoptera: Carabidae). International Journal of Invertebrate Reproduction and Development 9: 333–338. <https://doi.org/10.1080/01688170.1986.10510209>
- Schmidt J (2014) Three new *Anchomenus* Bonelli, 1810 from the west Palaearctic (Coleoptera: Carabidae: Platynini). Koleopterologische Rundschau 84: 13–29. http://www.zobodat.at/pdf/KOR_84_2014_0013-0029.pdf
- Sharp D (1903) Coleoptera II. Caraboidea. In: Sharp D (Ed.) Fauna Hawaiiensis 3, The University Press, Cambridge, 175–292.
- Shelford VE (1915) Elytral tracheation of the tiger beetles (Cicindelidae). Transactions of the American Microscopical Society 34: 241–253. <https://doi.org/10.2307/3221471>
- Simmons L (2014) Sexual selection and genital evolution. Austral Entomology 53: 1–17. <https://doi.org/10.1111/aen.12053>
- Sloane TG (1895) Studies in Australian Entomology. no. VII.–New genera and species of Carabidae (including some notes on previously described species, and synoptic lists of genera and species). Proceedings of the Linnean Society of New South Wales (2nd ser.) 9: 393–455.
- Sloane TG (1898) On Carabidae from West Australia, sent by Mr A M Lea (with descriptions of new genera and species, synoptic tables, &c.). Proceedings of the Linnean Society of New South Wales 23: 444–520.
- Sloane TG (1900) Studies in Australian Entomology. no. IX. New species of Carabidae (with notes on some previously described species, and synoptic lists of species). Proceedings of the Linnean Society of New South Wales 24: 553–584. <https://doi.org/10.5962/bhl.part.7682>
- Sloane TG (1903) Studies in Australian Entomology. no. XII. New Carabidae (Panageini, Bembidiini, Pogonini, Platysmatini, Platynini, Lebiini, with revisional lists of genera and species, some notes on

- synonymy, &c.). Proceedings of the Linnean Society of New South Wales 28: 566–642.
- Sloane TG (1915) Studies in Australian Entomology. no. XVII. New genera and species of Carabidae (Pamborini, Migadopini, Broscini, Cuneipectini, Nomiini, Pterostichini, Platynini, Oodini, Harpalini, and Lebiini). Proceedings of the Linnean Society of New South Wales 40: 438–473. <https://doi.org/10.5962/bhl.part.18880>
- Sloane TG (1920) The Carabidae of Tasmania. Proceedings of the Linnean Society of New South Wales 45: 113–178. <https://doi.org/10.5962/bhl.part.19535>
- Snedecor GW, Cochran WG (1980) Statistical Methods (7th edn). The Iowa State University Press, Ames, 507 pp.
- Sniderman, JMK, Porch N, Kershaw AP (2009) Quantitative reconstruction of Early Pleistocene climate in southeastern Australia and implications for atmospheric circulation. Quaternary Science Reviews 28: 3185–3196. <https://doi.org/10.016/j.quascirev.2009.08.006>
- Southwood TRE (1977) Habitat, the templet for ecological strategies? Journal of Animal Ecology 46: 337–365. <https://doi.org/10.2307/3817>
- Straneo SL (1941) Sui tipi dei Pterostichini (Coleopt. Carabid.) australiani dell collezione Castelnau nel Museo Civico di Genova, nota 3. Annali del Museo Civico di Storia Naturale Giacomo Doria 61: 83–94.
- Walker JJ (1921) Presidential address. Proceedings of the Linnean Society of New South Wales 46: 1–13. <https://doi.org/10.5962/bhl.part.14001>
- Wallace AR (1876) The geographical distribution of animals with a study of the relations of living and extinct faunas as elucidating the past changes of the Earth's surface. Harper & Brothers, Publishers, New York: vol. 1 – 503 pp.; vol. 2 – 607 pp.
- Waterhouse CO (1897) XVII. Description of a new coleopterous insect of the family Paussidae. Transactions of the Entomological Society of London 1897: 391–392.
- Waterhouse CO (1898) Description of a new species of *Calosoma* (Coleoptera, Geodephaga). Journal of Natural History 1: 98–99. <https://doi.org/10.1080/00222939808677927>
- White A (1843) Insects of New Zealand. In Richardson J, Gray JU (Eds) The Zoology on the Voyage of HMS Erebus and Terror, under the command of Captain Sir James Clark Ross, RN, FRS, during the years 1839 to 1843. Green and Longman, London: 2(4): 1–24.
- Whitehead DR (1974) An annotated key to described species of the genus *Glyptolenus* (Carabidae: Pterostichini: Agoni). Coleopterists Bulletin 28: 123–132.
- Wollaston TV (1864) Catalogue of the coleopterous insects of the Canaries in the collection of the British Museum. Taylor and Francis, London, 526 pp. [Appendix 140 pp.]

Supplementary material 1

Data file for cladistic analysis of Australian *Mecyclothorax* Sharp

Author: James K. Liebherr

Data type: NONA format data file

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Link: <https://doi.org/10.3897/dez.65.27424.suppl1>

Supplementary material 2

Supporting data for Mann-Whitney rank-sum test of differences in parameral setation for *M. eyrensis* and *M. peryphoides* males

Author: James K. Liebherr

Data type: Word format table.

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Link: <https://doi.org/10.3897/dez.65.27424.suppl2>

Revision of *Zosteragathis* Sharkey of Thailand (Hymenoptera, Braconidae, Agathidinae, Agathidini)

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<http://zoobank.org/5A043F9D-93FA-4DD7-873A-1A0101C849FE>

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Abstract

Received 10 May 2017
Accepted 31 July 2018
Published 14 August 2018

Academic editor:
Ralph Peters

Key Words

Insecta
identification key
taxonomy
systematics

Based on cladistic analyses recently conducted by Sharkey and Chapman, the genus *Zosteragathis* Sharkey is revised. Twenty-two species are reported from Thailand, three previously described species, *Z. samensis*, *Z. contrasta* and *Z. nuichuaensis*, and 19 new species, i.e., *Z. chaiyaphumensis*, *Z. eukos*, *Z. hinensis*, *Z. hongensis*, *Z. inthanonensis*, *Z. krachanensis*, *Z. lampangensis*, *Z. lampooensis*, *Z. luangensis*, *Z. ngamensis*, *Z. perknos*, *Z. petchaburiensis*, *Z. phahompokensis*, *Z. phuphanensis*, *Z. sakaeratensis*, *Z. sakonensis*, *Z. samensis*, *Z. surinensis*, *Z. taemensis*, *Z. tonensis*. Members of *Zosteragathis* are known from the Australian, Ethiopian, Oceania, Oriental, and eastern Palaearctic regions.

Introduction

Agathidinae is a moderately large subfamily the members of which are koinobiont endoparasitoids of lepidopterous larvae. For more general information on Agathidinae see Sharkey et al. (2006). As of 2005, roughly 1,000 species were described (Yu et al. 2005). The senior author (MJS), based on the number of new species in recent revisions (see below), believes that there are a magnitude more undescribed species. *Zosteragathis* is restricted to the Old World. It is very diverse with species richness in the hundreds, but most of these are undescribed. This paper is part of a series that investigates members of the massively paraphyletic genus *Bassus* s.l. (Sharkey and Clutts 2011, Sharkey et al. 2011a and b, Sharkey and Stelb 2012 and 2013, Sharkey and Chapman 2017a, b). The generic concept *Bassus* is now confined to a small clade restricted to The Palearctic and Oriental realms, *Zosteragathis* Sharkey (Sharkey and Chapman 2017a), includes 25 previously described species (24 currently recognized

as valid), all of which were previously included in the polyphyletic concepts of *Agathis* s.l., *Bassus* s.l. and *Therophilus* s.l. i.e.:

- Z. annuliferus* (Achterberg & Long, 2010), **comb. n.**, from *Therophilus*
- Z. annulus* (Chou & Sharkey, 1989), from *Bassus*
- Z. asper* (Chou & Sharkey, 1989), from *Bassus*
- Z. conformis* (Bhat & Gupta, 1977), from *Agathis*
- Z. contrasta* (Achterberg & Long, 2010), from *Therophilus* (as *contrastus*)
- Z. coryphe* (Nixon, 1950), from *Agathis*
- Z. depressa* (Chou & Sharkey, 1989), from *Bassus* (as *depressus*)
- Z. dravida* (Bhat & Gupta, 1977), from *Agathis*
- Z. elongator* (Achterberg & Long, 2010), from *Therophilus*
- Z. festiva* (Muesebeck, 1953), from *Agathis*
- Z. festivoidea* (Sharkey, 1996), from *Bassus*
- Z. fujianicus* (Chen & Yang, 2006), from *Bassus*
- Z. gracilis* (Bhat & Gupta, 1977), from *Agathis*

Z. lienhuachihensis (Chou & Sharkey, 1989), from *Bassus*
Z. lini (Chou & Sharkey, 1989), from *Bassus*
Z. masoni (Bhat & Gupta, 1977), from *Agathis*
Z. nigrolineatus (Achterberg & Long, 2010), from
Therophilus
Z. nuichuaensis (Achterberg & Long, 2010), from
Therophilus
Z. oranae (Watanabe, 1970), (syn. of *Agathis festiva*, by
Sharkey 1996)
Z. parasper (Achterberg & Long, 2010), from *Therophilus*
Z. punctiscutum (Achterberg & Long, 2010), from
Therophilus
Z. robusta (Achterberg & Long, 2010), from *Therophilus*
(as *robustus*)
Z. scutellatus (Achterberg & Long, 2010), from *Therophilus*
Z. sungkangensis (Chou & Sharkey, 1989), from *Bassus*
Z. tanycoleosus (Chen & Yang, 2006), from *Bassus*

Methods

Morphological terms: The length of the first metasomal median tergite is measured from the apex of the tendon emanating from the propodeum to the posterior border of the tergite. Metasomal median tergites are abbreviated as follows, T1 = metasomal median tergite 1, T2 = metasomal median tergite 2. T2–3 = metasomal median syntergite 2 + 3. Other terms are from Sharkey and Wharton (1997). Morphological terms used in this revision can be found in the Hymenoptera Anatomy Ontology (HAO; Yoder et al. 2010). To find definitions for any structure search for the term at <http://glossary.hymao.org>.

Museum acronyms

HIC Hymenoptera Institute Collection, University of Kentucky, Department of Entomology, Lexington, Kentucky, USA.
QSBG Queen Sirikit Botanic Gardens, Chiang Mai, Thailand.

Species description format: Descriptions are of the holotype; variation is given in parentheses. Color is not extensively described because the images serve this purpose; however color characters that are variable or of diagnostic significance are detailed. All species are treated with a diagnosis and distributional data. They are illustrated with color photos using a JVC digital camera mounted on a Leica MZ16 microscope and Automontag-eR stacking software.

Species delimitation: We used evidence from molecular data (COI and 28S) and morphology to arrive at species concepts. Details are given in Sharkey and Stoelb (2013). Table 1 gives details on the COI distances within species of *Zosteragathis* as well as distances to the nearest species.

Specimen collection: As part of the inventory of Thai insects, three Malaise traps at each of 30 different localities throughout Thailand were operated from 2007–2010, com-

Table 1. COI divergence data COI data for each species. If a species has more than one terminal, both intra- and interspecific uncorrected p-distances are reported. Interspecific p-distances are to the nearest OTU in the COI tree (not shown). Values are averaged if two or more comparisons are made.

Species	Intraspecific variation	Interspecific variation	Nearest species
<i>Z. contrasta</i>	0.318%	3.899%	<i>Z. taemensis</i>
<i>Z. eukos</i>	–	5.234%	<i>Z. ngamensis</i>
<i>Z. hongensis</i>	–	1.414%	<i>Z. sakonensis</i>
<i>Z. inthanonensis</i>	–	5.801%	<i>Z. ngamensis</i>
<i>Z. krachanensis</i>	–	4.683%	<i>Z. nuichuaensis</i>
<i>Z. lampangensis</i>	0.491%	5.2365%	<i>Z. inthanonensis</i>
<i>Z. lampooensis</i>	0%	1.514%	<i>Z. taemensis</i>
<i>Z. lunagensis</i>	–	0%	<i>Zosteragathis</i> sp. n. 2
<i>Z. ngamensis</i>	–	5.801%	<i>Z. inthanonensis</i>
<i>Z. nuichuaensis</i>	0%	3.038%	<i>Zosteragathis</i> sp. n. 2
<i>Z. perkno</i>	–	5.221%	<i>Z. ngamensis</i>
<i>Z. petchaburiensis</i>	–	6.428%	<i>Z. contrastus</i>
<i>Z. phahompokensis</i>	–	1.972%	<i>Z. tonensis</i>
<i>Z. sakonensis</i>	–	1.414%	<i>Z. hongensis</i>
<i>Z. samensis</i>	0.920%	4.074%	<i>Z. surinensis</i>
<i>Zosteragathis</i> sp. n. 2	–	0%	<i>Z. lunagensis</i>
<i>Z. surinensis</i>	–	4.074%	<i>Z. samensis</i>
<i>Z. taemensis</i>	–	1.514%	<i>Z. lampooensis</i>
<i>Z. tonensis</i>	–	1.972%	<i>Z. phahompokensis</i>

prising approximately 90 trap-years. The specimens dealt with here are primarily from these traps. Two numbers, beginning with the letters “H” and “T” are listed for each specimen collected by our collaborators in Thailand. The H-number is the specimen number. Specimen information is stored in the Symbiota database (Gries et al. 2014) under the Hymenoptera Institute Collection (HIC). (Symbiota Collections of Arthropods Network; <http://symbiota4.acis.ufl.edu/scan/portal/>). To search for a specimen in the database, do the following: Under the Search tab (upper left of the screen), select Search Collections. Deselect all collections, and scroll down the Southeast section, put a check in the box next to Hymenoptera Institute Collection, scroll back up and hit the Search > button (right side of screen). H-numbered specimens are stored with a 4-letter prefix (HICH) followed by a 6-digit number. Therefore, H660, as it appears in this publication, is stored as HICH000660. To search for this specimen, scroll down to the Specimen Criteria section, type this number in the box next to Catalog Number and hit the search button. This displays a page with a summary of the specimen information. Clicking on Full Record Details opens a new window with the full specimen record, including all available images. The T-number is the number associated with a single Malaise trap for a single trapping period (usually one week). A complete list of these numbers and associated collection events is available from the authors upon request.

Links to species maps in this paper were generated from the Symbiota database. These are not static maps and as georeferenced specimens are added to the database, the maps will update in real time such that a reader

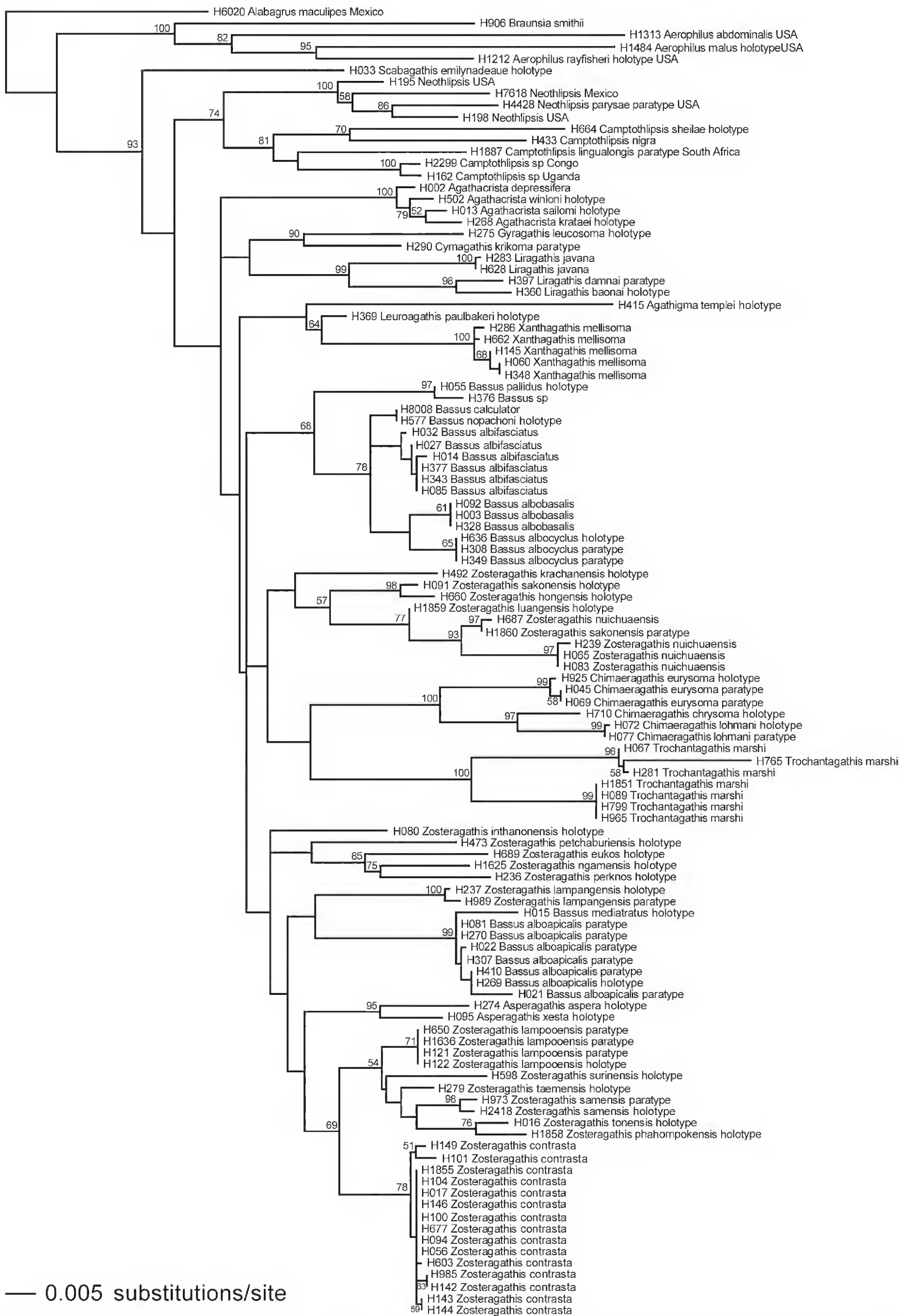


Figure 1. Tree of highest log-likelihood from 20 ML search reps of a combined COI+28S data set with bootstrap values $\geq 50\%$ (500 search replicates) plotted at the nodes. Tree modified from Sharkey and Chapman (2017a).

following a map link will see a map of all of the specimens of the taxon at hand in the database, including those that may have been added after this paper is published. Clicking on the dots on these maps links to the specimen record in the database.

Phylogenetic methods: The data set and analyses presented herein is from Sharkey and Chapman (2017a). In that paper, the *Zosteragathis* terminals were largely unnamed, leaving species descriptions for this paper. In short, we conducted maximum likelihood (ML) phylogenetic analyses on a concatenated COI + 28S dataset (1,313 total characters) using Garli (v. 2.01; Zwickl 2006). The 28S multiple alignment was assembled using the default settings on the MAFFT server (<http://mafft.cbrc.jp/alignment/server/>; v. 7; Katoh et al. 2006), and employing the Q-INS-i strategy which takes secondary RNA structure into account. All 28S bases were included in subsequent phylogenetic analyses. The data were partitioned by gene region and codon position (COI: 3 partitions; 28S: unpartitioned, total of 4 partitions). The most complex model available (GTR+I+G; Rodriguez et al. 1990) was applied to each partition as per recommendations of Huelsenbeck and Rannala (2004). A 20-replicate ML search for the tree of highest log-likelihood and a 500-replicate ML bootstrap analysis (Felsenstein 1985) were conducted using the default settings. Outgroup genera (*Alabagrus*, *Braunsia*, *Aerophilus*, *Camptothlipsis* and *Neothlipsis*) were selected based on two criteria: (1) they comprise genera that are members of three clades that are successively sister to the ingroup clade in the phylogeny in Sharkey and Chapman (2017b), and (2) full length sequences of COI and 28S were available for most of these OTUs. The data set analyzed herein is available from the authors upon request. All of the specimens for which we have DNA sequences are listed in Appendix I, including their accession numbers.

Phylogenetic considerations: Sharkey and Chapman (2017b) revised the agathidine tribes and showed that *Zosteragathis* falls within the Agathidini. They could not demonstrate the monophyly of *Zosteragathis*, but confounded with the choice of erecting four genera for morphologically uniform clades, or one genus for the lot, they opted for the latter. The cladogram in Figure 1 shows that none of basal clades that separate the four *Zosteragathis* clades have support, therefore it is entirely possible that the genus is monophyletic.

Key to Thai species of *Zosteragathis*

- 1 A. Mesoscutum pale, yellow to orange 2
 – B. Mesoscutum melanic, black 4



Results and discussion

Below is a discussion of the taxonomy of *Zosteragathis*, a key to the Thai species of this genus, and descriptions of each species.

Taxonomy

Zosteragathis Sharkey, 2017

Type species. *Zosteragathis samensis* Sharkey, 2017

Diagnosis. Most species can be recognized as members of this genus by the combination of finely microsculptured striae on T2 that end abruptly just anterior to the posterior margin of the tergite; this in combination with a pale colored band in the anterior half of T2, or T2 entirely black. Some species have reduced striae on T2 and are recognized by the lack of apomorphic structures that distinguish other closely related genera, e.g., claws not simple; interantennal space without a sharply declivous keel; T1 without prominent lateral carinae or medial carina; fore tarsus without spines or pegs.

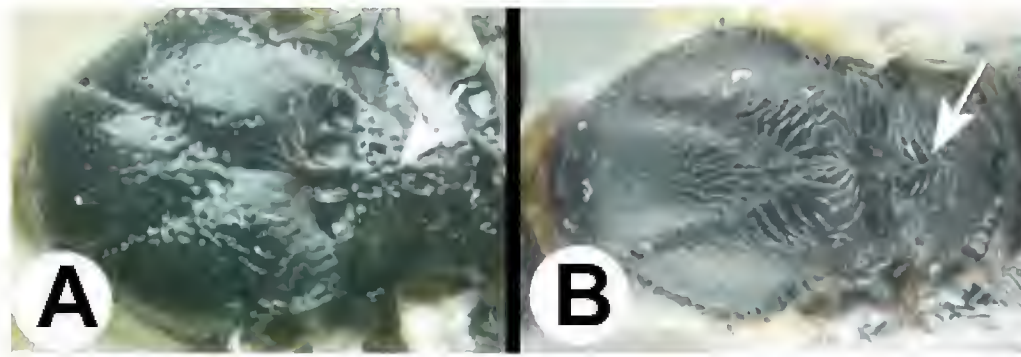
Description. See Sharkey and Chapman 2017a.

Biology. Hosts are unknown for all Thai species however there are records for three extra-Thailand species. These appear to suggest that the host range is wide. The records are: *Zosteragathis coryphe* was reared from *Phycodes radiata* (Sesioidea: Brachodidae) (Nixon 1950). *Zosteragathis festiva* (Muesebeck) was reared from *Grapholitha molesta*, oriental fruit moth, (Tortricoidea: Tortricidae) and many other Lepidoptera from a wide range of families, i.e., Blastobasidae, Gelechiidae, Cossidae, Carposinidae, Noctuidae, and Pyralidae. See Yu (2012) for a complete list. *Zosteragathis robusta* (Achterberg and Long) from Vietnam was reared from “*Omiodes indicata* (Lepidoptera: Pyralidae: Pyraustinae) on soybean (*Glycine max* (Linnaeus)), according to the label data”, (van Achterberg and Long 2010).

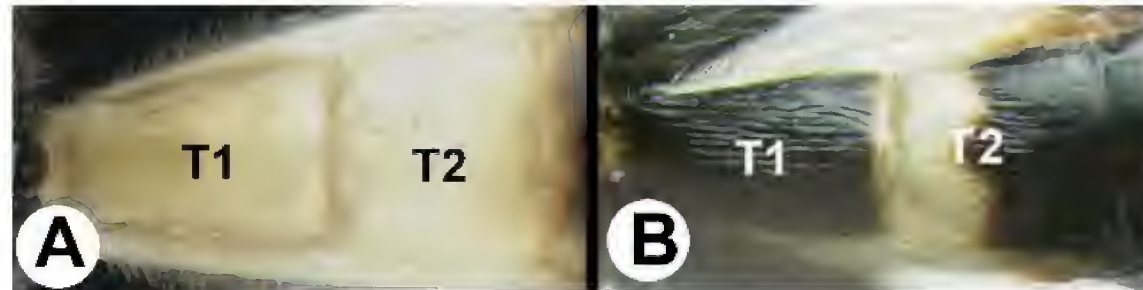
Distribution. Australian, Ethiopian, Oceania, Oriental, and eastern Palearctic regions.

Etymology. From the Greek *zoster*, meaning “belt or girdle” and *agathis* the type genus of the subfamily. *Zoster* is a reference to the diagnostic pale colored transverse band that is usually present on T2. The gender is feminine.

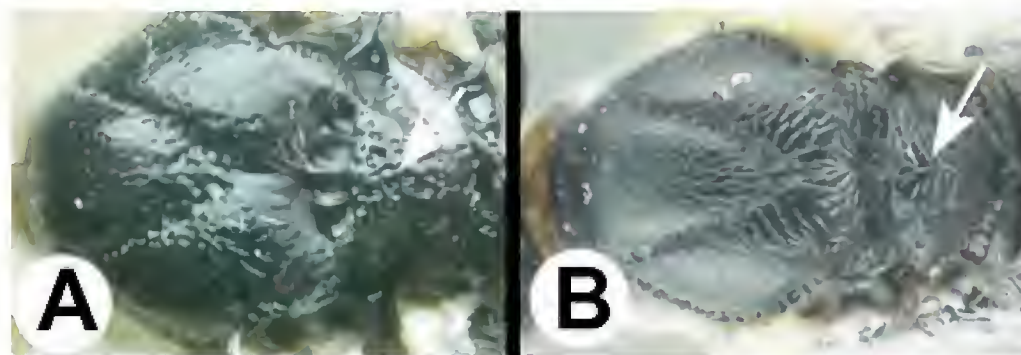
- 2 **A.** Scutellum rugose; T2 distinctly longer than wide; head mostly or entirely yellow to orange *Z. ngamensis*
- **B.** Scutellum smooth with punctures; T2 as wide as long or wider; head mostly or entirely black; pale color, if present restricted to the gena 3



- 3 **A.** T1 mostly or entirely pale (white to yellow) *Z. hongensis*
- **B.** T1 mostly or entirely melanic (brown to black) *Z. contrasta*



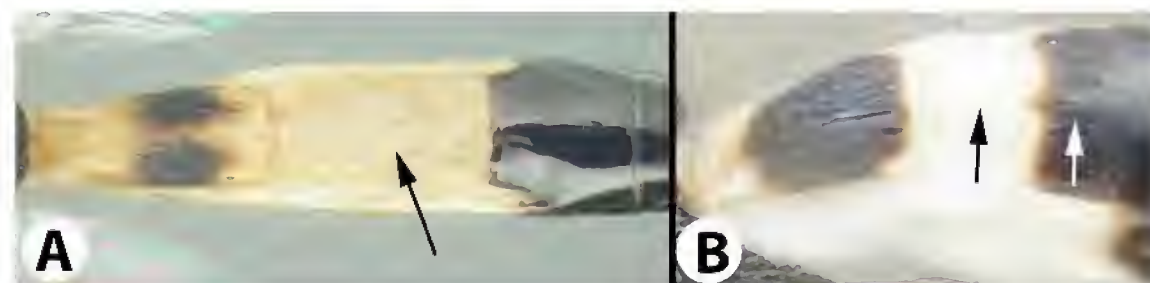
- 4 **A.** Scutellum rugose 5
- **B.** Scutellum smooth with punctures 7



- 5 **A.** T2 as wide as long or wider *Z. nuichuaensis*
- **B.** T2 distinctly longer than wide 6



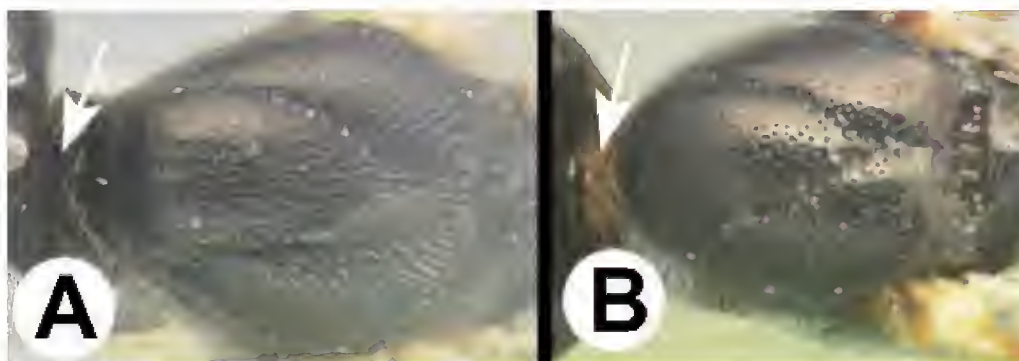
- 6 **A.** T2 entirely or almost entirely (80%) pale (white to yellow) *Z. krachanensis*
- **B.** T2 mostly pale (white to yellow) in anterior half and mostly melanic (brown to black) in posterior half .. *Z. luangensis*



- 7 **A.** T2 as wide as long or wider 18
- **B.** T2 distinctly longer than wide 8



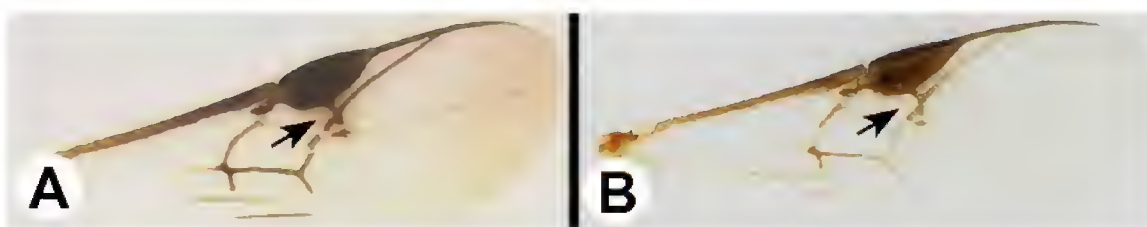
- 8 **A.** Pronotum melanic dorsomedially, concolorous with lateral surfaces of pronotum 9
- **B.** Pronotum pale dorsomedially (yellow to orange), contrasting with melanic lateral surfaces of pronotum..... 11



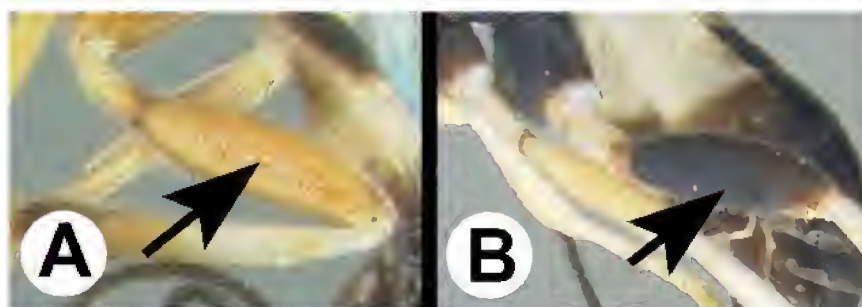
- 9 **A.** T2 entirely or almost entirely (>70%) pale (white to yellow)*Z. lampangensis*
- **B.** T2 entirely or almost entirely (>70%) melanic (dark brown to black)..... 10
- **C.** T2 mostly pale (white to yellow) in anterior half and mostly melanic (brown to black) in posterior half*Z. inthanonensis*



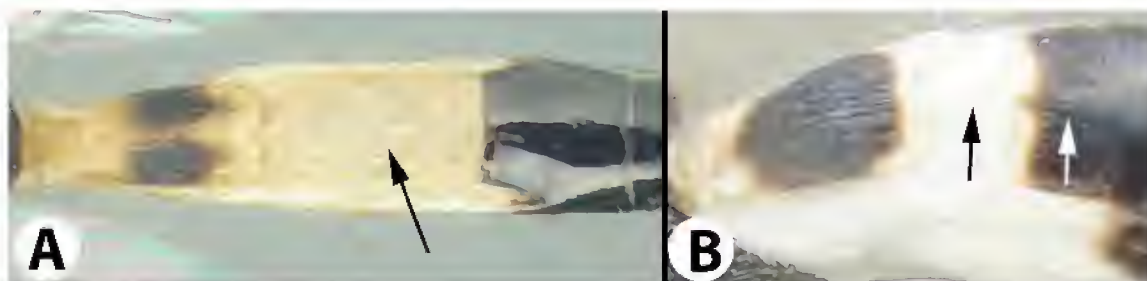
- 10 **A.** Fore wing with a small infusate area posterior to stigma; apex of T1 yellow*Z. inthanonensis*
- **B.** Fore wing without a small infusate area posterior to stigma; apex of T1 melanic (brown to black).....*Z. perknos*



- 11 **A.** Hind femur mostly or entirely pale, yellow to orange 12
- **B.** Hind femur mostly or entirely melanic, brown to black..... 13



- 12 **A.** T2 entirely or almost entirely (80%) pale (white to yellow)*Z. lampangensis*
- **B.** T2 mostly pale (white to yellow) in anterior half and mostly melanic (brown to black) in posterior half ... *Z. surinensis*



- 13 **A.** Striae of T2 curving towards the midline 14
- **B.** Striae of T2 relatively straight 15



- 14 **A.** T2 entirely or almost entirely (>70%) pale (white to yellow)*Z. lampangensis*
- **B.** T2 entirely or almost entirely (>70%) melanic (dark brown to black); or **C.** T2 mostly pale (white to yellow) in anterior half and mostly melanic (brown to black) in posterior half*Z. phuphanensis*



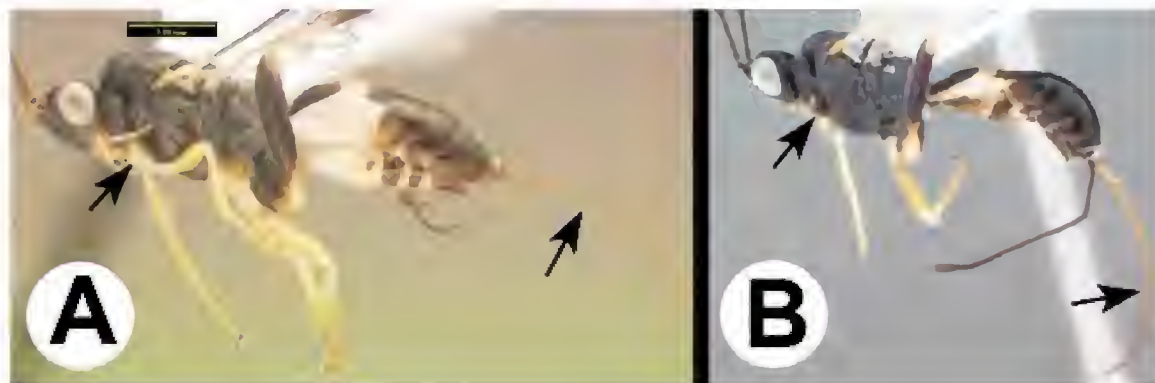
- 15 **A.** T2 entirely or almost entirely (>70%) pale (white to yellow)*Z. lampangensis*
 – **B.** T2 entirely or almost entirely (>70%) melanic (dark brown to black).....*Z. lampoensis*
 – **C.** T2 mostly pale (white to yellow) in anterior half and mostly melanic (brown to black) in posterior half 16



- 16 **A.** Exposed portion of ovipositor longer than body length.....*Z. tonensis*
 – **B.** Exposed portion of ovipositor equal to or shorter than body length..... 17



- 17 **A.** Fore coxa mostly or entirely yellow.....*Z. lampoensis*
 – **B.** Fore coxa mostly or entirely melanic*Z. hinensis*



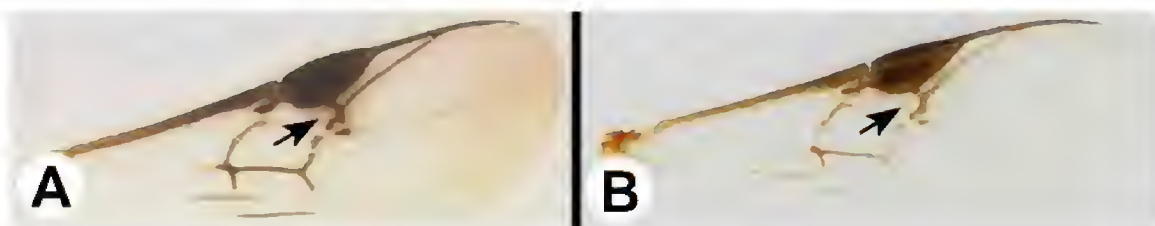
- 18 **A.** T2 entirely or almost entirely (>70%) pale (white to yellow)*Z. sakonensis*
 – **B.** T2 entirely or almost entirely (>70%) melanic (dark brown to black)..... 19
 – **C.** T2 mostly pale (white to yellow) in anterior half and mostly melanic (brown to black) in posterior half 22



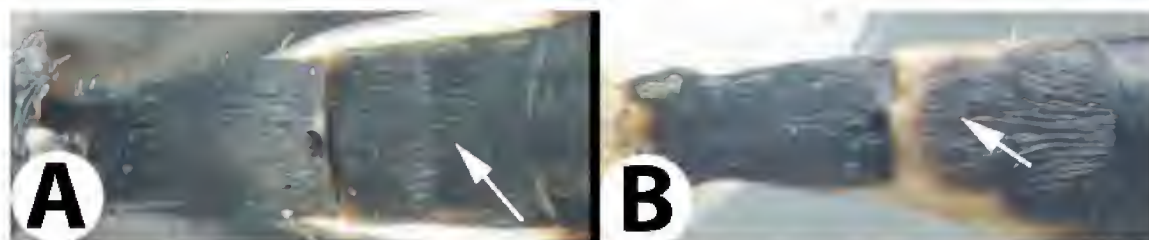
- 19 **A.** Hind femur mostly or entirely pale, yellow to orange *Z. sakaeratensis*
 – **B.** Hind femur mostly or entirely melanic, brown to black..... 20



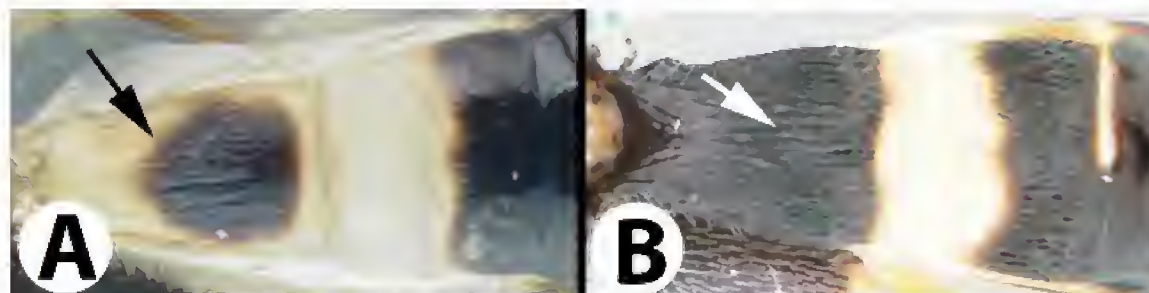
- 20 **A.** Fore wing with a small infuscate area posterior to stigma.....*Z. chaiyaphumensis*
 – **B.** Fore wing without a small infuscate area posterior to stigma..... 21



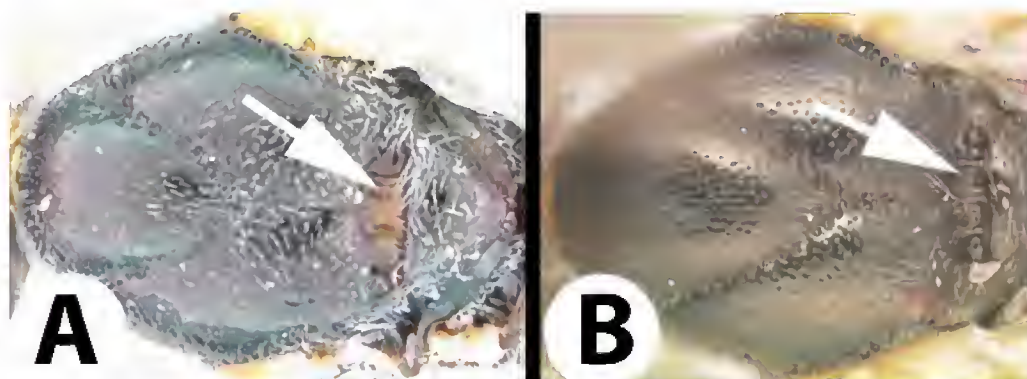
- 21 **A.** T2 almost entirely melanic *Z. eukos*
 – **B.** T2 mostly melanic, but pale, yellow to orange, anteriorly and anterolaterally *Z. petchaburiensis*



- 22 **A.** T1 extensively pale, white to yellow, basally *Z. phahompokensis*
 – **B.** T1 mostly or entirely melanic basally 23



- 23 **A.** Scutellar groove pale, yellowish brown, significantly lighter than remainder of mesonotum *Z. taemensis*
 – **B.** Scutellar groove melanic, concolorous with remainder of mesonotum *Z. samensis*



Species descriptions

Zosteragathis chaiyaphumensis Sharkey, sp. n.

<http://zoobank.org/E98CD31C-4FC2-469C-995B-CB9AFBC9B0C5>

Diagnosis. Fore wing with a small infuscate area posterior to stigma. T2 entirely or almost entirely (80%) melanic. T2 as wide as long or wider.

Description. Body length 5.6 mm. Ovipositor length 3.7 mm. Ovipositor 0.7× body length. Number of flagellomeres 32. Notauli sculpture not significantly wider posteriorly. Scutellum smooth with punctures. Mid tibia with 4 apical and 3 preapical spines. Hind tibia with 10 spines/pegs. Second submarginal cell diameter large, about same size as pedicel length. Wing hyaline with an infuscate patch posterior to stigma. T2 0.9× longer than wide. T2 entirely striate, striae converging anteromedially.

Color. head black except gena yellow; mesosoma black; fore and mid coxa black; T1 entirely black; anterior margin of T2 yellow.

Etymology. Named after the type locality Chaiyaphum Provence.

Material examined. Holotype: Female: *Thailand*, Chaiyaphum: Pa Hin Ngam NP, Mix deciduous forest, 15.578°N, 101.435°E, 419 m elev., Malaise trap, 19–25.v.2007 (H2442, T2601), Katae Sa-nog & Buakaw Adnafai. **Paratype:** Female: *Thailand*, Chiang Mai, Doi Chiangdao NP, Pha Tang substation, 19.416°N, 98.915°E,

526 m elev., Malaise trap, 3–9.v.2008 (H2434, T5802), S. Jugsu & A. Watwanich.

For a map of examined material, see: <https://bit.ly/2DZycUy>

Zosteragathis contrasta (Achterberg & Long)

Therophilus contrastus Achterberg & Long, 2010

Diagnosis. Head black; mesoscutum orange.

Description. Body length 5.2 mm. Ovipositor length 3.5 mm. Ovipositor 0.7× body length. Number of flagellomeres 34 (32–39). Sculpture of notauli slightly increasing in width posteriorly but not extending onto lateral lobes of mesoscutum. Scutellum smooth with punctures. Mid tibia with 2 apical and 3 preapical spines. Hind tibia with 7 spines/pegs. Second submarginal cell diameter small, not much larger than width of pedicel. Wing hyaline, without distinct infuscate areas. T2 1× longer than wide. T2 mostly smooth with hints of longitudinal striae especially medially. **Color:** head black except lower gena yellow; pro and mesothorax orange except ventral mesopleuron melanic; metathorax and propodeum melanic; fore and mid coxae mostly yellow; apex of T1 and lateral and anterior margins of T2 yellow.

Material examined. Holotype: not examined. **Paratypes:** not examined. **Non-type specimens:** All female: *Thailand:* Hua Khakhaer 6, iii.1986 (H5908, H5998,

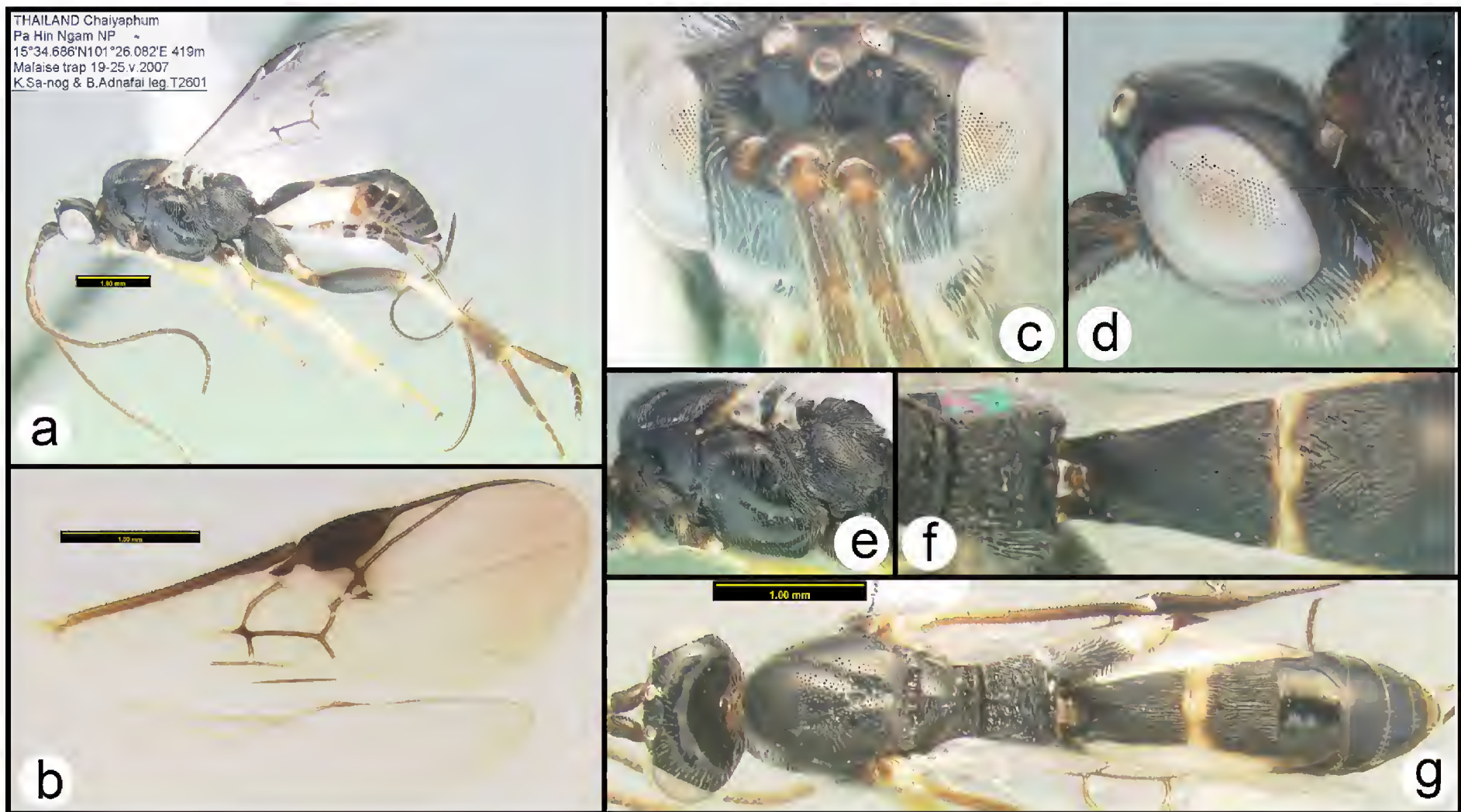


Figure 2. *Z. chaiyaphumensis*: a) lateral habitus. b) wings. c) dorsal head. d) lateral head. e) lateral mesosoma. f) dorsal propodeum and T1-2. g) dorsal habitus.

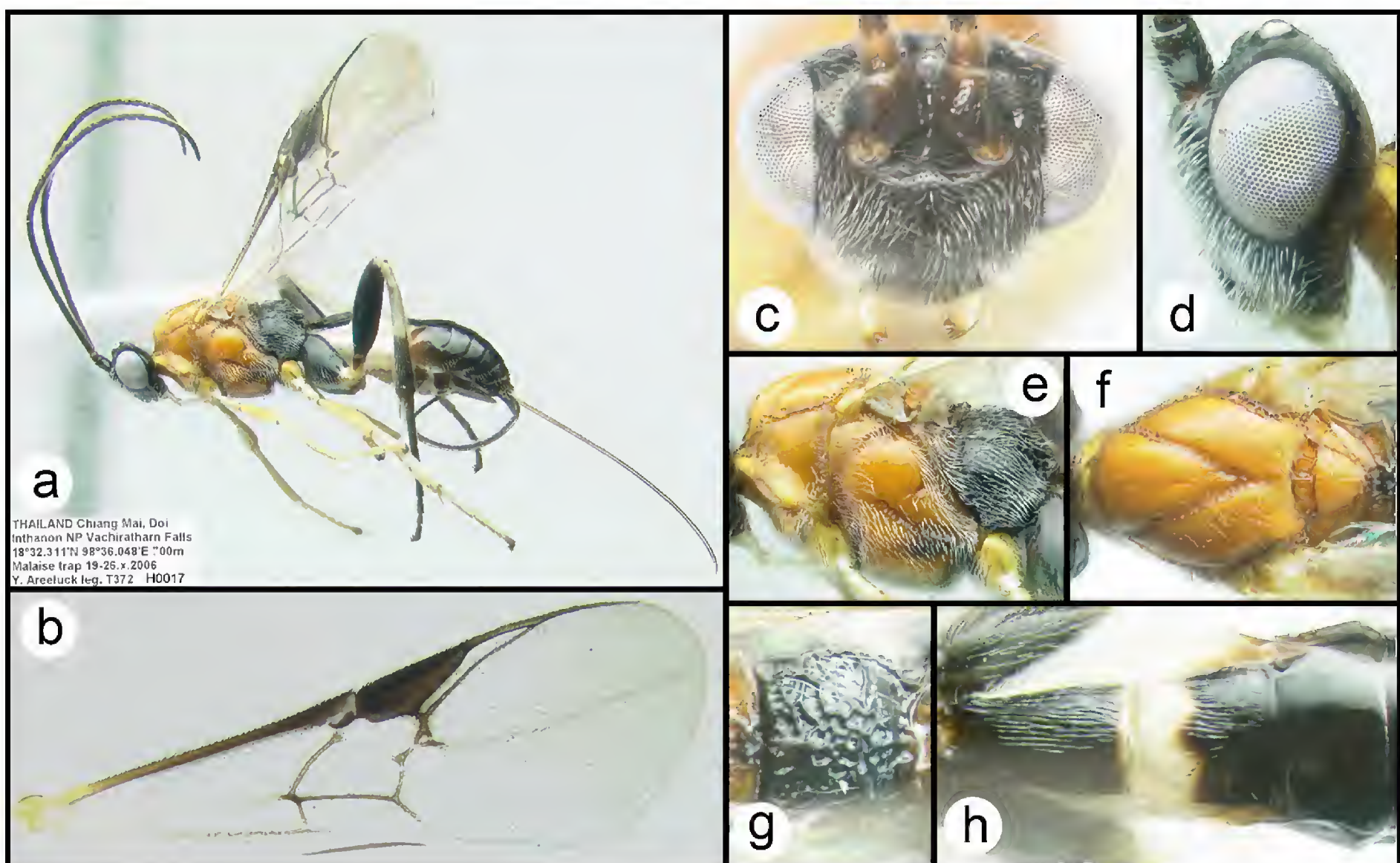


Figure 3. *Z. contrasta*: a) lateral habitus. b) fore wing. c) anterior head. d) lateral head. e) lateral mesosoma. f) dorsal mesoscutellum. g) propodeum. h) T1-3.

H5999), M.G. Allen; Chaiyaphum, Pa Hin Ngam NP, Dry dipterocarp, 15.635°N, 101.399°E, 698 m elev., Malaise trap, 18–24.viii.2006 (H1855, T448), Katae Sa-nog & Buakaw Adnafai; Chaiyaphum, Pa Hin Ngam NP, Dry ev-

ergreen next to creek, 15.676°N, 101.445°E, 461 m elev., Malaise trap, 19–23.xii.2006 (H5916, T1353), Katae Sa-nog & Buakaw Adnafai; Chaiyaphum, Pa Hin Ngam NP, Mixed deciduous forest (Thepana waterfall), 15.649°N,

- 101.418°E, 614 m elev., Malaise trap, 13–19.x.2006 (H5918, T662), Katae Sa-nog & Buakaw Adnafai; Chaiyaphum, Tat Tone NP, Chaiyapoom forest fire station, 16.013°N, 102.021°E, 195 m elev., Malaise trap, 19–23.xii.2006 (H100, T1372), Tawit Jaruphan & Orawan Budsawong; Chaiyaphum, Tat Tone NP, beside Sapsomboon substation, 16.013°N, 101.975°E, 648 m elev., Malaise trap, 5–12.v.2007 (H437, T2569), Tawit Jaruphan & Orawan Budsawong; Chiang Mai, Doi Chiang Dao WS, Nature trail, 19.4046°N, 98.9218°E, 491 m elev., Malaise trap, 30.ix-7.x.2007 (H5539, T3174), Songkran & Apichart; Chiang Mai, Doi Chiangdao NP, Headquarter, 19.405°N, 98.922°E, 491 m elev., Malaise trap, 1–8.iv.2008 (H924, T5780), 8–15.iv.2008 (H5979, T5792), S. Jugsu & A. Watwanich; Chiang Mai, Doi Inthanon NP, Vachirathan Falls, 18.539°N, 98.601°E, 700 m elev., Malaise trap, 21–27.ix.2006 (H5922, T341), 19–26.x.2006 (H017, T372), 17–24.xi.2006 (H094, T1861), 8–15.xii.2006 (H5913, T1933), 22–29.xii.2006 (H5923, T1935), Y. Areeluck; Chiang Mai, Doi Inthanon NP, campground pond, 18.544°N, 98.525°E, 1200 m elev., Malaise trap, 15–22.vii.2006 (H5930, T68), 9–16.viii.2006 (H5917, T175), Y. Areeluck; Chiang Mai, Queen Sirikit Botanic Garden, 18.881°N, 98.862°E, 811 m elev., Malaise trap, 4–13.iii.2009 (H399), 20–27.iii.2009 (H385), 3–18.iv.2009 (H643), 8–30.iv.2009 (H688), 30.iv-12.v.2009 (H341), 19–26.v.2009 (H312), 9–16.vi.2009 (H695), 16–23.vi.2009 (H569, H570, H571), 23–30.vi.2009 (H566, H567, H568), 30.vi-10.vii.2009 (H520), K. Kaewjanta & R. Sawkord; Kanchanaburi, Khuean Srinagarindra NP, Tha Thung-na, Chong Kraborg, 14.5°N, 98.884°E, 210 m elev., Malaise trap, 26.ii-5.iii.2009 (H534, H536, T4779), 12–19.iii.2009 (H985, T4781), 19–26.iii.2009 (H2437, T4780), Boonnam & Phumarin; Lampang, Chae Son NP, Campground#3, 18.831°N, 99.471°E, 487 m elev., Malaise trap, 8–14.x.2007 (H4112, T5324), 21–28.x.2007 (H4100, H4105, T5313), B. Kwannui & A. Sukpeng; Lampang, Chae Son NP, Hot spring, 18.835°N, 99.475°E, 493 m elev., Malaise trap, 1–8.xii.2007 (H5920, T2892), 14–21.xii.2007 (H5915, T2893), Boonruen & Acharapaun; Lampang, Chae Son NP, Nursery, 18.832°N, 99.469°E, 485 m elev., Malaise trap, 21–28.xi.2007 (H983), B. Kwannui & A. Sukpeng; Lampang, Chae Son NP, Youthcamp, 18.8304°N, 99.4709°E, 455 m elev., Malaise trap, 15–21.iv.2008 (H5532, T5418), B. Kwannui & A. Sukpeng; Lampang, Chae Son NP, beside office, 18.834°N, 99.473°E, 447 m elev., Malaise trap, 1–8.x.2007 (H5921, T2840), Bunruen Kwannui & Acharaporn Sukpeng; Loei, Phu Kradueng NP, Mixed deciduous forest south of Na Noy Forest Unit, 16.818°N, 101.794°E, 275 m elev., Malaise trap, 14–20.xi.2006 (H104, T1074), Suthin Gong-lasae; Loei, Phu Kradueng NP, Mixed deciduous, N Na Noy office, 16.803°N, 101.795°E, 276 m elev., Malaise trap, 14–21.v.2008 (H601, T5007), 21–28.v.2008 (H2405, H2414, T5015), Thonghuay Phatai; Thailand, Loei, Phu Ruea NP, Reservoir, 17.48°N, 101.356°E, 931 m elev., Malaise trap, 19–26.i.2007 (H101), Patikhom Tumtip; Mae Hong Son, Namtok Mae Surin NP, E Huai Fai Kor reservoir, 19.344°N, 97.988°E, Malaise trap, 27.i-3.ii.2008 (H451, T3496), 6–13.iv.2007 (H936, T6033), 9–16.ix.2007 (H984, T5891), 14–21.x.2007 (H994, T5917), 28.x-4.xi.2007 (H982, T5924), 18–25.xi.2007 (H980, T5942), A. Kamkhun & M. Kaewmanee; Mae Hong Son, Namtok Mae Surin NP, 19.36°N, 97.988°E, 228 m elev., Malaise trap, 30.iii-6.iv.2008 (H919, T6024), 4–11.v.2008 (H472, T3512), Manu Kaewmanee; Mae Hong Son, Namtok Mae Surin NP, E Huai Fai Kor reservoir, 19.344°N, 97.988°E, Malaise trap, 3–10.ii.2008 (H616, T3497), 4–11.v.2008 (H327, T3516), A. Kamkoon; Mae Hong Son, Namtok Mae Surin NP, Haad Saen, 19.348°N, 97.985°E, Malaise trap, 1–8.vi.2008 (H445, H446, H5976, T3527), 4–11.v.2008 (H311, T3508), J. Kaewmanee; Mae Hong Son, Namtok Mae Surin NP, Nature trail, 19.344°N, 97.988°E, 334 m elev., Malaise trap, 30.ix-7.x.2007 (H2420, T5901), 7–14.x.2007 (H969, T5904), 21–28.x.2007 (H959, T5921), Areerat Kamkhun; Mae Hong Son, Namtok Mae Surin NP, Visitor's center, 19.36°N, 97.988°E, 228 m elev., Malaise trap, 11–18.xi.2007 (H976, T5930), Manu Namadkum; Nakhon Nayok, Khao Yai NP, Lum Ta Kong View Point, 14.426°N, 101.391°E, 726 m elev., Malaise trap, 12–19.iv.2007 (H5909, T2124), Wirat Sukho; Nakhon Nayok, Khao Yai NP, secondary forest near Hnong Pakchee, 14.453°N, 101.364°E, 758 m elev., Malaise trap, 5–12.v.2007 (H142), Pong Sandao; Petchaburi, Kaeng Krachan NP, Panernthung, km27, 12.822°N, 99.371°E, Malaise trap, 11–18.i.2009 (H651, T4401), Sirichai; Phetchabun, Khao Kho NP, Deciduous forest at Ta Pol river, 16.543°N, 101.041°E, 242 m elev., Malaise trap, 26.v-2.vi.2007 (H491, T2557), Somchai Chachumnan & Saink Singtong; Phetchabun, Khao Kho NP, Mixed deciduous forest, 16.542°N, 101.041°E, 524 m elev., Malaise trap, 5–12.xii.2006 (H143, H144, H149, T1179), 19–26.xii.2006 (H146, T1184), 26.xii.2006-2.i.2007 (H5919, T1189), Somchai Chachumnan & Saink Singtong; Prachuab Khiri Khan, Khao Sam Roi Yot NP, 30m N, protection unit4, 12.268°N, 99.944°E, 1 m elev., Malaise trap, 24–31.v.2009 (H489, T4833), Yai Amnad; Prachuab Khiri Khan, Khao Sam Roi Yot NP, Don Tone Sone beach, 12.122°N, 99.968°E, 1 m elev., Malaise trap, 10–17.v.2009 (H2784), Yai Amnad; Prachuab Khiri Khan, Khao Sam Roi Yot NP, Khao Look Glang, 12.107°N, 99.955°E, Malaise trap, 1–8.ii.2009 (H378, H387, H392, T4187), 2–9.xi.2008 (H429, T4124), 9–16.xi.2008 (H2417, T4125), 23–30.xi.2008 (H402, T4140), 7–14.xii.2008 (H382, H669, T4142), 8–15.ii.2009 (H629, T4188), Yai, Amnad; Prachuab Khiri Khan, Khao Sam Roi Yot NP, Laem Sala beach, 12.204°N, 100.013°E, Malaise trap, 20–27.vii.2008 (H5902, T3014), Yai & Amnad; Prachuab Khiri Khan, Khao Sam Roi Yot NP, Nursery, 12.126°N, 99.958°E, Malaise trap, 29.vi-6.vii.2008 (H5900, T3049), 6–13.vii.2008 (H5912, T3035), Pan trap, 2–3.vii.2008 (H5903, T3034), Amnad & Yai; Prachuab Khiri Khan, Khao Sam Roi Yot NP, Saline wetland, Pa Gwad, N, 12.153°N, 99.972°E, Malaise trap, 28.xii.2008-4.i.2009 (H317, T4169), 25.i-1.ii.2009 (H2426, T4190), Yai & Amnad; Prachuab Khiri Khan, Khao Sam Roi Yot NP, foot of Khao Taen, 12.146°N, 99.966°E, 1 m elev., Malaise trap, 10–

17.v.2009 (H364, H2872, T4828), 17–24.v.2009 (H362, T4831), 24–31.v.2009 (H709, H711, T4834), Yai & Amnad; Sakon Nakhon, Phu Phan NP, Dry evergreen near house no. 1567, 16.81°N, 103.892°E, 512 m elev., Malaise trap, 16–22.vi.2007 (H1856), 22–28.vi.2007 (H5911, T2501), Winlon Kongnara; Suphanburi, Pu Toei NP, Huai Mongpae, red road, 14.95°N, 99.446°E, 300 m elev., Malaise trap, 24–31.vii.2008 (H5907, T3120); Suphanburi, Pu Toei NP, Phu Toei hill top, road, 14.955°N, 99.45°E, 650 m elev., Malaise trap, 24–31.vii.2008 (H5910, T3134), L. Saunbua; Suphanburi, Pu Toei NP, Pu Krathing waterfall, 14.815°N, 99.46°E, 200 m elev., Malaise trap, 21–28.v.2009 (H677), P. Wangkum; Surat Thani, Khao Sok NP, Headquarter, 8.915°N, 98.53°E, 115 m elev., Malaise trap, 31.viii-8.ix.2008 (H672, T3359), 17–24.iii.2009 (H603, H608, H609, H622, T4471), Buathong & Pongphan; Trang, Khaochong, 7.551°N, 99.789°E, 75 m elev., Malaise trap, 18–21.iii.2005 (H056); **Vietnam**, Dak Lak Prov., EASO National Park, 12.918°N, 108.633°E, Malaise trap, 18.iii.2009 (H7995).

For a map of examined material, see: <https://bit.ly/2q4eDp2>

Distribution. Vietnam and Thailand.

Zosteragathis eukos Sharkey, sp. n.

<http://zoobank.org/0F316EA6-9110-4218-8415-79F01AD086F6>

Etymology. *Eukos* is Greek for milky white; here it is a reference to the color of the base of the hind tibia.

Diagnosis. T2 almost entirely melanic and longer than wide; fore wing lacking infusate patch posterior to stigma; similar to *Z. annuliferus* (Achterberg and Long 2010) but dimensions of T1 and T2 differ.

Description. Body length 4.9 mm. Ovipositor length/body length ratio = 0.8. Interantennal space with a flat triangular elevation that narrows to a short ridge posteriorly and then divides into two short indistinct carinae that approach the median ocellus. Antenna with 32 flagellomeres. Third labial (penultimate) palpomere minute, barely visible and much smaller than apical palpomere. Scutellar groove with 3 longitudinal ridges. Fore tibia lacking thickened spines; mid tibia with 3 pegs; hind tibia with 10 pegs.

Specimens examined. Holotype female, THAILAND, Suphanburi, Pu Toei NP, car park, Pu Krathing waterfall, 14°48.922'N, 99°27.52'E, 200 m elev., Malaise trap, 21–28.iv.2009 (H689, T4610), Wangkum, leg.

For a map of examined material, see: <https://bit.ly/2I4SQEY>

Zosteragathis hinensis Sharkey, sp. n.

<http://zoobank.org/3D4A0CE0-16B9-442F-9B17-3110C1EADD9B>

Diagnosis. Mesoscutum black. Fore coxa mostly melanic. Hind femur melanic, brown to black. T2 mostly pale in anterior half and mostly melanic in posterior half. T2 as wide as long or wider.

Description. Body length 4.5 mm. Ovipositor length 3.6 mm. Ovipositor 0.8× body length.

Number of flagellomeres 31. Notauli sculpture not significantly wider posteriorly. Scutellum smooth with punctures. Mid tibia with 2 apical and 3 preapical spines. Hind tibia with 6 spines/pegs. Second submarginal cell diameter large, about same size as pedicel length. Wing hyaline with an infusate patch posterior to stigma. T2 0.9× longer than wide. T2 entirely striate, striae relative straight throughout.

Color. Head black; mesosoma black; fore and mid coxa black; posterior border of T1 yellow; T2 yellow in basal half.

Etymology. Named after the type locality Pa Hin Ngam National Park.

Material examined. Holotype: Female: **Thailand**, Chaiyaphum, Pa Hin Ngam NP, Deciduous forest, 15.666°N, 101.453°E, 357 m elev., Malaise trap, 1–7.vi.2007 (H278, T2472), Katae Sa-nog & Buakaw Adnafai.

For a map of examined material, see: <https://bit.ly/2E2Qcxq>

Zosteragathis hongensis Sharkey, sp. n.

<http://zoobank.org/DC9A51BD-C186-48FF-87DE-344387B377DA>

Diagnosis. Head mostly black; mesoscutum orange; T1 mostly and T2 entirely white of pale whitish yellow.

Description. Body length 3.6 mm. Ovipositor length 2.8 mm. Ovipositor 0.8× body length. Number of flagellomeres 30. Notauli sculpture not significantly wider posteriorly. Scutellum smooth with punctures. Mid tibia with 3 apical and 2 preapical spines. Hind tibia with 7 spines/pegs. Second submarginal cell diameter minute, about equal to width of pedicel. Wing hyaline, without distinct infusate areas. T2 0.8× longer than wide. T2 mostly smooth with fine wrinkles, only a hint of longitudinal striae. **Color:** head black except lower gena and clypeus yellow; pronotum and mesonotum orange; propodeum, mesopleuron and metapleuron black; T1 and T2 mostly or entirely white or pale whitish yellow; anterior margin of T3 white or pale whitish yellow.

Etymology. Named after the type locality Mae Hong Song Provence.

Material examined. Holotype: Female: **Thailand**, Mae Hong Son, Namtok Mae Surin NP, E Huai Fai Kor reservoir, 19.344°N, 97.988°E, 311 m elev., Malaise trap, 18–25.v.2008 (H660, T3518), Kamkoon, A. **Paratype:** Female: **Thailand**, Mae Hong Son, Namtok Mae Surin NP, Visitor's center, 19.3598°N, 97.9875°E, 228 m elev., Malaise trap, 20–27.iv.2008 (H3819, T6045), Areerat Kamkhun.

For a map of examined material, see: <https://bit.ly/2E2QgNG>

Zosteragathis inthanonensis Sharkey, sp. n.

<http://zoobank.org/44EBAC09-1B13-44BD-8AD1-0CCB808F5E05>

Diagnosis. Pronotum melanic dorsomedially, concolorous with lateral surfaces of pronotum.

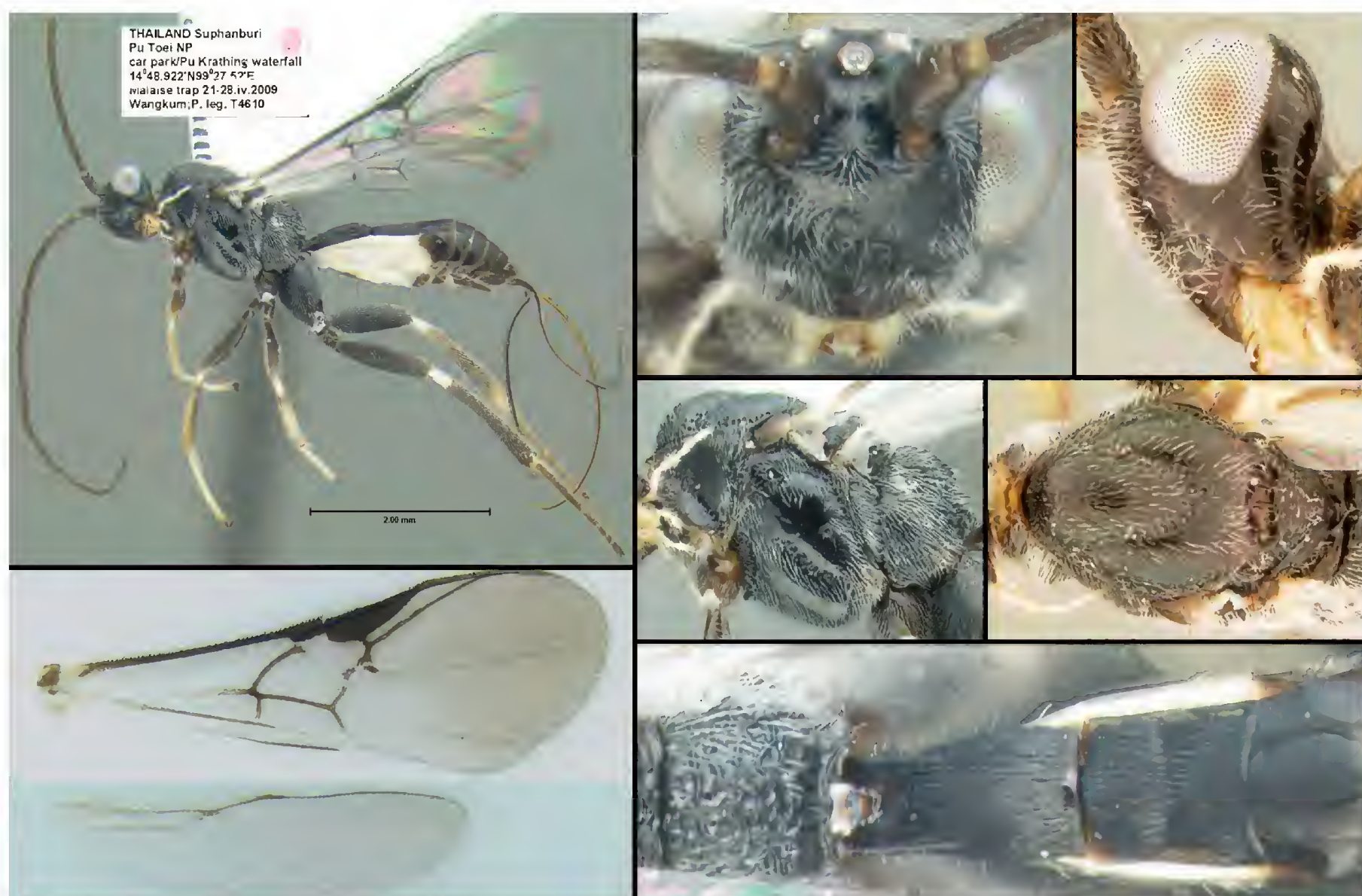


Figure 4. *Zosteragathis eukos* holotype female. **a)** lateral habitus. **b)** wings. **c)** anterodorsal head. **d)** lateral head. **e)** lateral mesosoma. **f)** dorsal thorax. **g)** propodeum and metasomal terga 1-3.

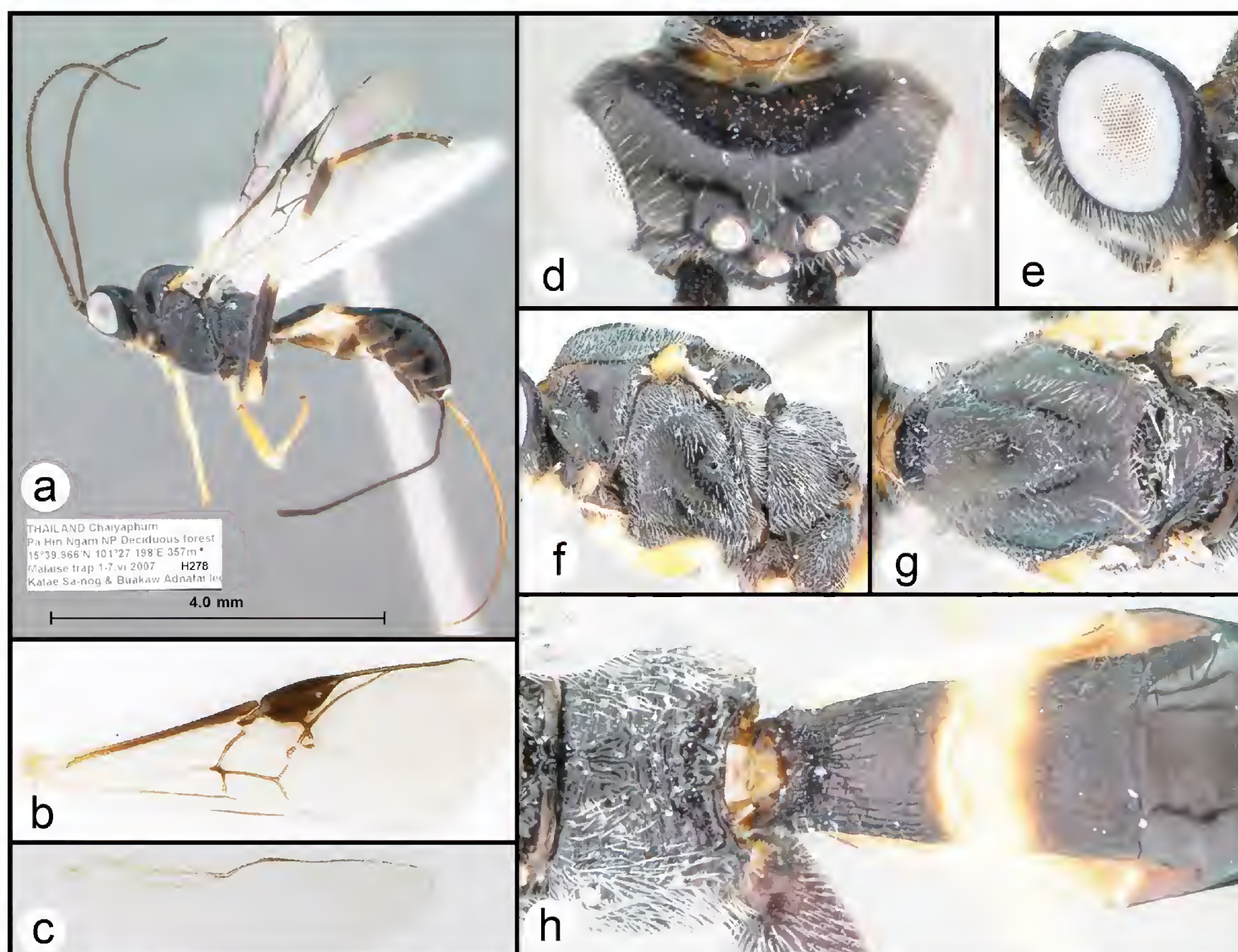


Figure 5. *Z. hinensis*: **a)** lateral habitus. **b)** fore wing. **c)** hind wing. **d)** dorsal head. **e)** lateral head. **f)** lateral mesosoma. **g)** dorsal mesoscutum **h)** dorsal propodeum and T1-3.

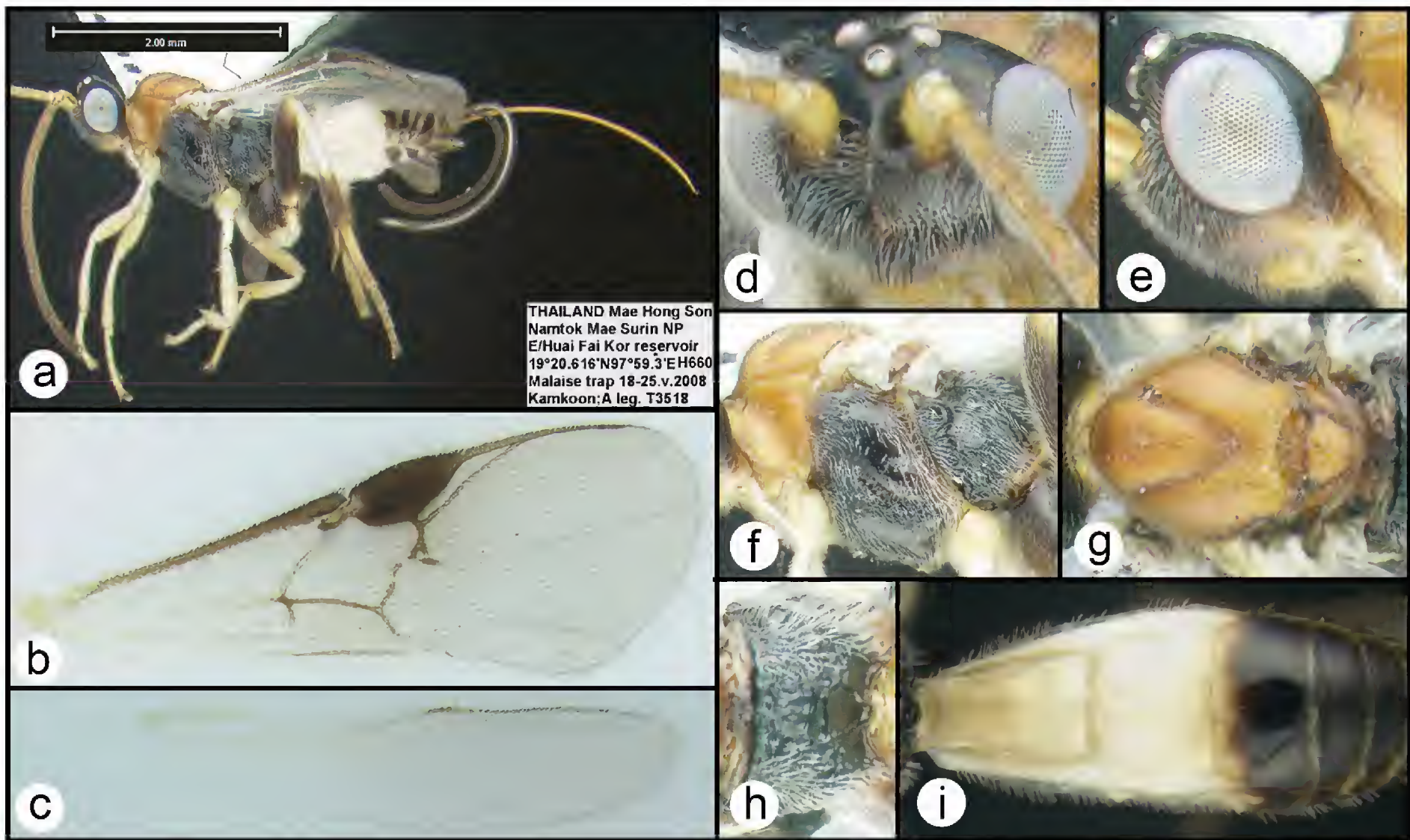


Figure 6. *Z. hongensis*: a) lateral habitus. b) fore wing. c) hind wing. d) anterior head. e) lateral head. f) lateral mesosoma. g) dorsal mesoscutum h) propodeum. i) T 1–5.

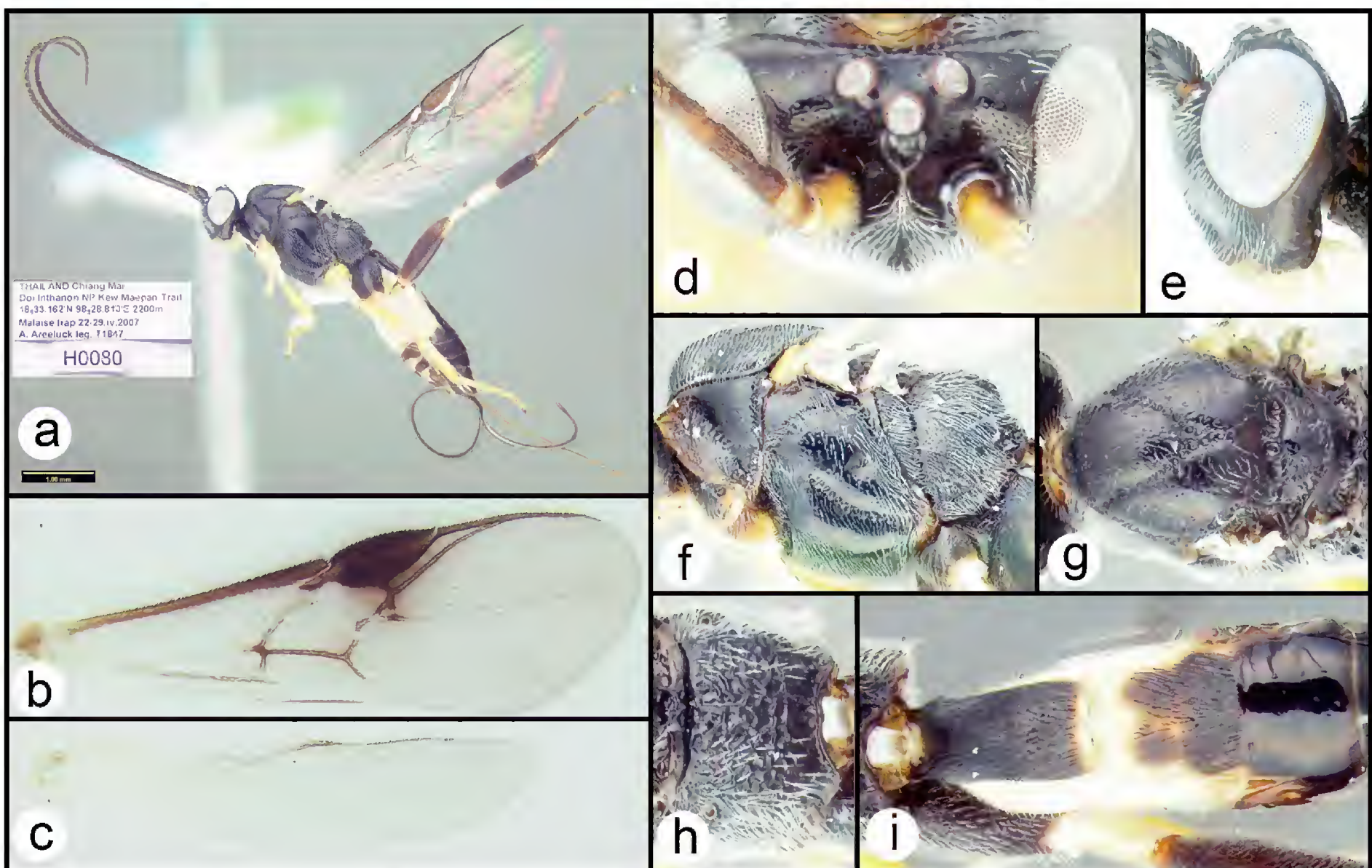


Figure 7. *Z. inthanonensis*: a) lateral habitus. b) fore wing. c) hind wing. d) dorsal head. e) lateral head. f) lateral mesosoma. g) dorsal mesoscutum h) propodeum. i) T1–3.

Scutellum sculpture smooth with punctures.

Description. Body length 4.7 mm. Ovipositor length 3.7 mm. Ovipositor $0.8\times$ body length. Number of flagellomeres 34. Notauli sculpture not significantly wider posteriorly. Scutellum smooth with punctures. Mid tibia with 2 apical and 3 preapical spines. Hind tibia with 6 spines/pegs. Second submarginal cell diameter small, slightly larger than pedicel width (varying to minute and about the same size as width of pedicel). Wing hyaline with an infuscate patch posterior to stigma. T2 $1.1\times$ longer than wide. T2 entirely striate, striae relative straight throughout. **Color:** head black; mesosoma black; fore and mid coxa yellow; posterior border of T1 yellow; T2 yellow anteriorly and anterolaterally (varying to yellow in entire anterior half).

Etymology. Named after the type locality Doi Inthanon National park.

Material examined. Holotype: Female: *Thailand*, Chiang Mai, Doi Inthanon NP, Kew Maepan Trail, 18.553°N, 98.48°E, 2200 m elev., Malaise trap, 22–29.iv.2007 (H080, T1847), Y. Areeluck.

Paratypes: All female: *Thailand*, Lampang, Chae Son NP, Behind youthcamp, 18.8308°N, 99.458°E, 445 m elev., Malaise trap, 14–21.ii.2008 (H3818, T5376), 7–14.ii.2008 (H5953, T5377), B. Kwannui & A. Sukpeng; Lampang, Chae Son NP, Mae Paan unit, 18.8274°N, 99.4118°E, 815 m elev., Malaise trap, 21–27.v.2008 (H5515, T5290), B. Kwannui & A. Sukpeng; Lampang, Chae Son NP, campground, lavatory, 18.832°N, 99.473°E, 467 m elev., Malaise trap, 21–30.v.2008 (H2440, T5305), B. Kwannui & A. Sukpeng.

For a map of examined material, see: <https://bit.ly/2uqJOjH>

Zosteragathis krachanensis Sharkey, sp. n.

<http://zoobank.org/CBD43CE1-12C1-4605-A5B0-845B450CD449>

Diagnosis. Scutellar triangle rugose; T2 elongate ($1.6\times$ longer than wide); t2 entirely pale yellow.

Description. Body length 6.7 mm. Ovipositor length 6.4 mm. Ovipositor $1.0\times$ body length. Number of flagellomeres broken after the 33rd flagellomere. Sculpture of notauli increasing in width posteriorly where it extends over onto lateral lobes of mesoscutum. Scutellum rugose. Mid tibia with 1 apical and 2 preapical spines. Hind tibia with 7 spines/pegs. Second submarginal cell diameter large, about as large as pedicel length. Wing hyaline with weak infuscation posterior to stigma. T2 $2\times$ longer than wide. T2 entirely and evenly striate, striae diverging anteriorly, otherwise approximately straight. **Color:** head and mesosoma melanic, except lower gena and clypeus yellow; fore and mid coxae yellow; T1 mostly pale yellow with a pair of large melanic spots; T2 entirely pale yellow.

Etymology. Named after the type locality Kaeng Krachan National Park.

Material examined. Holotype: Female: *Thailand*, Petchaburi, Kaeng Krachan NP, Panernthung, km 27,

12.822°N, 99.371°E, 950 m elev., Malaise trap, 18–25.iii.2009 (H492, T4732), Sirichai & Prasit.

For a map of examined material, see: <https://bit.ly/2utGnJc>

Zosteragathis lampangensis Sharkey, sp. n.

<http://zoobank.org/4F684A4F-BB25-4A31-8DB4-07A2BC5E34F5>

Diagnosis. Clypeus melanic. Mesoscutum black. Scutellum sculpture smooth with punctures. T2 entirely or almost entirely (80%) pale.

Description. Body length 4.2 mm. Ovipositor length 3.1 mm. Ovipositor $0.7\times$ body length. Number of flagellomeres 29. Notauli sculpture not significantly wider posteriorly. Scutellum smooth with punctures. Mid tibia with 4 apical and 4 preapical spines. Hind tibia with 9 spines/pegs. Second submarginal cell diameter minute, about equal to width of pedicel. Wing hyaline, without distinct infuscate areas. T2 $1\times$ longer than wide. T2 entirely striate, striae relatively straight. **Color:** head black; mesosoma black; fore and mid coxa yellow; anterior and posterior borders of T1 yellow; T2 yellow; anterior margin of T3 yellow.

Etymology. Named after the type locality Lampang Provence.

Material examined. Holotype: Female: *Thailand*, Lampang, Chae Son NP, behind visitor center, 18.835°N, 99.474°E, 421 m elev., Malaise trap, 1–8.ix.2007 (H237, T2832), Bunruean Kwannui & Acharaporn Sukpeng. **Paratype:** Female, *Thailand*, Petchaburi, Kaeng Krachan NP, Panernthung, km 27, 12.822°N, 99.371°E, 950 m elev., Malaise trap, 8–15.vi.2009 (H989, T5264), Sirichai.

For a map of examined material, see: <https://bit.ly/2pK371W>

Zosteragathis lampoensis Sharkey, sp. n.

<http://zoobank.org/482BC0EC-C427-4352-AE96-5BC323A27286>

Diagnosis. Subgenal groove poorly developed, shallow and narrow. Scutellum sculpture smooth with punctures. Mesoscutum black. Hind femur melanic. Fore wing not distinctly infuscate in apical half. T1 color mostly or entirely melanic (brown to black) in basal 1/5, sometimes extreme base pale. T2 distinctly longer than wide. Striae of T2 relatively straight. Exposed portion of ovipositor shorter than body length.

Description. Body length 4.6 mm. Ovipositor length 4.7 mm. Ovipositor $1.0\times$ body length. Number of flagellomeres 31. Notauli sculpture not significantly wider posteriorly. Scutellum smooth with punctures. Mid tibia with 3 apical and 3 preapical spines. Hind tibia with 10 spines/pegs. Second submarginal cell diameter minute, about equal to width of pedicel. Wing hyaline with an infuscate patch posterior to stigma. T2 $1.1\times$ longer than wide. T2 entirely striate, striae relative straight throughout.

Color. Head and mesosoma melanic, except tegula and lowermost extremity of gena yellow; fore coxa yellow.

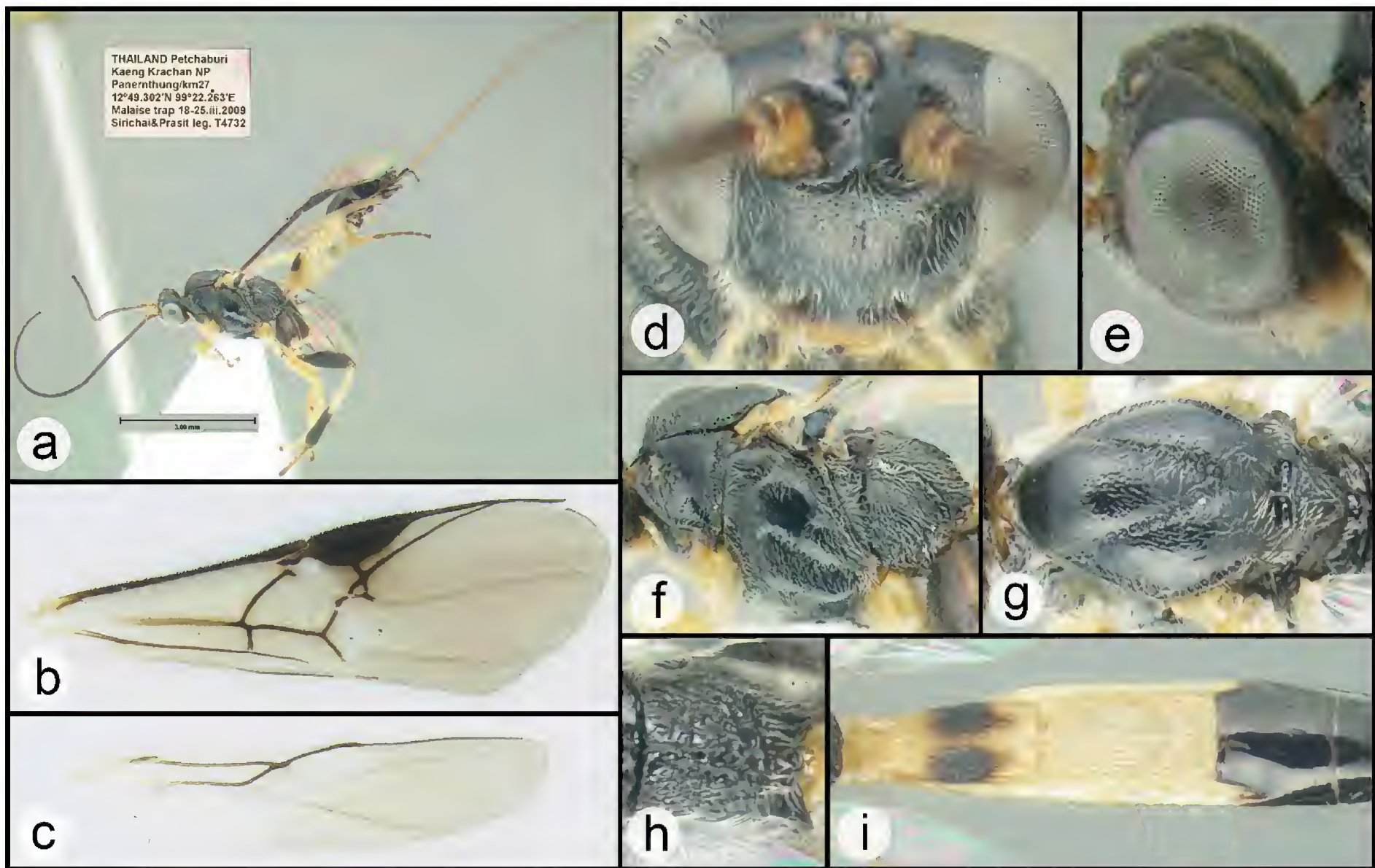


Figure 8. *Z. krachanensis*: a) lateral habitus. b) fore wing. c) hind wing. d) anterior head. e) lateral head. f) lateral mesosoma. g) dorsal mesoscutum h) propodeum. i) T1–3.

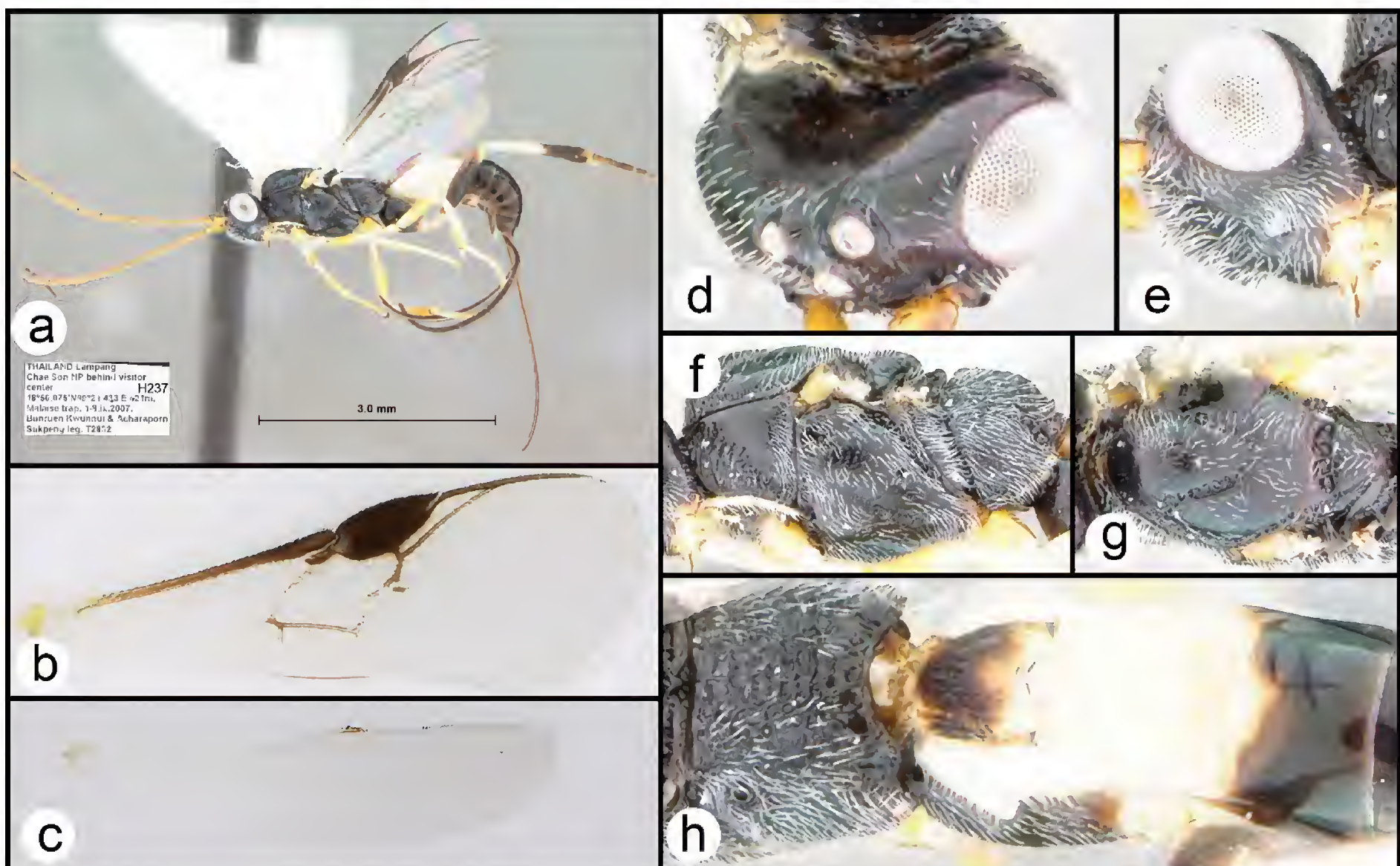


Figure 9. *Z. lampangensis*: a) lateral habitus. b) fore wing. c) hind wing. d) dorsal head. e) lateral head. f) lateral mesosoma. g) dorsal mesoscutum h) propodeum and T1–3.

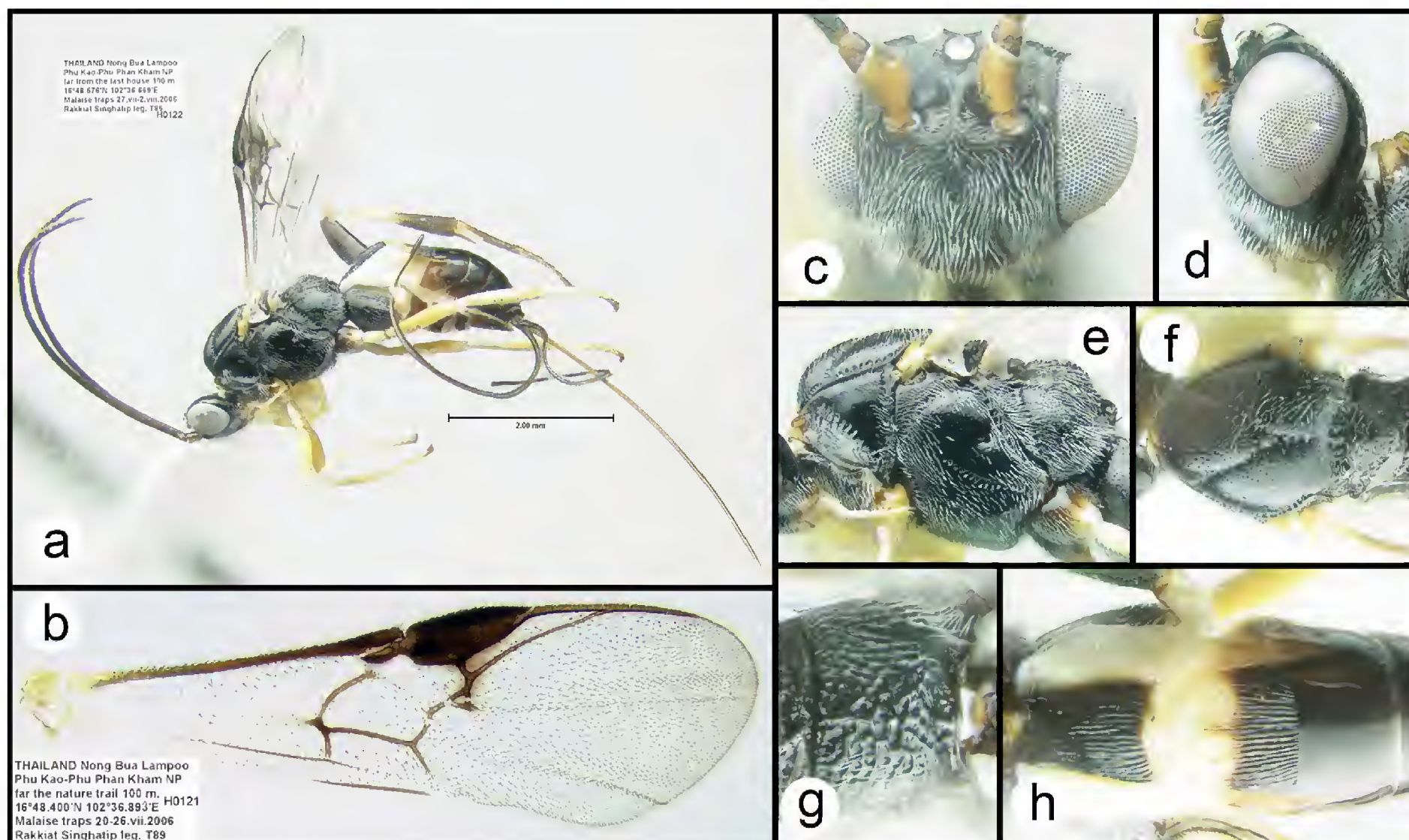


Figure 10. *Z. lampooensis*: **a)** lateral habitus. **b)** fore wing. **c)** anterior head. **d)** lateral head. **e)** lateral mesosoma. **f)** dorsal mesoscutum. **g)** propodeum. **h)** T1–3.

low; mid coxa mostly melanic; T1 mostly melanic except posterior margin pale yellow; T2 pale yellow anterior to transverse depression.

Etymology. Named after the type locality Nong Bua Lampoo Provence.

Material examined. Holotype: Female, *Thailand*, Nong Bua Lampoo, Phu Kao-Phu Phan Kham NP, far from the old house 100 m (east), 16.81°N, 102.614°E, 100 m elev., Malaise trap, 27.vii–2.viii.2006 (H122, T85), Rakkiat Singhatip. **Paratypes:** All female: *Thailand*, Nakhon Si Thammarat, Namtok Yong NP, TV aerial, 8.238°N, 99.805°E, 966 m elev., Malaise trap, 1–8. ix.2008 (H995, T3538), Paiboon; Phetchabun, Khao Kho NP, Mix deciduous forest, 16.542°N, 101.041°E, 524 m elev., Malaise trap, 26.vi–2.vii.2007 (H650, T2460), Somchai Chachumnan & Saink Singtong; Ubon Ratchathani, Pha Taem NP, Phu Krajeaw foothill, 15.6664°N, 105.5078°E, 238 m elev., Malaise trap, 2–9.vi.2007 (H1636, T2206), Tongcam & Banlu; Nong Bua Lampoo, Phu Kao-Phu Phan Kham NP, tank, 16.807°N, 102.615°E, 199 m elev., Malaise trap, 27.vii–2.viii.2006 (H121, T89), Rakkiat Singhatip.

For a map of examined material, see: <https://bit.ly/2G-ccq5J>

***Zosteragathis luangensis* Sharkey, sp. n.**

<http://zoobank.org/68E596E9-F85C-40E9-8945-0BFA8A916771>

Diagnosis. Ovipositor slightly more than 1/2 body length; scutellum rugose.

Description. Body length 4.0 mm. Ovipositor length 2.3 mm. Ovipositor 0.6× body length. Number of flagellomeres 30. Sculpture of notauli increasing in width posteriorly where it extends over onto lateral lobes of mesoscutum. Scutellum rugose. Mid tibia with 2 apical and 2 preapical spines. Hind tibia with 4 spines/pegs. Second submarginal cell diameter small, smaller than pedicel length, but larger than pedicel width. Wing hyaline with a weak infuscate area posterior to stigma. T2 1.2× longer than wide. T2 striate, striae straight and weak to absent anteriorly. **Color:** head black except lower gena and clypeus partly yellow; mesosoma black; fore and hind coxa melanic; T1 whitish yellow basally and apically; T2 whitish yellow in basal 1/2.

Etymology. Named after the type locality Thung Salaeng Luang National Park.

Material examined. Holotype: Female, *Thailand*, Phitsanulok, Thung Salaeng Luang NP, Moist evergreen forest, 16.844°N, 100.882°E, 557 m elev., Malaise trap, 25.viii–1.ix.2006 (H1859, T572), Pongpitak Pranee.

For a map of examined material, see: <https://bit.ly/2pMnf3r>

***Zosteragathis ngamensis* Sharkey, sp. n.**

<http://zoobank.org/F48AA80D-60AB-4E7C-A2C3-6B95C23C787A>

Diagnosis. Head, prothorax and mesothorax yellow; ovipositor short, about 1/2 body length; scutellar triangle rugose.

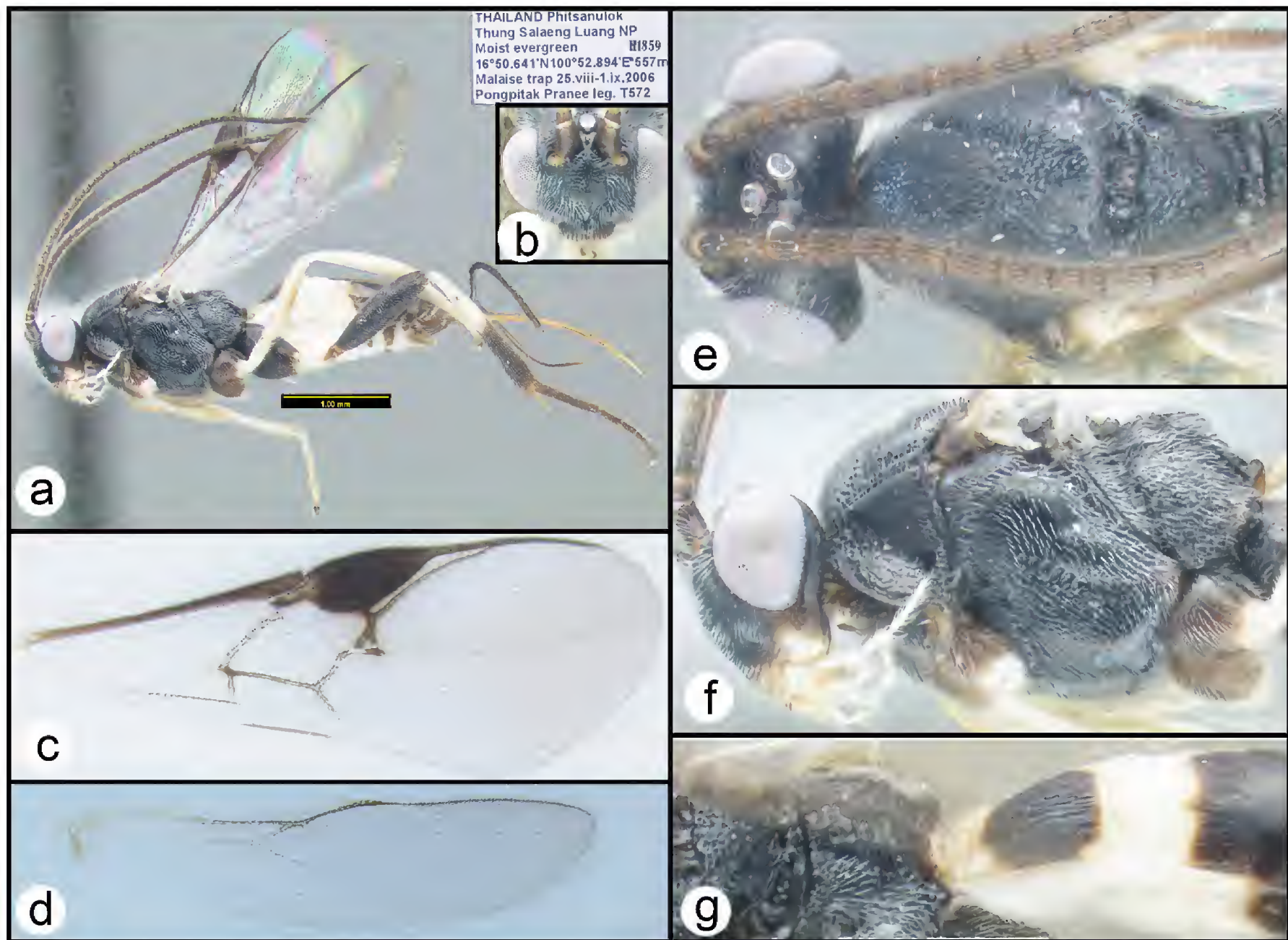


Figure 11. *Z. luangensis*: **a)** lateral habitus. **b)** anterior head. **c)** fore wing. **d)** hind wing. **e)** dorsal head and mesoscutum. **f)** lateral head and mesosoma. **g)** dorsal propodeum and T1–3.

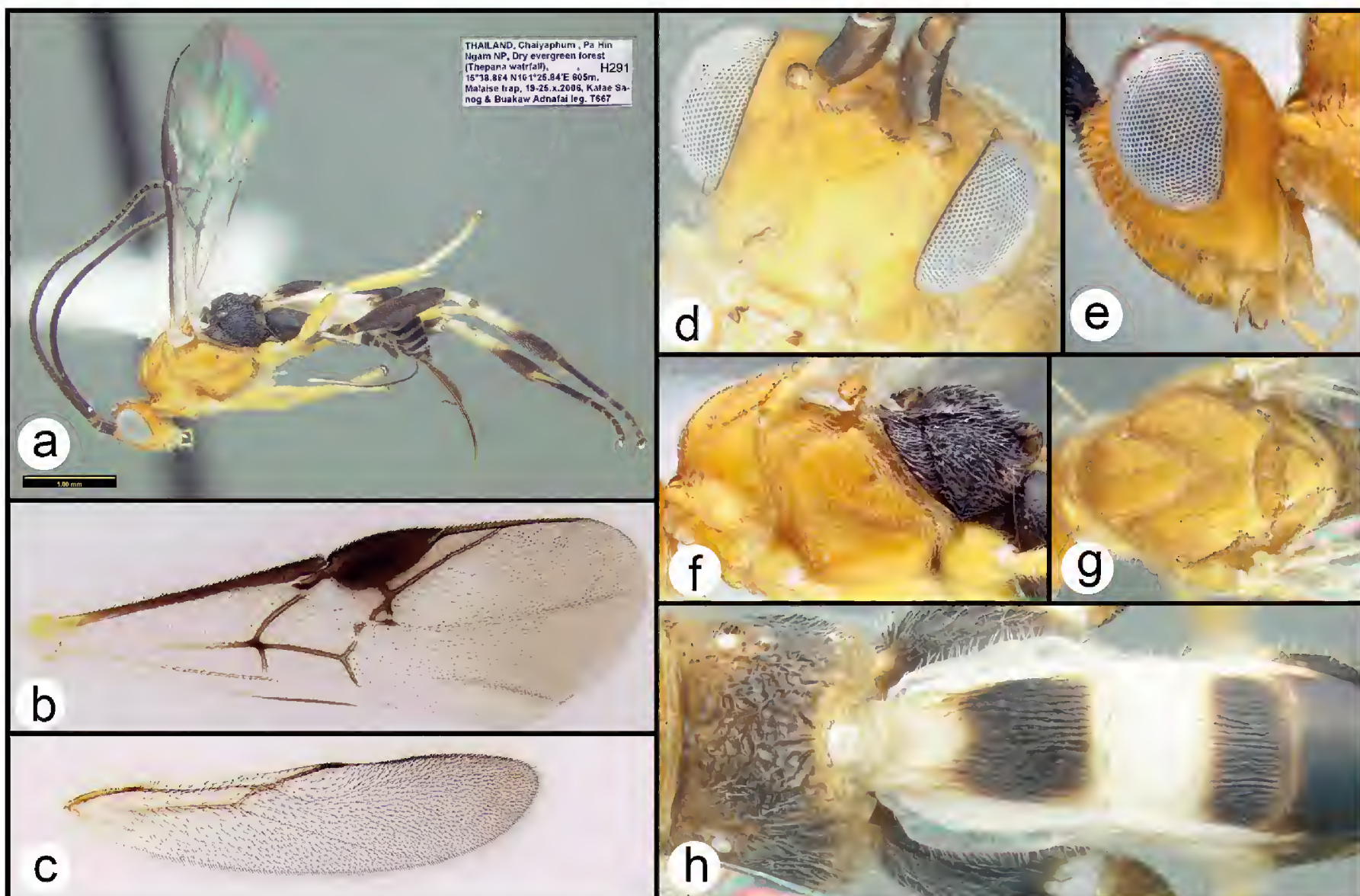


Figure 12. *Z. ngamensis*: **a)** lateral habitus. **b)** fore wing. **c)** hind wing. **d)** anterior head. **e)** lateral head. **f)** lateral mesosoma. **g)** dorsal mesoscutum. **h)** propodeum and T1–3.

Description. Body length 4.1 mm. Ovipositor length 2.0 mm. Ovipositor $0.5\times$ body length. Number of flagellomeres 34. Sculpture of notauli increasing in width posteriorly where it extends over onto lateral lobes of mesoscutum. Scutellum rugose. Mid tibia with no apical and 2 preapical spines. Hind tibia with 5 spines/pegs. Second submarginal cell diameter large, about as high as pedicel. Wing hyaline, apical half of wing weakly infusate, as is area posterior to stigma (infusate areas may not be evident unless lighting is optimal). T2 $1.2\times$ longer than wide. T2 entirely striate, striae relative straight throughout. **Color:** head, prothorax and mesothorax yellow, metathorax and propodeum black; fore and mid coxae yellow; basal 1/3 and apical margin of T1 yellow; anterior 1/2 of T2 yellow.

Etymology. Named after the type locality Pa Hin Ngam National Park.

Specimens examined. Holotype: Female, *Thailand*, Chaiyaphum, Pa Hin Ngam NP, Mixed deciduous forest (Thepana waterfall), 15.6486°N, 101.4179°E, 614 m elev., Malaise trap, 7–13.x.2006, Katae Sa-nog & Buakaw Adnafai. (H1625, T659). **Paratypes:** *Thailand:* Female, Chaiyaphum, Pa Hin Ngam NP, Dry evergreen forest near stream, 15.676°N, 101.445°E, 461 m elev., Malaise trap, 19–20.vi.2007, Katae Sa-nog & Buakaw Adnafai, (H277, T2482). Female, Chaiyaphum, Pa Hin Ngam NP, Dry evergreen forest (Thepana waterfall), 15.648°N, 101.431°E, 605 m elev., Malaise trap, 19–25.x.2006, Katae Sa-nog & Buakaw Adnafai. (H291, T667).

For a map of examined material, see: <https://bit.ly/2G-c89iQ>

Zosteragathis nuichuaensis (Achterberg & Long)

Therophilus nuichuaensis Achterberg & Long, 2010

Diagnosis. Scutellar triangle rugose.

Description. Body length 3.2 mm. Ovipositor length 2.7 mm. Ovipositor $0.8\times$ body length. Number of flagellomeres (26–28 in Thai specimens) incomplete in holotype. Sculpture of notauli increasing in width posteriorly where it extends over onto lateral lobes of mesoscutum. Scutellum rugose. Mid tibia with 2 apical and 3 preapical spines. Hind tibia with 6 spines/pegs. Second submarginal cell diameter large, almost as large as pedicel length. Wing hyaline, without distinct infusate areas. T2 $0.9\times$ longer than wide. T2 mostly smooth with striae indicated especially posteromedially (to entirely striate, with striae weaker medially), striae relatively straight. **Color:** head black except gena yellow ventrally; fore and mid coxae mostly melanic; apex of T1 and anterior half of T2 yellow.

Material examined. Holotype: not examined. **Paratypes:** not examined. **Non-type specimens:** All female: *Thailand*, Trang, Khoa Chong, Forest Research Stn., 7.551°N, 99.789°E, 75 m elev., xi.2005 (H083, T6372), viii.2005 (H065, T3595), D. Lohman; Trang, Khao Pu-Khao Ya NP, 7.551°N, 99.789°E, 75 m elev., Mal-

aise trap, 7–12.vi.2006 (H288, T1968), 31.iii–3.iv.2006 (H239, T2049), M. Sharkey; Trang, Khao Pu-Khao Ya NP, 7.551°N, 99.789°E, 147 m elev., Malaise trap, 3–5.viii.2005 (H5901, T1762), M. Sharkey; *Taiwan*, Taipei Co., Wulai, 24.87°N, 121.55°E, Malaise trap, 15.vii.2003, L. Stange & H. Wang.

For a map of examined material, see: <https://bit.ly/2pGpC8T>

Zosteragathis perknos Sharkey, sp. n.

<http://zoobank.org/1FC70495-DB98-45B3-857B-6CF146CB6025>

Diagnosis. Fore wing clear basally, infusate in apical half; T2 much narrower basally than apically; close to *Z. nigrolineatus* (Achterberg & Long, 2010), but differing in the dimensions of T2.

Description. Body length 6.2 mm. Ovipositor length/body length ratio = 0.8. Interantennal space with a flat triangular elevation that narrows to a short ridge posteriorly and then divides into two short indistinct carinae that approach the median ocellus. Antenna with 35 flagellomeres. Third labial (penultimate) palpomere small, 1/3 as long as apical palpomere. Scutellar groove with 3 longitudinal ridges. Fore tibia lacking thickened spines; mid tibia with 4 pegs; hind tibia with 8 pegs.

Etymology. *Perknos* is Greek for dusky; here it is a reference to the dark color of the base of the hind tibia.

Specimens examined. Holotype ♀, THAILAND, Chiang Mai, Doi Phahompok NP, Doi Phaluang, 20°1.06'N, 99°9.581'E, 1449 m elev., Malaise trap, 3–10.viii.2007 (H236, T2931), Wongchai, leg.

Paratypes: THAILAND: ♀, Petchaburi, Kaeng Krachan NP, Panernthung, km27, water pump, 12°49.151'N, 99°22.483'E, 970 m elev., Malaise trap, 17–24.x.2008 (H970, T4386), Sirichai leg. ♀, Mae Hong Son, Namtok Mae Surin NP, visitor's center, 19°21.593'N, 97°59.254'E, 228 m elev., Malaise trap, 26.viii–2.ix.2007 (H958, T5874), Manu Namadkum leg.

For a map of examined material, see: <https://bit.ly/2GbdAP7>

Zosteragathis petchaburiensis Sharkey sp. n.

<http://zoobank.org/15DCE0F9-7207-4D97-A957-C3A7C7CB7F61>

Diagnosis. Ovipositor longer than body; T2 almost entirely black; fore and mid femur partly black; propodeum smooth along posterior margin.

Description. Body length 3.6 mm. Ovipositor length 3.8 mm. Ovipositor $1.0\times$ body length. Number of flagellomeres 33. Notauli sculpture not significantly wider posteriorly. Scutellum smooth with punctures. Mid tibia with 7 apical and 2 preapical spines. Hind tibia with 10 spines/pegs. Second submarginal cell diameter small, smaller than pedicel length, but larger than pedicel width. Wing mostly hyaline, weakly infusate in distal half, not distinctly infusate posterior to stigma. T2 $1.2\times$ longer than

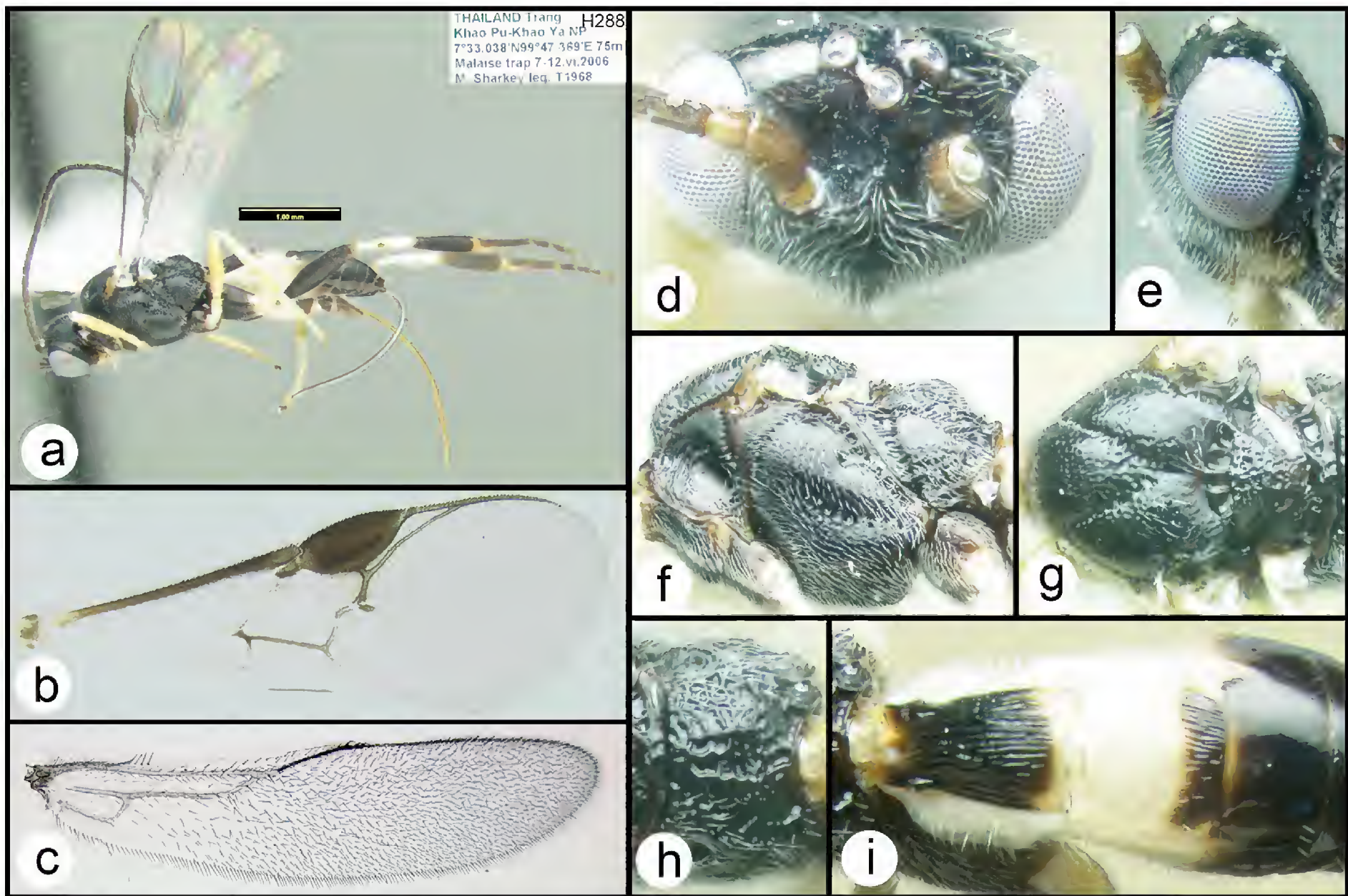


Figure 13. *Z. nuichuaensis*: **a)** lateral habitus. **b)** fore wing. **c)** hind wing. **d)** dorsal head. **e)** lateral head. **f)** lateral mesosoma. **g)** dorsal mesoscutum. **h)** propodeum. **i)** T1–3.

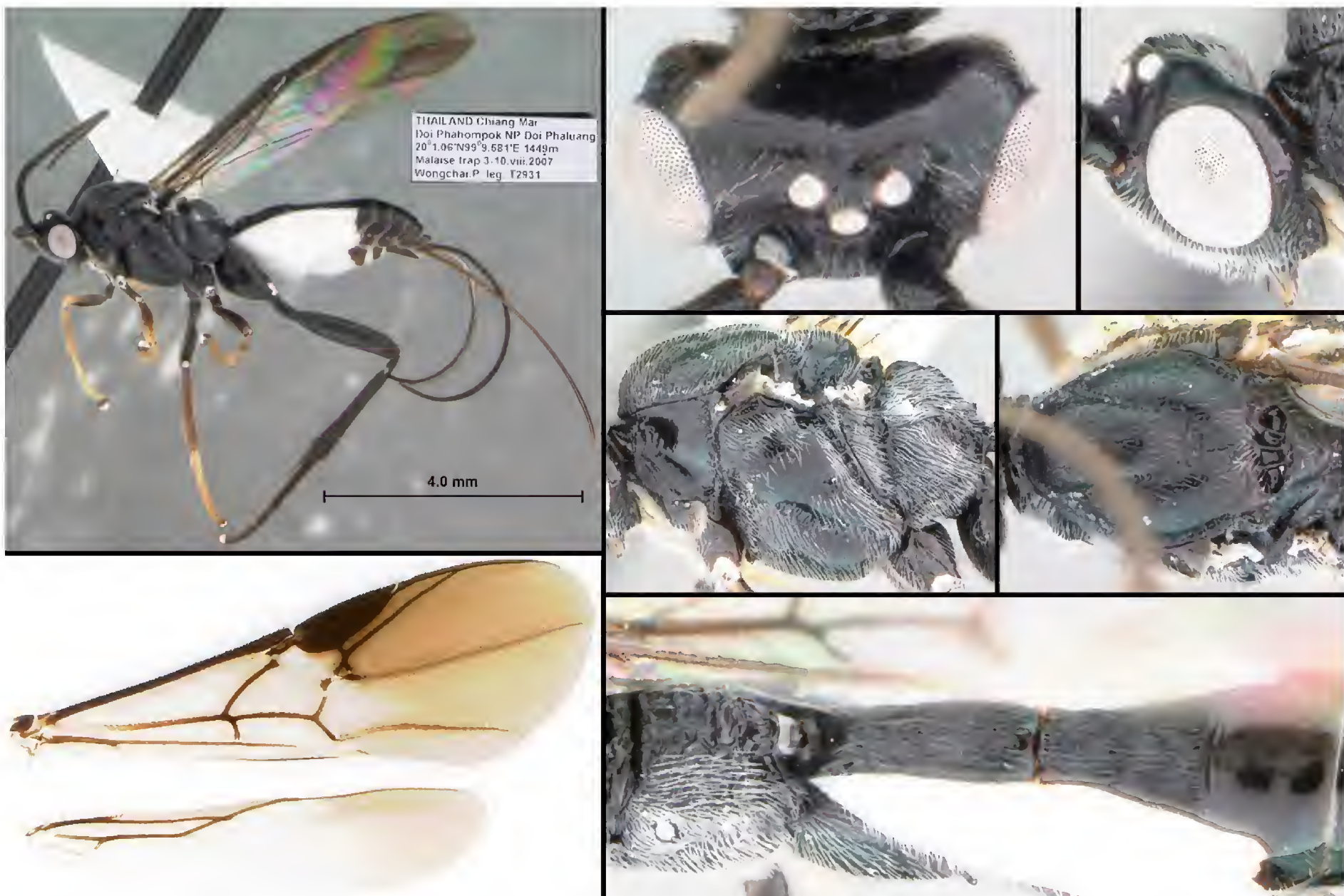


Figure 14. *Zosteragathis perkno* holotype female. **a)** lateral habitus. **b)** wings. **c)** dorsal head. **d)** lateral head. **e)** lateral mesosoma. **f)** dorsal thorax. **g)** propodeum and metasomal terga 1–3.

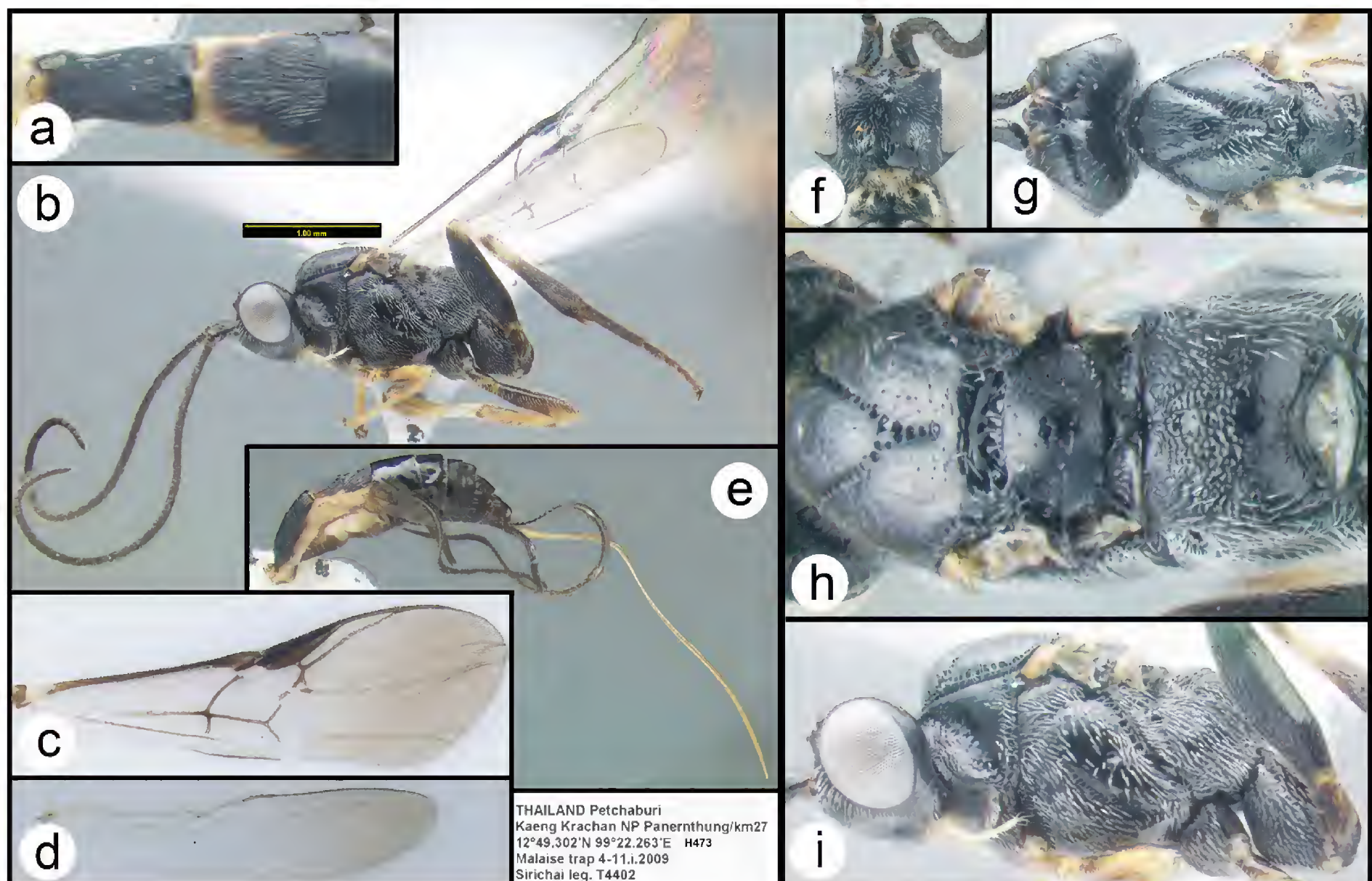


Figure 15. *Zosteragathis petchaburiensis*: **a)** T1–3. **b)** lateral head and mesosoma. **c)** fore wing. **d)** hind wing. **e)** lateral metasoma. **f)** anterior head. **g)** dorsal head and mesoscutum. **h)** dorsal mesosoma. **i)** lateral head and mesosoma.

wide. T2 entirely striate, striae converging somewhat posteromedially. **Color:** head black; mesosoma black; mid and fore coxa black; fore femur partly black; mid femur mostly black; T1 entirely black; T2 mostly black except anterior and anterolateral margins yellow.

Etymology. Named after the type locality Petchaburi Provence.

Specimens examined. Holotype: Female: *Thailand*, Petchaburi, Kaeng Krachan NP, Panernthung km 27, 12.822°N, 99.371°E, 950 m elev., Malaise trap, 4–11.i.2009 (H473, T4402), Sirichai.

For a map of examined material, see: <https://bit.ly/2umu41q>

***Zosteragathis phahompokensis* Sharkey, sp. n.**

<http://zoobank.org/85E264EF-33AC-4771-BD66-EF5D071F28B9>

Diagnosis. Scutellum smooth with punctures. T1 mostly or entirely pale in basal 1/5 or more. T2 mostly pale in anterior half and mostly melanic in posterior half.

Description. Body length 4.1 mm. Ovipositor length 3.2 mm. Ovipositor 0.8× body length. Number of flagellomeres 31. Notauli sculpture not significantly wider posteriorly. Scutellum smooth with punctures. Mid tibia with 2 apical and 4 preapical spines. Hind tibia with 7 spines/pegs. Second submarginal cell diameter large, about same size as pedicel length (to 1/3 length of pedicel but always

wider than pedicel). Wing hyaline, without distinct infuscate areas. T2 0.9× longer than wide. T2 mostly smooth with short longitudinal carinae restricted to area near median transverse depression. **Color:** head black except ventral gena and ventral clypeus yellow; mesosoma black; fore and mid coxa yellow; T1 yellow with large black patch posteromedially; T2 yellow in anterior half.

Etymology. Named after the type locality Doi Phahompokensis National Park.

Material examined. Holotype: Female: *Thailand*, Chiang Mai, Doi Phahompok NP, Headquarter, 19.966°N, 99.156°E, 569 m elev., Malaise trap, 28.ii-7.iii.2008 (H1858, T2939), Seesom, K. **Paratype:** Female: *Thailand*, Sakon Nakhon, Phu Phan NP, Behind national park office, 17.058°N, 103.975°E, 318 m elev., Malaise trap, 23–30.i.2007 (H097, T1527), Sailom Tongboonchai.

For a map of examined material, see: <https://bit.ly/2pIAjaK>

***Zosteragathis phuphanensis* Sharkey, sp. n.**

<http://zoobank.org/F1C9129E-DC7F-4106-81D4-FBB1B30D93FD>

Diagnosis. Scutellum smooth with punctures. Mesoscutum black. Fore wing with a small infuscate area posterior to stigma. T2 distinctly longer than wide. Striae of T2 curving towards the midline, especially anteromedially.

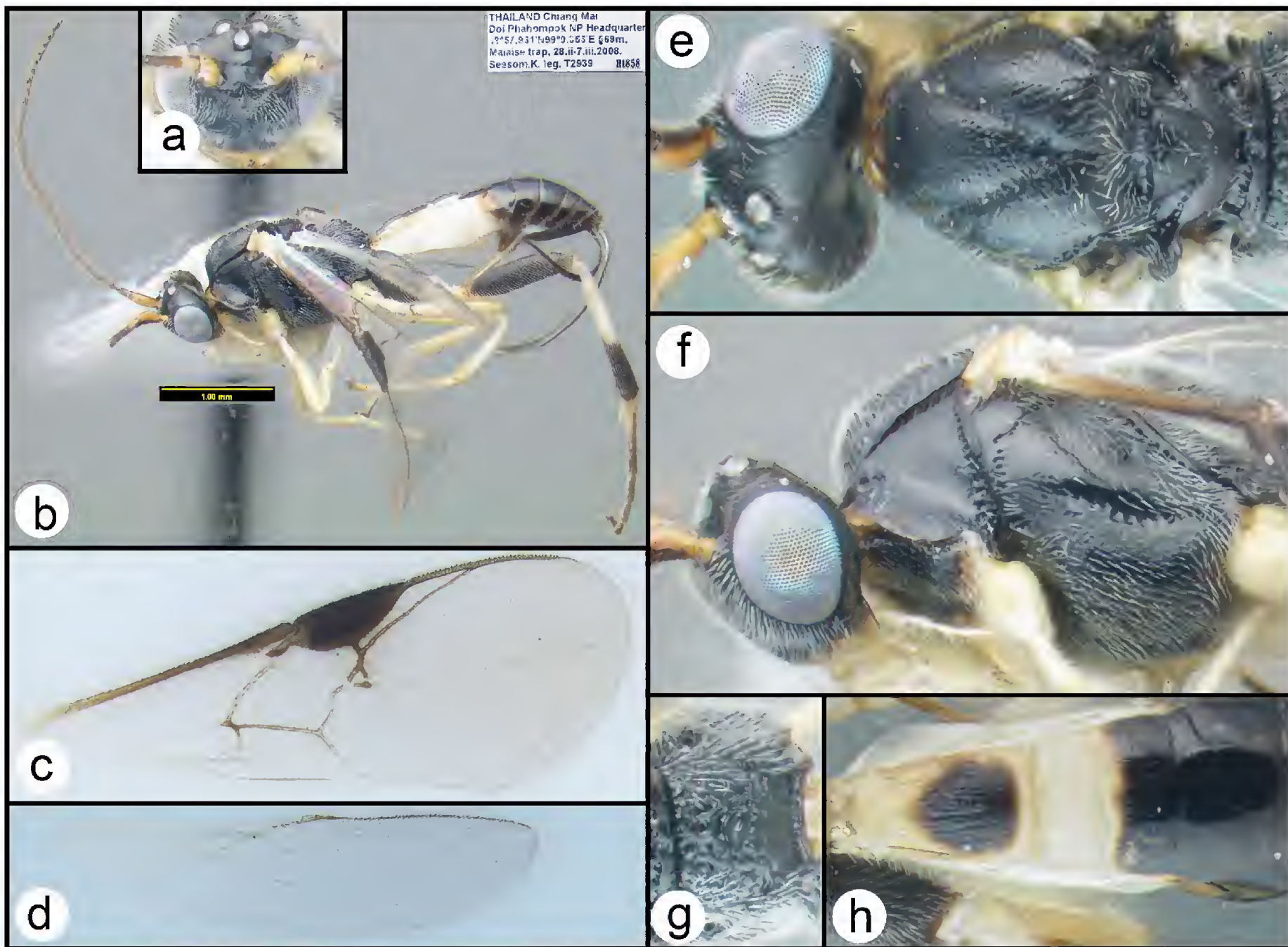


Figure 16. *Z. phahompokensis*: **a)** anterior head. **b)** lateral habitus. **c)** fore wing. **d)** hind wing. **e)** dorsal head and mesoscutum. **f)** lateral head and mesosoma. **g)** propodeum. **g)** propodeum. **h)** T1–3.

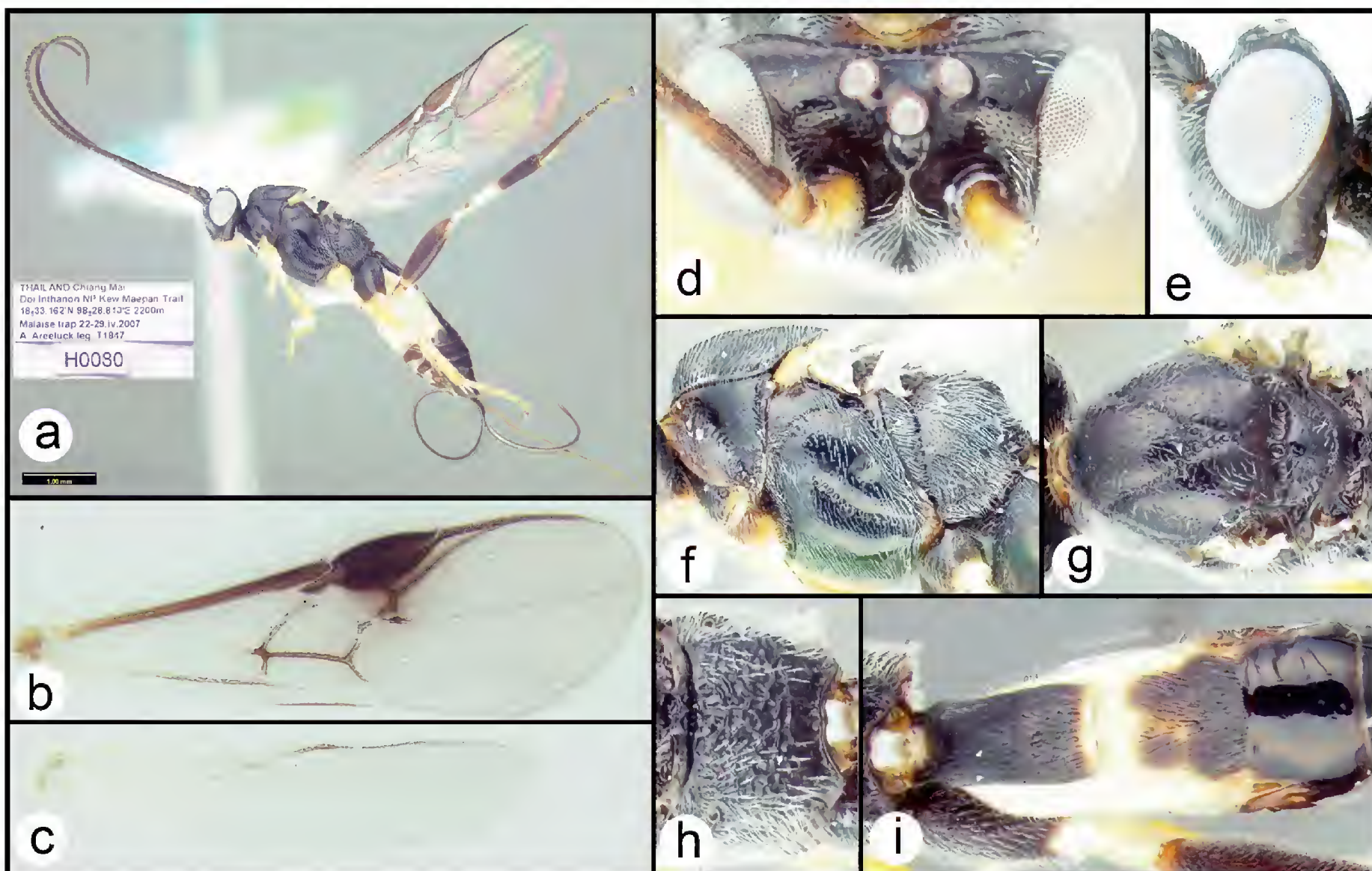


Figure 17. *Z. phuphanensis*: **a)** lateral habitus. **b)** fore wing. **c)** hind wing. **d)** dorsal head. **e)** lateral head. **f)** lateral mesosoma. **g)** dorsal mesoscutum. **h)** propodeum. **i)** T1–3.

Description. Body length 4.7. Ovipositor length 4.8. Ovipositor $1.0\times$ body length. Number of flagellomeres 32. Notauli sculpture not significantly wider posteriorly. Scutellum smooth with punctures. Mid tibia with 2–3 apical and 4 preapical spines. Hind tibia with 8 spines/pegs. Second submarginal cell diameter small, smaller than pedicel length, but larger than pedicel width. Wing hyaline with an infuscate patch posterior to stigma. T2 $1.1\times$ longer than wide. T2 entirely striate, striae converging medially.

Color. Head black except ventral extremity of gena yellow; mesosoma black; fore and mid coxa yellow; posterior margin of T1 yellow; T2 yellow anteriorly and anterolaterally.

Etymology. Named after the type locality Phu Phan National Park.

Material examined. Holotype: Female: *Thailand*, Sakon Nakhon, Phu Phan NP, Dry evergreen near house no.1567, 16.81°N , 103.892°E , 512 m elev., Malaise trap, 4–10.vi.2007 (H280, T1567), Winlon Kongnara. **Paratype:** Female, *Thailand*, Nakhon Si Thammarat, Namtok Yong NP, Behind campground lavatory, 8.174°N , 99.742°E , 80 m elev., Malaise trap, 29.x-5.xi.2008 (H550, T4253), U-prai;K.

For a map of examined material, see: <https://bit.ly/2DYkTUg>

Zosteragathis sakaeratensis Sharkey, sp. n.

<http://zoobank.org/39028CA9-4ABA-43C6-8845-457E9F88D7B9>

Diagnosis. Fore wing without a small infuscate area posterior to stigma. T2 entirely or almost entirely (80%) melanic. T2 as wide as long or wider.

Description. Body length 4.2 mm. Ovipositor length 2.8 mm. Ovipositor $0.7\times$ body length. Number of flagellomeres 29. Notauli sculpture not significantly wider posteriorly. Scutellum smooth with punctures. Mid tibia with 3 apical and 1 preapical spines. Hind tibia with 9 spines/pegs. Second submarginal cell diameter small, slightly smaller than pedicel length. Wing hyaline with a slight infuscation posterior to stigma. T2 $0.8\times$ longer than wide. T2 entirely striate, striae relative straight throughout. **Color:** fore coxa melanic; mid coxa yellow; hind femur yellowish brown; T1 and T2 mostly melanic; posterior margin of T1 pale; T2 with some pale infusions medially and anterolaterally.

Etymology. Named after the type locality Sakaerat Experimental Station.

Material examined. Holotype: Female: *Thailand*, Nakhon Ratchasima, 60 km S, Sakaeret Expt. Stn., 14.5°N , 101.917°E , 450 m elev., Malaise trap, 2–4.iii.1971 (H238), P&P Spangler.

For a map of examined material, see: <https://bit.ly/2Gvhsd0>

Zosteragathis sakonensis Sharkey, sp. n.

<http://zoobank.org/F7739620-FD6B-4ECE-8C7B-D960CD6A221C>

Diagnosis. Head black except clypeus and lower gena yellow, T1 and T2 predominantly pale yellow, T1 with a

large melanic spot in basal half, T2 with (or without) melanic infusion posteromedially; second submarginal cell minute pedicel much longer than cell height, diameter about equal to width of pedicel.

Description. Body length 3.6 mm. Ovipositor length 3.0 mm. Ovipositor $0.8\times$ body length. Number of flagellomeres 29. Notauli sculpture not significantly wider posteriorly. Scutellum smooth with punctures. Mid tibia with 2 apical and 3 preapical spines. Hind tibia with 6 spines/pegs. Second submarginal cell diameter minute, about equal to width of vein. Wing hyaline with an infuscate patch posterior to stigma. T2 weakly striate, striae almost absent anteromedially, weakly converging in posterior half. **Color:** head black except clypeus and lower gena yellow; mesosoma black; fore and mid coxae yellow; T1 and T2 predominantly pale yellow, T1 with a large melanic spot in basal half, T2 with melanic infusion posteromedially.

Etymology. Named after the type locality Sakon Nakhon Provence.

Material examined. Holotype: Female: *Thailand*, Sakon Nakhon, Phu Phan NP, Behind forest protection unit at Huay Wien Prai, 17.114°N , 104.005°E , 318 m elev., Malaise trap, 17–25.ii.2007 (H091, T1690), Sailom Tongboonchai. **Paratypes:** All female: *Thailand*, Surat Thani, Khao Sok NP, Headquarter, 8.9149°N , 98.5301°E , 115 m elev., Malaise trap, 2–9.xii.2008 (H3805, T3870), Pongphan; Phetchabun, Khao Kho NP, Mixed deciduous forest, 16.543°N , 101.041°E , 537 m elev., Malaise trap, 5–12.xii.2006 (H148, T1178), Somchai Chachumnan & Saink Singtong.

For a map of examined material, see: <https://bit.ly/2G-g3UTu>

Zosteragathis samensis Sharkey, sp. n.

<http://zoobank.org/39CBB49C-FAE4-4034-8677-D2B1CBF988DE>

Diagnosis. Fore coxa yellow. Hind femur black. T2 mostly pale in anterior half and mostly melanic in posterior half. Scutellum sculpture smooth with punctures. T2 dimensions as wide as long or wider.

Description. Body length 5.4 mm. Ovipositor length 3.3 mm. Ovipositor $0.6\times$ body length. Number of flagellomeres 31. Notauli sculpture not significantly wider posteriorly. Scutellum smooth with punctures. Mid tibia with 3 apical and 2 preapical spines. Hind tibia with 8 spines/pegs. Second submarginal cell diameter small, smaller than pedicel length, but larger than pedicel width. Wing hyaline with an infuscate patch posterior to stigma. T2 $0.9\times$ longer than wide. T2 entirely striate, striae weak anteromedially where they converge medially. **Color:** head black except gena yellow; mesosoma black; fore and mid coxa yellow; posterior margin of T1 yellow; anterior half of T2 yellow.

Etymology. Named after the type locality Khao Sam Roi Yot National Park.

Material examined. Holotype: Female: *Thailand*, Prachuab Khiri Khan, Khao Sam Roi Yot NP, Khao Look

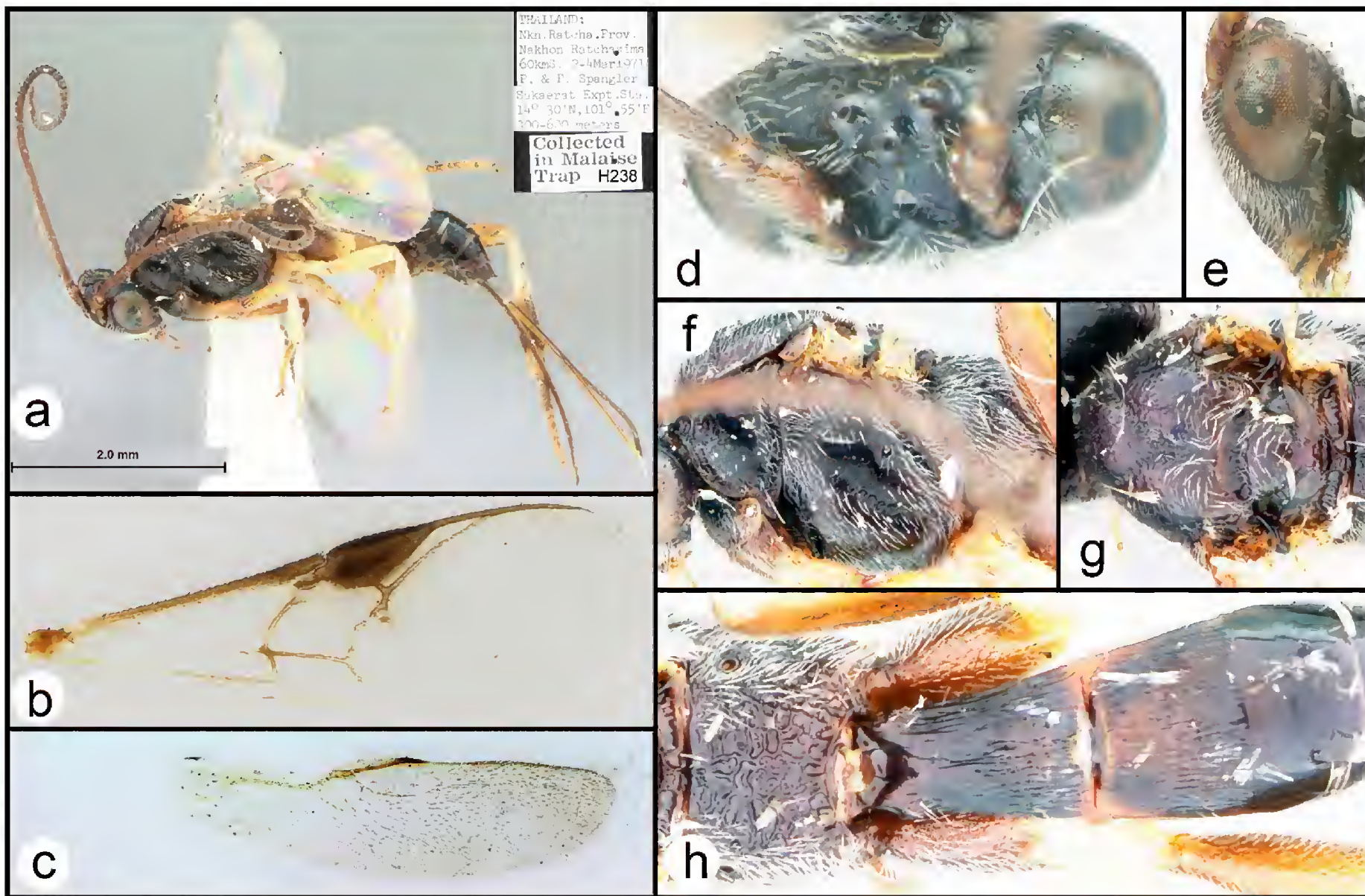


Figure 18. *Z. sakaeratis*: a) lateral habitus. b) fore wing. c) hind wing. d) dorsal head. e) lateral head. f) lateral mesosoma. g) dorsal mesoscutum. h) propodeum and T1–3.

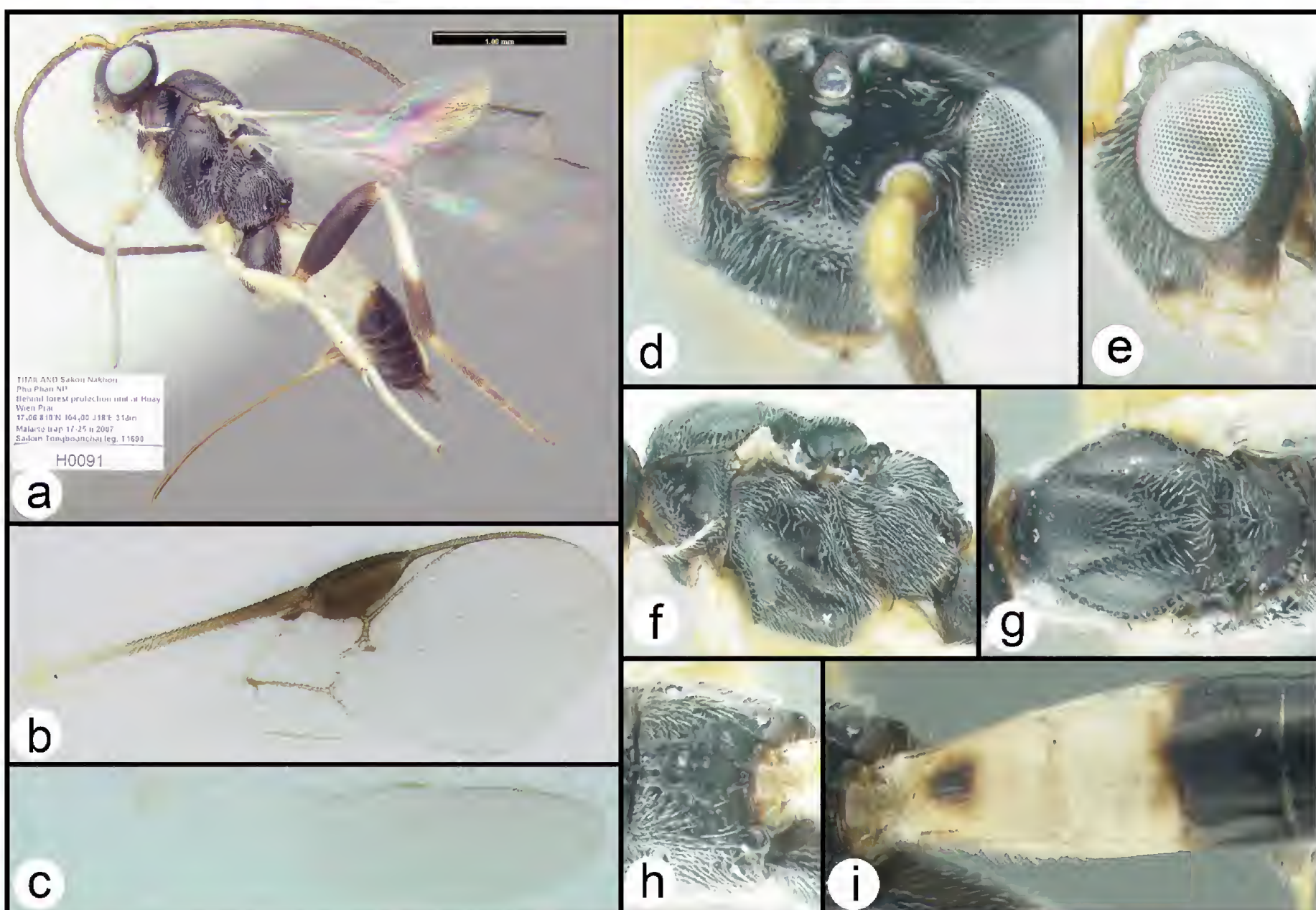


Figure 19. *Z. sakonensis*: a) lateral habitus. b) fore wing. c) hind wing. d) dorsal head. e) lateral head. f) lateral mesosoma. g) dorsal mesoscutum. h) propodeum. i) T1–3.

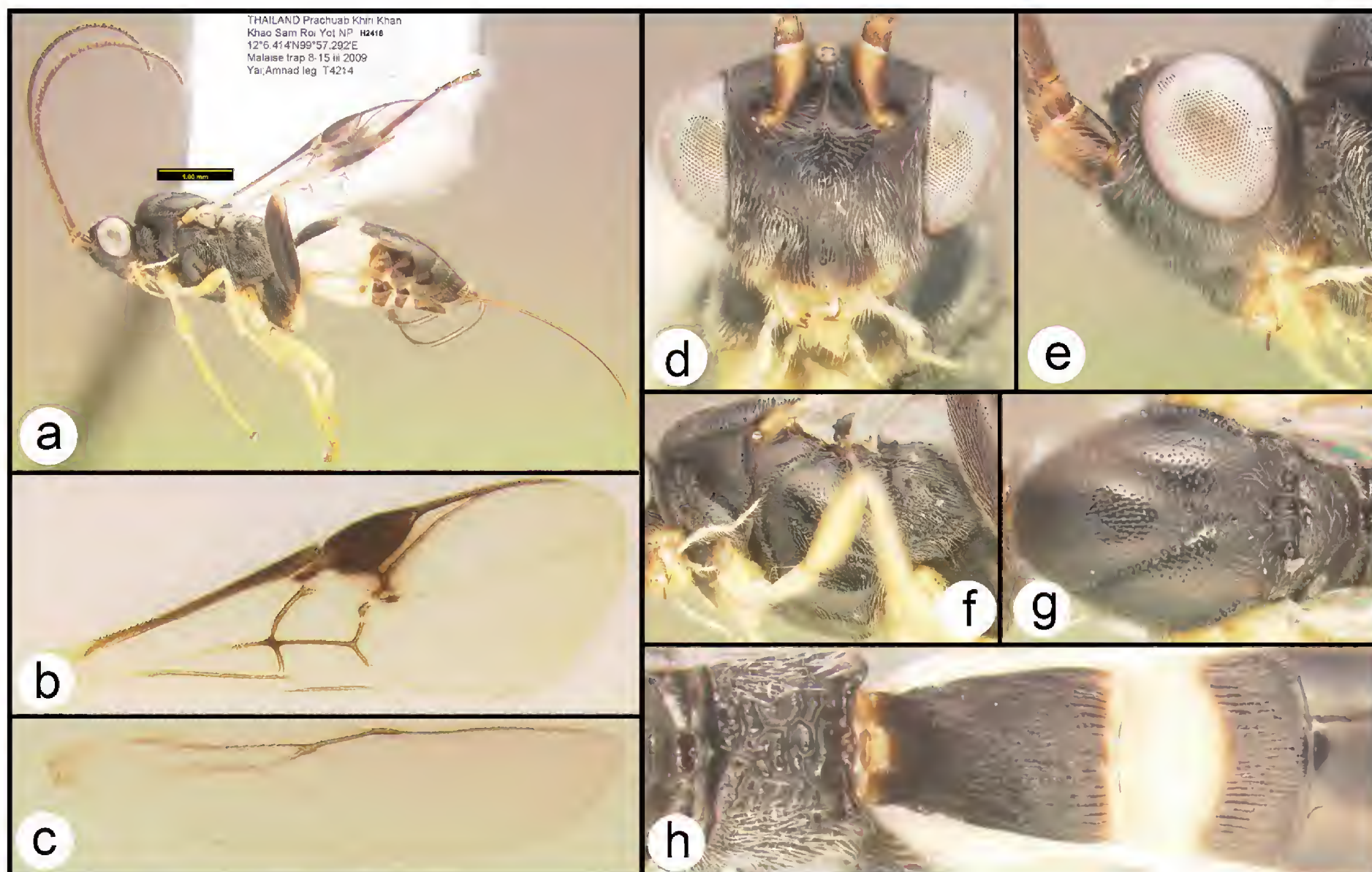


Figure 20. *Z. samensis*: **a)** lateral habitus. **b)** fore wing. **c)** hind wing. **d)** anterior head. **e)** lateral head. **f)** lateral mesosoma. **g)** dorsal mesoscutum. **h)** propodeum and T1–3.

Glang, 12.107°N, 99.955°E, 20 m elev., Malaise trap, 8–15.iii.2009 (H2418, T4214), Yai Amnad. **Paratypes:** All female: **Thailand**, Prachuab Khiri Khan, Khao Sam Roi Yot NP, foot of Khao Taen, 12.146°N, 99.966°E, 1 m elev., Malaise trap, 3–10.v.2009 (H638, H968, T4825), Yai Amnad; Prachuab Khiri Khan, Khao Sam Roi Yot NP, 30m N, protection unit4, 12.268°N, 99.944°E, 1 m elev., Malaise trap, 3–10.v.2009 (H973, T4824) 24–31.v.2009 (H490, T4833), Yai Amnad; Lampang, Chae Son NP, Youthcamp, 18.83°N, 99.471°E, 455 m elev., Malaise trap, 1–7.iv.2008 (H901, T5421), B. Kwannui & A. Sukpeng; Mae Hong Son, Namtok Mae Surin NP, Haad Saen, 19.348°N, 97.985°E, 257 m elev., Malaise trap, 27.iv-4.v.2008 (H481, T3507), Na-maadkam, M; Prachuab Khiri Khan, Khao Sam Roi Yot NP, Saline wetland, Pa Gwad, N, 12.153°N, 99.972°E, 1 m elev., Malaise trap, 15–22.iii.2009 (H670, T4216), Yai Amnad.

For a map of examined material, see: <https://bit.ly/2IZCper>

***Zosteragathis surinensis* Sharkey, sp. n.**

<http://zoobank.org/5FCED594-58B2-4EED-BD95-BC2D4A875A67>

Diagnosis. Hind femur yellow, hind coxa mostly yellow; hind tibia with many spines (9 or more).

Description. Body length 3.6 mm. Ovipositor length 3.4 mm. Ovipositor 1.0× body length. Number of flagellomeres 29. Notauli sculpture not significantly wider posteriorly. Scutellum smooth with punctures. Mid tibia with

3 apical and 3 preapical spines. Hind tibia with 11 spines/pegs. Second submarginal cell diameter large, larger than length of pedicel. Wing hyaline, without distinct infuscate areas. T2 1.2× longer than wide. T2 entirely striate, striae weak anteromedially, striae relatively straight. **Color:** head black except gena ventrally and clypeus yellow; mesosoma melanic; fore and mid coxae yellow; hind coxa yellow in apical half; hind femur yellow; apex of T1 yellow; T2 yellow in basal half.

Etymology. Named after the type locality Namtok Mae Surin National Park.

Material examined. Holotype: Female: **Thailand**, Mae Hong Son, Namtok Mae Surin NP, E Huai Fai Kor reservoir, 19.344°N, 97.988°E, 311 m elev., Malaise trap, 18–25.v.2008 (H598, T3518), Kamkoon, A.

For a map of examined material, see: <https://bit.ly/2IYZA91>

***Zosteragathis taemensis* Sharkey, sp. n.**

<http://zoobank.org/038CCAA1-97ED-42BB-8433-39D600685C15>

Diagnosis. Fore and mid coxae mostly melanic; scutellar groove pale; area posterior to fore wing stigma distinctly infuscate.

Description. Body length 6.1 mm. Ovipositor length 5.3 mm. Ovipositor 0.9× body length. Number of flagellomeres 34. Notauli sculpture not significantly wider posteriorly. Scutellum smooth with punctures. Mid tibia with 4 apical and 4 preapical spines. Hind tibia with 9 spines/

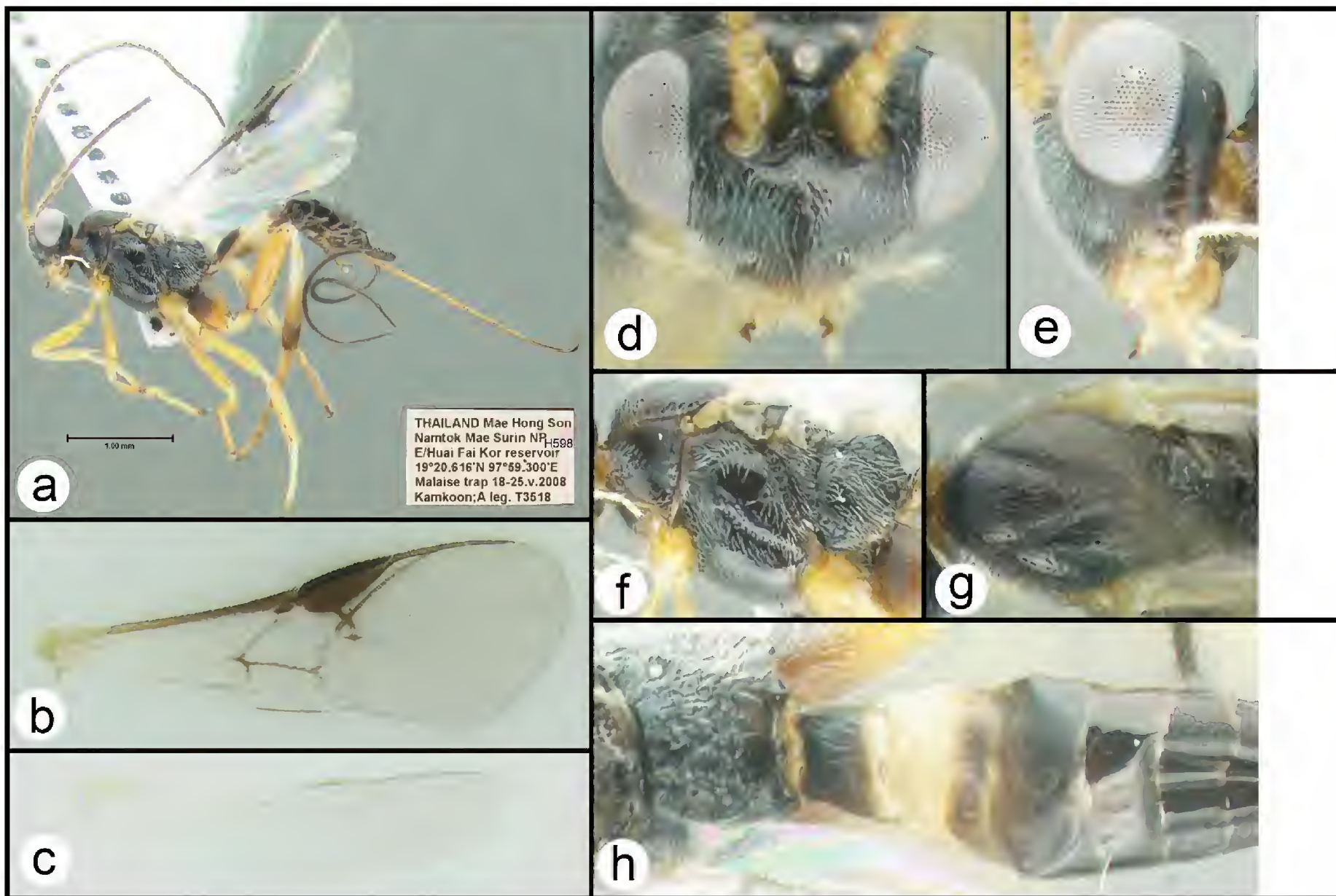


Figure 21. *Z. surinensis*: a) lateral habitus. b) fore wing. c) hind wing. d) anterior head. e) lateral head. f) lateral mesosoma. g) dorsal mesoscutum. h) propodeum and T1–3.

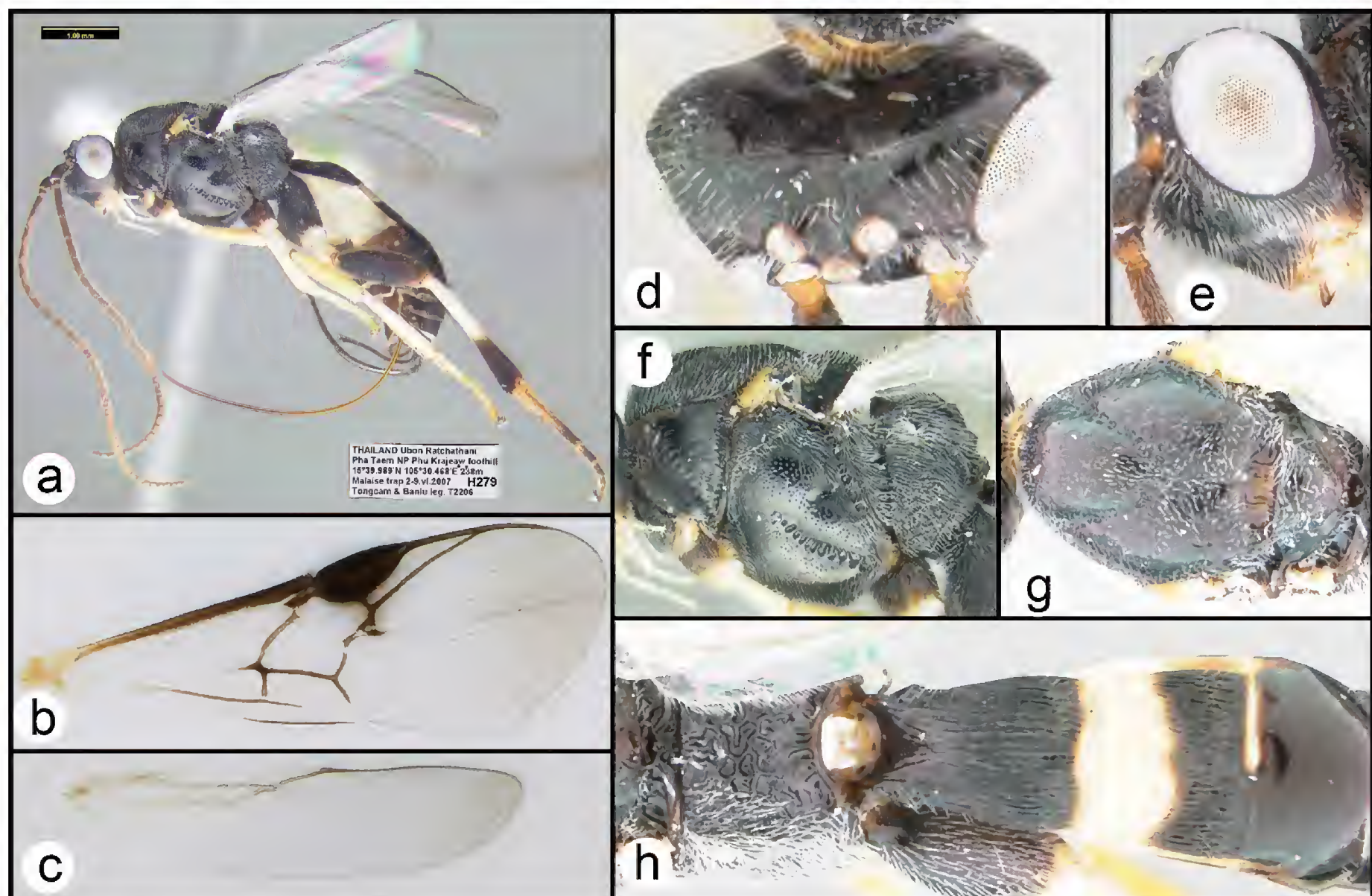


Figure 22. *Z. taemensis*: a) lateral habitus. b) fore wing. c) hind wing. d) dorsal head. e) lateral head. f) lateral mesosoma. g) dorsal mesoscutum. h) propodeum and T1–3.

pegs. Second submarginal cell diameter minute, about equal to width of vein. Wing hyaline with an infuscate patch posterior to stigma. T2 0.9× longer than wide. T2 entirely striate, semicircular pattern anteromedially, striae converging posterior to this pattern. **Color:** head black except ventral gena and ventral clypeus yellow; mesosoma black except scutellar groove pale; fore and mid coxae predominantly melanic; T1 black except posterior margin yellow; T2 yellow in anterior half.

Etymology. Named after the type locality Pha Taem National Park.

Material examined. Holotype: Female: *Thailand*, Ubon Ratchathani, Pha Taem NP, Phu Krajeaw foothill, 15.666°N, 105.508°E, 238 m elev., Malaise trap, 2–9.vi.2007 (H279, T2206), Tongcam & Banlu.

For a map of examined material, see: <https://bit.ly/2uq1wnv>

***Zosteragathis tonensis* Sharkey, sp. n.**

<http://zoobank.org/7B26BD3D-743D-41B7-8F4F-D86A7D4EA605>

Diagnosis. Ovipositor longer than body.

Description. Body length 4.5 mm. Ovipositor length 5.2 mm. Ovipositor 1.2× body length. Number of flagellomeres 31. Notauli sculpture not significantly wider posteriorly. Scutellum smooth with punctures. Mid tibia with 3 apical and 3 preapical spines. Hind tibia with 7 spines/pegs. Second submarginal cell diameter small, smaller than pedicel length, but larger than pedicel width. Wing hyaline with an infuscate patch posterior to stigma. T2 1.1× longer than wide. T2

entirely striate, striae relatively straight. **Color:** head black except ventral gena yellow; mesosoma black; fore and hind coxa black; posterior margin of T1 yellow; T2 mostly yellow in basal half with melanic tones posteromedially.

Etymology. Named after the type locality Tat Tone National Park.

Material examined. Holotype: Female: *Thailand*, Chaiyaphum, Tat Tone NP, Near stream, 15.98°N, 102.04°E, 305 m elev., Malaise trap, 12–19.vii.2006 (H016, T220), T. Jaruphan & O. Budsawong.

For a map of examined material, see: <https://bit.ly/2I-W47ZC>

Acknowledgements

We thank the staff at Queen Sirikit Botanic Garden in Chaing Mai, Thailand for sorting the many hundreds of samples and for the Thai park staff for operating Malaise traps and other collection devices. A special thanks to Chaweewan Hutacharern for managing the Thai end of the TIGER project. Special thanks also to Kees van Achterberg for lending specimens and types from Vietnam. Funding was provided by NSF grants DEB-0542864 and EF-0337220 and by Hatch projects KY008041 and KY008065 (to MJS). The information reported in this paper (No. 18-08-052) is part of a project of the Kentucky Agricultural Experiment Station and is published with the approval of the Director. Many thanks to Drs Jim Whitfield and Donald Quicke who reviewed the manuscript.

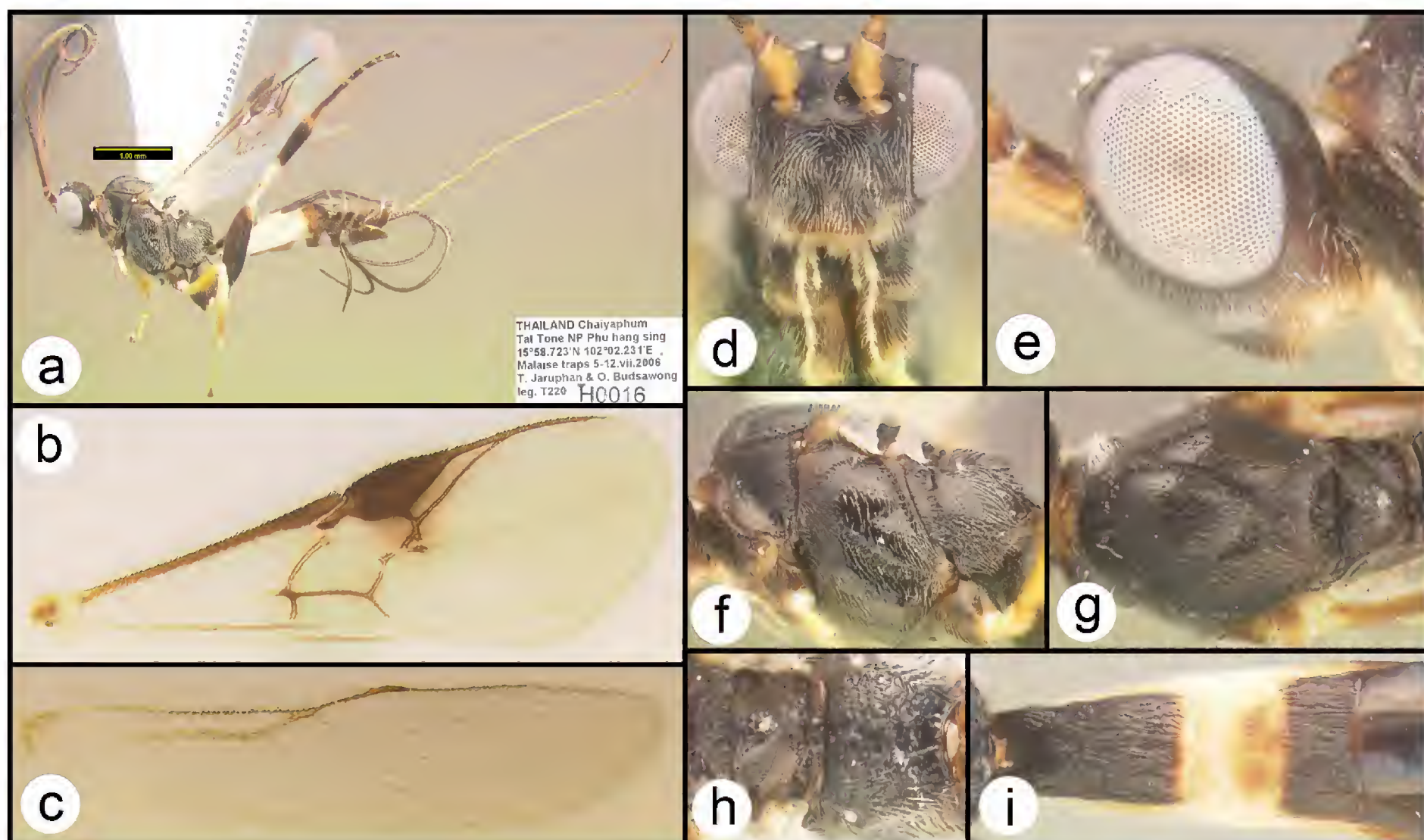


Figure 23. *Z. tonensis*: a) lateral habitus. b) fore wing. c) hind wing. d) anterior head. e) lateral head. f) lateral mesosoma. g) dorsal mesoscutum. h) scutellum and propodeum. i) T1–3.

References

- Achterberg C van, Long KD (2010) Revision of the Agathidinae (Hymenoptera, Braconidae) of Vietnam, with the description of forty-two new species and three new genera. *ZooKeys* 54: 1–184. <https://doi.org/10.3897/zookeys.54.475>
- Drummon AJ, Ashton B, Cheung M, Heled J, Kearse M, Moir R, Stones-Havas S, Thierer T, Wilson A (2009) Geneious version 6.1.5. <http://www.geneious.com> [accessed 1 April 2015]
- Felsenstein J (1985) Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39: 783–791. <https://doi.org/10.1111/j.1558-5646.1985.tb00420.x>
- Gries C, Gilbert EE, Franz NM (2014) Symbiota – A virtual platform for creating voucher-based biodiversity information communities. *Biodiversity Data Journal* 2014(2): e1114. <https://doi.org/10.3897/BDJ.2.e1114>
- Huelsenbeck JP, Rannala B (2004) Frequentist properties of Bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. *Systematic Biology* 53: 904–913. <https://doi.org/10.1080/10635150490522629>
- Nixon GEJ (1950) New Indian Braconidae bred from lepidopterous defoliators (Hymenoptera). *Annals and Magazine of Natural History* 12(3): 453–474. <https://doi.org/10.1080/00222935008654071>
- Rodriguez F, Oliver JL, Marin A, Medina JR (1990) The general stochastic model of nucleotide substitution. *Journal of Theoretical Biology* 142: 485–501. [https://doi.org/10.1016/S0022-5193\(05\)80104-3](https://doi.org/10.1016/S0022-5193(05)80104-3)
- Sharkey MJ, Chapman EG (2017a) Ten new genera of Agathidini (Hymenoptera: Braconidae: Agathidinae) from Southeast Asia. *Zootaxa* 660: 107–150. <https://doi.org/10.3897/zookeys.660.12390>
- Sharkey MJ, Chapman EG (2017b) Phylogeny of the Agathidinae (Hymenoptera: Braconidae) with a revised tribal classification and the description of a new genus. *Proceedings of the Entomological Society of Washington* 119 (Special Issue): 823–842. <https://doi.org/10.4289/0013-8797.119.SpecialIssue.823>
- Sharkey MJ, Clutts SA (2011) A revision of Thai Agathidinae (Hymenoptera: Braconidae), with descriptions of six new species. *Journal of Hymenoptera Research* 22: 69–132. <https://doi.org/10.3897/jhr.22.1299>
- Sharkey MJ, Clutts SA, Tucker EM, Janzen DH, Hallwachs W, Dapkey T, Smith MA (2011a) *Lytopylus* Forster (Hymenoptera, Braconidae, Agathidinae) species from Costa Rica, with an emphasis on specimens reared from caterpillars in Area de Conservación Guanacaste. *Zookeys* 130: 379–419. <https://doi.org/10.3897/zookeys.130.1569>
- Sharkey MJ, Parys KA, Clutts SA (2011b) A new genus of Agathidinae with the description of a new species parasitic on *Samea multiplicalis* (Guenee). *Journal of Hymenoptera Research* 23: 43–53. <https://doi.org/10.3897/jhr.23.1100>
- Sharkey MJ, Laurenne NM, Sharanowski BJ, Quicke DLJ, Murray D (2006) Revision of the Agathidinae (Hymenoptera: Braconidae) with comparisons of static and dynamic alignments. *Cladistics* 22: 546–567. <https://doi.org/10.1111/j.1096-0031.2006.00121.x>
- Sharkey MJ, Stoelb SAC (2012) Revision of *Therophilus* s.s. (Hymenoptera, Braconidae, Agathidinae) from Thailand. *Journal of Hymenoptera Research* 27: 1–36. <https://doi.org/10.3897/jhr.27.2832>
- Sharkey MJ, Stoelb SAC (2013) Revision of *Agathacrista* new genus (Hymenoptera, Braconidae, Agathidinae, Agathidini). *Journal of Hymenoptera Research* 33: 99–112. <https://doi.org/10.3897/jhr.33.4373>
- Sharkey MJ, Wharton RA (1997) Morphology and terminology. Manual of the New World genera of Braconidae (Hymenoptera). In: Wharton RA, Marsh PM, Sharkey MJ (Eds) Special Publication of the International Society of Hymenopterists. Vol. 1. International Society of Hymenopterists, Washington DC, 19–38.
- Watanabe C (1970) Notes on Braconid parasites of Lepidopterous leaf-rollers with descriptions of two new species (Hymenoptera, Braconidae). *Mushi* 43: 121–126.
- Yoder MJ, Mikó I, Seltmann KC, Bertone MA, Deans AR (2010) A gross anatomy ontology for Hymenoptera. *PLoS ONE* 5(12): e15991. <https://doi.org/10.1371/journal.pone.0015991>
- Yu DS, Achterberg C van, Horstmann K (2012) World Ichneumonidea 2012. Taxonomy, biology, morphology and distribution [Ichneumonidae]. Taxapad 2012 (Scientific names for information management) Interactive catalogue, Vancouver, Canada. [Flash drive]
- Zwickl DJ (2006) Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. PhD dissertation: The University of Texas at Austin. <https://code.google.com/archive/p/garli/> [accessed 1 April 2015]

Appendix 1

Table 2. Specimens used in the phylogenetic analyses, including specimen numbers, and GenBank and BOLD accession numbers and rough geographical information.

Taxon name	Number	Country: Region	Type status	COI	28S
<i>Aerophilus abdominalis</i>	H1313	USA: KY		ATRMK294-11	KP943685
<i>Aerophilus malus</i>	H1484	USA: WV	holotype	ATRMK309-11	KP943693
<i>Aerophilus rayfisheri</i>	H1212	USA: KY	holotype	ATRMK278-11	KP943675
<i>Agathacrista depressifera</i>	H002	Thailand: Phetchabun		KP943596	KC556782
<i>Agathacrista krataei</i>	H268	Thailand: Kalasin	holotype	KP943614	KC556781
<i>Agathacrista sailomi</i>	H013	Thailand: Chiang Mai	holotype	KX431796	KC556780
<i>Agathacrista winloni</i>	H502	Thailand: Phetchabun	holotype	ATRMK218-11	KC771135
<i>Agathigma templei</i>	H415	Thailand: Kamphaeng	holotype	ATRMK211-11	KX431753
<i>Alabagrus maculipes</i>	H6020	Mexico: Jalisco		ATRMK370-11	KP943698
<i>Asperagathis aspera</i>	H274	Thailand: Phetchabun	holotype	KX431797	KX431706
<i>Asperagathis xesta</i>	H095	Thailand: Chaiyaphum	holotype	KX431798	KX431707
<i>Bassus albifasciatus</i>	H014	Thailand: Sakon Nakhon		–	KX431714
<i>Bassus albifasciatus</i>	H027	Thailand: Trang		KX431800	KX431716

Taxon name	Number	Country: Region	Type status	COI	28S
<i>Bassus albifasciatus</i>	H032	Thailand: Trang		KX431799	KX431715
<i>Bassus albifasciatus</i>	H085	Thailand: Trang		KX431801	KX431719
<i>Bassus albifasciatus</i>	H343	Thailand: Chiang Mai		–	KX431718
<i>Bassus albifasciatus</i>	H377	Thailand: Nakhon Si Thammarat		–	KX431717
<i>Bassus alboapicalis</i>	H021	Thailand: Trang	paratype	KX431821	KX431767
<i>Bassus alboapicalis</i>	H022	Thailand: Trang	paratype	KX431819	KX431764
<i>Bassus alboapicalis</i>	H081	Thailand: Trang	paratype	KX431817	KX431762
<i>Bassus alboapicalis</i>	H269	Thailand: Trang	holotype	KX431820	KX431766
<i>Bassus alboapicalis</i>	H270	Thailand: Trang	paratype	KX431818	KX431763
<i>Bassus alboapicalis</i>	H307	Thailand: Surat Thani	paratype	ATRMK195-11	KX431765
<i>Bassus alboapicalis</i>	H410	Thailand: Nakhon Si Thammarat	paratype	–	KX431761
<i>Bassus albobasalis</i>	H003	Thailand: Phetchabun		KX431802	KX431721
<i>Bassus albobasalis</i>	H092	Thailand: Trang		–	KX431720
<i>Bassus albobasalis</i>	H328	Thailand: Phetchabun		JQ763436	KX431722
<i>Bassus albocyclus</i>	H308	Thailand: Phetchabun	paratype	–	KX431724
<i>Bassus albocyclus</i>	H349	Thailand: Chiang Mai	paratype	–	KX431725
<i>Bassus albocyclus</i>	H636	Thailand: Suphan Buri	holotype	ATRMK230-11	KX431723
<i>Bassus calculator</i>	H8008	Sweden: Stockholms län		–	KX431712
<i>Bassus mediatratus</i>	H015	Thailand: Chiang Mai	holotype	KX431816	KX431760
<i>Bassus nopachoni</i>	H577	Thailand: Kamphaeng	holotype	ATRMK223-11	KX431713
<i>Bassus pallidus</i>	H055	Thailand: Chanthaburi	holotype	–	KX431710
<i>Bassus</i> sp.	H376	Thailand: Phetchaburi		ATRMK204-11	KX431711
<i>Braunsia smithii</i>	H906	Thailand: Chiang Mai		ATRMK261-11	HQ667949
<i>Camptothlipsis lingualongis</i>	H1887	South Africa: Western Cape	paratype	ATRMK334-11	JN564494
<i>Camptothlipsis nigra</i>	H433	Thailand: Prachuap Khiri Khan		ATRMK430-11	HQ667951
<i>Camptothlipsis sheilae</i>	H664	Thailand: Kanchanaburi	holotype	ATRMK235-11	HQ667954
<i>Camptothlipsis</i> sp.	H162	Uganda: Homa Bay		–	KX431699
<i>Camptothlipsis</i> sp.	H2299	Congo: Pool		–	KX431698
<i>Chimaeragathis chrysoma</i>	H710	Thailand: Phetchaburi	holotype	ATRMK240-11	KX431738
<i>Chimaeragathis eurysona</i>	H045	Thailand: Trang	paratype	KX431805	KX431736
<i>Chimaeragathis eurysona</i>	H069	Thailand: Trang	paratype	KX431806	KX431737
<i>Chimaeragathis eurysona</i>	H925	Thailand: Phetchaburi	holotype	ATRMK265-11	KX431735
<i>Chimaeragathis lohmani</i>	H072	Thailand: Trang	holotype	KX431807	KX431739
<i>Chimaeragathis lohmani</i>	H077	Thailand: Trang	paratype	KX431808	KX431740
<i>Cymagathis krikoma</i>	H290	Thailand: Chaiyaphum	paratype	ATRMK192-11	KX431701
<i>Gyragathis leucosoma</i>	H275	Thailand: Nakhon Ratchasima	holotype	KX431794	KX431700
<i>Leuroagathis paulbakeri</i>	H369	Thailand: Prachuap Khiri Khan	holotype	–	KX431709
<i>Liragathis baonai</i>	H360	Thailand: Nakhon Si Thammarat	holotype	ATRMK200-11	KX431705
<i>Liragathis damnai</i>	H397	Thailand: Chiang Mai	paratype	ATRMK210-11	KX431704
<i>Liragathis javana</i>	H283	Thailand: Trang		KX431795	KX431702
<i>Liragathis javana</i>	H628	Thailand: Phetchabun		ATRMK228-11	KX431703
<i>Neothlipsis</i> sp.	H195	Thailand: Surat Thani		KP943607	KP943660
<i>Neothlipsis</i> sp.	H198	USA: KY		KX431793	KX431697
<i>Neothlipsis</i> sp.	H7618	Mexico: Yucatan		ATRMK403-11	KP943709
<i>Neothlipsis parysae</i>	H4428	USA: KY	paratype	ATRMK364-11	KX431696
<i>Scabagathis emilynadeauae</i>	H033	Thailand: Trang	holotype	KX431792	KX431695
<i>Trochantagathis marshi</i>	H067	Thailand: Trang		KX431809	KX431742
<i>Trochantagathis marshi</i>	H089	Thailand: Trang		KX431811	KX431745
<i>Trochantagathis marshi</i>	H1851	Thailand: Trang		–	KX431744
<i>Trochantagathis marshi</i>	H281	Thailand: Trang		KX431810	KX431743
<i>Trochantagathis marshi</i>	H765	Thailand: Ubon Ratchathani		ATRMK242-11	KX431741
<i>Trochantagathis marshi</i>	H799	Thailand: Suphan Buri		–	KX431746
<i>Trochantagathis marshi</i>	H965	Thailand: Nakhon Si Thammarat		ATRMK266-11	KX431747
<i>Xanthagathis mellisoma</i>	H060	Thailand: Trang		KX431812	KX431749
<i>Xanthagathis mellisoma</i>	H145	Thailand: Phetchabun		–	KX431748
<i>Xanthagathis mellisoma</i>	H286	Thailand: Chaiyaphum		ATRMK191-11	KX431751
<i>Xanthagathis mellisoma</i>	H348	Thailand: Chiang Mai		ATRMK199-11	KX431750
<i>Xanthagathis mellisoma</i>	H662	Thailand: Phetchaburi		ATRMK234-11	KX431752
<i>Zosteragathis contrasta</i>	H017	Thailand: Chiang Mai		KX431828	KX431783
<i>Zosteragathis contrasta</i>	H056	Thailand: Trang		KX431834	KX431790

Taxon name	Number	Country: Region	Type status	COI	28S
<i>Zosteragathis contrasta</i>	H094	Thailand: Chiang Mai		KX431833	KX431789
<i>Zosteragathis contrasta</i>	H100	Thailand: Chaiyaphum		KX431832	KX431787
<i>Zosteragathis contrasta</i>	H101	Thailand: Loei		KX431827	KX431781
<i>Zosteragathis contrasta</i>	H104	Thailand: Loei		–	KX431782
<i>Zosteragathis contrasta</i>	H142	Thailand: Nakhon Ratchasima		–	KX431779
<i>Zosteragathis contrasta</i>	H143	Thailand: Phetchabun		KX431829	KX431784
<i>Zosteragathis contrasta</i>	H144	Thailand: Phetchabun		KX431830	KX431785
<i>Zosteragathis contrasta</i>	H146	Thailand: Phetchabun		KX431831	KX431786
<i>Zosteragathis contrasta</i>	H149	Thailand: Phetchabun		KX431826	KX431780
<i>Zosteragathis contrasta</i>	H1855	Thailand: Chaiyaphum		ATRMK501-11	–
<i>Zosteragathis contrasta</i>	H603	Thailand: Surat Thani		ATRMK226-11	KX431791
<i>Zosteragathis contrasta</i>	H677	Thailand: Suphan Buri		–	KX431788
<i>Zosteragathis contrastus</i>	H985	Thailand: Kanchanaburi		–	KX431778
<i>Zosteragathis eukos</i>	H689	Thailand: Suphan Buri	holotype	ATRMK238-11	KX431755
<i>Zosteragathis hongensis</i>	H660	Thailand: Mae Hong Son	holotype	ATRMK233-11	KX431727
<i>Zosteragathis inthanonensis</i>	H080	Thailand: Chiang Mai	holotype	KX431814	KX431757
<i>Zosteragathis krachanensis</i>	H492	Thailand: Phetchaburi	holotype	ATRMK217-11	KX431728
<i>Zosteragathis lampangensis</i>	H237	Thailand: Lampang	holotype	KX431815	KX431758
<i>Zosteragathis lampangensis</i>	H989	Thailand: Phetchaburi	paratype	ATRMK271-11	KX431759
<i>Zosteragathis lampooensis</i>	H121	Thailand: Nong Bua Lam Phu	paratype	KX431822	KX431771
<i>Zosteragathis lampooensis</i>	H122	Thailand: Nong Bua Lam Phu	holotype	KX431823	KX431772
<i>Zosteragathis lampooensis</i>	H650	Thailand: Phetchabun	paratype	ATRMK232-11	KX431769
<i>Zosteragathis lampooensis</i>	H1636	Thailand: Ubon Ratchathani	paratype	ATRMK325-11	KX431770
<i>Zosteragathis luangensis</i>	H1859	Thailand: Phitsanulok	holotype	ATRMK329-11	KX431729
<i>Zosteragathis ngamensis</i>	H1625	Thailand: Chaiyaphum	holotype	ATRMK323-11	KX431754
<i>Zosteragathis nuichuaensis</i>	H065	Thailand: Trang		KX431803	KX431733
<i>Zosteragathis nuichuaensis</i>	H083	Thailand: Trang		KX431804	KX431734
<i>Zosteragathis nuichuaensis</i>	H239	Thailand: Trang		–	KX431732
<i>Zosteragathis petchaburiensis</i>	H473	Thailand: Phetchaburi	holotype	ATRMK216-11	KX431708
<i>Zosteragathis phahompokensis</i>	H1858	Thailand: Chiang Mai	holotype	ATRMK328-11	KX431777
<i>Zosteragathis sakonensis</i>	H091	Thailand: Sakon Nakhon	holotype	KX443589	KX431726
<i>Zosteragathis samensis</i>	H2418	Thailand: Prachuap Khiri Khan	holotype	ATRMK475-11	KX431775
<i>Zosteragathis samensis</i>	H973	Thailand: Prachuap Khiri Khan	paratype	ATRMK269-11	KX431774
<i>Zosteragathis surinensis</i>	H598	Thailand: Mae Hong Son	holotype	ATRMK225-11	KX431768
<i>Zosteragathis taemensis</i>	H279	Thailand: Ubon Ratchathani	holotype	KX431824	KX431773
<i>Zosteragathis tonensis</i>	H016	Thailand: Chaiyaphum	holotype	KX431825	KX431776
<i>Zosteragathis</i> sp. n. 1	H687	Thailand: Nakhon Si Thammarat		–	KX431730
<i>Zosteragathis</i> sp. n. 2	H1860	Thailand: Surat Thani		ATRMK330-11	KX431731

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Deutsche Entomologische Zeitschrift

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