ZooKeys 1073: 1–12 (2021)
doi: 10.3897/zookeys.1073.73241
https://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

A new *Diancta* species of the family Diplommatinidae (Cyclophoroidea) from Vanua Levu Island, Fiji

Estée Bochud[1,2], David Haberthür[3], Ruslan Hlushchuk[3], Eike Neubert[1,2]

1 *Natural History Museum of the Burgergemeinde Bern, Bernastrasse 15, CH-3005 Bern, Switzerland* **2** *Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland* **3** *Institute of Anatomy, University of Bern, Baltzerstrasse 2, CH-3012 Bern, Switzerland*

Corresponding author: Estée Bochud (estee.bochud@nmbe.ch)

Academic editor: Frank Köhler | Received 24 August 2021 | Accepted 18 October 2021 | Published 29 November 2021

http://zoobank.org/39EF7BB8-1A4E-45AA-B7C7-937ACB1DBD95

Citation: Bochud E, Haberthür D, Hlushchuk R, Neubert E (2021) A new *Diancta* species of the family Diplommatinidae (Cyclophoroidea) from Vanua Levu Island, Fiji. ZooKeys 1073: 1–12. https://doi.org/10.3897/zookeys.1073.73241

Abstract

A new species of *Diancta* of the staircase snail family Diplommatinidae is described from Mt. Savusavu, Vanua Levu Island, Fiji. Due to its left coiling shell and a constriction before the last whorl, it is placed in the genus *Diancta*. Micro-CT imaging reveals two apertural teeth and an inner lamella that is situated at the zone of constriction. The shell abruptly changes coiling direction by 45 degrees before the last whorl. Up to now, this coiling modus had not yet been documented for any species of Diplommatinidae from the Fiji Islands.

Keywords

Diancta, Diplommatinidae, Fiji, new species, Oceania, terrestrial malacology

Introduction

Micromolluscs are defined being smaller than 5 mm and can be found in all parts of the world. They belong to different gastropod groups, are diverse in their habitat needs, appearance and, due to their small size, certainly underexplored. Still, many new species are found in all parts of the world. Usually, little is known about their ecology, distribution patterns and morphological variability. Because of their limited dispersal capabilities and microhabitat needs, microsnails demonstrate a high endemism rate. Terrestrial island snails especially show a high endemism rate of about 75% (Proios et al. 2021). Although the Diplommatinidae are distributed worldwide, there is one group among the terrestrial island micromolluscs that is particularly well represented in the Indo-Pacific region from Southeast Asia to the south-west Pacific and Australia (Stanisic et al. 2010). It is also one of the most locally and regionally diverse land snail families (Webster et al. 2012), showing high endemism. For example, from the Papuan and Wallacean region, 127 species are known (Greke 2021), on Borneo nearly 170 diplommatinid taxa are found (Liew and Schilthuizen 2016), and on the Fiji islands 42 species had been documented so far (Neubert and Bouchet 2015).

Diplommatinids are known for having a zone of constriction close to the aperture (Egorov and Greke 2003), internal teeth and lamellar structures (Thiele 1929), while some genera are characterized by a change in the coiling direction of the shell axis (Webster et al. 2012). The shell of the new species presented here is remarkable because it changes its coiling direction upwards to the apex and again back to its original coiling axis. This coiling mode was not yet known for any other species of Diplommatinidae from Fiji Islands.

This study is based on a dry sample collected by Otto Degener in 1941 on the island Vanua Levu of Fiji, previously housed in the MCZ collection (Cambridge, Massachusetts, USA). It aims to provide further information on the land snail richness of the Fiji Islands, particularly that of Vanua Levu, by describing this new diplommatinid species and providing the first diplommatinid record from western Vanua Levu. Dating from the Late Eocene, Vanua Levu is the second largest island within the Fiji Archipelago, which consists of more than 332 volcanic islands (Neall and Trewick 2008). As is known for other Fijian islands, some areas are covered by isolated limestone blocks presenting ideal ecological niches for Diplommatinidae. Despite its large area of 5807 square kilometres, only two localities of Vanua Levu are known for diplommatids, Waivunia village and Netewa Peninsula, from which nine species have been identified so far (Neubert and Bouchet 2015; Barker and Narosamalua 2017).

So far, the Fiji Islands are home to the diplommatinid genera *Diancta* E. von Martens, 1864, *Moussonia* O. Semper, 1865 and *Palaina* O. Semper, 1865 (Neubert and Bouchet 2015). We tentatively assign the new species to the genus *Diancta* based on the zone of constriction as described in Martens (1864) and in Kobelt's (1902) emendation, "somewhat irregularly coiled". As is the case with many Pacific islands, the Fiji Archipelago remains malacologically underexplored (Greke 2017). Phylogenetic data are underrepresented in the available data, and none of the Fijian Diplommatinidae has so far been molecularly assessed. Subsequently, it is not clear whether the unusual shape of the shell is simply a species-specific trait or whether it belongs to another genus.

Internal structures, such as the lamellae or plicae, were examined using X-ray microtomographic (micro-CT) imaging. Unfortunately, the shell broke during removal from the sample holder. Some dry remains of the animal itself could be found inside the shell. This mummified tissue could potentially be used for DNA extraction and sequencing.

Methods

The description of this new species is based on a single dry shell from the type locality. There has been no living individual of this species collected or documented to date.

Before scanning, the shell was manually cleaned of dried mud and moss with a fine brush and distilled water.

All different perspectives of the shell were captured using a Leica MC190 HD digital camera connected to a Leica M205 C stereo microscope (Leica Microsystems GmbH, Wetzlar, Germany). The multifocal images were processed using the Leica proprietary software LAS X EDOF version 3.6.0.20104 (Leica Microsystems).

Micro-CT was conducted at the Anatomical Institute in Bern, Switzerland. The sample was mounted in a small custom-made cylindrical sample holder (3D-printed: https://git.io/Jc4De) and imaged on a Bruker SkyScan 1272 high-resolution microtomography machine (Control software version 1.4, Bruker microCT, Kontich, Belgium). The X-ray source was set to a tube voltage of 50.0 kV and a tube current of 200.0 µA, and the sample was imaged with an unfiltered x-ray spectrum. A set of 322 projection images of 1632 × 1092 pixels were taken at every 0.6° over a 180° recorded sample rotation. Every single projection was exposed for 339 ms. Three projections were averaged to reduce image noise. This resulted in a scan time of approximately 16 minutes. The projection images were then reconstructed into a 3D stack of images with NRecon (Version 2.0.0.5, Bruker microCT, Kontich Belgium). The whole process resulted in a dataset with an isometric voxel size of 7.5 µm. The 3D images and videos were visualized using the CTvox software Version 3.3.1 (Bruker microCT) and the Image J software version 1.53c 2020.

The raw data from the micro-CT scan as well as the reconstructions are-in the spirit of reproducible research-available online (Haberthür et al. 2021): https://doi.org/10.17605/OSF.IO/CSGKQ.

Measurements were made using the LAS X software measuring tool and are given in mm. Abbreviations used are: SH = shell height, SW = shell width, AH = aperture height, AW = aperture width, W = number of whorls after Kerney et al. (1983).

Museum abbreviations

NMBE	Natural History Museum of the Burgergemeinde Bern, Bern, Switzerland
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA.

Systematic part

Diplommatinidae L. Pfeiffer, 1856

Genus *Diancta* E. v. Martens, 1864

Diancta E. v. Martens, 1864: Type species: *Diplommatina constricta* Martens, 1864 [Moluccas, Indonesia].

Diagnosis. This species is placed in the genus *Diancta* because of the sinistral shell, constriction of the shell and closed umbilicus (Neubert and Bouchet 2015).

Diancta phoenix Bochud, sp. nov.

http://zoobank.org/12242324-0720-46A5-A9D6-0253E6140F10
Figs 1–4, Suppl material1–3

Type locality. Fiji, Cakaudrove Province, Vanua Levu Island, Vatumuvamode Mountain, Savusavu, -16.65°N, 178.53°E 63 m a.s.l. (original label text).

Type material. ***Holotype***. MCZ 394198 ex coll. Otto Degener., leg. Otto Degener, 6.1.1941. 1 shell, SH = 2.59, SW = 2.85, AH = 1.34, AW = 1.57, W = 6.25. The protoconch and peristome are the only remaining parts of the broken shell.

Etymology. The new species is named after the immortal saga bird that arises from its ashes. The species epithet is derived from the bird's name: Phoenix. It is a noun in apposition. Despite the broken holotype, this species is being kept "alive" by pictures, 3D prints and Micro-CT scans.

Description. shell sinistral, tiny (SH = 2.59 mm); pyramidal shaped; consisting of 6.25 whorls separated by a shallow suture; protoconch dull, smooth, 2.5 whorls; surface of teleoconch shell with radially aligned, regularly and finely formed axial ribs; ribs slightly curved; last whorl bears sharper ribs, ribbing pattern less regular, with a larger spacing between ribs; whorls rapidly increasing in size, shell constricted after four whorls; constriction site prominent, forming a bulge situated one whorl behind the aperture at the umbilicus; change of coiling axis after zone of constriction, turning the shell 45 degrees upward towards the apex; aperture large, about half shell height, slightly oval shaped and attached to the shell; two visible teeth located in the aperture; one small upper palatal tooth, and opposite a somewhat elongated basal tooth; peristome simple and continuous; inside shell, above ventral bulge, with an elongated palatal lamella opposite the very narrow constriction; columellar plate reduced; umbilicus closed.

Distribution. This species is known so far only from the type locality.

Remarks. According to the original label (Fig. 4), the shell was found in a place interpreted as Vatumuvamode on Mount Savu Savu. Close to the city of Savusavu in the South of Vanua Levu, there is a hill named Suva Suva. On topographic Fijian maps dated 1985, this hill is called mount Nasuvasuva (352 m a.s.l.). We were unable to allocate the mountain Savu Savu or a place called Vatumuvamode. It is difficult to say whether Degener's Savu Savu is a misspelling of Nasuvasuva, or whether he meant another place. The exact meaning of Vatumuvamode is also unclear. In the northwestern part of the island, a place called Savu Sau exists. A path leads from there to the Vuadomo waterfalls, reminiscent of Vatumuvamode. Since the shell was found in 1941 during World War II, and at a period when Fiji was a British colony, it is very likely that names of the places changed since then, or it belongs to an old village or defence site that is not shown on maps. However, the label and its interpretation seem contradictory and unresolvable. Additional sampling of more localities is needed to locate the exact type locality of the new species.

The shell was already quite eroded. The boundary between the protoconch and teleoconch is not clearly visible, while several ribs are partially removed or degraded. There is also no recognizable colouring on the shell. Because other shell specimens and

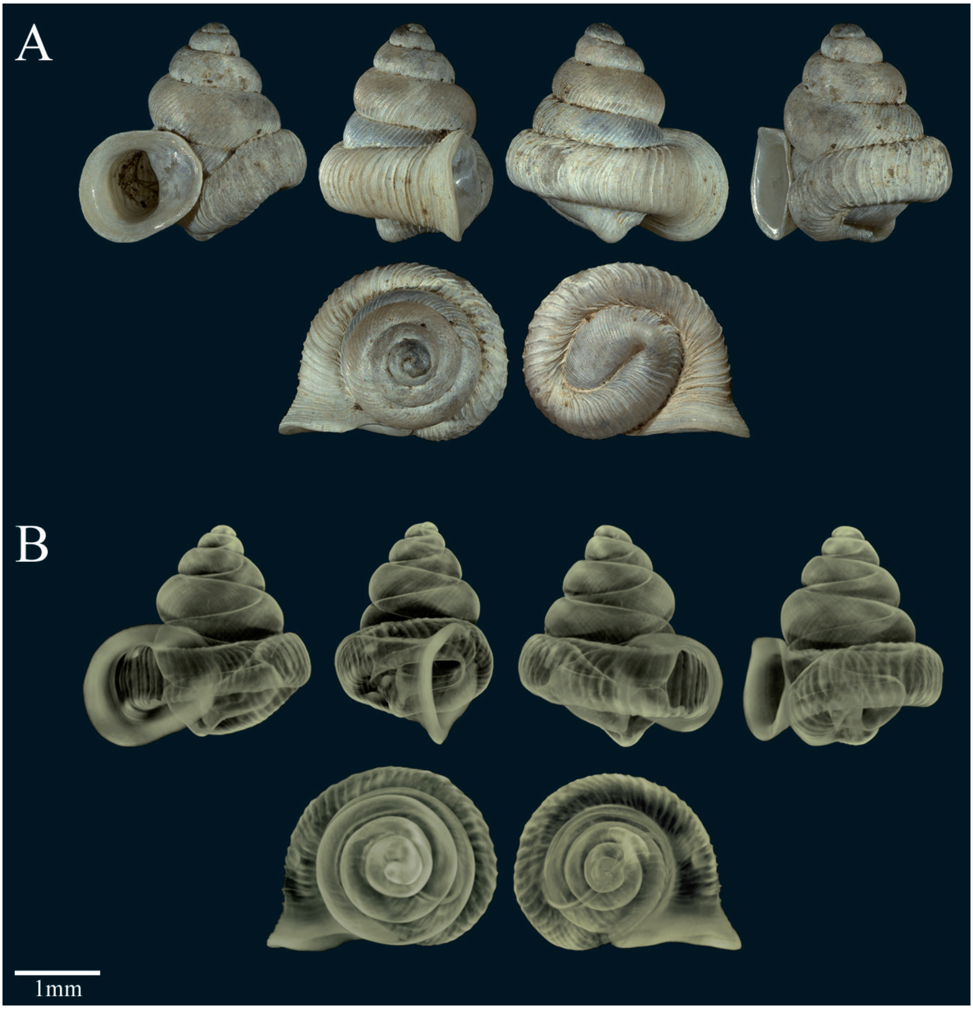


Figure 1A, B *Diancta phoenix* sp. nov. Holotype, MCZ 394198, SH = 2.59 mm **A** Different external views of the shell **B** Micro-CT views.

living animals of this species are lacking, it raises the question whether the specimen studied could be an aberrant shell of a species that has already been described. In any case, it is not possible to perform a comparative study on the morphology of shells, operculum, radula, and/or genitalia.

Other genera of Diplommatinidae with a directional change of the coiling axis include *Moussonia* O. Semper, 1865, *Opisthostoma* W. T. Blanford & H. F. Blanford, 1860, *Plectostoma* H. Adams, 1865, and *Whittenia* T.-S. Liew & Clements, 2020. *Moussonia monstrificabilis* Greke, 2017 changes coiling direction from dextral to sinistral, which is not the case in the newly described species. The aperture in *Opisthostoma* points towards the apex or the dorsal side of the shell due to an alteration in the coiling axis (Nurinsiyah and Hausdorf 2017). This is not seen in *Diancta phoenix* sp. nov. In

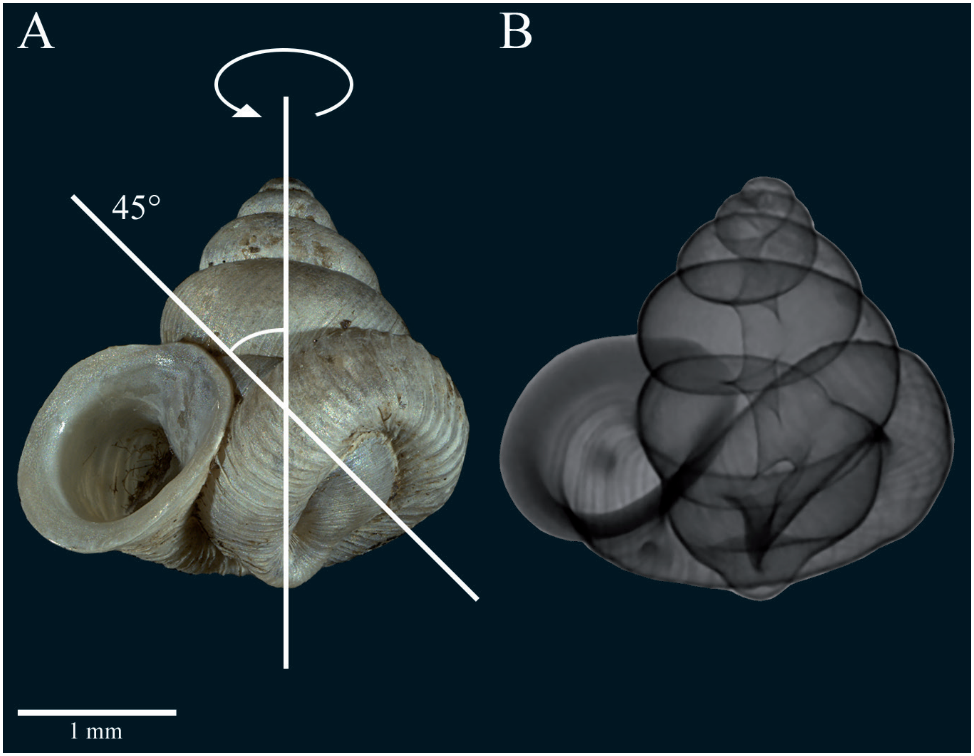


Figure 2A, B *Diancta phoenix* sp. nov., change in coiling axis by 45 degrees **A** Tilted view of the left coiled shell **B** Micro-CT picture, visualisation of the columella.

addition, the doubled peristome, mentioned in the original description of *Opisthostoma* by Blanford (1860), is missing. Usually, *Plectostoma* has a detached last whorl (Kobelt 1902; Egorov 2013; Liew et al. 2014b) and an "extraordinary prolongation backwards of the free portion" (Adams 1865). This is not the case for *D. phoenix* sp. nov. Liew and Gopalasamy (2020) described the new genus *Whittenia*, which conchologically resembles *Opisthostoma* but differs by the outer whorl being raised above the level of the apex, and distinguishing it also from our specimen. None of these character state combinations applies to the new species. In contrast, the penultimate whorl of the shell is constricted, as originally described by von Martens (1864) for the genus *Diancta*. Due to the upward bend in coiling, the last whorl wraps once again around the constricted whorl and gives a pyramidal appearance to the shell. In *Opisthostoma* and *Plectostoma*, the coiling axis changes, but, more importantly, the aperture ends detached from the shell or points in an upwards or other direction to that of the shell axis. For this reason, we assign the new species to *Diancta*.

Differential diagnosis. Applying the key of Neubert and Bouchet (2015) to the new species, identification attempts lead to the species *D. rotunda* Neubert & Bouchet, 2015, due to the sinistral shell and reduced columellar plate. This species has a small

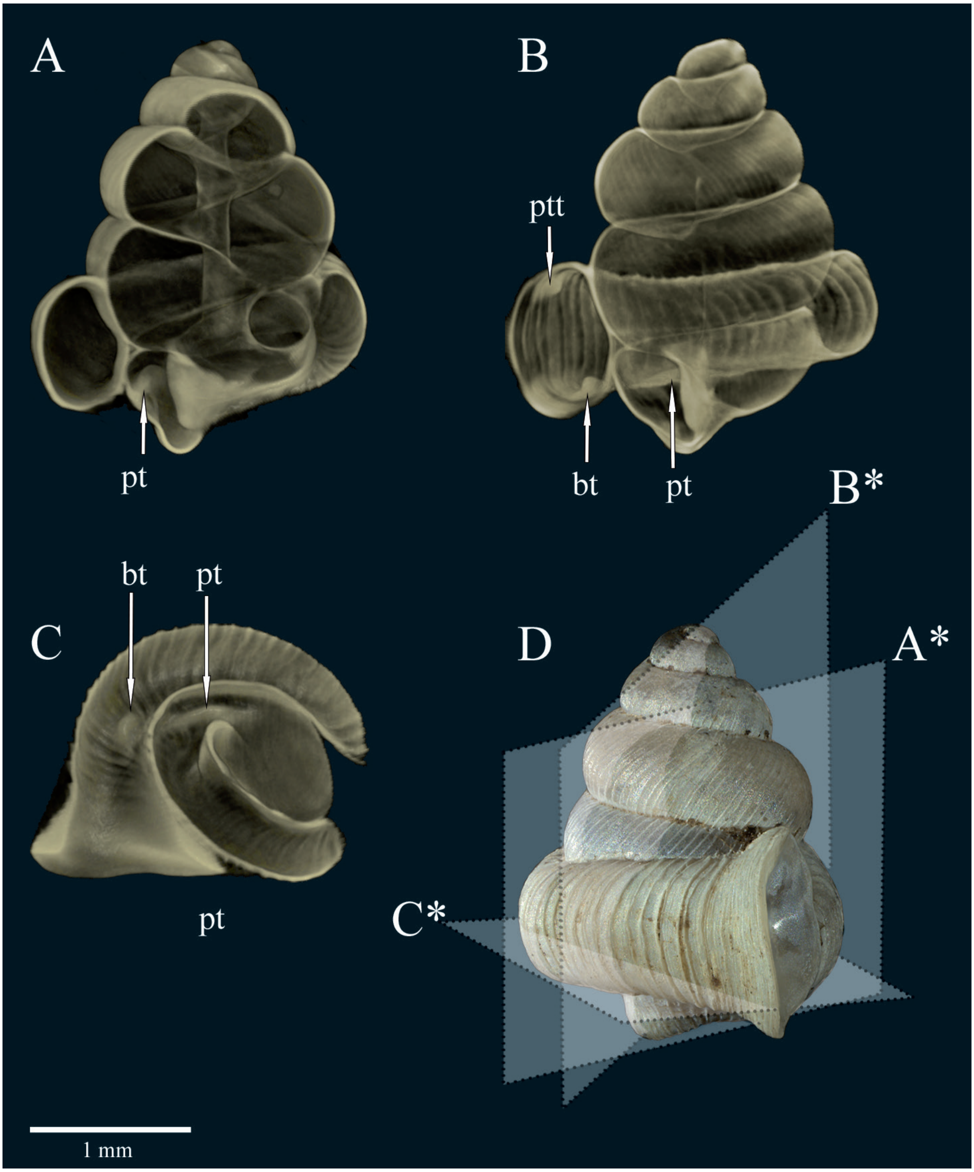
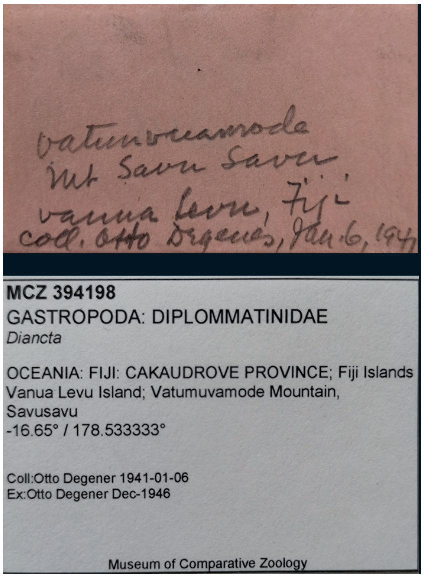


Figure 3A–D *Diancta phoenix* sp. nov., Micro-CT scans **A** Zone of constriction with palatalis = pt **B** Apertural teeth; palatal tooth (ptt) and basal tooth (bt) and palatalis **C** Additional view of the basal teeth and parietalis **D** Sectional planes through the shell to the corresponding letters **A*–C***.

palatal fold deep in the aperture and a shell height of 2.6 mm in the same size range as *D. phoenix* sp. nov., but it clearly differs by its quite bulbous penultimate whorl. Other species that are similar in size are *D. macrostoma* (Mousson, 1870) and *D. martensi* (H. Adams, 1866). With their strongly ascending last whorl, these two species are reminiscent of an incipient change in the coiling axis, as is the case for the newly described spe-



vatumuvamode
mt Savu Savu
vanua levu, Fiji
coll. Otto Degener, Jan. 6, 1941

MCZ 394198
GASTROPODA: DIPLOMMATINIDAE
Diancta

OCEANIA: FIJI: CAKAUDROVE PROVINCE; Fiji Islands
Vanua Levu Island; Vatumuvamode Mountain,
Savusavu
-16.65° / 178.533333°

Coll:Otto Degener 1941-01-06
Ex:Otto Degener Dec-1946

Museum of Comparative Zoology

Figure 4 original label from 1941 by Otto Degener and the interpreted label by MCZ, Harvard.

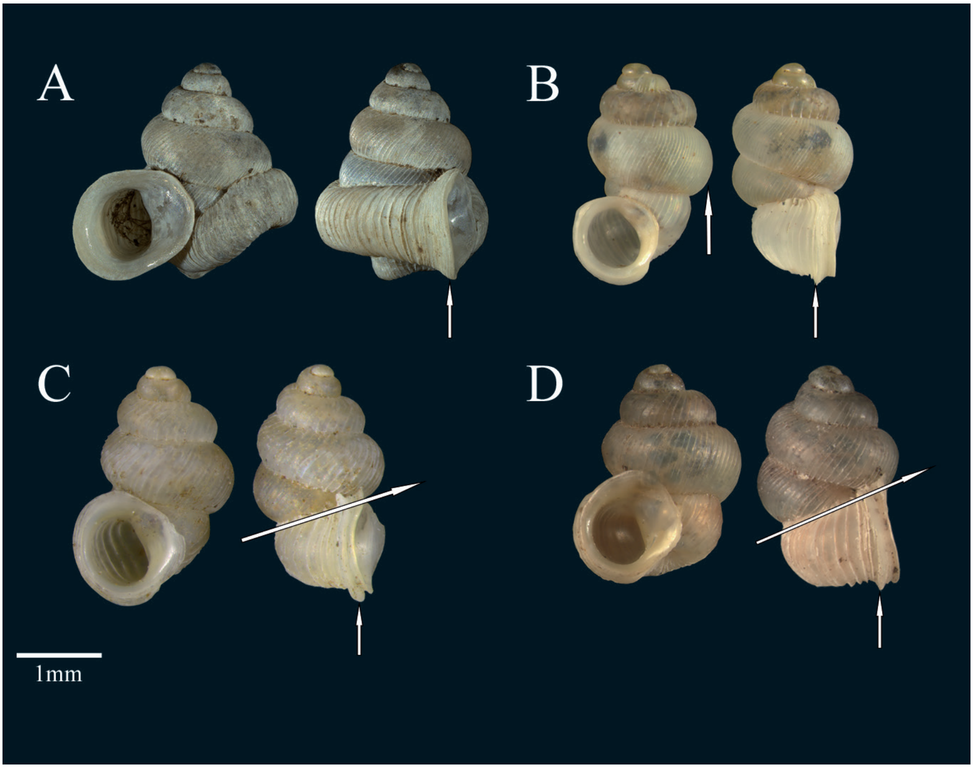


Figure 5A–D Comparison of *D. phoenix* sp. nov. with other Fijian species **A** *D. phoenix* sp. nov., with simple peristome**,** SH = 2.59 mm **B** *D. rotunda* Neubert and Bouchet, 2015, with bulbous penultimate whorl, SH = 2.65 mm **C** *D. macrostoma* (Mousson, 1870), SH = 2.84 mm and **D** *D. martensi* (H. Adams, 1866), SH = 2.62 mm, with strong ascending last whorl and double peristome.

cies. However, the missing shell features in the new species are the alteration of the coiling axis and the presence of frontally visible apertural teeth. The peristome of *Diancta phoenix* sp. nov. is simple and not doubled as in the other described species (Fig. 5).

Several species of Fijian *Diancta,* like *D. macrostoma* and *D. martensi,* share a strong ascending last whorl and a similar ribbing pattern. *Diancta phoenix* sp. nov. is distinguished from all Fijian species by the clear coiling axis twist of 45 degrees, the presence of a simple peristome, the umbilical bulge, its simple columella and the two teeth present in the aperture. To evaluate the variability of these traits, more specimens must be sampled. Changes in the coiling axis are documented for different snail groups and seem to have independently evolved several times (Páll-Gergely and Neubauer 2020).

Discussion

Diplommatinidae are mainly still assessed using shell characters. The original descriptions of the three genera from Fiji are quite short and have been emended via additional shell characters by subsequent authors such as Kobelt (1902) and Egorov (2013) The classification into genera, subgenera and species has already been regarded as difficult when focusing only on shell characters (Rundell 2008; Webster et al. 2012; Neubert and Bouchet 2015). For example, Köhler and Kessner (2020) found a high variation in shell ribbing in a single population of *Diplommatina fluminis* B. Rensch, 1931. Many species are only known from a single shell or a limited number of specimens, which hampers any serious conclusions about the variability of shell morphology. The risk that the specimen described herein is an aberrant form must be considered, due to the lack of comparative material from the type locality. However, the probability of finding a new species is quite high, considering that Diplommatinidae are very small in size, are local endemics and have only been documented in three localities from three regions of Vanua Levu. Clements et al. (2008) mentioned a mutant form, but also that the intraspecific variation among shell dimensions seems to be low. Therefore, we conclude that it is more probable to have a new species rather than an abnormal form, considering the clear differences in shell morphology compared to previously described species in Fiji.

For further sampling of fresh material, it is necessary to explore the northwestern part of the island in the Savu Sau region, as well as the Savu Savu mountain in the central-southern region, to find out exactly where the new species is found. The assignment to the genus *Diancta* is tentative. Here, the inclusion of the type species of the genus *Diancta*, *Diplommatina constricta* Martens, 1864, from the Moluccas in Indonesia, would be mandatory to confirm this generic assignment. Micro-CT is a highly useful and seldomly used method for revealing important diagnostic characters such as the inner dentition and the lamellae, especially in micromolluscs, which are difficult to handle. This method was malacologically pioneered and successfully used for assessing inner shell characters and variability in the genera *Plecostoma* and *Opisthostoma* (Liew et al. 2014a; Liew and Schilthuizen 2016), and far surpasses the need to break rare and valuable shells to expose internal structures (Budha et al. 2017).

Acknowledgements

We are deeply indebted to Adam J. Baldinger and Murat Recevik from the Museum of Comparative Zoology in Harvard for providing the holotype of the new species. We would like to thank Charles Huber, Bern, for his support when searching for more information on the locus typicus, as well as Merewalesi Vakarewa from the public library of Fiji, Angelika Principe from Zentralbibliothek Zürich, Matt Capper and Marita Manley from Talanoa Consulting, Suva, Fiji and Christine and Sam Tawake-Bachofner from Lawaki Beach House, Fiji for additional research and personal comments. Also, a great thank to Adrienne Jochum for improving the linguistic quality of our text. This work was supported by the NMBE.

References

Adams H (1865) Description of a new genus of Land-Shells from the Island of Labuan, Borneo. The Annals and Magazine of Natural History 15: 177–177. https://doi.org/10.1080/00222936508681785

Barker GM, Narosamalua J (2017) Netewa Peninsula Land snails. Operation Wallacea report.

Blanford WT, Blanford HF (1860) Contributions to Indian malacology, No. I. The Journal of the Asiatic Society of Bengal 29: 117–127.

Budha PB, Naggs F, Backeljau T (2017) The genus Diplommatina Benson, 1849 (Gastropoda: Caenogastropoda: Diplommatinidae) in Nepal, with the description of seven new species. European Journal of Taxonomy 337: 1–30. https://doi.org/10.5852/ejt.2017.337

Clements GR, Liew TS, Vermeulen J, Schilthuizen M (2008) Further twists in gastropod shell evolution. Biology letters 4: 179–82. https://doi.org/10.1098/rsbl.2007.0602

Egorov R, Greke K (2003) Treasure of Russian Shells. Volume 6. Terrestrial Pectinibranchia. Helicinidae, Cyclophoridae, Diplommatinidae, Cochlostomatidae, Aciculidae, Tateidae, Terrestribythinellidae, Pomatiidae, 43pp.

Egorov RV (2013) Treasure of Russian Shells. Supplement 3. A review of the genera of the terrestrial pectinibranch molluscs (synopsis mainly based on published data). Part III. Littoriniformes: Liareidae, Pupinidae, Diplommatinidae, Alycaeidae, Cochlostomidae. In: Roman Egorov. Moscow, 1–62.

Greke K (2017) Taxonomic review of Diplommatinidae (Caenogastropoda: Cyclophoroidea) from Wallacea and the Papuan Region. In: Biodiversity, biogeography and nature conservation in Wallacea and New Guinea, volume III, 151–316, pls 19.

Greke K (2021) New species and records of the Papuan Diplommatinidae (Caenogastropoda: Cyclophoroidea). 4: 111–134.

Haberthür D, Bochud E, Hlushchuk R, Neubert E (2021) Diancta phoenix. https://doi.org/10.17605/OSF.IO/CSGKQ

Kobelt W (1902) 16 Das Tierreich: eine Zusammenstellung und Kennzeichnung der rezenten Tierformen: 16. R. Friedländer und Sohn.

Köhler F, Kessner V (2020) The Diplommatinidae of Timor-Leste, with description of five new species (Gastropoda, Architaeniglossa, Cyclophoroidea). Molluscan Research 40: 236–246. https://doi.org/10.1080/13235818.2020.1777630

Liew TS, Schilthuizen M (2016) A Method for Quantifying, Visualising, and Analysing Gastropod Shell Form. PLoS ONE 11: e0157069.

Liew TS, Gopalasamy R (2020) Whittenia, a new genus of land snails from Perak, Peninsular Malaysia (Gastropoda: Diplommatinidae). The Raffles Bulletin of Zoology 35: 143–148. https://doi.org/10.1371/journal.pone.0157069

Liew T-S, Vermeulen JJ, Marzuki ME, Schilthuizen M (2014a) A cybertaxonomic revision of the micro-landsnail genus Plectostoma Adam (Mollusca, Caenogastropoda, Diplommatinidae), from Peninsular Malaysia, Sumatra and Indochina. ZooKeys 393: 1–107.

Liew TS, Kok A, Schilthuizen M, Urdy S (2014b) On growth and form of irregular coiled-shell of a terrestrial snail: Plectostoma concinnum (Fulton, 1901) (Mollusca: Caenogastropoda: Diplommatinidae). PeerJ 2: e383. https://doi.org/10.7717/peerj.383

Martens E von (1864) Über neue Cyclostomaceen und Helicinen aus dem indischen Archipel. Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin 1864: 116–121.

Neall VE, Trewick SA (2008) The age and origin of the Pacific islands: a geological overview. Philosophical Transactions of the Royal Society B: Biological Sciences 363: 3293–3308. https://doi.org/10.1098/rstb.2008.0119

Neubert E, Bouchet P (2015) The Diplommatinidae of Fiji – a hotspot of Pacific land snail biodiversity (Caenogastropoda, Cyclophoroidea). ZooKeys 487: 1–85. https://doi.org/10.3897/zookeys.487.8463

Nurinsiyah AS, Hausdorf B (2017) Revision of the Diplommatinidae (Gastropoda: Cyclophoroidea) from Java. Zootaxa 4312: e201.

Páll-Gergely B, Neubauer TA (2020) The value of a single character: the Paleogene European land snail Ferussina Grateloup, 1827 is likely a cyclophorid (Gastropoda, Caenogastropoda). ZooKeys 918: 29–40. https://doi.org/10.3897/zookeys.918.50135

Proios K, Cameron RA, Triantis KA (2021) Land snails on islands: building a global inventory. Frontiers of Biogeography 13(2): e51126 https://doi.org/10.21425/F5FBG51126

Rundell RJ (2008) Cryptic diversity, molecular phylogeny and biogeography of the rock- and leaf litter-dwelling land snails of Belau (Republic of Palau, Oceania). Philosophical Transactions of the Royal Society B: Biological Sciences 363: 3401–3412. https://doi.org/10.1098/rstb.2008.0110

Stanisic J, Shea M, Potter D, Griffths O (2010) Australian Land Snails Volume 1 – A field guide to eastern Australian species. The Australian Museum. Available from: https://publications.australian.museum/australian-land-snails-volume-1-a-field-guide-to-eastern-australian-species/publications.australian.museum/australian-land-snails-volume-1-a-field-guide-to-eastern-australian-species/ (July 7, 2021).

Thiele J (1929) Handbuch der systematischen Weichtierkunde. In: (Loricata: Gastropoda: Prosobranchia). Gustav Fischer, Jena, e376.

Webster NB, Van Dooren TJM, Schilthuizen M (2012) Phylogenetic reconstruction and shell evolution of the Diplommatinidae (Gastropoda: Caenogastropoda). Molecular Phylogenetics and Evolution 63: 625–638. https://doi.org/10.1016/j.ympev.2012.02.004

Supplementary material 1

Movie 1

Authors: David Haberthür

Data type: media

Explanation note: 360-degrees rotatable 3D shell model of *D. phoenix*.

Link: https://doi.org/10.3897/zookeys.1073.73241.suppl1

Supplementary material 2

Movie 2

Authors: Estée Bochud

Data type: media

Explanation note: Sagittal slicing through the 3D shell model of *D. phoenix* showing internal teeth and zone of constriction.

Link: https://doi.org/10.3897/zookeys.1073.73241.suppl2

Supplementary material 3

Movie 3

Authors: Estée Bochud

Data type: media

Explanation note: Transparent 3D model of *D. phoeni*x rotating upside down showing internal teeth, columella, ventral bulge and zone of constriction.

Link: https://doi.org/10.3897/zookeys.1073.73241.suppl3

ZooKeys 1073: 13–20 (2021)
doi: 10.3897/zookeys.1073.75598
https://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Two new species of cricket genus *Anaxiphomorpha* Gorochov, 1987 (Orthoptera, Trigonidiidae, Trigonidiinae) in China

Zhi Xin He[1], Li Bin Ma[1]

[1] *Shaanxi Normal University, 710119 Xi'an, China*

Corresponding author: Li Bin Ma (libinma@snnu.edu.cn)

Academic editor: T. Robillard | Received 22 September 2021 | Accepted 3 November 2021 | Published 29 November 2021

http://zoobank.org/6B382A8F-0F1B-439B-99D5-200D43E94075

Citation: He ZX, Ma LB (2021) Two new species of cricket genus *Anaxiphomorpha* Gorochov, 1987 (Orthoptera, Trigonidiidae, Trigonidiinae) in China. ZooKeys 1073: 13–20. https://doi.org/10.3897/zookeys.1073.75598

Abstract

Two new species, *Anaxiphomorpha nonggangensis* **sp. nov.** and *Anaxiphomorpha manereserratus* **sp. nov.**, are reported from Guangxi Province, China. Descriptions and illustrations for the new species and a key to all known species of *Anaxiphomorpha* are provided.

Keywords

Southern China, swordtail crickets, taxonomy, Trigonidiini, tropics

Introduction

The genus *Anaxiphomorpha* was established with *Anaxiphomorpha brachyapodemalis* Gorochov, 1987 as the type species. *Anaxiphomorpha* is recognized by a smaller body size, yellow coloration and special genitalia structure (epiphallus and ectoparamere possess multiple lobes or branches).

To date, seven species have been reported worldwide (Cigliano et al. 2021). Apart from two species, *Anaxiphomorpha brachyapodemalis* Gorochov, 1987 and *Anaxiphomorpha longiapodemalis* Gorochov, 1987 reported from Vietnam, the other five, *Anaxiphomorpha biserratus* Liu & Shi, 2015, *Anaxiphomorpha brevisparamerus* Liu & Shi, 2015, *Anaxiphomorpha longiserratus* Liu & Shi, 2015, *Anaxiphomorpha serratiprotuberus* Liu & Shi, 2015 and *Anaxiphomorpha hexagona* Ma, 2018 have been recorded from China. After comparing our new materials with the species of this genus, we concluded that two Chinese species are new for science. The distribution of *Anaxiphomorpha* species worldwide including the new species is also presented (Fig. 1).

Materials and methods

All specimens were collected at night with a sweep net. Specimens were preserved in ethanol during field work, and pinned and dry-preserved in the laboratory. Male genitalia were dissected from softened specimens. Photomicrographs of genitalia were collected using ToupCam Digital camera and bundled software (ToupTek, Hangzhou, China). Photographs of specimens were obtained using a VHX–6000 digital microscope (Keyence, Osaka, Japan).

Measurements

All specimens were measured using a ToupCam Digital camera and bundled software (ToupTek, Hangzhou, China). All the measurements are in millimeters (mm).

Abbreviations

BL	body length (from head to apical hindwing);
PL	pronotal length;
TL	tegmen length;
HFL	hind femur length;
OL	ovipositor length.

The specimens are deposited at the Museum of Flora and Fauna of Shaanxi Normal University, Xi'an, China (SNNU).

Taxonomy

Genus *Anaxiphomorpha* Gorochov, 1987

Type species. *Anaxiphomorpha brachyapodemalis* Gorochov, 1987

Key to known species of *Anaxiphomorpha*

1	Dorsally viewed, epiphallic lateral lobes apically acute	**2**
–	Dorsally viewed, epiphallic lateral lobes somewhat blunt of apex	**3**
2	Epiphallic transverse bridge and ectoparamere short	***A. brachyapodemalis***
–	Epiphallic transverse bridge and ectoparamere long	***A. longiapodemalis***
3	Epiphallic lateral lobes bifurcated as six significant branches	***A. hexagona***
–	Not as above and laterally viewed as following	**4**
4	Apex of epiphallic lateral lobes almost straight	***A. brevisparamerus***
–	Apex of epiphallic lateral lobes curved	**5**

5 Apex of epiphallic lateral lobes upward curved **6**
– Apex of epiphallic lateral lobes downward curved **8**
6 Epiphallic lateral lobes boot-like .... ***A. nonggangensis* sp. nov.**
– Epiphallic lateral lobes rod-like **7**
7 Epiphallic lateral lobes proximally bearing a protuberance .... ***A. manereserratus* sp. nov.**
– Not as above .... ***A. longiserratus***
8 Epiphallic lateral lobes long, medially raised and apically acute .... ***A. serratiprotuberus***
– Epiphallic lateral lobes short and apically blunt .... ***A. biserratus***

***Anaxiphomorpha nonggangensis* He & Ma, sp. nov.**
http://zoobank.org/960B75C1-468B-4D24-BADE-06F8D7F93D2E
Figs 1, 2, 3A, B, 4A–C

Material examined. ***Holotype.*** China: Male, Guangxi, Longzhou, Nonggang National Natural Reserve, 5.V.2019, 22.46°N, 106.96°E, Libin Ma & Tao Zhang leg. ***Paratypes.*** 7 males and 4 females, same information as holotype (SNNU).

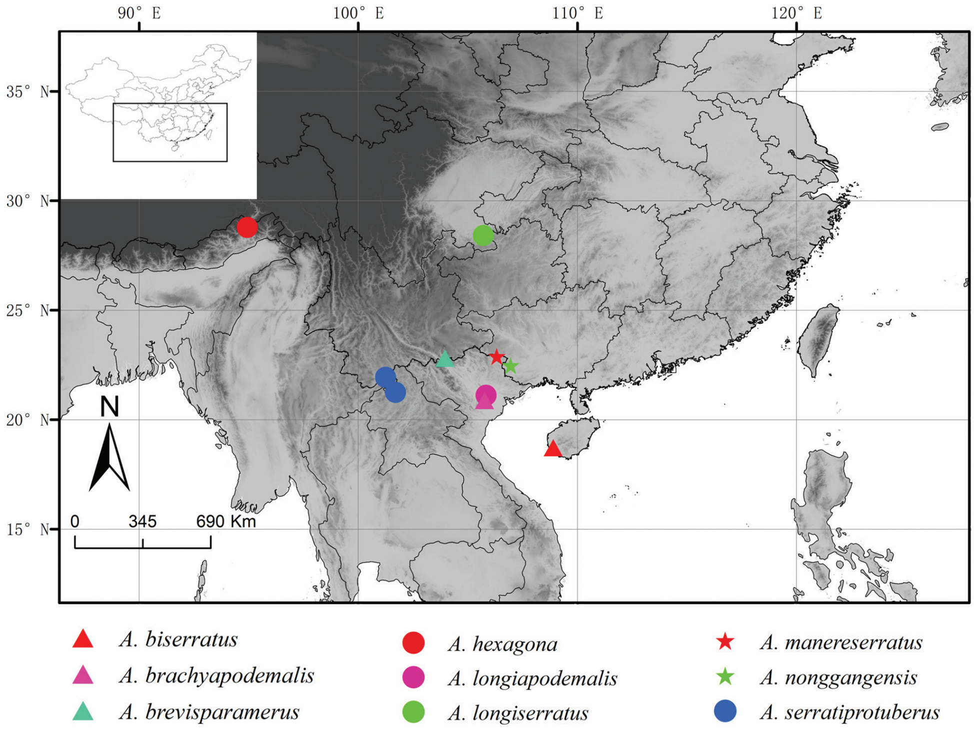


Figure 1. Known distribution of *Anaxiphomorpha* species, including the new species *A. nonggangensis* sp. nov. and *A. manereserratus* sp. nov..

Figure 2. Habitus (alive) of *A. nonggangensis* sp. nov. on leaf **A** male **B** female (photography: Zhang, Tao).

Diagnosis. Male (Figs 2A, 3A). Body size small. Head small and pubescent, slightly wider than anterior margin of pronotum; frontal rostrum as wide as antennal scape; eyes large and protruding forwards; apical three joints of maxillary palpi distinctly elongate, 5th joint truncated apically. Pronotum transverse, strongly widened posteriorly and distinctly longer than width of anterior one. Tegmina extending slightly over apex of abdomen, armed with one oblique vein; mirror slightly elongate; hindwings absent. Fore tibia armed with a large long-oval external tympanum, and without internal tympanum. Hind tibia bearing three dorsal spurs on two sides respectively, and bearing two apical spurs inside and three outside.

Genitalia (Fig. 4A–C). Lateral lobes of epiphallus slightly longer than median lobes, and possessing several teeth at outer margin, not narrowed apically in dorsal view, gradually narrowed apically in lateral view; median lobes shaped as boot and abruptly narrowed apically in lateral view. Etcoparameres transversely and truncated apically.

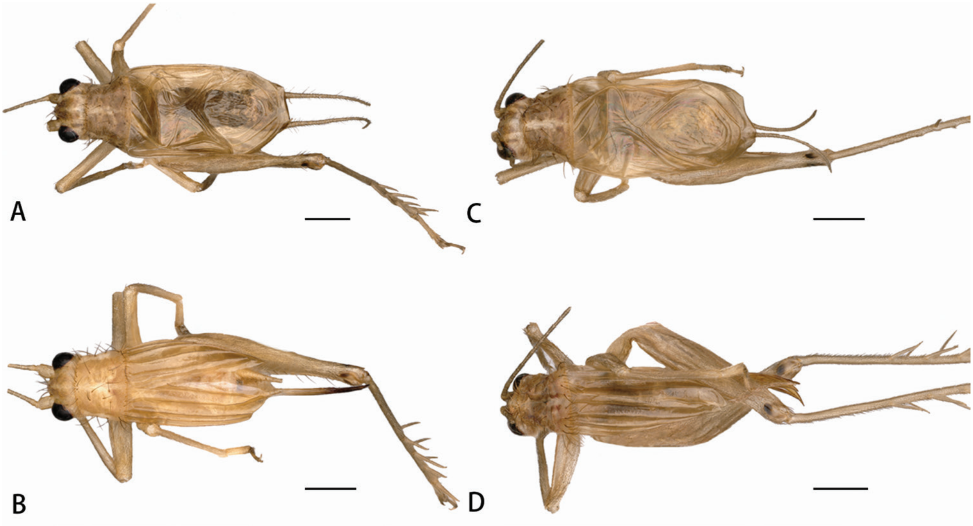


Figure 3. Habitus photographs. **A, B** *A. nonggangensis* sp. nov. **C, D** *A. manereserratus* sp. nov. **A, C** Male **B, D** Female. Scale bar: 1 mm.

Female (Figs 2B, 3B). Body slightly smaller than male. Tegmen rather convex, armed with five regular veins on dorsal field. Ovipositor blade-shaped.

Coloration. Body colored yellow. Dorsal area of head ornamented with four brown longitudinal stripes in ventral view, anterior half of abdomen colored dark brown in male or small part of middle abdomen colored dark in female. Apex of each hind femur bearing a small dark spot on two sides respectively. Ovipositor ventrally colored brown to dark brown and remainder yellowish.

Measurements. Male. BL 5.17–6.42, PL 0.98–1.19, TL 3.73–4.54, HFL 3.27–3.96. **Female.** BL 4.50–5.63, PL 0.99–1.17, TL 3.87–4.42, OL 2.22–2.67.

Etymology. The name refers its type locality, Nonggang National Natural Reserve.

Distribution. China (Guangxi) (Fig. 1).

Remarks. This species is very similar to *A. brevisparamerus* in the ectoparameres of the male genitalia, but different in the epiphallic lateral lobes of this new species, which are shaped as boot with an acute apex.

Anaxiphomorpha manereserratus **He & Ma, sp. nov.**

http://zoobank.org/9B5380BF-9334-4480-B796-4FE6DF673DB1
Figs 1, 3C–D, 4D–F, 5

Material examined. ***Holotype.*** China: Male, Guangxi, Jingxi, Longbang, 22.87°N, 106.32°E, 1.V.2019, Libin Ma & Tao Zhang leg. ***Paratypes.*** 10 males and 2 females, same information as holotype (SNNU).

Description. Male (Figs 3C, 5A). Body size small. Head small and pubescent, slightly wider than anterior margin of pronotum; frontal rostrum 1.2 times wider than

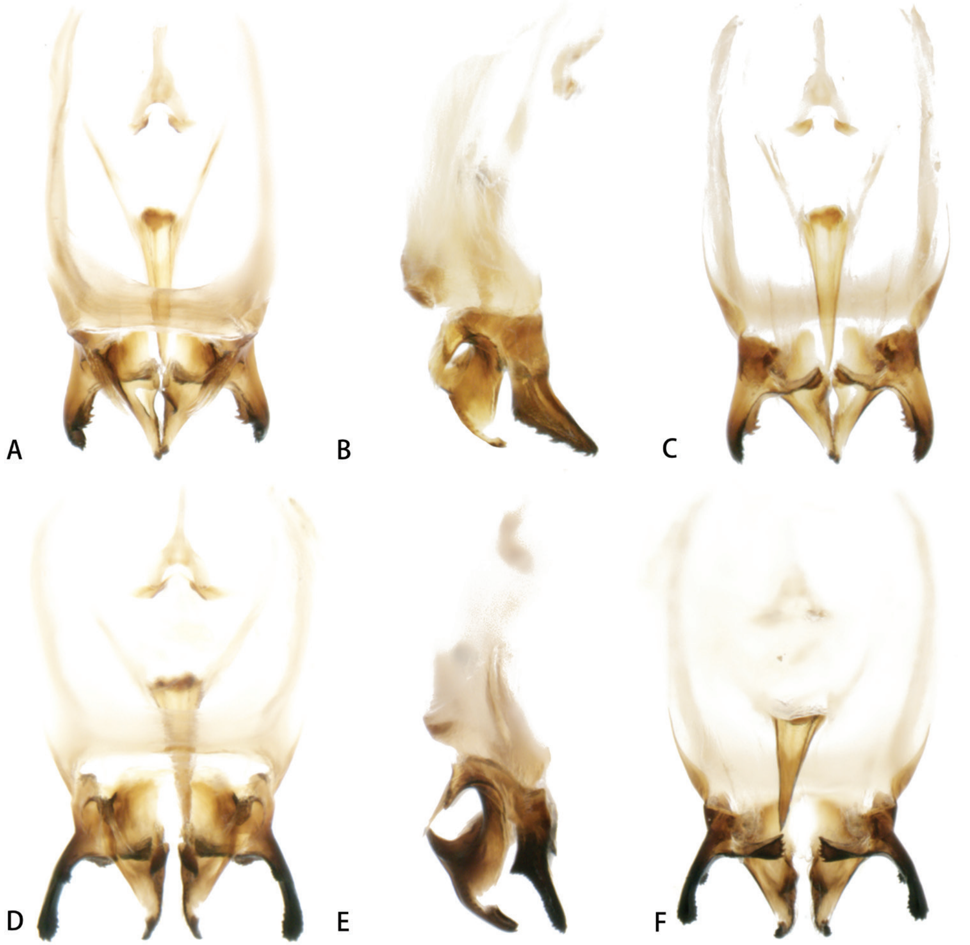


Figure 4. Male genitalia **A–C** *A. nonggangensis* sp. nov. **D–F** *A. manereserratus* sp. nov. **A, D** dorsal views **B, E** lateral views **C, F** ventral views.

antennal scape; eyes large and protruding forwards; apical three joints of maxillary palpi distinctly elongate, 5th joint truncated apically. Pronotum transverse, strongly widened posteriorly, and slightly wider than the anterior. Tegmina extending slightly over apex of abdomen, armed with one oblique vein; mirror slightly elongate; hindwings absent. Fore tibia armed with a large long-oval external tympanum; internal tympanum absent. Hind tibia bearing three dorsal spurs on two sides respectively, and bearing two apical spurs inside and three outside.

Genitalia (Fig. 4D–F). Lateral lobes of epiphallus slightly longer than median lobes in lateral view and possessing horned protuberances at inner margin proximally and outer margin medially, bearing several teeth at inner and outer margin and not narrowed apically in lateral view. Ectoparameres short and serrated apically.

Figure 5. Habitus (alive) of *A. manereserratus* sp. nov. on leaf **A** male **B** female (photography: Zhang, Tao).

Female (Figs 3D, 5B). Body slightly smaller than male. Tegmen rather convex, armed with five regular veins on dorsal field. Ovipositor blade-shaped.

Coloration. Body colored yellow. Dorsal area of head ornamented with four brown longitudinal stripes. Apex of each hind femur bearing a small dark spot in two sides respectively. Ovipositor ventrally colored brown to dark brown and remainder yellowish.

Measurements. Male. BL 4.92–6.05, PL 0.94–1.15, TL 3.42–4.09, HFL 3.56–4.17. **Female.** BL 4.65–4.94, PL 0.87–0.90, TL 3.21–3.33, OL 1.892.03.

Etymology. The name refers to the epiphallic median lobes almost as long as the lateral lobes.

Distribution. China (Guangxi) (Fig. 1).

Remarks. This species is very similar to *A. serratiprotuberus* and *A. longiserratus* in dorsal and ventral views of the male genitalia, but different in lateral view (epiphallic lateral lobes of the new species possessing horned protuberances at the inner margin proximally and the outer margin medially, and the ectoparameres of this new species are acute apically).

Acknowledgements

We thank staff of Nonggang National Nature Reserve, for their help in our field work. This work is supported by National Natural Science Foundation of China (No. 31750002, 32070474) and the Fundamental Research Funds for the Central Universities (GK202003049).

References

Cigliano MM, Otte D, Eades DC, Braun H (2021) Orthoptera species file online. Version 5.0/5.0. http://Orthoptera.SpeciesFile.org [accessed 6 Septemper 2021]

Gorochov AV (1987) On the fauna of crickets of the subfamily Gryllinae (Orthoptera, Gryllidae) of eastern Indochina. In: Medvedev LN (Ed.) Insect Fauna of Vietnam. Nauka, Moscow, 5–22.

Liu HY, Shi FM (2015) First record of the genus *Anaxiphomorpha* Gorochov (Orthoptera: Gryllidae) from China, with description of four new species. Zootaxa 3918: 433–438 https://doi.org/10.11646/zootaxa.3918.3.7

Ma LB (2018) *Anaxiphomorpha hexagona* sp. n., a new, unusual swordtail cricket collected from Motuo County, Xizang, China (Orthoptera: Grylloidea; Trigonidiidae; Trigonidiinae). Zootaxa 4418: 197–200. https://doi.org/10.11646/zootaxa.4418.2.10

ZooKeys 1073: 21–53 (2021)
doi: 10.3897/zookeys.1073.75539
https://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Songs and morphology in three species of the *Chorthippus biguttulus* group (Orthoptera, Acrididae, Gomphocerinae) in Russia and adjacent countries

Tatiana Tarasova[1], Dmitry Tishechkin[2], Varvara Vedenina[1]

1 *Institute for Information Transmission Problems, Russian Academy of Sciences, Bolshoy Karetny per.19, Moscow 127051 Russia* **2** *Department of Entomology, Faculty of Biology, Moscow State University, Leninskie Gory, Moscow 119234 Russia*

Corresponding author: Varvara Vedenina (vedenin@iitp.ru)

Academic editor: T. Robillard | Received 20 September 2021 | Accepted 30 October 2021 | Published 29 November 2021

http://zoobank.org/A991F9BF-945B-4491-9123-6222298863EA

Citation: Tarasova T, Tishechkin D, Vedenina V (2021) Songs and morphology in three species of the *Chorthippus biguttulus* group (Orthoptera, Acrididae, Gomphocerinae) in Russia and adjacent countries. ZooKeys 1073: 21–53. https://doi.org/10.3897/zookeys.1073.75539

Abstract

Songs and morphology are compared between *Chorthippus miramae* (Vorontsovsky, 1928) that was previously named as *C. porphyropterus* and two other closely related species, *C. brunneus* (Thunberg, 1815) and *C. maritimus* Mistshenko, 1951. We compare them because the calling song of *C. miramae* was previously shown to have song elements similar to those of other two species. One morphological character, the length of stridulatory file, appeared to be the best character to distinguish between all three species. For *C. maritimus* and *C. miramae*, we present the morphological descriptions since they are absent in the literature. We also establish the synonymy *C. maritimus* = *C. bornhalmi* Harz, 1971, **syn. n.** = *C. biguttulus eximius* Mistshenko, 1951, **syn. n.** In the song analysis, we analyse not only the sound but also the leg-movement pattern, which is very helpful to find a homology between various song elements. We show that the calling song of *C. miramae* usually contains two elements, one element being similar to the *C. brunneus* calling song, and another – to the *C. maritimus* calling song. Despite some similarities, the calling song elements in *C. miramae* have some peculiarities. The courtship song of *C. miramae* is similar to the *C. brunneus* song, whereas the rivalry songs of *C. miramae* comprise both the *maritimus*-like elements and the unique ones. *C. miramae* generally demonstrates a richer song repertoire than the other two species.

Keywords

Calling song, courtship song, grasshoppers, leg-movement pattern, rivalry song, stridulatory file

Introduction

In singing Orthoptera, the song is an important component of reproductive isolation. Acoustic signals are often used in taxonomy, when sibling species are similar in morphology, but different in songs. In grasshoppers of subfamily Gomphocerinae, the song is produced by stroking the stridulatory file of each hind femur across a raised vein on the fore wing. It is noteworthy that using both hind legs, the grasshoppers have two separate sound-producing devices, which must be coordinated with one another. The stridulatory movements of the two legs often differ in amplitude and pattern, and the legs can exchange roles from time to time, which leads to an increase of song complexity (e.g., Elsner 1974; Helversen and Elsner 1977; Helversen and Helversen 1994). To distinguish cryptic grasshopper species, not only the sound recordings but also the recordings of the leg movements are used by various authors (Helversen 1986; Gottsberger and Mayer 2007; Vedenina and Helversen 2003, 2009; Willemse et al. 2009; Vedenina et al. 2012; Tarasova et al. 2021).

Closely related grasshopper species belonging to the *Chorthippus biguttulus* group offer an excellent example of the cryptic species complex that can only be reliably identified by the male calling songs (Ragge and Reynolds 1988, 1998; Helversen 1989; Ragge et al. 1990; Bukhvalova 1993, 1998; Ingrisch 1995; Willemse et al. 2009; Sirin et al. 2010). This group includes four species with large ranges across Europe and Asia: *C. biguttulus* (Linnaeus, 1758), *C. brunneus* (Thunberg, 1815), *C. mollis* (Charpentier, 1825), and *C. maritimus* Mistshenko, 1951. Other species of this group with smaller ranges occur in southern Europe, namely, *C. jacobsi* Harz, 1975 and *C. yersini* Harz, 1975 in the Iberian Peninsula, *C. rubratibialis* Schmidt, 1978 in Italy and *C. bornhalmi* Harz, 1971 in the Balkans. Two additional species are endemic to Greece (Willemse et al. 2009) and two more to Anatolia (Sirin et al. 2010). Several species and subspecies only occur in Russia and adjacent territories, in particular, *C. porphyropterus* (Vorontsovsky 1928) (Benediktov 1999, 2005).

The main subject of the current study is one species of the *biguttulus* group, *C. porphyropterus*, which we name as *C. miramae* (Vorontsovsky, 1928 nec Ramme, 1936, 1951), and two closely related species, *C. brunneus* and *C. maritimus*, whose songs resemble song elements of *C. miramae*. Since in Russia and adjacent countries *C. brunneus*, *C. maritimus* and *C. miramae* often occur with two other species of the *biguttulus* group, *C. biguttulus* and *C. mollis*, we describe the main morphological differences from the latter two species as well.

Materials and methods

Localities where material was collected are shown in Fig. 1. All localities were numbered and all numbers are listed in Results, in the paragraph "Material examined". On the map, however, only localities with song recordings are numbered.

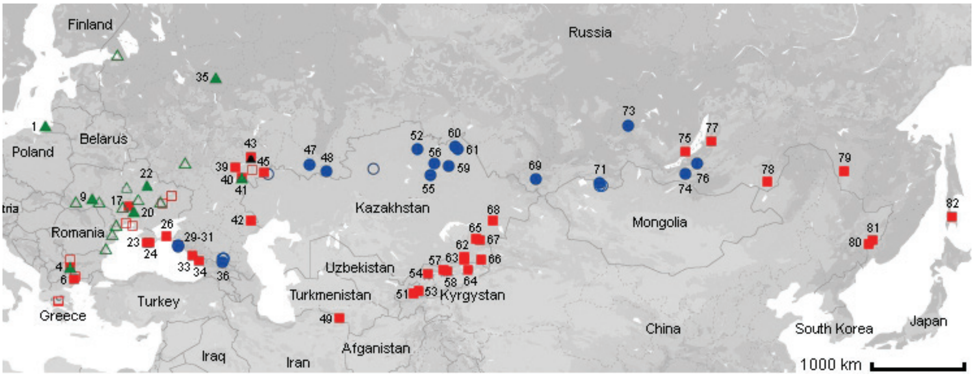


Figure 1. Map of localities where the specimens of *Chorthippus brunneus* (green triangles), *C. maritimus* (red squares) and *C. miramae* (blue circles) were collected. The localities with song recordings are numbered and marked by filled icons.

Morphological analysis

In all specimens studied, we measured the following morphological characters: the lengths of pronotum, forewing and hind femur, the width of costal and subcostal (C & Sc) areas of fore wing, the distance from the center of stigma to the tip of fore wing, the length of stridulatory file and the distance from the most distal stridulatory peg to the tip of knee (Table 1, Fig. 2). In 10 specimens of each sex and species, the body length, the width of fore wing and the number of stridulatory pegs were measured. These morphological features have been chosen on the basis of the literature (Ragge et al. 1988; Bukhvalova 1993; Benediktov 1999; Willemse et al. 2009).The length of pronotum was measured along the midline. The length of forewing was measured from the humeral plate to the tip of the wing; the widths of the C & Sc areas were measured at the point where costal area was of the greatest width (Fig. 2B). The length of hind femur was measured from the anterior margin of the upper basal lobe to the hind margin of the upper knee-lobe; the length of stridulatory file was measured from the most proximal peg to the most distal peg; the distance between stridulatory file to the tip of the knee was measured from the most distal peg to the hind margin of the upper knee-lobe (Fig 2C). Morphological studies were carried out with an MBS-9 light microscope at 8–56× magnification using an ocular micrometer. Material for the morphological analysis was taken from the Zoological Museum of Moscow State University (ZMMU) and the personal collections of V. Vedenina (CV).

All statistical analyses were performed using Excel 2016 and STATISTICA 12.0.0. To visualize and clarify the differences in morphology between the three species, a principal component analysis (PCA) was applied to 6 morphological characters (Fig. 3E).

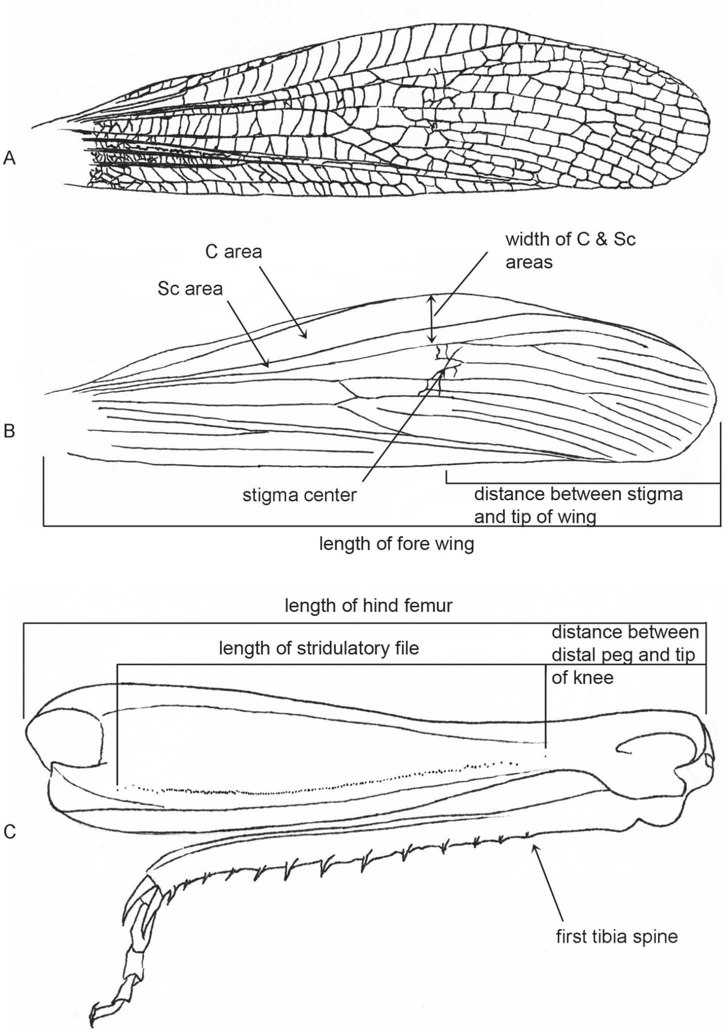


Figure 2. Morphology of fore wing and hind leg in *Chorthippus miramae* (Vorontsovsky) from Orenburg region **A** fore wing with complete venation **B** fore wing with main veins; **C** hind leg. The measured morphological characters are indicated with arrows and brackets.

Song recordings and analysis

The calling song was recorded from an isolated male; the courtship song was recorded when a male was sitting near a female; the rivalry song was recorded from males sitting near each other. Recordings of the calling and rivalry songs in the field were carried out with a MD-382 microphone (upper frequency limit 12.5 kHz; before 2008), or a Spirit IM-01 microphone (upper frequency limit 20 kHz), and an Elektronika-302-1 cassette recorder (upper frequency limit 10 kHz; before 2005), or a Sony Walkman MZ-NH900 minidisk recorder (sampling frequency 44.1 kHz). The signals were A/D

Table 1. Morphological measurements in three species of the *Chorthippus biguttulus* group. For each character, mean, standard deviation, min and max are shown. Abbreviations in brackets see in Fig. 2.

Number of specimens	**Males**			**Females**		
	C. miramae	***C. maritimus***	***C. brunneus***	***C. miramae***	***C. maritimus***	***C. brunneus***
	133	**122**	**53**	**50**	**28**	**35**
Length of pronotum, mm	3.14±0.25	3.25±0.23	3.06±0.15	4.17±0.36	4.26 ±0.25	3.89±0.27
	2.60–3.70	2.80–3.60	2.80–3.50	3.50–4.90	3.80–4.80	3.40–4.40
Length of fore wing, mm	14.06±0.89	14.87±1.09	14.30±0.82	17.49±1.46	17.78±1.18	17.12±1.29
	12.10–16.30	12.50–16.60	12.40–15.70	12.40–19.90	15.20–20.70	14.30–19.20
Length from stigma to tip of fore wing, mm	6.07±0.64	5.90±0.69	5.61±0.38	8.38±0.73	7.47±0.97	6.75±0.99
	4.30–7.70	4.50–7.30	4.60–6.20	6.60–10.80	5.80–9.90	4.10–8.30
Width of C & Sc areas, mm	10.53±0.96	9.52±0.84	9.05±0.61	7.58±0.65	7.20±0.75	7.10±0.64
	7.00–13.00	7.50–11.00	7.50–10.00	6.00–9.00	6.00–9.00	6.00–9.00
Length of hind femur, mm	10.09±0.58	10.21±0.61	9.57±0.41	13.21±1.09	13.48±0.99	12.21±0.99
	8.90–11.7	9.20–12.80	8.70–10.70	9.30–15.20	11.90–15.40	10.20–14.40
Length of stridulatory file, mm	5.78±0.87	4.41±0.55	3.13±0.25	7.35±0.76	5.45±1.04	4.29±0.99
	3.10–7.45	3.40–6.30	2.70–3.90	5.70–9.20	3.50–8.50	3.10–7.70
Length from last distal peg to tip of knee, mm	2.73±0.69	4.11±0.55	4.74±0.29	3.63±0.57	5.63±0.69	5.75±1.00
	1.60–5.05	2.20–5.50	4.20–5.40	2.60–4.90	4.10–7.00	2.30–7.40

converted with a PC card L-305 (L-Card Ltd., Russia). The ambient temperature near a singing male in the field was 20–40°C.

During stridulation of the males studied in laboratory, both the sound and the hind leg movements were recorded with a custom-built opto-electronic device (Helversen and Elsner 1977; Hedwig 2000). A piece of reflecting foil was glued to the distal part of each hind leg femur of a male and two opto-electronic cameras were focused on the illuminated reflecting dots. Each camera was equipped with a position-sensitive photodiode that converted the upward and downward movements of the hind legs into voltage signals. These signals, together with the recordings of the sounds (a microphone type 4191, ½ inch; a conditioning amplifier type 2690; Brüel & Kjaer, Nærum, Denmark), were A/D-converted with a custom-built PC card. The sampling rate was 1325 Hz for recording the stridulatory movements and 100 kHz for sound recordings. In the laboratory, the ambient temperature near a singing male was 30–32°C.

All recordings were analyzed with COOLEDIT 2.0 (Syntrillium, Seattle, WA) and TURBOLAB 4.0 (Bressner Technology, Gröbenzell, Germany). All statistical analyses were performed using Excel 2016 and STATISTICA 12.0.0.

For the song description we used the following terminology (Figs. 4, 6): *pulse* – the sound produced by one stroke of a hind leg (the shortest measurable unit or the first-order unit); *syllable* – the sound produced by one complete up and down movement of the hind legs, starting when the legs leave their initial position and ending when the legs return to their original position and representing the repeated unit of a stable structure (the second-order unit); *echeme* – series of consistent syllables separated by pauses (the third-order unit). We measured three characters in *C. brunneus* (echeme rate, echeme duration and pulse rate), four characters in *C. maritimus* (echeme rate and duration and syllable rate and duration) and seven characters in *C. miramae* (echeme rate, echeme duration and pulse rate for the *brunneus*-like echeme and echeme rate and duration and syllable rate and duration for the *maritimus*-like echeme). To visualize and clarify the differences in calling song between the three species, a PCA was applied to 5 song characters (Fig. 5E). We did not use echeme rate for both types of echemes because not all recorded males produced several echemes. When a character was equal to 0, we changed it to 0.01 by convention because we only used the logarithmic values for PCA.

Results

Nomenclatural notes

The names *Stauroderus mollis porphyroptera* and *S. miramae* (both currently included in the subgenus *Glyptobothrus* Chopard, 1951) were described by Vorontsovsky (1928a, b) in two papers on grasshoppers from Orenburg published in the same issue. *S. mollis porphyroptera* was described as a new variation and designated as a var. nov.; therefore, the authorship of Vorontsovsky in this case is beyond doubt (Vorontsovsky 1928a, p. 12). Vorontsovsky attributed the authorship of the *S. miramae* to Ramme, with the following comment: “For the identification of this species, as well as the form, I identified as a variety of the species *Stauroderus mollis*, I take the opportunity to express here my deep gratitude to E.F. Miram, who informed me that *S. miramae* has just been described from Crimea by Dr. Ramme as a new species.” (Vorontsovsky 1928a: 12, footnote). Actually, Ramme mentioned *Chorthippus miramae* for the first time only in 1939 without a description, specifying that this species “will be described in the near future” (Ramme 1939: 131). Therefore, the name *C. miramae* Ramme, 1939 is suggested to be a *nomen nudum*. Only in 1951, Ramme described this species based on material from Ukraine, Crimea, Southern and South-eastern European Russia, Caucasus, and Transcaucasia, with the type locality in Southern Crimea (Ramme 1951). On the other hand, Vorontsovsky (1928b) presented a short description of *C. miramae*. For this reason, he is the author of the taxon from Orenburg in spite of the fact that he attributed the authorship to Ramme. Further, the study of signals showed that *C. miramae* Vorontsovsky and *C. miramae* Ramme represent the different species (see below).

Summarizing the following three taxa were described in the papers mentioned above: *C. mollis porphyroptera* (Vorontsovsky 1928) from the type locality in Orenburg, *C. miramae* (Vorontsovsky, 1928) from the type locality in Orenburg, and *C. miramae* Ramme, 1951 from the type locality in Southern Crimea.

According to the study of Bukhvalova (1993) based on investigation of the male songs, the *Chorthippus biguttulus* group includes 5 species in Russia: *C. biguttulus* (Linnaeus, 1758), *C. brunneus* (Thunberg, 1815), *C. mollis* (Charpentier, 1825), *C. miramae* Ramme, 1939 and *C. yersini* Harz, 1975. The study of the songs of specimens from Crimea, Southern European Russia, North Caucasus, Central Asia, and the Russian Far East showed that *C. miramae* Ramme, 1939 *sensu* Bukhvalova (1993) is a good species, which is widespread throughout the southern part of Russia and adjacent territories. It was described as *C. biguttulus meridionalis* Mistshenko, 1950 from mountains of Central Asia (Mistshenko 1950), as *C. miramae* Ramme, 1951 from Crimea, and as *C. maritimus* Mistshenko, 1951 from the Russian Far East (Bey-Bienko and Mistshenko 1951). However, it differs from the taxa described by Vorontsovsky (1928a, b) from Orenburg (Bukhvalova 1998). The name *C. biguttulus meridionalis* Mistshenko, 1950 is invalid, since it is a junior homonym of *C. bicolor* var. *meridionalis* (Fruhstorfer, 1921). The name *C. miramae* Ramme, 1951 is a junior homonym of *C. miramae* (Vorontsovsky, 1928). As a result, the valid name of this taxon should be *C. maritimus* Mistshenko, 1951. It should be also noted that some authors improperly considered the date of publication of the name *C. miramae* Ramme to be 1939 (Bey-Bienko and Mistshenko 1951; Harz 1975; Bukhvalova 1993; Wosnessenskij 1996) and treated this taxon as a subspecies of *C. brunneus* (Bey-Bienko and Mistshenko 1951; Harz 1975).

C. bornhalmi Harz, 1971 was described from Croatia in the Balkans and has been shown to occur from Italy to Turkey (Willemse et al. 2009; Sirin et al. 2010). The range of *C. maritimus* extends from southern Ukraine to the Russian Far East. In the current study, we compare the morphology and songs in *C. bornhalmi* (from Bulgaria and Greece) and *C. maritimus*, and establish the synonymy *C. maritimus* Mistshenko, 1951 = *C. bornhalmi* Harz, 1971, syn. n.

C. biguttulus eximius Mistshenko, 1951 was described from Sukhumi, Abkhazia (Mistshenko 1951). A study of songs from the environs of the type locality (loc. 34 in Fig. 1) showed that this subspecies also is identical to *C. maritimus*. Since *C. maritimus* (as *C. biguttulus maritimus*) and *C. biguttulus eximius* were described in the same paper, we choose a valid name *C. maritimus* for this species and establish the synonymy *C. maritimus* = *C. biguttulus eximius* syn.n.

C. miramaellus Wosnessenskij, 1996 and *C. sinuatus* Mistshenko and Wosnessenskij, 1996 proposed by Wosnessenskij (1996) to replace *C. miramae* Ramme, 1951 and *C. biguttulus meridionalis* Mistshenko, 1950 respectively, are the junior synonyms of *C. maritimus* (Bukhvalova 1998). We suggest that *C. maritimus tsejensis* Bukhvalova, 1993 from North Ossetia, North Caucasus (Bukhvalova 1993) and *C. meridionalis karakalensis* Sytshev and Woznesenskij, 1995 from South-western Turkmenistan (Sychov and Voznesensky 1995) also belong to *C. maritimus*; however, additional studies are needed to clarify their status. It should be noted that M.M. Sychov and A.Yu. Voznesensky transliterated their own names in different ways in different papers, both in English and Latin; here we present their original spellings from the corresponding papers.

Benediktov (1999) reinvestigated material from Orenburg used by Vorontsovsky and concluded that *C. mollis porphyroptera* (Vorontsovsky, 1928) and *C. miramae* (Vorontsovsky, 1928) are synonyms. Benediktov (1999) compared the lengths of stridulatory files (the most characteristic feature of this species) in the type specimens of Vorontsovsky and found them to be identical. He proposed *C. porphyropterus* as the valid name, raising its rank, and changing its gender ending. However, according to chapter 24 of the International Code of Zoological Nomenclature (1999), when synonyms are established simultaneously, but are proposed at different ranks, the name proposed at a higher rank takes precedence. Consequently, the valid name of the taxon from Orenburg should be *C. miramae* (Vorontsovsky, 1928). Also, Benediktov (1999) established the synonymy *C. porphyropterus* = *C. biguttulus* forma *tomensis* Berezhkov, 1956, proposed the new combination *C. porphyropterus euchedickei* Helversen, 1989 for *C. biguttulus euchedickei* Helversen, 1989, and pointed out that *C. yersini* Harz, 1975 sensu Bukhvalova, 1993 is conspecific with *C. miramae* (Vorontsovsky, 1928). The true identity of *C. biguttulus* forma *tomensis* described known only from the bank of the Tom' River near Ust'-Iskitim, ca. 85 km south of Tomsk, Western Siberia (Berezhkov 1956), requires confirmation from song recordings from the type locality. The combination *C. biguttulus euchedickei* was restored by Willemse et al. (2009). The conspecificity of *C. yersini* sensu Bukhvalova, 1993 nec Harz, 1975 and *C. miramae* (Vorontsovsky, 1928) are absolutely correct.

Later on, Benediktov (2005) established the synonymy *C. porphyropterus* = *C. brunneus mistshenkoellus* Oliger, 1974 on the basis of investigation of the types of *C. brunneus mistshenkoellus* Oliger, 1974 from Tolyatti, Samara region. However oscillograms of the song of *C. maritimus* from Tolyatti (Benediktov and Mikhailenko 2017) cast doubt on this synonymy.

The status of *C. brunneus* (Thunberg, 1815) is unambiguous. In addition to the nominotypical subspecies, this species includes *C. brunneus mistshenkoellus* mentioned above and *C. brunneus brevis* Klingstedt, 1939 from Southern Finland (Klingstedt 1939), the statuses of which require further clarification.

In the current paper, we consider the following three taxa: *C. brunneus* (Thunberg, 1815), *C. maritimus* Mistshenko, 1951, and *C. miramae* (Vorontsovsky, 1928). *C. maritimus tsejensis* Bukhvalova, 1993, *C. meridionalis karakalensis* Sytshev et Woznesenskij, 1995, *C. brunneus mistshenkoellus* Oliger, 1974, and *C. brunneus brevis* Klingstedt, 1939 are excluded from the consideration since their statuses are unclear.

***Chorthippus brunneus* (Thunberg)**

Gryllus brunneus Thunberg, 1815: 256.

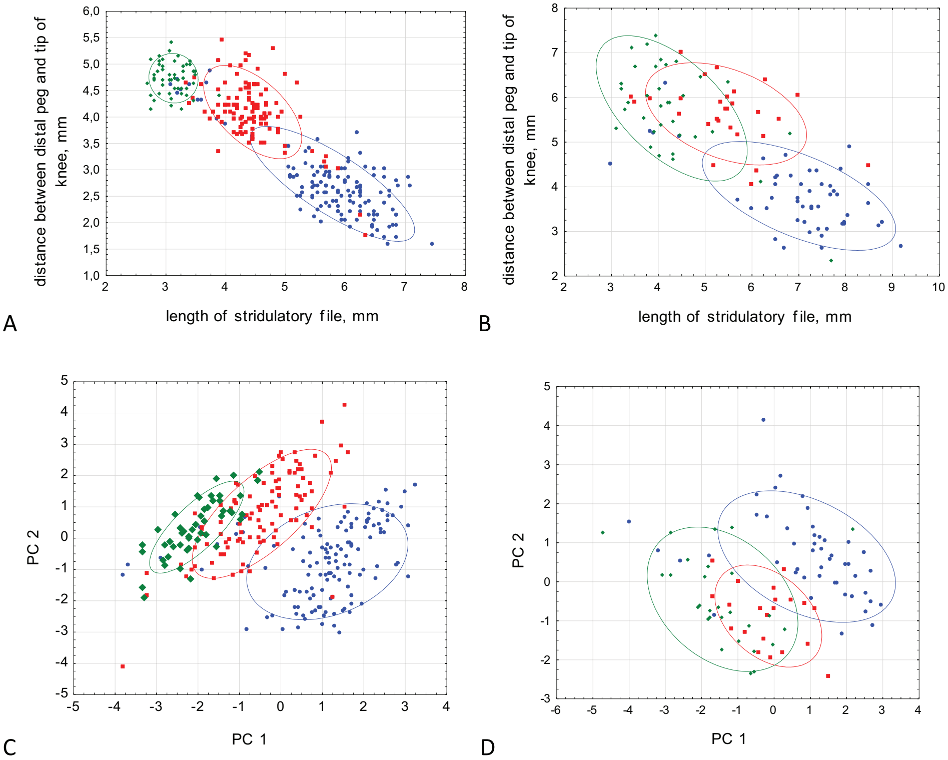
Material examined. Bulgaria: 4 Sofia region, lake Iskyr, 29.VI.2002, 1 ♂ 5 ♀, leg. V. Vedenina, song recordings in 1 ♂ (CV); **Moldova**: **10** Vinnitza region, Volchinetz, ab. 5 km W Mogilev-Podol'sky, 17.VII.1997, 1 ♂, leg. V. Vedenina (CV); **Romania**: **11** Dobrudzha region, 14 km S Constantza, Ephoria-Nord, 09.IX.1997, 2 ♂ 3 ♀, leg. A. Loginov (ZMMU); **Ukraine: 8** Ivano-Frankovsk region, environs of Mikulichin, 09–14.VIII.1996, 6 ♂ 1 ♀, leg. V. Vedenina (CV); **9** Khmelnitsky region, 28 km NNW of Kamenetz-Podolsky, near Beloe, 25.VI.2010, 1 ♂ 1 ♀, leg. V. Vedenina, song recordings in 1 ♂ (CV); **12** Odessa region, Kiliya district, environs of Vilkovo, 30.VI.1997, 2 ♂, leg. V. Vedenina (CV); **13** Odessa region, ab. 30 km NW of Belgorod-Dnestrovsky, near Krasnaya Kosa village, 29.VI.1997, 1 ♂, leg. V. Vedenina (CV); **16** Nikolaev region, Pervomaisk district, surr. of Kuripchino village, 27.06.1997, 1♂, leg. V. Vedenina (CV); **18** Cherkassy region, Kanev district, Kanev reserve, 12–18.VI.1996, 12 ♂ 5 ♀, leg. V. Vedenina (ZMMU); **19** Kirovograd region, environs of Aleksandriya, 04.VII.1997, 2 ♂ 2 ♀, leg. V. Vedenina (CV); **20** Nikolaev region, Pervomaisk district, environs of Kuripchino village, beach of

Yuzhny Bug river, 27.VI.1997, 1 ♂ 1 ♀, leg. V. Vedenina, song recordings in 2 ♂ (CV); **22** Poltava region, Mirgorod district., V.Sorochintzy, 27–28.VI.1985, 4 ♂ 5 ♀, 25–28.VII.1993, 3 ♂ 5 ♀, 24.VII–26.VIII.1994, 5 ♂, leg. V. Vedenina, song recordings in 6 ♂ (ZMMU, CV); **25** Dnipro region, Pavlograd district, Samara reserve, 12–15.VII.1996, 4 ♂ 4 ♀, leg. V. Vedenina (CV); **Russia: 1** Kaliningrad region, environs of Svetlogorsk, forest road, 16.VIII.2005, 3 ♂ 1 ♀, leg. N. Kulygina, song recordings in 1 ♂ (CV); **14** St-Peterburg, 27.08.1997, 1 ♂, leg. V. Vedenina (CV); **32** Voronezh region, Novaja Usman' district, near Maklok village, 29.VI.2006, 3 ♂, leg. N. Kulygina (CV); **35** Kostroma region, Manturovo district, environs of. Anosovo, 07–08.VIII.2009, 2 ♂ 1 ♀, leg. V. Vedenina, song recordings in 2 ♂ (CV); **40** Saratov region, Krasny Kut district, near D'yakovka, 17.VII.2004, 3 ♂, leg. D. Tishechkin, song recordings in 2 ♂ (ZMMU).

Distribution. (Fig. 1). The range of this species extends from Europe to the south-western part of European Russia. In Europe this species occurs over a wide range, excluding the central and southern part of the Iberian Peninsula and Greece (Ragge and Reynolds 1988, Sirin et al. 2010). Further to the east, it occurs in the Baltic republics, Belarus, Moldova, and Ukraine. The eastern border of the range lies on the longitude of the Saratov and Kostroma regions of Russia. The species tends to be mesophilic. The range of *C. brunneus* overlaps with that of *C. maritimus* in south-eastern Europe, Moldova, Ukraine, and the south-eastern part of European Russia.

Recognition. (Table 1, Fig. 3). The males of *C. brunneus* can be distinguished from the males of *C. miramae* and *C. maritimus* by a short stridulatory file (Fig. 3A). This, however, is not applicable to the females (Fig. 3B). Both sexes of *C. brunneus* are characterized by the lowest number of stridulatory pegs (58–93 in ♂, 51–95 in ♀.). In comparison with *C. miramae* and *C. maritimus*, both sexes of *C. brunneus* tend to have the shortest pronotum, the narrowest C & Sc areas of fore wing, and the stigma closest to the wing tip (Table 1). The PCA applied to 6 characters shows a substantial overlap between *C. brunneus* and *C. maritimus* (Fig. 3C, D). In PCA, however, we do not use the number of stridulatory pegs, since this value was measured for a small number of males. Meanwhile, it was previously shown that *C. brunneus* can be easily distinguished from all other species of the *C. biguttulus* group by the lowest number of stridulatory pegs, especially in nominate subspecies (Oliger 1974; Ragge and Reynolds 1988; Bukhvalova 1993; Willemse et al. 2009).

Calling song (Table 2, Figs. 4, 5). The calling song of *C. brunneus* consists of several short echemes repeated at the rate of about 0.3–2.1 /s. Each echeme lasts on average 0.1–0.4 s and has a relatively stable temporal structure. It consists of short pulses, which are grouped into 4–7 syllables (Fig. 4C). The gaps between the subsequent syllables can't be traced by the sound analysis, but they can be distinguished by the analysis of the leg movements. The two legs are moved with a large phase shift, and sometimes almost alternately (Fig. 4E). Each leg generates one short pulse during a straight upstroke, whereas two short pulses are produced during a two-step downstroke. The pulse duration and the pulse rate vary in the ranges of 7–8 ms and 91–111/s, respectively (at the temperature 29–30°C). The population from loc. 40, shows an extremely



Morphological characters	males		females	
	PC 1	PC 2	PC 1	PC 2
Length of pronotum	0,37	0,74	0,70	-0,43
Length of fore wing	0,28	0,90	0,58	-0,70
Distance from stigma to tip of fore wing	0,68	0,30	0,82	-0,13
Width of C & Sc areas	0,73	0,00	0,43	0,21
Length of stridulatory file	0,89	-0,31	0,86	0,35
Distance from last peg to end of knee	-0,76	0,61	-0,57	-0,77

E

Figure 3. Morphological differences between *Chorthippus brunneus* (green dots), *C. maritimus* (red dots), and *C. miramae* (blue dots). **A,B** length of stridulatory file vs. distance from the last stridulatory peg to the tip of knee in males (**A**) and females (**B**) **C,D** results of Principal Component Analysis based on 6 characters are shown for PC 1 and PC 2 in males (**C**) and females (**D**) **E** loadings of different characters to PC 1 and PC 2.

long echeme duration and low echeme and pulse rate (Table 2). Notably, the values are relatively stable within the same population.

Courtship and rivalry songs. The courtship and rivalry (Fig. 4F, G) songs of *C. brunneus* are similar to the calling song.

Chorthippus maritimus Mistshenko

Chorthippus miramae Ramme, 1939: 131, nomen nudum.

Table 2. Calling songs parameters of *Chorthippus brunneus*. For each parameter, medians, the lower and upper quartiles are shown.

Locality	Number of recorded males (measurements)	Temperature, ° C	echeme duration, s	echeme rate, /s	pulse rate, /s
1	1 (10)	32	0.2 0.1; 0.2	0.7 0.6; 0.9	125 115; 161
4	1 (9)	31–35	0.2 0.2; 0.2	1.1 0.7; 1.9	100 100; 122
9	1 (10)	24–25	0.2 0.2; 0.2	0.7 0.6; 0.8	143 143; 167
20	2 (16)	30	0.2 0.2; 0.2	2.1 1.0; 2.5	100 83; 111
22	6 (51)	29	0.2 0.2; 0.2	1.1 0.4; 1.3	91 83; 111
35	2 (20)	29–30	0.1 0.1; 0.1	1.1 0.7; 2.5	111 91; 129
40	2 (24)	28; 32–33	0.4 0.3; 0.5	0.3 0.2; 0.4	57 51; 66

Chorthippus meridionalis Mistshenko, 1950: 790.
Chorthippus biguttulus maritimus Mistshenko, 1951: 514.
Chorthippus miramae Ramme, 1951: 389.
Chorthippus biguttulus eximius Mistshenko, 1951: 515, syn. n.
Chorthippus bornhalmi Harz, 1971: 336, syn. n.
Chorthippus miramaellus Woznessenskij, 1996: 204.
Chorthippus sinuatus Mistshenko et Woznessenskij, 1996: 204.

Material examined. Bulgaria: 4 Sofia region, lake Iskyr, 29.VI.2002, 6 ♂ 5 ♀, leg. V. Vedenina (ZMMU); **5** Vraca region, ab. 3 km S of Vraca, Vracniki Balekan National Park, Memorial Botev, 30.VI.2002, 2 ♂, leg. V. Vedenina (CV); **Greece: 2** Phthiotis, environs of Timfristos, NE slope, 27.V.1998, 1 ♂, leg. V. Vedenina (CV); **3** Phthiotis, ab 40 km NW Lamia environs of Lautra Kaitsas, 26.V.1998, 3 ♂ 1 ♀, leg. V. Vedenina (CV); **6** Macedonia, Drama, Mt Falakro above Volakas, 5 km NE Elatia, 24.VII.2004, 1 ♂, leg. V. Vedenina, song recordings in 2 ♂ (CV); **7** Macedonia, Drama, W. Rodopi, 5 km NE Elatia, 23.VII.2004, 1 ♂ 1 ♀, leg. V. Vedenina (CV); **Ukraine: 15** Odessa region, near Sychavka, 03.VII.1997, 5 ♂, leg. V. Vedenina (ZMMU); **17** Kirovograd region, Novoukrainka district, environs of Pomoshnaya, 26.VI.1997, 2 ♂, leg. V. Vedenina, song recordings in 2 ♂ (CV); **21** Kherson region, Chernomorsky nature reserve, Solyonoozerny area, 25.VII–05.VIII.1995, 2 ♂ 1 ♀, leg. V. Vedenina (CV); **23** Crimea, Bakhchisaray district, 3–4 km E of Gluboky Yar, 11.VI.1997, 4 ♂, leg. D. Tishechkin, song recordings in 4 ♂ (ZMMU); **24** Crimea, Simferopol’ district, environs of Pereval’noe, 20.VI.1997, 3 ♂, leg. D. Tishechkin, song recordings in 3 ♂ (ZMMU); **25** Dnipro region, Pavlograd district, Samara reserve, 12–15.VII.1996, 6 ♂, leg. V. Vedenina (CV); **26** Crimea, Kerch peninsula, E shore of Kazantip bay, environs of cape Chagany, 26.VI.1997, 1 ♂, leg. D. Tishechkin, song recordings in 1 ♂ (ZMMU); **27** Kharkov region, Izjum district, Kamyshevacha, 15.VII.1996, 5 ♂ 1 ♀, leg. V. Vedenina (ZMMU); **28** Kharkov region, Izjum, Kremenetz hill, 15.VII.1996, 1

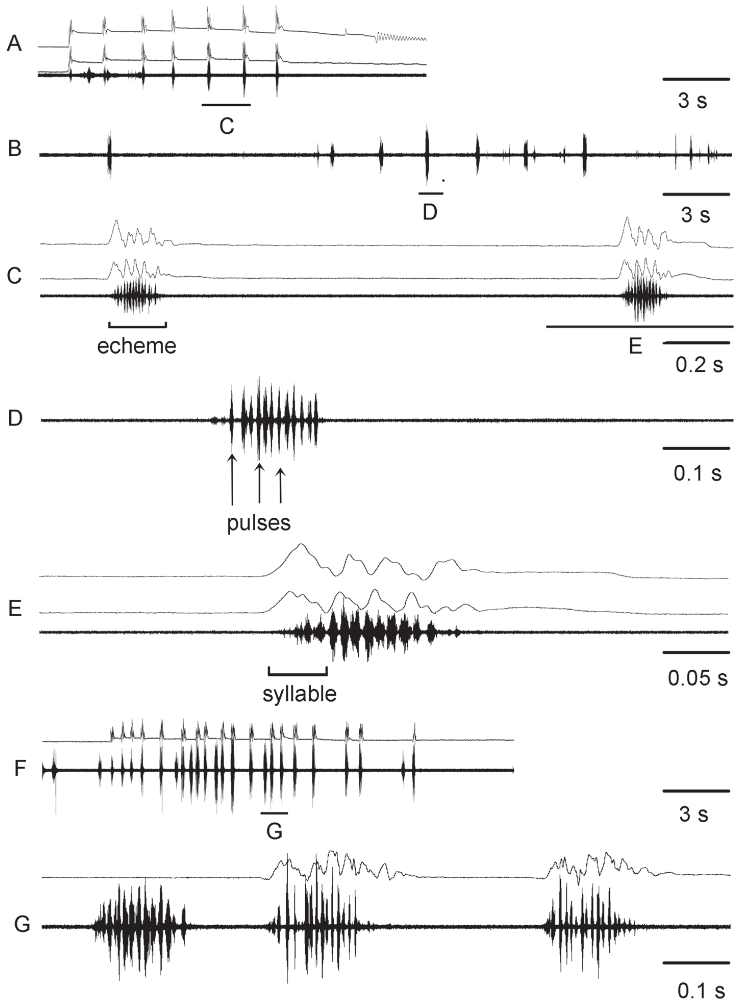


Figure 4. Oscillograms of calling songs **A–E** and rivalry songs **F,G** in *Chorthippus brunneus* from Kostroma region (**A**) Poltava region (**B**) and Saratov region (**F**). Song recordings are presented at four different speeds (faster oscillograms of the indicated parts of the songs shown in **C,D,E,G**). In all oscillograms the two upper lines are recordings of hind leg movements and the lower line is the sound recording. Different song parameters are indicated by brackets and arrows. The ambient temperature near a singing male was 29 – 32°C.

♂, leg. V. Vedenina (CV); **Abkhazia: 34** Sukhumi region, slopes near highway Sukhumi – Gagra, 21–22.X.2005, 5 ♂ 5 ♀, leg. V. Vedenina, song recordings in 3 ♂ (ZMMU); **Russia**: **33** Krasnodarsky krai, near highway Krasnaya Poljana – Adler, 22.X.2005, 4 ♂ 3 ♀, leg. V. Vedenina, song recordings in 4 ♂ (CV); **39** Saratov, slopes near Polivanovka, 28.VI.2020, 2 ♂, leg. V. Vedenina, song recordings in 2 ♂ (CV); **41** Saratov region, Krasnokutsk district, near D'yakovka, 28.VI.2020, 6 ♂ 1 ♀, leg., song recordings in 5 ♂ (CV); **43** Saratov region, SW from Khvalynsk, environs of Ul'yanino village, 19.VII.2005, 3 ♂, leg. D. Tishechkin, song recordings in 3 ♂ (ZMMU); **44** Saratov region, ab. 6 km NW of Ershov, 22.VI.2018, 3 ♂, leg. V. Vedenina (CV); **45** Saratov region, 15 km NE Ozinki, 23.VI.1996, 4 ♂, leg. D. Tishechkin, song recordings in 4 ♂ (ZMMU); **42** Krasnoyarsk region, Astrakhan‘ district, environs of Dosang railway station, 03.VII.2000, 1 ♂, leg. D. Tishechkin, song recordings in 1 ♂ (ZMMU); **75** Irkutsk region, Olkhon district, 20 km from Jelantsy to strait Olkhonskie vorota, 15.VII.2003, 4 ♂, leg. D. Tishechkin, song recordings in 4 ♂ (ZMMU); **77** Buryatia, Barguzin valley, Ina river, 4 – 5 km downstream from Ina, 17.VII.2007, 3 ♂, leg. D. Tishechkin, song recordings in 2 ♂ (ZMMU); **78** Chita region, Klichka range, ab. 15 km W Klichka, 22.VII.2003, 2 ♂, leg. D. Tishechkin, song recordings in 1 ♂ (ZMMU); **79** Amur region, 15 km S Svobodny, environs of Malaya Sazanka, 05.VII.1995, 4 ♂, leg. D. Tishechkin, song recordings in 4 ♂ (ZMMU); **80** Primorskiy kray, Pogranichny district, environs of Barabash-Levada, 20.VII.1995, 3 ♂, leg. D. Tishechkin, song recordings in 3 ♂ (ZMMU); **81** Primorskiy kray, Pogranichny district, Khanka lake, 15 km S Turiy Rog, 21.VII.2006, 3 ♂, leg. D. Tishechkin, song recordings in 3 ♂ (ZMMU); **82** Southern Sakhalin, environs of Sokol, 02.VIII.2015, 4 ♂, leg. D. Tishechkin, song recordings in 3 ♂ (ZMMU); **Kazakhstan: 62** Almaty region, 40 km N from Almaty, environs of Kara-Oi village, 12.VI.2017, 1 ♂, leg. D. Tishechkin, song recordings in 1 ♂ (ZMMU); **63** Almaty, botanical garden, 07.VII.1994, 3 ♂, leg. D. Tishechkin, song recordings in 3 ♂ (ZMMU); **65** Almaty region, ab. 20 km NE of Taldykorgan, 02.VII.2016, 4 ♂, 1 ♀, leg. V. Vedenina & T. Pushkar, song recordings in 1 ♂ (CV); **66** Kazakhstan, Almaty region, near Kapal, 01.VII.2016, 1 ♂, leg. V. Vedenina & T. Pushkar, song recordings in 1 ♂ (CV); **67** Kazakhstan, Almaty region, ab. 2.5 km W of Kapal, 02.VII.2016, 4 ♂ 4 ♀, leg. V. Vedenina & T. Pushkar, song recordings in 2 ♂ (ZMMU); **68** Urzhar region, 27 km SSE Taskesken, 5.5 km NW Karakol, 24.VI.2019, 1 ♂, leg. D. Tishechkin, song recordings in 1 ♂ (ZMMU); **Turkmenistan**: **49** Ahal region, Kaka district, 6–7 km S of Dushak, 14.V.2014, 3 ♂, leg. D. Tishechkin, song recordings in 3 ♂ (ZMMU); **Kyrgyzstan**: **51** Batken region, Leilek district, Turkestan range, 12 km S from Katran village, 11.VII.2014, 1 ♂, leg. D. Tishechkin, song recordings in 1 ♂ (ZMMU); **53** Batken region, N shore of Tortkul'skoye reservoir, 12 km WSW Batken, 09.VII.2014, 1 ♂, leg. D. Tishechkin, song recordings in 1 ♂ (ZMMU); **54** Jalal-Abad region, Chatkal range, Sary-Chelek nature reserve, environs of Arkyt, 22.VII.2008, 2 ♂, leg. D. Tishechkin, song recordings in 1 ♂ (ZMMU); **57** Chuy region, Jayyl district, Karakol river, 10 km upstream from confluence with Suusamyr, 07.VII.2016, 1 ♂, leg. D. Tishechkin, song recordings in 1 ♂ (ZMMU); **58** Chuy region, Djumgal river, between Baizak and Chaek, 30.VI.2014, 1 ♂, leg. D. Tishechkin, song recordings in 1 ♂ (ZMMU); **64** Issyk-Kul‘ region, Tossor river, 18 km E from Kadji-Sai, 15.VII.2013, 1 ♂, leg. D. Tishechkin, song recordings in 1 ♂ (ZMMU).

Distribution. (Fig. 1). *C. maritimus* is a widespread trans-Palearctic species. It includes *C. bornhalmi* from the Balkans and Anatolia (Willemse et al. 2009; Sirin et al. 2010; Skejo et al. 2018) and as *C. biguttulus eximius* from Sukhumi, Abkhazia (Mistshenko 1951). It also occurs in Moldova and southern Ukraine (Heller et al. 1998). In the territory of Russia, its range stretches from Krasnodarsky krai to Sakhalin along the southern border. This species also occurs in Caucasus, southern Kazakhstan, Turkmenistan, very likely Uzbekistan, Kyrgyzstan, Mongolia, northern-east China, Korea and Japan (Storozhenko 2002). The ranges of *C. maritimus* and *C. brunneus* overlap in Eastern Europe, Ukraine and the south-eastern part of European Russia. Moreover, *C. maritimus* and *C. brunneus* often occur syntopically. The range of *C. maritimus* also overlaps with the range of *C. miramae* in the south-eastern part of European Russia and in surroundings of the Baikal Lake, however, they do not occur in the same biotopes.

Recognition. (Table 1, Fig. 3). The males of *C. maritimus* can be distinguished from the males of *C. brunneus* by the longer stridulatory file (Fig. 3A) and the higher number of stridulatory pegs (see Description). These characters are also mentioned as the distinguishing features between *C. brunneus* and *C. bornhalmi* by other authors (Willemse et al. 2009; Skejo and Ivcovic 2015). The length of stridulatory file in *C. maritimus* is intermediate between those in *C. miramae* and *C. brunneus.* Both sexes of *C. maritimus* also tend to have the longest fore wings and pronotum in comparison with *C. miramae* and *C. brunneus* (Table 1). *C. maritimus* can be also distinguished from other species of the *biguttulus* group by the narrower costal area of fore wing. By contrast, *C. maritimus* differs from *C. mollis* by the wider costal area of fore wing and by the lower density of stridulatory pegs (Bukhvalova 1993; Oliger 1974). *C. bornhalmi* and *C. biguttulus eximius* are not different in morphology from *C. maritimus* from Ukraine and Russia.

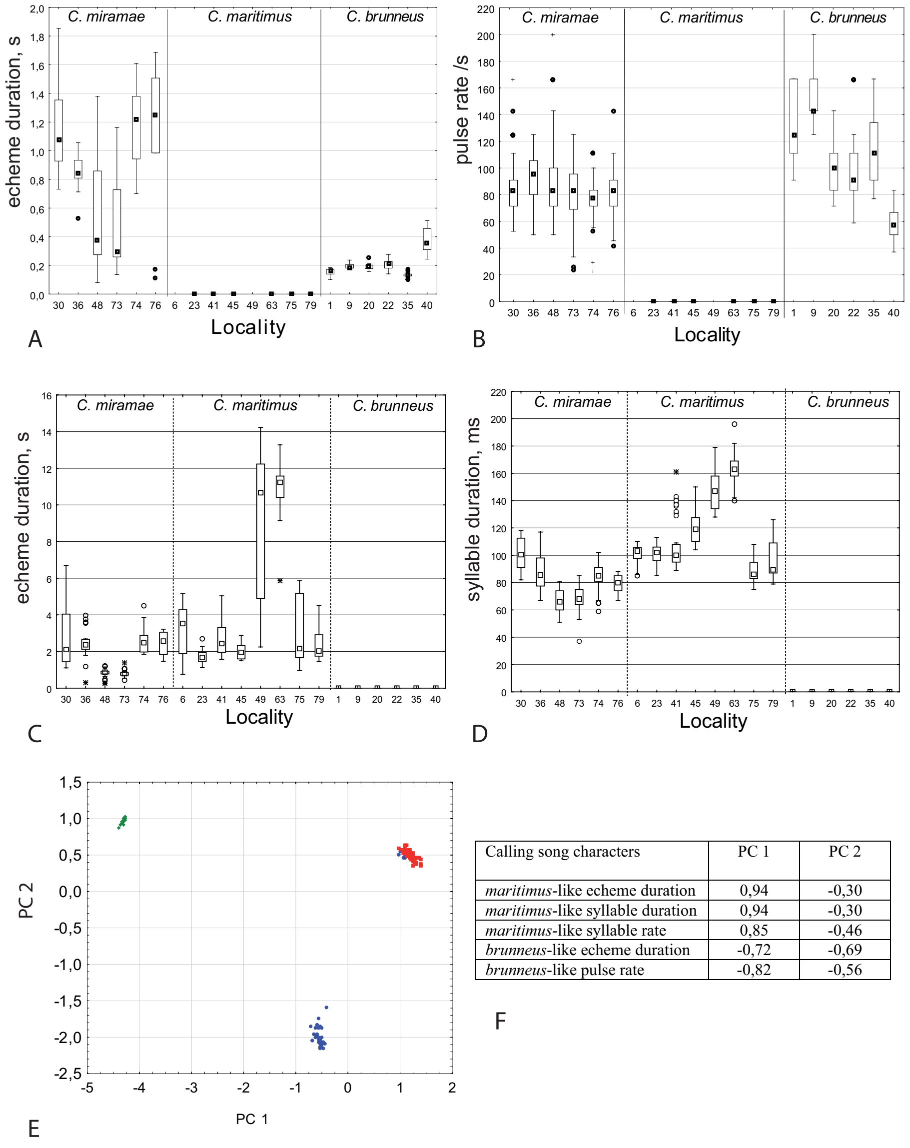
Description. (Table 1, Fig. 3). The head structure as in genus. Ratio length of vertical diameter of eye to maximum length of foveolae 2.8–3.4 in ♂, 3.0–3.2 in ♀; ratio minimum interocular distance to length of subocular groove 0.6–0.8 in ♂, 0.7–0.9 in ♀. Antennae filiform. Prozona is slightly shorter than metazona; median carina is distinct and continuous. Lateral pronotal keels are distinctly incurved, ratio between minimum and maximum widths 2.3–2.6 in ♂, 2.3–2.9 in ♀. In western populations keels are more angled, min/max width ratio up to 3.0. Tympanal aperture slit-like, 2.3–2.8 times in ♂, 2.6–2.8 in ♀ as long as broad. Fore and hind wings well developed in both sexes, wings far surpassing the apices of the hind knee. Costal area of fore wing has maximum width in the middle part or in the last third of the wing. Subcostal area narrow, its width 0.25–0.3 mm in ♂, 0.15–0.2 mm in ♀ (measured on the line of maximal width of costal area). Ratio width of fore wing to C & Sc areas 3.1–3.5 in ♂, 4.4–4.7 in ♀. Apical constriction (distance from C and Sc confluence to the wing tip) prolonged, ratio length of apical constriction to the wing length 3.3–3.8 in ♂, 3.5–3.8 in ♀. Stigma far from the wing tip, ratio length between stigma center and the wing tip to the wing length 2.4–2.7 in ♂, 2.3–2.5 in ♀. Hind femur gracile, ratio femur length to maximum width 4.4–4.6 in ♂, 4.4–4.7 in ♀. Stridulatory file consists of one row, its length nearly equal to the distance between last peg and tip of hind knee. The number of stridulatory pegs 100–168 in ♂, 104–157 in ♀. Body coloration varies from light straw to dark brown, sometimes with a red tone. The ventral side of the body lighter than dorsal side, and densely pubescent. Fore wings smoky, with a few dark spots in M area. Hind wings transparent at the base and slightly smoky in apical part, distal half of C area smoky or brownish. Hind femur in the inner side with black lengthwise line. Hind knees dark brown or blackish, particularly on upper lobe. Hind tibiae orange or reddish.

Measurements in mm. Body length: 15–18 in ♂, 19–26 in ♀, pronotum length: 3.1–3.4 in ♂, 4.1–4.4 in ♀, fore wing length: 14.1–15.5 in ♂, in 17.2–18.5 in ♀, fore wing width 3.1–3.4 in ♂, 3.2–3.5 in ♀, hind femur length: 9.8–10.6 in ♂, 12.8–14.1 in ♀.

Calling song (Table 3, Figs. 5, 6). The calling song of *C. maritimus* usually contains one to several echemes of median duration ranged from 1 to 4 s. In some populations (49, 62, 63), however, the median echeme duration is higher, ranging between 5–11.1 s (Table 3, Fig. 5C). The echeme rate also greatly varies between different populations (0.05–0.42 / s). The number of syllables per echeme varies in the range of 15 to 40, in populations with prolonged echemes – in the range from 40 to 70. The syllable duration is relatively stable within the same population; however, its median duration can vary between the populations in the range of 86–162 ms (Fig. 5D). At the beginning of each echeme, the sound is very soft, but then it reaches maximum loudness after the first third of the echeme duration, being constant until the echeme end (Fig. 6D). The syllables are generated by the leg movements with a small phase shift, which comprise the straight upstroke and stepwise downstroke (Fig. 6E, F). Both upstroke and downstroke have the similar duration. The leg upstroke generates a noisy sound with unclear structure and slightly increasing amplitude; the stepwise downstroke generates 4–5 distinct pulses. The pulses,

Table 3. Calling songs parameters of *Chorthippus maritimus*. For each parameter, medians, the lower and upper quartiles are shown.

Locality	Number of recorded males (measurements)	Temperature, ° C	echeme duration, s	echeme rate, /s	syllable duration, ms	syllable rate, /s
6	2 (10)	30	4.0	0.19	103	8.5
			3.6; 4.6	0.18; 0.19	99; 105	8.3; 9.1
17	2 (10)	32	1.0	0.20	129.5	9.4
			0.9; 1.1	0.18; 0.25	127; 132	8.6; 10.0
23	4 (40)	31–35	1.7	0.25	102	9.3
			1.5; 1.9	0.20; 4.5	96; 106	8.9; 9.5
24	3 (18)	24–25	1.4	0.3	104	8.8
			1.2; 1.6	0.29; 0.34	102; 112	8.5; 9.0
34	3 (14)	30	2.8	0.42	136	7.0
			2.0; 4.4	0.21; 0.46	119; 159	5.6; 8.1
39	2 (13)	29	2.1	0.24	103	9.2
			1.4; 2.7	0.22; 0.27	100; 106	9.0; 9.4
41	5 (15)	29–30	2.4	0.20	100	9.3
			2.0; 2.9	0.16; 0.22	95; 108	8.7; 9.9
43	3 (12)	28; 32–33	1.3	0.25	86	10.1
			1.2; 1.7	0.22; 0.28	81; 124	7.2; 10.8
45	4 (12)	32–36	2.0	0.23	119	7.8
			1.6; 2.3	0.19; 0.24	110; 127	7.2; 8.1
49	3 (25)	34–35	10.7	0.07	159	6.4
			4.9; 12.2	0.06; 0.08	157; 165	6.3; 6.5
54	1 (10)	35–39	3.2	0.16	135	7.0
			2.0; 5.2	0.13; 0.26	133; 136	6.9; 7.0
62, 63	4 (11)	30–32; 35	11.1	0.05	162	5.9
			7.8; 11.5	0.04; 0.05	134; 164	5.7; 6.1
75	4 (12)	31	2.2	0.14	86	10.1
			1.7; 5.2	0.13; 0.18	83; 94	9.7; 10.5
77	2 (15)	20; 27–30	2.5	0.13	133	7.0
			1.7; 5.2	0.12; 0.23	124; 147	6.3; 7.7
79	4 (13)	31	2.0	0.14	90	10.3
			1.7; 2.9	0.09; 0.18	87; 104	9.2; 10.7
80	3 (18)	38–40	2.1	0.13	87	10.9
			1.9; 2.5	0.07; 0.16	85; 90	9.6; 11.1
82	3 (20)	35–40	2.3	0.15	88	10.5
			1.8; 3.5	0.12; 0.18	85; 90	10.3; 11.2



Calling song characters	PC 1	PC 2
maritimus-like echeme duration	0,94	-0,30
maritimus-like syllable duration	0,94	-0,30
maritimus-like syllable rate	0,85	-0,46
brunneus-like echeme duration	-0,72	-0,69
brunneus-like pulse rate	-0,82	-0,56

F

Figure 5. Differences in calling songs between *Chorthippus brunneus*, *C. maritimus*, and *C. miramae* **A–D** box-plots for the *brunneus*-like echeme duration (**A**) for the *brunneus*-like pulse rate (**B**) for the *maritimus*-like echeme duration (**C**) and the *maritimus*-like syllable duration (**D**) medians (dots), first and third quartiles (boxes), the 10th and 90th percentiles (whiskers), and outliers (dots beyond whiskers) are shown **E** results of Principal Component Analysis based on 5 song characters are shown for PC 1 and PC 2 in *C. brunneus* (green dots), *C. maritimus* (red dots), and *C. miramae* (blue dots) **F** loadings of different characters to PC 1 and PC 2.

however, can be sometimes fuzzy. The durations and rates of echeme and syllable in *C. bornhalmi* (from loc. 6) and in *C. biguttulus eximius* (from loc. 34) fall into the range of values in *C. maritimus* from several localities (Table 3, Fig. 5C, D). The syllable structure is also quite similar in *C. bornhalmi* (Fig. 6E) and *C. biguttulus eximius* (Fig. 6F).

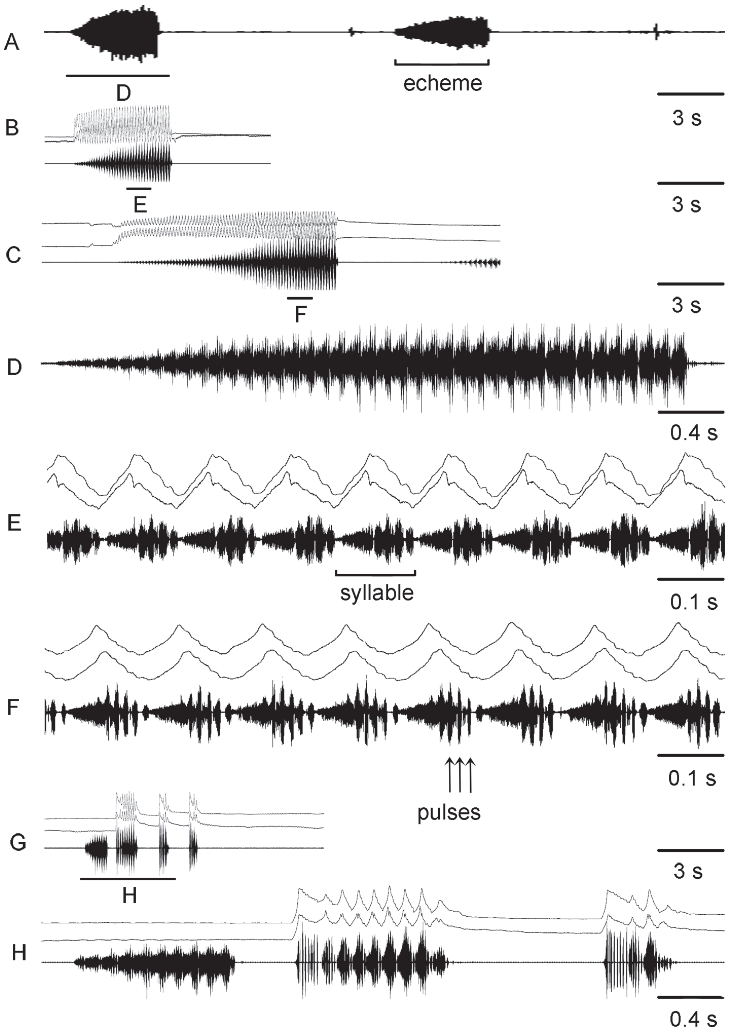


Figure 6. Oscillograms of calling songs **A–F** and rivalry songs **G,H** in *Chorthippus maritimus* from Primorskiy kray (**A**) Macedonia (**B**) Sukhumi region (**C**) and Saratov region (**G**). Song recordings are presented at three different speeds (faster oscillograms of the indicated parts of the songs shown in **D,E,F,H**). In all oscillograms the two upper lines are recordings of hind leg movements and the lower line is the sound recording. The ambient temperature near a singing male was 33 – 34°C in (**A**) and 29 – 30°C in other cases.

Courtship song. The courtship song of *C. maritimus* is similar to the calling song.

Rivalry song (Fig. 6G, H). The rivalry song of *C. maritimus* contains echemes of a shorter duration than the calling song. In some males the first syllable of the rivalry echeme lasts 1.5–2 times as long as the subsequent syllables, which results from the prolonged first downstroke (Fig. 6H). The pulses produced during the first downstroke are repeated twice as slowly as the pulses of the subsequent syllables. The subsequent 2–8 syllables are of the same structure as the syllables in the calling song.

Chorthippus miramae (Vorontsovsky)

Stauroderus miramae Vorontsovsky, 1928a: 12.
Stauroderus mollis porphyroptera Vorontsovsky, 1928b: 31, 34.
Chorthippus porphyropterus (Vorontsovsky, 1928): Benediktov, 1999: 42.

Material examined. Russia: 29 Krasnodarsky kray, environs of Gelendzhik, 06.X.2011, 8 ♂ 4 ♀, leg. V. Vedenina & L. Shestakov, song recordings in 3 ♂(ZMMU); **30** Krasnodarsky kray, Gelendzhik district, environs of Aderbievka, 07.VII.1997, 8 ♂ 8 ♀, leg. D. Tishechkin, song recordings in 4 ♂ (ZMMU); **31** Krasnodarsky kray, Gelendzhik district, environs of Praskoveevka; 12.VII.1997, 2 ♂, leg. D. Tishechkin (ZMMU); **36** N. Caucasus, N. Ossetia, environs of Alagir, Ardon river floodplain, 09.VIII.1990, 2 ♂ 2 ♀, leg. M. Bukhvalova, song recordings in 2 ♂ (ZMMU); **37** N. Caucasus, N. Ossetia, Sunzhensky range, environs of Elkhotovo, 10–12.VIII.1990, 2 ♂ 1 ♀, leg. M. Bukhvalova (ZMMU); **38** N. Caucasus, N. Ossetia, Sunzhensky range, environs of Bekan lake, 14.VIII.1985, 3 ♂ 3 ♀, leg. D. Tishechkin (ZMMU); **47** Orenburg region, environs of Studentzy, 14.VII.2012, 1 ♂, leg. V. Vedenina & L. Shestakov, song recordings in 1 ♂ (CV); **48** Orenburg region, environs of Guberlya railway station, 07–09.VII.1996, 37 ♂ 13 ♀, leg. D. Tishechkin, song recordings in 5 ♂ (ZMMU), 29.VI.2018, 1 ♂, leg. V. Vedenina & N. Sevastianov, song recordings in 1 ♂ (CV); **69** Altai Republic, ab. 26 km SE of Ongudai, environs of Kupchegen', 08.VIII.2017, 5 ♂ 3 ♀, leg. V. Vedenina & N. Sevastianov, song recordings in 1 ♂ (ZMMU); **70** Tyva republic, environs of Erzin, Tore-Kchan' lake, 31.VII.1989, 1 ♂ 1 ♀, leg. S. Byzov (ZMMU); **71** Tyva republic, environs of Erzin, Erzin river floodplain, 20.VII–06.VIII.1989, 3 ♂ 3 ♀, leg. M. Bukhvalova, song recordings in 3 ♂ (ZMMU); **72** Tyva republic, environs of Erzin, Tes-Kchem river floodplain, 03–06.VIII.1989, 3 ♂, leg. M. Bukhvalova (ZMMU); **73** Irkutsk region, Nizhneudinsk district, Uk river estuary, confluence with Uda, 02.VII.2003, 5 ♂, leg. D. Tishechkin, song recordings in 5 ♂ (ZMMU); **74** Buryatia, Selenginsk district, 5 km N from Novoselenginsk, Selenga river valley, 07.VII.2007, 5 ♂, leg. D. Tishechkin, song recordings in 5 ♂ (ZMMU); **76** Buryatia, Zaigrayevo district, 10 km Onokhoy, Bryanka river valley, 21.VII.2007, 3 ♂, leg. D. Tishechkin, song recordings in 3 ♂ (ZMMU); **Kazakhstan**: **46** West-Kazakhstan region, ab. 50 km W of Ural'sk, environs of Kamenka, 23.VI.2018, 5 ♂, leg. V. Vedenina & N. Sevastianov (ZMMU); **50** Kostanay region, Naurzum nature reserve, 04–11.VIII.1938, 13 ♂ 6 ♀, leg. Derevitskaya, 11.VIII–25.IX.1939, 3 ♂ leg. Pokrovskyi, 24.VII.1947, 1 ♂ A. Formozov (ZMMU); **52** Akmola region, Tselinograd district, ab. 4 km SWW from Zhaynak, 09.VII.2019, 3 ♂, leg. V. Vedenina, N. Sevastianov & T. Tarasova, song recordings in 1 ♂ (CV); **55** Akmola region, Arshaly district, 7 km N Vishnevka, Ishym river floodplain, 11.VII.2019, 3 ♂, leg. V. Vedenina, N. Sevastianov & T. Tarasova, song recordings in 2 ♂ (CV); **56** Akmola region, Jerementau district, 4.5 km NE from Baysary, 03.VII.2019, 2 ♂, leg. V. Vedenina, N. Sevastianov & T. Tarasova, song recordings in 2 ♂ (CV); **59** Pavlodar region, Ekibastuz district, ab. 3 km W of Schidert, 04.VII.2019, 6 ♂ 1 ♀, leg. V. Vedenina, N. Sevastianov & T.

Tarasova, song recordings in 3 ♂ (ZMMU); **60** Pavlodar region, Zhelezinsky district, near Pyatiryzhsk, 22.VII 1 ♂ 1 ♀ leg. Ingenitskyi (ZMMU), 05.VII.2019, 2 ♂, leg. V. Vedenina, N. Sevastianov & T. Tarasova, song recordings in 2 ♂ (CV); **61** Pavlodar region, Terenkol' district, bank of the Irtysh river, 05.VII.2019, 6 ♂, leg. V. Vedenina, N. Sevastianov & T. Tarasova, song recordings in 1 ♂ (CV).

Distribution. (Fig. 1). The range of this species stretches in the form of a ribbon from the Black Sea coast eastwards to Transbaikalia. *C. miramae* occurs in Krasnodarsky krai and Caucasus, Orenburg region, northern Kazakhstan, Altai, Tyva, Irkutsk region and Transbaikalia. The ranges of *C. miramae* and *C. maritimus* overlap in the south-eastern part of European Russia and in surroundings of Baikal Lake.

Recognition. (Table 1, Figs. 2, 3). *C. miramae* can be distinguished from most species of the *biguttulus* group by remarkably long stridulatory file (Fig. 2C). This feature was previously shown by Benediktov (1999), who described the last distal stridulatory peg to be situated at least at a level of the second tibial spine when tibia is attached to femur. Within the *biguttulus* group, a similarly long file is only shown in *C. biguttulus euhedickei* von Helversen, 1989, that occurs in the southern Balkans and Anatolia and in *C. maroccanus* Nadig, 1986, that occurs in North Africa (Ragge and Reynolds 1988; Willemse et al. 2009). The latter two taxa, however, are quite different from *C. miramae* in other morphological characters and songs. In other species of the *biguttulus* group, the length of stridulatory file is noticeably shorter, and the last distal stridulatory peg is situated at least at the level of the 4th tibial spine when the legs are bent (Benediktov 1999). Notably, in *C. miramae*, the number of stridulatory pegs is only slightly higher than in *C. maritimus*, and can't be considered as a good character. *C. miramae* tends to have the longest distance between stigma and the wing tip, and the broadest width of C & Sc areas in comparison to *C. maritimus* and *C. brunneus*. The PCA based on 6 morphological characters shows that *C. miramae* represents a separate cluster from *C. maritimus* and *C. brunneus*, but it is stronger in males than in females (Fig. 3C, D).

Description. (Table 1, Figs. 2, 3)**.** The head structure as in genus. Ratio length of vertical diameter of eye to maximum length of foveolae 3.2–3.6 in ♂, 2.8–3.2 in ♀; ratio minimum interocular distance to length of subocular groove 0.6–0.8 in ♂, 0.7–1.0 in ♀. Antennae filiform. Median carina distinct and continuous. Prozona slightly shorter than metazona. Lateral pronotal keels distinctly incurved, ratio minimum to maximum widths 2.1–2.6 in ♂, 2.4–2.6 in ♀. Tympanal aperture 2.8–3.3 times in ♂, 2.8–3.4 in ♀ as long as broad. Fore and hind wings well developed in both sexes, wings far surpassing the apices of the hind knee. Width of costal area of fore wing reaches its maximum in the middle or in the last third part (Fig. 2A, B). Width of subcostal area 0.3–0.35 mm in ♂, 0.2–0.23 mm in ♀ (measured along the line of maximal width of costal area). Ratio width of fore wing to width of C & Sc areas 3.0–3.2 in ♂, 4.3–4.5 in ♀. Length of apical constriction (distance from C and Sc confluence to the wing tip) is a quarter of the wing length. Ratio length between stigma center and the wing tip to the wing length 2.1–2.8 in ♂, 1.8–1.9 in ♀. Hind femur gracile, ratio femur length to maximum width 4.5–4.9 in ♂, 4.6–4.9 in ♀. Stridulatory file remarkably long in both sexes: distance between the last peg and the knee tip 2–2.7 times in ♂, 1.7–2.4 in ♀ as large as length of stridulatory file. In males, stridulatory pegs form one row and have different density along the file (Fig. 2C). Most proximal part of stridulatory file starts with several rare and dispersed pegs that are followed by more densely disposed pegs. The second part of stridulatory file more prolonged, consisting of more rare pegs with stable inter-peg intervals. In the third, most distal part the peg density decreases proportionally to the length of stridulatory file, and the pegs often do not lay in one raw. In females, stridulatory pegs arranged in one row and distributed rarer than in males. The peg density decreases from the proximal towards the distal parts. The number of stridulatory pegs 118–182 in ♂, 98–157 in ♀. Body coloration similar to coloration of *C. maritimus*.

Measurements in mm. Body length: 14–18 in ♂, 18–24 in ♀, pronotum length: 2.9–3.3 in ♂, 3.8–4.4 in ♀, fore wing length: 13.3–14.6 in ♂, in 16.4–18.3 in ♀, fore wing width 3.1–3.6 in ♂, 3.2–3.5 in ♀, hind femur length: 9.7–10.4 in ♂, 12.6–14.0 in ♀.

Calling song. (Table 4, Figs. 5, 7). The calling song of *C. miramae* includes the two types of randomly alternating echemes, typical *maritimus*-like and optional *brunneus*-like echemes. The first echeme type was present in the songs of all 34 males recorded, the second echeme type – in the songs of 28 males. The song usually starts with the *maritimus*-like echeme, which is similar to the *C. maritimus* calling song, but lasting shorter (the median duration varies in the range of 0.3–2.9 s). The number of syllables per echeme varies in the range of 5 to 35. Each echeme starts with the low-amplitude syllables. In short echemes, the amplitude reaches its maximum in about the echeme middle (Fig. 7F). In long echemes, the amplitude gradually increases, and keeps a constant level after about one quarter of an echeme (Fig. 7G). The syllables are about 1.5 times as short as the syllables in *C. maritimus*, lasting in the range of about 66–114 ms (Table 4). The syllable duration is rather stable within one population; however, it is more variable between populations. Oscillographic analysis shows no distinct pulses within the syllables in some populations, whereas distinct pulses are visible on the oscillograms of the songs from other populations. The shift between the two legs is greater in *C. miramae* than in *C. maritimus* (Fig. 7I, J).

The *brunneus*-like echemes are more often produced by the males from the Siberian and the east-european Russian populations, but they are rare in the songs from northern Kazakhstan. The echeme duration in *C. miramae* is almost three times as high as in *C. brunneus* (Fig. 5A). Similarly to *C. brunneus*, the *C. miramae* echeme consists of the short pulses, the amplitude of which gradually increases, reaching maximum intensity at about half of its duration, and then gradually decreases towards the end. The pulse duration and the pulse rate in *C. miramae* are almost the same as in *C. brunneus* (9–13 ms and 77–96 /s respectively, data are given for 29–30°C). However, the leg movement patterns are different in two species. In *C. miramae*, the *brunneus*-like echeme is produced by simple up and down leg-movements that vary in amplitude and duration (Fig. 7J). In *C. brunneus*, each leg generates a simple upstroke but a two-step downstroke (Fig. 4D). The oscillographic analysis of the *C. miramae* song shows that the pulses highly vary in amplitude and duration, whereas the pulses in the *C. brunneus*

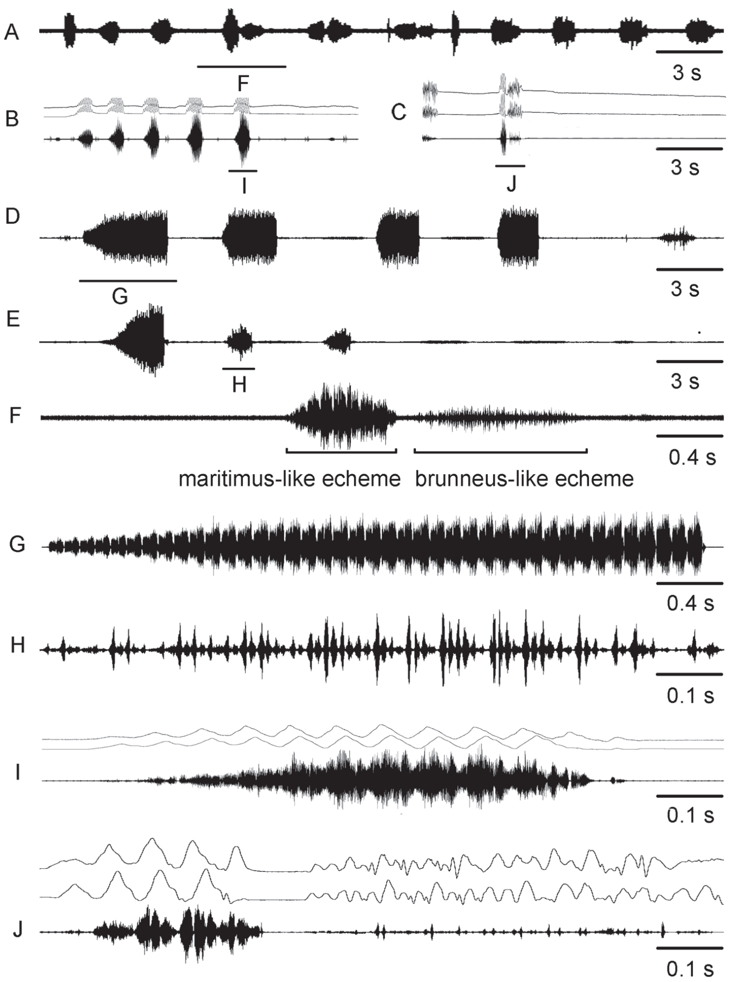


Figure 7. Oscillograms of calling songs of *Chorthippus miramae* from Orenburg region **A,** West-Kazakhstan region **C** and Buryatia **D,E**. Song recordings are presented at three different speeds (faster oscillograms of the indicated parts of the songs shown in **F–J**. At small scales (**A–D**) the *maritimus*-like echemes can be distinguished from the *brunneus*-like echemes by the higher amplitude. In all oscillograms the two upper lines are recordings of hind leg movements and the lower line is the sound recording. The ambient temperature near a singing male was 34 – 35 °C in (**A,E**) and 29 – 31°C in other cases.

song are much more stable in these parameters. In some males of *C. miramae*, the pulses are tended to group into syllables; the pulse number per syllable is unstable (Fig. 7H).

The order of the two echeme types in the *C. miramae* song is erratic, though there are some common variants in different populations. For example, several *maritimus*-like echemes are followed by one *brunneus*-like echeme (Fig. 7D). Another variant implies alternation of the two echeme types. A rarer case is when one *maritimus*-like echeme is followed by several echemes of the second type (Fig. 7A, E). The intervals between echemes of the same type may exceed the echeme duration 1.5–3 times for

Table 4. Calling songs parameters of *Chorthippus miramae*. For each parameter, medians, the lower and upper quartiles are shown.

Locality	Number of recorded males (measurements)	Temperature, °C	***maritimus*-like part**				***brunneus*-like part**		
			echeme duration, s	**echeme rate, /s**	**syllable duration, ms**	**syllable rate, /s**	**echeme duration, s**	**echeme rate, /s**	**pulse rate, /s**
29–30	7 (40)	25–28; 30–32	2.9	0.28	114	7.81	1.4	0.19	76.9
			1.8; 3.8	0.16; 0.29	99;135	7.16;8.53	1.0; 1.7	0.14; 0.20	66.7; 90.1
36	2 (20)	30	2.4	0.07	86	9.2	0.8	0.21	95.5
			2.2; 2.7	0.07; 0.07	78; 98	9.7; 11.3	0.8; 0.9	0.17; 0.22	81.7;102.8
48	6 (60)	28–30; 34	0.9	0.47	66	13.8	0.4	0.31	83.3
			0.8; 0.9	0.40; 0.59	60; 74	12.5; 14.9	0.3; 0.8	0.29; 0.37	71.4; 100
56	2 (15)	31	0.3	1.4	69	14.6	n/a	n/a	n/a
			0.3; 0.4	1.2; 1.8	61; 76	13.2; 16.3			
71	3 (13)	25–26; 30	0.8	0.40	76	10.5	1.0	n/a	47.6
			0.8; 1.1	0.36; 0.45	64; 91	9.6; 13.0	0.9; 1.2		23.4; 62.5
73	5 (26)		0.8	0.36	68	13.0	0.3	0.31	83.3
			0.7; 0.8	0.34; 0.44	64; 75	12.4; 14.3	0.3; 0.7	0.30; 0.33	70.2; 93.2
74	5 (20)	29–30	2.0	0.16	85	10.7	1.2	0.26	76.9
			2.0; 2.8	0.15; 0.17	81; 91	10.1; 11.2	1.0; 1.3	0.22; 0.28	71.4; 83.3
76	3 (10)	35	2.6	0.20	80	11.0	1.3	0.23	83.3
			1.9; 3.0	0.19; 0.21	75; 85	10.7; 11.6	1.0; 1.5	0.20; 0.30	71.4; 90.9

*n/a – non-applicable

the *maritimus*-like echemes, and 3–5 times for the *brunneus*-like echemes. An interval between the *maritimus*-like and the subsequent *brunneus*-like echemes can be very short (Fig. 7F, J), or can exceed the echeme duration 3–5 times.

Courtship song and female response song. (Fig. 8). The courtship song of *C. miramae* consists of the *brunneus*-like echemes. However, the courtship sound is much softer than in the calling song. The courtship echemes are shorter than in the calling song, not reaching 1 s (the median duration is about 0.4 s). The echemes are usually repeated at the rate of about 0.2–0.6/s, and their duration varies from 0.7 to 1.0 s. Pulses are short (6–9 ms), frequent (repeated at the rate of 61–95/s), and of a low amplitude (Fig. 8F). In some cases, the leg movements do not produce any sound at all (Fig. 8A, D).

A female produces the *brunneus*-like song in response to the male courtship or rivalry song (Fig. 8A, B). The female alternates her response echemes with the male echemes (Fig. 8D). The duration of the female echeme is similar to that in the male courtship, or 1.5–2 times longer than in the male courtship. The leg movement pattern in the female response song is similar to that in the male courtship song, but less regular (Fig. 8E, F). The pulses are longer (10–21 ms) and repeated at the rate of 43–77/s, especially in the first third of the echeme (Fig. 8D, E).

Rivalry song. (Fig. 9). Several males of *C. miramae* sitting close to each other produce a diversity of echemes of different duration, structure and leg movement pattern. For example, one can find a rivalry song similar to that of *C. maritimus*, which starts with the prolonged first syllable, which results from the prolonged first downstroke

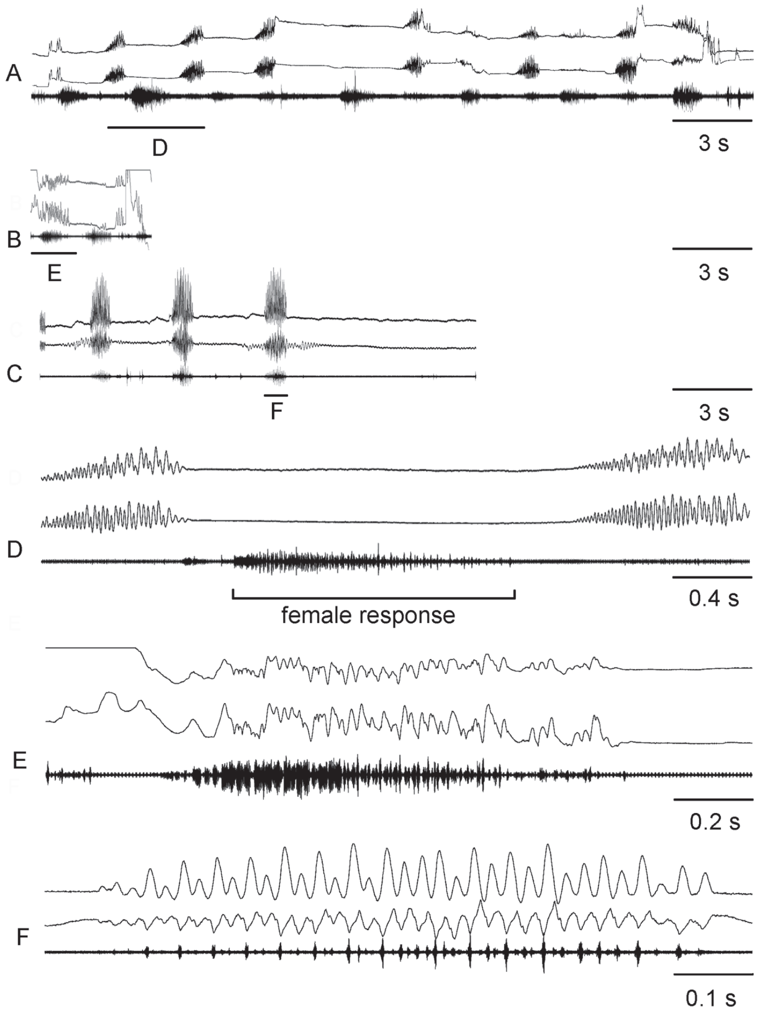


Figure 8. Oscillograms of courtship songs and female response songs in *Chorthippus miramae* from Pavlodar region **A** West-Kazakhstan region **B** and Altai republic **C**. Song recordings are presented at three different speeds (faster oscillograms of the indicated parts of the songs shown in **D–F**). During courtship, a male can produce audible (**C,F**) or silent (**A,D**) variants of song. Female responses with leg movements recordings (B, E) and without them (**A,D**) are shown. In all oscillograms the two upper lines are recordings of hind leg movements and the lower line is the sound recording. The ambient temperature near a singing specimen was 29 – 31°C.

(Fig. 9D, E). The pulses produced during the first downstroke follow twice as slowly as the pulses of the subsequent syllables. The subsequent syllables are of the same structure as in the *maritimus*-like echeme of the calling song.

Most often, the males produce single syllables similar to the first one with distinct pulses described above. These syllables are repeated at the rate of about 2–2.5 /s (Fig. 9F, G). Notably, the two legs may produce different number of the up and down strokes. Rarely, the males produce the *maritimus*-like echeme without the first syllable of distinct pulses (Fig. 9H).

The same male may produce echemes of different structure in the rivalry situations. Some females are actively responding to the male rivalry songs.

Discussion

What is the function of the long stridulatory file?

The morphological analysis conducted in the current study shows that one character, the length of stridulatory file, appears to be the most reliable character to distinguish *C. miramae*, *C. maritimus* and *C. brunneus*. The difference in the file length between *C. maritimus* and *C. brunneus* can be explained by the difference in the peg number. By contrast, the extremely long file in *C. miramae* is not due to the significant increase in the peg number, but due to the more widely spaced pegs in the distal part of the file.

The long stridulatory files are known in some other species of the *biguttulus* group. *C. biguttulus euchedickei* from the southern Balkans and north-western Anatolia (Willemse et al. 2009) and *C. maroccanus* Nadig, 1976 from north-western Africa (Ragge and Reynolds 1988), are also characterized by extraordinary long stridulatory files and the widely spaced distal pegs. In *C. brunneus brevis* Klingstedt 1939 from Southern Finland and north-east Russia (Ragge and Reynolds 1998; Benediktov 2017), the file length is much greater than in the nominate subspecies. In *C. brunneus brevis*, however, the increased length of the stridulatory file can be explained by the increase in the peg number. In one endemic of the *biguttulus* group in Anatolia, *C. relicticus* Sirin, Helversen & Ciplak, 2010, the peg number was shown to be extremely high (175–225 in male, 194–245 in female; Sirin et al. 2010). Unfortunately, the authors did not measure the length of stridulatory file in *C. relicticus*, but we assume that the file could be also long.

What could be a function of the long stridulatory file? The different parts of the long file can be used during stridulation to produce various song elements (Vedenina et al. 2007; Vedenina and Helversen 2009). This, however, is only evident in *C. biguttulus euchedickei* (Helversen 1989; Willemse et al. 2009). The calling song of this species consists of 1–3 typical loud echemes, similar to those in the nominate form, that are followed by 1–5 softer aftersongs (quiet parts of the song produced at the end of singing). Aftersongs are produced at a low position of the legs, and presumably the distal pegs are used for sound generation. In *C. miramae*, however, the long stridulatory file does not seem to be specifically involved in sound generation: at least, no song elements were found to be generated by distal pegs only. The leg movements in other species of the *biguttulus* group with a long file or high peg number have not been studied or studied only for certain song types.

It is noteworthy that stridulatory pegs function not only as a mechanic part of the stridulatory apparatus, but also as the mechanoreceptors (Hustert et al. 1999). It was

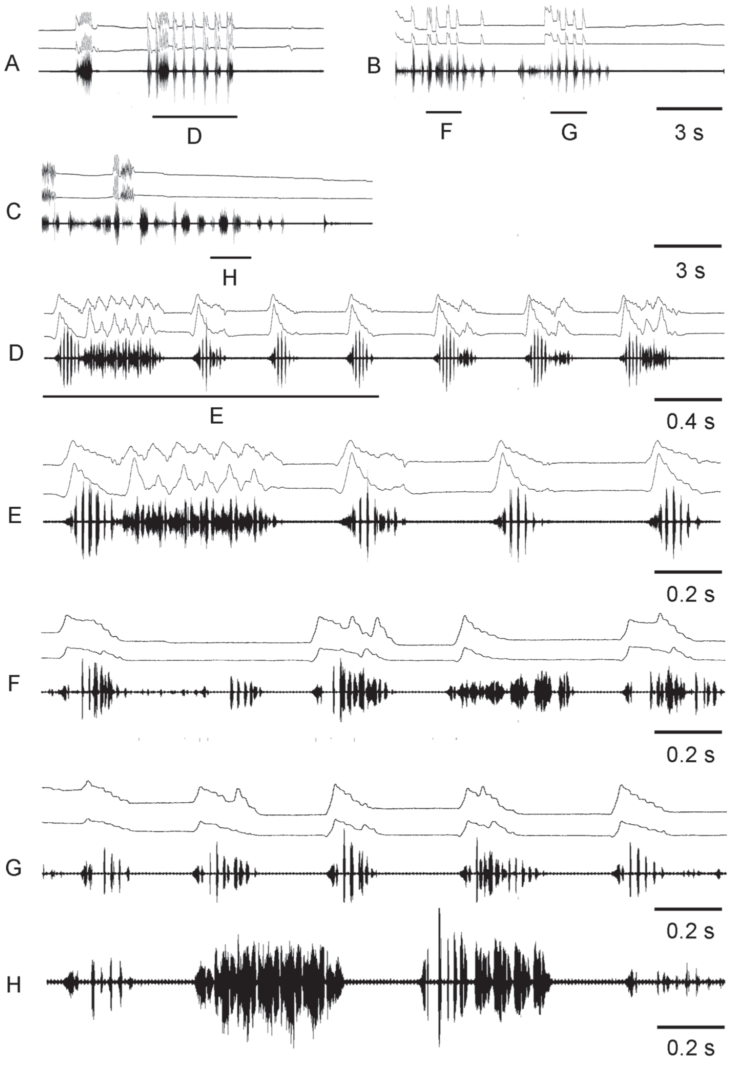


Figure 9. Oscillograms of rivalry songs in *Chorthippus miramae* from Altai republic **A** and Pavlodar region of Kazakhstan **B,C**. Song recordings are presented at three different speeds (faster oscillograms of the indicated parts of the songs shown in **D–H**). In all oscillograms the two upper lines are recordings of hind leg movements and the lower line is the sound recording. The ambient temperature near a singing male was 29 – 31°C.

shown in two distantly related species of Gomphocerinae, *C. biguttulus* and *Syrbula montezuma* (Saussure, 1861), that two sensory cells innervate each peg in themale and each tubercle in the female. These mechanoreceptors can deliver specific proprioceptive information about the contact between the stridulatory file and the vein of the fore wing. A subtle sensory control is required for measuring the pressure of the leg against the wing. The current study of the *C. miramae* songs shows that the loud *maritimus*-like echeme is apparently produced by legs being more pressed to the wings than during the softer *brunneus*-like echeme (Fig. 7). The latter echeme may be also produced with different leg pressure depending on the calling or courtship behavior; during courtship, the sound can be even absent despite the appropriate leg movements (Fig. 8).

In species of the *C. albomarginatus* group, the peg number and density differ only at the proximal parts of the stridulatory files (Vedenina and Helversen 2009). The various species of this group produce different and very conspicuous visual displays in a particular part of the courtship: during the stroke with the hind tibiae, the femora are kept at the extra-high, almost vertical, position. At this moment, the proximal pegs may participate in producing sound. Therefore, the divergence in visual display and the changes in the peg morphology in the *albomarginatus* group could strengthen each other. A similar assumption can be made for the evolution in song and the stridulatory file structure in the *biguttulus* group.

Peculiarities of the *Chorthippus miramae* song

The calling song of *C. miramae* is conspicuously different from the songs of *C. brunneus* and *C. maritimus*, by the presence of two types of echemes, which were recorded in 82% of males. In the calling songs of 18% of *C. miramae* males, however, only the *maritimus*-like echemes were recorded. The latter specimens, however, clearly belong to *C. miramae* based on morphology and courtship and rivalry songs.

Until now, the calling songs of *C. miramae* were only presented under the name *C. yersini* by Bukhvalova (1993) and *C. porphyropterus* by Benediktov (2005). Both authors claim the presence of the two echeme types. From the oscillograms presented, one could see many similarities with the songs of *C. maritimus* and *C. brunneus*. The current song analysis that includes not only the sound but also the leg-movement analysis indicates that both *maritimus*-like and *brunneus*-like elements have some peculiarities in the *C. miramae* song. The *maritimus*-like echemes rarely show the distinct pulses within syllable, whereas such pulses in the calling song of *C. maritimus* are typically present. This may be determined by the larger shift between the two legs in *C. miramae* than in *C. maritimus*. The *brunneus*-like echeme in the *C. miramae* song is produced by simple up and down leg-movements, whereas each leg generates a simple upstroke but a two-step downstroke in the *C. brunneus* song. The sound pulses, however, are of a similar temporal structure in both species. The similarities between the calling songs could explain why *C. miramae* is not found together with *C. maritimus* and *C. brunneus* in the same biotopes (despite the latter two species often occur syntopically). According to the concept of 'acoustic niches' (Bukhvalova 2006; Tishechkin and Bukhvalova 2009), the combination of the syllable rate and syllable temporal pattern determines the species 'place' in the acoustic environment of the grasshopper community. Since these song parameters overlap within the species pairs *C. miramae* / *C. maritimus* and *C. miramae* / *C. brunneus*, the absence of each pair in the same biotope is not surprising.

C. miramae generally demonstrates a richer song repertoire than the other two species. The courtship song of *C. miramae* is similar to the *brunneus*-like echeme, but the sound is very soft. In some cases, leg movements of *C. miramae* do not produce any sound at all, which may be interpreted by a female as a visual display. Notably, there is no specific courtship song in both *C. brunneus* and *C. maritimus*. As for a rivalry song, this is present in *C. maritimus* and *C. miramae* but not in *C. brunneus*. The rivalry song of *C. miramae* is similar to that in *C. maritimus*. It comprises the first syllable with distinct pulses lasting longer than the subsequent syllables with fuzzy pulses. More often, however, the rivalry repertoire in *C. miramae* includes short syllables similar to the first one in the *maritimus*-like echeme but repeated at the rate of 2–2.5/s.

In most species of the *biguttulus* group, the rivalry song is similar to the calling song (Ragge and Reynolds 1998). The rivalry song may be shorter than the calling song, but similar in temporal structure and usually does not contain any new elements. Only *C. maroccanus* produces a characteristic rivalry song containing two elements, one element similar to the calling song and the second unique element. Thus, *C. miramae* is another species of this group, in which the rivalry song is principally different from the calling song.

The relationship of *Chorthippus miramae* with other members of the *biguttulus* group

It has been suggested that the *biguttulus* group comprises many young, closely related species, some of which may be of hybrid origin. Some species of this group were found to hybridize in nature (e.g., Ragge 1976; Bridle and Butlin 2002; Kleukers et al. 2004; Nolen et al. 2020), whereas some of them were hybridized in laboratory in no-choice conditions and produced viable and fertile offspring (Helversen and Helversen 1975; Gottsberger and Mayer 2007). The similarity of the *C. miramae* song with the songs of *C. brunneus* and *C. maritimus* might suggest a hybrid origin of *C. miramae*.

One of the most well studied hybrid zones within the *biguttulus* group is a hybrid zone between *C. jacobsi* and *C. brunneus* in northern Spain (e.g., Bridle and Butlin 2002; Saldamando et al. 2005; Bridle et al. 2006). The calling song of *C. jacobsi* is similar to the song of *C. maritimus*, but of a shorter duration. Songs of F1, F2 and backcross hybrids between *C. jacobsi* and *C. brunneus* were intermediate between the songs of both parental species in all song parameters (Saldamando et al. 2005). At the same time, no combination of the parental song elements was found in the hybrid songs. Similarly, natural hybrids between *C. maritimus* (named as *C. bornhalmi*) and *C. brunneus* from north-eastern Italy were shown to sing intermediate songs (Kleukers et al. 2004). In European Russia and Ukraine, these two species often occur in the same biotope allowing them to hybridize. We suggest that the *C. brunneus* song with unusually long echeme duration and low echeme and pulse rate recorded from loc. 40 (Table 2) may be also attributed to the hybrid. F1 hybrids between *C. maritimus* and *C. brunneus* bred in our laboratory only revealed intermediate songs (unpublished data). It is therefore unlikely that *C. miramae* could evolve from the hybrids between *C. maritimus* and *C. brunneus*.

The number of stridulatory pegs in hybrids between *C. jacobsi* and *C. brunneus* (Saldamando et al. 2005) and *C. brunneus* and *C. bornhalmi* (Kleukers et al. 2004) were shown to be also intermediate between those in parental species. In *C. miramae*, the peg number is similar to that of *C. maritimus*, but significantly larger than that in *C. brunneus*.

Other results were obtained for hybrids between *C. biguttulus* and *C. mollis* (Helversen and Helversen 1975) and *C. brunneus* and *C. biguttulus* (Gottsberger and Mayer 2007). A combination of the parental song elements and even novel song elements were found in hybrids between *C. biguttulus* and *C. mollis*. Thus, the hybrid song may be considered as more complex in comparison with the parental songs. In hybrids between *C. albomarginatus* and *C. oschei* (unrelated species to the *biguttulus* group), the values of several song parameters were significantly larger or smaller than those in the parental songs (Vedenina et al. 2007). Notably, the leg-movement patterns appeared to be simpler in hybrids than these in both parentals. In hybrids between *C. brunneus* and *C. biguttulus*, the species-specific syllable structure was largely lost, because the leg-movement patterns were also simplified in comparison to the parental patterns (Gottsberger and Mayer 2007). These divergences in inheritance of different song parameters are likely the result from incompatibility of neuronal networks that control stridulatory leg movements in hybrids. This hypothesis was offered by Helversen and Helversen (1975). They suggested the two pattern-generating neuronal networks to be formed in the central nervous system of hybrids because of nonhomology of the parental elements. The outputs of the two networks converge in a common final pathway, probably at the level of the motoneurons, and may lead to the superimposed pattern of the hybrid song. In *C. brunneus*, *C. biguttulus*, and *C. mollis*, the song elements in terms syllable structure are suggested to be nonhomological. In *C. biguttulus*, for example, the first and the loudest pulse in each syllable is generated by an accentuated downstroke of the legs; each syllable is usually produced by three up-and-down leg movements; the two legs moving in slightly different patterns (e.g., Elsner 1974; Helversen and Helversen 1983, 1994). It is no coincidence that some authors attribute these three species to different subgroups of the *biguttulus* group (Willemse et al. 2009; Sirin et al. 2010). By contrast, syllable of the calling song in *C. brunneus*, *C. jacobsi* and *C. maritimus* (= *brunneus* subgroup) is produced by similar leg movements (simple upstroke and stepwise downstroke) and may be considered as homological element. It is therefore not surprising why hybrids between the species within the *brunneus* subgroup generate purely intermediate songs without novel elements or combination of the parental elements.

Considering all the aforesaid, what can we say about the origin of *C. miramae*? We hypothesize that this species could have evolved as a result of hybridization between other species of the *biguttulus* group, for example, between *C. biguttulus* and *C. maritimus*. The two species are vicariant: the first one occurs in the north, the second one – in the south. For example, in the Ukraine *C. biguttulus* is found more in the north, whereas *C. maritimus* more in the south. Eastwards, this border is shifting, the ranges overlap, and the species may occur syntopically. In the latter case, however, *C. maritimus* can be found in the first half of summer, whereas *C. biguttulus* – in the second half of summer. This indicates that the species tend not to meet, probably because the syllable rate in calling songs is quite similar; the syllable structure, however, is very different. Meanwhile, we do not exclude that hybridization may occur between these species when one of them is rare and another is abundant. To date, no laboratory hybrids were bred between them, and nothing is known about *biguttulus* × *maritimus* hybrid song. The hybridization experiments between these species could be a subject of future studies.

We also hypothesize that *C. miramae* could diverge from *C. maritimus*. The latter species is widespread in Anatolia, where it occurs in highlands, thus forming isolated populations. In Anatolia, there is also another species of the *biguttulus* group, *C. relicticus*, occurring very locally in the Southern Anatolian Taurus (Sirin et al. 2010). Its calling song is similar to the *brunneus*-like echeme of *C. miramae*, which is produced by simple up and down strokes of the legs moving in antiphase. Sirin et al. (2010) suggest that this species could have radiated from a *C. maritimus* (named as *C. bornhalmi* in the paper) like ancestor in an interglacial refugium. In southern territories, the members of the *biguttulus* group, being the cold-resistant species, are suggested to be isolated during interglacial periods and spread down and expanded their ranges during glacial periods. If we suggest the divergence of *C. miramae* from *C. maritimus*, the spreading of the former to the north could occur, on the contrary, during interglacial periods.

To test both hypotheses (hybrid origin of *C. miramae* or its divergence from a *C. maritimus*-like ancestor in a glacial refugium), it is necessary to conduct genomic studies. A recent analysis of mitochondrial and nuclear genomes in the *biguttulus* group in Western Europe (Nolen et al. 2020) shows that four species, *C. brunneus*, *C. biguttulus*, *C. rubratibialis* and *C. mollis*, experienced a long period of geographic isolation, followed by secondary contact and extensive introgression. According to Nolen et al. (2020), *C. mollis* was the first species to split, *C. biguttulus* was the next, followed by *C. rubratibialis* and *C. brunneus*. Mitochondrial genomes suggest that the radiation is relatively recent, dating to the mid-Pleistocene. Thus, the species of the *biguttulus* group must have experienced multiple episodes of contraction and expansion during the multiple glacial periods that affected the European continent. Taking this into account, it would be especially interesting to sample other species of the *biguttulus* group, especially those at or near the described refugia in Eurasia.

Acknowledgments

We are grateful to Lev Shestakov and Nikita Sevastianov (Institute for Information Transmission Problems, Moscow) for their help in the field trips and song recordings. We also highly appreciate the revision of our paper by Luc Willemse and Ionut Stefan Iorgu. The current study was partly supported by the Russian Foundation for basic Research (grant 20-04-00556). The contribution of D. Tishechkin was partly supported by the scientific project of the State Assignment of Moscow State University No. 121032300063-3.

The study was DT's idea; VV and DT organized the fieldwork; all authors recorded the grasshopper songs; TT made morphological measurements and song analysis; all authors discussed the results; VV and TT mainly wrote the manuscript.

References

Benediktov AA (1999) Little-known taxa of grasshoppers of the *Chorthippus biguttulus* group (Orthoptera, Acrididae, Gomphocerinae). Moscow University Biological Sciences Bulletin 54 (1): 41–45.

Benediktov AA (2005) Fauna and acoustic signals of the genus *Chorthippus* Fieb. (Orthoptera, Acrididae) from southern Siberia. Proceedings of the Russian Entomological Society 76: 118–130. [in Russian with English summary]

Benediktov AA (2017) To the knowledge of rare species of Acrididae from protected areas in north-western Russia*: Chorthippus brunneus brevis* (Orthoptera, Acrididae). Nature Conservation Research 2(2): 84–89. [in Russian with English summary] https://doi.org/10.24189/ncr.2017.003

Benediktov AA, Mikhailenko AP (2017) On the northern border of the range of *Chorthippus maritimus* in European Russia. Works of the Stavropol Department of Russian Entomological Society 13: 34–36. [in Russian]

Berezhkov RP (1956) Grasshoppers of Western Siberia. Tomsk University Publisher, Tomsk, 175 pp.

Bey-Bienko GJa, Mistshenko LL (1951) Locusts and grasshoppers of the USSR and adjacent countries. Part II. Academy of Sciences of USSR Publisher, Moscow-Leningrad, 287 pp. [pp. 381–667, in Russian, English translation of Russian original: Bey-Bienko GJa, Mistshenko LL (1964) Locusts and Grasshoppers of the U.S.S.R and Adjacent Countries. Part II. Jerusalem, Israel Program for Scientific Translations, 291 pp.].

Bridle JR, Butlin RK (2002) Mating signal variation and bimodality in a mosaic hybrid zone between *Chorthippus* species. Evolution 56: 1184–1198. https://onlinelibrary.wiley.com/doi/abs/10.1111/j.0014-3820.2002.tb01431.x

Bridle JR, Saldamando CI, Koning W, Butlin RK (2006) Assortative preferences and discrimination by females against hybrid male song in the grasshoppers *Chorthippus brunneus* and *Chorthippus jacobsi* (Orthoptera: Acrididae). Journal of Evolutionary Biology 19: 1248 – 1256. https://onlinelibrary.wiley.com/doi/full/10.1111/j.1420-9101.2006.01080.x

Bukhvalova MA (1993) Acoustic signals and morphological features of some grasshoppers of the *Chorthippus biguttulus* group (Orthoptera, Acrididae) of Russia and adjacent territories. Zoologicheskiy Zhurnal 72 (5): 55–65. [in Russian with English summary, English translation: Entomological Review 74 (1): 56–67 (1995)].

Bukhvalova MA (1998) New data on taxonomy of *Chorthippus biguttulus* group (Orthoptera, Acrididae) from Russia and adjacent countries. Zoologicheskiy Zhurnal 77 (10): 1128–1136. [in Russian with English summary, English translation: Entomological Review 78 (7): 867–875 (1998)].

Bukhvalova MA (2006) Partitioning of acoustic transmission channels in grasshopper communities. In: Drosopoulos S, Claridge MF (Eds) Insect Sounds and Communication. Physiology, Behaviour, Ecology and Evolution. CRC Press, Taylor and Francis Group, Boca Raton, London, New York, 199–205. https://doi.org/10.1201/9781420039337.ch14

Elsner N (1974) Neuroethology of sound in gomphocerine grasshoppers. I. Song patterns and stridulatory movements. Journal of Comparative Physiology 88: 72–102. https://doi.org/10.1007/BF00695923

Fruhstorfer H (1921) Die Orthopteren der Schweiz und der Nachbarländer auf geographischer sowie oekologischer Grundlage mit Berücksichtigung der fossilen Arten. Archiv für Naturgeschichte 87 (5): 1–262.

Gottsberger B, Mayer F (2007) Behavioral sterility of hybrid males in acoustically communicated grasshoppers (Acrididae, Gomphocerinae). Journal of Comparative Physiology 193: 703 – 714. https://link.springer.com/article/10.1007/s00359-007-0225-y

Harz K (1975) Die Orthopteren Europas ll. Series Entomologica 11, 939 pp.

Hedwig B (2000) A highly sensitive opto-electronic system for the measurement of movements. Journal of Neuroscience Methods 100: 165–171. https://doi.org/10.1016/S0165-0270(00)00255-7

Heller K-G, Korsunovskaya O, Ragge DR, Vedenina V, Willemse F, Zhantiev RD, Frantsevich L (1998) Check-List of European Orthoptera. Articulata Beiheft 7: 1–61.

Helversen O von, Elsner N (1977) The stridulatory movements of acridid grasshoppers recorded with an opto-electronic device. Journal of Comparative Physiology 122: 53–64. https://doi.org/10.1007/BF00611248

Helversen O von (1986) Courtship Song and Taxonomy of Grasshoppers in the *Chorthippus albomarginatus*-Group (Orthoptera: Acrididae). Zoologische Jahrbücher Systematik 113: 319 – 342.

Helversen O von (1989) Bemerkungen zu *Chorthippus hedickei* (Ramme 1942) und Beschreibung von *Chorthippus biguttulus euhedickei* n. ssp. Articulata 4: 26 – 34.

Helversen D von, Helversen O von (1975) Verhaltensgenetische Untersuchungen am akustischen Kommunikationssystem der Feldheuschrecken (Orthoptera, Acrididae). Journal of Comparative Physiology 104: 273 – 323. https://doi.org/10.1007/BF01379053

Helversen D von, Helversen O von (1983) Species recognition and acoustic localization in acridid grasshoppers: A behavioural approaC. Neuroethology and behavioral physiology. Springer, Berlin; Heidelberg; New York; Tokyo, 95–107. https://doi.org/10.1007/978-3-642-69271-0_8

Helversen O von, Helversen D von (1994) Forces driving coevolution of song and song recognition in grasshoppers. Fortschritte der Zoologie 39: 253–284.

Hustert R, Lodde E, Gnatzy W (1999) Mechanosensory pegs constitute stridulatory files in grasshoppers. Journal of Comparative Neurology 410: 444 – 456. https://onlinelibrary.wiley.com/doi/abs/10.1002/(SICI)1096-9861(19990802)410:3%3C444::AID-CNE7%3E3.0.CO;2-E

ICZN (International Commission on Zoological Nomenclature) (1999) International Code of Zoological Nomenclature. Fourth edition. International Trust for Zoological Nomenclature, London, xxix + 306 pp.

Ingrisch S (1995). Evolution of the *Chorthippus bigutulus* group (Orthoptera, Acrididae) in the Alps, based on morphology and stridulation // Revue Suisse de Zoologie. V. 100. P. 475–535.

Kleukers R, Odé B, Willemse F (2004) Hybridization of *Glyptobothrus brunneus* and *Glyptobothrus bornhalmi* in northeastern Italy (Orthoptera Acridomorpha). Memorie della Società Entomologica Italiana 82(2): 547 – 556.

Klingstedt H (1939) Taxonomic and cytological studies on grasshopper hybrids. I. Morphology and spermatogenesis of *Chorthippus bicolor* Charp. × *C. biguttulus* L. Journal of Genetics, 37 (3), 389–420. https://doi.org/10.1007/BF02982736

Mistshenko LL (1950) New data on the Central Asian fauna of harmful grasshoppers (Saltatoria – Orthoptera, Acridodea). Doklady Akademii Nauk SSSR, Novaya Seriya, 71 (4), 789–792. [in Russian]

Nolen ZJ, Yildirim B, Irisarri I, et al. (2020) Historical isolation facilitates species radiation by sexual selection: Insights from *Chorthippus* grasshoppers. Molecular Ecology 29: 4985–5002. https://doi.org/10.1111/mec.15695

Oliger IM (1974) Taxonomic significance of structural traits of the stridulation apparatus in species of the *biguttulus* group of the genus *Chorthippus* Fieb. (Orthoptera, Acrididae). Entomologicheskoye Obozrenie 53 (1): 81–90. [in Russian]

Ramme W (1939) Beiträge zur Kenntnis der palaearktischen Orthopterenfauna (Tettig. u. Acrid.). III. Mitteilungen aus dem Zoologischen Museum in Berlin 24 (1): 41–150.

Ramme W (1951) Zur Systematik, Faunistik and Biologie der Ortoperen von Südost-Europa und Vorderasien. Mitteilungen aus dem Zoologischen Museum in Berlin 27: 1–431. https://doi.org/10.1002/mmnz.4830270108

Ragge DR (1976) A putative hybrid in nature between *Chorthippus brunneus* and *C. biguttulus* (Orthoptera: Acrididae). Systematic Entomology 1: 71 – 74. https://doi.org/10.1111/j.1365-3113.1976.tb00033.x

Ragge DR, Reynolds WJ (1988) The songs and taxonomy of the grasshoppers of the *Chorthippus biguttulus* group in the Iberian Peninsula (Orthoptera: Acrididae). Journal of Natural History 22: 897 – 929. https://doi.org/10.1080/00222938800770611

Ragge D, Reynolds WJ (1998) The songs of the grasshoppers and crickets of western Europe. Harley Books, Colchester. 591 pp. https://brill.com/view/title/23975

Ragge DR, Reynolds WJ, Willemse F (1990) The songs of the European grasshoppers of the *Chorthippus biguttulus* group in relation to their taxonomy, speciation and biogeography (Orthoptera, Acrididae). Boletin de Sanidad Vegetal Plagas (Fuera de serie). 20: 239 – 245.

Saldamando CI, Miyaguchi S, Tatsuta H, Kishino H, Bridle JR, Butlin RK (2005) Inheritance of song and stridulatory peg number divergence between *Chorthippus brunneus* and *C. jacobsi*, two naturally hybridizing grasshopper species (Orthoptera: Acrididae). Journal of Evolutionary Biology 18: 703 – 712. https://onlinelibrary.wiley.com/doi/full/10.1111/j.1420-9101.2004.00838.x

Sirin D, Helversen O von, Ciplak B (2010) *Chorthippus brunneus* subgroup (Orthoptera, Gomphocerinae) in Anatolia with description of two new species: data suggest an Anatolian origin for the lineage. Zootaxa 2410: 1 – 28. https://doi.org/10.11646/zootaxa.2410.1.1

Skejo J, Ivković S (2015) *Chorthippus bornhalmi* in the heart of the Balkans (Acrididae: Gomphocerinae). Articulata 30: 81–90. http://dgfo-articulata.de/downloads/articulata/articulata_30_2015/Articulata%2030_Skejo-Ivkovic.pdf

Skejo J, Rebrina F, Szövényi G, Puskás G, Tvrtković N (2018) The first annotated checklist of Croatian crickets and grasshoppers (Orthoptera: Ensifera, Caelifera). Zootaxa 4533(1): 1–95. https://www.mapress.com/zt/article/view/zootaxa.4533.1.1

Storozhenko SYu (2002) To the knowledge of the genus *Chorthippus* Fieber, 1852 and related genera (Orthoptera: Acrididae). Far Eastern Entomologist 113: 1 – 16.

Sychyov MM, Voznesensky AYu (1995) Taxonomic structure of the *Chorthippus* "*biguttulus*-group" (Insecta Orthoptera Acrididae). Chteniya pamyati professora V.V. Stanchinskogo 2: 158–161. [in Russian with English summary]

Tarasova TA, Sevastianov NS, Vedenina VYu (2021) Songs and morphology in grasshoppers of the *Stenobothrus eurasius* group (Orthoptera: Acrdidae: Gomphocerinae) from Russia and adjacent countries: clarifying of taxonomic status. Zootaxa 4965 (2): 244–260. https://doi.org/10.11646/zootaxa.4965.2.2

Tishechkin DYu, Bukhvalova MA (2009) Acoustic communication in grasshopper communities (Orthoptera: Acrididae: Gomphocerinae): segregation of acoustic niches // Russian Entomological Journal 18(3): 165–188.

Vedenina VYu, Helversen O von (2003) Complex courtship in a bimodal grasshopper hybrid zone. Behavioural Ecology and Sociobiology 54: 44 – 54. https://link.springer.com/article/10.1007/s00265-003-0595-2

Vedenina VYu, Helversen O von (2009) A re-examination of the taxonomy of the *Chorthippus albomarginatus* group in Europe on the basis of song and morphology (Orthoptera: Acrididae). Tijdschrift voor Entomologie 152: 65 – 97. https://doi.org/10.1163/22119434-900000269

Vedenina VYu, Panyutin AK, Helversen O von (2007) The unusual inheritance pattern of the courtship songs in closely related grasshopper species of the *Chorthippus albomarginatus*-group (Orthoptera: Gomphocerinae). Journal of Evolutionary Biology 20: 260 – 277. https://doi.org/10.1111/j.1420-9101.2006.01204.x

Vedenina V, Sradnick J, Klöpfel A, Elsner N (2012) A narrow hybrid zone between the grasshoppers *Stenobothrus clavatus* and *S. rubicundus*: courtship song analysis. Biological Journal of Linnean Society 107: 383 – 397. https://doi.org/10.1111/j.1095-8312.2012.01935.x

Vorontsovsky PA (1928a) Materials to the knowledge of the fauna of Acridoidea of Orenburg region. Izvestiya Oreburgskoy Stantsii Zashchity Rasteniy 1: 5–25. [in Russian]

Vorontsovsky PA (1928b) On homologous series of colour variation in grasshoppers. Izvestiya Oreburgskoy Stantsii Zashchity Rasteniy 1: 27–39. [in Russian]

Wosnessenskij AJu (1996) New replacement names for one genus and two species of Acrididae (Orthoptera). Zoosystematica Rossica 4(2): 204.

Willemse F, Helversen O von, Odé B (2009) A review of *Chorthippus* species with angled pronotal lateral keels from Greece with special reference to transitional populations between some Peloponnesean taxa (Orthoptera, Acrididae). Zoologische Mededelingen 83(2): 319–507.

ZooKeys 1073: 55–117 (2021)
doi: 10.3897/zookeys.1073.71843
https://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

A review of the Larainae of Australia with description of seven new species and the new genus *Australara* (Coleoptera, Byrrhoidea, Elmidae)

Cheryl B. Barr[1], William D. Shepard[1]

[1] *Essig Museum of Entomology, 1101 Life Sciences Bldg. #4780, University of California, Berkeley, CA 94720 USA*

Corresponding author: Cheryl B. Barr (cbarr@berkeley.edu)

Academic editor: Mariano Michat | Received 20 July 2021 | Accepted 5 October 2021 | Published 29 November 2021

http://zoobank.org/18D5AF27-86E5-4D21-BCC5-27D09FB384DA

Citation: Barr CB, Shepard WD (2021) A review of the Larainae of Australia with description of seven new species and the new genus *Australara* (Coleoptera, Byrrhoidea, Elmidae). ZooKeys 1073: 55–117. https://doi.org/10.3897/zookeys.1073.71843

Abstract

The three genera and four species of Larainae (Elmidae) previously described from Australia are reviewed, and one new genus and seven new species are described: *Australara glaisteri* **gen. et sp. nov.**, *Ovolara lawrencei* **sp. nov.**, *Ovolara monteithi* **sp. nov.**, *Stetholus carinatus* **sp. nov.**, *Stetholus longipennis* **sp. nov.**, *Stetholus metatibialis* **sp. nov.**, and *Stetholus woronora* **sp. nov.** A lectotype is designated for *Hydora laticeps* (Carter & Zeck), and the first new collection records of the species are reported since its description in 1932. The occurrence in Australia of *Potamophilinus papuanus* Satô, described from Papua New Guinea, is reported. A key to the species, photographic images of the external morphology and male genitalia, distribution maps, and habitat and behavioral information, when known, are provided for all twelve species of Australian Larainae.

Keywords

aquatic beetles, *Hydora*, *Ovolara*, *Potamophilinus*, riffle beetles, *Stetholus*, new taxa, taxonomy

Introduction

The aquatic beetle family Elmidae is traditionally divided into two subfamilies, the Elminae and the Larainae. The Elminae are by far the most diverse of the two, with 123 genera and nearly 1,350 recognized species worldwide, whereas the Larainae have only

28 genera with nearly 160 species (Kodada et al. 2016). The laraines are poorly represented in Australia, with just three genera and four species described: *Hydora laticeps* (Carter & Zeck, 1932), *Ovolara australis* (King, 1865), *Ovolara leai* (Carter, 1926), and *Stetholus elongatus* Carter & Zeck, 1929. In the 90+ years since being described, little has been published on these taxa or the Australian Larainae in general. Larval rearing studies by Glaister (1985, 1992, 1999) resulted in the association of elmid adults and larvae, enabling her to publish an extensively illustrated identification guide to the larval Elmidae of Australia with keys and descriptive notes on taxonomy, distribution, and habitat (Glaister 1999). Calder (1992), for a Coleoptera identification workshop, produced an unpublished, illustrated adult key to the genera of Australian Elmidae, with taxonomic notes and species-level genitalic illustrations which included all of the described laraine species. Calder (1992) and Glaister (1999) first reported the presence of a fourth laraine genus, *Potamophilinus* Grouvelle, 1896, in Australia.

During a trip to north Queensland in 2001, we collected specimens of an undescribed genus and species and two undescribed species in the genera *Ovolara* and *Stetholus*. Specimens of a *Potamophilinus* species were also collected, which allowed us to identify and confirm the occurrence of *P. papuanus* Satô in Australia. Specimens of a second undescribed species of *Stetholus* were collected in New South Wales in 2019 by European colleagues Martin Fikáček, Matthias Seidel and Vít Sýkora, who provided them for this study. We and other collectors who have searched for enigmatic *Hydora laticeps*, known only from the type series collected more than 90 years ago, have failed to find additional specimens. However, during our recent examination of material on loan from museum collections, we discovered four previously unidentified specimens of *H. laticeps* in addition to three more new species of *Ovolara* and *Stetholus*. In this article, we describe these seven new species and one new genus, and review the subfamily Larainae of Australia which now includes 12 species in four genera.

Materials and methods

Institutional abbreviations

AM	The Australian Museum, Sydney, New South Wales, Australia
ANIC	Australian National Insect Collection, CSIRO, Canberra, Australian Capital Territory, Australia
EMEC	Essig Museum of Entomology, University of California, Berkeley, California, USA
MAGNT	Museum and Art Gallery of the Northern Territory, Darwin, Australia
NMPC	National Museum, Prague, Czech Republic
NMV	Museums Victoria, Melbourne, Victoria, Australia
QM	Queensland Museum, South Brisbane, Queensland, Australia
SAMA	South Australian Museum, Adelaide, South Australia, Australia
TMAG	Tasmanian Museum and Art Gallery, Hobart, Tasmania, Australia

Geographic abbreviations used in the text include: **ACT** = Australian Capital Territory; **NSW** = New South Wales; **QLD** = Queensland; **NQLD**, **NQ**, **N. Qld**. = north Queensland; **VIC** = Victoria.

Study material

The authors examined a total of 540 specimens during this project. These were borrowed from Australian institutional collections (AM, ANIC, QM, SAMA) or were collected by the authors and, in the case of one new species, by European colleagues.

Field techniques

Specimens collected by the authors were manually dislodged from surfaces and objects, then captured in aquatic nets, or were swept from streamside and emergent vegetation. The collections were placed in vials containing 95 % ethanol in the field and examined later in the laboratory. Related taxa collected with the laraines are reported in the species treatments as “Associated byrrhoid taxa.”

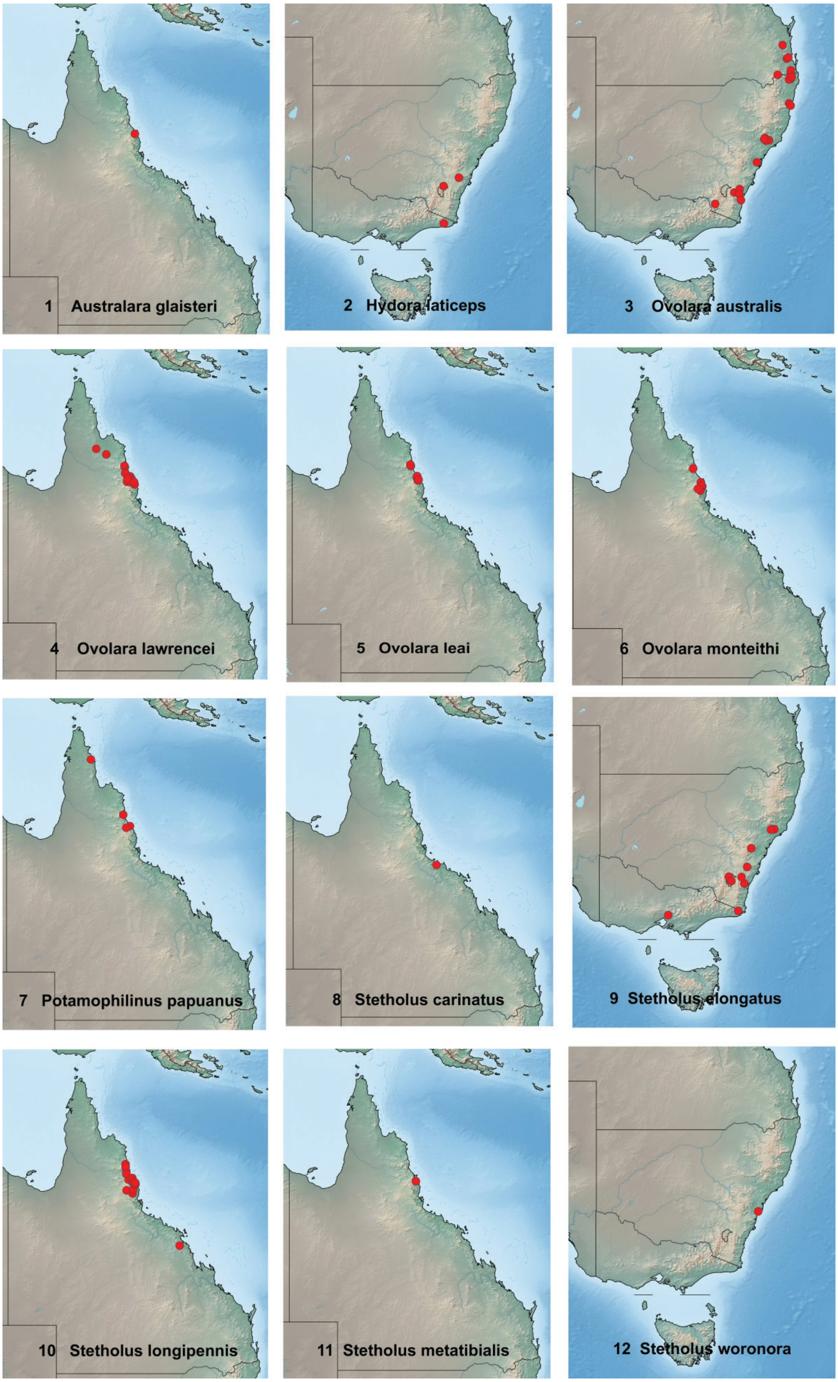
Laboratory procedures

Examination and measurement of specimens were done with a Leica MZ 12.5, fitted with an ocular micrometer, and an AO Spencer Model 25 stereo microscope. A series of species from each of the authors’ collection localities was dried and point-mounted after genitalic dissection. Specimens on loan also were often dissected for genitalic examination, and those previously glued to card mounts were remounted as was necessary. After study, the genitalia were placed in vials, each containing a drop of glycerin, and affixed to pins below the specimens. For almost all species with sufficient numbers, some specimens were further dissected to view other structures more accurately such as antennae, mouthparts, elytra, and metathoracic wings. The dissected parts were then slide mounted and examined. Measurements of body length consist of the pronotal length plus the elytral length taken at the midline, and do not include the head or the variable space between the pronotum and elytra; measurements of width are of both elytra at their widest point.

Specimen imaging and distribution mapping

Most of the habitus images were taken using a Visionary Digital BK Plus Lab System fitted with a Canon EOS 7D camera. Some of the images were provided by staff at museums where the specimens are housed, as noted in the figure legends and the Acknowledgments. The genitalia images were taken with a Syncroscopy AutoMontage ® system. Images were prepared and assembled using Adobe Photoshop Elements.

SimpleMappr, a free internet program (Shorthouse 2010), was used to create the species distribution maps (Figs 1–12). Geographical coordinates for specimens collected by the authors were obtained using a hand-held GPS unit. For museum speci-



Figures 1–12. Geographical distribution of species records **1** *Australara glaisteri* gen. nov., sp. nov. **2** *Hydora laticeps* **3** *Ovolara australis* **4** *Ovolara lawrencei* sp. nov. **5** *Ovolara leai* **6** *Ovolara monteithi* sp. nov. **7** *Potamophilinus papuanus* **8** *Stetholus carinatus* sp. nov. **9** *Stetholus elongatus* **10** *Stetholus longipennis* sp. nov. **11** *Stetholus metatibialis* sp. nov. **12** *Stetholus woronora* sp. nov.

men locality data, Google Earth Pro was used to acquire geographical coordinates for low-resolution mapping in the SimpleMappr format. This data was obtained from Google Earth maps containing the following attribution: "©2021 Google, Data SIO, NOAA, U.S. Navy, NGA, GEBCO; Data LDEO-Columbia, NSF, NOAA; Image Landsat / Copernicus."

Label data

Label data are reported verbatim in the Material Examined, but only the data of primary types (holotypes, lectotype) are enclosed within quotation marks. A single slash "/" indicates the end of a line of text, and a double slash "//" indicates the end of a label. Clarifications, corrections, or missing data may be provided within brackets "[ ]." An abbreviation found in the specimen data, besides those of depositories, is WDS-A-[#] = William D. Shepard aquatic field collection number.

Taxonomy

Species checklist and distribution of Australian Larainae

Australara glaisteri sp. nov.: NQLD
Hydora laticeps (Carter & Zeck, 1932): ACT, NSW, VIC
Ovolara australis (King, 1865): NSW, QLD
Ovolara lawrencei sp. nov.: NQLD
Ovolara leai (Carter, 1926): NQLD
Ovolara monteithi sp. nov.: NQLD
Potamophilinus papuanus Sâto, 1973: NQLD
Stetholus carinatus sp. nov.: NQLD
Stetholus elongatus Carter & Zeck, 1929: ACT, NSW, VIC
Stetholus longipennis sp. nov.: NQLD
Stetholus metatibialis sp. nov.: NQLD
Stetholus woronora sp. nov.: NSW

Key to the species of Australian Larainae

1 Pronotum without a distinct transverse impression or impressions anterior to the middle **2**
– Pronotum with a distinct transverse impression or impressions anterior to the middle 7
2 Body elongate; prosternum not produced anteriorly to form a chin piece; apices of hind tibiae extending beyond elytral apices **6**
– Body oval or elliptical; prosternum produced anteriorly to form a chin piece; apices of hind tibiae not extending beyond elytral apices ... ***Ovolara* Brown**........ **3**

3 Antennomeres 3–11 forming a stout, ovoid club; pronotum sculptured, midline with a shallow longitudinal sulcus at anterior 2/3 and a broad costa at posterior 1/3 (Fig. 23) .... ***Ovolara australis* (King)**

– Antennomeres 3–11 forming an elongate club; pronotum without a prominent longitudinal sulcus or costa **4**

4 Elytron without an accessory basal stria between striae 1 and 2; male genitalia with penis tapered and narrow, parameres clasping tip at apical 1/3 (Fig. 26); pronotal basal margin protuberant between the prescutellar foveae (Fig. 25) .... ***Ovolara lawrencei* sp. nov.**

– Elytron with a very short accessory basal stria of 1–3 punctures between striae 1 and 2, rarely obscure; male genitalia not as above; pronotal basal margin not or only weakly protuberant between prescutellar foveae **5**

5 Male genitalia with penis narrower at apex than at midlength, parameres not clasping tip (Fig. 31); apical elytral punctures large and deep, similar to those more basal (Fig. 30) .... ***Ovolara monteithi* sp. nov.**

– Male genitalia with penis wider at apex than at midlength, parameres clasping tip (Fig. 29); apical elytral punctures smaller and shallower than those more basal (Fig. 28) .... ***Ovolara leai* (Carter)**

6 Pronotum with basal, sublateral carinae**;** mesoventrite with a moderately wide, deep mesoventral cavity (Figs 15, 20) .... ***Hydora laticeps* Carter & Zeck (in part)**

– Pronotum without basal, sublateral carinae**;** mesoventrite with a slit-like mesoventral cavity contained within a narrow, anterior projection (Fig. 13) .... ***Australara glaisteri* sp. nov.**

7 Elytra with angulate apices; pronotum mostly flat; pronotal posterior angles explanate, each with a distinct oval depression (Fig. 32) .... ***Potamophilinus papuanus* Satô**

– Elytra with rounded apices; pronotum convex; pronotal posterior angles not explanate, at most moderately depressed **8**

8 Eyes hemispherical, very protuberant; maxillary palpi narrow at apices; prosternum moderately long anterior to coxae (Fig. 22)... .... ***Hydora laticeps* Carter & Zeck (in part)**

– Eyes ovoid, not very protuberant; maxillary palpi wide and oblique at apices; prosternum very short anterior to coxae ... ***Stetholus* Carter & Zeck**................**9**

9 Pronotum without basal sublateral carinae **10**

– Pronotum with basal sublateral carinae **11**

10 Antennae distinctly clavate; pronotum moderately sculptured (Fig. 36); male genitalia heavily sclerotized, penis slightly longer than parameres (Fig. 37).......... .... ***Stetholus elongatus* Carter & Zeck**

– Antennae slender, almost moniliform; pronotum lightly sculptured (Fig. 38); male genitalia moderately sclerotized, with penis at least 2 × longer than parameres (Fig. 39) .... ***Stetholus longipennis* sp. nov.**

11 Length (excluding head) 5.0 mm or longer; pronotal sublateral carinae very short (Fig. 41) .... ***Stetholus woronora* sp. nov.**

– Length (excluding head) 4.0 mm or shorter; pronotal sublateral carinae 1/3–1/2 as long as pronotum **12**

12 Metatibiae with posterior surfaces glabrous and shiny; elytral accessory basal stria between striae 1 and 2 with several distinct punctures (Fig. 40) .... ***Stetholus metatibialis* sp. nov.**

– Metatibiae entirely setose; elytral accessory stria with only a few faint punctures (Fig. 34) ....***Stetholus carinatus* sp. nov.**

***Australara* gen. nov.**

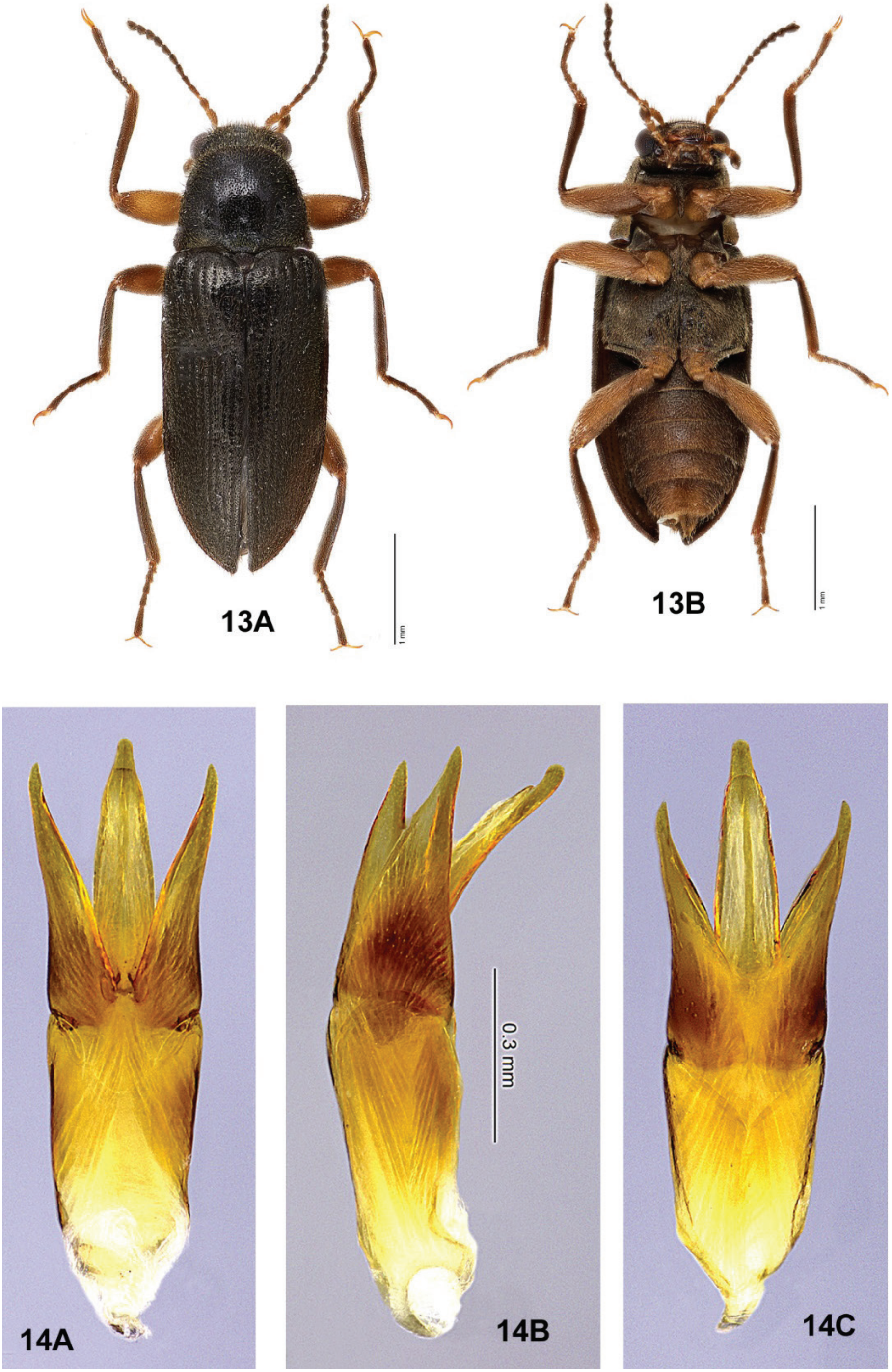
http://zoobank.org/47BFA6C2-8BDE-4CFB-B7A7-C4299E45CAFB

Type species. *Australara glaisteri* sp. nov.

Differential diagnosis. *Australara* (Fig. 13) is distinguished by the following characters: Body shape elongate; antennae subserrate, thin, very long; eyes moderately protuberant; maxillary palpi long and robust, apices tapered, sensory areas oblique and narrowly oval; labial palpomere 3 apex with white, digitiform, sensory area; pronotum with two faint, anterior transverse impressions laterad of the midline, basal sublateral carinae absent; prosternum moderately short anterior to procoxae, not extending beneath head; prosternal process spinose; mesoventrite with a narrow projection from the anterior margin containing a slit-like mesoventral cavity to receive the prosternal process; apices of hind tibiae exceeding the elytral apex.

Stetholus species (Figs 34–42), with similarly elongate bodies, are differentiated by the antennae (shorter, distinctly clavate), maxillary palpi (apical sensory area strongly oblique to base of palpomere 4 and widely open); prosternum (very short anterior to the procoxae), mesoventrite (mesoventral cavity large and deep, not within an anterior projection), and length of the hind legs (tibiae not exceeding elytral apices). *Hydora* (Figs 15B–D, 17–20, 22), like *Australara*, has an elongate body, long hind legs, and similar maxillary palpi, but differences include characteristics of the eyes (hemispherical, very protuberant), pronotum (with basal sublateral carinae), and mesoventrite (mesoventral cavity deep and moderately wide, not within an anterior projection).

Description. Body elongate; setose, setae longer and more dense on venter than on dorsum. Antenna thin, very long, antennomeres 3–11 subserrate; eye moderately protuberant, subcircular at base; maxillary palpus long and robust, palpomere 4 with apex tapered, sensory area oblique, narrowly oval. Pronotum lightly sculptured with a pair of faint anterior transverse impressions and a pair of elongate basal sublateral impressions. Elytron marginate, shallowly punctate and striate, apex acute. Prosternum moderately short anterior to procoxae, not extending anteriorly beneath head; prosternal process long, spinose, carinate. Mesoventrite with a narrow projection from the anterior margin containing a slit-like mesoventral cavity. Abdominal ventrites 1 and 2



Figures 13, 14. *Australara glaisteri* gen. nov., sp. nov., male **13** habitus **A** dorsal **B** ventral (photographs courtesy of the Australian National Insect Collection, CSIRO, Zhenhua Liu) **14** male genitalia **A** dorsal view **B** lateral view **C** ventral view.

combined much shorter than ventrites 3–5 combined. Legs long, slender, apex of hind tibia extending beyond elytral apex.

Etymology. From the Latin *australis*, meaning southern, in reference to the Southern Hemisphere as well as the continent of Australia, plus *Lara*, the type genus of the subfamily Larainae.

Distribution. Known only from the type locality in north Queensland, Australia (Fig. 1).

Comments. Described from only three specimens, all males, from one locality. The larva is unknown.

***Australara glaisteri* sp. nov.**

http://zoobank.org/BA2ACE21-58F3-41FD-92A8-7107B10055D9
Figs 1, 13, 14

Type locality. Mulgrave River south of Gordonvale; 17.1028°S, 145.7875°E; north Queensland, Australia.

Type material. *Holotype*, male. "AUSTRALIA**:** Queensland / 1 km S Gordonvale / 18 I 2001 94 ft / Mulgrave River (WDS-A-1371 on reverse) // William D. / Shepard, leg. // HOLOTYPE / Australara / glaisteri / Barr & Shepard" [red label, handwritten]. Dry pinned. Deposited in the Australian National Insect Collection, Canberra; ANIC Database Number 25-077640**.** ***Paratypes*** (2). Same data as for holotype // PARATYPE / *Australara* / *glaisteri* / Barr & Shepard [yellow label, printed] (2 ♂♂ EMEC).

Differential diagnosis. *Australara glaisteri* (Figs 13, 14) may be separated from other laraine species by the characters given in the generic diagnosis: *Hydora laticeps* (Figs 15–22) shares some similarities, but differs by having strong sublateral pronotal carinae, whereas *A. glaisteri* has none. Unlike *A. glaisteri*, *Stetholus* species (Figs 34–42) have shorter, distinctly clavate antennae, and the prosternum is very short anterior to the procoxae. The male genitalia of *A. glaisteri* (Fig. 14) are unusual, with the penis curved strongly in a dorsal direction.

Description (n = 3). Male. *Body:* Size 3.7–4.0 mm long, 1.4–1.5 mm wide; elongate, 2.5–3 × longer than wide. Dorsal color very dark brown; venter medium brown; head black; first 2 antennomeres, basal palpomeres, coxae, trochanters, femora yellow-brown; tibiae, tarsi, apical antennomeres, apical palpomeres brown. All surfaces with short to moderately long yellow setae, setae more dense ventrally than dorsally; dorsal cuticle shiny. ***Head:*** Densely and finely punctate, punctures 1 diameter apart or less; moderately setose, setae moderately long. Frons moderately protuberant between eyes, with adjacent lateral excavations and a pair of fossae above antennal bases; frontoclypeal suture straight. Antenna with eleven antennomeres, very long, thin, forming a loose, slightly asymmetrical club; antennomere 1 longest, ~ 3 × longer than wide, slightly curved; antennomere 2 ovoid; antennomeres 3–10 subserrate, with antennomeres 5–10 subequal in size; antennomere 11 broadly ovoid. Eye finely faceted, almost circular at base, moderately protuberant; dorsal margin with fringe of long, curved setae. Clypeus transverse, very short, ~ 7 × wider than long; anterior margin weakly emarginate; disc granulate; lateral margins with long setae. White membranous area visible between clypeus and labrum. Labrum rectangular, > 2 × wider than long, longer and wider than clypeus; anterior margin straight; disc granulate, very setose; lateral margins broadly rounded with long, yellow setae. Mandible with three teeth, apical pointed, 2nd triangular, 3rd smallest and triangular; lateral margins with several long setae. Maxillary palpus long, robust, setose, with four palpomeres; palpomere 1 short, annular; palpomere 2 twice as long as wide; palpomere 3 shorter and wider than 2, wider apically; palpomere 4 wide, ovoid, apex angled obliquely, ventral surface with a narrowly oval, white sensory area. Galea and lacinia long, finger-like, both with long setae. Labial palpus long, robust, yellow, with three setose palpomeres; palpomere 1 short and narrow, annular; palpomere 2 twice as wide as 1; palpomere 3 conical, apex with white, digitiform, sensory area. ***Pronotum:*** Shape nearly quadrate, slightly wider than long, widest at base; 0.9–1.0 mm long, 1.1–1.2 mm wide; disc densely punctate, punctures spaced ~ 1 diameter apart. Anterior margin thickened, straight; anterior angles obsolete; lateral margins weakly sinuate, marginate; posterior angles depressed, lateral margins raised, variably produced with tips generally blunt; posterior margin weakly trisinuate. Disc moderately convex; two faint, anterior transverse impressions laterad of the midline at anterior 1/4; two faint to distinct shallow, elongate, sublateral impressions ~ 1/3 length of pronotum; two prescutellar foveae joined by a shallow, transverse impression. ***Scutellar shield:*** As long as wide, apex rounded; flat; densely setose. ***Elytron:*** 2.8–3.0 mm long, 0.7–0.8 mm wide. Elytra conjointly 2 × as long as wide; generally parallel-sided; laterally compressed at basal 1/2; lateral margins strongly marginate. Humerus inflated, elytral base slightly depressed; disc moderately convex at anterior 1/4 median to humerus; moderately depressed at anterior 1/4–1/3 posterior to humerus; then weakly convex to apex. Disc with ten small, shallowly punctate, weakly impressed striae, intervals nearly flat; short, faint, accessory basal stria with close to ten punctures between striae 1 and 2; striae 2 and 3 end before apex; disc punctures of variable size, separated by < 1 diameter, more distinct basally, smaller and closer apically. ***Metathoracic wings:*** Macropterous. ***Prosternum:*** Moderately short anterior to procoxae, disc very setose with widely spaced punctures; prosternal process spinose, long, 5 × longer than wide, carinate with carina extending anterior of procoxae, apex narrowly rounded. ***Mesoventrite:*** Very setose; surface elevated at midline anterior to mesocoxae to form a narrow projection from the anterior margin with two carinae enclosing a slit-like mesoventral cavity; area anterior to mesocoxae shallowly excavated for procoxae; disc depressed between mesocoxae; posterior margin emarginated medially. ***Metaventrite:*** Broadly rectangular; very setose, moderately granulate; anterior margin moderately produced between mesocoxae; disc laterally convex, medially with a shallow, wide concave area surrounding discrimen; discrimen extending from anterior 1/4 to posterior margin, deeply incised; metakatepisternal suture distinct. ***Legs:*** Long, slender, of similar lengths; each leg with femur and tibia subequal in length; tarsus with tarsomere 5 distinctly shorter than tarsomeres 1–4 combined. Coxae and femora yellow-brown; tibiae brown, each with a pair of stout spines at ventral apex; meso- and metatibiae with posterior surfaces shallowly sulcate, yellow-brown, glabrous, shiny; tarsi brown; claws simple, long, sharply acute. ***Abdomen:*** Strongly convex, lateral margins concealed by elytra; densely setose and moderately granulate; with five ventrites, ventrites 1–4 of subequal length, ventrite 5 slightly longer; ventrite 1 with a long, narrow median, triangular intercoxal projection; ventrite 5 posterior margin with a median emargination. ***Aedeagus:*** Approximately 3.5 × longer than wide, generally parallel-sided at basal 3/4; phallobase longer than parameres, penis slightly longer than parameres (Fig. 14). Parameres, in dorsal view (Fig. 14A), widest at base; lateral margins nearly parallel at basal 1/2, then weakly divergent at apical 1/2; medial margin weakly arcuate; apex produced, acute. Penis, in dorsal view, widest basally, lateral margins evenly convergent to rounded apex; no visible corona; basal apophyses short, < 1/4 as long as phallobase, straight, broad, blunt at tips. In lateral view (14B), penis strongly curved dorsally above parameres at ~ 30° angle, apex rounded; paramere triangular, apex produced, acute. Fibula absent.

Variation. The three specimens varied in size from 3.7–4.0 mm long and 1.4–1.5 mm wide. Because the small series of *A. glaisteri* is all male, it was not possible to make a comparison with the female of the species. Among the three, the two shallow, elongate, sublateral pronotal impressions vary from faint to distinct. Also, the posterior pronotal angles differ in the amount to which they are produced, the shape of the angle (nearly 90° to acute), and whether the tip is truncate, blunt, or sharp. It is possible that the median emargination on the posterior margin of abdominal ventrite 5 is a male characteristic not present in females.

Etymology. The specific epithet *glaisteri*, a noun in the genitive case, is given in honor of Alena Glaister of Monash University, VIC, who devised a successful method of rearing Australian larval elmids to adults, thereby enabling their association. She published an extensively illustrated identification guide to the larval Elmidae of Australia with keys and descriptive notes on taxonomy, distribution, and habitat. Few elmid researchers have attempted such work, and none have produced larval keys covering so many taxa.

Distribution. Known only from the type locality in north Queensland, Australia (Fig. 1).

Habitat. At the collection site during low water stage, the Mulgrave River was mostly shallow, with warm, clear water and a fairly swift current over a substrate of sand and gravel. Decomposing wood and log jams, where *Australara* and other laraines were found, were abundant along the banks of the wide channel. The locality is at ~ 30 m elevation and bordered by a town and sugarcane fields not far from the ocean. Local residents told us that in past years saltwater crocodiles frequented the river until the sugarcane farmers shot them out.

Associated byrrhoid taxa. Elmidae: Larainae: *Ovolara leai, O. monteithi* sp. nov., *Stetholus longipennis* sp. nov.; Elminae: *Austrolimnius* spp., *Graphelmis pallidipes* (Carter), *Kingolus* spp., *Notriolus* spp., *Simsonia* spp.

Genus *Hydora* Anon. [Broun], 1882

Type species. *Pachycephala picea* Broun, 1881.

Diagnosis. Body elongate, sides subparallel; antennae loosely clavate; eyes large, prominent; pronotum with two basal sublateral carinae; prosternum not extended anteriorly beneath head; elytra striate-punctate, punctation sometimes reduced (New Zealand species), each elytron with one accessory basal stria between striae 1 and 2, elytral apices narrowly rounded; tarsi each with tarsomere 5 subequal to or shorter than tarsomeres 1–4 combined; abdominal ventrites 1 and 2 combined shorter than ventrites 3–5 combined.

Distribution. The genus *Hydora* has an interesting geographic distribution, with ten recognized species occurring in New Zealand (7), Australia (1), and Argentina and Chile (2) (Spangler and Brown 1981; Lambert et al. 2014). There are many currently undescribed species in New Zealand and one in Chile (R. Leschen, V. Sýkora, in litt.).

Habitat and behavior. There is no information available pertaining to the habitat and behavior of *Hydora* in Australia, except for the fact that at least half of the known specimens were collected at lights. In New Zealand, larvae and adult *Hydora* are common on the bottom substrate, or on vegetation, including bryophytes, at the margins of moderate to fast flowing streams (Lambert et al. 2014). Adults can sometimes be found running around on the emergent parts of boulders and have been observed in mass swarms above the water surface (Lambert et al. 2014).

Comments. In this genus the prosternal process may or may not have a median longitudinal carina, depending on the species. Some New Zealand species do, and some do not (Broun 1914; Lambert et al. 2014). No carinae were mentioned in the descriptions of the prosternal processes of the two species from Austral South America, *Hydora annectens* Spangler & Brown and *H. lenta* Spangler & Brown (Spangler and Brown 1981), and upon examining specimens of those species, we found none. The description of *H. laticeps* from Australia stated that the process is without a carina (Carter & Zeck 1932), but this is debatable. The prosternal process is discussed in the Comments section of the species treatment. The larva was keyed and illustrated at the generic level in Glaister (1999) based on New Zealand specimens.

Hydora laticeps (Carter & Zeck, 1932)

Figs 2, 15–22

Type locality. Upper Shoalhaven River, Tallong; 34.700°S, 150.083°E (approximate); New South Wales, Australia (lectotype deposited in the Australian Museum, Sydney). Note: The geographic coordinates given in the AM database place the type locality north of Tallong, whereas the Shoalhaven River is to the south.

Type material examined (2). *Lectotype* male (here designated). New South Wales. "Australian Museum / K 579881 // Tallong / N.S.W. / FHTaylor // Stetholus /

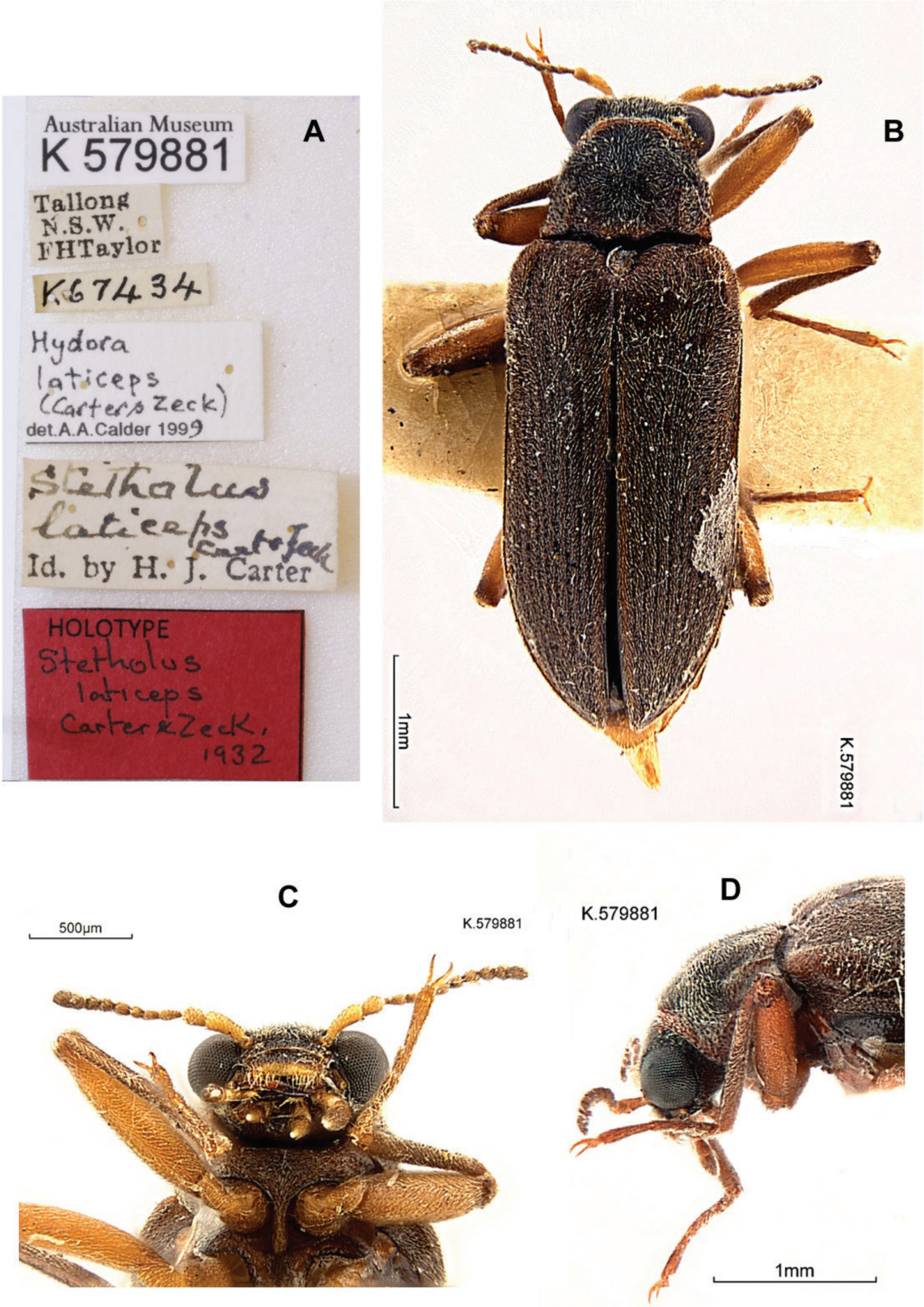


Figure 15. *Hydora laticeps*, lectotype male **A** specimen labels **B** dorsal habitus **C** ventral head and prosternum **D** lateral head and pronotum (photographs courtesy of the Australian Museum, Natalie Tees).

laticeps / Carter & Zeck / Id. by H. J. Carter // K67434 // HOLOTYPE / Stetholus / laticeps / Carter & Zeck, / 1932 [red label] // Hydora / laticeps / (Carter & Zeck) / det. A.A.Calder 1999 // LECTOTYPE / Stetholus laticeps / Carter & Zeck, 1932" [red label, handwritten]. Deposited in the Australian Museum, Sydney. ***Paralectotype* male (here designated). New South Wales.** Australian Museum / K 579882 // Tallong / N.S.W. / FHTaylor // K69264 // Stetholus / laticeps / Carter 1932 // PARATYPE / Stetholus laticeps / Carter & Zeck, / 1932 [blue label] // Hydora / laticeps / (Carter & Zeck) / det. A.A.Calder 1999 // PARALECTOTYPE / *Stetholus laticeps* / (Carter & Zeck, 1932) [yellow label, printed]. Deposited in the Australian Museum, Sydney.

Type material examined from photographs (2). *Paralectotype* males (here designated). New South Wales. Tallong / N.S.W. / FHTaylor // Stetholus / laticeps C & Z / Id. by H. J. Carter // Hydora / laticeps (C&Z) / det. A.Calder 1992 // Genitalia prep. / HH-224 ♂/ A. Calder 19~~87~~92 // PARALECTOTYPE / *Stetholus laticeps* / (Carter & Zeck, 1932) [yellow label, printed] (1 ANIC); Tallong / N.S.W. / FHTaylor // Stetholus / elongatus / C & Z / Id. by H. J. Carter // Paratype [blue label, printed] // PARATYPE [blue label, printed] // Genitalia prep. / HH-247 ♂/ A.Calder 1997 // ANIC / Image // PARALECTOTYPE / *Stetholus laticeps* / (Carter & Zeck, 1932) [yellow label, printed] (1 ANIC).

Other material examined (4). Australian Capital Territory. AUSTRALIA: / Lyneham / at light / A.C.T. 22.xii.66 / B.P.Moore (1♂ 1♀ ANIC). **Victoria.** Cann River, E.Vic. / 28.i.1967. / G. Monteith // EX UQIC / DONATED / 2011 (2♀♀ QM).

Differential diagnosis (n = 8). *Hydora laticeps* (Figs 15–22) is the only species of *Hydora* known to occur in Australia. It can be distinguished from other Australian laraines by a combination of the following characters: Eyes protuberant, hemispherical; maxillary palpi narrow at the apices; pronotum with strong basal, sublateral carinae and without a distinct transverse impression at anterior 1/3; and prosternum moderately long anterior to the coxae but not extending beneath head. *Stetholus* species (Figs 34–42) have ovoid eyes, not usually prominent; maxillary palpi each with palpomere 4 wide and oblique at the apex; pronotum with a distinct transverse impression; and prosternum very short and narrow anterior to the coxae.

Australara glaisteri (Fig. 13) most obviously differs by its lack of sublateral pronotal carinae and by the mesoventrite having an anterior projection containing a slit-like mesoventral cavity; the eyes are also not quite as protuberant.

Redescription (n = 2). Male lectotype and male paralectotype. *Body:* Size 4.2 mm long, 1.6 mm wide (lectotype); size 4.0 mm long, 1.5 mm wide (paralectotype); elongate, parallel-sided. Color light to dark brown; head and pronotum darkest; antennae, mouthparts, legs, venter lightest. Dorsum with fine, pale setae, short on elytra, longer on head and pronotum; venter with long, dense setae. ***Head:*** Eye large, protuberant, hemispherical. Antenna with antennomere 1 elongate, antennomere 2 ovoid, antennomeres 3–11 smaller, weakly clavate. Labrum emarginate anteriorly, lateral margins with long setae. Maxillary palpus long, robust, setose; palpomere 4 much enlarged, ovoid, apex blunt with small, oval sensory area. Labial palpus shorter, palpomere 4 conical, apex pointed with very small, circular sensory area. ***Pronotum:*** Shape generally trapezoidal, 0.9 mm long, 1.1 mm wide (at base); anterior angles obscure, lateral margins crenulate, posterior angles acute, depressed; disc weakly sculptured except for two distinct, basal, sublateral carinae, 1/2 the pronotal length; two shallow, obscure transverse impressions laterad of midline at anterior 1/5–1/4. ***Elytron:*** 3.2–3.3 mm long, 0.7–0.8 mm wide (at base); lateral margin narrowly marginate, apex narrowly rounded, acute; disc with ten rows of moderately striate punctures, accessory basal stria present between striae 1 and 2; disc in lateral view flattened at anterior 1/2. ***Prosternum:*** Moderately long anterior to coxae, not extending beneath head; prosternal process narrow, curved, posterior 1/3 semi-carinate with a short, faint row of granules at midline, tip narrowly rounded. ***Mesoventrite:*** Longer than prosternum; mesoventral cavity deep and moderately wide ***Metaventrite:*** Very convex, especially in lateral view. ***Legs:*** Long and slender. Tibia of all legs with a pair of stout spines at ventral apex; meso- and metatibia with posterior surfaces shallowly sulcate, glabrous, shiny. Tarsus with tarsomere 5 shorter than tarsomeres 1–4 combined; covered with short, dense setae; claws simple, slender, acute. ***Abdomen:*** Ventrite 1 triangular intercoxal projection moderately narrow; ventrite 5 nearly truncate at apex. ***Aedeagus:*** Phallobase longer than parameres and penis, penis slightly longer than parameres (Fig. 16). Phallobase open dorsally. In dorsal view (Fig. 16A), parameres broad, with lateral margins gradually convergent, apices bluntly rounded; medial margins parallel-sided at basal 2/3 then gradually divergent, margins appearing more sclerotized than rest of parameres. Penis slightly longer than parameres, approximately as wide at base as paramere base; lateral margins widened and arcuate just distal to base, then evenly convergent to apex; apex narrow, nipple-like, laterally flattened, tip narrowly rounded; no corona visible; basal apophyses short, 1/4–1/3 as long as phallobase, straight, broad, blunt at tips. Fibula absent. In lateral view (Fig. 16B), paramere nearly straight dorsally at apical 3/4, weakly arcuate ventrally, tip broadly rounded and slightly wider than paramere tip.

Variation. There is some size variation among the known specimens, particularly between males and females. Specimens from the type series, all males (n = 4), measured 4.0–4.3 mm long, 1.4–1.6 mm wide. Carter and Zeck (1932) stated in the type description "Dimensions: 5 × 1.5 mm" but the length probably included the head. Among the specimens examined (including two from the type series), the females (n = 3), 4.5–5.2 mm long, 1.7–1.8 mm wide, are considerably larger than the males (n = 3), 4.0–4.5 mm long, 1.4–1.6 mm wide. In addition, the females (Figs 20B, 22B) have prosternal processes broader than those of the males (Fig. 15C), and noticeably narrower maxillary palpi. The prosternal processes of the two male specimens examined from the type series (Fig. 15C) are slightly narrower than those of the non-type male. The surface of the prosternal process varies, and may be convex, depressed only between the procoxae, or entirely flat except posterior to coxae, but in all specimens the process is granulate, swollen, and an indistinct carina is usually visible. Non-sexual variation was also observed in the morphology of the elytral punctures (size and depth), pronotum (width, lateral margins, posterior angles, sculpturing); and prosternal process (width, surface features). On the pronotum, two shallow, anterior, transverse impressions are present laterad of the midline. In most specimens the impressions are weak or altogether ob-

Figure 16. *Hydora laticeps*, lectotype; male genitalia **A** dorsal view **B** lateral view **C** ventral view.

scure (Figs 17–19), but they are quite obvious in one of the two non-type specimens from Cann River (Fig. 22A). In addition, the single male non-type specimen from Lyneham (Fig. 21A, C) has a slightly broader aedeagus than the two specimens examined from the type series (Fig. 16A, C). This variability in external morphology and male genitalia raises the possibility that more than one species is involved.

Lectotype designation. It appears that none of the four known specimens from the type series of *Stetholus laticeps* was given a holotype or paratype label at the time of description, and those subsequently added to the specimens were not done so by the authors. In their description, Carter and Zeck (1932) stated that they had "five examples" and that the holotype was "in Coll. Carter," but did not mention designating paratypes. Two specimens were deposited at the Australian Museum 35 years apart: According to the original register of specimens, the first (Fig. 15) was presented by H. J. Carter in 1936, and bears an old, handwritten determination label saying "Stetholus laticeps Carter & Zeck Id. by H. J. Carter" (Fig. 15A). The specimen was subsequently given a holotype label by an unknown person, i.e., it was not written in the same hand as the determination label by Carter and appears much newer. This specimen is here designated as the lectotype to fix the concept of *Hydora laticeps* (Carter & Zeck). The second specimen (Fig. 17) was obtained from the late E. H. Zeck in 1971, lacks an

Figures 17–19. *Hydora laticeps*, paralectotype males; dorsal habitus with specimen labels **17** AM specimen (photograph courtesy of the Australian Museum, Natalie Tees) **18** ANIC specimen (photograph courtesy of Vít Sýkora, Charles University, Prague, Czech Republic) **19** ANIC specimen (photograph courtesy of the Australian National Insect Collection, CSIRO).

original determination label, and likewise bears a newer paratype label; it is designated a paralectotype.

There are also two specimens housed at Australian National Insect Collection. One of them bears the surprising, original determination label "Stetholus elongatus C & Z Id. by H. J. Carter" and two printed paratype labels, one older and one newer (Fig. 19). Probably the identification predated the description of *S. laticeps* by Carter and Zeck in 1932, however, Tallong was not among the localities cited in their 1929 description of *S. elongatus* (Carter and Zeck 1929). The other specimen has an original determination label, "Stetholus laticeps C & Z Id. by H. J. Carter," but has no paratype label (Fig. 18). These two specimens are likewise designated as paralectotypes. We were unable to examine the ANIC specimens because they were on loan to another researcher, but we were provided with habitus images (Figs 18, 19) and measurements of body length for this article.

The location of the fifth specimen from the type series is unknown. Lambert et al. (2014) cited the SAMA as a specimen depository for the species, but we have examined their material and found no specimens of *H. laticeps*, so this report was in error.

Distribution. *Hydora laticeps* is known from only three localities in Australia: the Shoalhaven River near Tallong, New South Wales, the type locality; Lyneham, Australian Capital Territory; and Cann River, eastern Victoria (Fig. 2).

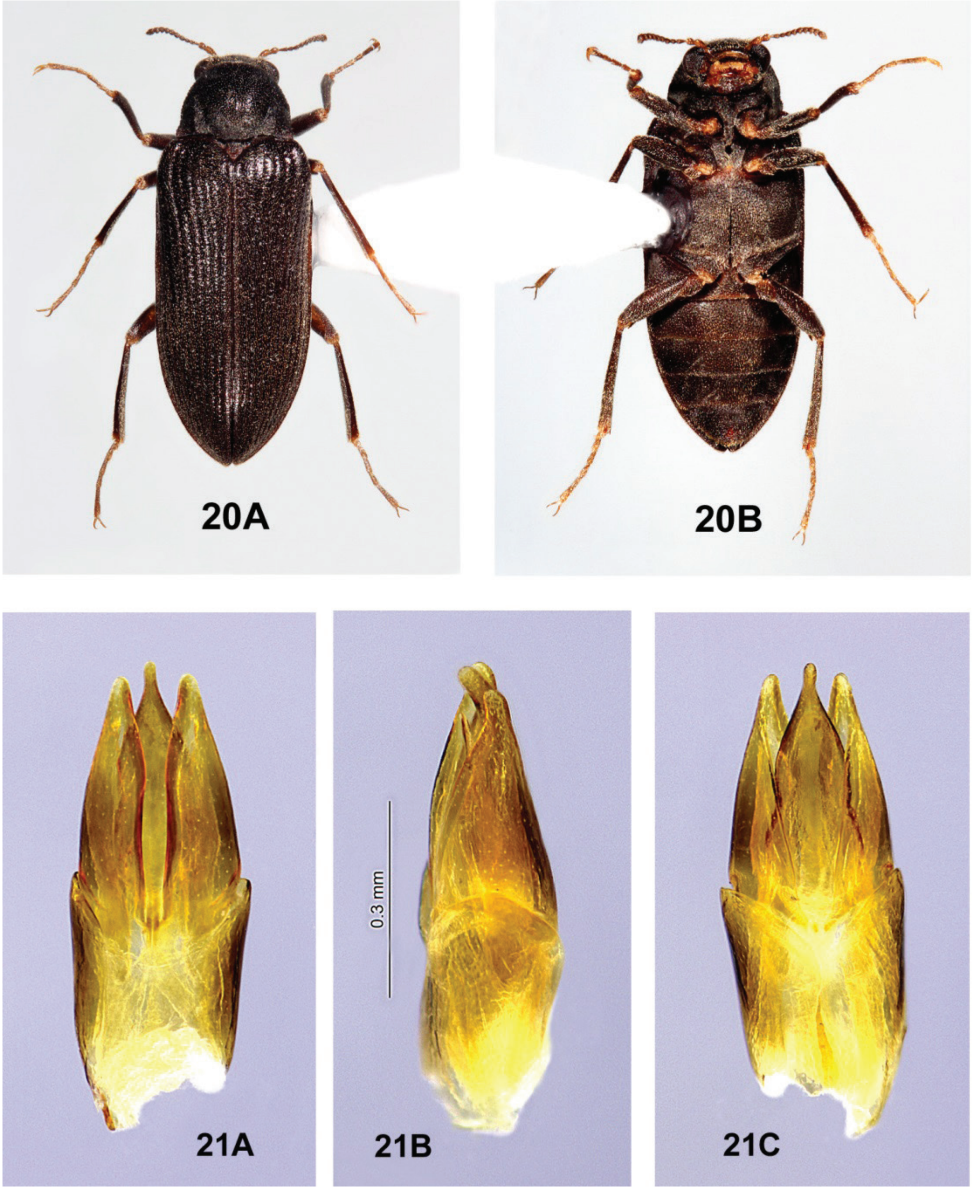
Associated byrrhoid taxa. Elmidae: Larainae: *Stetholus elongatus* (AM, ANIC, NMV, SAMA); Elminae: *Notriolus* sp. (AM).

Comments. *Hydora laticeps* was originally described in the genus *Stetholus* by Carter and Zeck (1932), and subsequently reassigned to *Hydora* by Hinton (1935). Hinton stated that he studied only the description and figures, not actual specimens, and gave no specific reasons for the new combination.

In the diagnosis following their description, Carter and Zeck (1932: 203) noted that the prosternal process of *S. laticeps* lacks a carina, in contrast to *Stetholus elongatus* Carter & Zeck (1929) which has a carina. The actual situation is less clear-cut. The surface of the apical 1/2-1/3 of the process is convex to varying degrees and may be somewhat granulate at the midline, resembling an indistinct carina. However, this is a poor diagnostic character because dense setation can make examination difficult.

When Carter and Zeck (1932) described *S. laticeps* they made no mention that *S. elongatus*, described by them in 1929, was present in the Upper Shoalhaven River as well. That *S. elongatus* was collected with *H. laticeps* at the type locality is evidenced by museum specimens with locality labels identical to those of *H. laticeps*: "Tallong N.S.W. FH Taylor." This raised the question as to whether the missing specimen of *H. laticeps* might bear a *S. elongatus* label, as does one of the ANIC specimens, and thus has been overlooked. Unfortunately, examination of all known *S. elongatus* specimens with collection labels as above (AM, 3 specimens; ANIC, 3; NMV, 2; SAMA, 4) revealed no misidentifications.

Until now, *Hydora laticeps* has been known only from its type locality, the Upper Shoalhaven River near Tallong, New South Wales, Australia. In the 90+ years since the type series was collected, deliberate attempts to re-collect it have been unsuccessful.



Figures 20, 21. *Hydora laticeps*, non-types from Lyneham, ACT **20** female habitus, 4.5 mm long **A** dorsal **B** ventral **21** male genitalia **A** dorsal view **B** lateral view **C** ventral view.

Examination of unidentified museum specimens for this project resulted in the discovery of four additional specimens from two new localities, all of which were collected at light. The four type specimens available are all males, the Lyneham specimens are male and female, and the Cann River specimens are both female. In the absence of males, the latter two specimens are assumed to be *H. laticeps* due to external morphological similarities. The larva of the species is unknown.

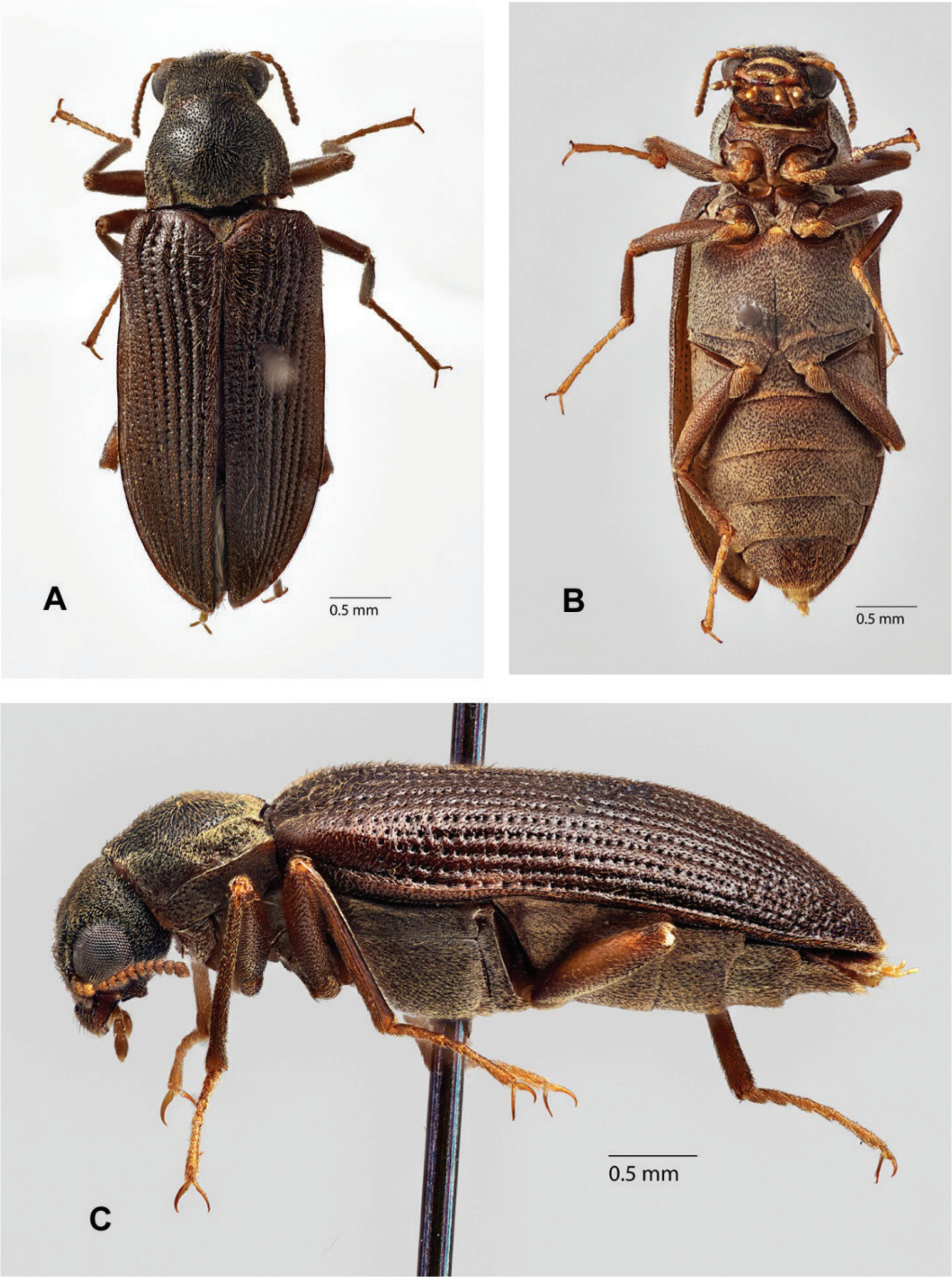


Figure 22. *Hydora laticeps*, non-type female from Cann River, VIC **A** dorsal habitus **B** ventral habitus **C** lateral habitus (photographs courtesy of the Queensland Museum, Geoff Thompson).

As mentioned in the Variation section, is possible that not all of the specimens are conspecific because of mophological variation which is apparent even among those from the type series. However, there is not enough evidence at present to assign any to a species other than *H. laticeps*. DNA analysis would be helpful in this regard if fresh material could be obtained. A recent attempt to obtain DNA from a specimen in the type series failed due to its age (V. Sýkora, in litt.), and even the youngest of the specimens is at least 54 years old.

Genus *Ovolara* Brown, 1981

Type species. *Lutochrus australis* King, 1865.

Diagnosis. Body oval or elliptical; antennae clavate, either compact or elongate; pronotum with two short, basal, sublateral carinae; pronotal disc without a transverse impression; elytra striate-punctate, each elytron with or without an accessory basal stria between striae 1 and 2, apices rounded; prosternum with a chin piece, a shelf-like, anterior extension beneath the head; prosternal process broad, with or without a distinct median longitudinal carina; mesotibiae glabrous and shiny on the posterior surfaces; apices of hind tibiae not exceeding apices of elytra; tarsi each with tarsomere 5 as long as tarsomeres 1–4 combined; abdominal ventrites 1 and 2 combined shorter than 3–5 combined (Figs 23–26, 28–31).

Distribution. *Ovolara* is endemic to Australia, with four species occurring in New South Wales and Queensland (Figs 3–6)

Habitat and behavior. *Ovolara* adults are most often associated with marginal or emergent stream vegetation and debris packs. Depending on the species, they may occur in areas of slow current (*O. australis*) or in fast water and rapids (*O. leai*). When captured or disturbed, *Ovolara* does not take flight as quickly as many other laraines. Specimens of all species have been collected at lights.

Comment. King (1865) described the type species of the genus in *Lutochrus*, a misspelling of *Lutrochus* Erichson, 1847. Brown (1981) subsequently erected the genus *Ovolara* to include the type species, *Lutrochus* [sic] *australis* as well as *Hydrethus leai* Carter, 1926 (Brown 1981). He believed the genus to be most closely related to *Hydora*. The larva was keyed and illustrated in Glaister (1999) at the generic level.

The external morphology of the species is very similar except for that of *O. australis*. Comparison of the male genitalia is the best way to distinguish the species.

Ovolara australis (King, 1865)

Figs 3, 23, 24

Type locality. Parramatta River; 33.7644°S, 151.0076°E; New South Wales, Australia (lectotype deposited in the Australian Museum, Sydney).

Material examined (114). New South Wales. AUSTRALIA: NSW / Jerrabattgulla Creek at / Ballalaba, E Capt. Flat / 35°38'36"S,149°36'19"E / 4-I-2001, coll. C. B. Barr (9 EMEC); AUSTRALIA: NSW / 6.4 km ENE of Guthega / 7 I 2001 438 ft / Piper's Creek (WDS-A-1357 on reverse) // William D. / Shepard, leg. (2 EMEC); AUSTRALIA: NSW / 13 km E Braidwood / 3 I 2001 / Mongarlowe River (WDS-

Figures 23, 24. *Ovolara australis*, male **23** habitus, 4.1 mm long **A** dorsal **B** ventral **24** male genitalia **A** dorsal view **B** lateral view **C** ventral view.

A-1345 on reverse) // William D. / Shepard, leg. (2 EMEC); AUSTRALIA: NSW / Deua Nat Park / 4 I 2001 453' / Black lights / S35°45'00" E149°54'53" (WDS-A-1346 on reverse) // William D. / Shepard, leg. (2 EMEC); same locality; Deua River (WDS-A-1348 on reverse) (1 EMEC); Australia: N.S.W. / Paterson River Nr. / Lostock Nov. 9 /2001 G. Challet (14 EMEC); AUSTRALIA: NSW / Allyn River / 9 Nov 2001 / G. Challet, leg. (8 EMEC); AUSTRALIA: N.S.W. / Tuross River nr. / Bodalla; Nov 3 / 2001; G. Challet (6 EMEC); Mebbin St. For. / NSW 18km W of / Uki 23-24 Nov. / 1982 J.Doyen (47 ANIC, 2 EMEC); AUSTRALIA: NSW, 2km N Nana / Glen (30°6'3"S, 153°'23.6"E), 11 / November 2006, coll. D. Britton // Weedy river bank / MV lamp, Britton 2006/052 // Australian Museum / K 579954 (1 AM); same data as for preceding; Australian Museum / K 579955 (1 AM); 15 km NE Kyogle / At black light / 20.xi.1984 / D.J.Scambler / Australian Museum / K 579974 (1 AM); same data as for preceding; Australian Museum / K 579975 (1 AM); Bruxner Park, Via / Coff's Harbour, / 25.ii.1967. N.S.W. / G. Monteith (1 QM); NSW, Eccleston 4 km / N 27/11/95 C.Watts // SAMA / 25-47747 (2 SAMA); NSW, Williams R. / nr Dungog 27/11/95 / C.Watts //SAMA / 25-47748 (1 SAMA). **Queensland.** Canungra Creek, / 4 ml. S. of Canungra, Qld / 25.XII.1974 / G. B. Monteith (9 QM); Upper Canungra Creek, / via Canungra, S.E. Qld. / 2.i.1973 / I.Naumann (1 QM); NSW [QLD], Cedar Creek / Dayboro 10 km S / 23/11/95 C.Watts // SAMA / 25-47737 (1 SAMA); Condamine R. / Killarney / 6-11-32 / H Hacker (1 QM); N. Pine R. / 23-[illegible]-32 H Hacker (1 QM); Young's X-ing / Petrie, Q. / 2.X.59 / I.C.Yeo / (1 QM).

Differential diagnosis (n = 114). *Ovolara australis* (Figs 23, 24) can be distinguished from other species of *Ovolara* by the following characters: Antennae ending in stout, moderately tight, ovoid clubs; pronotum distinctly sculptured, with a shallow, median, longitudinal sulcus at the anterior 2/3 and a broad, median, longitudinal costa at the posterior 1/3; each elytron with an accessory basal stria between striae 1 and 2; male genitalia unique. *Ovolara lawrencei* (Fig. 25), *O. leai* (Fig. 28) and *O. monteithi* (Fig. 30) have elongate antennal clubs and mostly unsculptured, smooth pronota without sulci or distinct costae; *O. lawrencei* lacks elytral accessory striae. The male genitalia of *O. lawrencei* (Fig. 26) are the most similar, but the penis of *O. australis* (Fig. 24) is abruptly constricted at the apex with the adjacent paramere apices rounded, while that of *O. lawrencei* is tapered and narrow near the apical 1/3 and the paramere inner margins are linear and clasping.

Variation. The only difference observed among individuals is the degree of pronotal sculpturing, especially the depth of the median longitudinal sulcus. Measured specimens vary in size from 3.3–4.2 mm long and 1.4–1.7 mm wide (n = 30). There is little size difference between males, 3.3–4.1 mm long, 1.4–1.7 mm wide (n = 19), and females, 3.4–4.2 mm long, 1.5–1.7 mm wide (n = 11), with individuals of both at the small and large ends of the size range.

Distribution. *Ovolara australis* occurs in New South Wales and south Queensland, Australia (Fig. 3).

Habitat, behavior, and life history. The authors found *O. australis* adults to be numerous in blackwater streams beneath undercut clumps of emergent vegetation in areas of sluggish flow. The species also has been taken at black light by the authors and other collectors. One female specimen, collected in January, was dissected and found to have 20+ eggs in her abdomen, indicating that January is within the reproductive period of the species.

Associated byrrhoid taxa. Elmidae: Larainae: *Stetholus elongatus*; Elminae: *Austrolimnius metasternalis* Carter & Zeck, *A.* spp., *Coxelmis novemnotata* (King), *Kingolus aeratus* (Carter), *K. quatuormaculatus* (King), *K. metallicus* (King), *K. tinctus* Carter & Zeck, *K.* spp., *Notriolus maculatus* (Carter), *N. minor* (Carter & Zeck), *N. quadriplagiatus* (Carter), *N. setosus* Carter & Zeck, *N.* spp., *Simsonia tasmanica* (Blackburn), *Simsonia* spp. Psephenidae: *Sclerocyphon striatus* Lea.

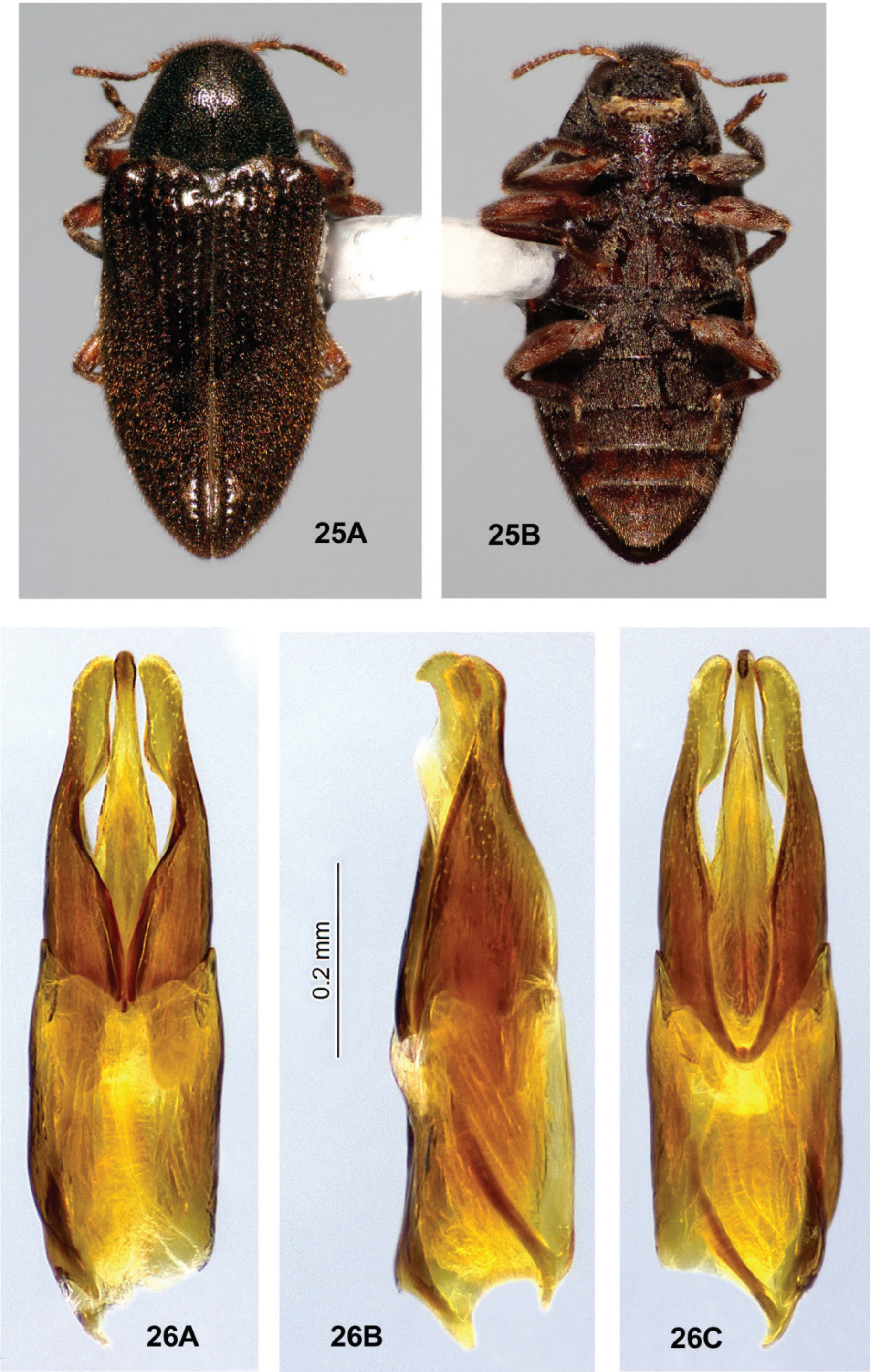
Comments. *Ovolara australis,* the type species of the genus, was originally described by King (1865) in *Lutochrus*, a misspelling of *Lutrochus* Erichson, 1847; it was moved to *Ovolara* by Brown (1981). The larva of this species has been reared to the adult by Glaister (A. Glaister, in litt.).

Ovolara lawrencei sp. nov.

http://zoobank.org/6631CC2C-FA3D-4053-A72A-9ED64B97B80A
Figs 4, 25–27

Type locality. Emerald Creek east of Mareeba; 16.9851°S, 145.4740°E; north Queensland, Australia (Fig. 27).

Type material. ***Holotype* male**. "AUSTRALIA: no. QLD / Emerald Creek at Hwy. 1 / E of Mareeba / 16°59'12"S, 145°28'21"E / 17-I-2001, coll. C.B. Barr // HOLOTYPE / Ovolara / lawrencei / Barr & Shepard" [red label, handwritten]. Dry pinned. Deposited in the Australian National Insect Collection, Canberra; ANIC Database Number 25-077641. ***Paratypes* (77).** Same data as for holotype (1 ANIC, 3 EMEC, 1 QM); AUSTRALIA: Queensland / Emerald Creek Store / 17 I 2001 / Emerald Creek / S16°59'12" E145°28'21" (WDS-A-1369 on reverse) // William D. / Shepard, leg. (2 EMEC); AUSTRALIA: no. QLD / Rocky Creek at Hwy. 1 / ~5 rd.km. NE of Atherton / 17°10'54"S, 145°26'59"E / 11-I-2001, coll. C.B.Barr (1 AM, 1 ANIC, 6 EMEC); AUSTRALIA: Queensland / 5 km N Atherton / 11 I 2001 / Rocky Creek (WDS-A-1364 on reverse) // William D. / Shepard, leg. (2 EMEC); AUSTRALIA: no. QLD / Pattersons Cr. at Boar / Pocket Rd. 3 rd.km. N off / Hwy.52, SW Gordonvale / 11-I-2001, C. B. Barr // 17°12'06"S / 145°40'08"E (1 AM, 4 EMEC, 1 QM); AUSTRALIA: Queensland / 17 km SW Gordonvale /11 I 2001 1883 ft / Patterson's Creek (WDS-A-1365 on reverse) // William D. / Shepard, leg. (2 EMEC); AUSTRALIA: no. QLD / Bushy Creek at Hwy. 44 / just W of Julatten / 16°36'40"S, 145°20'10"E / 17-I-2001, coll. C.B. Barr (1 ANIC, 5 EMEC); AUSTRALIA: Queensland / just W of Julatten / 17 I 2001 / Bushy Creek (WDS-A-1367 on reverse) // William D. / Shepard, leg. (1 AM, 3 EMEC, 1 QM); AUSTRALIA: no. QLD / Hunters Creek at Hwy. 44 / 5 rd. km. N Mount Molloy / 16°38'00"S, 145°19'27"E / 17-I-2001, coll. C. B. Barr (1 ANIC, 5 EMEC); AUSTRALIA: Queensland / 5 km N Mount Molloy



Figures 25, 26. *Ovolara lawrencei* sp. nov., male **25** habitus, 3.0 mm long **A** dorsal **B** ventral **26** male genitalia **A** dorsal view **B** lateral view **C** ventral view.

Figure 27. *Ovolara lawrencei* sp. nov., type locality, and *Stetholus longipennis* sp. nov., collection locality: Emerald Creek, east of Mareeba, QLD, Australia (photograph courtesy of David Rentz, James Cook University, Smithfield, QLD).

/ 17 I 2001 / Hunters Creek / S16°38’00” E145°19’27” (WDS-A-1368 on reverse) // William D. / Shepard, leg. (1 AM, 3 EMEC, 1 QM); 17.21S 145.56E / Babinda, NQld / J.G.Brooks / without date (3 ANIC); same data as for preceding // Genitalia prep. / HO-252 ♂ / A.Calder 1997 (1 ANIC); same data as for preceding // Genitalia prep. / HO-253 ♂ / A.Calder 1997 (1 ANIC); same data as for preceding // Genitalia prep. / HO-278 ♀ / A.Calder 1997 (1 ANIC); Barron R. / Cairns, N.Q. / Apr. 1946 / J. G. Brooks // Australian Museum / K 579980 (3 AM); Davies Creek, NQ / Oct. 1950 / J.G.Brooks // J.G. Brooks / Bequest, 1976 (2 ANIC); 15.11S 143.52E GPS / Hann River [tributary Morehead River (P. Zborowski, in litt.)] QLD / 14 Jan. 1994 at light / P.Zborowski & / E.D.Edwards (1 ANIC); 16.38S 145.19E QLD / Hunter Creek / 16 Dec. 1994 / P.Zborowski // flowing, clear stream, / sandy bottom, part / shade: rainforest (1 ANIC); Kuranda / QUEENSLAND / F. H. TAYLOR / 5-10-35 // Hydrethus leai Cart. / Genitalia prep. / HO-257 ♂ / A.Calder 1997 (1 ANIC); Kuranda, N. Qld. / 28.xii.1963 / G. Monteith // EX UQIC / DONATED / 2011 (10 QM); L’tle Mulgrave R. / N.Q. 16.xii.67 / J.G. Brooks // J.G. Brooks / Bequest, 1976 // Genitalia prep. / HO-261 ♂ / A.Calder 1997 (1 ANIC); 15.46S 144.15E GPS / Shepherd Creek QLD / 17 Jan. 1994 / water sweep / P. Zborowski, / E.D. Edwards (3 ANIC); Stewart’s Crk / Daintree, NQ / 16 Sept. 1969 / J.G. Brooks // J.G. Brooks / Bequest, 1976 (1 ANIC); same data as for preceding // Genitalia prep. / HO-258 ♂ / A.Calder 1997 (1 ANIC). Paratypes all with the following label: PARATYPE / *Ovolara* / *lawrencei* / Barr & Shepard [yellow label, printed].

Other material examined (11). Barron Falls / QLD 12.xii.64 / J.G.Brooks (1 ANIC); locality as in preceding / 2.i.1965 / J.G.Brooks // J.G. Brooks / Bequest, 1976 // Genitalia prep. / HO-276 ♀ / A.Calder 1997 (1 ANIC); AUSTRALIA: no. QLD / Clohesy River at Hwy. 1 / 22 rd. km. NE of Mareeba / 11-I-2001, coll. C.B. Barr (1 EMEC); AUSTRALIA: Queensland / 22.2 km NE Mareeba / 11 I 2001 / Clohesy River (WDS-A-1363 on reverse) // William D. / Shepard, leg. (6 EMEC); Upper Daintree R. / Via Daintree, N.Qld. / 27.xii.1964. / G. Monteith // EX UQIC / DONATED / 2011 (1 QM). AUSTRALIA: no. QLD / Fishery Creek at / Hwy. 1, Fishery Falls / 17°11’10”S, 145°53’11”E / 18-I-2001, C. B. Barr (1 EMEC).

Differential diagnosis. *Ovolara lawrencei* (Figs 25, 26) can be distinguished from other species of *Ovolara* (Figs 23, 24, 28–31) by a combination of the following characters: Antennae clavate, elongate; pronotum mostly smooth, unsculptured, except basal margin triangularly protuberant between the prescutellar foveae; pronotal basal sublateral carinae generally shorter than the length of the scutellar shield; elytra without accessory basal striae between striae 1 and 2; and elytral punctures large and deep from base to apex. The aedeagus (Fig. 26) is unique, with the paramere inner margins linear and clasping the apical 1/3 of the tapered, narrow penis.

The other three species of *Ovolara* have elytral accessory striae of varying lengths, sometimes as short as 1–3 punctures. In addition, *Ovolara australis* (Fig. 23) has an antenna with a stout, moderately tight, ovoid club; pronotum sculptured, with a distinct longitudinal sulcus and costa; and an aedeagus (Fig. 24) with the penis abruptly constricted at the apex and the adjacent paramere apices rounded. In *O. leai* (Fig. 28), the pronotal mediobasal margin is less-prominently raised; the pronotal basal sublateral carinae are as long as or longer than the scutellar shield; the apical elytral punctures are smaller and shallower than those more basal; and the aedeagus (Fig. 29) has a penis that is abruptly constricted at the middle and paramere apices that are rounded, each bearing an inner tooth. *Ovolara monteithi* (Fig. 30) has the pronotal base flat; the pronotal basal sublateral carinae as long or longer than the scutellar shield; and the aedeagus (Fig. 31) with the lateral margins of the penis evenly convergent to an acute apex. All species, except for *O. australis*, are quite similar, and most of the above characters are somewhat variable and overlapping. Fortunately the male genitalia (Fig. 26) are distinctive and diagnostic, and are therefore the best, most reliable, identification tool.

Description (n = 89). ***Body:*** Size 2.9–3.3 mm long, 1.3–1.4 mm wide (n = 19). Dorsal color dark brown; head black; first two antennomeres and mouthparts yellow or yellow-brown; trochanters, basal 2/3 of femora, most of abdomen yellow-brown or red-brown; apical antennomeres, coxae, tibiae, tarsi brown. Dorsum covered with short, dense, erect and semi-erect yellow setae, cuticle shiny beneath setae; venter covered with longer, dense, semi-erect and recumbent setae. ***Head:*** Densely punctate, punctures nearly contiguous. Eye weakly protruding, finely faceted, with a dorsal fringe of very long, dark setae curved over eye. Antenna with eleven antennomeres; antennomere 1 longest, arcuate, with long setae near apex; antennomere 2 subspherical, with long setae; antennomere 3 small, narrow, much longer than wide; antennomere 4 smallest; antennomeres 3–11 forming a tight, elongate club; antennomere 11 largest, apex round. Frons smooth, without impressions or carinae; frontoclypeal suture distinct, straight. Clypeus broadly rectangular, 3 × wider than long; anterior margin nearly straight; disc coarsely and densely punctate. Labrum 2 × as wide as long; disc densely punctate; anterior margin with short, dense yellow setae, anterolateral angles with dense brushes of long, yellow, curved setae. Mandible with three apical teeth; prostheca with apical setae; mola with four ridges. Maxillary palpus with four palpomeres, 3 + 4 capitate, all very setose; palpomere 1 short, annular; palpomere 2 subcylindrical, 2 × as long as wide, with tuft of long setae on medial surface; palpomere 3 conical, as long as 2 but wider; palpomere 4 conical, longer and much wider than 2, apex obliquely truncate with an oval, concave, pale yellow sensory area. Labial palpus with three palpomeres; palpomere 1 short, annular; palpomere 2 half as long as 3; palpomere 3 glabrous, rectangular, slightly longer than wide, weakly flattened, apex with oval sensory area. ***Pronotum:*** Shape trapezoidal, slightly wider than long, widest at base; 0.7–0.8 mm long, 0.9–1.1 mm wide; densely punctate, punctures ~ 1 diameter apart. Anterior margin arcuate; lateral margins weakly arcuate to nearly straight, narrowly marginate; posterior margin strongly arcuate laterally, nearly straight anterior to scutellar shield; anterior angles obsolete, posterior angles almost 90°. Disc mostly smooth, slightly flattened anteromedially; two short, basal, sublateral carinae ~ 1/6 pronotal length; two small prescutellar foveae; disc anterolateral to each fovea broadly, shallowly depressed; pronotal base between prescutellar foveae protuberant. ***Scutellar shield:*** Subpentagonal; anterior margin straight, apex rounded; disc flat, finely setose. ***Elytron:*** 2.2–2.5 mm long, 0.7 mm wide. Elytra conjointly almost 2 × as long as wide; nearly parallel-sided from base to middle; lateral margins narrowly marginate. Elytral base usually deeply depressed between humerus and scutellar shield; disc flattened medially at 1/4 length from base; disc with ten striae, without an accessory basal stria between striae 1 and 2; striae 2, 3, 9, and 10 ending before reaching posterior margin; punctures large and deep from base to apex, spaced < 1 diameter apart; diameters smaller in rows closer to suture, becoming larger laterally; intervals slightly raised. ***Metathoracic wings:*** Macropterous. ***Prosternum:*** Extending anteriorly beneath head, as long anterior to procoxae as length of prosternal process; anterior margin narrowly marginate; prosternal process broad, margined, with low median longitudinal carina; process arcuate between procoxae, expanded laterally posterior to coxae, apex broadly triangular. ***Mesoventrite:*** Short, wide; with a deep, broad, V-shaped mesoventral cavity to receive prosternal process; anteromedial margin raised; posterior margin nearly straight. ***Metaventrite:*** Broadly rectangular, anterior margin straight; disc posteromedially depressed, laterally convex; discrimen deeply incised; short, shallow metakatepisternal suture present; disc laterally with numerous, scattered, large punctures, posteromedial depressed area devoid of punctures. ***Legs:*** Setose; relatively short, similar in length, each leg with femur slightly shorter than tibia; tarsus with tarsomere 5 as long as 1–4 combined, protarsomere 5 with a single long, curved seta at dorsal apex; claws simple, slender, acute. Coxae brown, metacoxae deeply sulcate; femora with basal 3/4 yellow-brown or red-brown, apical 1/4 brown; tibiae brown, straight, mesotibiae with posterior surfaces glabrous, shiny; tarsi brown. ***Abdomen:*** Five ventrites; all punctate, punctures spaced one diameter apart; ventrite 1 with equilaterally triangular intercoxal projection; ventrites 2–4 broadly rectangular; ventrites 3 and 4 each with a pair of small lobed processes on posterolateral margins and with posterior margin thickened and slightly raised; ventrite 5 densely setose; broadly triangular, lateral margins weakly arcuate to widely rounded apex. ***Aedeagus:*** Phallobase, parameres and penis equally long (Fig. 26). Phallobase open dorsally, long, tubular, with parameres deeply inserted. Parameres in dorsal view (Fig. 26A) with lateral margins weakly sinuate, straight and parallel-sided in basal 1/2 then slightly converging, parallel-sided in apical 1/4; with inner margins abruptly and widely divergent, forming an enclosed, central opening; apices at apical 1/3 broadly clasping tip of penis, broadly rounded. Penis in dorsal view (Fig. 26A) with lateral margins evenly tapered to near apex, apex narrowly rounded to acute; penis laterally flattened near apex, dorsal surface with two thin, dark carinae; no visible corona; basal apophyses 1/3–1/2 as long as phallobase, straight, very broad, blunt at tips. In lateral view (Fig. 26B), penis and paramere apices broad, curved ventrally, hooked; penis apex slightly wider than paramere apex. Fibula absent. ***Ovipositor:*** Well-sclerotized; elongate; baculum slightly longer than gonocoxites; proximal gonocoxite short, narrowly rectangular, curved; distal gonocoxite long and slender, medial margins nearly straight, lateral margins weakly arcuate; gonocoxites separate at bases and medially, contiguous at apices; stylus short, slender, 3 × longer than wide.

Variation. Very little morphological variation was noted, except for small differences in the length of the pronotal sublateral carinae. Sizes range from 2.9–3.3 mm long and 1.3–1.4 mm wide (n = 19). The females measured are slightly larger than the males, but the female sample size is considerably smaller: females 3.0–3.3 long, 1.3–1.4 mm wide (n = 5); males 2.9–3.1 mm long, 1.3 mm wide (n = 14).

Etymology. The specific epithet *lawrencei*, a noun in the genitive case, is given in honor of John F. Lawrence, arguably the most influential and prolific coleopterist of our time. An excellent review of his life and career was published by Newton et al. (2000), although somewhat prematurely because Lawrence has by no means retired.

Distribution. *Ovolara lawrencei* occurs in north Queensland, Australia (Fig. 4).

Habitat and behavior. *Ovolara lawrencei* was collected by the authors in small to large streams at elevations ranging from 18–654 m. All but one of these were sand-bottomed with logs and debris, some with boulders, and one had a bedrock substrate. Their waters were warm to cool, clear and colorless to brown-stained, with currents varying from sluggish to fast. At Emerald Creek (Fig. 27), the type locality at an elevation of ~ 415 m, the stream was large with a substrate of sand, gravel and boulders. *Ovolara lawrencei* specimens were found in areas of slow current among streamside vegetation, grassy margins, and debris packs, and also in faster current on logs and rocks. The beetles “played dead” in the net, remaining immobile for a period of time, and were difficult to see amongst the netted debris. The easiest method to locate them was to hold the net and debris in the water and wait for them to pop up to the surface. They did not fly readily. Specimens have been taken at light, including those collected by Monteith (G. Monteith, in litt.).

Associated byrrhoid taxa. Elmidae: Larainae: *Ovolara leai* (Carter*), O. monteithi* sp. nov., *Potamophilinus papuanus* Satô, *Stetholus longipennis* sp. nov.; Elminae: *Austrolimnius* spp., *Graphelmis pallidipes* (Carter), *Kingolus* spp., *Notriolus taylori* Carter & Zeck, *Notriolus* spp., *Simsonia* spp. Psephenidae: *Sclerocyphon basicollis* Lea.

Ovolara leai (Carter, 1926)

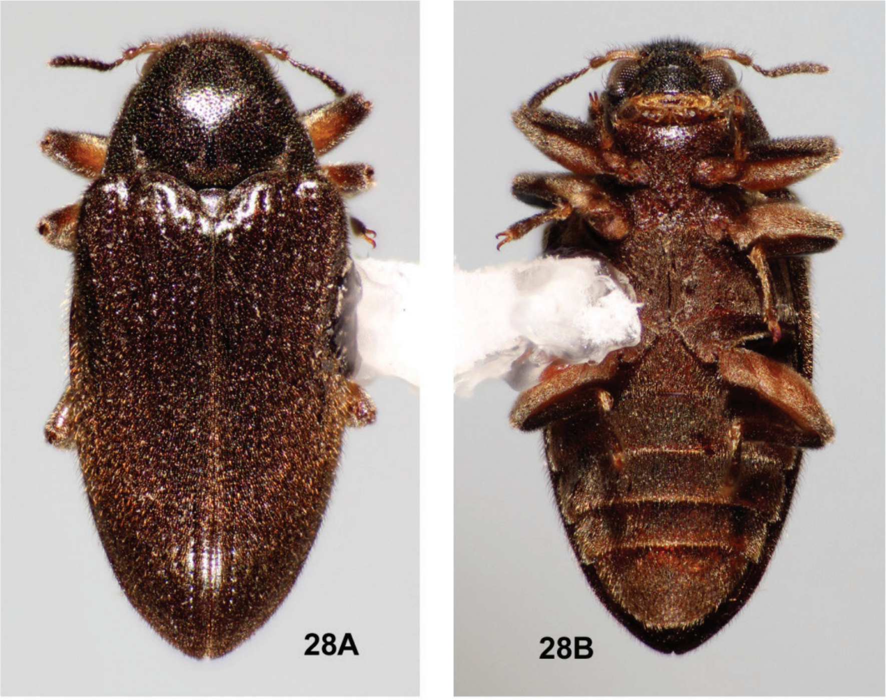
Figs 5, 28, 29

Type locality. Cairns District; 16.9167°S, 145.7500°E; north Queensland, Australia (holotype deposited in the South Australia Museum, Adelaide). Note: The geographic coordinates given in the SAMA database place the type locality, "Cairns District," in the middle of Cairns.

Material examined (78). AUSTRALIA: no. QLD / Freshwater, Freshwater / Cr. at Ryan Weare Park / 16°53'13"S, 145°42'05"E / 18-I-2001, coll. C.B. Barr (3 AM, 21 EMEC); AUSTRALIA: Queensland / Freshwater / 18 I 2001 / Freshwater Creek / S16°53'13" E145°42'05" (WDS-A-1370 on reverse) // William D. / Shepard, leg. (3 EMEC); AUSTRALIA: no. QLD / Mulgrave River at Hwy. 1 / 1 rd. km. S of Gordonvale / 17°06'10"S, 145°47'15"E / 18-I-2001, coll. C. B. Barr (3 AM, 21 EMEC); AUSTRALIA: Queensland / 1 km S Gordonvale, 18 I 2001 94 ft / Mulgrave River / (WDS-A-1371 on reverse) // William D. / Shepard, leg. (4 ANIC, 8 EMEC); QLD. Gordonvale / Apr. 1946 / J.G.Brooks // J. G. Brooks / Bequest, 1976 (1 ANIC); same data as for preceding // Genitalia prep. / HO-277 ♀ / A.Calder 1997 (1 ANIC); Mulgrave River, QLD / at Goldsborough / 2 Jan. 1965 / J.G.Brooks (Q 148) (1 ANIC); Crystal Cascades / Cairns, N.Qld. / 30.xii.1963. / G. Monteith (6 QM); Stewarts Ck. / Daintree N.Q. / 24.9.67. J.G.B. // J. G. Brooks / Bequest, 1976 (1 ANIC); same data as for preceding / 24.ix.67 Q356 / J.G.Brooks. // J. G. Brooks / Bequest, 1976 // Ovolara sp / (needle) / det. A.A.Calder 1997 (1 ANIC); same data as for preceding // Genitalia prep. / HO-311 ♀ / A.Calder 1999 // *Hydrethus* / *australis* / E.B. Britton det. 1972 (1 ANIC; gold coated for SEM); Upper Daintree R. / Via Daintree, N.Qld. / 27.xii.1964. / G. Monteith (5 QM).

Differential diagnosis (n = 78). *Ovolara leai* (Figs 28, 29) can be distinguished from other species of *Ovolara* (Figs 23–26, 30, 31) by a combination of the following characters: Antennae clavate, elongate; pronotum mostly smooth, unsculptured, with base only weakly protuberant between prescutellar foveae, if at all; pronotal basal sublateral carinae as long as or longer than the scutellar shield; elytron each with a very short, accessory basal stria of 1–3 punctures between striae 1 and 2, rarely obscure; apical elytral punctures smaller and shallower than those more basal; and the aedeagus (Fig. 29) with a penis that is abruptly constricted at the middle, and paramere apices that are rounded, each bearing an inner tooth.

Ovolara australis (Fig. 23) has an antenna with a stout, moderately tight, ovoid club; a sculptured pronotum with a distinct longitudinal sulcus and costa; and an aedeagus (Fig. 24) with the penis abruptly constricted at the apex and the adjacent paramere apices rounded. *Ovolara lawrencei* (Fig. 25) has a pronotum with the basal margin triangularly protuberant between the prescutellar foveae; pronotal basal sublateral carinae generally shorter than the length of the scutellar shield; no elytral accessory basal striae; elytral punctures large and deep from base to apex; and unique aedeagus (Fig. 26) with the paramere inner margins linear and clasping the apical 1/3 of the tapered, narrow penis. *Ovolara monteithi* (Fig. 30) has the pronotal base flat; apical



Figures 28, 29. *Ovolara leai*, male **28** habitus, 3.4 mm long **A** dorsal **B** ventral **29** male genitalia **A** dorsal view **B** lateral view **C** ventral view.

elytral punctures large and deep; and the aedeagus (Fig. 31) with the penis lateral margins evenly convergent to an acute apex. All species, except for *O. australis*, are fairly similar externally, and the above characters are somewhat variable and overlapping. Fortunately the male genitalia (Fig. 29) are distinctive and diagnostic.

Variation. Very little morphological variation was noted except for differences in the number punctures in the elytral accessory stria (1–3, rarely obscure), which sometimes varies between elytra on the same individual. Small differences in the length of the pronotal sublateral carinae were also observed. Measured specimens vary in size from 3.1–3.5 mm long and 1.4–1.5 mm wide (n = 18). The females are slightly larger than the males: females 3.3–3.5 mm long, 1.4–1.5 mm wide (n = 7); males 3.1–3.4 mm long, 1.4–1.5 mm wide (n = 11).

Distribution. *Ovolara leai* occurs in north Queensland, Australia (Fig. 5).

Habitat. The authors collected this species from only two localities: Freshwater Creek at Freshwater, a large, sand-bottomed stream at an elevation of 5 m; and the Mulgrave River just south of Gordonvale, a wide, sand-bottomed river at 9 m. In both, the water was warm and clear, and the current swift. In the Mulgrave River, *O. leai* was collected from wood in rapids formed by log jams. Specimens from the QM collected by Monteith were most likely from lights (G. Monteith, in litt.).

Associated byrrhoid taxa. Elmidae: Larainae: *Australara glaisteri* sp. nov., *Ovolara lawrencei* sp. nov., *O. monteithi* sp. nov., *Potamophilinus papuanus*, *Stetholus longipennis* sp. nov.; Elminae: *Austrolimnius* spp., *Graphelmis pallidipes*, *Kingolus* spp., *Notriolus* spp., *Simsonia* spp. Psephenidae: *Sclerocyphon basicollis, S. minimus* Davis.

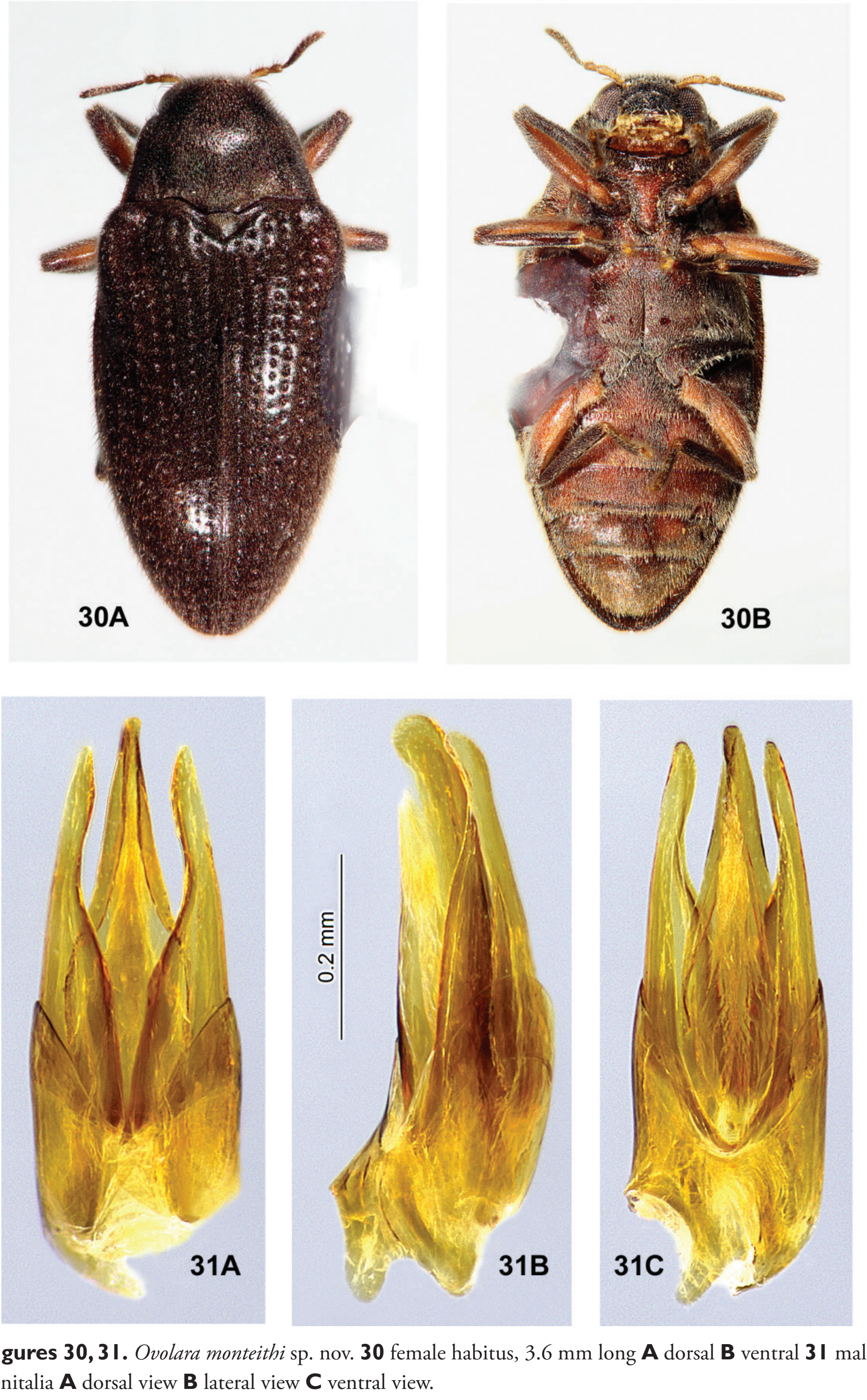
Comments. Carter (1926) described *O. leai* in *Hydrethus* Fairmaire, 1889; it was moved to *Ovolara* by Brown (1981). The geographic coordinates for the type locality, "Cairns District," listed in the SAMA database, place it in the middle of Cairns. The authors collected *O. leai* from Freshwater Creek only ~ 6 km northwest of Cairns.

***Ovolara monteithi* sp. nov.**

http://zoobank.org/27D3BBAB-05F6-4E22-8480-C7E0F25A99E7
Figs 6, 30, 31

Type locality. Millaa Millaa Falls Park; 17.495°S, 145.611°E; Millaa Millaa, north Queensland, Australia.

Type material. ***Holotype* male**. "Millaa Millaa, / 9.i.1964, N.Qld. / G. Monteith // EX UQIC / DONATED / 2011 // HOLOTYPE / Ovolara / monteithi / Barr & Shepard" [red label, handwritten]. Dry pinned. Deposited in the Queensland Museum, South Brisbane; Registration Number QM T250614. ***Paratypes* (33).** Same data as for holotype (2 EMEC, 4 QM); QLD. Gordonvale / Apr. 1946 / J.G.Brooks // J. G. Brooks / Bequest, 1976 // Genitalia prep. / HO-259 ♂ / A.Calder 1997 (1 ANIC); Henrietta Ck., / Palmerston Nat. / Pk., N.Qld. / 29.xii.1964. / G. Monteith // EX UQIC / DONATED / 2011 (2 EMEC, 6 QM); same data as for preceding; 5.xii.1965 (2 QM); same locality; Henrietta Ck., / Palmerston Nat. Pk. / 29.xii.1964. N.Qld. /



Figures 30, 31. *Ovolara monteithi* sp. nov. **30** female habitus, 3.6 mm long **A** dorsal **B** ventral **31** male genitalia **A** dorsal view **B** lateral view **C** ventral view.

H.A.Rose. / UQIC / SPECIMEN (2 QM); Stewarts Ck. / Daintree N.Q. / 24.ix.67 Q356 / J.G.Brooks. // J. G. Brooks / Bequest, 1976 // Genitalia prep. / HO-262 ♂ / A.Calder 1997 (1 ANIC); "The Boulders" Via / Babinda, N.Qld. / 15.xii.1966. / B. Cantrell // EX UQIC / DONATED / 2011 (4 QM); Upper Mulgrave / River, N.Qld. / 1-3.xii.1965. / G. Monteith // EX UQIC / DONATED / 2011 (1 QM); Upper Mulgrave River, / 30.iv.1970, N.Qld, / G. B. Monteith // EX UQIC / DONATED / 2011 (2 EMEC, 6 QM). Paratypes all with the following label: PARATYPE / *Ovolara / monteithi* / Barr & Shepard [yellow label, printed].

Differential diagnosis. *Ovolara monteithi* (Figs 30, 31) can be distinguished from other species of *Ovolara* (Figs 23–26, 28, 29) by a combination of the following characters: Antennae clavate, elongate; pronotum smooth, unsculptured, pronotal base flat; pronotal basal sublateral carinae as long or longer than the scutellar shield; each elytron with a short accessory basal stria of 1–3 punctures between striae 1 and 2; apical elytral punctures large and deep; and aedeagus (Fig. 31) with the penis lateral margins evenly convergent to an acute apex.

Ovolara australis (Fig. 23) has an antenna with a stout, moderately tight, ovoid club and a sculptured pronotum with a distinct longitudinal sulcus and costa; and an aedeagus (Fig. 24) with the penis abruptly constricted at the apex and the adjacent paramere apices rounded. *Ovolara lawrencei* (Fig. 25) has the pronotal basal margin protuberant between the prescutellar fovea; the pronotal basal sublateral carinae generally shorter than the length of the scutellar shield; no elytral accessory striae; and a unique aedeagus (Fig. 26) with the paramere inner margins linear and clasping the apical 1/3 of the tapered, narrow penis. In *O. leai* (Fig. 28), the apical elytral punctures are smaller and shallower than those more basal; and the aedeagus (Fig. 29) has a penis that is abruptly constricted at the middle, and paramere apices that are rounded, each bearing an inner tooth. All species, except for *O. australis*, are fairly similar externally, and the above characters are somewhat variable and overlapping. Fortunately the male genitalia (Fig. 31) are distinctive and diagnostic.

Description (n = 34). ***Body:*** Size 2.9–3.6 mm long, 1.2–1.5 mm wide (n = 11). Dorsal color medium to dark brown; head black; first two antennomeres, trochanters, basal 3/4 of femora yellow or yellow-brown; tibiae brown or black; apical antennomeres, tarsi brown; venter including coxae yellow-brown or red-brown. Dorsum covered with short, dense, erect and semi-erect, pale yellow setae, cuticle shiny beneath setae; venter covered with longer, dense, semi-erect and recumbent setae. ***Head:*** Densely punctate, punctures < 1 diameter apart, sometimes nearly contiguous. Eye weakly protruding, finely faceted, with a dorsal fringe of long setae curved over eye. Antenna with eleven antennomeres; antennomere 1 elongate, nearly cylindrical, arcuate, with long setae near apex; antennomere 2 subspherical with long, curved setae; antennomere 3 elongate, narrow; antennomere 4 smallest; antennomeres 3–11 forming a tight, elongate club; antennomere 11 largest, apex round. Frons smooth, without impressions or carinae; frontoclypeal suture distinct, weakly arcuate. Clypeus broadly rectangular, 3 × wider than long, anterior margin arcuate; disc coarsely punctate. Labrum 2 × wider than long; disc punctate; anterior margin with short, dense, pale yellow setae, anterolateral angles with dense brushes of long, yellow, curved setae. Maxillary palpus with four palpomeres, 3 + 4 capitate, all very setose; palpomere 1 annular, short; palpomere 2 fusiform, 2 × as long as wide, with tuft of long setae on medial surface; palpomere 3 asymmetrical, wider than long; palpomere 4 subovoid, longer and wider than 2, apex obliquely truncate with an oval, pale yellow sensory area. Labial palpus with three palpomeres; palpomere 1 short, annular; palpomere 2 elongate, narrow; palpomere 3 glabrous, rectangular, flattened, much wider than palpomere 2, apex truncate with oval sensory area. ***Pronotum:*** Shape trapezoidal, wider than long, widest at base; 0.7–0.9 mm long, 0.9–1.2 mm wide; densely, finely punctate, punctures 1.0–1.5 diameters apart. Anterior margin arcuate; lateral margins nearly straight, narrowly marginate; posterior margin strongly arcuate laterally, straight anterior to scutellar shield; anterior angles obsolete, posterior angles almost 90°. Disc mostly smooth, slightly flattened; two basal, sublateral carinae as long as 1/4 pronotal length or shorter; disc shallowly depressed around bases of carinae; two small prescutellar foveae, anterolateral disc slightly depressed or not. ***Scutellar shield:*** Subtriangular; disc weakly convex, finely setose. ***Elytron:*** 2.2–2.7 mm long, 0.6–0.8 mm wide. Elytra conjointly almost 2 × as long as wide, widest at 1/2 distance from base; lateral margins narrowly marginate. Humerus inflated, moderately prominent; elytral base depressed between humerus and scutellar shield; disc evenly convex, with ten striae and a very short, accessory, basal stria of 1–3 punctures between striae 1 and 2; striae 2, 3, 9, and 10 ending before reaching posterior margin; punctures deep and moderately large from base to apex, diameters smaller in rows closer to suture, becoming larger laterally; intervals mostly flat. ***Metathoracic wings:*** Macropterous. ***Prosternum:*** Extending anteriorly beneath head, shorter anterior to procoxae than length of prosternal process; anterior margin narrowly marginate; prosternal process broad, widely margined, with a low, rounded, median longitudinal carina; process arrowhead-shaped, narrowed and arcuate between procoxae, expanded laterally posterior to coxae, broadly triangular at apex, tip rounded. ***Mesoventrite:*** Short, wide; with a deep, broad, U-shaped mesoventral cavity to receive prosternal process; anteromedial margin raised; posterior margin nearly straight. ***Metaventrite:*** Broadly rectangular, anterior margin straight; disc posteromedially depressed, laterally convex; discrimen more deeply incised posteriorly than anteriorly; metakatepisternal suture shallow; disc laterally with irregularly spaced, large punctures, medially devoid of punctures. ***Legs:*** Setose; relatively short, similar in length, each leg with femur slightly shorter than tibia; tarsus with tarsomere 5 as long as 1–4 combined, protarsomere 5 with a single long, curved seta at dorsal apex; claws simple, short, slender, acute. Coxae yellow-brown or red-brown, metacoxae deeply sulcate; femora with basal 3/4 yellow or yellow-brown, apical 1/4 brown; tibiae brown or black, straight; mesotibiae with posterior surfaces flat, glabrous, shiny; tarsi brown. ***Abdomen:*** Five ventrites; all punctate, punctures spaced one diameter apart; ventrite 1 with equilaterally triangular intercoxal projection; ventrites 2–4 broadly rectangular, each with a pair of small lobed processes on posterolateral margins; ventrites 3 and 4 with posterior margin thickened and slightly raised; ventrite 5 densely setose, slightly flattened, broadly triangular, lateral margins weakly curved to widely rounded apex.

Aedeagus: Phallobase short, shorter than parameres and penis; penis slightly longer than parameres (Fig. 31). Phallobase open dorsally with parameres deeply inserted. Parameres in dorsal view (Fig. 31A) widest basally, narrowest at apical 1/3; lateral margins gradually convergent; medial margins gradually divergent in basal 2/3, moderately arcuate in apical 1/3, apices narrowly rounded. Penis in dorsal view (Fig. 31A) with lateral margins evenly convergent to acute apex; penis laterally flattened near apex, dorsolateral margins with two thin, dark carinae; no visible corona; basal apophyses long, 2/3–3/4 as long as phallobase, straight, broad, blunt at tips. Paramere in lateral view (Fig. 31B) subtriangular at basal 2/3, dorsal margin weakly arcuate, ventral margin nearly straight; narrowed abruptly at apical 1/3, apex curved ventrally, rounded at tip. Penis in lateral view (Fig. 31B) with apex curved ventrally, tip broadly rounded, wider than paramere tip. Fibula absent.

Variation. Very little morphological variation was noted except for differences in the number of punctures (1–3) in the elytral accessory striae, which is sometimes variable between elytra on the same individual. Differences were also observed in the length of the pronotal sublateral carinae which can be up to 1/4 the length of the pronotum or shorter. Measured specimens vary in size from 2.9–3.6 mm long and 1.2–1.5 mm wide (n = 11). The sizes of the males and females overlap, but the females are generally larger than the males: females 3.2–3.6 long, 1.3–1.5 mm wide (n = 6); males 2.9–3.4 mm long, 1.2–1.4 mm wide (n = 5).

Etymology. The specific epithet *monteithi*, a noun in the genitive case, is given in honor of Geoffrey Monteith of the Queensland Museum who has collected > 200,000 insects, including nearly all of the specimens of Elmidae housed there.

Distribution. *Ovolara monteithi* occurs in north Queensland, Australia (Fig. 6).

Habitat. The specimens collected at the type locality, Millaa Millaa Falls Park on the Atherton Tableland, were taken at mercury vapor light near a large waterfall at 780 m elevation (G. Monteith, in litt*.).* The other six collection localities included streams and small rivers in rainforest, remnant rainforest, and farmland habitats at elevations from 20–850 m. Most of the QM specimens were collected at mercury vapor lights near streams and rivers (G. Monteith, in litt.).

Associated byrrhoid taxa. Elmidae: Larainae: *Australara glaisteri* sp. nov., *Ovolara lawrencei* sp. nov.*, O. leai*, *Potamophilinus papuanus*, *Stetholus longipennis* sp. nov.

Genus *Potamophilinus* Grouvelle, 1896

Type species. *Potamophilus longipes* Grouvelle, 1892.

Differential diagnosis. Pronotum with a wide, U-shaped, transverse impression at the anterior third, without basal sublateral carinae; pronotal posterior angles blunt, not distinctly bidentate; elytral apices angulate; prosternal process carinate, broad between procoxae, abruptly narrowed and spinose between mesocoxae, acuminate apically; apices of metatibiae exceeding apices of elytra; abdominal ventrites 1+2 longer than 3+4+5, ventrite 1 very long, ventrite 2 long, ventrites 3–5 each very short, loosely fitted to epipleura. *Potamophilinus* is easily differentiated from all other Australian laraine genera by the above characteristics of the pronotum, elytral apices and prosternal process. Although *Potamophilus* Germar and *Parapotamophilus* Brown have not been reported from Australia, like *Potamophilinus* they occur in Papua New Guinea and therefore are being included here in the generic diagnosis. *Potamophilus* differs by having the pronotal posterior angles acute, distinctly bidentate; elytral apices acute, divergent; apices of metatibiae just reaching apices of elytra; abdominal ventrites 1+2 shorter than ventrites 3+4+5. *Parapotamophilus* has the pronotum without a transverse impression; elytral apices rounded; prosternal process broad, not spinose; abdominal ventrites 1+2 shorter than ventrites 3+4+5.

Distribution. Thirteen species of *Potamophilinus* occur from eastern Asia to Australia.

Comments. Grouvelle (1896) erected *Potamophilinus* and designated *Potamophilus longipes* Grouvelle, 1892, as the type species.

In his unpublished checklist of elmid species, Calder (1992) listed an undescribed species of *Potamophilinus* from north Queensland based on three specimens in ANIC labeled "W. Claudie River / Iron Range, NQ / 13 May 1971 / J.G.Brooks". We examined the specimens and concluded that they are *P. papuanus* Satô, described from New Guinea, by comparison with paratypes of that species, the original description, and the male genitalia. Lawrence and Britton (1994) first reported the genus from Australia, probably from Calder's determination. As mentioned in the differential diagnosis, two other genera of Larainae besides *Potamophilinus* occur in nearby Papua New Guinea, *Potamophilus* and *Parapotamophilus.* Possibly they too will be found in Australia in the future. Glaister (1999) keyed and illustrated larvae from the Northern Territory which she assumed to be *Potamophilinus*, but this was not verified by rearing to adult.

Potamophilinus papuanus **Satô, 1973**

Figs 7, 32, 33

Type locality. Wum, Upper Jimi Valley, NE New Guinea (Papua New Guinea) (holotype deposited in the Bishop Museum, Honolulu, Hawaii). Geographic coordinates unavailable.

Paratypes examined (2). NEW GUINEA (NE) / Wum, Upper Jimmi [Jimi] V. / 840 m. VII-17-'55 // J.L. Gressitt / Collector // Paratype / Potamophilinus / papuanus M. Sato / DET. M. SATO 1972 (1 EMEC); NEW GUINEA (NE) / Wau, Morobe Distr. / 1200 m, 25-30.IV.62 // Light Trap / J. Sedlacek / BISHOP // Paratype / Potamophilinus / papuanus M. Sato / DET. M. SATO 1972 (1 EMEC).

Other material examined (13). AUSTRALIA: no. QLD / Freshwater, Freshwater / Cr. at Ryan Weare Park / 16°53'13"S, 145°42'05"E / 18-I-2001, coll. C.B. Barr (2 EMEC); AUSTRALIA: Queensland / Freshwater / 18 I 2001 / Freshwater Creek / S16°53'13" E145°42'05" (WDS-A-1370 on reverse) // William D. / Shepard, leg. // Potamophilinus / papuanus / W. D. Shepard (1 ANIC, 4 EMEC); AUSTRAL-

IA: Queensland / Emerald Creek Store / 17 I 2001 / Emerald Creek / S16°59'12" E145°28'21" (WDS-A-1369 on reverse) // William D. / Shepard, leg // Potamophilinus / papuanus / W. D. Shepard (2 EMEC); Upper Daintree R. / Via Daintree, / 27.xii.1964. N.Qld. / G. Monteith // EX UQIC / DONATED / 2011 (1 QM); W. Claudie River / Iron Range, NQ / 13 May 1971 / J.G.Brooks (3 ANIC).

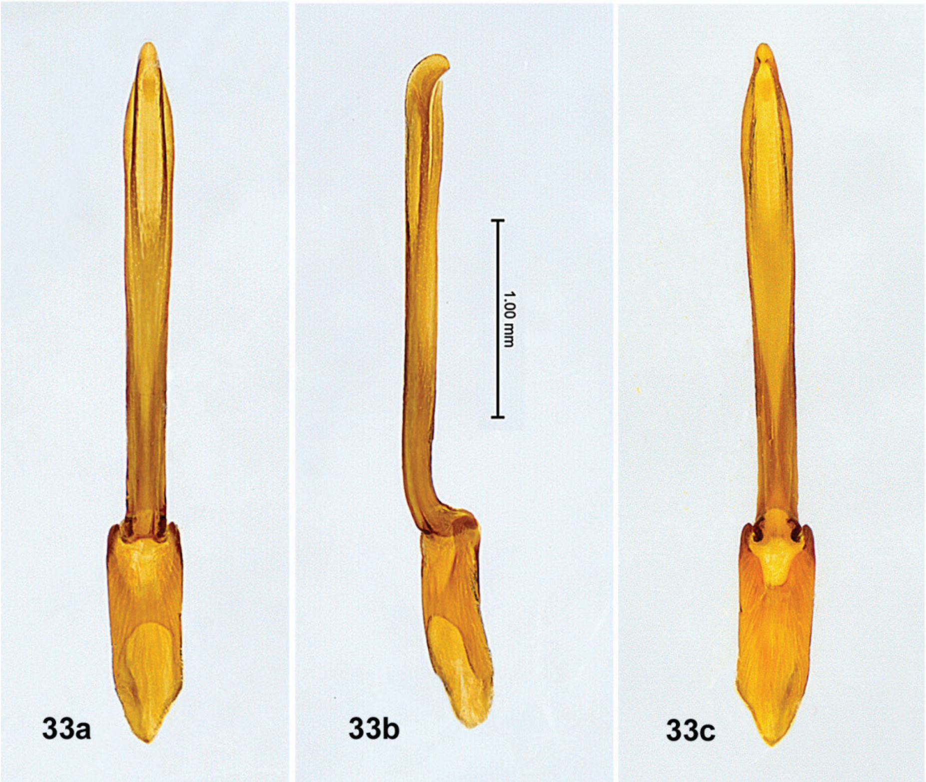
Differential diagnosis (n = 15). Body (Fig. 32) elongate, sides subparallel; antennae loosely clavate, not reaching to middle of pronotum; maxillary palpi each with tip of palpomere 4 obliquely truncate, elliptical; labial palpi with tip of palpomere 3 truncate, oval; pronotum flat, with a wide, U-shaped, transverse impression at anterior 1/3, without basal sublateral carinae; pronotal anterior angles depressed, posterior angles blunt, each with a large, adjacent oval depression; elytra striate-punctate, apices angulate; pro- and mesofemora broad and anteriorly flattened to slightly concave; prosternal process very long, carinate, broad between procoxae, abruptly narrowed and spinose between mesocoxae, apex acuminate; apices of metatibiae exceeding apices of elytra; abdomen with six visible ventrites, loosely fitted to epipleura; aedeagus (Fig. 33) very long and slender; penis and parameres abruptly angled at base; parameres fused with penis basally and appressed apically. *Potamophilinus papuanus* (Fig. 32) is easily differentiated from all other Australian laraines by characteristics of the pronotum, elytral apices, prosternal process, and unusual male genitalia (Fig. 33).

Variation. Measured specimens from Australia vary in size from 4.4–4.9 mm long and 1.7–2.1 mm wide (n = 11). The females are larger than the males, but the sample size is small: females 4.6–4.9 mm long, 1.8–2.1 mm wide (n = 6); males 4.4–4.7 mm long, 1.7–1.9 mm wide (n = 5). In the species description, Satô (1973) reported a much wider size range in Papua New Guinea specimens: 4.2–5.6 mm long, 1.6–2.1 mm wide. In measurements of two specimens from the type series, the male is a full millimeter shorter than the female. The species is sexually dimorphic with males having the elytral apices truncate and angulate, and females having the elytral apices broadly rounded except for each with a deflexed, triangular tooth near the inner margin (visible in posterior view).

Distribution. *Potamophilinus papuanus* occurs in Papua New Guinea, north Queensland (Fig. 7) and possibly the Northern Territory (Glaister 1992, 1999), Australia.

Habitat and life history. Our few records of *P. papuanus* are from large, sand-bottomed creeks with warm, clear water where specimens were collected from logs and branches in fast current. In the NT, *Potamophilinus* larvae occur among matted roots at margins of sandy streams (A. Glaister, in litt.). Three adult females, all collected in January, were dissected in the lab and had eggs in their abdomens: two had four eggs each and one had > 20 eggs. Therefore, January is within the reproductive period of the species. One of the specimens examined from New Guinea was collected in a light trap, as was the QM specimen although not labeled as such (G. Monteith, in litt.*).*

Associated byrrhoid taxa. Elmidae: Larainae: *Ovolara lawrencei* sp. nov., *O. leai*, *O. monteithi* sp. nov., *Stetholus longipennis* sp. nov.; Elminae: *Austrolimnius* spp., *Graphelmis pallidipes*, *Notriolus taylori*, *Notriolus* spp., *Simsonia* spp.



Figures 32, 33. *Potamophilinus papuanus*, male **32** habitus, 4.6 mm long **A** dorsal **B** ventral **33** male genitalia **A** dorsal view **B** lateral view **C** ventral view.

Comments. *Potamophilinus papuanus* was described from Papua New Guinea, and its occurrence in Australia is not listed in the world elmid catalog by Jäch et al. (2016). In order to confirm the species identification we examined two paratypes of *P. papuanus* from New Guinea and compared Satô's illustration of the male genitalia (Satô 1973) with the genitalia of four Australian specimens from north Queensland.

Genus *Stetholus* Carter & Zeck, 1929

Type species. *Stetholus elongatus* Carter & Zeck, 1929.

Diagnosis. Body elongate, sides subparallel; antennae clavate, either compact or elongate, reaching at least to middle of pronotum; labrum with lateral brushes of long, curved setae; maxillary palpi long, prominent, enlarged apically, each with nearly half of palpomere 4 composed of a ventral, widely open, white sensory area obliquely angled from the apex to the base; pronotum with or without basal sublateral carinae; pronotal disc with a shallow to moderately deep, transverse, broadly V-shaped impression generally at anterior 1/3–1/2; elytra striate-punctate, laterally compressed at basal 1/2, apices rounded; prosternum very short anterior to procoxae; prosternal process moderately narrow, with a median longitudinal carina; apices of hind tibiae not exceeding apices of elytra; abdominal ventrites 1–2 combined shorter than 3–5 combined (Figs 34–42).

Distribution. *Stetholus* is endemic to Australia, with species occurring in Queensland, the Australian Capital Territory, New South Wales and Victoria (Figs 8–12). There was a record in the Atlas of Living Australia (ALA) https://www.ala.org.au/ database of a specimen from Tasmania, but the specimen was misidentified therefore the record was erroneous (S. Grove, in litt.). It has since been deleted.

Habitat and behavior. Adults are usually found in fast or turbulent water in rocky chutes, below waterfalls and spillways, on log jams and boulders in rapids, and among root masses in the current, often in large aggregations. They fly readily when disturbed. Specimens also have been collected with light traps and flight intercept traps (A. Glaister, in litt.; G. Monteith, in litt.).

Comments. Three of the five known species exhibit secondary sexual dimorphism with the females having the posterior 1/4 of the elytron slightly explanate lateral to stria 11. This is most pronounced in *S. longipennis* sp. nov., but is less so and somewhat variable in *S. elongatus* and *S. woronora* sp. nov. The larva of *Stetholus* was keyed and illustrated by Glaister (1999).

Stetholus carinatus sp. nov.

http://zoobank.org/602C85EB-0E6E-4893-9087-F2F1F0ACB765
Figs 8, 34, 35

Type locality. Upper North Creek, Mt. Elliot, Bowling Green Bay National Park southeast of Townsville; 19.490° S, 146.974° E; north Queensland, Australia.

Type material. *Holotype* male. "Mt Elliot NP, N.E.QLD / (Upper North Ck, 1000m) / 3-5 Dec 1986 / Monteith, Thompson&Hamlet / Flight intercept trap // HOLOTYPE / Stetholus / carinatus / Barr & Shepard" [red label, handwritten]. Dry pinned. Deposited in the Queensland Museum, South Brisbane; Registration Number QM T250616.

Differential diagnosis. The single male specimen of *S. carinatus* (Figs 34, 35) is characterized by the following: shorter (3.7 mm) than other *Stetholus* species (3.9 mm or longer) (Figs 36–42); pronotum with a pair of distinct, long, basal sublateral carinae; elytron with a short, faint, accessory basal stria with a few punctures between striae 1 and 2; mesotibiae with posterior surfaces glabrous and shiny, metatibiae entirely setose; male genitalia unique (Fig. 35) (those of *S. metatibialis* are unknown). The species is separated from all other *Stetholus* except *S. metatibialis* (Fig. 40), which it most closely resembles, by the long, basal sublateral pronotal carinae. *Stetholus carinatus* differs from *S. metatibialis* as follows: length shorter (3.7 mm vs. 3.9 mm); metatibiae entirely setose; elytron with accessory stria obscure.

Description (n = 1). Holotype male. *Body:* Size 3.7 mm long, 1.4 mm wide; elongate, ~ 2 × longer than wide. Dorsal color dark brown; head black; first two antennomeres, palpi, venter, coxae, trochanters, femora yellow or yellow-brown. Short yellow setae on all surfaces. ***Head:*** Densely and finely punctate, punctures < 1 diameter apart or nearly contiguous; densely setose. Vertex with a faint V-shaped impression, open anteriorly, extending from antennal bases towards occiput; frontoclypeal suture arcuate. Antenna with eleven antennomeres; antennomeres 1 and 2 yellow-brown with long, coarse, dark setae; antennomere 1 longest, ~ 3 × longer than wide, curved; antennomere 2 spherical; antennomeres 3–11 brown with dense yellow setae, subserrate, together forming an elongate club; antennomeres 7–11 of equal width, antennomere 11 short with bluntly rounded apex. Eye finely faceted, suboval at base, not protuberant; fringe of long, curved, black setae at dorsal margin. Clypeus convex, broadly rectangular, weakly emarginate; disc densely setose, anterior and lateral margins with long setal fringe. Labrum rectangular, longer and slightly narrower than clypeus; setose; anterior margin emarginate with a band of short, yellow setae; lateral margins with dense fringes of long, yellow setae, each margin with a discrete tuft of longer, darker, curved setae (setal origin unclear, possibly mandibular). Maxillary palpus yellow, with four setose, palpomeres; palpomere 1 short, annular; palpomere 2 twice as long as wide; palpomere 3 nearly as long as 2, wider apically; palpomere 4 wide, ovoid, ventral surface with a broadly oval, slightly concave, white sensory area angled obliquely from the apex to the base. Labial palpus yellow, glabrous, with three palpomeres; palpomeres 1 and 2 short, annular; palpomere 3 broadest, apex truncate with a narrowly oval, flat, white sensory area. ***Pronotum:*** Shape generally trapezoidal, wider than long, widest at base; 0.9 mm long, 1.1 mm wide; disc densely punctate, punctures spaced < 1 diameter apart. Anterior margin arcuate; anterior angles obsolete; lateral margins weakly sinuate, moderately explanate at basal 2/3; posterior angles 90°, sharp, widely excavated; posterior margin weakly trisinuate. Disc weakly convex with a shallow, transverse V-shaped impression at apical 1/3; two basal, sublateral carinae 1/3–1/2 as long as pronotum, bordered by impressions, medial

Figures 34, 35. *Stetholus carinatus* sp. nov., holotype male **34** habitus, 3.7 mm long **A** dorsal **B** ventral **35** male genitalia **A** dorsal view **B** lateral view **C** ventral view.

impressions shallow, elongate; two small, shallow prescutellar foveae. ***Scutellar shield:*** Longer than wide, apex rounded; flat; densely setose. ***Elytron:*** 2.8 mm long, 0.7 mm wide. Elytra conjointly 2 × as long as wide; anterior 2/3 parallel-sided; posterior 1/3 widest; lateral margins narrowly marginate. Humerus inflated, elytral base depressed medially; disc weakly convex at anterior 1/4 then flattened. Disc with ten punctate, weakly impressed striae, intervals flat; accessory basal stria between striae 1 and 2 short, faint, with few punctures; punctures of striae 2 and 3 very small and obscure near base; striae 3 and 4 join near apex; disc punctures mostly separated by one diameter, smaller apically. ***Metathoracic wings:*** Macropterous. ***Prosternum:*** Very short anterior to procoxae. Prosternal process very narrow, long, 4 × longer than wide; parallel-sided posterior to coxae; apex narrowly rounded; surface tomentose. ***Mesoventrite:*** Short, very setose, with a deep mesoventral cavity to receive prosternal process. ***Metaventrite:*** Broadly rectangular; very setose; posterior 1/2–2/3 with a moderately wide, shallow, median depression, laterally convex; discrimen extending almost from anterior to posterior margin, narrowly incised at posterior 1/2; metakatepisternal suture distinct; disc laterally with shallow, closely spaced punctures; medially punctures mostly obscured by a broad, triangular patch of long, dense, recumbent, yellow setae. ***Legs:*** Of similar lengths; each leg with femur and tibia subequal in length; tarsus with tarsomere 5 longer than tarsomeres 1–4 combined; claws simple, long, sharply acute. Coxae yellow, metacoxae deeply sulcate; femora yellow, dorsal surfaces of each with a narrow brown stripe, apices brown; tibiae brown, each with a pair of spines at ventral apex, mesotibiae with posterior surfaces flat, yellow-brown, glabrous, shiny; tarsi yellow-brown. ***Abdomen:*** Five ventrites; ventrite 1 longest, ventrite 4 shortest, ventrites 2, 3, and 5 subequal in length; ventrites 1–3 weakly flattened at midline, ventrites 4 and 5 convex; ventrite 1 with a margined, triangular, intercoxal projection; ventrites 2–4 with lateral margins each produced to form a small, rounded lobe which clasps the epipleuron; ventrites 4 and 5 with moderately deep impressions at anterolateral margins; ventrite 5 apex broadly rounded. Ventrites covered with shallow, closely spaced punctures; ventrite 1 with punctures more widely spaced, ventrites 2–5 with punctures more closely spaced; medial punctures mostly obscured by dense covering of yellow setae, longest at median 1/5 of ventrites 3–5. ***Aedeagus:*** Phallobase much shorter than parameres, penis slightly longer than parameres (Fig. 35). Parameres, in dorsal view (Fig. 35A), widest basally; lateral margins weakly arcuate at basal 2/3, then parallel at apical 1/3; median margins straight and moderately divergent at basal 1/2, then arcuate to abruptly narrowed, strongly produced tips at apical 1/3; apices narrow, acute. Penis evenly convergent at basal 3/4, then abruptly narrowed at apical 1/4, apex very narrowly rounded; no visible corona; basal apophyses moderately long, 1/2 as long as phallobase, straight, very broad, blunt at tips. In lateral view (Fig. 35B), penis bent and abruptly angled above parameres near midpoint. Fibula absent.

Etymology. The specific epithet *carinatus*, an adjective in the nominative singular derived from the Latin meaning keeled, refers to the presence of a pair of basal, sublateral carinae on the pronotum.

Distribution. North Queensland, Australia. Known only from the type locality on the north slope of Mt. Elliot (Fig. 8).

Habitat. Geoff Monteith, one of the collectors, described the area thus: "Mt. Elliot is a high, isolated, rainforest-capped mountain with a strikingly unique and endemic fauna" (G. Monteith, in litt.). The specimen was collected using a flight intercept trap at 1000 m elevation.

Stetholus elongatus Carter & Zeck, 1929

Figs 9, 36, 37

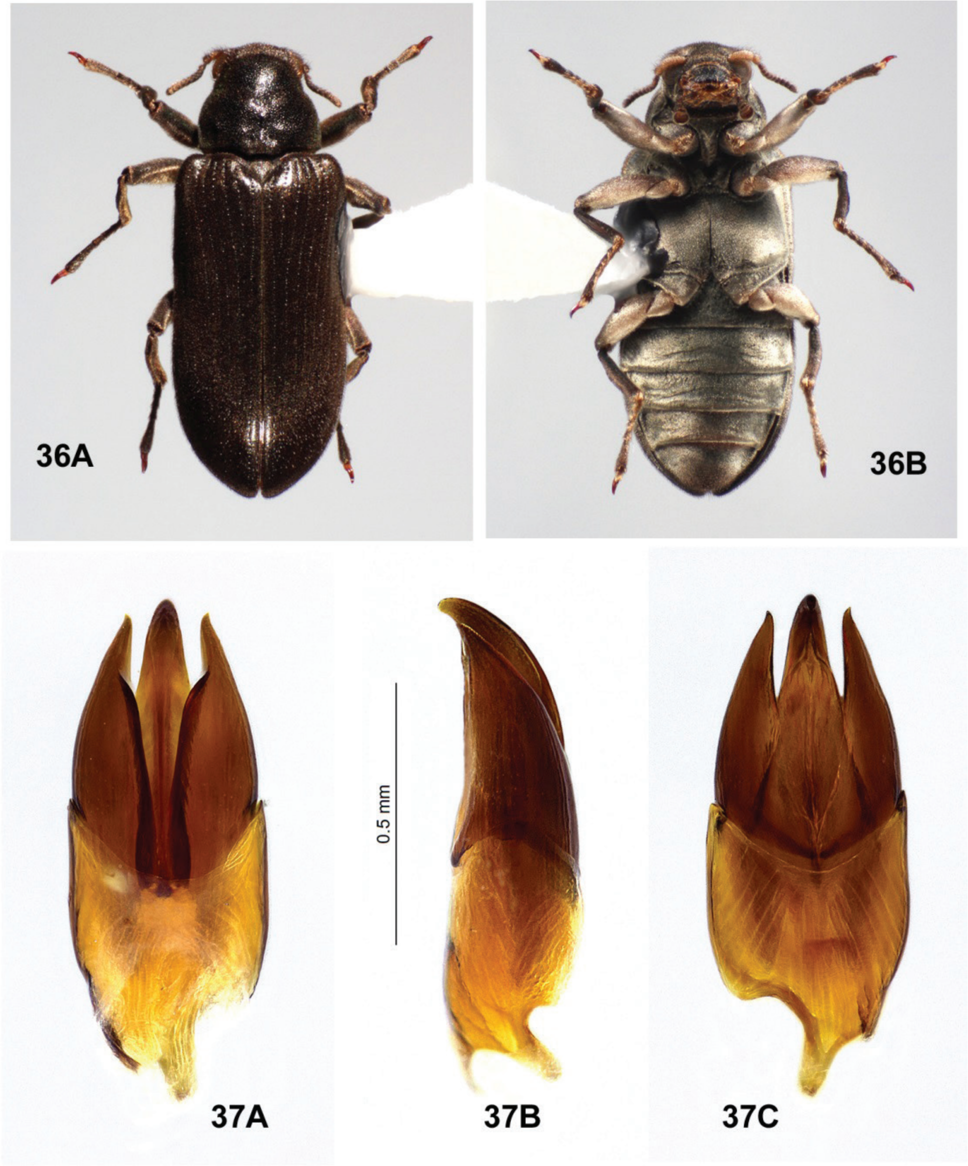
Type locality. Allyn River at Gresford; 32.350°S, 151.750°E; New South Wales, Australia (holotype deposited in the Australian Museum, Sydney).

Paratypes examined (5). Gresford / Allyn R., N.S.W. / Oct. 1926 / H. J. Carter // PARATYPE [blue label] (4 ANIC, 1 SAMA).

Other material examined (56). Australian Capital Territory. Kambah Pool / Murrumbidgee / River ACT / 1.i.1978 / J.F.Lawrence (3 ANIC); AUSTRALIA: ACT / Murrumbidgee River / Point Hut Xing S Canberra / 35°33'55"S,149°03'56"E / 1-I-2001, coll. C. B. Barr (9 EMEC, 3 QM); AUSTRALIA: ACT / Murrumbidgee River at / Casuarina, E Cotter Dam / 35°19'41"S,148°57'01"E / 2-I-2001, coll. C. B. Barr (4 ANIC, 9 EMEC, 3 QM); AUSTRALIA: ACT / Gigerbine [Gigerline] NR, Angle / Crossing 31 XII 2000 / Murrumbidgee River (WDS-A-1337 on reverse)// William D. / Shepard, leg. (3 EMEC). **New South Wales.** AUSTRALIA: NSW / Deua NP, Deua River at / Deua River Campground / 35°45'00"S, 149°54'53"E / 4-I-2001, coll. C. B. Barr (8 EMEC); AUSTRALIA: NSW / Deua NP, Deua R / Cmpgd. 4 I 2001 / Deua River (WDS-A-1348 on reverse) // William D. / Shepard, leg. (3 EMEC); Tallong / N.S.W. / FHTaylor (2 ANIC, 4 SAMA); same locality // On submerged / sticks in the / Shoalhaven R. (2 ANIC); AUSTRALIA: NSW / NW of Braidwood / 3 I 2001 / Shoalhaven River (WDS-A-1344 on reverse) // William D. / Shepard, leg. (2 EMEC); Pierce's Pass, / Blue Mtns., N.S.W. / 5.xii.1971 / G.B.Monteith (1 QM).

Differential diagnosis (n = 61). *Stetholus elongatus* (Figs 36, 37) can be distinguished from other species of *Stetholus* (Figs 34–35, 38–42) by a combination of the following characters: Antennae distinctly clavate; pronotum moderately sculptured, lacking basal sublateral carinae; metatibia usually with a narrow, elongate bare area of variable length at the posterobasal 1/3; male genitalia (Fig. 37) stout and heavily sclerotized. *Stetholus woronora* (Fig. 41) most closely resembles S. *elongatus* but has short, basal sublateral pronotal carinae. Although the male genitalia of the two species are similarly stout and heavily sclerotized, the penis of *S. elongatus* (Fig. 37) is narrow and tapered at the apex, while that of *S. woronora* (Fig. 42) is wide and bulbous near the apex. *Stetholus longipennis* (Figs 38) is usually shorter than *S. elongatus* (Fig. 36) (4.1–4.6 mm long vs. 4.7–5.3 mm, excluding the head), has slender, elongate antennae, and the male genitalia are strikingly different (Figs 39, 37).

Variation. The examined females exhibit minor secondary sexual dimorphism with the lateral margin of the elytra slightly explanate at the posterior 1/4 laterad to



Figures 36, 37. *Stetholus elongatus* **36** female habitus, 5.2 mm long **A** dorsal **B** ventral **37** male genitalia **A** dorsal view **B** lateral view **C** ventral view.

stria 11; in males, stria 11 is just inside the lateral margin, which is not explanate. The metatibia of both sexes has a posterior, linear bare patch which varies in length but is restricted to the basal 1/2, and nearly always the basal 1/3. This character is occasionally obscure, and is probably the result of abrasion of the setae. Otherwise, except for minor differences in the depth and extent of the pronotal impressions, the specimens examined are quite uniform. Measured specimens vary in size from 4.7–5.3 mm long and 1.8–2.1 mm wide (n = 12). The males and the females are of similar size: males

5.0–5.1 mm long, 1.8–2.1 mm wide (n = 7); females 4.7–5.3 mm long, 1.8–2.1 mm wide (n = 5). Carter & Zeck (1929) reported a body length of 5.0–6.0 mm in their species description which likely included the length of the head.

Distribution. *Stetholus elongatus* occurs in the Australian Capital Territory, New South Wales, and Victoria (A. Glaister, in litt.), Australia (Fig. 9).

Habitat and behavior. The habitat and behavior of this species is as described for the genus. Populations can be enormous in suitable habitats. Specimens also have been collected in light traps (A. Glaister, in litt.).

Associated byrrhoid taxa. Elmidae: Larainae: *Hydora laticeps*, *Ovolara australis*; Elminae: *Austrolimnius* spp., *Coxelmis novemnotata*, *Kingolus metallicus*, *K. tinctus*, *K.* spp., *Notriolus maculatus*, *N. minor*, *N. setosus*, *N.* spp., *Simsonia* spp. Psephenidae: *Sclerocyphon basicollis*, *S. minimus*, *S. striatus.*

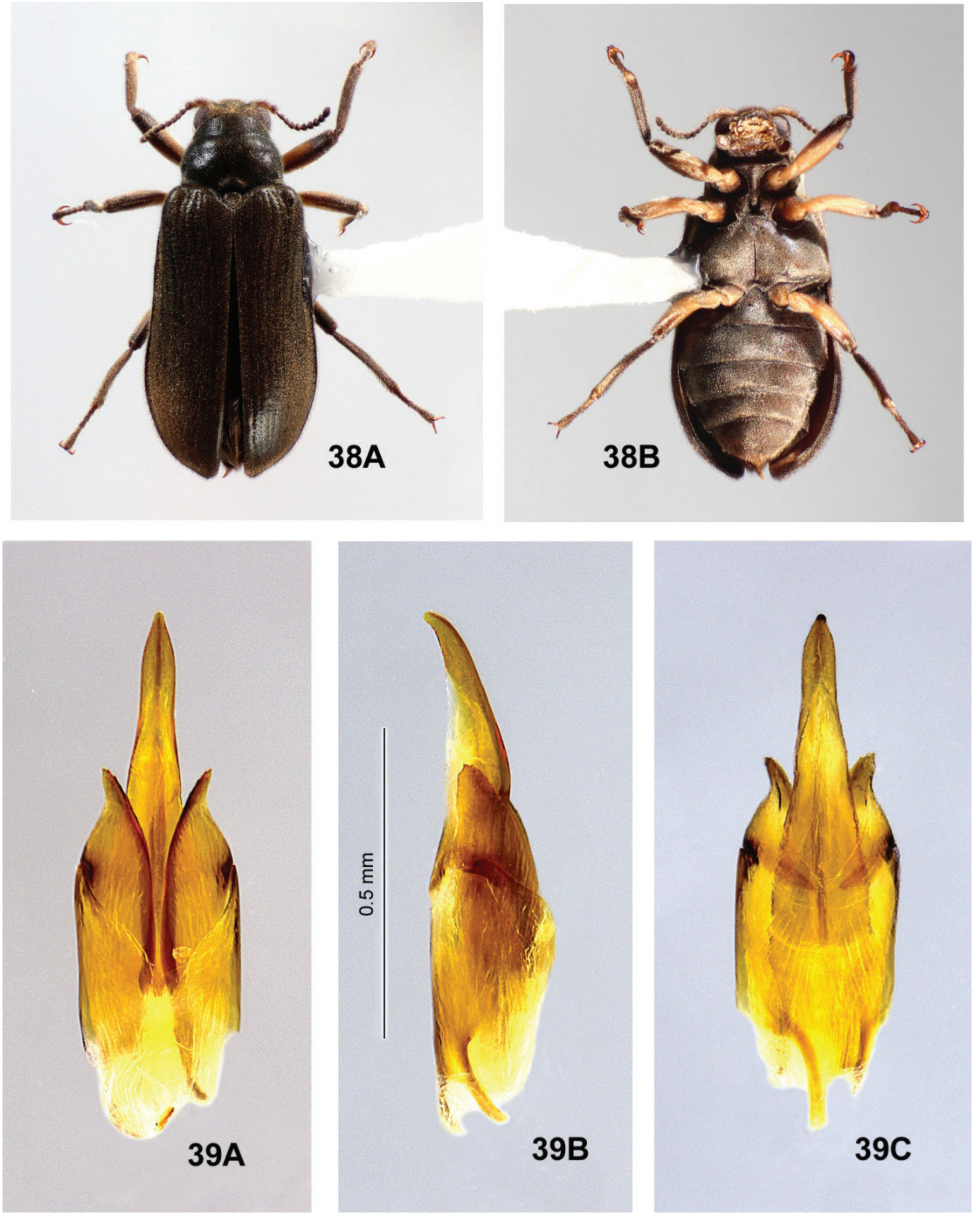
Comments. As noted in the *Hydora laticeps* Comments, there are specimens of *S. elongatus* in the AM, NMV and SAMA which bear locality labels identical to those of *H. laticeps.* Carter & Zeck (1929, 1932) made no mention of the *S. elongatus* specimens from Tallong, or that the two species co-occur. The larva of this species has been reared to the adult by Glaister (A. Glaister, in litt.).

Stetholus longipennis sp. nov.

http://zoobank.org/4A0A3280-EACD-42E2-9851-7BB81665144D
Figs 10, 27, 38, 39

Type locality. Hunters Creek north of Mount Molloy; 16.6324° S, 145. 3254° E; north Queensland, Australia.

Type material. *Holotype* male. "AUSTRALIA: Queensland / 5 km N Mount Molloy / 17 I 2001 / Hunters Creek / S16°38'00" E145°19'27" (WDS-A-1368 on reverse) // William D. / Shepard, leg. // HOLOTYPE / Stetholus / longipennis / Barr & Shepard" [red label, handwritten]. Dry pinned. Deposited in the Australian National Insect Collection, Canberra; ANIC Database Number 25-077642. ***Paratypes* (108).** Same data as for holotype (1 AM, 1 ANIC, 13 EMEC, 1 QM); AUSTRALIA: no. QLD / Hunters Creek at Hwy. 44 / 5 rd. km. N Mount Molloy / 16°38'00"S, 145°19'27"E / 17-I-2001, coll. C. B. Barr (5 EMEC, 1 QM); AUSTRALIA: no. QLD / Bushy Creek at Hwy. 44 / just W of Julatten / 16°36'40"S, 45°20'10"E / 17-I-2001, coll. C.B.Barr (1 EMEC); AUSTRALIA: no. QLD / Emerald Creek at Hwy. 1 / E of Mareeba / 16°59'12"S, 145°28'21"E / 17-I-2001, coll. C.B. Barr (6 EMEC); AUSTRALIA: Queensland / Emerald Creek Store / 17 I 2001 / Emerald Creek / S16°59'12" E145°28'21" (WDS-A-1369 on reverse) // William D. / Shepard, leg. (1 AM, 9 EMEC); AUSTRALIA: no. QLD / Freshwater, Freshwater / Cr. at Ryan Weare Park / 16°53'13"S, 145°42'05"E / 18-I-2001, coll. C.B. Barr (6 EMEC); AUSTRALIA: Queensland / Freshwater / 18 I 2001 / Freshwater Creek (WDS-A-1370 on reverse) // William D. / Shepard, leg. (2 EMEC); AUSTRALIA: no. QLD / Mulgrave River at Hwy. 1 / 1 rd. km. S of Gordonvale / 17°06'10"S, 145°47'15"E / 18-I-2001,



Figures 38, 39. *Stetholus longipennis* sp. nov., male **38** habitus, 4.2 mm long **A** dorsal **B** ventral **39** male genitalia **A** dorsal view **B** lateral view **C** ventral view.

coll. C. B. Barr (5 EMEC, 1 QM); AUSTRALIA: Queensland / 1 km S Gordonvale, 18 I 2001 94 ft / Mulgrave River / (WDS-A-1371 on reverse) // William D. / Shepard, leg. (1 AM, 1 ANIC, 2 EMEC, 1 QM); AUSTRALIA: no. QLD / Fishery Creek at / Hwy. 1, Fishery Falls / 17°11'10"S, 145°53'11"E / 18-I-2001, C. B. Barr (6 EMEC); AUSTRALIA: Queensland / Fishery Falls / 18 I 2001 / Fishery Creek (WDS-A-1372 on reverse) // William D. / Shepard, leg. (1 AM, 1 ANIC, 2 EMEC); QLD. Babinda / Apr. 1946 / J.G.Brooks (3 ANIC); 16.03S to 16.05S / 145.28E Cape / Tribulation area / QLD 21-28Mar.1984 / A.Calder & T.Weir // on rocks / in stream (1 ANIC); 16.03S to 16.05S / 145.28E QLD, Cape / Tribulation area / 1-11 May 1992 / J.F.Lawrence // on rocks / in stream (1 ANIC); same data as for preceding // Genitalia prep. / HS-243 ♂ / A.Calder 1997 (1 ANIC); same data as for preceding // Genitalia prep. / HS-274 ♀ / A.Calder 1997 (1 ANIC); QLD. Cardstone / 23 Jan. 1965 / J.G.Brooks / at light (4 ANIC); same data as for preceding // Genitalia prep. / HS-307 ♀ / A.Calder 1999 (1 ANIC); Cardstone, N.Q. / 23.i.65. J.G. & / J.A.G.Brooks // Genitalia prep. / HS-241 ♂ / A.Calder 1997 (1 ANIC); Crystal Cascades / Via Cairns, N.Qld. / 22.xii.1964. / G. Monteith // EX UQIC / DONATED / 2011 (7 QM); same locality / H.A.Rose. (1 QM); Crystal Cascades / Cairns, N.Qld. / 30.xii.1963. / G. Monteith // EX UQIC / DONATED / 2011 (1 QM); QLD. Gordonvale / Apr. 1946 / J.G.Brooks // J. G. Brooks / Bequest, 1976 (4 ANIC); Little Mulgrave R. / Gordonvale, N.Q. / Apr. 1946 / J. G. Brooks // Australian Museum / K 579979 (2 AM); Mossman, Q. / 25 Mar 1967 / M.S. Upton (1 ANIC); Mossman Gorge / Via Mossman, N.Qld. / 25-26. xii.1964. / G. Monteith // EX UQIC / DONATED / 2011 (2 QM); Mt. Molloy, Q. / Station Creek, at light / 30.xii.69 J.G.Brooks (1 ANIC); 32km S [N?] of Ravenshoe, Q. / (17.38S, 145.29E) / K.Hyde // 12.ii.1966, Genitalia prep. / HS-239 ♂ / A.Calder 1997 (1 ANIC); same data as for preceding // Genitalia prep. / HS-240 ♂ / A.Calder 1997 (1 ANIC); Upper Daintree R. / Via Daintree, / 27.xii.1964. N.Qld. / G. Monteith // EX UQIC / DONATED / 2011 (3 QM); Upper Finch Hatton / Ck., Via Finch / Hatton, N.Qld. / 3.i.1965. / G. Monteith // EX UQIC / DONATED / 2011 (1 QM); Upper Mulgrave River, / 30.iv.1970, N.Qld, / G. B. Monteith // EX UQIC / DONATED / 2011 (2 QM). Paratypes all with the following label: PARATYPE / *Stetholus* / *longipennis* / Barr & Shepard [yellow label, printed].

Other material examined (17). Archers Ck., Q. / Mt. Garnet Rd., / 28.xii.1964 / J.G.Brooks (1 ANIC); Bellenden Ker Range, NQ / Cableway Base Stn, 100m / 17 Oct.-9 Nov. 1981 / EARTHWATCH/QLD. MUSEUM / MV light, rainforest // A.N.I.C. / COLEOPTERA / Voucher No. / 83-0610 [green label] // Stetholus / sp. 1 / det. T. A. Weir 1983 (1 QM); Cardstone, N.Q. / 23.i.65. J.G. & / J.A.G.Brooks (4 ANIC); Cardstone QLD / 10-13.iii.1966 / K. Hyde (1 ANIC); Henrietta Ck., / Palmerston Nat. / Pk., N.Qld. / 29.xii.1964. / G. Monteith // EX UQIC / DONATED / 2011 (1 QM); Millstream at Archers / Ck. N. Q. Mt. Garnet / Rd. 28.xii.64 / J.G. Brooks (1 ANIC); same data as for preceding // Genitalia prep. / HS-306 ♀ / A.Calder 1999 (1 ANIC); same data as for preceding // Genitalia prep. / HS-308 ♀ / A.Calder 1999 (1 ANIC); Mossman Gorge / Via Mossman, N.Qld. / 25-26.xii.1964. / G. Monteith // EX UQIC / DONATED / 2011 (1 QM); 3 mls.W. of / Mossman, Q. / 14 Mar. 1964 / I.F.B.Common / & M.S.Upton (1 ANIC); 32km S [N?] of Ravenshoe, Q. / (17.38S, 145.29E) / K.Hyde // 16.ii.1966 (3 ANIC); Spring Ck. N. Q. / Heberton Rd. / 30.xii.64 / J.G. Brooks (1 ANIC).

Differential diagnosis. *Stetholus longipennis* (Fig. 38, 39) can be distinguished from other species of *Stetholus* (Figs 34–37, 40–42) by a combination of the following characters: Length usually shorter than or equal to 4.6 mm; antennae slender, almost moniliform; pronotum smooth or lightly sculptured, sublateral carinae absent; metatibiae entirely setose; male genitalia with penis very slender and much longer than parameres. Conversely, *S. metatibialis* (Fig. 40) and *S. carinatus* (Fig. 34) both have long, distinct sublateral pronotal carinae; *S. woronora* (Fig. 41) has very short carinae; and all three have distinctly clavate antennae. *Stetholus elongatus* (Fig. 36) also lacks pronotal carinae, but is usually longer than 4.6 mm and the antennae are clavate. The male genitalia of *S. longipennis* (Fig. 39) are strikingly different from those of other *Stetholus* (Figs 35, 37, 42) excluding *S. metatibialis* for which males are currently unknown.

Description (n = 127). ***Body:*** Size 4.1–4.6 long, 1.6–1.8 wide (n = 21). Color dark brown to black dorsally and ventrally, but appearing lighter due to layer of dense, short, yellow setae; first two antennomeres, trochanters, basal 2/3–3/4 of femora yellow; apical antennomeres, coxae, tibiae, tarsi dark brown. ***Head:*** Punctures shallow, fine, evenly spaced; setae fine, yellow, recumbent to erect. Vertex with faint V- or U-shaped impression, open anteriorly, extending from near antennal bases to a distinct median impression; frontoclypeal suture arcuate. Antenna with eleven antennomeres; antennomere 1 longest, 3 × longer than wide, curved; antennomere 2 spherical; both with long, curved setae; antennomere 3 ovoid; antennomeres 4–11 each subspherical, widening slightly towards antennal apex, forming a slender, elongate, almost moniliform, club. Eye finely-faceted, suboval at base, moderately protuberant; dorsal and posteroventral margin with fringe of long, curved, black setae. Clypeus convex, broadly rectangular, emarginate anteriorly, densely setose. Labrum rectangular, longer and slightly narrower than clypeus; setose; anterior margin weakly emarginate, with band of short, yellow setae; lateral margins each with a wide, dense band of long, curved setae. Mandible with two teeth, outermost acute apically, innermost truncate apically; prostheca shelf-like, very thin, apically with coarse, long setae; molar area large, moderately oval, surface striate; lateral edge basally with a partially free lobe with several thin setae. Maxillary palpus black, setose, with four palpomeres; palpomere 1 short, annular, with inner apical border spine-like; palpomere 2 twice as long as wide; palpomere 3 as long as 2, wider apically; palpomere 4 wide, ventral surface with a subcircular, concave, white sensory area angled obliquely from the apex to the base. Labial palpus black, glabrous, with three palpomeres; palpomeres 1 and 2 short, annular; palpomere 3 longer, wider, quadrate, apex truncate with an oval, concave, white sensory area. ***Pronotum:*** Shape generally trapezoidal, wider than long, widest at base; length 0.8–1.0 mm, width 1.2–1.3 mm; disc with distinct punctures evenly spaced ~ 1 diameter apart, deeper near lateral margins; densely setose, with short, fine, yellow setae and longer, coarser, dark setae. Anterior margin arcuate; anterior angles obsolete; lateral margins bisinuate; posterior angles 90°, blunt, depressed; posterior margin weakly trisinuate. Disc slightly convex; shallow, broadly V-shaped, transverse impression at apical 1/4–1/2; basal 1/2 with two faint to distinct, oblique, lateral depressions and two large, deep prescutellar foveae; pronotal margin inflated posterior to fovea. ***Scutellar shield:*** Cordate; posterior apex slightly raised; finely setose. ***Elytron:*** 3.3–3.6 mm long, 0.8–0.9 mm wide. Elytra conjointly ~ 2 × as long as wide, widest near posterior 1/3; apices together forming a triangular notch between. Humerus prominently inflated, elytral base depressed medially; disc at 1/4–1/3 distance from base with a shallow depression from suture to stria 5. Disc with 10 punctate, weakly impressed striae, intervals flat; punctures very fine, spaced one diameter apart, obsolete apically; accessory basal stria between striae 1 and 2 long; stria 3 ending before apex; striae 4 and 5 joining before apex; striae 10 and 11 joining and ending before apex. ***Metathoracic wings:*** Macropterous. ***Prosternum:*** Very short anterior to procoxae; prosternal process moderately narrow, 3 × longer than wide, margined, with a median longitudinal carina, apex narrowly rounded. ***Mesoventrite:*** Short; disc convex between mesocoxae with a deep mesoventral cavity to receive prosternal process. ***Metaventrite:*** Broadly rectangular; disc with a median, round concavity near anterior margin and a wide median depression covering posterior 1/2–2/3; discrimen extending from concavity to posterior margin; metakatepisternal suture distinct; disc with small, shallow, variably spaced punctures mostly obscured by dense, fine, recumbent, yellow setae. ***Legs:*** Of similar lengths; each leg with femur and tibia subequal in length; tarsus slender, with tarsomere 5 slightly longer than tarsomeres 1–4 combined; claws simple, moderately large, sharply acute. Coxae dark brown, metacoxae deeply sulcate; femora yellow, dorsal surfaces of each with a narrow brown stripe, apical 1/4–1/3 dark brown; tibiae dark brown, mesotibiae with posterior surfaces nearly glabrous, shiny; metatibiae entirely setose, weakly arcuate. ***Abdomen:*** Five convex ventrites, each with a shallow depression near lateral margin; ventrite 1 with a margined, broadly triangular, intercoxal projection; ventrites 2–4 broadly rectangular, with lateral margins each produced to form a small lobe of varying size, largest on ventrites 3 and 4, which clasps the epipleuron; posterior border of ventrite 5 with a broadly rounded apex. Ventrites covered with shallow punctures spaced 1–2 diameters apart, mostly obscured by dense covering of yellow setae; setae longer at median 1/5 of ventrites 3–5. ***Aedeagus:*** Phallobase lightly sclerotized, open dorsally, fused to short parameres; penis very long, nearly as long as phallobase and parameres together (Fig. 39). In dorsal view (Fig. 39A), parameres with lateral margins sinuate, convergent from junction with phallobase to near apex then strongly divergent and curved laterally; median margins nearly parallel at basal 2/3 then strongly divergent; apices acute. Penis beyond paramere tips with lateral margins nearly parallel almost to acute apex; no visible corona; dorsal median longitudinal carina with darker sclerotization present; basal apophyses very long, nearly as long as phallobase, straight, very broad, blunt at tips. In lateral view (Fig. 39B), paramere triangular, moderately convex dorsally, nearly flat ventrally; apex broadly rounded to truncate with a few, small, irregular teeth; penis curved, tip ventrally directed. Fibula absent. **Ovipositor:** Moderately sclerotized; oval in outline, 2 × longer than wide; baculum ~ 2 × longer than gonocoxite; proximal gonocoxite subrectangular, wide and short; distal gonocoxite narrow and short, ~ 2 × as long as wide, length equal to proximal gonocoxite length, median and lateral margins arcuate, together separate basally but contiguous medially to apices; stylus very narrow.

Variation. The females exhibit minor secondary sexual dimorphism with the lateral elytral margin slightly explanate at the posterior 1/4 laterad of stria 11; in males, stria 11 is just inside the lateral margin, which is not explanate. Measured specimens vary from 4.1–4.6 long and 1.6–1.8 wide (n = 21). The females are slightly larger than the males: females 4.3–4.6 mm long, 1.8 mm wide (n = 8); males 4.1–4.5 mm long, 1.6–1.8 mm wide (n = 13). The width of the prosternal process varies a bit between individuals. Otherwise, except for minor differences in the depth and extent of pronotal impressions, the specimens are quite uniform.

Etymology. The specific epithet *longipennis*, an adjective in the nominative singular derived from the Latin *longi* (long) plus *pennis* (penis), refers to the male genitalia in which the length of the penis greatly exceeds the length of the parameres (Fig. 39).

Distribution. *Stetholus longipennis* occurs in north and central Queensland, Australia (Fig. 10).

Habitat and behavior. *Stetholus longipennis* was collected by the authors from medium to large sand-bottomed streams with logs and debris, some with boulders, and a small river at elevations ranging from 5–417 m (Fig. 27). All had clear water which varied from warm to cool. The beetles were collected from logs and rocks in fast current or rapids, and from a spillway. The adults fly readily from the net, and also have been taken at lights. At the type locality, Hunters Creek, the stream was well-shaded, with many logs and much debris, and many *S. longipennis* were concentrated on a concrete spillway below a bridge.

Associated byrrhoid taxa. Elmidae: Larainae: *Australara glaisteri* sp. nov., *Ovolara lawrencei* sp. nov., *O. leai*, *O. monteithi* sp. nov., *Potamophilinus papuanus*; Elminae: *Austrolimnius* spp., *Graphelmis pallidipes*, *Kingolus* spp., *Notriolus taylori*, *Notriolus* spp., *Simsonia* sp. Psephenidae: *Sclerocyphon basicollis*, *Sclerocyphon minimus*.

Stetholus metatibialis **sp. nov.**

http://zoobank.org/37506188-9496-40B4-BC38-10BE15FF63D3
Figs 11, 40

Type locality. Mt. Bellenden Ker northwest of Babinda; 17.2672° S, 145.8700° E; Wooroonooran National Park, north Queensland, Australia.

Type material. ***Holotype* female.** "Bellenden Ker Range, NQ / Cable Tower 3 [now Tower 6], 1054m / 17 Oct.-5 Nov. 1981 / EARTHWATCH/QLD. MUSEUM // A.N.I.C. / COLEOPTERA / Voucher No. / 83-0611" [green label] // "HOLOTYPE / Stetholus / metatibialis / Barr & Shepard" [red label, handwritten]. Dry pinned. Deposited in the Queensland Museum, South Brisbane; Registration Number QM T250615.

Differential diagnosis. The single female specimen of *S. metatibialis* (Fig. 40) is characterized by an elongate-oval body shape; labrum "moustache" composed of two discrete, lateral tufts of very long, dark, curved setae (setal origin unclear, possibly mandibular) (Fig. 40C); long pronotal basal sublateral carinae; and posterior surfaces of both the meso- and metatibiae glabrous and shiny. While other species of *Stetholus* may have similar labral tufts, none are as long and distinctive. The metatibia of *S.*

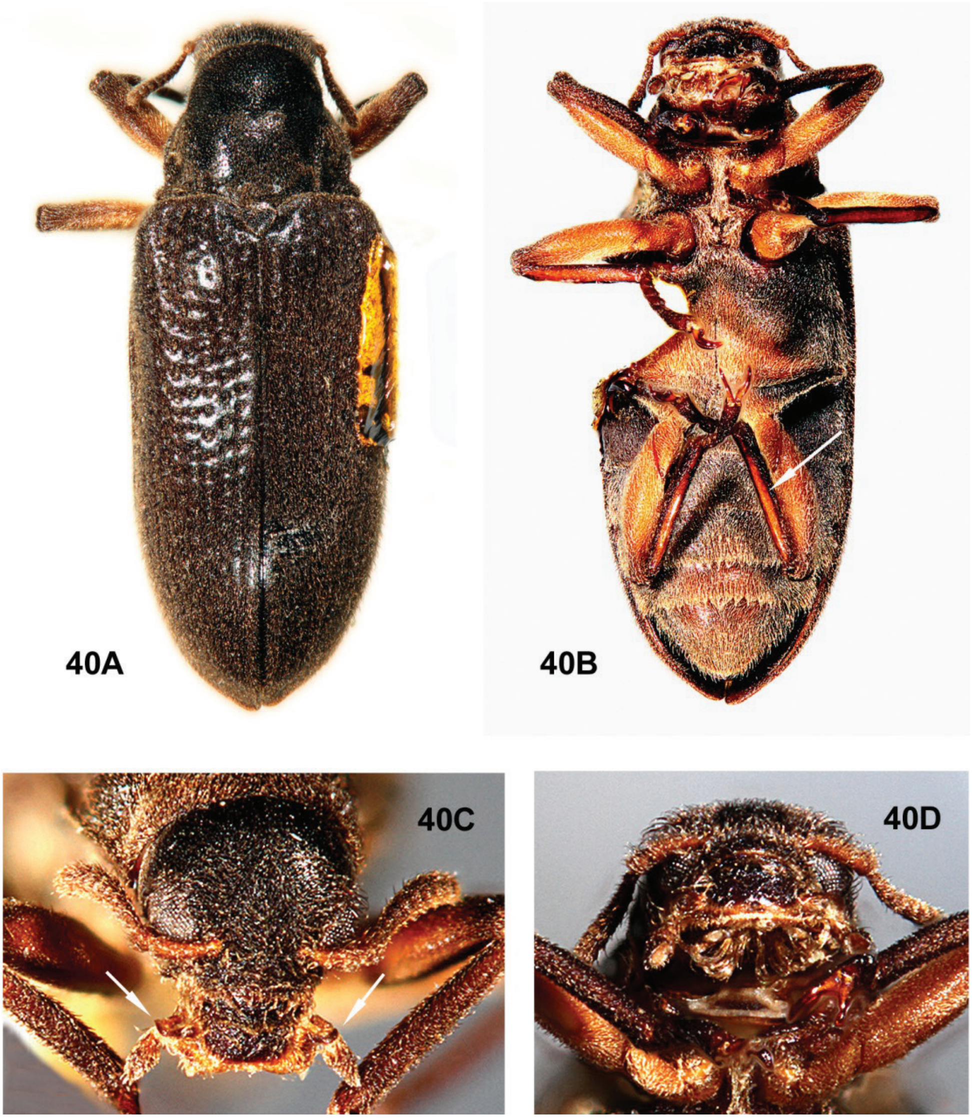


Figure 40. *Stetholus metatibialis* sp. nov., holotype female, 3.9 mm long **A** dorsal habitus **B** ventral habitus **C** head, frontal view **D** head, ventral view.

elongatus (Fig. 36) has a narrow, elongate, posterior bare area of variable length, usually at the basal 1/3, as opposed to that of *S. metatibialis* in which the posterior surface is entirely bare; the metatibiae of the others are entirely setose. *Stetholus elongatus* and *S. longipennis* (Fig. 38) lack pronotal sublateral carinae. *Stetholus metatibialis* (Fig. 40) bears a superficial resemblance to *Ovolara* species (Figs 23–26, 28–31) because of its elongate-oval body and strongly punctate elytra, however it is easily separated by the very short prosternum anterior to the procoxae (vs. prosternum long, extended anteriorly) and the presence of a transverse pronotal impression (vs. no impression).

Description (n = 1). Holotype female. ***Body:*** Size 3.9 mm long, 1.4 mm wide; elongate-oval. Dorsal color dark brown; head black; venter mostly brown; first two antennomeres, posterior metaventrite, coxae, trochanters, femora, posterior face of meso- and metatibiae yellow-brown. Setae of dorsal surfaces short, yellow, semi-erect and recumbent, setae of ventral surfaces long and recumbent. ***Head:*** Densely setose and punctate, punctures < 1 diameter apart or nearly contiguous. Vertex with a faint V-shaped impression, open anteriorly, extending from antennal bases towards occiput; frontoclypeal suture straight, obscure. Antenna with 11 tomentose antennomeres; antennomeres 1 and 2 yellow-brown with coarse, yellow setae; antennomere 1 longest, ~ 3 × longer than wide, curved; antennomere 2 ovoid; antennomeres 3–11 brown with dense yellow setae, together forming a tight, elongate club; antennomeres 7–11 of equal width, antennomere 11 longer than all but antennomeres 1 and 2, apex bluntly rounded. Eye finely faceted, suboval at base, weakly protuberant; dorsal margin with fringe of long, curved setae. Clypeus transverse, convex, anterior margin straight; disc densely setose, lateral margins with longer setae. Labrum trapezoidal, wider than long, 2 × longer and slightly narrower than clypeus; densely setose; anterior margin weakly emarginate with band of short, yellow setae; lateral margins with dense fringes of long, yellow setae, each margin with a discrete tuft of very long, dark, curved setae extending to maxilla (setal origin unclear, possibly mandibular). Maxillary palpus with four setose palpomeres; palpomere 1 yellow, short, annular; palpomere 2 yellow, 2 × as long as wide; palpomere 3 yellow, nearly as long as 2, wider apically; palpomere 4 brown, longest and widest, ovoid, ventral surface with a broadly oval, slightly concave, pale sensory area angled obliquely from the apex to the base. Labial palpus yellow, glabrous, with three palpomeres; palpomeres 1 and 2 yellow, annular, short and narrow; palpomere 3 brown, conical, much longer and wider than others, apex truncate with a narrowly oval, flat, slightly concave, pale sensory area. ***Pronotum:*** Shape generally trapezoidal, slightly wider than long, widest at base; 1.0 mm long, 1.1 mm wide; disc densely punctate, punctures evenly spaced ~ 1 diameter apart. Anterior margin arcuate; anterior angles obsolete; lateral margins sinuate and arcuate, moderately explanate; posterior angles raised, protruding, acute, posterior margin weakly trisinuate. Disc weakly convex, more convex at basal 1/2; distinct, transverse V-shaped impression at apical 1/3–1/2; two distinct, basal, sublateral carinae 1/3–1/2 as long as pronotum, bordered by shallow medial impressions and lateral excavations; two shallow, indistinct prescutellar foveae. ***Scutellar shield:*** Cordate, longer than wide, apex rounded; flat; densely setose. ***Elytron:*** 2.9 mm long, 0.7 mm wide. Elytra conjointly 2 × as long as wide; anterior 2/3 almost parallel-sided; margins narrowly marginate. Humerus inflated, elytral base depressed medially; disc convex at anterior 1/3, flattened at 1/3–1/2 distance from base, then weakly convex to apex. Disc with ten strongly punctate, weakly impressed striae, intervals slightly raised, sutural interval more so; accessory basal stria of 6 punctures between striae 1 and 2 short; striae 3 and 4 join near apex; disc punctures large and deep at basal 2/3, becoming much smaller and shallower towards apex, separated by one diameter. ***Prosternum:*** Very short anterior to procoxae, marginate anteriorly. Prosternal process moderately narrow, long, 4 × longer than wide; nearly parallel-sided between coxae then slightly widened towards rounded apex; laterally marginate, medially sulcate at basal 1/2, carinate at apical 1/2; surface tomentose. ***Mesoventrite:*** Short, marginate, densely setose, with a deep mesoventral cavity to receive prosternal process. ***Metaventrite:*** Broadly rectangular; very setose; anterior margin marginate, bordered posteriorly by a small, transverse excavation; disc with discrimen extending almost from anterior to posterior margin, deeply incised at posterior 2/3; disc laterad to discrimen very convex; metakatepisternal suture distinct. Disc laterally with large, variably spaced punctures; punctures obscured medially by a broad, triangular patch of very long, dense, recumbent, yellow-orange setae. ***Legs:*** Of similar lengths; each leg with femur and tibia nearly subequal in length; foreleg stouter than the others; tarsus with tarsomere 5 longer than tarsomeres 1–4 combined, distinctly expanded at 1/3 distance to apex; claws simple, large, sharply acute. Pro- and mesocoxae yellow; metacoxae yellow medially, brown laterally, deeply sulcate; femora yellow, dorsal surfaces of each with a narrow brown stripe, apices brown; tibiae brown, meso- and metatibiae with posterior surfaces yellow-brown, glabrous, shiny; tarsi brown. ***Abdomen:*** Five ventrites; ventrites 2 and 3 subequal in length, ventrite 4 shortest, ventrite 5 longest; ventrites convex; ventrite 1 with a wide, triangular, intercoxal projection; ventrites 2–4 with lateral margins each produced to form a small, rounded lobe which clasps the epipleuron; ventrites 3 and 4 depressed basally, raised at posterior margins; ventrite 5 with impressions at basomedial and basolateral margins, apex rounded. Ventrites covered with shallow punctures variably spaced one or more diameters apart; punctures of ventrites 3–5 medially obscured by dense covering of yellow setae.

Etymology. The specific epithet *metatibialis* is an adjective in the nominative singular derived from the Greek *meta* meaning after or posterior, and the Latin *tibia,* the lower portion of a leg. *Metatibialis* points to the diagnostic character present on the hind tibia, specifically, the glabrous posterior surface (Figs 40D).

Distribution. North Queensland, Australia. Known only from the type locality in the Bellenden Ker Range in Wooroonooran National Park, west of Bellenden Ker and northwest of Babinda (Fig. 11).

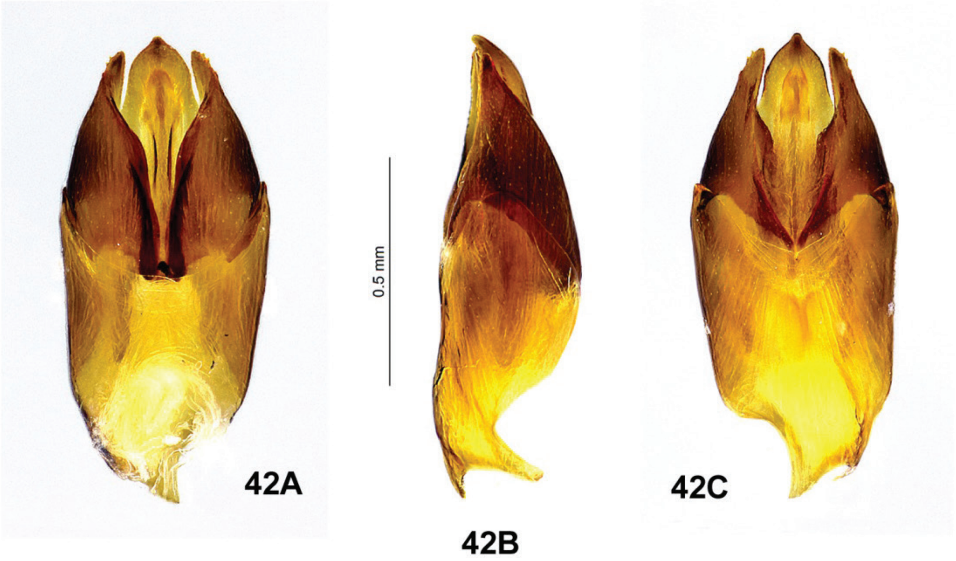
Habitat. The single specimen was taken at UV light trap at an elevation of 1054 m on the east slope of Mt. Bellenden Ker. According to the project leader “the whole place is solid rainforest and there are many endemics at higher elevations” (G. Monteith, in litt.).

Stetholus woronora **sp. nov.**

http://zoobank.org/8185A9F0-AE2F-4945-B5AF-AA78CB6F55BD
Figs 12, 41–43

Type locality. Woronora River north of Engadine; 34.0465° S, 151.0062° E; New South Wales, Australia (Fig. 43).

Type material. *Holotype* male. “AUSTRALIA: NSW / Woronora River, N / Engadine, S Sydney / -34.04652, 151.00621 / 10 m, 23.xi.2019 // Fikáček, Seidel / & Sýkora lgt. / AU-2019-34 // HOLOTYPE / Stetholus / woronora/ Barr & Shepard”



Figures 41, 42. *Stetholus woronora* sp. nov., holotype male **41** habitus, 5.2 mm long **A** dorsal **B** ventral **42** male genitalia **A** dorsal view **B** lateral view **C** ventral view.

[red label, handwritten]. Dry pinned. Deposited in the Australian National Insect Collection, Canberra; ANIC Database Number 25-077643. ***Paratypes* (9).** Same data as for holotype (4 ANIC, 3 EMEC, 2 NMPC). Paratypes all with the following label: PARATYPE / *Stetholus* / *woronora* / Barr & Shepard [yellow label, printed].

Differential diagnosis. *Stetholus woronora* (Figs 41, 42) can be distinguished from other species of *Stetholus* (Figs 34–40) by a combination of the following characters: Body large, > 5.0 mm long; antennae clavate; pronotum with very short, basal sublateral carinae; male genitalia stout and heavily sclerotized. *Stetholus elongatus* (Fig. 36) most closely resembles *S. woronora* but lacks pronotal carinae; the male genitalia are somewhat similar but the penis of *S. elongatus* (Fig. 37) is narrow and tapered at the apex whereas that of *S. woronora* (Fig. 42) is wide and bulbous. The other three species of *Stetholus* are much shorter (4.5 mm or less) and do not have similarly stout, heavily sclerotized genitalia (those of *S. metatibialis* are unknown). Furthermore, *S. longipennis* (Fig. 38) lacks sublateral pronotal carinae; *S. metatibialis* (Fig. 40) and *S. carinatus* (Fig. 34) both have much longer, more prominent carinae.

Description (n = 10). ***Body:*** Size 5.2–5.6 mm long, 1.9–2.2 mm wide (n = 9). Color black except first two antennomeres, trochanters and basal 2/3 of femora yellow-brown or light red-brown. All surfaces covered with short pale yellow or longer black setae. ***Head:*** Heavily punctate and setose, with many long, erect and semierect, curved, black setae and much shorter pale yellow setae. Eye finely faceted, suboval at base, weakly protuberant; with a dorsal and posteroventral fringe of long, curved, black setae. Antenna with eleven antennomeres; antennomere 1 3 × longer than wide, curved; antennomere 2 spherical; both with long, curved, black setae; antennomeres 3–11 forming an elongate club. Frons with a distinct Y-shaped impression, upper arms nearly reaching antennal bases, frons depressed between; frontoclypeal suture straight. Clypeus broadly rectangular, emarginate anteriorly, convex, densely setose. Labrum narrower than clypeus, trapezoidal, widest at base, weakly emarginate; anterior margin with band of short, pale yellow setae, lateral margins with long, dense brushes of light and dark, curved setae. Maxillary palpus black, setose, with four palpomeres; palpomere 1 short; palpomeres 2 and 3 longer; palpomere 4 longer and wider, ventral surface with a circular to oval, concave, white sensory area angled obliquely from the apex to the base. Labial palpus black, glabrous, with three palpomeres; terminal palpomere quadrate, apex with oval white sensory area. ***Pronotum:*** Shape generally trapezoidal, slightly wider than long, widest at base; 1.1–1.3 mm long, 1.3–1.5 mm wide; disc heavily and evenly punctate and setose; punctures deep, spaced mostly 1 diameter apart; setae either short, fine, pale yellow or longer, stout, dark. Anterior margin arcuate; anterior angles obsolete; lateral margins weakly trisinuate; posterior angles 90°, depressed; posterior margin weakly trisinuate. Disc with a shallow, broadly V-shaped, transverse impression from anterior 1/3–1/2 contiguous with a short, median, longitudinal impression; two shallow, oblique, lateral impressions at posterior 1/3; two very short, basal, sublateral carinae; two deep prescutellar foveae. ***Scutellar shield:*** Subtriangular with margins weakly arcuate, apex acute, raised; velvety in appearance due to very dense, short, pale yellow setae unlike that of pronotum and elytra. ***Elytron:*** 4.0–4.4 mm long, 1.0–1.1 mm wide. Elytra conjointly 2 × as long as wide, slightly widened at apical 1/3; apices together evenly rounded with a small notch between. Setae short, fine, pale yellow. Humerus prominently swollen; anterior margin narrowly depressed inside of humerus, especially at base of interval 6; disc at

Figure 43. *Stetholus woronora* sp. nov., type locality: Woronora River, north of Engadine, NSW, Australia (photograph courtesy of Martin Fikáček, National Museum, Prague, Czech Republic).

1/3 distance from base with a shallow depression from suture to stria 4. Disc with 10 punctate striae; punctures small and spaced < 1 diameter apart, stronger anteriorly, fainter posteriorly; accessory basal stria between striae 1 and 2 long; stria 3 ending before posterior margin, striae 4 and 5 joining and ending just before posterior margin. ***Metathoracic wings:*** Macropterous. ***Prosternum:*** Very short anterior to procoxae, margined; prosternal process very setose, moderately narrow, 3 × longer than wide, with a distinct median longitudinal carina, apex rounded. ***Mesoventrite:*** Short, wide; disc concave between mesocoxae, with a deep mesoventral cavity to receive prosternal process; covered with short yellow setae. ***Metaventrite:*** Broadly rectangular; with a wide, circular, median depression covering posterior 3/4; discrimen as long as median depression; metakatepisternal suture present; disc heavily punctate, punctures small and often contiguous; disc covered with short, dense, yellow setae. ***Legs:*** Of different lengths, fore leg shortest, hind leg longest; each leg with femur shorter than tibia; mesotibia narrower than pro- and metatibia; tarsus with tarsomere 5 slightly longer than tarsomeres 1–4 combined; claws large, simple, acute. Coxae black, metacoxae deeply sulcate; femora yellow-brown or light red-brown each with dorsal surfaces and apical 1/3 black; tibiae black; mesotibiae with posterior surfaces flat, glabrous, shiny; metatibiae weakly arcuate; tarsi black. ***Abdomen:*** Five convex ventrites, each with a shallow depression near lateral margin; ventrite 1 with margined, broadly triangular, intercoxal projection; ventrites 2–4 widely rectangular, with lateral margins each produced to form a small lobe of varying size, those of ventrites 3 and 4 largest, which clasps the epipleuron; ventrite 5 with lateral margins evenly curved with broadly rounded apex. Ventrites covered with shallow, often contiguous, punctures, and semi-erect and recumbent yellow setae. ***Aedeagus:*** Mostly well-sclerotized; short, broad, widest at apex of phallobase; phallobase longer than parameres, parameres slightly shorter than penis; phallobase open dorsally (Fig. 42). In dorsal view (Fig. 42A), parameres broad at base, abruptly digitate at apices; medial margin darkly sclerotized at basal 2/3 due to folding of the margin ventrally, inner surface flat against penis; medial margin weakly divergent at basal 1/2, arcuate and strongly divergent at apical 1/2, sinuate before apex; lateral margins evenly arcuate with four, small, sharp teeth near apex. Penis very broad, less well-sclerotized than parameres, medially inflated at basal 2/3 between parameres forming a longitudinal, margined, flat-topped carina; apex bell-shaped, tip produced and bent ventrally; no visible corona; basal apophyses moderately long, 1/2–2/3 as long as phallobase, straight, very broad, transversely truncate at tips. In lateral view (Fig. 42B), aedeagus widest midway between apex and base; paramere broadly triangular in outline, moderately convex dorsally, moderately concave ventrally, apex acute; penis apex narrowly rounded, curved ventrally slightly above paramere apex. In ventral view (Fig. 42C), parameres with arcuate median margins, thickened at basal 1/3; penis with tip longitudinally carinate, fibula absent. ***Ovipositor:*** Well-sclerotized; elongate, 2.5 × longer than wide; baculum 1/4 longer than gonocoxite; proximal gonocoxite subrectangular except widened medially at base, with two teeth; distal gonocoxite 2 × longer than proximal gonocoxite, base 2 × wider than apex, apex broader than middle, median margins straight, lateral margins sinuate; stylus narrow, 1/4–1/3 length of distal gonocoxite.

Variation. Females exhibit minor secondary sexual dimorphism with the lateral margin of the elytra very slightly explanate at the posterior 1/4 laterad to stria 11; in males, stria 11 is just inside the lateral margin, which is not explanate. The specimens vary from 5.2–5.6 mm long and 1.9–2.2 mm wide (n = 9). Males are slightly larger than the females, but the sample size is small, particularly for females: males 5.3–5.6 mm long, 2.0–2.2 mm wide (n = 6); females 5.2–5.5 mm long, 1.9–2.1 mm wide (n = 3). Except for small differences in the depth and extent of the pronotal impressions, the specimens are otherwise quite uniform.

Etymology. The specific epithet *woronora*, a noun in the genitive case, refers to the type locality of the species, the Woronora River (Fig. 43). Woronora is an Aboriginal place name meaning black rocks in the Dharug (or Darug) language.

Distribution. New South Wales, Australia. Known only from the type locality south of Sydney (Fig. 12).

Habitat. Although the Woronora River normally has pools interspersed with riffles at the type locality, collector Sýkora (in litt.) reported that due to a severe drought "the river there is pretty much just a small stream and we were surprised there was still some water, given the drought at that time." The specimens were obtained by "water collecting in a small rapids of a small stream in rocky pool" (Sýkora, in litt.) at an elevation of 10 m (Fig. 43).

Associated byrrhoid taxa. Elmidae: Elminae: *Kingolus* sp., *Notriolus* sp., *Simsonia* sp.

Discussion

Distribution, biogeography, and biodiversity

The family Elmidae has both high species richness and endemicity in Australia, but most of that is found in the subfamily Elminae rather than in the Larainae. The vast majority of the described species of both subfamilies are known from along the eastern coast of the continent from Queensland to Victoria. A few elmine species occur in other states, but laraines are known only from Queensland, New South Wales, the Australian Capital Territory, and Victoria. Although island state Tasmania shares five elmine species with the main continent, laraines are apparently absent. This could be an oversight because Tasmania has many streams and rivers, some most likely with suitable habitat.

The Australian Wet Tropics bioregion, characterized by high seasonal rainfall, extends along the northeast coast of Queensland from Cooktown to near Townsville, and is topographically varied with mountain ranges containing deep gorges and fast-flowing rivers which quickly descend to the coastal plain. Although it encompasses only 0.01 % of Australia, the Wet Tropics sustains a large proportion of the continent's terrestrial plant and vertebrate species, 25 % of which are regional endemics (McKie et al. 2005). The region was placed on the World Heritage list in 1988 in recognition of the high biodiversity and endemism of its rainforest flora and fauna https://www.environment.gov.au/heritage/places/world/wet-tropics.

Intensive surveys of the insects and other invertebrates of the Wet Tropics conducted in the 1980s focused on species diversity, altitudinal zonation, faunal turnover, and biogeography (Yeates and Monteith, 2008). Numerous studies involving aquatic insects were reviewed by Connolly et al. (2008), who concluded that the biodiversity of Wet Tropics streams is high compared to the rest of the continent. The elmids are no exception to this pattern of high biodiversity. Of the 12 species of Larainae known from Australia, eight are found only in north Queensland, including six of the seven newly described species. Five species of laraines, a surprising number, were identified from two rivers and their tributaries, the Daintree and the Mulgrave. It has been determined that the aquatic invertebrate fauna of the Australian Wet Tropics is chiefly of Gondwanan origin, but it also contains some Asian-derived elements (Connolly et al. 2008, McKie et al. 2005).

The island of New Guinea and Australia are part of the same continental land mass which separated from Gondwana ~ 96 mya. They formed a single, continuous landmass during the Pleistocene ice age ~ 18,000 years ago until rising sea levels separated them ~ 10,000 years ago. Today, only ~ 150 km separate the tip of the Cape York Peninsula in far north Queensland from Papua New Guinea. Therefore, it is not surprising to find shared fauna between the two, including unusual mammal groups (monotremes and marsupials) and several insect taxa (Yeates and Monteith 2008, Surbakti et al. 2021). Nonetheless, phylogenetic studies of Wet Tropics invertebrates suggest that species from New Guinea and far northern Australia have had little influence (Yeates and Monteith 2008). Instead, their closest relatives are found in coastal rainforests further south in Queensland and New South Wales. So far only one species of laraine shared with New Guinea has been found, *Potamophilus papuanus*. This species has not only been collected from the Wet Tropics, but also from the Iron Ranges further north in the Cape York Peninsula, an area that shows a much greater faunal overlap with New Guinea (Yeates and Monteith 2008). Besides *Potamophilinus*, the elmine genera *Austrolimnius* Carter & Zeck, *Coxelmis* Carter & Zeck, *Graphelmis* Delève, and *Simsonia* Carter & Zeck occur both in Australia and New Guinea. Other laraine genera that occur in New Guinea are *Parapotamophilus* Brown and *Potamophilus* Germar, with one and two species, respectively. It would be interesting to discover if any of these taxa are shared as well.

Exploring Australian elmid biodiversity: past research and future potential

Taxonomic research on Australian elmids was dominated by H. J. Carter and E. H. Zeck from 1926–1948, who described many new genera and species, including three of the four laraine species. H. E. Hinton named many more species in his monograph on *Austrolimnius*, an elmine, in 1965. Until now, there has been a 50+ year hiatus since any new Australian elmid taxa have been described. In the interim, ground-breaking descriptive work on the larval fauna was undertaken by Alena Glaister who developed techniques for rearing larvae to adults, thus establishing associations and enabling larval identification (Glaister 1985, 1992, 1999).

Australia has experienced very little focused elmid collecting, both historically and currently, and its elmid diversity is not very well known. The early elmid researchers (e.g., H. J. Carter, E. H. Zeck, H. E. Hinton) worked predominately with museum specimens or relied on local naturalists to send them material. In the 1980s, through the efforts of Geoff Monteith and others who extensively surveyed the Wet Tropics insect and invertebrate fauna, many elmids were captured primarily with light traps or flight intercept traps (Yeates and Monteith 2008). Since then, only a few collectors have added elmid specimens to museum collections. Aquatic invertebrates, particularly the Ephemeroptera, Trichoptera, and Chironomidae (Diptera), have been the focus of numerous surveys as well as ecological studies in the past (Connolly et al. 2008, McKie et al. 2005), but elmids have gotten at most passing mention in the literature despite their abundance in suitable habitats. An exception is a paper on the role of a few species in wood decomposition (McKie and Cranston 1998).

The results of our limited fieldwork in Australia speak volumes to the opportunity for future survey work and taxonomic research, as our experience with laraines in the

Wet Tropics of north Queensland illustrates: During a two day period, at seven stream/river sites on major roads, we collected an undescribed genus, three undescribed species, and a species not yet reported from Australia. Three more new species from that region were found in loan material from the Queensland Museum. Likewise, our elmine collections from north Queensland have proven mostly impossible to identify, and undoubtedly contain many undescribed species because the old taxonomic literature contains relatively few species from north Queensland. Even the more thoroughly explored states of New South Wales and Victoria still hold surprises: *Hydora laticeps*, previously known only from the type locality for nearly 90 years, was identified from museum specimens collected near Canberra and in coastal Victoria. And most unexpected of all, *Stetholus woronora* sp. nov. was found just two years ago in the suburbs of Sydney.

Acknowledgments

We are especially indebted to Alena Glaister (Monash University, Clayton, VIC) who served as our knowledgeable guide during a collecting trip to eastern Australia in 2000-2001. More recently, she provided us with unpublished details from her elmid research for this article. Andrew Calder served as our host at the Australian National Insect Collection in 2000-2001 and shared information about his work with the Elmidae. This project would not have been possible if John Lawrence (ANIC) had not returned to us specimens left at ANIC, for which we are very grateful. Our European colleagues Martin Fikáček, Vít Sýkora (NMPC and Charles University, Prague, Czech Republic), and Matthias Seidel (University of Hamburg, Hamburg, Germany) collected the *Stetholus woronora* specimens and generously offered them for inclusion in this paper. In addition, Sýkora and Fikáček shared their specimen and habitat information and provided photographs used in this article. The following curators and collection managers are thanked for providing vital information about the specimens in their care, and in several cases, for specimen loans: Derek Smith and Chris Reid (AM); Adam Slipinski, Lingzi Zhou, and Hermes Escalona (ANIC); Ken Walker (NMV); Graham Brown (MAGNT); Geoff Monteith, Terry Miller, Christine Lambkin, Karin Koch, and Susan Wright (QM); Ben Parslow (SAMA); and Simon Grove (TMAG). Alisha Steward (Dept. of Environment and Science, Brisbane, QLD) and Jill Lancaster (University of Melbourne, Parkville, VIC) provided information on aquatic ecology studies. David Rentz (James Cook University, Smithfield, QLD) went out of his way to photograph Emerald Creek, a type locality, for us. Specimen images were provided by Natalie Tees (AM), Zhenhua Liu (ANIC), Ken Walker (NMV), Geoff Thompson (QM), and Ben Parslow (SAMA). Images of the male genitalia were taken by Rachel Diaz-Bastin (California Academy of Sciences, San Francisco, CA). We are grateful that Kipling Will (University of California, Berkeley, CA) authorized access to his imaging system for the habitus photographs during a time of severe restriction to campus facilities; without his assistance this article would have been significantly delayed.

The authors have no funding to report, and declare that no competing interests exist.

References

Anonymous [Broun T] (1882) Alteration of generic names. The Annals and Magazine of Natural History (Series V) IX (53): 409. https://doi.org/10.1080/00222938209459067

Broun T (1914) Descriptions of new genera and species of Coleoptera. Bulletin of the New Zealand Institute 1(3): 143–266.

Brown HP (1981) Key to the world genera of Larinae (Coleoptera, Dryopoidea, Elmidae), with descriptions of new genera from Hispaniola, Colombia, Australia, and New Guinea. The Pan-Pacific Entomologist 57(1): 76–104.

Calder AA (1992) Illustrated keys and notes to the genera of adult Australian Elmidae. Coleopteran Identification Workshop, Murray–Darling Freshwater Research Centre, Albury (New South Wales, Australia), February 1992. [Unpublished]

Carter HJ (1926) Revision of the Australasian species of *Anilara* (Fam. Buprestidae) and *Helmis* (Fam. Dryopidae), with notes, and descriptions of other Australian Coleoptera. The Proceedings of the Linnean Society of New South Wales 51(2): 59–71.

Carter HJ, Zeck EH (1929) A monograph of the Australian Dryopidae. Order-Coleoptera. The Australian Zoologist 6(1): 179–190.

Carter HJ, Zeck EH (1932) Four new species of Dryopidae, together with notes on the family. The Australian Zoologist 7(3): 202–205.

Connolly NM, Christidis F, McKie B, Boyero L, Pearson R (2008) 12. Diversity of invertebrates in Wet Tropics streams: Patterns and processes. In: Stork N, Turton S (Eds) Living in a dynamic tropical forest landscape. Wiley-Blackwell, UK, 161–177. https://doi.org/10.1002/9781444300321.ch12

Glaister A (1985) Laboratory rearing of Australian elmid larvae (Elmidae: Coleoptera). Australian Society of Limnology Bulletin 10: 51–58.

Glaister A (1992) Illustrated keys to late instar larvae of some Australian Elmidae. Coleopteran Identification Workshop, Murray–Darling Freshwater Research Centre, Albury (New South Wales, Australia), February 1992. [Unpublished]

Glaister A (1999) Guide to the Identification of Australian Elmidae Larvae (Insecta: Coleoptera). Cooperative Research Centre for Freshwater Ecology Identification Guide No. 21. Cooperative Research Centre for Freshwater Ecology, Thurgoona, NSW, 48 pp.

Grouvelle A (1896) Note sur les subdivisions génériques de Potamophiliens (Col.). Bulletin de la Société Entomologique de France 4: 77–79. https://doi.org/10.3406/bsef.1896.21786

Hinton HE (1935) Notes on the Dryopoidea (Col.). Stylops 4: 169–179. https://doi.org/10.1111/j.1365-3113.1935.tb00660.x

Jäch MA, Kodada J, Brojer M, Shepard WD, Čiampor F Jr (2016) World Catalogue of Insects Volume 14. Coleoptera: Elmidae and Protelmidae. Brill, Leiden, Boston, 318 pp. https://doi.org/10.1163/9789004291775

King RL (1865) Description of Australian species of Georyssides and Parnides. The Transactions of the Entomological Society of New South Wales 1: 158–161.

Kodada J, Jäch MA, Čiampor F Jr (2016) 19.2 Elmidae Curtis, 1830. In: Beutel RG, Leschen RAB (Eds) Coleoptera, Beetles, Volume 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). In: Beutel RG, Kristensen NP (Eds) Handbook of Zoology, Arthropoda: Insecta, Second Edition. Walter de Gruyter, Berlin, 561–589. https://doi.org/10.1649/0010-065x(2007)61[492:cbvmas]2.0.co;2

Lambert P, Maier CA, Leschen RAB (2014) A new species and lectotype designations for New Zealand *Hydora* (Elmidae: Larainae) with a world checklist. New Zealand Entomologist 2014: 1–20. https://doi.org/10.1080/00779962.2014.963910

Lawrence JF, Britton EB (1994) Australian Beetles. Melbourne University Press, Carlton, Victoria, 192 pp. https://doi.org/10.1071/9780643100695

McKie BGL, Cranston PS (1998) Keystone coleopterans? Colonization by wood-feeding elmids of experimentally immersed woods in south-eastern Australia. Australian Journal of Marine and Freshwater Research 49: 79–88. https://doi.org/10.1071/mf97086

McKie BG, Pearson RG, Cranston PS (2005) Does biogeographical history matter? Diversity and distribution of lotic midges (Diptera: Chironomidae) in the Australian Wet tropics. Austral Ecology 30: 1–13. https://doi.org/10.1111/j.1442-9993.2005.01408.x

Newton AF, Matthews EG, Muona J (2000) John F. Lawrence — coleopterist *par excellence*. Invertebrate Taxonomy 14: 721–731. https://doi.org/10.1071/it00041

Satô M (1973) Notes on dryopoid beetles from New Guinea. Pacific Insects 15(3–4): 463–471.

Shorthouse DP (2010) SimpleMappr, an online tool to produce publication-quality point maps. https://www.simplemappr.net [Accessed on 7.14.2021]

Spangler PJ, Brown HP (1981) The discovery of *Hydora*, a hitherto Australia-New Zealand genus of riffle beetles, in austral South America (Coleoptera: Elmidae). Proceedings of the Entomological Society of Washington 83: 595–606.

Surbakti S, Balke M, Hendrich L (2021) Discovery of the Australian diving beetle *Neobidessodes mjobergi* (Zimmerman, 1922) in New Guinea (Coleoptera, Dytiscidae, Hydroporinae). Check List 17(2): 633–636. https://doi.org/10.15560/17.2.633

Yeates DK, Monteith GB (2008) 13. The invertebrate fauna of the Wet Tropics: Diversity, endemism and relationships. In: Stork N, Turton S (Eds) Living in a dynamic tropical forest landscape. Wiley-Blackwell, UK, 178–191. https://doi.org/10.1002/9781444300321.ch13

ZooKeys 1073: 119–175 (2021)
doi: 10.3897/zookeys.1073.57241
https://zookeys.pensoft.net

CHECKLIST

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

An annotated checklist of the amphibians and reptiles of North Padre Island, Texas, USA, with comparisons to adjacent barrier island and mainland herpetofauna

Mike Duran[1]

1 *220 Rainbow Dr. № 12083; Livingston, TX 77399, USA*

Corresponding author: Mike Duran (pmlodingi@yahoo.com)

Academic editor: Anthony Herrel | Received 11 August 2020 | Accepted 26 September 2021 | Published 29 November 2021

http://zoobank.org/09630BBB-42CD-40CA-AF43-B86FB8B7470A

Citation: Duran M (2021) An annotated checklist of the amphibians and reptiles of North Padre Island, Texas, USA, with comparisons to adjacent barrier island and mainland herpetofauna. ZooKeys 1073: 119–175. https://doi.org/10.3897/zookeys.1073.57241

Abstract

Padre Island is the world's longest barrier island and includes the longest stretch of undeveloped barrier island in the world. Largely due to harsh environmental conditions and difficult access, only cursory and incomplete checklists and subjective estimates of abundance have been produced. The results of an inventory of amphibians and reptiles of North Padre Island conducted 2002–2020, including the results of extensive field surveys conducted 2002–2003, are reported herein. Natural history museum and iNaturalist records are summarized and compared among North and South Padre and Mustang islands and the mainland portion of the seven counties in which the islands occur. The conservation status of rare species and extirpation of others is noted. The morphology and taxonomic status of some unique occurrences are discussed. Eleven species of amphibians and 39 species of reptiles presently occur or have occurred naturally or as introduced or accidental species on North Padre Island. Twelve species of amphibians and 50 species of reptiles occur or have occurred on North Padre, South Padre, and Mustang islands. Thirty-one species of amphibians and 93 species of reptiles have been reported from the seven counties in which the islands occur.

Keywords

Reptiles, amphibians, checklist, inventory, Padre Island, Texas, Mustang Island, North Padre Island, conservation, historical record, museum, iNaturalist

Introduction

Extending for 178 km along the southern Texas coast, from Packery Channel in Corpus Christi to the Rio Grande River delta at the southern tip of the state, Padre Island is the world's longest barrier island (Fig. 1; Tunnell and Judd 2002; National Park Service 2020). It is part of a barrier island chain that extends discontinuously along most of the Texas coast. Padre Island was divided into North and South Padre islands (NPI and SPI) when the Mansfield Channel was dredged in 1957. Historically, Mustang and Padre islands were separated by Corpus Christi Pass, before Packery Channel was dredged through the pass in 2005. North Padre Island is 122 km long and encompasses ~ 50,000 hectares. Including the frequently immersed tidal flats, the width of the island varies from ~ 275 m to ~ 11.5 km. The width of the consistently terrestrial part of the island varies from ~ 275 m to ~ 4.5 km. The northern 4.4 km of North Padre Island, within the Corpus Christi city limits, is urbanized and includes numerous saltwater canals and a few small man-made freshwater ponds. The southern 114 km of North Padre Island lies within the Padre Island National Seashore (PINS), established in 1962, which contains the longest undeveloped stretch of barrier island in the world (Tunnell and Judd 2002). Prior to this inventory, only cursory and incomplete checklists, based on limited or no field work, have been produced (Rabalais 1975; Baker and Rabalais 1978). This is the first inventory that includes extensive field work, as well as verification and enumeration of museum and other verifiable records.

Formation of Padre Island and the Laguna Madre

Several models have been proposed to explain the formation of Padre and other barrier islands. The consensus among coastal geologists today, while recognizing that no one model exclusively explains barrier island formation, postulates that at the end of the Holocene, ~ 5,000–4,500 years ago, rising sea levels reached ~ 4.6 m above where they are today, and sandbars and shoals parallel to the shoreline began to form. When the sea reached its current level, ~ 2,800–2,500 years ago, those sandbars and shoals coalesced to form Padre Island and created bays and lagoons between the island and the mainland (LeBlanc and Hodgson 1959; Tunnel 2002).

Padre and other barrier islands are ever-changing as winds and currents regularly alter beaches, dunes, and tidal inlets. During extreme tidal events, freshwater wetlands and grasslands may be flooded with saline water from the Gulf of Mexico and hypersaline water from the inland lagoon. Dunes erode to depressions and flats. Storm surges sometimes alter the island suddenly, creating wash-over channels, closing or opening of passes, and flooding inland lagoons with sea water.

The lagoon formed inland of Padre Island, the Laguna Madre, was mostly isolated from the Gulf of Mexico prior to the dredging of Mansfield Channel in 1957 and received little freshwater inflow; together with the Laguna Madre de Tamaulipas, it became the largest of only six hypersaline bays and lagoons in the world (Javor 1989; Tunnell 2002). Prior to the dredging of the Gulf Intracoastal Waterway, the Laguna

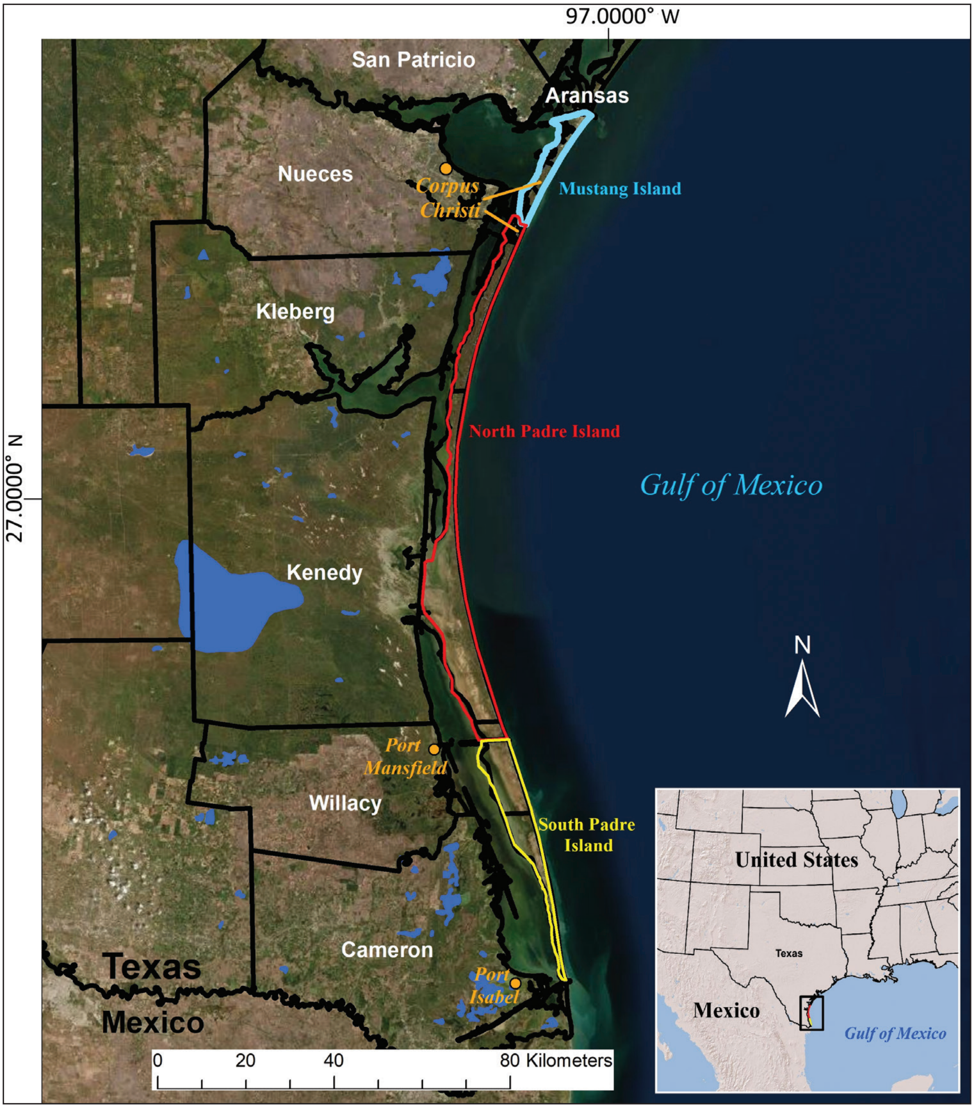


Figure 1. Map of seven-county study area including the South Texas barrier islands.

Madre was separated into the Upper Laguna Madre and Lower Laguna Madre by a frequently inundated land bridge, which appears on most maps as the Saltillo Flats, but is locally known by various names, including the Salt Flats, Kenedy Flats, Laguna Madre Flats, and most commonly, the Land Cut, a reference to the Intracoastal Waterway, which was cut through the flats in the 1940s. Salinity levels in the Upper Laguna Madre have been moderate in recent years: Olsen (2014) measured a mean salinity level of 44.1 psu (practical salinity units in parts per thousand concentration of sodium chloride) for the period of his study (1982–2012). Historically, the salinity of the upper Laguna Madre has varied from brackish (0.5–30 psu), after wet hurricanes, to brine (> 80 psu), during droughts, and has reached extremes over 100 psu, a level toxic to most organisms (Tunnell 2002). Due to relatively greater sea water and freshwater exchange, the salinity of the Lower Laguna Madre, while consistently hypersaline, has never risen to the briny extremes of the Upper Laguna Madre.

Vegetation, ecological zones, and climate

Laine and Ramsey (1998) developed a Geographic Information System (GIS) coverage layer for PINS which grouped vegetation into 12 categories. They calculated that ~ 28% of landscape within PINS was composed of areas that were mostly not vegetated by vascular plants (thus mostly unsuitable for amphibians and reptiles), including algal flats (~ 22%), unconsolidated shore (~ 5%), and wash-over channels (~ 1%). They calculated that 22% of PINS occurred within the Laguna Madre. Of the remaining habitats, Laine and Ramsey (1998) calculated that 45.6% are classified as emergent wetlands and inland water, 28.5% are classified as grasslands, and 12.5% are classified as sparsely vegetated. Nelson et al. (2000) reported 456 species of plants in 77 families and 259 genera from PINS. They reported that the five most common families are Poaceae (20.8%), Asteraceae (12.5%), Fabaceae (9.6%), Cyperaceae (6.4%), and Euphorbiaceae (4.2%). Diamond et al. (2017) added 36 new species to the PINS plant list and delineated 16 terrestrial plant associations within PINS, among which grasslands made up 48.0% of the vegetation, tidal saline vegetation made up 33.19%, dune and foredune communities together made up 9.37%, and herbaceous wetlands made up 8.74%. A few shrublands and woodlands accounted for < 1% of the vegetation.

While plant communities on North Padre Island are generally interdigitating and unevenly distributed, an idealized spatial vegetation profile is helpful to visualize the distribution of ecological zones from the Gulf of Mexico, proceeding westward to the Laguna Madre (adapted from Judd et al. 1977 and Diamond et al. 2017):

1. A forebeach zone at the shoreline of the Gulf of Mexico is unvegetated but sometimes partially to entirely littered with planktonic marine plants in the genus *Sargassum*.
2. A Gulf facing, sparsely vegetated, back-beach and foredune zone (Fig. 2a), usually not more than 50 m wide, within which the most conspicuous vegetation includes beach morning-glory (*Ipomoea imperati*), shoreline purslane (*Sesuvium portulacastrum*), and goat's foot convolvulus (*I. pes-caprae*). Grasses and forbs such as sea oats (*Uniola paniculata*) and beach evening primrose (*Oenothera drummondii*) are also apparent among patches of bare sand.
3. Just westward of the foredunes, a moderately vegetated rolling dune/swale complex (Fig. 2b) occurs where dunes that may reach 10 m elevation or more surround interstitial wetter swales. This complex includes at least three plant associations that make up ~ 8.2% of island vegetation (Diamond et al. 2017). Among the most conspicuous plants in this zone are sea oats (*U. paniculata*), camphorweed (*Heterotheca subaxillaris*), wooly croton (*Croton punctatus*), and partridge pea (*Chamaecrista fasciculata*.
4. An emergent wetland zone (Fig. 2c), most apparent on the northern part of the island, occurs as low-lying mid-island flats and depressions or ephemeral pools and lakes. Semi-aquatic and salt-tolerant plants apparent in this zone include cattails (*Ty-*

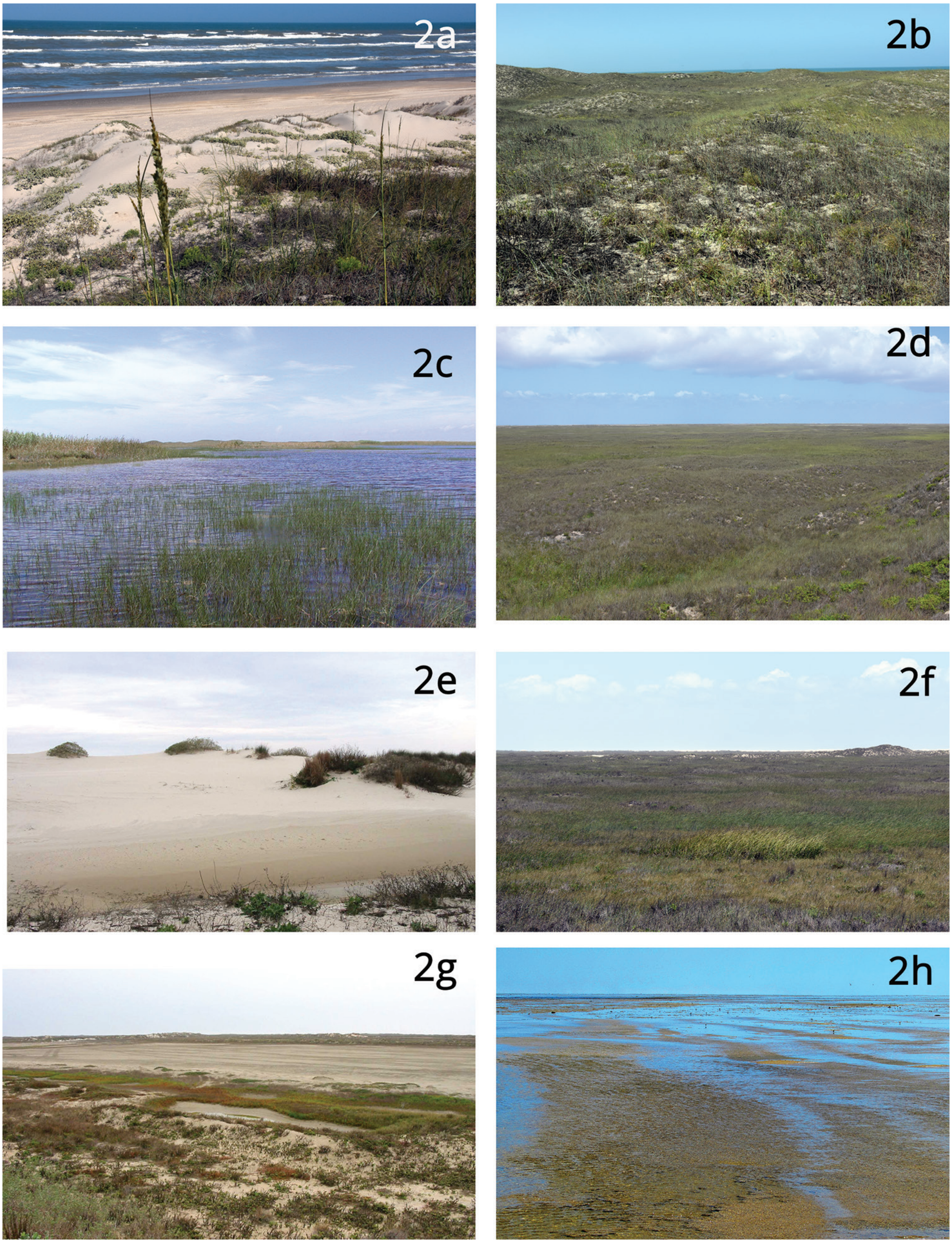


Figure 2. Major ecological zones of North Padre Island **a** back beach and foredunes **b** dune/swale complex **c** emergent wetlands **d** mid-island grasslands **e** sand dunes (back island dunes) **f** grassland/wetland matrix **g** saline flats **h** wind tidal flats (photograph by John Karges).

pha domingensis), cordgrass (*Spartina* sp.), and sedges, including common threesquare (*Schoenoplectus pungens*), beaksedges (*Rhynchospora* sp.), umbrella-sedges (*Fuirena* sp.), and fimbrys (*Fimbristylis* sp.). This zone includes ~ 16 ha of near-monoculture stands of the invasive common reed (*Phragmites australis*), which mostly occurs in and around a narrow 6-km ephemeral lake that begins ~ 22 km south of Packery Channel, but it is present in many wet areas throughout the island.

5. Mid-island grasslands (Fig. 2d), where seacoast bluestem (*Schizachyrium littorale*), gulfdune paspalum (*Paspalum monostachyum*), and bushy bluestem (*Andropogon glomeratus*) are dominant. The Seacoast Bluestem – Gulfdune Paspalum Grassland plant association makes up ~ 48% of island vegetation (Diamond et al. 2017). The generalized profile does not adequately describe the spatial setting of grasslands, which often occur as an overlapping matrix with emergent wetlands (Fig. 2e). Padre Island grasslands are infrequently flooded and relatively species-rich mid-island rolling flats dotted with low (mostly 0.5–1.5 m) vegetated dunes.
6. Sand dunes (Fig. 2f), sometimes called "back-island dunes," mostly occur within a few hundred meters of the Laguna Madre but may occur in any part of the island. They are composed of deep, dry, and shifting sands and are sparsely vegetated to unvegetated.
7. Saline flats (Fig. 2g) are irregularly tidally inundated and range from sparsely vegetated to relatively densely vegetated with halophytic species such as bushy sea oxeye (*Borrichia frutescens*), turtleweed (*Batis maritima*), saltgrass (*Distichlis spicata*), and shoregrass (*Monanthochloe littoralis*.
8. Wind tidal flats (Fig. 2h) are unvegetated or covered with a mat of the alga *Lyngbya confervoides*.
9. The Laguna Madre, a hypersaline lagoon, the ecological health of which depends on the health of seagrass meadows. According to Onuf (2006), ~ 75% of the substrate of the Laguna Madre is covered by seagrasses, mostly shoal grass (*Halodule wrightii*) and manatee grass (*Syringodium filiforme*).

According to NOAA (2021), Padre Island becomes considerably drier from the northern end at Corpus Christi, which receives 80.5 cm of rainfall per year, to the midpoint at Port Mansfield which receives 65.8 cm per year. Port Isabel, at the southern end of Padre Island, receives ~ 73.4 cm per year. The vegetation of North Padre Island gradually becomes less dense, north to south, i.e., the northern end vegetation is relatively lush and dense, while much of the landscape near either side of the Mansfield Channel is sparsely vegetated with extensive areas of bare sand.

Average annual temperatures become slightly warmer, north to south, with Corpus Christi at 22.3 °C, Port Mansfield 22.8 °C, and Port Isabel 23.1 °C. In some years, temperatures never drop below freezing. Most of the rainfall occurs in late summer and early fall, particularly at the southern end, where Port Isabel receives ~ 35% of its annual rainfall in September and October (NOAA 2021; https://www.ncdc.noaa.gov/cdo-web).

Materials and methods

A review of the relevant literature and museum specimens was conducted, through 08 October 2020, for the five counties in which the islands occur (Cameron, Kenedy, Kleberg, Nueces, Willacy) and for the two counties adjacent to Corpus Christi Bay (Aransas and San Patricio; hereafter "the seven counties"). Museum records were reviewed in September 2021, and new species added after 08 October 2020 are included. Research grade iNaturalist records for the South Texas barrier islands were compiled through 08 October 2020. Research grade iNaturalist observations of new species added between 08 October 2020 and 12 September 2021 are also included. For the most recent review of the museum database, I obtained most of the records through Vertnet.org (2021). The museum and iNaturalist searches of the seven counties captured a few records from San José Island, Harbor Island, South Bird Island, and other islands in the Laguna Madre and Corpus Christi Bay. Those records are labelled "other islands" (**OI**).

For the 2002–2003 surveys, I used ArcView 3.3 with the Hawth Tools extension, Random, to randomly select fifteen study sites on North Padre Island within six ecological zones (see previous section for discussion of ecological zones) within three geographical zones. Herpetofauna were sampled in six ecological zones: 1) back-beach and foredunes, 2) dune/swale complex 3) grasslands, 4) wetlands, 5) grassland/wetland complex, and 6) sand dunes. Herpetofauna were not sampled on the forebeach, saline flats, or wind tidal flats. The northernmost study site, just inside the PINS boundary, 13.8 km south of Packery Channel, was 102 km north of the southernmost study site, 250 m north of the Mansfield Channel. Two sites were selected non-randomly so that wetlands would be adequately sampled. The original design was based on ecological zones delineated by Laine and Ramsey III (1998), the only spatial vegetation layer available at that time. Subsequent vegetational analyses, all references to plant associations, and scientific and common names for plants of PINS, follow Diamond et al. (2017). Unless another source is cited, distance and area measurements were calculated using ArcGIS 10.8 (ESRI 2011).

Aquatic surveys were conducted opportunistically at all permanent ponds and most ephemeral pools from ~ 18 km south of Packery Channel to ~ 27 km south of Packery Channel and at ephemeral pools that occurred within or near the randomly selected study sites. During 2002 and 2003, road-searching and calling frog surveys were conducted from the southern end of Park Road 22, north to the intersection of Park Road 22 with State Highway 360. Calling-frog surveys were conducted and audio-recorded opportunistically (during and after heavy rainfall), and at predetermined points for 10 minutes (after the methodology of Mossman et al. 1998; North American amphibian monitoring program protocol 2012). Seines, dip nets, and funnel-type minnow traps were used to sample tadpoles, sirens, and newts. Turtles were trapped in hoop traps baited with sardines and chicken livers and were observed with binoculars and verified with photos. Calling-frog, road searching, and some visual encounter surveys continued, intermittently, into 2019.

Field work and trap installation and removal was performed by a team that consisted of The Nature Conservancy and National Park Service (**NPS**) personnel and volunteers. For terrestrial and semi-aquatic species, our team installed two variations of drift-fence/pitfall arrays. The first consisted of three equally spaced drift-fence arms, which originated at a center 19-liter pitfall buried to the rim and extended 7 m to 19-liter pitfalls at the ends and at midpoints, so that each array included seven pitfalls. The second type of array consisted of a 1.2 m × 1.2 m × 45.7 cm box, constructed after the design of Burgdorf et al. (2005), with a plywood top and

Figure 3. Reptile and amphibian trap array in grassland near the midpoint of North Padre Island. Two of four ~ 15 m arms of the array have been installed. *Cemophora lineri* (Texas scarletsnake) was captured in the center box at this study site.

bottom, hardware cloth wrapped around the sides, and funnel entrances built from hardware cloth on each of the four sides of the box (Fig. 3). A drift fence originating at each funnel opening extended approximately 15 m from the box. A 19-liter pitfall was buried to the rim at the end of each fence. Drift fences, fashioned from hardware cloth or nylon erosion-control fencing, were 91.4 cm high and were buried 20–25 cm in the ground. Traps were opened periodically May-October 2002. Turtle trapping was conducted in May 2003. Visual encounter surveys were conducted along transects within a square kilometer surrounding the study site random point. Visual encounter surveys were also conducted opportunistically and non-randomly throughout the island in areas which may have been under-sampled by the random-sampling protocol. Voucher specimens for each species and any specimens found dead on roads or in traps were collected and deposited in the University of Texas Biodiversity Collections (**TNHC**) or the Biodiversity Research and Teaching Collections at Texas A&M University (**TCWC**). Only tissue was collected from federally or state listed species. Most captured animals were photographed.

Scientific and common names follow Crother (2017), except for the genera *Bufo* (Pauly et al. 2009), *Masticophis* (Myers et al. 2017), and *Rana* (Yuan et al. 2016).

This work was performed under the authority of Texas Parks and Wildlife Department scientific research permit SPR-0302-204, US National Park Service scientific research and collecting permits PAIS-2003-SCI-0008, PAIS-2009-SCI-0012, and PAIS-2014-SCI-0006, and US Fish and Wildlife Service permit TE820085-0.

Abbreviations used in this paper are as follows:

AMNH	American Museum of Natural History
ASNHC	Angelo State Natural History Collection
BPP	Bayesian Phylogenetics and Phylogeography
GIS	Geographic information system
NOAA	National Oceanic and Atmospheric Administration
NPI	North Padre Island
NPS	US National Park Service
OI	other islands
PINS	Padre Island National Seashore
SPI	South Padre Island
TAMUK	Texas A&M University at Kingsville
TCWC	Biodiversity Research and Teaching Collections at Texas A&M University
TNHC	University of Texas Biodiversity Collections
UMMZ	University of Michigan Museum of Zoology
URL	Uniform Resource Locator (link)
VSR	Ventral scale rows

Results

Forty-four institutions held 14,830 specimens from the seven counties including 1751 specimens from the South Texas barrier islands held by 26 institutions and 47 specimens held by six institutions from San José Island, Harbor Island, South Bird Island, and other small man-made and natural islands in the Laguna Madre and Corpus Christi Bay (Table 1, 2; Suppl. material 1). There were 4904 iNaturalist research grade observations from the South Texas barrier islands as of 08 October 2020.

Eleven amphibian and 36 reptile species occur or have occurred naturally or as introduced or accidental species on North Padre Island (Table 2; Suppl. material 1). Of those, eight species of amphibians and 27 species of reptiles are represented or were represented by specimens in natural history collections. Three species of amphibians and nine species of reptiles that occur on North Padre Island are known only from iNaturalist observations; one of those amphibians is known only from an audio file. Two species of reptiles are known only from museum specimens.

Nine amphibian and 39 reptile species currently occur or historically occurred on Mustang Island. Twenty-one reptile species and four amphibian species occur or have occurred on SPI. In all, there are 47 species of reptiles and 12 species of amphibians that occur or have occurred naturally or as introduced or accidental

Table 1. Museums which contain amphibian and reptile specimens from the mainland portion of the seven adjacent counties (**ML**), Mustang Island (**MI**), North and South Padre (**NPI** and **SPI**), other small islands in the Laguna Madre and Corpus Christi Bay adjacent to Mustang Island (**OI**).

Inst code	Institution name	ML	MI	NPI	OI	SPI	Total
AMNH	American Museum of Natural History	4 900	32	338	28	51	**5 349**
TNHC	U. of Texas at Austin - Texas Natural History Collections	1 882	232	55	13	13	**2 195**
TCWC	Texas A&M U. Biodiversity Research and Teaching Collections	1 306	76	151	3	18	**1 554**
USNM	National Museum of Natural History, Smithsonian Institution	616	8	46	1	6	**677**
BUMMC	Baylor University, Mayborn Museum Complex	472	7	17		50	**546**
UTA	U. of Texas at Austin - Texas Natural History Collections	371	18	12		63	**464**
ASNHC	Angelo State Natural History Collection	108	19	315			**442**
KU	University of Kansas Biodiversity Institute	389	22	1	1	8	**421**
LSUMZ	Louisiana State University Museum of Natural Science	396	4	5		1	**406**
UMMZ	University of Michigan Museum of Zoology	404		1		1	**406**
UF	Florida Museum of Natural History	311	6	1	1		**319**
MVZ	Museum of Vertebrate Zoology, UC Berkeley	113	169	3			**285**
FMNH	Field Museum of Natural History	277					**277**
MCZ	Museum of Comparative Zoology, Harvard University	204		7			**211**
CM	Carnegie Museum of Natural History	156	5	11			**172**
SDNHM	San Diego Natural History Museum	162	2	1			**165**
LACM	Natural History Museum of Los Angeles County	100	16	1			**117**
UCM	University of Colorado Museum of Natural History	83	12	2			**97**
UMNH	Natural History Museum of Utah	72				1	**73**
ANSP	Academy of Natural Science Philidelphia	65					**65**
CHAS	Chicago Academy of Sciences	65					**65**
UBCBBM	University of British Columbia Beaty Biodiversity Museum	59					**59**
NCSM	North Carolina Museum of Natural Sciences	57					**57**
CAS	California Academy of Sciences	54	1				**55**
CUMV	Cornell University Museum of Vertebrates	49				1	**50**
MSUM	Michigan State University Museum	45					**45**
UAZ	University of Arizona Museum of Natural History	44					**44**
UTEP	University of Texas at El Paso Biodiversity Collections	36	1	1			**38**
BYU	Monte L. Bean Museum, Brigham Young University	29				2	**31**
OMNH	Sam Noble Oklahoma Museum of Natural History	17				7	**24**
CLO	Macaulay Library Audio and Video Collection	21					**21**
AUM	Auburn University Museum of Natural History	19					**19**
FHSM	Fort Hays Sternberg Museum of Natural History	10	6	1			**17**
SLU	Southeastern Louisiana University	8	2				**10**
GSU	Georgia Southern University	7	1				**8**
NBMB	New Brunswick Museum	8					**8**
ISM	Illinois State Museum	7					**7**
MSB	Museum of Southwestern Biology	7					**7**
PMNS	Perot Museum of Nature and Science	5		2			**7**
BSNS	Buffalo Society of Natural Sciences	5					**5**
MPM	Milwaukee Public Museum	5					**5**
YPM	Yale Peabody Museum	3		0			**3**
PBDB	Paleobiology Database	2					**2**
OSUM	Sam Noble Oklahoma Museum of Natural History	2					**2**
Total		**12 951**	**639**	**971**	**47**	**222**	**14 830**

Table 2. Museum and iNaturalist records of amphibians and reptiles of the South Texas barrier islands. **ML** = mainland; **MI** = Mustang Island; **NPI** = North Padre Island; **SPI** = South Padre Island; **OI** = San José Island (in Aransas Co.) and other natural and manmade islands in the Laguna Madre and Corpus Christi Bay.

Taxon	iNaturalist Observations				Museum specimen records						All
	MI	NPI	SPI	iNatTot	MI	ML	NPI	OI	SPI	MusTot	totals
AMPHIBIA	144	206	37	387	144	5 789	64	3	33	6 033	6 420
Anura	144	206	37	387	144	4 797	64	3	33	5 041	5 428
Bufonidae		30	18	94	132	1 028	9			1 169	1 263
Bufo cognatus						4				4	4
Bufo debilis						38				38	38
Bufo horribilis						2				2	2
Bufo nebulifer	46	18	18	82	8	447	7			462	544
Bufo speciosus					124	528				652	652
Bufo woodhousii		12		12		8	2			10	22
Rhinella marina						1				1	1
Eleutherodactylidae	3		4	7		184			3	187	194
Eleutherodactylus planirostris			2	2					2	2	4
Eleutherodactylus campi	3		2	5		184			1	185	190
Hylidae	64	95	14	173	3	1 052	15		28	1 098	1 271
Acris blanchardi						72				72	72
Hyla cinerea	9	21		30	1	486	14			501	531
Hyla squirella	55	66	10	131	2	80			28	110	241
Hyla versicolor complex						19				19	19
Osteopilus septentrionalis			1	1							1
Pseudacris clarkii		8		8		239	1			240	248
Pseudacris streckeri						80				80	80
Smilisca baudinii				3		76				76	79
Microhylidae	14	11		25		512	2		2	516	541
Gastrophryne carolinensis	14	9		23		3	2			5	28
Gastrophryne olivacea		2		2		364				364	366
Hypopachus variolosus						145			2	147	147
Ranidae	16	9	1	26	4	851	8	2		865	891
Rana berlandieri	14	7	1	22	3	597	7			607	629
Rana catesbeianus	2	1		3	1	76				77	80
Rana sphenocephala		1		1		178	1	2		179	180
Scaphiopodidae	1	61		62	5	1 170	30	1		1 206	1 268
Scaphiopus couchii						794				794	794
Scaphiopus hurterii	1	61		62	5	235	30	1		271	333
Spea bombifrons						90				90	90
Spea multiplicata						51				51	51
Caudata						992				992	992
Ambystomatidae						132				132	132
Ambystoma mavortium						132				132	132
Salamandridae						217				217	217
Notophthalmus meridionalis						216				216	216
Notophthalmus viridescens						1				1	1
Sirenidae						643				643	643
Siren intermedia						643				643	643
REPTILIA	1 317	2 637	563	4 517	495	7 162	907	44	189	8 797	13 314
Crocodylia	321	1	174	496		5				5	501
Alligatoridae	321	1	174	496		5				5	501
Alligator mississippiensis	321	1	174	496		5				5	501

Taxon	iNaturalist Observations				Museum specimen records						All
	MI	NPI	SPI	iNatTot	MI	ML	NPI	OI	SPI	MusTot	totals
Squamata	704	2 504	227	3 435	476	6 403	889	41	175	7 984	11 419
Sauria	508	1 910	216	2 634	424	3 105	773	21	171	4 494	7 128
Anguidae	9	1 107	1	1 117	13	101	18	3	1	136	1 253
Ophisaurus attenuatus	9	1 107	1	1 117	13	101	18	3	1	136	1 253
Crotaphytidae						1				1	1
Crotaphytus collaris						1				1	1
Dactyloidae	455	139	145	739	3	201				204	943
Anolis carolinensis	53	30	19	102	3	191				194	296
Anolis sagrei	402	109	126	637		10				10	647
Eublepharidae						2				2	2
Coleonyx brevis						2				2	2
Gekkonidae	7	38	3	48	2	220	2			224	272
Hemidactylus mabouia						4				4	4
Hemidactylus turcicus	7	38	3	48	2	216	2			220	268
Iguanidae						5				5	5
Ctenosaura acanthura						1				1	1
Ctenosaura pectinata						3				3	3
Ctenosaura similis						1				1	1
Phrynosomatidae	14	509	53	576	385	1 816	718	14	155	3 088	3 664
Cophosaurus texanus						2				2	2
Holbrookia propinqua	13	509	49	571	379	966	717	10	154	2 226	2 797
Holbrookia subcaudalis						75				75	75
Phrynosoma cornutum			1	1	6	180	1	2		189	190
Sceloporus consobrinus						117				117	117
Sceloporus cyanogenys						5				5	5
Sceloporus grammicus						195				195	195
Sceloporus olivaceus	1		3	4		139		1	1	141	145
Sceloporus variabilis						136		1		137	137
Urosaurus ornatus						1				1	1
Scincidae	2	37	2	41	2	268	11		1	282	323
Plestiodon obsoletus	1	6		7		54	7			61	68
Plestiodon tetragrammus			2	2		132			1	133	135
Scincella lateralis	1	31		32	2	82	4			88	120
Teiidae	21	80	12	113	19	491	24	4	14	552	665
Aspidoscelis gularis			7	7	1	380			6	387	394
Aspidoscelis laredoensis						1				1	1
Aspidoscelis sexlineatus	21	80	5	106	18	110	24	4	8	156	262
Serpentes	196	594	11	801	52	3 298	116	20	4	3 490	4 291
Colubridae	166	584	9	759	45	2 594	94	19	4	2 756	3 515
Arizona elegans	7	6	1	14	6	41	8		1	56	70
Cemophora lineri		1		1		12	1			13	14
Coluber constrictor		11		11		90	2			92	103
Coniophanes imperialis						64				64	64
Diadophis punctatus	1			1							1
Drymarchon melanurus						83				83	83
Drymobius margaritiferus						18				18	18
Farancia abacura						3				3	3
Ficimia streckeri						11				11	11
Haldea striatula						43				43	43
Heterodon kennerlyi						3				3	3
Heterodon platirhinos		3		3	3	15	8			26	29
Hypsiglena jani						7				7	7
Lampropeltis annulata		5		5	4	37	15			56	61
Lampropeltis calligaster						10				10	10
Lampropeltis gentilis	2			2							2
Lampropeltis getula complex						13		1		14	14
Lampropeltis holbrooki	14			14	2	24				26	40
Lampropeltis splendida	2			2		12				12	14
Leptodeira septentrionalis						13				13	13
Masticophis flagellum	25	61	5	91	12	133	25		3	173	264

Taxon	iNaturalist Observations				Museum specimen records						All
	MI	NPI	SPI	iNatTot	MI	ML	NPI	OI	SPI	MusTot	totals
Masticophis schotti						122				122	122
Nerodia clarkii	43	1		44	3	45		16		64	108
Nerodia cyclopion						5				5	5
Nerodia erythrogaster						20				20	20
Nerodia fasciata						3				3	3
Nerodia rhombifer		4		4		163	2			165	169
Opheodrys aestivus						56				56	56
Pantherophis emoryi	19	19		38		161	4			165	203
Pantherophis obsoletus	1			1		17				17	18
Pituophis catenifer		4		4		79				79	83
Regina grahami						7				7	7
Rhinocheilus lecontei						10				10	10
Salvadora grahamiae			2	2		70				70	72
Sonora semiannulata						51				51	51
Storeria dekayi	1	13	1	15		188	1			189	204
Tantilla gracilis		9		9		52	3			55	64
Tantilla nigriceps						49				49	49
Thamnophis marcianus	10	33		43	14	341	8	1		364	407
Thamnophis proximus	41	413		454	1	519	17			537	991
Thamnophis sirtalis						4				4	4
Tropidoclonion lineatum		1		1				1		1	2
Elapidae						113				113	113
Micrurus tener						113				113	113
Leptotyphlopidae	1			1		102				102	103
Rena dulcis	1	1		1		102				102	103
Pythonidae						1				1	1
Python regius						1				1	1
Typhlopidae	1		1	2		6				6	8
Indotyphlops braminus	1		1	2		6				6	8
Viperidae	28	10	1	39	7	482	22	1		512	551
Agkistrodon contortrix						3				3	3
Agkistrodon piscivorus						106		1		107	107
Crotalus atrox	28	7	1	36	7	363	3			373	409
Sistrurus tergeminus		3		3		10	19			29	32
Testudines	292	132	162	586	19	754	18	3	14	808	1 394
Cheloniidae	88	64	35	187	11	1	12		11	35	222
Caretta caretta	2	10	1	13	3		2		1	6	19
Chelonia mydas	81	26	23	130	2	1	4		8	15	145
Eretmochelys imbricata		2	1	3	4		2		1	7	10
Lepidochelys kempii	5	26	10	41	2		4		1	7	48
Chelydridae	1	1		2							2
Chelydra serpentina	1	1		2							2
Dermochelyidae			1	1			3			3	4
Dermochelys coriacea			1	1			3			3	4
Emydidae	187	65	109	361	1	405	3	3	2	414	775
Malaclemys terrapin						34			2	36	36
Pseudemys nelsoni			7	7							7
Terrapene carolina	2			2		3				3	5
Terrapene ornata	3			3		29		2		31	34
Trachemys scripta						8				8	8
Trachemys scripta elegans	182	65	95	342	1	331	3	1		336	678
Trachemys scripta scripta			7	7							7
Kinosternidae	15	2		17	7	80				87	104
Kinosternon flavescens	15	2		17	7	80				87	104
Testudinidae						212			1	213	213
Gopherus berlandieri						212			1	213	213
Trionychidae	1		17	18		56				56	74
Apalone spinifera	1		17	18		56				56	74
Total Amphibians and Reptiles	1 461	2 843	600	4 904	639	12 951	971	47	222	14 830	19 734

species on North and South Padre and Mustang islands (hereafter "the South Texas barrier islands" or "the islands").

By comparison, 31 amphibian species and 93 reptile species occur in the seven counties that include or are adjacent to the barrier islands. Eleven species of amphibians and 22 species of reptiles that occur on the mainland, do not occur on the islands. Seven species of reptiles and one amphibian species that occur on Mustang Island do not occur on the other barrier islands. Five amphibian species and seven reptile species that occur on North Padre Island do not occur on the other islands. Three amphibian species and six reptile species that occur on South Padre Island are not known from the other barrier islands.

Six species recorded during the 2002–2003 surveys were first records of those species from North Padre Island: *Pseudacris clarkii* (spotted chorus frog), *Bufo woodhousii* (Woodhouse's toad), *Cemophora lineri* (Texas scarletsnake), *Pantherophis emoryi* (Great Plains ratsnake), *Gastrophryne carolinensis* (eastern narrow-mouthed toad), and *Hyla squirella* (squirrel tree frog). Subsequently, in coordination with staff at PINS, I confirmed four more species not previously known from North Padre Island: *Rana sphenocephala* (southern leopard frog), *Chelydra serpentina* (common snapping turtle), *Rena dulcis* (plains threadsnake), and *Bufo nebulifer* (gulf coast toad). The records for *R. sphenocephala*, *B. woodhousii, G. carolinensis*, and *C. serpentina* were the first records for Kleberg County (Seabury et al. 2005; Duran and Hall 2013; Walker 2019). *Cemophora lineri* and *Heterodon platirhinos* (eastern hognose snake) have not been observed on the island since our team captured specimens in 2002.

Species accounts

The species accounts that follow characterize and enumerate records for each current, past, or potential species or subspecies that occur, possibly occur, or were previously thought to occur, on Padre and Mustang islands. Specimens contained in museum collections, iNaturalist observations, and records based on verifiable photos are included. Audio recordings are included as Suppl. materials.

Results from this inventory (2002–2021) are compared to a checklist of amphibians and reptiles of PINS (only PINS; Rabalais (1975) and a checklist of the herpetofauna of North Padre Island and Mustang Island by Baker and Rabalais (1978). For some species, a short account adequately describes the significance of its presence on the island, while a lengthier account is presented to address the unique nature of some occurrences. I discuss ecological associations for specimens we captured or observed, which is not meant to imply that those species do not occur in other ecological associations. For all mentions of iNaturalist, the citation is iNaturalist.org (accessed 08 October 2020). For unique iNaturalist observations an URL is included, and links to all iNaturalist records from the islands are available in Suppl. material 1.

Class Amphibia

Order Anura

Family Bufonidae

***Bufo nebulifer* Girard, 1854**
Gulf Coast toad
Fig. 4a

Notes. There are six museum specimens of *B. nebulifer* from NPI, with imprecise locality information, collected in 1891 (USNM 45349–52 and 46150). Our team did not detect *B. nebulifer* during the 2002–2003 surveys. Baker and Rabalais (1978) reported that *B. nebulifer* was not known from NPI but that it was known from residential areas of Mustang Island. A *Bufo nebulifer* photographed in 2007 (photo voucher, TNHC 101563) by a PINS biologist became the first verifiable record in over a century; however, in recent years the *B. nebulifer* population on the NPI has gone from nearly undetectable to relatively common as 18 iNaturalist observations were posted 2017–2021. There have been 46 observations posted on iNaturalist from Mustang Island in recent years and 18 from SPI. I located 386 specimens from the seven counties, six specimens, all collected in the 1970s, from Mustang Island, and one specimen from South Padre Island, collected in 1891. Moore (1976) reported that *B. nebulifer* was present on Mustang Island during his 1971 study, but that it was less common than *B. speciosus* and that he did not observe evidence of *B. nebulifer* reproduction.

Bufo nebulifer breeds in ephemeral pools and wetlands but may be found in much drier habitats and under artificial lighting. The one specimen photographed during this inventory was found in the parking lot of the Malaquite Visitor Center within PINS.

***Bufo speciosus* Girard, 1854**
Texas toad

Notes. Baker and Rabalais (1978) reported that *B. speciosus* had been collected on the north end of NPI, but I found no other evidence that *B. speciosus* occurs or has occurred there or on SPI. Baker and Rabalais (1978) also reported that *B. speciosus* was abundant on Mustang Island, which the museum record supports: I located 121 specimens from Mustang Island, including 51 specimens collected on one night in 1968 and 24 specimens collected on one night in 1954. I did not find any specimens collected after 1968 from Mustang Island; however, Moore (1976) reported that *B. speciosus* was the most common anuran he observed during his 1971 study on Mustang Island. I found 580 specimens from the seven counties. It appears that *B. speciosus* has been extirpated from Mustang Island.

Bufo woodhousii Girard, 1854
Woodhouse's toad
Fig. 4b

Notes. The first record for *B. woodhousii* from NPI and Kleberg County was collected during the 2002–2003 surveys. Another specimen collected in 2004 was the basis for a Kleberg County record published by Seabury et al. (2005). The species was not mentioned by Rabalais (1975) or Baker and Rabalais (1978). The species is not known from Mustang Island or from the counties adjacent to Mustang Island. After our observations of *B. woodhousii* on NPI in 2002, this species was not recorded there again until an observation was posted to iNaturalist in September 2018.

Three specimens from Mustang Island in the TCWC collection were identified as hybrids of *B. woodhousii* and *B. speciosus* (TCWC 93746-48) by the collector (J. K. Baker). I examined those specimens and observed that two of the specimens have weak cranial crests, which are rarely, and then only indistinctly, present in *B. speciosus* but always present in *B. woodhousii*; one of the specimens appears to have a faint mid-dorsal stripe, which is rarely and then only weakly present in *B. speciosus*, but usually present in *B. woodhousii*. While these characteristics provide some morphological support for Baker's identification, the specimens fall within the range of variation for *B. speciosus*. Because *B. woodhousii* is not known from Mustang Island, hybrids are unlikely, but it is possible that *B. woodhousii* was extirpated before any observations were recorded.

Dixon (2013) reported that a disjunct population of *B. woodhousii* is known on the mainland from the southern Texas counties of Brooks, Cameron, Hidalgo, Kenedy, and Willacy. I found nine museum specimens from Brooks (1), Cameron (3), Hidalgo (1), and Kenedy (4) counties (Table 3). It seems likely that *B. woodhousii* occurs or occurred in the Sand Sheet portion of northern Willacy County, but I was unable to find a specimen or other verifiable record from that county. The species was not thought to occur in Willacy County by Brown (1950), Axtell (1963), or Raun and Gehlbach (1970). Tipton et al. (2012) and Dixon (2013) reported that the species may have been extirpated from the inland portion of the southern Texas counties, but an iNaturalist observation of an individual observed in Kenedy County on 29 October 2015 and submitted in 2018, became the first verifiable South Texas mainland record since 1975 (https://www.inaturalist.org/observations/13049736). During the 2002–2003 surveys, *Bufo woodhousii* was observed or captured mostly in emergent and ephemeral wetlands but was also observed and captured in dry and sparsely vegetated foredunes and in an asphalt parking lot.

Family Microhylidae

Gastrophryne carolinensis Holbrook, 1835
Eastern narrow-mouthed toad
Fig. 4c; Suppl. material 2

Notes. During the 2002–2003 surveys, I made several audio recordings of *G. carolinensis* (Suppl. material 2; iNaturalist observation https://www.inaturalist.org/observa-

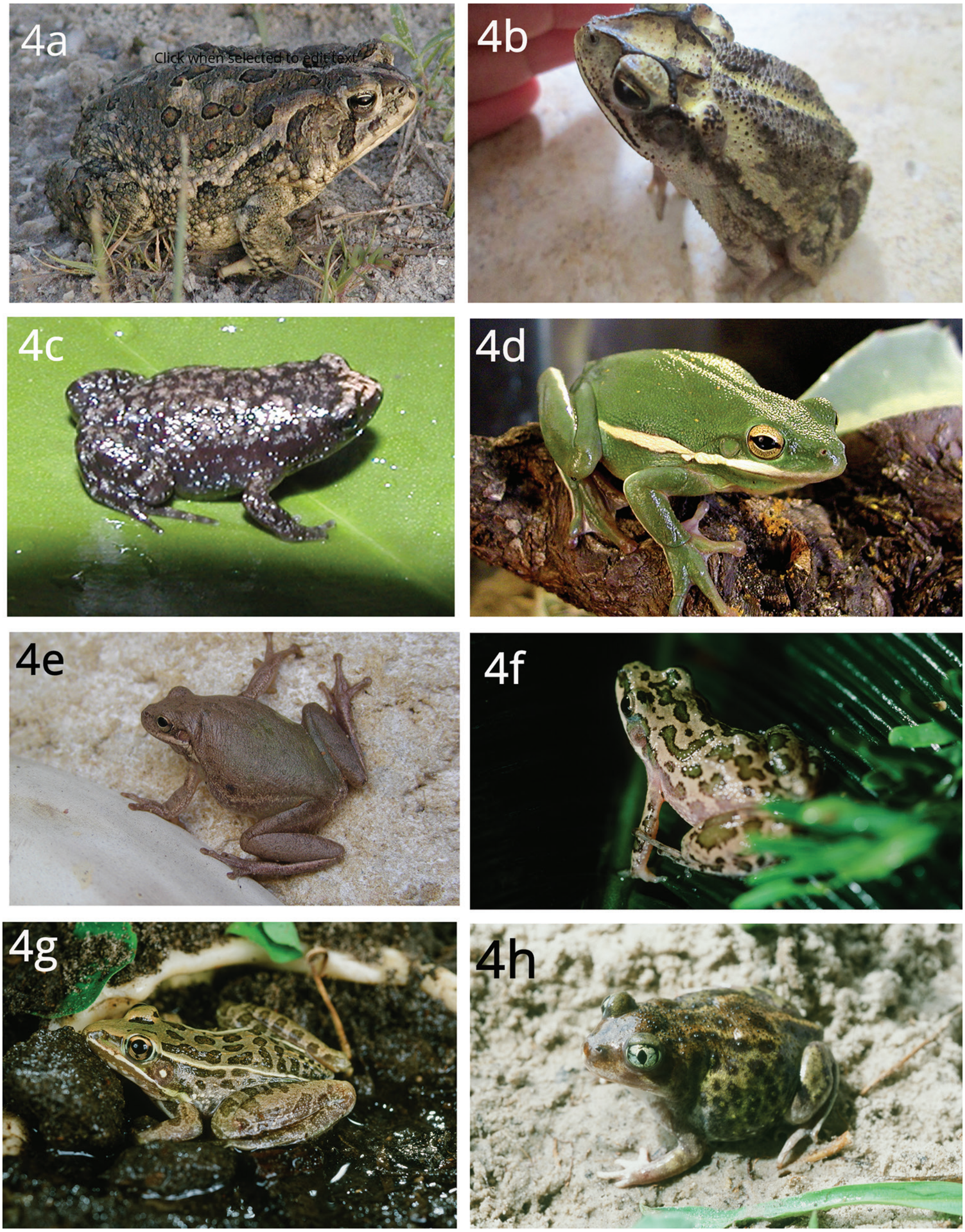


Figure 4. Eight Anurans found on North Padre Island **a** *Bufo woodhousii* (Woodhouse's toad) **b** *Bufo nebulifer* (Gulf Coast toad; photograph by Alicia Walker) **c** *Gastrophryne carolinensis* (eastern narrow-mouthed toad) **d** *Hyla cinerea* (Green treefrog) **e** *Hyla squirella* (squirrel treefrog) **f** *Pseudacris clarkii* (spotted chorus frog) **g** *Rana berlandieri* (Rio Grande leopard frog) **h** *Scaphiopus hurterii* (Hurter's spadefoot).

tions/12052215), which were the first verifiable records for that species from Kleberg County or from the South Texas barrier islands. I collected three *Gastrophryne* tadpoles from a seasonally inundated wetland and raised them until shortly after metamorpho-

Table 3. All known mainland occurrences of *Bufo woodhousii* in South Texas.

Inst Code	Cat #	Scientific Name	Date	County	Locality	Collector/observer
BUMMC	R 19809	Bufo woodhousii	10.9.1941	Kenedy	Armstrong	Brown, Bryce C.
TCWC	20830	Bufo woodhousii	11.4.1965	Brooks	12 mi SW Falfurrias	THS Field Meet
AMNH	A174386	Bufo woodhousii	2.7.1966	Kenedy	4.5 mi S Riviera	Ernest A. Liner & L.D. Wilson
AMNH	A183140	Bufo woodhousii	8.4.1968	Kenedy	3.4 mi N Armstrong on US Hwy 77	Allan H. Chaney
AMNH	A183141	Bufo woodhousii	8.4.1968	Kenedy	3.4 mi N Armstrong on US Hwy 77	Allan H. Chaney
AMNH	A183142	Bufo woodhousii	8.4.1968	Kenedy	3.4 mi N Armstrong on US Hwy 77	Allan H. Chaney
UTA	8382	Bufo woodhousii	8.8.1975	Cameron	Near San Benito	1, J. L. Darling
UTA	8383	Bufo woodhousii	8.8.1975	Cameron	Near San Benito	1, J. L. Darling
INAT	13049736	Bufo woodhousii	29.10.2015	Kenedy	Kenedy County (obscured)	Bryan Calk
KU	294840	Bufo woodhousii	na	Cameron	Brownsville	J.C. Lee

sis, when they could be identified as *G. carolinensis*. I photographed them (Fig. 4c), but a predator took the specimens before they could be preserved. Two museum specimens (TNHC 96013, 96014) collected in emergent wetlands in 2015 by PINS staff member Alicia Walker were the first specimens of *G. carolinensis* from Kleberg County and the South Texas barrier islands (Walker 2019). Five audio recordings of *G. carolinensis* were posted to iNaturalist in 2017. All specimens were collected or observed in emergent wetlands and ephemeral pools within the grassland/wetland matrix.

Gastrophryne olivacea Hallowell, 1856
Great Plains narrow-mouthed toad

Notes. There were no records for *G. olivacea* for the South Texas barrier islands until a photo was posted on iNaturalist in 2017 (https://www.inaturalist.org/observations/3447802; photo voucher TNHC 112542). I could not confirm the identification with certainty, but the observer describes characteristics not shown in the photo that would confirm the identification (T. LaDuc, pers. comm.). In March 2020, the first observation of *G. olivacea* from Mustang Island was entered on iNaturalist (https://www.inaturalist.org/observations/40571319). The animal shown is not a typical *G. olivacea* but neither is it typical *G. carolinensis*. I located 316 museum specimens from the mainland portion of the seven counties. Rabalais (1975) characterized the species as possible for PINS.

Family Eleutherodactylidae

Eleutherodactylus campi Stejneger, 1915
Rio Grande chirping frog

Notes. This species was once found mostly in northeastern Mexico and in the Rio Grande Valley of Texas but has expanded its range to include isolated populations in southern Louisiana and most of the eastern third of Texas to the Red River. It is often

Table 4. Sea turtle iNaturalist and museum records from the South Texas barrier islands. **MI** = Mustang Island; **NPI** = North Padre Island; **SPI** = South Padre Island iNat = iNaturalist observation (accessed 06 Oct 2020); Mus = Museum Specimens (Vertnet.org, accessed 02 Oct 2020).

	iNaturalist Observations					Museum Specimen Records				All Totals
	MI	NPI	SPI	iNatTot	MI	ML	NPI	SPI	MusTot	
Cheloniidae	**88**	**64**	**35**	**187**	**11**	**1**	**12**	**11**	**35**	**222**
Caretta caretta	2	10	1	13	3		2	1	6	19
Chelonia mydas	81	26	23	130	2	1	4	8	15	145
Eretmochelys imbricata		2	1	3	4		2	1	7	10
Lepidochelys kempii	5	26	10	41	2		4	1	7	48
Dermochelyidae			**1**	**1**			**3**		**3**	**4**
Dermochelys coriacea			1	1			3		3	4

found in plants and other items transported from the Rio Grande Valley (AmphibiaWeb 2021). Our team did not detect *E. campi* on NPI and there are no other records, but there are three iNaturalist observations from Mustang Island and two from SPI. There are three museum records from SPI and 184 museum records from the mainland portion of the seven counties. It seems likely that *E. campi* will eventually show up on NPI or that it is already there and has not yet been reported.

Eleutherodactylus planirostris Cope, 1862

Greenhouse frog

Notes. *Eleutherodactylus planirostris* is native to Cuba, the Bahamas, the Cayman Islands, and the Turk and Caicos Islands (AmphibiaWeb 2021) but is now found in coastal areas around the Gulf of Mexico from Florida to the Yucatan Peninsula of Mexico. There are two museum records from SPI. The same records were posted on iNaturalist: https://www.inaturalist.org/observations/62578832 and https://www.inaturalist.org/observations/62578829). The species has not been recorded in the rest of the study area.

Osteopilus septentrionalis Duméril & Bibron, 1841

Cuban tree frog

Notes. *Osteopilus septentrionalis* is native to the Bahamas, Cayman Islands and Cuba and has been introduced to other Caribbean Islands, most of Florida, and is spottily distributed in coastal areas from Georgia to Texas (AmphibiaWeb 2021). There is only one record for the species from the study area, an iNaturalist observation from Port Isabel in Cameron County. It was not found on the islands but is included here because of its potential to disrupt invaded ecosystems. It preys on a variety of animals including other amphibians and reptiles. In urban areas in Florida, *O. septentrionalis*, by predation and competition, has displaced some native frogs including (but not limited to)

Hyla cinerea (green treefrogs) and *H. squirella* (squirrel treefrog). The University of Florida Department of Wildlife Ecology recommends capturing and humanely euthanizing any *O. septentrionalis* found (Johnson 2017).

Family Hylidae

Hyla cinerea Schneider, 1799

Green treefrog
Fig. 4d

Notes. During and after rains during warmer months in 2002 and 2003 our team recorded conspicuous choruses of *H. cinerea* at all calling-frog stations and collected one of the 14 museum specimens from NPI. The historical record indicates that the species is considerably less common in other years. Rabalais (1975) characterized the species as "uncommon." I located 474 specimens from the mainland portion of the seven counties but only one specimen and nine iNaturalist observations from Mustang Island and no records from South Padre Island. Most observations during this inventory were in emergent wetlands during the breeding season.

The status of this species in southern portion of the study area is unclear. I heard choruses of *H. cinerea* at The Nature Conservancy's Southmost Preserve, in Cameron County, in 2002. There are ten museum specimens from Cameron County but no iNaturalist records. There are 34 museum specimens and zero iNaturalist observations from Kenedy County. The newest specimen from Cameron County was collected in 1941, and the newest specimen from Kenedy County was collected in 1976. The only record of any kind from the mainland portion of the counties south of Nueces County is an iNaturalist audio recording made in 2015 near Port Mansfield in Willacy County: https://www.inaturalist.org/observations/1480951. The status of the species in southern Texas deserves further study.

Hyla squirella Bosc, 1800

Squirrel treefrog
Fig. 4e; Suppl. material 3

Notes. There were no records for *H. squirella* from NPI until I photographed and audio recorded it during the 2002–2003 surveys. The calls were recorded in emergent wetlands during breeding season (Suppl. material 3; iNaturalist Observation https://www.inaturalist.org/observations/49370292), but I was unable to collect a specimen during those early surveys. There are two museum records from Mustang Island and 28 from South Padre islands but none from NPI. Sixty-six iNaturalist observations from NPI, 55 from Mustang Island, and ten from SPI based on photos and calls, were posted from 2015 to 2020. The species was not mentioned by Rabalais (1975) or by Baker and Rabalais (1978).

There is still only one mainland museum record collected from the study area south of Kleberg County of a specimen taken near Port Mansfield, in Willacy County in 2015. That specimen was also posted to iNaturalist where the collector commented that it was a single individual calling from a roadside ditch. The 28 museum records from Cameron County were all from a small area in the urbanized portion of southern SPI.

Pseudacris clarkii Baird, 1854

Spotted chorus frog
Fig. 4f

Notes. Our team did not observe or hear *P. clarkii* in 2002, but in 2003 I made audio recordings and collected a specimen (TCWC 93884) in temporarily flooded grasslands during drought-ending tropical rains. That specimen remains the only specimen of *P. clarkii* collected from the South Texas barrier islands, and among the eight research grade iNaturalist observations, the only observation based on a photo (https://www.inaturalist.org/observations/12007443). The species is not known from museum or iNaturalist records from SPI or Mustang islands. Only 18 of the 231 museum specimens from the study area have been collected since 1990. Rabalais (1975) categorized *P. clarkii* as "possible." Baker and Rabalais (1978) did not mention it.

Family Ranidae

Rana berlandieri Baird, 1859

Rio Grande leopard frog
Fig. 4g

Notes. There are seven museum specimens of *R. berlandieri* from NPI and three from Mustang Island residing in the collections I surveyed. I found 584 specimens from the mainland portion of the seven counties. During the 2002–2003 surveys, I collected two specimens and audio-recorded the species at most ephemeral and man-made ponds in the 24 km south of Packery Channel.

I collected one specimen that was particularly noteworthy because of its locality: TCWC 93885 was collected ~ 80.5 km south of the southern end of Park Road 22. That locality is a narrow, arid, and sparsely vegetated part of the island between two wash-over channel depressions that sometimes hold freshwater but are periodically flooded with saline water from the Gulf of Mexico and hypersaline water from the Laguna Madre. Permanent or long-lasting freshwater, usually associated with *R. berlandieri*, is not present. When I last visited that site in June 2018, the ponds only supported halophytic vegetation around its edges, which were crusted with salt. The survival strategies and dynamics of that population segment deserve further study.

Rana catesbeiana **Shaw, 1802**

American bullfrog

Notes. A 2018 iNaturalist observation, based on an audio file, is the first and only record of *Rana catesbeiana* on NPI (https://www.inaturalist.org/observations/8027494). Other experienced listeners have concurred on the identification of that call, but because of the poor quality of the recording, I cannot confirm with complete certainty that the call is that of *R. catesbeiana*. The NPI record is from the northern tip of the island, near Packery Channel. The species is relatively common in Aransas, Nueces, and San Patricio counties and much of the United States but uncommon in the counties adjacent to Padre Island. There were 77 museum specimens from the seven counties. The species requires relatively permanent freshwater for its long-lived larvae, therefore its habitat on NPI is probably limited to several small man-made ponds within the urbanized northernmost part of the island and three manmade ponds in the northern part of the Padre Island National Seashore. The lake that occurs near the middle of the island, from ~ 22.5 km south of Packery Channel to ~ 27 km south of Packery Channel is periodically dry but, in some years, might hold water long enough for *R. catesbeiana* reproduction. There is little to no habitat for the species in the southern 143 km of Padre Island. The species is a non-native and invasive in the western United States, where it competes with and preys on native fauna. Its recent arrival on North Padre and Mustang islands might be considered invasive.

Rana sphenocephala **Cope, 1886**

Southern leopard frog
Suppl. material 4

Notes. There is one *Rana sphenocephala* specimen from Padre Island (TNHC 65562), which was also the first and only specimen from Kleberg County (Duran and Hall 2013). There are no other records for the South Texas barrier islands or from the inland portion of the counties adjacent to Padre Island south of Nueces County. There are 176 museum specimens from the mainland counties adjacent to Mustang Island. In 2013, I made an audio recording of *R. sphenocephala* (Suppl. material 4; iNaturalist observation: https://www.inaturalist.org/observations/314642), which was only the second verifiable record for the islands and the first within PINS. That recording may include *R. berlandieri* calling at the same time, but that is not clear. The species was not mentioned by either Rabalais (1975) or Baker and Rabalais (1978).

Dorsolateral ridges inset posteriorly at the groin in *R. berlandieri* usually distinguish it from *R. sphenocephala*, but dorsolateral ridges of some *Rana* specimens from NPI are not distinctly inset. We examined many specimens in the field and could never say that any of them were distinctly typical of *R. sphenocephala*. While morphological differences between the species were not consistently differentiating, their calls are quite different and perhaps better evidence of their occurrence on the island than specimens or photos. The audio file of *R. sphenocephala* calling may also include *R. berlandieri* calling at the same time. Hillis (1981) reported on sympatric populations of three ranid species and identified pre-mating isolating mechanisms, including staggered breeding times and habitat.

Family Scaphiopodidae

Scaphiopus couchii **Baird, 1854**
Couch's spadefoot

Notes. I did not find verifiable records of *Scaphiopus couchii* from the South Texas barrier islands. It is mentioned here because Baker and Rabalais (1978) reported that a specimen had been collected "from a freshwater pond area along Park Road 22 north of the entrance to the National Seashore," but I did not locate that specimen. It may not exist or may have been re-identified. I found 792 *S. couchii* specimens from the mainland portion of the seven counties.

Scaphiopus hurterii **Strecker, 1910**
Hurter's spadefoot
Fig. 4h

Notes. I located 30 museum specimens from NPI, nine of which were collected during the 2002–2003 surveys. I found five museum specimens from Mustang Island and 235 from the mainland portion of the seven counties. There are 61 iNaturalist observations from NPI, one from Mustang Island and none from South Padre Island. *Scaphiopus hurterii* was captured 34 times during the 2002–2003 surveys at four study sites, all in flooded grasslands within grassland/wetland matrices. It was audio-recorded at every stop on the calling-frog survey route. The species is conspicuous during and after rains but nearly undetectable by the casual observer during dryer times.

Class Reptilia

Order Testudines
Families Cheloniidae and Dermochelyidae (sea turtles)

Padre Island National Seashore Division of Sea Turtle Science and Recovery has conducted a sea turtle monitoring, research, and recovery program since the 1970s (https://www.nps.gov/pais/learn/seaturtles.htm). The program is centered around monitoring and recovery of Kemp's Ridley Sea Turtle (*Lepidochelys kempii*) but has recorded the presence of four additional species: Loggerhead Sea Turtle (*Caretta caretta*), Green Sea Turtle (*Chelonia mydas*), Leatherback Sea Turtle (*Dermochelys coriacea*), Hawksbill Sea Turtle (*Eretmochelys imbricata*). Dozens of staff and volunteers patrol the beaches for Kemp's Ridley nests each summer. Eggs are excavated and hatched in the lab. Hatchling releases, which usually occur from June-August each year, are popular public events. I was not charged with conducting field surveys for sea turtles, but we did

Figure 5. Eight reptiles that occur on North Padre Island **a** *Eretmochelys imbricata* (Hawksbill sea turtle) **b** *Chelydra serpentina* (common snapping turtle) **c** *Malaclemys terrapin* (diamondback terrapin) **d** *Trachemys scripta* (pond slider) **e** *Ophisaurus attenuatus* (slender glass lizard) **f** *Hemidactylus turcicus* (Mediterranean house gecko) **g** *Holbrookia propinqua* (keeled earless lizard) **h** *Phrynosoma cornutum* (Texas horned lizard; photograph by Jerry Batey).

occasionally encounter sea turtles on the beach, including the Hawksbill Sea Turtle shown in Figure 5a. Table 4 is a compilation of iNaturalist observations and museum specimens of sea turtles from the islands and surrounding waters, but given the serendipitous nature of sea turtle observations, Table 4 does not accurately represent the true relative abundance of these species.

Family Chelydridae

Chelydra serpentina Linnaeus, 1758

Common snapping turtle
Fig. 5b

Notes. A photo taken by a PINS staff member in 2007 (TNHC 86867) is the only verifiable record of *Chelydra serpentina* from the South Texas barrier islands, though Baker and Rabalais (1978) reported that a live specimen had washed up on an NPI beach near the Malaquite Visitor Center. The species is not known from the counties adjacent to North and South Padre Island (Dixon 2013). I witnessed a PINS visitor attempting to release a red-eared slider (*Trachemys scripta elegans*) into the Gulf of Mexico surf in 2007 and suspect *C. serpentina* may have arrived on the island as a similar misguided rescue attempt. Baker and Rabalais (1978) speculated that freshwater Chelonians might be washed into the Gulf by flooding, then carried out of their native range by longshore currents. There is no evidence that *C. serpentina* occurs on the islands naturally.

Family Emydidae

Malaclemys terrapin Schoepff, 1793

Diamondback terrapin
Fig. 5c

Notes. There were no specimens or iNaturalist observations of *M. terrapin* from the South Texas barrier islands until one juvenile was collected, and another juvenile was photographed in an urbanized part of southernmost South Padre Island in February and March 2019 (Guadiana et al. 2020). The live specimen (photo voucher TNHC 114470; Fig. 5c), which was collected ~200 m west of the forebeach, is now housed in the Gladys Porter Zoo in Brownsville, Texas. The photo of the other specimen (TNHC 114630) appears to have been taken on the wet sand of the forebeach. Those localities are ~ 180 km south of the nearest localities in Corpus Christi Bay. Within the study area, there are 30 museum specimens from estuarine bays and marshes in Aransas, Nueces, and San Patricio counties. There are 80 museum specimens in all of Texas. Salt secreting glands allow *M. terrapin* to adjust to changing salinity, but there are no verifiable records from the hypersaline Laguna Madre, and it is rarely observed in 100% seawater; I found only one iNaturalist record (https://www.inaturalist.org/observations/21335833) and one museum specimen (TNHC 7421) from the seaward side of a Texas barrier island or peninsula: both were found on the Bolivar Peninsula, one near Rollover Pass and one near the mouth of Galveston Bay. Brackish marshes, usually associated with the species, are mostly absent along the shores of the Upper Laguna Madre and sparse along the shores of the Lower Laguna Madre. The species might enter the Upper Laguna Madre during times of lower salinity, then leave as salinity levels rise, a process characterized as “behavioral osmoregulation” by Dunson and Mazzotti (1989). The form that occurs in this part of the range is generally assigned to the subspecies *M. t. littoralis* (Texas diamondback terrapin), but the South Padre Island specimens could not be assigned to subspecies based on morphological characteristics described by Ernst and Lovich (2009) (Drew Davis, pers. comm.). Determining the subspecies by genetic or morphological means might provide a clue about how these animals arrived on SPI so far out of their native range.

***Terrapene carolina* Linnaeus, 1758**
Common box turtle

Notes. There were three *T. carolina* museum records from the mainland portion of the study area and two iNaturalist observations from Mustang Island. The mainland occurrences are individual records separated by decades (Suppl. material 1), which suggests they are introductions, probably released pets. While the study area is on the edge of the range for the species, there is no evidence to suggest that it has established reproducing populations there.

***Terrapene ornata* Agassiz, 1857**
Ornate box turtle

Notes. There are no museum specimens of *T. ornata* from the South Texas barrier islands and no records of any kind from NPI or SPI. Three iNaturalist observations from Port Aransas on Mustang Island have been entered since 2013. Baker and Rabalais (1978) also reported having seen two *Terrapene* sp. road-killed on Mustang Island. I found 24 museum specimens from the adjacent counties. Box turtles are popular pets. In Texas they may be legally taken from the wild for non-commercial purposes. They often escape or are released back into the wild, far from where they were collected.

***Trachemys scripta* Wied-Neuwied, 1838**
Pond slider
Fig. 5d

Notes. *Trachemys scripta* is easily observed on any visit to the three manmade ponds within the Padre Island National Seashore. Our team trapped 24 pond sliders in hoop traps in those ponds. No other turtle species were observed. *Trachemys scripta* was photographed but not collected. I located four museum specimens from NPI, two from Mustang Island, and 287 from the adjacent counties. *Trachemys scripta* from the study area is usually assigned to the subspecies *T. s. elegans* (red-eared slider), but there are seven iNaturalist observations (several of which appear to be the same individual) identified as *T. s. scripta* (yellow-bellied slider) from the South Padre Island Birding and Nature Center at the southern tip of SPI. The yellow-bellied slider is native to the eastern half of the US, but both subspecies have established introduced populations all over the US and Europe.

Family Kinosternidae

Kinosternon flavescens **Agassiz, 1857**
Yellow mud turtle

Notes. Baker and Rabalais (1978) reported that *K. flavescens* was common on Mustang Island and that it had been observed on the northern end of PINS, but the only verifiable records for *K. flavescens* from NPI I found were two iNaturalist observations of road-killed turtles from the northern end of the island entered on 22 and 24 September 2017. The nearest mainland record from those observation is 13.6 km across the Laguna Madre near Oso Bay, and the nearest mainland freshwater habitat for *K. flavescens* is 7.7 km across the Laguna Madre. Because Baker and Rabalais (1978) reported that the species was "common" on Mustang Island, and because there are seven museum records from Mustang Island since 1960 and 15 iNaturalist observations more recently, it is likely that *K. flavescens* is reproducing on Mustang Island. The species is not easily trapped in hoop traps, so our methodology might not have been adequate to determine if *K. flavescens* occurs as a reproducing population on NPI. There are 79 museum specimens from the seven counties and no records from SPI.

Family Testudinae

Gopherus berlandieri **Agassiz, 1857**
Texas tortoise

Notes. Several occurrences of *Gopherus berlandieri* on the South Texas barrier islands have been recorded, but there is little evidence that suggests the occurrences are natural. One specimen of a *G. berlandieri* (AMNH 9307) appears to have been collected on the southern end of Padre Island in 1917. Baker and Rabalais (1978) found a *G. berlandieri* with a painted carapace dead on the road on Mustang Island and a dead tortoise on the beach on NPI. Baker and Rabalais (1978) also reported that a live tortoise had been found just north of the Mansfield Channel, which divides North and South Padre islands; it is not clear whether they observed that animal themselves or if that was an anecdotal record. I did not find those specimens in natural history collections. Judd and Rose (2000) speculated that *G. berlandieri* populations occur on the barrier islands but offered no evidence of naturally occurring populations. In 2002, Frank Judd told me that he once found a live *G. berlandieri* on SPI but believed that was a human-aided occurrence and did not believe that tortoises occur on SPI naturally (Frank Judd, pers. comm.).

Little habitat for *G. berlandieri* is present on the South Texas barrier islands, and I could find only two reports of naturally occurring tortoises on deep sand: Neill (1958; citing pers. comm. with JR Dixon) reported a tortoise from "sand dunes" near Port Isabel on the mainland, and an iNaturalist observation posted in 2021 appears to show tortoise tracks on mainland sand dunes, also near Port Isabel (https://www.inaturalist.org/observations/74145383). While *G. berlandieri* often occurs on soils with a moderate sand content in the upper soil horizon, it is usually found on moderately clayey or loamy soils (Bury and Smith 1986; Kazmeier et al. 2001). Habitat of *G. berlandieri* at the Atascosa National Wildlife Refuge, adjacent to the Laguna Madre in Cameron County, was described by Bury and Smith (1986) as "lomas" (clay dunes). There is some evidence that the composition of vegetation on the islands also may not be suitable for tortoises, e.g., Scalise (2011) found cactus in 98% of scat of *G. berlandieri* that represented 29.8% of their diet. Cacti (mostly *Opuntia* sp.) occur on the barrier islands but not in the densities usually associated with *G. berlandieri* (Scalise 2011). Habitat for *G. berlandieri* appears to be limited on the South Texas barrier island and there is no evidence of reproducing populations, but the re-appearance of single individuals, probably via human-aided transport, is likely to continue to occur.

Class Reptilia

Order Crocodilia
Family Alligatoridae

Alligator mississippiensis Daudin, 1802

American alligator

Notes. There are no museum records from the South Texas barrier islands and only two from the seven counties, but the museum database is not a good indicator of the abundance an animal whose adult length may be 1.8–5 m (Conant and Collins 1998). While the species is relatively common in the southern and southeastern United States, it is listed by the U.S. Fish and Wildlife Service as threatened by similarity of appearance to rare crocodilians. There is no evidence that alligators have occurred on NPI naturally, but adult alligators have appeared there several times over the years, accidentally or via human introduction; it would not be surprising if it appeared there as an accidental visitor again.

Just prior to the 2002–2003 surveys, NPS had introduced three *A. mississippiensis* to a manmade pond within PINS according to the Natural Resource Manager at the time (Darrel Echols, pers. comm.). In consultation with experts, NPS later determined that alligators had probably never occurred naturally on the island and removed them. In 2007 an individual was found on Big Shell Beach, ~ 40 km south of the southern end of Park Road 22. That animal had been tagged ~ 500 km away, across the Gulf of Mexico at a national wildlife refuge in Louisiana (Buzz Botts, National Park Service, pers, comm.). I added that observation to iNaturalist (https://www.inaturalist.org/observations/20228712), which is the only iNaturalist observation on NPI. Then in 2021, PINS reported on their Facebook page that another alligator washed up on NPI which had also been tagged in Louisiana https://www.facebook.com/FriendsPINS/posts/173996127976128). Those occurrences provide support for the hypothesis that Gulf of Mexico currents play a role in the transport of out-of-range species to the South Texas barrier islands. Alligators will survive in manmade ponds for years, but natural populations require marshy habitat with access to deeper fresh or brackish water (Joanen and McNease 1972). Those habitat types are not found on NPI or the mainland bordering the Upper Laguna Madre, but they are found to the north and south where the species occurs in Nueces and Cameron counties. In Kleberg County, alligators are found within and around the city of Kingsville where they were probably introduced. They are not found west of NPI and the Laguna Madre in Baffin Bay. The Cameron County population is separated from the main alligator population by ~ 125 km of unsuitable habitat, which raises a question about their natural occurrence there, but alligators were first reported from Cameron County by Baird (1859) based on a report by US army officer Stewart Van Vliet, probably around the time of the Battle of Resaca de Palma (on 9 May 1846), during the Mexican-American War. There are 321 iNaturalist observations from the water in and around Mustang Island, and 174 iNaturalist observations from SPI, in or around the Laguna Atascosa Federal Wildlife Refuge. The observations from Mustang and SPI probably include multiple observations of the same individuals.

Order Squamata
Suborder Sauria
Family Anguidae

Ophisaurus attenuatus Cope, 1880

Slender glass lizard
Fig. 5e

Notes. *Ophisaurus attenuatus* is one of the most frequently observed reptiles on NPI. I located 17 museum specimens and 1012 iNaturalist observations. During the 2002–2003 surveys, the species was trapped 14 times at all eight study sites between the north end of PINS and the 35-mile-marker. A phenomenon resembling a mass movement of glass lizards was reported on iNaturalist from 24 February to 20 June 2017, when Jon McIntire of Corpus Christi, Texas, reported 938 observations, mostly on Park Road 22 and Bird Island Basin Road on NPI. He reported that the surrounding grasslands had recently been control-burned. The species is less frequently seen on Mustang Island, with five iNaturalist observations and 16 museum specimens. There is only one iNaturalist record and no museum records for the species on SPI; potential observers on SPI rarely venture into the island far from the beach, so the species is probably more common on SPI than that single record might imply. There were 91 museum records from the mainland portion of the seven counties.

Family Gekkonidae

Hemidactylus turcicus Linnaeus, 1758

Mediterranean house gecko
Fig. 5f

Notes. *Hemidactylus turcicus* is an introduced species native to the Mediterranean region. The earliest specimens I found from Texas were collected in Cameron County in 1953 (TNHC 23057–23060 It is now common on and around manmade structures on the South Texas barrier islands and across the southern United States. The only museum specimens of *H. turcicus* from NPI were collected in 1980 and 1982 (TCWC 93823 and 93845). We did not observe the species during the 2002–2003 surveys, but between 2017 and 2020, 38 iNaturalist observations from NPI were entered; all but two of those were observed in the northernmost residential part of the island. There are four museum specimens and seven iNaturalist observations from Mustang Island. I found 200 museum specimens from the mainland portion of the seven counties.

Family Phrynosomatidae

Holbrookia propinqua Baird & Girard 1852

Keeled earless lizard
Fig. 5g

Notes. *Holbrookia propinqua* is probably the most abundant reptile on the South Texas barrier islands, certainly the most observable. I located 724 museum specimens from NPI and 1916 specimens from the seven counties. During the 2002–2003 surveys, it was trapped 93 times. Another 128 observations were recorded, and hundreds of casual observations by the survey team were not recorded. On NPI, it is most abundant in the back beach/foredunes ecological zone, but it is common on deep dry sand throughout the island. A primary component of *H. propinqua* habitat is deep sand, which is the primary soil component on the islands and of an ~ 800,000 ha area that extends westward from the Land Cut and includes parts of several counties in southern Texas. That area, commonly known as the Sand Sheet, has been altered by grazing, farming, and invasive, nonnative, grasses, mostly Kleberg bluestem (*Dichanthium annulatum*) and buffelgrass (*Pennisetum ciliare*), which has led to its decline on the mainland.

Holbrookia subcaudalis Cope, 1880

Tamaulipan spot-tailed earless lizard

Notes. The catalogue of reptiles and amphibians for the collection kept at Texas A&M, Kingsville (TAMUK) contained an entry for *H.* (*lacerata*) *subcaudalis* (TA-

MUK 1879) collected in 1968 from the “Dunn Ranch” on NPI, but that specimen was missing when I examined the collection in 2002 and missing when the collection was transferred to AMNH in 2005. Prior to the creation of PINS, most of NPI was part of the Dunn Ranch. When PINS staff speak of the Dunn Ranch, they are generally referring to one of several sites where historical ruins remain. According to the collectors of the TAMUK specimen, the locality was probably the Green Hill site, ~ 1.3 km SW of the 25-mile marker (Thomas Shirley, pers. comm.) although it is possible that they were referring to the Black Hills site, ~ 1.5 km southwest of the 10-mile marker. Our team did not observe the lizard during a nonrandom visual encounter search at the southernmost site and did not trap it in a pitfall array ~ 2 km north of the Green Hill site. I conducted walking surveys at the site six times in subsequent years.

The questionable Dunn Ranch specimen was the only specimen of that species from the South Texas barrier islands. Axtell (1998) commented that the locality or identification of that specimen was probably erroneous. The species is known from just across the Laguna Madre in Kleberg County, along the clayey shores of Baffin Bay, but it avoids deep sand, so it is not likely to occur on NPI.

Both *H. lacerata* and *H. subcaudalis* have been the focus of a considerable amount of survey work and research following a 2011 ruling by the U. S. Fish and Wildlife Service that a listing of threatened or endangered, pursuant to the Endangered Species Act of 1973, may be warranted.

Phrynosoma cornutum Harlan, 1825

Texas horned lizard
Fig. 5h

Notes. Rabalais (1975) listed *P. cornutum* as “possible” for PINS and Baker and Rabalais (1978) reported that it was “common” on Mustang and northern Padre Island in the 1950s and 1960s. I found seven museum specimens from Mustang Island; the most recent of those was 1967. I found one specimen collected on NPI in 1967 but no iNaturalist records. I located 126 museum specimens from the inland portion of the seven counties; of those, 108 had collection dates, and only 15 of the specimens with dates were collected after 1970, and only two were collected since 1987. There are five museum specimens and possibly an obscured iNaturalist record from a small natural island in Corpus Christi Bay. I received a photo of a horned lizard from that island taken in 2013 and have since received other anecdotal accounts of recent observations of *P. cornutum* on that island. *Phrynosoma cornutum* has apparently been extirpated from the South Texas barrier islands. It is listed as a threatened species in Texas.

Subfamily Sceloporinae

Four species of Sceloporine lizards are known from the mainland portion of the seven counties: *Sceloporus consobrinus* (prairie lizard), *S. olivaceus* (Texas spiny lizard), *S. variabilis* (rosebellied lizard), and *S. cyanogenys* (blue spiny lizard). No Sceloporine lizards are known from NPI or Mustang Island, but a specimen of *S. olivaceus* was collected on South Padre Island in 1916 (AMNH 8159), and two iNaturalist observations from the urbanized portion of southernmost South Padre Island were entered in March and May of 2020. Sceloporine lizards are unlikely to occur in the undeveloped portions of the islands, partly due to lack of perching structure, but they might be able to establish reproducing populations if introduced to urbanized parts of the islands.

Family Polychrotidae

***Anolis carolinensis* Voigt, 1832**
Green anole

Notes. *Anolis carolinensis* is an abundant fixture of urban backyards and woodlands throughout the southeastern United States. There are no museum records from NPI and only two from Mustang Island but there are iNaturalist records from all urbanized areas of the South Texas barrier islands. Across its range, *A. carolinensis* is rarely observed in undeveloped areas and is probably absent from undeveloped portions of the islands due to lack of perching structures. I found 84 museum records from the seven counties.

***Anolis sagrei* Duméril & Bibron, 1837**
Brown anole

Notes. *Anolis sagrei* is another mostly urban species, native to Cuba and The Bahamas. It was first collected in the United States in Florida in 1935. The first records from Texas were specimens collected in Cameron County in 1986. I found nine museum specimens from the seven counties and 637 iNaturalist observations from the islands since 2009. One hundred nine of those came from NPI, all from the urbanized northern tip of the island.

Family Scincidae

***Plestiodon obsoletus* Baird & Girard, 1852**
Great Plains skink
Fig. 6a

Notes. Our team captured *P. obsoletus* ten times at five different localities from near the northern boundary of PINS to 56 km down the island, in wetlands, xeric grasslands, and dunes. We collected three specimens. There were seven specimens from NPI in museums and 47 specimens from the seven counties but none from South Padre or Mustang Islands. There is one iNaturalist record for Mustang Island based on a photo taken in 1985 (https://www.inaturalist.org/observations/2578244).

Scincella lateralis **Say, in James, 1822**

Little brown skink
Fig. 6b

Notes. I located four museum specimens and 31 iNaturalist observations of *S. lateralis* from NPI and two museum specimens and only one iNaturalist record from Mustang Island. There are no records from SPI. I found 82 museum specimens from the seven counties. Our team captured *S. lateralis* at seven localities from the northern boundary of PINS to 56 km down the island. All except one of the observations were in moist grasslands/wetlands. The exception was an individual that was trapped at study site 11, which was in sparsely vegetated foredunes.

In earlier versions of their online list, NPS had listed *Plestiodon septentrionalis* (prairie skink) as a species that occurs on PINS mostly based on a specimen in the NPS vertebrate collection (formerly PAIS 2025; now TCWC 93804) that had been identified as *P. septentrionalis* but has since been reidentified as *S. lateralis*. There is no evidence that the *P. septentrionalis* occurs on the barrier islands but no reason to think that it might not.

Family Teiidae

Aspidoscelis gularis **Baird & Girard, 1852**

Common spotted whiptail

Notes. *Aspidoscelis gularis* was classified as "uncommon" by Rabalais (1975). It was not mentioned by Baker and Rabalais (1978). Our team did not observe *A. gularis* during the 2002–2003 surveys. I found two specimens (AMNH 8157, 8158), collected in 1916, and one iNaturalist record (observed in 2017) from South Padre Island. I found three specimens labelled *A. gularis* from NPI (UMMZ 54001 and 54004 and ASNHC 235), but upon examination of photos and consultation with the curators, I determined that all three were *A. sexlineata*. There is one specimen from Mustang Island (TNHC 50473). The Mustang Island specimen is too faded to identify to species, and there is insufficient evidence to dispute the locality, but in my experience, unique localities represented by single specimens are often misidentifications or mislocations. The species is common in the inland portion of the seven counties, where I located 274 museum specimens. In Duran (2004) I reported that I found a museum specimen (AMNH R-168649) 4 km south of the Port Mansfield on South Padre Island, but I later determined that specimen probably came from the mainland side of the Laguna Madre.

Aspidoscelis sexlineata **Linnaeus, 1766**

Six-lined racerunner
Fig. 6c

Notes. *Aspidoscelis sexlineata* was captured and photographed 46 times. Team members recorded another 16 observations during visual encounter surveys and made many more casual observations. I located 24 specimens in museum collections from NPI, eighteen from Mustang Island, five from South Padre Island, and 145 specimens from the mainland. The species was observed in the back-beach, foredunes, grasslands, emergent wetlands, and dunes.

Trauth (1992) described a subspecies of the six-lined racerunner, the yellow-headed racerunner (*A. s. stephansae*; originally *A. s. stephansi*, emended by Trauth 1995), from Kenedy, Willacy Brooks, and Jim Hogg counties. The localities for some specimens Trauth (1992) examined to describe *A. s. stephansae* were within a sandy ecological zone just across the Laguna Madre from NPI. Trauth (1992) described *A. s. stephansae* as, on average, smaller (< 70 mm) than *A. s. sexlineata* (eastern six-lined racerunner), with a distinctive yellow coloration on the face. Some of the specimens that we captured had bright yellow faces extending from the snout to the nape (Fig. 6c). The snout to vent length was < 70 mm for all specimens during the 2002–2003 surveys. Another characteristic by which Trauth and McAllister (1996) distinguished the subspecies was the relative position of horizontal stripes: In contrast to other *A. sexlineata*, the yellow-headed race purportedly has no vertebral stipe, paravertebral stripes converge just posterior to the rump and extend onto the anterior one fourth of the tail, dorsolateral stripes extend onto the tail, and lateral stripes blend into the bright ventrolateral surface of the tail. Based on limited analysis, I could not determine if the NPI specimens could be assigned to *A. s. stephensae*.

iNaturalist recognizes the taxon, but no observations of *A. s. stephensae* have been entered, while 12 specimens have been identified as *A. sexlineata* within the taxon's purported range as defined by Trauth (1992). Because identification of the subspecies is based on external morphology and pattern, and apparently no one can identify it based on those characteristics, further analysis is needed to determine if this is a valid taxon.

Suborder Serpentes, Family Colubridae

Arizona elegans Dixon, 1960

Glossy snake

Notes. I found eight museum specimens of *Arizona elegans* from NPI, six from Mustang Island, and one from SPI (as of 08 October 2020). Another iNaturalist observation from SPI was entered in April 2021 and was deposited into the TNHC collection. I found 36 museum specimens from the seven counties. Since the species is nocturnal and often fossorial, historical records are not good indicators of its relative abundance. During the 2002–2003 surveys, we observed one *A. elegans*. Between 2013 and 2020, seven iNaturalist observations were entered for Mustang Island and six were entered for NPI. Rabalais (1975) referred to *A. elegans* on NPI as "fairly common." Baker and Rabalais (1978) referred to *A. elegans* as "common" on both NPI and Mustang Island. Glossy snakes in the study area are usually assigned to the subspecies *A. e. arenicolus* (Texas glossy snake).

Coluber constrictor Linnaeus, 1758

North American racer
Fig. 6d

Notes. I collected one road-killed *C. constrictor* (TCWC 93867) on Park Road 22, north of PINS where it passed through a flooded grassland/wetland. A team member observed one on the beach ~ 3 km south of the southern end of Park Road 22. Figure 6d is a PINS file photo of a *C. constrictor* on the beach, on wet sand near the surf. *Coluber constrictor* is a habitat generalist, but I did not find any mentions of *C. constrictor* on beaches in the literature. I found three iNaturalist records for *C. constrictor* on beaches in California, Florida, and Virginia. There are two museum specimens and eleven iNaturalist records from NPI but no records of any kind from Mustang or South Padre islands. There is an iNaturalist observation of a bird in flight carrying a *C. constrictor*; the photograph was taken on Mustang Island, but it is impossible to know where the bird caught the snake. There were 83 specimens from the mainland portion of the seven counties. Both Dixon (2013) and Werler and Dixon (2000) show the range of the subspecies, *C. c. oaxaca* (Mexican racer), extending from Mexico northeast along the coast to Aransas County, Texas. The racer I collected (TCWC 93867) was intermediate in key morphometrics between *C. c. oaxaca* and the *C. c. flaviventris* (yellow-bellied racer). Museum specimens of both subspecies are catalogued in each of the seven counties adjacent to the South Texas barrier islands. Werler and Dixon (2000) describe *C. c. flaviventris* as usually having seven supralabial scales and *C. c. oaxaca* as having eight, and both subspecies will usually have 17 or fewer dorsal scale rows at midbody. The specimen collected had a dark green dorsum and yellow ventrum, most like *C. c. flaviventris*, but it had six supralabials on one side and eight on the other and 15 dorsal scale rows, so it could not be assigned to subspecies based on those features. Burbrink et al. (2007) performed genetic analysis which appeared to indicate that *C. constrictor* may be composed of six independently evolving lineages not concordant with most recognized subspecies. No samples within the range of *C. c. oaxaca* were included in that analysis.

Drymarchon melanurus Cope, 1860

Central American indigo snake

Notes. I found one museum record for the islands (TAMUK 5526), a road-killed snake collected on Park Road 22, just north of the PINS entrance station. That specimen is among numerous specimens from the TAMUK collection (later moved to AMNH) that have been lost. I spoke with the collector and former curators and confirmed that the record is legitimate (Donna Shaver, Allan Chaney, pers. comm.). There were 64 museum records from the seven counties: only three of those were from the counties adjacent to Mustang Island. The Nature Conservancy ecologist, Lee Elliott, captured a *D. melanurus* in the surf near Bob Hall pier on the northern end of NPI and released

Figure 6. Eight reptiles that occur on North Padre Island **a** *Plestiodon obsoletus* (great plains skink **b** *Scincella lateralis* (little brown skink) **c** *Aspidoscelis sexlineatus* (six-lined racerunner) **d** *Coluber constrictor* (North American racer) **e** *Heterodon platirhinos* (eastern hognose snake) **f** *Lampropeltis triangulum annulata* (Tamaulipan milksnake) **g** *Masticophis flagellum* (coachwhip) **h** *Nerodia rhombifer* (diamondback watersnake).

it in the dunes (Lee Elliott, pers. comm.). Specimens from that part of the range are mostly identified as the subspecies *D. m. erebennus* (Texas indigo snake), which is a large, highly mobile, and conspicuous species. The absence of anecdotal reports and road-kills may indicate that the snake is an occasional visitor to the island. It is a powerful swimmer that probably crosses the Laguna Madre occasionally and might populate the island if conditions there became preferable, but historical and recent evidence does not indicate that it is or has been a permanent resident.

Heterodon platirhinos **Latreille, 1801**

Eastern hognose snake
Fig. 6e

Notes. Our team collected two road-killed specimens (TCWC 93872, TCWC 93873) and captured and examined three others during the 2002–2003 surveys. The road-killed specimens were surrounded by a grassland/wetland matrix. The trapped specimens were all from one location which was in a transition zone between sparsely vegetated foredunes and a more densely vegetated grassland on deep but stable sand. Photos of three of those specimens are the only iNaturalist records for the species from the South Texas barrier islands. There are eight museum specimens from NPI prior to the 2002–2003 surveys but no records of any kind from the South Texas barrier islands after that. Baker and Rabalais (1978) said that *H. platirhinos* on NPI was "one of the more common snakes on Mustang Island, particularly around the town of Port Aransas, which abounds with toads." The historical record does not support the Baker and Rabalais (1978) assessment, as there are only three museum specimens and no other type of records from Mustang Island. The last of the Mustang Island specimens was collected in 1991. Whether the apparent decline of *H. platirhinos* on Mustang Island is related to the previously discussed extirpation of *Bufo speciosus* (a primary prey item), should be investigated further. I found 15 museum specimens from the mainland portion of the seven counties.

Lampropeltis getula **Linnaeus, 1766**

Eastern kingsnake

Notes. There are no records for *Lampropeltis getula* from NPI or SPI. One specimen from NPI (UMMZ 224256) had been labelled "*L. getulus*," but in consultation with the curator of that collection, I determined that specimen was a mislabeled *L. triangulum*. Within the study area, two species or subspecies have been recognized: *L. g. holbrooki* (Stejneger 1903) and *L. g. splendida* (Baird & Girard 1853). Baker and Rabalais (1978) referred to *L. g. splendida* as "common" on Mustang Island and "possible" for NPI. Pyron and Burbrink (2009) proposed changes to the taxonomy and distribution boundaries of the *Lampropeltis getula* complex, which would elevate both subspecies to full species status. Widely followed taxonomic sources such as Crother et al. (2017), The Reptile Database (2021), and iNaturalist (2021) have adopted that taxonomy. Following that arrangement has created some confusion about the correct identification and taxonomy of kingsnakes on Mustang Island and the seven counties. Werler and Dixon (2000) noted that the seven counties adjacent to the South Texas barrier islands and much of central Texas lie within a broad area of intergradation between the subspecies, *L. g. splendida* and *L. g. holbrooki*, which led observers and collectors to identify specimens of both species or subspecies in the study area: Thirteen museum specimens were labelled *L. getula* ssp., 26 were labelled *L. holbrooki*, and twelve were labelled *L. splendida*. For this report I retained the subspecies arrangement of Blaney (1977) and used the verbatim museum labels for Table 2. There are 21 iNaturalist observations from Mustang Island identified as *L. holbrooki* and three identified as *L. splendida*. On Mustang Island, morphological characteristics of kingsnakes are sometimes more like *L.* (*g.*) *holbrooki* and sometimes more like *L* (*g.*) *splendida*, but it seems unlikely that there are two independently evolving kingsnake species on the island. Variation in coloration and pattern displayed by kingsnakes on Mustang Island should probably be regarded as phenotypic variations among genetically similar individuals, i.e., morphotypes, not different species.

Lampropeltis triangulum **Kennicott, 1861**

Milksnake
Fig. 6f

Notes. Our team observed four *L. triangulum* and took two as specimens (TCWC 93878, 93879) during the 2002–2003 surveys. Those observations were all within the grassland wetland matrix. Following the taxonomic arrangement prevalent at the time (Williams 1978), I labelled those specimens *L. t. annulata*. Ruane et al. (2014) proposed reducing the 14 previously recognized subspecies of *L. triangulum* to six species and redefined the distribution of those species. Widely followed taxonomic sources like Crother et al. (2017), iNaturalist (2021), and The Reptile Database (2021) adopted the Ruane et al. (2014) proposals. According to that arrangement, the species that occupied the seven counties would become *L. annulata*. Chambers and Hillis (2020) questioned the validity of the Ruane et al. (2014) analysis, stating that "over-reliance on the program Bayesian Phylogenetics and Phylogeography (BPP), without adequate consideration of its assumptions and of sampling limitations, resulted in over-splitting of species in this study." Chambers and Hillis (2020) did not propose a new taxonomic arrangement but demonstrated that the BPP program can be used to support "virtually *any* geographic partition of samples in this potential continental cline as species." Of the 14 specimens from NPI in museum databases, eight were originally labelled *L. t. annulata*, five were labelled *L. triangulum* ssp. and one was labelled *L. t. gentilis*. One museum specimen from Mustang Island was labelled *L. t. annulata* and three were labelled *L. triangulum* ssp. In Table 2, I retain the verbatim museum labels. On iNaturalist, which is following the Ruane et al. (2014) arrangement, two photos from Mustang Island have been identified as *L. gentilis*. The nearest mainland iNaturalist observation of *L. gentilis* is near Somerville, Texas, 323 km from the Mustang Island observations.

Masticophis flagellum Say, in James, 1822

Coachwhip
Fig. 6g

Notes. *Masticophis flagellum* was the most observed and most captured snake species during the 2002–2003 surveys. It was trapped 21 times at seven study sites, which spanned 94 km and four ecological zones: grasslands, emergent wetlands, sparsely vegetated foredunes, and dune/swell complexes. from Study Site 1 near Bird Island Basin to Study Site 17, near the Mansfield Channel. I took one specimen (TCWC 93880). There were 25 museum specimens from NPI, thirteen from Mustang Island, and 148 from the seven counties. There are 61 iNaturalist observations from NPI, 25 from Mustang Island, and five from SPI.

Nerodia rhombifer Hallowell, 1852

Diamondback watersnake
Fig. 6h

Notes. *Nerodia rhombifer* was observed four times and captured once near the man-made pond along the road to Bird Island Basin. There were two museum specimens from NPI and none from Mustang Island. There are four iNaturalist record for NPI, and none from Mustang Island. I found 163 specimens from the mainland portion of the seven counties. Mostly a fish eater and dependent on permanent fresh water, the species is probably only found on the northern end of NPI in and around the several manmade ponds.

Nerodia clarkii Baird & Girard, 1853

Saltmarsh Snake

Notes. *Nerodia clarkii* is regularly observed along the shorelines of Nueces, Corpus Christi, and Oso bays, and Mustang Island, but an iNaturalist observation of a road-killed specimen, near the northern end of NPI, just south of the Nueces County line, is the only verifiable occurrence of the species on NPI or in Kleberg County (https://www.inaturalist.org/observations/8105046). There are 33 iNaturalist observations and 18 museum records from Mustang Island. Forty-three more museum specimens have been taken around Corpus Christi Bay, in the counties of Nueces, San Patricio, and Aransas. The southern edge of the range of the species is an elastic boundary where the brackish water of Corpus Christi Bay meets the hy-

Figure 7. Comparison of *Cemophora lineri* (Texas scarletsnake) specimen from North Padre Island with *C. lineri* specimen from San Patricio County **a** *Cemophora lineri* (Texas scarletsnake) from North Padre Island **b** *Cemophora lineri* from San Patricio County. Note that the colors of the NPI specimen are duller than those of the scarletsnake from the mainland.

persaline water of the Laguna Madre. *Nerodia clarkii* could enter the upper Laguna Madre when higher precipitation lowers salinity, then retreat into Corpus Christi Bay when salinity rises, an example of "behavioral osmoregulation" (Dunson and Mazzotti, 1989).

Cemophora lineri Weinell & Austin 2017

Texas scarletsnake
Fig. 7a, b

Notes. There is only one record for *Cemophora lineri* from NPI or the South Texas barrier islands, an individual I captured in a grassland near the mid-point between the end of Park Road 22 and the Mansfield Channel in 2002 (photo voucher, TNHC 86866; Fig. 7a). Seemingly rare throughout the range, like other fossorial snakes, *C. lineri* may be more common than the sparse historical record implies; hundreds of square kilometers of suitable habitat within its range are privately-owned and largely inaccessible. It is listed as "threatened" by the state of Texas. Because of its rarity and the unique nature and atypical morphology of this lone barrier island specimen, a more detailed discussion follows.

Aufenburg (1948) collected the first specimens of what were probably *C. lineri* on U.S. Naval Air Station, Corpus Christi, on the mainland, near the northern end of NPI. At that time the nearest known occurrence of *Cemophora* sp. was > 1000 km from Auffenberg's observations, so it is difficult to fault Aufenburg for stating: "There is no doubt that these snakes were accidentally brought in from Pensacola, Florida, from which station we received much air cargo." It is not impossible that Auffenberg (1948) was right about the source of those snakes and the specimens were lost before they could be analyzed (Williams et al. 1966, citing personal communication with Auffenberg). Referring to that possibility, Brown (1950) called it "a doubtful species," but most researchers later concluded that those specimens were probably from southern Texas (Williams et al. 1966; Williams and Wilson 1967).

Williams et al. (1966) found that scutellation and other morphological features of the only two *Cemophora* specimens from southern Texas (AMNH 75307 [holotype] and BCB 10993 [paratype]) were distinctly different from *Cemophora* specimens known from the southeastern United States and described a new subspecies, *C. coccinea lineri* (Texas scarletsnake). During a more extensive review of the genus, Williams and Wilson (1967) confirmed that morphometrics of *C.* (*c.*) *lineri* were different from the two previously recognized subspecies, *C. c. coccinea* (Florida scarletsnake) and *C. c. copei* (northern scarletsnake).

Williams et al. (1966) reported that one of the more distinct differences between *C.* (*c.*) *lineri* and the southeastern *Cemophora* was the significantly higher number of ventral scale rows (VSR) for *C.* (*c.*) *lineri*: They found that the VSR count of 59 specimens of *C. c. coccinea* was 158–185 ($\bar{x}$= 174.0) and VSR count of 180 *C. c. copei* specimens was 150–180, ($\bar{x}$= 165.3). For the two *C.* (*c.*) *lineri* specimens available for the original description, VSR were 188 and 195, ($\bar{x}$= 191.5). The comparisons led Williams and Wilson (1967) to hypothesize that *C.* (*c.*) *lineri* was more closely related to the more geographically distant *C. c. coccinea* than to the nearer *C. c. copei*, which they attributed to climactic conditions that led to a splitting of *C. coccinea* during the Pleistocene. Weinell and Austin (2017) proposed elevating the subspecies to *C. lineri* based on their genetic analysis; that analysis indicated that *C. lineri* diverged from the *C. coccinea* in the Pliocene or early Pleistocene and that *C. lineri* is monophyletic, while *C. c. coccinea* and *C. c. copei* are paraphyletic. Crother et al. (2017) and other taxonomic sources adopted that taxonomy.

In addition to their genetic work, Weinell and Austin (2017) performed a phenotypic analysis of five southern Texas specimens (including the NPI specimen: TNHC 86866) and the two specimens used by Williams et al. (1966) in the original description. In rough concurrence with Williams et al. (1966), they found that *C. lineri* differed most distinctly from *C. coccinea* in the number of VSR (178–195; $\bar{x}$= 186.1). The results of that analysis provided evidence that the forms are morphologically dissimilar as well as genetically distant from the southeastern *Cemophora*. In reporting the VSR count, Weinell and Austin (2017) included the VSR count for the NPI specimen (178). Excluding the NPI specimen from that analysis would leave its VSR count outside the range of variation of other known specimens of *C. lineri* but within the range of variation and near the mean for *C. c. coccinea*. There are no published data on *C. lineri* morphometrics which includes more specimens, but in unpublished notes, The Nature Conservancy zoologist, John Karges, analyzed eleven morphometric features of the ten *C. lineri* specimens residing in natural history collections in the late 1970s (John Karges, pers. comm.): the VSR count of the NPI specimen is still well outside of the range of variation in VSR in that larger dataset (183–197, $\bar{x}$= 188.5).

As it is with other reptiles and amphibians on NPI, the colors of the *C. lineri* I photographed on NPI are duller than those of other *C. lineri* I have observed in the study area on the mainland. Figure 7a is the snake I captured on NPI and Figure 7b is a *C. lineri* I photographed in San Patricio County.

Pantherophis emoryi **Baird & Girard, 1853**

Great Plains ratsnake
Fig. 8a

Notes. During the 2002–2003 surveys, our team collected two road-killed *P. emoryi* of the four NPI specimens in museum databases (TNHC 85143, TCWC 93868). The road-kills were surrounded by inundated emergent wetlands within a grassland/wetland matrix. Our team captured and photographed three more specimens at two study sites; both sites were on the edge of an inundated emergent wetland surrounded by an extensive grassland/wetland matrix. Between 2015 and 2020, nineteen iNaturalist observations from NPI and 19 from Mustang Island were entered. Rabalais (1975) characterized the species as "possible." It was not mentioned by Baker and Rabalais (1978). I found 147 museum specimens from mainland portion of the seven counties.

Pituophis catenifer **Schlegel, 1837**

Gopher snake

Notes. I found no museum specimens of *P. catenifer* from the barrier islands, but an iNaturalist record of a 2006 observation (https://www.inaturalist.org/observations/2580986) was entered in 2016. Subsequently, three iNaturalist observations from the northernmost, urbanized part of the island, were entered for snakes observed in 2015, 2019, and 2020. Rabalais (1975) referred to *P. catenifer* as "uncommon." Given the sparse historical record, *P. catenifer*, a large-bodied snake that is probably capable of swimming across the Laguna Madre, may occur only as a vagrant on the islands, but further study might reveal that it occurs as a reproducing population. I located 74 museum specimens from the inland portion of the seven counties. In southern Texas, specimens are generally identified as the subspecies, *P. c. sayi* (bullsnake).

Storeria dekayi **Holbrook, 1839**

Dekay's brown snake

Notes. There is one 1982 museum specimen of *S. dekayi* from NPI, which is the only specimen from the South Texas barrier islands. Our team did not detect the species during the 2002–2003 surveys. There are now 13 iNaturalist records from NPI, one from Mustang Island, and one from SPI. I found 188 museum specimens from the inland portion of the seven counties.

Tantilla gracilis Baird & Girard, 1853

Flathead snake
Fig. 8b

Notes. *Tantilla gracilis* is largely fossorial, thus rarely observed, so they are probably more common on NPI than the three museum specimens and nine iNaturalist observations suggest. During the 2002–2003 surveys, our team captured three *T. gracilis* (TCWC 93900) at three study sites, all within the grassland/wetland matrix. There are no records for Mustang or South Padre islands. I found 52 *T. gracilis* museum specimens from the inland portion of the seven counties.

Thamnophis marcianus Baird & Girard, 1853

Checkered gartersnake
Fig. 8c

Notes. *Thamnophis marcianus* is common and conspicuous across most of its range. Our team observed this species three times. One road-killed specimen (TCWC 93901) was collected. I found eight museum specimens from NPI, fourteen from Mustang Island, one from Harbor Island (near Port Aransas), and 327 records from the inland portion of the seven counties. There are ten iNaturalist observations for Mustang Island and 33 from NPI. All observations are closely associated with wetlands and ponds within the grassland/wetland matrix. Its distribution is probably limited by the availability of freshwater to the northern 27 km of the island.

Thamnophis proximus Rossman, 1963

Western ribbonsnake
Fig. 8d

Notes. During the 2002–2003 survey our team captured *Thamnophis proximus* four times and collected six road-killed specimens (TCWC 93902–93908). All observations were closely associated with emergent wetlands within the grassland/wetland matrix. Baker and Rabalais (1978) reported that the species was more common on Mustang Island than on NPI, but museum and iNaturalist observations indicate that the species is and has been more common on NPI. I found 17 museum records and 413 iNaturalist observations from NPI. There was one museum specimen and 41 iNaturalist observations from Mustang Island. The distribution of this semi-aquatic fish-eating species on NPI is probably limited to the northern 27 km of the island by the availability of freshwater. Specimens that occur in the area are usually identified as the subspecies, *T. p. orarius* (Gulf Coast ribbonsnake).

Tropidoclonion lineatum **Hallowell, 1856**

Lined snake
Fig. 8e

Notes. A single museum specimen of *Tropidoclonion lineatum* (AMNH 171739) was collected in 1980 on South Bird Island, a 10.9 ha island in the Laguna Madre, ~ 75 m from NPI and ~ 2.0 km northwest of the western end of Bird Island Basin Road. There are no other records of *T. lineatum* from the South Texas barrier islands or from the seven adjacent counties (Werler and Dixon 2000; Dixon 2013). This locality is ~ 138 km from the nearest locality to the northeast in Calhoun County and ~ 156 km from the nearest locality to the northwest in Duval County. I could not locate the collectors (Richard R. Schmidt and C. Byrd) for comment. The species is spottily distributed from the north-central United States to south-central Texas.

Family Leptotyphlopidae

Rena dulcis **Baird & Girard, 1853**

Texas threadsnake
Fig. 8f

Notes. *Rena dulcis* is known from the South Texas barrier islands from one photo taken by PINS staff in 2010. That snake was uncovered ~ 46 cm underground while digging a hole for a fence post. There is an iNaturalist record from the north end of Mustang Island, but the photo submitted with that record is not detailed enough to determine with certainty if the snake is *R. dulcis* or the non-native *Indotyphlops braminus* (Brahminy threadsnake; https://www.inaturalist.org/observations/1270983). There are 101 museum records from the seven counties. *Rena dulcis* is fossorial and not easily observed, so it is probably more common on NPI (and possibly Mustang Island) than the sparse historical record implies.

Family Viperidae

Crotalus atrox **Baird & Girard, 1853**

Western diamondback rattlesnake
Fig. 8g

Notes. Baker and Rabalais (1978) reported that the western diamondback rattlesnake was “very common” on NPI and Mustang islands from the foredunes through the vegetated barrier flats. We received a few anecdotal reports and one photo during the 2002–2003 surveys, but our team did not observe *C. atrox*. I found three museum specimens and seven iNaturalist records from the northern end of NPI, seven museum specimens and 28

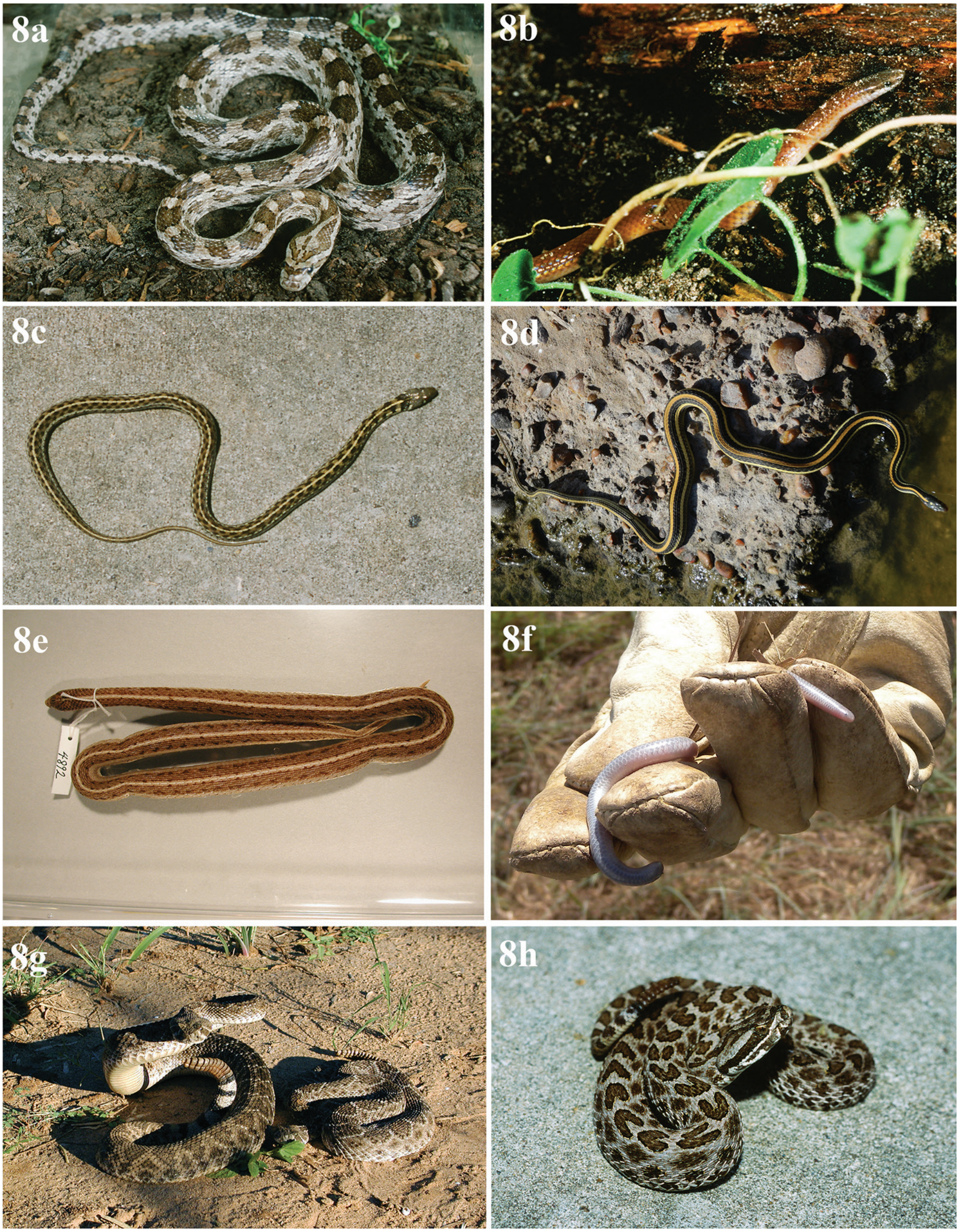


Figure 8. Eight reptiles that occur on North Padre Island **a** *Pantherophis emoryi* (Great Plains ratsnake) **b** *Tantilla gracilis* (flathead snake) **c** *Thamnophis marcianus* (checkered garter snake) **d** *Thamnophis proximus* (western ribbon snake) **e** *Tropidoclonion lineatum* (lined snake) from South Bird Island, just offshore of NPI **f** *Rena dulcis* (Texas threadsnake; PINS file photo) **g** *Crotalus atrox* (western diamond-backed rattlesnake) **h** *Sistrurus tergeminus* (western massasauga).

iNaturalist records from Mustang Island, one iNaturalist records from SPI, and 358 museum specimens from the seven counties. While it is clearly not uncommon, the historical record does not support the Baker and Rabalais (1978) contention that *C. atrox* is "very common." I have avoided the use of subjective classifications of abundance, but historical records for *C. atrox* are sparse compared to species such as *Masticophis flagellum* or *Holbrookia propinqua*. Observing this large venomous reptile may be frightening and memorable, and observations may be reported and repeated out of proportion to its abundance.

Sistrurus tergeminus **Say, 1823**
Western Massasauga
Fig. 8h

Notes. During the 2002–2003 surveys, out team captured five *S. tergeminus*. I located 19 museum specimens and three iNaturalist records from NPI but no records from Mustang or South Padre islands. There are ten museum specimens and one iNaturalist observation from the mainland portion of the seven counties. Baker and Rabalais (1978) reported that *S. catenatus* (*S. tergeminus*) was common on NPI but unknown from Mustang Island. At the time of the 2002–2003 surveys, two subspecies, *S. t. tergeminus* and *S. t. edwardsi* were recognized, but the snakes observed were morphologically intermediate between those subspecies, per the diagnostic characteristics described by Werler and Dixon (2000) and could not be assigned to subspecies. Kubatko et al. (2011) and Ryberg et al. (2015) report that the genetic distance between *S. t. tergeminus* and *S. t. edwardsi* is not significant. Currently most authoritative sources do not follow the subspecies arrangement.

Summary and discussion

Given the dynamic nature of barrier island geomorphology and the resulting equally dynamic arrangement of ecological zones, it is not surprising to find evidence of fluctuations in the occurrence and abundance of herpetofauna over the time-period for which we have records. Some species said to be abundant in the historical record were found to be rare or absent during all or part of this study period (2002–2020), and some species found to be abundant during the study period were absent or sparsely represented in the historical record. In some cases, failure to observe a species for decades has led me to presume they have been extirpated. The variability between time periods is particularly evident for Bufonids (true toads). Moore (1976) reported that the Texas toad (*Bufo speciosus*) was the most abundant anuran on Mustang Island during his 1971 study, but with no verifiable records since 1970, *B. speciosus* appears to have been extirpated from Mustang Island (there is no evidence it ever occurred on NPI or SPI). The gulf coast toad (*B. nebulifer*), which is quite conspicuous when present and abundant on the mainland, was not detected during the 2002–2003 surveys. There were no records for North Padre Island between 1891 and 2007 and not another until 2017 when choruses could be heard within the city limits of Corpus Christi on northernmost Padre Island. Woodhouse's toad (*B. woodhousii*) was not known from the islands until our team collected and audio-recorded it numerous times during the 2002–2003 surveys; it was not reported again until 2018. In a region known for extended droughts, *B. nebulifer* and *B. woodhousii* may fail to reproduce in some years and may experience periodic population declines that make them nearly undetectable (Perchman and Wilbur 1994; Green 2003; Brown et al. 2012). The natural history of Bufonids on the South Texas barrier islands, particularly examining how their prey and predator communities and their preferred habitats have been altered, warrants further study. Determining the mechanisms of the fluctuations would help inform conservation actions for the species. The eastern hognose snake (*Heterodon platirhinos*), which preys on Bufonids, also appears to experience noticeably fluctuating population densities: the species was consistently observed and collected from the 1960s through the 1990s, and our team recorded five individuals during the 2002–2003 surveys, but no *H. platirhinos* have been reported from the islands since that time. The last *H. platirhinos* specimen collected from Mustang Island was in 1991, a few years after *B. speciosus* appears to have been extirpated. While the evidence for interacting population fluctuations between Bufonids and *H. platirhinos* on the islands is circumstantial, further study is needed. The most high-profile extirpation is that of the Texas horned lizard (*Phrynosoma cornutum*), which is listed as an endangered species by the state of Texas and is the Texas state lizard. Baker and Rabalais (1978) referred to *P. cornutum* as the most common lizard on Mustang Island. It is still present on nearby San José Island, on another small island in Corpus Christi Bay, and on the mainland. Natural or human-aided repopulation of the species on Mustang Island might be possible if the threats which led to the extirpation are identified and mitigated.

Non-marine species that are extirpated from islands may later repopulate naturally despite the ecological barrier posed by saltwater. Baker and Rabalais (1978) reported finding a Texas tortoise (*Gopherus berlandieri*) and a common snapping turtle (*Chelydra serpentina*) dead on the beach and speculated that some turtles arrive there after being washed into the surf and carried along by longshore currents. Additional evidence supports that hypothesis: In 2007 and again in 2021, a live alligator, which had been tagged in Louisiana, washed up on an NPI beaches. In 2008, tons of debris, much of it lumber from destroyed houses, washed up on NPI beaches a few days after hurricane Katrina struck Louisiana and Mississippi (while that is the most extreme, debris from Gulf Coast storms commonly washes up on NPI beaches). In an extensive review of the literature, Neill (1958) provides many examples of non-marine amphibians and reptiles living in or adapting to saline environments including a common slider (*Trachemys scripta*) trapped in a brackish canal in the Sabine Wildlife Refuge (Cagle and Chaney 1950) and a speckled kingsnake (*Lampropelis getula holbrooki*) in brackish water in Cameron Parish, Louisiana (he cited personal communication with JR Dixon). On Merritt Island, Florida, Neill (1958) observed southern leopard frogs (*Rana sphenocephala*) and green treefrogs (*Hyla cinerea*) jumping into water "too salty to drink" He also heard eastern narrow-mouthed toads (*Gastrophryne carolinensis*) calling from *Salicornia* flats, and he collected *C. serpentina* on a tidal flat. Sissom et al. (1990) reported that one of the three man-made ponds within PINS was "too salty to be classified as freshwater," and that they did not observe any vertebrates using the pond.

However, we trapped *T. scripta* in hoop traps on each of four trap days and observed three introduced *A. mississippiensis* (frequently found in brackish water) in the pond. I found this iNaturalist observation, entered by The Nature Conservancy Zoologist John Karges, of a slender glass lizard (*Ophisaurus attenuatus*) swimming ~ 100 m from shore near Port O'Conner (https://www.inaturalist.org/observations/82288781) and this observation of *Masticophis flagellum* swimming 1.2 km from shore in Mesquite Bay (https://www.inaturalist.org/observations/95038106). The Nature Conservancy biologist, Lee Elliott, observed an indigo snake (*Drymarchon melanurus*) swimming in the surf near Bob Hall Pier on North Padre Island (Lee Elliott, pers. comm.). That species is large, conspicuous, and highly mobile. It is relatively common on the mainland and may occur on the island accidentally. Similarly, the gopher snake (*Pituophis catenifer*), another large, conspicuous snake, for which there were anecdotal accounts but no museum records or verifiable observations until 2006, may occur on the island occasionally or accidentally. The unexpected appearance of a diamondback terrapin (*Malaclemys terrapin*) on the seaward side of southernmost Padre Island, might be a natural range expansion, human-aided introduction, or another example of a reptile being carried outside of its native range by Gulf of Mexico currents.

Several species found on NPI differ in relative abundance and/or morphology from their mainland counterparts. Padre Island herpetofauna are generally paler than mainland specimens; in particular, *B. woodhousii*, *M. flagellum*, and the great plains ratsnake (*Pantherophis emoryi*) found on the island exhibit a ground color that is often nearly white, and the reds and yellows of the Texas scarletsnake (*Cemophora lineri*) that we observed were duller than its mainland counterpart. The ventral scale row count of one *C. lineri* specimen was found to be outside of the range of variation for that species but within the range of variation and near the mean for *C. c. coccinea* (this may be a single aberrant individual). The only Ranid found in the mainland counties adjacent to Padre Island is the Rio Grande leopard frog (*Rana berlandieri*), while both *R. berlandieri* and *R. sphenocephala* are found on NPI. The external morphology of some Ranid specimens found on North Padre Island are intermediate between *R. berlandieri* and *R. sphenocephala*, therefore calls are the most definitive record of occurrence for those species (Suppl. material 4). Prior to a single recent iNaturalist record, the only Gastrophrynid known from the South Texas barrier islands was *G. carolinensis*, while only the western narrow-mouthed toad (*G. olivacea*) was known from the inland counties. Additionally, *G. carolinensis* is found in the Kleberg County portion of NPI, while that species is not found on the adjacent mainland in Kleberg County.

Several non-native species of amphibians and reptiles have established breeding populations in southern Texas. Two non-native lizards, the Mediterranean gecko (*Hemidactylus turcicus*) and the brown anole (*Anolis sagrei*) have well-established populations in southern Texas, including many records from the South Texas barrier islands. *Anolis sagrei* are known to displace native green anoles (*A. carolinensis*). iNaturalist records have been posted for the Cuban treefrog (*Osteopilus septentrionalis*) on the southern end of South Padre Island. There are no other records for that species within 480 km of Corpus Christi, Texas, but the species is well-established in Florida and along the Gulf Coast. The invasion of Florida by Cuban treefrogs has severely impacted native ecosystems and has led to localized extirpations of other frogs in urban areas (Johnson 2017). Texas and federal wildlife agencies and organizations should proactively develop recommendations and protocols for dealing with an inevitable invasion by that species. The Brahminy blindsnake (*Indotyphlops braminus*) is well-established in Cameron and Hidalgo counties and a single iNaturalist record for South Padre Island was entered in 2015. The American bullfrog (*R. catesbeiana*) is an invasive species in the western United States where it competes with and preys on native species. While Padre Island is nestled within the native range of *R. catesbeiana*, its appearance on the island, documented in 2018 by an audio recording of a single individual, might be considered invasive.

There were a few species that appeared on previous checklists for NPI that our team did not detect. While it is unlikely that any of the unconfirmed species occur in abundance, it is possible that some of the species may yet be found on the island. The Texas coral snake (*Micrurus tener*) probably appeared on previous checklists of North Padre Island herpetofauna (Rabalais 1975; NPS 1984) because of misinterpretation of locality information of one specimen collected at the PINS headquarters when it was on the mainland in Corpus Christi. While little typical habitat for *M. tener* is found on NPI, it is possible that *M. tener* may yet be observed on the island. Couch's spadefoot (*Scaphiopus couchii*) appeared on a previous checklist because Baker and Rabalais (1978) said that a specimen had been collected on NPI, but I found no specimens or other verifiable evidence of its occurrence there. Likewise, *B. speciosus* was common on Mustang Island until the mid-1970s, so Rabalais (1975) and Baker and Rabalais (1978) understandably thought it might occur on NPI. While there is no evidence that *S. couchii* or *B. speciosus* ever occurred on NPI, they are common on the mainland and may yet be detected on the island. The lesser siren (*Siren intermedia*) and the spotted newt (*Notophthalmus meridionalis*) appeared on previous checklists because of their nearby occurrence on the mainland. Those species require poorly drained, generally clayey, soils (Judd 1983; Gelback et al. 1991). Most NPI soils are sandy but some ponds in the northern 27 km of the island are poorly drained because their substrates are covered in layers of decaying vegetation. Those ponds are difficult to access, and our sampling efforts were insufficient to say with certainty that *S. intermedia* and *N. meridionalis* do not occur on the islands. The lack of verifiable records for the common whiptail (*Aspidoscelis gularis*) is a bit of a mystery. It was listed by Rabalais (1975) as uncommon and Allan Chaney told me he thought he had observed it, but I did not observe it and could find no evidence that it occurs there.

The basic methodology of the 2002–2003 study was completed by the US National Park Service in consultation with their partners prior to my being tasked with coordinating the inventory There were some things I wish I could have done differently. In short, the original design called for random selection of study sites, where we would conduct drift-fence/pitfall trapping in the spring and early summer only. It is standard practice to employ a random sampling scheme in hopes that future researchers will be able to mimic the methodology, but this study area is 50,000 ha, it extends for 122 km, resources were limited, and the primary objective was to determine presence/absence. The freedom to directly target specific species in specific areas at specific times, should have been a primary component of the plan. Random selection, stratified by ecological zones and geography, also caused study areas to be unevenly distributed within stratifications, leaving some gaps that were under-sampled. While spring sampling is a standard feature of most amphibian and reptile and monitoring plans in much of the United States, in coastal southern Texas, where more than 30% of rainfall usually occurs in September and October, a more effective plan would have specified that some drift-fence/pitfall trapping would occur in the fall. While we did continue with visual encounter and calling-frog surveys throughout the year, we were only allowed to conduct drift-fence/pitfall trapping in the spring and early summer.

Acknowledgements

The US National Park Service at Padre Island National Seashore (NPS) was instrumental in funding, permitting, and assisting with various components of the project; I owe a special debt of gratitude to several NPS staff, including Travis Clap, Donna Shaver, Wade Stablein, Alicia Walker, Darrel Echols, and especially William "Buzz" Botts. Thanks to the numerous people who braved the harsh conditions of the barrier island to assist in the field, including Lynne Duran, Mark Gallyoun, Kristi Fazioli, Brent Koza, Dimitria Guerrero, Brianna Young, Nicki Hayes, Rod Miller, and Lisa Williams. I owe thanks to numerous professional herpetologists and naturalists who contributed their expert opinions and knowledge to the project, including Frank Judd, Allan Chaney, Jim Dixon, Graham Hickman, Ralph Axtell, Michael Forstner, and Nancy Rabalais. Collection curators who provided data are too numerous to mention, but I owe special thanks to Charles Dardia (CUMV), Linda Ford, David Dickey, and David Kizirian (AMNH), Gregory Schneider (UMMZ), and especially Travis LaDuc (TNHC) and Toby Hibbitts (TCWC) for their expert opinions and patience as I pestered them with dozens of inquiries over the years. This work would not have been possible without the contributions of The Nature Conservancy support staff over the years, including Debbie Benesh, Jim Bergen, Bill Carr, Lee Elliott, Mark Gallyoun, Steven Gilbert, John Karges, Carter Smith, and Lisa Williams. Thanks to Lee Elliott for editing the vegetation section of this manuscript. A big thanks to Lisa Williams, John Karges, and an anonymous reviewer, whose editing and technical reviews greatly improved this manuscript. And finally, I would like to thank my former employer, The Nature Conservancy (http://nature.org), whose commitment to science-based conservation made this work possible.

References

AmphibiaWeb. 2021. University of California, Berkeley, CA, USA. https://amphibiaweb.org [accessed 4 Sep 2021]

Auffenberg WA (1948) Airplane introduces *Cemophora coccinea* to Texas. Herpetologica 4: e212. https://www.jstor.org/stable/27669632

Axtell RW (1963) A reinterpretation of the distribution of *Bufo w. woodhousii* Girard, especially on the southeastern margin of the range. Herpetologica 19(2): 115–122. https://www.jstor.org/stable/3890546

Axtell RW (1998) *Holbrookia lacerata*. An interpretive atlas of Texas lizards, No. 20. Self-published, 12 pp.

Baird SF and Girard C (1853) Catalogue of North American reptiles in the Museum of the Smithsonian Institution. Smithsonian Miscellaneous Collections 2(5): iii–172. https://doi.org/10.5962/bhl.title.5513

Baker JK, Rabalais N (1978) Terrestrial vertebrates of Mustang and North Padre islands. Unpublished manuscript. Padre Island National Seashore Archives, 29 pp.

Blaney RM (1977) Systematics of the common kingsnake *Lamprpeltis getulus* (Linnaeus). Tulane Studies in Zoology and Botany 19(3–4): 47–103. https://www.biodiversitylibrary.org/page/4300709

Brown BC (1950) An annotated check list of the reptiles and amphibians of Texas. Baylor University Press, Waco, Texas, 265 pp.

Brown B, Kiehl K, Wilkinson L (2012) Advantages of long-term multi-scale monitoring assessing the current status of the Yosemite toad (*Anaxyrus* [*Bufo*] *canorus*) in the Sierra Nevada, California, USA. Herpetological Conservation and Biology 7(2): 115–131. http://herpconbio.org/Volume_7/Issue_2/Brown_etal_2012.pdf

Burbrink FT, Fontanella F, Pyron A, Guiher TJ, Jimenez C (2007) Phylogeography across a continent: The evolutionary and demographic history of the North American racer (Serpentes: Colubridae: Coluber constrictor) Molecular Phylogenetics and Evolution 47 (2008): 274–288. https://doi.org/10.1016/j.ympev.2007.10.020

Burgdorf SJ, Rudolph DC, Conner RN, Saenz D, Schaefer RR (2005) A successful trap design for capturing large terrestrial snakes. Herpetological Review 36(4): 421–424. https://www.srs.fs.usda.gov/pubs/25008

Bury RB, Smith EL (1986) Aspects of the ecology and management of the tortoise Gopherus berlandieri at Laguna Atascosa, Texas. The Southwestern Naturalist 31(3): 387–394. https://doi.org/10.2307/3671844

Chambers EA and Hillis DM (2020) The multispecies coalescent over-splits species in the case of geographically widespread taxa. Systematic Biology 69(1): 184–193. https://doi.org/10.1093/sysbio/syz042

Conant R, Collins JT (1998) A field guide to the reptiles and amphibians of eastern and central North America. Third edition, expanded. Houghton Mifflin Co., Boston, Massachusetts, 616 pp.

Crother BI (Ed.) (2017) Scientific and standard English names of amphibians and reptiles of North America north of Mexico, with comments regarding confidence in our understanding. Society for the Study of Amphibians and Reptiles Herpetological Circular 43: 1–102. https://repository.si.edu/handle/10088/33975

Crother BI, Boundy J, Burbrink FT, Ruane S (2017) Squamata (in part) – Snakes. In: Crother BI (Ed.) Scientific and standard English names of amphibians and reptiles of North America north of Mexico, with comments regarding confidence in our understanding. Society for the Study of Amphibians and Reptiles Herpetological Circular 43: 59–80. https://repository.si.edu/handle/10088/33975

Diamond DD, Elliott LF, Treuer-Kuehn A, Singhurst JR, Peterson A (2017) Vegetation classification and mapping of Padre Island National Seashore: Final project report. Natural Resource Report NPS/GULN/NRR – 2017/1449. National Park Service, Fort Collins, Colorado, 124 pp.

Dixon JR (2000) Amphibians and Reptiles of Texas, 2nd Ed. Texas A&M University Press, College Station, Texas, 421 pp.

Dixon JR (2013) Amphibians and Reptiles of Texas, 3rd Ed. Texas A&M University Press, College Station, Texas, 477 pp.

Dunson WA, Mazzotti FJ (1989) Salinity as a limiting factor in the distribution of reptiles in Florida Bay: A theory for the estuarine origin of marine snakes and turtles. Bulletin of Marine Science 44(1): 229–244. https://www.ingentaconnect.com/content/umrsmas/bullmar/1989/00000044/00000001/art00018

Duran CM (2004) An inventory of reptiles and amphibians of Padre Island National Seashore, San Antonio Missions Historical Park, and Palo Alto Battlefield National Historic Site. Final report to the US Department of Interior, National Park Service, 159 pp.

Duran CM, Hall DW (2013) Geographic distribution. *Rana sphenocephala* (southern leopard frog). Herpetological Review 44(4): 622.

Echternacht AC (1999) Possible causes for the rapid decline in population density of green anoles, A*nolis carolinensis* (Sauria: Polychrotidae) following invasion by the brown anole, *Anolis sagrei*, in the southeastern United States. Anolis Newsletter 5: 22–27.

Ernst CH, Lovich JE (2009) Turtles of the United States and Canada, 2nd Ed. Johns Hopkins University Press, Baltimore, Maryland, 840 pp.

ESRI (2011) ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.

Guadiana CJ, Robinson PS, Schalk MJ, Davis DR (2020) New county records of amphibians and reptiles from South Texas, USA. Herpetological Review 51(4): 799–803. https://scholarworks.utrgv.edu/cgi/viewcontent.cgi?article=1120&context=eems_fac

Gelback FR, Gordon R, Jordan JB (1991) Aestivation of the salamander, *Siren intermedia*. American Midland Naturalist 89(2): 455–468. https://doi.org/10.2307/2424051

Green DM (2003) The ecology of extinction: Population fluctuation and decline in amphibians. Biological Conservation 111: 331–343. https://doi.org/10.1016/S0006-3207(02)00302-6

Hillis DM (1981) Premating isolating mechanisms among three species of the *Rana pipiens* complex in Texas and southern Oklahoma. Copeia 1981: 312–319. https://doi.org/10.2307/1444220

iNaturalist.org web application. https://www.inaturalist.org [accessed 08 October 2020]

Javor B (1989) Hypersaline Environments. Springer-Verlag, New York, 328 pp. https://doi.org/10.1007/978-3-642-74370-2

Joanen T, McNease L (1972) A telemetric study of adult male alligators on Rockefeller Refuge, Louisiana. Procedures of the Annual Conference of Fish and Wildlife Agencies 26: 252–75.

Johnson, SA (2017) The Cuban Treefrog (*Osteopilus septentrionalis*) in Florida. Department of Wildlife Ecology, UF/IFAS Extension, document WEC218.

Jones WD (1999) Padre Island National Seashore: An administrative history. US National Park Service: https://irma.nps.gov/DataStore/DownloadFile/476200

Judd FW (1983) Status of *Siren intermedia texana*, *Notophthalmus meridionalis*, and*Crotaphytus reticulatus*. Final report submitted to the Office of Endangered Species, United States Fish and Wildlife Service, Department of Interior, 64 pp.

Judd FW, Lonard RWE, Sides SL (1977) The vegetation of South Padre Island, Texas in relation to topography. Southwestern Naturalist 22: 3 1–48. https://doi.org/10.2307/3670462

Judd FW, Rose FL (2000) Conservation status of the Texas tortoise (*Gopherus berlandieri*). Occasional Papers of the Museum of Texas Tech University, Number 196: 1–11. https://doi.org/10.5962/bhl.title.143474

Kazmaier, R, Hellgren, E, Ruthven D (2001). Habitat Selection by the Texas Tortoise in a Managed Thornscrub Ecosystem. The Journal of Wildlife Management 65(4): 653–660. https://doi.org/10.2307/3803016

Kubatko LS, Gibbs HL, Bloomquist EW (2011) Inferring species-level phylogenies and taxonomic distinctiveness using multilocus data in *Sistrurus* rattlesnakes. Systematic Biology 60: 393–409. https://doi.org/10.1093/sysbio/syr011

Laine SC, Ramsey EW III (1998) Landcover classification for Padre Island National Seashore. Report and GIS products delivered to the National Park Service. United States Biological Service, Biological Resource Division, Lafayette, Louisiana, 23 pp.

LeBlanc RJ, Hodgson WD (1959) Origin and development of the Texas shoreline. Transactions of the Gulf Coast Association of Geologic Societies 9: 197–220. https://archives.datapages.com/data/gcags/data/009/009001/0197.htm

Moore RH (1976) Reproductive habits and growth of *Bufo speciosus* on Mustang Island, Texas with notes on the ecology and reproduction of other anurans. Texas Journal of Science 27(1): 173–178.

Mossman MJ, Hartman LM, Hay R, Sauer JR, Dhuey BJ (1998) Monitoring long-term trends in Wisconsin frog and toad populations. In: Lannoo MJ (Ed.) Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, Iowa, 169–198. https://doi.org/10.2307/j.ctt20q20cw.24

Myers EA, Burgoon JL, Ray JM, Martinez-Gomez JE, Matias-Ferrer N, Mulcahy DG, Burbrink FT (2017) Coalescent species tree inference of *Coluber* and *Masticophis*. Copeia, 105(4): 642–650. https://doi.org/10.1643/CH-16-552

Nagy ZT, Lawson R, Ulrich J, Wink M (2004) Molecular systematics of racers, whipsnakes and relatives (Reptilia: Colubridae) using mitochondrial and nuclear markers. Journal of Zoological Systematics and Evolutionary Research 42: 223–233. https://doi.org/10.1111/j.1439-0469.2004.00249.x

National Oceanic and Atmospheric Administration. Climate data online.https://www.ncdc.noaa.gov/cdo-web/ [accessed 18 June 2021]

National Park Service (2020) Padre Island: The longest stretch of undeveloped barrier island in the world. http://www.nps.gov/pais/index.htm [accessed 15 June 2021]

Neill WT (1958) The occurrence of amphibians and reptiles in saltwater areas and a bibliography. Bulletin of Marine Science of the Gulf and Caribbean 8: 1–97.

Nelson A, Goetze J, Negrete B, Macke L, Wilburn T, Day A, Lucksinger A (2000) A floristic survey of Padre Island National Seashore, Texas, with comparisons to other barrier islands along the Texas coast. Final Report to Padre Island National Seashore, 100 pp.

North American Amphibian Monitoring Program (2012) North American Amphibian Monitoring Program, Protocol Description. http://www.pwrc.usgs.gov/naamp/index.cfm?fuseaction=app.protocol

Olsen Z (2014) Potential impacts of extreme salinity and surface temperature events on population dynamics of black drum, *Pogonias cromis*, in the Upper Laguna Madre, Texas. Gulf of Mexico Science 2014(1–2): 60–68. https://doi.org/10.18785/goms.3201.06

Onuf CP (2006) The Laguna Madre. In: Hanley L, Altsman D, DeMay R (Eds) Seagrass Status and Trends in the Northern Gulf of Mexico: 1940–2002. United States Geological Survey scientific investigations report 2006–5287 https://pubs.usgs.gov/sir/2006/5287/

Pauly GB, Hillis DM, Cannatella DC (2009) Taxonomic freedom and the role of official lists of species names. Herpetologica 64: 115–128. https://doi.org/10.1655/08-031R1.1

Pechmann JHK, Wilbur HM (1994) Putting declining amphibian populations in perspective: Natural fluctuations and human impacts. Herpetologica 50: 65–84. https://www.jstor.org/stable/3892876

Pyron RA, Burbrink FT (2009) Lineage diversification in a widespread species: roles for niche divergence and conservatism in the common kingsnake, *Lampropeltis getula*. Molecular Ecology 18: 3443–3457. https://doi.org/10.1111/j.1365-294X.2009.04292.x

Rabalais N (1975) Padre Island National Seashore checklist of reptiles and amphibians. Padre Island National Seashore informational bulletin No. 4, 2 pp.

Rappole JH, Klicka J (1991) Status of the Black-spotted Newt (*Notophthalmus meridionalis*) in Texas and New Mexico. A report to the US Fish and Wildlife Service, 66 pp.

Raun GG, Gehlbach FR (1972) Amphibians and reptiles in Texas: taxonomic synopsis, bibliography, and county distribution maps. Dallas Museum of Natural History, Bulletin 2: 1–66. [+ 140 maps]

Ruane SR, Bryson Jr W, Pyron RB, Burbrink FT (2014) Coalescent species delimitation in milksnakes (Genus *Lampropeltis*) and impacts on phylogenetic comparative analyses. Systematic Biology 63(2): 231–250. https://doi.org/10.1093/sysbio/syt099

Ryberg WA, Harvey JA, Blick A, Hibbitts TJ, Voelker G (2015) Genetic structure is inconsistent with subspecies designations in the western massasauga *Sistrurus tergeminus*. Journal of Fish and Wildlife Management, September 2015. https://doi.org/10.3996/122014-JFWM-093

Scalise JL (2011) Food habits and selective foraging by the Texas tortoise. MS Thesis, Texas State University, San Marcos, Texas, 28 pp.

Seabury RE, Hall DW, Pauly GB (2005) Geographic distribution: *Bufo woodhousii* (Woodhouse's toad). Herpetological Review 36(2): e198.

Sissom SL, Koehn RD, Lemke D (1990) A baseline study of three ponds within the Padre Island National Park. Final Report to Padre Island National Seashore, 70 pp.

Smith HM, Chiszar D, Staley II JR, Tepedelen K (1994) Population relationships in the corn snake *Elaphe guttata* (Reptilia: Serpentes). Texas Journal of Science 46(3): 259–292.

Stejneger L (1903) The reptiles of the Huachuca Mountains, Arizona. Proceedings of the US National Museum 25: 149–158. https://repository.si.edu/bitstream/handle/10088/13672/1/USNMP-25_1282_1902.pdf

Tipton BL, Hibbitts TL, Hibbitts TD, Hibbitts TJ, LaDuc TJ (2012) Texas Amphibians: A Field Guide. University of Texas Press, Austin, Texas, 330 pp. https://doi.org/10.7560/737358

Trauth SE (1992) A new subspecies of six-lined racerunner, *Cnemidophorus sexlineatus* (Sauria, Teiidae), from southern Texas. Texas Journal of Science 44: 437–443.

Trauth SE (1995) An emendation to the subspecies name of *Cnemidophorus sexlineatus stephensi* (Sauria: Teiidae). Bulletin of the Chicago Herpetological Society 30(4): e68.

Trauth SE, McAllister CT (1996) *Cnemidophorus sexlineatus*. Society for the Study of Amphibians and Reptiles. Catalogue of Amphibians and Reptiles 628: 1–12 pp. https://repositories.lib.utexas.edu/bitstream/handle/2152/44718/0628_Cnemidophorus_sexlineatus.pdf?sequence=1

Tunnell Jr JW, Judd FW (Eds; 2002) Laguna Madre of Texas and Tamaulipas. Gulf Coast Studies No. 2. Texas A&M University Press, College Station, Texas, 346 pp.

Tunnell Jr JW (2002) Geology, climate, and hydrography. In: Tunnel Jr JW, Judd FW (Eds) The Laguna Madre of Texas and Tamaulipas. Gulf Coast Studies No. 2. Texas A&M University Press, College Station, Texas, 346 pp.

Vertnet.org (2020) Museum database. http://vertnet.org [accessed 08 October 2020]

Walker A (2019) Geographic distribution. *Gastrophryne carolinensis*. Herpetological Review 50(1): e96.

Weinell JL, Austin CC (2017) Refugia and speciation in North American Scarlet Snakes (*Cemophora*). Journal of Herpetology 51(1): 161–171. https://doi.org/10.1670/15-125

Werler JE, Dixon JR (2000) Texas Snakes. University of Texas Press, Austin, Texas, 437 pp.

Williams KL (1978) Systematics and natural history of the American milk snake, *Lampropeltis triangulum*. Milwaukee Public Museum Contributions in Biology and Geology. 2: 1–258.

Williams KL, Brown BC, Wilson LD (1966) A new subspecies of the colubrid snake, *Cemophora coccinea* (Blumenbach), from southern Texas. Texas Journal of Science 18(1): 85–88.

Williams KL, Wilson LD (1967) A review of the colubrid snake genus *Cemophora* Cope. Tulane Studies in Zoology 13(4): 103–124.

Yuan ZY, Zhou WW, Chen X, Payarkov Jr NA, Chen HM, Jan-Liaw NH, Chou WH, Matzke NJ, Iizuka K, Min MS, Kuzmin SL, Zhang YP, Cannatella DC, Hillis DM, Che J (2016) Spatiotemporal diversification of the true frogs (Genus: *Rana*): A historical framework for a widely studied ground of model organisms. Systematic Biology 65: 824–842. https://doi.org/10.1093/sysbio/syw055

Supplementary material 1

Museum and iNaturalist records for Aransas, Cameron, Kenedy, Kleberg, Nueces, San Patricio, and Willacy counties, Texas, and iNaturalist records for North and South Padre and Mustang islands, Texas

Authors: Mike Duran

Data type: Collections.

Explanation note: This is an excel file containing attributes of all museum and iNaturalist records for Aransas, Cameron, Kenedy, Kleberg, Nueces, San Patricio and Willacy counties, Texas, including North and South Padre and Mustang islands.

Link: https://doi.org/10.3897/zookeys.1073.57241.suppl1

Supplementary material 2

***Gastrophryne carolinensis* calling, 08 July 2003.**

Authors: Mike Duran

Data type: Sound file.

Explanation note: Audio of *Gastrophryne carolinensis* calling on the night of July 8, 2003.

Link: https://doi.org/10.3897/zookeys.1073.57241.suppl2

Supplementary material 3

***Hyla squirella* calling 08 July 2003**

Authors: Mike Duran

Data type: Sound file.

Explanation note: Audio of *Hyla squirella* calling on the night of July 8, 2003.

Link: https://doi.org/10.3897/zookeys.1073.57241.suppl3

Supplementary material 4

***Rana sphenocephala* and possibly *R. berlandieri* calling, 10 February 2013**

Authors: Mike Duran

Data type: Sound file.

Explanation note: Audio of Rana sphenocephala and possibly R. berlandieri calling on the night of February 10, 2013.

Link: https://doi.org/10.3897/zookeys.1073.57241.suppl4

ZooKeys 1073: 177–199 (2021)
doi: 10.3897/zookeys.1073.75583
https://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Two new species and new records of Otocepheidae (Acari, Oribatida) from Yunnan, Southwest China

Lihao Zheng[1,2,3], Jun Chen[2,3]

1 *Guang'an Vacational and Technical College, Guang'an, China* **2** *Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China* **3** *College of Life Sciences, University of Chinese Academy of Sciences, Beijing, 100049, China*

Corresponding author: Jun Chen (chenj@ioz.ac.cn)

Academic editor: Vladimir Pesic | Received 21 September 2021 | Accepted 1 November 2021 | Published 30 November 2021

http://zoobank.org/C77F098C-FCCC-4AE8-A0EA-043289FDD592

Citation: Zheng L, Chen J (2021) Two new species and new records of Otocepheidae (Acari, Oribatida) from Yunnan, Southwest China. ZooKeys 1073: 177–199. https://doi.org/10.3897/zookeys.1073.75583

Abstract

This work includes taxonomic data on four species of oribatid mites of the family Otocepheidae from Yunnan, China. Two new species of the genera *Basiceramerus* and *Eurostocepheus* are described, respectively. *Basiceramerus ovatus* **sp. nov.** differs from *B. bangladeshensis* Corpuz-Raros & Gruèzo, 2008 by the wavy marginalis passing the base of the adanal setae, prodorsal condyles well separated from median ones, a ventral ridge present, and the anal plate foveolate; it differs from *B. igorotus* Corpuz-Raros & Gruèzo, 2011 from Vietnam by the wavy marginalis passing the base of the adanal setae, a connected tutorium and lamelliform expansion, a ventral ridge present, a smooth genital plate, and seta an_2 located close to the median margin of the anal opening; it differs from *B. igorotus* from the Philippines by the lamellar setae inserted behind the tip of the lamella, separated prodorsal condyles, lyrifissure *im* posterior to *gla*, genital plate smooth, anal plate foveolate, and the wavy marginalis passing the base of the adanal setae. *Eurostocepheus* (*Eurostocepheus*) *sinutus* **sp. nov.** differs from other known species of this genus by having a ventral groove between the genital aperture and the ventral ridge, eight pairs of notogastral setae, and distinctly shorter and thinner notogastral setae p_1, p_2, p_3, h_3. *Eurostocepheus* (*Eurostocepheus*) *aquilinus* Aoki, 1965 and *E.* (*E.*) *mahunkai* Mondal & Kundu, 1999 are reported for the first time from China.

Keywords

Basiceramerus, China, *Eurostocepheus* (*Eurostocepheus*), oribatid mites, taxonomy

Introduction

During identification of the oribatid mite material collected from Yunnan, Southwest China, we found four otocepheid species; among them two species are new to science belonging to the genera *Basiceramerus* and *Eurostocepheus*, and the others, *Eurostocepheus* (*Eurostocepheus*) *aquilinus* Aoki, 1965 and *E.* (*E.*) *mahunkai* Mondal & Kundu, 1999, are new records for China.

Basiceramerus was proposed by Corpuz-Raros with *Basiceramerus upelbensis* Corpuz-Raros, 1979 as the type species. Currently, the genus comprises six species, which are distributed in the subtropics of Asia: the Philippines, Bangladesh and Vietnam (Subías 2004, online version 2021). Before the present study, this genus had not been reported from China. The species herein described follows the generic characters (based on data from Corpuz-Raros 1979; Corpuz-Raros and Gruèzo 2008): fused median notogastral condyles present, apodemata II and apodemata *sj* long, 4 pairs genital, 1 pair aggenital, 2 pairs anal, 3 pairs adanal setae present, and leg setae *u* setiform (L-type) on tarsi I, thorn-like (S-type) on tarsi II–IV.

Eurostocepheus Aoki, 1965, which is distinguished from other genera of Otocepheidae mainly by its disproportionately dilated pedotectum II and conspicuously developed costula, comprises two subgenera: *Eurostocepheus* (*Eurostocepheus*) Aoki, 1965 and *Eurostocepheus* (*Cerostocepheus*) Mahunka, 1973. The main subgeneric difference lies in the number of genital setae, either 4 or 5 pairs respectively. Nine species of this genus, all from the Oriental region, were hitherto reported (Subías 2004, online version updated in 2021); among them only one species, *Eurostocepheus* (*E.*) *heterotrichus* Wen, 1999, has been recorded in China (Wen 1999; Chen, Liu and Wang 2010). A revised generic diagnosis and an identification key to known subgenera and species of this genus were given by Ermilov and Starý (2017).

In the following study, the two new species *Basiceramerus ovatus* sp. nov., *Eurostocepheus* (*Eurostocepheus*) *sinutus* sp. nov., are described and illustrated based on adults, and expanded descriptions and illustrations of *E.* (*E.*) *aquilinus* and *E.* (*E.*) *mahunkai* based in part on new information are provided.

Materials and methods

Specimens were mounted in lactic acid on temporary cavity slides for measurement and illustration. The body length was measured in lateral view, from the tip of the rostrum to the posterior edge of the ventral plate. Notogastral width refers to the maximum width in dorsal aspect. Lengths of body setae were measured in lateral aspect. All body measurements are presented in micrometers. Formulae for leg setation are given in parentheses according to the sequence trochanter-femur-genu-tibia-tarsus (famulus included). Formulae for leg solenidia are given in square brackets according to the sequence genu-tibia-tarsus.

General terminology used in this paper follows that of Grandjean (1934), Ermilov and Starý (2017), Norton (1977), Norton and Behan-Pelletier (2009).

Abbreviations and notations

Prodorsum: *ro*, *le*, *in*, *bs*, *ex*–rostral, lamellar, interlamellar, bothridial and exobothridial setae, respectively; *cos*–costula; *tu*–tutorium; *spa.l*–lamelliform expansion; *tbd*, *tbv*–dorsal and ventral bothridial plate, respectively; *cpm*, *cpl*–medial and lateral prodorsal condyles, respectively.

Notogaster: *c*, *la*, *lm*, *lp*, *h*-row, *p*-row–notogastral setae; *cnm*, *cnl*–medial and lateral notogastral condyles, respectively; *vm*–vitta marginalis; *ia*, *im*, *ip*–anterior, middle, posterior lyrifissures, respectively; *ih*, *ips*–same, associated with setal rows *h* and *p*, respectively; *gla*–opisthonotal gland opening.

Coxisternum and lateral podosoma: *1a*, *1b*, *1c*, *2a*, *3a*, *3b*, *3c*, *4a*, *4b*, *4c*–setae of epimeres I–IV; *met*–mentotectum; *st*–sternal apodeme; *ap1*, *ap2*, *ap sj*–apodeme I, II, sejugal, respectively; *Pd I*, *Pd II*–pedotectum I, II respectively; *spd*–sub pedotectum; *fep*–epimeral foramen; *dis*–discidium; *opp*–postpodosomal ornamentation.

Anogenital region: *g*, *ag*, *an*, *ad*–genital, aggenital, anal and adanal setae, respectively; *vr*–ventral ridge; *iag*, *iad*–aggenital, adanal lyrifissure respectively.

Gnathosoma: *a*, *m*–anterior, middle seta of gena; *h*–hypostomal seta of mentum; *v*, *l*, *d*, *cm*, *acm*, *ul*, *su*, *vt*, *lt*, *sup*, *inf*–palp setae; ω–palp tarsal solenidion; *ep*–postpalpal seta; *cha*, *chb*–cheliceral setae; *cht*–tooth on dorsal chelicerae; *rbr*–rutellar brush; Tg–Trägårdh's organ.

Legs: σ, φ, ω–solenidia of genu, tibia and tarsus, respectively; *ε*–famulus of tarsus I; *d*, *l*, *v*–dorsal, lateral, ventral setae, respectively; *ev*, *bv*–basal trochanteral setae; *ft*, *tc*, *it*, *p*, *u*, *a*, *s*, *pv*–tarsal setae; Tr, Fe, Ge, Ti, Ta–trochanter, femur, genu, tibia, tarsus of legs, respectively.

Taxonomy

Basiceramerus ovatus sp. nov.

http://zoobank.org/E8AFB948-9A53-47EF-9A1A-CFF080297747
Figures 1–5

Diagnosis. Body size (*N* = 4): 990–1360 × 540–650. Two pairs of prodorsal condyles present, similar in shape, broadly rounded, median prodorsal condyles close to each other but not fused. Lateral notogastral condyles triangular, with a tiny convex at bottom. One median notogastral condyle, rounded. Ten pairs of notogastral setae. Vitta marginalis distinct. A wavy marginalis, like vitta marginalis, passing the base of adanal setae, ended at level of anterior margin of anal opening.

Description. ***Measurements.*** Body length: 1020 (holotype, male), 990–1360 (paratypes, two males and one female), body width: 540 (holotype, male), 540–650 (paratypes, two males and one female). Setae length and mutual distance (holotype, male): *ro* 120, *le* 140, *bs* 130, *in* 110, *ex* 20; *c*, *la*, *lm*, *lp*, h_1, h_2, h_3, p_1, p_2, p_3 range 80–100; *c*–*c* 370, *la*–*la* 430, *lm*–*lm* 470, *lp*–*lp* 470.

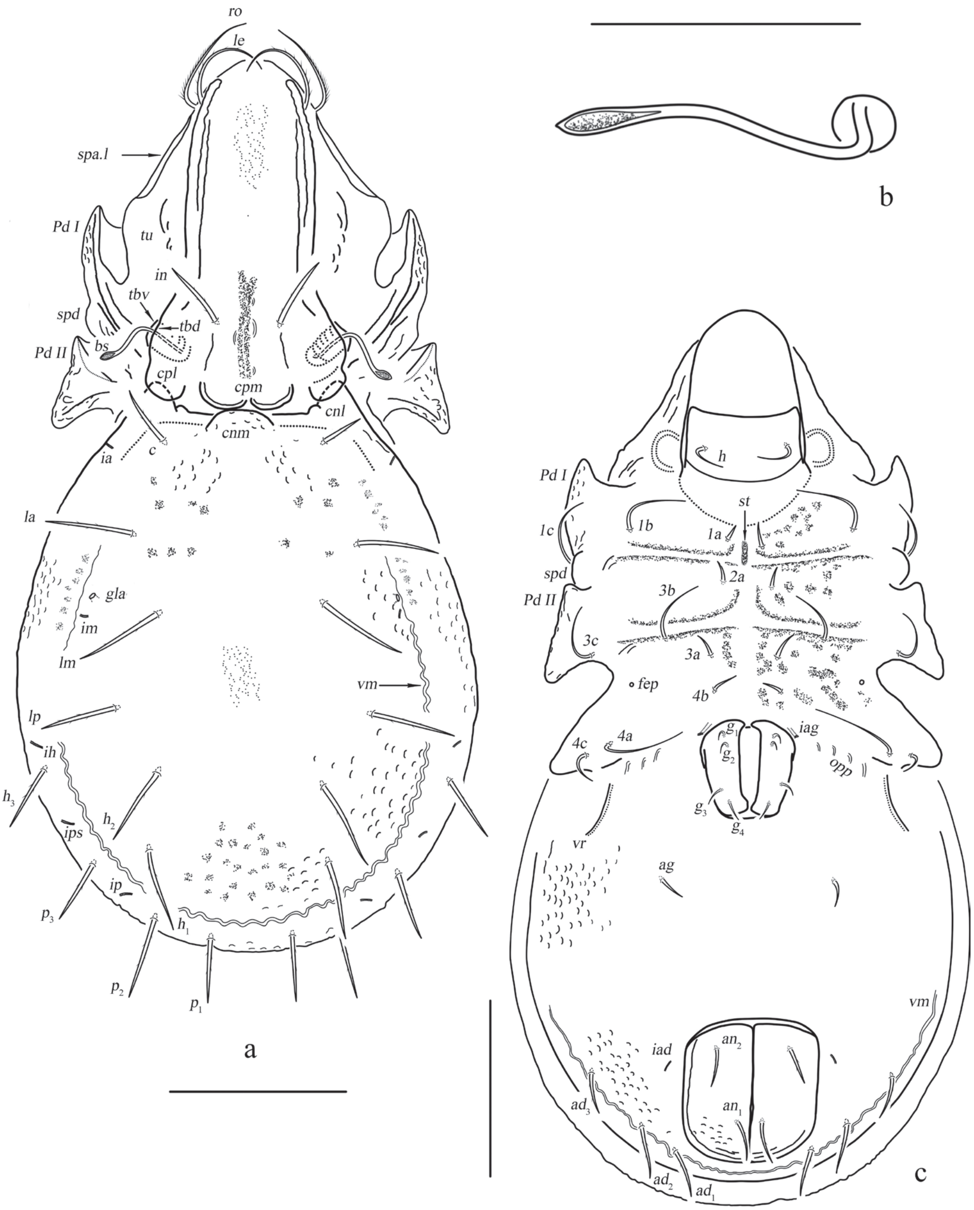


Figure 1. *Basiceramerus ovatus* sp. nov. adult: **a** dorsal view (legs not illustrated) **b** bothridial seta **c** ventral view (legs not illustrated). Abbreviations and notations explained in text. Scale bars: 200 µm (**a, c**); 100 µm (**b**).

Integument. Body color light brownish. Surface of notogaster foveolate.

Prodorsum. Rostrum rounded. Rostral setae moderately curved inward, densely barbed outside. Lamellar setae inserted behind tip of lamella, curved inward, roughened outside. Interlamellar setae barbed and setiform, a pair of longitudinal wrinkles

Figure 2. *Basiceramerus ovatus* sp. nov., adult, microscope images: **a** dorsal view **b** ventral view **c** lateral view. Abbreviations and notations explained in text. Scale bars: 200 μm (**a–c**).

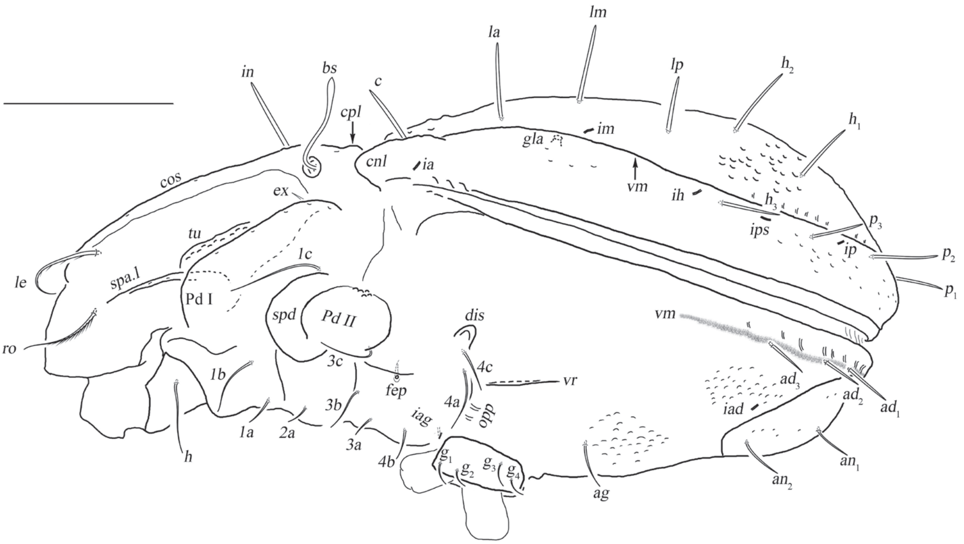


Figure 3. *Basiceramerus ovatus* sp. nov. adult: lateral view (legs not illustrated). Abbreviations and notations explained in text. Scale bar: 200 μm.

extending from its bottom backward to outer margin of median prodorsal condyles. Exobothridial setae short. Bothridial seta with a fusiform head. Tutorium developed, almost touching lamelliform expansion. Lamelliform expansion pointing to bottom of seta *ro*. Bothridium opening laterally, dorsal bothridial plate nearly straight, ventral bothridial plate broadly rounded in dorsal view. Two pairs of prodorsal condyles present, similar in shape, broadly rounded, median prodorsal condyles close to each other but not fused. Mutual distance between ventral bothridial plates nearly equal with that between lateral prodorsal condyles.

Notogaster. L/W of notogaster about 1.3. Lateral notogastral condyles triangular, with a tiny convex at bottom. One median notogastral condyle present, rounded. Ten pairs of notogastral setae, glabrous, setiform, nearly equal in length. Setae *lm* and lyrifissures *im* located nearly same level. All lyrifissures (*im*, *ip*, *ih*, *ips*, except *ia*) well visible in dorsal view, *ip* located between p_2 and p_3, *ips* between h_3 and p_3. Opisthonotal gland openings located anterior and very close to *im*. Vitta marginalis distinct.

Epimeral and lateral podosomal regions. Apodemes II and sejugal apodeme well developed, apodemes III invisible, epimeral foramen present, pedotectum II with anterior and posterior expansions nearly equal in size. Sternal apodeme well visible. Epimeral setal formula 3-1-3-3. Seta *4a* inserted between *4b* and *4c*, and closer to *4c*. Postpodosomal ornamentation well developed.

Anogenital region. Genital plates smooth. Four pairs of genital setae (mutual distances $g_1–g_1 \approx g_2–g_2 \approx g_4–g_4 < g_3–g_3$). Aggenital lyrifissures located close and anterolateral to genital aperture. One pair of aggenital, two pairs of anal (mutual distances an_1–

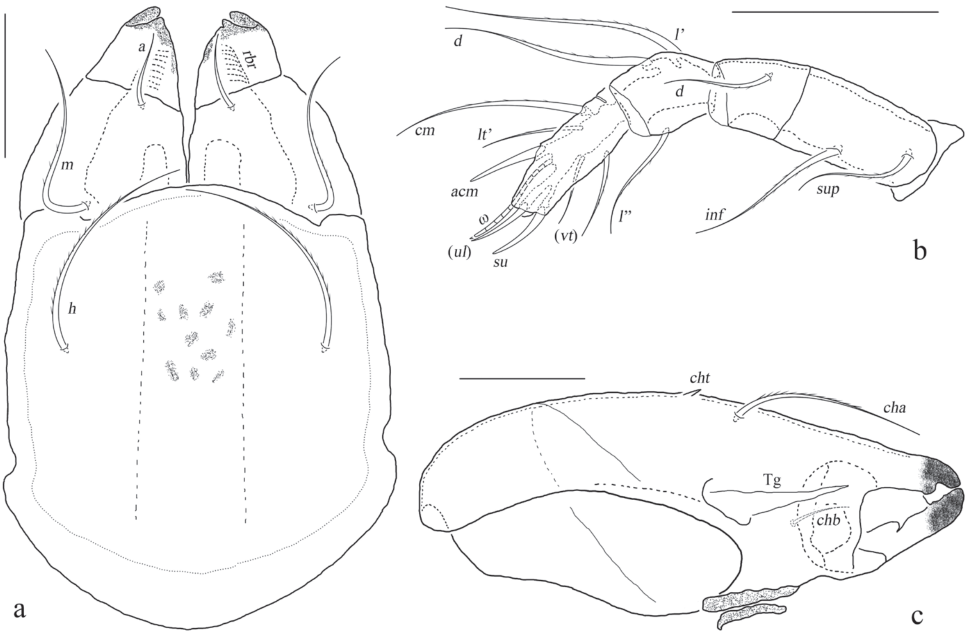


Figure 4. *Basiceramerus ovatus* sp. nov. adult: **a** subcapitulum, ventral view **b** left palp, abaxial view **c** left chelicera, adaxial view. Abbreviations and notations explained in text. Scale bars: 50 µm.

$an_1 < an_2$–an_2, seta an_1 located close to median margin of anal opening) and three pairs of adanal setae similar in length. Setae ad_3–ad_3 well below level of anterior margin of anal opening. Anal plate foveolate. Lyrifissures *iad* located in diagonal position and close to anal aperture, below level of anterior margin of anal opening. A wavy marginalis, like vitta marginalis, passing the base of adanal setae, ending beyond level of anterior margin of anal opening.

Gnathosoma. Subcapitular setae barbed, flagelliform at tips. Rutellum pantelobasic, with typical dentation and rutellar brush. Chelicera chelate-dentate; with a minute denticle proximal to seta *cha*; *cha* longer than *chb*, both of them barbed; Trägårdh's organ narrowly triangular. Palp with usual setal formula: 0-2-1-3-8 (+ω); setae of trochanter to tibia barbed. Tarsus with four short, blunt distal eupathidia–*acm*, *su*, (*ul*); other tarsal setae smooth or with sparse, inconspicuous barbs; base of solenidion ω constrainted by surface of tarsusand thus adjacent to setae *ul'*, *ul"* medioanteriorly. Postpalpal setae erect, smooth.

Legs. Monodactylous. Claw of each leg strong and smooth. Formulae of leg setation and solenidia (Table 1): I (1-4-3-4-16) [1-2-2], II (1-4-3-3-15) [1-1-2], III (2-3-1-2-15) [1-1-0], IV (1-2-2-2-12) [0-1-0]. Leg setae *u* setiform (L-type) on tarsi I, thorn-like (S-type) on tarsi II–IV.

Material examined. ***Holotype*:** male (in alcohol, ZLH-12-225): China, Yunnan Province, Ruili City, Nongdao Town, Nankaiba Village, 23°54'51.19"N, 97°33'58.69"E, 835 m a. s. l., in soil and debris under bush, 23 October 2012.

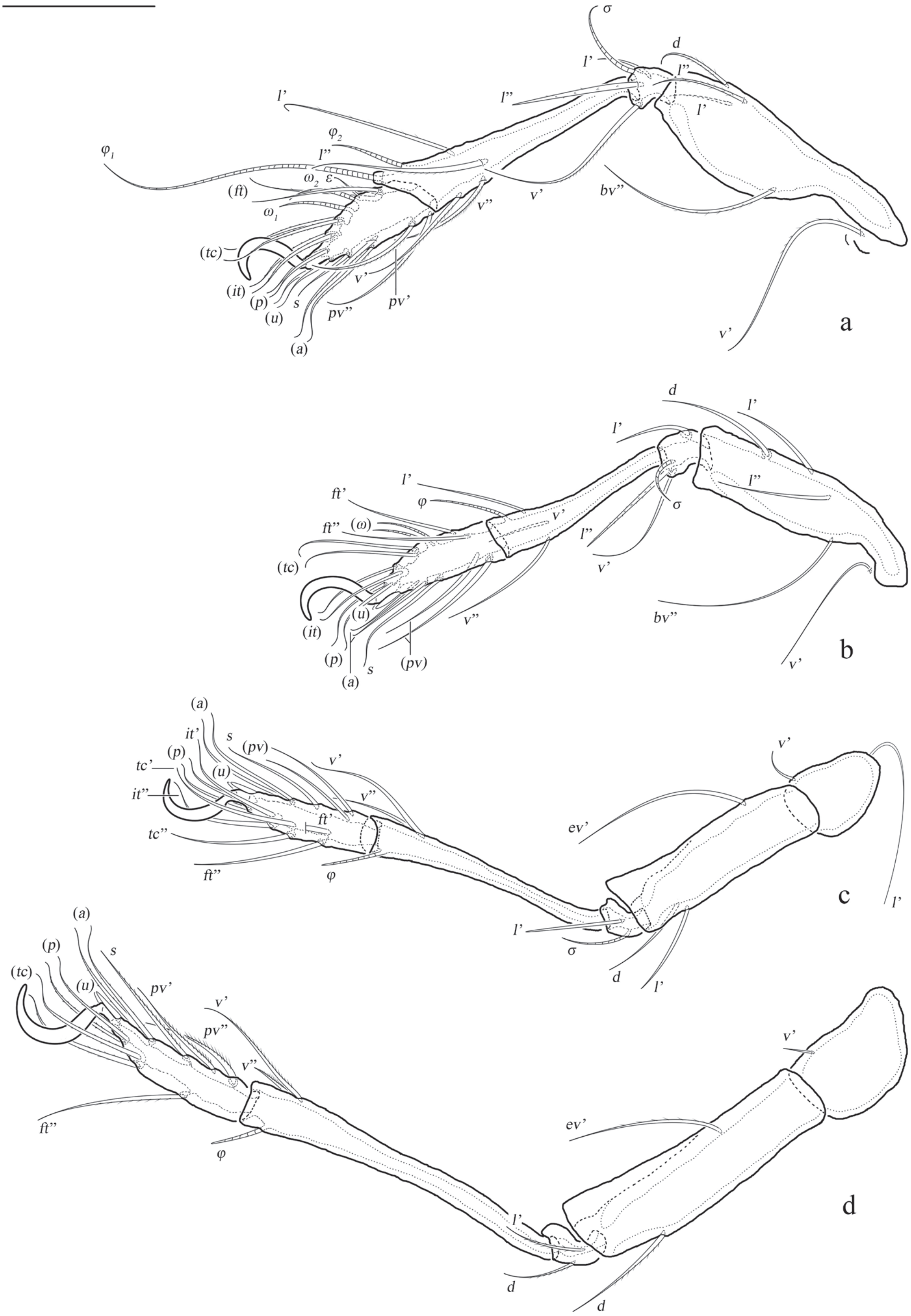


Figure 5. *Basiceramerus ovatus* sp. nov., adult: **a–d** leg I–IV, left, antiaxial view. Abbreviations and notations explained in text. Scale bars: 100 μm (**a–d**).

Table 1. Leg setation and solenidia of adult *Basiceramerus ovatus* sp. nov. Roman letters refer to normal setae, Greek letters to solenidia (except ε=famulus). Single prime (') marks setae on the anterior and double prime (") setae on the posterior side of a given leg segment. Parentheses refer to a pair of setae. Tr – trochanter, Fe – femur, Ge – genu, Ti – Tibia, Ta – tarsus.

Leg	Tr	Fe	Ge	Ti	Ta
I	*v'*	*d*, (*l*), *bv"*	(*l*), *v'*, σ	(*l*), (*v*), φ_1, φ_2	(*ft*), (*tc*), (*it*), (*p*), (*u*), (*a*), *s*, (*pv*), ε, ω_1, ω_2
II	*v'*	*d*, (*l*), *bv"*	(*l*), *v'*, σ	*l'*, (*v*), φ	(*ft*), (*tc*), (*it*), (*p*), (*u*), (*a*), *s*, (*pv*), ω_1, ω_2
III	*l'*, *v'*	*d*, *l'*, e*v'*	*l'*, σ	(*v*), φ	(*ft*), (*tc*), (*it*), (*p*), (*u*), (*a*), *s*, (*pv*)
IV	*v'*	*d*, e*v'*	*d*, *l'*	(*v*), φ	*ft"*, (*tc*), (*p*), (*u*), (*a*), *s*, (*pv*)

***Paratypes*:** two females (in alcohol, ZLH-12-225): same data as holotype; one female (in alcohol, ZLH-12-259): China, Yunnan Province, Yingjiang County, Daonong Village, 24°40'2.568"N, 97°35'54.24"E, 924 m a. s. l., in soil and debris under bush, 31 October 2012. All type specimens were collected by Lihao Zheng.

Type deposition. All type specimens are deposited in the collection of the Institute of Zoology, Chinese Academy of Sciences, Beijing (IZAS).

Etymology. The specific name "*ovatus*" is from Latin for "egg" refers to the oval notogaster in dorsal view.

Remarks. The new species is morphologically similar to *B. bangladeshensis* Corpuz-Raros & Gruèzo, 2008 from Bangladesh and *B. igorotus* Corpuz-Raros & Gruèzo, 2011 from the Philippines and Vietnam (Ermilov and Anichkin 2013) in having two median prodorsal condyles. However, the new species differs from *B. bangladeshensis* by the wavy marginalis, like vitta marginalis, passing the base of adanal setae (vs. none), prodorsal condyles well separated from the median ones (vs. all prodorsal condyles touching at base), ventral ridge present (vs. none), anal plate foveolate (vs. granulate, without foveolae). The species *B. igorotus* was reported from the Philippines and Vietnam by Corpuz-Raros and Gruèzo (2011) and Ermilov and Anichkin (2013) respectively. The latter recorded instances of intraspecific or geographical variability based on their specimens from Vietnam: body size larger and more elongate, interlamellar setae shorter, lamellar setae longer, lateral notogastral condyles narrower, medial notogastral condyles touching base of lateral notogastral condyles, genital plate smooth in the Vietnamese specimens. The new species differs from *B. igorotus* from Vietnam by the wavy marginalis passing the base of adanal setae (vs. none), tutorium and lamelliform expansion nearly touching (vs. well separated), ventral ridge present (vs. none), genital plate smooth (vs. finely striate), seta *an*$_1$ located close to the median margin of the anal opening (vs. *an*$_1$ well removed from median margin of anal opening); it differs from *B. igorotus* from the Philippines by the lamellar setae inserted behind the tip of the lamella (vs. lamellar setae arising outside the base of cuspis), separated prodorsal condyles (vs. prodorsal condyles all touching at base), *im* posterior to *gla* (vs. *im* anterior to *gla*), genital plate smooth (vs. finely striate), anal plate foveolate (vs. granulate), wavy marginalis, like vitta marginalis, passing the base of adanal setae (vs. none).

***Eurostocepheus* (*Eurostocepheus*) *sinutus* sp. nov.**

http://zoobank.org/2500C6A8-CB6A-44BF-9C05-1B85F9F80471
Figures 6–8

Diagnosis. Body size: 1500 × 850. Body ratio (length/width): 1.8. Body surface relatively smooth. Costula strong, a little "S" shaped curved, largest width of mutual distance anteriorly, curved inward around setae *le*. Pedotecta II disproportionately dilated, with smaller anterior parts and larger posterior parts projecting lateroposteriad. Eight pairs of notogastral setae, *c*, *la*, *lm*, *lp* setiform and slightly barbed distally, p_1, p_2, p_3, h_3 short and ciliform. Epimeral setal formula 3-1-3-3. A pair of ventral grooves between genital aperture and ventral ridge present.

Description. ***Measurements*** (holotype, female). Body length: 1500, body width: 850. Setae length and mutual distance: *ro* 230, *le* 230, *bs* 150, *ex* 20; *c*, *la*, *lm*, *lp* range 210–250; p_1, p_2, p_3, h_3 range 40–60; *c–c* 370, *la–la* 430, *lm–lm* 470, *lp–lp* 470.

Integument. Body color dark brownish. Body surface relatively smooth.

Prodorsum. Rostrum broadly rounded. Rostral setae curved inward, densely barbed outside. Lamellar setae inserted behind tip of costula, curved inward, roughened externally. Interlamellar setae slightly barbed. Bothridial setae with a long fusiform head and a curved peduncle in dorsal view. Exobothridial setae short, hardly visible in dorsal view. Costula strong, weakly "S" shaped, largest width of mutual distance anteriorly, curved inward around setae *le*. Bothridium opening laterally, dorsal bothridial plate nearly straight, ventral bothridial plate invisible in dorsal view. Tutorium developed weakly. Lamelliform expansion curved and pointing to base of seta *ro* in lateral view. Two pairs of prodorsal condyles present, lateral prodorsal condyles broadly flattened and wide, median prodorsal condyles drop-shaped.

Notogaster. L/W of notogaster about 1.1. Surface of notogaster relatively smooth in dorsal view, without visible foveola or granules. Anterior margin of notogaster distinctly moved forward. Lateral notogastral condyles trapezoid, with triangular tip outside, which markedly anterior to medial prodorsal condyles. Median notogastral condyles absent. Eight pairs of notogastral setae, *c*, *la*, *lm*, *lp* longer than others distinctly, setiform and slightly barbed distally, p_1, p_2, p_3, h_3 short and ciliform. All lyrifissures well visible, *ip* located between p_1 and p_2 on left side while it between p_2 and p_3 on right side, *ips* between h_3 and p_3. Opisthonotal gland openings located close to lyrifissure *im*. Vitta marginalis distinct. Lyrifissures *im* and setae *lm* almost located at same level.

Epimeral and lateral podosomal regions. Pedotecta II disproportionately dilated, with smaller anterior parts and larger posterior parts projecting lateroposteriad. Epimeral border I well visible. Apodemes I, II and sejugal apodeme well developed, epimeral foramen present. Sternal apodeme well developed. Epimeral setal formula 3-1-3-3. Epimeral setae slightly barbed, seta *4a* inserted between *4b* and *4c*, and closer to *4c*. Postpodosomal ornamentation present.

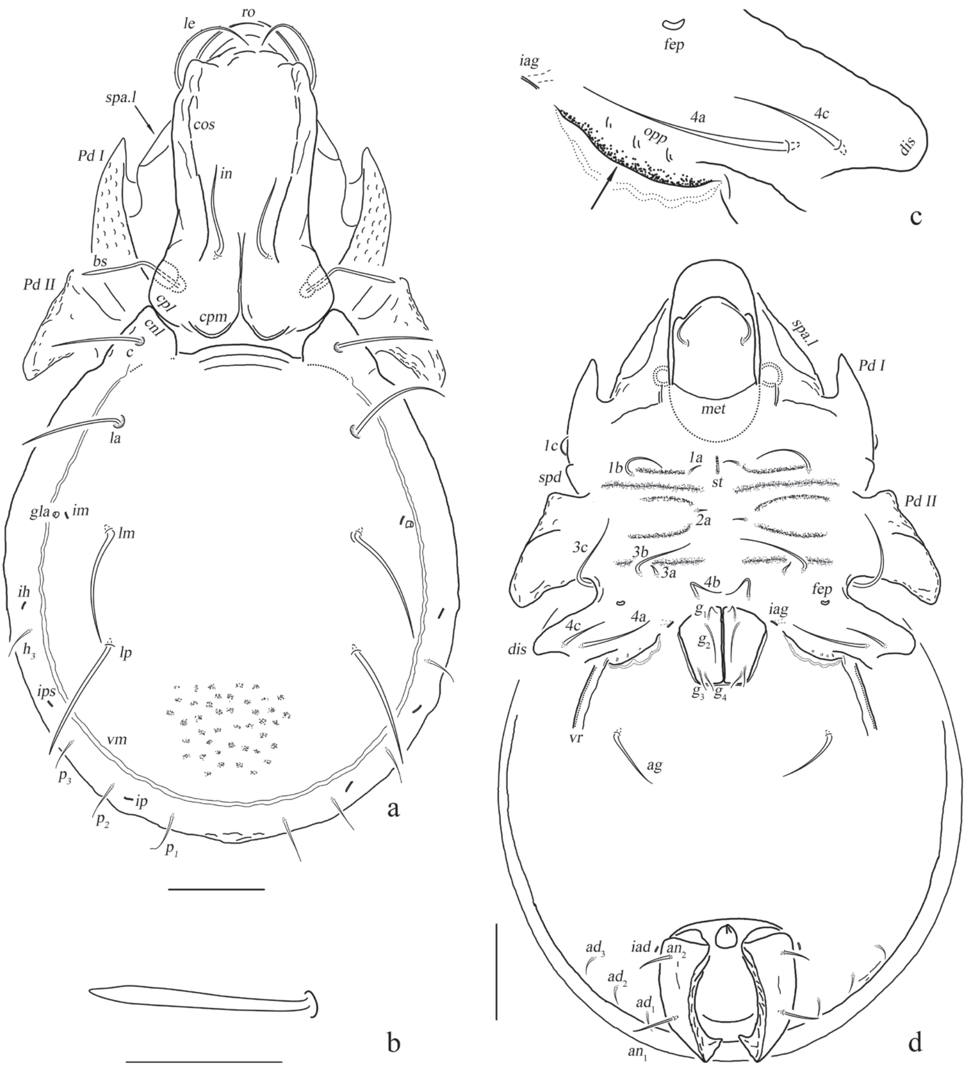


Figure 6. *Eurostocepheus (Eurostocepheus) sinutus* sp. nov., adult: **a** dorsal aspect (legs removed) **b** bothridial seta **c** epimeron IV (left, part), showing ventral groove (arrow) **d** ventral aspect (legs and mouthparts removed). Abbreviations and notations explained in text. Scale bars: 200 μm (**a, d**); 100 μm (**b**).

Anogenital region. Genital plates relatively smooth. Four pairs of genital setae (mutual distances g_1–g_1≈g_2–g_2≈g_4–g_4<g_3–g_3, g_2 longer than the rest). Aggenital lyrifissures located close and anterolateral to genital aperture. A pair of ventral groove present between genital aperture and ventral ridge. One pair of aggenital, two pairs of anal (mutual distances an_1–an_1<an_2–an_2) and three pairs of adanal setae short, similar in length. Setae ad_3–ad_3 below level of anterior margin of anal opening. Adanal lyrifissures located in diagonal position and close to anal aperture, below level of anterior margin of anal opening.

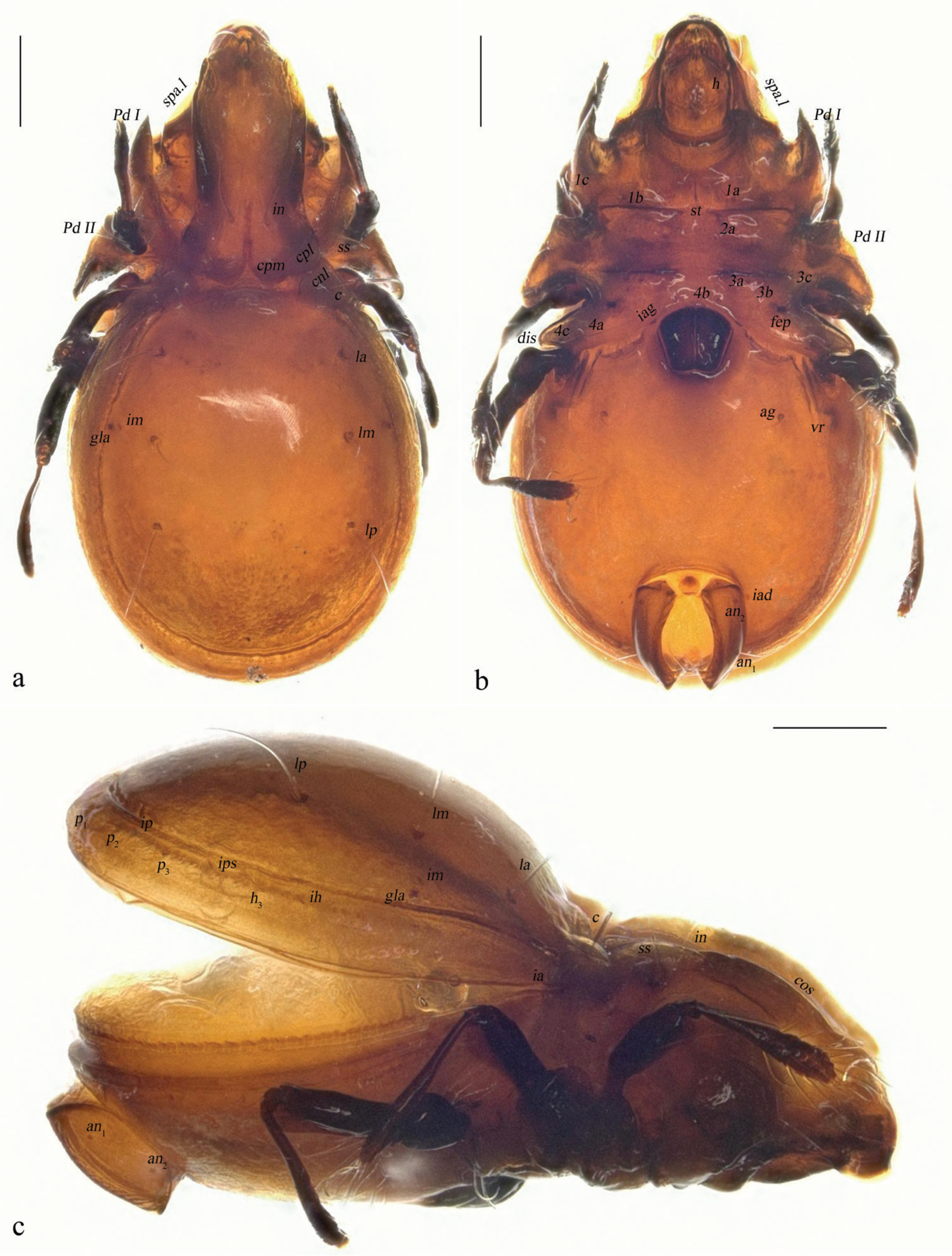


Figure 7. *Eurostocepheus (Eurostocepheus) sinutus* sp. nov., adult, microscope images: **a** dorsal view **b** ventral view **c** lateral view. Abbreviations and notations explained in text. Scale bars: 200µm.

Gnathosoma. Subcapitular setae barbed. Rutellum pantelobasic, with typical dentation and rutellar brush. Chelicera chelate-dentate; with a minute denticle proximal to seta *cha*; *cha* longer than *chb*; Trägårdh's organ narrowly triangular. Palp with

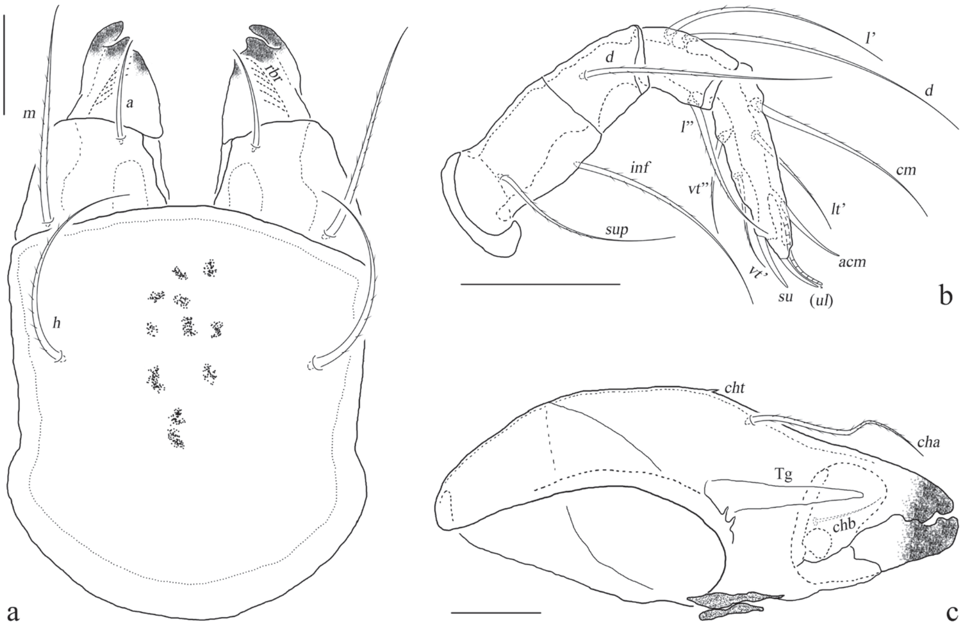


Figure 8. *Eurostocepheus (Eurostocepheus) sinutus* sp. nov., adult: **a** subcapitulum, ventral view **b** right palp, abaxial view **c** left chelicera, adaxial view. Abbreviations and notations explained in text. Scale bars: 50 µm.

usual setal formula: 0-2-1-3-8 (+ω); setae of trochanter to tibia barbed. Tarsus with four short, blunt distal eupathidia–*acm*, *su*, (*ul*); base of solenidion ω constrainted by surface of tarsus, and thus adjacent to setae *ul'*, *ul"* medioanteriorly. Postpalpal setae erect, smooth.

Legs. Monodactylous. Claw of each leg strong and smooth. Formulae of leg setation and solenidia (Table 3): I (1-4-3-4-16) [1-2-2], II (1-4-3-3-15) [1-1-2], III (1-2-1-2-15) [1-1-0], IV (1-2-2-2-12) [0-1-0]. Leg setae *u* setiform (L-type) on tarsi I, thorn-like (S-type) on tarsi II–IV.

Material examined. ***Holotype*:** female (in alcohol, ZLH-12-276): China, Yunnan Province, Yingjiang County, Taiping Town, Huilonghe Reservoir, 24°40'20"N, 97°45'28"E, 1769 m a. s. l., litter and soil under moss, 24 October 2012, collected by Lihao Zheng.

Type deposition. Type specimen is deposited in the collection of the IZAS.

Etymology. The specific name "*sinutus*" is from Latin for "sinus" refers to the ventral groove between genital aperture and ventral ridge.

Remarks. As possessing the conspicuously developed costula and the distinctly dilated posterior pedotecta II, which are diagnostic characters of the genus, this new species should be placed into the genus *Eurostocepheus*. The new species can be easily distinguished from other known species of this genus by its huge body size, eight pairs of notogastral setae and its ventral groove between the genital aperture and the ventral ridge.

Eurostocepheus (*Eurostocepheus*) *aquilinus* Aoki, 1965

New record for China
Figures 9–10

Eurostocepheus aquilinus Aoki, 1965: 334–339, figs 142–146; Ermilov, Niedbała and Anichkin 2012: 23.

Diagnosis. Body size: 1000 × 510. Body ratio (length/width): 2.0. Costula strong, thin anteriorly, and thick posteriorly. Lamelliform expansion sigmoid and passing between base of setae *ro* and *le* in lateral view. Ten pairs of notogastral setae nearly equal in length. Sternal apodeme short and rounded. Epimeral setal formula 3-1-3-2. Epimeral setae slightly barbed, seta *1a*, *2a*, *3a* short and thin, hardly visible.

Description. ***Measurements*** (ZLH-20-029, male). Body length: 1000, body width: 510. Setae length and mutual distance: *ro* 130, *le* 140, *bs* 150, *in* 60, *ex* 20; notogastral setae range 70–110. Mutual distance: *c–c* 140, *la–la* 190, *lm–lm* 210, *lp–lp* 310, h_2–h_2 220, h_1–h_1 210.

Integument. Body color dark brownish. Body surface covered with foveola.

Prodorsum. Rostrum rounded. Both rostral setae and lamellar setae curved inward, slightly barbed outside. Lamellar setae inserted behind tip of costula. Interlamellar setae slightly barbed. Bothridial setae with a long fusiform head and a curved peduncle. Exobothridial setae short, hard to see in dorsal view. Costula strong, thin anteriorly, and thick posteriorly. Bothridium opening laterally, dorsal bothridial plate nearly straight, ventral bothridial plate invisible in dorsal view. Tutorium fainted. Lamelliform expansion sigmoid and passing between bases of setae *ro* and *le* in lateral view. Lateral prodorsal condyles broadly rounded, median prodorsal condyles absent. Mutual distance between ventral bothridial plate nearly equal with that between lateral prodorsal condyles.

Notogaster. L/W of notogaster about 1.3. Lateral notogastral condyles triangular. Median notogastral condyles absent. Ten pairs of notogastral setae nearly equal in length. All lyrifissures well visible, *ip* located between p_2 and p_3, *ips* between h_3 and p_3. Opisthonotal gland openings located close to lyrifissure *im*. Vitta marginalis distinct. Lyrifissures *im* and setae *lm* located nearly same level.

Epimeral and lateral podosomal regions. Epimere I with distinct, long ridge extend to pedotectum I. Apodemes I, II and sejugal apodeme well developed. Sternal apodeme short and rounded. Epimeral setal formula 3-1-3-2. Epimeral setae slightly barbed, seta *1a*, *2a*, *3a* short and thin, hardly visible.

Anogenital region. Genital plates sculptured irregularly with several strong furrows. Four pairs of genital setae (largest mutual distance is g_3–g_3). Aggenital lyrifissures located close and anterolateral to genital aperture. One pair of aggenital, two pairs of anal (mutual distances an_1–an_1<an_2–an_2) and three pairs of adanal setae similar in length. Setae ad_3–ad_3 below level of anterior margin of anal opening. Adanal lyrifissures located longitudinally and close to anal aperture, below level of anterior margin of anal opening.

Gnathosoma. Subcapitular setae barbed. Rutellum pantelobasic, with typical dentation and rutellar brush. Chelicera chelate-dentate; with a minute denticle proximal to

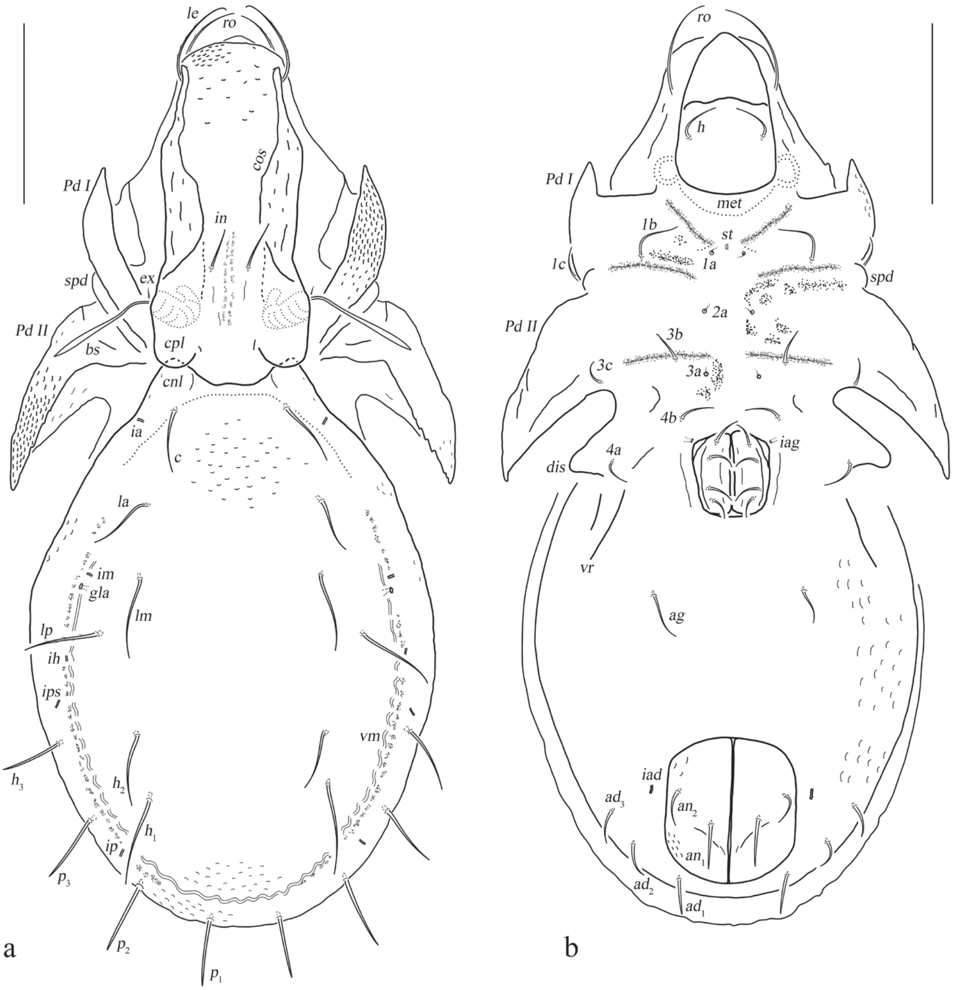


Figure 9. *Eurostocepheus (Eurostocepheus) aquilinus* Aoki, 1965, adult: **a** dorsal aspect (legs removed) **b** ventral aspect (legs and mouthparts removed). Abbreviations and notations explained in text. Scale bars: 200 μm.

seta *cha*; *cha* longer than *chb*; Trägårdh's organ narrowly triangular. Palp with usual setal formula: 0-2-1-3-8 (+ω); setae of trochanter to tibia barbed. Tarsus with four short, blunt distal eupathidia–*acm*, *su*, (*ul*); base solenidion **ω** constrainted by surface of tarsus, and thus adjacent to setae *ul'*, *ul"* medioanteriorly. Postpalpal setae erect, smooth.

Legs. Monodactylous. Claw of each leg strong and smooth. Formulae of leg setation and solenidia (Table 2): I (1-4-3-4-16) [1-2-2], II (1-4-3-3-15) [1-1-2], III (1-2-1-2-15) [1-1-0], IV (0-2-2-2-12) [0-1-0]. Leg setae *u* setiform (L-type) on tarsi I, thorn-like (S-type) on tarsi II–IV.

Material examined. One male (in alcohol, ZLH-20-029): China, Yunnan Province, Ruili County, Nongdao Town, Nankaiba, 23°55'49"N, 97°32'7"E, 752 m a. s. l., litter and soil under fern, 25 May 2020, collected by Lihao Zheng.

Figure 10. *Eurostocepheus (Eurostocepheus) aquilinus* Aoki, 1965, adult, microscope images: **a** dorsal view **b** ventral view **c** lateral view. Abbreviations and notations explained in text. Scale bars: 200 µm.

Table 2. Leg setation and solenidia of adult *Eurostocepheus (Eurostocepheus) aquilinus* Aoki, 1965.

Leg	Tr	Fe	Ge	Ti	Ta
I	*v*’	*d*, (*l*), *bv*”	(*l*), *v*’, σ	(*l*), (*v*), φ_1, φ_2	(*ft*), (*tc*), (*it*), (*p*), (*u*), (*a*), *s*, (*pv*), ε, ω_1, ω_2
II	*v*’	*d*, (*l*), *bv*”	(*l*), *v*’, σ	*l*’, (*v*), φ	(*ft*), (*tc*), (*it*), (*p*), (*u*), (*a*), *s*, (*pv*), ω_1, ω_2
III	*v*’	*d*, *l*’, e*v*’	*l*’, σ	(*v*), φ	(*ft*), (*tc*), (*it*), (*p*), (*u*), (*a*), *s*, (*pv*)
IV	-	*d*, e*v*’	*d*, *l*’	(*v*), φ	*ft*”, (*tc*), (*p*), (*u*), (*a*), *s*, (*pv*)

Specimen deposition. Specimen is deposited in the collection of the IZAS.

Remarks. The specimen checked in this study is almost coincident (shape of lamelliform expansion, different kind of epimeral setae in shape, etc.) with the original description given by Aoki. Here, we provide a supplementary description of this species with new figures and information about morphological characters of this species.

***Eurostocepheus* (*Eurostocepheus*) *mahunkai* Mondal & Kundu, 1999**

New record for China

Figures 11–14

Eurostocepheus (*Eurostocepheus*) *mahunkai* Mondal & Kundu, 1999: 180–186, figs 1–16.

Diagnosis. Body size: 830 × 420. Body ratio (length/width): 2.0. Mutual distance of costula gradually narrow from base to tip. Two pairs of prodorsal condyles present, lateral prodorsal condyles broadly rounded, with bottom straight, median prodorsal condyles rounded, not conspicuous, well separated from each other. Lateral notogastral condyles trapezoid, with triangular tip outside. Epimeral setal formula 3-1-3-3. Genital plates with longitudinal furrows.

Description. ***Measurements*** (holotype, male). Body length: 830, body width: 420. Setae length and mutual distance: *ro* 120, *le* 130, *bs* 100, *in* 160, *ex* 10; notogastral setae range 150–190; *c*–*c* 170, *la*–*la* 220, *lm*–*lm* 180, *lp*–*lp* 230, h_2–h_2 240, h_1–h_1 130.

Integument. Body color light brownish. Body surface densely foveolate (not well visible on notogaster).

Prodorsum. Rostrum broadly rounded. Rostral setae moderately curved inward, densely barbed outside. Lamellar setae inserted behind tip of costula, curved inward, roughened externally. Interlamellar setae slightly barbed. Bothridial setae with a long fusiform head and a strongly curved peduncle. Exobothridial setae short. Mutual distance of costula gradually narrow from base to tip. Bothridium opening laterally, dorsal bothridial plate nearly straight, ventral bothridial plate triangular in dorsal view. Tutorium fainted. Two pairs of prodorsal condyles present, lateral prodorsal condyles broadly rounded, with bottom straight, median prodorsal condyles rounded, not conspicuous, well separated from each other. Mutual distance between

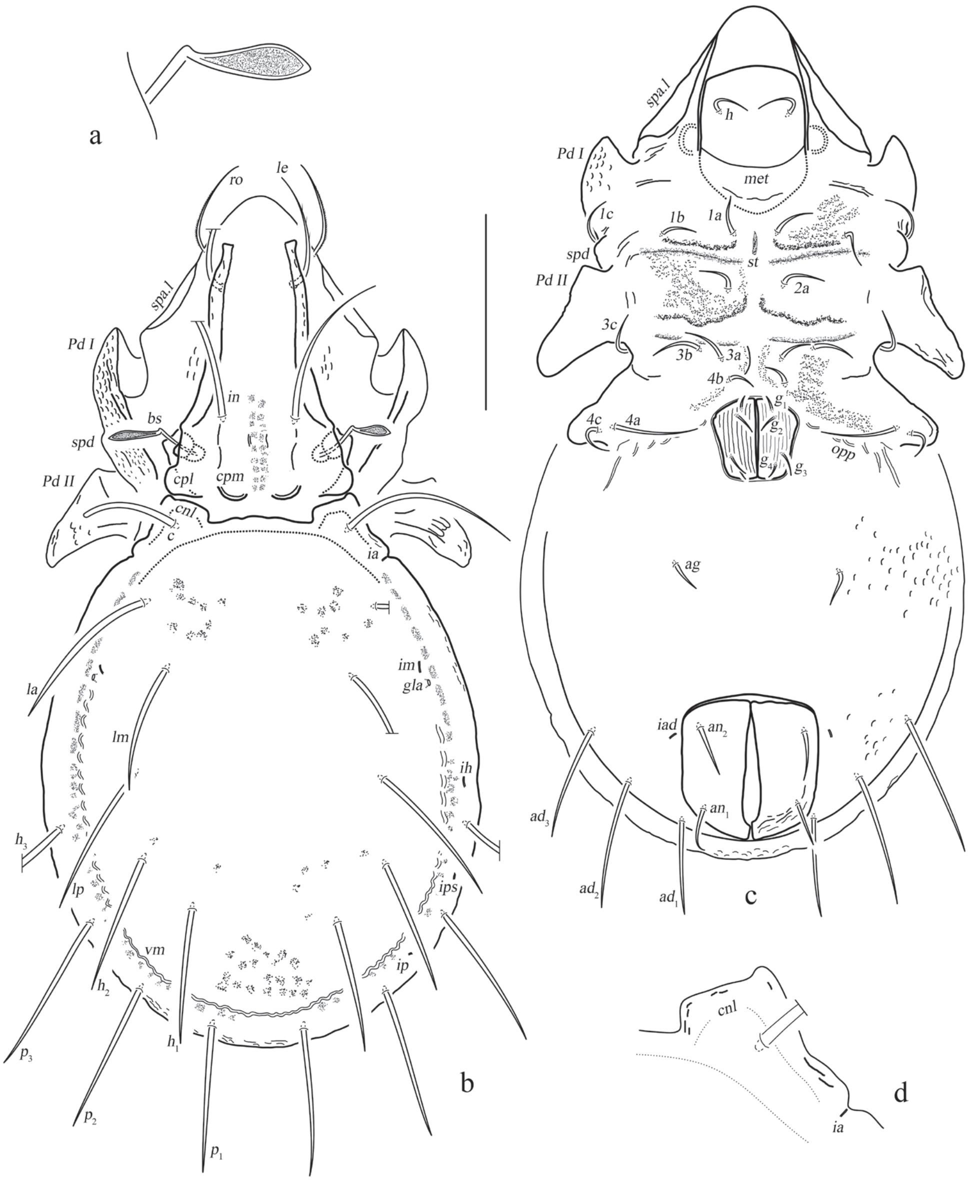


Figure 11. *Eurostocepheus (Eurostocepheus) mahunkai* Mondal & Kundu, 1999, adult: **a** bothridial seta **b** dorsal aspect (legs removed) **c** ventral aspect (legs and mouthparts removed) **d** lateral notogastral condyle (right). Abbreviations and notations explained in text. Scale bars: 200 μm.

ventral bothridial plate nearly equal with that between lateral prodorsal condyles. Subpedotectum well developed.

Notogaster. L/W of notogaster about 1.2. Surface of notogaster relatively smooth in dorsal view. Anterior margin of notogaster slightly curved forward. Lateral notogastral condyles trapezoid, with triangular tip outside. Median notogastral condyles

Figure 12. *Eurostocepheus* (*Eurostocepheus*) *mahunkai* Mondal & Kundu, 1999, adult, microscope images: **a** dorsal view, ventral view **c** lateral view. Abbreviations and notations explained in text. Scale bars: 100 µm.

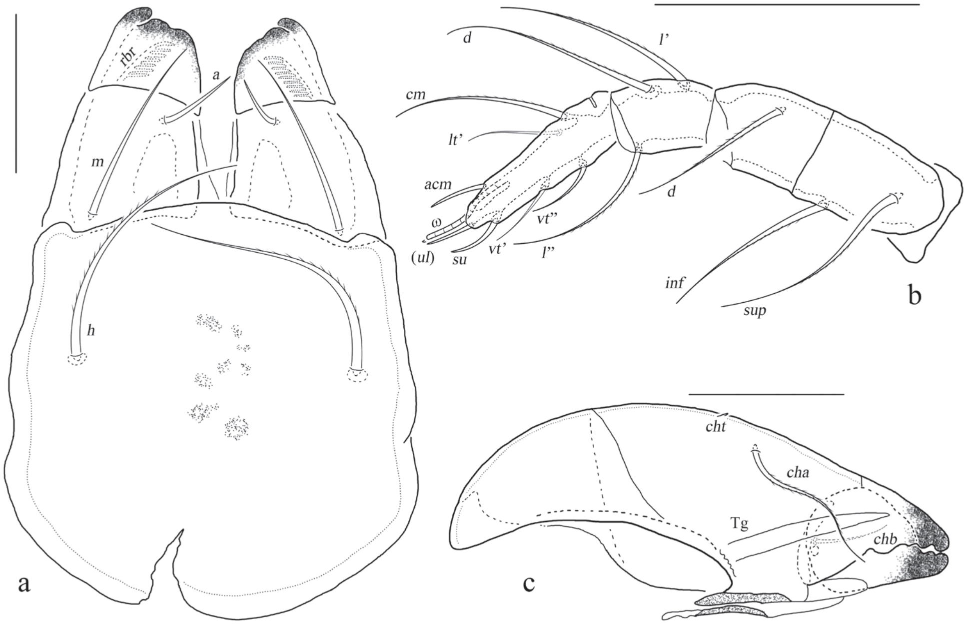


Figure 13. *Eurostocepheus (Eurostocepheus) mahunkai* Mondal & Kundu, 1999, adult: **a** subcapitulum, ventral view **b** left palp, abaxial view **c** left chelicera, adaxial view. Scale bars: 50 μm.

absent. Ten pairs of notogastral setae slightly barbed, setiform. A pair of notchs present in external margin of anterior notogaster, beside lyrifissure *ia*. All lyrifissures well visible, *ip* located between p_2 and p_3, *ips* between h_3 and p_3. Opisthonotal gland openings located posterior and close to lyrifissure *im*. Vitta marginalis distinct. Lyrifissures *im* and setae *lm* located nearly same line.

Epimeral and lateral podosomal regions. Epimere I with distinct, long, transverse ridge. Apodemes I, II and sejugal apodeme well developed, apodeme III short. Sternal apodeme well developed. Epimeral setal formula 3-1-3-3. Seta *4a* inserted between *4b* and *4c*, and closer to *4c*. Postpodosomal ornamentation present.

Anogenital region. Genital plates covered with longitudinal furrows. Four pairs of genital setae (mutual distances $g_1–g_1 \approx g_2–g_2 \approx g_4–g_4 < g_3–g_3$). Aggenital lyrifissures located close and anterolateral to genital aperture. One pair of aggenital, two pairs of anal (mutual distances $an_1–an_1 \approx an_2–an_2$) and three pairs of adanal setae similar in length. Setae $ad_3–ad_3$ below level of anterior margin of anal opening. Adanal lyrifissures located in diagonal position and close to anal aperture, below level of anterior margin of anal opening.

Gnathosoma. Subcapitular setae barbed, flagelliform at tips. Rutellum pantelobasic, with typical dentation and rutellar brush. Chelicera chelate-dentate; with a minute denticle proximal to seta *cha*; *cha* longer than *chb*, both of them barbed; Trägårdh's organ narrowly triangular. Palp with usual setal formula: 0-2-1-3-8 (+ω); setae of trochanter to tibia barbed. Tarsus with four short, blunt distal eupathidia–*acm*, *su*, (*ul*); other tarsal setae smooth or with sparse, inconspicuous barbs; base of solenidion ω constrainted by surface of tarsus, and thus adjacent to setae *ul'*, *ul"* medioanteriorly. Postpalpal setae erect, smooth.

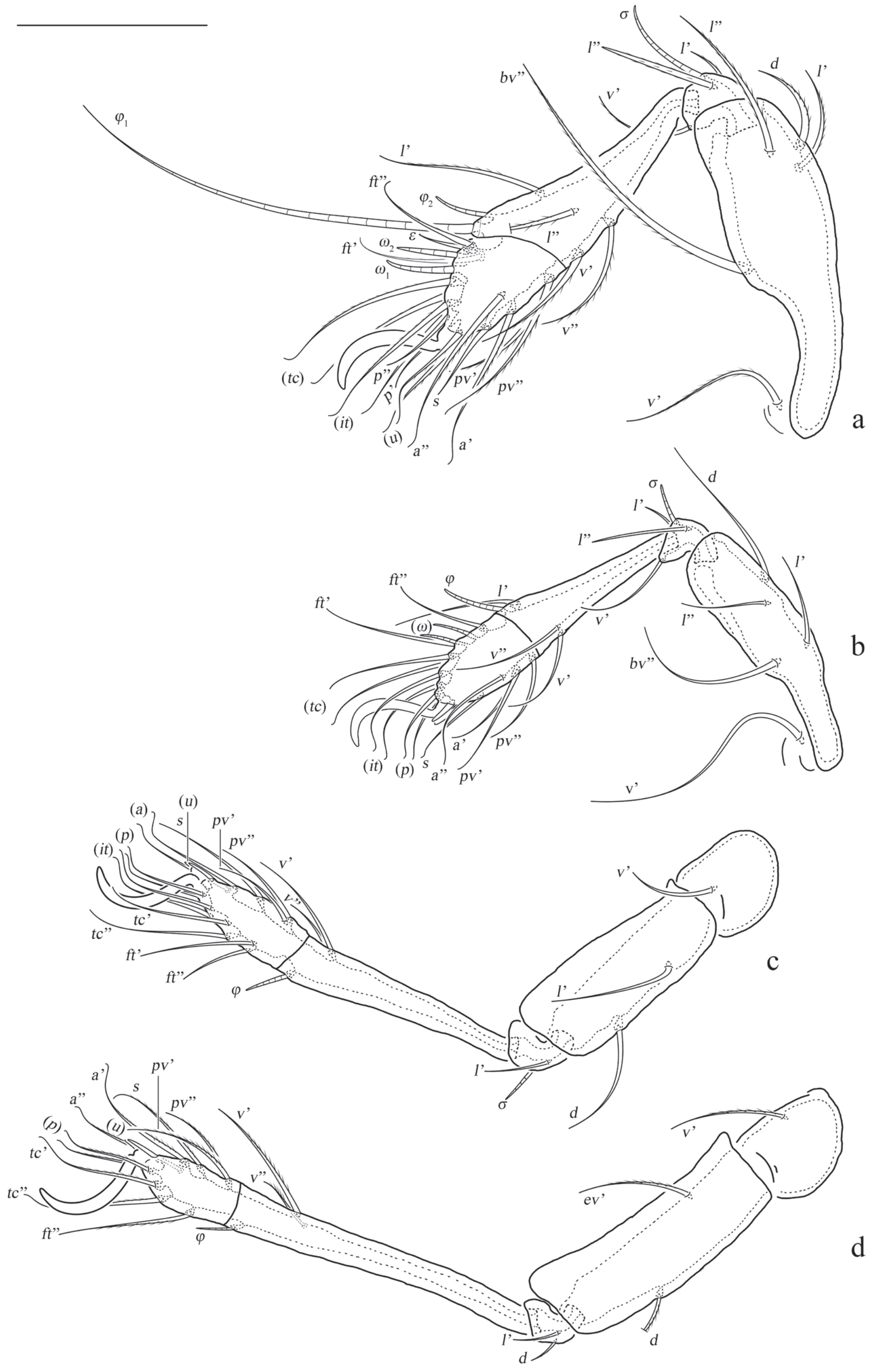


Figure 14. *Eurostocepheus (Eurostocepheus) mahunkai* Mondal & Kundu, 1999, adult: **a** subcapitulum, ventral view **b** left palp, abaxial view **c** left chelicera, adaxial view. Scale bars: 50 µm.

Table 3. Leg setation and solenidia of adult *Eurostocepheus (Eurostocepheus) sinutus* sp. nov. and *Eurostocepheus (Eurostocepheus) mahunkai* Mondal & Kundu, 1999.

Leg	Tr	Fe	Ge	Ti	Ta
I	*v'*	*d*, (*l*), *bv"*	(*l*), *v'*, σ	(*l*), (*v*), φ_1, φ_2	(*ft*), (*tc*), (*it*), (*p*), (*u*), (*a*), *s*, (*pv*), ε, ω_1, ω_2
II	*v'*	*d*, (*l*), *bv"*	(*l*), *v'*, σ	*l'*, (*v*), φ	(*ft*), (*tc*), (*it*), (*p*), (*u*), (*a*), *s*, (*pv*), ω_1, ω_2
III	*v'*	*d*, *l'*, e*v'*	*l'*, σ	(*v*), φ	(*ft*), (*tc*), (*it*), (*p*), (*u*), (*a*), *s*, (*pv*)
IV	*v'*	*d*, e*v'*	*d*, *l'*	(*v*), φ	*ft"*, (*tc*), (*p*), (*u*), (*a*), *s*, (*pv*)

Legs. Monodactylous. Claw of each leg strong and smooth. Formulae of leg setation and solenidia (Table 3): I (1-4-3-4-16) [1-2-2], II (1-4-3-3-15) [1-1-2], III (1-2-1-2-15) [1-1-0], IV (1-2-2-2-12) [0-1-0]. Leg setae *u* setiform (L-type) on tarsi I, thorn-like (S-type) on tarsi II–IV.

Material examined. One male (in alcohol, ZLH-12-229): CHINA, Yunnan Province, Ruili City, Nongdao Town, 23°59'49.1"N, 97°39'10.79"E, 1150 m a. s. l., primary forest, litter and soil under bamboo, 24 October 2012, collected by Lihao Zheng.

Specimen deposition. Specimen is deposited in the collection of the IZAS.

Remarks. The specimen collected from Yunnan, Southwest China is morphologically coincident (shape of costula, unsmooth genital plates, epimeral setal formula, etc) with *E.* (*E.*) *mahunkai* described and illustrated by Mondal and Kundu (1999) from Darjeeling, Bengal, India, except for the shape of lateral notogastral condyles (trapezoid in our specimen vs. triangular in Mondal and Kundu's description). Considering that there is intraspecific variation in the shape of notogastral or prodorsal condyles in Otocepheidae (Aoki 1967; Zheng and Chen 2020), we identified this specimen as *E.* (*E.*) *mahunkai*, which has not been recorded in China before.

Acknowledgements

We cordially thank Dr Schatz and Dr Vladimir Pesic (Subject editor of Zookeys) for their thorough review to this manuscript and many valuable comments. This work was supported by the National Natural Science Foundation of China (No. 32070421, 31372155), the National Science & Technology Fundamental Resources Investigation Program of China (Grant No. 2019FY101800), the Second Tibetan Plateau Scientific Expedition and Research (STEP) program (Grant No. 2019QZKK050100101), and the Key Laboratory of Dry-hot Valley Characteristic Bio-Resources Development at university of Sichuan Province (Grant No. GR-2018-C-04).

References

Aoki J (1965) A preliminary revision of the family Otocepheidae (Acari, Cryptostigmata). I. Subfamily Otocepheinae. Bulletin of the National Science Museum 8(3): 258–341.

Aoki J (1967) A preliminary revision of the family Otocepheidae (Acari, Cryptostigmata). II. Subfamily Tetracondylinae. Bulletin of the National Science Museum 10(3): 297–359.

Chen J, Liu D, Wang HF (2010) Oribatid mites of China: a review of progress, with a checklist. Zoosymposia 4: 186–224. https://doi.org/10.11646/zoosymposia.4.1.14

Corpuz-Raros LA (1979) Philippine Oribatei (Acarina). 1. Preliminary list of species and description of forty new species. The Philippine Agriculturist 62(1): 33–38.

Corpuz-Raros LA, Gruèzo WS (2008) A revision of the genus *Basiceremaeus* Corpuz-Raros 1979 (Acari: Oribatida: Otocepheid) including the description of a new species from Bangladesh. Asia Life Scienses 17(2): 179–187.

Corpuz-Raros LA, Gruèzo WS (2011) New species and records of Oribatida and other soil-inhabiting mites (Acari) mainly from Luzon and Mindanao Islands, Philippines. Asia Life Sciences 20(1): 31–67.

Ermilov SG, Anichkin AE (2013) Oribatid mites (Acari: Oribatida) of fungi from Dong Nai Biosphere Reserve, Southern Vietnam. Persian Journal of Acarology 2(2): 195–208. https://doi.org/10.3161/000345413X669513

Ermilov SG, Niedbała W, Anichkin AE (2012) Oribatid mites of Dong Nai Biosphere Reserve (= Cat Tien National Park) of Southern Vietnam, with description of a new species of *Pergalumna* (Acari, Oribatida, Galumnida). Acarina 20(1): 20–28. https://doi.org/10.31610/zsr/2011.20.2.200

Ermilov SG, Starý J (2017) Contribution to the knowledge of the oribatid mite genus *Eurostocepheus* (Acari, Oribatida, Otocepheidae). Systematic and Applied Acarology 22(5): 640–652. https://doi.org/10.11158/saa.22.5.4

Grandjean F (1934) Les poils des epimeres chez les Oribates (Acariens). Bulletin du Museum 6(6): 504–512.

Mahunka S (1973) Neue und interessante Milben aus dem Genfer Museum IX. Otocepheid species from Ceylon (Oribatida). Redia 54: 83–103.

Mondal BK, Kundu BG (1999) A new species of the genus *Eurostocepheus* (Acari: Oribatei, Otocepheidae) from Darjeeling, India. Records of the Zoological Survey of India 97(1): 179–186.

Norton RA (1977) A review of F. Grandjean's system of leg chaetotaxy in the Oribatei (Acari) and its application to the family Damaeidae. In: Dindal DL (Ed.) Biology of oribatid mites. Syracuse: SUNY College of Environmental Science and Forestry, 33–61.

Norton RA, Behan-Pelletier VM (2009) Oribatida. In: Krantz GW, Walter DE (Eds) A Manual of Acarology. Texas Tech University Press, Lubbock, 430–564.

Subías LS (2004) Listado sistemático, sinonímico y biogeográfco de los ácaros oribátidos (Acariformes: Oribatida) del mundo (excepto fósiles). [Version 16, updated March 2021] http://bba.bioucm.es/cont/docs/RO_1.pdf [Accessed on: 2021-9-1]

Wen ZG (1999) The first report of the genus *Eurostocepheus* from China, with description of a new species (Acari: Oribatida: Otocepheidae). Acta Zootaxonomica Sinica 24(4): 376–379. http://en.cnki.com.cn/Article_en/CJFDTotal-DWFL199904002.htm

Zheng LH, Chen J (2020) Three new species of the subgenus *Otocepheus* (*Acrotocepheus*) (Acari, Oribatida, Otocepheidae) from China. Zookeys 934: 1–23. https://doi.org/10.3897/zookeys.934.49862

ZooKeys 1073: 201–204 (2021)
doi: 10.3897/zookeys.1073.76830
https://zookeys.pensoft.net

CORRIGENDA

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Corrigenda: A parasitic insect on a parasitic plant: a new species of the genus *Formicoccus* Takahashi (Hemiptera, Coccomorpha, Pseudococcidae) from Ishigaki Island, Japan. ZooKeys 1060: 171–182. https://doi.org/10.3897/zookeys.1060.71652

Hirotaka Tanaka[1,2], Kenji Suetsugu[3], Satoshi Kamitani[4]

1 *Faculty of Agriculture, Ehime University, Tarumi 3-5-7, Matsuyama, Ehime 790-8566, Japan* **2** *The Kyushu University Museum, Hakozaki 6-10-1, Higashi-ku, Fukuoka, 812-8581, Japan* **3** *Department of Biology, Graduate School of Science, Kobe University, 1-1 Rokkodai, Nada-ku, Kobe, 657-8501, Japan* **4** *Entomological Laboratory, Faculty of Agriculture, Kyushu University, Motooka 744, Fukuoka, 819-0395, Japan*

Corresponding author: Hirotaka Tanaka (coccoidea@gmail.com)

Academic editor: Roger Blackman | Received 21 October 2021 | Accepted 29 October 2021 | Published 30 November 2021

http://zoobank.org/6A053084-4C27-4CA3-8462-8AE6A40800C8

Citation: Tanaka H, Suetsugu K, Kamitani S (2021) Corrigenda: A parasitic insect on a parasitic plant: a new species of the genus Formicoccus Takahashi (Hemiptera, Coccomorpha, Pseudococcidae) from Ishigaki Island, Japan. ZooKeys 1060: 171–182. https://doi.org/10.3897/zookeys.1060.71652. ZooKeys 1073: 201–204. https://doi.org/10.3897/zookeys.1073.76830

Dr. Sunil Joshi (Division of Insect Systematics, National Bureau of Agricultural Insect Resources, Bangalore Karnataka, India) kindly pointed out that the genus name used in Tanaka et al. (2021) was misspelt, and the paper also did not include *Formicococcus tectonae* Joshi, Bindu & Gullan, 2020 in the key to adult females of *Formicococcus* species in the Oriental region. We regret these mistakes. The corrected genus name of the species described in Tanaka et al. (2021) is "*Formicococcus*", not "*Formicoccus*". The specific name *yoshinoi* is deemed to have been published in combination with the original spelling *Formicococcus* under Article 11.9.3.2 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999). Furthermore, the corrected key to adult females of *Formicococcus* species in the Oriental region is provided here.

Key to adult females of *Formicococcus* species in the Oriental region (adapted and modified from Takahashi 1930, 1940; Tang 1992; Williams 2004; Joshi et al. 2020)

1 Antennae with 9 segments .... ***F. schimae* Takahashi, 1929**

– Antennae with 6–8 segments **2**

2 Cerarii numbering 17–18 pairs **3**

– Cerarii numbering 16 or fewer pairs **4**

3 Anal ring with 6 setae **7**

– Anal ring with 8 or more setae **8**

4 Cerarii numbering fewer than 6 pairs; only one type of ventral oral collar tubular duct present .... ***F. yoshinoi* Tanaka, sp. nov.**

– Cerarii numbering 11–16 pairs; 2 types of ventral oral collar tubular ducts present **5**

5 Penultimate cerarii (C17) with 9–12 conical setae .... ***F. tripurensis* Williams, 2004, in part**

– Penultimate cerarii (C17) with 2–8 conical setae **6**

6 All cerarian setae conical without flagellate apex. Dorsal setae short and stiff, each 10–20 µm long, not associated with trilocular pores. Translucent pores present on hind coxa and tibia .... ***F. robustus* (Ezzat & McConnell, 1956), in part**

– All cerarian setae conical with a flagellate apex. Dorsal setae each thick and stiff, 17–65 µm long, with flagellate apex; many dorsal setae associated with 1 or 2 trilocular pores. Translucent pores present only on hind coxa, absent from or very rare on hind tibia.... ***F. tectonae* Joshi, Bindu & Gullan, 2020**

7 Circulus absent .... ***F. lingnani* (Ferris, 1954)**

– Circulus present **10**

8 Circulus absent .... ***F. dispersus* Williams, 2004**

– Circulus present **9**

9 Anal ring with more than 10 setae .... ***F. cinnamomi* Takahashi, 1928**

– Anal ring with fewer than 10 setae ..... ***F. polysperes* Williams, 2004, in part**

10 Dorsal surface of each anal lobe moderately to heavily sclerotised **11**

– Dorsal surface of each anal lobe membranous, except for possible weak sclerotisation around some setal collars only **14**

11 Many dorsal setae conical, those on midline of abdomen associated with trilocular pores forming dorsal cerarii .... ***F. monticola* (Green, 1922)**

– Dorsal setae not conical, each one short, slender and stiff, or elongate and flagellate, not forming dorsal cerarii on midline of abdomen **12**

12 Dorsal setae short and stiff, 15–25 µm long **13**

– Dorsal setae long and flagellate, mostly 55–75 µm long .... ***F. matileae* Williams, 2004**

13 Anal lobe cerarii (C18) with 4 conical setae. Penultimate cerarii (C17) with 7 conical setae .... ***F. burckhardti* Williams, 2004**

– Anal lobe cerarii (C18) with 6 conical setae. Penultimate cerarii (C17) with 4 or 5 conical setae .... ***F. bambusicola* (Takahashi, 1930)**

14 All cerarii containing short, conical setae **18**

– Either all cerarii with many long, conical, or flagellate setae forming tufts, or some cerarii on head and thorax containing paired flagellate setae............ **15**

15 Abdominal cerarii with short and conical setae only. Cerarii on head and thorax with long paired flagellate setae. Oral collar tubular ducts on venter absent from thorax. Abdominal segments not strongly lobed laterally.......... .... ***F. acerneus* Williams, 2004**

– All cerarii each with many elongate cerarian setae, either conical or flagellate, forming tufts, cerarian setae often extending onto venter even in teneral specimens. Oral collar tubular ducts on venter present on thorax. Abdominal segments usually strongly lobed laterally **16**

16 Multilocular disc pores present on ventral abdominal margins. Most dorsal setae on head and thorax long, each 50–100 µm long.............................. **17**

– Multilocular disc pores absent from ventral abdominal margins. Most dorsal setae on head and thorax short, each 25–40 µm long...... ***F. formicarii* (Green, 1922)**

17 Most cerarian setae conical although elongated, sometimes with flagellate tips. Hind femur without translucent pores ...... ***F. simplicior* (Green, 1922)**

– All cerarian setae elongated and flagellate. Hind femur with translucent pores. .... ***F. formicarius* (Newstead, 1900)**

18 Anal lobe cerarii (C18) each mostly with 2 conical cerarian setae............. **19**

– Anal lobe cerarii (C18) each mostly with more than 2 conical cerarian setae. **21**

19 Penultimate cerarii (C17) each with 2 conical cerarian setae **20**

– Penultimate cerarii (C17) each mostly with more than 2 conical cerarian setae.. ***F. erythrinae* Williams, 2004**

20 Conical cerarian setae on anal lobe cerarii (C18) with flagellate tips. Dorsal setae mostly longer than anal ring length .... ***F. macarangae* (Takahashi, 1940)**

– Conical cerarian setae on anal lobe cerarii (C18) without flagellate tips. Dorsal setae mostly shorter than anal ring length .... ***F. sibolangiticus* Williams, 2004**

21 Ventral oral collar tubular ducts present anterior to abdomen, on head only or head and thorax... **25**

– Ventral oral collar tubular ducts absent from head and thorax, confined to abdomen.. .... **22**

22 Cerarii on head not clearly separated; boundaries of cerarii on head not clear .... ***F. citricola* (Tang, 1992)**

– Cerarii on head mostly clearly separated; boundaries of cerarii on head clear **23**

23 Ventral setae thick, stout, and curved, including anal lobe bar setae, cisanal, and obanal setae............................... ***F. tripurensis* Williams, 2004, in part**

– Ventral setae slender and flagellate, including anal lobe bar setae, cisanal, and obanal setae **24**

24 Hind coxae noticeably wider and larger than anterior coxae. Multilocular disc pores on venter absent from abdominal segment IV. Most cerarii on head and thorax with slender cerarian setae.......... ***F. cameronensis* (Takahashi, 1951)**

– Hind coxae with same shape as anterior coxae, only slightly larger. Multilocular disc pores on venter present on abdominal segment IV. Most cerarii on head and thorax with conical cerarian setae.. ***F. robustus* (Ezzat & McConnell, 1956), in part**

25 Most dorsal setae short and weakly knobbed, except for conspicuously long flagellate setae on abdominal segment VIII on either side of anal ring.. ***F. latens* Williams, 2004**

– Dorsal setae all short and pointed. Setae situated on either side of anal ring little if any longer than other dorsal setae.. **26**

26 Most dorsal setae anterior to abdominal segment VIII short and thick, 6–10 µm long; base of most setae ca. as wide as a trilocular pore and often wider. Ventral oral collar tubular ducts absent from opposite ocular cerarii (C3) and from margins of mesothorax and metathorax.. ***F. polysperes* Williams, 2004, in part**

– Most dorsal setae anterior to abdominal segment VIII short and slender, 10–17 µm long; base of most setae narrower than trilocular pores. Ventral oral collar tubular ducts present opposite ocular cerarii (C3) and on margins of mesothorax and metathorax..................... ***F. mangiferacola* Williams, 2004**

References

International Commission on Zoological Nomenclature (1999) International Code of Zoological Nomenclature (4th edn.). International Trust for Zoological Nomenclature, London, 306 pp.

Joshi S, Bindu JK, Gullan PJ, Sajeev TV, Anoop EV (2020) A new species of mealybug (Hemiptera: Coccomorpha: Pseudococcidae) from *Tectona grandis* L.f. (Lamiaceae) in southern India. Zootaxa 4718: 391–400. https://doi.org/10.11646/zootaxa.4718.3.7

Tanaka H, Suetsugu K, Kamitani S (2021) A parasitic insect on a parasitic plant: a new species of the genus *Formicoccus* Takahashi (Hemiptera, Coccomorpha, Pseudococcidae) from Ishigaki Island, Japan. ZooKeys 1060: 171–182. https://doi.org/10.3897/zookeys.1060.71652