

# Distribution of the genus *Boeckella* (Crustacea, Copepoda, Calanoida, Centropagidae) at high latitudes in South America and the main Antarctic biogeographic regions

Claudia S. Maturana<sup>1,2</sup>, Sebastián Rosenfeld<sup>2,3</sup>, Javier Naretto<sup>1,2,4</sup>,  
Peter Convey<sup>5</sup>, Elie Poulin<sup>1,2</sup>

**1** Laboratorio de Ecología Molecular, Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile. Las Palmeras 3425, Ñuñoa, Santiago, Chile **2** Instituto de Ecología y Biodiversidad (IEB), Las Palmeras 3425, Ñuñoa, Santiago, Chile **3** Laboratorio de Ecosistemas Marinos Antárticos y Subantárticos, Universidad de Magallanes, casilla 113-D, Punta Arenas, Chile **4** ONG Costa Humboldt, Canónigo Madariaga 570, Ñuñoa, Santiago, Chile **5** British Antarctic Survey (BAS), Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

Corresponding author: Claudia S. Maturana ([cmaturana.ciencias@gmail.com](mailto:cmaturana.ciencias@gmail.com))

Academic editor: D. Defaye | Received 7 September 2018 | Accepted 10 May 2019 | Published 10 June 2019

<http://zoobank.org/7B7ACD8-5C9D-4DB8-8E55-1DA1BF8ED0F3>

**Citation:** Maturana CS, Rosenfeld S, Naretto J, Convey P, Poulin E (2019) Distribution of the genus *Boeckella* (Crustacea, Copepoda, Calanoida, Centropagidae) at high latitudes in South America and the main Antarctic biogeographic regions. ZooKeys 854: 1–15. <https://doi.org/10.3897/zookeys.854.29614>

## Abstract

Copepods are present in numerous aquatic environments, playing key roles in food webs, and are thought to be useful indicators of environmental change. *Boeckella* is a calanoid copepod genus distributed mainly in the Southern Hemisphere, with 14 species reported at higher southern latitudes in South America and Antarctica. We present an updated database of these 14 species of *Boeckella* generated from a combination of three sources: 1) new field sampling data, 2) published records, and 3) Global Biodiversity Information Facility (GBIF), to provide a comprehensive description of the geographic distribution of the genus south of latitude 40°S in southern South America and the three main terrestrial biogeographic regions of Antarctica. The database includes 380 records, 62 from field sampling, 278 from the literature and 40 from GBIF. Southern South America, including the Falkland/Malvinas Islands, had the highest species richness and number of records (14 and 297, respectively), followed by the sub-Antarctic islands (5 and 34), South Orkney Islands (2 and 14), South Shetland Islands (1 and 23), Antarctic Peninsula (1 and 10)

and finally continental Antarctica (1 and 2). *Boeckella poppei* Mrázek, 1901 is the only representative of the genus, and more widely the only terrestrial/freshwater invertebrate, currently reported from all three main biogeographic regions in Antarctica (sub-Antarctic islands, maritime and continental Antarctic). Future development of molecular systematic studies in this group should contribute to assessing the correspondence between morphological taxonomy and molecular evolutionary radiation.

## Keywords

Antarctica, Falkland/Malvinas Islands, freshwater ecosystems, sub-Antarctic islands, Patagonia

## Introduction

Knowledge of the diversity and distribution of organisms over space and time can provide information about changes in the composition of communities in different environments, particularly in sensitive ecosystems such as those in freshwater. Such information can also be used in biogeographic and niche modelling studies, contributing to understand the ecology of a given taxon. However, despite international efforts to increase the digitization of catalogues of specimens in museums and other repositories, even today only a small proportion of the total worldwide records are estimated to have been made available online through the efforts of the Global Biodiversity Information Facility (Ariño 2010).

Copepods are thought to be one of the most abundant metazoan groups in the world (Huys and Boxshall 1991), colonizing virtually all aquatic habitats (Bayly and Boxshall 2009) from the deepest ocean abyss (Bradford-Grieve 2004) to high mountain lakes in the Himalayas (Sommaruga 2010) and Andes (Zagarese et al. 1997), and from hydrothermal springs (Ivanenko 2006; Ivanenko and Defaye 2006) to the frozen lakes of Antarctica (Bayly et al. 2003; Convey et al. 2008). They play fundamental ecological roles, being key components of food webs in both marine and freshwater ecosystems, and in some cases being recognized as useful indicators of environmental change (Gerten and Adrian 2002; Hays et al. 2005). However, the lack of updated and accessible data limits the ability to assess the impact of environmental change on their diversity and distribution. Species of the order Calanoida have undergone considerable adaptive radiation and diversification. They inhabit a great variety of aquatic environments (Adamowicz et al. 2010), with tolerance of a wide conductivity gradient (De los Ríos et al. 2010). Although the number of freshwater species is considerable (21% of the total species described), the majority of diversity is present in the marine environment (Jaume et al. 2004). Because of this, most studies to date have focused on marine copepods.

*Boeckella* is a freshwater calanoid copepod genus that currently includes 42 described species restricted to the Southern Hemisphere (Bayly 1992a), with some discrete records of *B. triarticulata* (G.M. Thomson, 1883) from Mongolia and several introduced populations in Italy (Bayly 1992b; Ferrari and Rossetti 2006, Alfonso and Belmonte 2008). *Boeckella* is one of the most representative groups of calanoids in the freshwater ecosystems of southern South America, Australasia (Australia, New Zealand, Tasmania, New Caledonia) and various sub-Antarctic and cool temperate islands

(Marion and Prince Edward Islands, Crozet Islands, Kerguelen Islands, Heard Island, Macquarie Island, Campbell Island, Amsterdam Island and South Georgia). *Boeckella poppei* is the only calanoid species recorded in continental and maritime Antarctica (Bayly 1992b; Pugh et al. 2002; Bissett et al. 2005; Maturana et al. 2018).

Fourteen species of *Boeckella* have been reported from higher southern latitudes (beyond 40°S) in South America, including Patagonia and Tierra del Fuego, Falkland/Malvinas Islands, various sub-Antarctic islands and Antarctica (Pugh et al. 2002; Bayly et al. 2003). According to the latest taxonomic and phylogenetic studies (Bayly 1992b; Adamowicz et al. 2007), these 14 are considered taxonomically valid species (Walter and Boxshall 2018).

The present study provides an updated database of these 14 species of *Boeckella*, using a combination of recent sampling data, published records available in the literature and records from GBIF, giving a comprehensive description of the geographic distribution of the genus *Boeckella* at high latitudes in southern South America and the three main terrestrial biogeographic regions of Antarctica (sub-Antarctic islands, maritime and continental Antarctica; Convey 2013). This database will underpin future comprehensive systematic research on the genus, including the application of molecular phylogenetic approaches, allowing reconstruction of the regional evolutionary history of the genus, and in particular its members in the sub-Antarctic and Antarctic regions.

## Methods

### Data collation and construction of the database

The dataset (Maturana et al. 2018, <https://doi.org/10.15468/zc6y59>) was filtered by the area of interest, defined as South America at latitudes beyond 40°S, which encompasses most of the Patagonian and sub-Antarctic Provinces (Cabrera and Willink 1980; Morrone 2004; Sanches Osés and Pérez-Hernández 2005; Morrone 2006) and includes sub-polar forest and grassland ecoregions (Olson et al. 2001), along with the classically defined terrestrial biogeographic regions of Antarctica (Holdgate 1977; Convey 2017). The latter include the core sub-Antarctic islands (South Georgia, Prince Edward Islands, Macquarie Island, Heard Island, Crozet and Kerguelen Islands), maritime Antarctica (west coast of the Antarctic Peninsula, South Shetland Islands, South Orkney Islands, South Sandwich Islands) and continental Antarctica.

*Boeckella* records across this region were collated from three main sources: 1) recent field sampling data, 2) published literature and 3) data present in GBIF. Duplicate records were removed in combining these data to construct a unified database. To evaluate the quality of the collated data, all records were checked for mismatches between reported geographic location and the associated metadata, and taxonomically dubious records were excluded from the geospatial analysis.

Two main ecoregions in South America were considered for the purpose of geospatial analyses, the subpolar forest and grassland ecoregions as defined in the Ter-

restrial Ecoregions of the World (Olson et al. 2001) shape file (<https://databasin.org/datasets/68635d7c77f-1475f9b6c1d1dbe0a4c4c>; accessed 07/07/2018). Subpolar forest here includes the union of the Valdivian temperate forest and the Magallanes temperate forest ecoregions, and the grassland ecoregion includes the union of the Patagonian steppe and the Falkland/Malvinas Islands, which are on the continental shelf. The definitions of the continental, maritime and sub-Antarctic regions are as described in Convey (2017). All spatial analysis were carried out on the unified database.

### Recent sampling data

New material was collected from multiple locations in southern South America between Sierra Baguales in Chilean Patagonia (50°45.015'S; 72°25.158'W) and the Diego Ramirez archipelago (56°31.345'S; 68°43.622'W). In the Falkland/Malvinas Islands we collected from multiple ponds between Port San Carlos (51°27.690'S; 58°46.763'W) and North Arm (52°00.121'S; 59°17.407'W).

New Antarctic material was collected from the South Shetland Islands and Palmer Land in the southern Antarctic Peninsula under the framework of Antarctic Expeditions ECA53 and ECA54 of the Chilean Antarctic Institute (INACH). Samples from Alexander Island in the southern Antarctic Peninsula, South Orkney Islands and South Georgia were obtained during British Antarctic Survey (BAS) expeditions (2016–2017 and 2017–2018). Samples from Kerguelen and Crozet Islands were obtained under the PROTEKER project during the French Polar Institute Paul Emile Victor (IPEV) expedition (2017).

### Sample collection

Collections were made from the shoreline, scooping individuals from the water column of lakes, ponds and small pools using a zooplankton net (200 µm pore diameter) at locations across sub-Antarctic islands (Crozet, Kerguelen and South Georgia), maritime Antarctic (i.e. west side of Antarctic Peninsula, South Shetland Island and South Orkney Islands), part of the sub-polar forest ecoregion and Falkland/Malvinas Islands. Samples were immediately preserved in ethanol (99%), except for a small number of collected specimens that were preserved using formalin (5%) for morphological analysis. GPS positions were recorded for each sample location.

### Taxonomic identification

Morphological observations were performed under a stereomicroscope (LEICA EZ4) at 3.5× magnification. For determination to species level, the fifth leg was removed from male specimens and observed under an inverted microscope at 10× and 20× for confirmation of diagnostic characters as described by Bayly (1992a, 1992b).



## Published literature

All available information was collated from the scientific literature reporting sampling or taxonomic revision of *Boeckella* species in southern South America, the sub-Antarctic islands, maritime and continental Antarctica. We included *Boeckella* records from 1855 to 1997 listed in the historical review of Menu-Marque et al. (2000), and additional information available in the literature from 1997 to present. Only records including the geographic location (coordinates) or approximate (identifiable) location of reported samples were incorporated in the database.

## Digital database GBIF

All georeferenced records for the genus *Boeckella* for the targeted study area were retrieved from the GBIF database on 30 July 2018. Records lacking precise geographic location (coordinates) were assigned georeferences by identification from the description of the reported collection locality included in the relevant metadata. The species list was updated to exclude erroneous or suspect records, rule out possible synonymies and include current taxonomy.

## Data Resources

The data underpinning the analysis reported in this paper are deposited at GBIF, the Global Biodiversity Information Facility (Maturana et al. 2018).

## Results

### Database Summary

A total of 815 unfiltered records were retrieved from all sources combined. Of these, 380 records were from the targeted study area (Maturana et al. 2018, <https://doi.org/10.15468/zc6y59>). Most records (278) were obtained from the published literature, followed by new sampling records (62), which represented more than 15% of the dataset analyzed. The GBIF database contributed further 40 records.

### Dubious records

*Boeckella silvestrii* Daday, 1901, described in South America, has also been reported by GBIF in the South Orkney (<https://www.gbif.org/occurrence/1056439704>) and South Shetland Islands (<https://www.gbif.org/occurrence/1056871457>). Previously,

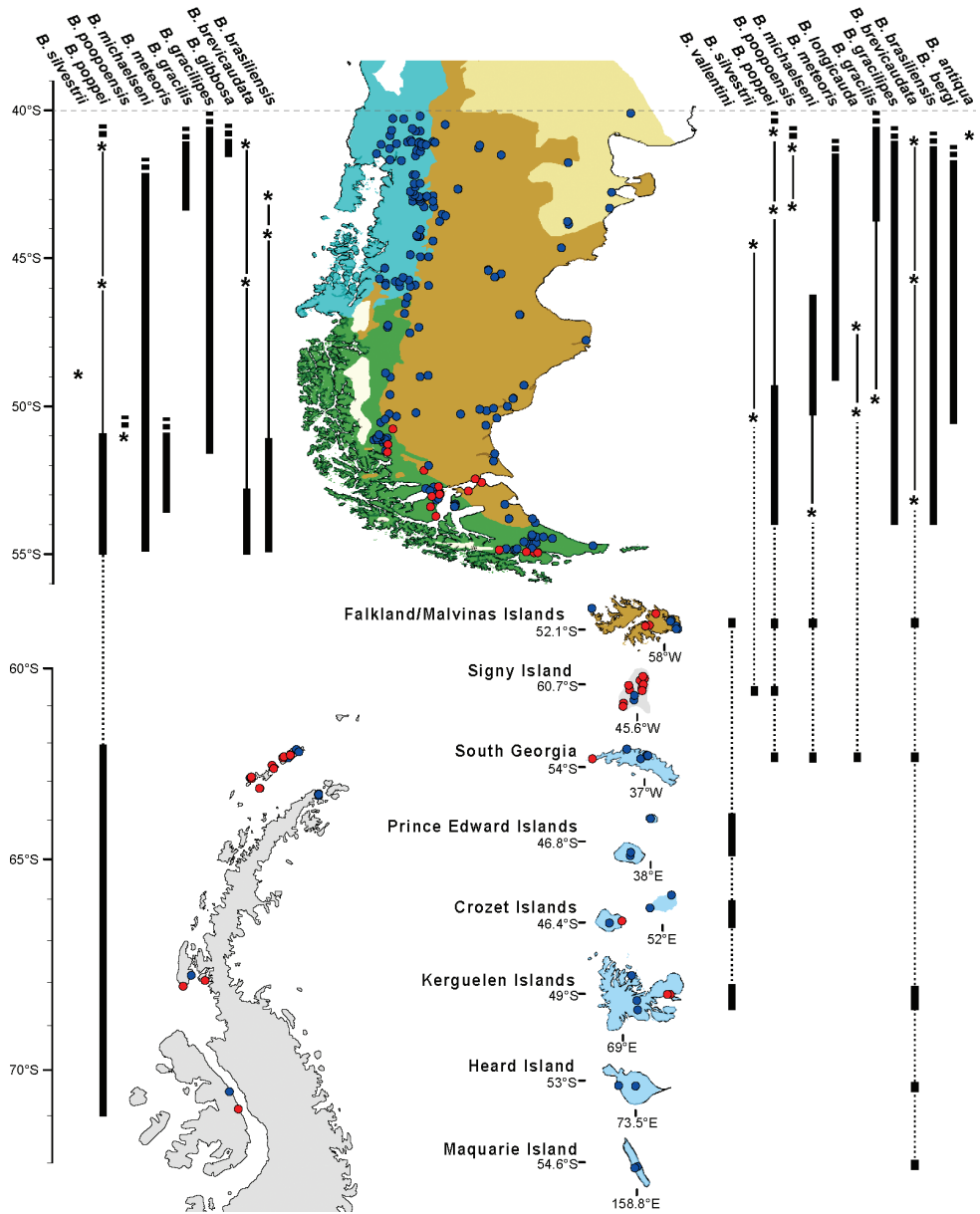
Harding (1941) reported *B. silvestrii* in the South Shetland Islands, now attributed to *B. poppei* (Pugh et al. 2002). Therefore, the identification of *B. silvestrii* in the South Orkney Islands could be the result of a repeated source of confusion from this previous erroneous identification.

*Boeckella longicauda* (Daday, 1901) has only been reported in the literature from southern Argentina (Menu-Marque et al. 2000), but there is a unique record from South Georgia, which is deposited in the Natural History Museum of London. This record is likely to be an erroneous identification and may correspond to *B. poppei*, as Bayly (1992a) commented that the morphology of the fifth leg of the male of *B. longicauda* is very similar to *B. poppei*, and probably the individual that Daday reviewed could be a variant of *B. poppei* (Bayly 1992a). Daday's review of the genus retained this species mainly on the basis of the shape of the female's urosome, which is very different from the morphology of *B. poppei*. It is also worth noting that *B. longicauda* was the only *Boeckella* species from southern South America that was not included in the phylogeny of Adamowicz et al. (2007). It is therefore important that the validity of this species be confirmed using both morphological and molecular techniques.

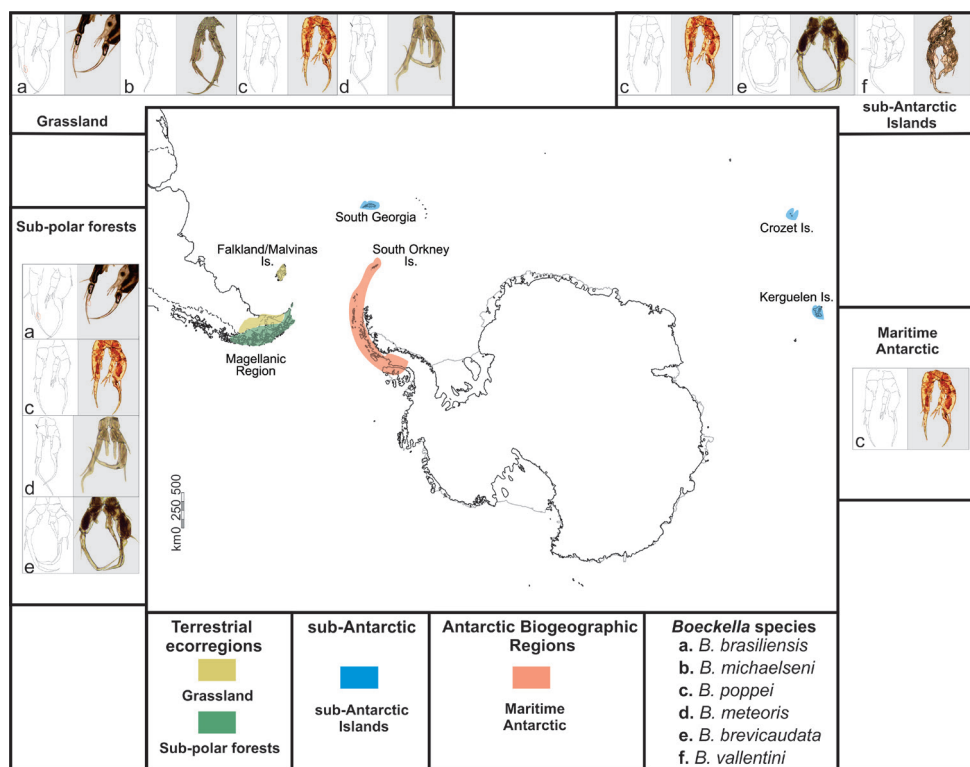
## Species richness

Fourteen species were recorded across the targeted study area (Fig. 1). Southern South America, including the Falkland/Malvinas Islands, contributed the highest number of records (297) and species richness (14) followed by the sub-Antarctic islands (34 and 5), South Orkney Islands (14 and 2), South Shetland Islands (23 and 2) and finally a single species (*B. poppei*) in continental Antarctica. Almost all records of *B. poppei* in Antarctica were from the maritime Antarctic (45), with seven records from the western Antarctic Peninsula (islands in Marguerite Bay and South Peninsula between 67°47'S; 68°54'W and 71°20'S; 68°17'W), and only two records from the continental Antarctic (Prince Charles Mountains, Enderby Sector). Although there was a small difference in species richness between the sub-polar forest (10 species) and grassland ecoregions (13 species) in southern South America, there are fewer records (102) from the latter region than from the forest (195).

Within the grassland ecoregion, four species were reported from the Falkland/Malvinas Islands (*B. brevicaudata* (Brady, 1875), *B. michaelseni* (Mrázek 1901), *B. poppei* and *B. vallentini* Scott, 1914), of which only *B. vallentini* is not shared with continental South America, rather being found on the sub-Antarctic Prince Edward Islands, Crozet Islands and Kerguelen Islands (and notably not South Georgia, the geographically closest sub-Antarctic island). All other species reported from the Falkland/Malvinas Islands are also reported from at least one of the sub-Antarctic islands (Kerguelen, Heard, South Georgia and Prince Edward Islands). South Georgia had the highest number of records (16) and species (4) of any sub-Antarctic island.



**Figure 1.** Spatial distribution of 14 *Boeckella* species from the targeted study area. The western (left side) and eastern (right side) of southern South America (green/blue: subpolar forest; brown: grassland), sub-Antarctic islands (light blue) and maritime Antarctic regions (light grey) obtained from records (red: obtained from field sampling; blue: obtained from literature and GBIF database) of all combined data sources. \*: discrete outlier records; dash bars: distribution extended north of 40°S; dashed lines: geographic discontinuity. Records from East Antarctic were not included.



**Figure 2.** Map of the sampling locations in South America, sub- and maritime Antarctica. Six species were identified following the traditional taxonomic key (Bayly 1992a). *Boeckella poppei* is present across the three Antarctic biogeographic regions. Drawings of the fifth male leg are modifications from Bayly (1992a).

Based on our sampling data, we identified six species distributed mainly in southern South America (*B. brevicaudata*, *B. meteoris* Kiefer, 1928, *B. poppei*, *B. brasiliensis* (Lubbock, 1855)), the Falkland/Malvinas Islands (*B. michaelsoni*) and the sub-Antarctic islands (*B. vallentini*), adding 62 new records to the existing data (Fig. 2). These new records are generally consistent with the existing literature and GBIF data, with the exceptions of (i) new records reporting *B. brasiliensis* in Sierra Baguales and the surroundings of Punta Arenas, (ii) *B. brevicaudata* in Otway Sound, (iii) *B. meteoris* in Tierra del Fuego, and (iv) *B. poppei* in Puerto Natales, Yendegaia National Park, Tierra del Fuego and Brunswick Peninsula in the Magallanes region, Robert and Greenwich Islands in the South Shetland Islands in northern maritime Antarctica, and finally the southernmost locality of Fossil Bluff on Alexander Island (71°20'S; 68°17'W). *Boeckella poppei* is known to occur slightly further south in the same geological formation on southern Alexander Island in pools at Mars and Ares Oases (71°50'S; 68°15'W), which represent the true known southern limit of this species (P. Convey pers. obs.), but these records have not been formally published.

## Discussion

Increasing availability of data and the application of new molecular biological analyses and modeling techniques have generated the need for revision of the geographic distribution of many taxa. The present compilation and classification of *Boeckella* records represents a contribution to biodiversity knowledge and to the biogeographic distribution of members of the genus across three large-scale biogeographic regions in Antarctica and two ecoregions in southern South America. It is also appropriate to note here that recent research has recognized that the long-used three region classification of Antarctic terrestrial biogeographic regions does not express the full regional complexity of terrestrial biogeography in Antarctica, with 16 “Antarctic Conservation Biogeographic Regions” now recognized within the continent, five of which are contained in the maritime Antarctic as considered in the current study (Terauds et al. 2012; Terauds and Lee 2016).

Six of the 14 species of *Boeckella* occurring at high latitudes recorded in this study have been reported as exclusively distributed south of 40°S in South America (*B. brevicaudata*, *B. vallentini*, *B. silvestrii*, *B. antiqua* Menu-Marque & Balseiro 2000, *B. michaelseni* and *B. longicauda* Daday 1901). In particular, *B. silvestrii*, reported from 44° to 50°S on the Argentine Patagonian Plateau (Menu-Marque et al. 2000), and *B. antiqua*, which has never been recorded in any location since its original description from an ephemeral pond in Argentine grassland (Menu-Marque and Balseiro 2000; Pérez et al. 2012; Garcia and Dieguez 2014). In contrast, other species showed much wider distributions, in particular *B. poppei* which has been reported across the three Antarctic biogeographical zones (sub-Antarctic islands, maritime and continental Antarctic), as well as in southern South America.

The distribution of *B. poppei* is exceptional within the genus, including the Andean Region in South America (Morrone 2006) and the three biogeographic regions in Antarctica. Furthermore, the distribution of this taxon is unique in the Antarctic terrestrial and freshwater fauna. This species thus provides an important opportunity to evaluate possible historical and contemporary dispersal across major continental biogeographic provinces (see also Chown and Convey 2007). Pugh et al. (2002) suggested that the presence of *B. poppei* in Beaver Lake (eastern continental Antarctica) might be the result of an anthropogenic introduction, and more generally that all maritime and continental Antarctic non-marine crustaceans may have reached these regions through recent introduction events associated with human activities. However, several palaeolimnological studies of lake sediments have confirmed that this species has been present in both the maritime and continental Antarctic regions for up to 9000 years (Jones et al. 2000; Bayly et al. 2003; Bissett et al. 2005).

The two ecoregions examined in southern South America were the richest in terms of number of species and records available (14 and 297, respectively), followed by the sub-Antarctic islands (5 and 34), the maritime Antarctic (2 and 47) and finally the continental Antarctic (1 and 2). There is an important geographic gap in available records between the western Antarctic Peninsula and Enderby Sector in continental Antarctica. In

a recent review of freshwater fauna in the south polar region, Dartnall (2017) reported only one record of *Boeckella* sp. in the region between Queen Maud Land (Schirmacher Oasis) and McMurdo Sound, including the Victoria Land Dry Valleys (Hansson et al. 2011). Although this seems to represent a low sampling effort, in reality, few, if any, suitable freshwater habitats are known to exist across this region today. For example, Hodgson et al. (2010) found the lowest species diversity yet observed in Antarctic lakes in the Dufek Massif and Shackleton Mountains, at the base and east of the Weddell Sea.

The presence of *B. vallentini* in the Falkland/Malvinas Islands and several sub-Antarctic islands (Kerguelen, Heard, South Georgia and Prince Edward Islands), but not in continental South America, must be noted (Table 1; Menu-Marque et al. 2000; Maturana et al. 2018). In the absence of molecular analyses, it is currently not possible to determine the phylogeographic relationship between these populations, and hence whether the Falkland/Malvinas acted as a source for current sub-Antarctic populations or vice versa. However, this is one of few known examples of the Falkland/Malvinas hosting terrestrial species that occur only from locations further south (i.e. sub-Antarctic and Antarctic regions). A second example is the terrestrial and supralittoral oribatid mite *Alaskozetes antarcticus* (Michael 1903), which occurs on sub-Antarctic South Georgia and throughout the maritime Antarctic, but not in South America (Block and Convey 1995).

The complexity of the morphology in this family of crustaceans, along with apparent plasticity in the diagnostic characters, can clearly lead to errors and considerable taxonomic and nomenclatural confusion (e.g. Bayly 1992a; Pugh et al. 2002). For example, Menu-Marque (2003) described *Karukinka fueguina* as a new genus and new species, but Adamowicz et al. (2007), in their study of Centropagidae phylogeny, found that *K. fueguina* genetically corresponds to *B. poppei* and concluded that *K. fueguina* is an aberrant version of *B. poppei*. Application of molecular systematics approaches to this group is required to limit misidentification, detect the existence of cryptic species, and assess the correspondence between currently recognized morphospecies and molecular

**Table 1.** List of the 14 species of *Boeckella* considered in this study with their distribution in the targeted study area. \*: Confirmed occurrence, \*\*: Dubious record

Species	South America	Falkland/ Malvinas Islands	Sub-Antarctic Islands	Antarctica
<i>Boeckella antiqua</i> Menu-Marque & Balseiro, 2000	*			
<i>Boeckella bergi</i> Richard, 1897	*			
<i>Boeckella brasiliensis</i> (Lubbock, 1855)	*			
<i>Boeckella brevicaudata</i> (Brady, 1875)	*	*	*	
<i>Boeckella gracilipes</i> Daday, 1901	*			
<i>Boeckella gracilis</i> (Daday, 1902)	*			
<i>Boeckella gibbosa</i> (Brehm, 1935)	*			
<i>Boeckella longicauda</i> Daday, 1901	*		**	
<i>Boeckella meteoris</i> Kiefer, 1928	*			
<i>Boeckella michaelsoni</i> (Mrázek, 1901)	*	*	*	
<i>Boeckella poopuensis</i> Marsh, 1906	*			
<i>Boeckella poppei</i> (Mrázek, 1901)	*	*		*
<i>Boeckella silvestrii</i> Daday, 1901	*		**	**
<i>Boeckella vallentini</i> (T. Scott, 1914)		*	*	

evolutionary units. To date, two studies on Centropagidae integrating morphological and genetic data are available (Adamowicz et al. 2007; Scheihing et al. 2009). However, neither addressed material from the Falkland/Malvinas Islands, sub-Antarctic islands or Antarctica. In the near future, such molecular studies should allow evaluation of different biogeographical scenarios regarding the origin of the contemporary freshwater biota in Antarctica. In this context, this study provides the first revision and comprehensive description of a major part of the geographic distribution of the genus *Boeckella*.

## Acknowledgements

This study utilized material obtained under several different projects and institutions, including South Atlantic Environment Research Institute (Falkland Islands/Islas Malvinas), FONDECYT 1161358, initiation FONDECYT program 11160391, INACH DT-04\_16, Institute of Ecology and Biodiversity (Chile) CONICYT PIA APOYO CCTE AFB170008, P05-002 ICM and Conicyt Ph.D. Grant (21150317) to C.M., and NERC core funding to the BAS “Biodiversity, Evolution and Adaptation” Team to P.C. We also appreciate the support of the following projects: J.N. (Conicyt Ph.D. Grant 21140632; INACH DG-03\_16), E.P. (regular Fondecyt project 1151336, PIA-CONICYT ACT172065), IPEV program PROTEKER (No. 1044). S.R. gives particular thanks to the Chilean Navy, the Commander in Chief of the III Naval Zone, Rear Admiral Ivo Brito, the Chief of General Staff, Vice Admiral José Miguel Rivera, the National Oceanographic Committee and the Naval Beagle Command, as well as the crew of the ship OPV 83 Marinero Fuentealba, and the helicopter and institutional logistics personnel. We also thank Roy Mackenzie and the staff of the lighthouse of Gonzalo Island for their invaluable support for the development of field research at the permanent ecological studies site implemented in the Diego Ramírez archipelago. S.R. and C.M. would like to thank Fernando Basualdo and Luciano Caputo for their valuable support to our fieldwork in Sierra Baguales and Última Esperanza. We especially thank Lafayette Eaton for English revision and editing and to Patricio De los Rios, Danielle Defaye and one anonymous reviewer for their helpful comments.

## References

- Adamowicz SJ, Menu-Marque S, Halse SA, Topan JC, Zemlak TS, Hebert PD, Witt JD (2010) The evolutionary diversification of the Centropagidae (Crustacea, Calanoida): a history of habitat shifts. *Molecular Phylogenetics and Evolution* 55: 418–430. <https://doi.org/10.1016/j.ympev.2009.12.008>
- Adamowicz SJ, Menu-Marque S, Hebert PD, Purvis A (2007) Molecular systematics and patterns of morphological evolution in the Centropagidae (Copepoda: Calanoida) of Argentina. *Biological Journal of the Linnean Society* 90: 279–292. <https://doi.org/10.1111/j.1095-8312.2007.00723.x>



- Alfonso G, Belmonte G (2008) Expanding distribution of *Boeckella triarticulata* (Thomson, 1883) (Copepoda: Calanoida: Centropagidae) in Southern Italy. *Aquatic Invasions* (2008) 3(2): 247–251 <https://doi.org/10.3391/ai.2008.3.2.17>
- Ariño AH (2010) Approaches to estimating the universe of natural history collections data. *Biodiversity Informatics* 7: 81–92. <https://doi.org/10.17161/bi.v7i2.3991>
- Bayly IAE (1992a) Fusion of the genera *Boeckella* and *Pseudoboeckella* (Copepoda) and revision of their species from South America and sub-Antarctic islands. *Revista Chilena de Historia Natural* 65: 17–63.
- Bayly IAE (1992b) The Non-marine Centropagidae: (Copepoda: Calanoida) of the World. Guides to the Identification of the Microinvertebrates of the Continental Waters of the World. SPB Academic Publishing, The Hague, 1–27.
- Bayly IAE, Boxshall GA (2009) An all-conquering ecological journey: from the sea, calanoid copepods mastered brackish, fresh and athalassic saline waters. *Hydrobiologia* 630: 39–47. <https://doi.org/10.1007/s10750-009-9797-6>
- Bayly IAE, Gibson JAE, Wagner B, Swadling KM (2003) Taxonomy, ecology and zoogeography of two east Antarctic freshwater calanoid copepod species: *Boeckella poppei* and *Gladioferens antarcticus*. *Antarctic Science* 15: 439–448. <https://doi.org/10.1017/S0954102003001548>
- Bissett A, Gibson JAE, Jarman SN, Swadling KM, Cromer L (2005) Isolation, amplification, and identification of ancient copepod DNA from lake sediments. *Limnology and Oceanography-Methods* 3: 533–542. <https://doi.org/10.4319/lom.2005.3.533>
- Block W, Convey P (1995) The biology, life cycle and ecophysiology of the Antarctic mite *Alaskozetes antarcticus*. *The Zoological Society of London* 236: 431–449. <https://doi.org/10.1111/j.1469-7998.1995.tb02723.x>
- Bradford-Grieve J (2004) Deep-sea benthopelagic calanoid copepods and their colonization of the near-bottom environment. *Zoological Studies* 43: 276–291.
- Cabrera A, Willink A (1980) Numero 13 de Serie de Biología. In: Secretaría General de la Organización de los Estados Americanos PRdDCyT (Ed.) Biogeografía de América Latina. Universidad de Texas, 1–122.
- Chown SL, Convey P (2007) Spatial and temporal variability across life's hierarchies in the terrestrial Antarctic. *Philosophical Transactions of the Royal Society of London: B Biological Sciences* 362: 2307–2331. <https://doi.org/10.1098/rstb.2006.1949>
- Convey P (2017) Antarctic Ecosystems. Reference Module in Life Sciences. Elsevier Inc., Cambridge, United Kingdom, 179–188. <https://doi.org/10.1016/B978-0-12-809633-8.02182-8>
- Convey P, Gibson JA, Hillenbrand CD, Hodgson DA, Pugh PJ, Smellie JL, Stevens MI (2008) Antarctic terrestrial life--challenging the history of the frozen continent? *Biological Reviews of the Cambridge Philosophical Society* 83: 103–117. <https://doi.org/10.1111/j.1469-185X.2008.00034.x>
- Daday E (1901) Diagnoses praecursoriae Copepodorum novorum e Patagonia. *Természetrájsz Füzetek* 24: 345–352.
- Dartnall HJG (2017) The freshwater fauna of the South Polar region: a 140-year review. *Papers and Proceeding of the Royal Society of Tasmania* 151: 19–58. <https://doi.org/10.26749/rstpp.151.19>

- De los Ríos P, Rivera R, Morrone JJ (2010) Calanoids (Crustacea: Copepoda) reported for Chilean inland waters. *Boletín de Biodiversidad de Chile* 3: 9–23.
- Ferrari I, Rossetti G (2006) New records of the centropagid *Boeckella triarticulata* (Copepoda: Calanoida) in northern Italy: evidence of a successful invasion? *Aquatic Invasions* 1: 219–222. <https://doi.org/10.3391/ai.2006.1.4.5>
- García PE, Dieguez MC (2014) Vulnerability of Patagonian planktonic copepods to fluctuations in temperature and UV radiation. *Crustaceana* 87: 291–304. <https://doi.org/10.1163/15685403-00003288>
- Gerten D, Adrian R (2002) Species-specific changes in the phenology and peak abundance of freshwater copepods in response to warm summers. *Freshwater Biology* 47: 2163–2173. <https://doi.org/10.1046/j.1365-2427.2002.00970.x>
- Hansson L-A, Hylander S, Dartnall HJG, Lidström S, Svensson J-E (2011) High zooplankton diversity in the extreme environments of the McMurdo Dry Valley lakes, Antarctica. *Antarctic Science* 24: 131–138. <https://doi.org/10.1017/s095410201100071x>
- Harding JP (1941) Lower Crustacea. British Graham Land Expedition 1934–1937 Scientific Reports. British Museum (Natural History), London, 319–322 pp.
- Hays GC, Richardson AJ, Robinson C (2005) Climate change and marine plankton. *Trends Ecology & Evolution* 20: 337–344. <https://doi.org/10.1016/j.tree.2005.03.004>
- Hodgson DA, Convey P, Verleyen E, Vyverman W, McInnes SJ, Sands CJ, Fernandez-Carazo R, Willemotte A, De Wever A, Peeters K, Tavernier I, Willems A (2010) The limnology and biology of the Dufek Massif, Transantarctic Mountains 82 degrees South. *Polar Science* 4: 197–214. <https://doi.org/10.1016/j.polar.2010.04.003>
- Holdgate MW (1977) Terrestrial Ecosystems in the Antarctic. *Philosophical Transactions of the Royal Society B: Biological Sciences* 279: 5–25. <https://doi.org/10.1098/rstb.1977.0068>
- Huys R, Boxshall GA (1991) Copepod evolution. The Ray Society, London, 1–468.
- Ivanenko VN (2006) Arthropoda, Crustacea, Copepoda. In: Desbrières D, Segonzac M, Bright M (Eds) *Handbook of Deep-sea Hydrothermal Vent Fauna*. Denisia, 316–317.
- Ivanenko VN, Defaye D (2006) Arthropoda, Crustacea, Copepoda. In: Desbrières D, Segonzac M, Bright M (Eds) *Handbook of Deep-sea Hydrothermal Vent Fauna*. Denisia, 318–355.
- Jaume D, Conradi M, López-Gonzalez JP (2004) 18. Copépodos. In: Barrientos JA (Ed.) *Curso Practico de Entomologia*. Universidad Autonoma de Barcelona, Barcelona, España, 303–331.
- Jones VJ, Hodgson DA, Chepstow-Lusty A (2000) Palaeolimnological evidence for marked Holocene environmental changes on Signy Island, Antarctica. *Holocene* 10: 43–60. <https://doi.org/10.1191/0959683000673046662>
- Maturana CS, Rosenfeld S, Naretto J, Convey P, Poulin E, Lopez Z, Gerard K, Jackson JA (2018) Occurrences of *Boeckella* at high latitudes in the Southern Hemisphere. Version 1.1. <https://doi.org/10.15468/zc6y59> [Accessed on: 2018-10-1]
- Menu-Marque S (2003) *Karukinka fueguina* n. gen., n. sp. (Copepoda, Calanoida, Centropagidae) from Tierra del Fuego. *Crustaceana* 75: 1229–1240. <https://doi.org/10.1163/156854002321518162>
- Menu-Marque S, Balseiro E (2000) *Boeckella antiqua* n. sp. (Copepoda, Calanoida, Centropagidae) from Patagonia. *Hydrobiologia* 429: 1–7. <https://doi.org/10.1023/A:1004023116688>

- Menu-Marque S, Morrone JJ, de Mitrovic CL (2000) Distributional pattern of the South American species of *Boeckella* (Copepoda: Centropagidae): a track analysis. *Journal of Crustacean Biology* 20: 262–272. <https://doi.org/10.1163/20021975-99990038>
- Morrone JJ (2004) Panbiogeografía, componentes bióticos y zonas de transición. *Revista Brasileira de Entomología* 48: 149–162. <https://doi.org/10.1590/S0085-56262004000200001>
- Morrone JJ (2006) Biogeographic areas and transition zones of Latin America and the Caribbean islands based on panbiogeographic and cladistic analyses of the entomofauna. *Annual Review of Entomology* 51: 467–494. <https://doi.org/10.1146/annurev.ento.50.071803.130447>
- Mrázek A (1901) Süßwasser-Copepoden. In: *Ergebnisse der Hamburger Magalhaenischen Sammelreise*. Hamburg, L. Friedrichsen, 1–29.
- Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D’Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P, Kassem KR (2001) Terrestrial ecoregions of the worlds: A new map of life on Earth. *Bioscience* 51: 933–938. [https://doi.org/10.1641/0006-3568\(2001\)051\[0933:Teotwa\]2.0.Co;2](https://doi.org/10.1641/0006-3568(2001)051[0933:Teotwa]2.0.Co;2)
- Pérez AP, Ferraro MA, Zagarese H (2012) The relative contributions of diet and associated microbiota to the accumulation of UV-absorbing mycosporine-like amino acids in the freshwater copepod *Boeckella antiqua*. *Freshwater Biology* 57: 993–1004. <https://doi.org/10.1111/j.1365-2427.2012.02760.x>
- Pugh PJA, Dartnall HJG, McInnes SJ (2002) The non-marine Crustacea of Antarctica and the Islands of the Southern Ocean: biodiversity and biogeography. *Journal of Natural History* 36: 1047–1103. <https://doi.org/10.1080/00222930110039602>
- Sanches Osés C, Pérez-Hernández R (2005) Historia y tabla de equivalencias de las propuestas de subdivisiones biogeográficas de la región Neotropical. *Primeras Jornadas Biogeográficas de la Red Iberoamericana de Biogeografía y Entomología Sistemática (RIBES XII.I-CYT-ED)*. In: Bousquets JL, Morrone JJ (Eds) *Regionalización Biogeográfica en Iberoamérica y Tópicos Afines*. Universidad de Mexico, Mexico DF, 145–169.
- Scheihing R, Cardenas L, Nespolo RF, Krall P, Walz K, Kohshima S, Labarca P (2009) Morphological and molecular analysis of centropagids from the high Andean plateau (Copepoda: Calanoidea). *Hydrobiologia* 637: 45–52. <https://doi.org/10.1007/s10750-009-9983-6>
- Sommaruga R (2010) Preferential accumulation of carotenoids rather than of mycosporine-like amino acids in copepods from high altitude Himalayan lakes. *Hydrobiologia* 648: 143–156. <https://doi.org/10.1007/s10750-010-0141-y>
- Terauds A, Chown SL, Morgan F, Peat HJ, Watts DJ, Keys H, Convey P, Bergstrom DM (2012) Conservation biogeography of the Antarctic. *Diversity and Distributions* 18: 726–741. <https://doi.org/10.1111/j.1472-4642.2012.00925.x>
- Terauds A, Lee JR (2016) Antarctic biogeography revisited: updating the Antarctic Conservation Biogeographic Regions. *Diversity and Distributions* 22: 836–840. <https://doi.org/10.1111/ddi.12453>
- Walter T, Boxshall G (2018) World of Copepods database. [accessed 24 June 2018]
- Zagarese HE, Feldman M, Williamson CE (1997) UV-B-induced damage and photoreactivation in three species of *Boeckella* (Copepoda, Calanoida). *Journal of Plankton Research* 19: 357–367. <https://doi.org/10.1093/plankt/19.3.357>

## **Supplementary material I**

### **Occurrences of *Boeckella* at high latitudes in the southern hemisphere. v1.1.**

Authors: Claudia S. Maturana, Sebastián Rosenfeld, Javier Naretto, Peter Convey, Elie Poulin

Data type: occurrence dataset

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.854.29614.suppl1>



# First record of the genus *Rasnitsynoryctes* Belokobylskij, 2011 (Hymenoptera, Braconidae, Doryctinae) in Vietnam, with the description of a new species

Khuat Dang Long<sup>1</sup>, Sergey A. Belokobylskij<sup>2,3</sup>

**1** Institute of Ecology and Biological Resources (IEBR), Vietnam Academy of Science and Technology (VAST), 18 Hoang Quoc Viet Road, Ha Noi, Vietnam **2** Zoological Institute of the Russian Academy of Sciences, Universitetskaya naberezhnaya 1, Saint Petersburg 199034, Russia **3** Museum and Institute of Zoology of the Polish Academy of Sciences, Wilcza 64, 00–679 Warsaw, Poland

Corresponding author: Sergey Belokobylskij ([doryctes@gmail.com](mailto:doryctes@gmail.com))

---

Academic editor: Jose Fernandez-Triana | Received 24 March 2019 | Accepted 1 May 2019 | Published 10 June 2019

---

<http://zoobank.org/1B76C98B-19B5-49DD-AD8F-721AB698C0E7>

---

**Citation:** Long KD, Belokobylskij SA (2019) First record of the genus *Rasnitsynoryctes* Belokobylskij, 2011 (Hymenoptera, Braconidae, Doryctinae) in Vietnam, with the description of a new species. ZooKeys 854: 17–24. <https://doi.org/10.3897/zookeys.854.34810>

---

## Abstract

The rare doryctine genus *Rasnitsynoryctes* Belokobylskij, 2011 is recorded for the braconid fauna of Vietnam for the first time. A new species of this genus, *R. vietnamicus* sp. nov., is described and illustrated.

## Keywords

Ichneumonoidea, new record, Oriental region, parasitoid

## Introduction

The peculiar monotypic Oriental genus *Rasnitsynoryctes* Belokobylskij, 2011, with type species *Rasnitsynoryctes alexandri* Belokobylskij, 2011, is a rare taxon from subfamily Doryctinae originally described from Malaysia (Belokobylskij 2011). The one of the most important features of this genus, presence of longitudinal and weakly convergent posteriorly sublateral furrows, is known in several others Old World genera: several taxa from the tribes Holcobraconini and Leptospathiini, *Eodendrus* Belokobylskij, 1998; *Hypodoryctes* Kokujev, 1900; *Halyscaea* Cameron, 1903 and *Sonanus* Belokobylskij et Konishi, 2001 from Doryctini, *Polystenus* Foerster, 1863; *Spathiostenus*

Belokobylskij, 1993 and *Terate* Nixon, 1943 from Hecabolini. *Rasnitsynoryctes* is additionally characterised by the fore wing with discal (discoidal) cell sessile anteriorly and vein CU1b (brachial) slanted towards base of wing (declivous); hind wing with subbasal (submedial) cell short and with more than three hamuli; inner spur of hind tibia transformed, sinuate and with inner expansion in apical third or submedially.

The hosts of the member from this genus are yet unknown. According to the large size of *Rasnitsynoryctes* specimens and by analogy to many other large-sized doryctines, species of this genus are probably parasitoids of Cerambycidae larvae or some other large xylophagous beetles inhabiting similar ecological niches.

In this paper we describe and illustrate the new species of the genus *Rasnitsynoryctes*, *R. vietnamicus* sp. nov., and additionally, this genus is recorded for the first time for the fauna of Vietnam.

## Materials and methods

The studied specimen is deposited in the Braconidae Collection of the Institute of Ecology & Biological Resources (IEBR), the Vietnam Academy of Science and Technology, Ha Noi, Vietnam.

Terminology used in this paper follows van Achterberg (1993), while sculpture terms are based on Harris (1979). The wing venation nomenclature follows van Achterberg (1993), with Belokobylskij and Maetô (2009) terminology shown in parentheses.

We used an Olympus SZ61 binocular microscope for study; measurement were carried out using an Olympus SZ40 binocular microscope; the photographs were made with a Sony 5000 digital camera attached to a Nikon SMZ 800N binocular microscope connected to a PC at IEBR and processed with Adobe Photoshop CS5 to adjust the size and background. Abbreviations used in this paper are as follows:

<b>POL</b>	minimum postocellar line;
<b>OOL</b>	minimum ocular-ocellar line;
<b>OD</b>	maximum diameter of posterior ocellus;
<b>MT</b>	Malaise trap;
<b>'Doryc. + number'</b>	code number indexing for Doryctinae specimens in the collection at IEBR;
<b>NR</b>	Nature Reserve.

## Taxonomy

### Genus *Rasnitsynoryctes* Belokobylskij, 2011

*Rasnitsynoryctes* Belokobylskij, 2011: 241.



**Type-species.** *Rasnitsynoryctes alexandri* Belokobylskij, 2011.

**Diagnostic characters.** Frons weakly concave. Eyes glabrous. Occipital carina dorsally complete, obliterate below at long distance above hypostomal carina. Malar suture absent. Postgenal bridge rather wide. Maxillary palpi long. Notauli complete. Precoxal sulcus narrow and long. Prepectal carina complete. Propodeum with finely delineated basolateral areas; lateral tubercles and propodeal bridge absent. Pterostigma of fore wing rather narrow. Marginal (radial) cell not shortened. Vein m-cu (recurrent) weakly antefurcal. Discal (discoidal) cell sessile anteriorly. Vein CU1a (parallel) arising from posterior 0.2–0.25 of apical margin of subdiscal (brachial) cell. Subdiscal (brachial) cell closed postero-apically by vein CU1b (brachial). Veins 2A and a (first and second transverse anal veins) absent. Hind wing with 5–6 hamuli. Marginal (radial) cell without additional transverse vein r. Subbasal (submedial) cell short; vein M+CU (first abscissa of mediocubital) 0.35–0.40 times as long as vein 1-M (second abscissa). Vein m-cu (recurrent) short, distinctly slanted toward base of wing. Fore tibia with short and thick spines arranged in almost single line. Hind coxa with distinct basoventral tooth. Hind tibia inner spur distinctly sinuate (Fig. 15) and with inner expansion in apical third. Basitarsus of hind tarsus 0.9–1.1 times as long as second-fifth segments combined. First metasomal tergite not petiolate, long and wide; acrosternite of first segment short, about 0.15 times as long as first tergite. Dorsope of first tergite large; spiracular tubercles situated in basal 0.25 of tergite. Second tergite with deep, weakly convergent posteriorly and fused with second suture sublateral furrows. Suture between second and third tergites rather deep, narrow, widely curved medially and laterally with distinct breaks. Second to sixth tergites with separate laterotergites. All tergites and laterotergites covered by very dense, short, white setae. Ovipositor apically with two obtuse, small dorsal nodes.

***Rasnitsynoryctes vietnamicus* Long & Belokobylskij, sp. nov.**

<http://zoobank.org/19483512-1317-41D9-BE8C-B2CC3F6BCB40>

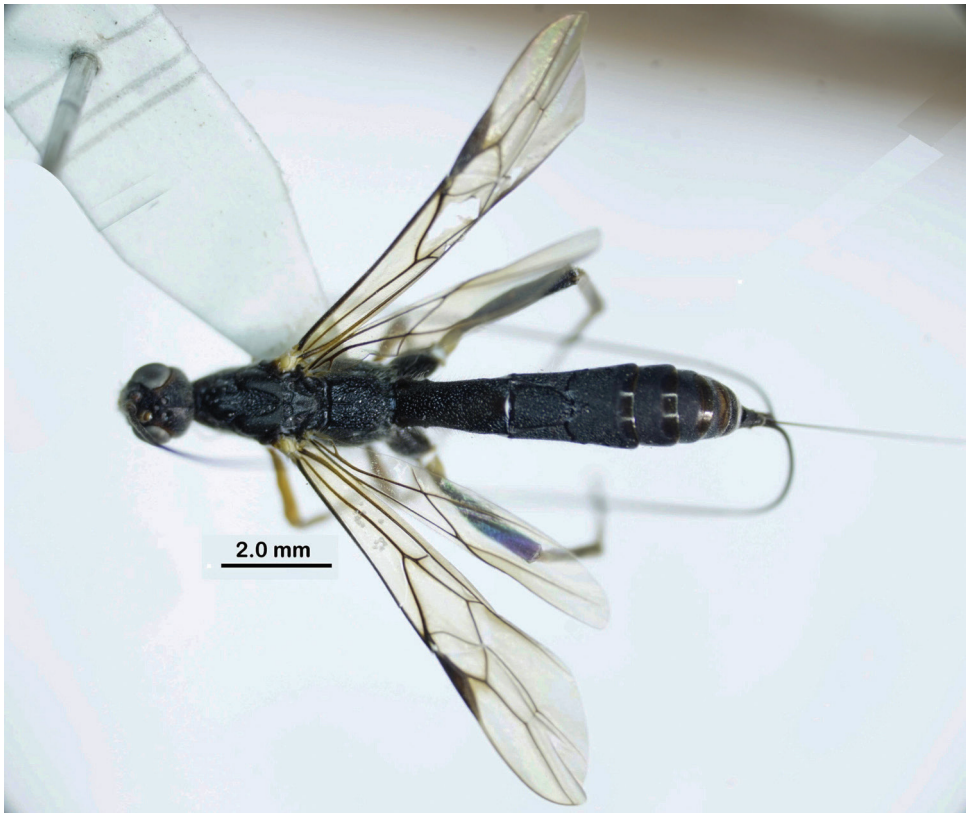
Figs 1–16

**Type material.** Holotype, female, “Doryc. 673”, NE Vietnam: Bac Giang, Son Dong, Yen Tu NR, 300 m, 4.vii.2010 (PT Nhi leg.) (IEBR).

**Comparative diagnosis.** The new species, *Rasnitsynoryctes vietnamicus* sp. nov., is very similar to the type species of the genus, *R. alexandri* Belokobylskij, 2011, from Malaysia; the differences between these species are showed in the key below after description.

**Description.** Female. Body length 11.7 mm, fore wing length 8.6 mm, ovipositor sheath 12.0 mm (Fig. 1).

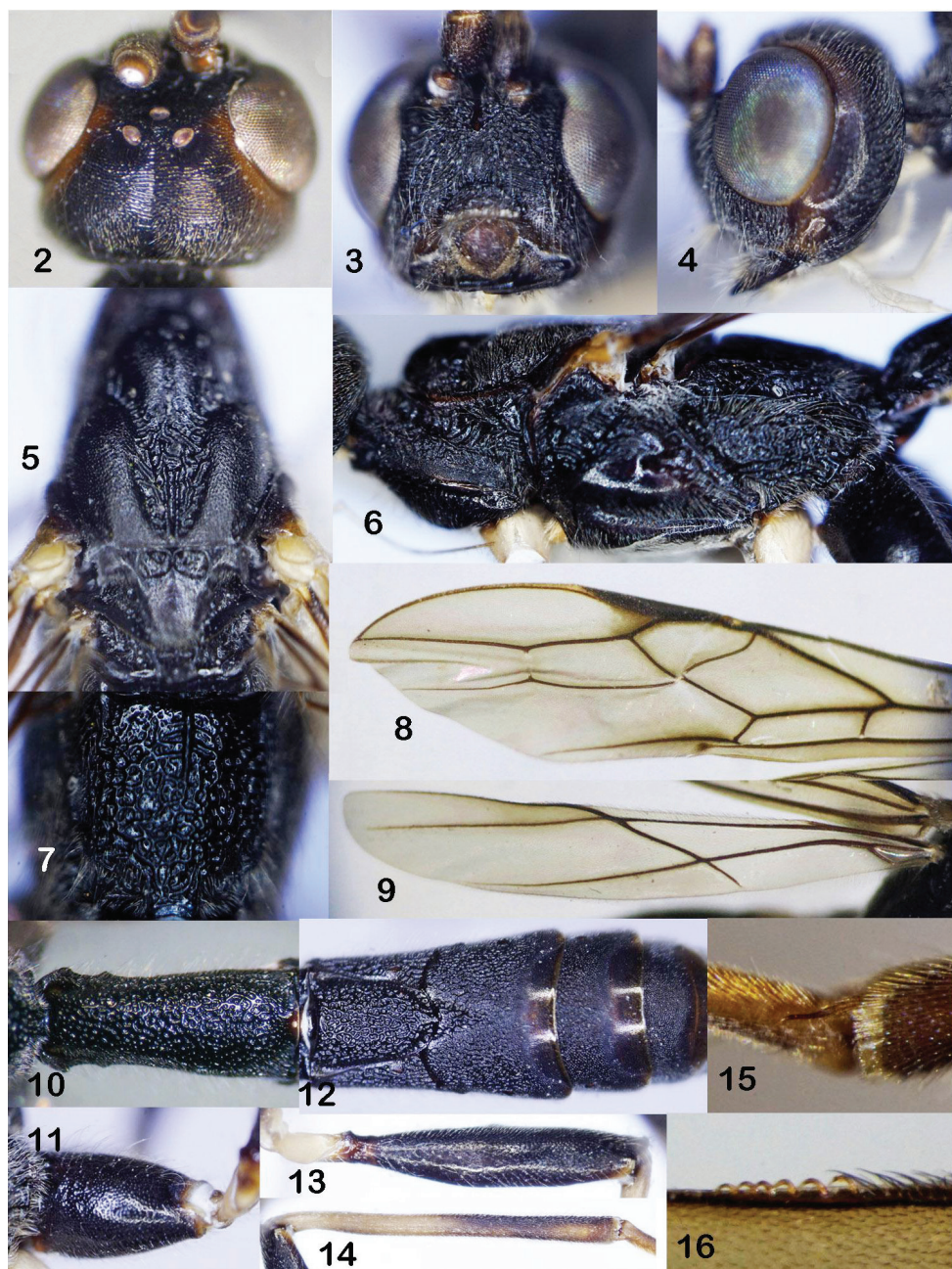
**Head.** Antennae with more than 48 segments (apical segments missing); scapus 1.4 times as long as its maximum width (14 : 10); third segment almost as long as fourth segment (27 : 26); middle segments 3.5–3.7 times as long as their width. Head width (dorsal view) 1.2 times its median length (64 : 52), head roundly narrowed behind eyes (Fig. 2), length of eye 1.6 times as long as temple (44 : 28); ocelli rather small,



**Figure 1.** Habitus in dorsal view of *Rasnitsynoryctes vietnamicus* sp. nov., female, holotype.

POL : OD : OOL = 7 : 5 : 8; in lateral view, eye 1.4 times as long as temple (25 : 18) (Fig. 4); maxillary palp 1.8 times as long as height of head (103 : 57); face width 1.4 times length of face and clypeus combined (35 : 25) (Fig. 3); malar space 0.7 times basal width of mandible (11 : 15); width of hypoclypeal depression equal to distance from edge of depression to eye (15 : 15); distance between tentorial pits 1.45 times distance from pit to eye (16 : 11); occipital carina not fused below with hypostomal carina above base of mandible but almost faded with patch of coarse rugosities near base of mandible.

*Mesosoma.* Length 2.3 times its height (77 : 34); mesoscutum highly and perpendicularly elevated above pronotum; median lobe of mesoscutum with distinct median longitudinal depression (Fig. 5); notauli deep, crenulate anteriorly, widened posteriorly, coarsely rugose (Fig. 5); pronotal sides largely crenulate medially, granulate ventrally (Fig. 6); prescutellar depression with only median carina, 0.3 times as long as scutellum (6 : 19); subalar depression wide and deep, with oblique rugosity; precoxal sulcus long, shallow, almost smooth (Fig. 6); metapleuron setose, coarsely rugose;



**Figure 2–16.** *Rasnitsynoryctes vietnamicus* sp. nov., female, holotype **2** head, dorsal view **3** head, front view **4** head, lateral view **5** mesonotum **6** mesosoma, lateral view **7** propodeum **8** fore wing **9** hind wing **10** first metasomal tergite **11** hind coxa, outer side **12** second-fifth metasomal tergites **13** hind femur, outer side **14** hind tibia, outer side **15** inner spur of hind tibia **16** hind wing hamuli.



propodeum with median carina in basal 0.3 of propodeum, without delineated areola (Fig. 7).

*Wings.* Length of fore wing 4.25 times as long as its maximum width (102 : 24) (Fig. 8); vein 1-R1 (metacarp) 1.5 times as long as pterostigma (58 : 38); length of pterostigma 4.75 times its width (38 : 8); vein r (radial) omitting before middle of pterostigma, 0.6 times as long as vein 2-SR (first radiomedial) and 0.35 times as long as vein 3-SR (second radial abscissa); r : 2-SR : 3-SR : SR1 (third radial abscissa) = 9 : 16 : 26 : 42; basal length of second submarginal (second radiomedial) cell 2.8 times its maximum width (36 : 13), 1.1 times length of subdiscal (brachial) cell basally (36 : 32); vein 1-CU1 : cu-a (nervulus) : 2-CU1 = 5 : 6 : 28; vein m-cu (recurrent) oblique. Length of hind wing 5.5 times as long as its maximum width (77 : 14); vein M+CU (first mediocubital abscissa) short, 0.3 times as long as vein 1-M (second mediocubital abscissa) (Fig. 9); vein M+CU : 1-M : r-m (basal) = 16 : 58 : 30.

*Legs.* Inner side of fore tibia with row of short robust spines; middle basitarsus 15.0 times as long as its width (60 : 4) and 0.9 times as long as tarsal segments 2–4 combined (60 : 68); hind coxa 1.6 times as long as its maximum width (52 : 35) (Fig. 11); hind femur, tibia and basitarsus 4.25, 14 and 12 times their maximum width, respectively (85 : 20; 140 : 14; 72 : 6) (Figs 13, 14); hind basitarsus 0.5 times as long as hind tibia (72 : 140); and 1.1 times as long as hind tarsal segments 2–5 combined (72 : 68); second segment of hind tarsus 0.4 times as long as basitarsus (38 : 72); fourth segment 0.5 times as long as fifth tarsal segment (without pretarsus) (7 : 14).

*Metasoma.* Metasoma 1.4 times as long as head and mesosoma combined (69 : 48); first metasomal tergite with large dorsope (Fig. 10); first tergite 2.3 times as long as its maximum width (86 : 38) (Fig. 10), 2.5 times as long as propodeum (86 : 35); second tergite with U-shaped medial area, emarginated by rather wide and crenulate lateral furrows fused with suture between second and third tergites (Fig. 12); medial length of second tergite 0.98 times its basal width (47 : 48), 1.1 times medial length of third tergite (47 : 43) (Fig. 12); ovipositor sheath slightly longer than body, and 1.4 times longer than fore wing (120 : 86).

*Sculpture and pubescence.* Frons rugose; vertex finely transversely striate; temple finely rugose-punctate; face largely rugose; clypeus and malar space with dense long setae; malar space largely rugose-punctate contrasting to rather smooth area between hypostomal carina and malar space; notauli largely rugose (Fig. 5); median and lateral lobes of mesoscutum rugose-coriaceous; scutellum finely and densely punctate; pronotum granulate ventrally, rugose dorsally; mesopleuron coriaceous; subalar depression with oblique rugosities; metapleuron setose, largely rugose; propodeum foveolate-rugose (Fig. 7); hind coxa finely and densely punctate laterally, finely rugose-punctate dorsally; first metasomal tergite and medial area of second tergite foveolate-rugose; third tergite largely rugose in basal 0.7, smooth in apical 0.3; fourth tergite largely rugose basally and laterally, finely rugose medially and almost smooth with sparse punctures apically; fifth–sixth tergites finely rugose-punctate basally and laterally, almost smooth apically; ovipositor sheath covered with short dense setae.

**Colour.** Black body; antenna brown; head mainly dark brown, subalar space brownish yellow; palpi white; fore and middle legs yellow, except coxa, trochanters and trochantellus cream white; hind coxa and femur black, trochanters and trochantellus yellow, hind tibia (except yellow basal area) and tarsus infusate; tegula yellow; fore wing subhyaline, its veins brown, outside area of vein r beneath pterostigma brownish; ovipositor sheath brown.

**Male.** Unknown.

**Etymology.** The new species is named after the country (Vietnam) where the holotype was collected.

**Distribution.** North-eastern Vietnam (Bac Giang Province).

### Key to *Rasnitsynoryctes* species

- 1 Vertex without medial longitudinal depression. Propodeum areolate-rugose, with delineated wide areola (Belokobylskij, 2011: fig. 8); first metasomal tergite 1.9 times as long as its apical width (Belokobylskij, 2011: fig. 28); median length of second tergite 0.7 times its basal width; hind wing with five hamuli (Belokobylskij, 2011: fig. 18); hind coxa light brown (Belokobylskij, 2011: fig. 20); hind trochanter pale brown; hind tibia mainly dark (Belokobylskij, 2011: fig. 19). Malaysia ..... ***Rasnitsynoryctes alexandri* Belokobylskij**
- Vertex with medial longitudinal depression. Propodeum foveolate-rugose, without delineated areola (Fig. 7); first metasomal tergite 2.3 times as long as its apical width (Fig. 10); median length of second tergite almost equal to its basal width (Fig. 12); hind wing with six hamuli (Fig. 16); hind coxa dark brown to black (Figs 11); hind trochanter whitish (Fig. 13); hind tibia mainly pale yellow, infusate apically (Fig. 14). Vietnam .....  
..... ***Rasnitsynoryctes vietnamicus* sp. nov.**

### Conclusions

The discovery of a new species from very rare Oriental genus *Rasnitsynoryctes* supports the opinion that our knowledge of the tropical and subtropical faunas of the parasitoid wasps is very incomplete even for such large-sized specimens (more than 10.0 mm length). Perhaps one of the main reasons for the rarity of such large specimens in a collection is related with peculiarities of their mode of life (preferring the tree canopies), behaviour, and food preferences related with potential hosts habitats. Further investigation of the relict tropical forests and collecting of such parasitoids by different methods and traps (including rearing from the potential hosts in infested plants, especially tree trunks or branches) in numerous habitats may allow to reveal more numbers of such specimens and taxa and to obtain more information about so called “rare” genera and taxa in the tropics.

## Acknowledgements

This research is funded by the Vietnam National Foundation for Science and Technology Development (NAFOSTED), grant No. 106-NN.05-2016.08, for the first co-author and by grant given of the Russian Foundation for Basic Research (project No 19–04–00027) and the Russian State Research Project No. AAAA-A19-119020690101-6 for the second co-author. Our thanks are expressed to the editor for the helpful comments on the manuscript; thanks are also due to Dr Pham Thi Nhi (IEBR) for providing the specimen.

## References

- Belokobylskij SA (2011) *Rasnitsynoryctes alexandri* gen. et sp. n., a new genus and species of the subfamily Doryctinae (Hymenoptera: Braconidae) from Malaysia. Russian Entomological Journal 20(3): 241–246. <https://doi.org/10.15298/rusentj.20.3.03>
- Belokobylskij SA, Maetô K (2009) Doryctinae (Hymenoptera, Braconidae) of Japan. Fauna mundi. Vol. 1. Warszawska Drukarnia Naukowa, Warszawa, 806 pp. <https://doi.org/10.3161/067.058.0107>
- Harris RA (1979) A glossary of surface sculpturing. Occasional papers of Laboratory Services/Entomology Department of Food and Agriculture division of Plant Industry, California 28: 1–34.
- van Achterberg C (1993) Illustrated key to the subfamilies of the Braconidae (Hymenoptera: Ichneumonoidea). Zoologische Verhandelingen 283: 1–189.

# Taxonomic study of the leafhopper genus *Oncopsis* (Hemiptera, Cicadellidae, Macropsinae) from Sichuan Province, China with description of two new species and a key to males

Hu Li<sup>1,2</sup>, Juan Li<sup>1</sup>, Ren-Huai Dai<sup>2</sup>

**1** Shaanxi Key Laboratory of Bio-resources, School of Biological Science & Engineering, Shaanxi University of Technology, Hanzhong, Shaanxi, 723000 China **2** Institute of Entomology of Guizhou University, The Provincial Key Laboratory for Agricultural Pest Management of Mountainous Region, Guiyang, Guizhou, 550025 China

Corresponding author: Ren-Huai Dai ([lihu@snut.edu.cn](mailto:lihu@snut.edu.cn), [rh dai69@163.com](mailto:rh dai69@163.com))

Academic editor: C.H. Dietrich | Received 15 January 2019 | Accepted 25 April 2019 | Published 10 June 2019

<http://zoobank.org/D69DBF2C-52BA-44F6-AC32-F2944B65E8BD>

**Citation:** Li H, Li J, Dai R-H (2019) Taxonomic study of the leafhopper genus *Oncopsis* (Hemiptera, Cicadellidae, Macropsinae) from Sichuan Province, China with description of two new species and a key to males. ZooKeys 854: 25–39. <https://doi.org/10.3897/zookeys.854.33117>

## Abstract

This paper deals with the leafhopper genus *Oncopsis* (Macropsinae) from Sichuan Province of China, and describes and illustrates two new species, *O. konkaensis* **sp. nov.** from Minya Konka (Sichuan), and *O. moxiensis* **sp. nov.** from Moxi Town (Sichuan), and provides a key to males and a geographic distribution map for *Oncopsis* species from Sichuan.

## Keywords

Auchenorrhyncha, China, distribution, morphology, taxonomy

## Introduction

The leafhopper genus *Oncopsis* Burmeister, 1838 includes more than 90 members (Dai et al. 2018, Li et al. 2018) around the world, and is the second largest group in the subfamily Macropsinae (Hemiptera: Cicadellidae). *Oncopsis* has been treated as a tribe



of the subfamily Eurymelinae recently (Dietrich and Thomas 2018), and has a distribution mostly in the Holarctic region. The type species is *Cicada flavicollis* Linnaeus, 1761. *Oncopsis* differs from other macropsine genera in having the face with coronal pits closer together than the ocelli, the usually transversely striate pronotum, the male pygofer without a process, and the s-shaped male dorsal connective that is usually produced into various processes from its inner ventral margin.

Almost all species of *Oncopsis* are oligophagous or monophagous on Betulaceae, including *Betula procurva* Litv., *B. turkestanica* Litv., *Alnus barbata* C.A.Mey., *A. hirsuta* (Spach) Rupr., *A. japonica* (Thunb.) Steud., *Duschekia* spp., and *Carpinus betulus* L. (Tishechkin 2016). Only one species, *Oncopsis krios* Mühlethaler, is an exception and is associated with *Ulmus* sp. (Ulmaceae) (Mühlethaler 2008). Sichuan Province is located in the Qinghai-Tibet, southwest and central China regions under the divisions of Zoogeographical Regions of China (Chen 1997), a key area for insect biodiversity. The first species of *Oncopsis* recorded in China, *O. fusca* (Melichar, 1902), was reported from Sichuan Province. Later, Xu et al. (2006), Dai and Li (2013), Kuoh (1992), Li et al. (2018) and Dai et al. (2018) described new species or reported *Oncopsis* from this area. To date, 14 species of *Oncopsis*, including the two new species described here, are known from Sichuan Province, which has more than 40% of the total number ( $n = 33$ ) of *Oncopsis* species distributed in China (Dai et al. 2018, Li et al. 2018).

In the present paper, the genus *Oncopsis* from Sichuan Province, China is reviewed, and two new species, *O. konkaensis*, sp. nov. from Minya Konka and *O. moxiensis*, sp. nov. from Moxi Town, are described and illustrated. A geographic distribution map and a key for identification of *Oncopsis* from Sichuan Province (based on male features) are provided.

## Materials and methods

Specimens were collected by sweep net. External morphology was observed under an Olympus SZX7 and BX43 microscopes. Male genitalia preparations were made by placing the whole abdomen in a boiling solution of 8% NaOH for 5 minutes, then rinsing with fresh water several times and transferring into glycerin on glass slides for examination, dissection, drawing, and photography. The dissected genitalia and remains of the abdomen were stored in micro vials containing glycerin for further examination.

Habitus images of adults were obtained with an Olympus SZX7 microscope associating with a Canon EOS 550D camera. Genitalia drawings were made and edited with Adobe Illustrator CS6 and Photoshop CS6.

The morphological terminology used in this work for the species descriptions follow the works of Anufriev (1967), Hamilton (1980), and Tishechkin (2017). The body length was measured from the apex of the head to the end of the forewings and is given in millimeters.

The type specimens of the new species are deposited in the Museum of Zoology and Botany, Shaanxi University of Technology, Hanzhong, China (**SUHC**), and the other examined specimens are deposited in the Institute of Entomology, Guizhou University, Guiyang, China (**GUGC**).

## Taxonomy

### Genus *Oncopsis* Burmeister, 1838

*Bythoscopus* (*Oncopsis*) Burmeister, 1838: 10.

*Zinneca* Amyot & Servile, 1843: 579; Hamilton 1980: 887 (synonymy).

**Type species.** *Cicada flavicollis* Linnaeus, 1761 [by subsequent designation, Westwood 1840].

**Distribution.** Palaearctic, Oriental, and Nearctic realms.

**Host.** Betulaceae and *Ulmus* spp. (Ulmaceae).

**Remarks.** *Oncopsis* can be distinguished from other genera of Macropsinae largely by the following combined features: face with coronal pits closer together than ocelli; frons usually with transverse striations or punctures; pronotum with transverse striations; forewing with three (rarely two or reticulate) anteapical and four apical cells; male pygofer without process at ventral margin; dorsal connective generally large, s-shaped in lateral aspect, and bearing large, forked or unforked process from inner ventral margin; dorsal connective usually articulating against upper margin of pygofer.

### *Oncopsis anchorous* Xu, Liang & Li, 2006

*Oncopsis anchorous* Xu, Liang & Li, 2006: 836

**Material examined.** 1 male [Holotype], 1 male and 1 female [Paratypes]: CHINA: Sichuan Province, Emeishan, 16-vii-1995, collected by Mao-Fa Yang (GUGC).

**Distribution.** Sichuan (Fig. 65).

### *Oncopsis furca* Liu & Zhang, 2003

*Oncopsis furca* Liu & Zhang, 2003: 181

**Material examined.** 1 male: CHINA: Sichuan Province, Tibetan Autonomous Prefecture of Garzê, Luding County, Moxi Town, Hailuoguo, 3000 m above sea level, 29-vii-2012, collected by Meng Jiao (GUGC).

**Distribution.** Sichuan (Fig. 65), Gansu, and Qinghai (Dai et al. 2018, Li et al. 2018).

***Oncopsis fusca* (Melichar, 1902)**

*Bythoscopus fuscus* Melichar, 1902: 120

*Oncopsis fusca* Metcalf 1966: 219; Lauterer and Anufriev 1969: 162

**Material examined.** None.

**Distribution.** Sichuan (Fig. 65), Tibet, and Hubei; Philippines, and Malaysia (Dai et al. 2018, Li et al. 2018).

***Oncopsis graciaedeagus* Li, Dai & Li, 2018**

*Oncopsis graciaedeagus* Li, Dai & Li, 2018: 31

**Material examined.** 1 male [Holotype], 5 males and 3 females [Paratypes]: CHINA: Sichuan Province, Tibetan Autonomous Prefecture of Garzê, Luding County, Moxi Town, Hailuogou, 3000 m above sea level, 29-vii-2012, collected by Hu Li, Zhi-Hua Fan, and Meng Jiao (GUGC).

**Distribution.** Sichuan (Fig. 65).

***Oncopsis hailuogouensis* Li, Dai & Li, 2018**

*Oncopsis hailuogouensis* Li, Dai & Li, 2018: 33

**Material examined.** 1 male [Holotype]: CHINA: Sichuan Province, Tibetan Autonomous Prefecture of Garzê, Luding County, Moxi Town, Hailuogou, 3000 m above sea level, 29-vii-2012, collected by Meng Jiao (GUGC).

**Distribution.** Sichuan (Fig. 65).

***Oncopsis kangdingensis* Dai & Li, 2013**

*Oncopsis kangdingensis* Dai & Li, 2013: 12

**Material examined.** 1 male [Holotype], 1 male and 7 females [Paratypes]: CHINA: Sichuan Province, Tibetan Autonomous Prefecture of Garzê, Kangding County, 2700 m above sea level, 10-viii-2010, collected by Yi Tang (GUGC).

**Distribution.** Sichuan (Fig. 65), Shanxi, and Yunnan (Dai et al. 2018, Li et al. 2018).

***Oncopsis konkaensis* Li, Li & Dai, sp. nov.**

<http://zoobank.org/4763F5C2-7588-4B82-A7F2-78256B2E2162>

Figs 1–3, 7–16, 65

**Type material.** *Holotype male*: CHINA: Sichuan Province, Tibetan Autonomous Prefecture of Garzê, Luding County, Minya Konka, Yajiageng, 3800 m above sea level, 13-viii-2015, collected by Hong-Ping Zhan (GUGC).

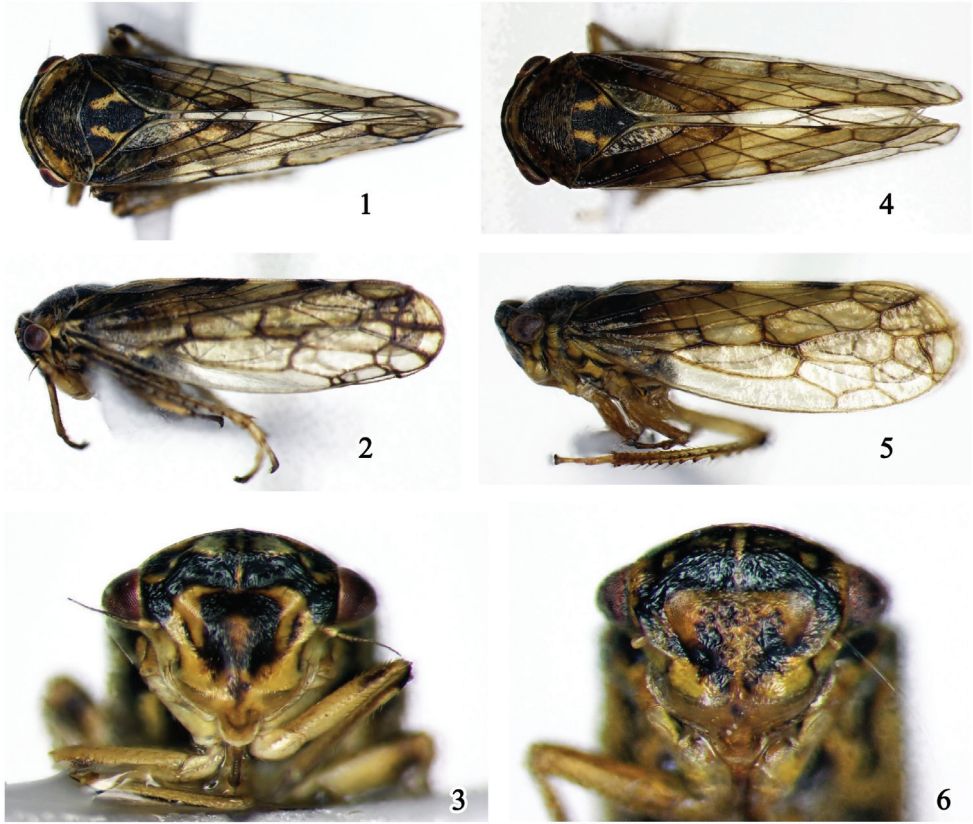
**Etymology.** The specific epithet was derived from the type locality, Minya Konka (Sichuan Province), where the species was collected, combined with the Latin suffix *-ensis*, meaning from a locality.

**Description.** [Holotype] **Body color.** Body background color (Figs 1, 2) yellowish. Crown (Fig. 1) with black transverse stripe. Face (Fig. 3) yellow, eyes reddish brown; antenna with pedicel and scape yellowish brown and flagellum dark brown; frons with approximately m-shaped black macula between eyes; frontoclypeus with n-shaped black macula at middle with two ends close to each other, and dark oblique striation near lateral margin; clypeus with brown markings. Pronotum (Fig. 1) dark brown medially, lighter anterolaterally. Scutellum (Fig. 1) black with pair of posteriorly diverging yellow submedial stripes. Forewing (Figs 2, 3) pale hyaline infused with brown, venation dark brown. Legs yellowish, marked with brown maculae.

**Body appearance.** Typically wedge-shaped. Head (Fig. 1) short, with parallel margins, broadly convex in dorsal view; width across eyes as wide as pronotum. Face including eyes (Fig. 3) slightly wider than long, distance between ocelli nearly  $4 \times$  that from ocellus to adjacent eye, frons with distinct rugae and longitudinal carina, clypeus with few scattered punctures. Pronotum (Fig. 1) with obvious closely-spaced transverse striations, anterior margin prominent frontally, and posterior margin concave medially, broader by  $2.6 \times$  length. Scutellum (Fig. 1) triangular, with coarse surface, middle length  $1.5 \times$  that of pronotum. Forewing (Figs 2, 3) hyaline, with three anteapical and four apical cells, veins well defined.

Male abdominal apodemes of second tergite (Fig. 9) weakly sclerotized, with rounded apex. Apodemes of second sternite (Fig. 10) basally broad, tapered to subacute apex, and pointed towards each other, distance between apodemes nearly  $2 \times$  their middle length.

**Male genitalia.** Pygofer side broad basally (Fig. 7), dorsal and caudal margin truncated, ventral margin with distal half expanded inwards, with scattered setae. Subgenital plate (Fig. 8) slender,  $0.6 \times$  length of ventral margin of pygofer. Aedeagus (Figs 11, 12) with broad basis, slender shaft, tapered to subacute end in lateral aspect, margins somewhat parallel, with round apex in ventral view, gonopore subapical. Dorsal connective (Fig. 13) s-shaped in lateral view, produced to large and long process from inner ventral margin bent ventrad beyond mid-length, apex bifurcate. Style (Fig. 14) with stout stem, dorsally bent, gradually widening to apex, with marginal setae, apical margin truncated. Connective (Figs 15, 16) typical of the genus.



**Figures 1–6.** Males of *Oncopsis* in dorsal (1, 4), and lateral (2, 5) views, and face (3, 6) 1–3 *O. konkaensis* sp. nov. 4–6 *Oncopsis moxiensis* sp. nov.

**Measurement.** Body length (including tegmen): 5.0 mm.

**Distribution.** Sichuan (Fig. 65).

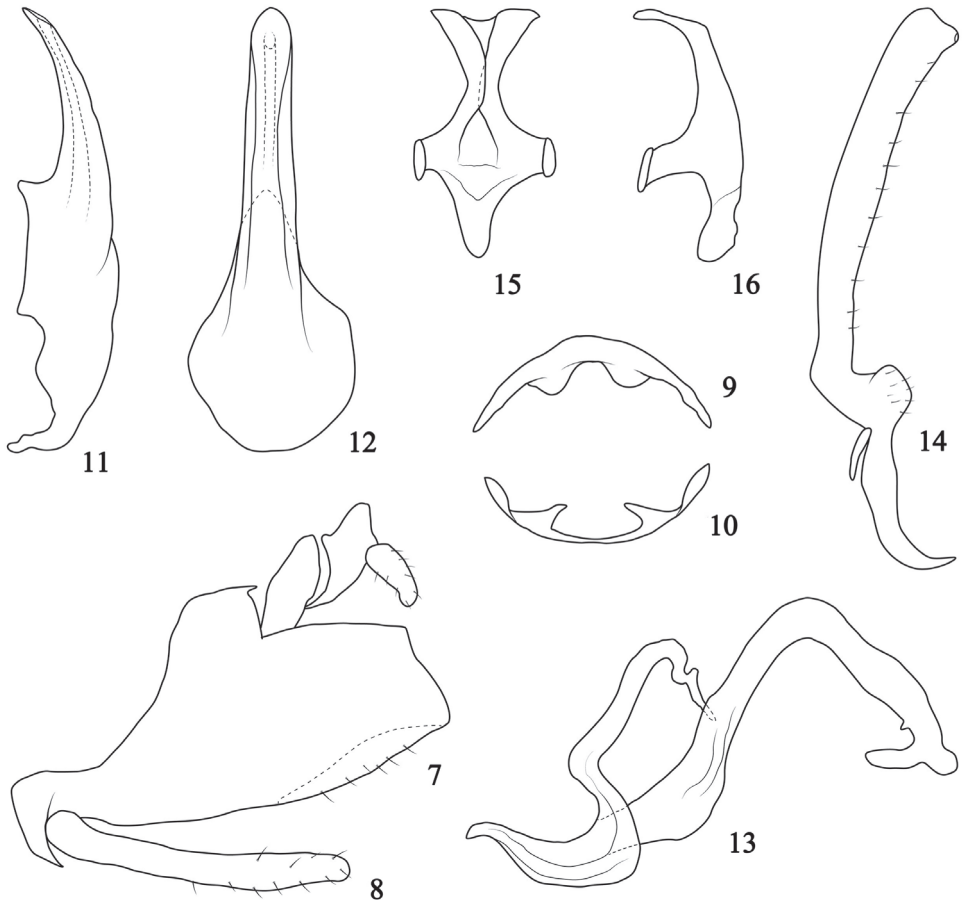
**Host.** *Betula* spp. (Betulaceae).

**Remark.** The new species differs from all other known members of *Oncopsis* by the unique shape of the dorsal connective, which has the medial process large and long, bent ventrad and bifurcated at the apex; also by the combined features of the aedeagus and pygofer.

### *Oncopsis kuluensis* Viraktamath, 1996

*Oncopsis kuluensis* Viraktamath, 1996: 185; Dai and Li 2013: 17.

**Material examined.** 3 males: CHINA: Sichuan Province, Emeishan National Natural Reserve, Jinding, 7-viii-1991, collected by Zi-Zhong Li (GUGC); 2 females: CHINA:



**Figures 7–16.** *Oncopsis konkaensis* sp. nov. **7** Male pygofer, lateral view **8** Subgenital plate, lateral view **9** 2<sup>nd</sup> abdominal tergal apodemes **10** 2<sup>nd</sup> abdominal sternal apodemes **11** Aedeagus, lateral view **12** Aedeagus, ventral view **13** Dorsal connective, lateral view **14** Style, dorsal view **15** Connective, dorsal view **16** Connective, lateral view.

Sichuan Province, Emeishan National Natural Reserve, Leidongping, 7-viii-1991, collected by Zi-Zhong Li (GUGC).

**Distribution.** Sichuan (Fig. 65) and India (Viraktamath 1996, Li et al. 2018).

### *Oncopsis ludingensis* Li, Dai & Li, 2018

*Oncopsis ludingensis* Li, Dai & Li, 2018: 36.

**Material examined.** 1 male [Holotype], 1 male and 5 females [Paratypes]: CHINA: Sichuan Province, Tibetan Autonomous Prefecture of Garzê, Luding County, Moxi



town, Hailuoguo, 3000 m above sea level, 29-vii-2012, collected by Li Hu, Fan Zhi-Hua and Jiao Meng (GUGC).

**Distribution.** Sichuan (Fig. 65).

***Oncopsis melichari* Lauterer & Anufriev, 1969**

*Oncopsis melichari* Lauterer & Anufriev, 1969: 163.

**Material examined.** None.

**Distribution.** Sichuan. Note: the distribution of *O. melichari* is excluded from the distribution map since the collected data, “the valley of the river Shubagu” of the original record (Lauterer and Anufriev 1969), cannot be matched with any known place names.

***Oncopsis moxiensis* Li, Li & Dai, sp. nov.**

<http://zoobank.org/224A1FE9-23CE-465F-8D22-A3BF6803BFDA>

Figs 4–6, 17–26, 65

**Type material. Holotype male:** CHINA: Sichuan Province, Tibetan Autonomous Prefecture of Garzê, Luding County, Moxi Town, Hailuoguo, 3600 m above sea level, 12-viii-2015, collected by Hong-Ping Zhan (GUGC).

**Etymology.** The specific epithet was derived from place name, Moxi Town, where the species was collected and the type locality is located, combined with the Latin suffix -ensis, meaning from a locality.

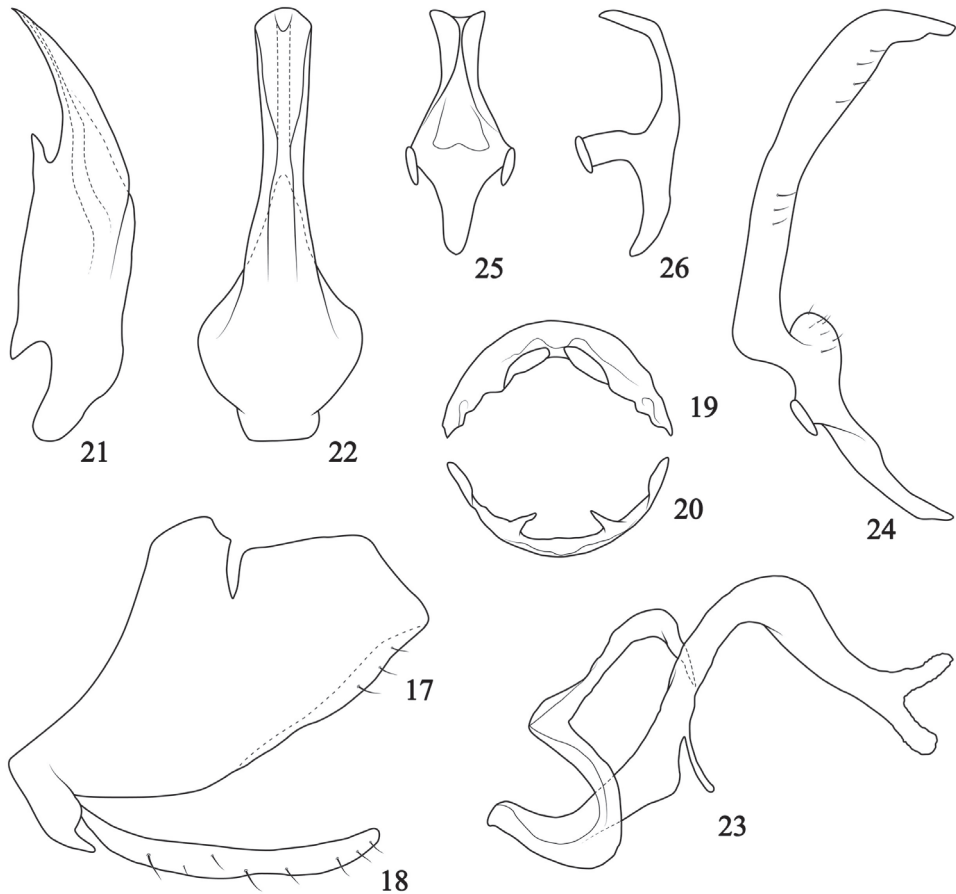
**Description.** [Holotype] **Body color.** Background yellow brown. Crown (Fig. 4) dark brown. Face (Fig. 6) yellow brown to dark brown, eyes brown, marked with reddish; antenna yellowish brown; frons dark to black except on ocelli and middle line; clypeus with central area dark or black on both sides of middle line, distal half chocolate. Pronotum (Fig. 4) dark brown with evenly dispersed darker spots. Scutellum and legs coloration similar to *O. konkaensis* sp. nov. Forewing (Figs 5, 6) with basal half dark brown and distal half yellowish brown.

**Body appearance.** Relatively stout. Head including eyes (Fig. 4) slightly narrower than pronotum. Face across eyes (Fig. 6) broader than long, central region with obvious punctures. Pronotum (Fig. 4) 2.5 × wider than long, with fore-margin strongly protruding forward, and hind margin slightly depressed in middle. Scutellum (Fig. 4) 1.2 × longer than pronotum. Other features as in *O. konkaensis* sp. nov.

Male abdominal apodemes of second tergite (Fig. 19) broad, close to each other, twisted caudally. Apodemes of second sternite (Fig. 20) relatively small, basally broad, tapered to acute or subacute apex, and pointed inwards; distance between apodemes nearly 3 × their middle length.

**Male genitalia.** Pygofer side (Fig. 17) basally broad, dorsal and caudal margins straight. Subgenital plate (Fig. 18) approximately 2/3 length of pygofer ventral margin. Aedeagus (Figs 21, 22) broad basally, shaft tapered to acute apex in lateral view, slightly





**Figures 17–26.** *Oncopsis moxiensis* sp. nov. **17** Male pygofer, lateral view **18** Subgenital plate, lateral view **19** 2<sup>nd</sup> abdominal tergal apodemes **20** 2<sup>nd</sup> abdominal sternal apodemes **21** Aedeagus, later view **22** Aedeagus, ventral view **23** Dorsal connective, lateral view **24** Style, dorsal view **25** Connective, dorsal view **26** Connective, lateral view.

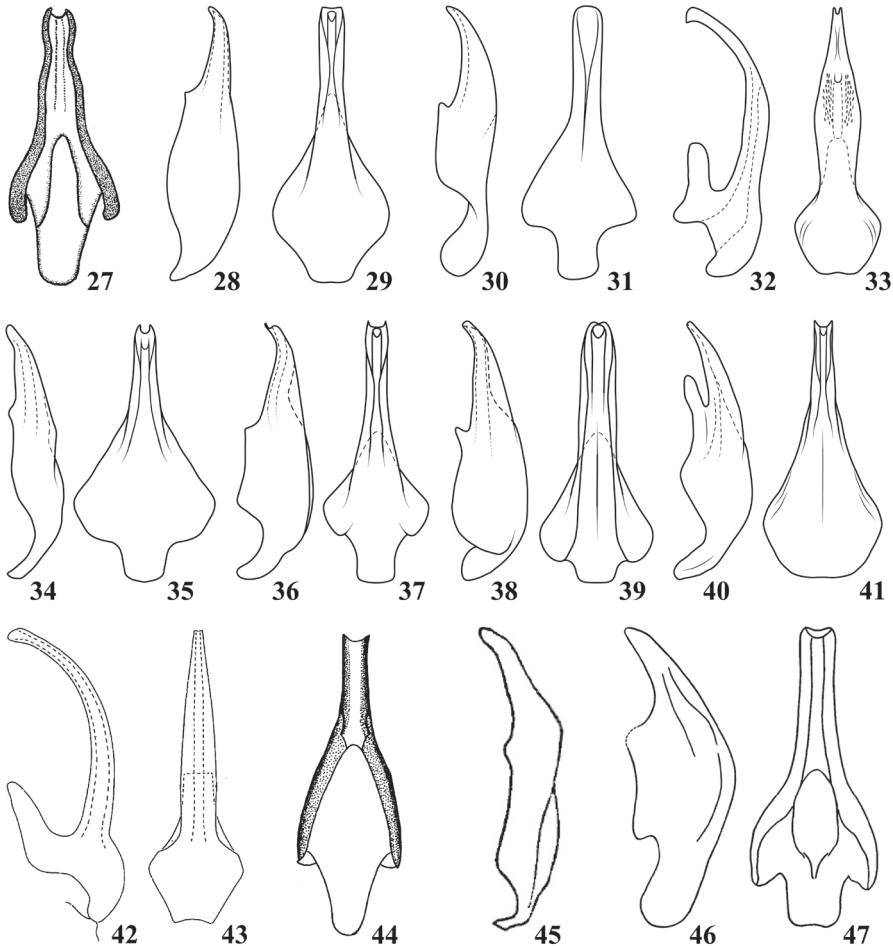
narrowed in middle, apex rounded in ventral aspect, gonopore apical. Dorsal connective (Fig. 23) with large process bent ventrocaudally from inner ventral margin with bifurcated end and sinuated margins; with extremely slender process pointed ventrad near base. Style apex bent dorsad and irregularly tapered (Fig. 24); connective (Figs 25, 26) typical.

**Measurement.** Body length (including tegmen): 5.4 mm.

**Distribution.** Sichuan (Fig. 65).

**Host.** *Betula* spp. (Betulaceae).

**Remark.** This species is similar to *Oncopsis konkaensis* sp. nov. in the body coloration and external morphology, and somewhat similar in the shape of the dorsal connective, but can be distinguished from the latter by the different coloration of the face, and the shapes of the aedeagus, style and the dorsal connective.



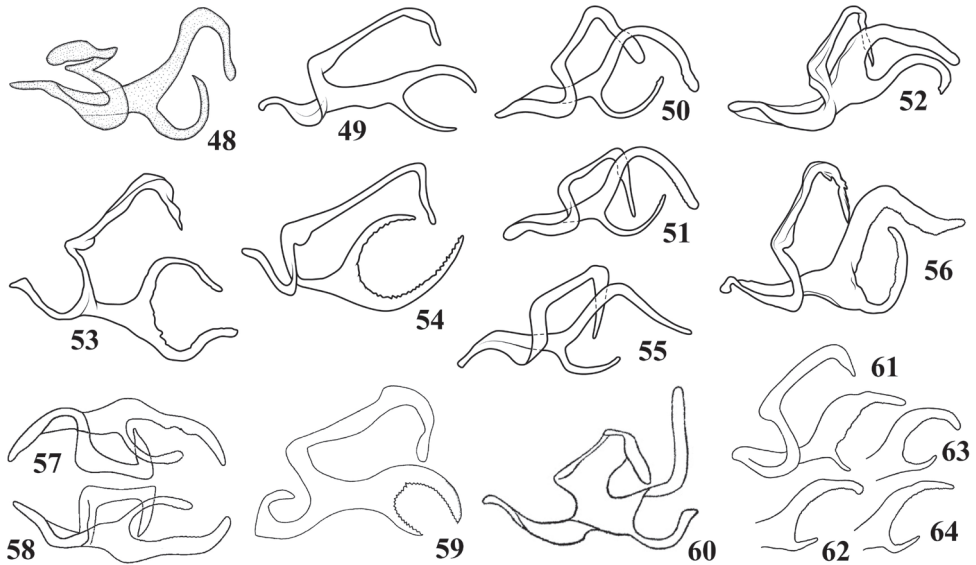
**Figures 27–47.** Aedeagus of *Oncopsis* in Sichuan, lateral (28, 30, 32, 34, 36, 38, 40, 42, 45–46) and ventral (27, 29, 31, 33, 35, 37, 39, 41, 43–44, 47) views 27 *O. anchorous* (after Xu et al. 2006) 28–29 *O. furca* 30–31 *O. fusca* (after Lauterer and Anufriev 1969) 32–33 *O. graciaeadeagus* 34–35 *O. hailuogouensis* 36–37 *O. kangdingensis* 38–39 *O. kuluensis* 40–41 *O. ludingensis* 42–43 *O. melichari* (after Lauterer and Anufriev 1969) 44 *O. nigrofasciata* (after Xu et al. 2006) 45 *O. trimaculata* (after Kuoh 1992) 46–47 *O. tristis* (after Tishechkin 2017).

### *Oncopsis nigrofasciata* Xu, Liang & Li, 2006

*Oncopsis nigrofasciatus* Xu, Liang & Li, 2006: 837.

*Oncopsis nigrofasciata*, Dai, Li and Li 2018: 130 (correction of gender of species name).

**Material examined.** 1 male: CHINA: Sichuan Province, Tibetan Autonomous Prefecture of Garzê, Kangding County, 2700 m above sea level, 10-viii-2005, collected by Yi Tang (GUGC); 1 female: CHINA: Sichuan Province, Tibetan Autonomous Prefecture of Garzê, Kangding County, 23-vii-2012, collected by Zhi-Hua Fan (GUGC).



**Figures 48–64.** Dorsal connectives of *Oncopsis* in Sichuan, lateral views **48** *O. anchorous* (after Xu et al. 2006) **49** *O. furca* **50–51** *O. fusca* (after Lauterer and Anufriev 1969) **52** *O. graciaedeagus* **53** *O. hailuoguoensis* **54** *O. kangdingensis* **55** *O. kuluensis* **56** *O. ludingensis* **57–58** *O. melichari* (after Lauterer and Anufriev 1969) **59** *O. nigrofasciata* (after Xu et al. 2006) **60** *O. trimaculata* (after Kuoh 1992) **61–64** *O. tristis* (after Tishechkin 2017).

**Distribution.** Sichuan (Fig. 65), Qinghai, Ningxia, Shanxi, Hebei, Yunnan, Shaanxi, and Jilin (Dai et al. 2018; Li et al. 2018).

### *Oncopsis trimaculata* Kuoh, 1992

*Oncopsis trimaculata* Kuoh, 1992: 272.

**Material examined.** None.

**Distribution.** Sichuan (Fig. 65).

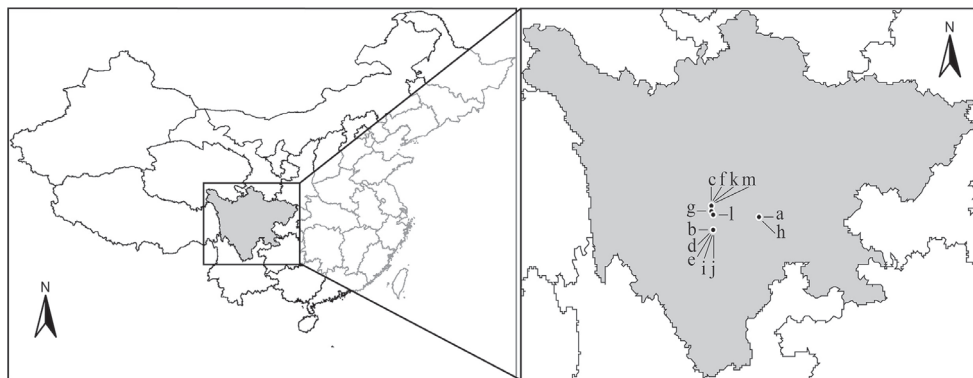
### *Oncopsis tristis* (Zetterstedt, 1840)

*Jassus tristis* Zetterstedt, 1840: 303.

*Oncopsis tristis*, Metcalf 1966: 231; Lauterer and Anufriev 1969: 165; Tishechkin 2017: 542.

**Material examined.** None.

**Distribution.** Sichuan (Fig. 65), western Europe to the Russian Far East including Sakhalin and Kurile Islands, Japan (Tishechkin 2017).



**Figure 65.** Map showing the distribution of species of *Oncopsis* in Sichuan Province, China. Key: a. *O. anchorous*; b. *O. furca*; c. *O. fusca*; d. *O. graciaedeagus*; e. *O. hailuogouensis*; f. *O. kangdingensis*; g. *O. konkaensis*; h. *O. kuluensis*; i. *O. ludingensis*; j. *O. moxiensis*; k. *O. nigrofasciata*; l. *O. trimaculata*; m. *O. tristis*.



**Figures 66–68.** Photographs showing the landscape and *Oncopsis* habitat at Hailuogou of Sichuan **66** a tip of the Hailuogou glacier **67** Vegetation **68** Potential host plant to *Oncopsis*.

**Key to species of *Oncopsis* from Sichuan Province, China based on male genitalia**

- 1      Aedeagal shaft (Figs 32, 42) strongly elongated and slender in lateral view..2
- Aedeagal shaft normal, stout and typical in lateral view.....3
- 2      Aedeagal shaft (Figs 32, 33) strongly tumid at middle in ventral view, and  
with fine protuberances on ventral margin..... *O. graciaeadeagus*
- Aedeagal shaft (Figs 42, 43) slightly inflated at middle in ventral view, with-  
out protuberances on ventral margin ..... *O. melichari*
- 3      Dorsal connective process clearly bifurcated from base or sub-base .....4
- Dorsal connective process (Figs 13, 23) not bifurcated from base or sub-base,  
only apex bilobed .....13
- 4      Process of dorsal connective with upper branch (Fig. 54) clearly shorter than  
lower one..... *O. kangdingensis*
- Process of dorsal connective with upper branch longer than or at least as long  
as lower one .....5
- 5      Process of dorsal connective with upper branch (Fig. 60) clearly bent dorsad ....  
..... *O. trimaculata*
- Process of dorsal connective with upper branch usually bent ventrad  
or caudad .....6
- 6      Process of dorsal connective branched from sub base .....7
- Process of dorsal connective branched from base.....8
- 7      Inner margin between two branches of process of dorsal connective (Fig. 49)  
smooth, not sinuate or serrated..... *O. furca*
- Inner margin between two branches of process of dorsal connective (Fig. 59)  
serrated ..... *O. nigrofasciata*
- 8      Both branches of process of dorsal connective (Figs 48, 53) slender and of  
almost equal length.....9
- Upper branch of process of dorsal connective distinctly wider and shorter  
than lower one .....10
- 9      Lower branch of process of dorsal connective (Fig. 48) bent dorsad; aedeagal  
shaft (Fig. 27) with lateral margins slightly sinuate in ventral view.....  
..... *O. anchorous*
- Lower branch of process of dorsal connective (Fig. 53) bent caudad; aedeagal  
shaft (Figs 34, 35) tapered to apex in ventral view..... *O. bailuogouensis*
- 10      Inner margin between two branches of process of dorsal connective  
smooth.....11
- Inner margin between two branches of process of dorsal connective  
sinuate.....12
- 11      Upper branch of process of dorsal connective (Figs 50, 51) bent ventrad and  
round at apex, lower branch longer than 1/2 length of upper one .... *O. fusca*
- Upper branch of process of dorsal connective (Fig. 55) bent caudad and suba-  
cute at apex, lower branch less than 1/2 length of upper one..... *O. kuluensis*



- 12 Aedeagal shaft (Figs 40, 41) tapered in ventral view; two branches of process of dorsal connective (Fig. 56) closer to each other, upper branch sinuate and pointed caudally, and lower one slender ..... *O. ludingensis*
- Aedeagal shaft (Figs 46, 47) with lateral parallel margins in ventral view; two branches of process of dorsal connective (Figs 61–64) away from each other, upper branch evenly bent caudally, and lower branch short..... *O. tristis*
- 13 Aedeagal shaft (Figs 11, 12) tapered to apex in ventral view; process of dorsal connective (Fig. 13) with apex bifurcated and ventrally pointed..... *O. konkaensis*
- Aedeagal shaft (Figs 21, 22) slightly narrowed at middle in ventral view; process of dorsal connective (Fig. 23) with apex bifurcated but ventrocaudally pointed ..... *O. moxiensis*

## Acknowledgments

We thank Hong-Ping Zhan (GUGC) for providing the specimens for the Macropsinae study, Drs Jin Hyung Kwon (referee) and Christopher H. Dietrich (referee and the subject editor) for reading and improving this paper, and giving valuable suggestions. The project was supported by a Young Talent Fund of University Association for Science and Technology in Shaanxi, China (no. 20170209).

## References

- Amyot CJB, Serville A (1843) Histoire naturelle des insects, Hémiptères. Librairie Encyclopédique de Roret, Rue Hautefeuille, Paris, 675 pp.
- Anufriev GA (1967) Notes on the genus *Oncopsis* Burmeister, 1838 (Homoptera, Auchenorrhyncha) with descriptions of new species from the Soviet Far East. Entomologisk Tidskrift 88(3–4): 174–184.
- Burmeister HCC (1838) Genera quaedam Insectorum Iconibus Illustravit et Descripsit, vol. 1. Rhynchota. Burmeister et Stange, Berolini, 76 pp. <https://doi.org/10.5962/bhl.title.8144>
- Chen X (1997) Insect biogeography. China Forestry Publishing House, Beijing, 102 pp.
- Dai R-H, Li H (2013) Five new species and a new record of genus *Oncopsis* from China (Hemiptera: Cicadellidae, Macropsinae). Entomologica Fennica 24(1): 9–20.
- Dai R-H, Li H, Li Z-Z (2018) Macropsinae from China (Hemiptera: Cicadellidae). China Agriculture Press, Beijing, 240 pp.
- Dietrich CH, Thomas MJ (2018) New eurymelinae leafhoppers (Hemiptera, Cicadellidae, Eurymelinae) from Eocene Baltic amber with notes on other fossil Cicadellidae. Zookeys 726: 131–143. <https://doi.org/10.3897/zookeys.726.21976>
- Hamilton KGA (1980) Contributions to the study of the world Macropsini (Rhynchota: Homoptera: Cicadellidae). The Canadian Entomologist 112: 875–932. <https://doi.org/10.4039/Ent112875-9>

- Kuoh CL (1992) Homoptera: Cicadelloidea In: Chinese Academy of Science (Ed.) The Comprehensive Scientific Expedition to the Qinghai-Xizang Plateau, Insects of the Hengduan Mountains Region, vol. 1. Science Press, Beijing, 243–316. [In Chinese with English summary]
- Lauterer P, Anufriev GA (1969) Contribution to the knowledge of the genus *Oncopsis* Burm. (Homoptera: Cicadellidae) from China and Far East. Acta Musei Moraviae 54: 161–168.
- Li H, Dai R-H, Li Z-Z (2018) Three new species of the leafhopper genus *Oncopsis* Burmeister, 1838 (Hemiptera: Cicadellidae, Macropsinae) from Sichuan Province of Southwestern China. Entomologica Fennica 28(1): 30–38.
- Liu ZJ, Zhang YL (2003) Description of two new species of Macropsinae (Homoptera: Cicadellidae) from China. Entomotaxonomia 25(3): 181–185. [In Chinese with English summary] <https://doi.org/10.3969/j.issn.1000-7482.2003.03.005>
- Melichar L (1902) Homopteren aus West China, Persien, und dem Süd-Ussuri-Gebiete. Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de St.-Petersbourg 7: 76–146.
- Metcalf ZP (1966) General catalogue of the Homoptera. Fasc. VI. Cicadelloidea. Pt 13. Macropsidae. United States Department of Agriculture, Agricultural Research Service, Washington, D.C., 261 pp.
- Mühlethaler R (2008) Description of a new species of the genus *Oncopsis* (Hemiptera: Cicadomorpha: Cicadellidae) from Greece. Acta Entomologica Slovenica 16(1): 5–10.
- Tishechkin DY (2016) Host plant shifts and transitions into new adaptive zones in leafhoppers: the example of Macropsinae (Homoptera: Auchenorrhyncha: Cicadellidae) of Russia and adjacent countries. Zootaxa 4121(2): 117–132. <https://doi.org/10.11646/zootaxa.4121.2.2>
- Tishechkin DY (2017) Review of the genus *Oncopsis* Burmeister, 1838 (Homoptera: Auchenorrhyncha: Cicadellidae: Macropsinae) of Russia and adjacent countries with description of a new species from Central Asia. Zootaxa 4216(6): 537–558. <https://doi.org/10.11646/zootaxa.4216.6.2>
- Viraktamath CA (1996) New Oriental Macropsinae with a key to species of the Indian subcontinent (Insecta: Auchenorrhyncha: Cicadellidae). Entomologische Abhandlungen, Städtisches Museum für Tierkunde Dresden 57(7): 183–200.
- Westwood JO (1840) An introduction to the modern classification of insects, vol. 2, Synopsis of the genera of British Insects. Longman, Orme, Brown, Green and Longmans, London, 158 pp.
- Xu P, Liang AP, Li ZZ (2006) Descriptions of two new species of *Oncopsis* Burmeister (Hemiptera, Cicadellidae, Macropsinae) from China. Acta Zootaxonomica Sinica 31(4): 835–839. [In Chinese with English summary]
- Zetterstedt JW (1840) Insecta Lapponica, 1. L. Voss, Lipsiae, 314 pp. <https://doi.org/10.5962/bhl.title.8242>





# A revision of the *Phelister haemorrhous* species group (Coleoptera, Histeridae, Exosternini)

Michael S. Caterino<sup>1</sup>, Alexey K. Tishechkin<sup>2</sup>

**1** Department of Plant & Environmental Sciences, Clemson University, Clemson, SC 29634 USA **2** California Dept. of Food and Agriculture Plant Pest Diagnostics Center, Sacramento, CA 95832 USA

Corresponding author: Michael S. Caterino ([mcateri@clemson.edu](mailto:mcateri@clemson.edu))

Academic editor: J. Klimaszewski | Received 3 April 2019 | Accepted 2 May 2019 | Published 10 June 2019

<http://zoobank.org/F358E361-E0B4-4A44-9782-E04688B82795>

**Citation:** Caterino MS, Tishechkin AK (2019) A revision of the *Phelister haemorrhous* species group (Coleoptera, Histeridae, Exosternini). ZooKeys 854: 41–88. <https://doi.org/10.3897/zookeys.854.35133>

## Abstract

The *Phelister haemorrhous* species group is established here, revising the seventeen included species, four of which are described as new. This group is named for and contains the type species of *Phelister*, so represents a core around which a modern concept of the dumping-ground genus *Phelister* may be developed. The group includes several common and well-known species in the Americas, including some of the only *Phelister* to exhibit distinctive coloration. Several of these are typically found in cattle dung, and have likely expanded beyond their native ranges as cattle spread throughout the Americas. The group contains the following species: *Phelister haemorrhous* Marseul, 1854, *Phelister affinis* J.E. LeConte, 1859, *Phelister parallelisternus* Schmidt, 1893, *Phelister mobilensis* Casey, 1916, *Phelister brevistriatus* Casey, 1916, *Phelister sonorae* **sp. nov.**, *Phelister warneri* **sp. nov.**, *Phelister puncticollis* Hinton, 1935, *Phelister subrotundus* (Say, 1825), *Phelister rouzeti* (Fairmaire, 1850), *Phelister rufinotus* Marseul, 1861, *Phelister thiemei* Schmidt, 1889, *Phelister parecis* **sp. nov.**, *Phelister bryanti* **sp. nov.**, *Phelister vernus* (Say, 1825), *Phelister chilicola* Marseul, 1870, and *Phelister bruchi* Bickhardt, 1920. We also designate the following new synonymies: *Phelister haemorrhous* Marseul (= *Phelister rubicundus* Marseul, 1889, **syn. nov.**); *Phelister subrotundus* (= *Phelister contractus* Casey, 1916, **syn. nov.**); *Phelister rouzeti* (Fairmaire) (= *Phelister fairmairei* Marseul 1861; **syn. nov.**, = *Phelister wickhami* Casey, 1916, **syn. nov.**); *Phelister rufinotus* Marseul, 1861 (= *Epierus marseulii* Kirsch, 1873, **syn. nov.**); and *Phelister thiemei* Schmidt, 1889 (= *Phelister stercoricola* Bickhardt, 1909, **syn. nov.**).

## Keywords

Histerinae, Neotropical biodiversity

## Introduction

With 91 described species, and many more undescribed, the largely Neotropical genus *Phelister* Marseul is one of the most species rich genera in the family Histeridae. Since its description it has served as a taxonomic dumping ground for a great diversity of small, generally non-descript Exosternini, even including some from outside the Neotropical realm, and phylogenetic analyses have revealed it to be para- and polyphyletic (Caterino and Tishechkin 2015). Recent revisions of some other Neotropical exosternine genera have marginally improved *Phelister*'s coherence by removing a number of species (to *Operclipygus* Marseul and *Baconia* Lewis (Caterino and Tishechkin 2013a, 2013b, respectively). However, exactly how to define *Phelister* itself has not become much clearer, and substantial additional phylogenetic work is needed to more fully understand relationships among the species currently included. Relationships to other as-yet-unrevised genera such as *Pseudister* Bickhardt, *Nunbergia* Mazur, and *Conchita* Mazur remain particularly obscure.

Beyond the phylogenetic questions surrounding *Phelister*, identification of species in the group is practically impossible without reference to type specimens. No comprehensive (or even partial) keys exist aside from some very local (e.g., Casey 1916) or outdated (Bickhardt 1916) treatments, and the species are very difficult to distinguish based solely on external characters in any case. Yet, accurate identification of some of the species of *Phelister* has practical significance, as some species have been cited in forensic investigations (e.g., *P. rufinotus* Marseul; Aballay et al. 2013) and others have been studied with regard for their potential to control of dung-breeding flies (*P. panamensis* LeConte; Summerlin et al. 1991), *P. rufinotus* and *P. haemorrhous* Marseul (Koller et al. 2002). The species (presumably all predatory) exhibit an interesting array of ecological associations, ranging from loose synanthropy to mammalian inquilinity to myrmecophily. Many also occur in great abundance and may make up substantial fractions of pitfall and flight intercept trap collections in the neotropics. So improved identification efficiency would significantly benefit biodiversity inventory work.

To begin to address these systematic impediments, we plan to revise the species of *Phelister* over a series of smaller treatments of putatively closely related groups of species. Here we begin with a group of 17 species loosely centered on the now firmly-established type of the genus, *Phelister haemorrhous* Marseul. Previous confusion over the type species of *Phelister* was resolved by the ICZN following an application to recognize Kryzhanovskij and Reichardt's (1976) designation of *P. haemorrhous* as the type (Caterino and Tishechkin 2013c, ICZN 2015). Our hypothesis of monophyly for this group is based on only a few shared characters (discussed more below), and the group does contain considerable diversity. But together they seem to represent a near continuum of forms, with many of them quite difficult to distinguish. The group is largely, though not completely supported as monophyletic in our recent global analysis of *Phelister* (Caterino and Tishechkin 2015). We attribute the exceptions mostly

to some inadequacies of search algorithms (across over 750 taxa), as well as a lack of molecular data for the majority of relevant species. Possible relationships among the species are discussed in further detail below, based on some more thorough analyses of a subset of taxa.

The species we attribute to the informal *P. haemorrhous* group include some of the most commonly encountered *Phelister* species in both North and South America. Several are associated with the dung of domestic cattle and horses. Additionally, the group includes nearly all of the *Phelister* species currently known to occur in the Nearctic realm. Interestingly, although the group's species collectively span the Americas, they are sparse in the wet tropics, and the species are most often encountered in the northern and southern subtropical/temperate zones. Furthermore, several of the species exhibit some red coloration, which has drawn an unusual amount of attention to them. Given these attributes, it is a relatively well-described group, with only a few new species, all of which exhibit fairly limited distributions and, in several cases, narrow ecological associations.

## Materials and methods

### Specimens

Type material of all species was examined by one or both of the authors. Other specimens examined were assembled from a large number of institutions:

<b>AKTC</b>	Alexey Tishechkin Collection, Sacramento, USA
<b>ASUC</b>	Arizona State University Collection, Tempe, USA
<b>NHMK</b>	Natural History Museum, London, UK
<b>CASC</b>	California Academy of Sciences Collection, San Francisco, USA
<b>CDFA</b>	California State Collection of Arthropods, Sacramento, USA
<b>CEMT</b>	Coleção de Entomologia, Universidade Federal do Mato Grosso, Cuiabá, Brazil
<b>CHJG</b>	Jeffrey P. Gruber Collection, Madison, USA
<b>CHND</b>	Nicolas Degallier Collection, Paris
<b>CHPWK</b>	Peter Kovarik Collection, Columbus, USA
<b>CHSM</b>	Slawomir Mazur Collection, Warsaw, Poland
<b>CMNC</b>	Canadian Museum of Nature, Ottawa, Canada
<b>CMNH</b>	Carnegie Museum of Natural History, Pittsburgh, USA
<b>CUAC</b>	Clemson University Arthropod Collection, Clemson, USA
<b>DVC</b>	David Verity Collection, Long Beach, CA
<b>DZUP</b>	Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil
<b>FMNH</b>	Field Museum, Chicago, USA
<b>FSCA</b>	Florida State Collection of Arthropods, Gainesville, USA

<b>INBIO</b>	Instituto Nacional de Biodiversidad, San Jose, Costa Rica
<b>LSAM</b>	Louisiana State Arthropod Museum, Baton Rouge, USA
<b>MCZC</b>	Museum of Comparative Zoology, Harvard University, Cambridge, USA
<b>MNHN</b>	Museum National d'Histoire Naturelle, Paris, France
<b>MSCC</b>	Michael Caterino Collection, Clemson, USA
<b>MSNG</b>	Museo Genova di Storia Naturale “Giacomo Doria”, Genova, Italy
<b>MTD</b>	Staatliches Museum für Tierkunde, Dresden, Germany
<b>SEMC</b>	Snow Entomology Museum, University of Kansas, Lawrence, USA
<b>TAMU</b>	Texas A&M University Collection, College Station, USA
<b>UNESP</b>	Universdade Estadual Paulista, Faculdade de Engenharia de Ilha Solteira, Ilha Solteira, Brazil
<b>USFQ</b>	Universidad San Francisco de Quito, Ecuador
<b>USNM</b>	National Museum of Natural History, Washington, USA
<b>WSUC</b>	Washington State University Insect Collection, Pullman, USA
<b>ZMHB</b>	Zoological Museum of Humboldt University, Berlin, Germany

We present brief diagnostic descriptions for most species, focusing on those character systems in which differences among species are typically found. They are not intended to be exhaustive descriptions of each species' morphology. We have attempted to make most of them consistent in character content and order, facilitating comparison as well as their reuse of descriptions in other contexts. The 'remarks' sections highlight the few most important key characters of each species. Much of the morphological terminology used is based on Wenzel and Dybas (Wenzel and Dybas 1941), but modified to follow more recent treatments (Helava et al. 1985, Ohara 1994, Kanaar 1997, Lawrence et al. 2011). We have presented an extensive discussion of Exosternini-specific morphological terminology in Caterino and Tishechkin (2013a), and refer the reader to the labeled illustrations there.

Material examined lists provide verbatim data only for holotypes and lectotypes, and summary data for all other material of described species, whether paratypes or non-type localities. Most of these represent lists of states or provinces within countries. For US states, counties are included. Within verbatim records, data are enclosed in double quotes, with data on separate labels separated by a slash '/'.

Conventional imaging was done using a Visionary Digital's 'Passport' portable imaging system, which incorporates a Canon D7 with MP-E 65mm 1–5×macro zoom lens. Images were stacked using Helicon Focus software (HeliconSoft, Kharkiv, Ukraine). SEM imaging was done on a Zeiss EVO 40 scope. Most specimens were sputter coated with gold, though some uncoated specimens were examined in 'variable pressure' mode. Following histerid conventions, total body length is measured from the anterior margin of the pronotum to the posterior margin of the elytra (to exclude preservation variability in head and pygidial extension), while width is taken at the widest point, generally near the elytral humeri. Ten specimens were measured wherever possible.

## Phylogenetic analyses

We reanalyzed a subset of taxa from the 750+ taxon data set of Caterino and Tishechkin (2015) to attempt to better resolve species within *Phelister* and to evaluate the level of support for the *haemorrhous* group as we delimit it here. This pruned data set included only small numbers of exemplars for those groups previously strongly supported as monophyletic. Specifically, it includes only four species of *Baconia*, two species of *Hypobletus*, two species of *Operclipygus*, and single exemplars of some other smaller but previously supported genera outside *Phelister*. We also reduced the number of outgroups to six (from 61). This reduced data set included a total of 231 taxa, including all described and undescribed *Phelister* and *Pseudister* spp., as well as many other new species of uncertain placement. All taxa were scored for 260 morphological characters. Approximately one-fourth were represented by some molecular data, including some combination of 18S (937 characters for 62 spp.), 28S (993 characters for 32 spp.), and cytochrome oxidase I (679 characters for 63 spp). We did not realign the length variable portions for this reduced dataset, maintaining homology assessments from the preceding analysis. For original alignment parameters see Caterino and Tishechkin (2015). This reduced data set is available as an online supplement (Suppl. material 1). Tree searching was performed in PAUP\* (v. 4.0a164; Swofford 2002) under the maximum parsimony criterion, running 1000 random sequence addition replicates, saving no more than 2500 trees for each replicate.

## Taxonomy

### The *Phelister haemorrhous* group

**Diagnosis.** Recognizing members of the *P. haemorrhous* group is difficult, given the general similarity prevailing throughout *Phelister*. However, most members exhibit most or all of the following character states. There is as yet no single and simple (non-homoplasious) synapomorphy to which we can point, even in genitalic morphology:

- Both mandibles have a strong tooth. A tooth on the right mandible is common outside the *P. haemorrhous* group; having both teeth is relatively uncommon;
- Outer subhumeral elytral stria present, but rarely in more than apical half. Many otherwise similar species have the outer subhumeral longer;
- Elytral striae 1–4 complete, 5<sup>th</sup> stria variable (but when abbreviated usually represented by a basal puncture); sutural stria abbreviated;
- Elytra often with rufescent maculae. There are very few bicolored species of *Phelister* outside this group;
- Body form elongate, less rounded than many *Phelister*;
- Lateral portion of pronotal disk bearing coarser punctures. More rarely present outside this group;

- Labrum broad, often weakly emarginate;
- Postmesocoxal stria usually well developed, ending freely or recurved anteriorly to mesepimeron;
- 1<sup>st</sup> abdominal ventrite with complete inner and abbreviated outer postmetacoxal stria;
- Males of several species have the pronotal keel more densely punctate than the females; most of these species are red-maculate;
- Aedeagus usually simple, with apices often variably separated; rarely with ventral dentate process;
- Median lobe with proximal apodemes divided into fine proximal and thick distal portions;
- Male eighth tergite lacking basal accessory sclerites;
- Most species occurring in temperate to seasonal subtropical areas, with few species known from wet tropics.

### Checklist of the species

#### ***Phelister haemorrhous* Marseul, 1854**

*Phelister egenus* Marseul, 1854b

*Phelister rubicundus* Marseul, 1889c, **syn. nov.**

#### ***Phelister affinis* JE LeConte, 1859**

*Phelister simplex* Casey, 1916

*Phelister solator* Marseul, 1861

#### ***Phelister parallelisternus* Schmidt, 1893**

#### ***Phelister mobilensis* Casey, 1916**

#### ***Phelister brevistriatus* Casey, 1916**

#### ***Phelister sonora*, sp. nov.**

#### ***Phelister warneri*, sp. nov.**

#### ***Phelister puncticollis* Hinton, 1935**

#### ***Phelister subrotundus* (Say, 1825)**

*Phelister rubricatus* Lewis, 1908

*Phelister sayi* Carnochan, 1915b

*Phelister frosti* Carnochan 1915b

*Phelister carnochani* Casey, 1916

*Phelister contractus* Casey, 1916, **syn. nov.**

#### ***Phelister rouzeti* (Fairmaire, 1850)**

*Phelister fairmairei* Marseul, 1861, **syn. nov.**

*Phelister wickhami* Casey, 1916, **syn. nov.**

*Phelister pimalis* Casey, 1916

*Phelister aztecus* Casey, 1916

#### ***Phelister rufinotus* Marseul, 1861**

*Epierus marseulii* Kirsch, 1873, **syn. nov.**



***Phelister thiemei* Schmidt, 1889***Phelister stercoricola* Bickhardt, 1909, syn. nov.***Phelister parecis*, sp. nov.*****Phelister bryanti*, sp. nov.*****Phelister vernus* (Say, 1825)***Phelister saunieri* Marseul, 1861***Phelister chilicola* Marseul, 1870*****Phelister bruchi* Bickhardt, 1920****Key to Species**

- 1 Protarsal claws modified, strongly bent at base, then straight (at least in males; Fig. 8C) ..... **2**
- Protarsal claws simple ..... **5**
- 2 Fifth elytral stria complete ..... **3**
- Fifth elytral stria abbreviated ..... **4**
- 3 Lateral pronotal stria absent; male prosternal carinal striae separate anteriorly, nearly or fully reaching anterior margin; metaventricle lacking distinct patches of punctures anteriad metacoxae; only known from Argentina ..... ***P. bryanti***
- Lateral pronotal stria present; male prosternal carinal striae meeting short of anterior margin, delimiting a small space (Fig. 5B); metaventricle with distinct patches of punctures anteriad metacoxae; northeastern Brazil ..... ***P. puncticollis***
- 4 Mesometaventral stria extending anteriad to midline of mesoventrite (Fig. 4E); frontal stria complete; only known from Sonora, Mexico ..... ***P. sonorae***
- Mesometaventral stria barely extending anteriad mesometaventral suture; frontal stria interrupted across much of middle of frons; elytral striae thin and finely impressed; elytra frequently with diffuse rufescent patches (Fig. 9B); known only from Chile ..... ***P. chilicola***
- 5 Lateral pronotal stria more or less complete, extending well posteriad pronotal midpoint ..... **6**
- Lateral pronotal stria abbreviated (not extending posteriad pronotal midpoint) or absent ..... **8**
- 6 Frontal stria complete ..... ***P. parecis***
- Frontal stria interrupted, usually broadly ..... **7**
- 7 Fifth elytral stria usually complete; body slightly larger and rounder (Fig. 6A); aedeagus expanded, rounded apically (Fig. 2I); Nearctic ..... ***P. subrotundus***
- Fifth elytral stria usually abbreviated; body smaller and more elongate (Fig. 6E); aedeagus narrower, almost straight in profile (Fig. 2J); mostly in Mexico, Central America, and northern South America, just extending into the southwestern US ..... ***P. rouzeti***

- 8 Lateral pronotal stria present but abbreviated, restricted to anterior half of pronotal margin; elytra (but not pygidia) often with red markings; southern neotropics and south temperate areas; aedeagus expanded apically, nearly spoon-shaped (Fig. 2K)..... ***P. rufinotus***
- Lateral pronotal stria absent, rarely detectable as disconnected punctures around anterior angle; red markings, if present, extending to pygidia..... **9**
- 9 Elytra with reddish markings ..... **10**
- Elytra unicolorous, usually black, rarely rufescent ..... **11**
- 10 Reddish markings extending onto pygidia and venter of apical abdominal segments (Fig. 1A); postmesocoxal stria recurved anteriad to mesepimeron (Fig. 1C); frontal stria frequently broadly interrupted across frons (Fig. 1B); larger, body length 1.85–2.3mm; widespread in Americas..... ***P. haemorrhous***
- Reddish markings (if present) restricted to elytra; postmesocoxal stria shorter, ending freely; frontal stria more nearly complete; smaller, body length 1.30–1.77mm; restricted to subtropical South America ..... ***P. thiemei***
- 11 Posterior ends of prosternal keel striae parallel and united before base (Fig. 3B); 5<sup>th</sup> dorsal elytral stria complete; posterior ends of inner metaventral striae tending to recurve mediad in front of metacoxae; south-central US into Mexico ..... ***P. parallelisternus***
- Posterior ends of prosternal keel striae ending freely; 5<sup>th</sup> dorsal elytral striae only very rarely complete; distribution varied ..... **12**
- 12 Epistoma with lateral marginal striae connecting to frontal stria at sides (Fig. 3C); mesometaventral stria distinctly more crenulated than marginal mesoventral stria (Fig. 3E); south-central and southeastern US..... ***P. mobilensis***
- Epistoma without lateral marginal striae; mesometaventral stria various..... **13**
- 13 Mesometaventral stria absent from middle (Fig. 9D); sutural and 5<sup>th</sup> dorsal striae absent; restricted to subtropical South America..... ***P. bruchi***
- Mesometaventral stria complete across middle; sutural and 5<sup>th</sup> dorsal striae present; North America ..... **14**
- 14 Frontal stria nearly complete, often interrupted, or obscured by punctures at middle; southwestern US..... **15**
- Frontal stria more broadly interrupted at middle or interrupted at middle and at sides..... **16**
- 15 Fifth elytral stria well impressed in at least apical half; body piceous; dorsal and ventral striae normally impressed; free-living, southern Arizona to Central America ..... ***P. brevistriatus***
- Fifth dorsal stria weak to absent; entire body rufescent; elytral and ventral striae more finely impressed; portions of ventral striae often effaced; middle and hind tibiae slender and only weakly spinose (Fig. 4G); likely a mammal burrow inquiline; only known from Arizona to Texas ..... ***P. warneri***

- 16 Frontal stria interrupted over antennal bases and at middle, represented at front by distinct, isolated lateral fragments (Fig. 1E); vestiges of lateral pronotal stria often detectable around anterior pronotal corners; ground punctation of metaventricle relatively fine and sparse (contrast elsewhere not as distinct); postmesocoxal stria longer, directed more posterolaterad; south-central US to Central America.....*P. affinis*
- Frontal stria usually absent across middle, though fine lateral fragments may be present; lateral pronotal stria not represented by anterior vestiges; ground punctation of pronotum, frons, and metaventricle unusually conspicuous (Fig. 9A); postmesocoxal stria short and turned out behind coxa; widespread in Nearctic.....*P. vernus*

### Species treatments

#### *Phelister haemorrhous* Marseul, 1854

Figs 1, 2; Map 1

*Phelister haemorrhous* Marseul, 1854: 476.

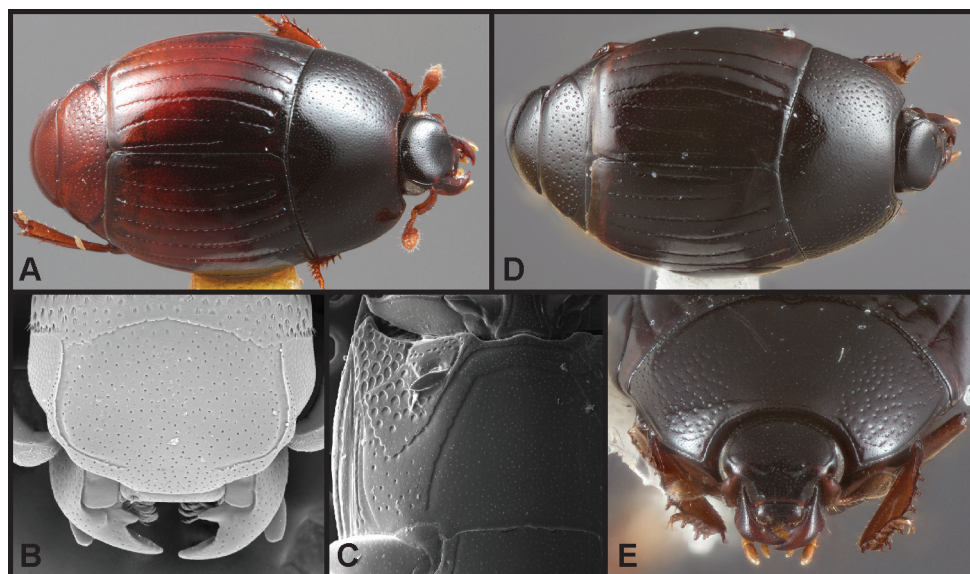
*Phelister egenus* Marseul, 1854: 480; Mazur 1984.

*Phelister rubicundus* Marseul, 1889: cxlvi; syn. nov.

**Type material.** **Lectotype**, hereby designated: “*Phelister haemorrhous* M., Italie?, Digot” [the question mark is written on the label]/ “Museum Paris, Coll. de Marseul 2842-90”/ “Type”/ “Lectotype *Phelister haemorrhous* Marseul, 1853, M.S.Caterino and A.K.Tishechkin des. 2010”, MNHN.

Types of synonyms. *Phelister rubicundus* Marseul, 1889: **Lectotype**, hereby designated: “Am. Mer” / “*Phelister rubicundus* Mars Type” / “Lectotype *Phelister rubicundus* Marseul, 1889, M.S.Caterino and A.K.Tishechkin des. 2010”, NHMUK. *Phelister egenus* Marseul, 1854b: **Lectotype**, hereby designated: “Carthagenae”, MNHN; Paralectotype with same data in NHMUK.

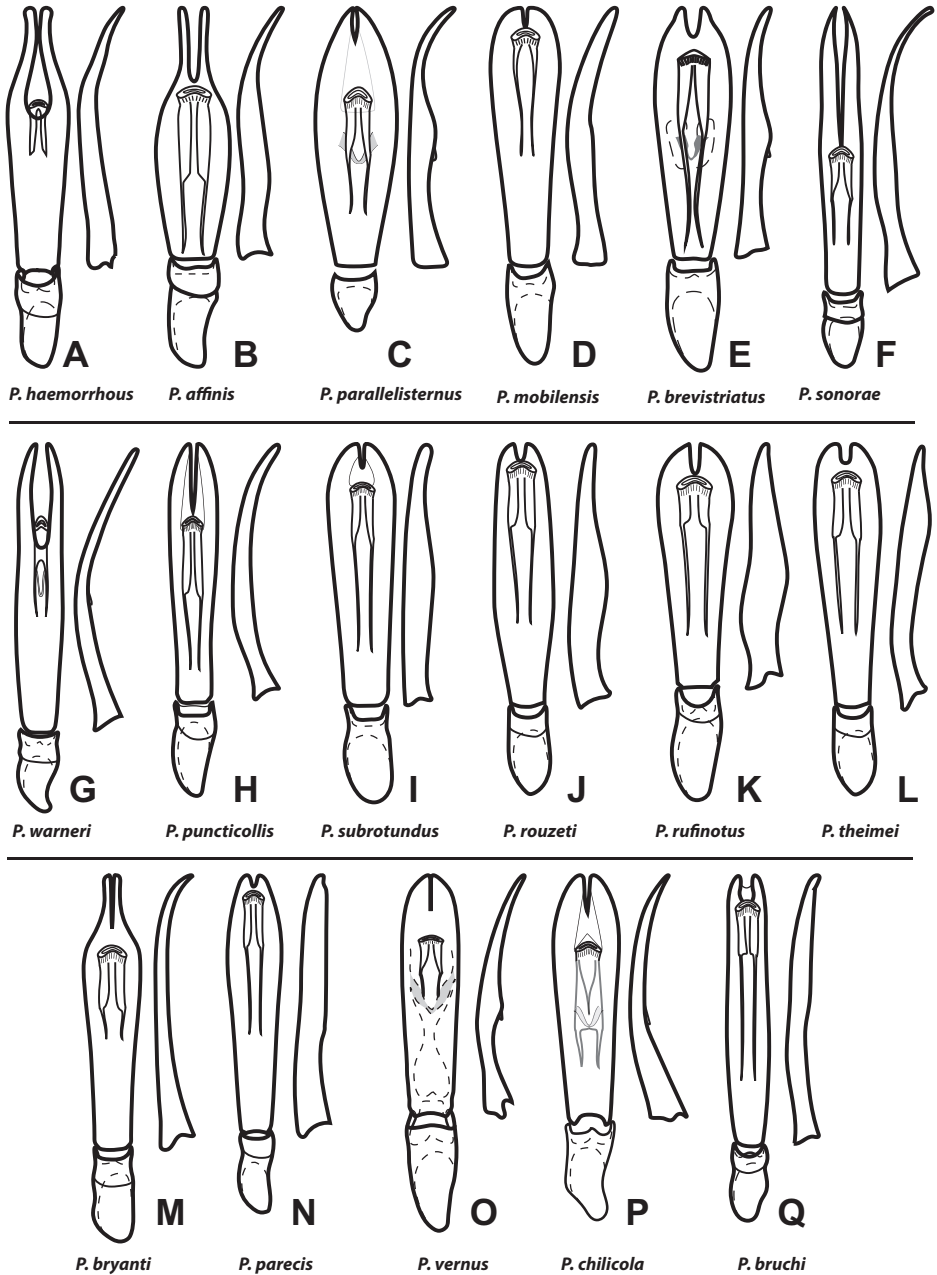
**Diagnostic description.** Length: 1.85–2.29 mm (avg. 2.03 mm); width: 1.58–1.89 mm (avg. 1.69 mm). Body elongate-oval, widest behind humeri, humeri slightly wider than base of pronotum; anterior of body black, posterolateral corners of elytra, pygidia, legs, and terminal abdominal ventrites distinctly reddish; entire dorsum finely punctulate, the pronotum more densely so than the elytra; frons finely punctulate, impressed along midline, supraorbital stria complete, frontal stria interrupted at middle, slightly sinuate at sides; labrum wide, distinctly emarginate apically; both mandibles with strong tooth on inner edges; pronotum lacking lateral and anterior submarginal striae; pronotal disk with larger punctures interspersed with finer punctures along lateral thirds; elytron with single, complete epipleural stria, outer subhumeral stria present in apical third, inner subhumeral stria absent, dorsal striae 1–4 com-



**Figure 1.** **A–C** *Phelister haemorrhous* Marseul: **A** Dorsal habitus **B** Head showing frontal and supraorbital striae and mandibular teeth **C** Meso- and metaventrals showing complete, recurved postmesocoxal stria **D–E** *Phelister affinis* JE LeConte **D** Dorsal habitus **E** Anterior view of head and pronotum showing fragmented frontal stria and rudiments of sublateral pronotal stria.

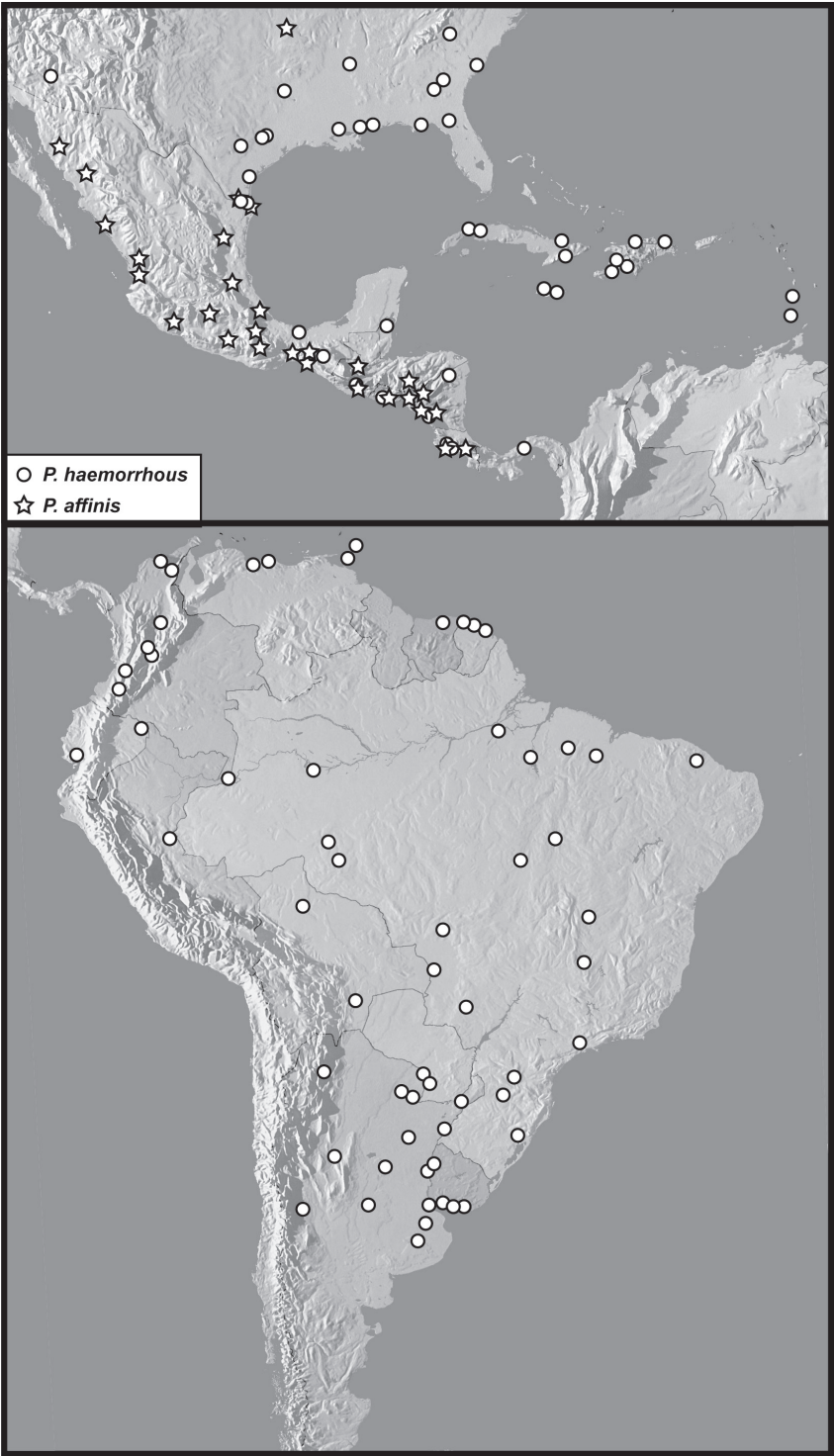
plete, stria 5 complete or abbreviated at base, and sutural stria obsolete in basal third, diverging from the suture anteriorly; propygidium with distinct secondary punctures separated by slightly greater than their widths, denser at sides; pygidium more finely punctate; prosternal keel with two complete striae, finely united by anterior arch, free, diverging posteriorly, finely punctulate between in both sexes; mesoventral marginal stria complete, weakly crenulate, continued at sides by postmesocoxal stria which recurves more or less evenly to anterolateral corner of metaventrals; mesometaventral stria complete, crenulate at middle, curving posteriorly to near inner corner of metacoxa; first abdominal ventrite with single, complete lateral stria; protibia with apex obliquely truncate, outer margin weakly rounded, bearing ca. six evenly spaced marginal spines; meso- and metatibiae weakly expanded to apex, mesotibia with ca. five marginal spines, more prominent toward apex, metatibia with distinct spines confined to apical fourth. Aedeagus with basal piece ca. one-fourth total length; tegmen widest just beyond middle, narrowed to apex, apices thin, with deep apical emargination; median lobe short, simple.

**Remarks.** As the type of the genus *Phelister*, *P. haemorrhous* is both typical in many respects, and somewhat unusual. Its distinctive posterior elytral and abdominal coloration is unmistakable, and this, in combination with dentate mandibles, a complete, recurved postmesocoxal stria, complete lateral pronotal stria, and presence of conspicuous lateral pronotal punctures, will easily distinguish it. There are cases where



**Figure 2.** Male genitalia of all *P. haemorrhous* group species, dorsal and lateral views: **A** *Phelister haemorrhous* Marseul **B** *Phelister affinis* JE LeConte **C** *Phelister parallelisternus* Schmidt **D** *Phelister mobilensis* Casey **E** *Phelister brevistriatus* Casey **F** *Phelister sonorae* sp. nov. **G** *Phelister warneri* sp. nov. **H** *Phelister puncticollis* Hinton **I** *Phelister subrotundus* (Say) **J** *Phelister rouzeti* (Fairmaire) **K** *Phelister rufinotus* Marseul **L** *Phelister thiemei* Schmidt **M** *Phelister bryanti* sp. nov. **N** *Phelister parecis* sp. nov. **O** *Phelister vernus* (Say) **P** *Phelister chilicola* **Q** *Phelister bruchi* Bickhardt.





**Map I.** Collecting records for *Phelister haemorrhous* (circles) and *P. affinis* (stars).



the reddish color is obscure, but the other characters in combination should still allow it to be recognized.

While the species' type locality is in Europe (Italy), it is clearly a Neotropical species. There is some uncertainty whether it was ever, in fact, collected in Europe. Vienna (1980) and Penati (2009) specifically dismiss its alleged (e.g., Mazur 1984, 1997) occurrence in Sardinia, and Penati (2009) furthermore makes a strong case that specimens reported from Sardinia as *P. haemorrhous*, in fact, represent a species of *Epierus* (Tribalinae). Earlier, Auzat (1925) suggested that no previous records of *Phelister* for Europe were *bona fide* (neither *P. haemorrhous* nor *P. rouzeti*). The label on the type of *P. haemorrhous* does include a question mark after 'Italie', and it seems most likely that Marseul received this in a mixed shipment and never, himself, believed the specimen to have originated in Italy.

This species was recently designated to be the type of *Phelister* following the suppression of an inadvertent designation of a *Baconia* species as *Phelister's* type (Caterino and Tishechkin 2013c; ICZN 2015).

**Biology.** This species is most commonly encountered in cattle dung. It has also been collected in pitfall traps using a few other types of bait, including human and pig dung. A few specimens have been taken in more general situations, in rotting vegetation (compost) and under the bark of rotten trees.

**Distribution.** *Phelister haemorrhous* is among the more widespread *Phelister* species, extending from Argentina into the southern United States, and possibly having been introduced into Europe (see caveats above). This wide distribution almost certainly owes to its common association with cattle dung, and it has probably expanded its range with cattle production in the New World. **Records:** **ARGENTINA:** Buenos Aires, Chaco, Córdoba, Corrientes, Entre Rios, Formosa, La Pampa, La Rioja, Mendoza, Misiones, Salta, San Juan; **BELIZE:** Orange Walk; **BOLIVIA:** Bení, Santa Cruz; **BRAZIL:** Amazonas, Ceará, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraná, Rio Grande do Sul, Rondônia, Santa Catarina, São Paulo, Tocantins; **COLOMBIA:** Amazonas, Antioquia, Cauca, Cundinamarca, Magdalena, Tolima, Valle de Cauca; **COSTA RICA:** Guanacaste, Puntarenas; **CUBA:** Habana, Sierra Bonilla; **DOMINICAN REPUBLIC:** Monte Cristi, Samaná; **ECUADOR:** Guayas, Napo; **EL SALVADOR:** San Salvador; **FRENCH GUIANA:** Cayenne, Sinnamary, St. Laurent du Maroni; **GRENADA;** **GUATEMALA:** Bobas; **HAITI:** Pic la Selle, Trouin; **JAMAICA:** Kingston; **MEXICO:** Chiapas, Veracruz; **NICARAGUA:** Granada, Region Norte Autónomo; **PANAMA:** Colón, Panamá; **PARAGUAY:** Alta Paraguay; **PERU:** Ucayali; **SAINT VINCENT & GRENADINES:** Saint Vincent; **SURINAME:** Pará, Saramacca; **TRINIDAD & TOBAGO:** St. George, Trinidad; **URUGUAY:** Canelones, Colonia, Montevideo, Salto, San José; **VENEZUELA:** Aragua, Capital, Sucre; **USA:** **Alabama:** Mobile; **Arizona:** Maricopa; **Florida:** Alachua, Franklin; **Georgia:** Tifton, Wheeler; **Louisiana:** East Baton Rouge, Iberville; **Mississippi:** Harrison, Jackson, Oktibbeha; **South Carolina:** Beaufort, Spartanburg; **Texas:** Brazos, Burleson, Cameron, Gillespie, Hidalgo, Nueces, Wood.

***Phelister affinis* JE LeConte, 1859**

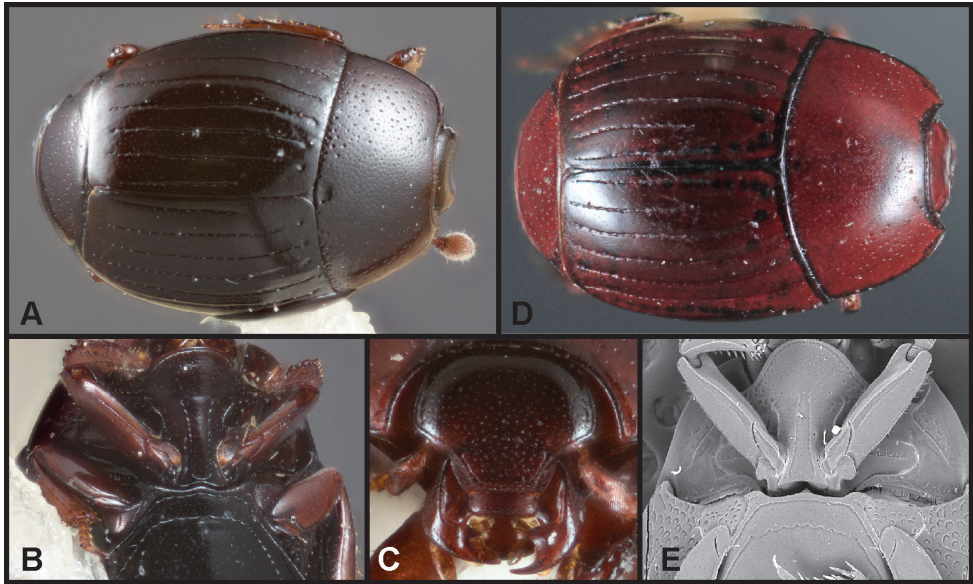
Figs 1, 3; Map 1

*Phelister affinis* JE LeConte, 1859: 311.*Phelister simplex* Casey, 1916: 230; Mazur 1997.*Phelister solator* Marseul, 1861: 164; Marseul 1870.

**Type material.** Neotype male, hereby designated: “Tejeria, Veracruz, MEX, VII:4:41” / “Col. by H. Dybas” / “Collection R. L. Wenzel” / “*Phelister* #68 det R. Wenzel” / “Compared with type *Phelister affinis* LeC. RLW’51; see type notes under *solator*”; dissected by Rupert Wenzel (FMNH). The type(s) of this species aren’t known, despite searches in the most likely repository (MCZC) and others (FMNH, CMNH, USNM), and despite the apparent fact that Wenzel studied a supposed type in 1951 (labels on specimen). Due to the extreme similarity among members of *Phelister*, we feel that a Neotype designation is necessary to anchor a specific concept for this species.

Types of synonyms. **Lectotype** of *Phelister solator* Marseul, of undetermined sex, hereby designated: “*Phelister solator*, Mexic. Sallé 20” / “Coll. Desbordes” / “TYPE”, MNHN. **Lectotype** of *Phelister simplex* Casey, of undetermined sex, hereby designated: “Lee Co Tex” / “Casey bequest 1925” / “TYPE USNM 38453” / “*simplex* Csy”, USNM.

**Diagnostic description.** Length: 1.73–2.01 mm (avg. 1.94 mm); width: 1.50–1.73 mm (avg. 1.65 mm). Body elongate-oval, widest behind humeri, humeri slightly wider than base of pronotum; body more or less uniformly piceous; entire dorsum finely punctulate, the pronotum more densely so than the elytra; frons finely punctulate, impressed along midline, supraorbital stria complete, frontal stria interrupted at sides and at middle, slightly sinuate laterally; labrum wide, distinctly emarginate apically; both mandibles with strong tooth on inner edges; pronotum usually with distinct fragments of submarginal stria in anterior corners; pronotal disk with larger punctures interspersed with finer punctures along lateral thirds; elytron with single, complete epipleural stria, outer subhumeral stria present in apical third, inner subhumeral stria absent, dorsal striae 1–4 complete, stria 5 present in apical half-two-thirds, very rarely complete, but nearly always with a basal puncture, and sutural stria obsolete in basal third, diverging from the suture anteriorly; propygidium with distinct secondary punctures separated by slightly greater than their widths; pygidium more finely punctate; prosternal keel with two complete striae, finely united by anterior arch, free, diverging posteriorly, finely punctulate between in both sexes; mesoventral marginal stria complete, smooth, continued at sides by postmesocoxal stria which runs posteriad two-thirds of the distance to metepipleuron; mesometaventral stria complete, weakly crenulate to smooth, angulate mediad mesocoxa, extending posteriad to near inner corner of metacoxa; first abdominal ventrite with single, complete lateral stria; protibia with apex obliquely truncate, outer margin weakly rounded, bearing ca. six evenly spaced marginal spines; meso- and metatibiae weakly expanded to apex, mesotibiae



**Figure 3.** **A–C** *Phelister parallelisternus* Schmidt: **A** Dorsal habitus **B** Ventral view showing prosternal and meso- and metaventral striae **C–E** *Phelister mobilensis* Casey: **C** Frontal view showing complete epistomal stria **D** Dorsal habitus **E** Ventral view (SEM) showing prosternal and meso- and metaventral striae.

with ca. five marginal spines, more prominent toward apex, metatibia with distinct spines confined to apical fourth. Aedeagus with basal piece a little over one-fourth total length; tegmen widest just beyond middle, abruptly narrowed to thin, divided apices; median lobe more than half tegmen length, proximal apodemes thin near base, thickened toward gonopore.

**Remarks.** This species was previously synonymized with *Phelister contractus* Casey by Mazur (1997), in error. Having studied its type, we instead synonymize *P. contractus* with *P. subrotundus* Say (below).

**Biology.** Label data indicate rather generalist habitat preferences, having been collected in cow, horse, and gopher tortoise dung, under decayed leaves, in rotting breadfruit, in fire-scorched *Yucca* L., and in rotten *Opuntia* Miller, and the species even exhibits some facultative myrmecophily, with records from nests of both *Acromyrmex* Mayr and *Azteca* Forel ants.

**Distribution.** This species occurs from Central America through Mexico, just into the south-central United States. **Records:** **COSTA RICA:** Guanacaste, Puntarenas, San José; **EL SALVADOR:** La Libertad, San Salvador; **GUATEMALA:** Baja Verapaz, Escuintla, Santa Rosa; **HONDURAS:** Choluteca, Francisco Morazán; **MEXICO:** Chiapas, Colima, Hidalgo, Michoacán, Morelos, Nayarit, Oaxaca, Sinaloa, Sonora, Tamaulipas, Veracruz; **NICARAGUA:** Granada, León, Madriz, Managua, Zelaya; **USA: Oklahoma:** Latimer; **Texas:** Cameron, Hidalgo.

***Phelister parallelisternus* Schmidt, 1893**

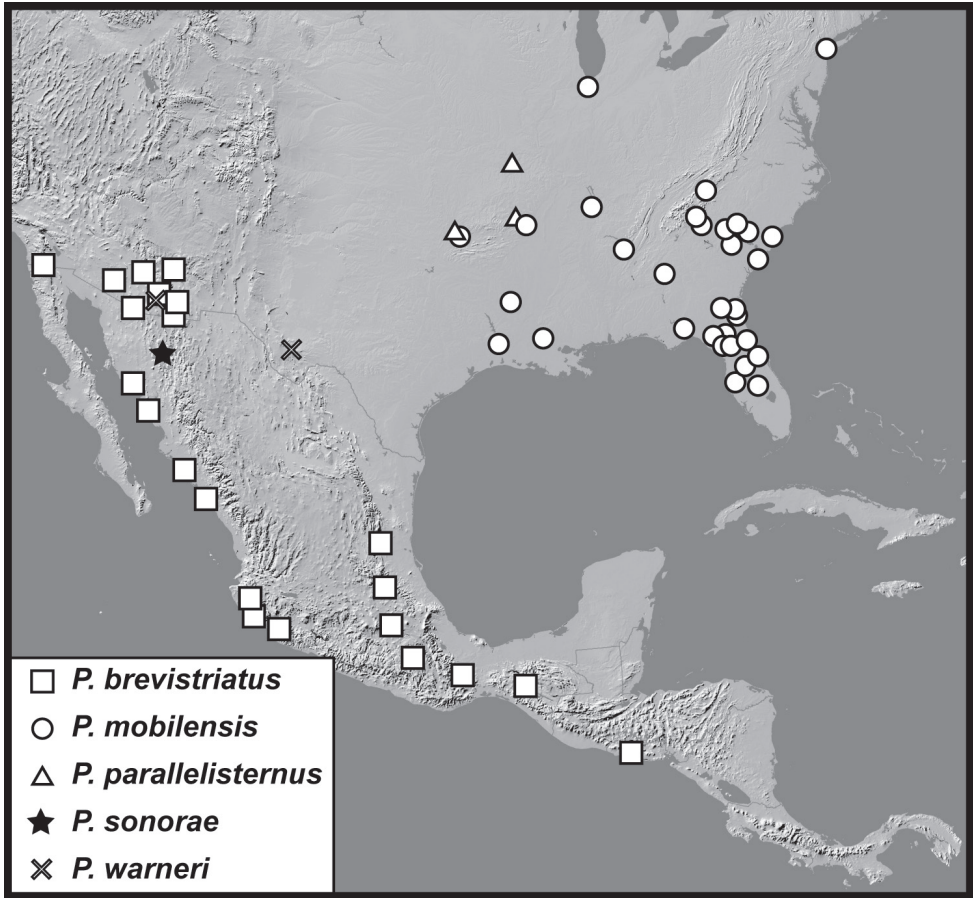
Figs 2, 3; Map 2

*Phelister parallelisternus* Schmidt, 1893b: 86.

**Type material.** **Lectotype** of undetermined sex, hereby designated: “Mexico” / “parallelisternus Sch.” / “parallelisternum [sic]” / “Type” / “coll. J.Schmidt” / “LECTOTYPE *Phelister parallelisternus* Schmidt 1893, M.S. Caterino & A.K. Tishechkin des. 2010” (ZHMB); one paralectotype of undetermined sex is also designated at ZMHB: “Mexico”, and one at MNHN: “Mexique, col. Bickhardt”.

**Diagnostic description.** Length: 1.65–1.93 mm (avg. 1.78 mm); width: 1.22–1.58 mm (avg. 1.46 mm). Body elongate-oval, widest at humeri, humeri slightly wider than base of pronotum; body uniformly dark rufescent to piceous; frons finely but distinctly punctulate, somewhat depressed along midline; supraorbital stria complete, frontal stria interrupted across middle; labrum wide, distinctly emarginate apically; both mandibles with strong tooth on inner edges; pronotum with coarse ground punctation throughout, with larger punctures becoming more densely intermingled toward sides; prescutellar impression distinct; lateral and anterior marginal pronotal striae continuous, complete, slightly crenulate at front; submarginal pronotal striae absent; elytron with single, complete, crenulate epipleural stria, outer subhumeral stria present in apical one-third to one-half, inner subhumeral stria absent, dorsal striae 1–5 complete (5<sup>th</sup> rarely abbreviated from base); sutural stria present in posterior three-fourths; ground punctation of pygidium and propygidium similarly fine, propygidium with secondary punctures small, sparse, mostly separated by two to three times their widths; prosternal lobe with truncate to weakly emarginate anterior margin, with fine marginal stria; prosternal keel with two complete striae parallel and distinctly united by basal arch, variably connected anteriorly, with faint, secondary basal striae nearer procoxa, finely punctulate between in both sexes; mesoventrite distinctly projecting, marginal stria complete, crenulate, continued at sides by postmesocoxal stria which runs posteriad nearly to metepipleuron; mesometaventral stria complete, weakly crenulate, arched weakly onto basal one-fourth of mesoventrite, extended posteriad by lateral metaventral stria to near inner corner of metacoxa; metaventral disk with few secondary punctures anteromedial metacoxae; first abdominal ventrite with complete inner lateral stria, outer lateral stria nearly complete, often fragmented at base; protibia with apex obliquely truncate, outer margin weakly rounded, bearing 5–6 marginal spines; meso- and metatibiae weakly expanded to apex, mesotibia with ca. five marginal spines, more prominent toward apex, metatibia with distinct spines confined to apical fourth. Aedeagus with distinct ventral process, just basad middle, basal piece short, less than one-fourth total length; tegmen with sides rounded, widest just beyond middle, apices narrowly separated, apical emargination narrow and shallow; median lobe approximately one-half tegmen length, proximal apodemes thin near base, thickened toward gonopore.





**Map 2.** Collecting records for *Phelister brevistriatus* (squares), *P. mobilensis* (circles), *P. parallelisternus* (triangles), *P. sonora* (star), and *P. warneri* (diagonal cross).

**Remarks.** This species is quite similar to *P. affinis*, but can be consistently distinguished by its parallel and rather narrowly separated prosternal striae, and its complete 5<sup>th</sup> dorsal stria. Its frontal stria is interrupted at the middle, but not at the sides, and it never appears to show any indication of a sublateral pronotal stria.

**Biology.** The only indications of habits for this species come from a few Oklahoma specimens sifted from ‘bay’ litter. A couple of specimens were also collected using flight interception traps.

**Distribution.** The known distribution of this species is oddly disjunct. The types and other early specimens (NHMUK) bear no more specific locality than Mexico. Yet all recent specimens we have seen are from the south-central United States, specifically Oklahoma, Arkansas, and Missouri. It is most surprising that no specimens have been seen from Texas. **Records: USA: Arkansas:** Faulkner; **Missouri:** Pike; **Oklahoma:** Latimer.

***Phelister mobilensis* Casey, 1916**

Figs 2, 3; Map 2

*Phelister mobilensis* Casey, 1916: 232.

**Type material.** **Lectotype**, hereby designated: “Ala. Mobile” / “Casey bequest 1925” / “Type USNM 38450” / “*mobilensis* Csy.” / “Lectotype *Phelister mobilensis* Casey, M.S.Caterino and A.K.Tishechkin des. 2010”, USNM. Four paralectotypes: two with same data as type, two from “Pensacola, Fla.”, all USNM.

**Description.** Length: 1.85–2.05 mm (avg. 1.93 mm); width: 1.58–1.73 mm (avg. 1.59 mm). Body uniformly dark rufescent to piceous, elongate oval, widest just behind midline; frons finely but distinctly punctulate; supraorbital stria complete, fine across vertex; frontal stria well impressed along inner margin of eyes, fragmentary to obsolete along upper epistomal margin, but continued anteriad along lateral and, generally, apical margins of epistoma; labrum transverse, at most weakly emarginate apically; mandibles both with strong tooth along incisor margin; pronotum strongly narrowed anteriorly, very finely punctate at middle but rather coarsely so in lateral thirds; prescutellar impression distinct; lateral and anterior marginal striae continuous, the anterior diverging slightly from the margin and crenulate; lateral submarginal striae absent; elytra with single, complete epipleural striae; outer subhumeral stria present in apical half only; inner subhumeral stria absent; dorsal elytral striae 1–4 complete, 5<sup>th</sup> present in apical half only, sutural stria just slightly longer than 5<sup>th</sup>; propygidium almost uniformly coarsely punctate, punctures separated by less than their widths; pygidium much more finely and sparsely punctate; prosternal lobe shape evenly rounded, with marginal stria obsolete toward sides; prosternal keel narrowed from base to apex; keel striae separate basally, converging between coxae, narrowly separated, parallel anteriad; anterior mesoventral margin weakly produced; marginal mesoventral stria complete, weakly crenulate; mesometaventral stria arching weakly onto basal third of mesoventrite; metaventral disk weakly punctate, with lateral stria nearly complete to inner corner of metacoxa; postmesocoxal stria extending posterolaterad, mostly straight, ending short of apex of metepisternum; abdominal ventrite 1 with one complete and one fragmentary lateral striae, impunctate at middle, increasingly punctate to sides; protibia with apex truncate, outer margin weakly rounded, bearing ca. five prominent, evenly spaced marginal spines; meso- and metatibiae weakly expanded to apex, mesotibia with ca. five marginal spines, more prominent toward apex, metatibia with distinct spines along most of margin; aedeagus gradually widened toward apex, apically rounded with short, narrow apical emargination; median lobe with simple basal apodemes, ca. half tegmen length.

**Remarks.** *Phelister mobilensis* exhibits one highly distinct character, a stria on the epistoma lining its anterior and lateral margins, which is continuous with the lateral portion of the otherwise interrupted frontal stria. Other unusual characters include particularly spinose front and middle tibiae, and a meso-metaventral stria which is distinctly more crenulate than the marginal mesoventral stria.



**Biology.** Label data indicate quite generalized habitat preferences, with records from dung (dog and chicken), decaying vegetation, *Geomys* Rafinesque burrows, and fungi. Specimens have also been collected using flight interception traps and Lindgren funnel traps.

**Distribution.** This species is found primarily near the Gulf and Atlantic coasts of the southeastern United States. Records from Indiana and New York could use additional confirmation. **Records:** **USA:** **Alabama:** Russell, Shelby; **Arkansas:** Pulas-ki; **Florida:** Alachua, Duval, Gilchrist, Highlands, Hillsborough, Lake, Leon, Levy, Marion, Nassau, Orange, Polk, Putnam; **Georgia:** Burke, Charlton; **Indiana:** Lake; **Louisiana:** Calcasieu; East Baton Rouge, Natchitoches; **New York:** [state record only - AMNH]; **North Carolina:** Transylvania; **Oklahoma:** Latimer; **South Carolina:** Aiken, Anderson, Bamberg, Barnwell, Beaufort, Georgetown, Oconee, Richland; **Tennessee:** Benton.

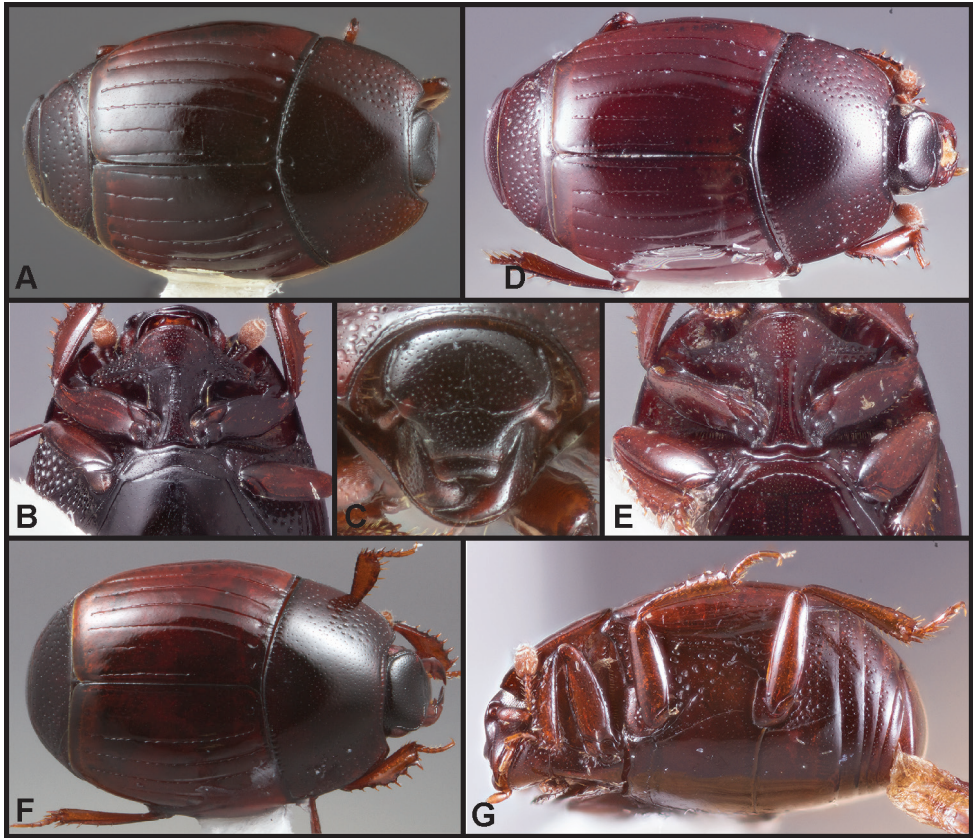
*Phelister brevistriatus* Casey, 1916

Figs 2, 4; Map 2

*Phelister brevistriatus* Casey, 1916: 233.

**Type material.** **Holotype** of undetermined sex: “Tucson, Arizona, Wickham” / “Casey bequest 1925” / “TYPE USNM 38452” / “*brevistriatus* Csy.”, examined in 2011 (USNM).

**Description.** Length: 1.81–2.29 mm (avg. 2.03 mm); width: 1.50–1.89 mm (avg. 1.69 mm). Body uniformly dark rufescent to piceous, elongate oval, widest just behind midline; frons finely but distinctly punctulate; supraorbital stria complete, fine across vertex; frontal stria well impressed along inner margin of eyes, continuing mediad above epistoma, but variably interrupted, often in a dense, linear field of punctures along frontal midline, ends generally curved upward, rarely complete and simple; labrum transverse, at most weakly emarginate apically; mandibles both with strong tooth along incisor margin; pronotum with sides subparallel at bases, weakly curved inward to front, disk very finely punctate at middle but rather coarsely so in lateral thirds; prescutellar impression weak, generally present; lateral and anterior marginal striae continuous, the anterior diverging slightly from the margin and crenulate; lateral submarginal striae absent; elytra with single, complete epipleural striae; outer subhumeral stria present in apical half only; inner subhumeral stria absent; dorsal elytral striae 1–4 complete, 5<sup>th</sup> present in apical half and represented by a basal puncture, sutural stria slightly longer than fifth; propygidium almost uniformly coarsely punctate, punctures separated by less than their widths; pygidium much more finely and sparsely punctate; prosternal lobe shape evenly rounded, with more or less complete marginal stria; prosternal keel striae separate basally, converging between coxae, thence diverging weakly, usually connected by anterior arch, males with striae more widely separated, and punctures between striae slightly denser and more conspicuous; anterior mesoventral margin weakly produced; marginal mesoventral stria



**Figure 4.** **A–C** *Phelister brevistriatus* Casey: **A** Dorsal habitus **B** Ventral view showing prosternal and meso- and metaventral striae **C** Frontal view showing median portion of frontal stria **D–E** *Phelister sonora* sp. nov.: **D** Dorsal habitus **E** Ventral view showing prosternal and meso- and metaventral striae **F–G** *Phelister warneri* sp. nov. **F** Dorsal habitus **G** Lateral view showing fine meso- and metaventral striae and slender tibiae with reduced lateral spines.

complete, smooth; mesometaventral stria more distinctly crenulate, arching anteriorly to middle of mesoventrite; metaventral disk impunctate, lateral stria nearly complete to inner corner of metacoxa; postmesocoxal stria extending posterolaterad, wavering, becoming fragmented posteriad, ending well short of metepisternum; abdominal ventrite 1 with complete inner and fragmentary outer lateral striae, disk impunctate at middle, increasingly punctate to sides; protibia with apex obliquely truncate, outer margin weakly rounded, bearing 6–7 prominent, marginal spines; meso- and metatibiae weakly expanded to apex, mesotibiae with ca. six marginal spines, more prominent toward apex, metatibia with distinct spines along apical third of margin; aedeagus with distinct ventral process near middle, tegmen in dorsal view gradually widened toward apex, apically abruptly narrowed, with short, rather wide apical emargination; median lobe with long, basal apodemes distinctly thicker toward gonopore, nearly as long as tegmen.

**Remarks.** Of the *Phelister* species occurring in the southwestern United States and northwestern Mexico, this species can generally be recognized by its frontal stria, which, while usually complete, tends to connect to a series of median longitudinal frontal punctures. These are not always present, however. It seems to be closely related to the two following species, both of which have distinctive characters of their own. *Phelister sonora* has modified protarsal claws (perhaps in the male only), while *Phelister warneri* has more finely impressed dorsal striae, and more finely spinose middle and hind tibiae.

**Biology.** Label data reveal varied habits for this species. Many specimens were collected in cow dung. A few specimens were taken directly from kangaroo rat (*Dipodomys* Gray) burrows, and many others were collected using black pitfall traps in the vicinity of *Dipodomys* burrows, so facultative mammal inquilinism appears likely. Several specimens were also taken from the debris piles of leafcutter ants (*Atta mexicana* (Smith) and *Atta* sp.)

**Distribution.** This species ranges from the southwestern United States through Mexico into northern Central America. **Records:** **EL SALVADOR:** San Salvador, **MEXICO:** Chiapas, Colima, Hidalgo, Jalisco, Oaxaca, Puebla, San Luis Potosí, Sinaloa, Sonora; **USA:** **Arizona:** Cochise, Gila, Maricopa, Pima, Pinal, Santa Cruz; **California:** Imperial, Riverside; **New Mexico:** Hidalgo.

*Phelister sonora* sp. nov.

<http://zoobank.org/53CAD355-2FEF-48FE-84B4-1573E869F0BA>

Figs 2, 4; Map 2

**Type material.** **Holotype male:** “MEX., Sonora Don [sp?], 14 Aug, 1957, David Lauck, small mud pond”/”*Phelister affinis* det S. Mazur”/”Caterino/Tishechkin Exos-ternini voucher EXO-03591”; deposited in USNM.

**Diagnostic description.** Length: 1.97 mm; width: 1.58 mm. This species is externally very difficult to distinguish from *P. brevistriatus*, especially given the variability and wide geographic distribution of that species (within which *P. sonora* occurs). With only a single specimen of this species, we can confidently cite only: male protarsal claws strongly bent at base, straight in apical three-fourths; frons narrower, with frontal stria less strongly impressed, weakly interrupted in denser frontal punctation; ground punctation of pronotal disk coarser and deeper; 5<sup>th</sup> dorsal elytral stria nearly complete, continued between stria and basal puncture by a weak crease; male prosternal keel striae not as widely separated, and surface between striae not very conspicuously punctate; aedeagus lacking distinct ventral process, tegmen narrow, only slightly widened at middle, apices acute, separated, apical emargination incised to middle of tegmen; median lobe with short, basal apodemes distinctly thicker toward gonopore, only ca. one-third as long as tegmen.

**Remarks.** As mentioned in the description, externally this species mostly falls within the range of variation for most characters of *P. brevistriatus*. Aside from the very distinctive aedeagus, and unusual, probably sex-limited, bent protarsal claw, the only distinguishing feature is the longer 5<sup>th</sup> dorsal elytral stria. More material of this species

will be necessary to confirm these differences, and hopefully to support the consistency of some other minor characters.

**Etymology.** We name the species for the state and region of its origin.

**Biology.** Nothing is known of the biology of this species.

**Distribution.** This species is only known from Sonora, Mexico.

***Phelister warneri* sp. nov.**

<http://zoobank.org/3A7CF0EF-94DC-4ADE-ADDF-8A3B6B839743>

Figs 2, 4; Map 2

**Type material. Holotype male:** “USA: AZ: Cochise Co., Birch Rd., 4.1 mi. E of Hwy 191, 31°58'43"N, 109°46'4"W; vii.17-29.2011; black cup pitfalls; W.B.Warner” / “Caterino/Tishechkin Exosternini Voucher EXO-03588”; deposited in ASUC; Paratypes (11): 4: same data as type; 2: same locality but vii.29-viii.14.2011; 3: same locality but vii.30-ix.5.2012; 1: same locality but vii.14-28.2011; 1: AZ: Cochise Co. Hwy 186 at Blue Sky Rd.; 32°12'52"N, 109°46'54"W, vii.17-29.2011, ex black cup barrier pitfall; W.B. Warner; 1: AZ: Cochise Co., 1.5 mi S. jct. Hwys 191 and 181; 31°51'44"N, 109°41'59"W; vii.14-28.2011; black cup barrier pitfall; W.B. Warner. Deposited in MSCC, AKTC, FMNH, and WBWC. Additional material: TX: Brewster Co., Marathon Iron Mt. Ranch, v.12.1976, R. Gordon, in burrow of *Cynomys ludovicianus* (USNM).

**Diagnostic description** Length: 1.73–2.09 mm (avg. 1.88 mm); width: 1.46–1.69 mm (avg. 1.57 mm). This species is externally very difficult to distinguish from *P. brevistriatus*, as well as *P. sonoreae*. The following characters should be sufficient to distinguish *P. warneri*: body distinctly rufescent, with the elytra (except for a linear area right along the suture) vaguely lighter/brighter red than most of the rest of the body, the lateral regions of the pronotum sometimes appearing similarly lighter; frontal stria often interrupted at sides as well as medially, rarely obsolete across the front; frontal disk usually with enlarged median punctures, but not organized into a linear cluster as they are in *P. brevistriatus*; ground punctation of pronotum more distinct, grading more gradually into denser lateral pronotal punctures; male protarsal claws ‘normal’, curved, not bent at base (distinct from *P. sonoreae*); elytral striae shallowly and rather finely impressed, 5<sup>th</sup> dorsal elytral stria confined to posterior third of elytron, typically fragmented, rarely entirely obsolete; meso- and metatibiae narrower, slightly more elongate, with marginal spines fewer in number and size; 1<sup>st</sup> abdominal ventrite with little or no vestige of outer lateral stria; aedeagus with short basal piece ca. one-fifth total aedeagus length; tegmen rather narrow, dorsoventrally flattened, with small ventral process, tegmen sides subparallel, undulating, apices slightly convergent but separate, apical emargination broad and deep, ca. one-third tegmen length; median lobe ca. one-third tegmen length, with simple proximal apodemes.

**Etymology.** In naming this species for Mr. Bill Warner, we are pleased to recognize his many contributions to our knowledge of histerid biology, taxonomy, and distribution. His efforts led to the discovery of this species, and many others.

**Biology.** The type series of this species was collected in the same place, and even in the same black cup pitfall traps, as numerous specimens of *P. brevistriatus*. Black cup pitfalls evidently often attract mammal nest inquilines (the cup imitates a burrow entrance; WB Warner, pers. comm.), and we suggest that *P. warneri* is a specialized inquiline. The single specimen from Texas was collected in a burrow of black-tailed prairie dog (*Cynomys ludovicianus*), supporting this assertion. This potential host does extend into southeastern Arizona.

**Distribution.** This species is mainly known from a single locality in southeastern Arizona. An additional male (which we have dissected) from Brewster Co., Texas, however, conforms in all respects to the diagnosis above. So, the species must be more widespread.

### *Phelister puncticollis* Hinton, 1935

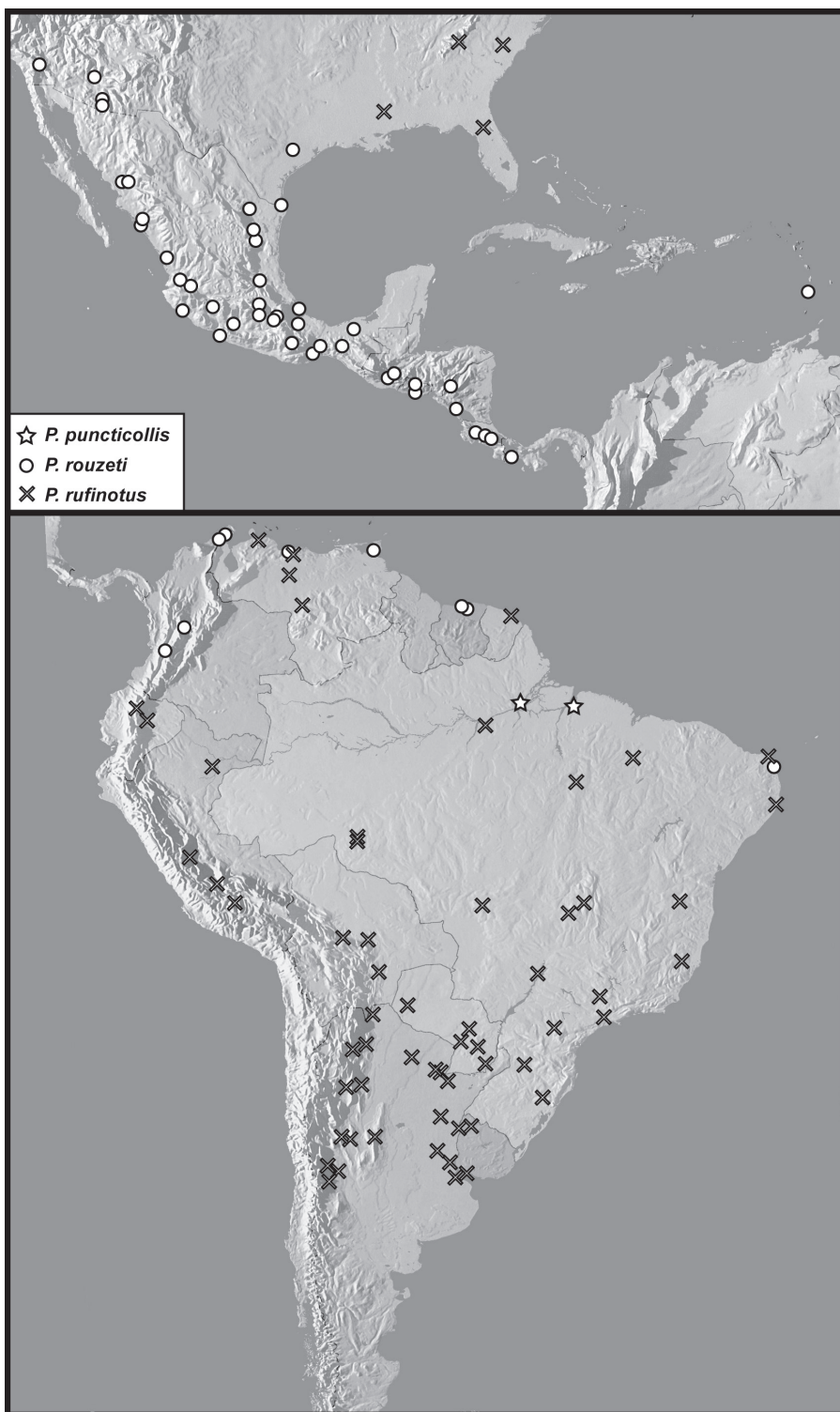
Figs 2, 5; Map 3

*Phelister puncticollis* Hinton, 1935c: 64.

**Type material.** **Holotype** of undetermined sex: “H.H. Smith, S. Amer” / “Monte Alegre” [Pará] / “*Phelister puncticollis* Type Hntn.” / “G. Lewis Coll. B.M.1926-369”, NHMUK.

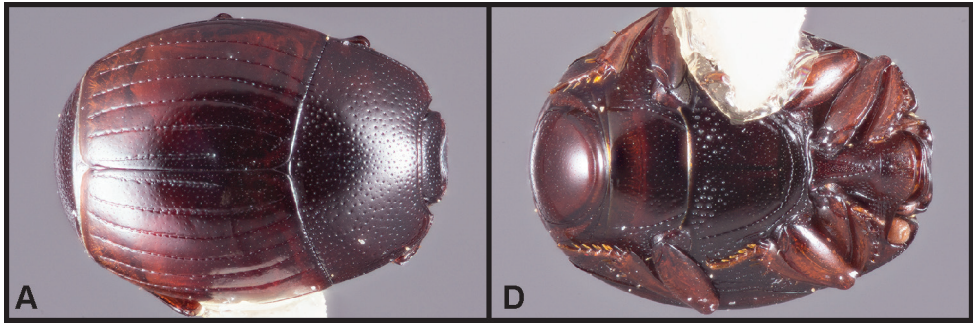
**Diagnostic description.** Length: 1.54–1.65 mm (avg. 1.59 mm); width: 1.30–1.38 mm (avg. 1.29 mm). Body elongate oval, dark rufescent, with elytra lighter toward their apices; frons depressed along midline, disk strongly punctate; frontal striae obsolete between antennal insertions; labrum short, weakly emarginate; both mandibles with distinct median tooth, that of right mandible small; entire pronotal disk almost uniformly punctate, only slightly less dense at middle; prescutellar impression distinct, though somewhat obscured by discal and posterior marginal punctures; marginal pronotal stria complete along lateral and anterior margins, crenulate anteriorly; lateral submarginal stria complete at sides, curving mediad at front, ending freely behind eye; elytra with complete outer subhumeral stria, inner subhumeral stria absent; dorsal elytral striae 1–5 complete, sutural stria obsolete in basal one-third, all striae distinctly crenulate; propygidium almost uniformly punctate, with small round punctures separated by approximately their diameters; pygidial punctures smaller and sparser, fading to indistinct at apex; prosternal lobe short, with fine, complete marginal stria; prosternal keel with striae united anteriorly to form a triangle, the male’s more densely punctate within; mesoventrite weakly projecting at middle; marginal mesoventral stria complete, evenly arched anteriad between inner corners of mesocoxae; mesometaventral stria arched strongly forward to mesoventral midpoint, extended by inner mesoventral stria to metacoxa; metaventral disk with distinct ground punctation and coarser punctures along most of posterior third; 1<sup>st</sup> abdominal ventrite with complete inner lateral stria and fragments of outer lateral stria; protibia with lateral margin strongly rounded, with 6–7 marginal spines, apex obliquely truncate, with two small apical spurs; protarsal claws somewhat unevenly curved, slightly bent at base; meso- and metatibiae evenly widened to apices, with few weak marginal spines confined to apical halves; basal piece of aedeagus ca. one-fourth total aedeagus





**Map 3.** Collecting records for *Phelister puncticollis* (stars), *P. rouzeti* (circles), and *P. rufinotus* (diagonal crosses).





**Figure 5.** A-B *Phelister puncticollis* Hinton: **A** Dorsal habitus **B** Ventral view.

length; tegmen narrow at base, widened toward narrowly rounded apex, apical emargination narrow, incised ca. one-fourth of tegmen length, ventral process absent; median lobe with long proximal apodemes, evenly differentiated into thicker and thinner portions.

**Remarks.** This species is similar to *P. bryanti* described below, but differs in the presence of a submarginal pronotal stria, abbreviated, united male prosternal striae, and the presence of punctures on the metaventricle in front of the metacoxae. The aedeagus of *P. puncticollis* is narrow and evenly rounded to the apex, whereas that of *P. bryanti* is abruptly narrowed.

**Biology.** Nothing is known of the biology of this species.

**Distribution.** We have only seen specimens from Pará state, Brazil, including the types, and only three additional specimens, from Belém and Benevides. One specimen was collected in the nest of the fire ant *Solenopsis saevissima* (Smith).

### ***Phelister subrotundus* (Say, 1825)**

Figs 2, 6; Map 4

*Hister subrotundus* Say, 1825: 39.

*Phelister subrotundus*: Marseul 1853: 487.

*Phelister rubricatus* Lewis, 1908: 158; Mazur 1997: 29.

*Phelister subrotundus* var. *sayi* Carnochan, 1915: 213; Mazur 1997: 29.

*Phelister subrotundus* var. *frosti* Carnochan, 1915: 213; Mazur 1997: 29.

*Phelister carnochani* Casey, 1916: 291; Mazur 1984: 285.

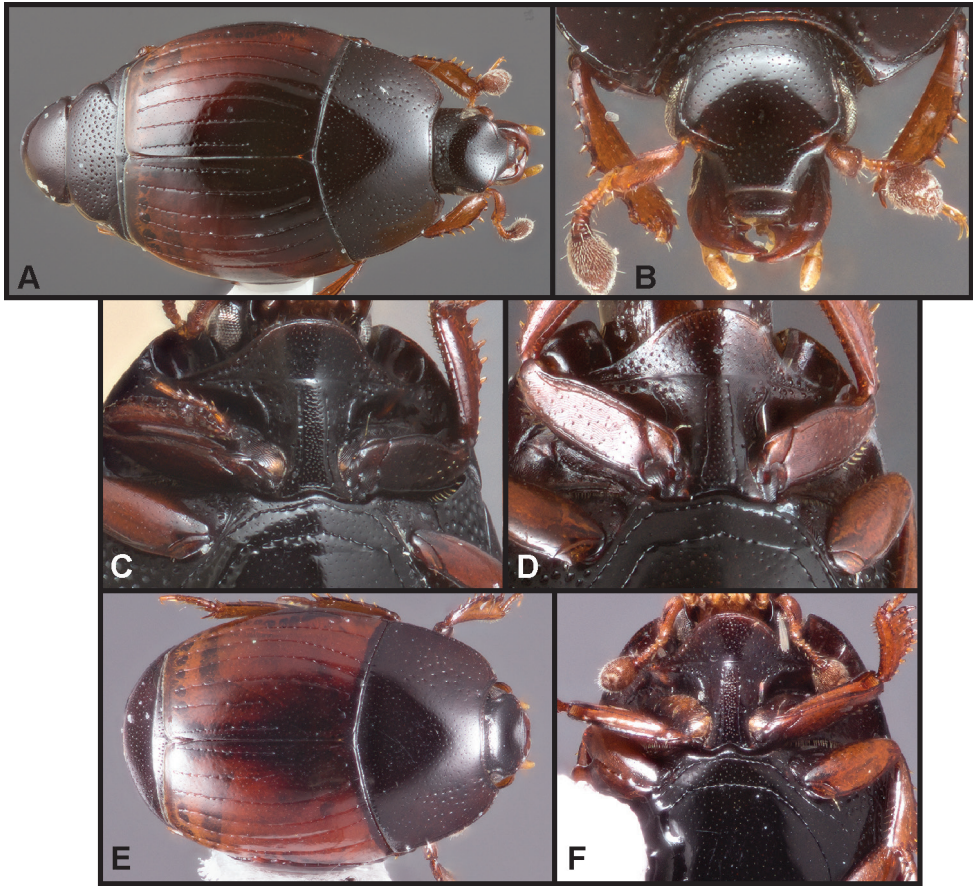
*Phelister contractus* Casey, 1916: 230, syn nov. (previously synonymized with *P. affinis* by Mazur (1997), in error).

*Phelister subrotundatus*: Mazur 1984: 286 (misspelling).

**Type material.** **Neotype** of *Hister subrotundus* Say, hereby designated: [pale pinkish round disk] / “892” / “NEOTYPE *Hister subrotundus* Say Desg. Caterino & Tishechkin, 2011”, MCZC. This common, widespread, and somewhat variable Nearctic species needs to be represented by a physical type so as to establish the identity of *P. subrotundus*, in the event that later work reveals it to represent multiple species.

Types of synonyms. **Lectotype** of *Phelister rubricatus* Lewis hereby designated: “Type” [red bordered disk] / “Dane Co., Wis. IX.30.99” / “G.Lewis Coll. B.M.1926-369” / “Phelister rubricatus Lewis Type” / “LECTOTYPE Phelister rubricatus Lewis M.S. Caterino and A.K. Tishechkin des. 2010”, NHMUK; Paralectotype: “Eddyville, IA” (interpreted by G. Lewis [1908] as Eddyville, Ja. [sic]) / “G.Lewis Coll. B.M.1926-369” / “Phelister rubricatus Lew. Cotype” / “PARALECTOTYPE Phelister rubricatus Lewis M.S. Caterino and A.K. Tishechkin des. 2010”, NHMUK. **Holotypes** of Carnochan’s ‘varieties’, *P. subrotundus* var. *sayi* and *P. subrotundus* var. *frosti*, are in MCZ (#26012 and 26013, respectively.) **Lectotype** of *Phelister carnochani* Casey hereby designated: “Alab 2289” / “Casey bequest 1925” / “TYPE USNM 38448” / “carnochani Csy. sayi Csy nec Carn.” / “LECTOTYPE Phelister carnochani Casey M.S. Caterino and A.K. Tishechkin des. 2019, USNM. **Holotype** of *Phelister contractus* Casey: “Lee Co Tex” / “Casey bequest 1925” / “TYPE USNM 38447” / “contractus Csy.”, USNM. This species was previously synonymized, in error, with *Phelister affinis* by Mazur (1997). Wenzel (unpub. notes) agrees with our assessment.

**Diagnostic description.** Length: 1.54–1.85 mm (avg. 1.69 mm); width: 1.30–1.62 mm (avg. 1.52 mm). Body elongate-oval, widest behind humeri, mostly piceous, posterolateral corners of elytra and legs generally reddish; entire dorsum finely punctulate, the pronotum more densely so than the elytra; frons finely punctulate, impressed along midline, supraorbital stria complete, frontal stria interrupted at middle, slightly sinuate at sides; labrum wide, weakly emarginate apically; both mandibles with strong tooth on inner edges; pronotum with more or less complete lateral submarginal stria incurved and crenulate anteriorly, ending freely, and diverging slightly from pronotal margin posteriorly, where it is weakly abbreviated; pronotal disk with larger punctures interspersed with finer punctures along lateral thirds; elytron with single, complete epipleural stria, outer subhumeral stria present in apical third, inner subhumeral stria absent, dorsal striae 1–5 complete, sutural stria obsolete in basal third; propygidium with distinct secondary punctures decreasing in density posteriad; pygidium more finely punctate; prosternal keel with two complete striae, weakly convergent and free anteriorly, usually united along basal margin of keel; male prosternal keel with coarser and denser punctures, the striae often more widely separated and more nearly parallel; mesoventral marginal stria complete, weakly crenulate, close to anterior mesoventral margin, often with corresponding median ‘point’, continued at sides by postmesocoxal stria which ends freely midway between the meso- and metacoxae; mesometaventral stria complete, crenulate at middle, arched anteriad distinctly onto mesoventrite (with weakly parallel median ‘point’ to mesoventral stria), curving posteriad to near inner corner of metacoxa; first abdominal ventrite with complete inner lateral stria and abbreviated outer lateral stria; protibia with apex obliquely truncate, outer margin weakly rounded, bearing ca. six evenly spaced marginal spines; meso- and metatibiae weakly expanded to apex, mesotibia with ca. five marginal spines, more prominent toward apex, metatibia with distinct spines confined to apical fourth. Aedeagus with basal piece ca. one-fourth total length; tegmen widened toward apex, apex evenly rounded, with shallow apical emargination; median lobe ca. two-thirds tegmen length, with differentiated basal and distal proximal apodemes.



**Figure 6.** **A–D** *Phelister subrotundus* (Say): **A** Dorsal habitus **B** Frontal view showing frontal striae **C** Prosternum and mesoventrite of male **D** Prosternum and mesoventrite of female **E–F** *Phelister rouzeti* (Fairmaire) **E** Dorsal habitus **F** Ventral view of prosternum of male and meso- and metaventrites showing striae.

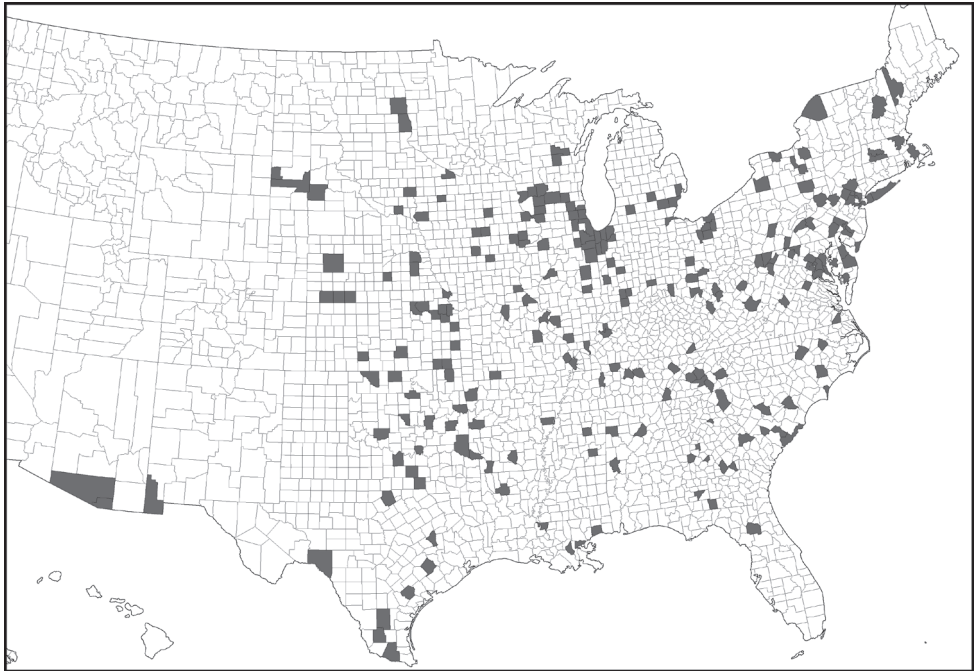
**Remarks.** Among species occurring in the United States, *P. subrotundus* is easily separated by the following character states: elytra reddish posterolaterally; frons depressed, with frontal stria interrupted; submarginal pronotal stria present, more or less complete, curved mediad anteriorly and diverging from margin posteriorly; prosternal striae converging anteriorly to nearly parallel, intervening punctures denser in male; elytral stria 1–5 complete. Below we refer to this species and following four (*P. rufinotus*, *P. thiemei*, *P. rouzeti*, and *P. parecis*) informally as the *P. rufinotus* complex, and their close relationship is supported by phylogenetic analyses to date.

**Biology.** The species has diverse and general habits, having been collected very commonly in dung, as well as in decaying vegetation, leaf litter, seaweed on the beach, in pocket gopher (*Geomys*) burrows, and even with a few ant species (in the genera *Aphaenogaster* Mayr and *Formica* L.). A few of the specimens from pocket gopher burrows, including one from Arkansas and four from Georgia, are unusually small and

have a posteriorly abbreviated sublateral pronotal stria. Males from both localities were dissected and do not differ in any obvious way from others of the species, so we have not considered them distinct. Further study should more carefully address this possibility with molecular data. Interestingly, a long series from *Geomys bursarius* (Shaw) burrows from St Clair Co, Illinois, do not exhibit these differences.

**Distribution.** This is the most abundant and widespread *Phelister* species in North America, occurring from southeastern Canada to Florida, west to South Dakota and Arizona. We have not seen any records from Mexico, but it occurs in several US border counties, and must occur south of the border as well. **Records:** **CANADA:** **Ontario:** Quebec; **USA:** **Alabama:** Blount, Greene, Marion; **Arizona:** Pima, Santa Cruz; **Arkansas:** Calhoun, Lafayette, Lee, Little River, Scott, Washington; **Delaware:** Kent, Sussex; **District of Columbia;** **Florida:** Alachua; **Georgia:** Baker, Burke, Clarke, Dodge, Lamar, Peach, Talbot, Thomas, Wheeler; **Illinois:** Campaign, Coles, Cook, Grundy, Iroquois, Jackson, Jo Daviess, Kane, Kankakee, Lake, Mason, McHenry, Pope, St. Clair, Will; **Indiana:** Boone, Brown, Franklin, Jasper, Lake, LaPorte, Laurel, Lawrence, Monroe, Newton, Parke, Porter, Starke, Tippecanoe, Vanderburgh; **Iowa:** Butler, Cedar, Dickinson, Dubuque, Johnson, Marshall, Monroe, Muscatine, Plymouth, Story, Warren; **Kansas:** Bourbon, Decatur, Doniphan, Douglas, Jefferson, Kiowa, Labette, Leavenworth, Miami, Montgomery, Norton, Pottawatomie, Rawlins, Riley, Sedgwick, Shawnee; **Kentucky:** Bell, Henderson; **Louisiana:** Bienville, Orleans, St. Charles, West Feliciana; **Maine:** Oxford; **Maryland:** Anne Arundel, Calvert, Charles, Garret, Montgomery, Prince George's, Somerset, Talbot, Washington; **Massachusetts:** Hampden, Hampshire, Middlesex, Plymouth; **Michigan:** Ingham, Kalamazoo, Macomb, Washtenaw, Wayne; **Minnesota:** Brown; **Mississippi:** Harrison, Oktibbeha, Pontotoc; **Missouri:** Boone, Marion, Mississippi, Pike, Saint Louis, Scott, Taney, Washington, **Nebraska:** Clay, Lancaster, Lincoln, Saunders; **New Jersey:** Bergen, Camden, Cape May, Gloucester, Hudson, Morris, Passaic, Sussex, Union; **New Hampshire:** Grafton; **New Mexico:** Hidalgo; **New York:** Cattaraugus, Kings, Monroe, Nassau, Onondaga, Orange, Richmond, Seneca, St. Lawrence, Suffolk, Tompkins; **North Carolina:** Buncombe, Duplin, Edgecombe, Jackson, New Hanover, Swain, Wake; **North Dakota:** Cass, Richland; **Ohio:** Ashland, Clermont, Cuyahoga, Franklin, Hocking, Lucas, Medina, Ross, Scioto, Summit, Wayne; **Oklahoma:** Cleveland, Comanche, Craig, Grant, Hughes, Latimer, Marshall, McCurtain, Payne, Sequoyah, Woods; **Pennsylvania:** Bradford, Cambria, Chester, Dauphin, Fulton, Luzerne, Monroe, Montgomery, Perry, Philadelphia; **South Carolina:** Anderson, Bamberg, Charleston, Dorchester, Florence, Pickens, Richland; **South Dakota:** Jackson, Lawrence, Minnehaha, Pennington, Yankton; **Tennessee:** Benton, Blount, Davidson, Hamilton, Montgomery, Morgan, Sevier, Wilson; **Texas:** Brazos, Colorado, Dallas, Denton, Duval, Erath, Goliad, Hidalgo, Jim Hogg, Montague, Val Verde; **Virginia:** Arlington, Fairfax, Nansemond, Nelson, Spotsylvania; **West Virginia:** Berkeley, Braxton, Grant, Greenbrier, Mason, Mineral, Preston, Putnam, Wayne; **Wisconsin:** Crawford, Dane, Iowa, Jefferson, Kenosha, Lafayette, Richland, Sauk, Shawano, Walworth, Waupaca.





**Map 4.** United States county map shading counties with records of *Phelister subrotundus*. Not shown are records from southern Ontario and Quebec, Canada (see Bousquet & Laplante 2006). No records have been found from Mexico.

***Phelister rouzeti* (Fairmaire, 1850)**

Figs 2, 6; Map 3

*Paromalus rouzeti* Fairmaire, 1850: 421.

*Phelister rouzeti*; Marseul, 1853: 488.

*Phelister fairmairei* Marseul, 1861: 172; **syn. nov.** (previously synonymized with *P. rufinotus*, Mazur, 1997, in error)

*Phelister wickhami* Casey, 1916: 231, **syn. nov.**

*Phelister pimalis* Casey, 1916: 233; Mazur 1997: 29.

*Phelister aztecianus* Casey, 1916: 233; Mazur 1997: 29.

**Type material. Lectotype** hereby designated: “Bondy fourmis Rouzet” / “certe Mexicanum” [handwritten, perhaps by Marseul] / “LECTOTYPE *Paromalus rouzeti* Fairmaire M.S. Caterino & A.K. Tishechkin des. 2010”, MNHN.

Types of synonyms. **Lectotype** *Phelister fairmairei* Marseul hereby designated: “Caracas Sallé” / “G.Lewis Coll. B.M.1926-369” / “LECTOTYPE *Phelister fairmairei* Marseul M.S. Caterino and A.K. Tishechkin des. 2010”, NHMUK. One paralectotype, same data as lectotype, NHMUK. **Lectotype** of *Phelister wickhami* Casey hereby designated: “Tepehuanes Dgo. Mex. Wickham” / “Casey bequest 1925” / “TYPE USNM 38449”

/ “wickhami Csy.” / “LECTOTYPE *Phelister wickhami* Casey M.S. Caterino and A.K. Tishechkin des. 2010.”, USNM. **Lectotype** of *Phelister pimalis* Casey hereby designated: “Ari” / “Casey bequest 1925” / “TYPE USNM 38454” / “pimalis Csy.” / “LECTOTYPE *Phelister pimalis* Casey M.S. Caterino and A.K. Tishechkin des. 2019.”, USNM. One paralectotype with same data, USNM. **Lectotype** of *Phelister aztecanus* Casey hereby designated: “San Angel D.F. Mex” / “Casey bequest 1925” / “TYPE USNM 38455” / “aztecanus Csy.” / “LECTOTYPE *Phelister aztecanus* Casey M.S. Caterino and A.K. Tishechkin des. 2019.”, USNM. One paralectotype with same data, USNM.

**Diagnostic description.** Length: 1.38–1.77 mm (avg. 1.57 mm); width: 1.10–1.46 mm (avg. 1.32 mm). Body elongate-oval, widest behind humeri; body color varied, common with much of elytra (posterolaterally) reddish, more rarely entirely piceous dorsally, legs typically golden reddish, though darker in piceous specimens; elytra and pronotum very finely punctulate; frons finely punctulate, impressed along midline, supraorbital stria complete, frontal stria interrupted at middle, slightly sinuate at sides; labrum wide, not or only weakly emarginate apically; both mandibles with strong tooth on inner edges; pronotum with more or less complete lateral submarginal stria incurved and crenulate anteriorly, ending freely, and diverging slightly from pronotal margin posteriorly, where it is often weakly abbreviated; pronotal disk with distinct, elongate secondary punctures along lateral thirds; base of pronotum with cluster of larger punctures in front of suture; elytron with single, complete epipleural stria, outer subhumeral stria present in apical third, inner subhumeral stria absent, dorsal striae 1–4 complete, fifth stria usually present in just over apical half, rarely complete, sutural stria present in apical two-thirds; propygidium with distinct secondary punctures decreasing in density posteriad; pygidium more finely punctate; prosternal keel with two complete striae, weakly convergent to subparallel, occasionally sinuate, free anteriorly, usually united along basal margin of keel; male prosternal keel with coarser and denser punctures, the males’ striae often more widely separated; mesoventral marginal stria complete, continued at sides by sinuate postmesocoxal stria which ends freely midway between the meso- and metacoxae; mesometaventral stria complete, crenulate at middle, arched anteriorly onto mesoventrite at middle, continued posteriad to near inner third of metacoxal margin; first abdominal ventrite with complete inner lateral stria and abbreviated outer lateral stria; protibia with apex obliquely truncate, outer margin weakly rounded, bearing ca. five evenly spaced marginal spines plus a larger apical marginal spine separated from others by a greater gap; meso- and metatibiae weakly expanded to apex, mesotibia with ca. five marginal spines, more prominent toward apex, metatibia with distinct spines mainly in apical half. Aedeagus with basal piece ca. one-fifth total length; tegmen simple, widest near middle, converging to apex, apex distinctly emarginate; median lobe ca. two-thirds tegmen length, with differentiated basal and distal proximal apodemes.

**Remarks.** Although its distribution is rather broad, *P. rouzeti* seems to be primarily native to western Mexico and southwestern North America. Its distribution only barely overlaps with that of *P. subrotundus*, its closest relative, from which it can be separated by its more elongate body form, usually abbreviated 5<sup>th</sup> elytral stria, and its narrower, more tapered aedeagus. Where it overlaps in distribution with *P. rufinotus*, in northern



South America, the complete submarginal pronotal stria of *P. rouzeti* will distinguish them. Although the species was originally described from France (Bondy, northeast of downtown Paris), it has never since been recorded in the country, despite dedicated attempts to recollect it (Auzat 1925; M Secq, pers. comm.). While an introduction followed by extirpation cannot be ruled out, it seems more likely that the original specimen was mislabeled, and that the species has never inhabited Europe.

**Biology.** Label data indicate varied habits for this species, with records from fire-scorched *Yucca*, rotten *Opuntia*, under bark of *Celtis* L., on a fermenting orange, in cow, dog, and horse dung, and in sifted riparian ‘dirt’.

**Distribution.** This widespread species occurs from the southwestern and south-central United States, through Mexico and Central America into northern South America. The species also occurs on several islands in the West Indies. As a common cow dung associate, its range has likely expanded in post-Columbian times. **Records:** **BRAZIL:** Rio Grande do Norte; **COLOMBIA:** La Guajira, Magdalena, Palmira, Tolima; **COSTA RICA:** Guanacaste, Heredia; **EL SALVADOR:** La Libertad, San Salvador; **GUATEMALA:** Escuintla; **MEXICO:** Chiapas, Colima, Distrito Federal, Guerrero, Jalisco, México, Michoacán, Morelos, Nayarit, Nuevo León, Oaxaca, Puebla, San Luis Potosí, Sinaloa, Sonora, Tabasco, Tamaulipas, Veracruz; **NICARAGUA:** Granada, Madriz; **PANAMA:** Chiriquí; **SAINT VINCENT & GRENADINES:** Saint Vincent; **SURINAME:** Pará, Saramacca; **TRINIDAD & TOBAGO:** Trinidad; **VENEZUELA:** Aragua; **USA: Arizona:** Florida, Maricopa, Pima, Santa Cruz; **California:** Riverside, **Texas:** Cameron, Colorado.

### *Phelister rufinotus* Marseul, 1861

Figs 2, 7; Map 3

*Phelister rufinotus* Marseul, 1861: 170.

*Epierus marseulii* Kirsch 1873: 136, syn. nov.

**Type material.** Type locality: “Bresil, Rio-Janeiro”. We have been unable to find any specimens that we believe to validly represent syntypes of *Phelister rufinotus*. Marseul specimens (with circular, green, handwritten labels) are present in MNHN and in NHMUK, but all of these represent other localities and appear to have been collected later ([18]’63’ and [18]’68) than the species was described. A couple of specimens in the NHMUK are labeled with variations on Rio de Janeiro, but none as typical for Marseul types, and lacking collection dates, it’s impossible to tell if these might have been extant in 1861. We considered designating a Neotype from among the later Marseul-identified specimens. However, we feel that the species is now adequately characterized, and that this would not serve a critical need.

Types of synonyms. **Lectotype** of *Epierus marseulii* Kirsch, hereby designated: “Pozuzu M. Kirsch” / “Statl. Museum für Tierkunde, Dresden” / “*Epierus marseulii*” / “*Phelister rufinotus* Mars. n. syn.” / “LECTOTYPE *Epierus marseuli* [sic] Kirsch M.S. Caterino and A.K. Tishechkin des. 2010”, MTD.



**Figure 7.** A–B *Phelister rufinotus* Marseul: **A** Dorsal habitus **B** Prosternum and mesoventrite of male. C–D *Phelister thiemei* Schmidt: **A** Dorsal habitus **B** Prosternum and mesoventrite of male.

**Diagnostic description.** Length: 1.46–1.69 mm (avg. 1.56 mm); width: 1.30–1.50 mm (avg. 1.34 mm). Body elongate-oval, widest just behind humeri; body piceous to rufescent, most of elytra and legs usually contrastingly reddish (elytra sometimes nearly black); dorsum very finely punctulate, the pronotum more densely so than the elytra, especially in the outer thirds; frons finely punctulate, impressed along midline, supraorbital stria complete, frontal stria interrupted at middle, inner ends pointing toward epistoma; labrum wide, weakly emarginate apically; both mandibles with distinct tooth on inner edges; pronotal lateral submarginal stria abbreviated, present in anterior half only; pronotal disk with vague antescutellar impression, with crenulations along posterior margin; elytron with single, complete epipleural stria, outer subhumeral stria present in apical half, inner subhumeral stria absent, dorsal striae 1–4 complete, fifth variable, but at least weakened in basal third if not obsolete, sutural stria obsolete in basal third; propygidium with sparse secondary punctures decreasing in density posteriad; pygidium with secondary punctures fewer and finer, diminishing to apex; prosternal keel with two complete striae, weakly sinuate, subparallel at base, slightly converging toward apex, free anteriorly; male prosternal keel with coarser and denser punctures, the striae often more widely separated; mesoventral marginal stria complete, smooth, continued at sides by postmesocoxal stria which ends freely near side of mesoventrite; mesometaventral stria complete, very weakly crenulate, arched anteriad nearly to midline of mesoventrite extended posteriad by lateral metaventral stria toward middle of metacoxa, ending short of it; first abdominal ventrite with complete inner lateral stria and abbreviated outer lateral stria; protibia rather narrow, with apex obliquely truncate, outer margin weakly rounded, bearing ca. five evenly spaced

marginal spines, the spine of the apical corner larger and slightly disjunct; meso- and metatibiae weakly expanded to apex, mesotibia with ca. five marginal spines, more prominent toward apex, metatibia with distinct spines confined to apical third. Aedeagus with basal piece ca. one-fourth total length; tegmen widened toward apex, spoon-shaped, apex rounded, with narrow apical emargination; median lobe ca. two-thirds tegmen length, with differentiated proximal and shorter distal proximal apodemes.

**Remarks.** This species is highly variable, but it can nearly always be recognized by its abbreviated submarginal pronotal stria. It is most often distinctly reddish on the elytra, but many all-black individuals have been seen, throughout the range. Its legs are nearly always distinctly golden in contrast to a piceous venter.

This species was previously synonymized with *P. fairmairei* Marseul 1861. We have studied that type and believe that *P. fairmairei* is instead identical to *P. rouzeti* (see above).

**Biology.** Label data indicate broad ecological associations with records from cow dung, decaying vegetation, meat- and dung-baited pitfalls, and gopher tortoise droppings. The species also exhibits distinct tendencies toward facultative myrmecophily, with numerous records from *Acromyrmex* and *Solenopsis* Westwood, and even a few from *Eciton* Latreille ('with prey').

**Distribution.** This species occurs most abundantly in southern South America, though numerous records also indicate that it occurs well into the tropics, with records in nearly every other country in the continent. There are several records from the Gulf Coast of the United States (Carolinas, Mississippi and Florida) that would seem likely to represent an introduction, given the lack of intervening records. This is another species that may well have expanded its distribution with the spread of cattle production. **Records:** **ARGENTINA:** Buenos Aires, Catamarca, Chaco, Cordoba, Corrientes, Entre Rios, La Rioja, Mendoza, Salta, San Juan, Santa Fe, Tucuman; **BOLIVIA:** Cochabamba, Santa Cruz; **BRAZIL:** Distrito Federal, Espírito Santo, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraná, Pernambuco, Rio Grande do Norte, Rio Grande do Sul, Rondônia, Santa Catarina, São Paulo, Tocantins; **ECUADOR:** Napo, Pinchincha; **FRENCH GUIANA:** Cayenne; **PARAGUAY:** Boquerón, Caaguazú, Caazapá, Cordillera, Itapúa, San Pedro; **PERU:** Apurímac, Ayacucho, Junín, Loreto; **URUGUAY:** Colonia, Salto; **VENEZUELA:** Aragua, Bolívar, Falcón, Guárico; **USA: Florida:** Alachua; **Mississippi:** Jones; **North Carolina:** Jackson; **South Carolina:** Chesterfield.

### *Phelister thiemei* Schmidt, 1889

Figs 2, 7; Map 5

*Phelister thiemei* Schmidt, 1889: 338.

*Phelister stercoricola* Bickhardt, 1909: 223, syn. nov.

**Type material. Lectotype**, hereby designated: "Matto grosso" / "Thiemei" / "Type" / "coll. J.Schmidt" / "Thiemei Schm." / "LECTOTYPE *Phelister thiemei* Schmidt 1889, M.S. Caterino & A.K. Tishechkin des. 2010", ZMHB.



**Map 5.** Collecting records for *Phelister bryanti* (stars), *P. parecis* (circles), and *P. thiemei* (squares; filled squares represent state records only for *P. thiemei*).

Types of synonyms. **Lectotype** of *Phelister stercoricola* Bickhardt hereby designated: “Montevideo, J. Tremoleras” / “Type” / “stercoricola Bickh.” / “LECTOTYPE *Phelister stercoricola* Bickhardt, 1909 M.S. Caterino & A.K. Tishechkin des. 2010”, ZMHB; five paralectotypes with same data, four in ZMHB, one in NHMUK.

**Diagnostic description.** Length: 1.30–1.77 mm (avg. 1.53 mm); width: 1.06–1.50 mm (avg. 1.32 mm). This species is extremely similar to both *P. rufinotus* and *P. rouzeti*, differing principally in the following features: Body elongate-oval, widest behind humeri; nearly always distinctly bicolored, with much of elytra (posterolaterally) reddish, rarely entirely piceous dorsally; frontal stria complete to narrowly interrupted; lateral submarginal pronotal stria absent; dorsal elytral striae 1–4 complete, 5<sup>th</sup> variable, complete to abbreviated from base; prosternal keel striae subparallel to sinuate;

male prosternal keel with coarser and denser punctures; mesometaventral stria closer, almost subparallel to mesoventral stria; aedeagus with basal piece ca. one-fourth total length; tegmen simple, widest just beyond middle, subparallel in apical third, apex shallowly emarginate, tegmen in lateral view thickest toward apex; median lobe ca. two-thirds tegmen length, with differentiated basal and distal proximal apodemes.

**Remarks.** We have characterized this species rather broadly. The typical form, from Mato Grosso, has a complete frontal stria and abbreviated 5<sup>th</sup> dorsal stria. Considerable variation is observed in these characters from other areas, with the frontal stria more often interrupted elsewhere. Typical *P. stercoricola* (which we synonymize here) exemplifies this alternative, with an interrupted frontal stria and complete 5<sup>th</sup> dorsal elytral stria. However, while there is some variation in genitalic shape over this range (mainly in the degree of apical expansion and approximately parallel sides of the tegmen), there is inadequate consistency to support multiple species at present. More careful study over this species' range may conclude otherwise. Specimens from the Cochabamba region of Bolivia frequently exhibit anterior fragments of a lateral submarginal pronotal stria, but we have dissected these as well and find them to fit within this broad concept of *P. thiemei*. *Phelister rufinotus* occurs broadly over much of the same range as this species, but we have generally had little difficulty separating them, on the basis of (in *P. rufinotus*) a partial lateral submarginal pronotal stria, and the spoon-shaped aedeagus.

**Biology.** Label data provide limited clues into the habits of this species; a few specimens were collected in cow dung or in pitfalls baited with human dung. Numerous specimens were simply collected by flight interception traps.

**Distribution.** This species is known from a fairly broad area from southeastern Bolivia and southeastern Brazil in the north through Uruguay and Paraguay south across central Argentina. **Records:** **ARGENTINA:** Buenos Aires, Cordoba, Corrientes, Entre Rios, Mendoza, San Luis; **BOLIVIA:** Cochabamba, Santa Cruz; **BRAZIL:** Mato Grosso, Minas Gerais, Rio Grande do Norte, Rio Grande do Sul, São Paulo; **PARAGUAY:** Caazapá, Misiones; **URUGUAY:** Canelones, Rocha; **VENEZUELA:** Aragua.

***Phelister parecis* sp. nov.**

<http://zoobank.org/5F177312-1062-4453-940C-7035402D19F0>

Figs 2, 8; Map 5

**Type material. Holotype male:** "BRASIL: Mato Grosso, Chapada dos Parecis, 14°15.85'S, 59°14.03'W, 25.xi-16.xii.2000" / "Caterino Tischechkin Exosternini Voucher EXO-00146", deposited in DZUP. Paratypes (5): 2: Same data as type (CHND, FMNH); 1: PARAGUAY: Paraguari, Compañía Naranjo, 5 November 2000, C. Aguilar" / "Caterino Tischechkin Exosternini Voucher EXO-00147"; 2: PARAGUAY: Cordillera, Naranjo, 3.xi.2000, C. Aguilar" (CHND, MSCC).

**Diagnostic description.** Length: 1.34–1.62 mm (avg. 1.48 mm); width: 1.14–1.30 mm (avg. 1.26 mm). Body elongate oval, dark rufescent to piceous, the elytra more distinctly rufescent; frons depressed along midline, lacking secondary punctures,



with complete frontal stria; labrum weakly emarginate; both mandibles with strong inner marginal tooth; pronotum with fine but distinct ground punctation, with coarser punctures in the lateral thirds, as well as along the basal margin; prescutellar impression distinct; marginal pronotal stria complete around sides and front; lateral submarginal pronotal stria complete along sides, very close to marginal stria, curving inward at front, nearly merging with marginal stria behind eye, strongly crenulate; elytra with single, complete epipleural stria, outer subhumeral stria present in posterior one-half, inner absent, dorsal striae 1–5 complete, the 5<sup>th</sup> hooked weakly at base, sutural stria present in apical two-thirds; propygidium with conspicuous, round secondary punctures separated by ca. their diameters, only slightly smaller and sparser in apical half; pygidium with very small, sparse secondary punctures throughout; prosternal lobe bluntly rounded, with complete marginal stria; prosternal keel with complete striae, sinuate, united anteriorly, with denser intervening punctures in the male; mesoventrite moderately produced, with complete marginal stria close to margin, continued at sides by long postmesocoxal stria that extends two-thirds of the distance to the posterior corner of the metepisternum; mesometaventral stria weakly arched onto base of mesoventrite, angulate at sides, lateral metaventral stria extending nearly to middle of front edge of metacoxa; 1<sup>st</sup> abdominal ventrite with complete inner lateral stria and fragments of outer behind metacoxa; protibia with outer edge rounded, bearing four moderately strong teeth, with prominent spines, apex obliquely truncate; protarsal claws unmodified; meso- and metatibiae weakly expanded to apices, bearing marginal spines, principally in the apical half on the metatibia; basal piece ca. one-fourth aedeagus length; tegmen narrow, only weakly expanded to apex, not very dorsoventrally flattened, rather thick in apical half; median lobe over half tegmen length, proximal apodemes differentiated with thin basal portions long.

**Remarks.** This species is very closely related to the *P. rufinotus* complex, and we considered the possibility that it represented a variant of one of these. But it is consistently distinct, over several localities, in the complete lateral submarginal pronotal stria, the complete 5<sup>th</sup> dorsal stria, and the complete frontal stria. Its aedeagus (from only one available male) is narrower than others in this complex, as well.

**Biology.** Nothing is known of the biology of this species.

**Distribution.** This species is known from only three locations, from Mato Grosso, Brazil to southern Paraguay.

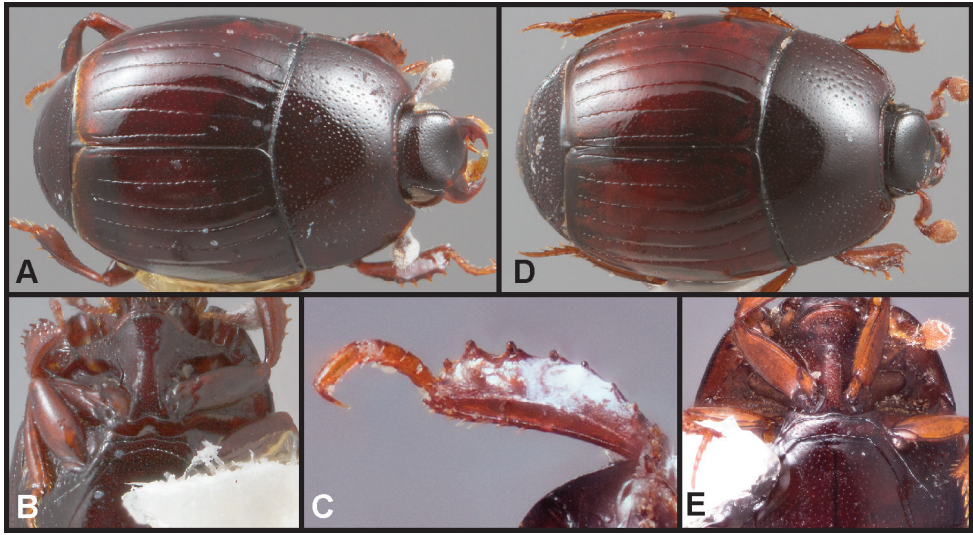
***Phelister bryanti* sp. nov.**

<http://zoobank.org/3B92666E-C64C-4A82-98C0-510275B0D62A>

Figs 2, 8; Map 5

**Type material. Holotype male:** “Rio San Javier, Santa Fe, Argentine. G.E. Bryant. San Joaquin 5.1.1912” / “G. Bryant Coll. 1919-147” / “*Phelister subrotundus* Say, H. Desbordes det. 1932” / “Caterino Tishechkin Exosternini Voucher EXO-00144”, deposited in NHMUK. 2 paratypes, same data as type (NHMUK).





**Figure 8.** **A–C** *Phelister bryanti* sp. nov. **A** Dorsal habitus **B** Prosternum and mesoventrite of male **C** Bent protarsal claws **D–E** *Phelister parecis* sp. nov. **D** Dorsal habitus **E** Ventral view showing prosternal and meso- and metaventral striae.

**Diagnostic description.** Length: 1.50–1.77 mm (avg. 1.62 mm); width: 1.22–1.38 mm (avg. 1.29 mm). Body broadly elongate oval, piceous, with conspicuous ground punctation, especially on pronotum; frons depressed along midline, lacking secondary punctation, with complete supraorbital stria; frontal stria obsolete between antennal bases; labrum moderately emarginate apically; both mandibles with strong inner marginal tooth; pronotal disk with few coarser secondary punctures at sides of disk and along basal margin; prescutellar impression present, but small; marginal pronotal stria complete along sides and front, crenulate anteriorly; submarginal pronotal striae absent; elytra with single, complete epipleural stria; outer subhumeral stria present in apical half only, inner absent, elytral striae 1–5 complete, sutural stria present in apical two-thirds or slightly more; propygidium with few sparse secondary punctures, mostly in basal half; pygidium with ground punctures only; prosternal lobe bluntly rounded, with complete marginal stria; prosternal keel with complete striae parallel over most of length, slightly divergent basad, connected basally by transverse stria, free anteriorly; mesoventrite moderately strongly produced, with complete marginal stria, continued at sides by postmesocoxal stria which diverges sinuately onto metaventricle; mesometaventral stria subangulate at middle, reaching midpoint of mesoventrite, curving posteriad at sides rather distant from mesocoxa, continued by lateral metaventral stria nearly to middle of metacoxa; 1<sup>st</sup> abdominal ventrite with single, complete lateral stria; protibia with outer margin weakly rounded, widest near middle, with 5–6 weakly developed teeth bearing marginal spines, apex obliquely truncate; protarsal claws (of male only?) strongly bent at base, straight to apex; meso- and metatibiae elongate, thin, mesotibia with ca. five thin marginal spines, those of metatibia very fine

and mostly near apex; basal piece ca. one-fourth total aedeagus length; tegmen moderately flattened dorsoventrally, lacking ventral process, sides widening to near apex, then abruptly narrowed to thin, elongate apices, apical emargination narrow; median lobe ca. one-third tegmen length, with proximal apodemes differentiated into thin and longer thick portions.

**Remarks.** This species appears quite similar to *P. puncticollis*, but is distinct in lacking a sublateral pronotal stria, its impunctate metaventrite, and separate male prosternal striae. The aedeagus of *P. bryanti* is highly distinct, being abruptly narrowed apically, where that of *P. puncticollis* is narrow and evenly rounded to the apex.

**Etymology.** This species is named for the collector of the entire type series, GE Bryant, a British coleopterist, best known for his work on Chrysomelidae.

**Biology.** Nothing is known of the biology of this species.

**Distribution.** This species is only known from the type locality in northeastern Argentina, and the types' labels bear no ecological data.

### *Phelister vernus* (Say, 1825)

Figs 2, 9; Map 6

*Hister vernus* Say, 1825: 40.

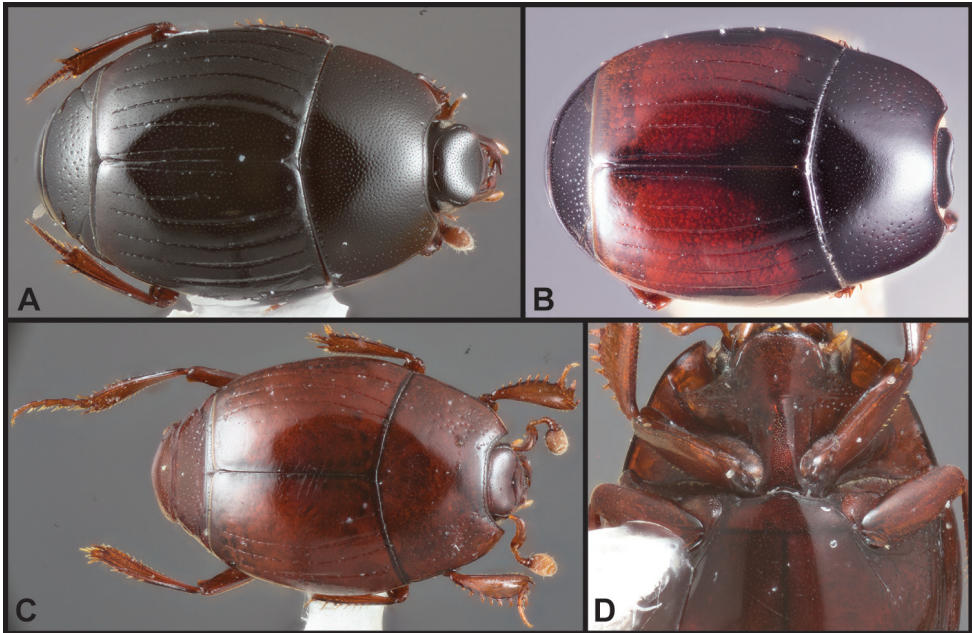
*Phelister vernus*; Marseul, 1853: 478.

*Phelister saunieri* Marseul, 1861: 162; Bickhardt, 1916: 214.

**Type material.** Neotype of *Hister vernus* Say, hereby designated: [reddish round disk] / “H. vernus Say.” / “NEOTYPE *Hister vernus* Say Desg. Caterino and Tishechkin, 2011”, MCZC. This common, widespread, and somewhat variable Nearctic species needs to be represented by a physical type so as to precisely establish its identity.

Types of synonyms. **Lectotype** of *Phelister saunieri* Marseul hereby designated: “11 *Phelister saunieri* M vernus Say Rochester Bouses Mai” / “6(11<sup>a</sup>) *Phelist. Saunieri* M Et Un. Rochester” / “TYPE” / “MUSEUM PARIS Coll. de Marseul 2842-90” / “LECTOTYPE *Phelister saunieri* Marseul, 1861 M.S. Caterino and A.K. Tishechkin des. 2010”, MNHN.

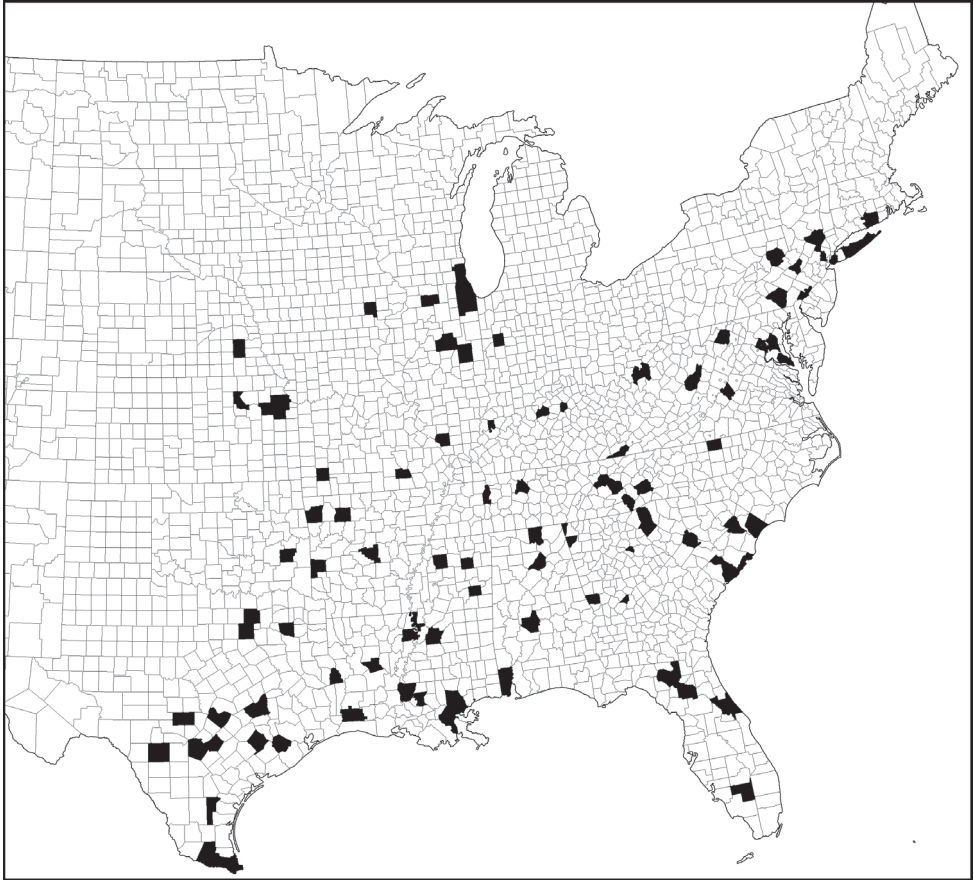
**Diagnostic description.** Length: 1.73–2.05 mm (avg. 1.95 mm); width: 1.50–1.77 mm (avg. 1.62 mm). Body elongate oval, piceous, with very distinct ground punctation throughout, especially distinct on pronotum; frons depressed along midline, supraorbital stria complete, frontal stria present along eyes, but broadly interrupted across front; labrum shallowly emarginate at apex; mandibles both with strong inner marginal tooth; prescutellar impression distinct, posterior margin of pronotum also with crenulate marginal punctures; lateral one-fifth of pronotal disk with elongate, coarser punctures; marginal pronotal stria complete along sides and front, only weakly crenulate in front; submarginal stria absent; marginal epipleural stria complete; outer subhumeral stria present in posterior one-third, inner subhumeral absent; dorsal elytral striae 1–4 complete, 5<sup>th</sup> present in apical half (some-



**Figure 9.** **A** *Phelister vernus* (Say), dorsal habitus **B** *Phelister chilicola*, dorsal habitus **C–D** *Phelister bruchi* Bickhardt: **C** Dorsal habitus **D** Ventral view showing prosternal and meso- and metaventral striae.

times also as basal puncture), sutural stria present in apical two-thirds; propygidium with small secondary punctures interspersed with ground punctures, separated by ca. twice their diameters; pygidium with ground punctures only; prosternal lobe narrowly rounded, subtruncate apically, marginal stria somewhat distant from margin, may be interrupted at middle; prosternal keel with striae converging from base, subparallel in apical half, similarly punctate in both sexes; mesoventral stria sinuate, following anterior margin, deeply impressed, continued by postmesocoxal stria, curving laterad behind coxa; mesometaventral stria somewhat quadrate, weakly arcuate across base of mesoventrite, angulate posteriad, with lateral mesoventral striae only weakly diverging to inner corners of metacoxae; 1<sup>st</sup> abdominal ventrite with complete inner lateral stria, outer abbreviated at base, and diverging behind metacoxa; protibia with outer margin weakly rounded, and rather strongly dentate, with five marginal spines, apex truncate; meso- and metatibiae weakly expanded to apex, mesotibia with ca. five marginal spines, more prominent toward apex, metatibia with distinct spines mainly in apical half. Aedeagus with basal piece almost one-third aedeagal length, tegmen more or less parallel sided, rounded to apex, with narrow, closed apical emargination; in lateral view tegmen rather flattened, thickened and with ventral dentate process near its midpoint; median lobe short, ca. one-third tegmen length, with differentiated thick and thin proximal apodemes.

**Remarks.** Among US species of *Phelister*, *P. vernus* is easily distinguished by its broadly interrupted frontal stria, its lack of submarginal pronotal stria, and its conspic-



**Map 6.** United States county map shading counties with records of *Phelister vernus*. No records have been confirmed for either Canada or Mexico.

uous pronotal ground punctation. It also lacks any hint of reddish coloration, common in the broadly sympatric *P. subrotundus*.

**Biology.** Label data associated with specimens indicate varied habits, having been collected from cow dung, mushrooms, ‘stable sweepings’, and even in the nest of a shrew.

**Distribution.** There is a published record from Ontario (Davies 1991), but neither we nor Bousquet and Laplante (2006) have seen any specimens from Canada. Otherwise, the species is common and widely distributed across the eastern Nearctic.

**Records: USA: Alabama:** Blount, Dallas, Madison, Mobile; **Arkansas:** Pulaski, Newton, Polk, Washington; **Connecticut:** New London; **District of Columbia;** **Florida:** Alachua, Columbia, Hendry, Putnam, Suwanee, Volusia; **Georgia:** Clarke, Chattooga, Dade, Harris, Peach; **Illinois:** Champaign, Cook, Dupage, Jackson, Lake, Lee, McClean, Will; **Indiana:** Tippecanoe, Vanderburgh; **Iowa:** Johnson; **Kansas:** Douglas, Jefferson, Leavenworth, Riley, Shawnee; **Kentucky:** Franklin, Jefferson; **Louisiana:** Calcasieu, East Baton Rouge, Grant, Jefferson, Madison, Orleans, Pointe Coupee, St. Charles, St. Tammany, West Feliciana; **Maryland:** Prince George’s, St. Mary’s; **Missis-**



**sippi:** Hinds, Issaquena, Oktibbeha, Panola, Pontotoc; **Missouri:** Carter, Lawrence; **Nebraska:** Lancaster; **New Jersey:** Essex, Passaic; **New York:** Kings, Orange, Queens, Suffolk; **North Carolina:** Buncombe, Jackson, Rockingham; **Oklahoma:** Latimer; **Pennsylvania:** Delaware, Lancaster, Luzerne, Northampton, Philadelphia; **South Carolina:** Anderson, Charleston, Dorchester, Florence, Horry, Lexington, Pickens; **Tennessee:** Benton, Davidson, Knox, Sevier; **Texas:** Bexar, Brazos, Burleson, Cameron, Collin, Colorado, Dallas, Fort Bend, Gillespie, Guadalupe, Hidalgo, Jim Wells, Sabine, Travis, Uvalde, Wood; **Virginia:** Fairfax, Lee, Nelson; **West Virginia:** Hampshire, Jackson, Mason, Pocahontas; **Wisconsin:** Kenosha.

***Phelister chilicola* Marseul, 1870**

Figs 2, 9; Map 7

*Phelister chilicola* Marseul, 1870: 79.

**Type material.** **Lectotype**, hereby designated: “*Phelister chilicola*, Chili, [????] 68” / “Museum Paris, Coll. de Marseul 2842-90” / “Type” / “Lectotype *Phelister chilicola* Marseul, 1870, M.S. Caterino & A.K. Tishechkin des. 2010”, MNHN.

**Diagnostic description.** Length: 1.73–2.17 mm (avg. 2.02 mm); width: 1.50–1.81 mm (avg. 1.66 mm). Body elongate oval, widest behind humeri, piceous with the apices of the elytra and the legs typically castaneous to rufescent, the ground punctation fine but distinct; frons depressed along midline, lacking secondary punctures; supraorbital stria complete, frontal stria fine, interrupted at middle for ca. width of labrum, inner ends weakly recurved dorsad; labrum weakly emarginate; mandibles both with distinct inner marginal tooth, that of left mandible slightly larger; pronotal disk with few coarser secondary punctures at sides and row of coarse punctures along posterior margin; prescutellar impression present but weak; marginal pronotal stria complete along sides and front, not distinctly crenulate anteriorly; submarginal pronotal stria absent; elytra with single, complete epipleural stria, outer subhumeral stria present in apical half, inner subhumeral stria absent; dorsal striae 1–4 complete, 4<sup>th</sup> rarely abbreviated at base, 1 and 2 weaker apically, 5<sup>th</sup> stria present in apical half, sutural stria present in apical two-thirds; propygidium with small, sparse secondary punctures, mainly in basal half; pygidium with ground punctation only; prosternal lobe evenly rounded, with complete marginal stria; prosternal lobe with two complete striae converging slightly toward front, the intervening punctures not sexually dimorphic in density; mesoventrite weakly projecting, with complete marginal stria, continued at sides by postmesocoxal stria which diverges to sides, ending freely before reaching middle of metepisternum; mesometaventral stria straight to angulate at middle, often reaching middle of mesoventrite, continued at sides by well-impressed lateral metaventral stria which reaches middle of metacoxa; 1<sup>st</sup> abdominal ventrite with complete inner lateral stria, the outer generally abbreviated from both base and apex; protibia with outer margin distinctly rounded, widest near middle, with five weakly developed teeth bearing marginal spines; protarsal claws of both sexes strongly bent

at base, then straight; meso- and metatibiae evenly widened to apices, with few weak marginal spines confined to apical halves; basal piece of aedeagus ca. one-fourth entire aedeagus length; tegmen dorsoventrally flattened, with weak ventral process ca. one-third from base, tegmen widening toward apex, sides rounded, apices bluntly rounded, with narrow, rather shallow apical emargination; median lobe a little over one-half tegmen length, proximal apodemes thin at bases, thicker over apical two-thirds.

**Remarks.** This species is superficially similar to other red-marked species, such as *P. haemorrhous*, *P. rufinotus*, and *P. thiemei*. However, it is clearly and easily distinguished from any of these by its thin elytral striae, modified protarsal claws (in both sexes), and more diffuse reddish coloration of the elytra only. The aedeagus is also quite distinct from any of these, particularly in the obvious ventral process of the tegmen, and in the short proximal apodemes of the median lobe.

**Biology.** None of the specimens we have seen include any biological data.

**Distribution.** This species is known only from Central Chile, ranging from Santiago Province in the north to Valdivia in the south. **CHILE:** Cautín, Concepción, Nuble, Osorno, Santiago, Valdivia.

### *Phelister bruchi* Bickhardt, 1920

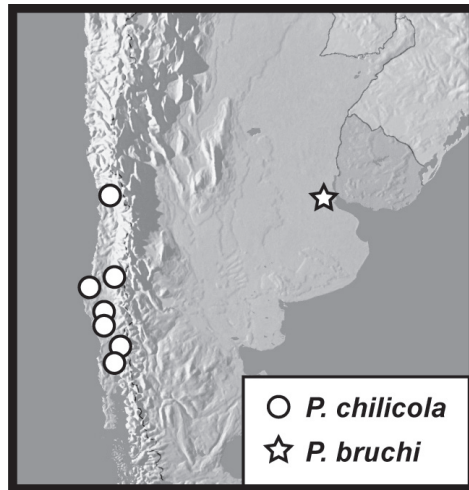
Figs 2, 9; Map 7

*Phelister bruchi* Bickhardt, 1920: 237.

**Type material. Lectotype** of undetermined sex, hereby designated: “Rep. Argentina, Prov. Buenos Aires 17.X.1919” / “ex nido de *Ctenomys*” / “*Phelister Bruchi* Bickh. H. Bickhardt det. 1920.” / “LECTOTYPE *Phelister bruchi* Bickhardt, 1920 M.S. Caterino and A.K. Tishechkin des. 2010”, ZMHB. 8 paralectotypes designated (on 6 pins) with same data as lectotype, ZMHB. There are two other probable syntypes (unmarked and undesignated) in FMNH.

**Diagnostic description.** Length: 2.01–2.05 mm (avg. 2.04 mm); width: 1.73–1.77 mm (avg. 1.76 mm). Body elongate oval, moderately depressed, rather pale rufescent; frons with fine ground punctation, weakly depressed at middle, frontal stria interrupted briefly at middle; labrum deeply emarginate, apical margin subcarinate; mandibles both strongly toothed along inner edge; pronotum with sides strongly convergent, only weakly curved, disk impunctate at middle, with sparse larger punctures at sides; prescutellar impression very small, fine; punctures along basal margin weak; marginal pronotal stria complete along sides and front; submarginal striae absent, but three gland openings conspicuous along lateral margins; elytra with single, complete epipleural stria, outer subhumeral stria very short and apical, inner subhumeral stria absent; dorsal elytral striae 1–3 complete (3<sup>rd</sup> may be weakly abbreviated apically), 4<sup>th</sup> present in basal third, and maybe as apical fragments, 5<sup>th</sup> and sutural striae absent; propygidium with sparse small punctures separated by 2–3× their diameters, also with faint wavy microsculpture near base; pygidium with only very small and ground





**Map 7.** Collecting records in southern South America for *Phelister chilicola* (circles) and *P. bruchi* (star).

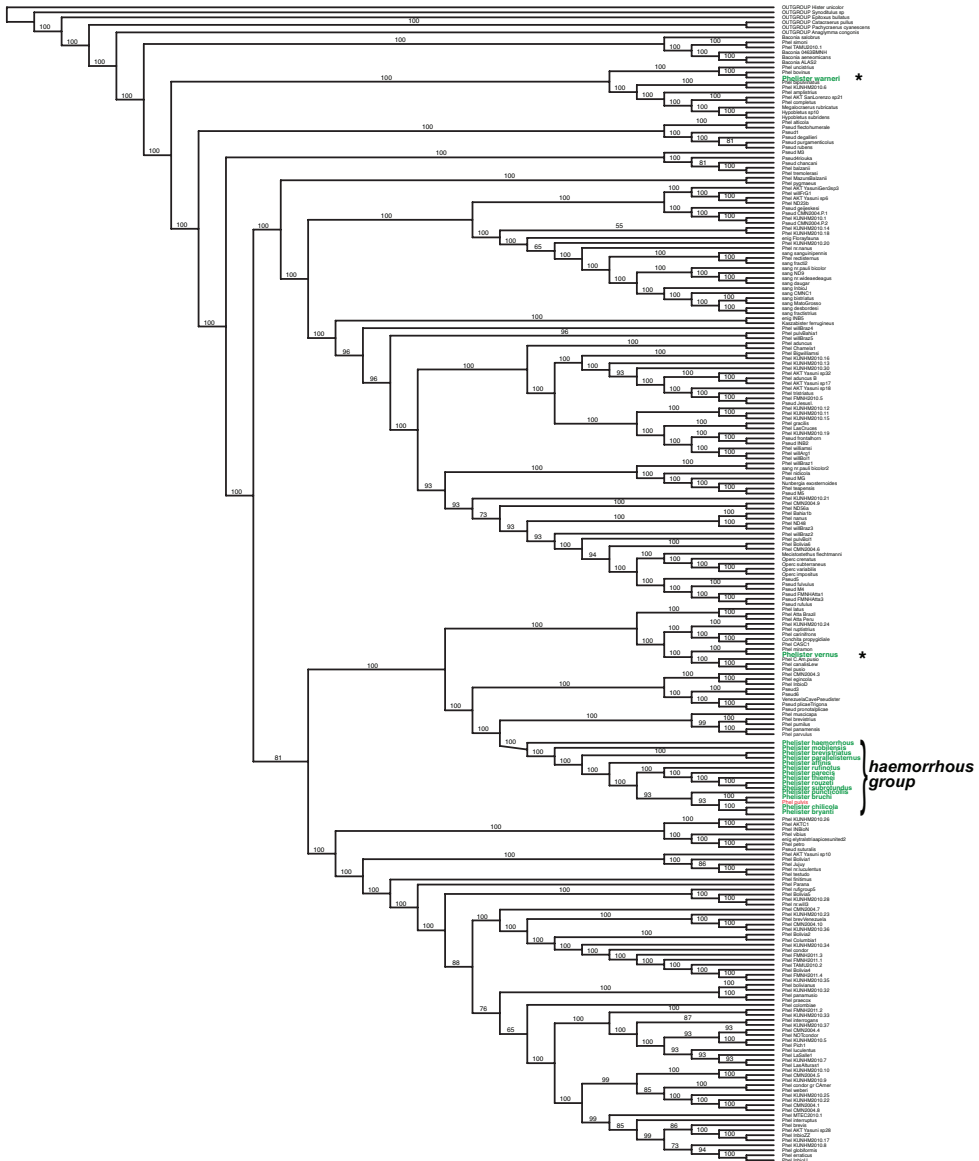
punctuation; prosternal lobe rather elongate, with complete marginal stria; prosternal keel narrow, lacking striae; mesoventrite projecting, with marginal stria fine, merging with margin at middle, thus appearing interrupted; mesometaventral stria absent from mesoventrite; postmesocoxal stria present curving strongly laterad behind coxa; lateral metaventral stria present, extending from inner margin of mesocoxa ca. two-thirds the distance to outer corner of metacoxa; 1<sup>st</sup> abdominal ventrite with only weak fragments of a lateral stria; all legs rather elongate and slender; protibia with lateral margin rounded, with 6–7 marginal spines, apex obliquely truncate; protarsi elongate, with almost straight protarsal claws; meso- and metatibiae narrow and elongate, with rather fine, elongate marginal spines, those of metatibia restricted to apical half; basal piece short, ca. one-sixth total length of aedeagus narrow, sides subparallel, apices bluntly rounded, with shallow apical emargination; median lobe long, ca. four-fifths tegmen length, proximal apodemes differentiated into thick and longer thin portions.

**Biology.** This species has only been collected once to our knowledge, from burrows of *Ctenomys* Blainville (tuco-tucos). Its habitus, with long thin legs and weakly impressed striae, reflects its probable status as an obligate inquiline in these burrows.

**Distribution.** This species is only known from the type locality, in Buenos Aires province, Argentina.

## Results and discussion

In our reduced analysis of *Phelister* (sensu lato) a single ‘best’ island of trees was found (saving the maximum 2500 trees) of 10777 steps. Continuing with an unconstrained search, beginning with these shortest starting trees, one shorter island of trees of 10766 steps was found. The majority rule consensus of these is presented in Figure 10. Fifteen



**Figure 10.** Majority rule consensus of 1000 trees of 10766 steps from parsimony search. Majority rule consensus indices are shown on branches. Taxa that are highlighted in green are members of the *Phelister haemorrhous* group, as delimited in this paper (including two not resolved to be part of the same clade, *P. vernus* and *P. warneri*). One species, *P. pulvis*, resolved among *P. haemorrhous* group species but excluded from the group is highlighted in red.

of the included species are resolved in a single clade. However, there are two problems. The first is that two species that we have included in the *haemorrhous* group based on overall morphology do not fall in it in these analyses. Omission of one of these, *Phelister vernus*, corresponds to some of our own uncertainties with its assignment. It instead falls

out with a Central American group of *Phelister* species that includes *P. pusio* Erichson, *P. canalis* Lewis, and *P. miramon* Marseul. The latter placement is somewhat intriguing, in that *P. miramon* was considered initially to be *P. vernus* (in Marseul's writing on his own label for the type of *P. miramon*). However, we have studied type(s) of *P. miramon* (Caterino & Tishechkin, unpublished notes), and, despite some external similarities, it represents a distinct species with a very different type of aedeagus from anything in the *P. haemorrhous* group. This phylogenetic result may be driven more by superficial external characters than more significant internal ones. More surprising is the wide separation of our new species *P. warneri* from the *P. haemorrhous* group. This may also be driven by some unique external characters associated with its inquilinous habits, as its aedeagus shares several characteristics with other species in the *haemorrhous* group (especially *P. brevistriatus* and *P. sonora*, which we suggest to be its closest relatives.)

The second problem is that *Phelister pulvis* Marseul falls among members of the *P. haemorrhous* group, though we have not included it in this revision. It is difficult to see the basis for its inclusion, as its external similarity is minimal, lacking most of the characters that we list above as diagnostic for the *haemorrhous* group. This unlikely result is probably driven by the lack of male genitalic data available for *P. pulvis*, hindering its placement with species we do consider to be its more likely relatives.

Within the *haemorrhous* group, *P. haemorrhous* itself is resolved as sister to all other members of the group, with the North American *P. mobilensis* then sister to the remainder. *Phelister brevistriatus* and *P. parallelisternus* are united as sister groups, somewhat surprisingly to the exclusion of *P. affinis*. What we informally refer to as the 'rufinotus complex' is resolved as a clade. Remaining relationships show relatively little correspondence with obvious morphological characters, and demand more comprehensive analysis. Only four of these species are yet represented by any molecular data (*P. haemorrhous*, *P. subrotundus*, *P. rufinotus*, and *P. vernus*). More comprehensive data will be necessary to reveal more valuable insights into relationships.

## Acknowledgments

We are very grateful to numerous colleagues who provided specimens, data, and other assistance with material, including Roger Booth, Martin Brendell, Christine Taylor, Alfred Vogler, and Max Barclay (NHMUK), David Kavanaugh and Jere Schweickert (CASC), Andrew Cline (CDFA), Fernando Vaz-de-Mello (CEMT), Robert Anderson and François Genier (CMNC), Bob Davidson and John Rawlins (CMNH), Lúcia Massutti de Almeida (DZUP), Margaret Thayer, Al Newton, James Boone, and Crystal Maier (FMNH), Mike Thomas and Paul Skelley (FSCA), Angel Solís (INBIO), Chris Carlton and Victoria Bayless (LSAM), Phil Perkins (MCZC), Thierry Deuve, and Azadeh Taghavian (MNH), Olaf Jäger (MTD), Michael Ivie and Erich Speissberger (MTEC), Zack Falin and Andrew Short (SEMC), Ed Riley (TAMU), Carlos Flechtmann (UNESP), Gary Hevel, David Furth, and Terry Erwin (USNM), Bernd Jaeger and Manfred Uhlig (ZMHB), Stéphane Brûlé, Pierre-Henri Dalens, Eddy Poirier, and

Julien Touroult (SEAG - Société entomologique Antilles-Guyane), Jeffrey Gruber, Peter Kovarik, David Verity, William Warner, and Slawomir Mazur. For assistance with fieldwork and permits we thank Carlos Flechtmann and his students (Silvia Tanabe, Julius Cerqueira, and Bruno Ferreira), Lúcia Massutti de Almeida, Fernando Leivas, Daniel Moura, Kleber Mise, Paschoal Grossi, and Fernando Vaz-de-Mello. We would like especially to thank Nicolas Dégallier for assistance with museum work at MNHN, for sharing data on types he borrowed, and for evaluating a preliminary version of the manuscript. This project was supported by National Science Foundation grant DEB 0949790; partial support came from the Louisiana State University Agricultural Center, USDA/NIFA, under project number SC-1700527, and NSF grants DEB 9815394 and DEB 0516311, as well as the Schlinger Foundation. Technical Contribution No. 6756 of the Clemson University Experiment Station.

## References

- Aballay FH, Arriagada H, Flores GE, Centeno ND (2013) An illustrated key to and diagnoses of the species of Histeridae associated with decaying carcasses in Argentina. *ZooKeys* 261: 61–84. <https://doi.org/10.3897/zookeys.261.4226>
- Auzat V (1925) Histeridae gallo-rhéniens. *Miscellanea Entomologica* (suppl.): 99–114.
- Bickhardt H (1909) Beiträge zur Kenntnis der Histeriden III. *Entomologische Blätter* 5: 220–224.
- Bickhardt H (1916) Coleoptera. Fam. Histeridae. In: Wytzman P (Ed.) *Genera Insectorum*. Junk, The Hague, 302 pp.
- Bickhardt H (1920) Neue Histeriden aus den Nestern eines argentinischen Nagers. *Entomologische Blätter* 16: 236–239.
- Bousquet Y, Laplante S (2006) The Insects and Arachnids of Canada. Part 24. Coleoptera: Histeridae. NRC Research Press, Ottawa, 485 pp.
- Carnochan FG (1915) Notes on the genus *Phelister* (Histeridae). *Psyche* 22: 213–214. <https://doi.org/10.1155/1915/70781>
- Casey TL (1916) *Memoires on the Coleoptera VII*. New Era Printing Co., Lancaster, PA, 390 pp.
- Caterino MS, Tishechkin AK (2013a) A systematic revision of *Baconia* Lewis (Coleoptera, Histeridae, Exosternini). *ZooKeys* 343: 1–297. <https://doi.org/10.3897/zookeys.343.5744>
- Caterino MS, Tishechkin AK (2013b) A systematic revision of *Operclipygyus* Marseul (Coleoptera, Histeridae, Exosternini). *ZooKeys* 271: 1–401. <https://doi.org/10.3897/zookeys.271.4062>
- Caterino MS, Tishechkin AK (2013c) Case 3610: *Phelister* Marseul, 1853 (Insecta, Coleoptera, Histeridae): proposed conservation of usage. *Bulletin of the ICZN* 70: 12–14. <https://doi.org/10.21805/bzn.v70i1.a3>
- Caterino MS, Tishechkin AK (2015) Phylogeny and generic limits in New World Exosternini (Coleoptera: Histeridae: Histerinae). *Systematic Entomology* 40: 109–142. <https://doi.org/10.1111/syen.12095>

- Davies A (1991) Family Histeridae – hister beetles. In: Bousquet Y (Ed.) Checklist of beetles of Canada and Alaska. Agriculture Canada, Publication 1861/E, 135–141.
- Fairmaire L (1850) Description de quelques coléoptères nouveaux d'Europe et de France. *Annales de la Société Entomologique de France* (2)7: 419–427.
- Helava JVT, Howden HF, Ritchie AJ (1985) A review of the New World genera of the myrmecophilous and termitophilous subfamily Hetaeriinae. *Sociobiology* 10: 127–386.
- Hinton HE (1935) New American Histeridae. *Stylops* 4: 57–65. <https://doi.org/10.1111/j.1365-3113.1935.tb00556.x>
- ICZN (2015) Opinion 2364 (Case 3610) *Phelister* Marseul, 1853 (Insecta, Coleoptera, HISTERIDAE): usage conserved. *Bulletin of the ICZN* 72: 231–232. <https://doi.org/10.21805/bzn.v72i3.a7>
- Kanaar P (1997) Revision of the genus *Paratropus*. *Zoologische Verhandelingen* 315: 1–185.
- Kirsch T (1873) Beiträge zur Kenntniss der Peruanischen Käferfauna. *Berliner Entomologische Zeitschrift* 17: 121–152.
- Koller WW, Gomes A, Rodrigues SR (2002) Fimicolous Histeridae Coleoptera in Campo Grande, MS, Brazil. *Brazilian Journal of Biology* 62: 473–478. <https://doi.org/10.1590/S1519-69842002000300011>
- Kryzhanovskij OL, Reichardt AN (1976) Beetles of the Superfamily Histeroidea. *Fauna SSSR, Novaya Seriya* 111: 1–432.
- Lawrence JF, Ślipiński A, Seago AE, Thayer MK, Newton AF, Marvaldi AE (2011) Phylogeny of the Coleoptera based on morphological characters of adults and larvae. *Annales Zoologici* 61: 1–217. <https://doi.org/10.3161/000345411X576725>
- LeConte JE (1859) Description of new species in the coleopterous family Histeridae. *Proceedings of the Academy of Natural Sciences Philadelphia* 11: 310–317.
- Lewis G (1908) On new species of Histeridae and notices of others. *Annals and Magazine of Natural History* 8: 137–160. <https://doi.org/10.1080/00222930808692465>
- Marseul SA (1853) Essai Monographique sur la Famille des Histerides, comprenant la description et la figure au trait des genres et des espèces, leur distribution méthodique, avec un résumé de leurs moeurs et de leur anatomie. *Annales de la Société Entomologique de France* (3)1: 131–160, 177–294. <https://doi.org/10.5962/bhl.title.9221>
- Marseul SA (1854) Essai monographique sur la famille des Histerides. *Annales de la Société Entomologique de France* (3)1 (1853): 447–553.
- Marseul SA (1861) Supplément a la monographie des Histerides. *Annales de la Société Entomologique de France* (4)1: 141–184. <https://doi.org/10.5962/bhl.title.11082>
- Marseul SA (1870) Descriptions d'espèces nouvelles d'Histerides. *Annales de la Société Entomologique de Belgique* 13: 55–158.
- Marseul SA (1889) Descriptions de nouvelles espèces d'Histerides du genre *Phelister* (3e et dernière partie). *Bulletin de la Société Entomologique de France* 1889: 146–147.
- Mazur S (1984) A World Catalogue of Histeridae. *Polskie Pismo Entomologiczne* 54: 1–376.
- Mazur S (1997) A world catalogue of Histeridae. *Genus (Supplement)*: 1–373.
- Ohara M (1994) A revision of the superfamily Histeroidea of Japan. *Insecta Mastumurana (N.S.)* 51: 1–283.

- Penati F (2009) An updated catalogue of the Histeridae (Coleoptera) of Sardinia, with faunistic, zoogeographical, ecological and conservation remarks. *Zootaxa* 2318: 197–280.
- Say T (1825) Description of new species of *Hister* and *Hololepta*, inhabiting the United States. *Journal of the Academy of Natural Sciences of Philadelphia* 5: 32–47.
- Schmidt J (1889) Neue Histeriden. *Entomologische Nachrichten* 21: 329–341. <https://doi.org/10.1002/mmnd.48018890124>
- Schmidt J (1893) Zwölf neue Phelister. *Entomologische Nachrichten* 19: 81–91.
- Summerlin JW, Roth JO, Fincher GT (1991) Predation by two species of histerid beetles on the horn fly. *Southwestern Entomologist* 16: 45–49.
- Swofford DL (2002) PAUP\*. Phylogenetic Analysis Using Parsimony (\*and Other Methods). Vienna P (1980) Fauna d'Italia XVI. Coleoptera Histeridae. Calderini, Bologna, 373 pp.
- Wenzel RL, Dybas HS (1941) New and little known Neotropical Histeridae. *Fieldiana, Zoology* 22: 433–472. [+ plates]

## Supplementary material I

### Exosternini phylogenetic data

Authors: Michael S. Caterino, Alexey K. Tishechkin

Data type: (Morphological and molecular character state data)

Explanation note: This dataset is a reduced (in numbers of taxa) from that published in Caterino and Tishechkin 2015. It contains 260 morphological characters followed by 2609 nucleotide characters, representing the 18S, 28S, and COI genes, scored for 231 taxa (including outgroups).

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.854.35133.suppl1>



# Taxonomic revision of *Mordellistena hirtipes* species complex with new distribution records (Insecta, Coleoptera, Mordellidae)

Dávid Selnekovič<sup>1</sup>, Ján Kodada<sup>1</sup>

<sup>1</sup> Department of Zoology, Faculty of Natural Sciences, Comenius University in Bratislava, Ilkovičova 6, SK-84215, Bratislava, Slovakia

Corresponding author: Dávid Selnekovič ([david.selnekovic@gmail.com](mailto:david.selnekovic@gmail.com))

---

Academic editor: A. Smith | Received 10 December 2018 | Accepted 27 April 2019 | Published 10 June 2019

---

<http://zoobank.org/04C4ED1B-F1A7-4490-A4ED-84CAB29BC3C9>

---

**Citation:** Selnekovič D, Kodada J (2019) Taxonomic revision of *Mordellistena hirtipes* species complex with new distribution records (Insecta, Coleoptera, Mordellidae). ZooKeys 854: 89–118. <https://doi.org/10.3897/zookeys.854.32299>

---

## Abstract

A taxonomic revision of species related to *Mordellistena hirtipes* Schilsky, 1895 is presented. Five species among the *M. hirtipes* complex are recognised: *M. hirtipes* Schilsky, 1895, *M. pseudohirtipes* Ermisch, 1965, *M. purpurascens* Costa, 1854, *M. balearica* Compère, 1985, and *M. irritans* Franciscolo, 1991. Descriptions, differential diagnoses, an identification key, and new distributional records are provided. Principal Component Analysis is performed for visualisation of differentiation between taxa. The following taxonomic acts are proposed: *Mordellistena podlussanyi* Czető, 1990 and *M. aegea* Franciscolo, 1949 are proposed as junior subjective synonyms of *M. hirtipes* Schilsky, 1895; *M. fageli* Ermisch, 1969 and *M. pseudohirtipes krotosensis* Czető, 1990 are proposed as junior subjective synonyms of *M. pseudohirtipes pseudohirtipes* Ermisch, 1965; *M. geronensis* Ermisch, 1977 and *M. istricea* Ermisch, 1977 are proposed as junior subjective synonyms of *M. purpurascens* Costa, 1854.

## Keywords

taxonomy, identification key, distribution, new synonym, morphometry, Principal Component Analysis (PCA)

## Introduction

*Mordellistena* Costa, 1854 is the largest genus within the family Mordellidae Latreille, 1802, comprising approximately 800 described species (Horák 2011). Adults are commonly found on flowers where they feed on pollen and nectar. Larvae are found in the stems of herbaceous plants or in decaying wood.

The Western Palaearctic species are conventionally assigned to species groups proposed by Ermisch (1956, 1969b), based on combinations of morphological characters. There are no studies focused on the phylogeny of Palaearctic species of genus *Mordellistena*, and thus the phylogenetic relationships among its species remain unresolved.

The present study is focused on nine morphologically related taxa, which represent a complex within *M. confinis* species group (Ermisch 1956, 1969b, Batten 1977). The unique character shared by all species of the complex is the expanded second segment of maxillary palpi in males, bearing very long setae on the ventral surface (Figs 4A, 6C, 7C). Additional characters are a strongly convex body and unique shape of parameres (Figs 5D–G, 6E–H, 7G–J, 8, 9).

Species belonging to this complex were described by Costa (1854), Schilsky (1895), Ermisch (1965, 1969a, 1977), Compte (1985), and Franciscolo (1949, 1991). Most of descriptions appeared to be insufficient for proper identification and after examination of type material, it became clear that some of the taxa are conspecific. In the present paper, we provide redescriptions of *M. hirtipes* Schilsky, 1895, *M. pseudohirtipes* Ermisch, 1965, and *M. purpurascens* Costa, 1854. Important diagnostic characters are visualised in drawings and photographs. We also performed Principal Component Analysis (PCA) based on morphometric measurements. This method is widely used in taxonomical research of invertebrates to help separate putative species in difficult species-complexes, to visualise differentiation between species and to evaluate the importance of peculiar morphometric characters (Kucharczyk et al. 2012, Przybycień and Waclawik 2015).

Examination of material from several localities in Western Palaearctic revealed new distribution records and new biological information for *M. hirtipes* Schilsky, 1895, *M. pseudohirtipes* Ermisch, 1965, and *M. purpurascens* Costa, 1854.

## Materials and methods

Dried specimens were relaxed in water with a few drops of acetic acid to allow for the dissection. Specimens were observed using Leica MZ16 stereomicroscope with magnification up to 120×, illuminated with diffuse light (neon bulb, 6400 K). Dissected body parts for drawings were temporarily mounted on slides in glycerine. Drawings were prepared using Leica drawing tube attached to Leica DM 1000 microscope, scanned and traced in Adobe Illustrator CS6. Dissected body parts were after examination mounted on the same card as respective specimen using dimethyl hydantoin formaldehyde (DMHF) or put to genitalia microvials filled with glycerine and pinned with the respective

specimen. Measurements were taken using ocular micrometre. Intervals of measured values are followed by data in parentheses: arithmetic mean  $\pm$  standard deviation,  $n$  = number of measured specimens. Total length (TL) was measured from the anterior margin of pronotum to the apices of elytra; elytral length (EL) was measured from the apex of scutellar shield to the apices of the elytra; elytral width (EW) was measured at the widest point of elytra. Digital photographs were taken using Canon EOS 5D mark II camera attached to Zeiss Axio Zoom.V16 stereomicroscope. Image stacks were produced manually, combined using Zerene Stacker software and edited in Adobe Photoshop CC.

Terminology used in morphological descriptions follows Lawrence and Ślipiński (2010) and is supplemented by terminology used by Lu et al. (1997) for the genitalia.

Specimen data are given in the following format: number of specimens and sex, depository: exact data from labels in quotation marks; slash indicates separate labels; author's remarks are given in square brackets.

Principal Component Analysis (PCA) was conducted in PAST 3.12 software (Hammer et al. 2001), based on variance-covariance matrix of 12 morphometric characters: HL, HW, PL, PW, EL, EW, PTiL, MsTiL, MtTiL, RPrL, BRPr, and LPrL. Measurements were taken from 59 male specimens (including holotypes / lectotypes) assigned to eight taxa (*M. hirtipes* Schilsky, 1895, *M. podlussanyi* Czető, 1990, *M. aegae* Franciscolo, 1949, *M. pseudohirtipes pseudohirtipes* Ermisch, 1965, *M. pseudohirtipes krotosensis* Czető, 1990, *M. fageli* Ermisch, 1969, *M. geronensis* Ermisch, 1977, and *M. istricea* Ermisch, 1977). Lectotype of *M. purpurascens* was not measured because of its bad condition. Plot created in PAST 3.12 was subsequently edited in Adobe Illustrator CS6.

All nomenclatorial acts follow regulations of ICZN (1999).

Overall 149 specimens from following depositories were examined:

- CSB** collection of Dávid Selnekovič, Bratislava, Slovakia  
**HNHM** Hungarian Natural History Museum, Budapest, Hungary  
**MCST** Museo Civico di Storia Naturale, Trieste, Italy  
**MNCN** Museo Nacional de Ciencias Naturales, Madrid, Spain  
**MNHU** Museum für Naturkunde der Humboldt Universität, Berlin, Germany  
**MZFN** Museo Zoologico dell'Università Federico II, Naples, Italy  
**SNSD** Senckenberg Naturhistorische Sammlungen, Dresden, Germany

Abbreviations of measured characters:

<b>BLPr</b>	basal part of left paramere length	<b>LabL</b>	length of labrum
<b>BRPr</b>	basal part of right paramere length	<b>LabW</b>	width of labrum
<b>EL</b>	length of elytra	<b>LPrL</b>	length of left paramere
<b>EW</b>	width of elytra (combined)	<b>MsTiL</b>	length of mesotibiae
<b>HL</b>	length of head	<b>MsTrL</b>	length of mesotarsi
<b>HW</b>	width of head	<b>MtTiL</b>	length of metatibiae

<b>MtTrL</b>	length of metatarsi	<b>St8W</b>	width of sternite VIII
<b>PL</b>	length of pronotum	<b>TVtL</b>	length of terminal abdominal ventrite
<b>PTiL</b>	length of protibiae	<b>TL</b>	total length
<b>PTrL</b>	length of protarsi	<b>TPaLL</b>	length of terminal segment of maxillary palpi
<b>PW</b>	width of pronotum	<b>TPaLW</b>	width of terminal segment of maxillary palpi.
<b>PygL</b>	length of pygidium		
<b>RPrL</b>	length of right paramere		
<b>St8L</b>	length of sternite VIII		

## Data resources

The data underpinning the analyses reported in this paper are deposited at GBIF, the Global Biodiversity Information Facility, <https://doi.org/10.15468/pkhkul>

## Taxonomy

### *Mordellistena* Costa, 1854

*Mordellistena* Costa, 1854: 16 [type species: *Mordellistena confinis* Costa, 1854: 18]

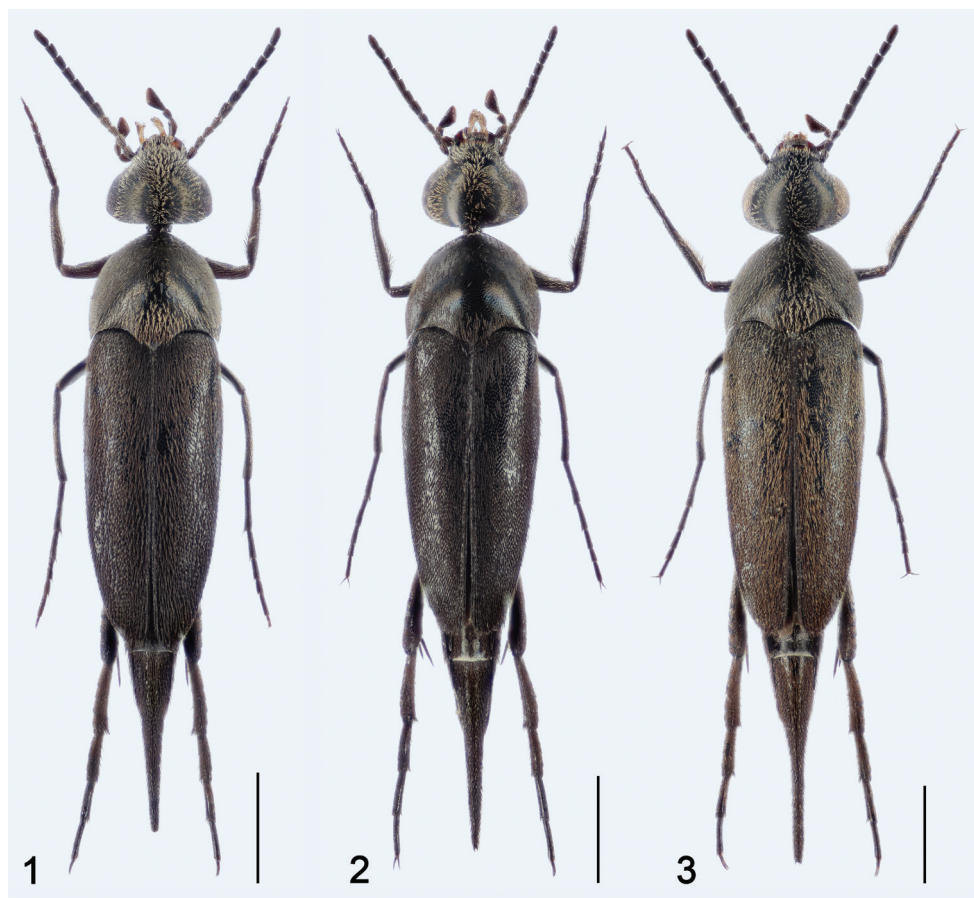
### *Mordellistena hirtipes* species complex

**Diagnosis.** Integument including legs and maxillary palpi completely black; metatibial spurs black; pubescence of dorsum yellowish, sometimes darkened in apical portions of elytra but never completely dark. Antennomeres I–IV shorter and narrower than following ones (Figs 5A, B, 6A, B, 7A, B). Maxillary palpomere II expanded in males, bearing very long setae on ventral surface (Figs 4A, 6C, 7C). Metatibiae at least with three lateral ridges, all parallel to apical margin of tibia. Metatarsomeres I and II with ridges.

### *Mordellistena* (s. str.) *hirtipes* Schilsky, 1895

Figs 1, 4A, B, 5A–J

*Mordellistena hirtipes* Schilsky, 1895: 46 (original description); Heyden et al. 1906: 455 (catalogue); Csiki 1915: 35 (catalogue); Schaufuss 1916: 766 (distribution); Ermisch 1963: 62 (distribution); Ermisch 1965: 268 (distribution); Batten 1976: 168 (distribution); Batten 1977: 171–173 (distribution, figures, key); Horák 1990: 136 (lectotype and paralectotypes designation, figures); Odnosum 2003: 36–37, 40, 46 (key, figures, distribution); Horák 2008: 98 (catalogue, distribution); Odnosum 2010: 153, 192–194 (key, description, figures, distribution); Samin et al. 2016: 24 (distribution); Ruzzier et al. 2017: 152 (distribution).



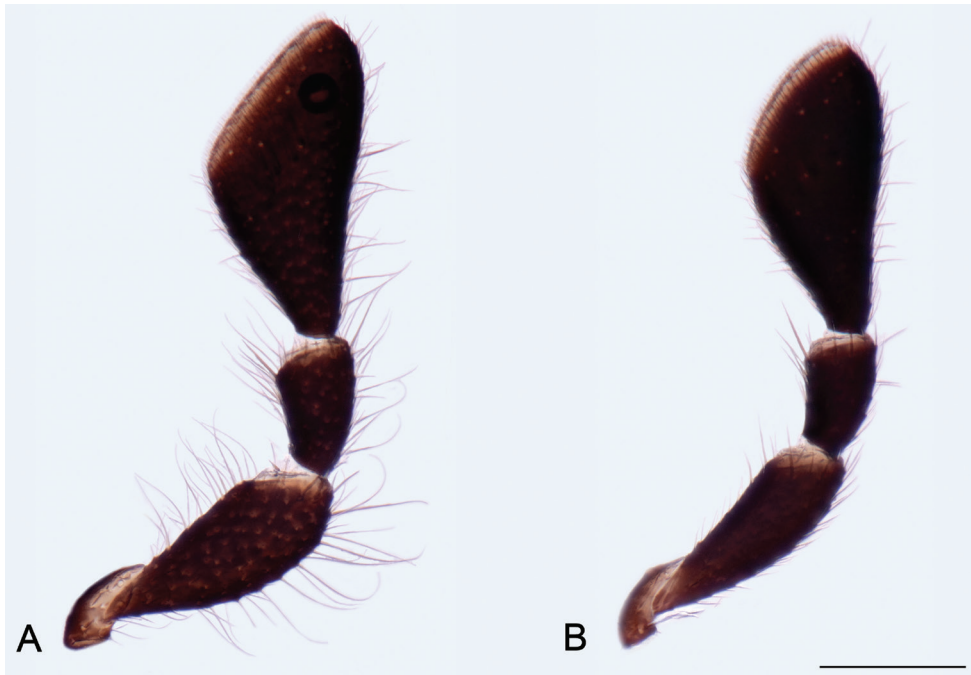
**Figures 1–3.** **1** *Mordellistena hirtipes* Schilsky, 1895, male **2** *M. pseudohirtipes* Ermisch, 1965, male **3** *M. geronensis* Ermisch, 1977, male. Scale bar: 0.50 mm.

*Mordellistena aegae* Franciscolo, 1949: 90, 93 syn. nov. (original description); Batten 1977: 169 (remarks); Horák 2008: 96 (catalogue).

*Mordellistena podlussanyi* Czető, 1990: 26–29 syn. nov. (original description); Horák 2008: 100 (catalogue).

**Type locality.** Attalia [Turkey].

**Type material examined.** *M. hirtipes*: LECTOTYPE (by designation of Horák (1990: 136)): 1 ♂, MNHU: “Attalia Reitter [hand written] / *hirtipes* Schils. [hand written] / Type [red label] / Zool. Mus. Berlin / [card with dissected genitalia] / LECTOTYPUS [red label] / *Mordellistena hirtipes* Schils. J. Horák det. 1985”; PARALECTOTYPES (by designation of Horák (1990: 136)): 4 ♂♂, 3 ♀♀, MNHU: “Attalia Reitter [hand written] / Coll. Schilsky / Type [red label] / Zool. Mus. Berlin / PARALECTOTYPUS [red label] / *Mordellistena hirtipes* Schils. J. Horák det. 1985”; 17 ♂♂, 9 ♀♀, MNHU: “♂ [or] ♀ / Coll. Schilsky / Type [red label] / Zool. Mus. Berlin / PARALECTOTYPUS [red label] / *Mordellistena hirtipes* Schils. J. Horák det. 1985”; 1 ♀, MNHU: “Syrien Kaifa.



**Figure 4.** *Mordellistena hirtipes* Schilsky, 1895, maxillary palpi: **A** male **B** female. Scale bar 0.10 mm.

Reitter. / Coll. Schilsky / Type [red label] / Zool. Mus. Berlin / PARALECTOTYPUS [red label] / *Mordellistena hirtipes* Schils. J. Horák det. 1985"; 1 ♀, MNHU: "Morea Hagios Wlassis Brenske / *hirtipes* [hand written] / Type [red label] / Zool. Mus. Berlin / PARALECTOTYPUS [red label] / *Mordellistena hirtipes* Schils. J. Horák det. 1985". *M. aegea*: HOLOTYPE: 1 ♂, MCST: "Pod. Sper. Coo 7. VII.–VIII. [Podere sperimentale, Kos Island; hand written] / 7. VII.–VIII. Pod. Sper. Coo [hand written] / 19 [blue label] / [card with dissected median lobe] / Olo [hand written] Typus / [cover slides with dissected parameres and sternite VIII] / *Mordellistena aegea* n. sp. DET. FRANCESCOLO / HOLOTYPE *Mordellistena aegea* Franciscolo, 1949 D. Selnekovič labelled 2018 / *Mordellistena* (s. str.) *hirtipes* Schilsky, 1895 D. Selnekovič det. 2018". *M. podlussanyi*: HOLOTYPE: 1 ♂, HNHM: "♂ / [transparent plastic board with dissected genitalia] / Krotos KRÉTA / 1981. V. 12. leg. Podlussány / Holotypus *Mordellistena podlussanyi* Czető, 1988 [red label, hand written] / *Mordellistena* (s. str.) *hirtipes* Schilsky, 1895 D. Selnekovič det. 2017".

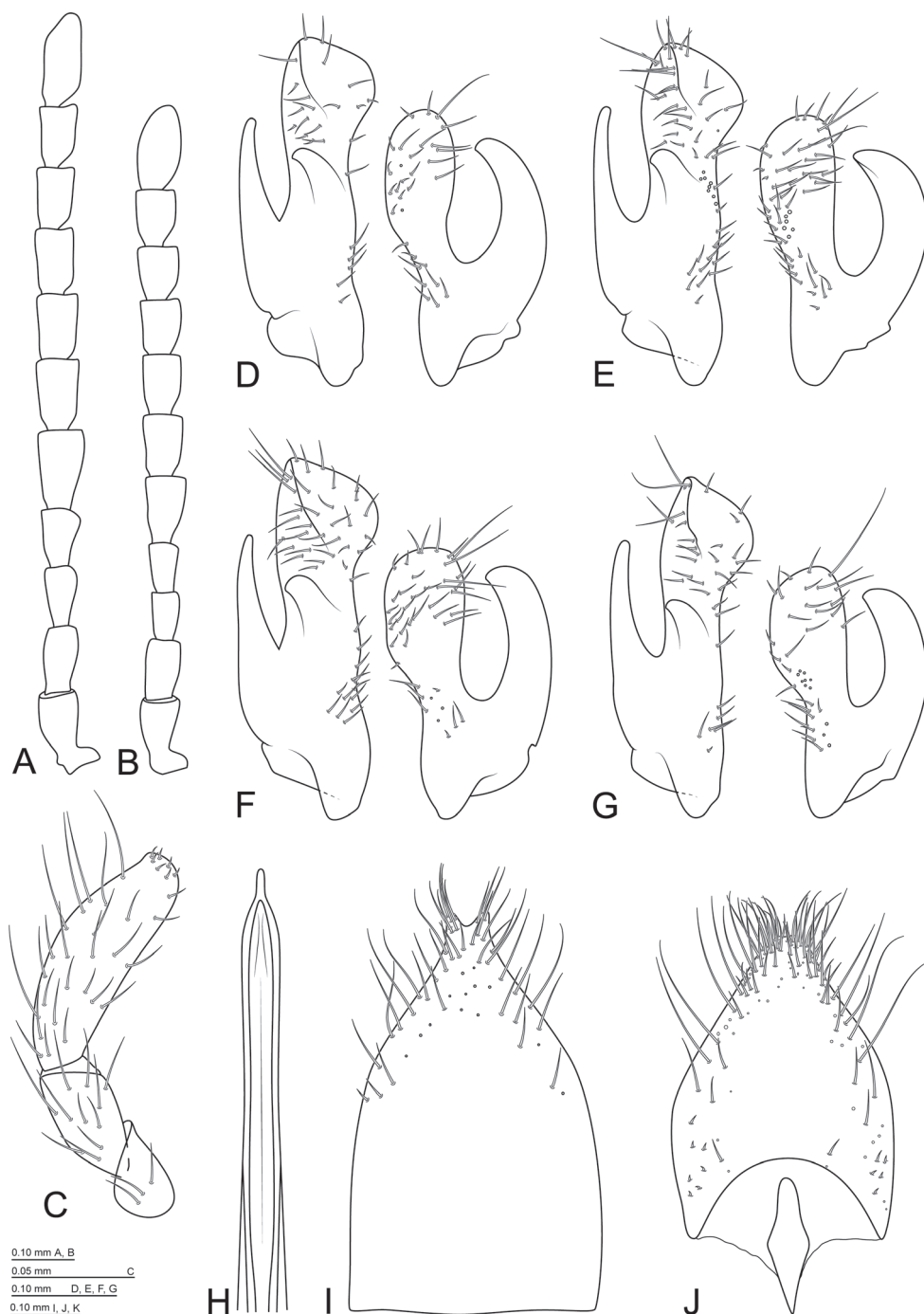
**Additional material examined. Croatia:** 1 ♂, HNHM: "Dalmatia leg. Endrödy-Younga / Dubrovnik Ins. Lokrum / 1958. VIII. 7. Kätscher / *Mordellistena hirtipes* Schils. det. R. Batten 1979 / *Mordellistena* (s. str.) *hirtipes* Schilsky, 1895 D. Selnekovič det. 2017". **Cyprus:** 1 ♂, HNHM: "Cyprus Laranka Glaszner / *Mordellistena hirtipes* Schils. det. R. Batten 1979 / *Mordellistena* (s. str.) *hirtipes* Schilsky, 1895 D. Selnekovič det. 2017"; 12 ♂♂, 2 ♀♀, CSB: "Cyprus W, Limassol env., Germasogeia Reservoir 34°45'19"N, 33°05'36"E, 27. IV. 2018 D. Selnekovič leg. / *Mordellistena* (s. str.) *hirtipes* Schilsky, 1895 D. Selnekovič det. 2018". **Greece:** 1 ♂, SNSD: "♂ / Insel Rhodos 24.5.–5.8.62 /



Stadt Rhodos Umg. Dr Mand / Genitalpräparat / MORDELLISTENA pseudohirtipes Erm. K. Ermisch det. 19 / Mordellistena (s. str.) hirtipes Schilsky, 1895 D. Selnekovič det. 2017"; 1 ♂, HNHM: "Crete Biró / Ins. Dia 25.–29. V. / Mordellistena hirtipes Schils. det. R. Batten 1980 / Mordellistena (s. str.) hirtipes Schilsky, 1895 D. Selnekovič det. 2017". **Montenegro:** 3 ♂♂, 3 ♀♀, CSB: "Montenegro SW Bar city env. 42°07'56"N, 19°07'33"E, 22. VI. 2011 D. Selnekovič / Mordellistena (s. str.) hirtipes Schilsky, 1895 D. Selnekovič det. 2012". 2 ♂♂, 3 ♀♀, CSB: "Montenegro SW Bar city–Volujica hill 242°04'16"N, 19°06'10"E, 20. VI. 2011 D. Selnekovič / Mordellistena (s. str.) hirtipes Schilsky, 1895 D. Selnekovič det. 2012". 2 ♂♂, 2 ♀♀, CSB: "Montenegro SW Bar city–Stari Bar 42°05'31"N, 19°07'58"E, D. Selnekovič 19. VI. 2011 / Mordellistena (s. str.) hirtipes Schilsky, 1895 D. Selnekovič det. 2012". 1 ♂, CSB: "Montenegro SW Bar city, on Daucus 42°06'N, 19°06'E, 19. VI. 2011 D. Selnekovič 2011 / Mordellistena (s. str.) hirtipes Schilsky, 1895 D. Selnekovič det. 2012". **Spain:** 1 ♂, 1 ♂, SNSD: "Spanien, Prov. Gerona Tossa de mar A. Kampf, VII–VIII 35 / Paratypus Mordellistena geronensis Ermisch / Mordellistena (s. str.) hirtipes Schilsky, 1895 D. Selnekovič det. 2017". 1 ♂, SNSD: "Nordostspanien Costa brava 27. 7. 53 Dr David / Paratypus / PARATYPUS Mordellistena (s. str.) geronensis Ermisch, 1977 Selnekovič labelled 2017 [red label] / Mordellistena (s. str.) hirtipes Schilsky, 1895 D. Selnekovič det. 2017".

**Differential diagnosis.** Parameres of *M. hirtipes* are shorter in proportion to the body dimensions than in *M. pseudohirtipes* and *M. purpurascens* (EL/LPrL ratio in *M. hirtipes*: 7.87–9.17 ( $8.48 \pm 0.40$ ,  $n = 14$ ), *M. pseudohirtipes*: 4.65–7.17 ( $5.89 \pm 0.71$ ,  $n = 25$ ) and *M. purpurascens*: 4.42–5.84 ( $4.98 \pm 0.35$ ,  $n = 19$ ); EL/RPrL ratio in *M. hirtipes*: 10.07–11.89 ( $11.10 \pm 0.50$ ,  $n = 14$ ), *M. pseudohirtipes*: 5.91–8.63 ( $7.42 \pm 0.72$ ,  $n = 25$ ) and *M. purpurascens*: 5.57–6.94 ( $6.19 \pm 0.41$ ,  $n = 19$ ). Ventral branch of the right paramere is in *M. hirtipes* (Fig. 5D–G) usually distinctly shorter than the dorsal one whereas in *M. pseudohirtipes* (Fig. 6E–H) and *M. purpurascens* (Fig. 7G–J) it is subequal or longer. Basal part of the left paramere is in *M. hirtipes* (Fig. 5D–G) distinctly shorter than in *M. purpurascens* (Fig. 7G–J). Sides of elytra less convergent apically than in *M. pseudohirtipes* and *M. purpurascens*. Terminal maxillary palpomere in females shorter and broader, its inner angle is more acute (Fig. 4B) than in *M. pseudohirtipes* (Fig. 6D) and *M. purpurascens* (Fig. 7D).

**Redescription.** Measurements: TL: ♂♂ 3.21–3.95 mm ( $3.51 \pm 0.24$  mm,  $n = 13$ ), ♀♀ 2.79–4.68 mm ( $3.44 \pm 0.52$  mm,  $n = 9$ ); HL: ♂♂ 0.72–0.93 mm ( $0.81 \pm 0.06$  mm,  $n = 14$ ), ♀♀ 0.67–0.80 mm ( $0.74 \pm 0.04$  mm,  $n = 9$ ); HW: ♂♂ 0.87–1.02 mm ( $0.94 \pm 0.05$  mm,  $n = 14$ ), ♀♀ 0.77–0.96 mm ( $0.87 \pm 0.06$  mm,  $n = 9$ ); PL: ♂♂ 1.04–1.33 mm ( $1.17 \pm 0.11$  mm,  $n = 14$ ), ♀♀ 0.94–1.20 mm ( $1.09 \pm 0.08$  mm,  $n = 9$ ); PW: ♂♂ 1.06–1.37 mm ( $1.23 \pm 0.10$  mm,  $n = 14$ ), ♀♀ 0.98–1.29 mm ( $1.16 \pm 0.10$  mm,  $n = 9$ ); EL: ♂♂ 2.34–2.96 mm ( $2.65 \pm 0.19$  mm,  $n = 14$ ), ♀♀ 2.08–2.79 mm ( $2.48 \pm 0.21$  mm,  $n = 9$ ); EW: ♂♂ 1.10–1.43 mm ( $1.25 \pm 0.11$  mm,  $n = 14$ ), ♀♀ 1.10–1.36 mm ( $1.23 \pm 0.09$  mm,  $n = 9$ ); PTiL: ♂♂ 0.70–0.87 mm ( $0.77 \pm 0.05$  mm,  $n = 14$ ), ♀♀ 0.56–0.73 mm ( $0.65 \pm 0.06$  mm,  $n = 9$ ); PTrL: ♂♂ 0.65–0.74 mm ( $0.71 \pm 0.03$  mm,  $n = 11$ ), ♀♀ 0.57–0.66 mm ( $0.63 \pm 0.03$  mm,  $n = 7$ ); MsTiL: ♂♂ 0.83–1.10 mm ( $0.97 \pm 0.08$  mm,  $n = 14$ ), ♀♀ 0.78–1.01 mm ( $0.87 \pm 0.07$  mm,  $n = 9$ ); MsTrL: ♂♂ 1.06–1.30 mm ( $1.16 \pm 0.06$  mm,  $n = 11$ ), ♀♀ 0.91–1.13 mm ( $1.05$



**Figure 5.** *Mordellistena hirtipes* Schilsky, 1895: **A** antenna, male **B** antenna, female **C** labial palpus, female **D** parameres, lectotype **E** parameres, holotype of *M. podlussanyi* **F** parameres, Greece **G** parameres, Spain **H** aedeagal median lobe **I** sternite VIII, male **J** sternite VIII, female.

$\pm 0.07$  mm,  $n = 9$ ); MtTiL: ♂♂ 0.69–0.91 mm ( $0.81 \pm 0.05$  mm,  $n = 14$ ), ♀♀ 0.66–0.86 mm ( $0.76 \pm 0.06$  mm,  $n = 9$ ); MtTrL: ♂♂ 1.48–1.87 mm ( $1.67 \pm 0.11$  mm,  $n = 10$ ), ♀♀ 1.33–1.69 mm ( $1.51 \pm 0.11$  mm,  $n = 9$ ); PygL: ♂♂ 1.42–1.85 mm ( $1.58 \pm 0.12$  mm,  $n = 13$ ), ♀♀ 1.17–1.56 mm ( $1.37 \pm 0.12$  mm,  $n = 9$ ); TVtL: ♂♂ 0.54–0.87 mm ( $0.68 \pm 0.10$  mm,  $n = 13$ ), ♀♀ 0.44–0.79 mm ( $0.63 \pm 0.11$  mm,  $n = 9$ ); LPrL: 0.29–0.35 mm ( $0.31 \pm 0.02$  mm,  $n = 14$ ); RPrL: 0.22–0.26 mm ( $0.24 \pm 0.01$  mm,  $n = 14$ ); St8L: ♂♂ 0.57–0.63 mm ( $n = 2$ ); St8W: ♂♂ 0.38–0.40 mm ( $n = 2$ ).

Habitus illustrated in Fig. 1. Body slender, widest at the end of anterior third of elytra. Integument black. Head and pronotum covered with yellowish pubescence; pubescence on elytra yellowish in proximal half, gradually darkened towards apices, sometimes with reddish or violet metallic sheen; venter covered with yellowish pubescence, darkened along posterior margins of ventrites 3–5.

Head moderately convex dorsally, wider than long, widest before middle, HW/HL ratio: ♂♂ 1.10–1.23 ( $1.17 \pm 0.04$ ,  $n = 14$ ), ♀♀ 1.13–1.23 ( $1.17 \pm 0.03$ ,  $n = 9$ ). Dorsal surface with microreticulation and small round punctures bearing short setae; ventral surface with transverse microreticulation and sparse, small punctures bearing short setae; small medial triangular part before gula without punctures. Occipital margin rounded in dorsal aspect, straight or slightly concave if seen from behind. Eyes oval, finely faceted with short interfacetal setae. Anterior margin of clypeus straight. Labrum transverse, approximately two times as wide as long, anterior margin straight; surface with microreticulation and small, round punctures bearing short setae. Antennae rather long, slightly serrate (Fig. 5A, B); antennomeres I–IV subequal in length, slightly shorter and slenderer than following ones; antennomeres V–X in males 1.40–1.60 $\times$ , in females 1.20–1.30 $\times$  as long as wide; antennomere XI oval,  $\sim 2.30\times$  as long as wide. Mandibles symmetrical, bidentate, lateral portions microreticulated with short setae, outer distal portion with group of seven long sensilla; mola well developed, minutely dentate; protheca well developed, setose. Galea gradually expanded toward apex, covered with apically expanded sensilla; lacinia setose medio-apically, reaching half of length of galea. Maxillary palpomere II distinctly expanded with long setae on ventral side in males (Fig. 4A); not expanded, without long setae in females (Fig. 4B); maxillary palpomere III short,  $\sim 1.50\times$  as long as wide; terminal maxillary palpomere broadly securiform, inner angle situated around middle, TPall/TPalW ratio: ♂♂ 1.95–2.20 ( $2.09 \pm 0.09$ ,  $n = 14$ ), ♀♀ 1.95–2.20 ( $2.10 \pm 0.08$ ,  $n = 9$ ). Terminal labial palpomere fusiform, bearing sparse long sensilla on whole surface, and group of short sensilla at apex (Fig. 5C).

Pronotum moderately convex, approximately as long as wide, widest just behind middle, PW/PL ratio: ♂♂ 1.00–1.09 ( $1.05 \pm 0.03$ ,  $n = 14$ ), ♀♀ 1.02–1.07 ( $1.06 \pm 0.02$ ,  $n = 9$ ). Surface finely microreticulate, with small, rasp-like punctures bearing flat seta. Anterior margin rounded, slightly produced mesally, anterior angles broadly rounded; lateral carinae emarginated in lateral aspect; posterior margin forming short mesal lobe, emarginated before posterior angles; posterior angles rectangular in lateral aspect. Posterior marginal bead interrupted before posterior angles. Hypomeron triangular with round concavity posteriorly. Prosternum in front of procoxae narrow, expanded laterally; prosternal process incomplete, narrow, slightly constricted in the

middle. Scutellar shield small, triangular, covered with small, round punctures bearing short setae. Mesoventral process  $\sim 0.50\times$  as wide as mesofemur, parallel-sided, truncate at apex. Metaventrite strongly convex in the middle; surface weakly microreticulated with small, transversally confluent, rasp-like punctures; posterior margin in the produced mesally; discrimen rather indistinct. Metanepisternum trapezoidal, narrowed posteriorly, dorsal margin emarginated, ventral margin straight.

Elytra long, narrow, widest in anterior 1/3, EL/EW ratio: ♂♂ 2.02–2.26 ( $2.12 \pm 0.08$ ,  $n = 14$ ), ♀♀ 1.88–2.07 ( $2.01 \pm 0.05$ ,  $n = 9$ ). Surface with weak transverse microreticulation and rasp-like punctures bearing flat setae. Lateral margins regularly rounded, apices separately rounded.

Protibiae in males expanded basally, bearing fringe of long setae in basal 1/3; PTiL/PTrL ratio: ♂♂ 1.02–1.17 ( $1.08 \pm 0.05$ ,  $n = 11$ ), ♀♀ 0.95–1.12 ( $1.03 \pm 0.05$ ,  $n = 7$ ). Protarsomere I as long as two following tarsomeres combined; protarsomere IV simple, parallel-sided, shallowly emarginate at apex. Claws on protarsi with three, on meso and metatarsi with four denticles. Mesotibiae slightly bent inwards; mesotarsus longer than tibia, MsTiL/MsTrL ratio: ♂♂ 0.78–0.89 ( $0.82 \pm 0.03$ ,  $n = 11$ ), ♀♀ 0.79–0.90 ( $0.83 \pm 0.03$ ,  $n = 9$ ). Metacoxae large, anterior margin straight, posterior margin broadly rounded. Metatibiae bearing short subapical ridge and 3–4 lateral ridges parallel with apical margin of tibia, reaching 1/3 of tibial width. Metatibial spurs black, inner one  $\sim 1.30\times$  as long as outer one. Metatarsomere I bearing 4–5 short ridges, metatarsomere II bearing 2–3 ridges, metatarsomeres III and IV without ridges. Metatarsus  $\sim 2.00\times$  as long as metatibia, MtTrL/MtTiL ratio: ♂♂ 1.97–2.18 ( $2.07 \pm 0.06$ ,  $n = 10$ ), ♀♀ 1.89–2.11 ( $1.98 \pm 0.06$ ,  $n = 9$ ).

Pygidium long, slender, narrowly truncate at apex, PygL/TVtL ratio: ♂♂ 2.00–3.04 ( $2.36 \pm 0.26$ ,  $n = 13$ ), ♀♀ 1.76–3.14 ( $2.22 \pm 0.37$ ,  $n = 9$ ). Apical margin of terminal abdominal ventrite arcuate.

Male genitalia: sternite VIII with long setae in apical part, apical margin produced and weakly bilobed mesally (Fig. 5I), St8L/St8W ratio: ♂♂ 1.49–1.59 ( $n = 2$ ). Sternite IX long, slender, arrow-shaped, with medial longitudinal keel at apex. Parameres (Fig. 5D–G) rather short, EL/LPrL ratio: 7.87–9.17 ( $8.48 \pm 0.40$ ,  $n = 14$ ); EL/RPrL ratio: 10.07–11.89 ( $11.10 \pm 0.50$ ,  $n = 14$ ); LPrL/RPrL ratio: 1.24–1.37 ( $1.31 \pm 0.04$ ,  $n = 14$ ). Left paramere with short basal part, LPrL/BLPr ratio: 1.88–2.12 ( $1.98 \pm 0.08$ ,  $n = 14$ ); dorsal branch expanded and obliquely truncate apically; ventral branch slender, slightly bent medially, pointed at apex. Right paramere rather short, ventral branch distinctly shorter than dorsal one, dorsally bent; dorsal branch expanded and rounded apically. Median lobe long, slender, apical part slightly expanded (Fig. 5H). Phallobase with short tubular process (approximately 1/6 of total length) and long, slender furca.

Female genitalia: sternite VIII with apical protuberance and long setae alongside apical and lateral margins, spiculum ventrale short, broadly clavate (Fig. 5J); St8L/St8W ratio: ♀ 1.36 ( $n = 1$ ).

**Sexual dimorphism.** Females are usually more robust; with shorter antennae. Maxillary palpomere II is not expanded in females and without long setae on ventral side. Terminal maxillary palpomere is shorter in females, with angles more rounded. Protibiae are not expanded in females, without long setae in basal portion.

**Distribution.** Croatia, Cyprus, France, Greece, Iran, Israel, Jordan, Macedonia, Montenegro, Romania, Spain, Syria, Turkey, Turkmenistan, Ukraine. *Mordellistena hirtipes* is reported here for the first time from Croatia, Montenegro, and Spain. Csiki (1915) mentioned also “Österreich” (Austria); however, this information is probably based on a misidentification.

**Biology.** Adults were found on the flowers of *Daucus* sp. (Apiaceae) and *Helichrysum* sp. (Asteraceae) on dry grasslands and in urban environment.

**Remarks.** Franciscolo (1949) described *M. aegea* based on three specimens from Kos island (Greece). Batten (1977) mentioned that this species does not belong to the *micans* group because the antennomere IV and V are equal in length. Examination of holotype revealed that this specimen belongs to *M. hirtipes*. We consider this taxon as a junior synonym of *M. hirtipes*.

Czető (1990) described *M. podlussanyi* based on a single male specimen from Crete. He mentioned in the original description that the maxillary palpomere II is not dilated. Examination of the holotype actually revealed, that the palpomere is expanded, and any other differences which could separate this taxon from *M. hirtipes* were found. This interpretation is also supported by the results of PCA analysis (Fig. 10A). We propose *M. podlussanyi* as a junior synonym of *M. hirtipes*.

In HNHM collections, there are three specimens of *M. hirtipes*, labelled by Reitter as holotype and paratypes. However, these specimens are not mentioned in original description and labels were probably added subsequently, after the description. These specimens are not parts of the type series.

### ***Mordellistena* (s. str.) *pseudohirtipes* Ermisch, 1965**

Figs 2, 6A–J

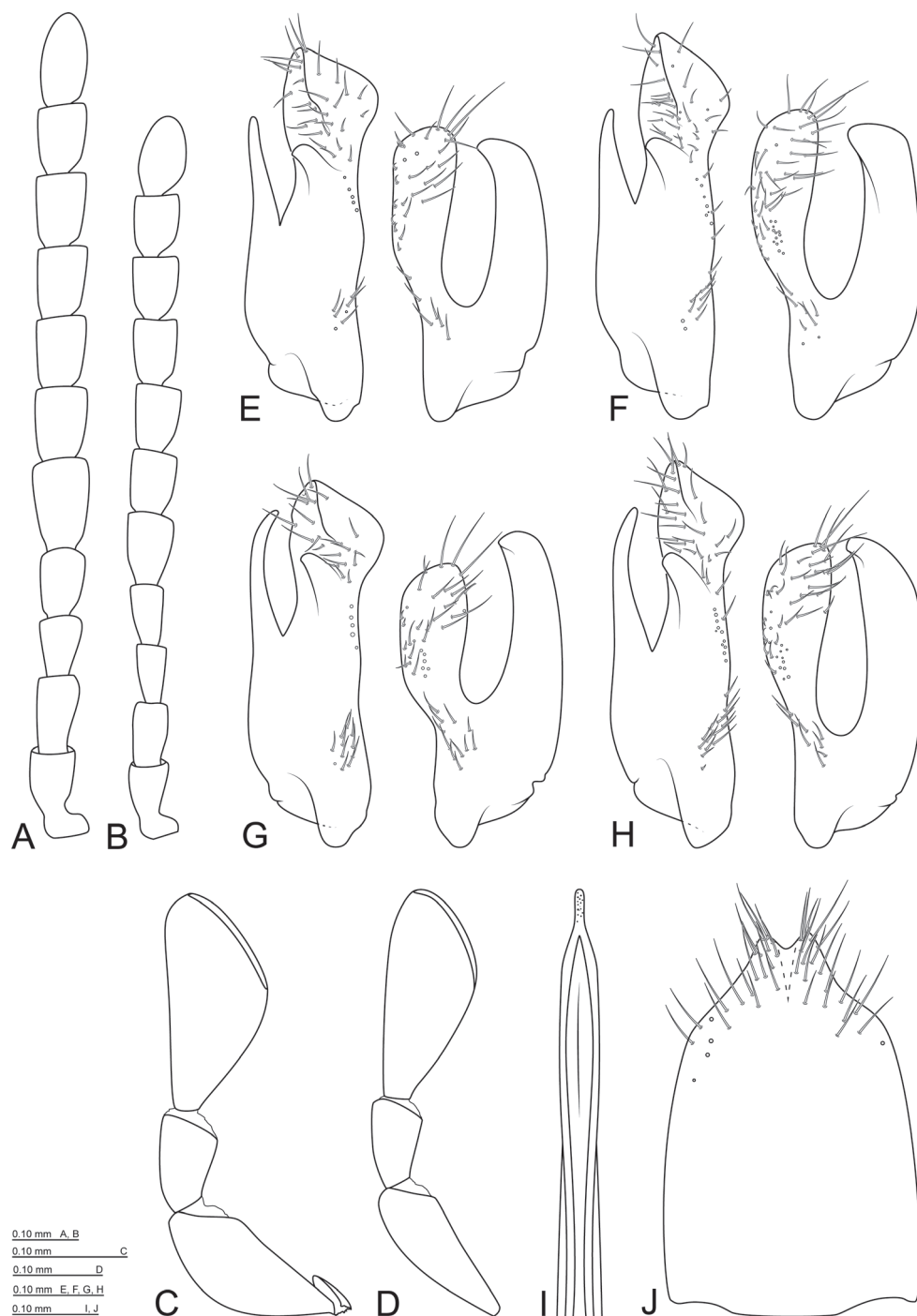
*Mordellistena pseudohirtipes* Ermisch, 1965: 268 (original description); Batten 1976: 168 (distribution); Batten 1977: 171–173 (distribution, figures, key); Plaza 1983: 574 (distribution, biology); Czető 1990: 28–29 (description, figure); Franciscolo 1995: 12 (distribution); Horák 2008: 100 (distribution); Odnosum 2010: 153, 194–195 (key, description, distribution); Ruzzier 2013: 109 (distribution).

*Mordellistena fageli* Ermisch, 1969: 112 syn. nov. (original description); Batten 1976: 168 (distribution); Plaza 1983: 575–576 (distribution, biology); Horák 1983: 13 (remarks); 2008: 97 (distribution).

*Mordellistena pseudohirtipes krotosensis* Czető, 1990: 28 syn. nov. (original description); Horák 2008: 100 (distribution).

**Type locality.** Nessebar env., Bulgaria.

**Type material examined.** *M. pseudohirtipes pseudohirtipes*: HOLOTYPE: 1 ♂, SNSD: “♂ / Genitalpräparat / Bulgaria Umg. Nessebar Juli 1961 leg. BECH / Holotypus [red label] / MORDELLISTENA pseudohirtipes Erm. K Ermisch det. 19 / Coll. ERMISCH Leipzig Ankauf 1970 / Staatl. Museum für Tierkunde Dresden”; PARATYPE: 1 ♀,



**Figure 6.** *Mordellistena pseudohirtipes* Ermisch, 1965: **A** antenna, male **B** antenna, female **C** maxillary palpus, male **D** maxillary palpus, female **E** parameres, holotype **F** parameres, holotype of *M. pseudohirtipes* ssp. *krotosensis* **G** parameres, holotype of *M. fageli* **H** parameres, France **I** aedeagal median lobe **J** sternite VIII, male.



SNSD: “♀ / Bulgaria Umg. Nessebar Juli 1961 leg. BECH / Allotypus [red label] / MORDELLISTENA pseudohirtipes Erm. K Ermisch det. 19 / Coll. ERMISCH Leipzig Ankauf 1970 / Staatl. Museum für Tierkunde Dresden”. *M. pseudohirtipes krotosensis*: HOLOTYPE: 1 ♂, HNHM: “[transparent plastic board with dissected genitalia] / ♂ / Krotos KRÉTA / 1981. V. 12. leg. Podlussány / Holotypus Mordellistena pseudohirtipes Ermisch, 1965 ssp. krotosensis, Czető 1988 [red label] / Mordellistena (s. str.) pseudohirtipes Ermisch, 1965 D. Selnekovič det. 2017”. *M. fageli*: HOLOTYPE: 1 ♂, SNSD: “♂ / Genitalpräparat / Portugal: Algrave Caldas de Monchique V–1960 G. Fagel / R. I. Sc. N. B. I. G. 22.145 / Holotypus [red label] / coll. ERMISCH, Leipzig, Ankauf 1970 / Staatl. Museum für Tierkunde Dresden / HOLOTYPUS Mordellistena (s. str.) fageli Ermisch, 1969 D. Selnekovič labelled 2017 [red label] / Mordellistena (s. str.) pseudohirtipes Ermisch, 1965 D. Selnekovič det. 2017”; PARATYPE: 1 ♀, SNSD: “♀ / Portugal: Algarve Caldas de Monchique V–1960 G. Fagel / R. I. Sc. N. B. I. G. 22.145 / Allotypus [red label] / coll. ERMISCH, Leipzig, Ankauf 1970 / Staatl. Museum für Tierkunde Dresden / ALLOTYPUS (PARATYPUS) Mordellistena (s. str.) fageli Ermisch, 1969 D. Selnekovič labelled 2017 [red label] / Mordellistena (s. str.) pseudohirtipes Ermisch, 1965 D. Selnekovič det. 2017”.

**Additional material examined. Algeria.** 1 ♂, SNSD: “Algérie: Algérois, Kaddous 3–V–1954 G. Fagel / R. I. Sc. N. B. I. G. 19.867 / coll. ERMISCH, Leipzig, Ankauf 1970 / Staatl. Museum für Tierkunde Dresden / “Mordellistena (s. str.) pseudohirtipes Ermisch, 1965 D. Selnekovič det. 2017” [in collection as *M. fageli*]. **Bulgaria.** 1 ♂, SNSD: “♂ / Nessebar, Bulgaria 28. 5. – 10. 6. 1963 Karl Bleyl / MORDELLISTENA pseudohirtipes Erm. K. Ermisch det. 19”; 1 ♂, CSB: “Bulgaria mer. occ. Sandanski (→ Liljanovo) 5. – 10. 1976 Karel Majer lgt. / Mordellistena (s. str.) pseudohirtipes Ermisch, 1965 D. Selnekovič det. 2016”. **France.** 2 ♂♂, SNSD: “♂ / Genitalpräparat / France Basses Alpes St. Michel l’Observat. 24. 7 – 10. 8. 63 Rudkjöb. / MORDELLISTENA pseudohirtipes Erm. K. Ermisch det. 19”; 1 ♂, SNSD: “♂ / Ardèche 10. 7. 65 Banne Balazuc / MORDELLISTENA pseudohirtipes Erm. K. Ermisch det. 19; 1 ♂ SNSD: “♂ / Genitalpräparat / Südfrankreich Camargue, 13. 6. 1952, leg. Freude / Mordellistena Lopezi Ermisch det. K. Ermisch 63” [in collection as *M. lopezi*]; 1 ♂, SNSD: “♂ / Genitalpräparat / Pyrenées or. Umg. Banyuls 30. 5.–10. 6. 53 / Mordellistena Lopezi Ermisch det. K. Ermisch 63” [in collection as *M. lopezi*]; 1 ♂, SNSD: “Banyuls Pyr. or. VI. 53 J. u. B. Bechyne / Museum Frey München” [in collection as *M. lopezi*]; 1 ♂, SNSD: “♂ / Gall. mer. Agay (Var) 18. 7. 58 W. Liebmann / Genitalpräparat” [in collection as *M. lopezi*]; 1 ♂, SNSD: “♂ / Genitalpräparat / Fr. Ardèche Bois de Paiolive 1. 7. 66 Balazuc [hand written] / Paratypus / Staatl. Museum für Tierkunde Dresden / PARATYPUS Mordellistena (s. str.) geronensis Ermisch, 1977, Selnekovič labelled 2017 [red label] / Mordellistena (s. str.) pseudohirtipes Ermisch, 1965 D. Selnekovič det. 2017” [in collection as *M. geronensis*]. **Georgia.** 1 ♂, SNSD: “♂ / Genitalpräparat / SSSR–Gruzie Tbilisi 7.57 R. Dvořák / MORDELLISTENA pseudohirtipes Erm. K. Ermisch det. 19 / Coll. ERMISCH Leipzig Ankauf 1970 / Staatl. Museum für Tierkunde Dresden”; 2 ♂♂, SNSD: “♂ / SSSR–Gruzie Tbilisi 7.57 R. Dvořák / MORDELLISTENA pseudohirtipes Erm. K. Ermisch det. 19”. **Greece.** 1 ♂, SNSD: “♂ / Genitalpräparat / Athos Daphni A. Schatzmayr / MORDELLISTENA pseudohirtipes Erm. K. Ermisch det. 19”; 1 ♂,

SNSD: “♂ / Genitalpräparat / Ephesus / J. Sahlb. / MORDELLISTENA pseudohirtipes Erm. K. Ermisch det. 19”; 1 ♂, HNHM: “Creta Biró / Amari 4. VII. 06 / Mordellistena pseudohirtipes Erm. det. R. Batten 1980 / Mordellistena (s. str.) pseudohirtipes Ermisch, 1965 D. Selnekovič det. 2017”. **Israel.** 1 ♂, CSB: “Israel Jerusalem 25. III. 2001, ??? leg. / Mordellistena s. str. pseudohirtipes Ermisch, 1965 D. Selnekovič det. 2014”; 1 ♂, HNHM: “Izrael Rehovot 1965. V. 20. Dr. Erdös / coll. Dr. J. Erdös / Mordellistena pseudohirtipes Erm. det. R. Batten 1980 / Mordellistena (s. str.) pseudohirtipes Ermisch, 1965 D. Selnekovič det. 2017”. **Italy.** 1 ♂, SNSD: “♂ / Genitalpräparat / Sicilia Magara d. V. 16. 5. 61 W. Liebmam” [in collection as *M.lopezi*]. **Macedonia.** 1 ♂, SNSD: “♂ / Veles, Mac. 23. – 25. 5. 55. leg. F. Schubert / Genitalpräparat / MORDELLISTENA pseudohirtipes Erm. K. Ermisch det. 19”. **Montenegro.** 2 ♂♂, 1 ♀, CSB: “Montenegro S Skadarske jazero lake N, Virpazar village env. D. Selnekovič 21. VI. 2011 / Mordellistena pseudohirtipes Ermisch, 1965 D. Selnekovič det. 2012”. **Spain.** 1 ♂, SNSD: “♂ / Genitalpräparat / Son Española 1–VI–1958 R. López / Paratypus [red label] / Mordellistena Lopezi Ermisch det. K. Ermisch / Mordellistena (s. str.) pseudohirtipes Ermisch, 1965 D. Selnekovič det. 2017” [in collection as *M.lopezi*]; 1 ♂, SNSD: “♂ / Genitalpräparat / SEVILLA Hi. m. Marismas, V. 1943 G. Frey, C. Koch / Mordellistena Lopezi Ermisch det. K. Ermisch 63 / Mordellistena (s. str.) pseudohirtipes Ermisch, 1965 D. Selnekovič det. 2017” [in collection as *M.lopezi*]; 1 ♂, CSB: “Spain, Málaga, Lagunas de Archidona, 800m 37°06'N, 04°18'40"W, 12.–14. V. 2018 E. Jendek / Mordellistena (s. str.) pseudohirtipes Ermisch, 1965 D. Selnekovič det. 2018”. **Ukraine.** 2 ♂♂, SNSD: “♂ / Genitalpräparat / Umgeb. Jalta Krim, Ende Juli 1965 leg. F. Hieke / MORDELLISTENA pseudohirtipes Erm. K. Ermisch det. 19”; 1 ♂, HNHM: “Krim Jaila 17. VI. 1956 leg. L. Horváth / Mordellistena pseudohirtipes Erm. det. R. Batten 1980 / Mordellistena (s. str.) pseudohirtipes Ermisch, 1965 D. Selnekovič det. 2017”.

**Differential diagnosis.** From *M. purpurascens* it differs in shorter parameres (EL/LPrL ratio: *M. pseudohirtipes*: 4.65–7.17 ( $5.89 \pm 0.71$ ,  $n = 25$ ), *M. purpurascens*: 4.42–5.84 ( $4.98 \pm 0.35$ ,  $n = 19$ ); EL/RPrL ratio: *M. pseudohirtipes*: 5.91–8.63 ( $7.42 \pm 0.72$ ,  $n = 25$ ), *M. purpurascens*: 5.57–6.94 ( $6.19 \pm 0.41$ ,  $n = 19$ )). Basal part of the left paramere (Fig. 6E–H) is shorter than in *M. purpurascens* (Fig. 7G–J). Body usually smaller (TL: *M. pseudohirtipes*: ♂♂ 2.47–4.05 mm ( $3.20 \pm 0.43$  mm,  $n = 25$ ) ♀♀ 3.26–4.47 mm ( $3.68 \pm 0.56$  mm,  $n = 3$ ), *M. purpurascens*: ♂♂ 3.10–4.42 mm ( $3.75 \pm 0.35$  mm,  $n = 19$ ), ♀♀ 3.31–4.42 mm ( $3.82 \pm 0.36$  mm,  $n = 14$ )). Differences between *M. hirtipes* are mentioned above.

**Redescription.** Measurements: TL: ♂♂ 2.47–4.05 mm ( $3.20 \pm 0.43$  mm,  $n = 25$ ) ♀♀ 3.26–4.47 mm ( $3.68 \pm 0.56$  mm,  $n = 3$ ); HL: ♂♂ 0.64–0.93 mm ( $0.75 \pm 0.09$  mm,  $n = 25$ ), ♀♀ 0.77–1.04 mm ( $0.87 \pm 0.12$  mm,  $n = 3$ ); HW: ♂♂ 0.70–1.06 mm ( $0.87 \pm 0.11$  mm,  $n = 29$ ), ♀♀ 0.87–1.20 mm ( $0.99 \pm 0.15$  mm,  $n = 3$ ); PL: ♂♂ 0.83–1.29 mm ( $1.05 \pm 0.14$  mm,  $n = 25$ ), ♀♀ 1.06–1.42 mm ( $1.19 \pm 0.16$  mm,  $n = 3$ ); PW: ♂♂ 0.83–1.39 mm ( $1.07 \pm 0.17$  mm,  $n = 29$ ), ♀♀ 1.12–1.67 mm ( $1.31 \pm 0.25$  mm,  $n = 3$ ); EL: ♂♂ 1.88–3.02 mm ( $2.37 \pm 0.31$  mm,  $n = 25$ ), ♀♀ 2.44–3.35 mm ( $2.75 \pm 0.42$  mm,  $n = 3$ ); EW: ♂♂ 0.81–1.46 mm ( $1.09 \pm 0.18$  mm,  $n = 25$ ), ♀♀ 1.17–1.69 mm ( $1.35 \pm 0.24$  mm,  $n = 6$ ); PTiL: ♂♂ 0.57–0.91 mm ( $0.70 \pm 0.10$  mm,  $n = 25$ ), ♀♀ 0.65–0.90 mm ( $0.74 \pm 0.11$  mm,  $n = 6$ ); PTrL: ♂♂ 0.52–0.84 mm ( $0.63 \pm 0.08$  mm,  $n = 24$ ), ♀♀ 0.60–0.80 mm ( $0.68 \pm 0.09$ ,  $n = 3$ ); MsTiL: 0.71–1.17 mm ( $0.87 \pm$

0.12 mm,  $n = 25$ ), ♀♀ 0.86–1.25 mm ( $0.99 \pm 0.18$  mm,  $n = 3$ ); MsTrL: ♂♂ 0.83–1.34 mm ( $1.02 \pm 0.15$  mm,  $n = 13$ ), ♀♀ 1.04–1.35 mm ( $n = 2$ ); MrTrL: ♂♂ 0.60–0.92 mm ( $0.74 \pm 0.09$  mm,  $n = 25$ ), ♀♀ 0.74–1.04 mm ( $0.84 \pm 0.14$  mm,  $n = 3$ ); MrTrL: ♂♂ 1.27–1.98 mm ( $1.59 \pm 0.20$  mm,  $n = 17$ ), ♀♀ 1.51–2.05 mm ( $n = 2$ ); PygL: ♂♂ 1.29–1.96 mm ( $1.54 \pm 0.18$  mm,  $n = 29$ ), ♀♀ 1.39–1.75 mm ( $1.57 \pm 0.14$  mm,  $n = 3$ ); TVtL: ♂♂ 0.56–1.25 mm ( $0.73 \pm 0.13$  mm,  $n = 25$ ), ♀♀ 0.50–0.71 mm ( $0.64 \pm 0.10$  mm,  $n = 3$ ); LPrL: 0.33–0.46 mm ( $0.40 \pm 0.03$  mm,  $n = 25$ ); RPrL: 0.26–0.37 mm ( $0.32 \pm 0.03$  mm,  $n = 25$ ); St8L: ♂ 0.47 mm ( $n = 1$ ); St8W: ♂ 0.31 mm ( $n = 1$ ).

Habitus given in Fig. 2. Body strongly elongate, slender, widest just behind humeri. Integument black, mouthparts sometimes paler. Pubescence on head pale yellowish, on pronotum yellowish to dark grey, on elytra yellowish in anterior 1/2, darkened towards apices, or completely dark grey, sometimes with reddish or purplish metallic sheen, on pygidium dark grey, on venter yellowish, darkened along posterior margins of abdominal ventrites.

Head moderately convex dorsally, wider than long, widest just before middle, HW/HL ratio: ♂♂ 1.08–1.23 ( $1.15 \pm 0.03$ ,  $n = 25$ ), ♀♀ 1.11–1.16 ( $1.13 \pm 0.02$ ,  $n = 3$ ). Dorsal surface weakly microreticulated with small, round punctures bearing short setae. Occipital margin rounded in dorsal aspect, straight, or slightly concave seen from behind. Eyes oval, completely reaching occiput, not expanded onto ventral surface, finely faceted, with short interfacetal setae. Anterior margin of clypeus straight. Labrum transverse, anterior margin straight or very slightly emarginate; surface microreticulation with small, round punctures and setae. Antennae slightly serrate (Fig. 6A, B); antennomeres I–IV subequal in length; antennomeres V–X longer and wider, in males  $\sim 1.30\times$ , in females  $\sim 1.20\times$  as long as wide; terminal antennomere elongate oval,  $\sim 1.90\times$  as long as wide. Galea gradually expanded toward apex, covered with apically expanded sensilla. Maxillary palpi (Fig. 6C–D) black; palpomere I very short; palpomere II distinctly expanded, with long setae on ventral side in males, not expanded, rather long and narrow in females; palpomere III short,  $\sim 1.50\times$  as long as wide; terminal palpomere in males broadly securiform, with inner angle situated around the middle, in females slenderer, with inner angle situated in apical 1/3; TPall/TPalW ratio: ♂♂ 1.80–2.30 ( $2.07 \pm 0.11$ ,  $n = 25$ ), ♀♀ 2.05–2.31 ( $2.21 \pm 0.12$ ,  $n = 3$ ).

Pronotum moderately convex, approximately as long as wide, PW/PL ratio: ♂♂ 0.97–1.12 ( $1.02 \pm 0.03$ ,  $n = 25$ ), ♀♀ 1.04–1.18 ( $1.10 \pm 0.06$ ,  $n = 3$ ). Surface finely transversally microreticulate, covered with rasp-like punctures, distance between punctures 2.00–4.00 times as long as the diameter, each puncture bears flat, pointed seta. Anterior margin rounded, slightly produced mesally, anterior angles broadly rounded; lateral carinae emarginated in lateral aspect; posterior margin forming short mesal lobe, emarginated before posterior angles; posterior angles in lateral aspect rectangular, acute. Posterior marginal bead interrupted before posterior angles. Scutellar shield small, triangular, with small, rasp-like punctures bearing setae. Metanepisternum trapezoidal, narrowed posteriorly, ventral margin straight, dorsal margin emarginate.

Elytra long and narrow, moderately convex, widest at the end of anterior 1/4, EL/EW ratio: ♂♂ 2.02–2.40 ( $2.18 \pm 0.10$ ,  $n = 25$ ), ♀♀ 1.99–2.08 ( $2.04 \pm 0.04$ ,  $n = 3$ ). Surface with weak transverse microreticulation and rasp-like punctures, these are larger and more densely arranged than those on pronotum, each puncture

bears flat seta. Lateral margins rather strongly convergent, regularly rounded; apices separately rounded.

Profemora slender, in males somewhat stouter than in females. Protibiae straight, in males distinctly expanded in basal half, here with fringe of long, thick setae; PTiL/PTrL ratio: ♂♂ 1.02–1.24 ( $1.11 \pm 0.05$ ,  $n = 25$ ), ♀♀ 1.02–1.13 ( $1.09 \pm 0.05$ ,  $n = 3$ ). Protarsomere I in females as long as two following tarsomeres combined, in males slightly longer; protarsomere IV simple, slightly shorter than previous one, shallowly emarginate at apex; terminal protarsomere slightly shorter than previous two tarsomeres combined. Claws on protarsi with three denticles, on meso- and metatarsi with four denticles. Mesotibiae slightly bent medially; mesotarsus longer than tibia, MsTiL/MsTrL ratio: ♂♂ 0.79–0.90 ( $0.83 \pm 0.03$ ,  $n = 13$ ), ♀♀ 0.85–0.92 ( $n = 2$ ). Metacoxae large, anterior margin slightly emarginated, posterior margin broadly rounded. Metatibiae bearing short subapical ridge and 3–4 lateral ridges parallel to apical margin of tibia, reaching 1/3 of tibial width. Metatibial spurs black, long, inner one  $\sim 1.30\times$  as long as outer one. Metatarsomere I bearing 3–5 short ridges, metatarsomere II bearing 2–3 ridges, metatarsomere III without ridges. Metatarsus  $\sim 2.00\times$  as long as metatibia, MtTrL/MtTiL ratio: ♂♂ 2.02–2.32 ( $2.18 \pm 0.07$ ,  $n = 17$ ), ♀♀ 1.98–2.00 ( $n = 2$ ).

Pygidium long and slender, PygL/TVtL ratio: ♂♂ 1.82–2.47 ( $2.19 \pm 0.15$ ,  $n = 23$ ), ♀♀ 1.88–2.79 ( $2.22 \pm 0.32$ ,  $n = 6$ ). Apical margin of terminal ventrite arcuate.

Male genitalia: sternite VIII rather short, setae present in apical 1/3, apical protuberance short, slightly bilobed at apex (Fig. 6J); St8L/St8W ratio: ♂♂ 1.50–1.53 ( $n = 2$ ). Sternite IX long, slender, arrow-shaped, with medial longitudinal keel in apical part. Parameres (Fig. 6E–H) rather long, EL/LPrL ratio: 4.65–7.17 ( $5.89 \pm 0.71$ ,  $n = 25$ ), EL/RPrL ratio: 5.91–8.63 ( $7.42 \pm 0.72$ ,  $n = 25$ ), LPrL/RPrL ratio: 1.12–1.39 ( $1.26 \pm 0.06$ ,  $n = 25$ ). Left paramere: dorsal branch expanded apically, obliquely truncate at apex; ventral branch narrow, slightly bent medially, pointed at apex, LPrL/BLPr ratio: 1.73–2.24 ( $1.95 \pm 0.11$ ,  $n = 25$ ). Right paramere: dorsal branch rather narrow, slightly expanded, rounded at apex; ventral branch as long as or slightly shorter than dorsal branch, bent dorsally in apical part, pointed at apex. Median lobe long, slender, slightly expanded in apical part (Fig. 6I). Phallobase with short tubular process (approximately 1/6 of total length) and long, slender furca.

**Sexual dimorphism.** Females are more robust than males, their protibiae are not expanded in basal 1/3 and without fringe of long setae. Maxillary palpomere II is not expanded in females and without long setae on ventral side. Terminal maxillary palpomere is slenderer in females and its inner angle is situated more distally than in males. Antennae are somewhat shorter in females.

**Distribution.** Algeria, Azerbaijan, Bulgaria, Croatia, Cyprus, France, Georgia, Greece, Israel, Italy, Macedonia, Montenegro, Morocco, Portugal, Spain, Turkey, Ukraine. *Mordellistena pseudohirtipes* is reported here for the first time from Israel and Montenegro.

**Biology.** Adults were collected on the flowers of Apiaceae plants on dry grasslands. Plaza (1983) mentioned that *M. pseudohirtipes* was collected in Spain on following plant species: *Thapsia villosa*, *Daucus carota* (both Apiaceae) and *Ruta montana* (Rutaceae).

**Remarks.** *Mordellistena fageli* was placed in the *pentas*-group in the original description, based on the dark pubescence and three ridges on the metatarsomere II. In fact, as Horák (1983) already mentioned, this species belongs to *M. hirtipes* complex, based on the strongly convex body and expanded maxillary palpomere II. Examination of type material did not reveal any characters which could separate this taxon from *M. pseudohirtipes*. In the plot from PCA analysis (Fig. 10A), *M. fageli* is placed just next to the cluster of *M. pseudohirtipes*, in the same plane along the PC 1 axis. We consider these taxa as conspecific and propose *M. fageli* as a junior synonym of *M. pseudohirtipes*.

Czető (1990) described *M. pseudohirtipes krotosensis* based on two male specimens from Crete island. Characters such as length of the body, length of pygidium and colouration of pubescence, that he used for differentiation of the subspecies, are subjects of individual variability. Results of PCA (Fig. 10A) show, that holotype of *M. pseudohirtipes krotosensis* is placed within the cluster of the nominotypical subspecies. After examination of holotype we consider this subspecies as a junior synonym of *M. pseudohirtipes pseudohirtipes*.

In Ermisch's collection, there is a series of specimens named *Mordellistena lopezi*. Such species has not been described, and in fact, all the specimens belong to *M. pseudohirtipes*, except the one labelled as "Type", which belongs to *M. purpurascens*.

### ***Mordellistena* (s. str.) *purpurascens* Costa, 1854**

Figs 3, 7A–K

*Mordellistena purpurascens* Costa, 1854: 17 + Plate XXI (original description, figure); Gemminger and Harold 1870: 2113 (catalogue, as syn. of *Mordellistena pumila* (Gyllenhal, 1810)); Emery 1876: 95 (as syn. of *Mordellistena micans* (Germar, 1817)); Baudi di Selve 1877: 827 (as syn. of *M. micans*); Heyden et al. 1883: 142 (catalogue, as syn. of *M. micans*); Schilsky 1898: 77 (as syn. of *M. micans*); Heyden et al. 1906: 456 (catalogue, as syn. of *M. micans*); Csiki 1915: 37 (catalogue, as syn. of *M. micans*); Ermisch 1977: 169 (misidentification); Batten 1977 (misidentification); Kaszab 1979: 72, 74 (misidentification); Franciscolo 1991: 172–173 (remarks); Odnosum 2003: 36–46 (misidentification); Odnosum 2005: 100–108 (misidentification); Horák 2008: 100 (misidentification); Odnosum 2010: 199 (misidentification); Ruzzier 2013: 110 (misidentification).

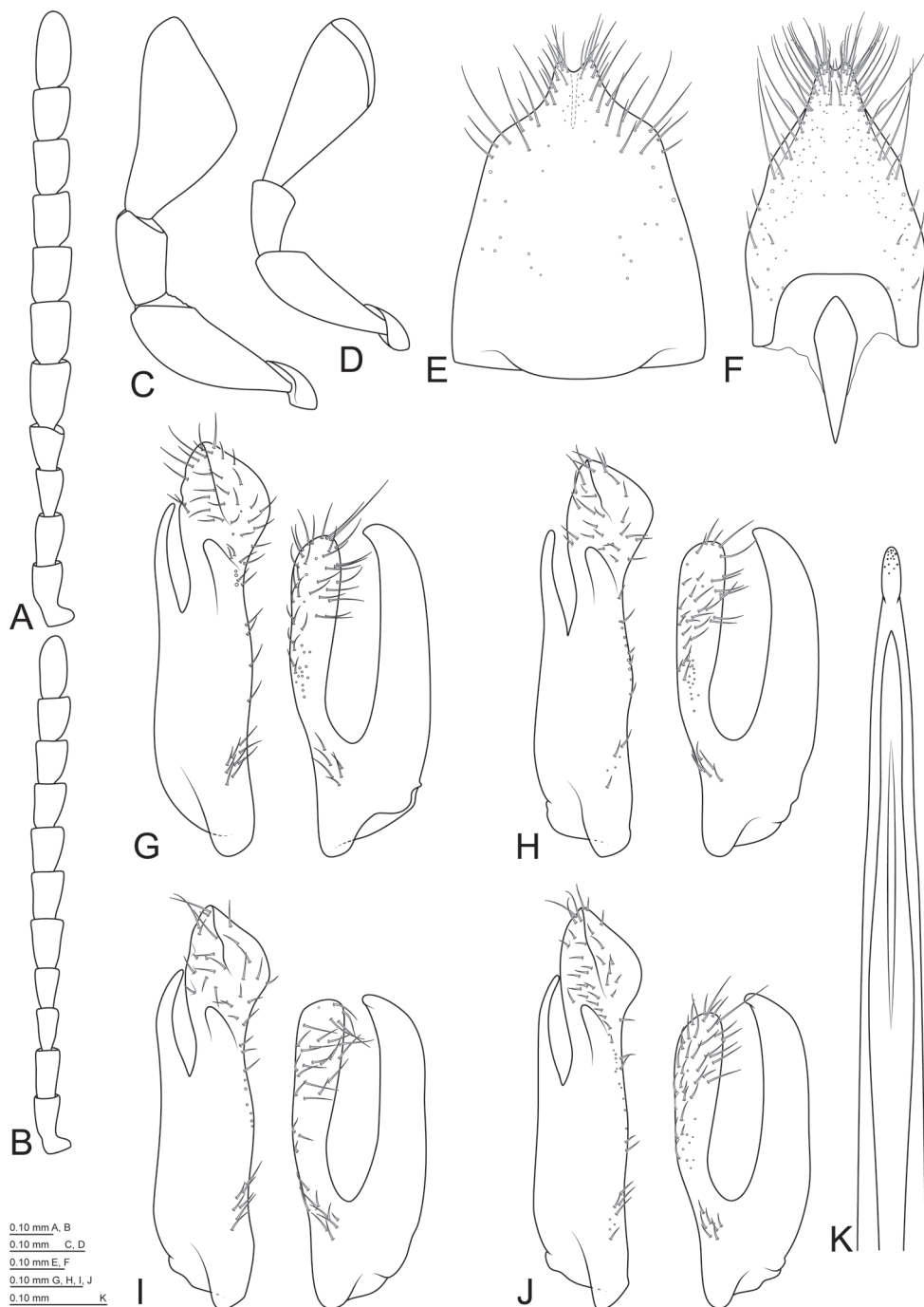
*Mordellistena geronensis* Ermisch, 1977: 169 syn. nov. (original description in the key); Kaszab 1979: 72–73 (figures, key); Franciscolo 1991: 171–172 (key, figures); Horák 2008: 98 (distribution).

*Mordellistena istrica* Ermisch, 1977: 169 syn. nov. (original description in the key); Kaszab 1979: 73 (key); Horák 2008: 98 (distribution).

**Type locality.** Naples, Italy.

**Type material examined.** *M. purpurascens*: LECTOTYPE, here designated, glued, genitalia in separate microvial, right metatarsus missing: 1 ♂, MZFN: "Mordellistena





**Figure 7.** *Mordellistena purpurascens* Costa, 1845: **A** antenna, male **B** antenna, female **C** maxillary palpus, male **D** maxillary palpus, female **E** sternite VIII, male **F** sternite VIII, female **G** parameres, lectotype **H** parameres, holotype of *M. geronensis* **I** parameres, holotype of *M. istricea* **J** parameres, France **K** aedeagal median lobe, holotype.



purpurascens n. Napoli [hand written by Costa] / LECTOTYPE *Mordellistena purpurascens* Costa, 1854 D. Selnekovič det. 2019" [red label]. *M. geronensis*: HOLOTYPE: 1 ♂, SNSD: "♂ / Genitalpräparat / [card with dissected genitalia, right antenna and right protarsus] / Spanien, Prov. Gerona, Tossa de mar, A. Kampf. VII–VIII 35 / Holotypus [red label] / Holotypus *Mordellistena geronensis* Ermisch / Staatl. Museum für Tierkunde Dresden"; PARATYPES: 1 ♀, SNSD: "Spanien, Prov. Gerona, Tossa de mar, A. Kampf, V–VI 35 / sp.? grupe micans, det. Ermisch 1940 / Paratypus / PARATYPUS *Mordellistena* (s. str.) *geronensis* Ermisch, 1977, Selnekovič labelled 2017 [red label] / *Mordellistena* (s. str.) *purpurascens* Costa, 1854, D. Selnekovič det. 2019"; 2 ♂♂, 2 ♀♀, SNSD: "♂ [or] ♀ / Ardèche, 10. 7. 65, Banne, J. Balazuc / Paratypus / PARATYPUS *Mordellistena* (s. str.) *geronensis* Ermisch, 1977, Selnekovič labelled 2017 [red label] / *Mordellistena* (s. str.) *purpurascens* Costa, 1854, D. Selnekovič det. 2017"; 1 ♂, SNSD: "♂ / Ardèche, Sammzon, 8. 7. 65, Balazuc / Paratypus / PARATYPUS *Mordellistena* (s. str.) *geronensis* Ermisch, 1977, Selnekovič labelled 2017 [red label] / *Mordellistena* (s. str.) *purpurascens* Costa, 1854, D. Selnekovič det. 2017". *M. istrice*: HOLOTYPE: 1 ♂, SNSD: "♂ / [card with dissected genitalia] / Pola, Istr. F. Lang / [blank red circular label] / MORDELLISTENA istriian [illegible handwriting] det. Ermisch 1952 / Type [red label] / Holotypus *Mordellistena istrice* Ermisch / *Mordellistena* (*Mordellistena*) *geronensis* Ermisch det. P. Leblanc 2007 / *Mordellistena* (s. str.) *purpurascens* Costa, 1854 D. Selnekovič det. 2019"; PARATYPES: 1 ♀, SNSD: "Plomin, Warmehang 14. 6. 1965 / Istrien K. Wellschmied / Paratypus / PARATYPUS *Mordellistena* (s. str.) *istrice* Ermisch, 1977, Selnekovič labelled 2017" [red label]; 1 ♂, SNSD: "♂ / Corsica / Paratypus / PARATYPUS *Mordellistena* (s. str.) *istrice* Ermisch, 1977, Selnekovič labelled 2017 [red label] / *Mordellistena* (*Mordellistena*) *geronensis* Ermisch det. P. Leblanc 2007 / *Mordellistena* (s. str.) *purpurascens* Costa, 1854 D. Selnekovič det. 2019"; 1 ♂, 1 ♀, SNSD: "12. 7. 14 Gallia m. Agay Rapp / Paratypus / PARATYPUS *Mordellistena* (s. str.) *istrice* Ermisch, 1977, Selnekovič labelled 2017" [red label].

**Additional material examined. Greece:** 1 ♂, 2 ♀♀, CSB: "Greece N, Corfu – Kavos, 39°24'16"N, 20°05'53"E, F. Repta leg., 28. VIII. 2011 / *Mordellistena purpurascens* Costa, 1854, D. Selnekovič det. 2019". **Italy:** 1 ♂, CSB: "IT–Sicilia, Madonia, Termini, Sciara, M San Calogero, ex. 1, 2.–3. 6. 2011, M. Šárovec, 3. 8 / *Mordellistena purpurascens* Costa, 1854, D. Selnekovič det. 2019"; 1 ♂, SNSD: "♂ / Gavoi Sard. 750m 21.–26. 8. 55 J. Kless 78 / *Mordellistena Lopezi* Ermisch det. K. Ermisch / *Mordellistena* (s. str.) *purpurascens* Costa, 1854 D. Selnekovič det. 2019" [in collection as *M. lopezi*]; 1 ♂, SNSD: "♂ / Genitalpräparat / ITALIA mer. Capaccio Hüdepohl VI. 64 / *Mordellistena* (s. str.) *purpurascens* Costa, 1854 D. Selnekovič det. 2019" [in collection as *M. lopezi*]. **Montenegro:** 4 ♂♂, 4 ♀♀ CSB: "Montenegro SE, 42°06'N, 19°06'E, Bar–centrum, on *Daucus* sp., D. Selnekovič 19. VI. 2011 / *Mordellistena purpurascens* Costa, 1854, D. Selnekovič det. 2019"; 1 ♀ CSB: "Montenegro SE, BAR env., 42°07'56"N, 19°07'33"E, 22. VI. 2011 / *Mordellistena* (s. str.) *purpurascens* Costa, 1854, D. Selnekovič det. 2019"; 1 ♂ HNHM: "Dalmatia Horváth / Zelenika 906. VIII. / *Mordellistena pseudohirtipes* Erm. det. R. Batten

1979 / *Mordellistena* (s. str.) *purpurascens*, Costa, 1854 D. Selnekovič det. 2019". **Morocco:** 1 ♂, CSB: Morocco Moyen Atl, Khenifra 15km E M. Šárovec 11. VII. 2007 / *Mordellistena purpurascens* Costa, 1854 D. Selnekovič det. 2019"; 4 ♂♂, 3 ♀♀, CSB: "Morocco Moyen Atl, Khenifra 10km I M. Šárovec 30. V. 2007 / *Mordellistena purpurascens* Costa, 1854 D. Selnekovič det. 2019". **Spain:** 1 ♂, SNSD: "♂ / Genitalpräparat / Son Españalet 1–VI–1958 R. López / Typus [red label] / *Mordellistena Lopezi* Ermisch det. K. Ermisch / *Mordellistena* (s. str.) *purpurascens* Costa, 1854 D. Selnekovič det. 2019" [in collection as *M. lopezi*].

**Differential diagnosis.** *M. purpurascens* closely resembles *M. hirtipes* and *M. pseudohirtipes*. The differences are described under these species.

**Redescription.** Measurements: TL: ♂♂ 3.10–4.42 mm ( $3.75 \pm 0.35$  mm,  $n = 19$ ), ♀♀ 3.31–4.42 mm ( $3.82 \pm 0.36$  mm,  $n = 14$ ); HL: ♂♂ 0.77–0.97 mm ( $0.85 \pm 0.06$  mm,  $n = 19$ ), ♀♀ 0.78–0.96 mm ( $0.86 \pm 0.06$  mm,  $n = 14$ ); HW: ♂♂ 0.91–1.17 mm ( $1.01 \pm 0.07$  mm,  $n = 19$ ), ♀♀ 0.84–1.12 mm ( $0.98 \pm 0.09$  mm,  $n = 14$ ); PL: ♂♂ 1.06–1.44 mm ( $1.23 \pm 0.10$  mm,  $n = 19$ ), ♀♀ 1.04–1.44 mm ( $1.25 \pm 0.11$  mm,  $n = 14$ ); PW: 1.10–1.56 mm ( $1.30 \pm 0.13$  mm,  $n = 19$ ), ♀♀ 1.13–1.58 mm ( $1.35 \pm 0.14$  mm,  $n = 13$ ); EL: ♂♂ 2.44–3.35 mm ( $2.81 \pm 0.27$  mm,  $n = 19$ ), ♀♀ 2.50–3.38 mm ( $2.88 \pm 0.27$  mm,  $n = 14$ ); EW: ♂♂ 1.15–1.59 mm ( $1.35 \pm 0.13$  mm,  $n = 19$ ), ♀♀ 1.19–1.66 mm ( $1.43 \pm 0.15$  mm,  $n = 14$ ); ATiL: ♂♂ 0.71–0.93 mm ( $0.81 \pm 0.07$  mm,  $n = 19$ ), ♀♀ 0.65–0.91 mm ( $0.75 \pm 0.08$  mm,  $n = 14$ ); ATrL: ♂♂ 0.64–0.84 mm ( $0.72 \pm 0.07$  mm,  $n = 15$ ), ♀♀ 0.62–0.80 mm ( $0.69 \pm 0.06$  mm,  $n = 13$ ); ITiL: ♂♂ 0.91–1.23 mm ( $1.03 \pm 0.10$  mm,  $n = 19$ ), ♀♀ 0.86–1.23 mm ( $1.01 \pm 0.12$  mm,  $n = 14$ ); ITrL: ♂♂ 1.12–1.64 mm ( $1.27 \pm 0.15$  mm,  $n = 9$ ), ♀♀ 1.02–1.34 mm ( $1.16 \pm 0.10$  mm,  $n = 14$ ); PTiL: 0.78–1.08 mm ( $0.88 \pm 0.08$  mm,  $n = 19$ ), ♀♀ 0.75–1.05 mm ( $0.88 \pm 0.08$  mm,  $n = 14$ ); PTrL: 1.64–2.18 mm ( $1.87 \pm 0.19$  mm,  $n = 9$ ), ♀♀ 1.48–2.16 mm ( $1.77 \pm 0.21$  mm,  $n = 11$ ); PygL: ♂♂ 1.50–2.12 mm ( $1.86 \pm 0.18$  mm,  $n = 19$ ), ♀♀ 1.35–1.98 mm ( $1.67 \pm 0.20$  mm,  $n = 14$ ); TVtL: ♂♂ 0.58–0.87 mm ( $0.77 \pm 0.10$  mm,  $n = 18$ ), ♀♀ 0.60–0.92 mm ( $0.77 \pm 0.08$  mm,  $n = 14$ ); RPrL: 0.52–0.64 mm ( $0.56 \pm 0.03$  mm,  $n = 19$ ); LPrL: 0.41–0.51 mm ( $0.45 \pm 0.03$  mm,  $n = 19$ ); St8L: ♂♂ 0.65–0.80 mm ( $0.70 \pm 0.07$  mm,  $n = 3$ ); St8W: ♂♂ 0.49–0.52 mm ( $0.50 \pm 0.01$  mm,  $n = 3$ ).

Habitus illustrated in Fig. 3. Body strongly elongate, slender, widest behind anterior 1/4 of elytra. Integument black, anterior margin of clypeus and mandibles somewhat paler. Pubescence on head and thorax yellowish; on elytra yellowish in anterior half, gradually darkened apically; on venter yellowish, darkened along posterior margins of ventrites 3 and 4 and completely dark grey on terminal ventrite and pygidium.

Head convex dorsally, wider than long, widest about middle, HW/HL ratio: ♂♂ 1.11–1.23 ( $1.19 \pm 0.03$ ,  $n = 19$ ), ♀♀ 1.06–1.19 ( $1.14 \pm 0.03$ ,  $n = 14$ ). Dorsal surface weakly microreticulated, with small, round punctures, each bearing short seta. Ventral surface with weak transverse microreticulation and sparsely arranged, round punctures, each bearing short seta. Occipital margin rounded in dorsal aspect, straight if seen from behind. Eyes oval, completely reaching occiput, not expanded onto ventral surface, finely faceted, with short interfacetal setae. Anterior margin of

clypeus straight. Labrum transverse, LabW/LabL: ♂♂ 2.04–2.27 ( $2.15 \pm 0.10$ ,  $n = 5$ ), ♀♀ 1.88–2.38 ( $2.21 \pm 0.20$ ,  $n = 5$ ), anterior margin straight or very shallowly emarginate mesally; surface covered with small, round punctures, each bearing seta. Antennae slightly serrate, expanded from antennomere V (Fig. 7A, B); antennomeres I and II short, subequal in length and width; antennomere III equal in length and slightly slenderer than previous two; antennomere IV slightly longer and wider than previous one; antennomeres V–X wider than previous four, in males  $\sim 1.60\times$ , in females  $\sim 1.30\times$  as long as wide; antennomere XI elongate oval,  $\sim 2.20\times$  as long as wide. Galea gradually expanded apically, covered with apically expanded sensilla. Maxillary palpi (Fig. 7C–D) black; palpomere I very short; palpomere II in males expanded with long setae on ventral side, in females slenderer, without long setae; palpomere III short,  $\sim 1.80\times$  as long as wide, in males with long setae on ventral side; terminal palpomere securiform, in males wider than in females, inner angle situated around middle in males, in terminal 1/3 in females; TPalL/TPalW ratio: ♂♂ 1.72–2.16 ( $1.96 \pm 0.10$ ,  $n = 17$ ), ♀♀ 2.08–2.34 ( $2.21 \pm 0.09$ ,  $n = 14$ ).

Pronotum moderately convex, slightly wider than long, PW/PL ratio: ♂♂ 0.97–1.10 ( $1.05 \pm 0.03$ ,  $n = 19$ ), ♀♀ 1.00–1.15 ( $1.07 \pm 0.04$ ,  $n = 13$ ). Surface weakly microreticulated with small, rasp-like punctures, distance between punctures  $1.50\text{--}2.00\times$  as long as puncture diameter, each puncture bearing flat seta. Anterior margin rounded, slightly produced mesally, anterior angles broadly rounded; lateral carinae rounded in dorsal aspect, shallowly but distinctly emarginate in lateral aspect; posterior margin forming short mesal lobe, emarginated laterally before posterior angles; posterior angles rectangular, pointed in lateral aspect. Posterior marginal bead interrupted before posterior angles. Prosternum in front of procoxae narrow, laterally expanded. Scutellar shield small, triangular, with small punctures bearing short setae. Mesoventral process ca. half as wide as mesofemora. Metaventricle large, posterior margin produced mesally between metacoxae; longitudinal discrimen rather indistinct. Metanepisternum trapezoidal, slightly narrowed posteriorly, dorsal margin emarginate, ventral margin straight.

Elytra long, narrow, widest at end of anterior 1/4, EL/EW ratio: ♂♂ 1.97–2.23 ( $2.08 \pm 0.07$ ,  $n = 19$ ), ♀♀ 1.83–2.15 ( $2.02 \pm 0.07$ ,  $n = 14$ ). Dorsal surface covered with weak transverse microreticulation and rasp-like punctures, distance between punctures  $\sim 1.50\times$  as long as puncture diameter; each puncture bearing flat seta. Lateral margins regularly rounded, apices separately rounded.

Protibiae straight, basal part in males slightly expanded and bearing distinct fringe of long setae; PTiL/PTiL ratio: ♂♂ 0.98–1.24 ( $1.13 \pm 0.06$ ,  $n = 15$ ), ♀♀ 0.98–1.17 ( $1.10 \pm 0.05$ ,  $n = 13$ ). Protarsomere I in females as long as two following tarsomeres combined, in males slightly longer; protarsomere IV simple, parallel-sided, very shallowly emarginated at apex. Claws on protarsi rather long, slender, with three denticles, on meso- and metatarsi with four denticles. Mesotibiae slightly bent medially; mesotarsus longer than tibia, MsTiL/MsTiL ratio: ♂♂ 0.75–0.90 ( $0.84 \pm 0.04$ ,  $n = 9$ ), ♀♀ 0.82–0.95 ( $0.88 \pm 0.04$ ,  $n = 14$ ). Metacoxae large, anterior margin straight, posterior margin broadly rounded. Metatibiae bearing short subapical ridge and 3–4 lateral ridges parallel to apical tibial margin, reaching 1/3 of tibial width. Metatibial spurs black, inner one

~1.30× as long as outer one. Metatarsomere I bearing in males 5, in females 3–4 short lateral ridges; metatarsomere II bearing 2–3 ridges; metatarsomeres III and IV without ridges. Metatarsus ~2.00× as long as metatibia, MtTrL/MtTiL ratio: ♂♂ 2.00–2.33 ( $2.13 \pm 0.10$ ,  $n = 10$ ), ♀♀ 1.90–2.18 ( $2.01 \pm 0.07$ ,  $n = 11$ ).

Pygidium long, slender, PygL/TVtL ratio: ♂♂ 1.88–3.32 ( $2.43 \pm 0.35$ ,  $n = 18$ ), ♀♀ 1.88–2.64 ( $2.18 \pm 0.17$ ,  $n = 14$ ). Apical margin of terminal abdominal ventrite arcuate.

Male genitalia: sternite VIII rather short, with long setae in apical part, apical protuberance rather short, slightly bilobed at apex (Fig. 7E); St8L/St8W ratio: ♂♂ 1.26–1.32 ( $1.28 \pm 0.02$ ,  $n = 4$ ). Sternite IX long, slender, arrow-shaped, with medial longitudinal keel apically. Parameres (Fig. 7G–J) rather long, EL/LPrL ratio: 4.42–5.84 ( $4.98 \pm 0.35$ ,  $n = 19$ ), EL/RPrL ratio: 5.57–6.94 ( $6.19 \pm 0.41$ ,  $n = 19$ ); LPrL/RPrL ratio: 1.16–1.30 ( $1.24 \pm 0.03$ ,  $n = 19$ ). Left paramere with very long basal part, LPrL/BLPr ratio: 1.50–1.91 ( $1.76 \pm 0.09$ ,  $n = 19$ ); dorsal branch strongly expanded apically, obliquely truncate at apex; ventral branch slender, slightly bent medially. Right paramere rather long with long branches; ventral branch longer than dorsal one, pointed at apex; dorsal branch rather narrow, slightly expanded apically, rounded at apex. Median lobe (Fig. 7K) long, slender, apical part narrow or slightly expanded. Phallobase with short tubular process (approximately 1/6 of total length) and long, slender furca.

Female genitalia: sternite VIII (Fig. 7F) with slightly bilobed apical protuberance, long setae situated at apex and alongside lateral margins; spiculum ventrale short, broadly clavate; St8L/St8W ratio: 1.62 ( $n = 1$ ).

**Sexual dimorphism.** Females are more robust, with protibiae not expanded and without fringe of long setae in basal part. Maxillary palpomere II not expanded in females and without long setae on ventral side. Terminal maxillary palpomere is wider in males, with its inner angle situated approximately in the middle (Fig. 7C), in females it is generally slenderer, with its inner angle situated in terminal 1/3 (Fig. 7D). Antennae are shorter in females; antennomeres V–X ~1.60× as long as wide in males, ~1.30× in females.

**Distribution.** Croatia, France, Greece, Italy, Montenegro, Morocco, Spain. *Mordellistena purpurascens* is reported here for the first time from Greece and Montenegro. Odnosum (2003, 2005, 2010) reported *M. purpurascens* from Kazakhstan, Turkmenistan, Tajikistan, and Ukraine. However, based on the figures of parameres provided in all the three mentioned studies, it is obvious that he referred to a different species (see Discussion).

**Biology.** Adults were collected by the first author in Montenegro, in urban environment of Bar on the flowers of *Daucus* sp. (Apiaceae).

**Remarks.** *Mordellistena purpurascens* was described by Costa (1854) and referred to be found in several localities in former “Regno di Napoli” (southern parts of present Italy). Series of *M. purpurascens* in Costa’s collection in MZFN contains only two specimens. One of them with the original label “*Mordellistena purpurascens* n. Napoli” is designed here as a lectotype. The other specimen labelled “S. Severina” without identification label belongs to a different species from the *gemellata*-group (sensu Ermisch 1956). Genitalia of the lectotype were examined for the first time for the purposes of the present study (Fig. 7G).

Ermisch (1977) briefly described two new species *M. geronensis* and *M. istrica* as a part of an identification key. He differentiated these species from each other based on the shape of the apical part of the median lobe (expanded in *M. istrica*, not expanded in *M. geronensis*). Shape of the apical part of median lobe depends on the observation method (dry/wet, card mounted/slide mounted). After examining the series of slide mounted median lobes of both taxa, we did not find any differences in the shape. Examination of the male genitalia from type specimens of *M. purpurascens* (Fig. 7G), *M. geronensis* (Fig. 7H) and *M. istrica* (Fig. 7I) revealed that these taxa are conspecific. We thus propose *M. istrica* and *M. geronensis* as the junior synonyms of *M. purpurascens*.

Type series of *M. istrica* includes a female paratype (Pola, Croatia), which we were not able to assign to *M. purpurascens* or *M. pseudohirtipes*. Type series of *M. geronensis* includes a male paratype (Bois de Paiolive, Ardèche, France), which in fact belongs to *M. pseudohirtipes*, and three paratypes (Tossa de mar, Spain; Costa Brava, Spain), which belong to *M. hirtipes*. In Ermisch's collection, there is a series of specimens named *Mordellistena lopezi*. Such species has not been described. Specimen labelled as "Typus", in fact, belongs to *M. purpurascens*, the rest of the specimens belongs to *M. pseudohirtipes*.

### ***Mordellistena* (s. str.) *balearica* Compte, 1985**

Fig. 8

*Mordellistena balearica* Compte, 1985: 63–64 (original description); Horák 2008: 96 (distribution).

**Type locality.** Palma de Mallorca, Majorca.

**Type depositary.** According to the original description (Compte 1985), holotype should be deposited in MNCN. However, despite of the effort of the curator, the specimen was not found.

**Diagnosis.** *Mordellistena balearica* was described based on a single male specimen from Mallorca. According to the original description, this species closely resembles *M. pseudohirtipes* and can be distinguished from this species by longer antennae (antennomeres V–X two times longer than wide) and different shape of parameres (Fig. 8) (Compte 1985). All characters mentioned in the original description suggest that this taxon is conspecific with *M. pseudohirtipes*; unfortunately, the authors did not have the opportunity to study the type.

**Distribution.** Known only from type locality.

**Remarks.** Compte (1985) mentioned following information: "This specimen, together with other specimens collected by P. López in Majorca, which current location I don't know, was studied by the specialist Mr Ermisch, who considered it as a new species for science, called *M. balearica*, a name that seems to have remained *in litteris*". There are several specimens collected by P. López in Mallorca in Ermisch's collection (SNSD) labelled by Ermisch as *M. balearica* which in fact all belong to *M. thuringiaca* Ermisch, 1963.

***Mordellistena* (s. str.) *irritans* Franciscolo, 1991**

Fig. 9

*Mordellistena irritans* Franciscolo, 1991: 168–173 (original description); Franciscolo 1995: 12 (distribution); Horák 2008: 98 (distribution).

**Type locality.** Lampedusa Is., Italy.

**Type depository.** Museo d'Aumale, Terrasini, Palermo, Italy: 1 ♀ holotype, 1 ♂ paratype (Franciscolo 1991). Not examined.

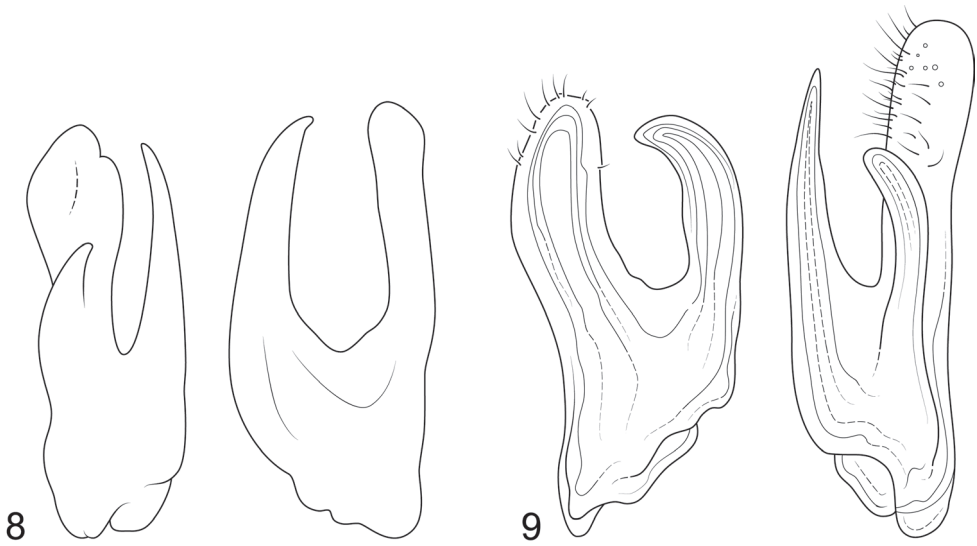
**Diagnosis.** *Mordellistena irritans* can be assigned to *M. hirtipes* complex based on the expanded maxillary palpomere II in males and the shape of parameres. This species can be distinguished from all other species in the complex by the characteristic shape of the left paramere with dorsal branch parallel-sided and rounded at apex (Fig. 9).

**Distribution.** Known only from the type locality.

**Key to the species of *M. hirtipes* species complex**

- 1 Dorsal branch of the left paramere not expanded, parallel-sided, rounded at apex (Fig. 9).....***M. irritans***
- Dorsal branch of left paramere expanded apically, obliquely truncate at apex.... **2**
- 2 Parameres shorter, EL/LPrL ratio: 7.87–9.17 ( $8.48 \pm 0.40$ ,  $n = 14$ ); EL/RPrL ratio: 10.07–11.89 ( $11.10 \pm 0.50$ ,  $n = 14$ ); basal part of left paramere short; ventral branch of the right paramere usually distinctly shorter than the dorsal one (Fig. 5D–G). Terminal segment of maxillary palpi in females shorter and broader, inner angle is more acute (Fig. 4B). Pubescence on pronotum and elytra yellowish, somewhat darkened posteriorly .....***M. hirtipes***
- Parameres longer, EL/LPrL ratio: 4.42–7.17, EL/RPrL ratio: 5.57–8.63; basal part of left paramere longer; ventral branch of right paramere equally long or longer than the right one (Figs 6E–H, 7G–J). Terminal segment of maxillary palpi in females slenderer, its inner angle is rounded (Figs 6D, 7D). Pubescence on pronotum and elytra sometimes completely dark greyish.....**3**
- 3 Parameres shorter, EL/LPrL ratio: 4.65–7.17 ( $5.89 \pm 0.71$ ,  $n = 25$ ), EL/RPrL ratio: 5.91–8.63 ( $7.42 \pm 0.72$ ,  $n = 25$ ); basal part of left paramere shorter (Fig. 6E–H). Pubescence on pronotum and elytra sometimes almost completely dark greyish .....***M. pseudohirtipes***
- Parameres longer, EL/LPrL ratio: 4.42–5.84 ( $4.98 \pm 0.35$ ,  $n = 19$ ), EL/RPrL ratio: 5.57–6.94 ( $6.19 \pm 0.41$ ,  $n = 19$ ); basal part of left paramere longer (Fig. 7G–J). Pubescence on pronotum and elytra yellowish, darkened posteriorly but not completely dark greyish .....***M. purpurascens***





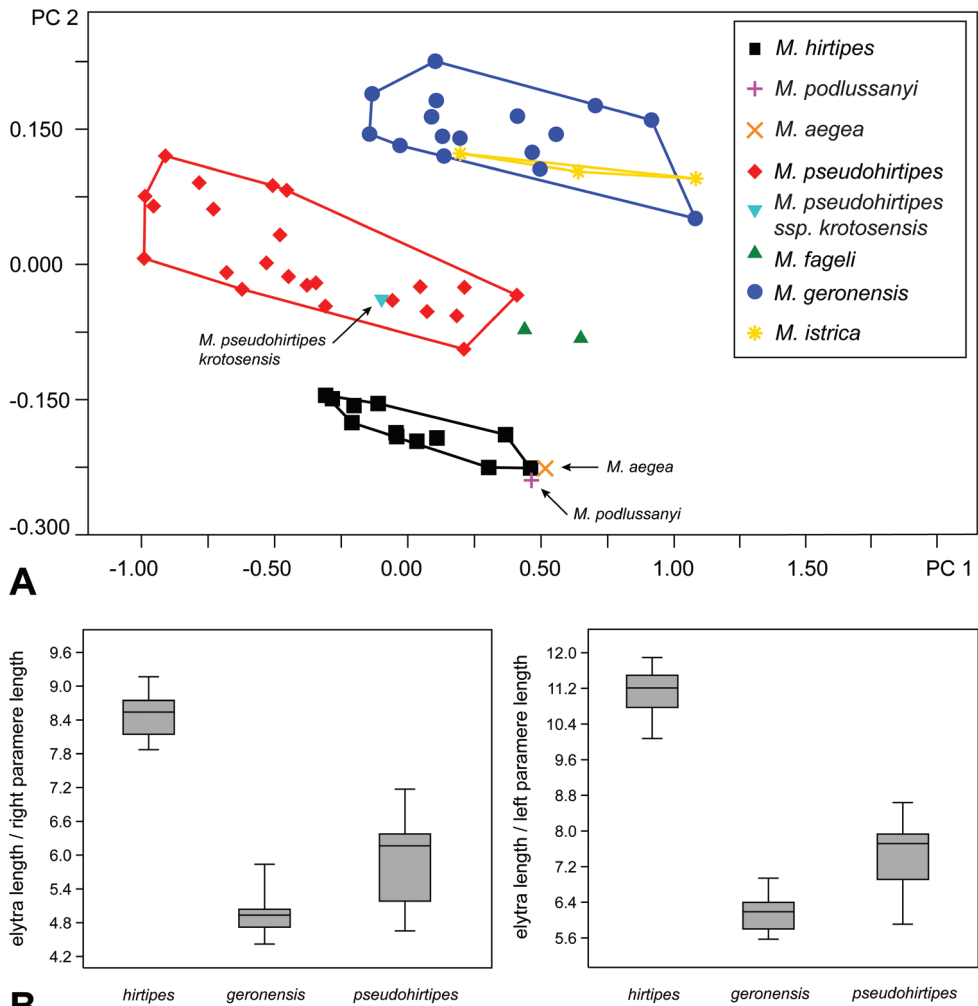
**Figures 8–9.** **8** *Mordellistena balearica* Compte, 1985, parameres (Compte 1985, modified) **9** *M. irritans* Franciscolo, 1991, parameres (Franciscolo 1991, modified).

## Results of PCA analysis

Principal Component Analysis (PCA) was conducted based on following morphometric characters: HL, HW, PL, PW, EL, EW, PTiL, MsTiL, MtTiL, RPrL, BRPr, and LPrL. Characters were measured in 59 male specimens, including holotypes / lectotype of every taxon. The first two principal components describe 91.03% (PC 1) and 6.32% (PC 2) of variation. PC 1 correlates mostly with elytral length (loading 0.66), elytral width (loading 0.37) and pronotal width (loading 0.35); PC 2 correlates with characters measured on parameres: left paramere length (loading 0.68), right paramere length (loading 0.56), basal part of left paramere length (loading 0.43).

Visualisation of the results of PCA analysis (Fig. 10A) shows clear distinction of *M. hirtipes*, *M. pseudohirtipes*, and *M. purpurascens* along the PC 2 axis. Cluster of *M. istrica* overlaps with cluster of *M. geronensis*; *M. pseudohirtipes krotosensis* is placed within the cluster of *M. pseudohirtipes pseudohirtipes*; *M. fageli* is placed next to the cluster of *M. pseudohirtipes* in one plane along the PC 1 axis, and *M. podlussanyi* and *M. aegea* are placed next to cluster of *M. hirtipes*. Results of PCA correspond with hypotheses based on observations of morphological characters.

Length of elytra and length of parameres are characters, that reach the highest loadings in PCA analyses. Ratios of these characters (EL/RPrL, EL/LPrL) are useful for identification and are used in diagnoses. Differences in values of selected ratios are presented in Fig. 10B.



**Figure 10.** **A** Results of Principal Component Analysis (PCA) **B** Box-plots showing differences between species in selected ratios. Top and bottom of the boxes represent first and third quartiles, transverse band represents the median and whiskers represent maximum and minimum.

## Discussion

The family Mordellidae is taxonomically very challenging and thus rather poorly known. Most of the original descriptions are insufficient for proper identification and differentiation of the species, especially those published before the 1950s (before K Ermisch provided a more precise method of description). There are still some species which were described as several different taxa, sometimes even by the same author (e.g., *M. pseudohirtipes* Ermisch, 1965 = *M. fageli* Ermisch, 1969). Characters used for the differentiation of these taxa were usually misinterpreted (e.g., the shape of the

median lobe in *M. geronensis* Ermisch, 1977 and *M. istrica* Ermisch, 1977) or they are subjects of the intraspecific variability (e.g., the dark coloration of the pubescence in *M. fageli* Ermisch, 1969). In other cases, the insufficient descriptions in combination with overlooking of the type specimens led to a misinterpretation of the taxa. It can be seen for example in some species described by Achille Costa (1854). Revision of the type specimens in his collection deposited in MZFN revealed that several species described by him were incorrectly interpreted by the subsequent authors as completely different species, one of them is *M. purpurascens* Costa, 1854 treated in the present paper. This species was considered by the subsequent authors as a synonym of either *M. pumila* (Gyllenhal, 1810) (Gemminger and Harold 1870) or *M. micans* (Germar, 1817) (Emery 1876; Baudi di Selve 1877; Heyden et al. 1883, 1906; Schilsky 1898; Csiki 1915). Later it was treated again as a valid species by Ermisch (1977), Ermisch in Kaszab (1979) and Batten (1977) but none of these authors had studied the types and it is obvious, based on their figures of the genitalia that the specimens considered by them as *M. purpurascens* belong to a different species. Their misinterpretations were later followed by Odnosum (2003, 2005, 2010) who published several new distribution records for *M. purpurascens* which were then included in the catalogue by Horák (2008). Only the examination of the lectotype of *M. purpurascens* Costa, 1854 done by the first author revealed that it is conspecific with the types of *M. geronensis* Ermisch, 1977 and *M. istrica* Ermisch, 1977. As it can be seen from this example, examination and redescriptions of the type specimens are essential for the future studies, especially in such taxonomically difficult and species-rich family as Mordellidae.

We live in the era of the global biodiversity crisis caused by the anthropogenic interventions in the natural ecosystems. But how does these changes affect the diversity and distribution patterns of Mordellidae beetles is not known. Despite of the great effort of the authors such as Ermisch (e.g., 1956, 1965, 1969a), Horák (e.g., 1990, 2008) and Odnosum (e.g., 2003, 2005, 2010) who have summarised and published a vast number of distributional records, the information about distribution and ecology of many Palearctic species is still very poor and several species are reported only from a single locality stated in the original description. It is very important to gather and provide new distributional and ecological records, however, it is also essential to pay effort to correct identification of the specimens to guarantee the accuracy of the published biological data.

## Acknowledgments

We wish to thank Olaf Jäger (SNSD), Ottó Merkl (HNHM), Andrea Colla (MCST), Roberta Improta (MZFN), and Bernd Jäger (MNHU) for providing us with the type material. Financial support was provided partially by the Slovak Research and Development Agency, Project No.: APVV-15-0147 and by Comenius University in Bratislava, grant no. UK/70/2018.

## References

- Batten R (1976) Mordellidae (Coleoptera) from the South of France and Pyrenees. *Entomologische Berichten* 36: 164–171.
- Batten R (1977) Two new Mordellidae (Coleoptera) from Southern Europe, and a key to the *Mordellistena micans* group. *Entomologische Berichten* 37: 167–176.
- Baudi di Selve F (1877) Coleotteri eteromeri esistenti nelle collezioni del R. Museo zoologico di Torino ed in altre italiane. Eteromeri delle famiglie susseguenti a quella dei tenebrioniti nei limiti della fauna europaea e circummediterranea. *Atti della Reale Accademia delle Scienze di Torino* 13: 765–866, 1027–1183.
- Compte A (1985) Mordellidae de las islas Baleares (Coleópteros). *Boletim da Sociedade Portuguesa de Entomologia* 3 (Suppl. 1): 57–66.
- Costa A (1854) Parte I a. Coleotteri, Eteromeri. Famiglia de'Mordellidei — Mordellidea. In: *Fauna del regno di Napoli ossia enumerazione de tutti gli animali che abitano le diverse regioni di questo regno e la acque che la bagnano contenente la descrizione de'nuovi o poco esattamente conosciuti noc figure ricavete da originali vivente e dipinte al naturale*. Gaetano Sautto, Naples, 32 pp. [plates XX–XXII]
- Csiki E (1915) Mordellidae. In: Junk W, Schenkling S (Eds) *Coleopterorum Catalogus*. Pars 63. W. Junk, Berlin, 84 pp.
- Czető Z (1990) New Mordellidae (Coleoptera) from the Mediterranean Region, and a key to the genus *Mordellistenula* Sthegolewa-Barowskaya. *Folia Entomologica Hungarica* 51: 25–30.
- Emery MC (1876) Essai monographique sur les Mordellides de l'Europe et des contrées limitrophes. *L'Abeille: Journal d'Entomologie* 14: 1–128.
- Ermisch K (1956) Mordellidae. In: Horion A (Ed.) *Faunistik der mitteleuropäischen Käfer*. Band V: Heteromera. *Entomologische Arbeiten aus dem Museum G. Frey, Tutzing bei München*, 269–329.
- Ermisch K (1963) Die Mordelliden der Insel Cypren (Coleoptera, Heteromera, Mordellidae). *Notulae Entomologicae* 43: 49–67.
- Ermisch K (1965) Neue Mordelliden von der Balkanhalbinsel (Coleoptera, Mordellidae). *Reichenbachia* 5: 251–272.
- Ermisch K (1969a) Neue Mordelliden aus Europa, Nordafrika und dem Nahen Osten (Coleoptera, Mordellidae). *Entomologische Blätter* 65: 104–115.
- Ermisch K (1969b) 79. Familie: Mordellidae. In: Freude H, Harde KW, Lohse GA (Eds) *Die Käfer Mitteleuropas*. Band 8. Terebrida, Heteromera, Lamellicornia. Goecke & Evers, Krefeld, 160–196.
- Ermisch K (1977) Die *Mordellistena*-Arten Ungarns und benachbarter Gebiete sowie Beschreibung einer neuen *Hosbihanonomia*-Art aus Siebenbürgen (Coleoptera, Mordellidae). *Folia Entomologica Hungarica (Series Nova)* 30: 151–177.
- Franciscolo ME (1949) XIII° contributo alla conoscenza dei Mordellidi (Coleoptera: Heteromera). *Memorie della Società Entomologica Italiana* 28: 81–95.
- Franciscolo ME (1991) Su alcuni Mordellidi e Scaptiidi (Coleoptera – Heteromera) delle Isole Pelagie. *Naturalista Siciliano, Series 4*, 15: 167–178.

- Franciscolo ME (1995) Famm. Mordellidae. In: Angelini F, Audisio P, Bologna MA, De Biase A, Franciscolo ME, Nardi G, Ratti E, Zampetti MF, Coleoptera Polyphaga XII (Heteromera escl. Lagriidae, Alleculidae, Tenebrionidae). In: Minelli A, Ruffo S, La Posta A (Eds) Checklist delle specie della fauna italiana. Ed. Calderini, Bologna, 11–13.
- Gemminger M, Harold B de (1870) Familia LVIII. Mordellidae. In : Catalogus coleopterorum hucusque descriptorum synonymicus et systematicus. Tom VII. Tenebrionidae, Nilionidae, Pythidae, Melandryidae, Lagriidae, Pedilidae, Anthicidae, Pyrochroidae, Mordellidae, Rhipidophoridae, Cantharidae, Oedemeridae. EH Gummi, München, 2105–2117.
- Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological Statistics software package for education and data analysis. Palaeontologia Electronica: 4, 1–9. [http://palaeo-electronica.org/2001\\_1/past/issue1\\_01.htm](http://palaeo-electronica.org/2001_1/past/issue1_01.htm).
- Heyden L von, Reitter E, Weise J (1883) Catalogus coleopterorum Europae et Caucasi. Editio tertia. Libraria Nicolai, Berlin, 228 pp. <https://doi.org/10.1002/mmnd.48018830225>
- Heyden L von, Reitter E, Weise J (1906) Catalogus coleopterorum Europae, Caucasi et Armeniae Rossicae. Editio secunda. Friedländer & Sohn, Berlin, 774 pp.
- Horák J (1983) Revision der *Mordellistena*-Arten aus der *pentas*-Gruppe (Coleoptera, Mordellidae). Entomologische Abhandlungen 47: 1–13.
- Horák J (1990) Typenrevision einiger wenig bekannter Arten aus der Gattung *Mordellistena* Costa (Insecta, Coleoptera, Mordellidae). Entomologische Abhandlungen 53: 125–142.
- Horák J (2008) Mordellidae. In: Löbl I, Smetana A (Eds) Catalogue of Palaearctic Coleoptera. Vol. 5. Tenebrionoidea. Apollo Books, Stenstrup, 87–105.
- Horák J (2011) The world genera system of family Tumbling Flower Beetles (Coleoptera: Mordellidae) and its distribution in the Czech Republic. Unpublished Bachelor Thesis, Czech University of Life Sciences, Prague.
- ICZN (1999) International Code of Zoological Nomenclature (4<sup>th</sup> edn). International Trust for Zoological Nomenclature, London, 306 pp. <https://doi.org/10.5962/bhl.title.50608>
- Kaszab Z (1979) Felemás lábfejűes bogarak II. Heteromera II. (Mordellidae), Fauna Hungariae, 134. Akadémiai Kiadó, Budapest, 100 pp.
- Kucharczyk H, Kucharczyk M, Stanisławek K, Fedor P (2012) Application of PCA in Taxonomy Research – Thrips (Insecta, Thysanoptera) as a Model Group. In: Sanguansat P (Ed.) Principal Component Analysis – Multidisciplinary Applications. InTech, Rijeka, 111–126. <https://doi.org/10.5772/2694>
- Lawrence JF, Ślipiński A (2010) Mordellidae Latreille, 1802. In: Leschen RAB, Beutel RG, Lawrence JF (Eds) Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim), Vol. 2. Walter de Gruyter, Berlin-New York, 533–537. <https://doi.org/10.1515/9783110911213.533>
- Lu W, Jackman JA, Johnson PW (1997) Male genitalia and phylogenetic relationships in North American Mordellidae (Coleoptera). Annals of the Entomological Society of America 90: 742–767. <https://doi.org/10.1093/aesa/90.6.742>
- Odnosum VK (2003) Mordellid beetles (Coleoptera, Mordellidae) in the fauna of Kazakhstan and Middle Asia. Communication 2. Vestnik Zoologii 37: 33–49.

- Odnosum VK (2010) Zhuki gorbatki (Coleoptera, Mordellidae). Fauna Ukrainy. Volume 19. Part 9. Naukova Dumka, Kiev, 264 pp.
- Plaza E (1983) Mordellidae (Col.) de la provincial de Madrid. Actas del I Congreso Ibérico de Entomologia 2: 567–577.
- Przybycień M, Waclawik B (2015) Morphometric measurements of *Bryodaemon* (Coleoptera: Curculionidae): contribution to phylogeny. Baltic Journal of Coleopterology 15: 129–136.
- Ruzzier E (2013) Taxonomic and faunistic notes on Italian Mordellidae (Coleoptera Tenebrionoidea) with redescription of *Falsopseudotomoxia argyroleura* (Franciscolo, 1942) n. comb. Bollettino della Società Entomologica Italiana 145: 103–115. <https://doi.org/10.4081/BollettinoSEI.2013.103>
- Ruzzier E, Ghahari H, Horák J (2017) A checklist of the Iranian Mordellidae (Coleoptera: Tenebrionoidea). Zootaxa 4320: 146–158. <https://doi.org/10.11646/zootaxa.4320.1.8>
- Samin N, Etebarian HR, Sakenin H, Ghahari H, Mirutenko V (2016) A faunistic study of some Coleoptera families from Iran. Ukrainska Entomofaunistyka 7: 21–24.
- Schaufuss C (1916) Calwer's Käferbuch. Einführung in die Kenntnis der Käfer Europas. Ed. 6, Vol. 2. E. Schweizerbart, Stuttgart, 709–1390.
- Schilsky J (1895) Mordellidae. In: Küster HC, Kraatz G (Eds) Die Käfer Europa's. Nach der Natur beschrieben, Heft 31. Bauer & Raspe, Nürnberg, 1–100.



# Allometry and morphological trait relationship in the sexually dimorphic Chinese dobsonfly, *Acanthacorydalid asiatica* (Wood-Mason, 1884) (Megaloptera, Corydalidae)

Chengquan Cao<sup>1</sup>, Pei Yu<sup>2</sup>, Fumio Hayashi<sup>2</sup>

**1** College of Life Science, Leshan Normal University, Leshan, Sichuan 614004, China **2** Department of Biology, Tokyo Metropolitan University, Minamiosawa 1-1, Hachioji, Tokyo 192-0397, Japan

Corresponding author: Chengquan Cao ([chqcao1314@163.com](mailto:chqcao1314@163.com))

---

Academic editor: B. Price | Received 7 January 2019 | Accepted 29 April 2019 | Published 10 June 2019

---

<http://zoobank.org/F1AE4704-EA30-4820-9E38-263202DD2420>

---

**Citation:** Cao C, Yu P, Hayashi F (2019) Allometry and morphological trait relationship in the sexually dimorphic Chinese dobsonfly, *Acanthacorydalid asiatica* (Wood-Mason, 1884) (Megaloptera, Corydalidae). ZooKeys 854: 119–129. <https://doi.org/10.3897/zookeys.854.32897>

---

## Abstract

Male insects with large weapons such as horns and elongate mandibles would be expected to invest more on such structures than other parts of the body for advantages in male to male competition for mating. In male genitalia, however, intermediate size provides a better fit for more females than small or large sizes, and such a male would leave more offspring regardless of their body size. These predictions were tested using a static allometry analysis between body size and other trait sizes. *Acanthacorydalid asiatica* is a large dobsonfly (Megaloptera) and males have conspicuously large mandibles used as weapons. We examined the hypothesis that the male mandibles of this sexually dimorphic species are sexually selected to enlarge, whereas the male genitalia are stable to be intermediate regardless of a great variation in body size. The results, as predicted, showed positive allometry between male body size and mandible length but negative allometry between male body size and ectoproct length (a male grasping structure). Sperm are transferred through a small spermatophore attached externally to the female genital opening, so it may be evolutionarily unnecessary to develop an enlarged male genital size. In contrast, there may be a trade-off between male mandible size and wing length, because of negative allometry between body size and wing length in males but isometry between them in females.

## Keywords

Male genitalia, morphological trade-off, sexually selected trait, static allometry

## Introduction

Many groups of animals develop secondary sexual traits mostly in males but a few in females (reviewed by Emlen 2008; Rico-Guevara and Hurme 2019). In insects, exaggeration in male mandibles, horns, legs, and eye spans is well known, and sexual selection is recognized as a key driver of it (Emlen and Nijhout 2000; Lavine et al. 2015). Studies of the morphological evolution of sexually selected traits often attempt to explain how selection has shaped them, and static allometry has been a useful tool in generating hypotheses about selection on morphology (Eberhard et al. 2009, 2018). Static allometry is a measure of the proportional size of a particular structure in a population of conspecific individuals that have different body sizes but are at the same ontogenetic stage (Eberhard et al. 2009, 2018; Voje 2016; O'Brien et al. 2018). The allometric equation is represented as  $y = ax^b$ , where  $a$  and  $b$  are constants (Huxley 1932). In the log-log relationship between body size ( $x$ ) and one body trait ( $y$ ) ( $\log_{10} y = b \log_{10} x + \log_{10} a$ ) in conspecific individuals, the three kinds of relationships arise depending on the slope  $b$  of this regression; positive allometry ( $b > 1$ ) in which larger individuals show disproportionately large traits, negative allometry ( $b < 1$ ) in which larger individuals show disproportionately smaller traits, and isometry ( $b = 1$ ) in which the trait size increases proportionately with body size. There are usually isometric relationships between body size and other body parts. In this case, the body proportion does not differ between small and large individuals. Male sexually selected traits such as horns, mandibles, and visual display devices have generally positive allometry with body size (reviewed by Emlen and Nijhout 2000; Kodric-Brown et al. 2006; Bonduriansky 2007; Voje 2016; Eberhard et al. 2018; O'Brien et al. 2018), although the presence or absence of positive allometry cannot be used simply to infer the presence or absence of sexual selection if the function of the traits is unknown (e.g., Bonduriansky 2007). On the other hand, male genital size shows negative allometry or little correlation with male body size in most insect species examined, offering a one-size-fits-all hypothesis of male genital size (reviewed by Eberhard et al. 1998, 2018; Eberhard 2009; Voje 2016). If intermediate-sized genitalia provide a better fit or better tactile stimulation for more females in the population than small genitalia or large genitalia, males with intermediate-sized genitalia would leave more offspring regardless of their body size (Eberhard et al. 1998).

The order Megaloptera is a minor insect group including only two families, 35 genera, and 397 species in the world (Rivera-Gasparín et al. 2019), and little attention has been paid to its behavior. However, this order of insects includes three genera in which the male develops exaggerated traits and conspicuous sexual dimorphism is known. In *Corydalus*, distributed in North to South America, and *Acanthacorydalus*, known from Asia, positive allometry is reported between male body size and mandible size (Liu et al. 2015; Álvarez et al. 2017). These males are known to combat with their mandibles (Liu et al. 2015; Álvarez et al. 2017). In *Platyneuromus* in Central America, the exaggerated male postocular flanges show the positive allometry with male body size, although the function of this postocular flange is still unknown (Liu et al. 2015;

Ramírez-Ponce et al. 2017). Thus, sexual selection may affect the development of male mandibles and postocular flanges of these insects. However, the morphometric data sets of previous studies were based on small sample size collected from a variety of localities, because it is usually difficult to collect them in the field. Samples combined multiple populations may mislead the obtained results if local adaptations occur, particularly in the case that some populations are large while others are small in body size. For best understanding of the phenomenon of sexual dimorphism, the morphometric analysis of a single population and comparative studies along the geographic range of a species must be used. Therefore, in this study, we reexamined the allometric relationships of male and female morphological traits of a single population of the Chinese dobsonfly, *Acanthacorydalis asiatica* (Wood-Mason, 1884).

We also examined the allometric relationships of male genital size of this species. In Megaloptera, *Corydalus bidenticulatus* Contreras-Ramos, 1998 is the only species for which the relationship between body and genital size has been studied, and a negative allometry is reported although based on only nine males and statistically marginal at  $P = 0.05$  in correlation analysis (Álvarez et al. 2017). Two types of sperm transfer are known in insects; one is ejaculation of sperm or sperm-including spermatophores internally to the female reproductive organs and the other is transfer of sperm via an externally attached spermatophore to the female (Simmons 2001; Chapman 2013). In Megaloptera, males use an external spermatophore (Hayashi 1992, 1993, 1996, 1999; Liu et al. 2015). In this study, the size of male ectoprocts grasping female abdominal tip at mating (Liu et al. 2015) was analyzed allometrically to examine whether this apparatus supports the one-size-fits-all hypothesis (Eberhard et al. 1998). If so,  $b$  in the allometric equation is expected  $<1$ , and the coefficient of variation (CV) in genital traits should be lower than those in other traits (Eberhard et al. 1998).

## Material and methods

The genus *Acanthacorydalis* includes some of the most remarkable dobsonflies in the world by their large body size and elongated male mandibles (Liu et al. 2005; Cao and Liu 2013). This genus is endemic to Asia and mainly distributed in the Oriental realm, and there are eight species currently recorded from China, India, and Vietnam (Yang and Liu 2010). China has a rich fauna of this genus with six species distributed from southern and southwestern to northern China (Yang and Liu 2010). The larva, an aquatic predator, lives in the relatively large river beds and the final-instar larva leaves water to pupate in the riverside soils (Cao and Liu 2013).

Adult *A. asiatica* were obtained by rearing large larvae collected from Panzhihua, Sichuan Province, China. These larvae were collected on 12 April 2015 and brought to the laboratory to be kept in large plastic tanks (40 cm wide, 60 cm long, and 20 cm high) in which water obtained from underground was circulated 10 cm in depth. Chironomid larvae and shrimps were made available as food. Fully-grown larvae were replaced to the same-sized tanks but filled with wet soil (5 cm deep) for pupation. These

tanks were covered with nets to prevent larvae escaping. When adults emerged, they were kept in a large rearing cage covered with fine wire nets (8 m wide, 25 m long, and 3.5 m high) in which several trees and grasses were planted and an artificial pond was set. Fruit (broken water melon) was given as food because the adult megalopterans can be reared by giving sugar solution, fermented milk, and/or fruit (Hayashi 1993, 1996, 1999; Villagomez and Contreras-Ramos 2017). In this cage, adults mated freely and laid egg masses. Water temperature in the larval tanks ranged from 10 to 20 °C, but air temperature and photoperiod were under natural conditions at Leshan, Sichuan, China. After the adults died, they were preserved as pinned dry specimens with wings spread (Fig. 1). The prothorax length (PL), head width between the outer left and right eye margins (HW), mandible length (ML), forewing length (WL) from the basal part to the tip of cubital vein, and ectoproct length of male genitalia (GL) were measured carefully with a digital slide caliper to the nearest 0.01 mm (Fig. 1). These five body parts are relatively hard structures, which allowed us to measure them even in the dried specimens. Usually, the right mandible, wing, and ectoproct were measured, but if the right ones were broken, the left ones were used for measurements, although in a few cases both were broken.

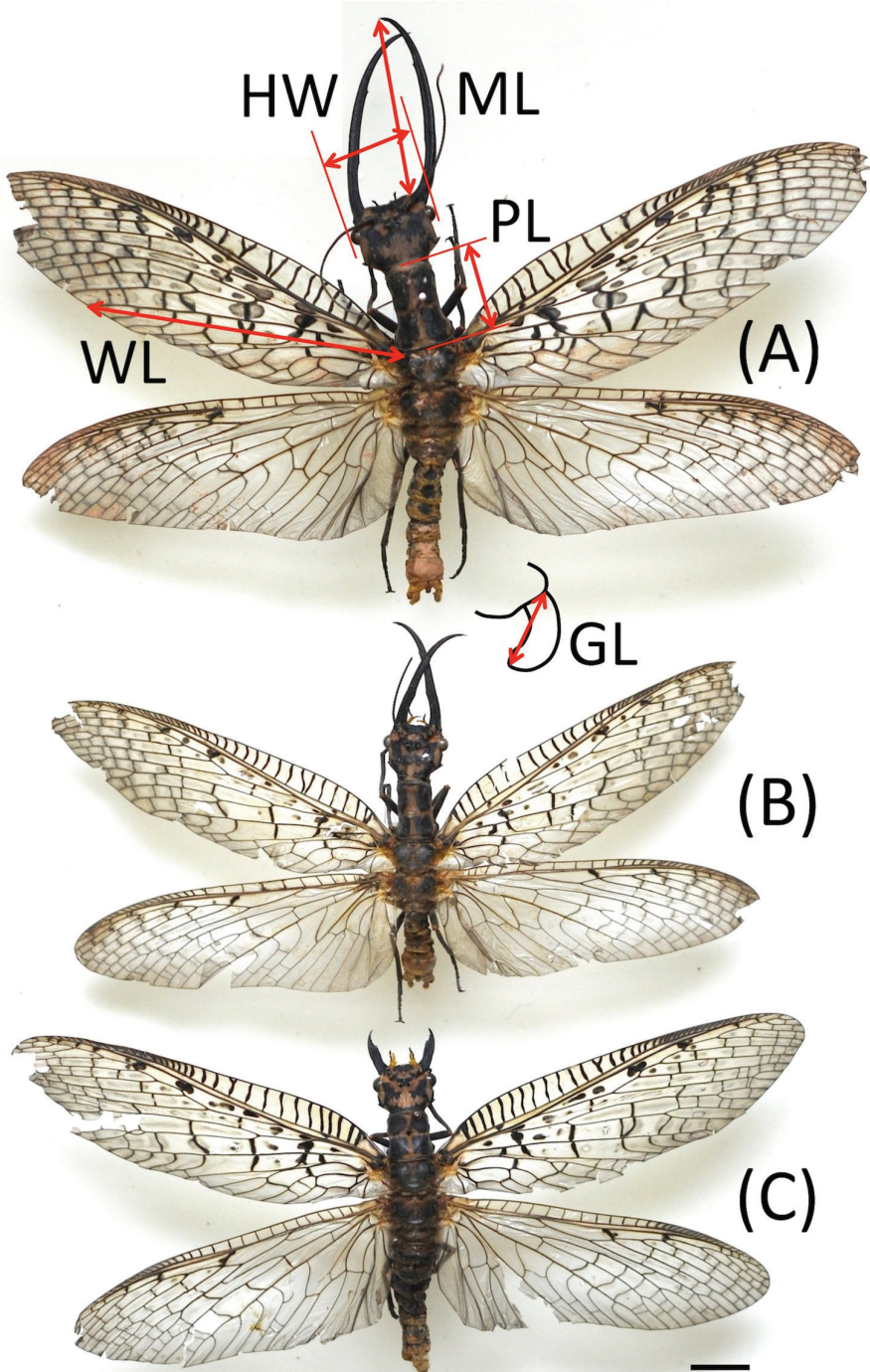
The mean value ( $\pm$  SD) and CV (%) were calculated for all measured parameters. As in Liu et al. (2015), PL was used as an index of the body size, and the allometric relationships with PL were calculated for HW, ML, WL, and GL after all data were  $\log_{10}$ -transformed. The regression slope was calculated by major axis regression for males and females, respectively, because the standard least-squares method tends to produce underestimations (McArdle 1988). The 95% and 99% confidence limits of the slope were also calculated. Sexual differences of the slope and intercept of regressions were tested by the analysis of covariance (ANCOVA) using likelihood ratio statistics for slopes and using Wald statistics for intercepts when the slopes are common (R Development Core Team 2017).

## Results

Males were larger than females on the average and there was a great size variation in male morphological traits; CV was greater in males than females (Table 1, Fig. 1). Among male traits, CV was largest in ML and smallest in GL, suggesting the mandible length varies individually, but the ectoproct length is rather stable.

HW was correlated linearly with PL in log-log relationship both in males ( $R^2 = 0.946$ ,  $P < 0.0001$ ) and females ( $R^2 = 0.813$ ,  $P < 0.0001$ ), and the slope of the regression line was 0.829 in males and 0.773 in females (Fig. 2A). The slopes were less than 1 both in males and females ( $P_s < 0.01$ ), and did not differ between the sexes (ANCOVA,  $P = 0.434$ ). However, the intercepts of the regressions differed between the sexes ( $P < 0.0001$ ), suggesting that the head width is larger in females than males compared with same body size.

ML was always greater in males than females (Fig. 2B). ML was correlated linearly with PL in log-log relationship both in males ( $R^2 = 0.916$ ,  $P < 0.0001$ ) and females

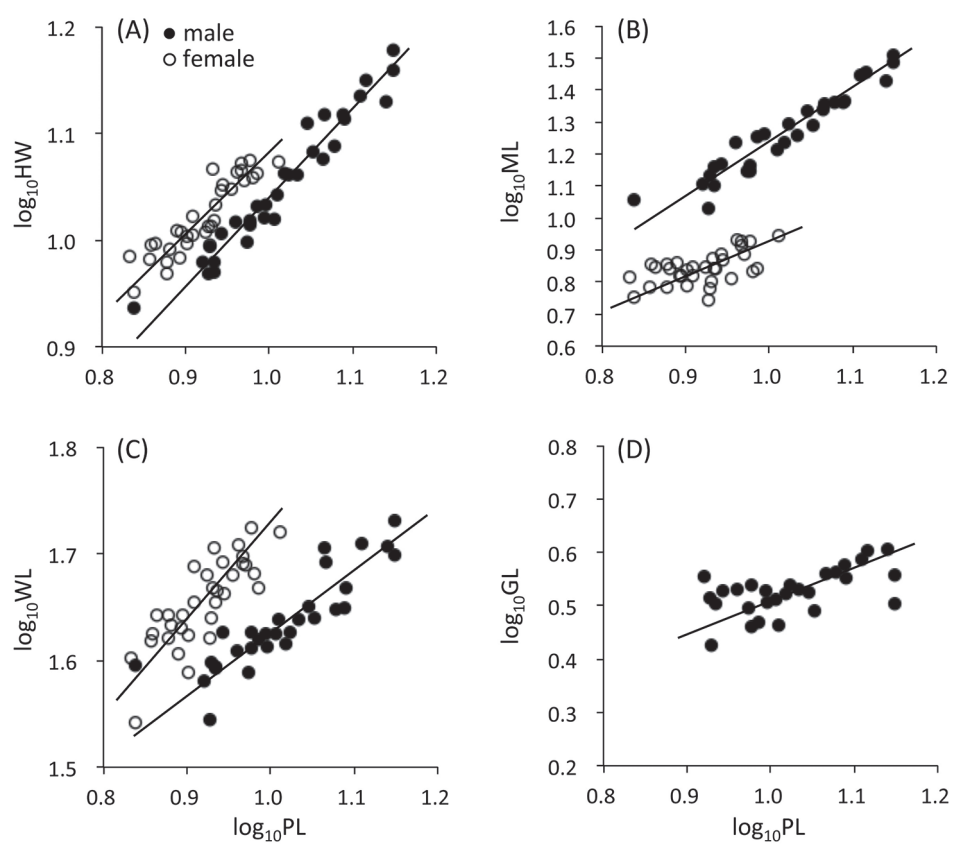


**Figure 1.** *Acanthacorydalis asiatica* in the dorsal view. **A** Large male **B** small male **C** female. Abbreviations: HW, head width; GL, genital (ectoproct) length in the lateral view; ML, mandible length; PL, prothorax length; WL, wing length. Scale bar: 10 mm.



**Table 1.** The prothorax length (PL), head width (HW), mandible length (ML), wing length (WL), and genital length (GL) of male and female *Acanthacorydalis asiatica*.

Sex	Males					Females			
Body part	PL (mm)	HW (mm)	ML (mm)	WL (mm)	GL (mm)	PL (mm)	HW (mm)	ML (mm)	WL (mm)
N	31	31	29	30	28	33	33	33	33
Mean	10.56	11.44	19.27	43.43	3.38	8.37	10.53	7.02	45.36
SD	1.86	1.70	5.93	4.51	0.33	0.87	0.85	0.82	4.19
CV%	17.63	14.83	30.76	10.38	9.73	10.37	8.07	11.74	9.23



**Figure 2.** Log-log relationships between the prothorax length (PL) and the head width (HW in **A**), mandible length (ML in **B**), wing length (WL in **C**), and genital (ectoproct) length (GL in **D**) in male and female *Acanthacorydalis asiatica*. Regression lines: **A**  $y = 0.829x + 0.211$  in males and  $y = 0.773x + 0.310$  in females **B**  $y = 1.663x - 0.428$  in males and  $y = 1.113x - 0.181$  in females **C**  $y = 0.582x + 1.046$  in males and  $y = 0.903x + 0.823$  in females **D**  $y = 0.605x - 0.094$  in males. For statistical tests, see the text.

( $R^2 = 0.342$ ,  $P < 0.001$ ), and the slope of the regression line was 1.663, significantly larger than 1 ( $P < 0.01$ ), in males and 1.113, not different from 1 ( $P > 0.05$ ), in females (Fig. 2B). The slopes differed significantly between the sexes (ANCOVA,  $P < 0.05$ ),



suggesting that the mandible length shows the positive allometry with their body size in males, but isometric in females.

WL was correlated linearly with PL in log-log relationship both in males ( $R^2 = 0.774$ ,  $P < 0.0001$ ) and females ( $R^2 = 0.664$ ,  $P < 0.0001$ ), and the slope of the regression line was 0.582, significantly lower than 1 ( $P < 0.01$ ) in males and 0.903, not different from 1 ( $P > 0.05$ ), in females (Fig. 2C). The slopes differed significantly between the sexes (ANCOVA,  $P < 0.005$ ), suggesting that the wing length shows the negative allometry with their body size in males, but isometric in females, and the wing is usually shorter in males than females compared with same body size.

GL was correlated linearly with PL in log-log relationship in males ( $R^2 = 0.336$ ,  $P < 0.005$ ), and the slope of the regression line was 0.605 which was significantly lower than 1 ( $P < 0.01$ ), suggesting the ectoproct length shows the negative allometry with male body size (Fig. 2D).

## Discussion

Males of *Acanthacorydalis* species combat each other for access to females or limited resources (tree sap) that attract females (Liu et al. 2015). They use mandibles as weapons for their combat and the exaggerated mandibles may be favored by sexual selection, because males had longer mandibles than females and the allometry between body and mandible sizes was positive in males but isomeric in females. CV of the mandible length was also greatest among male traits examined in this study. Thus, mandibles are condition-dependent traits in males (House et al. 2015). In Megaloptera, positive allometry between body and weapon sizes is also reported in males of seven species of *Corydalus* in the Americas, three species of *Acanthacorydalis* in Asia, and two species of *Platyneuromus* in Central America (Liu et al. 2015; Álvarez et al. 2017; Ramírez-Ponce et al. 2017). In addition, 22 species of *Corydalus* in America are suggested to have elongated male mandibles fitting this allometric phenomenon (Contreras-Ramos 1998). In *Corydalus* and *Acanthacorydalis*, males have elongated mandibles, but in *Platyneuromus*, males have large flanges at the lateral sides of the head, spread like a fan, although the function is still unknown (Glorioso and Flint 1984; Ramírez-Ponce et al. 2017). The molecular phylogenetic tree of all genera of the subfamily Corydalinae of Megaloptera suggests that these three genera are included in the same lineage with the New World *Chloronia* which lacks any weapons in males, and therefore male weapons are thought to have evolved independently (Liu et al. 2015). In *Corydalus bidenticulatus*, positive allometry is reported between male body size and antenna length (Álvarez et al. 2017). In the present study, we cannot examine this, because most specimens were preserved after spending life in a large rearing cage and lost antennae.

For insects, resources used for adult body development are limited to those acquired during larval periods. Males suffer in how they allocate the limited resources to weapons and other body parts of adults. Much allocation to weapons is costly and, hence, trade-offs occur between weapons and other male traits such as wing size (e.g.,

Kawano 1995, 1997), ejaculate size (review by Simmons et al. 2017), nuptial gift size (Liu et al. 2015), and immune system (Körner et al. 2017; also see Pomfret and Knell 2006; McCullough and Emlen 2013). If males have two or more types of weapons, a trade-off is also important in allocating more resources to which type of weapons (Kojima and Lin 2017). In the present study, mandibles had positive but wings had negative allometries with body size in males, while both traits were isometric in females. Liu et al. (2015) reported the same tendency in three species of *Acanthacorydalis*, but no such tendencies in six species of *Corydalis* with enlarged male mandibles and two species of *Platyneuromus* with enlarged male head flanges, although specimens from multiple collecting sites were combined for analysis. Thus, in *Acanthacorydalis*, large males possess disproportionately large mandibles but small wings compared with small males, which is quite similar to the common results of stag beetles (Kawano 1997). However, such a trade-off must be demonstrated directly. Despite the accumulating evidence for resource allocation trade-offs in insects, these trade-offs are not universal (Simmons and Emlen 2006; McCullough and Emlen 2013). In the future, flight ability will be compared between large and small males to reveal the cost of disproportionately developed wings in *Acanthacorydalis*, compared with *Corydalis* and *Platyneuromus* likely to have proportionate wings.

Male genital size of *Acanthacorydalis asiatica* was only slightly influenced by variation in body size as supported by its lowest CV, and the allometric relationship was negative between body size and genital size. Although based on small sample size, the negative allometry was also obtained in American *Corydalis bidenticulatus* (Álvarez et al. 2017). The low influence of body size on genital size may be interpreted as evidence of stabilizing selection for it. Eberhard et al. (1998) considered that this is achieved by cryptic sexual selection and called it the one-size-fits-all hypothesis of insect male genitalia. If intermediate-sized genitalia provide a better fit or better tactile stimulation for more females in the population than small genitalia or large genitalia, the males with that-sized genitalia would leave more offspring, regardless of their body size (Eberhard et al. 1998, 2018). In insects, sperm are transferred to the female by direct ejaculation into the bursa copulatrix, deposition of a small spermatophore in the bursa copulatrix, or an external spermatophore attached to the female genital opening from which sperm enter the bursa copulatrix (Simmons 2001; Chapman 2013). Males of Megaloptera use the external spermatophore which is attached to the female within a few minutes at mating (Hayashi 1992, 1993, 1996, 1998; Liu et al. 2015). They lack the intromittent organ such an aedeagus (Liu et al. 2016). All the previous studies on genital allometries were done for insects with direct ejaculation or internally deposited spermatophores (reviewed by Eberhard et al. 1998, 2018; Eberhard 2009; Voje 2016). Thus, the present study reveals that the one-size-fits-all hypothesis also applies to male genitalia of Megaloptera with insemination via an externally attached spermatophore. Ectoprocts, which grasp the female abdominal tip, may be unnecessary to be enlarged with male body size. Insemination using an external spermatophore also occurs in crickets and bushcrickets in Orthoptera and some species in these taxa have male weaponry

just like Megaloptera (e.g., Kelly 2005; Kim et al. 2011). It would be interesting to examine whether or not the same allometric relationship of genitalia occur between these sexually dimorphic Megaloptera and Orthoptera, which are distant phylogenetically (holometabolous and hemimetabolous, respectively), but similar in mating behavior.

## Acknowledgements

We thank Tamotsu Kusano for helping statistical tests, and Suting Li and Yaqian Fang for assisting field sampling and laboratory rearing. We also thank Atilano Contreras-Ramos for his invaluable comments on the early version of this manuscript.

## References

- Álvarez HA, García-Chávez JH, Cebada-Ruiz JA (2017) Do social environments affect the use of exaggerated traits in the dobsonfly *Corydalus bidenticulatus*? *Entomological Science* 20: 168–176. <https://doi.org/10.1111/ens.12249>
- Bonduriansky R (2007) Sexual selection and allometry: a critical reappraisal of the evidence and ideas. *Evolution* 61: 838–849. <https://doi.org/10.1111/j.1558-5646.2007.00081.x>
- Cao C, Liu X (2013) Description of the final-instar larva and pupa of *Acanthacorydalus orientalis* (McLachlan, 1899) (Megaloptera: Corydalidae) with some life history notes. *Zootaxa* 3691: 145–152. <https://doi.org/10.11646/zootaxa.3691.1.5>
- Chapman RF (2013) *The Insects: Structure and Function*, 5<sup>th</sup> edition. Cambridge University Press, Cambridge, 929 pp.
- Contreras-Ramos A (1998) Systematics of the Dobsonfly Genus *Corydalus* (Megaloptera: Corydalidae). Thomas Say Publications in Entomology: Monographs. Entomological Society of America, Lanham, Maryland, 360 pp.
- Eberhard WG (2009) Static allometry and animal genitalia. *Evolution* 63: 48–66. <https://doi.org/10.1111/j.1558-5646.2008.00528.x>
- Eberhard WG, Huber BA, Briceño RD, Salas I, Rodríguez V (1998) One size fits all? Relationships between the size and degree of variation in genitalia and other body parts in twenty species of insects and spiders. *Evolution* 52: 415–431. <https://doi.org/10.1111/j.1558-5646.1998.tb01642.x>
- Eberhard W, Rodríguez RL, Polihronakis M (2009) Pitfalls in understanding the functional significance of genital allometry. *Journal of Evolutionary Biology* 22: 435–445. <https://doi.org/10.1111/j.1420-9101.2008.01654.x>
- Eberhard WG, Rodríguez RL, Huber BA, Speck B, Miller H, Buzatto BA, Machado G (2018) Sexual selection and static allometry: the importance of function. *Quarterly Review of Biology* 93: 207–250. <https://doi.org/10.1086/699410>
- Emlen DJ (2008) The evolution of animal weapons. *Annual Review of Ecology, Evolution, and Systematics* 39: 387–413. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173502>

- Emlen DJ, Nijhout HF (2000) The development and evolution of exaggerated morphologies in insects. *Annual Review of Entomology* 45: 661–708. <https://doi.org/10.1146/annurev.ento.45.1.661>
- Glorioso MJ, Flint Jr OS (1984) A review of the genus *Platyneuromus* (Insecta: Neuroptera: Corydalidae). *Proceedings of the Biological Society of Washington* 97: 601–614.
- Hayashi F (1992) Large spermatophore production and consumption in dobsonflies *Protohermes* (Megaloptera, Corydalidae). *Kontyû* 60: 59–66.
- Hayashi F (1993) Male mating costs in two insect species (*Protohermes*, Megaloptera) that produce large spermatophores. *Animal Behaviour* 45: 343–349. <https://doi.org/10.1006/anbe.1993.1039>
- Hayashi F (1996) Insemination through an externally attached spermatophore: bundled sperm and post-copulatory mate guarding by male fishflies (Megaloptera: Corydalidae). *Journal of Insect Physiology* 42: 859–866. [https://doi.org/10.1016/0022-1910\(96\)00037-6](https://doi.org/10.1016/0022-1910(96)00037-6)
- Hayashi F (1998) Multiple mating and lifetime reproductive output in female dobsonflies that receive nuptial gifts. *Ecological Research* 13: 283–289. <https://doi.org/10.1046/j.1440-1703.1998.00272.x>
- Hayashi F (1999) Rapid evacuation of spermatophore contents and male post-mating behaviour in alderflies (Megaloptera: Sialidae). *Entomological Science* 2: 49–56.
- House CM, Jensen K, Rapkin J, Lane S, Okada K, Hosken DJ, Hunt J (2015) Macronutrient balance mediates the growth of sexually selected weapons but not genitalia in male broad-horned beetles. *Functional Ecology* 30: 769–779. <https://doi.org/10.1111/1365-2435.12567>
- Kawano K (1995) Horn and wing allometry and male dimorphism in giant rhinoceros beetles (Coleoptera: Scarabaeidae) of tropical Asia and America. *Annals of the Entomological Society of America* 88: 92–99. <https://doi.org/10.1093/aesa/88.1.92>
- Kawano K (1997) Cost of evolving exaggerated mandibles in stag beetles (Coleoptera: Lucanidae). *Annals of the Entomological Society of America* 90: 453–461. <https://doi.org/10.1093/aesa/90.4.453>
- Kim H, Jang Y, Choe JC (2011) Sexually dimorphic male horns and their use in agonistic behaviors in the horn-headed cricket *Loxoblemmus doenitzi* (Orthoptera: Gryllidae). *Journal of Ethology* 29: 435–441. <https://doi.org/10.1007/s10164-011-0277-x>
- Kodric-Brown A, Sibly RM, Brown JH (2006) The allometry of ornaments and weapons. *Proceedings of the National Academy of Sciences of the United States of America* 103: 8733–8738. <https://doi.org/10.1073/pnas.0602994103>
- Körner M, Vogelweith F, Foitzik S, Meunier J (2017) Condition-dependent trade-off between weapon size and immunity in males of the European Earwig. *Scientific Reports* 7: 7988. <https://doi.org/10.1038/s41598-017-08339-6>
- Lavine L, Gotoh H, Brent CS, Dworkin I, Emlen DJ (2015) Exaggerated trait growth in insects. *Annual Review of Entomology* 60: 453–472. <https://doi.org/10.1146/annurev-ento-010814-021045>
- Liu X, Hayashi F, Lavine LC, Yang D (2015) Is diversification in male reproductive traits driven by evolutionary trade-offs between weapons and nuptial gifts? *Proceedings of the Royal Society of London B* 282: 14–20. <https://doi.org/10.1098/rspb.2015.0247>

- Liu X, Lü Y, Aspöck H, Yang D, Aspöck U (2016) Homology of the genital sclerites of Megaloptera (Insecta: Neuropterida) and their phylogenetic relevance. *Systematic Entomology* 41: 256–286. <https://doi.org/10.1111/syen.12154>
- Liu X, Yang D, Ge S, Yang X (2005) Phylogenetic review of the Chinese species of *Acanthacorydalis* (Megaloptera, Corydalidae). *Zoologica Scripta* 34: 373–387. <https://doi.org/10.1111/j.1463-6409.2005.00197.x>
- McArdle BH (1988) The structural relationship: regression in biology. *Canadian Journal of Zoology* 66: 2329–2339. <https://doi.org/10.1139/z88-348>
- McCullough EL, Emlen DJ (2013) Evaluating the costs of a sexually selected weapon: big horns at a small price. *Animal Behaviour* 86: 977–985. <https://doi.org/10.1016/j.anbehav.2013.08.017>
- O'Brien DM, Allen CE, Van Kleeck MJ, Hone D, Knell R, Knapp A, Christiansen S, Emlen DJ (2018) On the evolution of extreme structures: static scaling and the function of sexually selected signals. *Animal Behaviour* 144: 95–108. <https://doi.org/10.1016/j.anbehav.2018.08.005>
- Pomfret JC, Knell RJ (2006) Immunity and the expression of a secondary sexual trait in a horned beetle. *Behavioral Ecology* 17: 466–472. <https://doi.org/10.1093/beheco/arj050>
- R Development Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ramírez-Ponce A, Garfías-Lozano G, Contreras-Ramos A (2017) The nature of allometry in an exaggerated trait: the postocular flange in *Platyneuromus* Weele (Insecta: Megaloptera). *PLoS ONE* 12: e0172388. <https://doi.org/10.1371/journal.pone.0172388>
- Rico-Guevara A, Hurme KJ (2019) Intrasexually selected weapons. *Biological Reviews* 94: 60–101. <https://doi.org/10.1111/brv.12436>
- Rivera-Gasperín SL, Ardila-Camacho A, Contreras-Ramos A (2019) Bionomics and ecological services of Megaloptera larvae (dobsonflies, fishflies, alderflies). *Insects* 10: 86. <https://doi.org/10.3390/insects10040086>
- Simmons LW (2001) *Sperm competition and its evolutionary consequences in the insects*. Princeton University Press, Princeton, 434 pp.
- Simmons LW, Emlen DJ (2006) Evolutionary trade-off between weapons and testes. *Proceedings of the National Academy of Sciences of the United States of America* 103: 16346–16351. <https://doi.org/10.1073/pnas.0603474103>
- Simmons LW, Lüpold S, Fitzpatrick JL (2017) Evolutionary trade-off between secondary sexual traits and ejaculates. *Trends in Ecology & Evolution* 32: 964–976. <https://doi.org/10.1016/j.tree.2017.09.011>
- Villagomez F, Contreras-Ramos A (2017) First records of adult feeding in Megaloptera (Corydalidae, Corydalinae) from Mexico and their possible relationship with the increase in life span. *Zootaxa* 4341: 287–290. <https://doi.org/10.11646/zootaxa.4341.2.11>
- Voje KL (2016) Scaling of morphological characters across trait type, sex, and environment: a meta-analysis of static allometries. *American Naturalist* 187: 89–98. <https://doi.org/10.1086/684159>
- Yang D, Liu X (2010) *Fauna sinica, Insecta Vol. 51 Megaloptera*. Science Press, Beijing, 457 pp. [in Chinese]





# Genus *Pempeliella* Caradja, 1916 and *P. bayassensis* Leraut, 2001 (Lepidoptera, Pyralidae) in Italy

Manuela Pinzari<sup>1</sup>, Mario Pinzari<sup>2</sup>

**1** Dipartimento di Biologia, Università di Roma Tor Vergata, Via della Ricerca Scientifica 1, 00133, Roma, Italy

**2** Piazza Francesco Morosini 12, 00136 Roma, Italy

Corresponding author: *Manuela Pinzari* ([manuela.pinzari@uniroma2.it](mailto:manuela.pinzari@uniroma2.it)); *Mario Pinzari* ([mario.pinzari@uniroma3.it](mailto:mario.pinzari@uniroma3.it))

Academic editor: *Colin Plant* | Received 10 April 2019 | Accepted 1 May 2019 | Published 10 June 2019

<http://zoobank.org/6DF94F38-18DA-47DB-B57E-FF98E22B6C76>

**Citation:** Pinzari M, Pinzari M (2019) Genus *Pempeliella* Caradja, 1916 and *P. bayassensis* Leraut, 2001 (Lepidoptera, Pyralidae) in Italy. ZooKeys 854: 131–144. <https://doi.org/10.3897/zookeys.854.35351>

## Abstract

*Pempeliella bayassensis* has been reported for the first time in Italy. This species has been confused with *P. ornatella* for a long time. Our study of the historical collections of Carlo Prola and Federico Hartig, and also newly collected materials from central Italy, allowed us to verify the presence of *P. bayassensis* in Italy. At present, this species is known only in central Italy (Lazio), where it coexists with *P. ornatella* and *P. sororiella*. We also provide information on the geographical distribution of the genus *Pempeliella* in Italy. In northern Italy we found *P. ornatella* and *P. sororiella*, and in the south (Puglia), *P. sororiella*. In Sardinia, *P. matilella*, which has been confused with *Delplanqueia cortella* in the past, coexists with *P. sororiella*.

## Riassunto

Viene segnalata per la prima volta in Italia *Pempeliella bayassensis*. Da sempre confusa con *ornatella*, per verificare la presenza in Italia della specie è stato effettuato lo studio delle collezioni storiche di Carlo Prola ed Federico Hartig e di materiale più recente raccolto in Italia centrale. Allo stato attuale, *P. bayassensis* sembra essere presente soltanto nel centro Italia ove convive con *ornatella* e *sororiella*. Inoltre diamo nota della distribuzione geografica in Italia delle specie appartenenti al genere *Pempeliella*. In particolare, nel nord sono presenti soltanto *P. ornatella* e *P. sororiella*. Nel sud è presente solo *sororiella* nelle Puglie. In Sardegna convivono *P. sororiella* e *P. matilella*, precedentemente confusa con *Delplanqueia cortella*.

## Keywords

distribution, *matilella*, *ornatella*, *sororiella*, sister species

## Introduction

In 2001 the genus *Pempeliella* Caradja, 1916 was adjusted (Leraut 2001a, 2001b) to include several European species: *P. ornatella* (Denis & Schiffermüller, 1775), which is present in almost all European countries and to Central Asia and Morocco; *P. lecerfella* (Lucas, 1933), in Morocco; *P. matilella* (Leraut, 2001), a Sardinian-Corsican endemism; *P. ardosiella* (Ragonot, 1887), in Spain, Gibraltar, and France but excluding Corsica; *P. sororiella* (Zeller, 1839), throughout southern Europe, from Spain to the Balkan Peninsula and also European Turkey; and *P. bayassensis*, in France and Morocco (Leraut 2001b), Spain (Gaston et al. 2014), and Switzerland (Schmid 2016). Leraut (2001a) excluded *Moitrelia italogallicella* (Millière, 1883) and *Delplanqueia cortella* (Constant, 1884) from the genus *Pempeliella*. Slamka and Plant (2016) described as new *P. bulgarica* Slamka & Plant, 2016, from Bulgaria and also recorded it in Turkey and Hungary. It is externally closely similar to *Pempeliella sororiella* (Zeller, 1839), but easily distinguished by male and female genitalia.

In Italy, four species belonging to the genus *Pempeliella* were included in the checklist of the Italian fauna: *P. cortella*, *P. italogallicella*, *P. ornatella*, and *P. sororiella* (Bassi et al. 1995).

We have collected *P. bayassensis* since 1989 in an ongoing survey of the Lepidoptera fauna in central Italy (Pinzari et al. 2010; Pinzari 2009, 2016a, 2016b; Pinzari and Sbordoni 2013; Pinzari et al. 2013a, 2013b, 2015, 2016b, 2017b, 2018a, 2018b, 2018c, 2019). This species has been confused with *P. ornatella* for a long time, and *P. sororiella* is easily mistaken for *P. bulgarica* Slamka & Plant, 2016. According to Leraut (2001), to clarify our understanding of the distribution of *Pempeliella* species in Italy and also verify the accuracy of the historical faunistic information in the literature of the last century, we studied recently collected specimens from central Italy in ours and other private collections, and specimens from every Italian region preserved in the historical collections of the Museo civico di Zoologia di Roma and the Museo di Zoologia dell'Università la Sapienza di Roma.

We provide information on the geographical distribution of the genus *Pempeliella* in Italy and the first records of *P. bayassensis* in Italy.

## Materials and methods

### Species identification and distribution in Italy

We examined the collections of Mario Pinzari (Rome), Zerun Zerunian (Assisi), Carlo Prola (Museo civico di Zoologia di Roma, MCZR), and Federico Hartig (Museo di Zoologia dell'Università la Sapienza di Roma, MZUR).

For the taxonomic identifications of specimens, we examined either the external habitus (wingspan and wing pattern) or dissected the genitalia, using the characters reported by Leraut (2001, 2012, 2014), Leraut G.H.C. (2012), and Slamka and Plant (2016). Genital parts were glycerol-preserved in microtubes, which had their ends closed with vinyl glue; the microtubes were put under the specimens themselves.

To match up ancient specimens in the museum collections with the past literature, we recorded the collocation of the species (Hartig's collection, boxes no. 17a and 18a; Prola's collection, original collocation unknown) and the determination labels under the specimens. After our study, all specimens of the Hartig (MZUR) and Prola (MCZR) collections were returned to the museums and placed in a new collocation on the basis of our species determination. We added another determination label under the original label for each specimen.

To show an updated distribution of the genus *Pempeliella* in Italy, we mapped the collection sites of both the materials examined and records from the literature.

### History of the genus *Pempeliella* in Italy

Four species were included in the check list of Italian fauna (Bassi et al. 1995): *P. cortella* (northern Italy and Sardinia); *P. italogallicella* (northern Italy); *P. ornatella ornatella* (= *gigantella* Amsel, 1932; Italian Peninsula and Sicily); and *sororiella sororiella* (northern Italy, Sicily, and Sardinia).

Speidel et al. (2013) and Leraut (2014) provided data on *P. sororiella* in all Italian regions, including Sicily and Sardinia; *P. ornatella* in continental Italy and Sicily; and *P. matilella* in Sardinia only.

In the following text, we report the precise citations of the studied species mentioned in past papers.

### *Pempeliella ornatella* (Denis & Schiffermüller, 1775)

Valle d'Aosta: Parco Naturale Mont Avic: 1 ♂, 2 ♀♀, sentiero da Magazzino al Lago Selva, 1600–1800 m, 11.VII.1993; 4 ♀♀ sentiero da Covarey a Serva Desot, 1400–1600 m, 14.VII.1993, 22.VII.1994; 1 ♂, 1 ♀, dintorni di Covarey, 1200 m ca, 18.VII.1993, 23.VII.1994 (lux); 1 ♀, Serva Desot, prati, 1600 m ca, 24.VI.1995; (Baldizzone 1996).  
Piemonte: Alpi Marittime, Viozene; Val Chisone, Fenestrelle, VII–VIII.1928; Alpi Biellesi, Piedicavallo, VII.1930; (Della Beffa 1941). S. Anna di Valdieri, dintorni del Lago sottano della Sella, 1900 m ca, 16.VII.1998; Terme di Valdieri, sentiero da Valasco superiore a Laghi Valscura e Claus, 2000–2300 m, 23.VII.1996, 30.VII.1997, 7.VIII.2001; Terme di Valdieri, Vallone del Gesso della Valletta, Pian della Casa, 1800 m, 24.VII.1997; Terme di Valdieri, Vallone del Gesso della Valletta, sentiero Pian della Casa al Colle del Mercantour, 1900–2200 m, 26.VII.2000; Entracque, Monte Ray, 1800 m, 20 and 24.VII.1999; Entracque, Valle della Rovina, Rocca Barbis, 1537–1800 m ca, 14.VII.1996, 20.VII.1997; S. Giacomo, vallone del Gesso della Barra: Gias Isterpis, 1380 m, 19.VII.1996 e sentiero per Rifugio Sori, 1600–1700 m ca, 19.VII.2000; Trinità, 1100 m, 24.VII.1996 (lux), 30.VII.1997 (lux), 13 and 14.VII.1998 (lux); Trinità, Vallone Grande, 1300 m ca, 15.VII.1996, 19.VII.1997, 13.VI.1999, 16.VI.2000; Trinità, sentiero per Colle della Garbella, 1550–1800 m, 30.VI.2000; Trinità, Valle del Sabbione, da Gias Ischietto a Gias dell'Adreit, 1200–1450 m ca, 13.VII.1996; (Baldizzone 2004). Parco Naturale delle Capanne del Marcarolo:

- Località, Cirimilla, Cascina Le Miniere, 300 m, 6.VI.2005 (lux); Strada-Cirimilla Capanne inferiori, 350 m, 26.V.2006 (lux); Cascina Cappellana, 450 m, 8.VI.2005 (lux), 21.VI.2005 (lux); Cascina Macerona, 500 m, 12.VI.2005 (lux), 21.VI.2005 (lux); Capanne inferiori, località Gli Olmi, 758 m, 9.VI.2003 (lux), 10.VI.2003 (lux), 19.VI.2003 (lux); (Baldizzone et al. 2013). Valdieri, luglio, agosto, (Turati and Verity 1911). Colle Fauniera (CN), Alpi Cozie, 3–6.VIII.2008, (Huemer 2009).
- Veneto: Alpi Bellunesi, Mas, M. Piai, 450 m, 25.VII.1937; Alpi Agordine, Falcade, 6.VII.1932 (Rocca leg.); (Della Beffa 1941).
- Trentino Alto Adige: Venezia Tridentina, Passo di Campolongo, 12.VII.1931 and S. Vigilio di Marebbe, 28.VI.1931 (Rocca leg.); Val S. Pellegrino, Someda, 15.VII.1938; (Della Beffa 1941). Brennero, Nord e Sud, (Hartig 1956). Tirolo, *Pempelia ornatella*, (Weiler (1877) in Burmann, 1995); *Pempelia ornatella* ssp. *gigantella*, Venosta: Juval VI al L(ume) (Reitberger H. leg); Val d'Adige: S. Maurizio-Moritzing (Hellweger M. leg); Castel Firmiano-Sigmundskron. Val d'Isarco: Bressanone (Hellweger M. leg); Adamello: Malga Bedole (Biasoli in H.81); Val d'Amola 1800 m ♂♀ 29.VII.1924 (Tr); Fresine nell'VIII (Turati E. leg); Tonale ♂ 29.VI.1943 (Prola G., G. e Carlo leg); Ortler: Gomagoi ♂ 3.VII.1929 (Astfäller B. leg); Trafoi-Stelvio (Eppelsheim F., Wocke M., Frey leg); S. Valentino (Rocca); Tures-Taufers e Riva-Rain (W.80); Alpi Sarentine: Collalbo ♂ 12.VI, ♂♀ 17.VII, Rosswagen 1650 m ♂ 18.VI.1947 (Hartig); Avelengo-Hafling ♀ 23.VI, ♂ 17.VII.1930 (Hager K. leg); Dolomiti Ortisei-St. Ulrich 1.VII, Selva-Wolkenstein, Rif. Di Cisles-Regensburgerhutte 21.VII (Schawerda K. leg); Val di Non e Mendola: Tret ♂ 8.VI.1931, 17.VI.1932 (Castelli G. leg); Romeno ♀ 7.VI.1928 (Anonymous collector); Brenta e Paganella: Pinzolo 2 ♀♀ 30.VI and 11.VII.1926, Campiglio ♂ 1.VIII.1926, ♀ 21.VII.1927 (F); ibid. VII–VIII.1933–1935 (Hartig leg); Sette Comuni: Lavarone ♂ 19.VIII.1930 (Fiori A. leg); ♂ 17.VII.1933 (Anonymous collector); (Hartig 1958). Ritten (BZ), 1021 m, 1992–1995, 2000; Passo Lavazé (TN), 1790 m, 1992–1995; Huemer 2002. Schlern Nature Park, Castelrotto (BZ), (Huemer 2007).
- Friuli Venezia Giulia: Alpi Carniche, Sappada, VII.1933; (Della Beffa 1941).
- Emilia Romagna: Sestola, Appennino Emiliano (Turati 1923; In Parenti 1962). Croara, colline bolognesi (Parenti 1962). Toscana: *Pempelia ornatella* Schiff., Forte dei Marmi, (Verity 1904). Umbria: 1 ♂, Monte Subasio (PG), Fonte Bregno, 1000 m, 7.VI.2006; 1 ♂, Monte Subasio (PG), Colle S. Rufino, 1000 m, 13.V.2007; Z. & I. Zerunian leg. 2 ♂♂, Monte Subasio (PG), Mortaro Grande, 1200 m, 16.VI.2015; Z. Zerunian leg. (Pinzari M et al. 2016).
- Lazio: Borbona (RI) Fraz. Vallemare, 1 ♂, Colle Marcone, 1121 m, 16.VI.1989 (gen. praep. PIRA 274, M. Pinzari), 1 ♂, 1 ♀, idem, 18.VI.2007, 1 ♂, idem, 27.VI.2008, 1 ♂, 1 ♀, idem, 13.VI.2009, 1 ♂, idem, 26.VI.2009, 1 ♀, idem, 22.VII.2009, 1 ♂, idem, 18.VI.2010, 1 ♀, idem, 10.VII.2010; M. Pinzari leg; Posta (RI), Fraz. Villa Camponeschi, 1 ♂, Colle Petruccio, 1000 m, 19.V.2007, 1 ♂, idem, 20.V.2007; A. Zilli leg. SIGHTINGS. Colle Petruccio, 1000 m, 29.VI.2007, fide A. Zilli. (Pinzari et al. 2010). Abruzzo: La Maielletta, VII.1961 1 ♂; Passo Lanciano, VII.1960 1 ♂, 1 ♀, VII.1961 (6 ♂♂); (Parenti 1962).

***Pempeliella matilella* (Leraut, 2001)**

Sardegna: Paratypes: 1 ♂, Italie, Sardaigne, Aritzo, “dint. Cant. Sa Casa”, 950 m, 24.VII.1936 (Conte Hartig) (prép. Gén. Leraut n° 6639; MNHN, Paris; 3 ♀♀, mêmes coordonnées, 1 ♀, Sardaigne, Aritzo, 3.VIII.1936 (H.G. Amsel); (Leraut 2001).

***Pempeliella sororiella* (Zeller, 1839)**

Piemonte: Terme di Valdieri, Vallone del Gesso della Valletta, sentiero Pian della Casa al Colle del Mercantour, 1900–2200 m, 26.VII.2000, (Baldizzone 2004).

Trentino Alto Adige: Trentino Alto Adige, Val Venosta, S. Valentino alla Muta, m. 1500 e Burgusio, m. 1300, VI.1939, (Della Beffa 1941). Brennero Sud, (Hartig 1956). Tirolo, *Pempeliella sororiella*, (Hellweger 1929 in Burmann 1995). Tirolo, Hartig *Pempeliella sororiella* (Burmann 1995); Dolomiti: 1 ♂ Schludersbach, 1 ♀, Val Popena (Mann In Mus. Vind. Htg) (Hartig 1958).

Friuli Venezia Giulia: Tagliamento, Cornino, 180 m, Peonis, Avasinis, 250 m. (Deutsch 2006).

Lazio: Fondi, S. Anastasia, 1 ♂, 1–12.VIII, Predota C. leg. (Hartig 1939). Borbona (RI) Fraz. Vallemare, 1 ♂, Colle Marcone, 1121 m, 2.VIII.2012, 1 ♂, idem, 15.VIII.2012 (gen. praep. PYRA 259, M.Pinzari), M. Pinzari leg. (Pinzari et al. 2013b).

Sicilia: Siracusa, giugno, Zeller leg. (Curò 1880; Minà Palumbo and Failla-Tebaldi 1889). Zappulla (ME), VII (Mariani, 1939).

Sardegna: Aritzo 29.VII, Sa Casa 24–29.VII. 1936, Strada per Desulo 8.VII. 1936, (Hartig and Amsel 1951).

***Pempeliella cortella* (Constant, 1884)**

Sardegna: Sa Casa 24–29.VII.1936; Aritzo 9–27.VII.1936; Piano di Sadali, 5.VII.1936; Strada per Desulo, 8.VII., 1936 (Hartig and Amsel 1951). This citation was attributed *P. matilella* after the study of Hartig’s collection by Pinzari and Pinzari (in press). At present, *P. cortella* (= *Delplanqueia cortella*) has not been revealed yet in Sardinia.

**Results**

We identified the species of *Pempeliella* in Italy and grouped the specimens following the publication by Leraut (2001). Our study of Hartig’s and Prola’s collections revealed that the specimens collected in Trentino ( $N = 15$ ) and Liguria ( $N = 2$ ) were *P. ornatella* and that the specimen from Puglia was *P. sororiella*.

In central Italy we found that there were only three of the four Italian species of *Pempeliella*: *P. ornatella*, *P. bayassensis* and *P. sororiensis*. In Latium, we collected: five males and three females of *P. bayassensis*; 13 males and 14 females of *P. ornatella*; two males and one female of *P. sororiella*. From Sardinia, four specimens of *P. sororiella* and 27 of *P. matilella* were identified in Hartig’s collection.

## Materials examined and newly collected

### *Pempeliella ornatella* (Denis & Schiffermüller, 1775)

Liguria: 1 ♂, (gen. praep. PIRA 534, M. Pinzari), Alpi Marittime, Carmo Langan, 14.VIII.1950, Prola leg. MCZR; 1 ♀, (gen. praep. PIRA 535, M. Pinzari), Alpi Liguri, Colla Melosa, 17.7.1985, (legit absent), MCZR; 1 ♂, (abdomen absent), Alpi Liguri (IM), Colla Melosa, 16.VII.1983, V. Raineri leg, MCZR. Piemonte: 1 ♀, (abdomen absent), Alpi Cozie, Sestriere, 23.VII.1950, Prola. Lombardia: 1 ♂, (gen praep. PIRA 519, M. Pinzari), colloc. *gigantella*, Alpi del Tonale, 29.VI.1943 Prola MCZR (Fig. 3 B).

Trentino Alto Adige: 2 ♂♂, (gen. Praep. PIRA 513, PIRA 516, M. Pinzari), Mad. di Campiglio, 13.VII.1933, and coll. Cte Hartig; 1 ♂, (gen. praep. PIRA 514, M. Pinzari), M. di Campiglio, Trentino, Italia, 1522 m, 20.VII.1933, 1 ♀, (gen praep. PIRA 515, M. Pinzari, Fig. 1A, C, idem, 10.VIII.1933, and coll. Cte. Hartig; 1 ♂, (gen. praep. PIRA 517, M. Pinzari, Fig. 1B, D), Alpi di Merano, Haflling, 900 (m), 2.VI.1931. All colloc. *gigantella*, Coll. Hartig MZUR. 1 ♂, M. di Campiglio, Trentino, Italia, 1522 m, 21.VII.1933, 1 ♂, idem, 15.VII.1933, and coll. Cte Hartig; 3 ♂♂, Mad. di Campiglio, 13.VII.1933, and coll. Cte Hartig; 1 ♂, determination label by E. Turati (Fig. 3B)., Mad. di Campiglio, 1515 m, 10.VII.1933, and coll. Cte Hartig (Fig. 3B); 1 ♂, M. di Campiglio Pfeiffertafel, 1600 (m), 13.VIII.1933, and coll. Cte Hartig. 1 ♀, Mad. di Campiglio, Via degli Orsi, 24.VII.1933, and coll. Cte Hartig; M. di Campiglio, 1522 m, 1 ♂, 27.VI.1935, 1 ♂, idem, 8.VII.1935, coll. Cte Hartig; 1 ♀, Mad. di Campiglio, 1515 m, 10.VII.1933, and coll. Cte Hartig, MZUR.

Lazio: 1 ♂, (gen. praep. PIRA 522, M. Pinzari), colloc. *gigantella*, M. Terminillo, m 1800, 16.VII.40 Prola leg. Coll. Hartig MZUR. Borbona (RI) Fraz. Vallemare, 1 ♂, (gen. praep. PIRA 274, M. Pinzari), Colle Marcone, 1121 m, 16.VI.1989, 1 ♂, 1 ♀, idem, 18.VI.2007, 2 ♂♂, 1 ♂, idem, 26.VI.2009, 1 ♀, idem, 22.VII.2009, 1 ♂, idem, 18.VI.2010, 1 ♀, idem, 10.VII.2010, 1 ♂, idem, 22.V.2011, 1 ♂, idem, 25.VI.2011, 1 ♀, idem, 8.VI.2012, 1 ♂, idem, 15.VI.2012, 1 ♂ (gen. praep. PIRA 278, M. Pinzari), idem, 16.VI.2012 1 ♀, idem, 22.VI.2012, 1 ♂, idem, 19.VI.2013, 1 ♀, idem, 5.VII.2013, 1 ♂, idem, 20.V.2014, 1 ♀, idem, 7.VI.2014, 1 ♀, idem, 7.VII.2014, 2 ♀♀, idem, 24.VI.2016, 1 ♂, 1 ♀, idem, 9.VII.2016, 1 ♀, idem, 19.VIII.2016, 1 ♀, idem, 17.VI.2017; M. Pinzari leg, Posta (RI) Fraz. Villa Camponeschi, 1 ♂, Colle Petruccio, 1000 m, 19.V.2007, 1 ♂, idem, 20.V.2007; A. Zilli leg.

Abruzzo: 1 ♂, (gen. praep. PIRA 521, M. Pinzari), colloc. *ornatella*, Abruzzo, Collelongo, m 1300, 28.VI.75, Prola leg. MCZR. 1 ♂, (gen. praep. PIRA 536, M. Pinzari), Abruzzo, Tufo, m. 900, 28.VI.75 Prola leg. MCZR.

### *Pempeliella matilella* Leraut, 2001

Sardegna: 1 ♀, Sard. centr., Aritzo, 6.VII.1936, 1 ♂, (gen. praep. PIRA 493, M. Pinzari), idem, 11.VII.1936, 1 ♀, (gen. praep. PIRA 488, M. Pinzari, Fig. 2A, C), idem,



28.VII.1936; 3 ♂♂, (gen. praep. PIRA 490, M. Pinzari, Fig. 2B, D), 2 ♀♀, (gen. praep. PIRA 487, M. Pinzari), Aritzo dint., Cant.sa Casa, 950 m, 24.VII.1936 (Fig. 3B); 2 ♂♂, (gen. praep. PIRA 491, M. Pinzari), idem, 29.VII.1936; all Cte Hartig leg.

### ***Pempeliella bayassensis* Leraut, 2001**

Lazio: 1 ♂, (gen. praep. PIRA 520, M. Pinzari), Colloc. *subornatella*, Lazio, M.te Flavio, 800 m, 30.V.1938, Hartig legit. MZUR. Borbona (RI), Fraz. Vallemare: 1 ♀, (gen. praep. PIRA 275, M. Pinzari), Colle Marcone, 1121 m, 27.VI.2008, 1 ♂, (gen. praep. PIRA 281, M. Pinzari), idem, 9.VII.2011, 1 ♀, (gen. praep. PIRA 280, M. Pinzari, Fig. 1E, G), idem, 24.VIII.2011, 1 ♂, (gen. praep. PIRA 277, M. Pinzari, Fig. 1F, H), idem, 18.V.2012, 1 ♂, idem, 19.VI.2013, 1 ♂, (gen. praep. PIRA 541, M. Pinzari), idem, 2.VI.2014, 1 ♀, idem, 6.VI.2014, 1 ♀, idem, 24.VI.2016; 1 ♀, (gen. praep. PIRA 276, M. Pinzari), Bivio Brignola, 1061 m, 1.VI.2012, M. Pinzari leg.

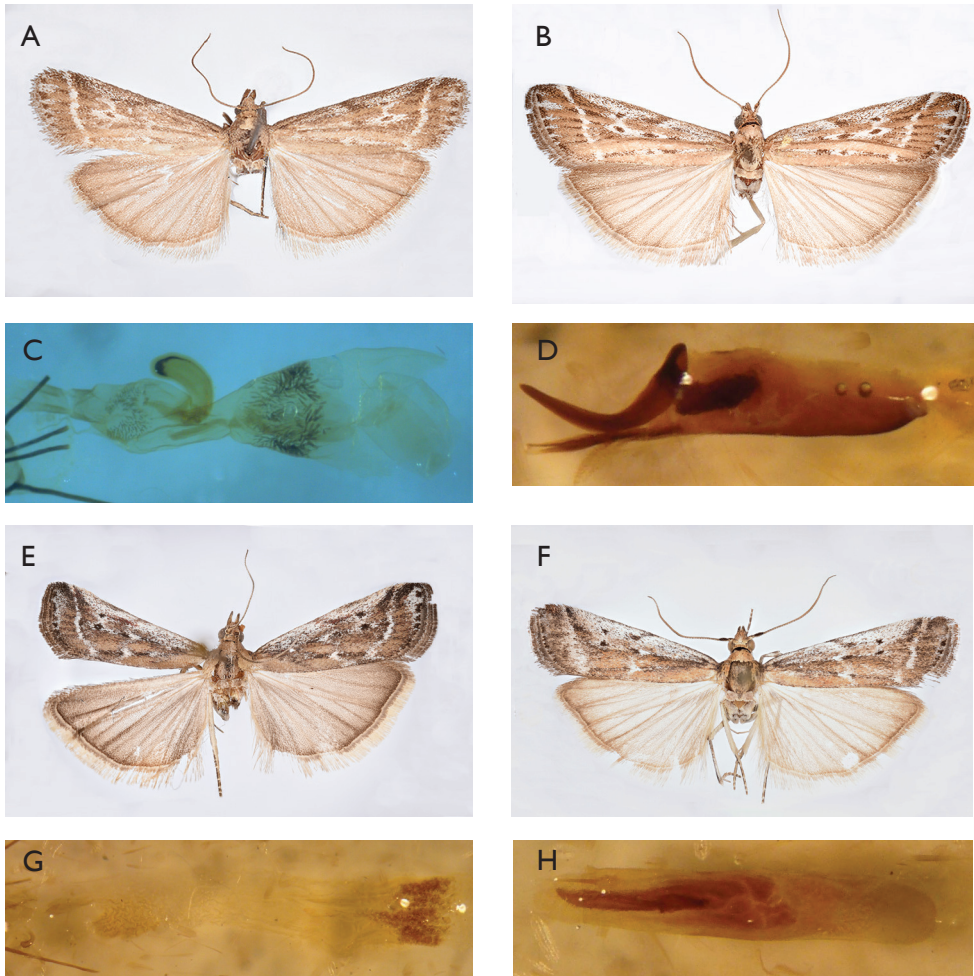
### ***Pempeliella sororiella* (Zeller, 1839)**

Veneto: 1 ♂, (gen. praep. PIRA 499, M. Pinzari), Lago di Garda, Torri Benaco, 6.VI.1940, Hartig leg. MZUR.  
Lazio: 1 ♂, (gen. praep. PIRA 555, M. Pinzari), Lazio, Fondi S.ta Anastasia, 1–12. VIII.1937, Predota leg. (Fig. 3B) MZUR. Borbona (RI) Fraz. Vallemare: 1 ♀, (gen. praep. PIRA 282, M. Pinzari), Colle Marcone, 1121 m, 2.VIII.2012, 1 ♂, (gen. praep. PYRA 259, M. Pinzari), idem, 15.VIII.2012, 1 ♂, (gen. praep. PYRA 537, M. Pinzari, Fig. 2F, H), idem, 29.VIII.2015, M. Pinzari leg.  
Puglie: 1 ♀, (gen. praep. PIRA 554, M. Pinzari, Fig. 2E, G), Puglie, Leuca dint. 6.VI.1941 Castellani leg (Fig. 3B), MZUR.  
Sardegna: 1 ♀, Sard. centr., Strada Desulo, 650 m, 8.VII.1936, Cte Hartig leg; 1 ♀, (gen. praep. PIRA 539, M. Pinzari), Aritzo, dint. Cant.sa Casa, 950 m, Cte Hartig leg. MZUR. 1 ♀, Sard. centr. Aritzo, 29.VII.1936, Cte. Hartig leg; 1 ♀, Aritzo, dint. Cant.sa Casa, 950 m, Cte Hartig leg. MZUR.

## **Distinguishing species**

### ***Pempeliella ornatella***

We examined 48 specimens of *P. ornatella* that were collected from northern and central Italy. In general, males and females of *P. ornatella* differed in wingspan (Mann-Whitney U test, wingspan,  $N_{\text{males}} = 29$ ,  $N_{\text{females}} = 19$ ,  $U = 30.00$ ,  $Z_{\text{adj}} = 5.26$ ,  $p < 0.00001$ ). Wingspan values were on average equal to  $24.48 \text{ mm} \pm \text{SE } 0.27$  ( $N = 29$ , range: 21–27,  $\text{SD} = 1.45$ ) in males and to  $21.16 \text{ mm} \pm \text{SE } 0.31$  ( $N = 19$ , range: 18–24 mm,  $\text{SD} = 1.34$ ) in females. Sexual dimorphism in wingspan was present when considering specimens of northern and central Italy either separately or as a whole (northern specimens: Mann-Whitney U test, wingspan,  $N_{\text{males}} = 13$ ,  $N_{\text{females}} = 4$ ,  $U = 6.50$ ,  $Z_{\text{adj}} = 2.24$ ,  $p = 0.000007$ ;



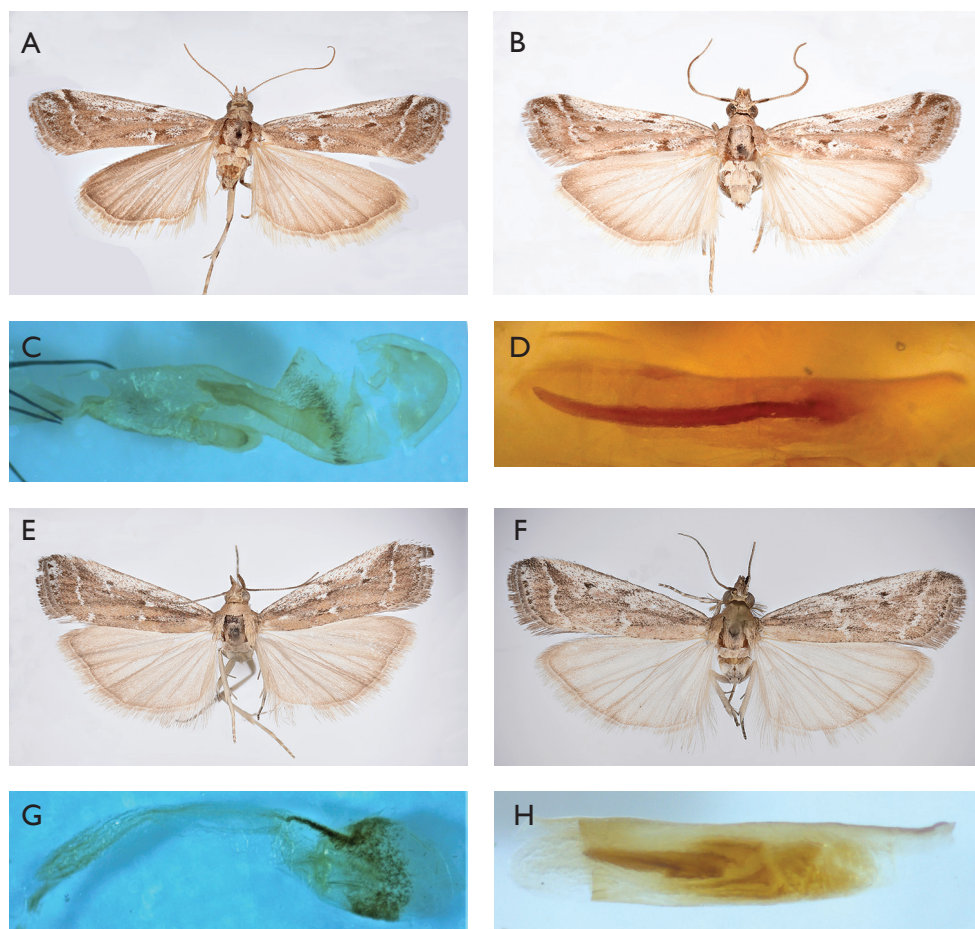
**Figure 1.** *Pempeliella* species in Italy. **A** *P. ornatella* ♀ (wingspan 21 mm) **B** *P. ornatella* ♂ (wingspan 24 mm) **C** *P. ornatella* ♀ bursa copulatrix (gen. praep. PIRA 515) **D** *P. ornatella* ♂ aedeagus (gen. praep. PIRA 517) **E** *P. bayassensis* ♀ (wingspan 21 mm) **F** *P. bayassensis* ♂ (wingspan 24 mm) **G** *P. bayassensis* ♀ bursa copulatrix (gen. praep. PIRA 280) **H** *P. bayassensis* aedeagus (gen. praep. PIRA 277).

central specimens: Mann-Whitney U test, wingspan,  $N_{\text{males}} = 15$ ,  $N_{\text{females}} = 15$ ,  $U = 6.00$ ,  $Z_{\text{adj}} = 4.51$ ,  $p = 0.025$ ).

The specimens of *P. ornatella gigantella* collected in the northern (n) Italy showed values of wingspan higher than *ornatella* in central Italy (cI) (males: Mann-Whitney U test, wingspan,  $N_n = 12$ ,  $N_{\text{cI}} = 15$ ,  $U = 50.5$ ,  $Z_{\text{adj}} = 1.99$ ,  $p = 0.046$ ; females: Mann-Whitney U test, wingspan,  $N_n = 4$ ,  $N_{\text{cI}} = 15$ , NS).

### *Pempeliella bayassensis*

We examined nine specimens of *P. bayassensis*. This species could be easily confused with *P. ornatella* due to their very similar habitus, and the two species are sympatric and



**Figure 2.** *Pempeliella* species in Italy. **A** *P. matilella* ♀ (wingspan 22 mm) **B** *P. matilella* ♂ (wingspan 22 mm) **C** *P. matilella* bursa copulatrix (gen. praep. PIRA 488) **D** *P. matilella* aedeagus (gen. praep. PIRA 490) **E** *P. sororiella* ♀ (wingspan 14 mm) **F** *P. sororiella* ♂ (wingspan 20 mm) **G** *P. sororiella* bursa copulatrix (gen. praep. PIRA 282) **H** *P. sororiella* aedeagus (gen. praep. PIRA 537).

coexist in central Italy. The size of *P. bayassensis* is smaller than *P. ornatella*. The wingspan showed a greater mean value in *P. ornatella* than in *P. bayassensis* (mean value  $\pm$  standard error: males,  $23.33 \pm 0.67$  mm, SD = 1.15,  $N = 3$ , range 22–24 mm; females,  $21.67 \pm 0.49$  mm, SD = 1.21,  $N = 6$ , range 20–23). *P. bayassensis* has a distinctive forewing post median line that is more curved in *bayassensis* than in *ornatella* (Fig. 1A, B, E, F). Accordingly, it could be identified only by external habitus. However, in doubtful cases, *P. bayassensis* can be easily recognized by characters of the genitalia (Fig. 1C, D, G, H).

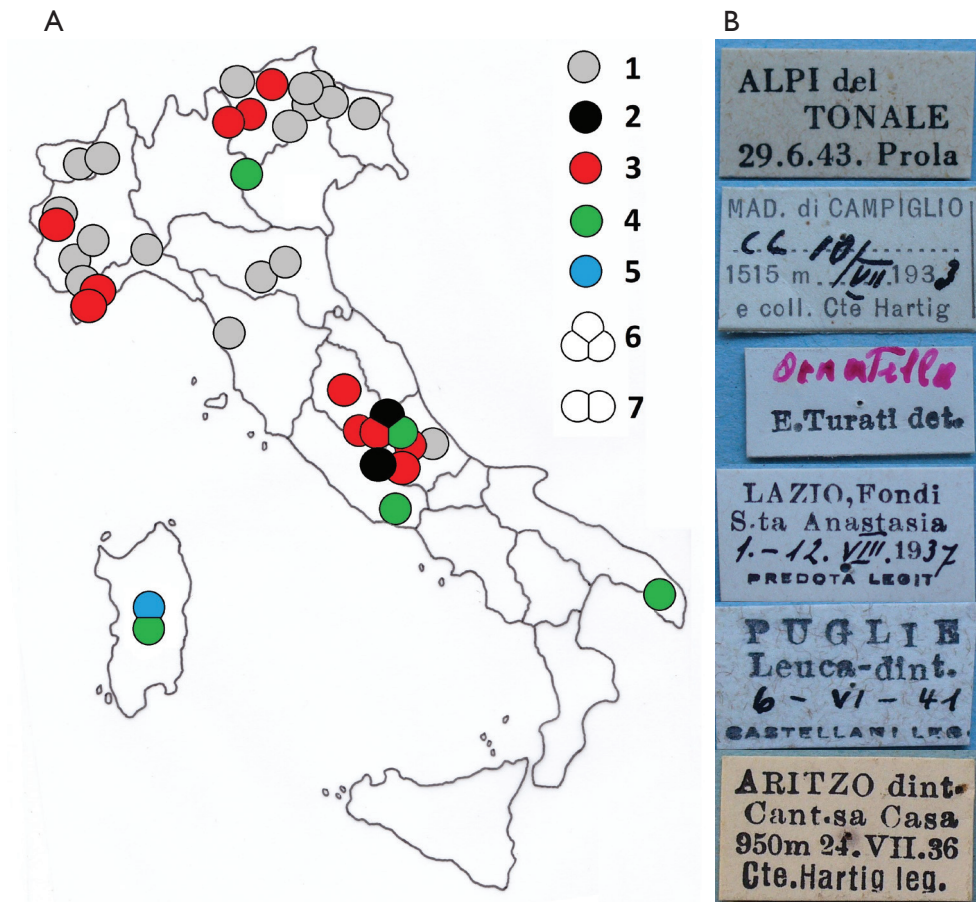
### *Pempeliella sororiella*

We examined 10 specimens of *P. sororiella*. This species can be easily confused with *P. bulgarica* due to their very similar habitus (Slamka and Plant 2016), but our examination of genitalia confirmed the species as *P. sororiella* (Fig. 2G, H).



## Distribution of species in Italy

The distribution map of materials examined shows that all moths from Trentino, Liguria, Emilia Romagna, and Toscana are *P. ornatella* (Fig. 3A). *Pempeliella sororiella* was found in northern Italy but never together with *P. ornatella*. In central Italy, we found three species, *P. ornatella*, *P. bayassensis*, and *P. sororiensis*. These species coexist in Latium, but *P. sororiella* and *P. bayassensis* were infrequent and difficult to sample by lamp. In eastern Latium, a single specimen of *P. bayassensis* (gen. praep. PIRA 520, M. Pinzari) was sampled in 1938 by Hartig at Monte Flavio. In Umbria and Abruzzi, all specimens were *P. ornatella*. In southern Italy (Apulia), there was only one specimen of *P. sororiella*, which was found in 1941 by Omero Castellani; it is preserved in Hartig's collection (MZUR). Currently, no species of *Pempeliella* have been recorded in Sicily. Finally, *P. matilella*, which was erroneously confused with *Delplanqueia cortella*, and *P. sororiella* were found to be in Sardinia.



**Figure 3.** *Pempeliella* species in Italy. **A** Distribution of genus *Pempeliella* Caradja, 1916 in Italy: 1) unverified quotations; 2) *P. bayassensis*; 3) *P. ornatella*; 4) *P. sororiella*; 5) *P. matilella*; 6) three and two (7) coexisting species. **B** Some historical entomological cards of the specimens in the map by: 1) Prola; 2) Hartig; 3) Turati; 4) Predota; 5) Castellani; 6) Hartig, are shown to the right of the map.

## Discussion

The historical collections studied include moths collected by several entomologists and in various regions of Italy. Our study of these collections and the published literature on *Pempeliella* allowed us to reconstruct the distribution of *Pempeliella* species in Italy. Our study revealed that *P. ornatella* is present in northern and central Italy, that *P. sororiella*, although is a less frequent species in Italy, is present through the peninsula and in Sardinia, that *P. matilella* is known only in Sardinia (Pinzari and Pinzari in press), and that *P. bulgarica* is not present in Italy. Finally, the main novelty of this paper is that *P. bayassensis*, which is present only in central Italy, is reported from Italy for the first time. Federico Hartig collected a single specimen of *P. bayassensis* in 1938 but it was misidentified as *P. ornatella*. We have since collected this species at Vallemare (Rieti) in Latium, where *P. bayassensis* coexists with *P. sororiella* and *P. ornatella*. At present, *P. bayassensis* has not been recorded yet in other localities in Italy.

## Acknowledgements

We thank Dr Roberto Casalini (Museo Civico di Zoologia di Roma) and Dr Emanuele Piattella (Museo di Zoologia dell'Università di Roma La Sapienza) for allowing the study of the specimens of Prola's and Hartig's collections, respectively, and Dr Richard Hewett (University of Salford, UK) for the review of the final version of the manuscript. Special thanks to Francesco Sacco (Associazione Romana di Entomologia, Rome) for the final photographs of specimens and Dr Flavia Gravina (University of Rome Tor Vergata) for making her laboratory available to make the final illustrations of genitalia.

## References

- Baldizzone G (1996) I microlepidotteri del Parco Naturale del Mont Avic e zone limitrofe (Valle d'Aosta – Val Chalamy – Alpi Graie orientali). *Revue Valdôtaine d'Histoire Naturelle* 50: 55–141.
- Baldizzone G (2005) I Microlepidotteri del Parco Naturale Alpi marittime (Italia, Piemonte) (Lepidoptera). *Bollettino Museo Regionale di Scienze Naturali* 22(1): 1–318.
- Baldizzone G, Cabella C, Fiori F, Varalda PG (2013) I Lepidotteri del Parco naturale delle Capanne di Marcarolo. *Memorie dell'associazione Naturalistica Piemontese* XII: 1–349.
- Bassi G, Passerin d'Entreves P, Speidel W, Zangheri S (1995). Lepidoptera Pyraloidea. In: Minelli A, Ruffo S, La Posta S (Eds) *Checklist delle Specie della Fauna Italiana* 87. Calderini, Bologna, 28 pp.
- Burmann K (1995) Beitrage zur Microlepidopteren-Fauna Tirols. XIX. Pyralidae-Phycitinae (Insecta: Lepidoptera). *Berichte des Naturwissenschaftlich-medizinischen Vereins in Innsbruck* 82: 297–309.
- Curò A (1880) Saggio di un catalogo dei Lepidotteri d'Italia. *Bollettino della Società Entomologica Italiana* 12: 51–92.

- Della Beffa G (1941) I Piralidi della catena alpina. Bollettino del Laboratorio sperimentale e Regio Osservatorio di fitopatologia Torino 17: 3–34.
- Deutsch H (2006) Contribution to the knowledge of the Lepidoptera of Friuli Venezia Giulia (North Italy). Part I: Province of Udine (Carnic Alps, Carnic Pre-Alps, Upper Tagliamento river). Gortania 27: 227–298.
- Gaston FJ, Ylla J, Redondo V, Macia R (2014) *Pempeliella bayassensis* Leraut, 2001 en la Peninsula Iberica (lepidoptera: Pyralidae, Phycitinae). SHILAP Revista de Lepidopterologia 42 (166): 261–264.
- Hartig F (1939) Contributo alla conoscenza della Fauna lepidotterologica dell'Italia centrale. Memorie della Società Entomologica Italiana 18: 186–198.
- Hartig F (1956) Prodromus dei Microlepidotteri della Venezia Tridentina e delle regioni adiacenti. Studi Trentini di Scienze Naturali 33: 89–148.
- Hartig F (1958) Microlepidotteri della Venezia Tridentina e delle regioni adiacenti. Studi Trentini di Scienze Naturali 35(2–3): 106–268.
- Hartig F, Amsel HG (1951) Lepidoptera sardinica. Fragmenta Entomologica 1: 3–159.
- Huemer P (2002) Biomonitoring der Schmetterlingsfauna in Waldstandorten Südtirols und Trients (Lepidoptera). Linzer biologische Beiträge 34(1): 199–264.
- Huemer P (2007) Biodiversity of butterflies and Moths (Lepidoptera) of the Schlern nature park (South Tyrol, Italy). Gredleriana 7: 233–306.
- Huemer P (2009) Auf der Suche nach Schmetterlingsendemiten (Lepidoptera) in den Cotti-schen Alpen (Prov. Cuneo, Italien). Wissenschaftliches Jahrbuch der Tiroler Landesmu-seen 2: 120–129.
- Leraut P (2001a) Contribution à l'étude des phycitesses paléarctiques (Lepidoptera, Pyralidae, Phycitinae). Revue française d'Entomologie 23(2): 129–141. [https://doi.org/10.1016/S0338-9898\(01\)80347-4](https://doi.org/10.1016/S0338-9898(01)80347-4)
- Leraut P (2001b) Contribution à l'étude des pyrales paléarctiques (Lepidoptera, Pyraloidea). Nouvelle Revue d'Entomologie (N.S.) 18(2): 173–185.
- Leraut GHC (2012) Découverte de la femelle de *Pempeliella bayassensis* P. Leraut, 2001. Alexanor 25(4): 227–230.
- Leraut P (2014) Moths of Europe. Vol. 4: Pyralids 2. N.A.P. Editions, Verrières le Buisson, 442 pp.
- Mariani M (1939) Fauna Lepidopterorum Siciliae (Catalogo ragionato). Memorie della Società Entomologica Italiana 17: 129–187.
- Minà Palumbo F, Failla-Tebaldi L (1889) Materiali per la Fauna lepidotterologica della Sicilia. Naturalista Siciliano 8(6): 129–140.
- Parenti U (1962) Ricerche sulla fauna Appenninica. LXIX. Microlepidotteri della Maiellet-ta (Appennino Centrale). Memorie del Museo Civico di Storia Naturale di Verona 10: 287–413. [3 pls]
- Pinzari M (2009) A comparative analysis of mating recognition signals in graylings: *Hipparchia statilinus* vs. *H. semele* (Lepidoptera: Nymphalidae, Satyrinae). Journal of Insect Behavior 22: 227–244. <https://doi.org/10.1007/s10905-008-9169-5>
- Pinzari M, Pinzari M, Zilli A (2010) Deep lepidopterological exploration of Mt Cagno and surroundings (Central Italy), a restricted mountain Massif and hotspot for butterfly and moth diversity. Bollettino dell'associazione Romana di Entomologia 65(1–4): 3–383.



- Pinzari M, Sbordoni V (2013a) Species and mate recognition in two sympatric Grayling butterflies: *Hipparchia fagi* and *H. Hermione genava* (Lepidoptera). *Ethology Ecology & Evolution* 25: 28–51. <https://doi.org/10.1080/03949370.2012.703244>
- Pinzari M, Pinzari M, Zilli A (2013b) Additions and corrections to the Lepidoptera fauna of Mt Cagno and surroundings (Central Italy), with first records of *Caloptilia honoratella* and *Buvatina stroemella* from Italy (Lepidoptera). *Bollettino dell'associazione Romana di Entomologia* 68: 51–72.
- Pinzari M (2016a) *Deraeocoris schach*, a new predator of *Euphydryas aurinia* and other heteropteran feeding habits on caterpillar web (Heteroptera: Miridae; Lepidoptera: Nymphalidae). *Fragmenta Entomologica* 48(1): 77–81. <https://doi.org/10.4081/fe.2016.163>
- Pinzari M (2016b) *Scythris clavella* (Zeller, 1855) in Italy (Lepidoptera, Gelechioidea, Scythrididae). *Journal of Entomological and Acarological Research* 48: 301–303. <https://doi.org/10.4081/jear.2016.5798>
- Pinzari M, Zerunian Z, Pinzari M (2016a) – Microlepidotteri di Assisi (Italia) (Lepidoptera). – *Bollettino dell'associazione Romana di Entomologia* 71(1–4): 107–200.
- Pinzari M, Pinzari M, Sbordoni V (2017b) Notes on Life-History of *Erycia furibunda* (Diptera: Tachinidae), A parasitoid of *Euphydryas aurinia provincialis* (Lepidoptera: Nymphalidae). *Redia* 100: 81–87.
- Pinzari M, Santonico M, Pennazza G, Martinelli E, Capuano RM, Paolesse R, Di Rao M, D'Amico A, Cesaroni D, Sbordoni V, Di Natale C (2018a) Chemically mediated species recognition in two sympatric Grayling butterflies: *Hipparchia fagi* and *Hipparchia hermione* (Lepidoptera: Nymphalidae, Satyrinae). *Plos ONE* 13(6): e0199997. <https://doi.org/10.1371/journal.pone.0199997>
- Pinzari M, Zerunian Z, Pinzari M (2018b) Is the alien species *Clepsis peritana* (Lepidoptera: Tortricidae) settling in Italy? *Journal of Entomological and Acarological Research* 50(7551): 1–3. <https://doi.org/10.4081/jear.2018.7551>
- Pinzari M, Cianferoni F, Martellos S, Dioli P (2018c) *Zelus renardii* (Kolenati, 1856), a newly established alien species in Italy (Hemiptera: Reduviidae, Harpactorinae). *Fragmenta Entomologica* 50(1): 31–35. <https://doi.org/10.4081/fe.2018.281>
- Pinzari M (in press) *Phylloneta sisyphia* (Araneae: Theridiidae), a predator of larvae of *Euphydryas aurinia* (Lepidoptera: Nymphalidae) and its parasitoid *Erycia furibunda* (Diptera: Tachinidae). *Acta Zoologica Bulgarica*.
- Pinzari M, Pinzari M, Sbordoni V (in press) Make it simply: the mating behaviour of *Euphydryas aurinia provincialis* (Lepidoptera: Nymphalidae). *European Zoological Journal* 86.
- Pinzari M, Cianferoni F, Fabiani A, Dioli P (in press) Predation by nymphs of *Picromerus bidens* (Heteroptera: Pentatomidae, Asopinae) on caterpillars of *Euphydryas aurinia provincialis* (Lepidoptera: Nymphalidae) in Italy. *Redia – Journal of Zoology* 102.
- Schmid J (2016) *Delplanqueia inscriptella* (Duponchel, 1836) new for the fauna of Switzerland and confirmation of the Swiss occurrence of *Pempeliella bayassensis* Leraut, 2001 (Lepidoptera: Pyralidae, Phycitinae). *Entomo Helvetica* 9: 35–39.
- Slamka F, Plant CW (2016) *Pempeliella bulgarica* sp. nov.: a new species closely related to *Pempeliella sororiella* (Zeller, 1839) (Pyraloidea, Pyralidae, Phycitinae) and some new synonymies. *The Entomologist's Record and Journal of Variation* 128: 99–111.

- Speidel W, Segerer A, Nuss M (2013) Fauna Europaea: Pyralidae. In: Karsholt O, van Nieukerken EJ (Eds) Fauna Europaea, moths. Version 2.6. <http://www.fauna-eu.org>. [Accessed on: 2019-1-13]
- Turati E, Verity R (1911–1912) Faunula Valderiensis nell'alta Valle del Gesso (Alpi Marittime). *Bollettino della Società entomologica italiana* 42–43: 168–233.
- Verity R (1904) Elenco dei lepidotteri raccolti sul litorale del Lucchese (Forte dei Marmi). *Bollettino della Società entomologica italiana* 36: 123–170.

# Molecular data reveal a new species of *Rhopalias* Stiles & Hassall, 1898 (Digenea, Echinostomatidae) in the Common opossum, *Didelphis marsupialis* L. (Mammalia, Didelphidae) in the Yucatán Peninsula, Mexico

Jorge López-Caballero<sup>1</sup>, Rosario Mata-López<sup>1</sup>, Gerardo Pérez-Ponce de León<sup>2</sup>

**1** Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México. Avenida Universidad 3000, Ciudad Universitaria, C. P. 04510; Mexico City, Mexico **2** Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México. Avenida Universidad 3000, Ciudad Universitaria, A. P. 70–153, C. P. 04510; Mexico City, Mexico

Corresponding author: Gerardo Pérez-Ponce de León ([ppdleon@ib.unam.mx](mailto:ppdleon@ib.unam.mx))

Academic editor: David Gibson | Received 14 March 2019 | Accepted 3 May 2019 | Published 10 June 2019

<http://zoobank.org/F870F686-0B4B-4B24-8583-73757950FDB1>

**Citation:** López-Caballero J, Mata-López R, Pérez-Ponce de León G (2019) Molecular data reveal a new species of *Rhopalias* Stiles & Hassall, 1898 (Digenea, Echinostomatidae) in the Common opossum, *Didelphis marsupialis* L. (Mammalia, Didelphidae) in the Yucatán Peninsula, Mexico. ZooKeys 854: 145–163. <https://doi.org/10.3897/zookeys.854.34549>

## Abstract

A new species of *Rhopalias* Stiles & Hassall, 1898 is described from the small intestine of the Common opossum, *Didelphis marsupialis* Linnaeus from the Yucatán Peninsula, Mexico. *Rhopalias oochi* **sp. nov.** is morphologically very similar to the type species of the genus, *Rhopalias coronatus* (Rudolphi, 1819) Stiles & Hassall 1898, a species widely distributed in opossums across Mexico. A molecular phylogenetic analysis using a mitochondrial gene (*cox1*), and the nuclear ribosomal internal transcribed spacer region (ITS1-5.8S-ITS2), of specimens of *R. coronatus* collected in several localities of Mexico revealed that those from the Yucatán Peninsula, originally recorded on morphological grounds as *R. coronatus* actually represented an independent genetic lineage. Maximum Likelihood and Bayesian Inference analyses were performed for each data set independently, and for the concatenated data set (ITS1-5.8S-ITS2 + *cox1*). All phylogenetic analyses showed that the specimens from Yucatán represented a monophyletic lineage, with high bootstrap support and Bayesian posterior probabilities. In addition, the genetic divergence estimated between *R. oochi* **sp. nov.** and two species of *Rhopalias*, *R. coronatus*, and *R. macracanthus* Chandler, 1932 that also occur in Mexican marsupials ranged between 7–8% and 16–17%, for *cox1*, and between 0.1–0.2% and 7% for the ITS region, respectively. The molecular evidence gathered in this study

(reciprocal monophyly in both phylogenetic analyses, and estimated genetic divergence) suggested that the specimens found in the intestine of *D. marsupialis* originally reported as *R. coronatus* from Yucatán, actually represent a new species. Morphological evidence was found through light and scanning electron microscopy to support the species distinction based on molecular data.

### Keywords

DNA, integrative taxonomy, phylogeny, Trematoda

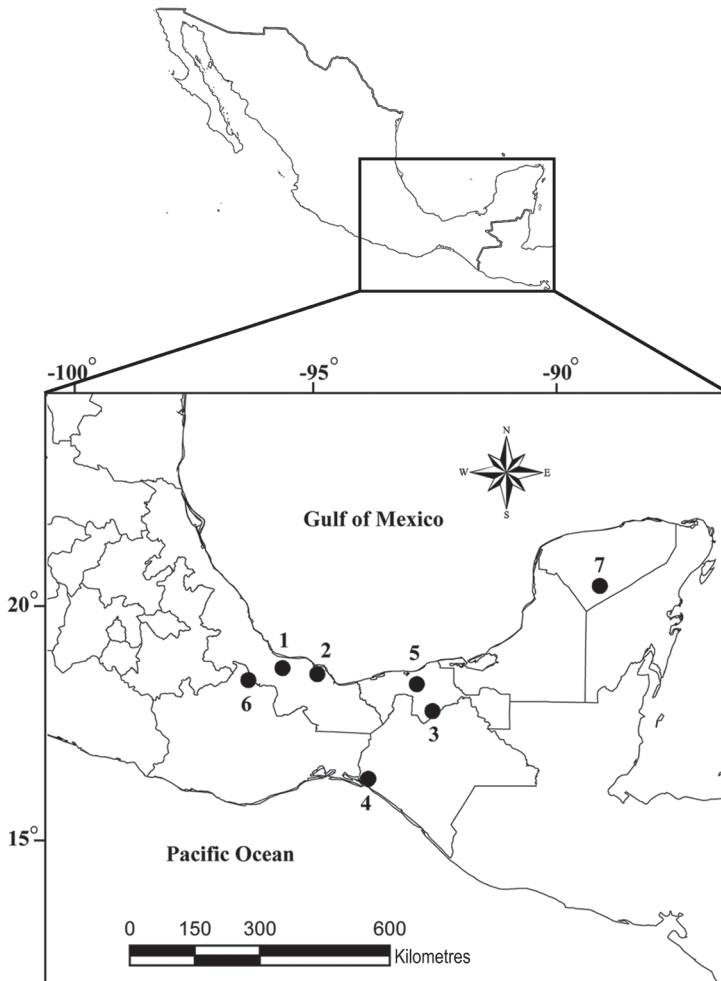
## Introduction

The genus *Rhopalias* Stiles & Hassall, 1898 includes six species of digenetic trematodes that infect the small intestine of didelphimorph marsupials of the New World (Haverkost and Gardner 2008). Members of this genus of echinostomatid trematodes (see Tkach et al. 2016) are distinguished by having two anterior tentacles armed with spines, which can be invaginated into a muscular pouch, one on each side of oral sucker (Kostadinova 2005). In a taxonomic review of the species of the genus *Rhopalias*, Haverkost and Gardner (2008) discussed the morphological characters that could be used for distinguishing among congeneric species, concluding that the number and size of tentacle spines, the presence or absence of oral and/or flanking spines, and the length of the muscular pouches are the most reliable characters. Nevertheless, they cautioned that a more extensive sampling of each species of *Rhopalias* was necessary to support the use of these characters for the species delimitation. Furthermore, with the exception of the sequence of the 28S rRNA gene from an individual of *R. macracanthus* Chandler, 1934, a parasite of the Virginia opossum, *D. virginiana* Kerr from the U.S. (Tkach et al. 2016), and genetic information about the other species of *Rhopalias* is lacking. The main objective of this study was to explore the genetic diversity among specimens of *R. coronatus* collected throughout a geographical range across southern Mexico, following a molecular prospecting approach in the search for cryptic species (sensu Blouin 2002). Molecular data were used in combination with a morphological study of newly sampled specimens of *R. coronatus*, and those deposited at the Colección Nacional de Helmintos (CNHE) to describe a new species of *Rhopalias*. Specimens originally recorded as *R. coronatus* from the Yucatán Peninsula by Acosta-Virgen et al. (2015) corresponded with an undescribed species. We describe the new species herein.

## Materials and methods

### Specimen sampling

In total, 44 specimens of opossums were collected between August 2011 and November 2013, in seven localities across southeastern Mexico (Fig. 1, Table 1). Hosts were collected under the collecting permit FAUT-0057 issued to GPPL by the Secretaría del



**Figure 1.** Sample collection sites of specimens of *Rhopalias* spp. in opossums across southeastern Mexico. **1** Tlacotalpan, Veracruz (TL) **2** Los Tuxtlas, Veracruz (LT) **3** Cunduacán, Tabasco (CU) **4** Agua Fria, Chiapas (AF) **5** Teapa, Tabasco (TE) **6** Soyaltepec, Oaxaca (SO) **7** Rancho Hobonil, Tzucacab, Yucatán (TZ). Numbers refer to map ID in Table 1.

Medio Ambiente y Recursos Naturales. The mammals were sacrificed with an overdose of pentobarbital sodium, necropsied, and all organs were separated in Petri dishes with 0.85% saline, and examined under a stereomicroscope. A small piece of host tissue was taken from each individual and saved for further DNA studies. These tissues are available upon request. Trematodes were removed from the intestine of their hosts, and washed in saline for 3–5 min. Some specimens were fixed by sudden immersion in hot 4% formaldehyde and stored in 70% ethanol for morphological analyses. For molecular study, eight specimens were washed with saline solution, preserved in 100% ethanol, and stored at -20 °C. These specimens were used for DNA extraction, including four

**Table 1.** Collecting localities, host species (Didelphidae) by locality, GenBank and Colección Nacional de Helmintos (CNHE) accession numbers. Map ID corresponds with numbers in Fig. 1.

Map ID	Locality (abbreviation)	Coordinates	Host (sample size)	Species	GenBank		CNHE
					cox1	ITS1-5.8S-ITS2	
1	Tlacotalpan, Veracruz (TL)	18°37'40"N, 95°40'40"W	<i>D. marsupialis</i> (5)	<i>R. coronatus</i>	MK982742–57	MK982805–06	9502, 9503
			<i>D. virginiana</i> (4)				
			<i>P. opossum</i> (2)	<i>R. macracanthus</i>	MK982783–85	MK982815	9509
2	Los Tuxtlas, Veracruz (LT)	18°34'21"N, 95°04'30"W	<i>D. marsupialis</i> (5)	<i>R. coronatus</i>	MK982674–99	MK982813–14	9499, 9500, 9501
			<i>D. virginiana</i> (1)				
			<i>P. opossum</i> (2)				
3	Cunduacán, Tabasco (CU)	17°34'17"N, 92°57'09"W	<i>D. virginiana</i> (3)	<i>R. coronatus</i>	MK982700, MK982702	–	9497
4	Agua Fría, Chiapas (AF)	16°15'26"N, 93°53'55"W	<i>D. marsupialis</i> (3)	<i>R. coronatus</i>	MK982703–41	MK982786–96	9488, 9489, 9491
			<i>D. virginiana</i> (2)				
			<i>P. opossum</i> (11)				
5	Teapa, Tabasco (TE)	17°33'49"N, 92°45'40"W	<i>D. marsupialis</i> (3)	<i>R. coronatus</i>	MK982701	MK982801	9498
6	Soyaltepec, Oaxaca (SO)	18°15'28"N, 96°24'00"W	<i>D. virginiana</i> (2)	<i>R. coronatus</i>	MK982758–74	MK982797–99, MK982807–12	9495
7	“Rancho Hobonil” Tzucacab, Yucatán (TZ)	20°00'58"N, 89°01'12"W	<i>D. marsupialis</i> (1)	<i>R. oochi</i> sp. nov.	MK982775–82	MK982800, MK982802–04	9504, 10926, 11069

specimens that were cut in half and the posterior half processed for morphology (hologenophores, sensu Pleijel et al. 2008), and four complete specimens. The four hologenophores and remaining seven specimens (paragenophores) were stained in Mayer’s paracarmine and mounted as permanent slides in Canada balsam. Specimens of *Rhopalias* were morphologically identified either as *R. coronatus* or *R. macracanthus* according with the description and morphometrical traits reported by Haverkost and Gardner (2008).

Amplification and sequencing of DNA

Individual worms fixed in 100% ethanol (or the posterior portion in some cases) were placed in tubes and digested overnight at 56 °C in a solution containing 10 mM Tris-HCl (pH 7.6), 20 mM NaCl, 100 mM Na<sub>2</sub> EDTA (pH 8.0), 1% Sarkosyl, and 0.1 mg/mL proteinase K. Following digestion, DNA was extracted from the supernatant using DNAzol reagent (Molecular Research Center, Cincinnati, Ohio) according to the manufacturer’s instructions. A fragment of the mitochondrial cytochrome *c* oxidase subunit 1 (cox1), and ITS1-5.8S-ITS2 were amplified by PCR, using the primers shown in Table 2.

All PCRs were performed at a final volume of 25 µl consisted of 2.5 µl of 10× PCR buffer, 2.5 µl of 10 mM of dNTPs mixture (200 µl each), 1.25 µl MgCl<sub>2</sub> (50 mM), 1.0 µl each primer (10 pmol), 2 µl DNA template, and 1 unit of Taq DNA polymerase (Biogenica, Mexico City), and the remaining volume of sterilized distilled water. The amplification program for cox1 consisted of: initial denaturation at 96 °C for 3 min,



**Table 2.** Primers used in the present study.

Locus	Primer	Sequence (5'–3')	Use	Reference
cox1	MplatCOX1dF	TGTAAACGACGGCCAGTTTWCITTRGATCATAAG	PCR <sup>†</sup>	Moszczyńska et al. 2009
	BARCOXR	ATAAACCTCAGGATGCCCAAAAAA	PCR	Razo-Mendivil (pers. comm.)
	M13F	TGTAAACGACGGCCAGT	SEQ <sup>‡</sup>	Messing (1993)
(ITS1-5.8S-ITS2)	BD1	GTCGTAACAAGGTTTTCGGTA	PCR & SEQ	Bowles and McManus (1993)
	BD2	TATGCTTAAATTCAGCGGT	PCR & SEQ	Bowles et al. 1995
	BD3	GAACATCGACATCTTGAACG	SEQ	Hernández-Mena et al. 2014
	BD4	ATAAGCCGACCTTCGGC	SEQ	Hernández-Mena et al. 2014

<sup>†</sup> = amplification; <sup>‡</sup> = sequencing.

followed by 35 cycles at 94 °C for 1 min, annealing at 50 °C for 45 s, extension at 72 °C for 1 min, followed by 10 min at 72 °C for final elongation. For the ITS1-5.8S-ITS2, the PCR conditions were: initial denaturation at 96 °C for 3 min, followed by 35 cycles at 94 °C for 1 min, annealing at 53 °C for 1 min, extension at 72 °C for 1 min, followed by a final elongation at 72 °C for 10 min. PCR products were treated with Exo-SAP-IT (Thermo Scientific), according to the manufacturer's instructions. Cox1 and ITS1-5.8S-ITS2 products were sequenced in both strands using the primers mentioned in the Table 2, by the High Throughput Genomics Unit at the University of Washington, USA, (<http://www.htseq.org./index.html>). Contigs were assembled using the platform Geneious v.5.1.7 (Drummond et al. 2010). As an additional check on accuracy, cox1 nucleotide sequences were translated using Mesquite v.2.75 (Maddison and Maddison 2011), and trematode mitochondrial genetic code. All the cox1 and ITS1-5.8S-ITS2 sequences generated in this study were deposited in the GenBank (Table 1).

## Phylogenetic analyses

DNA fragments of the cox1 and ITS region were aligned separately using the software Clustal W2 (Thompson et al. 1994) with a final manual adjusting in Mesquite v.2.75. The concatenated data set was aligned using the same software. Sequences of cox1 and ITS region of other species included within superfamily Echinostomatoidea Looss, 1899 available in the GenBank were used as outgroups. Maximum Likelihood (ML) and Bayesian Inference (BI) analyses were performed for each data set, and for the concatenated data set (ITS1-5.8S-ITS2 + cox1) partitioned by gene. The program jModeltest v.3.0 (Posada and Crandall 1998) was used for inferring the best model of evolution for each data set using the Akaike information criterion. The TVM + I + G and TPMuf + G substitution model were the best models for cox1 and ITS region, respectively. The ML trees were inferred using RAxML v.7.0.4 (Stamatakis 2006). Bootstrap resampling with 10,000 replicates assessed ML clade support. Additionally, Bayesian analyses were performed with the program MrBayes v.3.2.1 (Ronquist et al. 2012). The settings were two simultaneous runs with four Markov chains Monte Carlo (MCMC) for 10 million generations, sampling every 200 generations, a

heating parameter value of 0.2 and a ‘burn-in’ of 10%. A 50% majority-rule consensus tree representing the posterior probability distribution of clades was produced of the sampled trees. Phylogenetic trees were displayed with the program FigTree v.1.4.2 (Rambaut 2006). Finally, genetic divergence (p-value) was calculated for each data set using MEGA v.6.0 (Tamura et al. 2013).

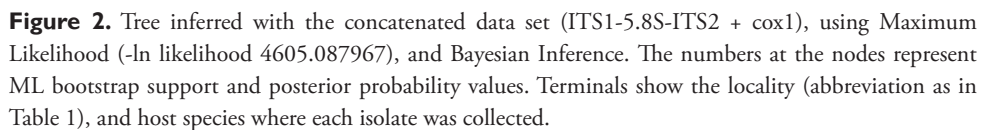
## Morphological analyses

Representative specimens of the species of *Rhopalias* were stained with Mayer’s paracarmine or Gomori’s trichrome, dehydrated through a graded ethanol series (70%, 80%, 90% [twice], and 100%), cleared in methyl salicylate, and mounted in Canada balsam. The specimens were observed using an Olympus BX81 light microscope. Some worms were drawn with the aid of a drawing tube attached to an Olympus BX53 light microscope. Likewise, in order to obtain a complete digital record of the morphological traits, specimens were observed through the Differential Interference Contrast method (DIC), using an Olympus Provis AX70 microscope. Photomicrographs of the specimens were obtained with a digital camera Evolution 5.0 MP. All specimens were measured using the software Image Pro-Plus v.7.0. Measurements are presented in micrometres ( $\mu\text{m}$ ) unless otherwise stated. For scanning electron microscope studies (SEM), the specimens were dehydrated in a graded series of alcohol solutions and then critical point dried with carbon dioxide. Specimens were mounted on metal stubs with carbon adhesive, and then gold coated and examined at 15kV in a Hitachi Stereoscan Model SU1510 SEM (Hitachi Ltd., Tokyo, Japan). Digital images of these specimens were obtained using digital imaging software attached to a computer. Specimens of the new species of *Rhopalias* were deposited in the Colección Nacional de Helmintos (CNHE), Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City (Table 1).

## Results

### Phylogenetic analysis

**Cox1.** One hundred twelve sequences of *cox1* were obtained in the present study, including 101 of *R. coronatus*, three of *R. macracanthus*, and eight of the new species. The final alignment included seven sequences from GenBank (as outgroups), and consisted of 119 sequences with 666 bp. Phylogenetic trees reconstructed by ML and BI yielded similar topologies with high bootstrap support and Bayesian posterior probabilities, respectively (see Suppl. material 1: Figure S1). The tree obtained with both reconstruction methods shows three major clades, the same ones that were obtained in the concatenated data set (Fig. 2). Clade I, corresponding to *R. coronatus* according to their morphology, included 101 sequences from six localities: 26 isolates from Los Tuxtlas (LT), 16 isolates from Tlacotalpan (TL), 17 from Soyoltepec (SO), 39 from Agua Fría



**ITS.** A subsample of 30 sequences of ITS1-5.8S-ITS2 region were obtained in this study from some specimens corresponding with each of the three genetic lineages of *Rhopalias* from the *cox1* analysis; samples included 25 individuals of *R. coronatus*, one of *R. macracanthus*, and four sequences of the new species. In addition, ITS sequences of other species included in the superfamily Echinostomatoidea were downloaded from GenBank and used as outgroups. The final alignment consisted of 32 sequences

with 1093 bp. Phylogenetic analyses by ML and BI yielded the same topology (see Suppl. material 2: Figure 2). Both topologies showed two major clades (and not three as the *cox1* tree), and relationships are supported by high bootstrap and posterior probability values. Clade I included 29 sequences from six localities: two isolates from Los Tuxtlas (LT), two isolates from Tlacotalpan (TL), nine from Soyoltepec (SO), eleven from Agua Fría (AF), one from Teapa (TE) and four isolates from Tzucacab (TZ). However, these four sequences formed a small subclade within Clade I, corresponding with the isolates of the new species; Clade II was composed by only one sequence of *R. macracanthus* from Los Tuxtlas (LT).

**Concatenated data set.** This data set consisted of ITS1-5.8S-ITS2 plus the *cox1* gene sequences. The final alignment included 32 sequences with 1759 bp. Phylogenetic analyses of this concatenated data set were also conducted using ML and IB methods, yielding the same topologies. The ML tree is shown in Figure 2. The tree yielded three major clades well supported by bootstrap and Bayesian posterior probability values. The first one included all samples of *R. coronatus*: two specimens from Los Tuxtlas (LT), two specimens from Tlacotalpan (TL), nine specimens from Soyoltepec (SO), eleven specimens from Agua Fría (AF), and one from Teapa (TE). The second clade included four isolates from Rancho Hobonil, Tzucacab (TZ), representing the new species. Clade III included only one sequence from Tlacotalpan (TL), corresponding with *R. macracanthus*. All the individuals sequenced from each of these three *Rhopalias* species, sampled in most of their geographic distribution in Mexico, formed monophyletic groups, with *R. coronatus* and the new species grouped as sister species (Fig. 2).

**Genetic divergence.** The genetic divergence estimated among populations of the new species with respect to *R. coronatus* and *R. macracanthus* ranged between 7–8% and 16–17%, for *cox1*, respectively; for the internal transcribed spacers, interspecific divergence between the new species and the other two species of *Rhopalias* varied 0.1–0.2% and 7%, respectively. The intraspecific divergence among isolates of the three species of *Rhopalias* ranged from 0–1% for *cox1*, was null for ITS.

### Family Echinostomatidae Looss, 1899

### Genus *Rhopalias* Stiles & Hassall, 1898

#### *Rhopalias oochi* sp. nov.

<http://zoobank.org/2AFA9155-52CE-4436-A95F-2B0E85F93C72>

Figures 3A–D, 4 A, D, E, 5A, D

**Synonym.** *Rhopalias coronatus* of Acosta-Virgen et al. (2015). Specimens deposited in the CNHE (9504).

**Type host.** *Didelphis marsupialis* Linnaeus, Common opossum (Mammalia: Didelphidae).



**Figure 3.** *Rhopalias oochi* sp. nov., parasite of *Didelphis marsupialis* from Yucatán, Mexico. **A** Microphotograph, ventral view of entire body **B** Line drawing, ventral view **C** Detail of the oral, flanking and tentacle spines, ventral view **D** Cirrus sac, vagina, and eggs, ventral view. Scale bars: 10  $\mu$ m (**A–C**); 400  $\mu$ m (**D**).

**Type locality.** Rancho Hobonil, Tzucacab, Yucatán state, Mexico (20°00'58"N, 89°01'12"W).

**Site in host.** Small intestine.

**Prevalence and intensity of infection.** 100% (1 of 1 opossum), infected with 15 trematodes.

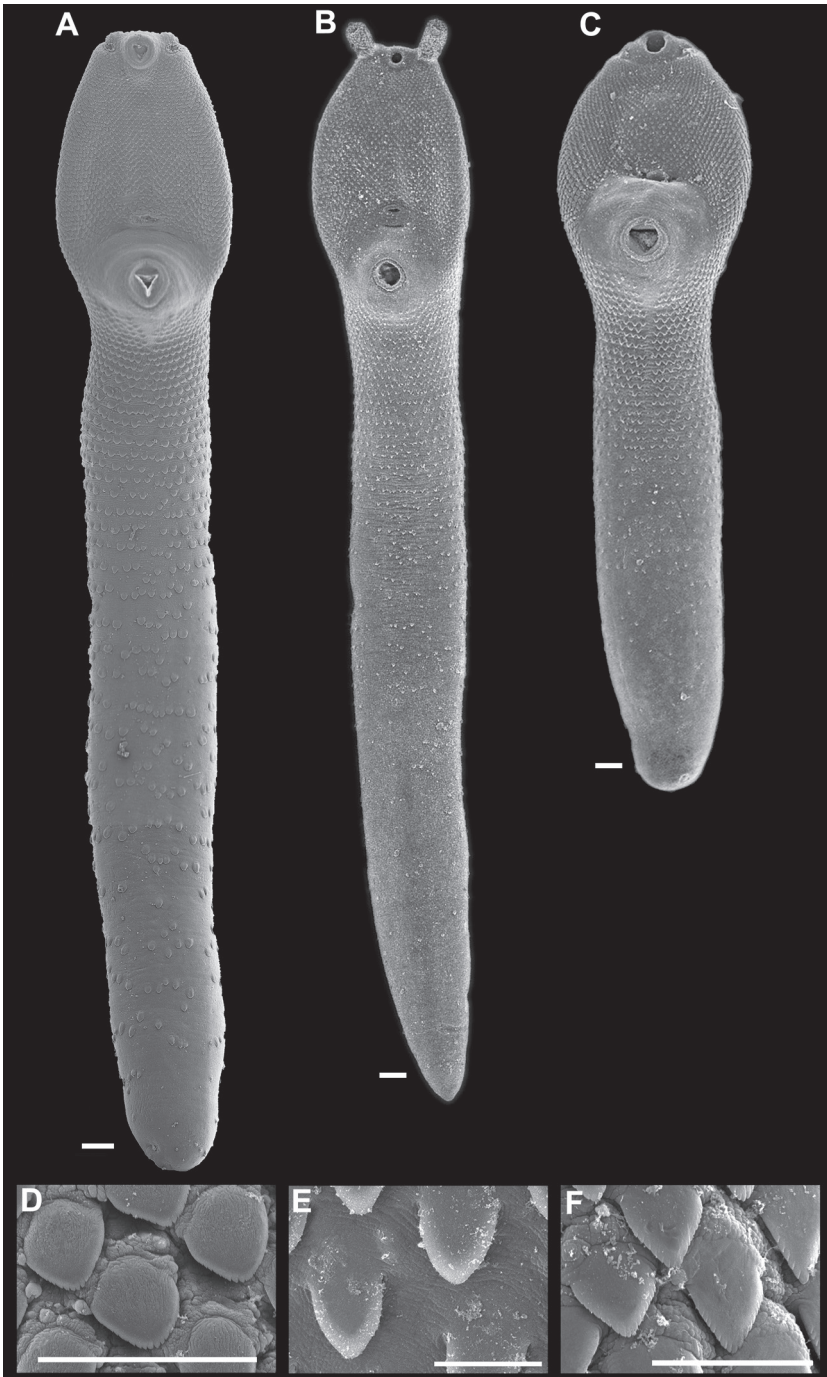
**Type specimens.** Holotype: CNHE 9504; paratypes: CNHE 10926 (3 specimens) and hologenophores CNHE 11069 (4 specimens).

**Etymology.** The specific epithet refers to the common name of the host where the new species was found. In the Mayan language, “ooch” means opossum.

**Description.** Based on 11 adult specimens (including 4 hologenophores). Measurements are given in Table 3. Trematodes with a long body, forebody concave, wider than hindbody, with a pair of armed retractile tentacles with 4–7 spines (Fig. 3A, B, C). Tegument covered with spines reaching posterior end of body (Fig. 4A). Tegument spines U-shaped, with distal tip pectinated (Fig. 4D, E). Oral and flanking spines present (Figs 3C, 5A, 5D). Muscular sacs long, reaching far beyond posterior margin of pharynx, and may or may not reach the anterior margin of ventral sucker (Fig. 3A, B). Oral sucker sub-terminal, rounded, well-developed, short prepharynx, pharynx muscular, and relatively long oesophagus; caecal bifurcation at short distance anterior to genital pore (Fig. 3B); long caeca extending to the posterior end of body (Fig. 3A). Ventral sucker muscular and subspherical, in the first third of body, larger than oral sucker (Figs 3A, B, 4A). Testes two, elongated, in tandem, contiguous, no overlapped, located in mid-body; anterior testis shorter than posterior testis (Fig. 3B). Cirrus sac long, claviform, containing a well-developed prostate complex and seminal vesicle, extending beyond ventral sucker and terminating near anterior border of ovary. Genital pore between ventral sucker and caecal bifurcation. Ovary slightly oval, postacetabular, pretesticular. Uterus intercaecal, between ovary and genital pore. Metraterm long (Fig. 4D). Vitelline follicles in lateral fields, beginning at mid-level between ventral sucker and ovary, ending at posterior end. Gravid specimens with few eggs, oval-shaped, operculated; embryonated eggs with thin shell.

**Remarks.** The genus *Rhopalias* currently contains six species as parasites of New World marsupials (Haverkost and Gardner 2008), i.e., *Rhopalias coronatus*, the type species; *Rhopalias horridus* (Diesing, 1850) Stiles and Hassall 1898; *Rhopalias baculifer* Braun, 1901; *Rhopalias macracanthus* Chandler, 1932; *Rhopalias caballeroi* Kifune & Uyema, 1982; and *Rhopalias caucensis* Rivillas, Caro, Carvajal & Vélez, 2004. *Rhopalias oochi* sp. nov. represents the seventh described species and is readily distinguished from five of the congeneric species, excepting *R. coronatus* by having tentacle sacs extending far beyond the posterior margin of pharynx. In their detailed morphological revision of the genus *Rhopalias*, Haverkost and Gardner (2008) provided a key to species of the genus and found that this character is reliable to distinguish between two groups of species. In *R. horridus*, the tentacle sacs surpass the posterior margin of pharynx to reach the mid-level of oesophagus; however, they never extend beyond the caecal bifurcation. In *R. oochi* sp. nov. the tentacle sacs extend to reach the anterior margin of ventral sucker. *Rhopalias horridus* further differ from the new species, and the remaining congeners by the large number of tentacle spines (> 30) (see key in Haverkost and Gardner 2008).





**Figure 4.** SEM micrographs of *Rhopalias* species. **A–C** Ventral view of the body of adult specimens showing the distribution of spines **D–I** Detail of the spines shape on the ventral surface of hindbody **A, D, E** *R. oochi* sp. nov. **B, F, G** *R. coronatus* **C, H, I** *R. macracanthus*. Scale bars: 100  $\mu$ m (**A–C**); 50  $\mu$ m (**D, E**); 10  $\mu$ m (**F, G**); 20  $\mu$ m (**H, I**).

The new species most closely resembles the type species, *R. coronatus*; in fact the specimens upon which the description of the new species is based were originally recorded as *R. coronatus* (see Acosta-Virgen et al. 2015). Genetic data revealed that they might actually represent a different species. In *R. coronatus* as in the new species tentacle sacs extend far beyond the posterior border of pharynx; in *R. coronatus*, both sacs usually surpass the anterior border of ventral sucker (although our observation of numerous voucher specimens indicate that the extension is variable among individuals); in the new species, the tentacle sacs consistently extend to almost reach the anterior border of ventral sucker, but never surpass it. Additionally, *R. coronatus* differ from the new species by having larger oral spines (at least four times larger), and by the distribution of vitelline follicles. In *R. coronatus* follicles extend between the posterior end of body and the posterior border of ventral sucker; instead, in *R. oochi* sp. nov. vitelline follicles do not reach the posterior end of body, and in the forebody, they reach the mid-level of cirrus sac. Morphometrically, most measurements are clearly overlapped between the new species and *R. coronatus* (except in oral spines size). We observed and measured 21 individuals of *R. coronatus* deposited at the CNHE. Our measurements, and those reported in other studies (see Table 3) indicate that *R. coronatus* is morphometrically quite variable. Furthermore, SEM study of the ultrastructure of the body surface provided additional evidence to distinguish the new species from *R. coronatus* and *R. macracanthus*; for these two species we collected specimens and some were fixed for a comparative SEM study (Fig. 4). In the three species body spines are denser in the forebody; however, the extension, size, and shape of spines clearly distinguish the three species. In *R. oochi* sp. nov., spines are robust and pectinate and they extend along the body almost to the posterior end (Fig. 4A, D, E); meanwhile, in *R. coronatus* spines are distributed to the mid-level of hindbody and are entire and tongue-shaped (Fig. 4B, F, G) and in *R. macracanthus*, even though spines extend more posteriorly, they are not as robust as in the new species; spines in *R. macracanthus* are pectinate and arrow-shaped (Fig. 4C, H, I).

## Discussion

Specimens of *Rhopalias* studied in the present study were identified morphologically either as *R. coronatus* or *R. macracanthus* following the descriptions by Haverkost and Gardner (2008). Identification was based on the length of the muscular sacs. The species *R. coronatus* possess muscular sacs almost reaching the anterior end of ventral sucker; meanwhile in *R. macracanthus* muscular sacs are short and slightly overpass the pharynx level. Additionally, spines of the retractile tentacles are very large in *R. macracanthus* (see Suppl. material 3: Figure S3C) in comparison with those of *R. coronatus*. Morphometrically, specimens of the three species are also different (see Table 3). Our study followed a molecular prospecting approach by considering *R. coronatus* as a trematode species that infects three species of marsupials distributed across a wide geographical range in southeastern Mexico (Blouin 2002; Criscione et al. 2005; Vilas et al. 2005). Our analyses showed that the specimens from the Yucatán Peninsula actually represented a separate species; phylogenetic trees showed all isolates from

**Table 3.** Measurements of *Rhopalias* spp. Measurements are presented in micrometers (µm) unless otherwise noted. Measurements above 1000 µm are expressed in millimeters.

	<i>R. oochi</i> sp. nov. (Present study) N= 7			<i>R. coronatus</i> (Present study) N= 15			<i>R. coronatus</i> (Haverkost & Gardner 2008) N= 22			<i>R. macracanthus</i> (Present study) N= 6		
	n	Mean	Range	n	Mean	Range	n	Mean	Range	n	Mean	Range
Body L	4	6.64 mm	6.42–6.70	15	4.69	2.94–6.66	22	4.440	2.160–9.360	6	3.36	2.78–3.75
Body W	4	727	622–810	15	611	320–770	22	735	219–1.58	6	680	514–680
VS L	7	484	420–543	15	330	190–530	22	376	150–840	6	308	257–340
VS W	7	417	355–464	15	330	190–480	22	350	150–816	6	304	273–332
OS L	6	177	168–189	15	180	100–245	22	183	93–344	6	159	141–174
OS W	6	160	139–194	15	167	99–200	22	180	88–325	6	162	149–174
Cirrus sac L	6	1.30	1.14–1.43	15	931	332–1.50	22	970	563–2.219	4	960	871–1.03
Cirrus sac W	6	283	248–317	15	281	132–400	20	203	119–500	4	319	174–431
Anterior testis L	4	528	500–572	15	386	255–515	21	333	156–625	6	277	195–356
Anterior testis W	4	149	146–154	15	189	135–227	21	167	100–281	6	220	130–350
Posterior testis L	4	722	672–770	15	535	322–655	21	499	256–919	5	412	299–520
Posterior testis W	4	140	137–147	15	175	112–232	21	149	75–281	5	164	123–217
Ovary L	5	222	112–233	14	175	75–232	21	169	75–344	6	151	97–175
Ovary W	5	178	162–193	14	162	95–217	20	178	88–350	6	149	86–180
Tentacle sac L	7	741	654–798	14	710	423–990	21	693	375–1.188	6	301	271–347
Tentacle sac W	7	155	137–189	14	146	109–200	21	137	63–238	6	132	125–143
Prepharynx L	5	103	90–118	15	80	30–120	22	39	0–313	6	78	56–97
Pharynx L	6	173	151–212	15	156	105–200	22	202	115–425	6	162	147–182
Pharynx W	6	96	84–111	15	81	47–135	21	104	30–244	6	99	91–112
Oesophagus L	4	312	300–339	15	285	200–422	20	186	0–606	6	19	10–30
Egg number	5	6	0–12	15	30	22–90	22	24	0–75	6	25	10–75
Eggs L	12	83	66–96	58	89	70–113	94	90	70–108	30	86	60–100
Eggs W	12	51	41–55	58	50	30–62	94	51	38–70	30	54	39–93
VS/OS ratio L	6	1:2.70	1:2.60–2.87	15	1:1.83	1:1.90–2.20		1:2.0*	1:1.61–2.44*	6	1:1.93	1:1.82–1.95
VS/OS ratio W	6	1:2.70	1:2.60–2.80	15	1:1.00	1:1.90–2.40		1:1.94*	1:1.70–2.50*	6	1:1.87	1:1.83–1.90
ANTVIT	4	1.66 mm	1.56–1.75	15	1.31	715–2.72	22	1.16	331–3.60	6	1.10	1.05–1.20
VSVIT	4	248	176–328	14	38	-130–237	22	51	-200–480	6	40	0–10
GP to anterior end	5	821	795–853	15	660	430–760		NM	NM	6	525	430–589
Oral spines L	14	9	7–12	30	39	22–58		NM	NM	24	10	12–20
Oral spines W	14	8	5–10	30	11	7–14		NM	NM	24	12	7–17
Tentacle spines L	18	23	15–32	30	36	33–55	22	56	32–67	24	135	112–152
Tentacle spines W	18	11	8–14	30	19	14–30		NM	NM	24	25	20–32

VS = Ventral Sucker; OS = Oral Sucker; ANTVIT = distance from the anterior end to the anterior margin of the vitellarium; VSVIT = distance from the anterior margin of the vitellarium to the posterior margin of the Ventral Sucker; GP = Genital Pore; NM = No mentioned; \* = Values estimated from original measurements in Haverkost and Gardner (2008).

that locality as a reciprocally monophyletic assemblage, separated from isolates of *R. coronatus*, and this two as the sister taxa of *R. macracanthus*. Even though the internal transcribed spacers (ITS1–5.8S–ITS2) exhibited lower resolution, the mitochondrial gene (cox1) revealed relatively high genetic divergence values (7–8%) supporting the distinction of the new species. This level of genetic divergence has been found in studies with other members of the superfamily Echinostomatoidea. For instance, Saijuntha et al. (2011) reported divergence levels of 8–16% between two species of *Echinostoma* Rudolphi, 1809. Even though the pertinence of using a genetic yardstick to distinguish parasite species has been questioned (Nadler and Pérez-Ponce de

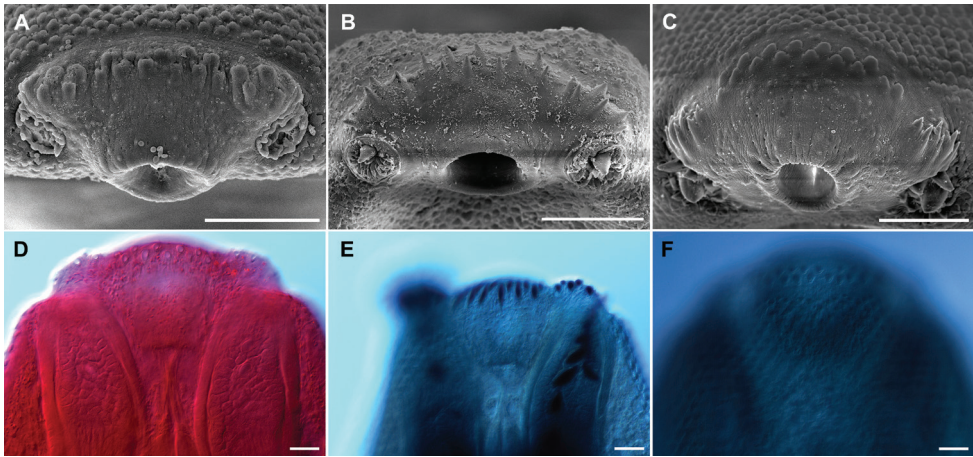
León 2011), the species delimitation criteria followed in our study is also based on a hypothesis-testing framework (see Adams 2002; Nadler 2002).

A closer look at the morphology of the specimens from Yucatán using light and scanning electron microscopy corroborated the molecular results, and the new species was described as a parasite of the Common opossum, *D. marsupialis*. *Rhopalias oochi* sp. nov. represents the seventh described species in the genus, and the 5<sup>th</sup> in marsupials distributed in Mexico. With the exception of *R. macracanthus*, a species described by Chandler (1932) in the Nearctic biogeographical region, from the Virginia opossum, in the U.S.A., all the other species included in the genus *Rhopalias* were originally described in marsupials from the Neotropical region. However, *R. macracanthus* was later found in South American marsupials, particularly in the Department of Santa Cruz, Bolivia (Haverkost and Gardner 2008). The type species, *R. coronatus* was described from the Common opossum, *D. marsupialis* in Brazil; *R. horridus* from the Water opossum, *Chironectes minimus* (Zimmerman) also in Brazil; *R. baculifer* from *D. marsupialis* in Brazil; *R. caballeroi* from *D. marsupialis* and from the Grey four-eyed opossum, *Philander opossum* (Linnaeus) in Brazil; and *R. caucensis* from *P. opossum* in Colombia (see Haverkost and Gardner 2008). According to García-Prieto et al. (2012) four species of *Rhopalias* have been recorded in Mexico, *R. baculifer* and *R. caballeroi* in restricted localities in the tropical rain forest of Los Tuxtlas, Veracruz, and other two species more widely distributed parasitizing three species of marsupials (*P. opossum*, *D. virginiana* and *D. marsupialis*), *R. coronatus*, and *R. macracanthus* in nine and 12 localities, respectively. A few additional records were more recently provided by Acosta-Virgen et al. (2015). Interestingly, in the region of Los Tuxtlas, Veracruz, where the three species of opossums are found in sympatry (see Cervantes et al. 2010), the four species of *Rhopalias* have been recorded. In our study, even though we sampled five individuals of *D. marsupialis*, one of *D. virginiana* and two of *P. opossum* from the same locality, we only collected specimens of *R. coronatus* and *R. macracanthus*.

Marsupials occurring across Mexico are heavily parasitized by helminths; at least 16 helminth taxa have been recorded for *D. marsupialis*, 30 for *D. virginiana*, and 17 for *P. opossum* across their distributional ranges in Mexico (Acosta-Virgen et al. 2015). The only study where DNA sequences were used to establish a more robust species delimitation for the helminth parasite fauna of marsupials is that of López-Caballero et al. (2015). These authors uncovered three genetic lineages for the acanthocephalan *Oligacanthorhynchus microcephalus* (Rudolphi, 1819) Schmidt, 1972, a species allegedly with a distribution from Brazil, where it was originally described, extended to the USA. The fact that we detected another new species of a marsupial parasite through the use of DNA sequences clearly indicated that future studies should consider the use of molecular tools that greatly enhance our ability to delimit species, and this will increase our understanding of the species diversity of marsupial parasites.

Finally, we consider that the use of SEM is fundamental in determining reliable characters that distinguish among echinostomid species because the presence of a wide array of spines along the body and around the oral sucker. In this case, SEM was very important in showing that the species *R. macracanthus* do possess oral spines, although they are not completely visible using light microscopy (see Fig. 5C–F). For instance,





**Figure 5.** Anterior end of *Rhopalias* species, showing the detail of the oral and flanking spines. **A–C** SEM micrographs **D–F** DIC micrographs, dorsal view **A, D** *R. oochi* sp. nov. **B, E** *R. coronatus* **C, F** *R. macracanthus*. Scale bars: 100  $\mu$ m (**A, B**); 50  $\mu$ m (**C**); 40  $\mu$ m (**D–F**).

Figure 5C shows the presence of 16 tongue-shaped oral spines in *R. macracanthus*, and these spines contrast in size and shape with flanking spines which are more visible. Haverkost and Gardner (2008) taxonomic key pointed out the lack of oral spines in *R. macracanthus*. However, our study demonstrated that these spines are present. Overall, the integrative taxonomy approach, where several sources of information are used to establish more robust species delimitation criteria, is highly recommended for a complete understanding of parasite diversity.

## Acknowledgements

We thank David Osorio, Luis García, Virginia León, Luis J. García, Sergio Guillén, Uriel Garduño, Karla Acosta, Manuel Servín, Samantha Contreras, and Sara Ramírez for their support during field work. To Rosamond Coates and David Cervera kindly granted permissions for sampling in the Estación de Biología Tropical, Los Tuxtlas, Veracruz and Rancho Hobonil, Tzucacab, Mérida, Yucatán, respectively. JLC thanks to families Medina-Castillo in Agua Fría, Chiapas, and Hernández in Finca Brasil, Tapachula, Chiapas. We are grateful with Berenit Mendoza Garfias for her technical support taking the SEM pictures and Ana Isabel Bieler Antolin for assistance taking DIC microphotographs; David Hernández-Mena for obtaining of ITS sequences and Laura Márquez and Nelly López, LaNaBio, for obtaining sequences with the automatic sequencer. JLC also thanks CONACyT for the scholarship received to complete his PhD studies within Posgrado en Ciencias Biológicas, UNAM. This study was partly founded by the Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica (PAPIIT-UNAM) IN202617 and 220113 to GPPL and RML, respectively.

## References

- Acosta-Virgen K, López-Caballero J, García-Prieto L, Mata-López R (2015) Helminths of three species of opossums (Mammalia, Didelphidae) from Mexico. *ZooKeys* 511: 131–152. <https://doi.org/10.3897/zookeys.511.9571>
- Adams BJ (2002) The species delimitation uncertainty principle. *Journal of Nematology* 33: 153–160.
- Blouin MS (2002) Molecular prospecting for cryptic species of nematodes: mitochondrial DNA versus internal transcribed spacer. *International Journal for Parasitology* 32: 527–531. [https://doi.org/10.1016/S0020-7519\(01\)00357-5](https://doi.org/10.1016/S0020-7519(01)00357-5)
- Bowles J, McManus DP (1993) Rapid discrimination of *Echinococcus* species and strains using a PCR-based method. *Molecular and Biochemical Parasitology* 57: 231–239. [https://doi.org/10.1016/0166-6851\(93\)90199-8](https://doi.org/10.1016/0166-6851(93)90199-8)
- Bowles J, Blair D, McManus DP (1995) A molecular phylogeny of the human schistosomes. *Molecular Phylogenetics and Evolution* 4: 103–109. <https://doi.org/10.1006/mpev.1995.1011>
- Braun M (1901) Zur Kenntnis der Säugetiere. *Zoologische Jahrbücher Systematik* 14: 311–348.
- Cervantes FA, Arcangeli-Álvarez J, Hortelano-Moncada Y, Borisenko AV (2010) DNA barcodes effectively identify the morphologically similar Common Opossum (*Didelphis marsupialis*) and Virginia Opossum (*Didelphis virginiana*) from areas of sympatry in Mexico. *Mitochondrial DNA* 21: 44–50. <https://doi.org/10.3109/19401736.2010.538051>
- Chandler AC (1932) Notes on helminth parasites of the opossum (*Didelphis virginiana*) in Southeast Texas with description of four new species. *Proceedings of the United States National Museum* 81: 1–15. <https://doi.org/10.5479/si.00963801.81-2939.1>
- Criscione CD, Poulin R, Blouin MS (2005) Molecular ecology of parasites: elucidating ecological and microevolutionary processes. *Molecular Ecology* 14: 2247–2257. <https://doi.org/10.1111/j.1365-294X.2005.02587.x>
- Diesing CM (1850) *Systema helminthum*. Vindobonae, Vienna, 588 pp.
- Drummond AJ, Ashton B, Buxton S, Cheung M, Cooper A, Duran C, Field M, Heled J, Kearse M, Markowitz S, Moir R, Stones-Havas S, Sturrock S, Thierer T, Wilson A (2010) Geneious v5.0.4. <http://www.geneious.com/>
- García-Prieto L, Falcón-Ordaz J, Guzmán-Cornejo C (2012) Helminth parasites of wild Mexican mammals: list of species, hosts and geographical distribution. *Zootaxa* 3290: 1–92. <https://doi.org/10.11646/zootaxa.3290.1.1>
- Haverkost TR, Gardner SL (2008) A review of species in the genus *Rhopalias* (Rudolphi, 1819). *Journal of Parasitology* 94: 716–726. <https://doi.org/10.1645/GE-1423.1>
- Hernández-Mena DI, García-Prieto L, García-Varela M (2014) Morphological and molecular differentiation of *Parastrigea* (Trematoda: Strigeidae) from Mexico, with the description of a new species. *Parasitology International* 63: 315–323. <https://doi.org/10.1016/j.parint.2013.11.012>
- Kifune T, Uyema N (1982) Report of the Fukuoka University Scientific Expedition to Peru, 1976. Part 3. Taxonomical studies on trematodes from marsupials and rodents with records of two crabs. *Medical Bulletin of Fukuoka University* 9: 241–256.



- Kostadinova A (2005) Family Echinostomatidae Looss, 1899. In: Jones A, Bray RA, Gibson DI (Eds) Keys to the Trematoda, vol. 2. CABI. Publishing and the Natural History Museum, Wallingford and London, UK, 9–64. <https://doi.org/10.1079/9780851995878.0009>
- Looss A (1899) Weitere Beiträge zur Kenntnis der Trematoden-Fauna Aegyptens zugleich Versuch einer natürlichen Gliederung des Genus *Distomum* Retzius. Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere 12: 521–784. <https://doi.org/10.5962/bhl.part.2037>
- López-Caballero J, Mata-López R, García-Varela M, Pérez-Ponce de León G (2015) Genetic variation of *Oligacanthorhynchus microcephalus* (Acanthocephala: Archiacanthocephala: Oligacanthorhynchidae), parasite of three species of opossums (Mammalia: Didelphidae) across central and southeastern Mexico. Comparative Parasitology 82: 175–186. <https://doi.org/10.1654/4742.1>
- Maddison DR, Maddison WP (2011) Mesquite: a modular system for evolutionary analysis v2.75 <http://mesquiteproject.org>
- Messing J (1993) M13 cloning vehicles. Their contribution to DNA sequencing. Methods in Molecular Biology 23: 9–22. [https://doi.org/10.1016/0076-6879\(83\)01005-8](https://doi.org/10.1016/0076-6879(83)01005-8)
- Moszczyńska A, Locke SA, McLaughlin JD, Marcogliese DJ, Crease TJ (2009) Development of primers for mitochondrial cytochrome *c* oxidase I gene in digenetic trematodes (Platyhelminthes) illustrates the challenge of barcoding parasitic helminths. Molecular Ecology Resources 9: 75–82. <https://doi.org/10.1111/j.1755-0998.2009.02634.X>
- Nadler SA (2002) Species delimitation and nematode biodiversity: phylogenies rule. Nematology 4: 615–625. <https://doi.org/10.1163/15685410260438908>
- Nadler SA, Pérez-Ponce de León G (2011) Integrating molecular and morphological approaches for characterizing parasite cryptic species: implications for parasitology. Parasitology 138: 1688–1709. <https://doi.org/10.1017/S003118201000168X>
- Pleijel F, Jondelius U, Norlinder E, Nygren A, Oxelman B, Schander C, Sundberg P, Thollesson M (2008) Phylogenies without roots? A plea for the use of vouchers in molecular phylogenetic studies. Molecular Phylogenetics and Evolution 48: 369–371. <https://doi.org/10.1016/j.ympev.2008.03.024>
- Posada D, Crandall KA (1998) Modeltest: testing the model of DNA substitution. Bioinformatics 9: 817–818. <https://doi.org/10.1093/bioinformatics/14.9.817>
- Rambaut A (2006) FigTree v1.3.1. Institute of Evolutionary Biology. University of Edinburgh, UK.
- Rivillas C, Caro E, Carvajal H, Vélez I (2004). Algunos trematodos digeneos (Rhopaliasidae, Opisthorchiidae) de *Philander opossum* (Marsupialia) de la costa pacífica colombiana, incluyendo *Rhopalias caucensis* sp. n. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 28: 591–600.
- Ronquist F, Teslenko M, Van Der Mark P, Ayres LD, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes v3.2: Efficient Bayesian Phylogenetic Inference and Model Choice Across a Large Model Space. Systematics Biology 61: 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Rudolphi CA (1809) Entozoorum sive vermium intestinalium. Historia Naturalis 1: 1–527.
- Rudolphi CA (1819) Entozoorum synopsis cui accedunt mantissa duplex et indices locupletissimi. Sumtibus Augusti Rücker, Berolini (Berlin), 811 pp. <https://doi.org/10.5962/bhl.title.9157>

- Saijuntha W, Sithithaworn P, Duenngai K, Kiatsopit N, Andrews RH, Petney TN (2011) Genetic variation and relationships of four species of medically important echinostomes (Trematoda: Echinostomatidae) in South-East Asia. *Infection, Genetics and Evolution* 11: 375–381. <https://doi.org/10.1016/j.meegid.2010.11.009>
- Schmidt GD (1972) Revision of the Class Archiacanthocephala Meyer, 1931 (Phylum Acanthocephala), with emphasis on Oligacanthorhynchidae Southwell et MacFie, 1925. *Journal of Parasitology* 58: 290–297. <https://doi.org/10.2307/3278091>
- Stamatakis A (2006) RAxML-VI-HP: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–90. <https://doi.org/10.1093/bioinformatics/btl446>
- Stiles CW, Hassall A (1898) Notes on parasites, an inventory of the genera and subgenera of the trematode family Fasciolidae. *Archives de Parasitologie* 1: 81–99.
- Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: Molecular Evolutionary Genetics Analysis v6.0. *Molecular Biology and Evolution* 30: 2725–29. <https://doi.org/10.1093/molbev/mst197>
- Thompson J, Higgins D, Gibson T (1994) Clustal W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research* 22: 4673–4680. <https://doi.org/10.1093/nar/22.22.4673>
- Tkach VV, Kudlai O, Kostadinova A (2016) Molecular phylogeny and systematics of the Echinostomatoidea Looss, 1899 (Platyhelminthes: Digenea). *International Journal for Parasitology* 46: 171–185. <https://doi.org/10.1016/j.ijpara.2015.11.001>
- Vilas R, Criscione CD, Blouin MS (2005) A comparison between mitochondrial DNA and the ribosomal internal transcribed regions in prospecting for cryptic species of platyhelminth parasites. *Parasitology* 131: 1–8. <https://doi.org/10.1017/S0031182005008437>

## Supplementary material I

### Figure S1. Tree inferred with *cox1* data set, using Maximum Likelihood and Bayesian Inference

Authors: Jorge López-Caballero, Rosario Mata-López, Gerardo Pérez-Ponce De León

Data type: phylogenetic tree

Explanation note: The numbers at the nodes represent ML bootstrap support and posterior probability values. Clade terminals represent localities and hosts from the worms were collected.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.854.34549.suppl1>

## Supplementary material 2

### Figure S2. Tree inferred with ITS region (ITS1 + 5.8S + ITS2) data set, using Maximum Likelihood and Bayesian Inference

Authors: Jorge López-Caballero, Rosario Mata-López, Gerardo Pérez-Ponce De León

Data type: phylogenetic tree

Explanation note: The numbers at the nodes represent ML bootstrap support and posterior probability values. Clade terminals represent localities and hosts from the worms were collected.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.854.34549.suppl2>

## Supplementary material 3

### Figure S3

Authors: Jorge López-Caballero, Rosario Mata-López, Gerardo Pérez-Ponce De León

Data type: species images

Explanation note: *Rhopalias coronatus* ex *Didelphis virginiana* from Los Tuxtlas, Veracruz. (A) Line drawing, ventral view (B) Microphotograph, ventral view of entire body. *Rhopalias macracanthus* ex *Philander opossum* from Tlacotalpan, Veracruz (C) Line drawing, ventral view. (D) Microphotograph, ventral view of entire body. Scale bars 1 mm (A, C); 20.2 mm (B, D).

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.854.34549.suppl3>

