

# Research on Chrysomelidae 7

*Edited by*

Caroline S. Chaboo & Michael Schmitt



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RESEARCH ON CHRYSOMELIDAE 7

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Fax: +359-2-870-42-82

[info@pensoft.net](mailto:info@pensoft.net)

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*Thomas Wagner*



## Editorial

Caroline S. Chaboo<sup>1</sup>, Michael Schmitt<sup>2</sup>

**1** Department of Entomology, W-436 Nebraska Hall, University of Nebraska, Lincoln, Nebraska, 68583-0514, USA **2** Ernst-Moritz-Arndt-Universität, Allgemeine & Systematische Zoologie, Loitzer Str. 26, D-17489 Greifswald, Germany

Corresponding author: *Caroline S. Chaboo* ([michael.schmitt@uni-greifswald.de](mailto:michael.schmitt@uni-greifswald.de))

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This special issue assembles a fine collection of authors and recent research that emerged from the 9<sup>th</sup> International Symposium on the Chrysomelidae, organised within the frame of the 25<sup>th</sup> International Congress of Entomology, held in September 2016, in Orlando, Florida, USA. This collection of research articles forms the core of volume 7 of Research on Chrysomelidae (RoC), a series that is devoted to all aspects of the biology of leaf and seed beetles. Editor Schmitt has been a co-editor in this series since volume 1 while this is author Chaboo's first participation as a co-editor.

The first volume of the RoC series originated as the brainchild of Pierre Jolivet, starting with volume 1 in 2008 (Editors: Pierre Jolivet, Jorge Santiago-Blay and Michael Schmitt; Brill publishers). The series was intended from conception, and we are happy to be right on target with RoC7 in 2017. Volumes 1 in 2008 and volume 2 in 2009 were presented in independent book formats; since 2011, the chrysomelid community has established a strong working relationship with the ZooKeys publishing team and this has produced volumes 3–6 (2011, 2013, 2015, and 2016). The RoC series mostly contains elaborated versions of research presentations at meeting conferences but also independently submitted papers. Their unconstrained appearance has helped inform and educate on Chrysomelidae systematics and biology.

The issue comprises 9 articles by 23 authors from 9 countries. The majority of articles were presented orally or as posters at the 25<sup>th</sup> ICE congress. The 9<sup>th</sup> International Symposium on the Chrysomelidae was the first that also included two contributions



on seed beetles (regrettably no manuscripts on seed beetles are included in the present volume). However, we hope this is a change of attitude to include Bruchinae under the umbrella of RoC. Until recently the community of seed beetle workers appeared completely separated from that of leaf beetle workers, reflecting that seed beetles were treated as a separate family, Bruchidae. Since the mode of life of leaf beetles, even of those that are regarded a “pest”, is different from that of seed beetles, the scientists working on the latter had their own agenda. Although the phylogenetic position of the “Bruchidae” within Chrysomelidae was established long ago, treating them as subfamily Bruchinae within the Chrysomelidae became accepted only since 1995. The opposite applies to the Megalopodidae and the Orsodacnidae, both formerly listed as subfamilies within Chrysomelidae. Luckily, leaf beetle workers still include these groups in their field of study, as the paper by Geovanni Rodriguez-Mirón and co-workers shows (pp. 47–64).

Several papers of RoC7 focus on faunistics, biogeography, and biology of leaf beetles in a certain region: Vivan Flinte & co-authors on Rio de Janeiro (pp. 5–22), David Furth on Mexico (pp. 23–46), Yongying Ruan et al. on Chinese flea beetles (pp. 103–120). Some other papers deal with taxonomy: Jesús Gómez-Zurita on Eumolpinae from New Caledonia (pp. 65–75), Rui-E Nie et al. on Galerucinae (pp. 91–102), Michael Schmitt and Gabriele Uhl on Palaearctic *Oulema*-species (pp. 121–130), Thomas Wagner on Afrotropical Galerucinae (pp. 131–137). One contribution deals with functional morphology: Yoko Matsumura and co-authors on traumatic mating in *Pyrrhalta maculicollis* (pp. 77–89).

This broad selection of taxa, topics, and methods demonstrates the attractiveness of leaf beetles as subjects of research in different fields. *Research on Chrysomelidae* provides a forum for diverse and fascinating results on these beetles. We, the editors and the publishers, want to promote further exchange of results and ideas pertaining to all aspects of Chrysomelidae biology among scientists working with different methods in different disciplines, but all on our favourites, the seed and leaf beetles.

Today, chrysomelid researchers and enthusiasts have many ways of sharing their research via the *Chrysomela* newsletter (established in 1979, over 200 recipients), emails,

and social media – Twitter (hashtag #leafbeetles) and a Facebook group ‘Chrysomelidae Forum’ (426 members today). As in 2008, we still believe firmly in the power of meeting face-to-face and in assembling articles in volumes like this one, especially since these provide powerful accelerators for research in a single step.

We look forward to seeing at our upcoming international meetings and in bringing more volumes like the present one into shape.

Caroline S. Chaboo, Michael Schmitt



# Chrysomelinae species (Coleoptera, Chrysomelidae) and new biological data from Rio de Janeiro, Brazil<sup>1</sup>

Vivian Flinte<sup>1</sup>, André Abejanella<sup>1</sup>, Mauro Daccordi<sup>2</sup>,  
Ricardo F. Monteiro<sup>1</sup>, Margarete Valverde Macedo<sup>1</sup>

**1** Av. Carlos Chagas Filho, 373. CCS, IB, Laboratório de Ecologia de Insetos, Universidade Federal do Rio de Janeiro, Ilha do Fundão, CEP 21941-590, Rio de Janeiro, RJ, Brazil **2** Museo Civico di Storia Naturale, Lungadige Porta Vittoria 9, 37129, Verona, Italy

Corresponding author: Vivian Flinte ([vflinte@gmail.com](mailto:vflinte@gmail.com))

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## Abstract

Chrysomelinae is one of the largest subfamilies in Chrysomelidae, yet much basic information remains unknown for Neotropical species. The present study aims to compile the first regional list of Chrysomelinae for the State of Rio de Janeiro, Brazil, and assemble natural history traits obtained from our fieldwork from 2005 to 2010 in Serra dos Órgãos National Park, a mountainous area of Atlantic forest. The species list was compiled from data from field work, collections, and literature, and recorded a total of 100 species, belonging to 21 genera in one tribe (Chrysomelini) and three subtribes: Chrysolinina (91 species), Chrysomelina (eight species) and Entomoscelina (one species). Of these, 91 species are new records for the state. Serra dos Órgãos National Park holds records of 43 species, with *Platyphora* being the most species-rich genus, and Solanaceae the most common host plant family. Some new records of reproductive mode (larviparous vs. oviparous) and larval behavior are also given. These Brazil Chrysomelinae species exhibited a clear seasonal pattern, with more species recorded in the hot and rainy season from October to January, and considerably fewer species from June to August, during the drier and colder months. The fraction of new records in comparison with published species and natural history information illustrates how little we know of Chrysomelinae in the state and in the country.

## Keywords

Atlantic forest, biodiversity, host plant, *Platyphora*, seasonality, viviparity

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<sup>1</sup> Contribution to the 9<sup>th</sup> International Symposium on the Chrysomelidae, Orlando, FL, USA, September 28, 2016

## Introduction

Chrysomelinae is the fifth largest subfamily of Chrysomelidae, after Galerucinae, Eumolpinae, Cassidinae and Cryptocephalinae (Reid 2006), with 3,000 species and 132 genera (Daccordi 1994, 1996, Riley et al. 2002), but these numbers vary among authors (see Seeno and Wilcox 1982, Reid 1995). Two tribes are generally recognized: Timarchini, which is monogeneric with *Timarcha* Latreille (ca. 100 species); and Chrysomelini containing the remainder (Seeno and Wilcox 1982, Daccordi 1994). However, there are still many problems concerning Chrysomelinae taxonomy. Daccordi (1996) listed 38 genera for the Neotropical region, out of which 31 are exclusive to the area. Some of the main contributions for Neotropical Chrysomelinae taxonomy and cataloguing are those by Jan Bechyně (e.g. 1954, 1958, 1980), which include many species descriptions and some regional lists, and, more recently, a key to the genera in Costa Rica by Wills Flowers (2004), modified from Bechyně and Springlova de Bechyně (1965). Both larvae and adults normally feed on leaves of the same host plant species and species tend to be monophagous or to feed on a narrow group of related plant species (Jolivet 1988). The same author pointed out that host plants are known for nearly 40% of Chrysomelinae genera, and data are largely lacking for tropical species. In the Neotropical area, Chrysomelinae are frequently associated with Solanaceae, Asteraceae, Apocynaceae, and Zygophyllaceae (Jolivet and Hawkeswood 1995). However, knowledge of Chrysomelinae biology is rare in this region, remaining so two decades after being underlined by Jolivet (1997).

Except for some ecological studies and species records confined to entomological collections, no list of species exists for the subfamily in the State of Rio de Janeiro or even in Brazil. Since we have conducted extensive research in a protected area in the state and have accumulated considerable biological information on Chrysomelidae species, our aim here is to compile the first regional list of Chrysomelinae in Brazil, and to assemble natural history traits for the species found in Serra dos Órgãos National Park, State of Rio de Janeiro.

## Materials and methods

For Chrysomelinae species list compilation for Brazil, four national collections were examined: Coleção entomológica do Laboratório de Ecologia de Insetos / Universidade Federal do Rio de Janeiro, Rio de Janeiro (**CLEI**); Museu Nacional / Universidade Federal do Rio de Janeiro, Rio de Janeiro (**MNRJ**), except species from Itatiaia; Coleção entomológica da Fundação Instituto Oswaldo Cruz, Rio de Janeiro (**CEIOC**); and Museu Paraense Emílio Goeldi, Belém (**MPEG**). The digital collection of the Museo del Instituto de Zoología Agrícola, Universidad Central de Venezuela (MIZA) was also consulted. Finally, the literature was searched for additional records. These records are indicated in Table 1. Location is given by the municipality within the State of Rio de Janeiro, which comprises 43,696 km<sup>2</sup> and represents less than 1% of the country's area. Taxonomy follows Daccordi (1994) and Seeno and Wilcox (1982).

For documentation of species' natural history and host plants, data assembled from field expeditions during different research projects conducted at Serra dos Órgãos National Park (22°26'56"S; 42°59'5"W), State of Rio de Janeiro, between 2005 and 2010 was used. The duration, months and number of participants of field expeditions per year are as follows: 2005 (1 or 2 days every month, 3 to 5 collectors); 2006 (2 to 4 days every month, 3 to 5 collectors); 2007 (2 to 4 days every month, 3 to 5 collectors); 2008 (1 or 2 days every month, 2 or 3 collectors); 2009 (1 or 2 days every month, 2 or 3 collectors); 2010 (1 or 2 days every month, 1 or 2 collectors).

### **Study Site**

The park covers an area of 20,024 ha of well-preserved Atlantic Rain Forest (see Veloso et al. 1991 for more on local vegetation) and is located ca. 100 km from Rio de Janeiro, in a mountainous area ranging from 80 m to 2263 m elevation. The climate is tropical, with a colder drier season from May to August, and a rainy warmer period from November to February (Flinte et al. 2009b). Mean annual temperature is around 18 °C, maximum of 38 °C and minimum of 0 °C. Annual precipitation varies between 1250 and 1500 mm (Flinte et al. 2008).

### **Species study and collection**

Species were sampled by a combination of manual collecting, sweep nets and malaise traps, during the conduction of other projects with Chrysomelidae in the park. When a species was initially found in the field, individuals in as many different developmental stages as possible were brought to the laboratory and reared in plastic containers for host plant confirmation and observations on behavior and biology. In an attempt to describe species seasonal distribution in the area, considering data on labels of specimens from all collections, we recorded the different months on which they were collected and summed the number of species per month (independent of year).

### **Identification and vouchers**

Chrysomelinae species were identified by Mauro Daccordi. Solanaceae host plants were identified by Lucia d'Ávila Freire de Carvalho (Jardim Botânico do Rio de Janeiro) and Luciano Bianchetti (Embrapa/Brasília), Asteraceae by Roberto Lourenço Esteves (Universidade do Estado do Rio de Janeiro), Convolvulaceae by Rosângela Simão-Bianchini (Herbário SP - Instituto de Botânica) and Malvaceae by Massimo Bovini (Jardim Botânico do Rio de Janeiro). Thiago Marinho Alvarenga (Universidade de Campinas) identified parasitoids. Species collected at Serra dos Órgãos National Park are deposited at CLEI-UFRJ, Rio de Janeiro, Brazil.

## Results and discussion

### General patterns of richness and distribution

The Chrysomelinae Neotropical fauna is thought to comprise ca. 38 genera (Daccordi 1996) and 1,020 species (Blackwelder 1944), but these are outdated numbers and no such information could be found specifically for Brazil. One hundred species occurring in the State of Rio de Janeiro were recorded, belonging to 21 genera in one tribe (Chrysomelini) and three subtribes: Chrysolinina, Chrysomelina and Entomoscelina (Table 1). Chrysolinina was represented by 91 species, followed by Chrysomelina with eight and Entomoscelina with only one species (Table 1). According to Daccordi (1996), there are many endemic Chrysolinina and Chrysomelina taxa in the Neotropical region, where they reach their maximum diversity. Only nine species are from previously published sources, the other 91 species we found are new records for the state. The genus with most species records was *Platyphora* ( $n = 39$ ) representing 42.4% of Chrysolinina found and 40% of total species records, followed by *Stilodes* ( $n = 13$ , 12.9% of all species recorded) and *Deuterocampta* ( $n = 11$ , 10.9%), genera restricted to the Neotropical region (Daccordi 1996). Indeed, *Platyphora* is the most species-rich genus in South America (Daccordi 1994), with approximately 500 species (Chaboo et al. 2014 and references therein).

The findings presented here also revealed a high diversity of species and genera, typical for the Atlantic rain forest, in comparison to other studies in South and Central America. Flowers (2004) documented 67 species in 11 genera for Costa Rica and, similar to our work, *Platyphora* and *Stilodes* were the most species-rich genera. During a six-year field study in a Mexican state, 47 species and eight genera were found; *Leptinotarsa*, *Calligrapha* and *Zygogramma* were the genera with most species records (Burgos-Solorio and Anaya-Rosales 2004). Chaboo and Flowers (2015) found 158 species and 18 genera for Peru, based on species catalogues.

Species were recorded from only 17 (18.5%) of the state's municipalities, and 62 species were known from only one location (Table 1). We found a similar pattern in an inventory of Cassidinae for the same state (Flinte et al. 2009a), with most records concentrated near the city of Rio de Janeiro and in large protected areas, such as Petrópolis and Teresópolis (Serra dos Órgãos National Park) and Itatiaia (Itatiaia National Park). The high number of single locality records is probably due more to sampling effort than to endemism, considering that species normally are not very abundant and are more easily collected manually than with traps.

### Biology and ecology of Chrysomelinae at Parque Nacional da Serra dos Órgãos

A total of 43 species were recorded from Serra dos Órgãos National Park (Table 1, under SONP; Figure 1), all Chrysomelini, 42 occurring within the subtribe Chrysolinina and only one from Chrysomelina (*Pixis columbina*). Within Chrysolinina, *Platyphora* was the genus with most species records (23 species) out of the 10 genera found,

**Table 1.** List of Chrysomelinae species. Chrysomelinae species from the State of Rio de Janeiro, indicating the municipality of the record and specific location, when available. Numbers indicate the source of information (see footnote below table). SONP = Serra dos Órgãos National Park; INP = Itatiaia National Park.

Species	Location
<b>Chrysomelini: Chrysoliniina – 15 genera and 91 species</b>	
<i>Calligrapha polyspila</i> (Germar, 1821) (Fig. 1A)	Angra dos Reis <sup>3</sup> , Itatiaia <sup>3</sup> , Paraty (Pedra Branca) <sup>1</sup> , Resende <sup>3</sup> , Teresópolis <sup>3</sup> (SONP <sup>1</sup> )
<i>Cosmogramma decora</i> Stål, 1859	Itatiaia (INP) <sup>1</sup>
<i>Cosmogramma fulvocincta</i> Stål, 1859	Itatiaia <sup>3</sup>
<i>Cosmogramma wygodzinskyi</i> Bechyně, 1948	Itatiaia <sup>4</sup>
<i>Cryptostetha hieroglyphica</i> Lucas, 1857	Itatiaia <sup>3</sup> (INP <sup>1</sup> )
<i>Cryptostetha notatifrons</i> Stål, 1863	Itatiaia <sup>3</sup>
<i>Deuterocampta achardi</i> Bechyně, 1944	Mendes <sup>4</sup>
<i>Deuterocampta crucnigra</i> Stål, 1859	Angra dos Reis <sup>3</sup>
<i>Deuterocampta fallax</i> Bechyně, 1950	Itaboraí <sup>2</sup> , Rio de Janeiro (Gávea <sup>4</sup> , Tijuca <sup>2</sup> )
<i>Deuterocampta humeralis</i> Bechyně, 1944	Petrópolis (SONP) <sup>3</sup>
<i>Deuterocampta leucomelaena</i> (Perty, 1832)	Itatiaia <sup>3,4</sup> (INP <sup>1</sup> )
<i>Deuterocampta pustulicollis</i> Stål, 1859	Macaé <sup>2,4</sup>
<i>Deuterocampta sedula</i> Stål, 1859 (Fig. 1B)	Teresópolis <sup>2</sup> (SONP <sup>1</sup> )
<i>Deuterocampta semistriata</i> (Fabricius, 1775)	Petrópolis (SONP) <sup>4</sup> , Rio de Janeiro (Rio de Janeiro <sup>4</sup> , Corcovado <sup>3</sup> )
<i>Deuterocampta stauroptera</i> (Wiedmann, 1821)	Rio de Janeiro (Botafogo <sup>4</sup> , Corcovado <sup>3</sup> , Gávea <sup>4</sup> , Rio de Janeiro <sup>3</sup> , Tijuca <sup>4</sup> )
<i>Deuterocampta undulata</i> Bechyně, 1950	Rio de Janeiro <sup>4</sup>
<i>Deuterocampta vitulosa</i> Bechyně, 1944	Rio de Janeiro (Engenho de Dentro <sup>4</sup> )
<i>Dorysterna cruentata</i> (Baly, 1858)	Cambuci (Funil) <sup>3</sup>
<i>Dorysterna dorsosignata</i> (Stål, 1857)	Itatiaia (INP) <sup>1</sup> , Rio de Janeiro (Corcovado <sup>2</sup> , Rio de Janeiro <sup>2</sup> )
<i>Dorysterna riopardensis</i> Bechyně, 1948	Nova Friburgo <sup>2</sup>
<i>Dorysterna salvatori</i> Bechyně, 1948	Teresópolis (SONP) <sup>1</sup>
<i>Elytrosphaera breviscula</i> Stål, 1858	Grande Rio (Baixada fluminense <sup>4</sup> )
<i>Elytrosphaera lahtivirtai</i> Bechyně, 1951	Itatiaia (INP) <sup>1</sup>
<i>Elytrosphaera noverca</i> Stål, 1858	Teresópolis (SONP) <sup>1</sup>
<i>Elytrosphaera xanthopyga</i> Stål, 1858 (Fig. 1C)	Itatiaia <sup>1,3</sup> , Resende <sup>3</sup> , Teresópolis <sup>2,3</sup> (SONP <sup>1</sup> )
<i>Eugonycha bryanti</i> Bechyně, 1946	Rio de Janeiro <sup>4</sup>
<i>Gavirga subaenea</i> Bechyně, 1946	Itatiaia <sup>4</sup>
<i>Grammodesma elongata</i> Bechyně, 1952	Itatiaia (INP) <sup>8</sup>
<i>Grammodesma luridipennis</i> (Baly, 1859)	Itatiaia (INP) <sup>8</sup>
<i>Grammodesma obliqua</i> (Stål, 1859)	Itatiaia <sup>3,4</sup> (PNI) <sup>8</sup>
<i>Grammodesma rubroaenea</i> (Stål, 1859) (Fig. 1D)	Teresópolis (SONP) <sup>1</sup>
<i>Grammodesma stulta</i> (Stål, 1859)	Rio de Janeiro (Corcovado <sup>2</sup> , Rio de Janeiro <sup>4</sup> , Tijuca <sup>2</sup> )
<i>Metastyla insignis</i> Achard, 1923	Rio de Janeiro (Corcovado <sup>2,4</sup> , Rio de Janeiro <sup>3</sup> , Tijuca <sup>2</sup> )
<i>Monocampta crucigera</i> (Sahlberg, 1823)	Angra dos Reis <sup>3</sup> , Itatiaia (Itatiaia <sup>3</sup> , Penedo <sup>3</sup> ), Rio de Janeiro (Alto da Boa Vista <sup>3</sup> , Corcovado <sup>3</sup> , Tijuca <sup>3,4</sup> ), Teresópolis <sup>2</sup> (SONP <sup>1</sup> )
<i>Platyphora acuminata</i> (Olivier, 1790)	Itatiaia <sup>3</sup>
<i>Platyphora angulata</i> Stål, 1858	Rio de Janeiro <sup>5</sup>
<i>Platyphora axillaris</i> (Germar, 1824) (Fig. 1E)	Angra dos Reis <sup>3</sup> , Itatiaia <sup>3</sup> , Nova Friburgo <sup>3</sup> , Rio de Janeiro (Gávea <sup>3</sup> , Tijuca <sup>3</sup> ), Silva Jardim <sup>1</sup> , Teresópolis <sup>2,3</sup> (SONP <sup>1,10</sup> ), Guapimirim (SONP) <sup>1</sup> , Três Rios <sup>3</sup>
<i>Platyphora biforis</i> (Germar, 1824)	Itatiaia <sup>3</sup> , Laje do Muriaé <sup>3</sup> , Rio de Janeiro <sup>2</sup>
<i>Platyphora bigata</i> (Germar, 1824) (Fig. 1F)	Teresópolis <sup>3</sup> (SONP) <sup>1</sup>
<i>Platyphora bullata</i> (Stål, 1858)	Nova Friburgo <sup>2</sup>
<i>Platyphora cincta</i> (Germar, 1821)	Itatiaia <sup>3</sup> , Teresópolis (SONP) <sup>3</sup>
<i>Platyphora congener</i> (Stål, 1858) (Fig. 1G)	Nova Iguaçu (ReBio do Tinguá <sup>3</sup> ), Rio de Janeiro (Tijuca <sup>3</sup> ), Teresópolis (SONP) <sup>1</sup>
<i>Platyphora conviva</i> (Stål, 1858)	Itatiaia <sup>3</sup> (INP <sup>1</sup> )

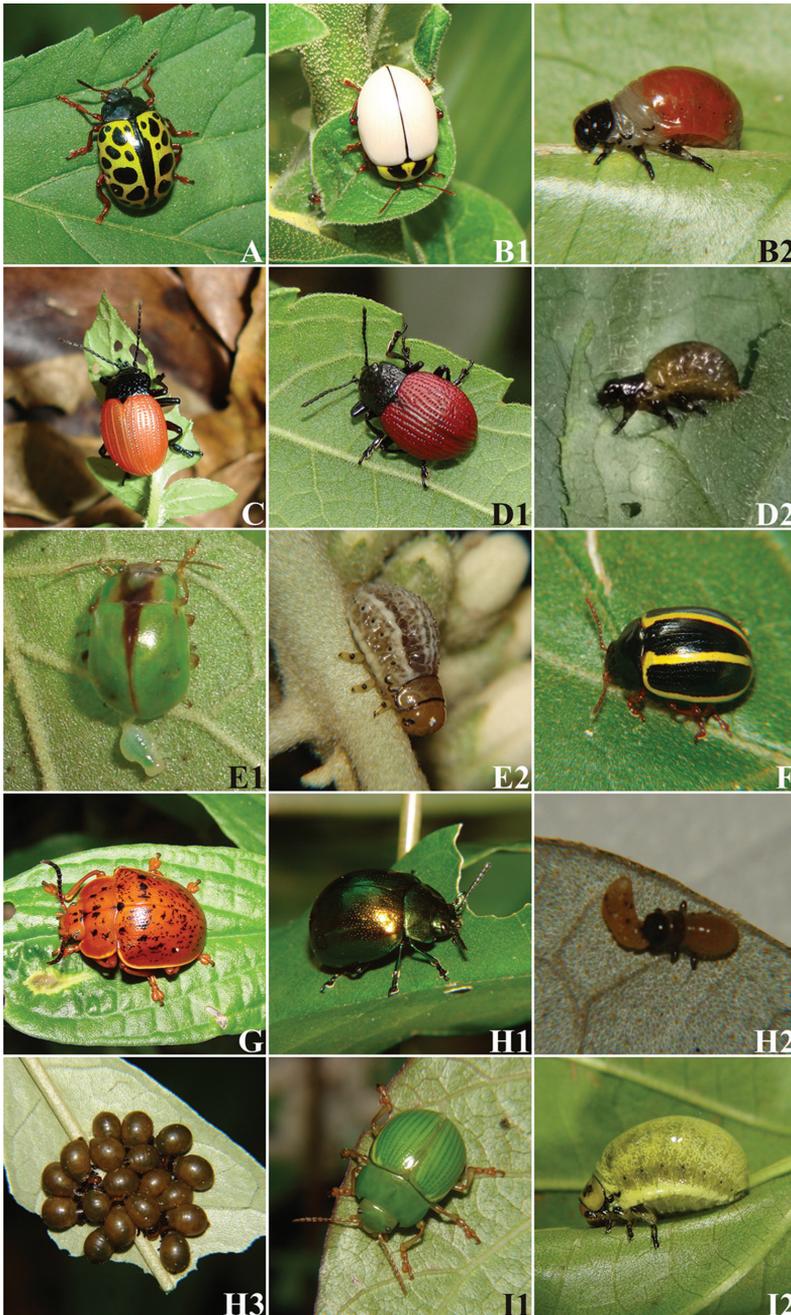
Species	Location
<i>Platyphora curticolis</i> (Stål, 1857) (Fig. 1H)	Teresópolis (SONP) <sup>1</sup>
<i>Platyphora dejeani</i> (Germar, 1824) (Fig. 1I)	Casimiro de Abreu (ReBio União) <sup>1</sup> , Itatiaia <sup>3</sup> , Nova Iguaçu (ReBio do Tinguá) <sup>1</sup> , Petrópolis <sup>1</sup> , Rio de Janeiro (Corcovado <sup>3</sup> , Tijuca <sup>3</sup> ), Teresópolis <sup>2,3</sup> (SONP) <sup>1</sup>
<i>Platyphora difficilis</i> (Stål, 1859) (Fig. 1J)	Teresópolis (SONP) <sup>1</sup>
<i>Platyphora dilatocollis</i> (Stål, 1858)	Cambuci (Funil) <sup>3</sup> , Itatiaia <sup>3</sup> , Teresópolis (SONP) <sup>1</sup>
<i>Platyphora fasciatomaculata</i> (Stål, 1857) (Fig. 1K)	Itatiaia (INP) <sup>1</sup> , Teresópolis (SONP) <sup>1</sup>
<i>Platyphora fervida</i> (Fabricius, 1775) (Fig. 1L)	Itatiaia <sup>3</sup> , Teresópolis <sup>2</sup> (SONP <sup>1,9</sup> )
<i>Platyphora figurata</i> (Germar, 1824)	Angra dos Reis <sup>3</sup> , Rio de Janeiro <sup>3</sup>
<i>Platyphora flavovittata</i> (Stål, 1858) (Fig. 1M)	Itatiaia <sup>3</sup> (INP <sup>1</sup> ), Teresópolis (SONP) <sup>1</sup>
<i>Platyphora fraterna</i> (Stål, 1857) (Fig. 1N)	Teresópolis (SONP) <sup>1</sup>
<i>Platyphora histrio</i> (Olivier, 1807)	Angra dos Reis <sup>3</sup> , Itatiaia <sup>3</sup> , Rio de Janeiro (Rio de Janeiro <sup>2</sup> , Corcovado <sup>3</sup> ),
<i>Platyphora irrorata</i> (Stål, 1857)	Itatiaia <sup>3</sup> , Rio de Janeiro (Corcovado <sup>3</sup> , Rio de Janeiro <sup>3</sup> )
<i>Platyphora itatiayensis</i> (Bechyně, 1950) (Fig. 1O)	Itatiaia <sup>3</sup> , Teresópolis (SONP) <sup>1</sup>
<i>Platyphora jucunda</i> (Stål, 1857) (Fig. 1P)	Itatiaia <sup>3</sup> , Teresópolis (SONP) <sup>1</sup>
<i>Platyphora langsdorfi</i> (Germar, 1824) (Fig. 1Q)	Teresópolis (SONP) <sup>1</sup>
<i>Platyphora pardalina</i> (Stål, 1858)	Itatiaia <sup>3</sup>
<i>Platyphora pastica</i> (Germar, 1824) (Fig. 1R)	Angra dos Reis <sup>3</sup> , Itatiaia <sup>3</sup> , Rio de Janeiro (Alto da Boa Vista <sup>3</sup> ), Teresópolis (SONP) <sup>1</sup>
<i>Platyphora pervicax</i> (Stål, 1859)	Itatiaia <sup>3</sup>
<i>Platyphora princeps</i> Gray, 1832	Itatiaia <sup>3</sup>
<i>Platyphora reticulata</i> (Fabricius, 1787)	Itatiaia <sup>3</sup> , Teresópolis (SONP) <sup>3</sup>
<i>Platyphora semiviridis</i> Jacoby, 1903	Itatiaia <sup>3</sup> , Resende <sup>6</sup>
<i>Platyphora signiceps</i> (Stål, 1857)	Itatiaia <sup>3</sup> , Petrópolis (SONP) <sup>3</sup>
<i>Platyphora</i> sp.	Itatiaia (INP) <sup>1</sup>
<i>Platyphora strigilata</i> (Stål, 1859)	Itatiaia <sup>3</sup> (INP <sup>1</sup> )
<i>Platyphora tessellata</i> (Olivier, 1807)	Teresópolis (SONP) <sup>3</sup>
<i>Platyphora variolaris</i> (Stål, 1859)	Nova Friburgo <sup>2</sup>
<i>Platyphora vidanoi</i> Daccordi, 1993 (Fig. 1S)	Itatiaia <sup>3</sup> (INP <sup>1</sup> ), Teresópolis (SONP) <sup>1</sup>
<i>Platyphora vigintiunopunctata</i> (Chevrolat, 1831)	Itatiaia <sup>3</sup> , Teresópolis (SONP) <sup>2</sup>
<i>Platyphora zikani</i> (Bechyně, 1950) (Fig. 1T)	Teresópolis (SONP) <sup>1</sup>
<i>Platyphora zonata</i> (Germar, 1824) (Fig. 1U)	Macaé (Parque Nacional da Restinga de Jurubatiba) <sup>1</sup> , Itatiaia <sup>3</sup> , Teresópolis (SONP) <sup>1</sup>
<i>Stilodes flavosignata</i> (Stål, 1859)	Nova Friburgo <sup>2</sup> , Rio de Janeiro (Rio de Janeiro <sup>2</sup> , Corcovado <sup>3</sup> ), Teresópolis (SONP) <sup>1</sup>
<i>Stilodes jocosa</i> (Stål, 1859)	Rio de Janeiro (Corcovado <sup>2,4</sup> )
<i>Stilodes nigriventris</i> (Germar, 1824)	Itaguaí <sup>2</sup> , Macaé (Restinga de Jurubatiba) <sup>1</sup> , Rio de Janeiro (Corcovado <sup>2,4</sup> )
<i>Stilodes peltasta</i> (Stål, 1865)	Rio de Janeiro (Corcovado <sup>2</sup> )
<i>Stilodes</i> sp. 1	Teresópolis (SONP) <sup>1,9</sup>
<i>Stilodes</i> sp. 2	Teresópolis (SONP) <sup>1</sup>
<i>Stilodes thetis</i> Stål, 1860 (Fig. 1V)	Itatiaia (INP) <sup>1</sup> , Teresópolis (SONP) <sup>1</sup>
<i>Stilodes trimaculicollis</i> Stål, 1859	Rio de Janeiro (Rio de Janeiro <sup>3</sup> , Corcovado <sup>2</sup> ), Teresópolis (SONP) <sup>1</sup>
<i>Stilodes (Eustilodes) cordata</i> Achard, 1923	Rio de Janeiro <sup>4</sup> , Teresópolis (SONP) <sup>1</sup>
<i>Stilodes (Eustilodes) cornuta</i> (Bechyně, 1947)	Itatiaia <sup>3</sup>
<i>Stilodes (Eustilodes) denticeps</i> (Stål, 1860)	Macaé <sup>4</sup>
<i>Stilodes (Grammomades) impuncticollis</i> (Stål, 1859) (Fig. 1W)	Itatiaia <sup>3</sup> , Laje do Muriaé <sup>3</sup> , Teresópolis <sup>2</sup> (SONP <sup>1,9</sup> )
<i>Stilodes (Iostilodes) bisbilineata</i> Stål, 1859	Itatiaia <sup>3</sup>
<i>Trichomela notaticollis</i> (Stål, 1858)	Itatiaia <sup>3</sup> , Teresópolis (SONP) <sup>3</sup>
<i>Trichomela xantholoma</i> (Stål, 1857) (Fig. 1X)	Teresópolis (SONP) <sup>1</sup>
<i>Zygogramma appendiculata</i> Stål, 1859 (Fig. 1Y)	Teresópolis (SONP) <sup>1</sup>

Species	Location
<i>Zygogramma novemstriata</i> Stål, 1859	Angra dos Reis <sup>3</sup>
<i>Zygogramma (Tritaenia) mendesi</i> Bechyně, 1948	Itatiaia <sup>3,4</sup> , Resende <sup>3</sup>
<i>Zygogramma (Tritaenia) virgata</i> (Stål, 1859)	Rio de Janeiro (Tijuca <sup>2</sup> )
<b>Chrysomelini: Chrysomelina – 5 genera and 8 species</b>	
<i>Lioplacis meridionalis</i> Bechyně, 1948	Itatiaia (INP) <sup>1</sup>
<i>Phaedon confinis</i> Klug, 1829	Angra dos Reis <sup>3</sup> , Itatiaia <sup>3</sup>
<i>Phaedon consimilis</i> Stål, 1860	Rio de Janeiro (Manguinhos <sup>3</sup> )
<i>Phaedon pertinax</i> Stål, 1860	Nova Friburgo <sup>4</sup> , Itatiaia <sup>3</sup> , Resende <sup>3</sup> , Rio de Janeiro (Manguinhos <sup>3</sup> )
<i>Pixis clavigera</i> Stål, 1860	Rio de Janeiro (Corcovado <sup>2</sup> )
<i>Pixis columbina</i> Stål, 1860	Itatiaia <sup>7</sup> , Teresópolis (SONP) <sup>1</sup>
<i>Plagioderma gounelli</i> Achard, 1925	Rio de Janeiro (Corcovado <sup>2</sup> , Tijuca <sup>2</sup> )
<i>Trochalonota badia</i> (Germar, 1824)	Rio de Janeiro (Anil <sup>2</sup> , Corcovado <sup>2</sup> , Tijuca <sup>3</sup> )
<b>Chrysomelini: Entomoscelina – 1 genus and 1 species</b>	
<i>Microtheca ochroloma</i> Stål, 1860	Rio de Janeiro (Deodoro <sup>2</sup> , Rio de Janeiro <sup>2</sup> )

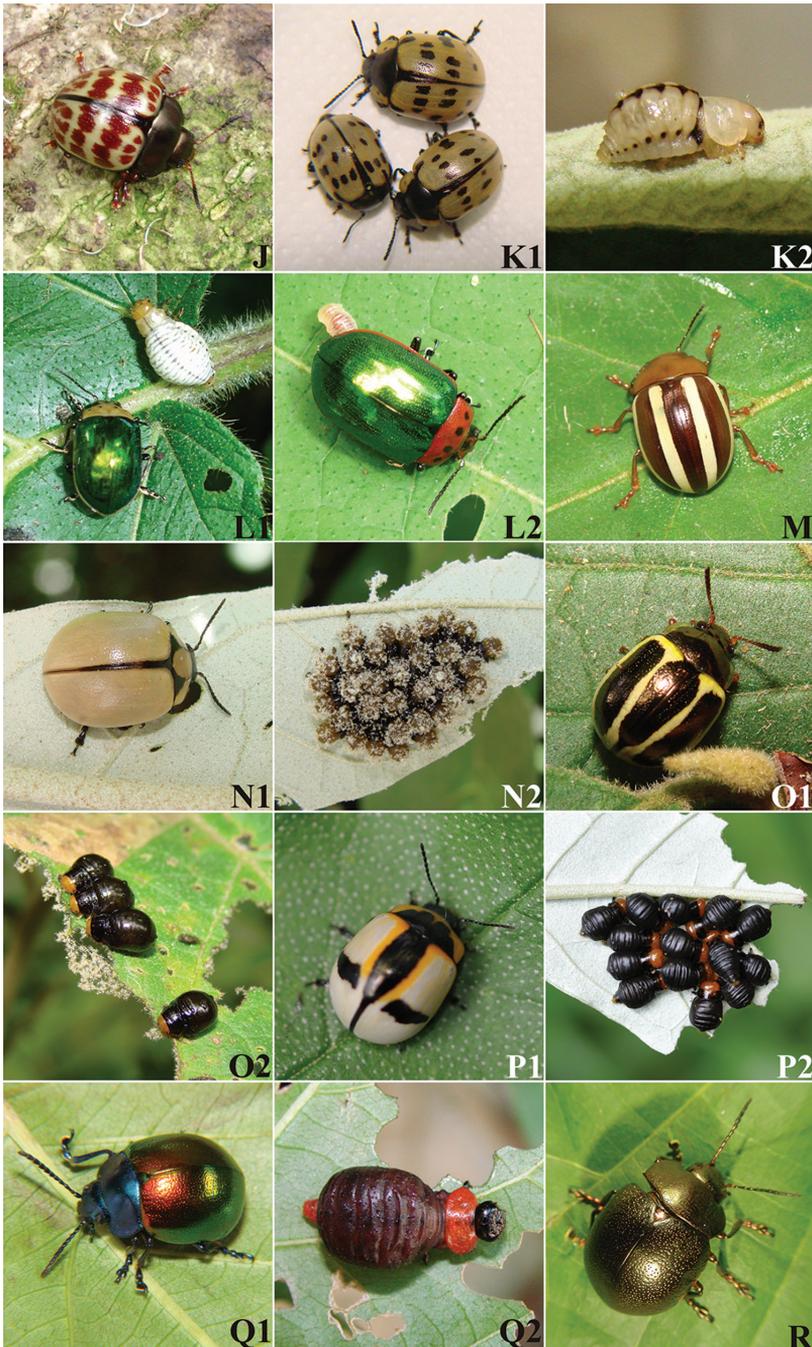
<sup>1</sup> CLEI; <sup>2</sup> MNRJ; <sup>3</sup> CEIOC; <sup>4</sup> MIZA; <sup>5</sup> MPEG; <sup>6</sup> Olckers 1998; <sup>7</sup> Bechyně 1958; <sup>8</sup> Sampaio and Monné 2016; <sup>9</sup> Flinte et al. 2009b; <sup>10</sup> Flinte et al. 2015.

followed by *Stilodes* (7) and *DeuteroCampta* (3), much like the pattern found generally over the state (Table 1). Species showed an enormous variation in color. Adult polymorphism expressed by variation in pronotum color was observed in *P. fervida*, (Fig. 1-L1, L2), while the degree of fusion in stripes on the elytra varied greatly among individuals in *Zygogramma appendiculata* (Fig. 1-Y1). Other species, such as *Platyphora axillaris* (Fig. 1-E1), *P. dejeani* (Fig. 1-I1) and *P. fraterna* (Fig. 1-N1), displayed strikingly similar coloration to the leaves of their host plant, while other species including *P. congener* (Fig. 1G), *Calligrapha polyspila* (Fig. 1A) and *Elytrosphaera xanthopyga* (Fig. 1C) were highly conspicuous to the human eye.

The subfamily in SONP exhibited a clear seasonal pattern (Fig. 2), with more species recorded in the hot rainy season, from October to January, than during the drier and colder months, between June and August. This seasonal pattern is well-established for the family Chrysomelidae in the area, with annual variation in temperature and precipitation and effects on host plant phenology being likely the main drivers of the temporal dynamics in these beetles (Flinte et al. 2009b, 2011, 2015). This is particularly so because many of the records were made at altitudes above 1000 m, where the pattern normally more closely resembles that found in the subtropical zone (e.g. Medeiros and Vasconcellos-Neto 1994, Nogueira-de-Sá et al. 2004). However, the present results are, to our knowledge, the first to examine the seasonal pattern for such a large number of Chrysomelinae species in a single area. Ideally, a standardized collecting effort across the year would better describe the seasonal differences we observe here. However, as we have conducted research in the area over many years, doing the same surveys at least once a month every year, we are confident that this represents the seasonal pattern of chrysomeline species occurrence in the area. Moreover, the Chrysomelinae species which were intensively studied over the year, *Platyphora axillaris* (Flinte et al. 2015), *P. fervida* and *Stilodes (Grammomades) impuncticollis* (Flinte et al. 2009b) exhibited the same low densities during the drier and colder months.



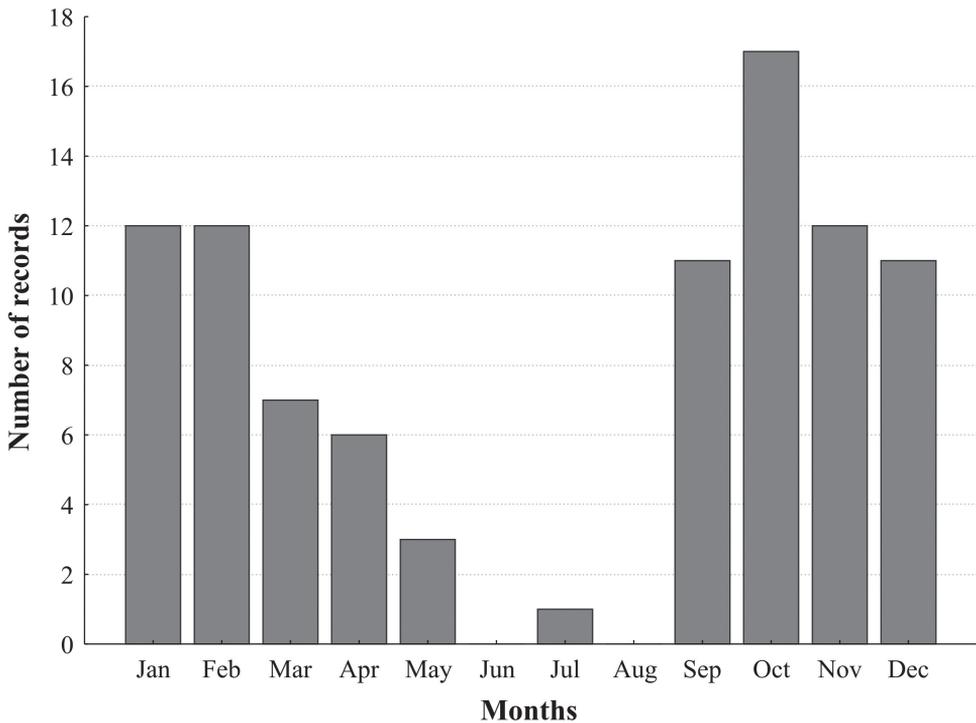
**Figure 1.** Chrysomelinae species in Rio de Janeiro. Some Chrysomelinae species occurring in Serra dos Órgãos National Park, State of Rio de Janeiro, Brazil. *Calligrapha polyspila* (A); *Deuterocampta sedula* adult (B1) and larva (B2); *Elytrosphaera xanthopyga* (C); *Grammodesma rubroaenea* adult (D1) and larva (D2); *Platyphora axillaris* adult (E1) and larva (E2); *Platyphora bigata* (F); *Platyphora congener* (G); *Platyphora curticolis* adult (H1), larval cannibalism (H2) and larval aggregation (H3); *Platyphora dejeani* adult (I1) and larva (I2).



**Figure 1.** Continued. *Calligrapha polyspila* (*Platyphora difficilis*) (J); *Platyphora fasciatomaculata* adult (K1) and larva (K2); *Platyphora fervida* yellow-pronotum adult and larva (L1) and red-pronotum female ovipositing (L2); *Platyphora flavovittata* (M); *Platyphora fraterna* adult (N1) and larval aggregation (N2); *Platyphora itaiayensis* adult (O1) and larvae (O2); *Platyphora jucunda* adult (P1) and larval aggregation (P2); *Platyphora langsdorfi* adult (Q1) and larva (Q2); *Platyphora pastica* (R).



**Figure 1.** Continued. *Platyphora vidanoi* (S); *Platyphora zikani* adult (T1) and young larvae (T2); *Platyphora zonata* (U); *Stilodes thetis* (V); *Stilodes* (*Grammomades*) *impuncticollis* adult (W1), eggs (W2) and larva (W3); *Trichomela xantholoma* (X); *Zygogramma appendiculata* polymorphic adults in copula (Y1), larvae feeding (Y2), larval cycloalexys (Y3), adult aggregation (Y4), egg mass (Y5), larva attacked by hemipteran nymph (Y6).



**Figure 2.** Seasonal distribution of Chrysomelinae. Number of Chrysomelinae species recorded on each month, obtained for 40 species from collections and fieldwork, in Serra dos Órgãos National Park, south-east Brazil.

Host plant and/or biological information were found for almost half of the species ( $n = 16$ ) (Table 2) that we (VF, AA, MVM, RFM) collected in the park ( $n = 35$ ). Solanaceae was the most common host plant family, followed by Convolvulaceae, Asteraceae, Malvaceae and Apocynaceae. As expected, this is a pattern that reflects *Platyphora* preference for Solanaceae (Jolivet and Hawkeswood 1995, Chaboo et al. 2014 and references therein). Intense host plant defoliation was observed in *Stilodes* (*Grammomades*) *impuncticollis* (Fig. 1-W1, W2, W3) on *Capsicum mirabile* (Solanaceae), *Platyphora fraterna* (Fig. 1-N1, N2) on *Solanum swartzianum* (Solanaceae) and *Zygogramma appendiculata* (Fig. 1-Y1, Y2, Y3) on *Callianthe rufinerva* (Malvaceae).

Maternal care was not recorded for any species in this study, although subsocial behavior is known in the subfamily for several species, including some *Doryphora* and *Prosicela* species (Windsor et al. 2013, Chaboo et al. 2014). Other interesting behavioral defenses were recorded, including larval cycloalexy in *Z. appendiculata* (Fig. 1-Y3) and *P. curticolis* (Fig. 1-H3), a defensive behavior of gregarious circular formation at rest (Jolivet et al. 1990, Vanconcellos-Neto and Jolivet 1994, Dury et al. 2014). Additionally, we recorded larvae of *P. fraterna* (Fig. 1-N2) attaching trichomes from *Solanum* host plant leaves to hairs on their backs, a behavior already described in *P. zonata* (Bernardi and Scivittaro 1991), which may contribute to larval camouflage. Larval

**Table 2.** Ecological data on Chrysomelinae species. Species at Serra dos Órgãos National Park with host plant record and/or biological data obtained from our research at the area. Published records are indicated by numbers (see footnote for references).

Species	Host plant family	Host plant species	Reproduction	Larvae
<i>Calligrapha polyspila</i>	Malvaceae <sup>1</sup>	?	oviparous <sup>1</sup>	?
<i>Deuterocampta sedula</i>	?	?	?	solitary
<i>Grammodesma rubroaenea</i>	Asteraceae	?	oviparous	solitary
<i>Platyphora axillaris</i>	Solanaceae <sup>2</sup>	<i>Solanum scuticum</i> <sup>2</sup>	larviparous <sup>2</sup>	solitary
<i>Platyphora curticolis</i>	Solanaceae	<i>Solanum swartzianum</i>	larviparous	aggregated
<i>Platyphora dejeani</i>	Convolvulaceae	<i>Ipomoea philomega</i>	oviparous	solitary
<i>Platyphora fervida</i>	Solanaceae <sup>3</sup>	<i>Solanum thotskyanum</i> <sup>3</sup>	larviparous	solitary
<i>Platyphora flavovittata</i>	Apocynaceae	?	oviparous	?
<i>Platyphora fraterna</i>	Solanaceae	<i>Solanum swartzianum</i>	larviparous	aggregated
<i>Platyphora itatiayensis</i>	Solanaceae	<i>Solanum megalochiton</i>	larviparous	aggregated
<i>Platyphora jucunda</i>	Solanaceae <sup>4</sup>	<i>Solanum swartzianum</i>	larviparous	aggregated
<i>Platyphora langsdorfi</i>	Convolvulaceae <sup>5</sup>	<i>Ipomoea philomega</i>	oviparous	solitary
<i>Platyphora zikani</i>	Solanaceae	<i>Solanum swartzianum</i>	larviparous	aggregated
<i>Stilodes (Grammomades) impuncticolis</i>	Solanaceae <sup>3</sup>	<i>Capsicum mirabile</i> <sup>3</sup>	oviparous	solitary
<i>Stilodes</i> sp. 1	Asteraceae	<i>Baccharis stylosa</i>	?	?
<i>Zygotogramma appendiculata</i>	Malvaceae	<i>Callianthe regnelli</i> , <i>Callianthe rufinerva</i>	oviparous	aggregated

<sup>1</sup> Grissell et al. 1987; <sup>2</sup> Flinte et al. 2015; <sup>3</sup> Flinte et al. 2009b; <sup>4</sup> Olckers 2000; <sup>5</sup> Jolivet and Hawkeswood 1995.

aggregations were observed in many species (Table 2), but also for adults of *Z. appendiculata* on young folded leaves in the field (Fig. 1-Y4). Larval gregarious behavior may serve to reduce individual risk against small invertebrate parasitoids and predators, and promote defense against larger predators through the cumulative effect of individuals' toxins (Grégoire 1988). Thanatosis ("feigning death") was observed in adults of *P. axillaris* (Fig. 1-E1), *P. fervida* (Fig. 1-L1, L2), and *P. fraterna* (Fig. 1-N1), and both in adults and larvae of *Stilodes (Grammomades) impuncticolis* (Fig. 1-W1, W3).

Seven oviparous and seven larviparous species were found, most being new records of reproductive biology (Table 2). Chrysomelinae is the subfamily of leaf beetles with the most diversity in reproductive biology, containing oviparous, ovoviviparous and viviparous species (Bontems 1988), sometimes in the same genus, and also different levels of social behavior (Chaboo et al. 2014). The last two types of development may be more costly to the mothers, but ensure a quicker development of the vulnerable larval stage, among other advantages, as proposed by Jolivet and Hawkeswood (1995) and Chaboo et al. (2014 and references therein), which is why it is sometimes considered to be a parental care preceding birth (Hinton 1981). Interestingly, viviparous species may result in solitary larvae, as in *P. axillaris* (Fig. 1-E2), or larval aggregations, as in *P. jucunda* (Fig. 1-P2). Oviparous species may also have solitary or gregarious larvae, as in *P. dejeani* (Fig. 1-I2) and *Z. appendiculata* (Fig. 1-Y2), respectively, although larval aggregations seem rarer in this type of reproduction. In their work on subsocial

neotropical Doryphorini, Windsor et al. (2013) found, among *Platyphora* species, two with solitary larvae and nine which formed larval aggregations, but all eleven species were larviparous. We observed a single case of larval cannibalism in the viviparous *P. curticolis* during laboratory rearing (Fig. 1-H2), a behavior already described for some Chrysomelinae genera (Wade 1994, Mafra-Neto and Jolivet 1996, Windsor et al. 2013) that grants nutritional benefits.

Except for the eggs of *Z. appendiculata*, which are laid in masses on the underside of its host plant leaves (Fig. 1-Y5), no other eggs of oviparous Chrysomelinae were found in the field. This is probably because chrysomelids often lay their eggs in the soil or in secluded parts of plants (Selman 1994). All oviparous species reared in laboratory laid chorion-covered yellowish eggs on the bottom of the vials or on leaves, normally grouped in clutches (Fig. 1-W2). In the field, the number of eggs of *Z. appendiculata* varied from 80 to 100 per group ( $90.4 \pm 8.3$  SD;  $n=7$  egg masses), and larval aggregations comprised between 10 and 233 individuals per group ( $49.2 \pm 38.7$ ;  $n=50$  groups). Larvae of different egg masses may cohabit the same aggregation of this species, since differently sized larvae were observed in the same aggregation. *Platyphora fraterna* larvae (Fig. 1-N2) were grouped in aggregations of  $24.9 \pm 13.1$  SD individuals ( $n=14$  groups), with a minimum of seven and maximum of 44 larvae per group. No pupa has yet been found in the field, but in the laboratory, prepupae always buried themselves in earth layer at the bottom of the vials. While pupation in Chrysomelinae may be arboreal or underground (Taki-zawa 1976), it seems that underground pupation is most common in our taxa as indicated by laboratory rearing.

Only a few observations on natural enemies of Chrysomelinae were made. Phoretic wasps of Pteromalidae (Hymenoptera) were found on adults of *Grammodesma rubroaenea* (Fig. 1-D1) and *Deuterocampta sedula* (Fig. 1-B1). Pteromalidae are well known parasitoids of chrysomeline larvae (Cox 1994). On one occasion, a *Podisus* (Hemiptera) nymph was seen preying on a larva of *Z. appendiculata* (Fig. 1-Y6). Many chrysomeline species presented unprotected larvae without any apparent behavioral defense, but several gain chemical defenses by the sequestration of host plants toxins or by synthesizing defensive compounds from plant precursors, especially in *Platyphora* (Pasteels et al. 2001, Termonia et al. 2002).

## Conclusions

The high proportion of new host, biological data and occurrence records in Rio de Janeiro reflects the limited knowledge we have about this subfamily in this immediate area. In Brazil, the picture is not very different, as no inventory for the subfamily has been compiled and the relatively few published records come from ecological studies such as Medeiros and Vasconcellos-Neto (1994), Medeiros et al. (1996), Macedo et al. (1998), Vasconcellos-Neto and Jolivet (1998), and Flinte et al. (2009b, 2015). However, Chrysomelinae is known to be very species-rich in Brazil, including known en-

dem species, such as *Elythrosphaera lahtivirtai* (Macedo et al. 1998). Because of their high host specificity (Jolivet 1988, Jolivet and Hawkeswood 1995) and low dispersal ability (Freijeiro and Baselga 2016) the chrysomelinae are expected to have many narrowly distributed species, especially in mountainous areas, as has already been found for other tropical Chrysomelidae species (García-Robledo et al. 2016, Macedo et al. 2016). These traits then would make these Brazil species especially vulnerable to extinction as the mountains within the Atlantic forest biome are largely degraded and threatened (Martinelli 2007).

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# Recent advances in the knowledge of Mexican Alticinae (Coleoptera, Chrysomelidae)<sup>1</sup>

David G. Furth<sup>1</sup>

<sup>1</sup> Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, USA

Corresponding author: David G. Furth ([furthd@si.edu](mailto:furthd@si.edu))

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## Abstract

The present study updates previously published biodiversity/faunistics of the flea beetles of Mexico published by the author after examination of 6132 specimens from 8 institutional collections. The following 9 genera were selected as indicators of the effects of known diversity only through examination of museum specimens (i.e., “indoor collecting”): *Alagoasa* Bechyné; *Asphaera* Chevrolat; *Capraita* Bechyné; *Disonycha* Chevrolat; *Kuschelina* Bechyné; *Omophoita* Chevrolat; *Prasona* Baly; *Systema* Chevrolat; and *Walterianella* Bechyné. From the specimens examined in these genera from the 8 collections, there were 394 new records for Mexican states of the 287 new species records representing 47% new records of the species recorded from those states. Total new state records 287 from 80 species. States with most new records: Chiapas (32); Nayarit (27); Sinaloa (24). 80 spp. (47%) with new state records. *Systema oberthuri* Baly is reported from Mexico for the first time. The current total of Alticinae in Mexico is 90 genera/626 species. The difficulties of the generic boundaries between *Systema* and *Prasona*, *Alagoasa* and *Kuschelina*; as well as the specific boundaries between *A. jacobiana* and *A. decemguttatus* and the specific level pattern variation in *Disonycha glabrata* and *Alagoasa decemguttatus* are discussed. *Kuschelina semipurpurea*, formerly placed in *Alagoasa*, is placed is considered as a new combination.

## Keywords

Mexico state records, Flea Beetles, indoor collecting, faunistics, new combinations, *Systema/Prasona* and *Alagoasa/Kuschelina* confusion, *Alagoasa decemguttatus*, *Omophoita octomaculata*, Mexican biodiversity

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## Introduction

For about 30 years I have been studying the biodiversity/faunistics of the Central American Alticinae (Furth and Savini 1996, 1998, Furth et al. 2003), especially the Mexican Alticinae (Furth 2004, 2006, 2009, 2013). The current project is a continuation of research about the biodiversity/faunistics, distribution, and biogeography of the Alticinae (Flea Beetles) of Mexico. The author has conducted extensive field work in the majority of the 32 Mexican states as well as examination and determination of thousands of Mexican specimens from many museums in North America. Two previous published surveys by the author were of individual selected states. The first one from Chihuahua and Sonora (Furth 2009) revealed 26 genera with 70 species from Chihuahua, including 44 species new to Chihuahua, 9 species new to Sonora, 10 species new to Mexico, and two species new to science. The second from Oaxaca (Furth 2013) discovered 68 genera with 275 species (113 species known only from Oaxaca) in that state alone elevating the total recorded Alticinae fauna of Mexico to 90 genera and 625 species. This Oaxaca study demonstrated a very strong biogeographic affinity to the Neotropical Region. Some of the species in this Oaxaca study were at the time unidentifiable morpho-species and some either far from their known distribution or even new to science. The last comprehensive list of the entire Mexican Alticinae fauna was over 10 years ago and a lot of new specimen data has become accessible. There are still many more specimens in the remaining Alticinae genera currently being studied by the author from the institutions mentioned in the current study as well as others in a few other North American and Mexican institutions. Some details of the Mexican Alticinae fauna as well as about Mexican biogeography were included in Furth (2006) which recorded 89 genera and 524 species of Alticinae in Mexico.

Some of the author's recent publications (mentioned above) concerning the Mexican fauna stressed the value of a combination of strategies for biodiversity research beginning with a comprehensive search of the literature examination, combined with fieldwork and extensive search of institutional collections. The current study concentrates on the latter of these strategies to uncover additional specimens and localities in order to better understand Mexican flea beetle diversity.

## Methods

During the past 10+ years the author has visited the institutions listed below and has pulled out all Alticinae from Mexico and borrowed them. For the current study nine genera, including the genera of the “Oedionychini/a” tribe/subtribe (*Alagoasa*, *Asphaera*, *Capraita*, *Kuschelina*, *Omophoita*, *Walterianella*), as well as a few other randomly selected genera (*Disonycha*, *Prasona*, *Systema*) were studied and determined to species. There were 6625 adult specimens studied and determined to species based on morphology and using literature and reference collections. The term species refers also to all taxa, including subspecies recorded from Mexico.

The institutional collections studied are: American Museum of Natural History (New York, New York, USA) [AMNH]; Monte L. Bean Museum of Brigham Young University (Provo, Utah, USA) [BYU]; Natural History Museum (London, United Kingdom) [NHM]; California Academy of Sciences (San Francisco, California, USA) [CAS]; California Department of Food and Agriculture, Sacramento, California, USA [CDFA]; University of California Berkeley (Berkeley, California, USA) [UCB]; University of California Davis, Davis, California, USA [UCD]; U.S. National Museum/NMNH (Washington, D.C., USA) [USNM]; and a few specimens donated to the author by R. Wills Flowers (Florida State University, Tallahassee, Florida, USA) [RWF]. Specimens were studied and determined using a Leica MZ-APO dissecting stereomicroscope, as well as specimen reference collections at the U. S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. USA [USNM/NMNH], relevant literature in the author's library and certain online references, e.g., MCZ Type Database.

The habitus photographic images were taken using the Visionary Digital BK Lab Imaging system outfitted with the Canon EOS 5D and a MP-E 65 mm 1–5× Canon macrolens. Stacked images were processed in part with Helicon Focus; final editing was done with Adobe PhotoShop. Specimens will be returned to their original institutional collections with some vouchers deposited at the USNM.

Images of adult species for Figures 4–6, 8–9 were taken randomly from the Internet by searching for the species name. Figures 1–3 were taken by the author; Figure 7 was taken by K. Darrow.

In Table 2 (totaled in Table 1) there are some new state records from multiple institutional collections, but each new state record is only counted once (e.g., for *Alagoasa acutangula* Nayarit is a new state record and was recorded from AMNH, CAS, CDF A, and UCB, but it is only counted as a single state record). The taxa in Table 2 are referred to in the text as species, but a few are subspecies names.

The author follows a less popular classification, i. e., Alticinae rather than Alticini, as explained in several publications, e.g., Furth and Lee (2000), Furth and Suzuki (1998), Mohamedsaid and Furth (2011).

**Table 1.** Indoor Collecting. Numbers of specimens examined, by institutional collection. For Specimens Examined, the number in parentheses are those not determined to species.

Collection	Specimens Examined	New State Records/Collection
AMNH	374 (9)	30
NHM	120 (14)	1
BYU	309 (33)	29
CAS	1412 (93)	105
CDF A	374 (20)	27
UCB	3131 (223)	150
UCD	846 (97)	46
USNM	59 (4)	6
TOTALS	6625 (493)	394/287*

\*Repeats/Actual

**Table 2.** List of determined species by institution with state records (new state records in bold print).

Genus	Species	Author	Distribution	AMINH	BMINH	BYU	CAS	CDEFA	NHIM	UCB	UCD	RWF	USNM	New Records	No. New Records
	<i>acutangula</i>	(Jacoby)	CHIS, COL, DGO, GRO, JAL, MEX, MOR, NL, OAX, VER	NAY		GRO, JAL,	CHIS, GRO, MOR, NAY, SIN, SLP	JAL, MICH, NAY	VER	CHIS, DGO, GRO, JAL, MICH, MOR, NAY, NL, PUE, SIN, VER	GRO, MOR, PUE, SIN		GRO, QRO	MICH, NAY, PUE, QRO, SIN, SLP	6
	<i>bipunctata</i>	(Chevrolat)	CHIS, DF, OAX, SLP, VER, YUC	CHIS, SLP, QRO, TAMPS, VER, YUC		PUE, SLP	VER		MOR, VER	CHIS, QRO, SLP, VER	SLP			MOR, PUE, QRO, TAMPS	5
	<i>chevrolati</i>	(Baly)	OAX, VER, YUC				VER		VER						
	<i>elypata</i>	(Jacoby)	CHIS, DGO, FGO, MICH, OAX, TAB, VER			VER		CHIS, VER	VER	CHIS, DGO, OAX, VER	CHIS, VER			DGO	1
	<i>donckieri</i>	(Jacoby)	GRO					PUE						PUE	1
	<i>extrema</i>	(Harold)	MOR, OAX, TAB, VER	CHIS, VER			CHIS		VER	VER	VER		YUC	CHIS, YUC	2
	<i>fimbriata</i>	(Forster)	GRO, MICH, MOR, OAX				MICH								
	<i>hoegeri</i>	(Jacoby)	OAX, VER				VER								
	<i>inconspicua</i>	(Jacoby)	DGO, JAL	JAL		JAL	SIN			DGO, JAL, SIN				SIN	1
	<i>jaobiana</i> * [comb. n.]	(Horn)		CHIH, CHIS, DGO, JAL, MOR, NAY, OAX, SON, SIN, YUC		GRO, SON	CHIS, MOR, NAY, SIN, SON	COL, JAL, NAY, SIN	MEX	CHIH, CHIS, DGO, GRO, JAL, NAY, OAX, SIN, SON	CHIH, JAL, MOR, SIN			SIN, YUC	2
	<i>lateralis</i>	(Jacoby)	COL, GRO, JAL, MEX, MICH, MOR, NAY, OAX	NAY		PUE	CHIH, COL, MOR, NAY, NL, SIN, VER	COL, JAL, NAY, SIN	VER	GRO, MOR, NAY, SIN, VER	CHIS, MOR			CHIH, CHIS, COL, NL, SIN, VER	6
	<i>longicollis</i>	(Jacoby)	OAX				VER							VER	1
	<i>semipurpurea</i> **	(Jacoby)	VER											CHIH	1
	<i>seriata</i>	(Baly)	GRO, MOR, OAX, PUE, VER	MOR			MOR, SLP, TAMPS, VER			CHIS, GRO				CHIS, SLP, TAMPS	3

*Alagausa*



Genus	Species	Author	Distribution	AMNH	BMINH	BYU	CAS	CDEA	NHM	UCB	UCD	RWF	USNM	New Records	No. New Records	
<i>Diomphya</i>	<i>antennata</i>	Jacoby	COL, DGO, GRO, JAL, MEX, MICH, MOR, OAX, VER		MEX		MICH, MOR, NAV, SIN, VER	SIN		CHIS, GRO, JAL, MICH, NAV, OAX, SIN, VER	CHIH, MICH, SIN, VER			CHIH, CHIS, NAV, SIN	4	
	<i>arizonae</i>	Casey	CHIH, DGO?, GRO, MOR							CHIH, COAH, NL, SON	CHIH, NL			COAH, NL, SON	3	
	<i>barberi</i>	Blake	GRO, SIN, VER				SIN	MICH		NAV, VER	SIN			MICH, NAV	2	
	<i>brevilineata</i>	Jacoby	DGO, GRO, JAL, MOR, OAX		MEX		CHIS, MOR	JAL		CHIS, JAL, NAV				CHIS, MEX, NAV	3	
	<i>brunneofasciata</i>	Jacoby	GRO, PUE, SLP							OAX, SIN				OAX, SIN	2	
	<i>collata</i>	(Fabricius)	CHIH, COAH, DE, DGO, GTO, JAL, MEX, MICH, MOR, OAX, PUE, TAB, VER, YUC				DGO, JAL, MEX, MOR, NAV, PUE, SIN, SON	SIN, VER		DE, JAL, NAV, SIN	NAV, SIN			NAV, SIN, SON	3	
	<i>dorsata</i>	Harold	MOR, OAX, TAB, VER, YUC			VER	CHIS, JAL, MOR, NAV, VER	JAL		CHIS, NAV, OAX, SLP, VER				CHIS, JAL, MOR, NAV, SLP	5	
	<i>figurata</i>	Jacoby	AGS, CHIH, CHIS, COAH, COL, DE, DGO, GRO, GTO, JAL, MEX, MICH, MOR, NAV, OAX, SIN, TAB, VER, YUC	CHIH	MEX	CHIH, JAL, SON	CHIH, MOR, NAV, SIN	JAL, MOR, SIN		CHIH, CHIS, COL, DE, DGO, GRO, GTO, JAL, MICH, NAV, OAX, SIN, SON, TAMP, VER	CHIH, CHIS, JAL, MICH, NAV, SIN, ZAC				SON, TAMP, ZAC	3
	<i>fimata</i>	LeConte	BC, CHIH, CHIS, DGO, GRO, HGO, JAL, MEX, MICH, MOR, NL, OAX, PUE, SLP, SON, TAB, VER, ZAC	COL, TAB	MEX	JAL, MEX	CHIS, GRO, NAV, PUE, SIN, SON, ZAC	JAL, MOR, SIN		BCS, CHIS, COL, DGO, GRO, JAL, MICH, NAV, NL, PUE, SIN, SON, VER	CHIH, JAL			BCS, COL, NAV, SIN	4	
	<i>glabrata</i>	(Fabricius)	BC, BCS, CAMP, CHIS, COL, DGO, GRO, JAL, MOR, NAV, OAX, PUE, SIN, SON, TAB, TAMP, YUC, VER	COL, TAB	JAL, MOR	SON	BCS, CHIH, CHIS, JAL, MEX, MOR, NAV, NL, SIN, SON, TAMP, VER	COL, JAL, NAV, SIN, SON		CAMP, CHIH, CHIS, COL, GRO, GTO, JAL, MICH, MOR, NAV, NL, OAX, QROO, SIN, SON, TAB, VER, YUC	GRO, JAL, MOR, NAV, SIN, SLP, SON, VER			CHIH, GTO, MEX, MICH, NL, QROO, SLP	7	
<i>guatemalensis</i>	Jacoby	CHIS, GRO, MOR, OAX, VER				CHIS			CHIS, GRO, JAL, TAB, VER	MOR, TAMP			JAL, TAB, TAMP	3		
<i>jalopensis</i>	Blake	VER				CHIS			CHIS, COL, SIN	VER			CHIS, COL, SIN	3		

Genus	Species	Author	Distribution	AMNH	BMINH	BYU	CAS	CDEA	NHM	UCB	UCD	RWF	USNM	New Records	No. New Records
	<i>knabi</i>	Blake	GRO							OAX, VER				OAX, VER CHIH, CHIS,	2
	<i>leptolineata texana</i>	Schaeffer	DGO, GRO, JAL, MOR, NL, OAX, QROO, TAMPS, YUC		MEX		NAY, SON			CHIH, CHIS, COL, MICH, OAX, VER	CHIS, MOR			COL, MEX, MICH, NAY, OAX, SON, VER	9
	<i>limbata</i>	Jacoby	DGO, MEX, MOR							DGO					
	<i>maculipes</i>	Jacoby	CHIS, VER	SON			BCS, DGO, SON	COAH		CHIS, TAMPS				BCS, COAH, DGO, SON, TAMPS	5
	<i>melanocephala</i>	Jacoby	VER				CHIS			CHIS, VER				CHIS	1
	<i>mexicana</i>	Jacoby	TAB, SLP, VER, YUC			TAMPS	VER			BC, CHIS, DGO, NAY, OAX, PUE, SON, TAB, VER				BC, CHIS, DGO, NAY, OAX, PUE, SON, TAMPS	8
	<i>militaris</i>	Jacoby	TAB, VER, YUC			CHIS	CHIS			CHIS				CHIS	1
	<i>nigrita</i>	Jacoby	OAX (Furth, 2013)					COL, NAY		NAY				COL, NAY	2
	<i>pluriligata</i>	LeComte	BC, CHIH, DGO, JAL, NAY, SIN, SLP, SON, VER		JAL	CHIH, JAL, SLP, SON	CHIS, JAL, NAY, SLP, SON, TAMPS, VER			CHIS, DGO, OAX, VER	CAMP, CHIH, DGO, MEX, MICH, SON			CAMP, CHIS, MEX, MICH, OAX, SIN, TAMPS	6
	<i>politula</i>	Horn	AGS, CAMP, CHIH, DF, DGO, GRO, GTO, HGO, JAL, MEX, MOR, OAX, PUE, QRO, SLP, SON, TAMPS, VER, ZAC	VER	DGO	CHIH	AGS, CHIS, DGO, JAL, NAY, SON			AGS, CHIH, DGO, GRO, GTO, HGO, JAL, MICH, NAY, NL, PUE, SLP, SON, ZAC	CHIH, DGO, HGO, JAL, PUE, ZAC			CHIS, MICH, NAY, NL	4
	<i>proena</i>	Casey	NAY	NAY			NAY								

*Disonycha*

Genus	Species	Author	Distribution	AMNH	BMINH	BYU	CAS	CDEA	NHM	UCB	UCD	RWF	USNM	New Records	No. New Records
	<i>quinquevittata</i>	(Larrelle)	CHIS, COL, GRO, OAX, QROO, TAB, TAMPS, VER					JAL		VER				JAL	1
	<i>reticulolis</i>	(Jacoby)	NAY, VER				VER				VER				
	<i>sallei</i>	(Baly)	VER												
<i>Disonycha</i>	<i>scriptipennis</i>	(Jacoby)	CHIS, COL, DGO, GRO, MOR, NAY, OAX, YUC				CHIS, NAY			CHIS, JAL, MICH, SIN	GRO, JAL, NAY			JAL, MICH, SIN	3
	<i>subaenea</i>	Jacoby	DGO, GRO, MOR, OAX							JAL				JAL	1
	<i>tenicornis</i>	Horn	CHIH, DGO, HGO				CHIS, SIN	HGO, JAL, SIN		CHIH, DGO, HGO, NL, SIN				CHIS, JAL, NL, SIN	4
	<i>trifasciata</i>	Jacoby	CHIS				CHIS			CHIS					
	<i>laeta</i>	(Perbosc)	TAMPS, VER	COL, NAY		CHIH	BC, MOR, NAY, NL, VER			BCS, DGO, GTO, JAL, NAY, SIN, SON				BC, BCS, CHIH, COL, DGO, GTO, JAL, MOR, NAY, NL, SIN, SON	12
	<i>modesta</i>	(Jacoby)	CHIH, CHIS, DE, DGO, GRO, GTO, HGO, MEX, MOR, OAX, PUE, SLP, TLAX, VER			CHIH	PUE			MEX	CHIH				
	<i>semipurpurea</i> ***	(Jacoby)		CHIH										CHIH	1
	<i>aequinoctialis</i>	(Linnaeus)	Mexico						TAB	TAB, VER				TAB, VER	2
	<i>aequinoctialis affinis</i> ?	(Jacoby)	Mexico ?							CHIS				CHIS	1
<i>Omophoita</i>	<i>cinetipennis</i>	(Chevrolat)	JAL, OAX, PUE, SLP, VER	SLP, VER			NL, SLP			PUE, SLP, VER	VER			NL	1
	<i>ocymaculata</i> **** Crotch (= some <i>aequinoctialis</i> & <i>punctulata</i> Bechyne & Bechyne)	(Crotch)	OAX, TAB, TAMPS, VER	CHIS, NAY, SLP, TAB, TAMPS, VER, YUC		NL, SLP, TAMPS	CHIS, MEX, NL, SLP, VER	VER	CHIS, TAB, VER	CAMP, CHIS, COAH, OAX, SLP, VER	SLP, TAMPS, VER			CAMP, CHIS, COAH, MEX, NAY, NL, SLP, YUC	8
	<i>quadrinotata centraliamericana</i>	Bechyne	OAX, TAB, VER	TAB, VER			CHIS, MEX, VER		TAB, VER	CHIS, TAB, VER	VER	VER		CHIS, MEX	2

Genus	Species	Author	Distribution	AMNH	BMINH	BYU	CAS	CDEA	NHM	UCB	UCD	RWF	USNM	New Records	No. New Records
	<i>recticollis</i>	(Baly)	CHIS, HGO, OAX, TAB, TAMPS, VER				VER			CHIS, VER					
	<i>violacea</i>	Jacoby	GRO	NAY			NAY			CHIS, JAL, MICH, NAY, SON	SIN			CHIS, JAL, MICH, NAY, SIN, SON	6
<i>Prasoma</i>	<i>viridis</i>	Baly	VER			PUE	VER	JAL?		PUE, VER				JAL?, PUE	2
	<i>abbreviata</i>	Jacoby	PUE			MOR	PUE, VER			PUE				MOR, VER	2
	<i>bitaeniata</i>	LeConte	CHIH			CHIH	BC				VER			BC, VER	2
	<i>blanda</i>	Melsheimer	BC?, CHIH, JAL, MICH, NL, SIN, SLP?, SON, TAB, VER			CHIH, JAL	NAY, NL, PUE, SLP, SON			CHIS, JAL, MOR, NAY, SIN, SLP	CHIH, COAH, JAL, SIN, SON			CHIS, COAH, MOR, NAY, PUE, SLP	6
<i>Systema</i>	<i>contigua</i>	Jacoby	CHIS, GRO, GTO, HGO, OAX, SON?, TAMPS, VER?, ZAC			CHIS, HGO, SLP	CHIS, VER	JAL		NAY, NL, PUE, QRO, SIN, SON, VER				JAL, NAY, NL, PUE, QRO, SIN, SLP, SON, VER	9
	<i>discicollis</i>	Clark	CAMP, CHIH, DE, DGO, GTO, JAL, MEX, MICH, TAB, TAMPS, VER?, ZAC	MICH		DGO	DE, JAL			DGO, HGO, MEX, MICH	JAL, MICH, ZAC			HGO	1

Genus	Species	Author	Distribution	AMNH	BMINH	BYU	CAS	CDEA	NHM	UCB	UCD	RWF	USNM	New Records	No. New Records
	<i>gracilentata</i>	Blake	NL	CHIH		CHIH, CHIS, SLP, SON, TAMPS	MOR, SLP, TAMPS, VER, ZAC	CHIS		CHIH, GRO, PUE, SIN, SLP, VER	CHIH, HGO, SLP, VER		QROO, ZAC	CHIH, GRO, HGO, MOR, PUE, QROO, SIN, SLP, SON, TAMPS, VER, ZAC	13
	<i>lucis</i>	Blake					BC							BC	1
	<i>marginata</i>	Jacoby	PUE, VER				CHIS							CHIS	1
	<i>nigropilgata</i>	Jacoby	AGS, CHIH, DE, DGO, GTO, GRO, JAL, MICH, MOR, OAX, PUE, VER			CHIH, CHIS, GRO, JAL, MOR, OAX, SLP, SON, VER	MOR, PUE, SIN, TAMPS, VER			DGO, GRO, GTO, JAL, MICH, MOR, PUE, SIN	CHIH, JAL, MOR, SIN			CHIS, SIN, SLP, SON, TAMPS	5
	<i>oberthuri</i>	Baly					CHIS							CHIS	1
	<i>pectoralis</i>	Clark	CHIS, GTO, OAX, VER				VER			CHIS, PUE, VER	GRO			GRO, PUE	2
	<i>s-litena</i>	(Linnaeus)	CHIS, GTO, TAB, VER			VER	VER	VER		CHIS, TAB, VER	VER				
	<i>sabini</i>	Jacoby	CHIS				CHIS				CHIS				
	<i>semitittata</i>	Jacoby	BCS, GRO, GTO, HGO, MEX, MOR, NL, OAX, SIN	CHIH		CHIH, SON	PUE	MOR		CHIH, CHIS, NAV, SON	CHIH, CHIS, JAL, NAV, PUE, SON, ZAC			CHIH, CHIS, JAL, NAV, PUE, SON, ZAC	7
	<i>subcostata</i>	Jacoby	MICH, MOR, VER				GRO	MICH		GRO, JAL, NAV, VER	MICH			GRO, JAL, NAV	3
	<i>subrigosa</i>	Jacoby	GTO, MICH, MOR				TAB	GRO		GRO, PUE	ZAC			GRO, PUE, TAB, ZAC	4
	<i>sulphurea</i>	Jacoby	CHIH, DGO, GRO, MOR, OAX							CHIH, CHIS, PUE, SON	GRO, MOR, PUE			CHIS, PUE, SON	3

*Systema*

Genus	Species	Author	Distribution	AMNH	BMINH	BYU	CAS	CDEA	NHM	UCB	UCD	RWF	USNM	New Records	No. New Records
<i>Systema</i>	<i>thoracica</i>	Jacoby	CAMP, HGO, PUE, QROO, TAB, VER	CHIS, MEX, VER			JAL, NAY, SLP, VER			CHIS, JAL, NAY, SIN, TAB, VER	JAL, VER			CHIS, JAL, MEX, NAY, SIN, SLP	6
	<i>undulata</i>	Jacoby	AGS, CAMP, GRO, GTO, MOR, VER			MOR	MEX			GRO, MICH				GRO, MEX, MICH, MOR	4
	<i>variabilis</i>	Jacoby	CHIH, CHIS, COL, DGO, GRO, GTO, MICH, MOR, NAY, OAX, VER			GRO, MOR, PUE, SLP, TAMPS, VER	CHIH, JAL, MOR, NAY, SIN, VER	JAL, SIN		CHIH, JAL, MICH, MOR, NAY, QRO, SIN, VER	CHIH, MICH, SIN, VER			JAL, PUE, QRO, SIN, SLP, TAMPS	6
	<i>biarvata</i>	(Chevrolat)	CHIS, VER				NAY, VER		VER	VER				NAY	1
<i>Waterianella</i>	<i>dwangoensis</i>	(Jacoby)	CHIH, DGO			SON	NAY, SON			DGO, JAL	CHIH, SIN		DGO	JAL, NAY, SIN, SON	4
	<i>inscripta</i>	(Jacoby)	OAX, SLP, VER			SLP	CHIS	VER		CHIS, VER				CHIS	1
	<i>oculata?</i>	(Fabricius)	VER				VER			VER					
	<i>signata</i>	(Jacoby)	CHIS, JAL, TAB, TAMPS, VER, YUC	QROO, VER, YUC			CHIS, MOR ?VER		VER	CHIS	SLP?			MOR, QROO, SLP?	2
	<i>sublimata</i>	(Jacoby)	OAX, TAB, VER, YUC	QROO, VER			CHIS, VER			CHIS, SLP, VER				CHIS, QROO, SLP	3
	<i>tenuicincta</i>	(Jacoby)	SLP, TAB, VER			SLP	CHIS, NAY, SLP, VER							CHIS, NAY	2
<i>tenustula</i>		(Schauffuss)	CHIS, COL? GRO, JAL, MICH, MOR, NAY, QROO, TAMPS, VER, YUC	VER, YUC		NAY, SLP	COL, JAL, MOR, NAY, OAX, SON	JAL, MICH, NAY	JAL	JAL, SON	MOR, NAY, SIN, VER	CHIS		COL, NAY, OAX, SIN, SLP, SON	6
	<b>TOTAL</b>														<b>287</b>

\*This species has apparently been confused with *A. 10-guttatus* (Fabricius); therefore, most *A. 10-guttatus* records are actually *A. jacobiana* (originally described and only known from USA: AZ, TX).

\*\* *Alagoasa semipurpurea* = comb. n., this species should be placed in *Kuschelina*.

\*\*\* *Kuschelina semipurpurea* = comb. n., see *Alagoasa*.

\*\*\*\* *aequinoctialis aequinoctialis* (= *cyanipennis octomaculata* Crotch & *punctulata* Bechyne & Bechyne). BUT, re Blake 1931 *O. aequinoctialis* (s.s.) has a black metasternum & black metafemora. Indeed there seems to be some differences consistent with this & an elytral pattern different where *aequinoctialis* (s.s.) has the median/central spots more rounded & only slightly angled whereas for *O. cyanipennis* 8-maculata they are more distinctly angled and slender.

## Results

Although 6625 Mexican Alticinae specimens from nine institutional collections were studied (see list in the Methods section above) some of these (493) that could not be determined reliably to recorded species (Table 1); therefore, a total of 6132 specimens were determined to species. Table 1 also demonstrates that a total of 394 new state records were found in these 8 collections, but 107 were repeated so that actually there are 287 new state records. The specimens studied belonged to a somewhat random assortment of genera, including the subtribe Oedionychina (*Alagoasa*, *Asphaera*, *Capraita*, *Kuschelina*, *Omophoita*, *Walterianella*) and *Disonycha*, *Prasona*, *Systema*. The genera with the most specimens belonged to *Alagoasa*, *Asphaera*, *Omophoita*, *Disonycha*, and *Systema*. Table 2 lists only the species in these genera with the new state records as discovered in the current study with those new state records in bold type; the full distribution of each species can be determined by combining these with the distributions in Furth (2006, 2009, 2013). Map 1 demonstrates the number of species by state as of Furth (2013) in comparison to the current study illustrating in Map 2 only the new species records by states and in Map 3 the total species per state.

As indicated in Table 2 the nine genera studied have a high percentage of new state records based only on examination of these institutional collections, as follows: *Alagoasa* (13 of 18 species with new state records of the 44 species recorded from Mexico) [see also Fig. 1]. However, the two apparent new state records (SIN and YUC) for *A. jacobiana* are not included as new records because of its confusion with *A. decemguttata*; *Asphaera* (4 of 4 species of the 10 species recorded from Mexico) [see also Fig. 2]; *Capraita* (2 of 2 species of the 4 species recorded from Mexico) [see also Fig. 3]; *Disonycha* (27 of 33 species of the 49 species recorded from Mexico) [see also Fig. 4]; *Kuschelina* (2 of 3 species of the 8 species recorded from Mexico) [see also Fig. 5]; *Omophoita* (6 of 7 species of the 13 species record from Mexico) [see also Fig. 6]; *Prasona* (1 of 1 species of the 1 species recorded from Mexico) [see also Fig. 7]; *Systema* (18 of 20 species of the 31 species recorded from Mexico) [see also Fig. 8]; and *Walterianella* (7 of 8 species of the 10 species recorded from Mexico) [see also Fig. 9]. Thus, there are 80 species of the 97, or almost 83% of the species examined from the nine institutional collections with new state records, and this is 47% of the total 170 species in these genera recorded from Mexico (Fig. 10).

Of special note in Table 2 are the confirmed species determinations that verify some questionable state records indicated in Furth (2006). They are as follows: *Disonycha guatemalensis* from Veracruz; *Omophoita affinis* from Mexico, a state record for a species only recorded previously as from the country of Mexico; *Systema bitaeniata* from Veracruz; *Systema blanda* from San Luis Potosi; *Systema contigua* from Sonora and Veracruz; *Systema undulata* from Guerrero and Morelos; *Walterianella venustula* from Colima.

*Systema oberthuri* Baly is reported for the first time from Mexico (Table 2; Fig. 12).

From the current study, it is evident that the numbers of recorded species have changed, in some cases significantly (see Maps 1, 2, 3). Map 2 shows these new records clearly (the details are in Table 2). The Mexican states with the most new species records are Chiapas (32), Nayarit (27), and Sinaloa (24).



Figure 1. *Alagoasa* Bechyné new state records versus previously recorded state records.

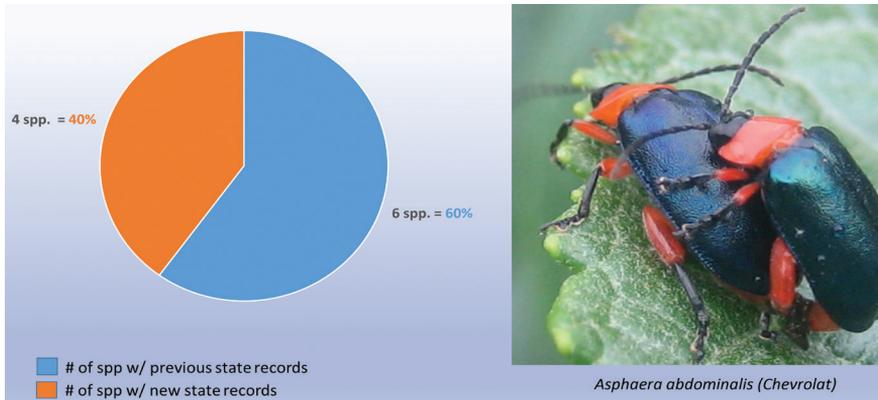


Figure 2. *Asphaera* Chevrolat new state records versus previously recorded state records.

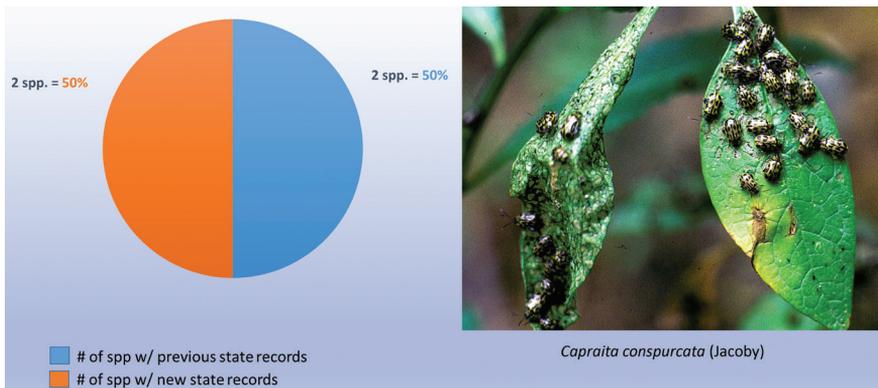


Figure 3. *Capraita* Bechyné new state records versus previously recorded state records.

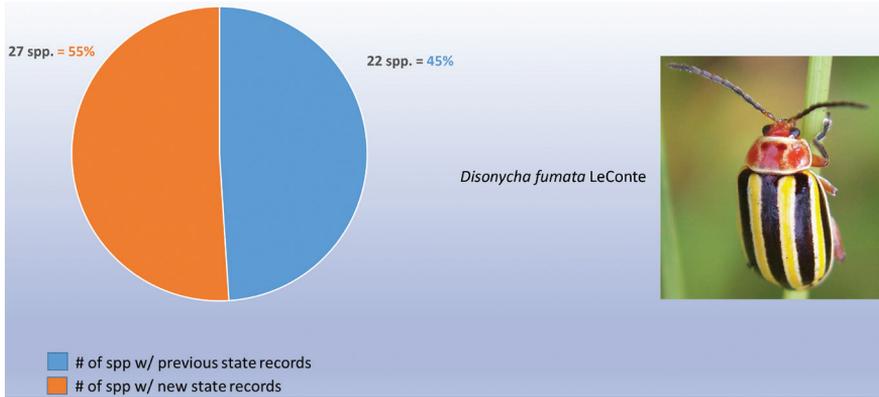


Figure 4. *Disonycha* Chevrolat new state records versus previously recorded state records.

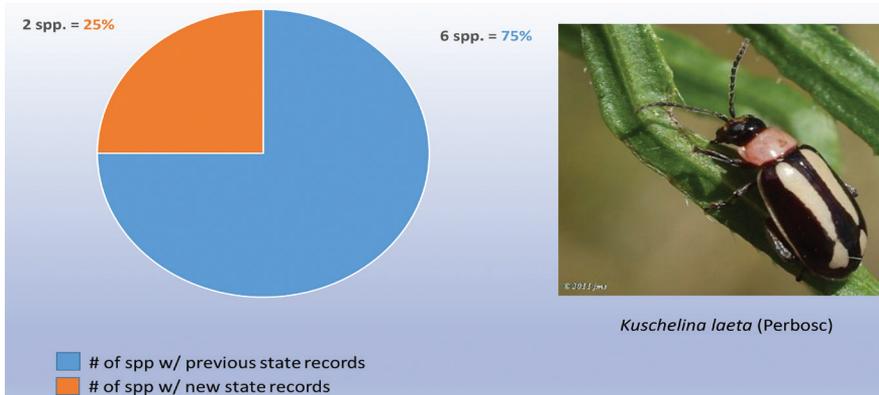


Figure 5. *Kuschelina* Bechyné new state records versus previously recorded state records.

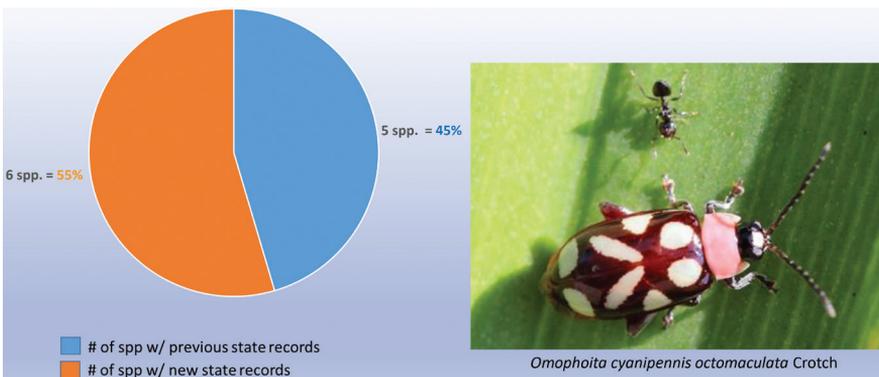
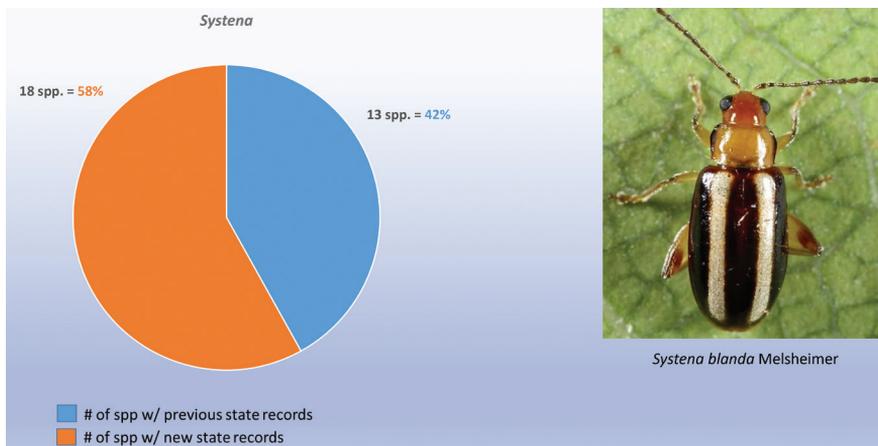


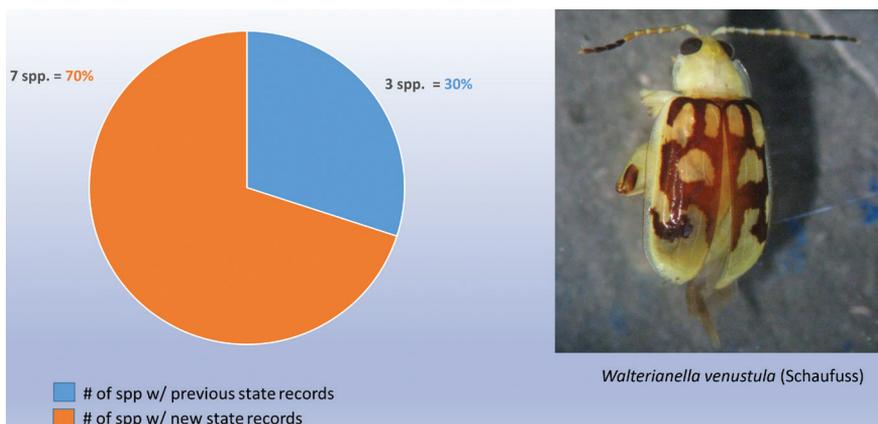
Figure 6. *Omophoita* Chevrolat new state records versus previously recorded state records.



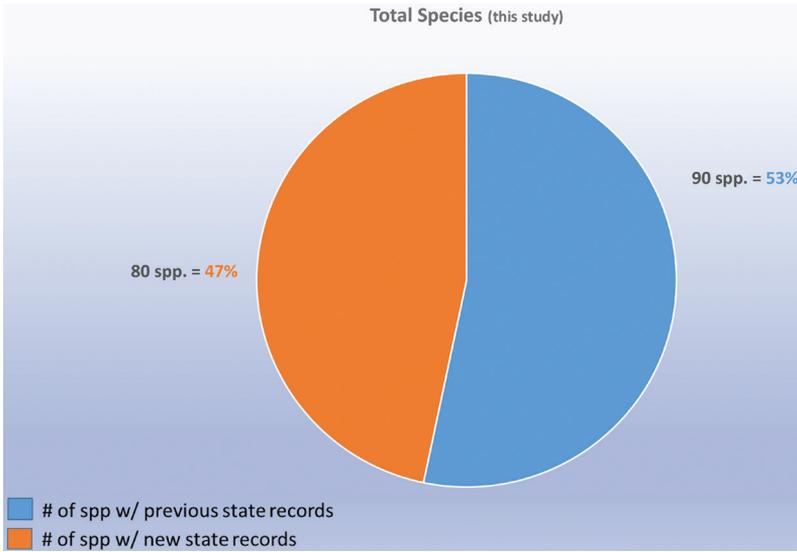
**Figure 7.** *Prasona* Baly new state records versus previously recorded state records.



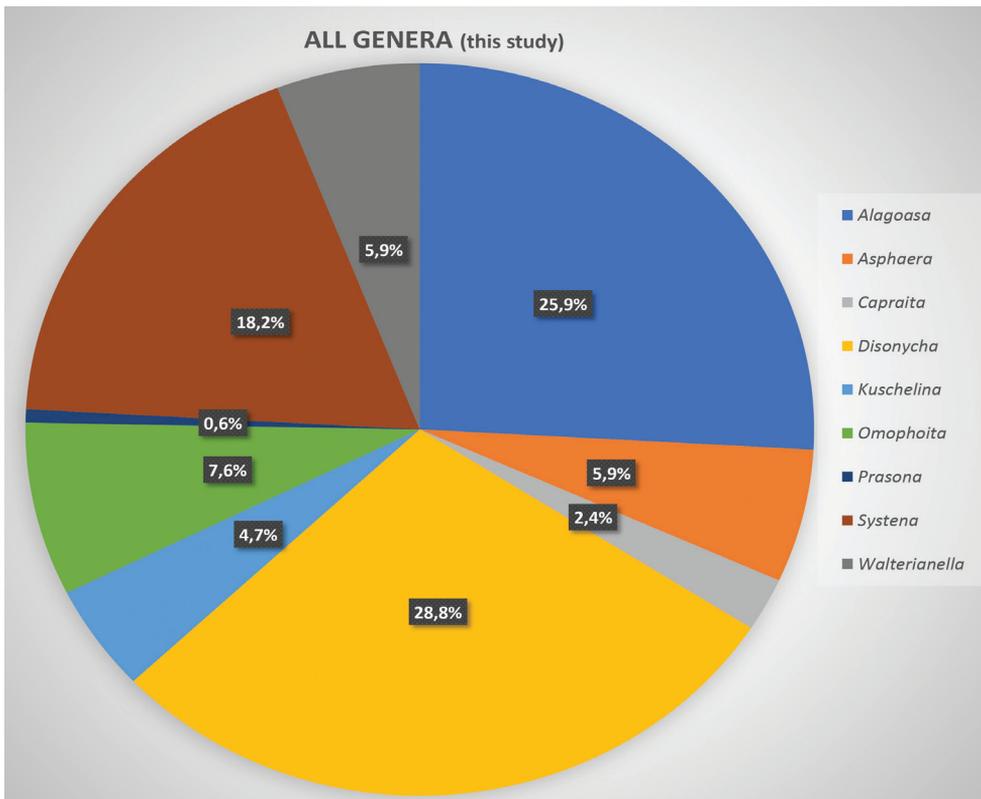
**Figure 8.** *Systema* Chevrolat new state records versus previously recorded state records.



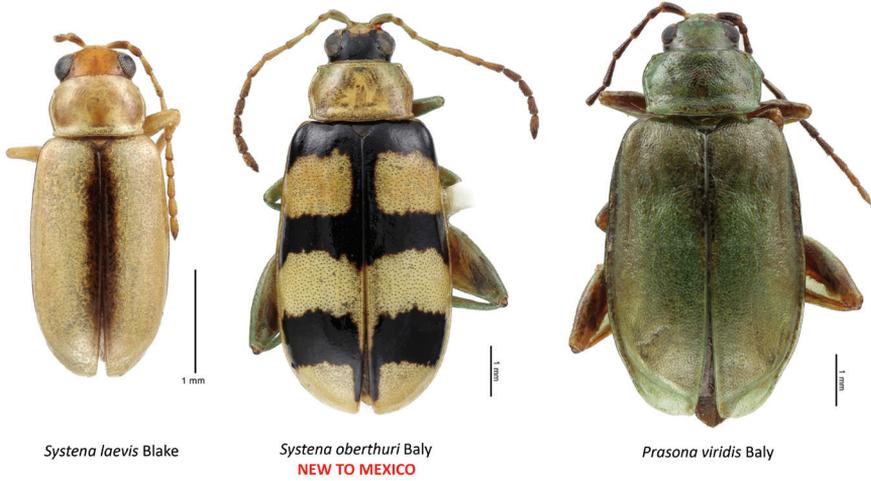
**Figure 9.** *Walterianella* Bechyné new state records versus previously recorded state records.



**Figure 10.** Summary of all new records for selected genera.

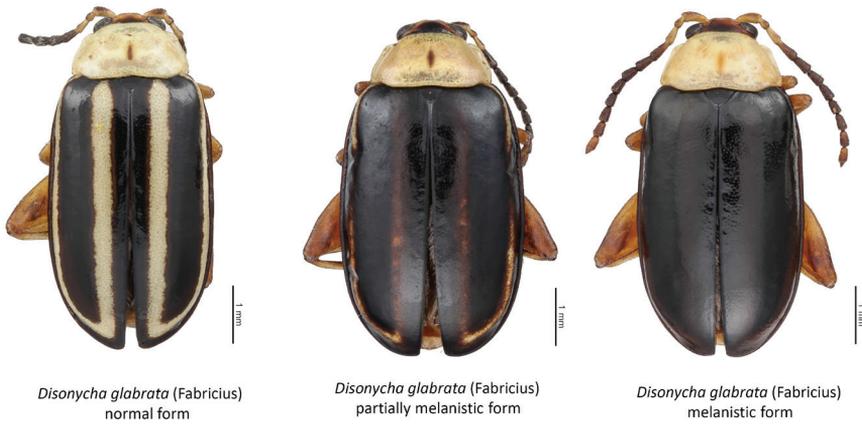


**Figure 11.** Summary of all genera with species percentages.



**Figure 12.** *Systema* and *Prasona* generic confusion.

Melanism only known from Chihuahua, Nayarit, Sonora, Sinaloa



**Figure 13.** *Disonycha glabrata* (Fabricius) species color forms.



Ex Biologia Centrali Americana, Jacoby, 1887  
(Figures 15, 18, 22)



Biologia Centrali Americana specimen  
Panama: V. de Chiriqui. Champion

**Figure 14.** *Alagoasa decemguttata* (Fabricius) intraspecific variation.

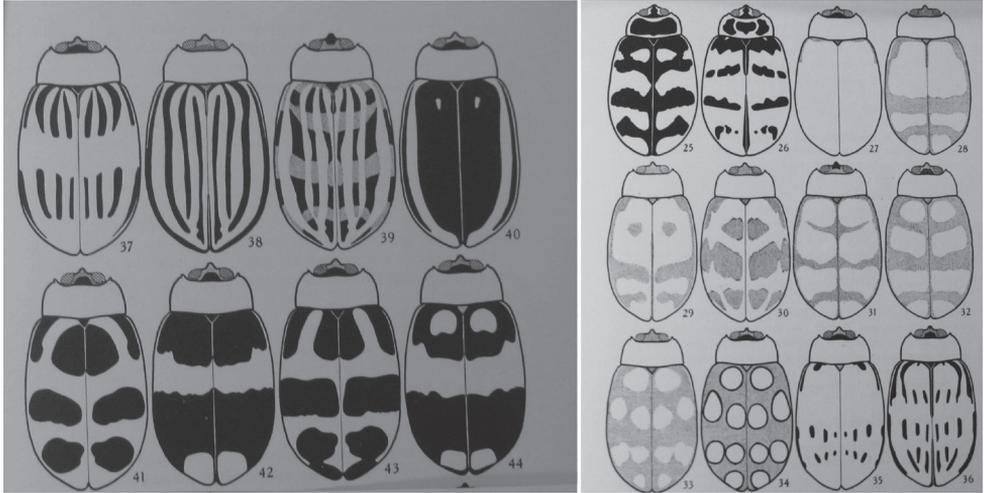


Figure 15. *Alagoasa decemguttata* intraspecific variation (ex Bechyné, 1955).



Figure 16. *Alagoasa jacobiana* (Horn) species confusion and intraspecific variation.

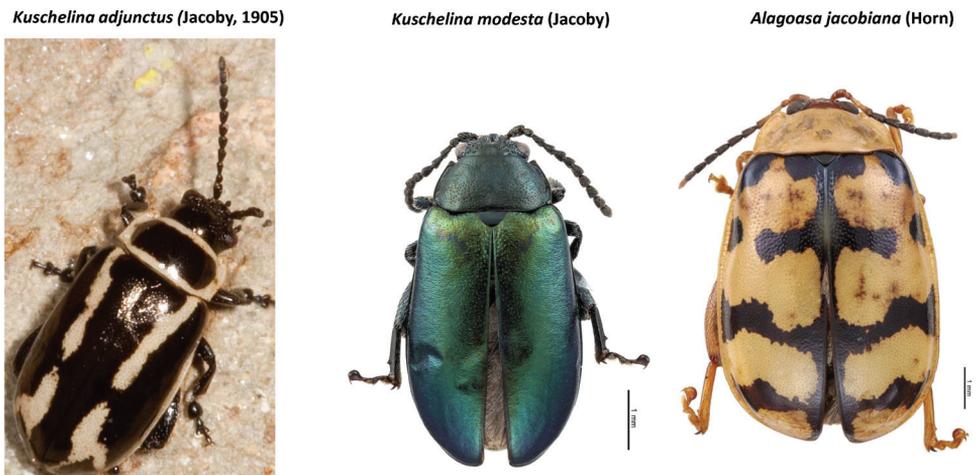


Figure 17. *Alagoasa* and *Kuschelina* generic confusion.

## División Política Estatal

Records of Oaxaca Study (Furth, 2013)



Map 1. Species numbers by states from Furth (2013).

## División Política Estatal

New Records



Map 2. New species records by states from the current study.



## Taxonomic problems

### Generic level confusion

*Systema* versus *Prasona* (Fig. 12). There has long been some confusion concerning the genus *Prasona* Baly as to whether it is synonymous with *Systema* Chevrolat. *Prasona viridis* Baly from Mexico is the type species (Baly 1861) and the only one recorded from Central America (Furth and Savini 1996) and eight other species from various parts of South America (Bechyné 1971). *Prasona* seems to have the primary characteristics of *Systema*, but seems only to differ in being much larger in size than species of *Systema*. *Prasona* was placed near *Systema* and *Cyrsylus* in the “catalog phylogeny” (Furth and Suzuki 1998) of Bechyné (1971).

*Alagoasa* versus *Kuschelina* (Fig. 17). *Kuschelina* Bechyné differs from *Alagoasa* Bechyné by having moniliform antennal segments; smaller eyes (diameter less than 3 times as small as width of frons); head (frons/vertex) rugosely punctured; male terminal sternite ventrally without depression; epipleura bent/slanted downward, i.e., visible in lateral view; elytral pleura narrow, not grooved or explanate; antero-lateral corners of pronotum only slightly protruding (not appearing to surround eyes/head; body shape elongate oval (not very rounded). The first placement of North American *Oedionychus* Berthold or *Oedionychis* Latreille (most *Alagoasa* were placed in one of these generic names previously) into *Kuschelina* was by Balsbaugh and Hays (1972) [for 14 spp.]. In Riley et al. (2003) there were 28 species of *Oedionychis* Latreille listed (following Wil-

cox 1975), but only one (*K. scripticollis* (Say) was noted as a new combination; however, many of the others are also technically new combinations, e.g., *K. amplivittata* (Blake), *K. barberi* (Blake), *K. flavocyanea* (Crotch), *K. jacobiana* (Horn), etc. Based on the above characters the author considers *K. semipurpurea* (Jacoby), formerly placed in *Alagoasa*, to be a new combination.

### Intra-specific variation:

*Disonycha glabrata* (Fabricius) (Fig. 13). Because of melanization of the elytra there are intermediate and dark forms; known only from Chihuahua, Nayarit, Sonora, and Sinaloa.

*Alagoasa decemguttatus* (Fabricius) (Figs 14, 15). Intra-specific variation in this species is well-documented in the literature (Jacoby 1886; Bechyné 1955).

### Species confusion (see Table 2):

*Alagoasa decemguttatus* versus *A. jacobiana* (Horn) (Figs 14, 16). *Alagoasa decemguttatus*: Some confusion with this species. According to Bechyné (1971) *A. decemguttatus* is only from South America and, therefore, most *A. decemguttatus* recorded from Mexico are probably *A. jacobiana*; therefore, some records for *A. jacobiana* may be new records because of this confusion.

*Alagoasa duodecimmaculata* (Jacoby): There is some confusion of this species with *A. trifasciata escuintla* Bechyné & probably most specimens are *A. trifasciata escuintla*. Its occurrence in Mexico is still somewhat in question (Furth 2006).

*Omophoita cyanipennis octomaculata* Crotch or *O. octomaculata*: There has historically been confusion about the exact identity of *O. aequinoctialis aequinoctialis*. In this study, the author considers records of *O. a. aequinoctialis* to consist of both *O. cyanipennis octomaculata* Crotch and *O. punctulata* (Bechyné & Bechyné). However, according to Blake (1931) *O. aequinoctialis* (s.s.) has a black metasternum and black metafemora. Indeed, there seems to be some consistent differences between these and an elytral pattern different where *aequinoctialis* (s.s.) has the median/central spots more rounded and only slightly angled, whereas for *O. cyanipennis octomaculata* they are more distinctly angled and slender.

### Discussion

Interesting that this study did not reveal new genera and only discovered one new species for Mexico (Furth 2004, 2006, 2009, 2013). This may indicate that the number of described species found in Mexico may be reaching the level of being relatively well known. Only one new species record for Mexico (*Systema oberthuri*) was discovered in this study. However, based on the author's previous and current research, there are certainly many additional undescribed species living within Mexico; probably as many as another 300–400

species. Few other Central American countries have been surveyed for Chrysomelidae. Only Costa Rica is relatively well-known with 350 species in 89 genera (Furth et al. 2003) with only 113 species in 43 genera known previously from the literature. Panama is poorly-known and has 270 species in 70 genera recorded (Furth and Savini 1996, 1998).

Indoor Collecting (Table 1):

The author is not aware of any references in the literature referring to “indoor collecting”, especially in the meaning used in this study. One interview in 2015 of Dr. Art Evans referred to this term for picking up a beetle collection, something the author of this study has been doing for 50 years. However, the meaning for the current study refers to visiting institutional or private scientific collections for the purposes of scientific research, e.g., systematic revisions, faunistics, biodiversity, biogeographical, etc. Most biologists interested in nature, prefer the fun of “outdoor collecting” coupled with subsequent study of material and data from this back home, “indoor collecting” can be just as fun and usually even more productive scientifically; as evidenced from the current study. This kind of work is certainly nothing new, all students and professional biologists conduct this kind of work because the wealth of information “hiding” in such collections is phenomenal, vast, full of valuable information that can help answer many scientific questions and enhance most studies, and for the most part except data already published (at least in entomology), not available elsewhere. The current study is an example of “indoor collecting” where a large percentage (47%) of new Mexican state records were discovered.

Although the choice of the 9 genera and 8 collections for this study was rather random they still provide a very good example of the scientific value of collections. The author plans to continue such research on the Mexican Flea Beetle fauna based on much more specimen material he has borrowed from the same (and eventually other) collections. The 8 collections sampled represent a large percentage of the collections not yet studied by the author likely to have material from Mexico, notable exceptions are the collections of the Los Angeles County Museum, Texas A. & M. University, and, of course, the Universidad Nacional Autónoma de Mexico.

There is no particular pattern to the states with the most new records (Map 2). This is probably only an artifact of the historical collecting of individuals whose material is associated with the nine collections sampled. One of the 3 states with the most new records is Chiapas that is one of several southern states with strong tropical biogeographical affinities (Furth 2013). As evident in Map 2, this study produced new state records in all but three states (Aguascalientes, Distrito Federal, Tlaxcala) and there were new records with 10 or more in 13 states, i.e., over 30%; this is a testament to the value of “indoor collecting”. In previous studies of the Mexican Alticinae fauna some records were questionable because of unclear label data, unclear assignment in the literature, etc. (Table 2), but in the current study of the specimens in these 8 collections some of these were confirmed or enhanced for 7 species (see results above) for eight of the state, including one for the country.

In the Results section above the author has pointed out and attempted to clarify the taxonomic confusion at the generic and specific levels that came to light during the current study. There is no real need to elaborate in detail about these. Resolution

of the confusion between *Systema* and *Prasona* requires considerably more study, but it is quite possible that *Prasona* will become a synonym of *Systema*. The confusion within the “Oedionychina” of *Alagoasa* and *Kuschelina* has caused some problems in faunistic studies in the Nearctic and Neotropical Regions, e. g., Riley et al. (2003). In the Results section above the author attempts to explain his interpretation of these two genera and to clarify the morphological differences, as well as to point out some new combinations created by this confusion.

Therefore, there are 80 species of the 96 species found in this study from 8 collections, or 83%, with new state records, and this is 47% of the total 170 species in these genera recorded from Mexico (Fig. 10). Figure 11 illustrates the nine genera in this study and their species percentages of the total.

In conclusion, the author hopes that not only does this study of a relatively few collections and genera significantly increase the knowledge of the Mexican Flea Beetle fauna, but also that it demonstrates the value of “indoor collecting” as an integral part of any biodiversity and faunistic research.

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# Comparative morphology of the spermatheca in Megalopodidae (Coleoptera, Chrysomeloidea)<sup>1</sup>

Geovanni M. Rodríguez-Mirón<sup>1</sup>, Santiago Zaragoza-Caballero<sup>1</sup>,  
Sara López-Pérez<sup>1</sup>

<sup>1</sup> *Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, A.P. 70-153, 04510 Mexico City, Mexico*

Corresponding author: *Geovanni M. Rodríguez-Mirón* ([geo20araa@yahoo.com.mx](mailto:geo20araa@yahoo.com.mx))

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## Abstract

The spermatheca is an organ that stores and maintains viability of sperm until fertilization. It has an important role in copulation and oviposition, and it is highly informative in species delimitation. Here, we present a comparative study of the spermathecal morphology in the coleopteran family Megalopodidae. The spermathecae of 34 species, representing 13 genera and all three subfamilies, were studied. Illustrations are newly provided for all species, except in 14 cases in which illustrations were reproduced from previously published literature. Our results show that each subfamily of Megalopodidae can be effectively differentiated based on the particular spermathecal anatomy. In addition, the spermathecal anatomy presents a range of variation within each subfamily, useful for diagnosing species and, in some cases, identifying groups of genera. For instance, the “American group” is thus recognized in this study.

## Keywords

Female genitalia, Zeugophorinae, Megalopodinae, Palophaginae, flagellum, taxonomic significance

## Introduction

The female internal reproductive organs in insects consist of several organs: a pair of ovaries with their respective oviducts, a median ectodermal tube, a vagina, a bursa cop-

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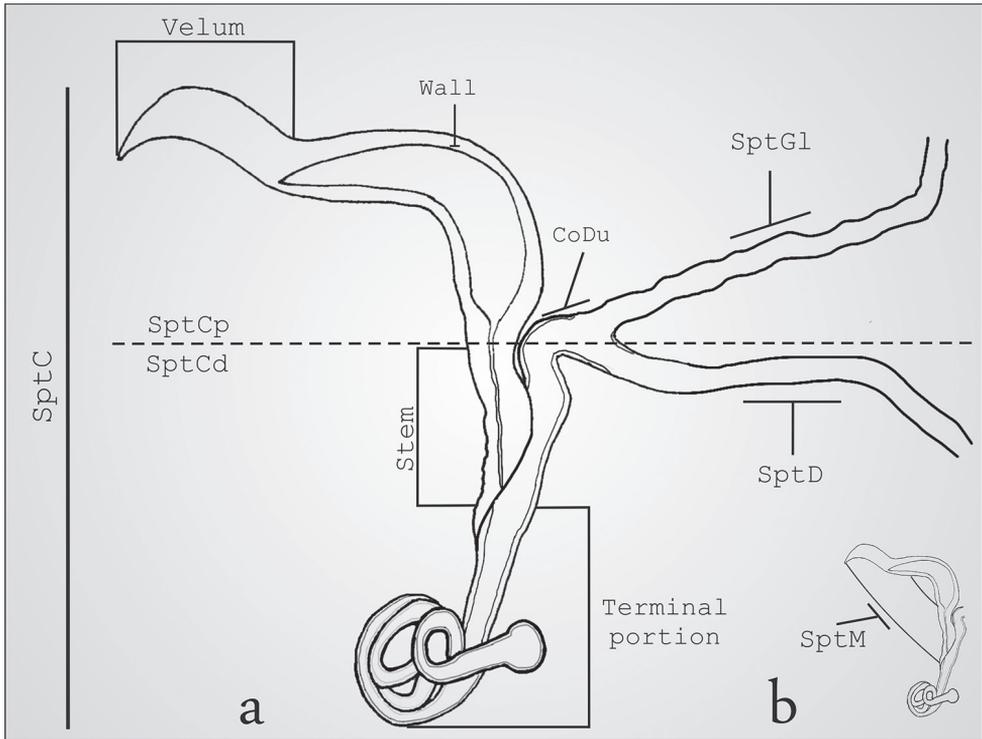
ulatrix and the spermatheca (Snodgrass 1935, Suzuki 1988, Triplehorn et al. 2005). The spermatheca (multiple spermathecae in some instances) is an invagination of the eighth abdominal segment (Snodgrass 1935); and its shape and number depend on the group of insects (Harterreiten-Souza and Pujol-Luz 2012, Pascini and Martins 2017). The spermatheca is an important organ that stores and maintains viability of sperm until fertilization, and it has an important role in copulation and oviposition (e.g. Gschwentner and Tadler 2000, De Marzo 2008, Harterreiten-Souza and Pujol-Luz 2012, Pascini and Martins 2017).

The order Coleoptera exhibits five patterns of spermathecal morphology (De Marzo 2008). These patterns are distinguished by the presence, absence or variations of the following structures: spermathecal capsule, spermathecal duct, and spermathecal gland (De Marzo 2008). The most widespread pattern is to have only one spermathecal capsule that stores sperm, and this capsule is connected with the bursa copulatrix by one spermathecal duct that allows the sperm to be transported to the spermathecal capsule after copulation (Gack and Peschke 1994, De Marzo 2008). In addition, there is only one spermathecal gland that secretes glycoproteins responsible for the migration of sperm from the bursa copulatrix to the spermathecal capsule (Fig. 1a) (Aslam 1961, Grodner and Steffens 1978, Suzuki 1988, De Marzo 2008, Matsumura and Suzuki 2008). Finally, the distal and proximal portions of the spermatheca are connected by a muscle (Fig. 1b), the contraction of which causes the sperm to be transferred to the bursa copulatrix (Rodríguez 1994).

Classification systems have mainly utilized characters of the external morphology, such as wing venation; however, most of these classifications change constantly because of symplesiomorphy and homoplasy within these character sets. Therefore, taxonomists have studied internal morphology and genital features, which, in combination with the features mentioned above, will contribute to a more stable classification (Aslam 1961, Kasap and Crowson 1979, Mann and Crowson 1983, Suzuki 1988, Wanat 2007, Santos and Rosado-Neto 2010). Male genitalia have been widely used to differentiate species, even between closely related taxa, because of their rapid divergence due to sexual selection (Arnqvist 1997, Flowers and Eberhard 2006, Zunino 2012).

The female internal reproductive organs have been used less frequently; however, they have also been found useful in diagnosing certain groups (Hernández and Ortuño 1992, Hernández 1993, Ferronato 2000, Gaiger and Vanin 2008). Histological differences and shape variations are useful in distinguishing species, species groups and even genera (Suzuki 1988, Candan et al. 2010). These variations render the spermatheca as a character complex with high taxonomic value. For example, spermathecal features have been used to separate and diagnose the tribes of Scarabaeinae (López-Guerrero and Halffter 2000); in Curculionidae and Carabidae, the spermathecae also allow the recognition of species and genera (Aslam 1961, Schuler 1963).

The spermatheca in Chrysomeloidea has been useful to define subfamilies, genera, species, and groups of species (Reid 1989, Hernández 1993, Biondi 2001, Borowiec and Świętojańska 2001, Borowiec and Skuza 2004, Borowiec and Opalinska 2007,



**Figure 1.** Structure of the spermatheca in Megalopodidae (*Mastostethus novemaculatus*). **a** general view, **b** spermathecal muscle.

Yus-Ramos 2008, Borowiec and Pomorska 2009, Bi and Lin 2013, López-Pérez et al. 2016, Rodríguez-Mirón and Zaragoza-Caballero 2017). Suzuki (1988) presented the first comprehensive study of the male and female genitalia of Chrysomelidae, and he described the spermathecae of two species of Megalopodidae, *Zeugophora annulata* (Baly, 1873), and *Temnaspis japonica* Baly, 1873. This author included these genitalic features in a phylogenetic analysis, proposing Megalopodinae and Zeugophorinae as sister taxa, and placing both subfamilies within Chrysomelidae. In a later study, Megalopodidae was ranked as a separate family based on larval anatomy, and the spermathecae of some species of Palophaginae were illustrated and described (Kuschel and May 1990, 1996).

Other megalopodid taxa that have had their spermathecae described and illustrated are: *Mastostethus* Lacordaire, 1845, *Agathomerus* Lacordaire, 1845, and *Megalopus* Fabricius, 1801 (Suzuki 2003). Additionally, Reid (1989, 1992, 1998) illustrated the spermathecae of *Zeugophora vitinea* (Oke, 1932), *Zeugophora williamsi* Reid, 1989, *Zeugophora javana* Reid, 1992, and *Zeugophora toroja* Reid, 1998. Finally, Sekerka and Vives (2013) described and illustrated the spermatheca of *Zeugophorella riedeli* (Medvedev 1996).

Megalopodidae currently consists of 552 described species, which are classified into three subfamilies (Megalopodinae, Zeugophorinae, and Palophaginae) (Rod-

riíguez-Mirón 2016). However, the spermathecae of only 5% of these species have been described. Herein, we describe and compare 34 species, representing 13 genera and two subgenera for one of these genera. This work presents a panorama of the diversity and complexity of the spermathecal capsule in Megalopodidae, with the objective of shedding light in future taxonomic and phylogenetic studies.

## Methods

The spermathecae of 34 species of Megalopodidae were examined. These species represent three subfamilies, 13 genera and two subgenera for one genus. Approximately 100 specimens were examined, distributed between the 34 species studied (Table 1). Illustrations from Suzuki (1988, 2003), Kuschel and May (1990, 1996), Reid (1989, 1992, 1998) and Sekerka and Vives (2013) were reproduced in the present study and were used to establish putative homologies among these structures.

For microscopic examination, the dried specimens were placed in hot water for 10 minutes to soften the tissues. Each abdomen was dissected along the abdominal pleura and boiled in a 10% KOH solution for five minutes. The spermatheca was dissected from the KOH preparation, washed with water, and mounted with glycerin in a glass slide for observation. Dissection and analysis were done using a Zeiss V–8 stereoscopic microscope. Photographs were made using a Zeiss Axio Zoom V–16 stereoscopic microscope equipped with an AxioCam MRC5 camera. After examination the spermatheca of each specimen was transferred to a microtube with glycerin, which was pinned underneath the specimen. The abdomen was attached to a white card using a drop of glue, also pinned underneath the specimen.

Specimens were borrowed from the following national and international museums and Institutions: BMNH–The Natural History Museum, London, U.K. (M. Geiser); MNHN–National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (A. Konstantinov); MZLU–Museum of Zoology Lund University, Lund, Sweden (Ch. Fägerström); NHMB–Naturhistorisches Museum Basel (M. Borner); CCFES–Z–Colección Coleopterológica de la Facultad de Estudios Superiores Zaragoza, UNAM, México (M. Ordóñez); CNIN–Colección Nacional de Insectos IBUNAM, UNAM, México (S. Zaragoza). Names in parentheses following each institution indicate the responsible curatorial person.

Spermathecal terminology follows Suzuki (1988) and Matsumura and Suzuki (2008) (Fig. 1). The following abbreviations are used in the descriptions and figures. SptC: spermathecal capsule; SptCp: proximal part of spermathecal capsule; SptCd: distal part of spermathecal capsule; CoDu: common duct; SptGl: spermathecal gland; SptD: spermathecal duct; SptM: spermathecal muscle.

**Table I.** Species studied.

Species	Geographic information in label	No. specimens
<b>Megalopodinae</b>		
<i>Agathomerus (Agathomeroides) flavomaculatus</i> (Klug, 1824)	Brazil	4
<i>Agathomerus (Eugathomerus) sellatus</i> (Germar, 1823)	Brazil	6
<i>Agathomerus rufus</i> (Klug, 1834)	Mexico	30
<i>Agathomerus signatus</i> (Klug, 1824)	Brazil	3
<i>Agathomerus</i> sp. * <sup>1</sup>	Panama	–
<i>Homalopterus tristis</i> Perty, 1832	Brazil	2
<i>Mastostethus hieroglyphicus</i> (Klug, 1834)	Mexico	9
<i>Mastostethus nigrocinctus</i> (Chevrolat, 1834)	Honduras, Costa Rica, Mexico	25
<i>Mastostethus novemaculatus</i> (Klug, 1834)	Mexico, Costa Rica	6
<i>Mastostethus variegatus</i> (Klug, 1824)	Brazil	1
<i>Megalopus inscriptus</i> Klug, 1824	Peru	3
<i>Megalopus</i> sp. 1	Costa Rica	2
<i>Megalopus</i> sp. 2 * <sup>1</sup>	Panama	–
<i>Poecilomorpha atripes</i> Lacordaire, 1845	South Africa	1
<i>Poecilomorpha cyanipennis</i> (Kraatz, 1879)	South Korea, Russia	4
<i>Pseudohomalopterus carinatus</i> Pic, 1920	Brazil	7
<i>Sphondylia</i> sp.	Africa	1
<i>Temnaspis septemmaculata</i> (Hope, 1831)	Laos	1
<i>Temnaspis japonica</i> Baly, 1873 * <sup>2</sup>	Japan	–
<i>Temnaspis</i> sp. * <sup>1</sup>	–	–
<i>Temnaspis speciosus</i> Baly, 1859	Bhutan, Nepal	4
<b>Zeugophorinae</b>		
<i>Zeugophora annulata</i> (Baly, 1873) * <sup>2</sup>	–	–
<i>Zeugophora californica</i> Crotch, 1874	USA	6
<i>Zeugophora indica</i> Jacoby, 1903	Kashmir, India	3
<i>Zeugophora javana</i> Reid, 1992 * <sup>3</sup>	Indonesia: West Java	–
<i>Zeugophora toroja</i> Reid, 1998 * <sup>4</sup>	Indonesia: West Java	–
<i>Zeugophora varians</i> Crotch, 1873	Canada, USA	4
<i>Zeugophora vitinea</i> (Oke, 1932) * <sup>5</sup>	Australia	–
<i>Zeugophora williamsi</i> Reid, 1989 * <sup>5</sup>	Australia	–
<i>Zeugophorella riedeli</i> (Medvedev, 1996) * <sup>6</sup>	New Guinea	–
<b>Palophaginae</b>		
<i>Cucujopsis setifer</i> Crowson, 1946 * <sup>7</sup>	Australia	–
<i>Palophagoides vargasorum</i> Kuschel, 1996 * <sup>8</sup>	Chile	–
<i>Palophagus australiensis</i> Kuschel, 1990 * <sup>7</sup>	Australia	–
<i>Palophagus bunyae</i> Kuschel, 1990 * <sup>7</sup>	Australia	–

\*Information previously published; 1: Suzuki (2003); 2: Suzuki (1988); 3: Reid (1992); 4: Reid (1998); 5: Reid (1989); 6: Sekerka and Vives (2013); 7: Kuschel and May (1990); 8: Kuschel and May (1996).

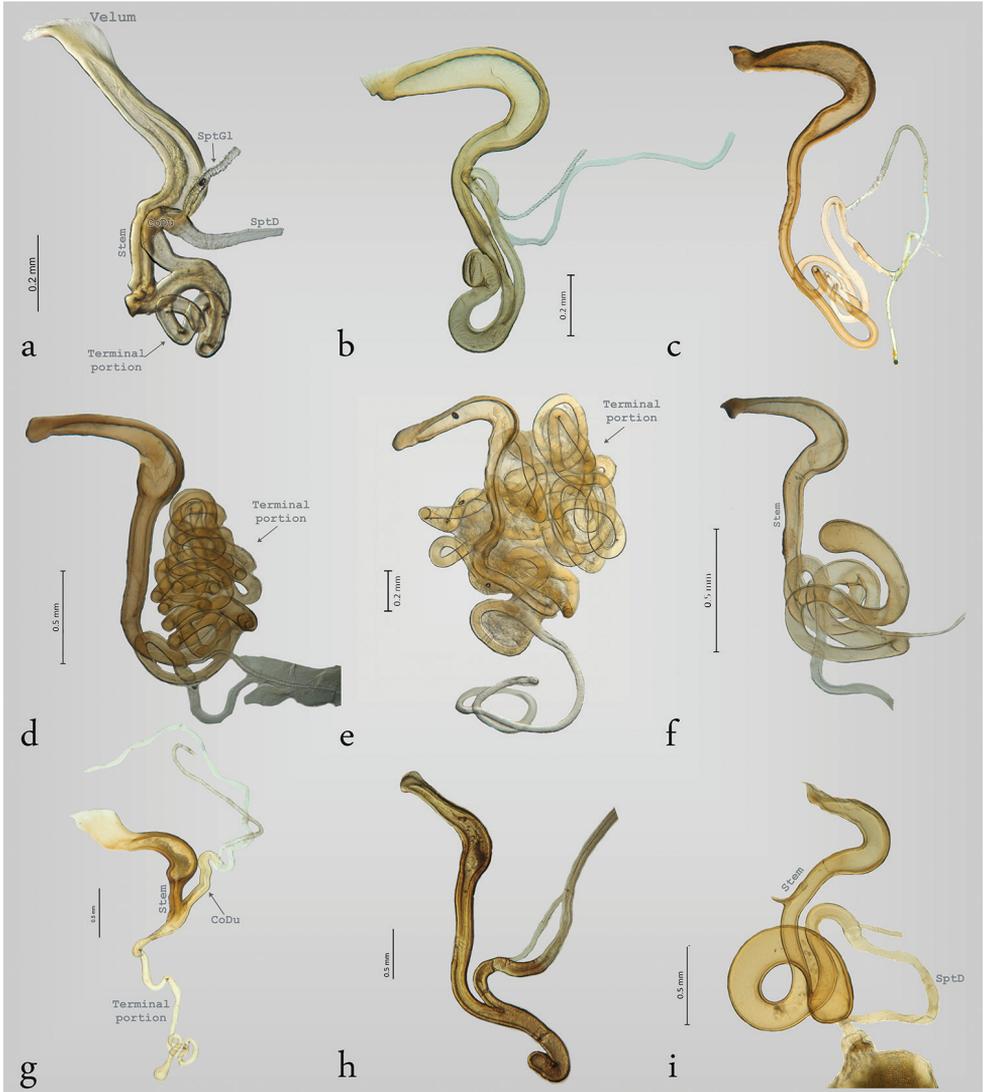
## Results

Our results showed that the three subfamilies of Megalopodidae can be effectively differentiated by their particular spermathecal anatomy (Table 2). We did not find intraspecific variation in the spermatheca. All subfamilies exhibit a spermathecal capsule (SptC), a spermathecal gland (SptGl) and a spermathecal duct (SptD); variations of these structures provide the diagnostic characters for these subfamilies (Fig. 1–6, Table 2). The SptD diameter and length are variable, and the length is always longer than the SptC (Figs 2i, 3a, b, i, 5b, 7a). The SptGl is wide and also longer than SptC (Figs 5a–d, 7b), except in Palophaginae where it is either shorter or the same size as the SptC (Figs 6g–j, Table 2). The SptC has wide walls and it is well sclerotized as in other coleopteran families (Figs 1–4). The shape of the SptC varies among the species of Megalopodidae (Figs 1–6).

In this study the SptC was divided in two portions, the proximal part of spermathecal capsule (SptCp) and the distal spermathecal part (SptCd) (Fig. 1a), following the homologies proposed by Suzuki (1988). The SptCp has a particular shape in each subfamily. Megalopodinae has a boomerang-shaped SptCp (Figs 1–3, 5a–c, 6a); in Zeugophorinae it is crane's neck-shaped (Figs 4, 5d, 6b–f); and in Palophaginae it is C-shaped (Fig. 6g–j, Table 2). In some species, the SptCp exhibits a prolongation of the apical wall called the velum (Figs 1, 2, 3a, b, 4a–c, 5a, b, 6a–f, h); it is less sclerotized than the rest of the SptC wall. The first part of the SptCd (=stem) (Fig. 1) is variable in length and sometimes is elongate (Figs 1–6). The SptCd has duct-shaped, the terminal portion in its last portion is globose (Figs 1, 2b, f–i). The SptCd is bifurcate (Figs 1, 2, 3a, i, 4a–b, 5a, d), ending the stem; this bifurcation could be a common duct (CoDu) between the SptGl and the SptD (Figs 2g, 3c, 4a, 6h).

In Megalopodinae, the differences among genera are especially evident in the shapes of the SptCp and SptCd. The genera *Agathomerus*, *Homalopterus* Perty, 1832, *Mastostethus*, and *Megalopus* (Figs 1, 2, 3a, b, 5a, 6a) have similar spermathecae; thus, they are proposed in this study as the “American group.” This group has a boomerang-shaped SptCp, with a velum. The SptCd is elongate, wide, and variable in length. The stem in the SptCd is long, and the apex of the SptC holds the spermathecal muscle (SptM) (Figs 1b, 5a). Some species have a stem with ornaments (Figs 2f, g, i). The terminal portion of the SptC in *A. flavomaculatus* (Klug, 1824) and *A. signatus* (Klug, 1824) is coiled and notably long (Figs 2d and 2e respectively); in *Megalopus inscriptus* Klug, 1824 (Fig. 3a) and *Megalopus* sp. 1 (Fig. 3b) it is shorter. The SptD can be wider and short as in *Megalopus* (Figs 3a, b), narrow and long as in *Mastostethus nigrocinctus* (Chevrolat, 1832) (Fig. 2g), or coiled as in *Homalopterus tristis* Perty, 1832 (Fig. 7a).

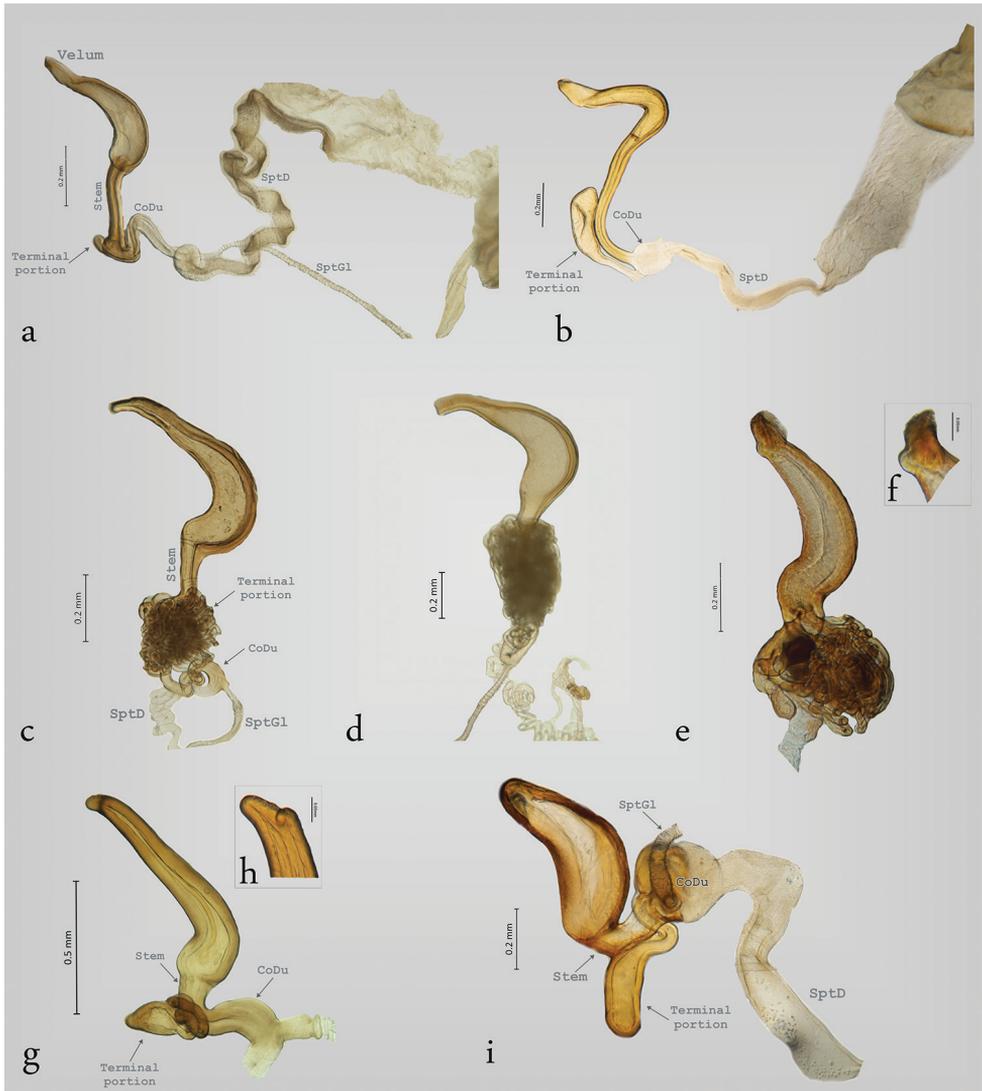
The apex of the SptCp in *Temnaspis* Lacordaire, 1845 (Figs 3c, d) does not have velum, and the internal part is abruptly narrowed towards the apex. The SptCd has a long stem that can have either two or three ramified ducts, as in *T. speciosus* Baly, 1859 and *T. septemmaculata* (Hope, 1831). These ducts are bifurcate and are connected between each other, forming a complex mass of ducts covering the stem. The CoDu



**Figure 2.** Structure of the spermatheca in Megalopodinae: *Agathomerus*, *Pseudohomalopterus*, *Homalopterus*, and *Mastostethus*. **a** *Agathomerus rufus* **b** *P. carinatus* **c** *A. (Eugathomerus) sellatus* **d** *A. (Agathomeroides) flavomaculatus* **e** *A. signatus* **f** *H. tristis* **g** *M. nigrocinctus* **h** *M. hieroglyphicus* **i** *M. variegatus*.

**Table 2.** Differences between the subfamilies of Megalopodidae.

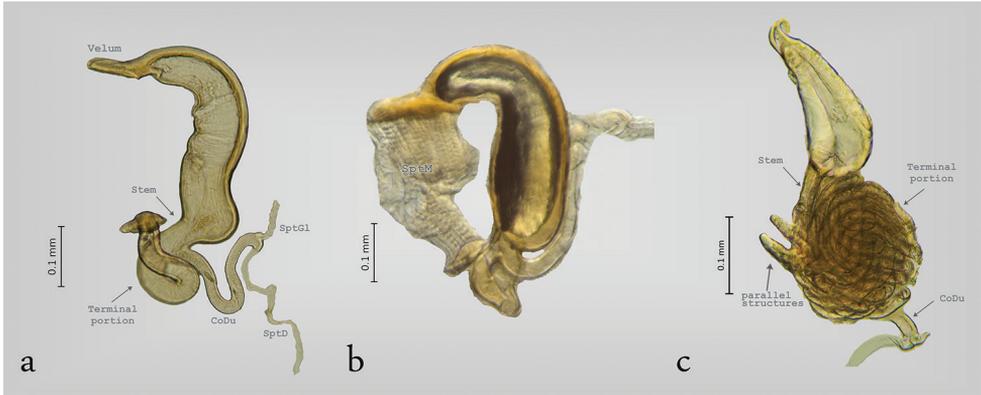
	SptC morphology	SptCp	SptGl	SptD	Hold the SptM
<b>Megalopodidae</b>	complex	boomerang-shaped	not branched and longer	very long	apex and the stem
<b>Zeugophorinae</b>	complex	crane's neck-shaped	branched and longer	very long	apex and the terminal portion
<b>Palophaginae</b>	simple	C-shaped	not branched and short	short	—



**Figure 3.** Structure of the spermatheca in Megalopodinae: *Megalopus*, *Temnaspis*, *Poecilomorpha*, *Sphondylia*. **a** *Megalopus inscriptus* **b** *Megalopus* sp. **c** *T. septemmaculata* **d** *T. speciosa* **e** *P. cyanipennis* **f** apex of the spermatheca in *P. cyanipennis* **g** *P. atripes*, **h** apex of the spermatheca in *P. atripes*, **i** *Sphondylia* sp.

is long and somewhat coiled, and it originates in the terminal portion of the SptC. Finally, the SptD is very variable in length and coils.

The genus *Poecilomorpha* Hope, 1840 has coarse walls in the SptCp, the apex is emarginate and without a velum (Fig. 3f, h), and its internal part is acuminate (Fig. 3e, g). The SptCd in *P. cyanipennis* (Kraatz, 1879) is divided in three branches connected between the SptCd and SptCp (Fig. 3e). The main connection is the stem, and the other two branches attach laterally and are interconnected with the stem; these branches lack rami-

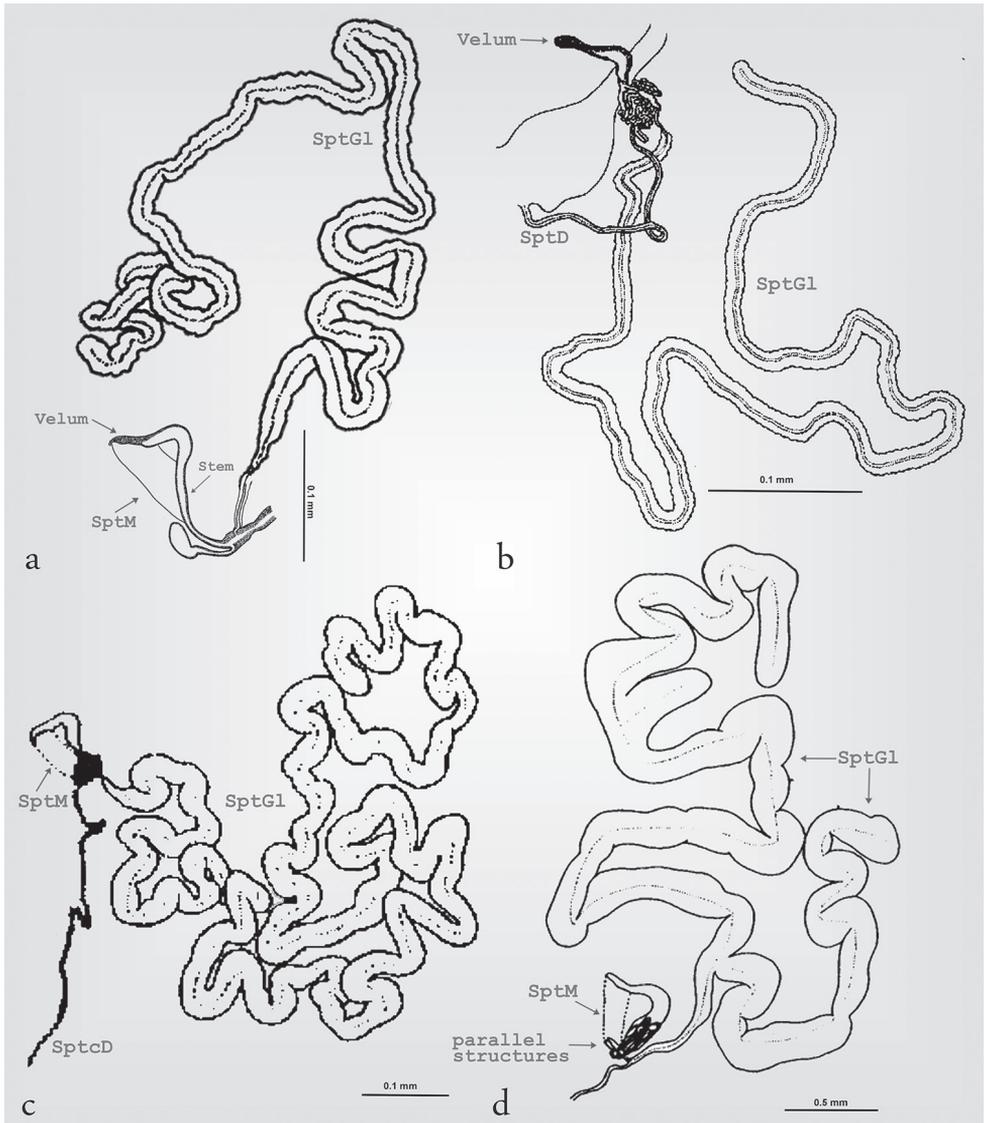


**Figure 4.** Structure of the spermatheca in Zeugophorinae **a** *Zeugophora californica* **b** *Z. varians* **c** *Z. indica*.

fications. All the lateral branches of the SptCd are coiled and form a mass. The CoDu has a diameter greater than that of the lateral ducts, and it is attached in the basal portion of SptCd. The SptCd in *P. atripes* Lacordaire, 1845 is globose and short (Fig. 3g), and the CoDu is thicker. The SptC in *Sphondylia* Weise, 1902 is different because of the tetrahedral form of the SptCp. The stem is short and is joined laterally to the terminal portion. The stem and the terminal portion are connected by the CoDu (Fig. 3i) that is globose, thick, and short. Finally, there is no connection with the SptCd.

The structure of the spermatheca in Zeugophorinae is notably different from Megalopodinae. The ventral wall of SptCp is narrow in *Zeugophora californica* Crothc (Fig. 4a), 1874 and *Zeugophora varians* Crothc, 1873 (Fig. 4b). The SptCd is elongate and twisted towards the apex, the stem is short, and the terminal portion in its last portion is fusiform (Fig. 4a, b). The apex and the terminal portion hold the SptM (Fig. 4b). The SptCd in *Zeugophora indica* Jacoby, 1903 (Fig. 4c), *Z. annulata* (Fig. 5d), and *Z. javana* (Fig. 6c) is an elongate and complex structure that is branched into three ramifications coiled in a subspherical mass (Suzuki 1988, Reid 1992). The terminal portion in its last portion presents two parallel structures that hold the SptM (Figs 4c, 5d). The SptGl is branched (Fig. 5d). The SptCd in *Z. toroja* (Fig. 6b), *Z. vitinea* (Fig. 6d), and *Z. williamsi* (Fig. 6e) is somewhat elongate, and it forms two terminal branches and do not form any type of mass. The last portion of SptCd is mound-shaped. Sekerka and Vives (2013) mentioned that *Z. riedeli* (Fig. 6f) has a characteristic velum and a long well coiled duct that is connected many times with the vasculum (= SptCp).

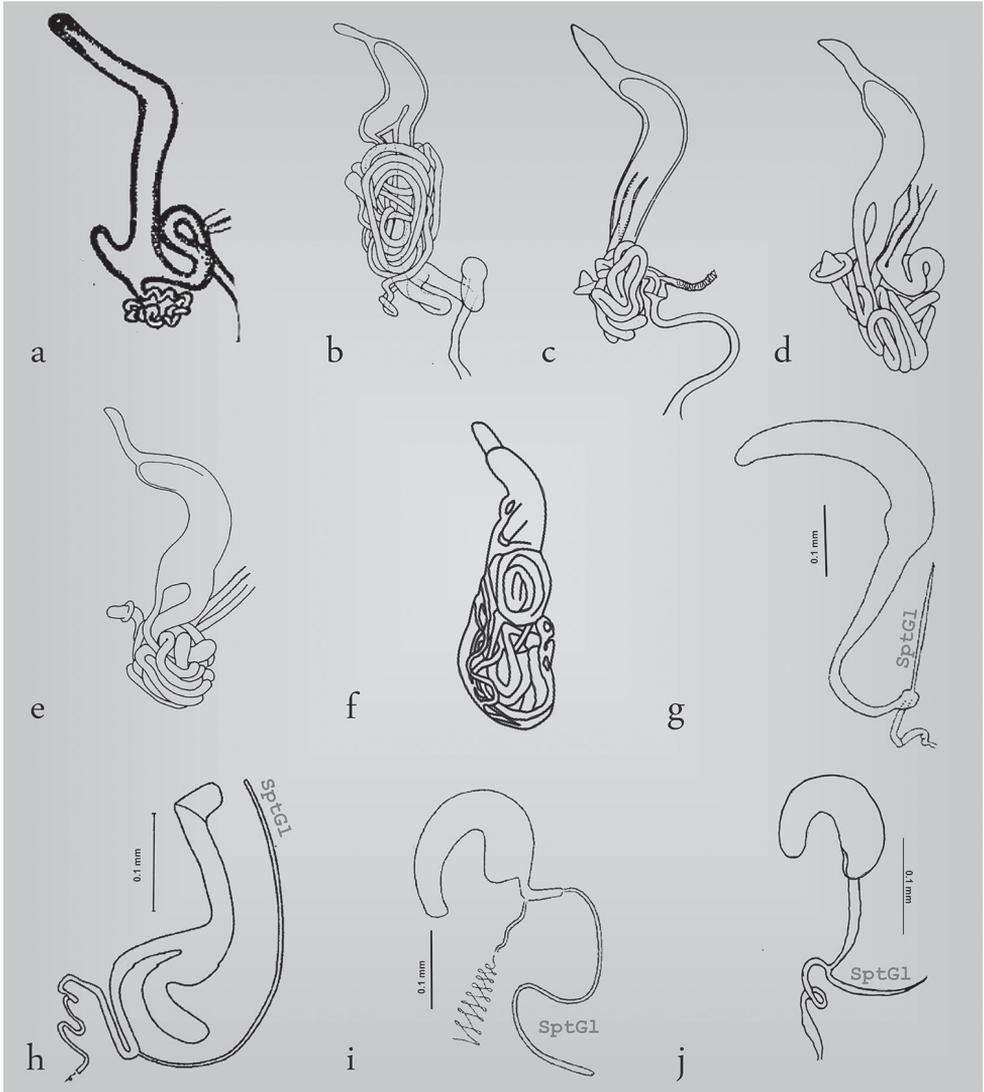
The subfamily Palophaginae (Figs 6g–j) has a simple spermatheca. The SptGl is short and narrow, and the SptCp is variable among the species. *Palophagus bunyae* Kuschel, 1990 (Fig. 6g), *P. australiensis* Kuschel, 1990 (Fig. 6h), and *Palophagoides vargasorum* Kuschel, 1996 (Fig. 6j) have an elongate SptCd. The SptGl and SptD are connected in the terminal portion. *Cucujopsis setifer* Crowson, 1946 (Fig. 6i) has the SptD reduced, and it is connected laterally with the SptCd. *Palophagus bunyae* (Fig. 6g) and *C. setifer* (Fig. 6i) have the SptD very long and coiled (Kuschel and May 1990, 1996).



**Figure 5.** Spermatheca and spermathecal gland in Megalopodinae (a–c) and Zeugophorinae (d). **a** *Agathomerus* sp. **b** *Temnaspis* sp. **c** *T. japonica* **d** *Zeugophora annulata*. Images from Suzuki (1988, 2003).

## Discussion

The structure of the spermatheca in Megalopodidae (Palophaginae + Zeugophorinae + Megalopodinae) is complex, and it is associated with a high diversity in forms. This variability affords characters with great taxonomic and phylogenetic value at various taxonomic levels. The structure of the spermatheca has been used to delimited species, that is the case of the genus *Mastostethus* (Rodríguez-Mirón and Zaragoza-Caballero 2017).



**Figure 6.** Structure of the spermatheca in Megalopodinae (a), Zeugophorinae (d–f) and Palophaginae (g–j). a *Megalopus* sp. 2 b *Zeugophora toroja* c *Z. javana* d *Z. vitinea* e *Z. williamsi* f *Zeugophorella riedeli* g *Palophagus bunyae* h *P. australiensis* i *Cucujopsis setifer* j *Palophagoides vargasorum*.

The spermatheca in Megalopodidae consists of a SptC, SptD, and SptGl, which is the arrangement that is the commonest in Coleoptera, including Chrysomeloidea, except in *Vesperus luridus* (Rossi, 1794) (Vesperiidae), which does not have an SptD or an SptGl (De Marzo 2008). The SptC of Coleoptera is usually well sclerotized, as in Megalopodidae (Figs 2–4), and this condition that helps with sperm storage (Suzuki 1988, Candan et al. 2010). However, the families Orsodacnidae and Vesperiidae have a membranous SptC (Suzuki 1988, Saito 1993).

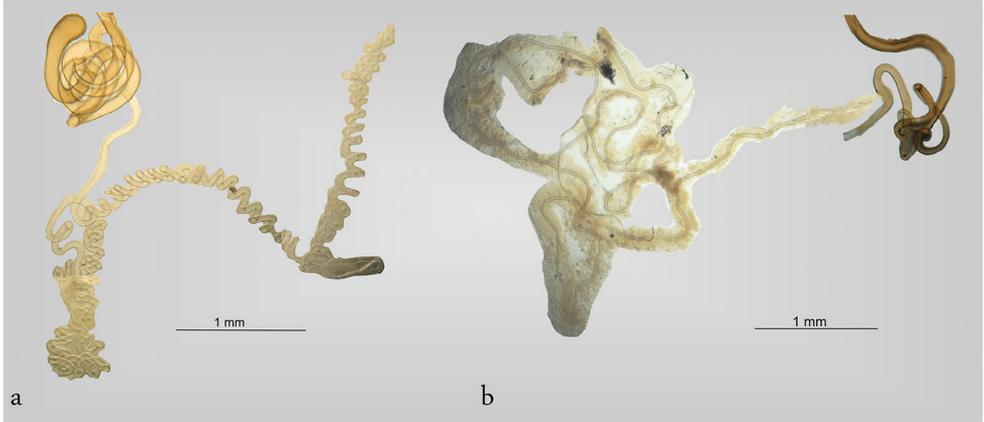
The SptC has a particular structure in the three subfamilies of Megalopodidae. The morphology of the SptCp and SptCd in Zeugophorinae and Megalopodinae is complex (Suzuki 1988, 2003), similar to that of Disteniidae where the SptC has a complex arrangement in the SptCd, the stem being globose, the SptCp being C-shaped, and the SptC being “?-shaped” (Lin and Murzin 2012, Bi and Lin 2013). In Chrysomelidae, Orsodacnidae and Cerambycidae the SptC is simple, C-shaped or hook-shaped, and the SptCd is wide (Suzuki 1988, Hernández 1993, Hernández and Ortuño 1992, Mergen 2004, Chamorro-Lacayo et al. 2006, Yus-Ramos 2008, Gui-Yi and Li 2012).

The C-shaped SptC is present in Palophaginae (Fig. 6i, j), the sister group of the remaining two subfamilies of Megalopodidae (Reid 1995, Marvaldi et al. 2009). Lamiinae (Cerambycidae) has a narrow SptCd and a wide SptCp (Hernández and Ortuño 1992, Hernández 2000, Lin et al. 2009). The SptCp in Vesperidae is like an elongate sack, and this character is considered a plesiomorphic state (Saito 1993, De Marzo 2008). Considering the last idea, the C-shaped SptC in Megalopodidae (Fig. 6i, j) could be considered as a plesiomorphic state present in a common ancestor of Orsodacnidae, Cerambycidae, Chrysomelidae, and Megalopodidae. Moreover, the complex arrangement of the SptC in Megalopodidae (Figs 2–5, 6a–f) could be considered as an apomorphic state. These changes, from simple to complex structure in the SptC, have been mentioned as an evolutionary change in Cerambycidae (Saito 1993) and Criocerinae (Matsumura et al. 2014).

The shape and length of the SptGl and SptD are not taxonomically or phylogenetically diagnostic among families. These structures should be considered as homoplastic, in view of the heterogeneity in Cerambycidae and Chrysomelidae (see Suzuki 1988, Saito 1993). Even so, the SptGl of Megalopodidae transitions from simple to complex. Palophaginae has a short SptGl (Fig. 6g, j) (Kuschel and May 1990, 1996), in contrast with Zeugophorinae and Megalopodinae (Figs 5a–d, 7b), where it is longer and thicker in comparison to the SptC. The SptGl in Zeugophorinae is branched (Fig. 5d) (Suzuki 1988, 2003).

The SptD in Megalopodidae is characterized by being longer than the SptC (Figs 2i; 3a, b; 5b; 7a). The SptD length has a close relationship with the flagellum length in males. That is the case of *Megalopus armatus* Lacordaire, 1845, where the flagellum goes until the spermatheca and leaves the spermatophore (Flowers and Eberhard 2006). This relationship has been found in some species of leaf beetles (Chrysomelidae), such as in *Chelymorpha alternans* Boheman, 1884 (Cassidinae) (Rodríguez et al. 2004) and in some species of *Lema* (subgenus *Lema*) Fabricius, 1798 (Criocerinae) where it is considered as a plesiomorphic state (Matsumura and Suzuki 2008). Also, a relationship between the SptD and the flagellum has been found in Staphylinidae (Gack and Peschke 1994).

The correlation of the lengths of the reproductive organs in Megalopodinae is characteristic of the genus *Megalopus*. However, in the genera *Homalopterus*, *Temnaspis*, and *Agathomerus*, this correlation is obscured because the SptD is very long and coiled (Figs 3c, d, 7a). Moreover, *A. flavomaculatus* (Fig. 2d) and *A. signatus* (Fig. 2e) have a very long SptCd, in contrast to *Megalopus*, where the SptD is shorter and not coiled, and the SptCd is short (Figs 3a, b, 6a). The length of the flagellum has been pointed



**Figure 7.** Spermathecal duct and gland in Megalopodidae (Megalopodinae). **a** spermathecal duct of *Homalopterus tristis* **b** spermathecal gland of *Agathomerus (Eugathomerus) sellatus*.

out as the main factor for fitness, where the selective pressure favors a longer flagellum as a result of sexual selection (e.g. Rodriguez et al. 2004, Matsumura and Suzuki 2008).

The SptM has an important function in reproduction. The SptC in Coleoptera is adapted in many ways to give two places of insertion of the muscle fibers, which form the SptM (De Marzo 2008). The surface of the SptC in Megalopodidae has two forms for connecting the muscle fibers. The first one is present in Megalopodinae, where the fibers connect the apex of the SptC with the stem (Figs 1b, 5a). The second way is where the apex is connected with the terminal portion; it is present in Zeugophorinae (Figs 4b, 5d). The SptM in Palophaginae has not been described.

Some characters in the spermathecae possibly diagnose genera or groups of genera. For example, the arrangement of the SptC is similar within the American group (*Agathomerus*, *Homalopterus*, *Megalopus*, and *Mastostethus*), but is different from that found in *Poecilomorpha*, *Temnaspis*, and *Sphondylia*, because of the presence of a velum in the American group. *Sphondylia* differs from the rest of the genera of Megalopodinae, due to the tetrahedral arrangement of the SptCp (Fig. 3i).

The walls thickness of SptC have differences among Megalopodinae. The apical portion in *Poecilomorpha* and *Temnaspis* is acuminate (Fig. 3c–e, g). These walls are gradually reduced in the American group (Figs 1, 2, 3a, b).

Within the subfamily Zeugophorinae, there are differences in the SptC. The genus *Zeugophorella* Sekerka, 2013 (Fig. 6f) has multiple connections between the SptCd and the SptCp. Such connections are not present in *Zeugophora* Kunze, 1818. Between the Nearctic species and the Asian species that were sampled in this study, there are differences in the arrangement of the SptC. The North American species (*Z. californica* and *Z. varians*) have a curved and elongate SptCp (Fig. 4a, b). Among the Old World species, *Z. indica*, *Z. annulata*, and *Z. javana* have an SptCd with a complex mass of ducts forming three branches (Figs 4c, 5d, 6c) (Suzuki 1988, Reid 1992). In addition, the structure that holds the SptM is different. In the Nearctic species, it is fusiform (Fig. 4a, b); in *Z. indica* and *Z. annulata* (Figs 4c, 5d), this structure is like two paral-

lel bars, and in *Z. javana* (Fig. 6c), *Z. vitinea* (Fig. 6d), and *Z. williamsi* (Fig. 6e), it is mound-shaped. *Zeugophora annulata* has been treated as part of the subgenus *Pedrillia* Westwood, 1864, but this subgenus was just synonymized with *Zeugophora* (Sekerka and Vives 2013). This taxonomic change was made because of the lack of diagnostic characters that validate the subgenus *Pedrillia*. The spermatheca provides characters to diagnose genera and subgenera. Particularly useful is the SptCd of the SptC, which is different between the North American species and the Asiatic species of *Zeugophora*.

## Conclusions

The present study compares the spermathecae of Megalopodidae, and it considers species from all three subfamilies (Megalopodinae, Zeugophorinae and Palophaginae). It describes for the first time this structure for 20 taxa.

We conclude that the SptCp variations are informative and useful in diagnosing these three subfamilies. In addition, the variations observed in the distal portion of the SptCd are diagnostic of several genera, and, in some cases, groups of genera, such as the American group.

Finally, we believe that the spermatheca has a high taxonomic value for diagnosing taxa at various ranks within Megalopodidae. However, further testing of this hypothesis, to be provided by phylogenetic analyses, will establish the phylogenetic signal and corroborate the homology hypothesis of this character complex.

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# Insights on the genus *Acronymolpus* Samuelson with new synonymies and exclusion of *Stethotes* Baly from the fauna of New Caledonia (Coleoptera, Chrysomelidae, Eumolpinae)

Jesús Gómez-Zurita<sup>1</sup>

<sup>1</sup> *Animal Biodiversity and Evolution, Institute of Evolutionary Biology (CSIC-Universitat Pompeu Fabra), 08003 Barcelona, Spain*

Corresponding author: Jesús Gómez-Zurita ([j.gomez-zurita@csic.es](mailto:j.gomez-zurita@csic.es))

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## Abstract

In this work, several taxonomic problems affecting the recently erected genus *Acronymolpus* Samuelson, 2015, endemic to New Caledonia, are addressed. Two of the three New Caledonian species described in *Stethotes* Baly are transferred to *Acronymolpus* and their priority is recognized over the names proposed in the revision of this genus. Moreover, different forms of *Acronymolpus* always found in sympatry, one reddish and larger, and the other black and smaller, were each given species status in that revision, but they are recognized here as the females and males, respectively, of the same species. The taxonomic summary of these discoveries is: (i) *A. bertiae* (Jolivet, Verma & Mille, 2007), **comb. n.** = *A. meteorus* Samuelson, 2015, **syn. n.**, and *A. turbo* Samuelson, 2015, **syn. n.**; and (ii) *A. jourdani* (Jolivet, Verma & Mille, 2013), **comb. n.** = *A. gressitti* Samuelson, 2015, **syn. n.**, and *A. joliveti* Samuelson, 2015, **syn. n.** New distribution data and the male genitalia and the spermatheca of the two valid species of *Acronymolpus* are described for the first time with reference to taxonomically important characters. Finally, the last New Caledonian species described in *Stethotes* is recognized here as a member of the endemic genus *Taophila* Heller: *T. mandjeliae* (Jolivet, Verma & Mille, 2010), **comb. n.**

## Keywords

Eumolpinae, New Caledonia, new combinations, new synonymys

## Introduction

The fauna of Eumolpinae in New Caledonia has received considerable attention in recent years, including the description of several genera and many species (e.g., Jolivet et al. 2007, 2010, 2013), the first molecular phylogenies of this fauna (Papadopoulou et al. 2013; Gómez-Zurita and Cardoso 2014), and some revisionary work (Gómez-Zurita 2011a, 2011b), including the revisions of two endemic genera, *Taophila* Heller and *Acronymolpus* Samuelson, both by the entomologist G. Allan Samuelson (2010, 2015). *Acronymolpus* is a member of the Eumolpini characterized, among other things, by a small but bulky, fusiform body (almost diamond shaped in the larger taxa), long antennae and a very short abdomen, with the first ventrite accommodating very large metacoxae and projecting a long, acute triangular process between them. The genus currently includes four species (Samuelson 2015). Important as this study is in highlighting the singularity of the Eumolpinae in the Western Pacific archipelago with a new endemic genus, it was still preliminary in (i) lacking descriptions of a highly relevant taxonomic character such as the penis, and (ii) not fixing an important taxonomic blunder with implications in Eumolpinae systematics and biogeography. Samuelson (2015) was well aware about the first problem, but considered it a necessary weakness “owing to the rarity of specimens, [whereby] three of the species are left intact and not compromised by dissecting” (Samuelson 2015: 94). Unfortunately, in his revision he did not correct the misinterpretation of previous authors, who described species clearly allied to *Acronymolpus* but placing them in a genus of a different tribe, the Typophorini *Stethotes* Baly.

In this article, the opportunity offered by the availability of new material of *Acronymolpus* from the Museum of Natural History of the University of Wrocław (MNHW, Wrocław) and the Hungarian Natural History Museum (HNHM, Budapest) is used to address the abovementioned problems and discuss their taxonomic and biogeographic implications. Because the solution to this taxonomic conundrum involves connections with the genus *Stethotes*, an additional observation and taxonomic act involving a species described in this genus but not related to *Acronymolpus* is presented in this manuscript, definitively excluding the presence of the former genus in New Caledonia.

## Materials and methods

The specific material for each taxon treated in the study, including all available label information, is given under each species treatment. Type material of *Stethotes bertiae* Jolivet, Verma & Mille, 2007 as well as a reassessment of other taxa mentioned in this study confirming the main conclusions presented in this work were kindly informed by G. Allan Samuelson (Bishop Museum, Honolulu, Hawai'i), after I shared these results with him. The specimens were dissected and studied using a Leica M80 stereomicroscope. Genitalia were mounted dry next to the specimen and pictures were taken to aid line drawings using a Leica DFC420 digital camera and stacking with the freely distributed software CombineZP (Alan Hadley, distributed by the author: alan@

micropics.org.uk). Beetle anatomic features were described using the standard nomenclature proposed by Lawrence et al. (2010) for exoskeletal parts and Wagner (2007) specifically for the spermathecae.

## Results and discussion

### Reassessment of a repeated geographic and taxonomic pattern

An interesting circumstance affecting *Acronymolpus*, unapproachable by A. Samuelson because of his scant material for study and zeal in avoiding dissection, is the fact that the four species that he described are known from two distant areas only, and each locality has two divergent forms of the genus. This repeated pattern may be suggestive of some kind of general process allowing the coexistence of related species of *Acronymolpus* only if they differ enough in some traits, at least anatomically. One of these forms is larger (3.0–3.3 mm), broader, more convex and reddish, and the other one is smaller (2.4–2.6 mm), more slender, less convex and black. These divergent forms would be, respectively, *A. turbo* Samuelson and *A. meteorus* Samuelson from Col d'Amieu and a nearby locality, and *A. jolivetii* Samuelson and *A. gressitti* Samuelson from Mont Panié. The availability for this study of MNHW material from a third locality in the Central Chain (L'Aoupinié) showed the coexistence of the same two forms.

However, the dissection of material from all known localities where *Acronymolpus* is present proved that what could be an interesting case of competitive exclusion or niche partitioning of some kind is nothing but sexual dimorphism. The large reddish specimens are always the females and the black, small specimens are the males of two species, one in Col d'Amieu and one in Mont Panié, respectively. Indeed, knowing that these divergent forms represent sexual dimorphic extremes, and that the characters that were used to distinguish them taxonomically are in fact secondary sexual traits, one can concentrate on the traits that help recognizing them as belonging to the same species. One that is obvious is punctation, which is stronger and deeper on the pronotum and even rugose on the elytra of the species in Col d'Amieu, and finer, distinct in the species in Mont Panié (Samuelson 2015). The sexual dimorphism hypothesis was particularly well grounded on data in the case of *A. meteorus* and *A. turbo*, for which a large number of specimens could be studied (see below), and helped establishing a number of relevant taxonomic acts for the genus *Acronymolpus*.

### Taxonomic findings

***Acronymolpus bertiae* (Jolivet, Verma & Mille, 2007), comb. n.**

= *Acronymolpus meteorus* Samuelson, 2015, **syn. n.**

= *Acronymolpus turbo* Samuelson, 2015, **syn. n.**

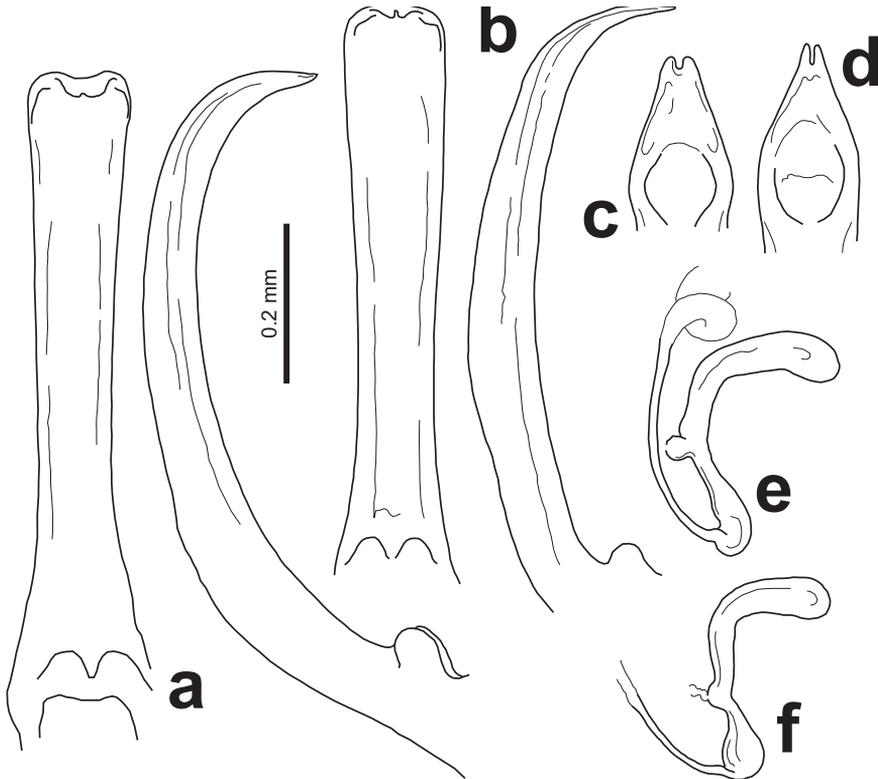
**Material examined. IBE-JGZ:** one male and one female, New Caledonia, Aoupinié, refuge, -21.14890 165.32348, 400 m, 29.xi.2008, leg. M. Wanat, beating rainforest, *Acronymolpus bertiae* (Jolivet, Verma and Mille) J. Gómez-Zurita det. 2017. **HNHM:** (1) one male, New-Caledonie, Col d'Amieu, 19.i.1977, leg. Dr. J. Balogh, *Acronymolpus bertiae* (Jolivet, Verma et Mille) J. Gómez-Zurita det. 2017. **MNHW:** (1) two females, New Caledonia, Col d'Amieu (6.5–7.0 km from gate), 21°35.2'S, 165°46.4'E, 450–470 m, 6.i.2007, leg. M. Wanat & R. Dobosz, night coll.; (2) one male, New Caledonia, Col d'Amieu (3 km from gate), 21°35.1'S, 165°47.8'E, 500 m, 6.i.2007, leg. M. Wanat, *Acronymolpus bertiae* (Jolivet, Verma et Mille) J. Gómez-Zurita det. 2017; (3) one male, New Caledonia, Col d'Amieu (3.0 km to gate), -21.58536 165.79319, 500 m, 16.xi.2008, leg. M. Wanat, *Acronymolpus bertiae* (Jolivet, Verma et Mille) J. Gómez-Zurita det. 2017; (4) one female, New Caledonia, Farino, Parc des Grandes Fougères, Pic Vincent track, -21.60948 165.77459, 600–670 m, 17.xi.2008, leg. M. Wanat; (5) one male and one female, New Caledonia, Farino, Parc des Grandes Fougères, track & forest N of Pic Vincent, -21.59929 165.77519, 670 m, 17.xi.2008, leg. M. Wanat, *Acronymolpus bertiae* (Jolivet, Verma et Mille) J. Gómez-Zurita det. 2017; (6) one male, New Caledonia, Sarramea, trail to Dogny, -21.6229 165.8684, 300–560 m, 9.xi.2010, leg. M. Wanat & R. Ruta, *Acronymolpus bertiae* (Jolivet, Verma et Mille) J. Gómez-Zurita det. 2017; (7) one male and one female, New Caledonia, Aoupinié, road to sawmill, 21°09'S, 165°19'E, 420–530 m, 7.ii.2004, leg. M. Wanat; (8) two males, New Caledonia, Aoupinié, gate to meteo station, 21°11'S, 165°17'E, 900–950 m, 8.ii.2004, leg. M. Wanat; (9) one female, New Caledonia, Aoupinié, Goipin road jct., 21°10.8'S, 165°18.1'E, 730 m, 17.i.2007, night coll., lamp & beating, leg. M. Wanat & R. Dobosz; (10) three males, New Caledonia, Aoupinié, 21°11.0'S, 165°17.5'E, 850–900 m, 18.i.2007, leg. M. Wanat & R. Dobosz; (11) two females, New Caledonia, Aoupinié, 21°11.0'S, 165°17.6'E, 650–800 m, 19.i.2007, leg. M. Wanat; (12) one male, New Caledonia, Aoupinié, -21.17539 165.30952, 700 m, 27.xi.2008, leg. M. Wanat; (13) one female, New Caledonia, Aoupinié, -21.18151 165.30048, 790–830 m, 27.xi.2008, leg. M. Wanat; (14) three males and one female, New Caledonia, Aoupinié, refuge, -21.14890 165.32348, 400 m, 29.xi.2008, leg. M. Wanat, beating rainforest; (15) one male, New Caledonia, Aoupinié, -21.18027 165.30005, 800–830 m, 20.xi.2010, ex *Pycnanandra benthami*, leg. M. Wanat & R. Ruta; (16) six males and two females, New Caledonia, Aoupinié, Goipin rd jct to gate, -21.1814 165.2879, 850–900 m [one with: 700–900 m], 20.xi.2010, leg. M. Wanat & R. Ruta; (17) one male and two females, New Caledonia, Aoupinié, meteo station to summit, roadside, -21.1788 165.2786, 950 m, 21.xi.2010, leg. M. Wanat & R. Ruta.

**Remarks.** Jolivet et al. (2007) described *Stethotes bertiae* based on three specimens collected at Col d'Amieu and compared the new species with *S. minuta* Jacoby, *S. similis* Gressitt and *S. mimica* Gressitt, all endemic from New Guinea (Gressitt 1966; Jolivet et al. 2007). The genus *Stethotes* was proposed with descriptions of nine species from Java, New Guinea, Borneo, and the Moluccas (Baly 1865–1867) and later shown to be particularly species-rich in New Guinea (Gressitt 1966; Medvedev 2009), but also

recorded from other areas in the Australasian region, including Fiji and Samoa (Maulik 1929; Bryant and Gressitt 1957). In this geographic context, it seemed reasonable to find the genus in New Caledonia as well. But the finding of *Stethotes bertiae* had implications beyond the discovery of a genus that had not been previously recorded from New Caledonia and is not known from Australia either. *Stethotes* belongs to the tribe Typophorini, a lineage most diverse in the Old World, particularly in South East Asia and in the Western Pacific, and this lineage is also the one thriving in Fiji, with important biogeographic connections with New Caledonia (Keppel et al. 2009). Interestingly, the vast majority of Eumolpinae in New Caledonia belong to the tribe Eumolpini (Gómez-Zurita 2011a; Papadopoulou et al. 2013; note that in these works, the names Colaspoi-dini and Nodinini were used instead of Eumolpini and Typophorini, respectively). To our knowledge, the only exceptions were *Rhyparida foaensis* (Jolivet, Verma & Mille, 2007) and three species of *Stethotes*, including *S. bertiae* (Gómez-Zurita 2011a).

The original description of *S. bertiae* was very generic, without much useful information on characters that could help in recognizing the correct generic placement of the species, except perhaps the two differentiated arrangements of elytral punctuation: confused at basal half and aligned at apical half of elytra. However, the original description included a photograph of the holotype (Jolivet et al. 2007: 91). *Stethotes bertiae* has the size, the characteristic fusiform shape, the long antennae, the strong punctuation (aligned at apical half of elytra), and most critically, entire tibiae of *Acronymolpus*, a character clearly showing that the species should not be placed in the Typophorini. Moreover, the revision of *Acronymolpus* included one species, *A. meteorus* Samuelson, also collected in the Col d'Amieu and the nearby Plateau de Dogny and sharing all the (apomorphic) peculiarities of *S. bertiae*. Among these, it is worth mentioning the heavy punctuation of pronotum and basal half of elytra, the reddish testaceous coloration of abdominal ventrites, and the finely wrinkled hypomera, referred to as "with heavy isodiametric sculpture" by Samuelson (2015). There is no doubt that Samuelson's species is the same that had been described years earlier by Jolivet et al. (2007), and this claim was recently confirmed by G. Allan Samuelson himself, upon our exchange of opinions, by comparing the type of *S. bertiae* with his own specimens (G. Allan Samuelson, pers. comm.).

The original work describing *Stethotes bertiae* included a drawing of the penis, but as it is customary in contributions by the authors of this species, the sexual organ was shown in lateral view, which is of very limited utility for identification purposes (Gómez-Zurita 2011b). In turn, the description of *A. meteorus* lacked any reference to genital structures. The dissection of the new material available for this species showed that they are all males, and male genitalia could be prepared and described focusing on taxonomically relevant characters for the first time (Fig. 1a, c): the penis is narrow and slender, narrower in median part and curved in lateral view, with apex tapering and more strongly bent ventrally, as described by Jolivet et al. (2007); distal end is flattened dorsoventrally, with sides straight and converging to blunt apex with a short median notch. The dissection of the specimens of *A. turbo*, sympatric and syntopic (judging from collection data shown in labels) with *A. meteorus* in every one of the sites where



**Figure 1.** Ventral and lateral views of the penises of **a** *Acronymlpus bertiae* (Jolivet, Verma & Mille) and **b** *A. jourdani* (Jolivet, Verma & Mille). Dorsal view of the distal ends of the penis of **c** *A. bertiae* and **d** *A. jourdani*. Spermathecae of **e** *A. bertiae* and **f** *A. jourdani*.

this species has been found, showed that they were all females and, as mentioned above, are interpreted here as conspecific with *A. bertiae*. The spermatheca of the species is described here for the first time (Fig. 1e): spermatheca slender, with nodulus and cornu feebly curved and more or less at right or slightly obtuse angle; cornu thicker than nodulus and blunt at apex; nodulus with bulging insertion of spermathecal gland at middle; spermathecal duct inserted nearly at base of nodulus and bent abruptly.

Based on this complete account, which takes into account geographical but mainly anatomical data and the recognition of sexual dimorphism in the species as described above, three taxonomic acts are necessary. The first is the transfer of *Stethotes bertiae* to the genus *Acronymlpus*, resulting in *Acronymlpus bertiae* (Jolivet, Verma & Mille, 2007), comb. n., and the other two are recognizing that *A. meteorus* (males) and *A. turbo* (females) are junior synonyms of this taxon; thus, *Stethotes bertiae* Jolivet, Verma & Mille, 2007 = *Acronymlpus meteorus* Samuelson, 2015, syn. n. and *Acronymlpus turbo* Samuelson, 2015, syn. n.

***Acronymolpus jourdani* (Jolivet, Verma & Mille, 2013), comb. n.**

= *Acronymolpus gressitti* Samuelson, 2015, **syn. n.**

= *Acronymolpus joliveti* Samuelson, 2015, **syn. n.**

**Material examined. HNHM:** (1) one male and one female, New-Caledonie, Mont Panié, 7.ii.1977, leg. Dr. J. Balogh, *Acronymolpus jourdani* (Jolivet, Verma et Mille) J. Gómez-Zurita det. 2017. **MNHW:** (1) one female, New Caledonia (N), Mandjélia (summit) 20°23.9'S, 164°31.9'E, 750–780 m, beating, montane rainforest, leg. M. Wanat & R. Dobosz, *Acronymolpus jourdani* (Jolivet, Verma et Mille) J. Gómez-Zurita det. 2017.

**Remarks.** A few years after the description of *S. bertiae*, Jolivet et al. (2013) described another species of *Stethotes*, *S. jourdani*, very similar to the former but with subtler punctuation and from localities further north in the island, in the Massif du Panié, including La Guen, Dawenia, and Wewec (Jolivet et al. 2013). As before, the species does not have any of the characters of the genus *Stethotes*, but these of *Acronymolpus* instead. Interestingly, it fits the description of the second blackish species of *Acronymolpus* described by A. Samuelson a couple of years later, *A. gressitti*, also collected from Mt. Panié. It is worth noting that both descriptions depart in a significant character: the size of the holotypes. The type of *S. jourdani* is reported as 4.0 mm long (Jolivet et al. 2013), while that of *A. gressitti* is 2.6 mm (Samuelson 2015). The measurement given by Jolivet et al. (2013) is far bigger than the largest *Acronymolpus* studied by Samuelson (2015). However, it is important to note that, judging from the figures in the article, the measurements in Jolivet et al. (2013) may not be reliable. *Samuelsonia gomyi* Jolivet et al., 2013 measures 2.5 mm and it shows slightly longer than the holotype of *S. jourdani*, figured alongside and possibly photographed with the same magnification as the former, since both show an identical scale bar of 2.0 mm (Jolivet et al. 2013, figs 7 and 8). Apart from this detail, the two species, *S. jourdani* and *A. gressitti*, match in their characters, as recognized by the author of the latter (G. Allan Samuelson, pers. comm.), including the four basal antennomeres paler, vertex deeply sulcate, smooth hypomera, and pronotal and elytral punctuation smaller than in *S. bertiae*.

Moreover, additional material, even if limited, made it possible to draw an analogy with the previous case whereby *A. joliveti* could be recognized as the female of *A. gressitti*. The spermatheca of this species was known due to the description of *A. joliveti*, and the only information available on the male genitalia was a drawing of the penis in lateral view (Jolivet et al. 2013: fig. 1). The spermatheca of *A. jourdani*, figured here from a specimen from Mandjélia, is identical to that figured by Samuelson (2015) from a specimen from Mt. Panié (Fig. 1f). This spermatheca is very similar to that of *A. bertiae*, but shows some relevant differences, including a straight nodulus longer than cornu, conspicuously dilated at base and constricted medially at both ends of bulging insertion of spermathecal gland. Here, the first complete description of the penis of *A. jourdani* is provided and is a very useful character to distinguish this species from *A. bertiae* (Fig. 1b, d). The penis is similar to that of *A. bertiae* with a less pronounced

ventral curvature and more gradually curved apex; and the apical end, as seen in dorsal view, has straight sides converging to an acute apex with a deep, narrow median cleft.

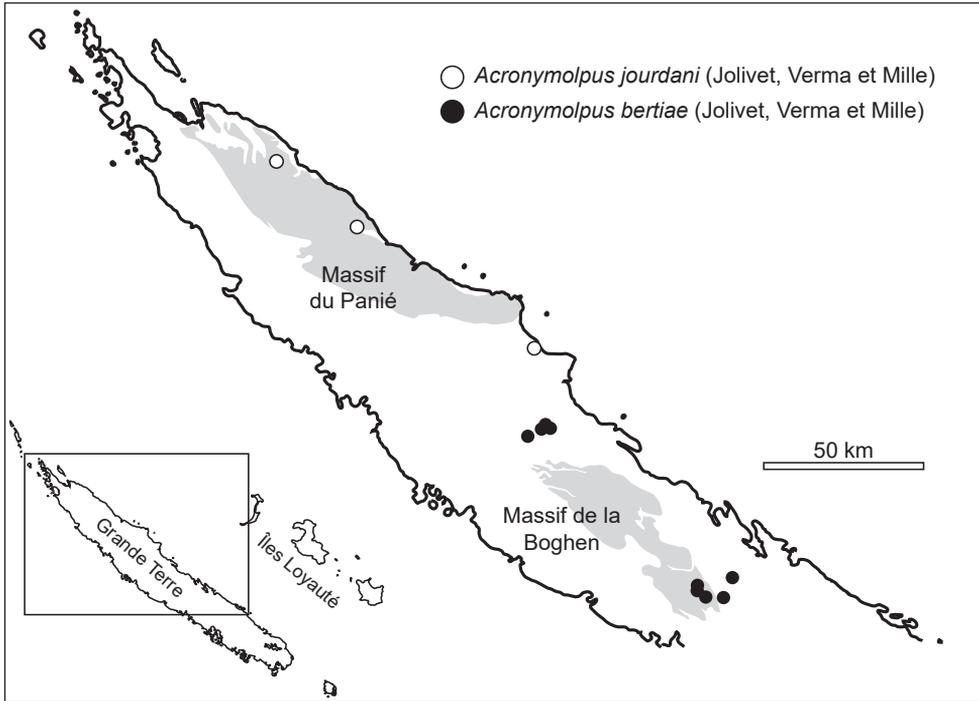
As before, three taxonomic acts are required, the first transferring *Stethotes jourdani* to *Acronymolpus*, to propose the new combination *Acronymolpus jourdani* (Jolivet, Verma & Mille, 2013), comb. n., and the second establishing that *A. gressitti* and *A. joliveti* are junior synonyms of this taxon, thus *Stethotes jourdani* Jolivet, Verma & Mille, 2013 = *Acronymolpus gressitti* Samuelson, 2015, syn. n. and *Acronymolpus joliveti* Samuelson, 2015, syn. n.

### ***Taophila mandjeliae* (Jolivet, Verma & Mille, 2010), comb. n.**

**Remarks.** A third species of Eumolpinae originally ascribed to *Stethotes*, *S. mandjeliae*, was described based on several specimens collected near the summit of Mt. Mandjélia, in the northern part of the Massif du Panié (Jolivet et al. 2010). However, conversely to the other species of *Stethotes* described by the same authors, this species does not belong to the genus *Acronymolpus*. This species unmistakably fits the nominotypical subgenus of *Taophila* instead (Gómez-Zurita and Cardoso 2014), allied to *T. subsericea* Heller, 1916 and *T. corvi* Samuelson, 2010, and easily recognizable by the elongate shape, bicolor antennae, angulated sides of pronotum, which is darker than elytra, marked humeri wider than pronotum, and tapering elytra with partially aligned punctures and stiff hairs, amongst others. It remains to be seen if this species had been previously described by Samuelson (2010), but it may be a valid taxon considering the local area endemism of the Massif du Panié and that no other *Taophila* s. str. had been reported in the area. Until the validity of the species is settled, it is appropriate to propose the following transfer: *Taophila mandjeliae* (Jolivet, Verma & Mille, 2010), comb. n.

### **Geography of *Acronymolpus* and exclusion of *Stethotes* from New Caledonia**

All the localities reported in this study where *S. bertiae* has been confirmed are in the Central Chain, in the northwestern and southeastern edges of the Massif de la Boghen (Fig. 2). Jolivet et al. (2010) reported *Stethotes bertiae* from Mt. Mandjélia, in the northern part of the Massif du Panié, and Jolivet et al. (2013) from a locality in Mt. Panié where they also found *Stethotes jourdani*. It is very likely that these two records relate to the latter species instead. Indeed, the two localities reported here for *A. jourdani* are in the northern part of the Massif du Panié, a separated geographic feature and different area of endemism in New Caledonia relative to the Central Chain and the Massif de la Boghen, where *A. bertiae* occurs (Fig. 2). The holotype of *A. joliveti*, one of the synonyms of *A. jourdani*, is from one locality south from the Massif du Panié, in the valley of one of the rivers discharging in the northern coast of Grande Terre, the Amoa (Samuelson 2015), not so distant from the range



**Figure 2.** Distribution of *Acronymolpus bertiae* (Jolivet, Verma & Mille) and *A. jourdani* (Jolivet, Verma & Mille) in New Caledonia.

of Aoupinié, where the other species, *A. bertiae*, has been found in the current study. However, they are clearly different species based on the analysis of external morphology and their genitalia.

New Caledonia is very rich in species of Eumolpinae of the Eumolpini tribe (Papadopoulou et al. 2013), but the fauna of the archipelago encompassed the Typophorini as well, including one species of *Rhyparida* and three species of *Stethotes* (Eumolpinae: Typophorini) described and reported from Grande Terre (Jolivet et al. 2007, 2010, 2013): *S. bertiae*, *S. jourdani*, and *S. mandjeliae*. This classification had an important implication relative to the biogeography of New Caledonia, namely that the island had been repeatedly colonized by Eumolpinae on, at the very least, three occasions. These would include a minimum of one colonization by Eumolpini, which may have given rise to the high diversity of species in this tribe that we see today in the island (Papadopoulou et al. 2013), once by the Typophorini *Rhyparida*, and at least once by *Stethotes* (Gómez-Zurita 2011a). However, the two most significant findings of this study contradict this interpretation, i.e., the recognition that none of these species supposedly of *Stethotes* belongs to the tribe Typophorini based on the absence of the defining traits of this tribe, and that they belong to two possibly related genera of Eumolpini, *Acronymolpus* in the case of *S. bertiae* and *S. jourdani*, and *Taophila* in the case of *S. mandjeliae*. The fauna of Chrysomelidae of New Caledonia is under intense

scrutiny and it is possible that native populations of *Stethotes* may be found in the future. However, at present, the genus must be removed from the faunistic catalogues of the archipelago, which stands out as a center for rich endemic diversity of Eumolpini that may have evolved *in situ* after one or very few colonization events by members of this tribe in the Late Eocene (Papadopoulou et al. 2013).

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# Traumatic mating by hand saw-like spines on the internal sac in *Pyrrhalta maculicollis* (Coleoptera, Chrysomelidae, Galerucinae)

Yoko Matsumura<sup>1</sup>, Haruki Suenaga<sup>2</sup>, Yoshitaka Kamimura<sup>3</sup>, Stanislav N. Gorb<sup>1</sup>

**1** Department of Functional Morphology and Biomechanics, Zoological Institute, Kiel University, Am Botanischen Garten 1-9, D-24118 Kiel, Germany **2** Sunshine A205, Nishiachi-chô 833-8, Kurashiki-shi, Okayama Pref., 710-0807, Japan **3** Department of Biology, Keio University, 4-1-1 Hiyoshi, Yokohama 223-8521, Japan

Corresponding author: Yoko Matsumura ([yoko.matsumura.hamupeni@gmail.com](mailto:yoko.matsumura.hamupeni@gmail.com))

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## Abstract

Morphology of the aedeagus and vagina of *Pyrrhalta maculicollis* and its closely related species were investigated. The internal sac of *P. maculicollis* bears hand saw-like spines, which are arranged in a row. Healing wounds were found on the vagina of this species, whose females were collected in the field during a reproductive season. However, the number of the wounds is low in comparison to the number of the spines. In addition, males of *P. tibialis* bear one spinous sclerite on the internal sac, but the female of this species show no wounds on the vagina. The vaginal wall is thicker in *P. maculicollis* and *P. tibialis* in comparison to other studied species, whose males bear no spinous sclerite. This thickening in *P. maculicollis* is likely a counter-adaptation to wound infliction. *Pyrrhalta maculicollis* has a narrow internal sac in comparison to that of other *Pyrrhalta* species. Narrow internal sacs with spines can be potentially disadvantageous because their movement during copulation likely enhances the risk of self-infliction. Males of *Pyrrhalta* species have tiny membranous projections densely covering the internal sac surface, and it is hypothesized that they prevent damaging their own internal sac during everting and withdrawing the internal sac with the spines.

## Keywords

Copulation, genitalia, insect, internal sac, leaf beetles, mating systems

## Introduction

Traumatic mating is one of the well-observed phenomena in invertebrate mating systems (Lange et al. 2013, Reinhardt et al. 2015). Morphology of trauma-causing structures and ways of inflicting traumas diversified in the course of evolution (Lange et al. 2013). Examples of traumatic mating can be divided into three categories: traumatic insemination, traumatic secretion transfer, and traumatic penetration (Lange et al. 2013). In cases of the former two categories, wounds function as the entrance of sperm or seminal secretions without spermatozoa into the female body, respectively. There is continuing debate about the function and significance of mating trauma caused in the examples of the third category (Lange et al. 2013). On the contrary, female counter-adaptations, as response to traumatic mating, are less studied: however, some exemplary cases of female adaptations are known. For example, seed beetle females possess the thickened vaginal wall, as response to the spiny male penis (Rönn et al. 2007). Bed bug females have a spermatheca that is an organ specialized to receive hypodermically injected sperm. Recent studies revealed that (1) physiological responses of this organ defend female body cavity against pathogens (Reinhardt et al. 2003) and that (2) the rubber-like protein, resilin, dominates in the wound inflicted areas of the organ to tolerate the traumatic cuticle penetration (Michels et al. 2015). Recently, additional examples of traumatic mating in a sea slug, earwig, and twisted wing parasite have been reported (Lange et al. 2014, Kamimura et al. 2016, Peinert et al. 2016). In one of the most mega-diversified group Coleoptera, hitherto only a few examples of traumatic mating are known: some Chrysomelidae (Bruchinae, Crudgington and Siva-Jothy 2000; Galerucinae, Flowers and Eberhard 2006), a species of Carabidae (Carabinae, Okuzaki et al. 2012), and as results of heterospecific mating in Carabidae (Sota and Kubota 1998).

In insects, male trauma inflicting structures usually locate in aedeagi, whose morphology is usually one of the best diagnoses especially in beetle systematics (Crowson 1981). Recently internal sac morphology is also described in many taxonomic papers. Possible wound inflicting structures, such as sharply pointed spines, have been described for many beetle groups, although it is usually unknown, whether they have a function in relation to traumatic mating. For example, regularly arranged spinous sclerites on the internal sac have been reported for the leaf beetles *Pyrrhalta maculicollis* and *P. sulcatipennis* (Nie et al. 2012, 2013). To examine the possibility of traumatic mating in species of this genus, we investigated morphology of the genitalia using species from Japan: *Pyrrhalta maculicollis*, *P. humeralis*, *P. tibialis*, and some members of the *Tricholochmaea semifulva* species complex (hereafter *Tricholochmaea semifulva* species complex) (Takizawa and Suenaga, unpubl. data). *Tricholochmaea semifulva* species complex was treated as *Pyrrhalta semifulva* before (Kimoto and Takizawa 1994) because of morphological affinity. Therefore *T. semifulva* species complex was chosen in the current paper for an outgroup comparison. Despite of a series of great works on *P. maculicollis* and related species on speciation (Nie et al. 2012, 2013, Zhang et al. 2014, 2015) and broad life history survey of Japanese leaf beetles (Takenaka 1963, Lee 1990, Kimoto and Takizawa 1994), we do not have much information on basic

mating biology of *Pyrrhalta* species and applied a correlational method among species for the current study. First the morphology of male genitalia was investigated and then whether female vaginas have wounds or not to test correlations between spinous structures and wounds existences. Possible counter-adaptations in the females were also examined by measuring thickness of the vagina. In addition, irrespective of the functional significance of traumatic mating, wound-inflicting organs might require related adaptations in the male morphology, although this perspective has been totally overlooked in previous studies. In male beetles with a wound inflictor on the internal sac of the aedeagus, it may potentially harm the internal sac surface during repeated eversion and withdrawal of the internal sac. Based on comparisons among related species with an outgroup species, we also discuss possible male co-adaptations to traumatic mating.

## Materials and methods

The male and female genitalia of the following four species were examined: *Pyrrhalta maculicollis*, *P. humeralis*, *P. tibialis*, and *Tricholochmaea semifulva* species complex with a special focus on *P. maculicollis*, which has spines on the internal sac. In regards to the scientific name, *P. maculicollis* had been treated as *Xanthogaleruca maculicollis* previously (e.g. Beenen 2010). However, in the latest taxonomic paper (Nie et al. 2013), the genus *Xanthogaleruca* was treated as a synonym of the genus *Pyrrhalta* and this is followed here.

Examined specimens were mainly collected in the Okayama prefecture, Japan with some exceptions. For *P. maculicollis* we used individuals also from the Kanagawa prefecture, Japan, for *P. tibialis* two specimens from the Hokkaido prefecture, for *P. humeralis* one specimen from the Ehime prefecture, and for *T. semifulva* species complex two samples from the Oita prefecture.

To show general morphology and measure body sizes and the dimensions of genital spines, we dissected and observed samples under the stereomicroscopes (Nikon SMZ 745: Nikon Corporation, Tokyo, Japan; Olympus SZX12: Olympus Corporation, Tokyo, Japan; Leica M205 A with the camera Leica DFC420 and the software LAS 3.8: Leica Microscopy GmbH, Wetzlar, Germany) and the light microscope Zeiss Axioplan equipped with the camera Zeiss Axio Cam MRc (Carl Zeiss Microscopy GmbH, Jena, Germany). Then the sizes were measured with aids of the software Fiji (Schindelin et al. 2012) using the segmented line tool based on the taken images. For spine length measurement, we measured the length of five spines per male, one from each apical-, subapical-, middle-, subbasal-, and basal section of the spine row. For measurement of relatively well-sclerotized structures we used 99.5 % ethanol fixed specimens for *Pyrrhalta maculicollis* and dried specimens for other species. Potassium hydroxide was used to macerate muscles, when necessary, for visualization of skeletal structures.

To understand three-dimensional configuration of the aedeagus of *Pyrrhalta maculicollis* the aedeagus was dissected out from 99.5 % ethanol preserved specimens, dehydrated up to 100 %, and dried with a critical point drier (E3100 CPDA/Quorum

Technologies LTD, Kent, UK). Then the sample was glued onto a thin-wall borosilicate glass capillary (120 × 1 mm, Hirschmann-Laborgeräte GmbH & Co. KG, Eberstadt, Germany) with super glue and scanned using the high-resolution micro-computed tomography ( $\mu$ CT) SkyScan 1172 (RJL Micro & Analytic GmbH, Karlsdorf-Neuthard, Germany) with a current of 250  $\mu$ A and a voltage of 40 kV. Segmentation of each structure was carried out using the software Amira 5.4 (Visualization Sciences Group, Mérégnac, France).

Some additional internal sac specimens of *Pyrrhalta maculicollis* were also dried with the same methods and sputter coated with gold-palladium (ca. 10 nm thickness) using the Leica EM SCD 500 High Vacuum Sputter Coater (Leica Microscopy GmbH) for detailed surface investigations using the Hitachi S4800 and TM3000 scanning electron microscopes (Hitachi High-Tech. Corp., Tokyo, Japan) at an accelerating voltage of 3 kV and ca. 15 kV, respectively. For interspecific comparisons, we also used internal sac samples dried at room temperature.

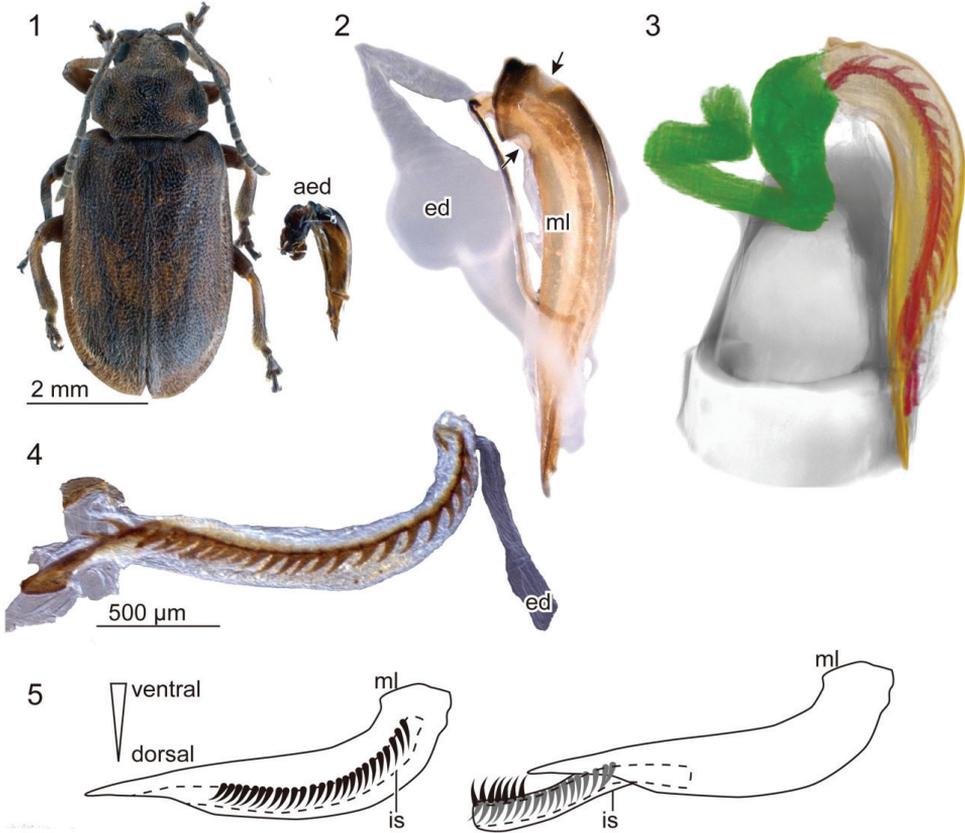
For interspecific comparisons of the vaginal wall thickness, we dissected female vaginas from freshly killed samples in phosphate-buffered saline (PBS; Carl Roth GmbH & Co. KG, Karlsruhe, Germany) and fixed with 2.5 % glutaraldehyde for one to three weeks. Two females per species were fixed except for *P. tibialis*, for which only one sample was treated. The samples were washed with PBS at least three times, dehydrated with a series of ethanol up to 100 % ethanol. Then they were gradually replaced with Epon 812 (Glycidether 100; Carl Roth GmbH & Co. KG), and finally the samples were embedded in the Epon resin. All procedures were processed at room temperature, but polymerisation was done at 60 °C for two days. Semi-thin sections (ca. 300–700 nm) were prepared using the Leica EM UC7 ultramicrotome (Leica Microscopy GmbH). Sections were stained with 0.1 % toluidine blue for three to four hours, and overstained dye was removed by retaining the slices in glycerine for two days. Images of the sections were then taken with the light microscope Zeiss Axioplan equipped with the camera Zeiss Axio Cam MRc. Following the method of Rönn et al. (2007), the areas of muscles and epidermis plus cuticle were measured with aids of the software Fiji.

A Fisher's exact probability test was adopted for comparing the occurrence rate of mating trauma among species. All statistical analyses were carried out using R 3.2.0 (R Core Team 2015).

## Results

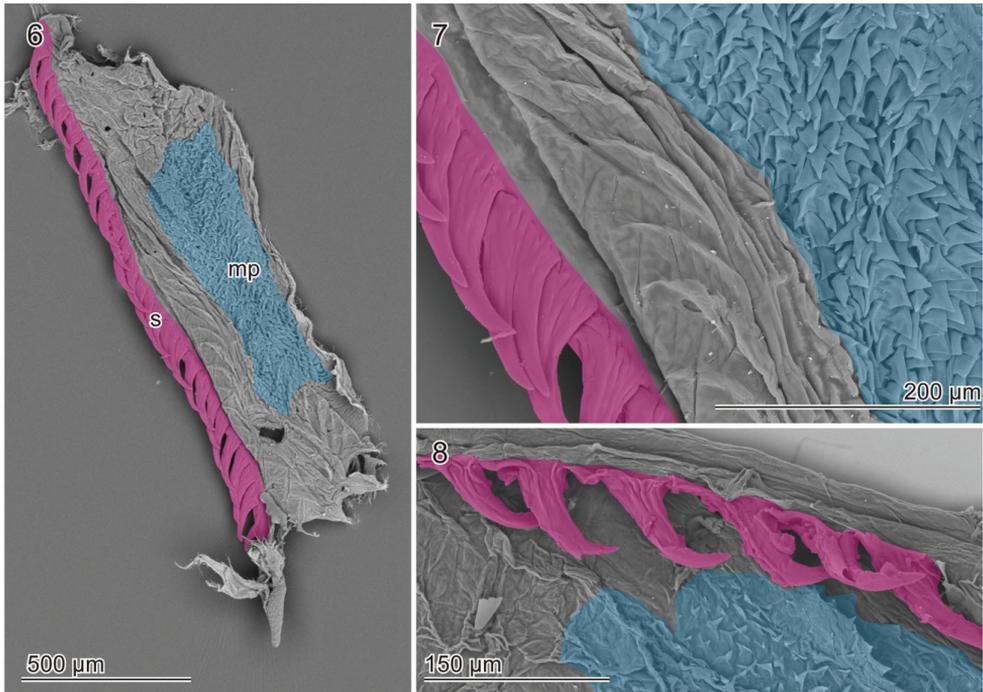
### Anatomy of the male aedeagus of *Pyrrhalta maculicollis*

The males have a relatively stout aedeagus (Fig. 1). The median lobe has two small membranous regions on the proximal part in the lateral view (Fig. 2, arrows). The distal part of the ejaculatory duct, which is located adjacent the aedeagus, is enclosed by well-developed circular muscles (Fig. 3). This section of the ejaculatory duct is



**Figures 1–5.** Aedeagus of *Pyrrhalta maculicollis* in the lateral view **1** relative size of the aedeagus compared to body size **2** the aedeagus and a part of the ejaculatory duct, muscles completely macerated. Two arrows point to the membranous areas of the median lobe **3** a micro CT scanned and segmented aedeagus and a part of the ejaculatory duct. The green structure represents the part of the ejaculatory duct with well-developed circular muscles, the yellow one represents the median lobe, and the red ones represent spines on the internal sac **4** the internal sac at rest with a part of the ejaculatory duct (ed) **5** schemes of the aedeagus at rest (left) and with partly evaginated internal sac during copulation (right). Abbreviations: aed, aedeagus; ed, ejaculatory duct; is, internal sac; ml, median lobe.

widened and its wall is folded at repose. When the surrounding muscles are macerated, this section is swollen (Fig. 2). Well-developed spines are situated on the ventral side of the internal sac, and the spines are caudally curved (Figs 3, 4). This means that the evaginated internal sac wears the spines pointing in the opposite direction (Fig. 5), which will result in anchoring the vagina during copulation (Figs 5, 13). The spines are pigmented and look like well-sclerotized structures. However, in the samples that had been dried at room temperature, the surface of the spines is slightly shrunk (Fig. 8) compared with that of critical-point dried samples (Figs 6, 7). The number and size of spines are variable among individuals within a population (Kanagawa, Japan; Table 1). The surface of the internal sac is largely covered with tiny projections (Figs 6, 7).



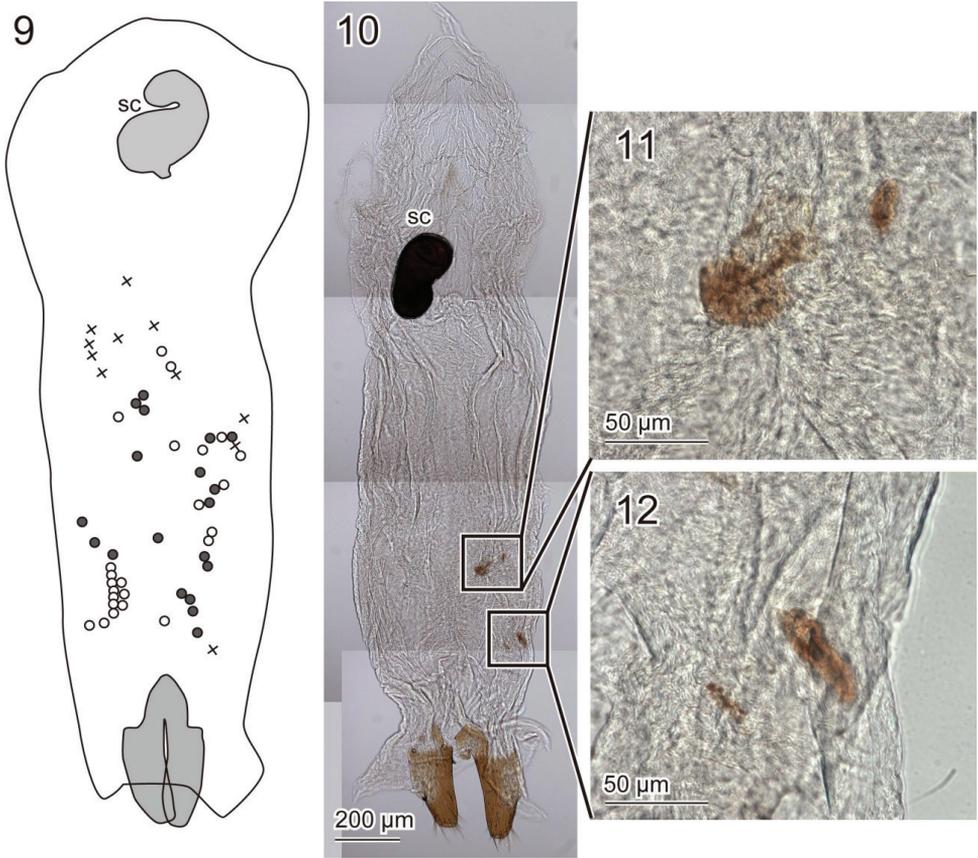
**Figures 6–8.** The internal sac membrane and spines of *Pyrrhalta maculicollis*. **6, 7** the sample was cut laterally, opened, dehydrated, and dried at the critical point **8** the sample dried at room temperature. The surfaces of the spines is slightly shrunken in comparison to that depicted in 7. Abbreviations: mp, membranous projections; s, spines; each is highlighted with blue and pink, respectively.

**Table I.** The measurements of the male spines in *Pyrrhalta maculicollis*, Kanagawa population in Japan.

	N	Mean ± S.D. (min.–max.)
Body size (mm)	6	6.00 ± 0.12 (5.84–6.11)
Spine number	7	23.6 ± 2.4 (20–8)
Spine size (μm)	7	126.2 ± 10.7 (110.8–145.0)
Internal sac length (μm)	7	2305 ± 83.9 (2204–2432)

### Copulatory wounds in female *Pyrrhalta maculicollis*

The vaginas of 13 female *Pyrrhalta maculicollis* were examined, collected during the reproductive season in the field (Kanagawa, Japan) and probably had already copulated. In most females ( $N = 11$ ),  $11.8 \pm 6.3$  (mean ± SD) wounds (2–25) were detected on both the ventral and dorsal sides of the vaginal wall, whereas no wound was found in the other two females. The sizes of wounds varied considerably and some were large enough to be visible under the stereomicroscope (Figs 10–12). Contrary to the male spines, the wounds were never aligned in a straight line (Figs 9–12). All wounds in females were observed in the caudal area posterior to the spermathecal capsule (Figs 9–12).

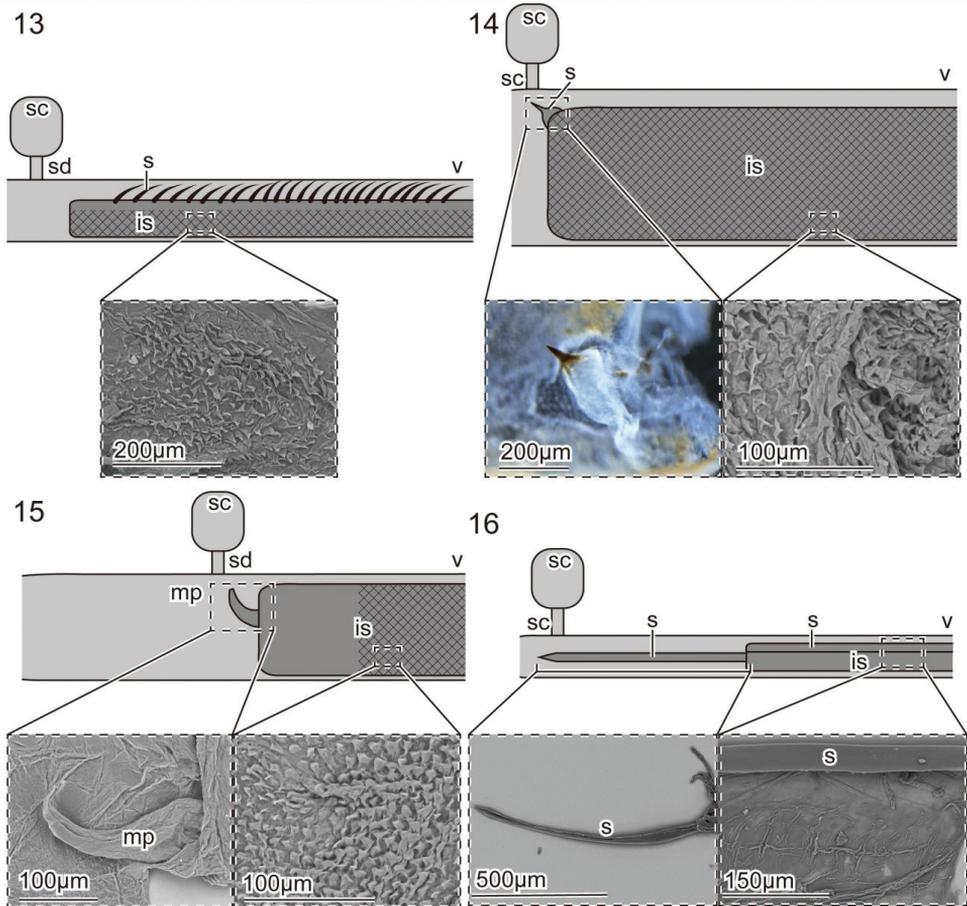


**Figures 9–12.** Wounds observed on the vagina of *Pyrrhalta maculicollis* **9** schemes of three female vaginas, which had largest numbers of wounds, are shown. Each symbol represents one individual **10** one representative with four wounds **11, 12** enlarged images of the wounds. Abbreviations: sc: spermathecal capsule.

### General morphology of male aedeagus in related species

The shape of the median lobe of the studied species is similar except for *Tricholochmaea semifulva* species complex, whose median lobe is relatively slender.

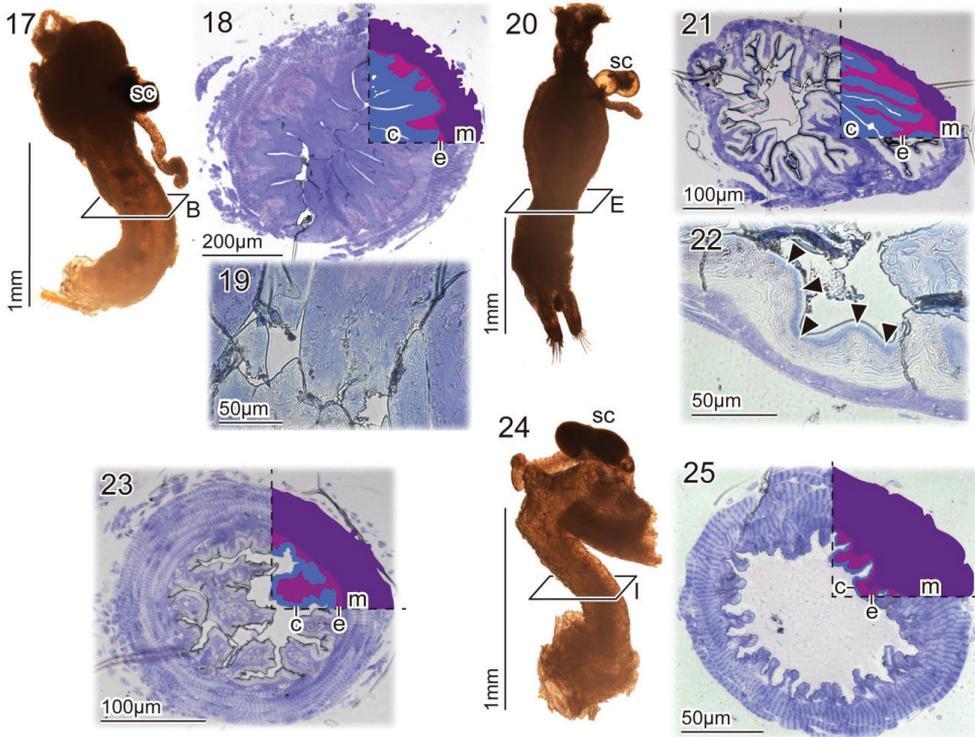
The internal sac of *Pyrrhalta tibialis* and *P. humeralis* is broader than that of *P. maculicollis* and *Tricholochmaea semifulva* species complex (Figs 13–16). In *P. tibialis*, a sclerotized and spinous sclerite is present near the orifice of the ejaculatory duct (Fig. 14). The surface is almost completely and densely covered with tiny membranous projections (Fig. 14). Remarkable sclerites are absent in *P. humeralis*, but membranous projections cover the proximal half of the internal sac, and a membranous rod is present on the tip of the internal sac (Fig. 15). Two long sclerites, as long as the internal sac, are situated on the tip of the internal sac and along the internal sac in *Tricholochmaea semifulva* species complex (Fig. 16). Membranous projections found in *Pyrrhalta* species are absent on the internal sac surface of *T. semifulva* species complex.



**Figures 13–16.** Schemes of hypothetical couplings between male and female genitalia, light microscopy (LM) and scanning electron microscopy (SEM) images of the male internal sac **13** *Pyrrhalta maculicollis* **14** *P. tibialis* **15** *P. humeralis* **16** *Tricholochmaea semifulva* species complex. The schemes were created using information on morphology and dimensions of both male and female genitalia, but the genital coupling has not been experimentally proven. The meshed areas in the male internal sacs show areas covered by tiny projections, as shown in the SEM images. All samples were dried at room temperature. Abbreviations: is, internal sac; mp, membranous projection; s, sclerite; sc, spermathecal capsule; sd, spermathecal duct; v, vagina.

### Vagina wall comparison among species

The vaginal wall of *Pyrrhalta maculicollis* and *P. tibialis* shows relatively well developed epidermis and cuticle layers, if compared to that of the other species (Figs 17–22), while muscles are well developed in *P. humeralis* and *Tricholochmaea semifulva* species complex (Figs 23–25). Proportions of the epidermis + cuticle areas to the area of the muscle layer are variable among species, and these values in *P. maculicollis* and *P. tibialis* are higher than those of the others: 1.76–1.85 ( $N = 2$ ) in *P. maculicollis*, 2.22–5.81 ( $N = 2$ ) in *P. tibialis*, 0.60 ( $N = 1$ ) in *P. humeralis*, 0.27–0.62 ( $N = 2$ ) in *T. semifulva* species



**Figures 17–25.** Female reproductive systems: **17–19** *Pyrrhalta maculicollis* **20–22** *P. tibialis* **23** *P. humeralis* **24–25** *Tricholochmaea semifulva* species complex. **18, 21, 23, 25** show the cross sections of the lower part of the vagina, where wounds were found in *P. maculicollis*; each cuticular, epidermal, and muscular layer are partly highlighted in the upper right corner. **19, 22** show enlarged parts of the cuticular, epidermal, and muscular layers; these samples were embedded in glycerine for two days before taking the images. Arrowheads in **22** point to the strip stained with toluidine blue. Abbreviations: c, cuticle; e, epidermis; m, muscles; sc, spermathecal capsule.

**Table 2.** The measurements of the areas of the vagina muscles and epidermal plus cuticular layers.

Species	N	Areas of muscles ( $\mu\text{m}^2$ )	Areas of epidermis and cuticle ( $\mu\text{m}^2$ )
<i>Pyrrhalta maculicollis</i>	2	102545 / 45674	180528 / 84607
<i>Pyrrhalta tibialis</i>	2	12574 / 40076	73012 / 88799
<i>Pyrrhalta humeralis</i>	1	27599	16555
<i>Tricholochmaea semifulva</i> species complex	2	38635 / 13166	23952 / 3601

complex (Table 2). The thick cuticular layers in *P. maculicollis* and *P. tibialis* are not strongly stained with toluidine blue. However staining patterns are different between the species, i.e. *P. maculicollis* cuticular layers are weakly and homogeneously stained (Fig. 19) and *P. tibialis* cuticular layers are not stained except for a stained stripe (Fig. 22, arrowheads).

Any possible healing wounds were not found in the vagina of *P. tibialis* ( $N = 5$ ) and *P. humeralis* ( $N = 4$ ), indicating that mating trauma, if any, occurs significantly less frequently in these species than in *P. maculicollis* (Fisher's exact probability test:  $P = 0.0025$ – $0.0063$ ). However, five small melanised patches were found in one out of four females of the *T. semifulva* species complex examined. Those patches were similar to the small ones in Figs 11, 12.

## Discussion

Among the examined *Pyrrhalta* spp., wounds were found significantly more in the vagina of *P. maculicollis*. This finding supports the view that the hand saw-like spines of the internal sac, which is characteristic of this species, are responsible for traumatic mating. Although we have neither compared virgin females with mated ones nor examined the genital coupling of the species, it is reasonable to estimate that the regularly arranged male spines are everted and face to the vaginal wall during copulations (Fig. 13). The everted spines must be arranged like anchoring to the vaginal wall (Fig. 13). However, the number of the wounds of the females, collected from the field, was less in comparison to the number of the spinous sclerites of the internal sac, and the traces of the wounds do not coincide with the male spine arrangement, as typically seen in ants with a similar hand saw-like spines (Kamimura 2007). This would mean that the spines of *P. maculicollis* are not stiff enough to always inflict wounds on the female vagina. In accordance with this view, the air-dried spines shrunk in comparison to the spines dried at the critical point. The spine surface can be less stiff than the spine internal part. Moreover, we found that the *P. tibialis* also has a plausible wound inflictor in the internal sac. On the contrary to *P. maculicollis*, however, we failed to detect wounds on five observed vaginas of *P. tibialis*. Additional studies are necessary to elucidate functions of the single spinous sclerite in *P. tibialis*.

As in the cases of seed beetles (Rönn et al. 2007), the high cuticular + epidermal layer area ratio in comparison to the muscle layer area in *P. maculicollis* vagina likely represents a counter-adaptation to traumatic mating, although we have not statistically analysed our data due to the small sample sizes. The relatively high cuticular + epidermal layer ratio was found also in *P. tibialis*, although it has not been confirmed that the spinous sclerite inflicts traumas during copulation in *P. tibialis*. It is conceivable that the material composition of the thickened cuticular layers is different between *P. maculicollis* and *P. tibialis*, because the staining of the cuticle layers differs between the species. Since toluidine blue strongly stains the rubber-like protein, resilin, which was demonstrated to enhance female tolerance against traumatic mating in bed bugs (Michels et al. 2015, 2016), we expected the highest stainability by toluidine blue in the vaginas of *P. maculicollis* among the species examined. However, resilin unlikely distributes much in the cuticle layers of *P. maculicollis* and the related species due to their low stainability by toluidine blue (Figs 19, 22). Thickening the vaginal wall alone is probably sufficient to be a counter-adaptation against the spinous sclerites on the internal sac in *P. maculicollis*. Judged from the observed thin cuticular layers in the

vagina of *T. semifulva* species complex, the thick vaginal cuticular layers likely represent a derived state in the genus *Pyrrhalta*. For estimating the origin of the female vaginal wall thickening, phylogenetic hypotheses of the relationship among different *Pyrrhalta* species should be developed in future studies.

The internal sac of *P. maculicollis* is relatively narrow in comparison to other *Pyrrhalta* species. The narrow internal sac would be problematic for bearing the spiny sclerites, since the spines may harm the internal sac, especially its dorsal surface, during its eversion and withdrawal (Fig. 5). It can be hypothesized that the presence of tiny and densely covering projections on the male internal sac presumably aid in avoiding such self-harming, and therefore represent possible male co-adaptation for traumatic mating. However, the tiny projections had likely evolved in *Pyrrhalta* and were found in all examined species of the genus. Accordingly, they must have other presently unknown functions, which have been preadaptations for the evolution of traumatic mating. The species rich galerucine genus *Pyrrhalta* contains more than 110 described species (Xue and Yang 2010, Nie et al. 2013), for which phylogenetic relationships at the species level are unknown. The morphology of the internal sac/vagina and the phylogeny of this group must be investigated comprehensively in future studies, for better understanding the genital evolution of this group.

In comparison to the seed beetles, whose spinous sclerites on the internal sac are arranged three dimensionally (Crudgington and Siva-Jothy 2000), the spines of *P. maculicollis*, which are arranged rather two-dimensionally, can be easily counted. Moreover, as shown in the present study, the spine number in this beetle is highly variable even within a population (Table 1). As well as possible variations among populations (see Dougherty et al. 2017 for a case of the seed beetle), it can cause mismatches between male and female genitalia. Some combinations may more severely harm females than others, enabling us to detect (1) female costs and (2) female counter adaptations. Despite that this species can potentially be a model system for future experimental studies of traumatic mating, hitherto no comprehensive study has been published for the mating biology of the *Pyrrhalta* spp. Establishment of rearing techniques are warranted especially for *P. maculicollis* to confirm our predictions on the trauma-causing functions of the genital spines with direct evidence.

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# How many genera and species of Galerucinae s. str. do we know? Updated statistics (Coleoptera, Chrysomelidae)<sup>1</sup>

Rui-E Nie<sup>1</sup>, Jan Bezděk<sup>2</sup>, Xing-Ke Yang<sup>1</sup>

<sup>1</sup> Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing, 100101, China <sup>2</sup> Mendel University, Department of Zoology, Zemědělská, 1, 613 00 Brno, Czech Republic

Corresponding authors: Jan Bezděk ([bezdek@mendelu.cz](mailto:bezdek@mendelu.cz)); Xing-Ke Yang ([yangxk@ioz.ac.cn](mailto:yangxk@ioz.ac.cn))

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## Abstract

Galerucinae s. str. is a rich group of leaf beetles. A new, up-to date checklist of Galerucinae genera in the world is provided, including the number of valid species of each genus. Genera and species were counted in literature published before the end of 2016. In summary, 7145 species (7132 recent, 13 fossils) and 192 subspecies from 543 genera (542 recent, 1 fossil) were quantified in Galerucinae s. str. In comparison with the previous catalogue of worldwide Galerucinae (Wilcox 1971–1973), an additional 91 valid genera, 1341 valid species (1337 recent, 4 fossils) and 38 subspecies have been published; 43 genera were synonymized, four genera were transferred into Alticini, two subgenera were elevated to genus rank, and one genus was downgraded to subgenus rank. The updated list of references to taxonomic publications on Galerucinae s. str. from the period 1971–2016 is provided.

## Keywords

Biodiversity, checklist, Chrysomeloidea, leaf beetles, worldwide

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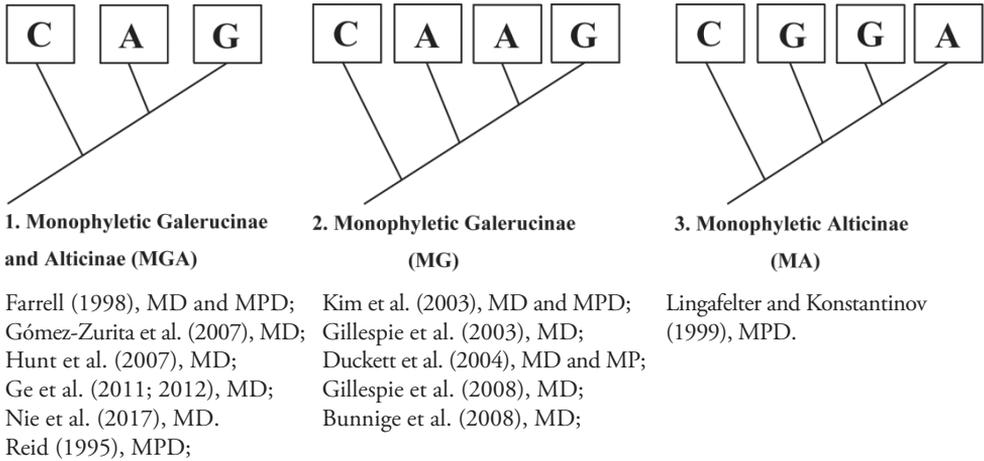
## Introduction

Galerucinae *sensu stricto* (i.e., not including Alticini) belongs to Chrysomelidae (Coleoptera) and is one of the largest groups of leaf beetles (Yang et al. 2015). Adult Galerucinae can be identified by an oval to oblong body, with the head visible from above and inserted into the prothorax. The front coxal cavity is either open or closed. Tarsi are pseudotetramerous with the third segment bifid, and the fourth segment very small in size, and nested in the third one. The hind femur is slender without a femoral spring. The antenna has eleven segments; the antennal insertions are situated close together in front or between the eyes. Frontal tubercles are usually present and well developed. The elytral sensilla patch is usually single (Samuelson 1996; Nadein and Bezděk 2014).

Galerucinae *s. str.* is a key group to study the phylogeny of Polyphaga. The adults and larvae of Galerucinae *s. str.* are herbivorous, and most of them show host specificity. The special relationship of Galerucinae *s. str.* and its host plants makes the group a good model to study the evolution of herbivorous beetles, the convergent evolution of insects and plants (Futuyma and McCafferty 1990), and the evolutionary mechanisms of biodiversity (Farrell et al. 1992; Mitter and Farrell 1991). In addition, many species are used for biological control of weeds or are important pest species of agriculture (Vencl and Morton 1998; Xue et al. 2007; Bunnige et al. 2008; Xue and Yang 2008; Nie et al. 2012).

Among Chrysomelidae, the closest relative to Galerucinae *s. str.* is Alticinae (or flea beetles) discussed further below. Both groups have very rich diversity. Nadein and Bezděk (2014) estimated 6500 species in ca. 600 genera within Galerucinae *s. str.*; and about 8000 species in 534 genera within Alticinae *s. str.* The two groups have very similar morphological characters. The key morphological character used to distinguish both groups is the metafemoral extensor tendon (MET) in the hind femora (also known as metafemoral spring, metafemoral apodeme, or Maulik's organ), which is a structure that permits large jumps for predator evasion (Furth and Suzuki 1990; Furth and Suzuki 1998; Nadein and Betz 2016). The presence of MET was not always mentioned in the descriptions of genera or species. Actually some species with slender hind femora have MET, such as *Mandarella* Duvivier, 1892. In contrast, some species with swell hind femora are without MET such as *Orthaltica* Crotch, 1873 (Furth and Suzuki 1994; Konstantinov and Prathapan 2008). Some genera are called “problematic genera” with the presence or absence of a MET and not fitting other characters. Recently, some researchers found that the MET may have multiple origins, evolving at least two or three times (Ge et al. 2011; 2012; Nie et al. 2017).

The phylogenetic relationship of Galerucinae *s. str.* and flea beetles has been disputed for many decades and is still unclear and controversial. Some recent investigations support the inclusion of the traditional alticines in Galerucinae, yet classification remains a challenge as neither the traditional “Galerucinae” nor the traditional “Alticinae” are monophyletic (Bouchard et al. 2011; Nadein and Bezděk 2014; Reid 2014). Other studies suggest considering both groups as subfamilies (e.g. Löbl and



**Figure 1.** The three hypotheses of the phylogeny of Galerucinae and Alticinae. The supporters of each hypothesis are listed below each. Note: MD = Molecular Data; MPD = Morphological Data.

Smetana 2010, Ge et al. 2011, 2012; Haddad and McKenna 2016). So far, three hypotheses of evolutionary relationships have been proposed based on morphological or molecular data (Fig. 1). Among these tree hypotheses, a sister group relationship of Galerucinae and Alticinae was supported by the most molecular or morphological analyses (Seeno and Wilcox 1982; Doguet 1994; Farrell 1998; Gómez-Zurita et al. 2007; Hunt et al. 2007; Bouchard et al. 2011; Ge et al. 2011, 2012; Nie et al. 2017). Some of the recently established groupings, based on DNA sequences, still need further in-depth analysis because they are phylogenetically and biogeographically incomplete (Biondi and D'Alessandro 2012). In this study there is no attempt to resolve the relationship of both groups. The reason Galerucinae and Alticinae are treated as two equal groups is strictly technical in order to count the genera and the species correctly.

Some important catalogues of Galerucinae s. str. have been published during the 20<sup>th</sup> century. Weise (1924) catalogued 3678 species from 305 genera. The last comprehensive Galerucinae catalogue published by Wilcox (1971–1973) included 5802 species (including fossil taxa) in 476 genera. The summarized generic arrangement (495 genera) was presented by Seeno and Wilcox (1982). However, the taxonomy of Galerucinae s. str. has not been summarized during the last 40 years. Many new species, new genera, new names, or new synonymies have been proposed. This work seeks to provide a new detailed, up-to date, summary of global Galerucinae s. str. taxonomy.

## Methods

All the currently valid genera names (in nomenclatorial sense, both recent and fossil) of subfamily Galerucinae s. str. in the world published before December 31, 2016 are listed.

The references are mainly based on the database Zoological records and Jan Bezděk's personal catalogue. Each genus includes the present number of recent species, subspecies and fossil species, generic distribution, list of subgenera and generic synonyms, and references to publications which influenced the number of genera and species from Wilcox's (1971–1973) catalogues to present (including important redescriptions). The references omitted in Wilcox's (1971–1973) catalogue are included.

For each genus, an outline of its present geographic distribution (based on Löbl and Smetana 2010) is provided. The abbreviation of fauna is as following:

- AFR** Afrotropical Region;
- AUR** Australian Region;
- NAR** Nearctic Region;
- NTR** Neotropical Region;
- ORR** Oriental Region;
- PAR** Palaearctic Region.

For genera with restricted distributions, the countries are listed. For the genera (e.g. *Pyrrhulta*, *Xanthogaleruca*, *Tricholochmaea*, *Galerucella*, *Galeruca*) with controversial classified rank, we follow the Palaearctic catalogue (Beenen 2010). The authorship of the genera published in Dejean (1836) follows the paper by Bousquet and Bouchard (2013).

Wilcox published his catalogue in four fascicles. The fascicles 1–3 (Wilcox 1971–1973) comprise the catalogue itself including precisely documented species and genera. The last fascicle (Wilcox 1975) included addenda, index, and references to the papers published in several previous years. For comparison of genera and species, we used only fascicles 1–3. The fourth fascicle will be included in subsequent publications.

## Results

Wilcox (1971–1973) published 5802 species (5793 recent species + 9 fossil ones) and 154 subspecies in 476 genera. As of the end of December 2016, Galerucinae *s. str.* contains 7145 species (7132 recent, 13 fossils) and 192 subspecies from 543 genera (542 recent, one fossil). Among these 543 genera, 91 novel valid genera (including one fossil) have been published since 1974. Since 1974, 1341 valid species (including four fossils) and 38 subspecies have been added. A total of 194 genera is listed in synonymy, of which 145 were listed as synonyms in Wilcox (1971–1973). After 1973, 43 genera were synonymized, four genera were transferred into Alticini, two subgenera were elevated to genus rank, and one genus was downgraded to subgenus. The detailed statistics on the number of genera, species and subspecies, geographic distribution, as well as the subgenera, the generic synonyms and references can be seen in Supplementary information/data 1.

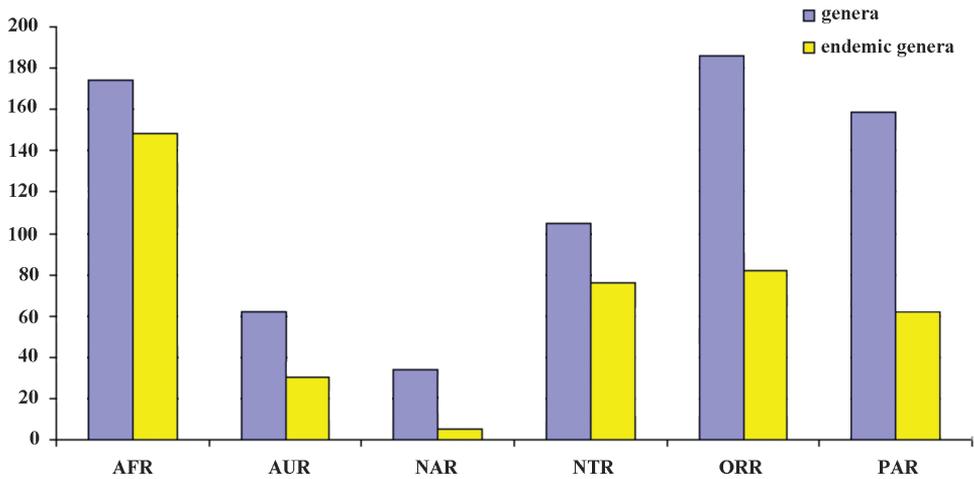
Since 1974, some genera have been increased by many species e.g. *Monolepta* (113 species), *Paleosepharia* (63 species), *Apophyllia* (47 species), *Paridea* (41 species), *Pyrrh-alta* (38 species), while 292 genera have not increased. Surprisingly, the species number decreased from 259 to 246 in African Monoleptites, a group deeply revised in last twenty years, because of many new synonyms. Similar decrease in species number is expected in other species-rich genera with color variability, e.g., *Diacantha* Chevrolat, 1836 (see Wagner 2017). The major contribution of new generic descriptions since Wilcox's (1971–1973) catalogue has been made by Medvedev (22 genera), Wagner (17 genera), Chen (eleven genera), Kimoto (seven genera), Mohamedsaid (seven genera), Silfverberg (six genera), Bezděk (five genera), Beenen (five genera), Clark (four genera), Shute (three genera), and Lopatin (two genera).

The distribution of Galerucinae s. str. is worldwide. Altogether 186 genera (34.3%) are distributed in the Oriental Region, followed by Afrotropical Region (174 genera, 32.0%), Palaearctic Region (159 genera, 29.1%), Neotropical Region (105 genera, 19.3%), Australian Region (62 genera, 11.4%), and Nearctic Region (34 genera, 6.3%). A very high level of generic endemism is exhibited for the Afrotropical Region where 148 genera from total 174 are endemic (31 genera are endemic for Madagascar) and for Neotropical Region with 76 endemic genera from total 105. In the Afrotropical Region high level of generic endemism in Galerucinae s. str. (85%) corresponds to Alticinae with 71% (Biondi and D'Alessandro 2010). In all other regions the level of generic endemism of Galerucinae s. str. is below 50%. For the total numbers of genera and endemic genera in all the regions see Fig. 2.

There are no cosmopolitan genera in Galerucinae s. str. The most diverse and most widely distributed genus is *Monolepta* with more than 700 species occurring in almost all the regions but missing in the Nearctic Region (Riley et al. 2003). Additional species-rich genera with wide distribution like *Luperus* Geoffroy, 1762 (97 species), *Luperodes* Motschulsky, 1858 (77 species), and *Calomicrus* Dillwyn, 1829 (85 species) are evidently polyphyletic and the future revisions will lead to the geographical restriction of these genera.

The distribution of many genera is shared with adjacent regions. For example, 37% of Oriental genera are endemic while 39% are shared with Palaearctic Region and additional 14% with Australian fauna. As expected only a low percentage (2%) of genera occurs in Nearctic/Neotropical regions and some another region (ORR-AFR 6%). On the other hand, 27 genera are shared with both Nearctic and Neotropical regions. It is necessary to mention that distribution of some genera is often only marginal in adjacent region (for example in the eastern border of Palaearctic and Oriental Regions). The generic endemism percentage in comparison with the percentage of the genera shared with other regions is graphed in Figs 3–8.

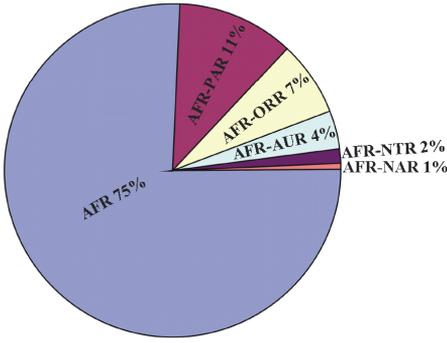
Among 92 genera proposed after Wilcox's (1971–1973) catalogue, the fauna of the Oriental region has increased by 36 genera (39.1%), followed by Palaearctic Region (24 genera, 26.1%), Afrotropical Region (22 genera, 23.9%), Neotropical Region (eight genera, 8.7%), Australian Region (six genera, 6.5%), and Nearctic Region (one genus, 1.1%).



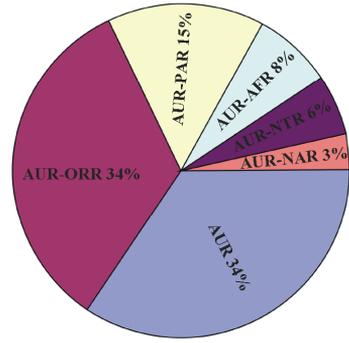
**Figure 2.** The numbers of genera and endemic genera in geographical regions.

The following taxa listed by Wilcox (1971–1973) or described later in Galerucinae *s. str.* have been transferred to other Chrysomelidae groups:

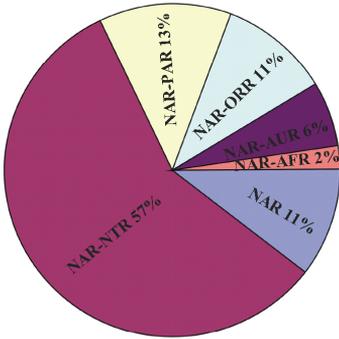
- *Hildebrandtina* Weise, 1910 belongs to Alticinae *s. str.* (see Biondi and D’Alessandro 2010, 2012).
- *Borbaita* Bechyné, 1958, *Micrantipha* Blackburn, 1896, *Neoclitena* Abdullah & Qureshi, 1968, *Philocalis* Dejean, 1836, and *Scelidopsis* Jacoby, 1888 were transferred to Alticinae *s. str.* by Wilcox (1975) and their position is widely accepted (see Seeno and Wilcox 1982; Döberl 2010).
- *Lochmaeina* Medvedev, 1956 and *L. rosea* Medvedev, 1956 are synonyms of *Sangariola* and *S. punctatostrigata* Motschulsky (Alticinae *s. str.*) (see Wilcox 1975).
- *Stenoluperus* Ogloblin, 1936 was synonymized with *Mandarella* Duvivier, 1892 which belongs to Alticinae *s. str.* (see e.g., Wilcox 1975; Medvedev 2012; Lee et al. 2016). However, its position is still questionable (Nie et al. 2017).
- *Luperodes antillarum* Blake, 1937 was synonymized with *Lysathia ludoviciana* Fall, 1910 which belongs to Alticinae *s. str.* (see Wilcox 1975, Virkki 1979).
- *Luperus uenoi* Kimoto, 1969 was transferred to *Mandarella* Duvivier, 1892 which belongs to Alticinae *s. str.* (see Lee et al. 2016).
- *Chaloenus* Westwood, 1862 belongs to Alticinae *s. str.* (see Konstantinov and Prathapan 2008).
- *Calomicrus sibiricus* (Csiki, 1916) was transferred to *Luperomorpha* Weise, 1887 which belongs to Alticinae *s. str.* by Bezděk (2007).
- *Oides neobengalensis* Rizvi & Kamaluddin, 2011 is synonym of *Clytra subfasciata* Lacordaire, 1848 which belongs to Clytrini of Cryptocephalinae (see Bezděk 2012, 2016).
- *Paramerista* Lopatin, 2011 is synonym of *Podontia* Dalman, 1824 and *Paramerista luteola* Lopatin, 2011 is synonym of *Podontia lutea* (Olivier, 1790) which belongs to Alticinae *s. str.* (see Bezděk 2012).



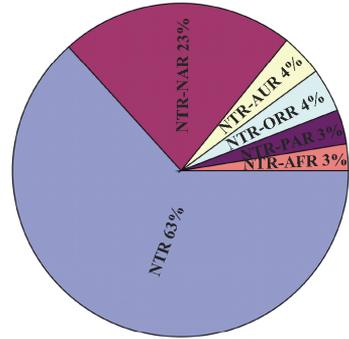
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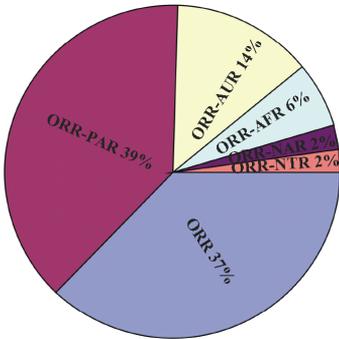
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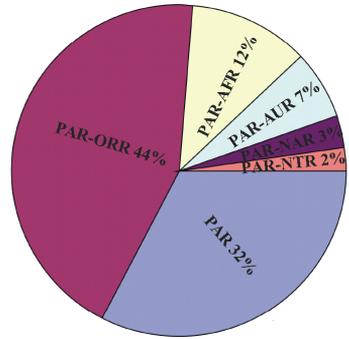
5



6



7



8

**Figures 3–8.** Distribution of genera of Galerucinae s. str. in the different zoogeographical regions showing generic endemism percentage and percentage of the genera shared with other regions. **3** Afrotropical Region (AFR) **4** Australian Region (AUR) **5** Nearctic Region (NAR) **6** Neotropical Region (NTR) **7** Oriental Region (ORR) **8** Palearctic Region (PAR).

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## **Supplementary material I**

### **Genera list and related files**

Authors: Rui-E Nie, Jan Bezděk, Xing-Ke Yang

Data type: species data

Explanation note: The list of all valid genera (both recent and fossil) of subfamily Galerucinae s. str. in the world.

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Link: <https://doi.org/10.3897/zookeys.720.13517.suppl1>

# Contributions to the knowledge of Chinese flea beetle fauna (II): *Baoshanaltica* new genus and *Sinosphaera* new genus (Coleoptera, Chrysomelidae, Galerucinae, Alticini)

Yongying Ruan<sup>1,2</sup>, Alexander S. Konstantinov<sup>3</sup>, K. D. Prathapan<sup>4</sup>, Xingke Yang<sup>1</sup>

**1** Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China **2** Postdoctoral Innovation Practice Base (College of Applied Chemistry and Biological Technology), Shenzhen Polytechnic, Shenzhen, China **3** Systematic Entomology Laboratory, USDA, ARS, Washington DC, USA **4** Department of Entomology, Kerala Agricultural University, Vellayani P.O., Trivandrum -695 522, Kerala, India

Corresponding author: Alexander S. Konstantinov ([alex.konstantinov@ars.usda.gov](mailto:alex.konstantinov@ars.usda.gov)); Xingke Yang ([yangxk@ioz.ac.cn](mailto:yangxk@ioz.ac.cn))

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## Abstract

Two new genera: *Baoshanaltica* **gen. n.** and *Sinosphaera* **gen. n.**, and two new species: *Baoshanaltica minuta* **sp. n.** and *Sinosphaera aptera* **sp. n.** from south-west China are described and illustrated. *Baoshanaltica* is compared to the allied moss-inhabiting genera *Cangshanaltica* Konstantinov et al. and *Phaelota* Jacoby, in addition to *Minota* Kutschera. *Sinosphaera* is compared to *Sphaeroderma* Stephens, *Omeisphaera* Chen & Zia, *Jacobyana* Maulik, and *Kamala* Maulik.

## Keywords

Alticini, beetle diversity, China, flea beetles, moss-inhabiting, new genera, new species

## Introduction

As currently understood, Chinese flea beetle fauna consists of 102 genera and 856 species (Ruan and Yang 2015, Ruan et al. 2017). However, new taxa are still being discovered, particularly in mountainous south-west China (e.g. Yunnan and Sichuan) and in particular in the habitats that are poorly sampled for leaf beetles not just in China but throughout the world: leaf litter and moss cushions. So far 30 species from 15 genera are known to occur in moss cushions in the world (Damaška and Konstantinov 2016). A discovery of a new genus and species of flea beetles in Baoshan mountains in Yunnan brings the number to 31 and 16 respectively (Table 1). *Baoshanaltica minuta* sp. n. and *Sinosphaera aptera* sp. n. described in this paper bring the total number of flea beetle genera known to occur in China to 104 and species to 858.

*Baoshanaltica* resembles another moss-inhabiting genus *Cangshanaltica* Konstantinov et al., 2013 and is compared with it, besides *Minota* Kutschera and *Phaelota* Jacoby. *Sinosphaera* gen. n. is allied to *Jacobyana* Maulik, *Kamala* Maulik, *Omeisphaera* Chen & Zia, and *Sphaeroderma* Stephens. Morphological comparisons between the new genera and their allies are given in “Results” part of the paper.

## Materials and methods

Observations of the male genitalia and habitus were made with a Zeiss Discovery V20 microscope and digital images were taken with an AxioCam HRC digital camera attached to it. Female genitalia were dissected and mounted on slides in glycerin, and photographed with Leitz Diaplan Microscope and the camera module of Blackberry Q10 mobile phone (with a resolution of 800MP). The morphological terminology follow Konstantinov (1998).

Abbreviations of collections:

- IZCAS** Institute of Zoology, Chinese Academy of Sciences, Beijing, China.  
**USNM** National Museum of Natural History, Washington DC, USA.

## Results

### *Baoshanaltica* Konstantinov & Ruan, gen. n.

<http://zoobank.org/FE1DABB6-4EA4-4652-A213-B620A9390AEC>

Figs 1–3

**Type species.** *Baoshanaltica minuta* Konstantinov & Ruan, sp. n.

**Etymology.** We name this genus after its type locality: Baoshan (保山) mountains, Yunnan province. The name is feminine.

**Distribution.** China.

Table 1. Flea beetle genera with species known to occur in moss cushions.

Genus name	Type species	Total number of species	Number of moss-inhabiting species	Biogeographic region
<i>Baoshanaltica</i> Konstantinov & Ruan, gen. n.	<i>Baoshanaltica minuta</i> Konstantinov & Ruan, sp. n.	1	1	Oriental
<i>Benedictus</i> Scherer, 1969	<i>Benedictus elisabethae</i> Scherer, 1969	27	7	Oriental
<i>Borinken</i> Konstantinov & Konstantinova, 2011	<i>Borinken ebyunqae</i> Konstantinov & Konstantinova, 2011	1	1	Neotropical
<i>Cangshanaltica</i> Konstantinov et al., 2013	<i>Cangshanaltica nigra</i> Konstantinov et al., 2013	2	2	Oriental
<i>Clavicornaltica</i> Scherer, 1974	<i>Clavicornaltica besuchetti</i> Scherer, 1974	20	1	Oriental
<i>Ivalia</i> Jacoby, 1887	<i>Ivalia viridipennis</i> Jacoby, 1887	57	1	Oriental
<i>Kiskeya</i> Konstantinov & Chamorro-Lacayo, 2006	<i>Kiskeya baorucae</i> Konstantinov & Chamorro-Lacayo, 2006	3	3	Neotropical
<i>Minota</i> Kutschera, 1859	<i>Haltica obesa</i> Walll, 1839	5	1	Palaearctic
<i>Mniophila</i> Stephens, 1831	<i>Haltica muscorum</i> Koch, 1803	6	3	Palaearctic
<i>Monotalla</i> Bechyné, 1956	<i>Monotalla guadeloupensis</i> Bechyné, 1956	6	2	Neotropical
<i>Nicaltica</i> Konstantinov et al., 2009	<i>Nicaltica selvanegra</i> Konstantinov et al., 2009	1	1	Neotropical
<i>Paraminota</i> Scherer, 1989	<i>Paraminota minima</i> Scherer, 1989	2	1	Oriental
<i>Paraminotella</i> Döberl & Konstantinov, 2003	<i>Paraminota nepalensis</i> Döberl, 1991	2	1	Oriental
<i>Phaelota</i> Jacoby, 1887	<i>Phaelota semifasciata</i> Jacoby, 1887	16	3	Oriental
<i>Stevenaltica</i> Konstantinov et al., 2014	<i>Stevenaltica normi</i> Konstantinov et al., 2014	2	2	Neotropical
<i>Ulrica</i> Scherer, 1962	<i>Sparnus minutus</i> Jacoby, 1889	5	1	Neotropical

**Host plant.** Possibly unknown species of moss.

**Description.** Body color and proportions. Body unicolorous, brown to dark brown, without slight metallic luster. Body ovate in dorsal view, highly convex in lateral view. Body length 1.40–1.55 mm (n=2). Body width (widest point of elytra) 1.05–1.10 mm. Body length to width, ratio 1.35–1.45. Pronotum width to length, ratio 1.50–1.60. Pronotum width at base to width at apex, ratio 1.05–1.10. Elytron length (measured along suture) to width of both, ratio 0.90–1.00. Elytron and abdomen length to height of the body (in lateral view), ratio 1.30–1.40. Length of elytron to length of pronotum, ratio 2.75–2.85. Width of elytra at base (measured across middle of humeral calli) to width of pronotum at base, ratio 1.25–1.30.

Head. Surface glabrous, dark brown, shiny, without punctures, except for supraorbital. Antennal calli poorly delimited with supracallinal, midfrontal, supraantennal, and suprafrontal sulci absent to poorly developed. Frontal ridge wider between antennal sockets than near clypeus. Each side of frontal ridge with few white, long setae. Top of frontal ridge separated from vertex by a more or less round impression. Width of frontal ridge to antennal sockets (counting surrounding ridges), ratio 2.50–2.60. Frontal ridge in lateral view moderately convex. Frontal ridge and anterofrontal ridge in frontal view form nearly straight angle. Vertex obviously concave at its lower part near frontal ridge.

Orbit as wide as transverse diameter of antennal socket. Inner margin of eye straight. Distance between eyes (just above antennal sockets) to transverse diameter of eye in frontal view, ratio 3.50–3.60. Longitudinal diameter of eye to transverse diameter of eye in frontal view, ratio 1.95–2.05. Sides of head below eyes converging ventrally. Labrum flat with 2 pairs of setae, without projections in middle. Anterior margin of labrum with shallow emargination in middle. Apical maxillary palpomere conical. Supraorbital pore well developed. Clypeus band-like in shape. Antennal sockets situated about middle of eye. Distance between antennal sockets to transverse diameter of one antennal socket, ratio 2.50–2.60.

Antennae stout and short, only slightly stretch over pronotum. Number of antennomeres: 11. First antennomere slightly as long as or slightly shorter than next two combined. Antennomere 2 longer than 3. Antennomere 5 about as long as antennomeres 4 and 6 separately. Distal antennomeres robust, wider than middle ones. Antennomere 7 in males with lobe projecting dorsally. Length to width of antennomere 9, ratio 1.20–1.25. Length to width of antennomere 10, ratio 1.05–1.10. Length to width of antennomere 11, ratio 1.45–1.55.

Prothorax. Pronotal surface glabrous, with a shallow and poorly defined transverse impression and two poorly defined lateral impressions near base. Pronotal punctures as large as elytral ones, their diameter 2–3 times smaller than distance between them. Anterolateral callosity of pronotum well developed, long, facing anterolaterally with obtuse denticle posteriorly. Anterior setiferous pore of pronotum situated close to middle of lateral margin. Sides of pronotum curved, somewhat sinuate. Pronotal base straight. Lateral margin of pronotum complete and strongly explanate. Posterolateral setiferous pore of pronotum protruding laterally beyond lateral margin.

Procoxal cavities open. Lateral sides of intercoxal prosternal process concave in middle, apex slightly wider than middle. Posterior end of intercoxal prosternal process slightly convex. Intercoxal prosternal process slightly extends beyond procoxae. Intercoxal prosternal process normally wide. Width of intercoxal prosternal process between procoxae to length of procoxa, ratio 0.65–0.70.

Elytra. Humeral calli absent. Hind wings absent. Impressions or ridges on elytron absent. Elytron with small punctures arranged in 8 rows; scutellar row of punctures absent. Interspaces slightly costate. Scutellum present, extremely small, triangular. Elytron with apex acute, covering entire abdomen. Sides strongly and evenly convex. Epipleura oblique outwardly, gradually narrowing from base to apex, nearly reaching apex. Width of epipleura greater than that of profemur. Epipleura basally much wider than apically. Elytra at base wider than base of pronotum.

Venter. Meso- and metasterna more or less flat, without elevated projection in middle. Metasternum slightly projecting forward. Abdominal ventrites 1 and 2 not fused. Abdominal ventrite 1 as long as remaining ventrites together. Abdominal ventrite 5 longer than ventrites 4, 3 and 2 together. First abdominal ventrite between coxa without longitudinal ridges. Anterior end of first abdominal ventrite normally wide and truncate.

Legs. Apical spur of protibia and mesotibia absent. Apical spur of metatibia relatively short and slender. Metafemoral spring present. Claw simple. Apical part of hind and middle tibia without excavation. Length (not counting trochanter) to maximum width of metafemur, ratio 1.90–1.95. Length to width of metatibia in lateral view, ratio 7.70–7.80. Width of metatibia at base to width at apex in dorsal view, ratio 0.50–0.60. Length of metatibia to length of first metatarsomere, ratio 4.50–4.60. Metatibia generally straight. Metatibia in cross section around its middle more or less cylindrical. Dorsal side of metatibia without sharp edge or small denticles. Metatarsomere 1 attached to apex of metatibia. Length of metafemur to metatibia, ratio 1.25–1.35. First protarsomere of male, length to width, ratio (in dorsal view) 1.40–1.50. Length of first protarsomere to length of second protarsomere, ratio 1.80–1.90. Width of first protarsomere to width of second protarsomere, ratio 0.95–1.00. Tarsomere 3 incised, deeply bilobed and slightly elongate. First metatarsomere of male, length to width, ratio (in dorsal view) 2.20–2.30. Length of first metatarsomere much less than half of metatibial length. First and rest three metatarsomeres make more or less straight line. Length of first metatarsomere to length of second metatarsomere, ratio 2.90–3.00. Width of first metatarsomere to width of second metatarsomere, ratio 1.00–1.05. Length of fourth metatarsomere to length of third metatarsomere, ratio 1.40–1.45.

Genitalia. Aedeagus slender, flattened in cross section, strongly and evenly curved in lateral view. Apex abruptly narrowed.

**Remarks.** In the general shape, *Baoshanaltica* resembles moss-inhabiting flea beetles from the genus *Cangshanaltica* Konstantinov et al., 2013, discovered in a neighboring mountain ridge in Yunnan and later found in northern Thailand (Damaška and Konstantinov 2016). However, *Baoshanaltica* can be differentiated from the latter by the following characters: frontal ridge generally narrow, wider between antennal

sockets than near clypeus, forming nearly straight angle with anterofrontal ridge (in *Cangshanaltica* frontal ridge wide, as wide between antennal sockets as near clypeus, forming one solid structure with anterofrontal ridge); anterolateral callosity of pronotum straight, facing anterolaterally with obtuse denticle posteriorly (in *Cangshanaltica* callosity convex, facing more anteriorly than laterally without denticle posteriorly); elytra with regular rows of punctures and convex interspaces (in *Cangshanaltica* elytral punctures placed irregularly and elytra without convex interspaces); metatibial spur short and slender (in *Cangshanaltica* metatibial spur long and more robust). From *Minota*, with which *Baoshanaltica* shares similarly shaped frontal ridge, absence of humeral calli, regular elytral punctuation and wide epipleuron, it can be differentiated by: presence of anterofrontal ridge (absent in *Minota*); poorly developed supracallinal sulci (well developed in *Minota*); and open procoxal cavities (closed in *Minota*). *Baoshanaltica* resembles apterous species of *Phaelota*, which are also moss-inhabiting. Both share characters such as two pairs of labral setae, robust distal antennomeres, presence of antebasal transverse impression on pronotum, regular elytral punctuation, wide elytral epipleura reaching almost up to elytral apex etc. However, *Baoshanaltica* can be easily differentiated from *Phaelota* based on the modified 7<sup>th</sup> antennomere in males (unmodified in *Phaelota*), open procoxal cavities (closed in *Phaelota*), metatibia which is not sexually dimorphic (sexually dimorphic in *Phaelota*) and eyes separated by a distance of 3.50–3.60 times transverse diameter of one eye (eyes separated by a distance of 1.6–2.3 times transverse diameter of one eye in *Phaelota*).

***Baoshanaltica minuta* Konstantinov & Ruan, sp. n.**

<http://zoobank.org/4CC8CD22-1BFE-4224-AD84-CC5B395B6D5B>

Figs 1–3

**Etymology.** The new species is named after its small body size.

**Distribution.** China.

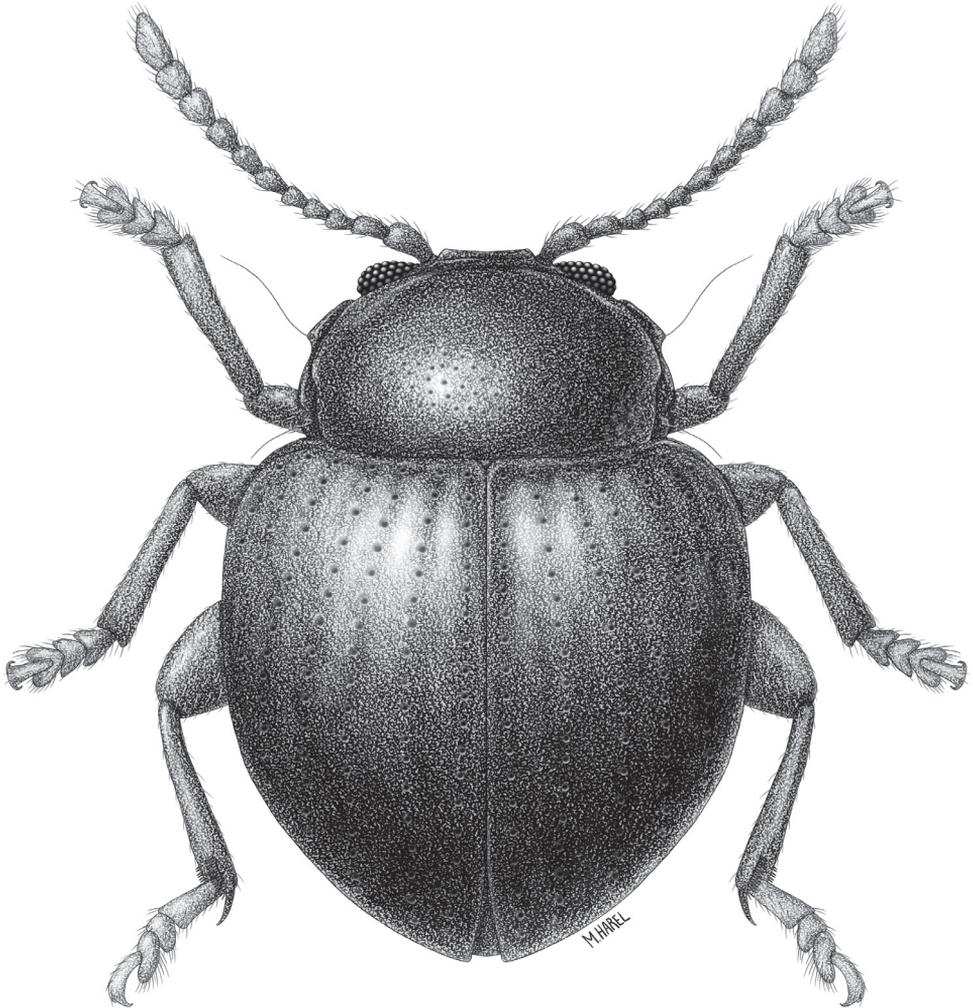
**Host plant.** Possibly unknown species of moss.

**Type material. Holotype,** ♂ (IZCAS), labels: 1) Yunnan, 60 km W Baoshan, Lujian Zhen, 11.VI.2012, N24.55'736 E99.48'332, h-2383 m, moss sifted, leg. A. Konstantinov. 2) Holotype. 3) *Baoshanaltica minuta* des. Konstantinov & Ruan, 2016.

**Paratype.** 1♂ (USNM), labels: 1) Yunnan, 60 km W Baoshan, Lujian Zhen, 111. VI.2012, N24.55'736 E99.48'332, h-2383 m, moss sifted, leg. A. Konstantinov. 2) Paratype *Baoshanaltica minuta* des. Konstantinov & Ruan, 2016.

**Description.** Dorsum and venter uniformly brown to dark brown, without metallic luster. Body oval in dorsal view, highly convex in lateral view. Body length: 1.40–1.55 mm (n=2). Body width (widest point of elytra): 1.05–1.10 mm.

Antennal calli poorly delimited with supracallinal, midfrontal, supraantennal, and suprafrenal sulci absent to poorly developed. Frontal ridge wider between antennal sockets than near clypeus. Top of frontal ridge separated from vertex by more or less round impression. Width of frontal ridge to antennal sockets (counting surrounding



**Figure 1.** *Baoshanaltica minuta* sp. n. (habitus).

ridges), ratio 2.50–2.60. Vertex shiny, without punctures, except for supraorbital, obviously concave at its lower part near frontal ridge. Distance between eyes (just above antennal sockets) to transverse diameter of eye in frontal view, ratio 3.50–3.60. Longitudinal diameter of eye to transverse diameter of eye in frontal view, ratio 1.95–2.05. Sides of head below eyes converging ventrally. Distance between antennal sockets to transverse diameter of one antennal socket, ratio 2.50–2.60. Proportions of *antennomeres* as follows: 13:7:6:7:7:6:8:8:9:10:15. Length to width of antennomere 9, ratio 1.20–1.25. Length to width of antennomere 10, ratio 1.05–1.10. Length to width of antennomere 11, ratio 1.45–1.55.

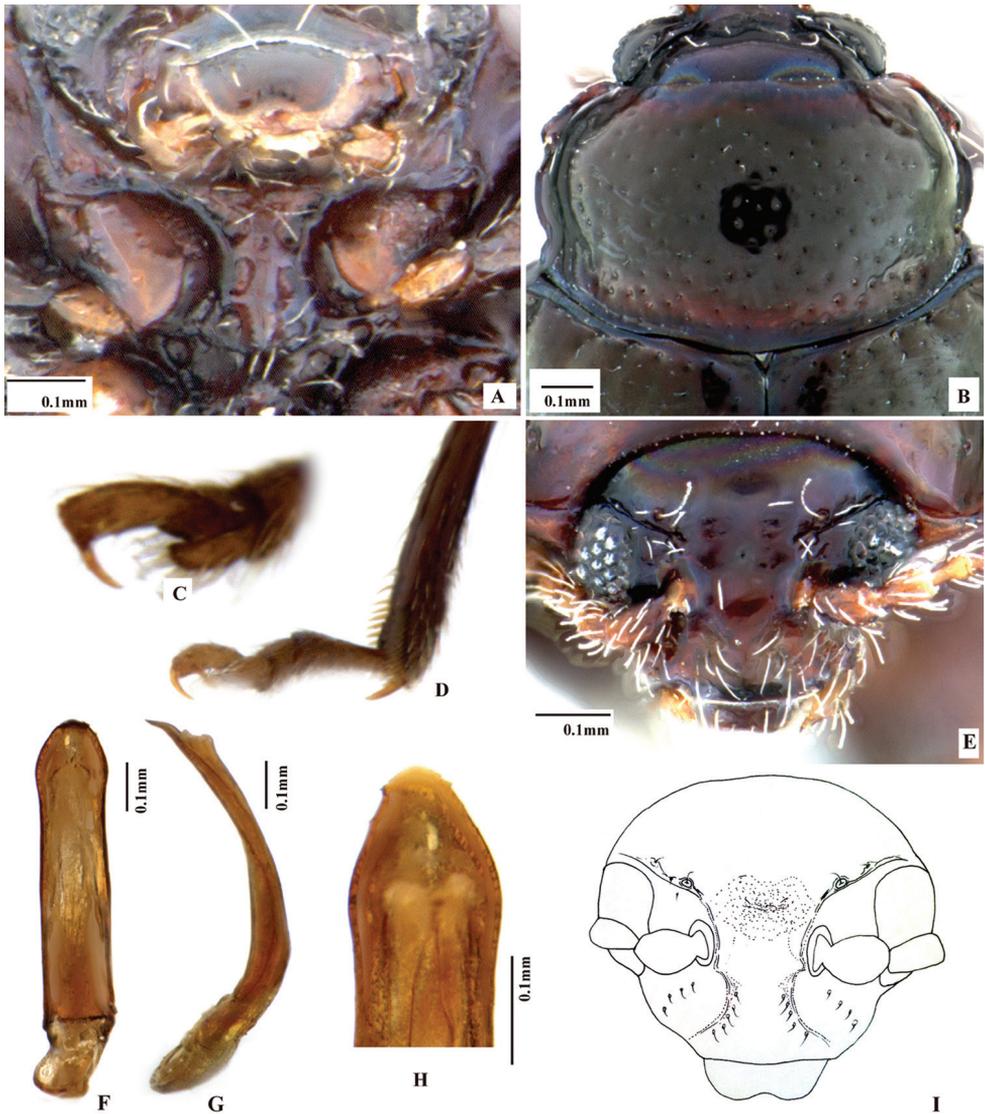
Pronotal surface glabrous, with punctures as large as elytral ones, their diameter 2–3 times smaller than distance between them. Sides of pronotum curved, somewhat



**Figure 2.** *Baoshanaltica minuta* sp. n. **A** habitus (holotype, male) **B** epipleuron **C** venter **D** lateral view of body.

angulate near middle. Posterolateral setiferous pore of pronotum protruding laterally beyond lateral margin. Elytral humeral callus absent. Hind wings absent. Elytron with small punctures arranged in 8 rows, scutellar row absent. Interspaces slightly costate.

Length (not counting trochanter) to maximum width of metafemur, ratio 1.90–1.95. Length to width of metatibia in lateral view, ratio 7.70–7.80. Width of metatibia at base to width at apex in dorsal view, ratio 0.50–0.60. Length of metatibia to length of first metatarsomere, ratio 4.50–4.60. First protarsomere of male, length to width,



**Figure 3.** *Baoshanaltica minuta* sp. n. **A** prosternum **B** pronotum **C** claw **D** tarsi of hind leg **E** frontal view of head **F** Aedeagus, ventral view **G** aedeagus, lateral view **H** apical part of aedeagus, dorsal view **I** frontal view of head (drawing).

ratio (in dorsal view), ratio 1.40–1.50. First metatarsomere of male, length to width, ratio (in dorsal view), ratio 2.20–2.30. Length of first metatarsomere to length of second metatarsomere, ratio 2.90–3.00.

Aedeagus slender, flattened in cross section, with long membranous window ventrally. In lateral view aedeagus strongly and evenly curved with apex abruptly bent ventrally. Apical denticle absent.

***Sinosphaera* Konstantinov & Ruan, gen. n.**

<http://zoobank.org/2E610C26-7999-4301-85F2-7E67C2E41793>

Figs 4–6

**Type species.** *Sinosphaera aptera* Konstantinov & Ruan, new species.

**Etymology.** The new genus is named for its spherical body outline. The name is feminine.

**Distribution.** China.

**Host plant.** Unknown.

**Description.** Body color and proportions. Dorsal surface without hair, glabrous, metallic bluish or greenish, shiny, pronotum very slightly darker than elytra. Ventral surface dark brown. Body spherical in dorsal view, moderately and evenly convex in lateral view. Body length: 2.60–2.80 mm (n=2). Body width (widest point of elytra): 1.80–2.00 mm. Body length to width, ratio 1.35–1.45. Pronotum width to length, ratio 1.90–2.00. Pronotum width at base to width at apex, ratio 1.25–1.35. Elytron length (measured along suture) to width of both, ratio 0.95–1.05. Elytron and abdomen length to height of body (in lateral view), ratio 1.50–1.55. Length of elytron to length of pronotum, ratio 2.60–2.70. Width of elytra at base (measured across middle of humeral calli) to width of pronotum at base, ratio 1.05–1.10.

Head. Vertex metallic blue, shiny, with extremely minute and distantly placed punctures. Vertex with small indentation or transverse impression above frontal ridge. Frontal ridge short, as wide between antennal sockets as near anterofrontal ridge, entering between antennal calli. Top of frontal ridge meet and merge with vertex. Width of frontal ridge to antennal sockets (counting surrounding ridges), ratio 2.30–2.35. Frontal ridge in lateral view moderately convex. Frontal ridge and anterofrontal ridge in frontal view gradually merge into each other. Frontal ridge and vertex in lateral view form convex line. Anterofrontal ridge lower near frontal ridge, higher laterally, concave in middle.

Antennal calli more or less triangular, at same level as surface of vertex, separated from each other by tip of frontal ridge, entering interantennal space. Width to length of antennal callus, ratio 1.40–1.45. Length of antennal calli smaller than length of frontal ridge. Supracallinal sulcus slightly and evenly curved, poorly developed. Suprafrontal sulcus straight, poorly developed. Supraorbital and orbital sulci very short and deep. Supraantennal sulcus long, stronger than supracallinal, but not as deep as orbital sulcus. Frontolateral sulcus poorly developed.

Orbit normally wide, as wide as transverse diameter of antennal socket. Supraorbital pore poorly developed, unrecognized. Inner margin of eye straight to very slightly concave in middle. Distance between eyes (just above antennal sockets) to transverse diameter of eye in frontal view, ratio 4.20–4.30. Longitudinal diameter of eye to transverse diameter of eye in lateral view, ratio 2.00–2.10. Sides of head below eyes converging ventrally. Labrum flat, without projections in middle. Anterior margin of labrum entire and straight. Number of labral setae: 3 pairs. Apical maxillary palpomere conical, length to width, ratio 1.70–1.80. Preapical maxillary palpomere proximally narrower than distally. Length to width, of preapical maxillary palpomere, ratio 1.00–

1.05. Length of apical to preapical maxillary palpomeres, ratio 1.55–1.60. Clypeus band like. Antennal sockets situated nearly at middle level of eye. Distance between antennal sockets to transverse diameter of one antennal socket, ratio 2.70–2.80.

Antennae. Antennae filiform, stretching over pronotum but not reaching half of elytron. Number of antennomeres 11. Length of antennomere 1 slightly greater than next two antennomeres combined. Antennomere 2 robust, longer and wider than 3. Antennomere 5 slightly longer than antennomere 4 and slightly shorter than 6 separately. Distal antennomeres slightly wider than middle ones. Length to width of antennomere 9, ratio 1.40–1.45. Length to width of antennomere 10, ratio 1.15–1.20. Length to width of antennomere 11, ratio 2.40–2.45.

Prothorax. Pronotal surface glabrous, with 2 antebasal, barely visible longitudinal impressions, laterally. Anterolateral corners of pronotum projected prominently forward. Anterolateral callosity of pronotum strongly developed, ovoid, without angulation, facing anteriorly. Anterior setiferous pore of pronotum situated close to anterior margin. Sides of pronotum weakly convex, strongly converging anteriorly. Pronotal base evenly convex. Lateral margin of pronotum complete and narrowly explanate. Posterolateral setiferous pore of pronotum not protruding laterally beyond lateral margin.

Procoxal cavities closed. Lateral sides of intercoxal prosternal process concave in middle, with apex much wider than middle. Posterior end of intercoxal prosternal process nearly straight. Intercoxal prosternal process normally wide, convex along its length, without ridge, slightly extends beyond procoxae. Width of intercoxal prosternal process between procoxae to length of procoxa, ratio 0.70–0.75.

Elytra. Elytra without humeral calli. Hind wings absent. Elytra at base wider than base of pronotum. Impressions or ridges on elytron absent. Elytron with punctures minute and confused. Scutellum present, small. Elytron with apex rounded, covering entire abdomen. Elytra with strongly and evenly convex sides. Epipleura oblique outwardly. Epipleura gradually narrowing from base to apex. Width of epipleura about equal to that of profemur. Epipleura basally much wider than apically. Epipleura reaches end of elytron.

Venter. Metasternum projecting forward, covers and conceals mesosternum. Metasternum without elevated projection in middle. Abdominal ventrites 1 and 2 not fused. Abdominal ventrite 1 longer than ventrites 2, 3, and 4 together. Abdominal ventrite 5 as long as ventrites 4 and 3 together. First abdominal ventrite between coxae without longitudinal ridges. Anterior end of first abdominal ventrite extremely wide and slightly convex.

Legs. Pro- and mesotibia without apical spur. Apical spur of metatibia tiny, slightly larger than other bristles. Metafemoral spring present. Claw appendiculate. Apical part of hind and middle tibia without excavation. Length (not counting trochanter) to maximum width of metafemur, ratio 2.50–2.55. Length to width of metatibia in lateral view, ratio 7.00–7.10. Width of metatibia at base to width at apex in dorsal view, ratio 0.60–0.65. Length of metatibia to length of first metatarsomere, ratio 4.65–4.70. Metatibia generally straight. Metatibia in cross section around its middle more or less cylindrical, flattens only very close to apex and also abruptly widens near apex in dorsal view. Dorsal side of metatibia without sharp edge or small denticles. Metatarsomere 1

attached to apex of metatibia. Length of metafemur to metatibia, ratio 1.10–1.20. First protarsomere of male, length to width, ratio (in dorsal view) 1.20–1.30. Length of first protarsomere to length of second protarsomere, ratio 1.70–1.75. Width of first protarsomere to width of second protarsomere, ratio 1.05–1.10. Incision of tarsomere 3 as long as wide. Tarsomere 3 subtriangular. First metatarsomere of male, length to width, ratio (in dorsal view) 1.90–2.00. Length of first metatarsomere much less than half of metatibial length. First and rest three metatarsomeres make more or less straight line. Length of first metatarsomere to length of second metatarsomere, ratio 1.50–1.55. Width of first metatarsomere to width of second metatarsomere, ratio 0.95–1.00. Length of fourth metatarsomere to length of third metatarsomere, ratio 0.95–1.00.

Genitalia. Aedeagus robust and short, slightly flattened in cross section, evenly and moderately curved, with apex gradually narrowed.

**Remarks.** *Sinosphaera* resembles *Omeisphaera* Chen & Zia and *Sphaeroderma* Stephens in having ovate body shape and similar, forward facing, anterolateral callosities of the pronotum. *Sinosphaera* can be easily differentiated from these genera by the short antebasal, lateral impression on the pronotum and closed procoxal cavities. They are open in *Omeisphaera* and *Sphaeroderma*, which are also lacking antebasal, lateral impression on the pronotum. In *Sinosphaera*, antennal calli are separated from each other by the top of the frontal ridge. They are connected in *Omeisphaera* and *Sphaeroderma*. *Sinosphaera* resembles *Kamala* in having ovate body shape, absence of humeral calli and closed procoxal cavities. However, they can be easily separated by the lack of antebasal impressions on pronotum (short longitudinal antebasal impressions present in *Kamala*), confused elytral punctation (elytral punctures form rows in *Kamala*) and the distal antennomeres only slightly wider than the middle ones (distal antennomeres form a dilated club in *Kamala*). *Jacobyana* superficially resembles *Sinosphaera* in being rounded, convex and posteriorly narrowed. Minutely punctate vertex and frons (vertex and frons coarsely punctate in *Jacobyana*), evenly convex posterior margin of pronotum (posterior margin of pronotum bisinuate in *Jacobyana*), closed procoxal cavities (procoxal cavities open in *Jacobyana*), confused elytral punctation (elytral punctures regularly arranged in *Jacobyana*) and absence of hindwings and humeral calli (both present in *Jacobyana*) will separate these two genera.

***Sinosphaera aptera* Konstantinov & Ruan, sp. n.**

<http://zoobank.org/85A7DF16-182B-44D1-A855-231DF85E5209>

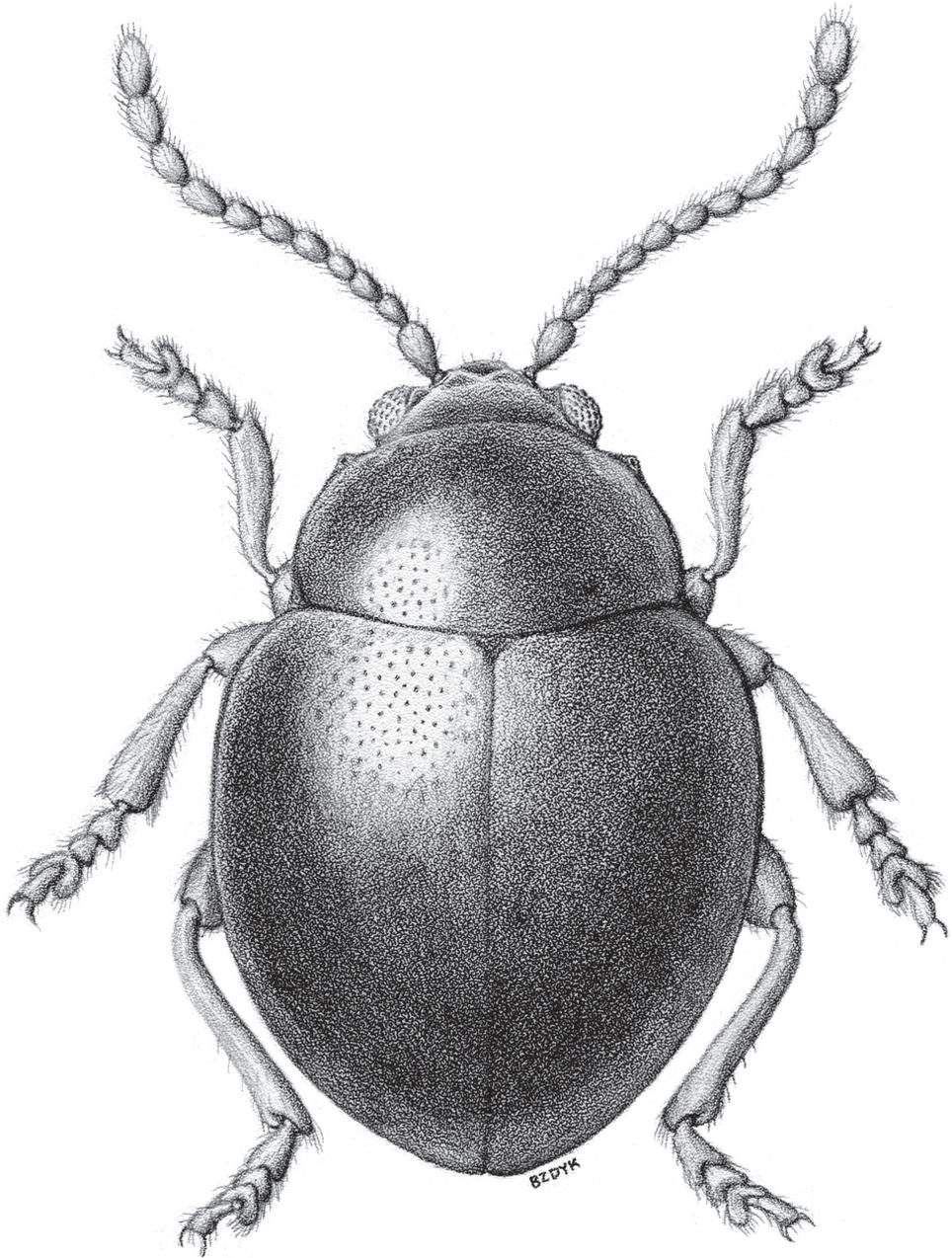
Figs 4–6

**Etymology.** This species is named after the absence of hindwings.

**Distribution.** China.

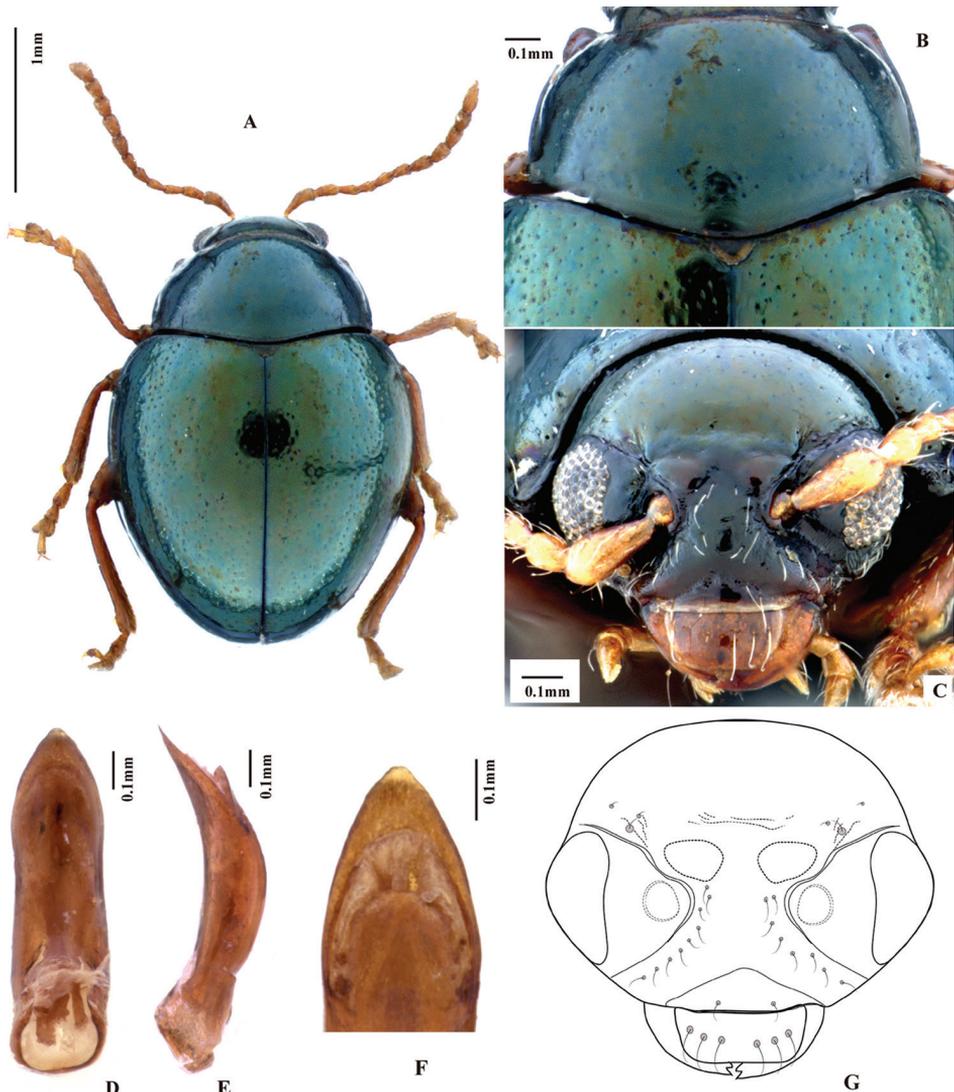
**Host plant.** Unknown.

**Type material.** **Holotype**, ♂ (IZCAS), labels: 1) CH, Sichuan, right bank of r. trib. of Lanhegou River, SSW of Jimi Vill., 2200–2600 m, 25.VI.2000, Belousov, Kabak, Davidian. 2) Holotype. 3) *Sinosphaera aptera* des. Konstantinov & Ruan, 2016.



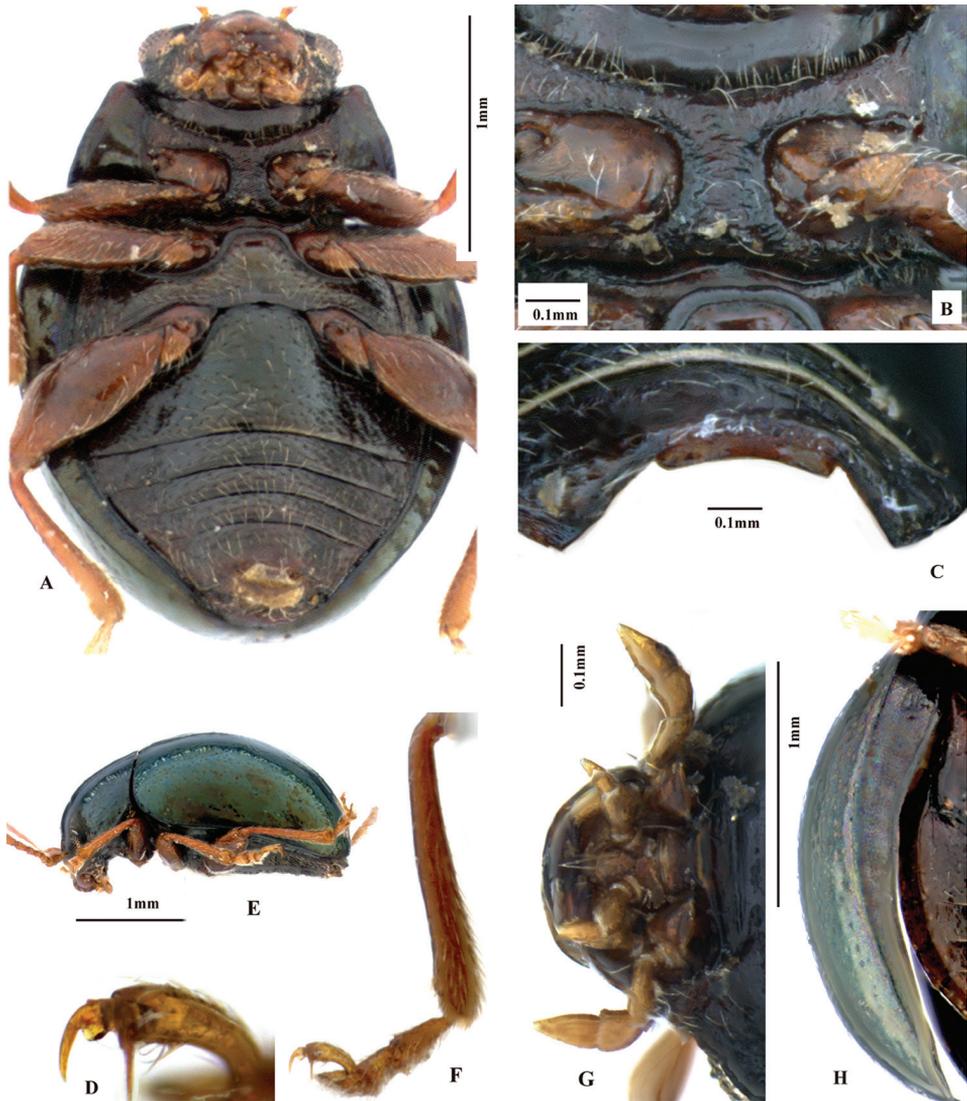
**Figure 4.** *Sinosphaera aptera* sp. n. (habitus).

**Paratypes.** 5♂ (USNM), labels: 1) CH, Sichuan, right bank of r. trib. of Lanhegou River, SSW of Jimi Vill., 2200–2600 m, 25.VI.2000, Belousov, Kabak, Davidian. 2) Paratype *Sinosphaera aptera* des. Konstantinov & Ruan, 2016.



**Figure 5.** *Sinosphaera aptera* sp. n. **A** habitus (holotype, male) **B** prothorax, dorsal view **C** head, frontal view **D** aedeagus, ventral view **E** aedeagus, lateral view **F** apical part of aedeagus, dorsal view **G** frontal view of head (drawing).

**Description.** Dorsal surface glabrous, metallic bluish or greenish, pronotum slightly darker than elytra. Body spherical in dorsal view, moderately and evenly convex in lateral view. Body length: 2.60–2.80 mm ( $n=2$ ). Body width (widest point of elytra): 1.80–2.00 mm. Body length to width, ratio 1.35–1.45. Pronotum width to length, ratio 1.90–2.00. Pronotum width at base to width at apex, ratio 1.25–1.35. Elytron length (measured along suture) to width of both, ratio 0.95–1.05. Length of elytron to length of pronotum, ratio 2.60–2.70. Width of



**Figure 6.** *Sinosphaera aptera* sp. n. **A** ventral view of holotype **B** prosternum **C** last ventrite of male **D** claw **E** lateral view of holotype **F** lateral view of hind tibia and tarsi **G** maxillary palpi and labial palpi **H** epipleuron.

elytra at base (measured across middle of humeral calli) to width of pronotum at base, ratio 1.05–1.10.

Vertex shiny, with extremely minute and distantly placed punctures bearing small setae, punctures larger at base of vertex. Anterofrontal ridge with wrinkles on surface facing antennal calli.

Antennae with antennomeres of following proportions: 20:10:8:10:9:9:10:11:10:10:15.

Distal antennomeres slightly wider than middle ones. Length to width of antennomere 9, ratio 1.40–1.45. Length to width of antennomere 10, ratio 1.15–1.20. Length to width of antennomere 11, ratio 2.40–2.45.

Pronotal surface glabrous with small, evenly spaced punctures, smaller than elytral punctures. Sides of pronotum weakly convex, strongly converging anteriorly. Pronotal base evenly convex.

Humeral calli of elytra absent. Hind wings absent. Elytral punctures larger than pronotal, confused.

Length (not counting trochanter) to maximum width of metafemur, ratio 2.50–2.55. Metatibia slender, its length to width in lateral view, ratio 7.00–7.10. Length of metatibia to length of first metatarsomere, ratio 4.65–4.70. First protarsomere of male, length to width, ratio (in dorsal view), 1.20–1.30. Length of first protarsomere to length of second protarsomere, ratio 1.70–1.75. Width of first protarsomere to width of second protarsomere, ratio 1.05–1.10.

Aedeagus relatively short with more or less convex ventral side and narrow groove stretching from basal opening to about 1/3 from apex. Apex gradually narrowed. Apical denticle of aedeagus absent.

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# *Oulema septentrionis* and *O. erichsonii* are neither conspecific nor melanic variants of *O. melanopus* as assessed by micro CT analysis of their lectotypes (Insecta, Coleoptera, Chrysomelidae, Criocerinae)<sup>1</sup>

Michael Schmitt<sup>1</sup>, Gabriele Uhl<sup>1</sup>

<sup>1</sup> Ernst-Moriz-Arndt-Universität, Allgemeine & Systematische Zoologie, Loitzer Str. 26, 17489 Greifswald, Germany

Corresponding author: Michael Schmitt ([michael.schmitt@uni-greifswald.de](mailto:michael.schmitt@uni-greifswald.de))

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## Abstract

The investigation of the type series of *Oulema septentrionis* (Weise, 1880) and *Oulema erichsonii* (Suffrian, 1841) using Micro-computed X-ray tomography ( $\mu$ CT) revealed that neither species is a melanic variant of *Oulema melanopus* (Linnaeus, 1758) as has been suggested previously. Lectotypes of *Oulema septentrionis* (Weise, 1880) and *Oulema erichsonii* (Suffrian, 1841) are designated based on the study of type material. The male genitalia of *O. septentrionis* and *O. erichsonii* differ to an extent in the shape of the median lobe and flagellum that their status as separate species – cautiously – confirmed by the present study.

## Keywords

Taxonomy, lectotype designation, 3D-reconstruction, aedeagus, flagellum, morphology

## Introduction

In the western Palearctic there are *Oulema* species with a red and with a blue pronotum. The discussion as to how many species we should accept is ongoing. In catalogues (e.g.

<sup>1</sup> Contribution to the 9<sup>th</sup> International Symposium on the Chrysomelidae, Orlando, FL, USA, September 28, 2016

Schmitt 2010) and identification keys (e.g. Kippenberg 1994) five species with blue pronotum are listed: *O. septentrionis* (Weise, 1880), *O. erichsonii* (Suffrian, 1841), *O. obscura* (Stephens, 1831) = *O. gallaeciana* (Heyden, 1870) see Cox (2000), and *O. tristis* (Herbst, 1786). *O. septentrionis* is sometimes regarded a subspecies or even variety of *O. erichsonii* (e.g. Mohr 1966). A fifth species with a blue pronotum was described in 1964 from Italy, *O. maggistrettiorum* Ruffo, 1964. A recent review of the species with red pronotum (Bezdek and Baselga 2015) considered five different species occurring in Europe: *O. melanopus* (Linnaeus, 1758), *O. duftschmidi* (Redtenbacher, 1874), *O. mauroi* Bezdek & Baselga, 2015, *O. rufocyanea* (Suffrian, 1847) and *O. verae* Bezdek & Baselga, 2015. A sixth species, *O. hoffmannseggii* (Lacordaire, 1845), is listed by e.g., Warchałowski (2003, 2010).

On the website of the NERC- Centre for Ecology & Hydrology the hypothesis was published that specimens identified as *Oulema septentrionis* in Ireland could actually be melanic forms of *O. melanopus*: “The taxonomic status of *O. septentrionis* in Ireland is currently under review as there is evidence from dissections of the aedeagal flagellum that specimens from Ireland and Normandy are a melanic form of *O. melanopus*. The final outcome of this work is awaiting publication” (<http://www.coleoptera.org.uk/species/oulema-septentrionis>, last accessed 11.05.2017). We examined the type specimens of *O. septentrionis* and *O. erichsonii* non-destructively under microCT in order to inspect the median lobe and flagellum of the aedeagus and compare them with the those in the red-necked *Oulema* species *O. melanopus* and *O. duftschmidi* - as these two latter can hardly be separated by external morphological characters. With this investigation we attempt to assess two hypotheses: first, that *O. septentrionis* is a melanic form of *O. melanopus* and second that *O. septentrionis* and *O. erichsonii* are conspecific. The latter assessment is based on a morphological species concept (“morphospecies”). As long as there is no sound information at hand as to possible cross-breeding (“biospecies”) and ecological relationships (“ecospecies”), we use morphospecies as a proxy for bio- and ecospecies.

## Material and methods

From the collection of the Museum für Naturkunde Berlin (ZMUH) we received the syntype series of *Oulema septentrionis* (Weise, 1880), consisting of 11 specimens. From the collection of the Martin-Luther Universität Halle (MLUH) we received a syntype series of 14 specimens for *Oulema erichsonii* (Suffrian, 1841). Three syntype specimens of *Oulema septentrionis* and one syntype specimen of *Oulema erichsonii* were microCT-scanned with an Xradia Micro XCT-200 (Carl Zeiss X-ray Microscopy Inc.), using the 4× object lens units, at 40 kV and 8 W, with a pixel size of 5.36 µm. Tomography projections were reconstructed using the reconstruction software provided by XRadia. Volume rendering of image stacks was performed by using Amira 5.6.0 (FEI Visualization Science Group, Burlington, USA) applying the “Volren” or “Voltex” function. Habitus photographs were taken by means of a Canon EOS 6D with the Canon MP-E 65 mm macro lens in a BK PLUS Lab system by Dun Inc. The flagella of *O. melanopus* and *O. duftschmidi* were photographed using the Direct to Sensor Microscope Lens

with a 10× Mitutoyo objective mounted on a Canon EOS 7D camera in a BK PLUS Lab system by Dun Inc. Obtained images stacks were processed using Zerene Stacker and Adobe Photoshop CS6.

## Data repository

The set of TIFF-files from the microCT scan of the three (former) syntype specimens of *Oulema erichsonii* is deposited at the MLUH, that of *Oulema septentrionis* at ZMHU, copies are accessible through MorphDBase (<https://www.morphdbase.de/> – OULEERIC\_1, OULEERIC\_2, OULESEPT\_1).

## Results

### *Oulema septentrionis* (Weise, 1880)

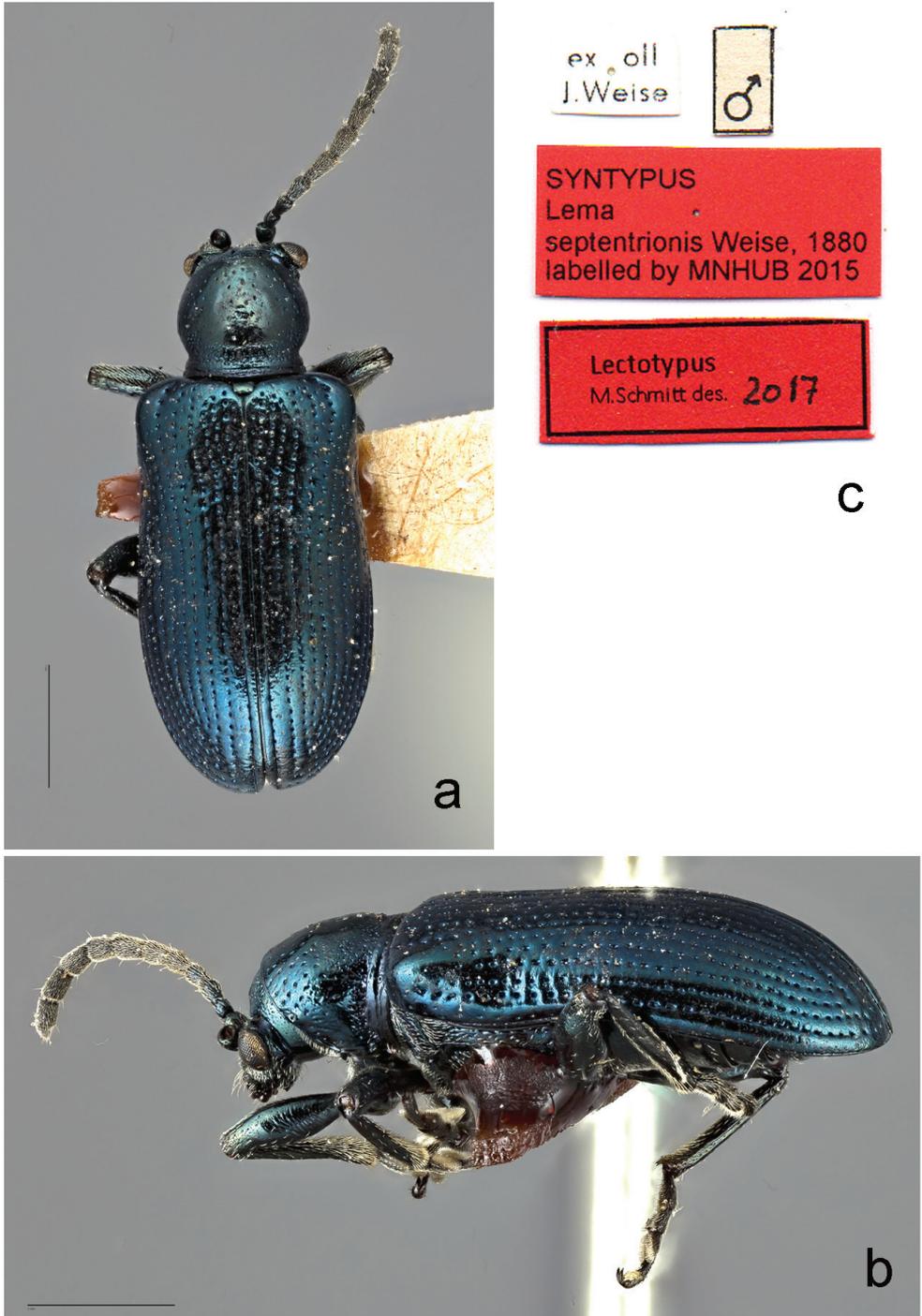
Of the 11 syntype specimens – all of them pinned - of *O. septentrionis* we scanned three specimens, among them one male that we designate here lectotype (Fig. 1 - male, pinned, Germany [with no locality information] / Weise, see Fig. 1c). Three of the paralectotypes have also no locality label. Nine specimens of the syntype series have the same red name label and an “ex coll. Weise label” as the lectotype (Fig. 1c). Of these, one has an additional handwritten label “septentrionis\*”, one a small label “Müggel” (probably Müggelsee/lake Müggel in Berlin), one is labelled “Styria Ludg”, and one “Stettin”. The two remaining specimens have a simple label “Typus”, one of them additionally a label “Müggel” and a name label “Lema septentrionis Wse. / L.N. Medvedev det. 1973”. All paralectotypes were additionally labelled “Paralectotypus / M.Schmitt des. 2017”.

The 3D reconstruction revealed that the tip of the apex of the median lobe is pointing straight forward. Seen from the side, the apex of the median lobe has a wedge-like shape with upper and lower outline forming an angle of 40° (Fig. 2a). The ostium is oval and semicircular towards the tip of the apex, with the distal third of the flagellum laying outside the median lobe (Fig. 2b). The flagellum has a thicker portion basally and a thinner towards the tip, the latter being about as long as the basal part (Fig. 2c).

### *Oulema erichsonii* (Suffrian, 1841)

The scanned syntype of *O. erichsonii* specimens was a male. This we designated here lectotype (Fig. 3).

Material examined: The specimens do not bear a locality label but only tiny labels in different colours showing an individual number. In the book of records maintained by Christian Wilhelm Ludwig Eduard Suffrian (1805–1876), the localities for each numbered specimen are listed. These are:

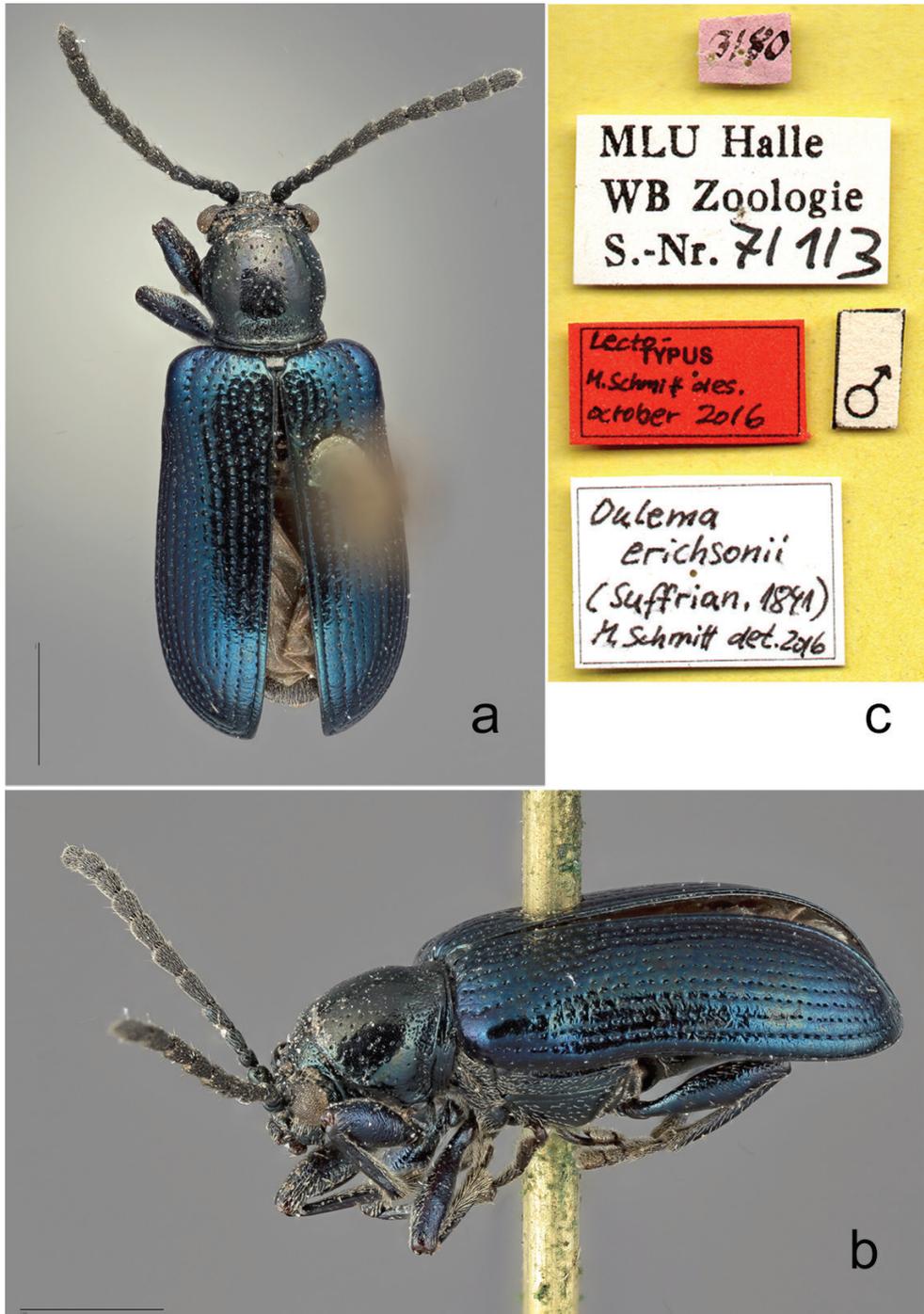


**Figure 1.** *Oulema septentrionis* (Weise, 1880), lectotype. **a** dorsal **b** lateral from left **c** labels. Scale bars: 1 mm.

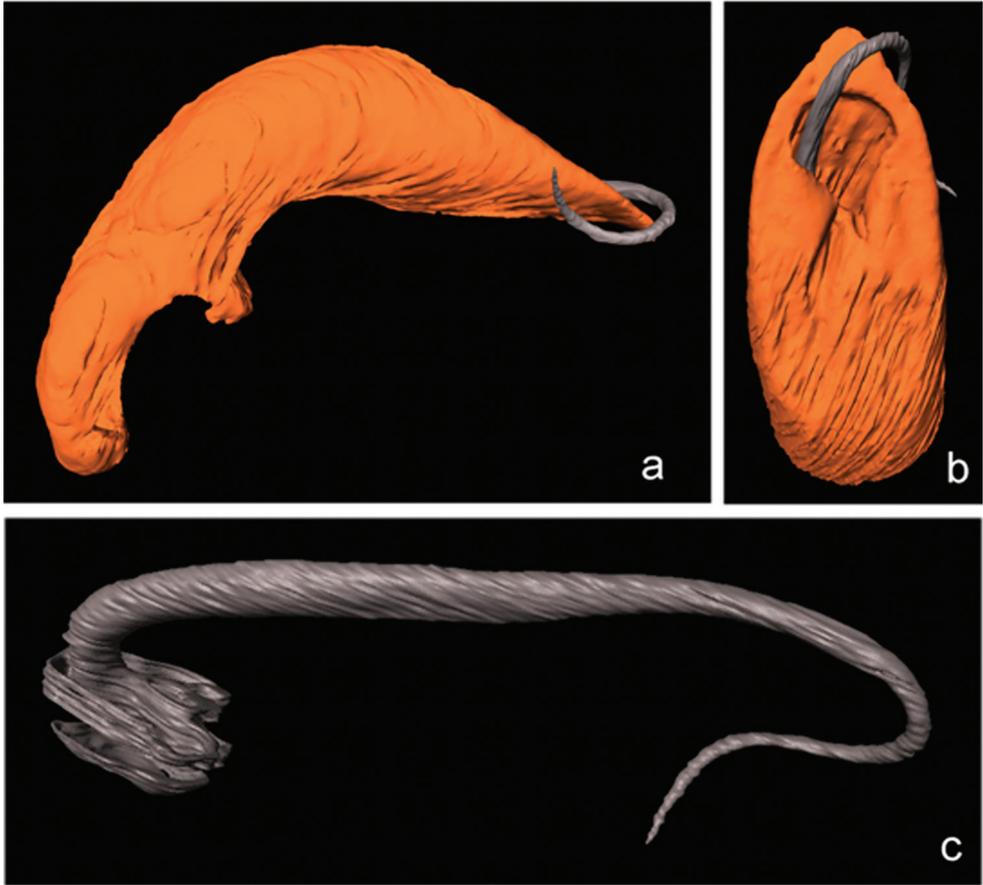


**Figure 2.** *Oulema septentrionis*, lectotype; **a:** median lobe with flagellum lateral **b** apex of median lobe with flagellum dorsal; **c:** flagellum (not to scale). 3D reconstructed microCT-scans.

**Lectotype** male, pinned, No. 3180 Elberfeld (Fig. 3), **Paralectotypes**, pinned: nos. 3178 & 3179 Kassel, no. 3181 Altenburg, no. 3174 Dortmund, all originally listed as “*Lema cyanella*”, nos. 4220, 4221, 4222, 4223 “Regio 1827”, probably meaning the environments of Aschersleben, where Suffrian lived and worked as a school teacher from 1825 until 1833 (Dohrn 1877). He entered nos. 4220–4223 as “*Lema cyanella* Gyl.” but explained in a note on the left margin of the page, obviously added later: “4220 ist eine neue Art, *L. Erichsonii* Mihi. Davon ist 4221.22. die var.  $\beta$ . mit schwarzem Halsstück, und 4123 var.  $\gamma$ . schwarz. Die Art ist durch Bau und Punktierung des Halsstücks, sowie durch den Bau der Flügeldecken hinreichend von *L. cyanella* Gyl. verschieden“ (4220 is a new species, *L. Erichsonii* mihi. Of these is 4221.22 the variety  $\beta$  with black thorax, 4123 var.  $\gamma$  black. The species is by shape and punctuation of the pronotum as well as by the shape of the elytra sufficiently different from *L. cyanella* Gyl.). No. 9883 Siegen, no. 11012 “Wald von Montabaur”, no. 19596 Münster, no. 27523 Moskau. The fourteenth specimen, no. 10162 from Mainz, is clearly an *Oulema obscura* (Stephens, 1831), so we put a name label accordingly on the pin. “*Lema cyanella* Gyl.” refers to Gyllenhal’s *Insecta suecica* (1813: 638), where this name is used for *Oulema obscura* (Stephens, 1831). All paralectotypes were additionally labelled “Paralectotypus / M.Schmitt des. 2017”.



**Figure 3.** *Oulema erichsonii* (Suffrian, 1841), lectotype. **a** dorsal **b** lateral from left **c** labels. Scale bars: 1 mm.



**Figure 4.** *Oulema erichsonii*, lectotype; **a** median lobe with flagellum lateral **b** apex of median lobe with flagellum dorsal **c** flagellum (not to scale). 3D reconstructed microCT-scans.

The 3D reconstruction revealed that the tip of the apex of the median lobe is slightly bent downwards (“ventrally”). Seen from the side, the apex of the median lobe has a wedge-like shape with upper and lower outline forming an angle of  $30^\circ$  (Fig. 4a). The ostium is broad and semicircular towards the tip of the apex, with the distal half of the flagellum laying outside the median lobe (Fig. 4b). The flagellum has a thicker portion basally and a thinner towards the tip, the latter being considerably longer than the basal part (Fig. 4c).

***Oulema melanopus* (Linnaeus, 1758) and *Oulema duftschmidi* (Redtenbacher, 1874)**

We compared the flagella of the above species with those of the species of which they were suspected melanic forms. One male of *O. melanopus*: GERM. RHEINL. / UNKEL



**Figure 5.** Flagella of **a** *Oulema duftschmidi* **b** *O. melanopus*, photos taken at the same magnification.

/ 29.93.92 SIEDE // BACHTÄLCHEN / KAHLSCHLAG / UNT. VERBASCUM // LEMA MELANOPUS (L.) S.STR. / SIEDE DET. 92. One male of *O. duftschmidi*: same data as before, but LEMA DUFT- / SCHMIDI REDT. / SIEDE DET. 92.

The flagella differ clearly from each other and from those of *O. erichsonii* and *O. septentrionis*. The flagellum of *O. melanopus* is short, stout, and only slightly curved, with a proportion of length/diameter=4.8. The flagellum of *O. duftschmidi* is long, slender, nearly semi-circular, without an inflexion point, and ca. 40 times longer than wide. Since the rim of the distal opening is complete, it is certain that the tips are not broken (Fig. 5).

## Discussion

Our study shows that *Oulema septentrionis* is not a melanic form of *Oulema melanopus*. The specimens from Ireland and Normandy identified as *Oulema septentrionis* by the authors of the website [www.coleoptera.org.uk](http://www.coleoptera.org.uk) must belong to a different species, provided that the shape of the flagella differ between the supposed *O. septentrionis* and the specimens we investigated.

The outer morphology of *Oulema melanopus* (Linnaeus, 1758) and of *O. duftschmidi* (Redtenbacher, 1874) is extremely similar. Until Nicole Berti's thorough investiga-

tion (1989) taxonomists treated the two forms as conspecific. Therefore, we used dissected specimens of both species for comparison with *O. septentrionis* and *O. erichsonii* (Fig. 5). The morphological comparison shows clearly that neither *O. septentrionis* nor *O. erichsonii* is conspecific with *O. melanopus* or *O. duftschmidi*.

The morphological differences in the aedeagus of the lectotypes of *Oulema septentrionis* and *O. erichsonii* concur with the differences in external morphology found in the literature (e.g., Weise 1893, Mohr 1966, Warchałowski 2003): *O. erichsonii* has a very finely punctate pronotum, whereas in *O. septentrionis* only the hind part of the pronotum is finely and deeply punctate. However, the elytral punctures appear very much the same, in contrast to the description in Mohr (1966). Altogether, the differences indicate that the two forms are separate morphospecies, which is also supported by Bukejs' (2010) study on their aedeagi. Since we have no information on whether these morphospecies interbreed, and if so, with viable offspring, it is uncertain if they are biospecies. Both species are repeatedly mentioned as feeding on *Nasturtium*, which goes back to Weise (1893). Still, there are no confirmations of this statement nor did we find the species when inspecting *Nasturtium* in the field. In conclusion, we cautiously treat *Oulema septentrionis* and *O. erichsonii* for taxonomic purposes as different species based on our morphological investigation.

Our study corroborates that Micro-computed X-ray tomography ( $\mu$ CT) can be used successfully for non-invasive, non-destructive investigation of internal structures of dried beetle specimens, e.g. old type material, as was e.g. demonstrated for Lepidoptera (Simonsen and Kitching 2014) and damselflies (Steinhoff and Uhl 2015). A pixel size of 5.36  $\mu$ m is sufficient to reveal the details necessary for a taxonomic analysis of the male copulatory apparatus in resting posture inside the specimen.

## Acknowledgements

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# Quo vadis biodiversity? Species richness following twenty years of taxonomic revisions on Afrotropical Galerucinae s. str. (Coleoptera, Chrysomelidae)<sup>1,2</sup>

Thomas Wagner<sup>1</sup>

<sup>1</sup> Universität Koblenz-Landau, Institut für Integrierte Naturwissenschaften – Biologie, Universitätsstr. 1, D-56070 Koblenz, Germany

Corresponding author: Thomas Wagner ([thwagner@uni-koblenz.de](mailto:thwagner@uni-koblenz.de))

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## Abstract

Galerucinae is one of the most species-rich leaf beetle group with its greatest diversity occurring in tropical forests. There are 1680 nominal species of Afrotropical Galerucinae s. str. (without Alticini) described. Considering global diversity estimations, many unknown species can be presumed. Several taxa traditionally placed in “Monoleptites”, have been revised in the last twenty years. To date 259 species have been re-examined, revealing in 139 valid species and 120 mainly newly recognized synonyms. This large number of synonyms can mainly be ascribed to highly variable colour patterns, a typical character used for the identification of many chrysomelid species. Genitalic structures and molecular work can support a more precise allocation to species. Within around 72,000 specimens of galerucines s. str. from 48 museums and private collections, only 107 species were newly described. After revising approximately 15% of the Afrotropical galerucine fauna their species richness decreased from 259 to 246 species, a pattern that appears to be similar to that for other African galerucine groups. Since the estimation of the extent of global diversity based mainly on insect species richness in tropical forests, our current study which is based on hard data suggests a much lower diversity than previously predicted.

## Keywords

Africa, Afrotropical, region, biodiversity, Galerucinae s. str., Monoleptites, revision, taxonomy

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<sup>1</sup> 51<sup>st</sup> contribution to the taxonomy, phylogeny, and biogeography of the Galerucinae.

<sup>2</sup> Contribution to the 9<sup>th</sup> International Symposium on the Chrysomelidae, Orlando, FL, USA, September 28, 2016

## Introduction

Galerucinae s. str. (without Alticini) is one of most diverse group of leaf beetles in tropical forests, including 1680 nominal species from Africa (Wagner 2006) and 7145 species worldwide (Nie et al. 2017). Among the highly diverse Galerucinae, *Monolepta* Chevrolat, 1836 is the largest genus of Galerucinae s. str., with nearly 700 described species in the world (Wagner 2007a). When a taxonomic and phylogenetic revision of Afrotropical *Monolepta* was started, it became clear that this genus as traditionally delimited was a non-monophyletic group (Wagner 1999, 2003, 2004). *Monolepta* and other taxa with a distinctly elongated first tarsomere of the hind-leg are placed in “Monoleptites” (Wilcox 1973). Subsequently, the relative length of the second to third antennomeres, and the shape of the pronotum were considered to place the “long-legged” African galerucines largely in three genera: *Monolepta* (second and third antennomere of same length, pronotum rectangular); *Candezea* Chapuis, 1879 (third antennomere much longer than second, pronotum rectangular); and *Barombiella* Laboissière, 1931 (third antennomere much longer than second, pronotum trapezoidal).

During a period of twenty years, our working group has revised approximately 85 % of the “Monoleptites” sensu Wilcox (1973). Besides redefining generic characters in the external morphology, we also studied the genitalic patterns of all the examined taxa for the first time. These were found to be valuable not only to distinguish species, but also to define genera as monophyletic groups within *Monolepta* (e. g. Wagner 2007a), *Candezea* (Wagner and Kurtscheid 2005), and *Barombiella* (Freund and Wagner 2003, Wagner and Freund 2003, Bolz and Wagner 2011). Some species were transferred to *Afrocrania* Hincks, 1949 (Middelhauve and Wagner 2001, Wagner 2007b). We found several phylogenetically isolated taxa that had to be transferred to newly described genera, e. g. *Fromaculepta* (Hasenkamp and Wagner 2000), *Afrocandezea* (Wagner and Scherz 2002, Scherz and Wagner 2007), *Afronaumannia* (Steiner and Wagner 2005), *Monoleptoides* (Wagner 2011), and *Bicolorizea* (Heunemann et al. 2015). These supra-specific taxa could be also identified as separate phylogenetic units by molecular data (Wagner in prep.). We included also short-legged *Bonesioides* Laboissière, 1925 (Freund and Wagner 2003), *Galerudolphia* Hincks, 1949 (Bolz and Wagner 2005) and the very short-legged *Ootheca* Chevrolat, 1836 in our revisions (Kortenhaus and Wagner 2010, 2011, 2012, 2013).

At present, some 250 species of Afrotropical Galerucinae s. str. have been revised and these data are used here as a case study on their general species richness. Global insect diversity caught the attention of entomologists, and a broader audience, in the 1980s, when data of canopy fogging in tropical forests were extrapolated to 30 million species of insects (Erwin 1982). This started a controversial discussion in the community (e.g., Stork 1988, Thomas 1990, Gaston 1991), but more detailed “calculations” led to a much lower number that levelled off at around six million species (Ødegaard 2000, Basset et al. 2012). The author’s empirical data of species revisions in a quite highly diverse tropical leaf-beetle group is used here to address the question, What is the global diversity of Galerucinae s. str.?

## Material and methods

Our revisions of Afrotropical galerucines are currently published in 40 papers with a taxonomic focus (Wagner and collaborators 1993–2017) based on around 72,000 specimens from 48 collections which includes all the major museum collections that house African insects.

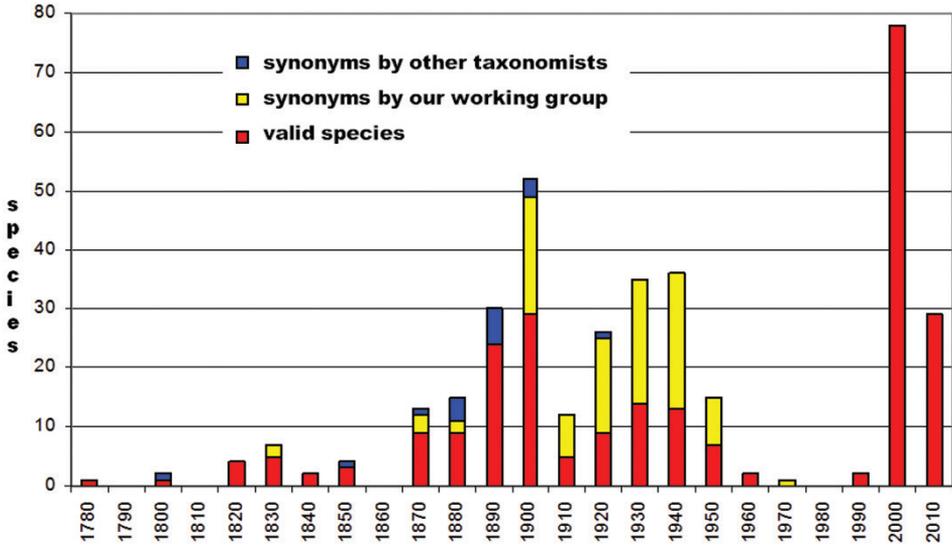
## Results

Up to now, 259 species have been re-examined, resulting in 139 valid species and 120, mainly newly recognized synonyms (Fig. 1). The high variability of colour pattern, a typical character for many chrysomelid species, caused the high number of synonyms (46%). Genitalic structures and molecular data can make more reliable species identification. The large number of specimens examined revealed only 107 new species described. After revising approximately 15% of the Afrotropical galerucine fauna, the species number decreased from 259 to 246 species.

## Discussion

The high polychromatism in many galerucine species is the cause of the majority of synonyms, since colour patterns were used by previous authors as very definite species specific characters. When species are widely distributed, the number of synonyms increase even more. *Monolepta vincta* Gerstaecker, 1871, has a pan-Afrotropical distribution and ten synonyms have been found for his species (Wagner 2005), six of these synonyms are provided in two publications of Victor Laboissière (1920a, b). This is not a reproach for Laboissière, who was the most productive taxonomist on the Galerucinae world-wide. The majority of species described by him are still valid, but in his early publications, his work was based on a very “classic”, Linnaean species concept, as it was customary for that time. Later in his career (e.g. Laboissière 1940), he used genitalic patterns for species identification, being one of the first taxonomists in Chrysomelidae to do so. Further examples of widely distributed African galerucines with a large number of synonyms are *Neobarombiella flavilabris* (Weise, 1903) with eleven and *Neobarombiella senegalensis* (Laboissière, 1923) with ten synonyms.

Other diverse Afrotropical Galerucinae s. str. appear to indicate a similar “over-description” rate. *Diacantha* Chevrolat, 1836 (syn. *Hyperacantha* Chapuis, 1879) is the second most diverse group of African galerucines in terms of some 120 described species. A few spot checks revealed there are a large number of synonyms in this genus too, and *Diacantha* might be another taxonomic “nightmare”, revealing a lower number of valid species subsequent to formal revision.



**Figure 1.** Numbers of described species of Afrotropical Galerucinae s. str. per decade revised between 2000 to 2016 by our working group with synonyms found.

On the other hand, revisions of tropical phytophagous insects can result in a strong increased number of species. Examples are the weevil genera *Euops* Schönherr, 1839 from New Guinea with 24 valid species before revision, and 160 additional new species there after (Riedel 2006), and the litter-dwelling *Trigonopterus* Fauvel, 1862 from the Sundaland area (mainly Malaysia, Indonesia) which was monotypic and comprised 98 species after being revised (Riedel et al. 2014). Alexander Riedel’s studies on East Asian weevils revealed six times more species after the revision of *Euops*, and a much larger increase in *Trigonopterus* with their cryptic life-history, whereas our conclusion brought decreased species richness to light. The results may reflect the two extremes along a continuum, but both data sets imply that more recent “calculations” on global insect diversity, with around six million species, are much more reasonable than the higher numbers “believed” before.

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