Proceedings of the Third International Tenebrionoidea Symposium, Arizona, USA, 2013

Edited by
Patrice Bouchard & Aaron D. Smith

Sofia–Moscow
2014
ZooKeys 415 (Special Issue)

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First published 2014
ISBN 978-954-642-736-6 (paperback)

Pensoft Publishers
12 Prof. Georgi Zlatarski Street, 1700 Sofia, Bulgaria
Fax: +359-2-870-42-82
info@pensoft.net
www.pensoft.net

Printed in Bulgaria, June 2014
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Editorial:
Third International Tenebrionoidea Symposium

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Academic editor: L. Penev
Received 23 January 2013 | Accepted 8 February 2014 | Published 12 June 2014


The Third International Tenebrionoidea Symposium (ITS) was held at Arizona State University in Tempe, Arizona USA on August 7th and 8th, 2013. Researchers from ten countries participated with a total of 36 attendees (Figure 1). It was the first formal meeting of the international tenebrionoid research community since the October 2005 in Lyon, France. Though the previous meetings did not list themselves as the beginning of a series, we consider it fitting to acknowledge them as the first two modern international meetings specifically organized for the sharing and dissemination of Tenebrionoidea research.

The 1st International Tenebrionid Symposium, entitled “Systematics and Biogeography of Tenebrionoidea”, was held in 2002 at the Zoologisches Staatssammlung, München (Germany) to honor Dr. Hans J. Bremer’s work on tenebrionids and celebrate the museum’s acquisition of his collection. This event organized by Dr. Martin Baehr resulted in a highly successful meeting.

The 2nd International Tenebrionoidea Symposium, entitled “Coleoptera Tenebrionoidea: Taxonomy, Biogeography, and Faunistics”, was held in 2005 at the Lyon Museum (France) following the acquisition of the remarkable tenebrionid collection of Jaroslav Picka. Following the symposium, many of the presentations were published in Cahiers Scientifiques (Fascicule 10). Again a highly successful meeting this time organized by Dr. Harold LaBrique.
To continue this successful tradition, and encourage tenebrionoid workers from around the world to meet, share their research, and form new collaborations, researchers in the US and Canada decided to host the 3rd International Tenebrionoidea Symposium. A steering committee was assembled with representatives from Arizona State University, California Academy of Sciences, the Canadian National Collection of Insects, and the Smithsonian Institution. Arizona State University in Tempe, Arizona was ultimately chosen to host the symposium due to its institutional support, excellent facilities, and multiple opportunities for field work both before and after the meeting. Presentations were given on August 7th and 8th, 2013.

Before the meeting, researchers visited US collections on both the west and east coasts and held a pre-meeting collecting trip through California, Nevada, Utah, and Arizona. Gustavo Flores had the most impressive itinerary of museum visits. After flying into New York City from Mendoza, Argentina, Gustavo visited the American Museum of Natural History (AMNH – New York, New York), the Smithsonian Institution (NMNH – Washington, D.C.), the C.A. Triplehorn Insect Collection at Ohio State University (OSUC – Columbus, Ohio), the Field Museum (FMNH – Chicago, Illinois), and Rolf Aalbu’s personal collection (RLAC – El Dorado Hills, California). In Sacramento, Gustavo joined Wolfgang Schawaller, Roland Grimm, and René Fouquè who had been working in the California Academy of Sciences (CASC – San Francisco, California), California Department of Food and Agriculture (CDFA – Sacramento,
California), and RLAC collections the prior week. Rolf, Gustavo, René, Roland, and Wolfgang then drove from Sacramento to Tempe while doing field work through California, Nevada, Utah, and north central Arizona (Figure 2).

During the meeting 21 presentations, seventeen 20-minute talks and four posters, where given (see http://insectbiodiversitylab.org/3ITS_presentations.html) ranging from species-level revisions to broad scale Tenebrionidae phylogenies and inventories, darkling beetles intercepted by USDA-APHIS during agricultural quarantine interceptions, and the first steps towards the construction of a Coleopteran Anatomy Ontology. Presentations were generally well received and elicited animated question and answer sessions.

Many of the attendees had previously corresponded by email, but never met in person. For example, Guodong Ren’s research group (Figure 3) has been remarkably productive, but this was the first time any of the American (North and South) or European visitors were able to meet him face to face. Others, such as Chuck Triplehorn (Figure 4) are well known to almost all attendees through both research and previous visits. Following the first day’s presentations, Bill Warner led an evening collecting expedition to Oak Flat Campground in Pinal County.

Group discussions were also held during the symposium on potential large scale tenebrionid projects that could be undertaken as a community, the organization of a Proceedings volume from the Symposium, collecting localities for the post-meeting trip, and potential localities and dates for the Fourth International Tenebrionoidea Symposium. Informal talks on these and other tenebrionoid related matters extend far into the evening and past the closing session on August 8th (Figure 5). Pat Bouchard agreed to act...
Figure 3. Visiting Chinese and US-based Chinese researchers. Left to right: Yuxia Yang, Li Zhong, Guodong Ren, Guanyang Zhang (ASU postdoc), Shanshan Liu, Caixia Yuan.

Figure 4. Dr. Charles A. Triplehorn showing off a Triplehornia metallica Matthews and Lawrence shirt made by his grandson.
as lead editor for a Proceedings volume in the journal Zookeys, for which we were and remain very grateful. Most articles included in this resulting special issue of ZooKeys are based on the contents of presentations during the Third International Tenebrionoidea Symposium, although papers submitted by all attendants were also welcome.

After the formal symposium, attendees went their separate ways, with some doing solo collecting and some visiting US museums (California Academy of Sciences and the University of Arizona Insect Collection to name just two). Twelve researchers from five countries went to the Beetle Infestation VI on August 10th hosted by Pat and Lisa Sullivan in Ramsey Canyon, Huachuca Mountains, one of the most biologically diverse localities in the United States, before collecting through southern and central Arizona (Figures 6 & 7) eventually disbursing into smaller field groups or heading home. While a full tally of tenebrionoid species collected in association with the symposium will likely never be assembled, the first author collected approximately 40 darkling beetles species during and after the meeting. Most of the species collected can be sight IDed, at least to genus, using Bugguide.

Many of the presentations, a list of collecting localities, and additional pictures from the symposium are online at: http://www.insectbiodiversitylab.org/3ITS.html.
Figure 6. Post meeting collecting. Marcin Kamiński and Andrew Johnston near Madera Canyon.

Figure 7. Post meeting afternoon break at Fred Skillman’s house, Cochise, AZ. Left to right: Wolfgang Schawaller, Pat Bouchard, Rolf Aalbu, Kojun Kanda, Andrew Johnston, Fred Skillman, Warren Steiner, Marcin Kamiński, René Fouquè.
Two researchers graciously volunteered to host the next symposium at their institutions: Gustavo Flores (CCT CONICET – Mendoza, Argentina) for 2016, or Guo-dong Ren (Hebei University – Baoding City, China) for 2015, and presented short talks highlighting the advantages of their respective cities. A survey was set up to allow the attendees of the Third symposium, current tenebrionoid researchers (those with at least one tenebrionioid manuscript in print), and graduate students working on tenebrionoids to vote for the host city of the Fourth International Tenebrionoidea Symposium. Voting was open until September 30th, 2013 and turnout was excellent. After over a month of voting, Mendoza, Argentina was chosen to host the next meeting in November 2015. See you in Mendoza!

Acknowledgements

We would like to express our gratitude to all of the attendees and the volunteers at ASU (Andrew Johnston and Guanyang Zhang) who helped make the symposium such a success. We are also deeply appreciative of the ASU-HIC, IISE, SoLS, Akis Consulting, and the NSF ARTS program (DEB-1258154) for providing facilities, supplies, catering, and partial travel funding. Lastly, we are grateful to Dr. Gustavo Flores for volunteering to host the 4th International Tenebrionoidea Symposium in Mendoza Argentina in November 2015.

Steering committee

Rolf Aalbu – California Academy of Science, San Francisco, CA USA
Patrice Bouchard – Canadian National Collection of Insects, Ottawa, Ontario CANADA
Kojun Kanda – Oregon State University, Corvallis, OR USA
Nico Franz – Arizona State University, Tempe, AZ USA
Aaron Smith – Arizona State University, Tempe, AZ USA
Warren Steiner – Smithsonian Institution, Washington, DC USA
Quentin Wheeler – Arizona State University, Tempe, AZ USA

Attendees (Current country of residence)

Rolf L. Aalbu (USA)  Shanshan Liu (China)
Jason T. Botz (USA)  James Pflug (USA)
Patrice Bouchard (Canada)  Guodong Ren (China)
Milton Campbell (Canada)  Wolfgang Schawaller (Germany)
Alejandro Castro Tovar (Spain)  Aaron D. Smith (USA)
Paulina Cifuentes Ruiz (Mexico)  Ronald Somerby (USA)
Adriana Li Colinas (Spain)  Warren Steiner (USA)
Rich Cunningham (USA)  
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Rene Fouque (Czech Republic)  
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Gael J. Kergoat (France)  

Larry Stevens (USA)  
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The Tenebrionidae of California: A Time Sensitive Snapshot Assessment

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Academic editor: P. Bouchard | Received 29 October 2013 | Accepted 1 February 2014 | Published 12 June 2014

http://zoobank.org/D530808E-29A0-444C-B87C-CD01AF10DDF7


Abstract

Due to a diversity of habitats and its geologic history, the US state of California hosts a spectacular assemblage of darkling beetle species (Coleoptera: Tenebrionidae). In addition to being part of the California Floristic Province, one of 34 global biodiversity hotspots identified by Conservation International, California also has additional areas which are parts of the Great Basin, Mojave, and Sonoran deserts. California is divided into nine floristic regions. Each region is assessed in terms of faunal composition and endemism. A “snapshot” of our present knowledge of the Tenebrionidae indicates that 447 currently recognized species, representing 108 genera, occur in California of which one hundred and ninety are endemic. California is compared to other nearby regions in diversity and endemism. An analysis of currently valid species vs a more realistic species account based on unpublished records of likely synonyms and known species yet to be described in the scientific literature is presented. The California Floristic Region, rather than other more arid parts of California, has the highest number of total and endemic species. Because of their high diversity and endemism, tenebrionids could potentially provide a valuable tool for monitoring the environment for conservation purposes.

Keywords

California, Floristic Regions, Tenebrionidae, Biodiversity, Hotspots, Conservation

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Introduction

The state of California is part of the California Floristic Province, one of 34 global biodiversity hotspots identified by Conservation International. Over 50 percent of the world’s plant species and 42 percent of all terrestrial vertebrate species are endemic to these 34 biodiversity hotspots, a total area which covers only 2.3 percent of the Earth’s land surface. The California Floristic Province includes most of western California and a small section of Baja California and Southwestern Oregon. On Conservation International’s California Floristic Province website, although numbers of endemic plants, birds, mammals and amphibians are listed, nothing is mentioned concerning insects.

California also includes areas not considered to be part of the California floristic province. These areas contain aspects of the Great Basin, Mojave, and Sonoran deserts.

In 2010 the Essig Museum of Entomology at University of California, Berkeley began CalBug (NSF-DBI: 0956389), a collaborative project among nine California museums with a goal to digitize and geographically reference over one million specimens from target groups and localities. Tenebrionidae was one of the focus groups in Coleoptera. However, to date, few tenebrionids (2%) have been digitized and georeferenced, all at Santa Barbara Museum of Natural History (SBMNH).

In 2005 Mike Caterino, formerly at SBMNH, solicited the author’s help in contributing to a web accessible list of “Beetles of California”. This was followed by a visit to the SBMNH in 2007 to provide additional identifications of beetles in the collection. The list, last updated in 2009, is posted on http://www.sbnature.org/collections/invert/entom/cbphomepage.php [accessed on December 9, 2013]. An updated list is present here (Fig. 1) that reflects a current “snapshot” of our knowledge of this fauna. It is also available online (http://insectbiodiversitylab.org/CaliforniaDarklingBeetles.html). To account for active research and our growing understanding of the California fauna, the list includes a separate column assessing the potential that each species will be synonymized in future works (see below). Both the current valid species list and a list excluding likely synonymous species, but including known undescribed species, are analyzed based on each species’ known occurrence in each of California’s nine floristic provinces to assess number of tenebrionid species in each province and their endemicity.

Materials and methods

Sources of Information other than the SBMNH list above include publications from early workers (LeConte, Horn, Motschulsky, Casey, Blaisdell, and others), modern workers

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1 See http://www.conservation.org/where/priority_areas/hotspots/Pages/hotspots_main.aspx [accessed on December 9, 2013].


3 See http://calbug.berkeley.edu/data.html [accessed on December 9, 2013].
(Doyen, Triplehorn, Somerby, Brown, Smith, and others)⁴, and modern revisions: Parts of the Coniontini (Doyen 1984), Cnodalonini (Doyen 1973), Amphidornini (Aalbu et al. 2012, Triplehorn and Thomas 2011), Edrotini (Pape et al. 2007), Stenosini (Papp 1981) and Asidini (Brown and Doyen 1991, Smith 2013) as well as complete revisions of the Cryptoglossini (Aalbu 2005) and Anepsiini (Doyen 1987). Other major sources of information include the Species Database of the California Academy of Sciences and information from the author’s personal collection (the Rolf L. Aalbu Collection – RLAC), as well as visits to all major beetle collections in California and many others outside of the state. Information for potential future species synonymies and undescribed species come from the authors’ research, discussions with other tenebrionid workers, and currently unpublished studies by the authors, Ron Somerby, and Charles Triplehorn.

To account for the many groups in which data has been accumulated but no recent revision has been published, the Tenebrionidae records from California were categorized in the following status groups based on their current and future status: 0), Known new but undescribed species; 1), Currently projected valid species and subspecies⁵; 2) Most likely synonyms, but synonymy not determined without further study; and 3), Known but unpublished synonyms. Published synonyms were omitted. The assessment was then divided into two categories: A.) Described Species Count: All species currently valid in the literature including known synonyms (groups 1, 2, and 3 above). B), Realistic Species Count: (groups 0, 1, and 2 above). Endemism was calculated on a strict basis (species endemic to specific regions which include parts of adjacent areas not in California were not considered).

For the purpose of this study, California is divided into nine floristic regions modified from a map by the Jepson Herbarium⁶ (Fig. 1). Four of these are not considered parts of the California Floristic Region. These are: Region 1, The Northern Great Basin Province, including the Warner Mountains and Modoc Plateau; Region 2, The Southern Great Basin Province, including the White and Inyo Mountains and intermountain valleys east of the Sierras Nevada’s and White Mountains; Region 3, The Mojave Desert and associated desert mountains; and Region 4, The Sonoran (Colorado) Desert and associated desert mountains.

Regions belonging to the California Floristic Region include: Region 5. The South Coast, including the Transverse and Peninsular Ranges and Channel Islands; Region 6, The Sierra Nevada Mountains; Region 7, The Central Valley; Region 8, The Central Coast, including the San Francisco Bay area and Coast Ranges; and Region 9, The Northern Coast, including the Cascade and Klamath Ranges as well as the Northern Coast Ranges. In these regions we examined species occurrence and regional endemism. Regional endemism was also calculated on a strict basis as described above.

⁴ All publications prior to 2002 are listed in Aalbu et al. 2002. Newer pertinent publications are listed in the reference section below.

⁵ Some of the early described species as Edrotines etc., described by early workers as Casey may potentially be synonyms.

Results and discussion

It is important to keep in mind that this study represents a snapshot in time and thus is subject to change as new information becomes available. However, this assessment is also a balance between future synonymies from previous descriptions (Casey and other early workers: *Coniontis*, various genera of edrotes) on one side and new species discoveries, as well as new foreign introductions, on the other. At present, we know of at least eight distinct new species.

A list of all described species is presented in phylogenetic order (Fig. 1). Differences in group numbers and endemics are presented in Table 1. Differences in species count categories (numbers, endemics and percent endemism) are shown in Table 2. It is notable that despite the differences in numbers, both analyses (described vs realistic) indicate a very similar percent endemism. Since this study is intended as a “snapshot” of our current knowledge, species counts and analysis, unless otherwise specified, include only groups 0, 1, and 2 (Realistic Species Count). This tenebrionid inventory of California thus includes 34 tribes, 118 genera and subgenera, 447 species and subspecies (including known new species). Of these, 190 are endemic to California. The present SBMNH web list includes 471 species from California. Of these, 10 are collection data errors. These included *Argoporis alutacea* Casey; *Asidopsis consentanea* Casey; *Asidopsis planata* (Horn); *Cryptoglossa variolosa* Horn; *Eleodes alticola* Blaisdell; *Eleodes subnitens* LeConte; *Neatus tenebrioides* Beauvois; *Platydema micans* Zimmerman; and *Stenomorpha obovatus* (LeConte) none of which are known to occur in California. Others are known but unpublished synonymies (status group 3).

The fauna is composed of the following subfamilies in descending species number: Pimeliinae (204), Tenebrioninae (168), Alleculinae (33), Diaperinae (23), Stenochiini (11), Lagriinae (7), and Phrenapatiniae (1). California is clearly a center of diversity for the family Tenebrionidae, representing 38% of all U.S. species. The most abundant tribes and genera in terms of species numbers are: Amphidorini (73 species), Edrotini (71 species), Coniontini (53 species), Alleculini (33 species), Opatrini (26 species), Asidini (25 species), and Helopini (21 species); and genera such as *Eleodes* (64 species), *Stenomorpha* (19 species), *Coniontis* (38 species), and *Metoponium* and *Helops* each with 21 species. A number of tribes such as Amphidorini, Coniontini, and Nyc- toporini, and genera such as *Eleodes*, *Coelocnemis*, *Nyctoporis*, *Asbolus*, *Coniontis*, and *Alaudes* also exhibit their greatest diversity in genera/species in California.

Compared to other known nearby geographical regions, California also has a high species per area diversity (1.05 per 1000 square miles) which is higher than the U.S. as a whole\(^7\) (.12) or even Mexico\(^7\) (.68), but not Baja California\(^7\) which has a species diversity of 5.47 (see Table 3). California shares species with the following adjoining areas in descending order: 1. Southwest U.S.: (including Arizona, 101, Nevada, 76; New Mexico, 23; and Utah, 42). 2. Mexico (mainland 32, Baja California, 68) and 3. Northwest U.S. (including Oregon, 56; Washington, 33; and Idaho, 32. A number of

\(^7\) Numbers probably 5–8 years old.
species are known only from the type and have undetermined California localities (16). Twenty species are cosmopolitan pests. See Fig. 1 for additional locality information.

The distribution of California tenebrionids can be divided into six patterns: 1), Widespread species, 2), Restricted but not especially hard to collect species (Caves, single canyons (*Eschatomoxys andrewsi* Aalbu & Thomas, *Eleodes (Caverneleodes) microps* Aalbu et al.), 3), Restricted but very difficult to collect species (*Eleodimorpha*, *Oxygonodera*), 4), Historically abundant but now difficult to collect species (*Eleodes (Mela-neleodes) quadricollis* Eschscholtz), 5) Introduced species composed of standard stored product pests as well as other introductions not associated with stored products (*Opatroides punctulatus* Brullé and *Gonocephalum* sp.) and 6) species only known from the type material with specific locality unknown. California also has some unusual darkling beetle occurrences and absences compared to the rest of North America. One is the presence of two species from the Asian tribe Laenini, which is otherwise absent on the continent. Another is the absence of the genus *Strongylium*, a species-rich genus found worldwide including in Arizona (2 species) and most of the rest of the United States.

### Table 1. Status Groups and Endemicity.

<table>
<thead>
<tr>
<th>Status group</th>
<th>Non endemic species</th>
<th>Endemic species</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>2</td>
<td>8</td>
<td>10</td>
</tr>
<tr>
<td>1</td>
<td>249</td>
<td>155</td>
<td>404</td>
</tr>
<tr>
<td>2</td>
<td>6</td>
<td>27</td>
<td>33</td>
</tr>
<tr>
<td>3</td>
<td>22</td>
<td>17</td>
<td>39</td>
</tr>
<tr>
<td></td>
<td>279</td>
<td>207</td>
<td>486</td>
</tr>
</tbody>
</table>

### Table 2. California Species, Described vs Realistic.

<table>
<thead>
<tr>
<th>Category</th>
<th>Status groups</th>
<th>Species</th>
<th>Endemics</th>
<th>Total</th>
<th>% Endemic</th>
</tr>
</thead>
<tbody>
<tr>
<td>A: Described</td>
<td>1, 2 &amp; 3</td>
<td>277</td>
<td>199</td>
<td>476</td>
<td>41.81%</td>
</tr>
<tr>
<td>B: Realistic</td>
<td>0, 1, &amp; 2</td>
<td>257</td>
<td>190</td>
<td>447</td>
<td>42.51%</td>
</tr>
</tbody>
</table>

### Table 3. Comparison of currently valid species/endemics per area for various regions.

<table>
<thead>
<tr>
<th>Region</th>
<th>Number of species</th>
<th>Number of endemics</th>
<th>% Endemism</th>
<th>Area (km²)</th>
<th>Species diversity per 1000 km²</th>
</tr>
</thead>
<tbody>
<tr>
<td>California*</td>
<td>447**</td>
<td>190</td>
<td>43%</td>
<td>423970</td>
<td>1.05</td>
</tr>
<tr>
<td>USA***</td>
<td>1184</td>
<td>?</td>
<td>&gt;60%</td>
<td>9827000</td>
<td>0.12</td>
</tr>
<tr>
<td>Mexico***</td>
<td>1340</td>
<td>723</td>
<td>54%</td>
<td>1973000</td>
<td>0.68</td>
</tr>
<tr>
<td>Baja California***</td>
<td>404</td>
<td>225</td>
<td>56%</td>
<td>73909</td>
<td>5.47</td>
</tr>
</tbody>
</table>

* Bordered by 3 states and Baja California.
** 34% of all U.S. species.
*** numbers probably 5–8 years old.
Regional analysis

For the purpose of this study, California was into 9 floristic regions (Fig. 2) to examine species occurrence and regional endemism. Regional endemism was also calculated on a strict basis as mentioned above. A list of all regional endemics is presented as well as total species numbers for the region and percent endemism (Fig. 3). These areas are ranked in Table 4. Adding the above data suggests that over 62% (62.11) of the endemic species in California are regional endemics while 43% (42.60) of all tenebrionids are endemic in terms of being regional endemics or multiple region endemics.

One may note that, somewhat surprisingly, subregions within the California Floristic Region have more regional endemic species (87) as well as California endemic species (124) despite the common association of tenebrionids with desert habitats, where they are always abundant (see Table 5). On this table, “all endemics” in the “unknown….” region refer to species where the type locality is simply listed as “California”. This “snapshot” assessment emphasizes how much remains to be done in this area, especially in revising tribes or genera which have not been looked at since their description, as well as rediscovering species of “unknown” California localities. Additional new species, as well as new introductions, will undoubtedly be discovered as well. It is hoped that this type of assessment can be useful in environment monitoring and conservation studies.

Table 4. Comparison of regional endemics and all endemics for California.

<table>
<thead>
<tr>
<th>Region</th>
<th>Endemic species</th>
<th>All species</th>
<th>% Endemic</th>
<th>% of all California Endemics</th>
</tr>
</thead>
<tbody>
<tr>
<td>5. South Coast &amp; Islands</td>
<td>42</td>
<td>171</td>
<td>24.56%</td>
<td>35.59%</td>
</tr>
<tr>
<td>8. Central Coast &amp; Bay</td>
<td>20</td>
<td>110</td>
<td>18.18%</td>
<td>16.95%</td>
</tr>
<tr>
<td>6. Sierra Nevada</td>
<td>16</td>
<td>100</td>
<td>16.00%</td>
<td>13.56%</td>
</tr>
<tr>
<td>4. Sonoran Desert</td>
<td>13</td>
<td>113</td>
<td>11.50%</td>
<td>11.02%</td>
</tr>
<tr>
<td>3. Mojave Desert</td>
<td>12</td>
<td>112</td>
<td>10.71%</td>
<td>10.17%</td>
</tr>
<tr>
<td>8. Central Valley</td>
<td>5</td>
<td>76</td>
<td>6.58%</td>
<td>4.24%</td>
</tr>
<tr>
<td>2. South Great Basin</td>
<td>5</td>
<td>55</td>
<td>9.09%</td>
<td>4.24%</td>
</tr>
<tr>
<td>9. North Coast</td>
<td>4</td>
<td>73</td>
<td>5.48%</td>
<td>3.39%</td>
</tr>
<tr>
<td>1: North Great Basin</td>
<td>1</td>
<td>29</td>
<td>3.45%</td>
<td>0.85%</td>
</tr>
</tbody>
</table>

Table 5. Comparison of species endemicity for California Floristic affinities.

<table>
<thead>
<tr>
<th>Floristic Region</th>
<th>All Endemics</th>
<th>Non Endemic</th>
<th>All Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Desert Areas</td>
<td>37</td>
<td>94</td>
<td>131</td>
</tr>
<tr>
<td>California Floristic Province</td>
<td>124</td>
<td>81</td>
<td>205</td>
</tr>
<tr>
<td>Both Areas</td>
<td>16</td>
<td>60</td>
<td>76</td>
</tr>
<tr>
<td>Unknown California locality, cosmopolitan or introduction</td>
<td>13</td>
<td>22</td>
<td>35</td>
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</tbody>
</table>
## Figures

### California Tenebrionidae (January 2014)

<table>
<thead>
<tr>
<th>Endemic Status</th>
<th>Group</th>
<th>Species</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>CA</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Pimilinae Cremnoterini</td>
<td>1</td>
<td>A. alticola</td>
<td>Fall, 1928</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>A. alticola</td>
<td>Fall, 1928</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>A. alticola</td>
<td>Fall, 1928</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>A. alticola</td>
<td>Fall, 1928</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>A. alticola</td>
<td>Fall, 1928</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>A. alticola</td>
<td>Fall, 1928</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>A. alticola</td>
<td>Fall, 1928</td>
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<tr>
<td></td>
<td>8</td>
<td>A. alticola</td>
<td>Fall, 1928</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>A. alticola</td>
<td>Fall, 1928</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>A. alticola</td>
<td>Fall, 1928</td>
</tr>
</tbody>
</table>

### Figures

Figure 1. Checklist of the California Tenebrionidae species with distributions and likelihood for future synonymy. Distribution numbers refer to California regions (Fig. 2) and the following: ME (Mexico) BC (Baja California) NV (Nevada) AZ (Arizona) ID (Idaho) UT (Utah) NM (New Mexico) OR (Oregon) WA (Washington) CA (Canada) U (unknown California distribution) C (refers to cosmopolitan pest), ASIA SA (South America), and OW (Old World).
Figure 1. Continue.
Figure 1. Continue.
Figure 1. Continue.
### California Tenebrionidae (January 2014)

<table>
<thead>
<tr>
<th>#</th>
<th>CA group</th>
<th>Species</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>369</td>
<td>1</td>
<td>Helops edwardsi Horn, 1870</td>
<td>3-5 OR</td>
</tr>
<tr>
<td>400</td>
<td>1</td>
<td>Helops fresnesensis Blanchard, 1931</td>
<td>7</td>
</tr>
<tr>
<td>401</td>
<td>1</td>
<td>Helops laetus LeConte, 1857</td>
<td>8 WA</td>
</tr>
<tr>
<td>402</td>
<td>1</td>
<td>Helops obtusangula Blanchard, 1921</td>
<td>5-6</td>
</tr>
<tr>
<td>403</td>
<td>1</td>
<td>Helops opacipes LeConte, 1859</td>
<td>1-9 5-7</td>
</tr>
<tr>
<td>404</td>
<td>1</td>
<td>Helops punctipes LeConte, 1866</td>
<td>6</td>
</tr>
<tr>
<td>405</td>
<td>1</td>
<td>Helops rutipes (LeConte), 1851</td>
<td>5 BC</td>
</tr>
<tr>
<td>406</td>
<td>1</td>
<td>Helops rugulosus LeConte, 1896</td>
<td>5</td>
</tr>
<tr>
<td>407</td>
<td>1</td>
<td>Helops rugulosus LeConte, 1896</td>
<td>5 7 0 6</td>
</tr>
<tr>
<td>408</td>
<td>1</td>
<td>Helops simulans Blanchard, 1921</td>
<td>5</td>
</tr>
<tr>
<td>409</td>
<td>1</td>
<td>Helops spinellus Horn, 1880</td>
<td>21 NV</td>
</tr>
<tr>
<td>410</td>
<td>1</td>
<td>Helops steinichioides Blanchard, 1925</td>
<td>6 8</td>
</tr>
<tr>
<td>411</td>
<td>1</td>
<td>Helops striolatus Horn, 1885</td>
<td>3 4</td>
</tr>
<tr>
<td>412</td>
<td>1</td>
<td>Helops tenebrosus LeConte, 1866</td>
<td>3 4 AZ</td>
</tr>
</tbody>
</table>

### Tenebrioninae Tribolium

<table>
<thead>
<tr>
<th>#</th>
<th>CA group</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>413</td>
<td>1</td>
<td>Gnathocerus cornutus (Fabricius) 1801</td>
</tr>
<tr>
<td>414</td>
<td>1</td>
<td>Gnathocerus maritimus (Fabricius) 1801</td>
</tr>
<tr>
<td>415</td>
<td>1</td>
<td>Leathesius orex Stiltz, 1983</td>
</tr>
<tr>
<td>416</td>
<td>1</td>
<td>Leathesius prosopis (Stiltz), 1904</td>
</tr>
<tr>
<td>417</td>
<td>1</td>
<td>Lypia latipalpila (Forster,1855)</td>
</tr>
<tr>
<td>418</td>
<td>1</td>
<td>Mecyclothorax angustus Horn, 1870</td>
</tr>
<tr>
<td>419</td>
<td>1</td>
<td>Mecyclothorax piceus Horn, 1870</td>
</tr>
<tr>
<td>420</td>
<td>1</td>
<td>Palorus sabuligerus (Wissmann), 1848</td>
</tr>
<tr>
<td>421</td>
<td>1</td>
<td>Palorus subdumicollis Weisebluth, 1964</td>
</tr>
<tr>
<td>422</td>
<td>1</td>
<td>Thaneus seditiosus LeConte, 1866</td>
</tr>
<tr>
<td>423</td>
<td>1</td>
<td>Tribolium australium Watts, 1993</td>
</tr>
<tr>
<td>424</td>
<td>1</td>
<td>Tribolium brevicorne LeConte, 1899</td>
</tr>
<tr>
<td>425</td>
<td>1</td>
<td>Tribolium castaneum Herbst, 1797</td>
</tr>
<tr>
<td>426</td>
<td>1</td>
<td>Tribolium confusum Jacobsthal du Val, 1868</td>
</tr>
<tr>
<td>427</td>
<td>1</td>
<td>Tribolium destructor Watts, 1993</td>
</tr>
<tr>
<td>428</td>
<td>1</td>
<td>Tribolium madorei (Chevrier), 1825</td>
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</table>

### Tenebrioninae Apocyphrini

<table>
<thead>
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<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>429</td>
<td>1</td>
<td>Acrophia anthracoides Schachtzchel, 1931</td>
</tr>
<tr>
<td>430</td>
<td>1</td>
<td>Acrophia chlordevisis Horn, 1870</td>
</tr>
<tr>
<td>431</td>
<td>1</td>
<td>Acrophia elenor Horn &amp; Kityama, 1980</td>
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</table>

### Tenebrioninae Alphitobii

<table>
<thead>
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<tbody>
<tr>
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<td>1</td>
<td>Alphitobius diaperinus (Panzer), 1797</td>
</tr>
<tr>
<td>433</td>
<td>1</td>
<td>Alphitobius marginatus Fabricius, 1781</td>
</tr>
<tr>
<td>434</td>
<td>1</td>
<td>Metopina marginata Horn, 1870</td>
</tr>
<tr>
<td>435</td>
<td>0</td>
<td>Nemasteus sp.</td>
</tr>
<tr>
<td>436</td>
<td>1</td>
<td>Tenobius mixtus Linneaus, 1758</td>
</tr>
<tr>
<td>437</td>
<td>1</td>
<td>Tenobius obscurus Fabricius, 1792</td>
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</table>

### Tenebrioninae Centromerini

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<th>#</th>
<th>CA group</th>
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</tr>
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<tbody>
<tr>
<td>438</td>
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<td>Scothobius paraleucus LeConte, 1859</td>
</tr>
<tr>
<td>439</td>
<td>1</td>
<td>Scothobius punctatus (Blanchard), 1933</td>
</tr>
<tr>
<td>440</td>
<td>1</td>
<td>Scothobius simplex (Blanchard), 1837</td>
</tr>
<tr>
<td>441</td>
<td>1</td>
<td>Scothobius wagneri (Blanchard), 1933</td>
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### Alleculinae Alleculini

<table>
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<td>442</td>
<td>1</td>
<td>Hymenoteropsis caseyi, 1891</td>
</tr>
<tr>
<td>443</td>
<td>1</td>
<td>Hymenoteropsis caseyi, 1891</td>
</tr>
<tr>
<td>444</td>
<td>1</td>
<td>Hymenoteropsis caseyi, 1891</td>
</tr>
<tr>
<td>445</td>
<td>1</td>
<td>Hymenoteropsis caseyi, 1891</td>
</tr>
<tr>
<td>446</td>
<td>1</td>
<td>Hymenoteropsis caseyi, 1891</td>
</tr>
<tr>
<td>447</td>
<td>1</td>
<td>Hymenoteropsis caseyi, 1891</td>
</tr>
<tr>
<td>448</td>
<td>1</td>
<td>Hymenoteropsis caseyi, 1891</td>
</tr>
</tbody>
</table>

Figure 1. Continue.
Figure 2. Geographic subdivisions of California from http://ucjeps.berkeley.edu/cguide.html#Map with Unit Boundaries with regions 1–9 outlined.
### Regional Endemic California Tenebrionidae (January 2014)

<table>
<thead>
<tr>
<th>REGION</th>
<th>Species present, Percent endemic</th>
</tr>
</thead>
<tbody>
<tr>
<td>1: The Northern Great Basin Province</td>
<td>20: 3.45%</td>
</tr>
<tr>
<td>including the Warner Mountains and Modoc Plateau</td>
<td>1 Elodes (Elodes) convexus Blaisdell 1921</td>
</tr>
<tr>
<td>2: The Southern Great Basin Province</td>
<td>55: 9.09%</td>
</tr>
<tr>
<td>including the White and Inyo Mountains and intermountain valleys east of the Sierra Nevadas’ and White Mountains</td>
<td>1 Aethontus subtilissimus LeConte, 1851</td>
</tr>
<tr>
<td>3: The Mojave Desert</td>
<td>112: 10.71%</td>
</tr>
<tr>
<td>and associated desert mountains</td>
<td>1 Ariacantha (airaveti) Papp, 1961</td>
</tr>
<tr>
<td>4: The Sonoran (Colorado) Desert</td>
<td>113: 11.50%</td>
</tr>
<tr>
<td>and associated desert mountains</td>
<td>1 Ariacantha andrewsi LeConte, 1902</td>
</tr>
<tr>
<td>5: The South Coast</td>
<td>178: 24.12%</td>
</tr>
<tr>
<td>including the Transverse and Peninsular Ranges and Channel Islands</td>
<td>1 Alephus longicornis Case, 1924</td>
</tr>
<tr>
<td>6: The Sierra Nevada Mountains</td>
<td>100: 16.00%</td>
</tr>
<tr>
<td>7: The Central Valley</td>
<td>76: 6.58%</td>
</tr>
<tr>
<td>including the San Francisco Bay area and Coast Ranges</td>
<td>1 Acropyga setosa Deyrolle &amp; Kianiya, 1960</td>
</tr>
<tr>
<td>8: The Central Coast</td>
<td>110: 16.18%</td>
</tr>
<tr>
<td>including the San Francisco Bay area and Coast Ranges</td>
<td>1 Acropyga setosa Deyrolle &amp; Kianiya, 1960</td>
</tr>
</tbody>
</table>

**Figure 3.** Regional Endemic California Tenebrionidae.
Acknowledgements

We would like to thank the Jepson Herbarium at UC Berkeley for use of their map, Mike Caterino for encouraging interest in California beetles and regional endemism within the state, Drs. Ronald Somerby and Charles Triplehorn for sharing their ongoing research, and the NSF ARTS program (DEB-1258154) for support of this study.

References

Review of the species of Paratenetus Spinola inhabiting America, north of Mexico (Coleoptera, Tenebrionidae)

Yves Bousquet¹, Patrice Bouchard¹⁺

¹ Canadian National Collection of Insects, Arachnids and Nematodes, Agriculture and Agri-Food Canada, Ottawa, Ontario, K1A 0C6, Canada

† http://zoobank.org/C1B72C11-229F-449C-8763-6898C950A3A7

Corresponding author: Yves Bousquet (yves.bousquet@agr.gc.ca)

Academic editor: A.D. Smith | Received 29 October 2013 | Accepted 7 January 2014 | Published 12 June 2014


Abstract

The North American (north of Mexico) species of the tenebrionid genus Paratenetus Spinola are reviewed and a key is presented for their identification. Five species are recognized, P. gibbipennis Motschulsky, P. fuscus LeConte, P. punctatus Spinola and two sp. n., P. exutus [type locality: Tabusintac, Nova Scotia] and P. texanus [type locality: Port Isabel, Cameron County, Texas]. Two syn. n. are proposed: P. cribratus Motschulsky, 1868 with P. gibbipennis Motschulsky, 1868 and P. crinitus Fall, 1907 with P. fuscus LeConte, 1850. A lectotype is selected for Paratenetus punctatus Spinola. A type species is designated for Storthephora Mäklin, 1875 (Storthephora denticollis Mäklin, 1875).

Keywords

Coleoptera, Tenebrionidae, North America, key
Introduction

The genus *Paratenetus* was proposed by Spinola in 1844 for two species, *P. lebasi* from Colombia and *P. punctatus* from the United States of America. The last mentioned species was represented by three specimens originating from the collection of Baron Dejean who received them from John Eaton LeConte. Subsequently, the genus received very little attention. In North America, John Lawrence LeConte described a new species in 1850 which he obtained during his trips to Lake Superior. In 1853–54, Victor de Motschulsky, a Russian Imperial Army Colonel, made a 10-month trip to the United States and Panama and collected at several locations including New York, Niagara Falls, Cleveland, Cincinnati, Lexington, Louisville, New Orleans, Mobile, Atlanta, Washington D.C., and Philadelphia. He described two species of *Paratenetus* in 1868 from the material he collected in Georgia. In 1907, Fall described a new species from New Mexico. Subsequently, the genus and some of its species were briefly cited in monographic works such as Blatchley (1910), Downie and Arnett (1996) and Aalbu et al. (2002a, b).

The purpose of this paper is to review the American species occurring north of Mexico and provide a key for their identification.

Material

The study is based on the examination of about 3110 specimens borrowed from the following collections:

- **AFC** Atlantic Forestry Centre, Fredericton, New Brunswick. Reginald P. Webster.
- **CAS** California Academy of Sciences, San Francisco, California. David H. Kavanaugh.
- **CMN** Canadian Museum of Nature, Gatineau, Quebec. François Génier.
- **CNC** Canadian National Collection of Insects, Archnides and Nematodes, Ottawa, Ontario.
- **CUIC** Cornell University Insect Collection, Ithaca, New York. James K. Liebherr.
- **DENH** Department of Entomology, University of New Hampshire. Donald S. Chandler.
- **ENMU** Department of Biology, Eastern New Mexico University, Portales, New Mexico. Darren A. Pollock.
- **FSC** Florida State Collection of Arthropods, Gainesville, Florida. Paul E. Skelley.
Methods

The photographs were made with a Leica Digital DC500 Imaging Workstation using Zerene Stacker software and retouched with Adobe Photoshop software.

For type specimens, complete verbatim label data are given with additional information enclosed within quotation marks; individual labels are separated by a slash (/).

The distribution maps were generated using the software SimpleMappr (http://www.simplemappr.net/).
Taxonomy

Genus *Paratenetus* Spinola, 1844
http://species-id.net/wiki/Paratenetus


**Etymology.** Spinola (1844: 117) mentioned that the name *Paratenetus* came from a Greek adjective which supposedly means “Digne d’être observé” (worthy of being observed). The idea for the name came from the peculiar shape of the palpi and particularly the flattening of the first two labial palpmere.

**Description** (based on species treated only). Body short, convex, pubescent; elytra with slanting setae in addition to erect setae. Epistoma with clypeolabral membrane exposed. Eyes present, prominent. Gena not sulcate. Antenna with last three antennomeres abruptly expanded, forming a distinct, loose club. Labial palpi short, penultimate palpomere swollen, last palpomere narrow, more or less fusiform; last maxillary palpomere large, at least twice as large apically than basally. Pronotum with sides denticulate, each denticle with one or two stiff setae; surface with relatively coarse punctures. Procoxae moderately separated. Mesepimeron not closing mesocoxal cavity. Elytra without striae, with relatively coarse punctures; epipleuron distinct and relatively wide up to apex. Abdomen with distinct membrane along posterior edge of ventrites 3 and 4. Intercoxal process of first ventrite relatively wide, more or less rounded apically. Tibia not expanded apically. Metatarsomere 1 elongate, as long as next two tarsomeres combined; penultimate tarsomere deeply lobate dorsally; last tarsomere not arising at apex of penultimate tarsomere. Tarsal claw simple, not pectinate. Tarsal formula 5–5–4. Defensive glands absent.

**Diversity.** This genus currently includes 57 species (Table 1) ranging collectively from Canada, as far north as southern Northwest Territories, south to Argentina.

**Taxonomic position.** Spinola (1844) originally placed *Paratenetus* in his Clérites Corynétoïdes (currently Cleridae: Korynetinae). Agassiz (1846: 119) listed it in the family “Tenebrionites.” Melsheimer (1853: 45) transferred the genus to the family Cryptophagidae. LeConte (1862: 232) moved *Paratenetus* back in the family Tenebrionidae, and placed it in the tribe Heterotarsini, a position that was followed by several authors including Horn (1870: 373), Gebien (1911: 471), Leng (1920: 236), Gebien (1941: 821) and Arnett (1962: 688). In 1918, Leng mentioned that “the genera *Paratenetus*, *Prataeus* and *Anaedus* seem to be near the Lagriidae on account of the similarity in their larval stages” and Böving and Craighead (1931: 42) moved the genera of Heterotarsini (except *Heterotarsus* Latreille) from the tenebrionids to the lagriids based also on the morphology of the larvae. The study of the ovipositor structures by Tschinkel and Doyen (1980: 367) supported also the position of *Paratenetus* within the subfamily Lagriinae rather than the subfamily Tenebrioninae. Ardoin (1961: 33)

We did not investigate the taxonomic position of the genus _Paratenetus_ but we accept, following Aalbu et al. (2002a; 2002b), its placement in the tribe Gonioderini of the subfamily Lagriinae within the Tenebrionidae.

**Biology.** The biology of members of _Paratenetus_ is poorly known. Many of the specimens seen in this study were collected in leaf litter in forested areas or in nests of the tent caterpillar genus _Malacosoma_ (Lepidoptera: Lasiocampidae). All three winged species have been collected at black light. Steiner (1995: 508) commented that _Paratenetus_ species pupate on the inner surfaces of rolled dead leaves (in which the larvae live) either hanging on fallen tree branches or on the ground.

**Notes.** There are two types of setae on the elytra of _Paratenetus_: erect and slanting. The slanting setae are characterized as subdepressed when the angle between the base of the seta and the elytra is between 10 and 40°, semierect when the angle is between 40 and 60°, and suberect when the angle is between 60 and 80°.

**Key to North American (north of Mexico) species of _Paratenetus_**

1. Metaventrite short, length along midline subequal to or shorter than length of abdominal ventrite 2 along midline ..............................................................
2. – Metaventrite longer, length along midline longer than length of abdominal ventrite 2 along midline .............................................................
3. 2
   – Elytra with very few, short erect setae.................._P. gibbipennis_ Motschulsky
   – Elytra with numerous, long erect setae.................._P. fuscus_ LeConte
4. 3
   – Antennomere 8 transverse. Metaventrite quite distinctly darker than first two abdominal ventrites in the vast majority of specimens, not or only slightly darker in a few specimens. Protibia of male without calcar..........................
   – Antennomere 8 subquadrate or slightly elongate. Metaventrite not darker than first two abdominal ventrites in the vast majority of specimens, slightly darker in a few specimens. Protibia of male with calcar..........................
5. 4
   – Pronotum with maximum width anterior of midlength (Fig. 3); punctures narrowly spaced, in part subcontiguous over lateral half [widely distributed in eastern North America] ..........................................._P. punctatus_ Spinola
   – Pronotum with maximum width at midlength (Fig. 4); punctures moderately dense, not subcontiguous even over lateral half [known only from Texas, Louisiana and Florida in North America] .........._P. texanus_ Bousquet & Bouchard
Table 1. Checklist of *Paratenetus* species of the world.

<table>
<thead>
<tr>
<th>Species</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. antennalis</em> Kulzer, 1958</td>
<td>Brazil</td>
</tr>
<tr>
<td><em>P. atricolor</em> Pic, 1934</td>
<td>Brazil</td>
</tr>
<tr>
<td><em>P. auritus</em> (Mäklin, 1875)</td>
<td>Brazil</td>
</tr>
<tr>
<td><em>P. bicoloricollis</em> Pic, 1939</td>
<td>Brazil</td>
</tr>
<tr>
<td><em>P. bordoni</em> Marcuzzi, 1994</td>
<td>Venezuela</td>
</tr>
<tr>
<td><em>P. brevipennis</em> Champion, 1886</td>
<td>Panama</td>
</tr>
<tr>
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**Paratenetus gibbipennis** Motschulsky, 1868

http://species-id.net/wiki/Paratenetus_gibbipennis

Figs 5, 10

*Paratenetus gibbipennis* Motschulsky, 1868: 193. Type locality: «Atlanta, Géorgie américaine» (original citation).

*Paratenetus cribratus* Motschulsky, 1868: 193. Type locality: «Géorgie américaine» (original citation). **syn. n.**

**Type material.** Motschulsky’s collection at ZMMU contains a single specimen, a female, under the name *P. gibbipennis*. It bears the following labels: “[green round disc] / [small brick red square label] / type [handwritten] / Paratenetus gibbipennis Motch Am. b. Mobile [handwritten on a rectangular green label].” The specimen is intact although many of the setae on the pronotum and elytra are gone. The provenance of the specimen is doubtful. In the key to the *Paratenetus* in his collection, Motschulsky (1868: 193) mentioned that the species was collected in Atlanta but Mobile is listed on one of the type labels. Motschulsky collected in both localities during his 10-month trip to America in 1853–54.

Motschulsky’s collection contains a single specimen, a male, under the name *P. cribratus*. It bears the following labels: “[green round disc] / Atlanta [handwritten] / type [handwritten] / Paratenetus cribratus Motch Am. bor. Atlanta [handwritten on a rectangular green label].” The specimen is missing the left antennomeres 3–11 and the posterior legs.

**Note about synonymy.** Motschulsky (1868) separated *P. gibbipennis* and *P. cribratus* on the account that the first species has the lateral denticles of the pronotum very short while the second species has strong denticles. From an examination of the types, we cannot sustain Motschulsky’s affirmation; the denticles are basically of the same size on both specimens.

**Diagnosis.** This species and *P. fuscus* differ from the other three species treated by having the metaventrite very short. *Paratenetus gibbipennis* differs from *P. fuscus* by having few short erect setae on the elytra.

**Description.** Body dorsally reddish yellow to dark reddish brown, legs paler, yellow to reddish yellow; antennal club not darkened in most specimens; metaventrite not darker than first two abdominal ventrites. Antennomere 8 subquadrat or very slight-
ly transverse. Pronotum with maximum width near midlength or slightly anterior to midlength; punctures moderately dense, not subcontiguous even over lateral half. Elytra very convex; slanting setae subdepressed, erect setae very few, short. Metaventrite short, length along midline clearly shorter than length of abdominal ventrite 2 along midline. Male protibia with calcar near middle along ventral surface; male mesotibia with short, in some specimens very short, more or less perpendicular preapical protuberance. Parameres with sides more or less parallel towards apex, apex not particularly acute (Fig. 5).

Length: 2.5–3.2 mm.

**Distribution.** This species ranges from southern Maine to southwestern Manitoba, south to central Texas, southwestern Alabama, and central South Carolina (Fig. 10).

**Records.** We have seen 660 specimens from the following localities. **CANADA.**


**Remarks.** Females are much more abundant in collections than males. Of 183 specimens randomly selected, 8 were males (4.4%) and 175 were females (95.6%). The males came from Georgia (n=1), Alabama (n=6), and Missouri (n=1). No males were found among the 160+ randomly selected specimens from Canada and the northern states.

Specimens were collected in January (n=1), February (n=1), March (n=89), April (n=64), May (n=8), June (n=61), July (n=20), August (n=95), September (n=31), October (n=38), November (n=6) and December (n=2).

Labels on specimens read “in leaf litter” (6 specimens); “in leaf litter of black birch and shrubs around and on areas of exposed rock” (71); “forest litter sifting” (2); “forest litter” (3); “moist forest berlese” (1).

**Paratenetus fuscus** LeConte, 1850
http://species-id.net/wiki/Paratenetus_fuscus
Figs 6, 11

**Paratenetus fuscus** LeConte, 1850: 223. Type locality: Lake Superior (inferred from the title of the book).

**Paratenetus crinitus** Fall, 1907: 253. Type locality: «Trout Spring [New Mexico]» (original citation). **syn. n.**

**Type material.** LeConte’s collection at MCZ contains a single male specimen under the name *P. fuscus*. It bears the following labels: “[pale green round disc] / Type 4684 [partially handwritten on a red square label] / P. fuscus Lec. [handwritten].” The specimen is intact.
Fall described *P. crinitus* from one specimen now at the MCZ. It bears the following labels: “Trout sp. N.M. May [handwritten] / crinitus. Type [partially handwritten] / M.C.Z Type 24612 [red square label] / H.C. Fall Collection.” The specimen is intact.

**Note about synonymy.** Fall (1907: 253) described his *P. crinitus* and mentioned that “in *crinitus* the metasternum is almost as short as in *fuscus*, which species is, however, very distinct by its subinflated elytra, more rounded sides of the prothorax and absence of erect hairs on the upper surface.” Obviously Fall did not study the syntype in LeConte’s collection since the specimen bears many erect hairs. LeConte never mentioned that character in his description and obviously Fall misidentified LeConte’s species. We have studied the type specimens of both species and find no structural differences to separate them.

**Diagnosis.** This species differs from *P. gibbipennis* by the character states listed in the description.

**Description.** Same character states as *P. gibbipennis* except for the following: slanting setae on elytra less depressed, semierect, occasionally even suberect; erect setae numerous, in seven or eight rows; metaventrite slightly longer, length along midline subequal to slightly shorter than length of abdominal ventrite 2 along midline.

**Distribution.** This species ranges from Quebec City to the Rocky Mountains in northeastern British Columbia, north to southern Northwest Territories, south to northern New Mexico, northeastern Kansas, and Maryland (Fig. 11).


Remarks. Females are a little more common in collections than males. Of 45 randomly selected specimens, 28 (62%) were females and 17 (38%) were males. Specimens were collected in February (n=1), March (n=30), April (n=58), May (n=8), June (n=40), July (n=7), August (n=19), September (n=14), October (n=5) and November (n=4).

*Paratenetus punctatus* Spinola, 1844

http://species-id.net/wiki/Paratenetus_punctatus

Figs 3, 8, 12

*Latridius pubescens* Say, 1826: 265 [*nomen dubium*]. Type locality: United States (inferred from title of the paper).


**Type material.** Most of Say’s entomological collection has been destroyed and we are unaware that a syntype of his *Latridius pubescens* survived. LeConte (1859: 325) based his interpretation of Say’s species on the original description. For nomenclatural stability, we believe it is best to consider *Latridius pubescens* Say as a [*nomen dubium*] and retain the long accepted name *Paratenetus punctatus* Spinola for this species.

Spinola (1844: 119) indicated that he had three specimens of *P. punctatus* which came from Dejean’s collection. These specimens were received for study from the Museo Regionale di Scienze Naturali in Turin (MRSN). The first specimen, probably a female, is labeled “Paratenetus punctatus Ekis 1974 [handwritten]”; the second, a male “Paralectotype Paratenetus punctatus Spinola Ekis 74 [handwritten]”; and the third, a female “Lectotype Paratenetus punctatus (Spinola) Ekis 74 [handwritten]”. The first two specimens correspond neither to our concept of *P. punctatus* nor to any other North American species we have seen. The specimens are in poor condition, with almost all the setae gone, but they appear to be conspecific. Although Spinola indicated that all three of his specimens came from the United States and were provided by “Mr. [John Eatton] LeConte,” these two specimens may have originated from Mexico, Central America or South America. The third specimen, a small individual (3.2 mm), fits
our concept of *P. punctatus* and is here selected as lectotype. The label “Lectotype *Paratenetus punctatus* Spinola des. Y. Bousquet 2012” has been attached to the specimen.

**Diagnosis.** Many specimens of *P. punctatus* can be separated from the other North American species of *Paratenetus* by their large size (3 mm or more). The vast majority of specimens of the other species are less than 3 mm long. Otherwise, the species can be separated from *P. exutus* in having the antennomere 8 subquadrate, the pronotum wider clearly anterior to the midlength, the punctuation on the pronotum coarser, the slanting setae on the elytra slightly longer and more erect and the protibia of the male with a calcar along ventral surface. From *P. texanus*, this species is best separated in having the pronotum widest anterior to the midlength and the punctures on the pronotum coarser and denser, in part subcontiguous along the lateral half.

**Description.** Body dorsally uniformly pale to dark reddish brown in most specimens, with the pronotum and head slightly darker than elytra and legs in some specimens; antennal club darker than antennomeres 1–8; metaventrite not darker than first two abdominal ventrites in the vast majority of specimens, slightly darker in a few specimens. Antennomere 8 subquadrate. Pronotum with maximum width anterior of midlength (Fig. 3); punctures narrowly spaced, in part subcontiguous over lateral half. Elytra less convex than for *P. gibbipennis* and *P. fuscus*; slanting setae semierect in the vast majority of specimens, suberect in some specimens, erect setae few. Metaventrite long, length along midline longer than length of abdominal ventrite 2 along midline. Male protibia with calcar near middle along ventral surface; male mesotibia with very short, preapical spine, oriented perpendicularly or obliquely to long axis of tibia. Parmers with sides more or less parallel to very slightly convergent towards apex; apex more or less rounded (Fig. 8).

Length: 3.0–4.0 mm.

**Distribution.** This species ranges from New Brunswick to southeastern Manitoba, south to eastern Texas, southern Mississippi, and southeastern Florida (Fig. 12).

**Records.** We have seen 1215 specimens from the following localities. Canada. 
Review of the species of Paratenetus Spinola inhabiting America, north of Mexico


**Remarks.** This species varies in regard to the punctation and setae. The punctation on the pronotum is coarse and in most specimens free on the disc and very close, in part subcontiguous over the sides; in some specimens the punctation is denser, being subcontiguous on the disc and contiguous all over the lateral sides. The slanting setae on the elytra are usually semierect but in some specimens they are less inclined and the erect setae are difficult to distinguish. The erect setae are usually short and moderately numerous but in some specimens, they can be relatively long or much more numerous; in such case the species can be confused with *P. fuscus* but is easily separated by the coarse, irregular punctation on the pronotum and by the longer metaventrite.
Females are more common in collections than males. Of 220 randomly selected specimens, 169 (77%) were females and 51 (23%) were males.

Specimens were collected in March (n=6), April (n= 89), May (n= 296), June (n= 384), July (n= 152), August (n= 67), September (n= 40), October (n= 9), November (n= 5), and December (n= 2).

Labels on specimens read “in overwintered nest remains of *Malacosoma americana* on *Prunus serotina* at mixed forest edge, shale barren area” (7 specimens), “shaken from and reared in moldy frass in old nest of *Malacosoma americana* on *Prunus serotina*” (13), “beaten from dead leaf clusters on cut branches of *Carpinus caroliniana* at forest edge” (6), “beaten from dead leaf clusters on branches of fallen *Populus deltoides*” (7), “beaten from dead leaf clusters on fallen broken branch of *Tilia americana* in shade, mixed forest” (2), “beaten from dead hanging leaf clusters on fallen *Ailanthus* in mixed forest” (6), “shaken from dead leaves on fallen branches of *Quercus rubra*” (4), “in moldy leaf clusters on fallen branch of *Quercus alba* in shade” (6), “beaten from dead leaves of wind-blown *Quercus rubra*” (1), “beaten from dead leaf clusters on fallen branches of *Quercus rubra* in mixed forest” (14); “at black light in longleaf pine and mixed oak, sand barrens” (23), “in moldy leaves on fallen branches of *Acer rubrum*” (4), “at black light in oak & longleaf pine sand barren” (5); “at black light; open sandy gap in mixed forest” (1); “at black light in mixed deciduous forest” (1); “at black light in mixed hardwood and loblolly pine forest” (1); “at black light in mixed pine and hardwood forest” (3); “beaten from dead leaf clusters on branches of *Castanea* out ca. 2 weeks earlier” (5); “at black light near mixed forest, farmed fields and tidal creek” (4); “beach drift” (1); “from pile of moldy thatch” (1); “in moldy leaf clusters on cut branches of *Prunus serotina*” (4); “in moldy leaf clusters on cut branches of *Morus*” (2); “beaten from dead leaf clusters on cut branches of *Acer rubrum* at mixed forest edge” (10); “in old nest of *Malacosoma* on *Prunus*” (2); “in dead leaves on branches of fallen oak” (1); “shaken from dead leaves on cut *Sassafras*” (7); “beaten from dead leaf clusters on fallen branch *Acer negundo* at mixed forest edge” (1); “at black light in tree canopy, mixed broken forest and residential area” (43); “at black light in mixed hardwood forest near pond and river” (8); “at black light in mixed forest, bluff above river” (2); “in old tent *Malacosoma americana*” (5); “at black light” (2); “in old tent nest of *Malacosoma americana* with moldy frass, on *Prunus serotina*” (1); “shaken from dry leaf (Vitis sp.) nest of *Sciurus carolinensis* in vine tangle ca. 3 m above ground” (1); “at black light at edge of clearing in mixed forest near drying vernal pool” (2); “at black light in mixed forest near vernal pools” (8); “at black light sheet in open mature mixed forest near river” (3); “beaten from dead leaf clusters on fallen branch of *Liriodendron* in mixed forest” (9); “beaten ex spruce” (1); “collected in tents *Malacosoma americana*” (12); “in web of *Malacosoma*” (3); “on *Pinus strobus*” (2); “ex. canopy trap” (34); “intercept trap” (1); “beating dead leaves” (8); “btng oak blowdown” (2); “leaf litter” (1); “dead moldy leaves” (1); “beating veg.” (2); “beating flowers” (2).
Paratenetus exutus Bousquet & Bouchard, sp. n.  
http://zoobank.org/E79EDDDF-59F8-4A43-880F-2A86CF8EB2F2  
http://species-id.net/wiki/Paratenetus_exutus  
Figs 1, 2, 7, 13

Type material. Holotype (♂) labeled “Tabusintac, N.S. 20-VI-1939 W.J. Brown / Holotype Paratenetus exutus Bousquet & Bouchard CNC No. 24035.” The specimen is deposited in the CNC.


Etymology. The specific name comes from the Latin participle exutus, -a, -um (deprived of) and alludes to the fact that the protibia of the male lacks the spikelike projection (calcar) found in the other American (north of Mexico) species.

Diagnosis. This species is best separated from P. punctatus and P. texanus in having the antennomere 8 transverse. The males are also easily recognized among the species treated here in having no calcar on the protibia and a relatively long apical spine, oriented more or less parallel to long axis of tibia, on the metatibia.

Description. Body dorsally pale reddish brown in most specimens, with the pronotum and head usually slightly darker than elytra and legs; antennal club darker than antennomeres 1–8, particularly in males; metaventrite quite distinctly darker than first
two abdominal ventrites in the vast majority of specimens, not or only slightly darker in a few specimens. Antennomere 8 transverse. Pronotum with maximum width at or very slightly anterior of midlength (Fig. 2); punctures narrowly spaced, in part sub-contiguous over lateral half. Elytra less convex than for *P. gibbipennis* and *P. fuscus*; slanting setae subdepressed, erect setae few. Metaventrite long, length along midline longer than length of abdominal ventrite 2 along midline. Male protibia without calcar near middle along ventral surface; male mesotibia with relatively long, apical spine, oriented more or less parallel to long axis of tibia. Parameres with sides convergent towards apex; apex more or less truncate (Fig. 7).

Length: 2.5–3.0 mm.

Figure 1. Dorsal habitus drawing of *Paratenetus exutus*. 
Distribution. This species ranges from Cape Breton Island to northwestern Alberta, south to east-central Texas, southern Alabama, and southern Florida (Fig. 13).


Remarks. While almost all specimens from Canada and northern United States had the metaventrite distinctly darker than the first two abdominal ventrites, this is not the case with the specimens from the southern states. There is also variation in the width of the antennomere 8. Most specimens have that antennomere distinctly transverse, some specimens from the southern states (particularly Louisiana) have the antennomere 8 only slightly transverse.

Females are more common in collections than males. Of 105 randomly selected specimens, 76 (72%) were females and 29 (28%) were males.

Specimens were collected in March (n= 9), April (n= 38), May (n= 84), June (n= 58), July (n= 79), August (n= 40), September (n= 22), October (n= 5), November (n= 3), and December (n= 2).

Labels on specimens read “at black light near mixed forest, farmed fields and tidal creek” (4 specimens); “at black light at edge of mixed forest and open turf on hill” (1); “in moldy leaf clusters on cut branches of Acer rubrum” (3); “beaten ex spruce” (35); “beaten ex fir” (10); “on Bumelia lanuginosa” (1); “ex. spruce” (1); “ex. canopy trap” (15); “ex. FIT, near upper meadow” (1); “ex. FIT, near lower meadow” (3); “ex. canopy malaise, near lower meadow” (9); “ex. canopy FIT, near lower meadow” (3); “malaise trap” (6).

Most specimens of this species in collections are identified under the name “Paratenetus inermis” Bsq. and Bouch.” since it was the intended name. Unfortunately, we realized that the name was already used by Champion only after the specimens were returned to their respective collections.
Paratenetus texanus Bousquet & Bouchard, sp. n.
http://zoobank.org/E4FC7175-796F-4270-966D-93B4EE8E681A
http://species-id.net/wiki/Paratenetus_texanus
Figs 4, 9, 14

Type material. Holotype (♂) labeled “Port Isabel, Tex. 20.X.1982 Lot 2 BF&JL Carr / Holotype Paratenetus texanus Bousquet & Bouchard CNC No. 24133.” The specimen is deposited in the CNC.


Etymology. The specific name derives from the name of the state of Texas where the species has been commonly collected.

Diagnosis. Members of this species can be distinguished from those of P. punctatus and P. exutus in having the punctures on the pronotum sparser, not subcontiguous even on the lateral half. They can also be distinguished from most adults of P. punctatus by their smaller size and from most adults of P. exutus by the subquadrate antennomere 8 and metaventrite of same color as the first two abdominal ventrites.

Description. Body dorsally yellow to pale reddish brown, with the pronotum and head usually slightly darker than elytra and legs; antennal club slightly darker than antennomeres 1–8 in many specimens, often reddish brown to partially piceous, yellowish and as pale as legs in some specimens; metaventrite not darker than first two abdominal ventrites. Antennomere 8 subquadrate. Pronotum with maximum width at midlength (Fig. 4); punctures moderately dense, not subcontiguous even over lateral half. Elytra less convex than P. gibbipennis and P. fuscus; slanting setae subdepressed, erect setae short. Metaventrite long, length along midline longer than length of abdominal ventrite 2 along midline. Male protibia with calcar near middle along ventral surface; male mesotibia with short, preapical spine, wide at base and oriented perpendicularly to long axis of tibia. Parameres with sides distinctly convergent towards apex; apex markedly acute (Fig. 9).

Length: 2.7–3.3 mm.

Distribution. This species is known from southeastern Florida, central Louisiana, and central and eastern Texas (Fig. 14). We have also seen specimens from the states of Chiapas, Nayarit and Tamaulipas in Mexico.

Records. We have seen 515 specimens, including the type material, from the following localities. United States of America. Florida. Dade Co.: Miami (FSC). Louisiana. Avoyelles Parish: Mansura (USNM). Cameron Parish: Holly Beach (LSAM, TAMU); nr. Oak Grove (TAMU). Texas. “60 mi SE Cotulla” (CNC). “15 mi SW Jct
FR 3073 & Hwy 16” (CNC). Anderson Co.: Elkhart (TAMU). Aransas Co.: Goose Island St. Park (LSAM, TAMU). Atascosa Co.: Pleasanton (USNM); Campbellton (TAMU). Bastrop Co.: Bastrop St. Pk. (FSC). Bee Co.: Beeville (USNM); Pettus (CNC). Bexar Co.: San Antonio (USNM). Brooks Co.: Falfurrias (CNC); 9 mi W Falfurrias (TAMU). Cameron Co.: Boca Chica (CNC, TAMU); 6 mi W Boca Chica Beach (TAMU); 6.7 mi

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W Boca Chica Beach (TAMU); Brownsville (CNC, CUIC, MCZ, TAMU, USNM); 4 mi ESE Brownsville (TAMU); 6 mi E Brownsville (TAMU); 10 mi E Brownsville (RLAC, LSAM); 12.5 mi E Brownsville (TAMU); 13.5 mi E Brownsville (TAMU); W of Harlingen (TAMU); Main Reservoir near Brownsville (RLAC); Resaca de las Palomas St. Pk. (RLAC); Resaca de La Palma St. Pk. (TAMU); Sabal Palm Grove Wildlife Sanctuary (RLAC, GMNH, LSAM, TAMU); nr. Southmost (USNM); ca. 2 mi E Los Fresnos (TAMU); Laguna Atascosa NWR (TAMU); 9.7 mi E jct Rt 1419 on hwy 4 (TAMU). Chambers Co.: Anahuac (USNM). Duval Co.: San Diego (USNM); Freer (TAMU); Sepulveda Ranch (TAMU); 3.5 mi S Realitos (TAMU). Fort Bend Co.: Brazos Bend St. Pk. (TAMU). Galveston Co.: Virginia Point (USNM); San Luis Pass (TAMU); 3.5 mi SW Jamaica Beach (TAMU); 7 mi SW Jamaica Beach (TAMU). Goliad Co.: Goliad (USNM). Hidalgo Co.: Santa Ana Nat. Wdlf. Ref. (LSAM, TAMU, USNM); Bentsen Rio Grande Valley St. Pk. (LSAM, TAMU); Anzalduas Park (TAMU); Delta Lake (TAMU). Jefferson Co.: 10 mi W Sabine Pass (TAMU). Jim Wells Co.: Ben Bolt (CNC); 1 mi N Ben Bolt (TAMU); Alice (USNM); 5 km W Alice (CMN); 1 mi N Premont (TAMU); 1.4 mi S Premont (TAMU). Karnes Co.: 1 mi NE Runge (TAMU). Kendall Co.: Boerne (USNM). Kenedy Co.: Sarita (CNC); 2 mi S Sarita (TAMU); 13 mi S Sarita (TAMU); 25.3 mi S Sarita (FSC); 31.8 mi S Sarita (TAMU); Armstrong (CNC); 1 mi S Armstrong (TAMU); Norias (TAMU); 5 mi N Norias (TAMU); 6 mi S Norias (TAMU); 8 mi S Norias (CNC); Loyola Beach, Baffin Bay (CNC); Baffin Bay (TAMU). Kleberg Co.: Kingsville (CUIC, TAMU); Riviera (CNC, TAMU); Riviera Beach (CNC); Velederos Creek (TAMU). Live Oak Co.: 17 mi SW George West (TAMU). Nueces Co.: Corpus Christi (USNM, TAMU). Refugio Co.: 8 mi E Refugio (TAMU); 7 mi S Woodsboro (TAMU). San Patricio Co.: Sinton (USNM); nr. Sinton (CNC); 3 mi N Sinton (TAMU); 7 mi N Sinton (TAMU); Welder Wildlife Refuge (CMN, FSC, TAMU); Welder Wildlife Refuge, 17 km NE Sinton (CMN); Lake Corpus Christi St. Pk. (LSAM). Starr Co.: 1.5 mi E Rio Grande City (LSAM). Tyler Co.: 4 mi E Spurger (TAMU). Willacy Co.: 8 miles SW Port Mansfield (TAMU). Mexico. Chiapas. El Aguacero, 16 km W Ocozocoautla (CMN); 5 km E Ocozocoautla (CMN); 2 km S Chicoasen (CMN); Cinco Cerros (CMN). Nayarit. 15 mi N Tepic (CNC). Tamaulipas. Mpio.San Carlos, Cerro del Diente (TAMU).

Remarks. The two specimens from Miami in Florida externally agree perfectly with those from Texas. One is a male and its genitalia are identical to those of specimens from Texas.

Males are more common in collections than females. Of 106 randomly selected specimens, 42 (40%) were females and 64 (60%) were males.

Specimens were collected in January (n=1), February (n=1), March (n= 65), April (n= 39), May (n= 89), June (n= 30), July (n=53), August (n= 21), September (n= 36), October (n= 108), November (n= 2), and December (n=6).

Labels on specimens read “at black light in Prosopis and Celtis forest, sandy soil” (6 specimens); “on Celtis” (1); “ex dry okra pod” (1); “cotton” (1); “collected on Celtis” (2); “fallen fruit Yucca treculeana” (1); “on flower Yucca treculeana” (2); “on Acacia Berlandieri Benth.” (1).

This new species occurs in Mexico and nine species have been reported from that country. We have examined the type material of the six species described by Champion and housed in BMNH, i.e., *Paratenetus constrictus*, *P. corticarioides*, *P. nigricornis*,
Figure 14. Map showing collection localities in America (north of Mexico) of Paratenetus texanus.

*P. punctulatus*, *P. tibialis*, and *P. villosus*, and none of them are conspecific with those of *P. texanus*. The three species not seen are *P. tropicalis* Motschulsky, *P. koltzei* Pic, and *P. mexicanus* Pic.

**Acknowledgments**

We would like to thank Matthew L. Gimmel for sharing independently-generated information on Nearctic *Paratenetus*. Thanks are due also to Go Sato for the habitus drawing, to Anthony Davies and Henri Goulet for the photographs, and to Darren A. Pollock and Matthew L. Gimmel for their constructive suggestions on the manuscript. We are grateful to the curators of the collections studied for access to the specimens under their care.

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Towards a revision of the South American genus *Praocis* Eschscholtz (Coleoptera, Tenebrionidae), with estimation of the diversity of each subgenus

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Abstract

A review of the subgenera of the South American genus *Praocis* Eschscholtz (Pimeliinae: Praociini) is presented. *Praocis* comprises 77 species and 8 subspecies arranged in nine subgenera distributed in arid lands from Central Peru and Bolivia to the Southern part of Patagonia in Chile and Argentina. For each subgenus of *Praocis*: *Praocis* Eschscholtz, *Mesopraocis* Flores & Pizarro-Araya, subgen. n., *Anthrasomus* Guérin-Méneville, *Filotarsus* Gay & Solier, *Postpraocis* Flores & Pizarro-Araya, subgen. n., *Hemipraocis* Flores & Pizarro-Araya, subgen. n., *Orthognoderes* Gay & Solier, *Praonoda* Flores & Pizarro-Araya, subgen. n., and *Praocida* Flores & Pizarro-Araya, subgen. n., we present a diagnosis using new and constant characters of adult morphology such as clypeal configuration, length and proportion of antennomeres 9, 10 and 11, arrangement of apical tomentose sensory patches on antennomeres 10 and 11, anterior margin of prosternum, lateral margin of elytron, ventral surface of profemora, and shape of protibiae. An identification key for the nine subgenera of *Praocis* is presented. Type species are designated for the five new subgenera; for *Mesopraocis*: *Praocis calderana* Kulzer, for *Postpraocis*: *Praocis pentachorda* Burmeister, for *Hemipraocis*: *Praocis*...
sellata Berg, for Praonoda: Praocis bicarinata Burmeister, for Praoidea: Praocis zischkai Kulzer, and for the previously described subgenus Orthogonoderes: Praocis subreticulata Gay & Solier. The current number of species and the estimated number of species to be described are presented. The distribution ranges of the subgenera, including new records from collections and recent expeditions, are given. Habitat preferences and a discussion of the biogeography of the genus are also presented.

**Keywords**
Taxonomy, Pimeliinae, Praociini, Praocis, key, diversity, South America

**Introduction**

The genus *Praocis* Eschscholtz belongs to the Praociini, an endemic Neotropical tribe of Pimeliinae with 151 species arranged in 15 genera (Flores and Pizarro-Araya 2012). *Praocis* is the most specious genus of the tribe (52% of the species). It comprises 77 species and 8 subspecies, arranged in nine subgenera (Flores and Pizarro-Araya 2012), distributed from central Peru to the southern part of Patagonia in Argentina and Chile. The distribution of *Praocis* species coincides with the whole distribution of the tribe (Fig. 1) and is related to the arrangement of the Andes mountain range in arid and semiarid lands of southern South America (Flores and Pizarro-Araya 2006).

The last revision of *Praocis* was made by Kulzer (1958) in the context of a tribal review. Kulzer (1958) classified the species of *Praocis* into 10 subgenera, six of which were new: *Mesopraocis*, *Postpraocis*, *Parapraocis*, *Hemipraocis*, *Praonoda*, and *Praocida*, plus the four previously recognized as valid by Solier (1840): *Praocis* s. str., *Anthrasomus* Guérin-Méneville 1834, *Orthogonoderes* Gay & Solier, 1840, and *Filotarsus* Gay & Solier, 1840. Kulzer (1958) did not characterize his new subgenera nor designate type species, but in his key he mentioned character states for identifying some of them except between *Anthrasomus* and *Filotarsus*, and between *Orthogonoderes* and *Praocida*, which can be keyed only by body size. Kulzer (1958) also failed to assess the geographic distribution of the subgenera, reporting only isolated localities of the species.

The subgeneric classification of the genus was recently reviewed (Flores and Pizarro-Araya 2012) and the genus was redefined on the basis of five constant character states. The subgenus *Parapraocis* was excluded from *Praocis* because its species exhibit different character states from those defining the genus and it was recognized as a separate genus within Praociini (Flores and Pizarro-Araya 2012).

In the current study we report new constant characters to define each *Praocis* subgenus, such as shape of clypeus, frons and clypeal suture, length and proportion of antennomeres 9, 10 and 11, arrangement of apical tomentose sensory patches on antennomeres 10 and 11, and ventral surface of profemora. We also used the characters defined by Kulzer: shape of anterior margin of prosternum, posterior angles of pronotum, lateral margin of pronotum, lateral margin of elytron, shape of body and apical process of protibiae.
The objectives of this study are to present elements for a revision of the genus *Praocis* by incorporating new constant characters from external morphology to define each subgenus, to designate type species for some subgenera that remain unavailable, to estimate the diversity of each subgenus, to detail the geographic distribution and habitat of each subgenus and to report new distributional records for some subgenera.

**Material and methods**

**Material examined.** The present study is based on an examination of specimens deposited in the following collections (we follow Arnett et al. 1993 where possible for collection abbreviations):

- **FMNH**  Field Museum of Natural History, Chicago, USA
- **IADIZA** Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza, Argentina
- **LEULS** Laboratorio de Entomología Ecológica, Universidad de La Serena, Chile
- **MACN**  Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina
- **MLPA**  Museo de La Plata, Buenos Aires, Argentina

*Figures 1–2. 1 Distribution area of the whole genus *Praocis* 2 Dorsal view of *Praocis (P.) bicentenario*, holotype (previously published in Flores and Pizarro-Araya 2012, Zootaxa 3336: Fig. 17; copyright Magnolia Press, reproduced with permission).*
**Type species.** For the subgenera *Praocis, Anthrasomus,* and *Filotarsus* the type species were designated prior to this study. For *Orthogonoderes* Gay & Solier (in Solier 1840) the authors characterized this new taxon but did not indicate the type species. We designate the type species of *Orthogonoderes* in this paper (Article 67.4 ICZN 1999) based on one of the six specific names available in the original publication (Article 67.2.1 ICZN 1999).

The remaining five names of the subgenera proposed by Kulzer (1958): *Mesopraocis,* *Postpraocis,* *Hemipraocis,* *Praonoda,* and *Praocida* are unavailable because Kulzer (1958) did not designate type species for these subgenera. To be available, every new genus-group name published after 1930 must, in addition to satisfying the provisions of Article 13.1 (ICZN 1999), be accompanied by the fixation of a type species in the original publication (Article 67.4.1 ICZN 1999). These five names will be made available for the first time in this article. To fix the current interpretation of these names and to ensure stability as these names were used in previous works (Peña 1966; Flores 2007, 2009; Alfaro et al. 2009; Flores et al. 2011; Flores and Pizarro-Araya 2012; Cortés-Contreras et al. 2013), we use the same names proposed by Kulzer (1958), present a diagnosis of each subgenus and hereby designate the type species on the basis of the specific names available for this nomenclatural act, the type specimens are not lost and the species is representative of the characters of the subgenus.

**Characters.** For each subgenus of *Praocis* we present a diagnosis using the following characters and character states:

Clypeal configuration (characters 1–3). The anterior margin of clypeus, in most subgenera, extends beyond the lateral expansion of frons (Fig. 3); in some species of *Filotarsus* it appears at same level as lateral expansion of frons. The width of the anterior margin of the clypeus, in most subgenera, does not exceed half the interocular width (Fig. 3), while in some species of *Filotarsus* it is equal to interocular width. The clypeal suture shows two different states: as horizontal groove (Fig. 4), the clypeus being lower than frons; and as vertical groove, in this state the clypeus and frons are at the same level (Fig. 3).

Length and proportion of antennomeres 9, 10 and 11 (characters 4–5) are very variable among subgenera. Antennomere 9 can be longer than antennomere 10 (Fig. 5) or equal in length to antennomere 10. Antennomere 11 is in most subgenera longer than antennomere 10 (Fig. 5), in *Orthogonoderes* it is shorter than antennomere 10 (Fig. 6) and equal in length to antennomere 10 in *Mesopraocis.*

Arrangement of apical tomentose sensory patches on antennomeres 10 and 11 (characters 6–7) are also variable among the subgenera. The apical tomentose sensory patches on antennomere 10 are arranged in two areas subequal in size (Fig. 6), or in a dorsally continuous semicircle (Fig. 5). On antennomere 11, the apical tomentose
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Sensory patches are located in a single area on the distal third (Fig. 6) or on the distal half of its surface (Fig. 5).

The anterior margin of the prosternum (character 8) presents two states: with a narrow sharp edge or lacking that edge. The lateral margin of the elytron (character 9) can be not defined, rounded, continuous between dorsal area of elytron and pseudopleuron, or well defined by a narrow, sharp carina-shaped edge or by a wide longitudinal, prominent edge. The ventral surface of the profemora (character 10) presents a row of setae on the anterior edge or lacks that row of setae. The shape of protibiae (character 11) varies between explanate, distal margin width exceeding 1/3 of protibial length, and not explanate, distal margin width equal to 1/4 of protibial length.

**Distribution.** With the distributional data published (Kulzer 1958; Peña 1966; Ferrú and Elgueta 2011; Flores and Pizarro-Araya 2012) and from specimens deposited in the examined collections we made approximate maps of the current geographic distribution for each subgenus. New records are reported for some subgenera and enlargement.
of their distribution. As a result of recent expeditions (Alfaro et al. 2009; Flores et al. 2011) we recorded the subgenera present on Pacific islands and Peninsula Valdés in the Atlantic Ocean. For distribution of the species we used the biogeographic classification by Morrone (2006).

**Estimation of the diversity of each subgenus.** Based on the types of known species (deposited at FMNH, MACN, MLPA, MNHUB, MNHN, MNNC, and NHMB) and the keys of Kulzer (1958), all specimens available in collections were determined and we identified specimens belonging to species to be described. Other unnamed species were found in collecting trips made for our projects in IADIZA and LEULS since 2001 until now. A list of the unnamed species by subgenus was made with these records and the diversity of each subgenus and of the whole genus was estimated, including the species to be described.

**Species list.** Based on the last revision of the genus (Kulzer 1958) and on most recent studies of types and new synonymies (Flores 2007, 2009; Flores and Pizarro-Araya 2010, 2012; Flores et al. 2011), we made a list of species included for each subgenus. Some species were described after Kulzer’s revision (Kaszab 1964, 1969; Molinari 1969; Marcuzzi 1977, 2001) or rediscovered (Flores 2007), so we assigned these species to some subgenus according to the diagnostic characters presented here.

**Results**

**Genus Praocis Eschscholtz, 1829**

http://species-id.net/wiki/Praocis

**Generic characteristics.** The species of *Praocis* can be recognized by having maxillary palps with last segment axe-shaped (apex twice as wide as base), antennomere 3 shorter than 4 + 5 combined, pronotum with anterior margin concave, width of posterior margin exceeding width of anterior margin, single lateral margin slender, expanded, remote from disc, and anterior angles rounded; mesosternum inclined forward, separated from prosternum; elytron with punctuate surface; apterous.

(1) **Subgenus Praocis (Praocis) Eschscholtz, 1829**

Figs 2, 15–16

**Type species.** *Praocis rufipes* Eschscholtz, 1829, subsequent designation by Guérin-Méneville (1834: 8-9).

**Diagnosis.** Clypeus with anterior margin extending beyond to lateral expansion of frons, width of anterior margin not exceeding half the interocular width, clypeal suture as a vertical groove, not covered by frons, clypeus and frons at same level; antennomere 10 wider than long, antennomere 9 longer than antennomere 10, antennomere 11 longer than antennomere 10; apical tomentose sensory patches on antennomere 10 in
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a dorsally continuous semicircle, on antennomere 11 on distal half; prosternum with a narrow edge on anterior margin; lateral margin of elytron well defined; ventral surface of profemora with a row of setae on anterior edge; protibiae explanate.

**Distribution.** Species of *Praocis* s. str. are endemic to central and southern Chile and occur from 26°South (Quebrada el León, Atacama Region) to 42°South (Carelmapu, Los Lagos Region) in the biogeographic provinces of Atacama, Coquimbo, Santiago, Maule and Valdivian Forest (Morrone 2006) (Fig. 15).

**New records.** We present new records for some Pacific islands. We recorded *Praocis* (*P.*) *spinolai* Gay & Solier for Damas (29°13’S, 71°31’W), Gaviota (29°15’S, 71°28’W) and Choros (29°15’S, 71°32’W) islands (Alfaro et al. 2009), *Praocis* (*P.*) *subaenea* Erichson and *Praocis* (*P.*) *curta* Solier for Chañaral Island (29°02’S, 71°36’W) (pers. obs), and *Praocis* (*P.*) *costata* Gay & Solier was recorded for Mocha Island (38°23’S, 73°52’W) (Flores and Pizarro-Araya 2012).

**Diversity.** This subgenus contains 18 species of which 2 species were recently described (Flores and Pizarro-Araya 2012), increasing 13 percent the number of species (Fig. 33).

**Habitat.** The distribution range of the subgenus extends from sea level to an altitude of ~1300 m. Most species are distributed between the Huasco coastal desert and the coastal shrub steppe (Gajardo 1994), with 4 and 10 species each, and are ecologically related to shrub and herbaceous vegetation (perennial and annual) characteristic of the Chilean Coastal Desert (CCD), in sandy soils or clayey, poorly-permeable soils (Flores and Pizarro-Araya 2012; Cortés-Contreras et al. 2013; collection data FMNH, IADIZA, LEULS, and pers. obs.). One species (*Praocis* (*P.*) *costata* Solier) inhabits deciduous woodlands of *Nothofagus* spp. (Gajardo 1994) in the Valdivian Forest biogeographic province (Morrone 2006) (Fig. 16).

**Species included.** *Praocis rufipes* Eschscholtz, 1829 (= *Sternodes mannerheimi* Fischer, 1844, male, synonymy by Motschulsky 1845) (= *Praocis interrupta* Solier, 1851, synonymy by Kulzer 1958); *Praocis costata* Gay & Solier in Solier, 1840 (= *Praocis ciliata* Germain, 1855, synonymy by Kulzer 1958); *Praocis sanguinolenta* Gay & Solier in Solier, 1840 (= *Praocis audouini* Solier, 1840, synonymy by Flores 2007); *Praocis quadrirunculata* Germain, 1855; *Praocis curta* Solier, 1840 (= *Praocis nigroaenea* Solier, 1840, synonymy by Kulzer 1958) (= *Praocis rugipennis* Germain, 1855, synonymy by Kulzer 1958); *Praocis hirtella* Kulzer, 1958a; *Praocis sulcata* Eschscholtz, 1829 (= *Sternodes mannerheimi* Fischer, 1844, female, synonymy by Motschulsky 1845) (= *Praocis rotundata* Laporte, 1840, synonymy by Flores and Pizarro-Araya 2010); *Praocis subsulcata* Gay & Solier in Solier, 1840; *Praocis spinolai* Gay & Solier in Solier, 1840; *Praocis aenea* Gay & Solier in Solier, 1840; *Praocis parva* Gay & Solier in Solier, 1840; *Praocis tibialis* Gay & Solier in Solier, 1840 (= *Praocis rufitarsis* Gay & Solier in Solier, 1840, synonymy by Flores 2007) (= *Praocis aenipennis* Germain, 1855, synonymy by Kulzer 1958); *Praocis subaenea* Erichson, 1834 (= *Praocis submetallica* Guérin-Méneville, 1834, synonymy by Flores 2007) (= *Praocis laevicosta* Curtis, 1845, synonymy by Kulzer 1958); *Praocis marginata* Germain, 1855; *Praocis elliptica* Philippi & Philippi, 1864 (= *Praocis angustata* Philippi & Philippi, 1864, synonymy by Kulzer 1958).

(2) Subgenus Praocis (Mesopraocis) Flores & Pizarro-Araya, subgen. n.
http://zoobank.org/C6C1EBD7-2CD9-4698-8D8A-A0823A43B03A
Figs 7, 17–18

Type species. Praocis calderana Kulzer, 1958, present designation.

Diagnosis. Clypeus with anterior margin extending beyond to lateral expansion of frons, width of anterior margin not exceeding half the interocular width, clypeal suture as a vertical groove, not covered by frons, clypeus and frons at same level; antennomere 10 wider than long, antennomere 9 of equal length to 10, antennomere 11 of equal length to 10; apical tomentose sensory patches on antennomere 10 in two areas subequal in size, on antennomere 11 on distal third; prosternum with a narrow edge on anterior margin; lateral margin of elytron not defined; ventral surface of profemora with a row of setae on anterior edge, protibiae very explanate.

Distribution. Species of Praocis (Mesopraocis) are endemic to northern Chile and occur from 25°South (Paposo, Antofagasta Region) to 31°South (Caleta Limari, Coquimbo Region) in the biogeographic provinces of Atacama and Coquimbo (Morrone 2006) (Fig. 17).

New records. We present new records for some Pacific islands. We recorded the species Praocis (Mesopraocis) pilula Laporte and Praocis (Mesopraocis) flava Kulzer for Damas (29°13'S, 71°31'W) and Gaviota Islands (29°15'S, 71°28'W) (Alfaro et al. 2009).

Diversity. This subgenus contains 4 species (Kulzer 1958) plus 1 species to be described, 5 species in total, with a 25 percent increase in the number of species (Fig. 33).

Habitat. The distribution range of the subgenus extends from sea level to an altitude of ~1325 m. All Mesopraocis species are associated with coastal dunes stabilized with vegetation or paleodunes in the transitional coastal desert of Chile and have nocturnal habits, remaining during the day under stones or plants (Cortés-Contreras et al. 2013, collection data FMNH, IADIZA, LEULS, MNNC, and pers. obs.) (Fig. 18).

Species included. Praocis pilula Laporte, 1840 (= Coelus hirticollis Solier, 1840, synonymy by Lacordaire 1859); Praocis calderana Kulzer, 1958; Praocis flava Kulzer, 1958; Praocis nitens Kulzer, 1959.

(3) Subgenus Praocis (Postpraocis) Flores & Pizarro-Araya, subgen. n.
http://zoobank.org/2EA923F4-48C6-4DA4-A0C7-A7E3B6714881
Figs 8, 19–20

Type species. Praocis pentachorda Burmeister, 1875, present designation.
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Diagnosis. Clypeus with anterior margin extending beyond to lateral expansion of frons, width of anterior margin not exceeding half the interocular width, clypeal suture as a vertical groove, not covered by frons, clypeus and frons at same level; antennomere

Figures 7–10. Dorsal view of Praocis species. 7 Praocis (Mesopraocis) calderana, paratype 8 Praocis (Postpraocis) pentachorda, lectotype (previously published in Flores 2009, Zootaxa 1985: Fig. 3; copyright Magnolia Press, reproduced with permission) 9 Praocis (Anthrasomus) chevrollatii nigra 10 Praocis (Filotarsus) peltata.
10 wider than long, antennomere 9 longer than antennomere 10, antennomere 11 longer than antennomere 10; apical tomentose sensory patches on antennomere 10 in two areas subequal in size, on antennomere 11 on distal half; prosternum with a narrow edge on anterior margin; lateral margin of elytron well defined; ventral surface of profemora without a row of setae on anterior edge, protibiae not explanate.

**Distribution.** Species of *Praocis* (*Postpraocis*) inhabit central and northern Chile and western and northern Argentina. They occur from 19°South (Termas de Enquela-ga, Colchane, Tarapacá Region, Chile) to 34°South in Chile (Rancagua) and 33°South in Argentina (Mendoza) in the biogeographic provinces of Atacama, Coquimbo, Santiago, Puna, Prepu and Monte (Morrone 2006) (Fig. 19).

**New records.** We present new records of *Praocis* (*Postpraocis*) *pentachord*a Burmeister for the Region Tarapacá of Chile and southern Bolivia and of *Praocis* (*Postpraocis*) *curtisi* Solier for the Pacific islands Damas (29°13'S, 71°31'W), Gaviota (29°15'S, 71°28'W) and Choros (29°15'S, 71°32'W) (Alfaro et al. 2009; Ferrú and Elgueta 2011; collection data).

**Diversity.** This subgenus contains 7 species/subspecies (Kulzer 1958; Flores 2007, 2009) plus 3 species to be described, 10 species in total, with a 43 percent increase in the number of species (Fig. 33).

**Habitat.** Species of *Praocis* (*Postpraocis*) have diurnal habits, remaining during the night under stones or plants. In central Chile they can be observed walking on coastal plains or in sandy places lying from sea level to an altitude of ~1300 m. In Argentina, northern Chile and Bolivia, they occur from 1600 m in high altitudinal valleys associated with the Andes mountain range to an altitude of 4200 m in the high Puna plateau, in sandy soils or clayey, poorly permeable soils (Ferrú and Elgueta 2011; Cortés-Contreras et al. 2013; collection data FMNH, IADIZA, LEULS, and pers. obs.) (Fig. 20).

**Species included.** *Praocis curtisi*i Solier, 1851; *Praocis costatula* Gay & Solier in Solier, 1840 (= *Praocis anguliformis* Philippi & Philippi, 1864, synonymy by Kulzer 1958); *Praocis pubescens* Philippi & Philippi, 1864; *Praocis pentachord*a Burmeister, 1875 (= *Praocis larraini* Marcuzzi, 2001, synonymy by Flores 2009); *Praocis pentachord*a minor Kulzer, 1958; *Praocis aenescens* Kulzer, 1958; *Praocis concinna* Burmeister, 1875.

(4) **Subgenus Praocis (Anthrasomus) Guérin-Méneville, 1834**

Figs 9, 21–22

**Type species.** *Anthrasomus chevrolatii* Guérin-Méneville, 1834, monotypy.

**Diagnosis.** Clypeus with anterior margin extending beyond to lateral expansion of frons, width of anterior margin not exceeding half the interocular width, clypeal suture as a horizontal groove covered by frons, clypeus lower than frons; antennomere 10 wider than long, antennomere 9 longer than antennomere 10, antennomere 11 longer than antennomere 10; apical tomentose sensory patches on antennomere 10 in two areas subequal in size, on antennomere 11 on distal half; prosternum with a narrow edge
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Figures 11–14. Dorsal view of Praocis species. 11 Praocis (Hemipraocis) sellata peninsularis, holotype (reproduced from Flores et al. 2011) 12 Praocis (Praonoda) bicarinata 13 Praocis (Orthogonoderes) ecostata, holotype 14 Praocis (Pracoidea) montana, holotype (previously published in Flores 2009, Zootaxa 1985: Fig. 9; copyright Magnolia Press, reproduced with permission).
on anterior margin; lateral margin of elytron not defined; ventral surface of profemora without a row of setae on anterior edge, protibiae not explanate.

**Distribution.** Species of *Praocis (Anthrasomus)* inhabit central Chile and occur from 28°South (Freirina, Atacama Region) to 33°South (San Fernando, Libertador General Bernardo O’Higgins Region) in the biogeographic provinces of Atacama, Coquimbo, and Santiago (Morrone 2006) (Fig. 21).

**Diversity.** This subgenus contains 5 species/subspecies (Kulzer 1958; Flores 2007) plus 1 species to be described, 6 species in total, with a 20 percent increase in the number of species (Fig. 33).

**Habitat.** Species of *Praocis (Anthrasomus)* have nocturnal habits, remaining during the day under stones or plants in coastal plains, gullies, and transverse valleys in semi-arid Chile. They occur from sea level to an altitude of 2800 m, in stony-clayey, poorly permeable soils (collection data FMNH, IADIZA, LEULS, and pers. obs.) (Fig. 22).


(5) **Subgenus Praocis (Filotarsus)** Gay & Solier in Solier, 1840

Figs 10, 23–24

**Type species.** *Filotarsus tenuicornis* Gay & Solier in Solier, 1840, monotypy and original designation by Solier (1840: 241).

**Diagnosis.** Clypeus with anterior margin extending beyond to lateral expansion of frons or at same level as lateral expansion of frons, width of anterior margin not exceeding half the interocular width or width of anterior margin same as interocular width, clypeal suture as a vertical groove, not covered by frons, clypeus and frons at same level or clypeal suture as a horizontal groove not covered by frons, clypeus lower than frons; antennomere 9 longer than antennomere 10, antennomere 11 longer than antennomere 10; apical tomentose sensory patches on antennomere 10 in a dorsally continuous semicircle, on antennomere 11 on distal half; prosternum with a narrow edge on anterior margin; lateral margin of elytron not defined; ventral surface of profemora without a row of setae on anterior edge, protibiae explanate.

**Distribution.** Species of *Praocis (Filotarsus)* inhabit central and northern Chile, western and northern Argentina, eastern Bolivia and southern Peru. They occur from 12°South (Cuzco, Peru) to 39°South (Neuquén, Argentina) in the biogeographic provinces of Puna, Atacama, Coquimbo, Santiago, Prepuna, Monte, and Central Patagonia (Morrone 2006) (Fig. 23).
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**Figures 15–18.**  
15 Distribution area of the subgenus *Praocis* (*Praocis*)  
16 Punta de Choros (Coquimbo Region, Chile), habitat of *Praocis* (*Praocis*) *spinolai*  
17 Distribution area of the subgenus *Praocis* (*Mesopraocis*)  
18 Chañaral de Aceituno, Huasco (Atacama Region, Chile), habitat of *Praocis* (*Mesopraocis*) *pilula*.

**Diversity.** This subgenus contains 14 species (Kulzer 1958; Flores 2009) plus 6 species to be described, 20 species in total, with a 43 percent increase in the number of species (Fig. 33).

**Habitat.** Species of *Praocis* (*Filotarsus*) have nocturnal habits, remaining during the day under stones or plants. In central Chile they can be observed in gullies and Coastal and Andean mountain ranges from 400 m to an altitude of 2500 m. In Argentina, Bolivia, northern Chile and Peru they occur from 1600 m in high altitudinal valleys associated with the Andes mountain range to an altitude of 5200 m in the high Puna plateau, in clayey, poorly permeable soils (Ferrú and Elgueta 2011; collection data FMNH, IADIZA, LEULS, and pers. obs.) (Fig. 24).
Species included. *Praocis tenuicornis* Gay & Solier in Solier, 1840; *Praocis castanea* Germain, 1855; *Praocis rufilabris* Gay & Solier in Solier, 1840; *Praocis uretai* Kulzer, 1958 (= *Praocis freyi* Marcuzzi, 1977, synonymy by Flores 2009); *Praocis reedi* Kulzer, 1958; *Praocis oblonga* Solier, 1851; *Praocis peltata* Erichson, 1834; *Praocis försteri* Kulzer, 1958; *Praocis obesa* Kulzer, 1958; *Praocis titschacki* Kulzer, 1958; *Praocis brevicornis* Kulzer, 1958; *Praocis weyrauchi* Kulzer, 1958; *Praocis peruana* Fairmaire, 1902; *Praocis grossa* Kulzer, 1958.


Type species. *Praocis sellata* Berg, 1889, present designation.

Diagnosis. Clypeus with anterior margin extending beyond to lateral expansion of frons, width of anterior margin not exceeding half the interocular width, clypeal suture as a horizontal groove not covered by frons, clypeus lower than frons; antennomere 9 longer than antennomere 10, antennomere 11 longer than antennomere 10; apical tomentose sensory patches on antennomere 10 in two areas subequal in size, on antennomere 11 on distal half; prosternum without a narrow edge on anterior margin; lateral margin of elytron well defined; ventral surface of profemora without a row of setae on anterior edge, protibiae explanate.

Distribution. The species of *Praocis* (*Hemipraocis*) occur from central Argentina (southern Mendoza 36°S and coastal Buenos Aires 36°S), to southern Argentina and Chile (northern Magellan Strait 52°S), in the biogeographic provinces of Patagonia, Monte and Pampa (Morrone 2006) (Fig. 25).

New records. We present a new record for the Peninsula Valdés in Argentina (Flores et al. 2011).

Diversity. This subgenus contains 8 species/subspecies (Kulzer 1958; Flores 2007, 2009; Flores et al. 2011) of which 2 subspecies were recently described (Flores et al. 2011), plus 8 species to be described, 16 species in total, with a 167 percent increase in the species number (Fig. 33).

Habitat. Species of *Praocis* (*Hemipraocis*) have diurnal and crepuscular habits, hiding during the night under shrubs, stones or buried in sand. They inhabit the Patagonian steppes and coastal Pampa from sea level to an altitude of 1700 m, in sandy soils or clayey, poorly permeable soils (Flores et al. 2011; collection data FMNH, IADIZA, and pers. obs.) (Fig. 26).

Species included. *Praocis sellata* Berg, 1889; *Praocis sellata bergi* Kulzer, 1958; *Praocis sellata bruchi* Kulzer, 1958 (= *Praocis sellata topali* Kaszab, 1964, synonymy by Flores et al. 2011); *Praocis sellata peninsularis* Flores & Carrara, 2011 (in Flores et al. 2011); *Praocis sellata granulipennis* Flores & Carrara, 2011 (in Flores et al. 2011);
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Praocis fimbriata Burmeister, 1875; Praocis striolicollis Fairmaire, 1883a (= Praocis denseciliata Fairmaire, 1883b, synonymy by Flores 2007) (= Praocis silvestrii Marcuzzi, 2001, synonymy by Flores 2009); Praocis inermis Burmeister, 1875 (= Praocis compacta Fairmaire, 1883b, synonymy by Flores 2007).

Figures 19–22. 19 Distribution area of the subgenus Praocis (Postpraocis) 20 Totoralillo Norte (Coquimbo Region, Chile), habitat of Praocis (Postpraocis) curtisii 21 Distribution area of the subgenus Praocis (Anthrasomus) 22 Socos (Coquimbo Region, Chile), habitat of Praocis (Anthrasomus) chevrolatii subcostata.
Subgenus *Praocis* (*Praonoda*) Flores & Pizarro-Araya, subgen. n.

http://zoobank.org/5D327D83-AAE6-4E40-B7BC-B338ADE4CA09

Figs 12, 27–28

**Type species.** *Praocis bicarinata* Burmeister, 1875, present designation.

**Diagnosis.** Clypeus with anterior margin extending beyond to lateral expansion of frons, width of anterior margin not exceeding half the interocular width, clypeal suture as a horizontal groove not covered by frons, clypeus lower than frons; antennomere 9 longer than antennomere 10, antennomere 11 longer than antennomere 10; apical tomentose sensory patches on antennomere 10 in two areas subequal in size, on antennomere 11 on distal half; prosternum without a narrow edge on anterior margin; lateral margin of elytron well defined; ventral surface of profemora without a row of setae on anterior edge, prothoracic explanate.

**Distribution.** The species of *Praocis* (*Praonoda*) occur from Neuquén and Rio Negro provinces in Argentina (40°S) to northern Tierra del Fuego Island (52°30′S) with the species *Praocis* (*Praonoda*) *bicarinata* as the unique species of *Praocis* inhabiting Tierra del Fuego. They inhabit the biogeographic provinces of Patagonia and Monte (Morrone 2006) (Fig. 27).

**Diversity.** This subgenus contains 2 species (Kulzer 1958) plus 2 species to be described, 4 species in total, with a 100 percent increase in the number of species (Fig. 33).

**Habitat.** Species of *Praocis* (*Praonoda*) have diurnal and crepuscular habits, hiding during the night under shrubs or stones. They inhabit the Patagonian steppes from sea level to an altitude of 1250 m, in sandy soils or clayey, poorly permeable soils (collection data FMNH, IADIZA and pers. obs.) (Fig. 28).

**Species included.** *Praocis bicarinata* Burmeister, 1875 (= *Praocis silphomorpha* Fairmaire, 1883a, synonymy by Berg 1884); *Praocis molinari* Kulzer, 1958.

Subgenus *Praocis* (*Orthognoderes*) Gay & Solier in Solier, 1840

Figs 13, 29–30


**Type species.** *Praocis subreticulata* Gay & Solier in Solier, 1840, present designation.

**Diagnosis.** Clypeus with anterior margin extending beyond to lateral expansion of frons, width of anterior margin not exceeding half the interocular width, clypeal suture as a horizontal groove covered by frons, clypeus lower than frons; antennomere 9 longer than antennomere 10, antennomere 11 shorter than antennomere 10; apical tomentose sensory patches on antennomere 10 in two areas subequal in size, on antennomere 11 on distal third; prosternum without a narrow edge on anterior margin;
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Figures 23–26. 23 Distribution area of the subgenus Praocis (Filotarsus) 24 Uspallata Valley (Mendoza, Argentina), habitat of Praocis (Filotarsus) oblonga 25 Distribution area of the subgenus Praocis (Hemipraocis) 26 Peninsula Valdés (Chubut, Argentina), habitat of Praocis (Hemipraocis) sellata peninsularis.

lateral margin of elytron well defined; ventral surface of profemora without a row of setae on anterior edge, protibiae explanate.

**Distribution.** Species of Praocis (Orthogonoderes) inhabit central and northern Chile, western and northern Argentina, western Bolivia and southern Peru. They occur from 12°South (Cuzco, Peru) to 38°South in Chile (Nahuelbuta) and 39°South in Argentina (Neuquén) in the biogeographic provinces of Puna, Atacama, Coquimbo,
Santiago, Maule, Prepuna, Monte, and Central Patagonia (Morrone 2006). One species (*Praocis (Orthogonoderes) insularis* Kulzer) has been recorded in the Guacolda island in the Pacific Ocean (28°S) (Kulzer 1958; Peña 1966) (Fig. 29).

**New records.** We present a new record of *Praocis argentina* Kulzer for the Atlantic coast in Argentina, the isthmus of Peninsula Valdés, 42°30’S.

**Diversity.** This subgenus contains 23 species (Kulzer 1958; Flores 2007, 2009) plus 10 species to be described, 33 species in total, with a 43 percent increase in the number of species (Fig. 33).

**Habitat.** Species of *Praocis (Orthogonoderes)* have diurnal and crepuscular habits, hiding during the night under shrubs or stones. In central Chile they can be observed in coastal dunes stabilized with vegetation or paleodunes, gullies, coastal plains, transverse valleys and Coastal and Andean mountain ranges from sea level to an altitude of 2700 m. In Argentina, Bolivia, Peru, and northern Chile, they occur from 1600 m high altitudinal valleys associated with the Andes mountain range to an altitude of 4200 m in the high Puna plateau, in sandy soils or in clayey, poorly permeable soils (Cortés-Contreras et al. 2013; collection data FMNH, IADIZA, LEULS, and pers. obs). The only species inhabiting Patagonian steppes, *Praocis (Orthogonoderes) argentina*, is recorded from 1700 m in southern Mendoza to sea level on the Atlantic coast in Argentina (collection data IADIZA, LEULS, and pers. obs.). *Orthogonoderes* is the only subgenus inhabiting both the Pacific and Atlantic coasts of South America (Fig. 30).

**Species included.** *Praocis cribrata* Gay & Solier in Solier, 1840; *Praocis adspersa* Germain, 1855; *Praocis depressicollis* Germain, 1855; *Praocis ecostata* Kulzer, 1958; *Praocis subreticulata* Gay & Solier in Solier, 1840; *Praocis dentipes* Germain, 1855; *Praocis pleuroptera* Gay & Solier in Solier, 1840 (= *Praocis convexa* Germain, 1855, synonymy by Flores 2007); *Praocis plicicollis* Germain, 1855; *Praocis laevicollis* Philippi & Philippi, 1864 (= *Praocis nitidicollis* Philippi & Philippi, 1864, synonymy by Kulzer 1958); *Praocis ebenina* Germain, 1855; *Praocis tibiella* Kulzer, 1958; *Praocis variolosa* Erichson, 1834; *Praocis variolosa laxepunctata* Kulzer, 1958; *Praocis penai* Kulzer, 1958 (incorrect original spelling: peñai, Article 32.5 ICZN 1999); *Praocis chilensis* (Gray, 1832); *Praocis insularis* Kulzer, 1958; *Praocis tibiella* Kulzer, 1958; *Praocis argentina* Kulzer, 1962; *Praocis magnoi* Molinari, 1969.

(9) **Subgenus Praocis (Praocida) Flores & Pizarro-Araya, subgen. n.**
http://zoobank.org/4B6EC138-1D93-4567-BB66-E3A6B1FC4593
Figs 14, 31–32

**Type species.** *Praocis zischkai* Kulzer, 1958, present designation.
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Figures 27–30. 27 Distribution area of the subgenus *Praocis* (*Praonoda*) 28 Southern Santa Cruz (Argentina), habitat of *Praocis* (*Praonoda*) *bicarinata* 29 Distribution area of the subgenus *Praocis* (*Orthogonoderes*) 30 Choros Bajos, (Coquimbo Region, Chile), habitat of *Praocis* (*Orthogonoderes*) *chilensis*.

**Diagnosis.** Clypeus with anterior margin extending beyond to lateral expansion of frons, width of anterior margin not exceeding half the interocular width, clypeal suture as a horizontal groove not covered by frons, clypeus lower than frons; antennomere 9 longer than antennomere 10, antennomere 11 longer than antennomere 10; apical tomentose sensory patches on antennomere 10 in two areas subequal in size, on antennomere 11 on distal third; prosternum without a narrow edge on anterior margin;
lateral margin of elytron well defined; ventral surface of profemora without a row of setae on anterior edge, protibiae explanate.

**Distribution.** Species of *Praocis* (*Praocida*) inhabit southern Peru, central and southern Bolivia and northern Argentina. They occur from 12°South (Cuzco, Peru) to 31°South in Cordoba (northern Argentina), in the biogeographic provinces of Puna, Chaco, and Pampa (Morrone 2006) (Fig. 31). *Praocida* is the only subgenus of *Praocis* inhabiting the biogeographic province of Chaco.

**New records.** We present a new record of *Praocis* (*Praocida*) *teniucosta* Kulzer for the mountains in South Buenos Aires province (38°S).

**Diversity.** This subgenus contains 4 species (Kulzer 1958; Flores 2009) plus 3 species to be described, 7 species in total, with a 75 percent increase in number of species (Fig. 33).

**Habitat.** Species of *Praocis* (*Praocida*) have nocturnal habits, hiding during the day under shrubs, stones or logs in clayey, poorly permeable soils. They occur from 1200 m in the Chacoan forest to an altitude of 4000 m in Puna (collection data FMNH, IADIZA and pers. obs.) (Fig. 32).

**Species included.** *Praocis tenuicosta* Kulzer, 1958; *Praocis zischkai* Kulzer, 1958; *Praocis kuscheli* Kulzer, 1958; *Praocis montana* Kulzer, 1958 (= *Praocis baloghi* Marczuzi, 2001, synonymy by Flores 2009).

**Species of *Praocis incertae sedis.** *Praocis pentagona* Lacordaire, 1830; *Praocis squalida* Lacordaire, 1830; *Praocis silphoides* Lacordaire, 1830; *Praocis spinipes* Laporte, 1840; *Praocis hirticollis* Laporte, 1840. Type material belonging to these five species is missing (Kulzer 1958; Flores and Pizarro-Araya 2010) and the original descriptions do not provide information for the subgeneric assignment.
Figure 33. Diversity of the subgenera of *Praocis*. Current number of species (dotted); number of species to be described or recently described (grey) and percentage of increasing of species for each subgenus (black).
Key to the subgenera of *Praocis*

1. Anterior margin of prosternum with a narrow, sharp edge .................. 2
   – Anterior margin of prosternum rounded, smooth, lacking edge .......... 6

2. Lateral margin of elytron well defined by a sharp edge carina-shaped, narrow or broad (Figs 2, 8), dorsal area of elytron well differentiated from pseudopleuron .................................................. 3
   – Lateral margin of elytron not defined, rounded (Figs 7, 9–10), surface continuous between dorsal area of elytron and pseudopleuron .................. 4

3. Apical tomentose sensory patches on antenomemore 10 arranged in a dorsally continuous semicircle (Fig. 3); ventral surface of profemora with a row of setae on anterior edge (Fig. 2) ............................................. *Praocis* Eschscholtz
   – Apical tomentose sensory patches on antenomemore 10 arranged in two areas subequal in size (Fig. 4); ventral surface of profemora lacking a row of setae on anterior edge (Fig. 8) .......................... *Postpraocis* Flores & Pizarro-Araya

4. Antennae very short, reaching only 1/4 of lateral margin of pronotum; antennomere 9 equal length as antenomemore 10; antenomemore 11 equal length as antenomemore 10; apical tomentose sensory patches on antenomemore 11 on distal third (Fig. 4); ventral surface of profemora with a row of setae on anterior edge (Fig. 7) .......................... *Mesopraocis* Flores & Pizarro-Araya
   – Antennae long, reaching or surpassing the midpoint of lateral margin of pronotum; antenomere 9 longer than antenomemore 10 (Fig. 3); antenomemore 11 longer than antenomemore 10 (Fig. 3); apical tomentose sensory patches on antenomemore 11 on distal half (Fig. 3); ventral surface of profemora lacking a row of setae on anterior edge .............................................

5. Apical tomentose sensory patches on antenomemore 10 arranged in two areas subequal in size (Fig. 4); dorsal area of elytron with 2 to 5 carinae; protibiae not explanate (Fig. 9) .................................. *Anthrasomus* Guérin-Méneville
   – Apical tomentose sensory patches on antenomemore 10 arranged in a dorsally continuous semicircle (Fig. 3); dorsal area of elytron lacking carinae; protibiae explanate (Fig. 10) .................................. *Filotarsus* Gay & Solier

6. Apical tomentose sensory patches on antenomemore 11 on distal half (Fig. 3) .... 7
   – Apical tomentose sensory patches on antenomemore 11 on distal third (Fig. 4) .... 8

7. Body spherical, wide, rounded seen from above; lateral margin of elytra as a wide, prominent edge; lateral margin of pronotum with a row of long, black or golden setae (Fig. 11) .......................... *Hemipraocis* Flores & Pizarro-Araya
   – Body elongate, narrow, subparallel seen from above, lateral margin of elytra as sharp edge carina-shaped; lateral margin of pronotum lacking a row of setae (Fig. 12) .......................... *Praonoda* Flores & Pizarro-Araya

8. Antennomere 11 shorter than antenomemore 10; clypeal suture as a horizontal groove covered by frons (Figs 4, 13) .......................... *Orthogonoderes* Gay & Solier
   – Antennomere 11 longer than antenomemore 10; clypeal suture as a horizontal groove not covered by frons (Figs 3, 14) .......................... *Praocida* Flores & Pizarro-Araya
Discussion

Estimation of the diversity of the whole genus

_Praocis_ currently contains 77 species and 8 subspecies (Flores and Pizarro-Araya 2012) arranged in 9 subgenera (Fig. 33). Taking into account the 34 currently undescribed species, the genus will have 119 species/subspecies (Fig. 33), with a 47 percent increase in the number of species in the entire genus. All these undescribed species fall within the present generic concept of _Praocis_. An assessment of the subgeneric characters presented herein among these species to be described show a preliminary affiliation as detailed in Fig. 33. Three species that did not fit in any generic concept of Praociini or subgeneric concept of _Praocis_ were recently described in a new genus, *Patagonopraocis* (Flores and Chani-Posse 2005).

Character states

A table was made with the character states used in the diagnoses (Table 1). This table summarizes the distribution of character states among the subgenera. It can be observed that each subgenus can be defined by a particular combination of these characters, stated in each diagnosis. For the characters here named 1-3, different species of *Filotarsus* present both the states found for each character, which are constant and well defined in all the species of the other subgenera, suggesting that in *Filotarsus* there are at least two groups of species which will be elucidated further by examining all the species of the subgenus and conducting a cladistic analysis of the group.

Some character states appear as unique for some subgenera such as antennomere 11 of equal length to 10 in *Mesopraocis* and antennomere 11 shorter than antennomere 10 in *Orthogonoderes*. One third of the characters analysed here are from the antennae, suggesting the importance of studying the length and proportion of antennomeres 9, 10 and 11 and the arrangement of the apical tomentose sensory patches on antennomeres 9, 10 and 11. Using these character states, we presented a preliminary identification key for the subgenera of _Praocis_.

Biogeography

The distribution of the whole genus _Praocis_ is related to the arrangement of the Andes mountain range in southern South America. The Andes are the only high mountain chain in the continent, running along the Pacific coast of South America from Venezuela down South to Tierra del Fuego, extending over 8500 km and separating xeric habitats both eastward and westward (Flores and Pizarro-Araya 2006). Among the genera of Pimeliinae, the distributional patterns of the nine subgenera of _Praocis_ were analysed in relation to the Andes mountain range. We found three distribution
Table 1. Characters studied and distribution of character states among the subgenera of *Praocis*.

<table>
<thead>
<tr>
<th>Characters</th>
<th>Character states</th>
<th>Subgenera</th>
</tr>
</thead>
<tbody>
<tr>
<td>1) Clypeus, anterior margin</td>
<td>A) extending beyond to lateral expansion of frons</td>
<td><em>Praocis s. str.</em></td>
</tr>
<tr>
<td></td>
<td>B) at same level as lateral expansion of frons</td>
<td>x</td>
</tr>
<tr>
<td>2) Clypeus, width of anterior margin</td>
<td>A) not exceeding half the interocular width</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>B) same width as interocular distance</td>
<td>x</td>
</tr>
<tr>
<td>3) Clypeal suture</td>
<td>A) as horizontal groove</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>B) as vertical groove</td>
<td>x</td>
</tr>
<tr>
<td>4) Antennomere 9</td>
<td>A) longer than antennomere 10</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>B) equal in length to antennomere 10</td>
<td>x</td>
</tr>
<tr>
<td>5) Antennomere 11</td>
<td>A) Longer than antennomere 10</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>B) shorter than antennomere 10</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>C) equal in length to antennomere 10</td>
<td>x</td>
</tr>
<tr>
<td>6) Apical tomentose sensory patches on antennomere 10</td>
<td>A) in two areas subequal in size</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>B) in a dorsally continuous semicircle</td>
<td>x</td>
</tr>
<tr>
<td>7) Apical tomentose sensory patches on antennomere 11</td>
<td>A) on distal third</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>B) on distal half</td>
<td>x</td>
</tr>
<tr>
<td>8) Prosternum</td>
<td>A) with a narrow edge on anterior margin</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>B) without edge on anterior margin</td>
<td>x</td>
</tr>
<tr>
<td>9) Lateral margin of elytron</td>
<td>A) well defined</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>B) not defined</td>
<td>x</td>
</tr>
<tr>
<td>10) Ventral surface of profemora</td>
<td>A) with a row of setae on anterior edge</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>B) without a row of setae on anterior edge</td>
<td>x</td>
</tr>
<tr>
<td>11) Protibiae</td>
<td>A) explanate</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>B) not explanate</td>
<td>x</td>
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</table>
Towards a revision of the South American genus Praocis Eschscholtz...

patterns: three endemic subgenera west of the Andes, in central and northern Chile, Praocis, Mesopraocis and Anthrasomus (Figs 15, 17, 21); three endemic subgenera east of the Andes, in Patagonian steppes, Monte, Chaco and eastern Puna (Argentina, Bolivia and Peru), Hemipraocis, Praonoda and Praocida (Figs 25, 27, 31); and three subgenera widely distributed on both sides of the Andes and inhabiting also high altitudes of the Andes, Postpraocis, Filotarsus and Orthogonoderes (Figs 19, 23, 29). Based on these distribution patterns, and despite the current lack of a phylogeny for the genus, we can hypothesize that the ancestor of all Praocis species was older than the uplift of these mountains and the distribution of the species of six current subgenera was affected by a vicariant event caused by the uplift of the Andes. This vicariant event, which was analyzed in known phylogenies of tribes and genera of Pimeliinae in South America, left genera and species both east and west of the Andes (Flores and Pizarro-Araya 2006).

Acknowledgements

We gratefully acknowledge to the organizers of the Third International Symposium on Tenebrionoida 2013 (Arizona, USA) for the invitation to write this paper presented at the meeting; to the curators for the loan of material: Margaret Thayer, James Boone (FMNH), Sergio Roig-Jüñent (IADIZA), Jorge Cepeda-Pizarro (LEULS), Arturo Roig-Alsina (MACN), Analía A. Lanteri, Nora Cabrera (MLPA), Claude Girard, Antoine Mantilleri (MNHN), Manfred Uhlig, Bernd Jaeger (MNHUB), Mario Elgueta D. (MNNC) and Eva Sprecher (NHMB); Margaret Thayer and Alfred Newton for their hospitality during the visit of GEF to FMNH; Nelly Horak for correction of the English language; Mariana Chani Posse and Aaron Smith for suggestions improving the manuscript; Remedios Marin for help with the artwork; two anonymous reviewers for suggestions for improving this paper and Patrice Bouchard (Editor) for his advise on nomenclatural questions. This study was supported by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, Argentina), by a grant PIP 112-201101-00987 (CONICET, Argentina) (GEF) and DIULS-PR13121-VACDDI001 from DIULS (Universidad de La Serena) (JPA).

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Towards a revision of the South American genus Praocis Eschscholtz...


A cladistically based reinterpretation of the taxonomy of two Afrotropical tenebrionid genera *Ectateus* Koch, 1956 and *Selinus* Mulsant & Rey, 1853 (Coleoptera, Tenebrionidae, Platynotina)

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Academic editor: P. Bouchard | Received 7 October 2013 | Accepted 12 December 2013 | Published 12 June 2014


Abstract

On the basis of a newly performed cladistic analysis a new classification of the representatives of two Afrotropical tenebrionid genera, *Ectateus* Koch, 1956 and *Selinus* Mulsant & Rey, 1853 sensu Iwan 2002a, is provided. *Eleoselinus* is described as a new genus. The genus *Monodius*, previously synonymized with *Selinus* by Iwan (2002), is redescribed and considered as a separate genus. Following new combinations are proposed: *Ectateus calcaripes* (Gebien, 1904), *Monodius laevisstriatus* (Fairmaire, 1897), *Monodius lamottei* (Gridelli, 1954), *Monodius plicicollis* (Fairmaire, 1897), *Eleoselinus villiersi* (Ardoin, 1965) and *Eleoselinus ursynowiensis* (Kamiński, 2011). Neotype for *Ectateus calcaripes* and lectotypes for *E. crenatus* (Fairmaire, 1897), *E. ghesquierei* Koch, 1956 and *Monodius malaisei malaisei* Koch, 1956 are designated to fix the taxonomic status of these taxa. The following synonymies are proposed: *Selinus monardi* Kaszab, 1951 and *Ectateus latipennis* Koch, 1956 with *E. crenatus* (Fairmaire, 1897). Identification keys are provided to all known species of *Ectateus sensu novum*, *Eleoselinus*, *Monodius* and *Selinus sensu novum*.

Keywords

Africa, ecoregions, cladistics, identification key, new genus, taxonomy, Pedinini
Introduction

Pursuant to the classification of the family Tenebrionidae presented by Bouchard et al. (2005, 2011) Platynotina Mulsant & Rey, 1853 is one of the eight subtribes within the tribe Pedinini Eschscholtz, 1829. At present Platynotina consists of over 60 genera distributed in Afrotropical, Indomalayan, Nearctic and Neotropical realms (Iwan 2002b; Kamiński 2013c; Kamiński and Raś 2012).

According to the results of a cladystic analysis performed by Iwan (2002a), Ectateus Koch, 1956 and Selinus Mulsant & Rey, 1853 are the members of the platynotoid evolutionary lineage within the subtribe Platynotina Mulsant & Rey, 1853. The representatives of both genera are distributed in the western parts of Central Africa (Iwan 2004a).

The current taxonomic concept of the genus Ectateus was proposed by Iwan (2002a) and modified by Kamiński and Raś (2011) to: circular depressions on the lateral sides of clypeus and genae, pronotum with anterior angles distinctly protruding anteriorly, elytral humeri not protruding outwards, apical part of epipleuron and fifth ventrite unbordered. The taxonomic concept of Selinus was also established by Iwan (2002a) and is as follows: upper edge of elytral base fused with humerus, anterior pronotal angles distinctly protruding anteriad, short metasternum and bursa copulatrix with two sacs. Unfortunately both of the above mentioned taxonomic concepts were based only on a few representatives of their genera. The preliminary study of the entomological material has shown that some of the representatives of Ectateus shares many morphological characters and distributional pattern with certain species of the Selinus and vice versa.

According to the results of a cladistic analysis performed by Iwan (2002a) Ectateus and Selinus are members of two sister clades. In the key to the genera of World Platynotina they are distinguished by the structure of 5th abdominal ventrite (Selinus – with bordering or border interrupted; Ectateus – without bordering) (Iwan 2002a). Unfortunately, this feature is no longer relevant which may easily lead to misidentification (five of seven species of Selinus do not match this character). Additionally, Ectateus and Selinus shares some unique (within whole subtribe) morphological features (e.g. slender antennomeres, specific clavae structure) and similar distributional pattern (Iwan 2002a, 2002b, Kamiński and Raś 2011). All this suggests that both of the mentioned genera can be more closely related than it was implied by Iwan (2002a).

The aim of this paper was to test the monophyly of Ectateus and Selinus and propose a stable classification for the representatives of these genera.

Material and methods

Morphological studies. The descriptive sequence used in this study is in accordance with Kamiński (2013b). Morphological terms follow Matthews et al. (2010); with additional specialized terms used for the male (Iwan 2001b, 2004b) and female genitalia (Banaszkiewicz 2006).
Measurements, taken using a filar micrometer, were as follows: width of anterior elytral margin (from humeral angle to scutellum); body length (from anterior margin of labrum to elytral apex); body width (maximum elytral width).

For examination of internal structures, specimens were dissected and whole abdomens were cleared in 10% cold potassium hydroxide overnight (Iwan 2000).

Images were taken using a Canon 1000D body with accordion bellows and Industar 61L/3 MC 50 mm f/2.8 lens, and with a Hitachi S-3400N SEM in MIIZ. Chosen SEM photographs were colored using Photoshop CS5.

**Entomological material.** This study was based on the material from the following collections:

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<thead>
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<th>Code</th>
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<td>BMNH</td>
<td>Natural History Museum, London, Great Britain</td>
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<td>JFCS</td>
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<td>Muséum d’histoire naturelle de la Ville de Genève, Geneva, Switzerland</td>
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<td>MIIZ</td>
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<td>MRAC</td>
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<td>ZMAS</td>
<td>Zoological Museum, Academy of Sciences, Sankt Petersburg, Russia</td>
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**Phylogenetic analysis.** Based on the results of a comparative analysis of the morphology of available material, including the type specimens, I propose a following synonymy: Selinus monardi Kaszab, 1951 and Ectateus latipennis Koch, 1956 with Ectateus crenatus (Fairmaire, 1897). Also, I disagree with the synonymy of Selinus calcaripes Gebien, 1904 with Ectateus curtulus (Fairmaire, 1893) proposed by Koch (1956) and I propose to treat this taxon as an independent species – not as a synonym of E. curtulus. For detailed information see the descriptions of these taxa included in the results section of this publication.

The operational taxonomic units (OTUs) representing the genus Ectateus consists of all (8) known species (considering above mentioned nomenclatural acts): E. crenatus (Fairmaire, 1897), E. curtulus (Fairmaire, 1893), E. ghesquierei Koch, 1956, E. laevistriatus (Fairmaire, 1897), E. lamottei (Gridelli, 1954), E. modestus (Fairmaire, 1887), E. ursynowiensis Kamiński, 2011 and E. villiersi Ardon, 1965. Also, all (7) known species of Selinus were included in the phylogenetic analysis: S. convexipennis Gebien, 1904, S. gravis Koch, 1956, S. malaisei Koch, 1956, S. medius Fairmaire,
1897, *S. planus* (Fabricius, 1792), *S. plicicollis* Fairmaire, 1897 and *S. striatus* (Fabricius, 1794). The above mentioned taxa form the ingroup. *Zidalus latipes* (Sahlberg, 1823) was used as the most distant outgroup on which the character polarization process was performed. According to Iwan’s (2002a) hypothesis the genus *Zidalus* Mulsant & Rey, 1853 is a sister clade to all afrotropical platynotoid genera.

*Lechius abacoides* (Fairmaire, 1902), *Pseudoselinus punctatostriatius* (Gerstaecker, 1854), *Upembarus upembaensis* Koch, 1956 were used to test the monophyly of the clade *Ectateus*+*Selinus*. According to the results of Iwan’s (2002a) cladistic analysis the genus *Lechius* Iwan, 1995 together with *Pseudoselinus* Iwan, 2002 and *Upembarus* Koch, 1956 form a sister clade to the *Ectateus* generic group (which includes *Ectateus* and *Selinus*). This hypothesis was supported by more recent studies (Iwan and Kamiński 2012, Kamiński 2012, Raś and Kamiński 2013).

The data matrix originated in Mesquite (Maddison and Maddison 2011). Parsimony analysis was conducted under equal weights in TNT (Goloboff et al. 2003). Most parsimonious tree was obtained by the “Implicit enumeration”. Jackknife support (absolute frequencies) was calculated with 36 removal probability using 2000 replicates. Consistency index (CI) and retention index (RI) were used to assess the fit of data to the cladograms (Farris 1989). The results were illustrated using WinClada (Nixon 2002).

**Species distribution.** The distribution of species was illustrated using DIVA-GIS version 7.5 (Hijmans et al. 2012). The raster layer used in Figs 41–44 was downloaded from naturalearthdata.com (“Made with Natural Earth. Free vector and raster map data”). The division of Afrotropical Realm into ecoregions was adopted after Olson et al. (2001).

**Results**

**Character matrix.** A matrix of 40 characters was constructed for 20 operational taxonomic units (Table 1). Characters used for phylogenetic analyses have been treated as unordered. The missing data for *Ectateus curtulus* are caused by the fact that this species is only known from one specimen (holotype, female). The character states are presented in this section.

**Head (characters 1–7)**
1. Antenna: (0) slender, longer than pronotum; (1) robust, shorter than pronotum.
2. Antennomeres from 7 to 11: (0) widened, their width greater than the length; (1) elongated, their length greater than the width (Fig. 3).
3. Circular depressions on the lateral sides of clypeus and genae: (0) absent (Fig. 1); (1) present (Fig. 2).
4. Fronto-clypeal suture: (0) fine (Fig. 1); (1) coarse, clearly visible (Fig. 2).
5. Indentation between frons and clypeus on the lateral edge: (0) shallow (Fig. 1); (1) deep (Fig. 2).
6. Anterior tentorial pit: (0) shallow; (1) deep, clearly visible (Fig. 4).
7. Anterior part of mentum: (0) not elongated; (1) elongated.
Table 1. Character matrix for the cladistic analysis of the species of *Ectateus* and *Selinus* (sensu Iwan 2002a), with selected outgroup taxa: *Z. latipes*, *L. abacoides*, *P. punctatostriatus*, *U. upembaensis* (see also text).

<table>
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<th>6</th>
<th>11</th>
<th>16</th>
<th>21</th>
<th>26</th>
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<tr>
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</table>

**Prothorax** (characters 8–18)

8. Anterior pronotal angles: (0) straight; (1) curved outwards (Fig. 5).
9. Lateral pronotal sides: (0) rounded; (1) sinusoidal (Fig. 5).
10. Pronotum: (0) widest at the middle (Fig. 5); (1) widest at the base (Fig. 6).
11. Pronotal margins: (0) not erected upwards; (1) strongly erected upwards (Raš and Kamiński 2013, Kamiński 2013c).
12. Ratio of prothorax width (tw) and pronotal disc height (dh): (0) < 5; (1) > 6 (Raš and Kamiński 2013, Kamiński 2013c).
13. Apophyseal depressions: (0) absent; (1) trapezoidal (Fig. 6); (2) rounded (Fig. 5).
14. Pronotal base: (0) the same width as elytral base; (1) narrower than elytral base.
15. Posterior pronotal angles: (0) not protruding towards elytra; (1) strongly protruding towards elytra.
16. Punctures on pronotal disc: (0) fine, the intervals between the punctures are greater than the 2 diameters of the puncture; (1) coarse, the intervals between the punctures are smaller than the diameter of the puncture.
17. Intercoxal process of prosternum: (0) flat or dented (Fig. 12); (1) bellied (Kamiński and Raš 2011: 650).
18. Intercoxal process of prosternum: (0) not widened at the apex; (1) strongly widened at the apex.
Mesothorax (characters 19–24)
19. Scutellum: (0) situated at the level of elytra; (1) impressed.
20. Elytral surface: (0) dull; (1) shiny.
21. Elytral intervals with transverse sculpture: (0) no; (1) yes (Fig. 8, 27).
22. Elytral intervals: flat (0); strongly convex (1).
23. Elytral striae: (0) impressed on whole length, with fine punctures (Fig. 9); (1) im-
pressed mainly near conspicuous punctures (Fig. 8).
24. Margins of elytra in basal part: (0) rounded; (1) subparallel (elytral humeri slightly
protruding outwards).

Metathorax (character 25)
25. Metaventrite: (0) without a coarse longitudinal depression; (1) with a coarse lon-
gitudinal depression.

Abdomen (characters 26–27)
26. 5th abdominal ventrite: (0) relatively narrow; (1) strongly widened (Fig. 10).
27. 5th abdominal ventrite: (0) unbordered (Fig. 10); (1) bordered (Fig. 11).

Legs (character 28–31)
28. Male protarsi widened: (0) no; (1) yes (Fig. 13).
29. Female protarsi widened: (0) no; (1) yes.
30. Male profemora (0) relatively wide (length/width = 3.2-3.6); (1) relatively slender
(length/width = 4.0-5.6).
31. Denticle at the apex of the inner face of male mesotibia: (0) small, sometimes ab-
sent; (1) large (Fig. 7).

Male and female genitalia (character 32–39)
32. Penis wide: (0) no (Figs 20-21); (1) yes, at least 4 times wider than clavae (Figs 14–19).
33. Clavae: (0) straight (Figs 14-19, 21); (1) curved, hook-shaped (Fig. 20).
34. Clavae: (0) short, their length less than half of the length of parameres; long, their
length more than half of the length of parameres (1).
35. Parameres strongly extended apically: (0) no; (1) yes (Fig. 18).
36. Parameres narrowest in the half of their length (0) no; (1) yes (Fig. 20).
37. Apex of parameres: (0) not fused (Fig. 20); (1) fused, not emarginated at apex (Figs
14, 16); (2) fused, emarginated at apex (Figs 15, 17).
38. Bursa copulatrix: (0) without additional sacs; (1) with 2 additional sacs (Fig. 23).
39. Paraproct longer than coxites: (0) no (Fig. 22); (1) yes.

Other (character 40)
40. Body size: (0) more than 10.0 mm; (1) less than 9.0 mm.

Phylogenetic analysis. The cladistic analysis yield a single most parsimonious
cladogram (Fig. 25) with a length of 57 steps, a consistency index (CI) of 74 and a re-
tention index (RI) of 90. According to the obtained cladogram the genera *Ectateus* and *Selinus*, in their current interpretations, are paraphyletic (Fig. 25). The *Ectateus* clade is supported by two synapomorphies: male protibia slender (length/width = 4.0-5.6) (char. 30:1) and clavae curved, hook-shaped (char. 33:1). Also one homoplasy was recovered for this clade – male protarsi relatively narrow (char. 28:0). The *Selinus* clade is supported by single synapomorphy – clavae long, their length more than half of the length of parameres (char. 34:1) – and two homoplasies: antennomeres from 7 to 11 elongated (their length greater than the width), anterior tentorial pit deep, clearly visible (char. 2:1, 6:1). The monophyly of the *Ectateus+Selinus* clade was supported during the analysis by the following two synapomorphies: ratio of prothorax width (tw) and pronotal disc height (dh) greater than 5 (char. 12: 0) and apophyseal depressions on pronotal disc present (char. 13:1).

Two main species groups were recovered within the *Ectateus* clade – *modestus* group and *villiersi* group. The branch support reported for these groups was relatively high (Fig. 25). The phylogenetic relationships within the *modestus* group were supported unequally. Relatively low Jackknife values were reported within the clade composed of *E. modestus*, *S. calcaripes*, *E. ghesquierei* and *E. crenatus*.

According to the results of a cladistic analysis the *modestus* group is characterized by following synapomorphies: fronto-clypeal suture coarse, clearly visible (char. 4:1), anterior pronotal angles curved outwards (char. 8:1), pronotal margins strongly erected upwards (char. 11:1), apophyseal depressions rounded (char. 13:2), pronotal base narrower than elytral base (char. 14:1), scutellum impressed (char. 19:1) and elytral intervals with transverse sculpture (char. 21:1). Additionally, one homoplasy was recovered: posterior pronotal angles strongly protruding towards elytra (char. 15:1).

Despite the fact that the species aggregated in the *modestus* group (Fig. 25) are homogeneous in their morphology the cladistic analysis revealed some species groups. According to the results *E. curtulus* is a sister taxon to all other *modestus* group species. This relationship is supported highly supported (Jackknife support = 91; char. 3:1, 6:1, 9:1). Unfortunately, *E. curtulus* is known only form a single specimen (holotype, female), therefore the above mentioned phylogenetic hypothesis should be reconsidered once the male specimen will be found.

The four remaining species occurred in two separate clades (Fig. 25). The first clade which consists of *E. ghesquierei* and *E. crenatus* is defined by the following synapomorphies: convex elytral intervals (char. 22:1) and a small body size (char. 40:1). The other clade composed of *E. modestus* and *E. calcaripes* comb. n. is only supported by a single homoplasy - antennomeres from 7 to 11 elongated (char. 2:1). However, these two species are very similar in general morphology – the females are almost impossible to separate or distinguish (Figs 45, 49).

According to the results of a cladistic analysis the *villiersi* group is characterized by following synapomorphies: anntenna robust, shorter than pronotum (char. 1:1), intercoxal process of prosternum bellied (char. 17:1) and metaventrite with coarse longitudinal depression (char. 25: 1).
Taking into consideration other significant morphological differences between modestus and villiersi groups (char. 1, 4, 8, 11, 13–15, 17, 19, 21, 25) it is reasonable to treat them as two separate genera.

Two main highly supported species group were recovered within the Selinus clade – convexipennis group and planus group (Fig. 25). The first group contains the type species (convexipennis) of Monodius Koch, 1956 (genus synonymized with Selina by Iwan in 2002a).

According to the results of a cladistic analysis the convexipennis group is characterized by following synapomorphies: 5th abdominal ventrite strongly widened (char. 26:1), female protarsi widened (char. 29:1), penis wide, at least 4 times wider than clavae (char. 32:1), apex of parameres fused (char. 37:1) and bursa copulatrix with 2 additional sacs (char. 38:1).

S. gravis occurred as a sister taxon to all other convexipennis group species, however this relationship is not highly supported (Fig. 25). The remaining species of the above mentioned group were divided into two separate clades (Fig. 25). The first one which consists of S. malisei, S. medius and S. plicicollis is defined by the following synapomorphies: margins of elytra in basal part subparallel (elytral humeri slightly protruding outwards) (char. 24:1), denticle at the apex of the inner face of male mesotibia large (char. 31:1), apex of parameres fused and emarginated at apex (char. 37:2). This clade is also supported by a single homoplasy – elytral surface shiny (char. 20:0). The second clade (S. convexipennis, S. laevistriatus and S. lamottei) is defined by two homoplasies: indentation between frons and clypeus on the lateral edge deep (char. 5:1) and posterior pronotal angles strongly protruding towards elytra (char. 15:1).

According to the results of a cladistic analysis the planus group is characterized by a following synapomorphy: paraproct longer than coxites (char. 39:1). Additionally, two homoplasies were recovered: pronotum widest at the base (char. 10:1) and 5th abdominal ventrite bordered (char. 27:1).

Because of significant morphological differences between convexipennis group and planus group, especially the ones concerning the male (char. 32, 37) and female genitalia (char. 38, 39), I propose to consider them as two separate genera.

On the basis of the aforementioned results I propose to classify the analyzed ingroup species in four genera: Ectateus (based on modestus group), Monodius stat. r. (based on convexipennis group), Eleoselinus gen. n. (based on villiersi group) and Selinus (based on planus group).

A new classification and diagnostic characters of the analyzed ingroups species are presented below.

Genus Ectateus Koch, 1956
http://species-id.net/wiki/Ectateus

Type species. *Anchophthalmus modestus* Fairmaire, 1887; by original designation.

**Diagnosis.** The following character combination is unique for *Ectateus* within the whole subtribe Platynotina: (1) fronto-clypeal suture coarse, clearly visible, (2) anterior pronotal angles curved outwards, (3) pronotal margins strongly erected upwards, (4) apophyseal depressions rounded, (5) pronotal base narrower than elytral base, (6) posterior pronotal angles strongly protruding towards elytra, (7) scutellum impressed, (8) elytral intervals with transverse sculpture (9) male protarsi relatively narrow, (10) male protibiae slender (length/width = 4.0–5.6) and (11) clavae curved, hook-shaped.

**Distribution.** *Ectateus* specimens have been collected in the following ecoregions of Central Africa (Cameroon, Central African Republic, Democratic Republic of the Congo, Equatorial Guinea, Gabonese Republic, Republic of Rwanda, Republic of the Congo, South Sudan): Albertine Rift montane forests, Angolan Miombo woodlands, Atlantic Equatorial coastal forests, East Sudanian savanna, Mount Cameroon and Bioko montane forests, Northeastern Congolian lowland forests, Northwestern Congolian lowland forests, Northern Congolian forest-savanna mosaic, Southern Congolian forest-savanna mosaic, Western Congolian forest-savanna mosaic (Fig. 41).

**Species included (5).** *Ectateus calcaripes* (Gebien, 1904), comb. n., *E. crenatus* (Fairmaire, 1897), *E. curtulus* (Fairmaire, 1893), *E. ghesquierei* Koch, 1956 and *E. modestus* (Fairmaire, 1887).

**Key to the species of Ectateus**

1. Clypeus and genae without depressions. Pronotal margins rounded. Elytral intervals with conspicuous punctures.........................*Ectateus curtulus*
   – Circular depressions on the lateral sides of clypeus and genae (Fig. 2). Pronotal margins sinusoidal (Fig. 5). Elytral intervals without punctures or punctures very fine (Fig. 8, 27) ...........................................................................2

2. Body size: 7.0–9.0 mm. Antennomeres form 7 to 11 transverse. Elytral striae with deep punctures; intervals convex (Fig. 8). ..................................................2
   – Body size: 11.5–14.0 mm. Antennomeres form 7 to 11 elongated. Elytral striae with superficial punctures; intervals flat (Fig. 27) ..............................................3

3. Pronotal disc with a longitudinal groove in the middle (Fig. 5). Male protibiae as in Fig. 33; mesofemorae simple .........................*Ectateus ghesquierei*
   – Pronotal disc without longitudinal groove. Male protibiae as in Fig. 34; mesofemorae with a large denticle on the posterior face (Fig. 35) ............

4. Intercoxal process protruding towards mesoventrite; peaked at the apex. Male protibiae as in Fig. 31 ..................................................*Ectateus calcaripes*
   – Intercoxal process not protruding towards mesoventrite; rounded at the apex. Male protibiae as in Fig. 32 ..................................................*Ectateus modestus*
Ectateus calcaripes (Gebien, 1904), comb. n.
http://species-id.net/wiki/Ectateus_calcaripes
Figs 3, 20, 27, 31, 41, 45


Notes. The types of Selinus calcaripes seems to be lost. According to the information provided by Iwan (2002b) they should be deposited in Naturhistorisches Museum collection (Basel, Switzerland). Unfortunately, the curators do not confirm this statement. Additionally, during the preparation of my recent scientific project – Phylogeny, biogeography and generic classification of the Ectateus generic group (Coleoptera: Tenebrionidae: Platynotina) – I have studied diverse entomological material concerning the subtribe Platynotina from several collections across the World and I did not managed to locate these specimens.

Based only on the original species descriptions Koch (1956) proposed to consider Selinus calcaripes as a synonym of Ectateus curtulus (Fairmaire, 1893). Unfortunately, the morphology of the holotype of Ectateus curtulus (damaged female – Fig. 47) do not correspond to Gebien’s (1904) description of Selinus calcaripes and Koch’s (1956) interpretation of Ectateus curtulus. Both publications refer rather to a morphological form that is very closely to Ectateus modestus and differs from it mainly by the structure of male protibiae (Figs 31–32). A consistent to the above mentioned descriptions morph was found in the studied material. It was included in the cladistic analysis as Selinus calcaripes.

The results of a cladistic analysis confirmed the aforementioned assumption that Ectateus curtulus and Selinus calcaripes represent two distinct morphological forms (Fig. 25). They can be easily distinguished by the structure of head (char. 3, 5), pronotum (char. 9) and elytra (elytral intervals with conspicuous punctures in E. curtulus). Additionally, the results shows that Selinus calcaripes is very closely related to Ectateus modestus – which is consistent with Gebien’s (1904) description and Koch’s (1956) interpretation.

Taking into consideration the difficulties associated with Selinus calcaripes I propose to designate a neotype to clarify the taxonomic status of this species. Additionally, on the basis of the results of a cladistic analysis I propose to treat this taxon as an independent species – not as a synonym of Ectateus curtulus.

Figures 1–7. Head, dorsal view (1, 2), ventral view (4); antenna (3); pronotal disc (5, 6); mesotibia (7). *E. calcaripes* (3), *E. crenatus* (2), *E. ghesquierei* (5), *M. medius* (7), *M. plicicollis* (4), *S. planus* (1, 6).

Redescription. Habitus as in Fig. 45. Body length = 11.5–14.0 mm. Elytra wider and longer than pronotum (width ratio elytra / pronotum = 1.1–1.2; length ratio elytra / the middle of pronotum = 2.4–2.6).

Dorsal side of head dull, with punctures (the intervals between the punctures are smaller than the diameter of the puncture). Frontoclypeal suture coarse. Clypeal emargination relatively deep (clypeal emargination width / depth ratio = 8.0–8.6). Mentum with median part narrow. Submentum with short base. Maxillary palp not widened (width of maxillary palp / length of 3rd antennomere = 1.0–1.1). Length of antennae greater than pronotal length (ratio antenna / pronotum from tip of anterior pronotal angle to tip of posterior pronotal angle = 1.1–1.2). 3rd antennomere relatively long (length ratio of antennomere 3rd / 2nd = 2.8–3.0).

Pronotal disc transverse (middle of pronotum length / width ratio = 0.4–0.5); dull, with coarse punctures (the intervals between the punctures are smaller than the diameter of the puncture). Anterior pronotal angles sharp and protruding outwards. Lateral margins of pronotal disc sinusoidal. Apophyseal and basal depressions on pronotal disc present; apophyseal depressions rounded. Pronotal hypomera dull; without punctures.

Elytra oblong (elytra length / width ratio = 1.1–1.2). Elytral striae with fine punctures; intervals non-convex, with transverse sculpture (Fig. 27). Elytral base slightly rounded. Elytral humeri rounded, not protruding laterad. Wings absent. Scutellum triangular; situated in a depression.

Intercoxal process protruding towards mesoventrite; peaked at the apex. Metaventrite reduced (length ratio cavity of hind coxa / metaventrite between the insertions of mid and hind coxae ca. 2). In both sexes abdominal process without tubercles; relatively narrow (process of 1st abdominal ventrite / process of metaventrite = 2.1–2.2). 5th abdominal ventrite without bordering; punctures fine (the intervals between the punctures are greater than the 2 diameters of the puncture).
Male legs. Protarsi slightly narrow. Protibiae as in Fig. 31. Mesotibiae and mesofemorae with large denticle. Metafemorae with an hair fringe. Female legs simple.

Male genitalia. Parameres narrowest in the half of their length; length equal to the 0.2 of the rest of aedeagal tegmen (Fig. 20). Clavae hook-shaped (Fig. 20). Female genitalia. Paraproct equal to coxites. Bursa copulatrix with a sclerite in the distal part. Spermatheca with narrow ducts.

**Distribution.** This species has been collected in the following ecoregions of Central Africa (Cameroon, Central African Republic, Democratic Republic of the Congo, South Sudan): Atlantic Equatorial coastal forests, East Sudanian savanna, Mount Cameroon and Bioko montane forests, Northeastern Congolian lowland forests, Northwestern Congolian lowland forests (Fig. 41).

**Ectateus crenatus** (Fairmaire, 1897)
http://species-id.net/wiki/Ectateus_crenatus
Figs 2, 8, 12, 34–36, 41, 46


*Selinus monardi* Kaszab, 1951: 2 (syn. nov.)


**Notes.** While describing *Ectateus latipennis*, Koch has noted that types of *Ectateus crenatus* were unknown to him. The characters used by Koch to separate those two species (body size, pronotum structure) were based only on the Fairmaire (1897) description. During the examination of available material I have not found any consistent morphological characters to separate those two species. Therefore, I propose to consider *E. latipennis* as a synonym of *E. crenatus*.

The examination of the type material representing *Selinus monardi* resulted in similar conclusions – there are no consistent morphological characters to separate it from *E. crenatus*.

Figures 8–13. Elytral disc (8, 9); 5th abdominal ventrite (10, 11), intercoxal process of pro sternum (12), male protarsi (13). *E. crenatus* (8, 12), *M. convexipennis* (10), *M. malaisei* (9), *M. plicicollis* (13), *S. striatus* (11).
Redescription. Habitus as in Fig. 46. Body length = 7.0–9.0 mm. Elytra wider and longer than pronotum (width ratio elytra / pronotum = 1.1–1.2; length ratio elytra / the middle of pronotum = 2.4–2.6).

Dorsal side of head shiny, with punctures (the intervals between the punctures are smaller than the diameter of the puncture). Frontoclypeal suture coarse. Clypeal emargination relatively deep (clypeal emargination width / depth ratio = 5.7–6.5). Mentum with median part narrow. Submentum with short base. Maxillary palp not widened (width of maxillary palp / length of 3rd antennomere = 1.0–1.2). Length of antennae greater than pronotal length (ratio antenna / pronotum from tip of anterior pronotal angle to tip of posterior pronotal angle = 1.1–1.3). 3rd antennomere relatively long (length ratio of antennomere 3rd / 2nd = 2.8–3.0).

Pronotal disc transverse (middle of pronotum length / width ratio = 0.5–0.6); shiny, with coarse punctures (the intervals between the punctures are smaller than the diameter of the puncture). Anterior pronotal angles sharp and protruding outwards. Lateral margins of pronotal disc sinusoidal. Apophyseal and basal depressions on pronotal disc present; apophyseal depressions rounded. Pronotal hypomera dull; without punctures.

Elytra oblong (elytra length / width ratio = 1.1–1.2). Elytral striae with coarse punctures (Fig. 8); intervals convex, with transverse sculpture and fine punctuation (Fig. 8). Elytral base slightly rounded. Elytral humeri rounded, not protruding laterad. Wings absent. Scutellum triangular; situated in a depression.

Intercoxal process protruding towards mesoventrite, peaked at the apex, slightly saddle-like. Metaventrite reduced (length ratio cavity of hind coxa / metaventrite between the insertions of mid and hind coxae ca. 2). In both sexes abdominal process without tubercles; relatively narrow (process of 1st abdominal ventrite / process of
A cladistically based reinterpretation of the taxonomy of two Afrotropical tenebrionid genera...

metaventrite = 2.1–2.2). 5th abdominal ventrite without bordering; punctures fine (the intervals between the punctures are greater than the 2 diameters of the puncture).

Male legs. Protarsi slightly narrow. Protibiae as in Fig. 34. Mesotibiae and mesofemorae with large denticle (Figs 35–36). Metafemorae with an hair fringe. Female legs simple.

Male genitalia. Parameres narrowest in the half of their length; length equal to 0.2 of the rest of aedeagal tegmen. Clavae hook-shaped. Female genitalia. Paraproct equal to coxites. Bursa copulatrix without sclerites. Spermatheca with narrow ducts.

**Distribution.** This species has been collected in the following ecoregions of Central Africa (Cameroon, Democratic Republic of the Congo, Equatorial Guinea, Gabonese Republic, Republic of the Congo): Atlantic Equatorial coastal forests, Northern Congolian forest-savanna mosaic, Northwestern Congolian lowland forests, Southern Congolian forest-savanna mosaic, Western Congolian forest-savanna mosaic (Fig. 41).

**Ectateus curtulus (Fairmaire, 1893)**
http://species-id.net/wiki/Ectateus_curtulus
Fig. 47


**Studied material.** Holotype (Fig. 47), female (MNHN): „l’Oubanghi”.

**Redescription.** Habitus as in Fig. 47. Body length ca. 12.5 mm. Elytra wider and longer than pronotum (width ratio elytra / pronotum ca. 1.2; length ratio elytra / the middle of pronotum ca. 2.6).

Dorsal side of head dull, with punctures (the intervals between the punctures are smaller than the diameter of the puncture). Frontoclypeal suture coarse. Clypeal emargination relatively deep (clypeal emargination width / depth ratio ca. 8.1). Mentum with median part wide. Submentum with short base. 3rd antennomere relatively long (length ratio of antennomere 3rd / 2nd ca. 3.0).

Pronotal disc transverse (middle of pronotum length / width ratio ca. 0.5); dull, with coarse punctures (the intervals between the punctures are smaller than the diameter of the puncture). Anterior pronotal angles sharp and protruding outwards. Lateral margins of pronotal disc rounded. Apophyseal and basal depressions on pronotal disc present; apophyseal depressions rounded. Pronotal hypomere dull, without punctures.

Elytra oblong (elytra length / width ratio ca. 1.2). Elytral striae with conspicuous punctures; intervals non-convex, with transverse sculpture and conspicuous punctuation (2 diameters apart). Elytral base slightly rounded. Elytral humeri rounded, not protruding laterad. Wings absent. Scutellum triangular; situated in a depression.

Intercoxal process protruding towards mesoventrite, peaked at the apex, slightly saddle-like. Metaventrite reduced (length ratio cavity of hind coxa / metaventrite be-
between the insertions of mid and hind coxae ca. 2). In both sexes abdominal process without tubercles; relatively narrow (process of 1st abdominal ventrite / process of metaventrite ca. 2.1). 5th abdominal ventrite without bordering; punctures fine (the intervals between the punctures are greater than the 2 diameters of the puncture).

Female legs simple.


**Distribution.** The only known specimen was collected in the Oubanghi (Central Africa). Because of the general character of the geographical reference it can not be translated into ecoregions.

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**Ectateus ghesquierei** Koch, 1956

http://species-id.net/wiki/Ectateus_ghesquierei

Figs 5, 33, 41, 48


**Redescription.** Habitus as in Fig. 48. Body length = 8.0–9.0 mm. Elytra wider and longer than pronotum (width ratio elytra / pronotum = 1.1–1.2; length ratio elytra / the middle of pronotum = 2.5–2.6).

Dorsal side of head dull, with punctures (the intervals between the smaller than the diameter of the puncture). Frontoclypeal suture coarse. Clypeal emargination relatively deep (clypeal emargination width / depth ratio = 9.0–9.3). Mentum with median part narrow. Submentum with short base. Maxillary palp not widened (width of maxillary palp / length of 3rd antennomere = 1.0–1.1). Length of antennae greater than pronotal length (ratio antenna / pronotum from tip of anterior pronotal angle to tip of posterior pronotal angle = 1.1–1.2). 3rd antennomere relatively long (length ratio of antennomere 3rd / 2nd = 2.7–3.0).

Pronotal disc transverse (middle of pronotum length / width ratio = 0.4–0.5); dull, with coarse punctures (the intervals between the punctures are smaller than the diameter of the puncture). Anterior pronotal angles sharp and protruding outwards. Lateral margins of pronotum sinusoidal. Apophyseal and basal depressions on pronotal disc present; apophyseal depressions rounded (Fig. 5). Pronotal hypomera shiny; without punctures.
Elytra oblong (elytra length / width ratio = 1.1–1.3). Elytral striae with conspicuous punctures; intervals convex, with transverse sculpture. Elytral base slightly rounded. Elytral humeri rounded, not protruding laterad. Wings absent. Scutellum triangular, situated in a depression.

Intercoxal process protruding towards mesoventrite, peaked at the apex, slightly saddle-shaped. Metaventrite reduced (length ratio cavity of hind coxa / metaventrite between the insertions of mid and hind coxae ca. 2). In both sexes abdominal process without tubercles; relatively narrow (process of 1st abdominal ventrite / process of metaventrite = 2.0–2.2). 5th abdominal ventrite without bordering; punctures fine (the intervals between the punctures are greater than the 2 diameters of the puncture).

Male legs. Protarsi slightly narrow. Protibiae as in Fig. 33. Mesotibiae with large denticle. Metatibiae without fringle of hairs. Female legs simple.

Male genitalia. Parameres narrowest in the half of their length; length equal to the 0.2 of the rest of aedeagal tegmen. Clavae hook-shaped. Female genitalia. Paraproct equal to coxites. Bursa copulatrix without sclerites. Spermatheca with narrow ducts.

**Distribution.** This species has been collected in the following ecoregions of Central Africa (Democratic Republic of the Congo, Republic of the Congo): Southern Congolian forest-savanna mosaic, Western Congolian forest-savanna mosaic (Fig. 41).

*Ectateus modestus* (Fairmaire, 1887)
http://species-id.net/wiki/Ectateus_modestus
Figs 32, 41, 49


umbe: T. Kipanzu, de, Singa à Mbomba V/VI-58, Dr R. Laurent”, female (MNHN):

Redescription. Habitus as in Fig. 49. Body length = 12.0–14.0 mm. Elytra wider
and longer than pronotum (width ratio elytra / pronotum = 1.1–1.2; length ratio
eytra / the middle of pronotum = 2.4–2.6).

Dorsal side of head dull, with punctures (the intervals between the punctures are
smaller than the diameter of the puncture). Frontoclypeal suture coarse. Clypeal emar-
gination relatively deep (clypeal emargination width / depth ratio = 8.0–8.4). Mentum
with median part narrow. Submentum with short base. Maxillary palp not widened
(width of maxillary palp / length of 3rd antennomere = 1.0–1.1). Length of antennae
greater than pronotal length (ratio antenna / pronotum from tip of anterior pronotal
angle to tip of posterior pronotal angle = 1.2–1.3). 3rd antennomere relatively long
(length ratio of antennomere 3rd / 2nd = 2.7–3.0).

Pronotal disc transverse (middle of pronotum length / width ratio = 0.4–0.5); dull,
with coarse punctures (the intervals between the punctures are smaller than the diam-
er of the puncture). Anterior pronotal angles sharp and protruding outwards. Lateral
margins of pronotum sinusoidal. Apophyseal and basal depressions on pronotal disc
present; apophyseal depressions rounded. Pronotal hypomera dull; without punctures.

Elytra oblong (elytra length / width ratio = 1.1–1.2). Elytral striae with fine punc-
tures; intervals non-convex, with transverse sculpture. Elytral base slightly rounded.
Elytral humeri rounded, not protruding laterad. Wings absent. Scutellum triangular;
situated in a depression.

Intercoxal process not protruding towards mesoventrite, rounded at the apex.
Metaventrite reduced (length ratio cavity of hind coxa / metaventrite between the in-
sertions of mid and hind coxae ca. 2). In both sexes abdominal process without tuber-
cles; relatively narrow (process of 1st abdominal ventrite / process of metaventrite ca.
2.0. 5th abdominal ventrite without bordering; punctures fine (the intervals between
the punctures are greater than the 2 diameters of the puncture).

Male legs. Protarsi slightly narrow. Protibiae as in Fig. 32. Mesotibiae and mes-
ofemorae with large denticle. Metafemorae with an hair fringe. Female legs simple.

Male genitalia. Parameres narrowest in the half of their length; length equal to 0.2
of the rest of aedeagal tegmen. Clavae hook-shaped. Female genitalia. Paraproct equal
to coxites. Bursa copulatrix with a sclerite in distal part. Spermatheca with narrow ducts.

Distribution. This species has been collected in the following ecoregions of Central
Africa (Angola, Democratic Republic of the Congo, Republic of Rwanda, Republic of
the Congo): Albertine Rift montane forests, Angolan Miombo woodlands, Atlantic
Equatorial coastal forests, Western Congolian forest-savanna mosaic (Fig. 41).
Genus *Eleoselinus* gen. n.
http://zoobank.org/D78C17B9-5607-472D-BE6F-D28B8C33E23F
http://species-id.net/wiki/Eleoselinus

**Type species.** *Ectateus villiersi* Ardoin, 1965; here designated.


Non-dimorphic legs distinguish *Eleoselinus* from: *Anchophthalmops, Anchophthalmus, Ectateus, Microselinus, Monodius, Phymatoplata, Platykochius, Platymedvedevia* and *Selinus*. From *Kochogaster* it can be easily distinguished by a triangular submentum and lack of sclerites in bursa copulatrix (Kamiński and Iwan 2013). Not parallel body sides separates *Eleoselinus* form *Quadrideres* and *Glyptopteryx*. Additionally, from the latter it can be distinguished by flat elytral intervals and slightly sinusoidal base of pronotum (Iwan 2002). Fine hairs covering the body surface, narrow apical segments of maxillary palps and long basal apophyses of aedeagal tegmen separates *Eleoselinus* from *Phallocentrion* (Iwan 2001a).

The following character combination is unique for *Eleoselinus* within the whole subtribe Platynotina: (1) antennta robust, shorter than pronotum, (2) shallow anterior tentorial pits, (3) presence of apophyseal and basal depressions on pronotal disc, (4) intercoxal process of prosternum bellied, (5) metaventrite with coarse longitudinal depression, (6) 5th abdominal ventrite unbordered, (7) non dimorphic legs and maillary palps, (8) elytral intervals with fine punctures, (9) curved, hook-shaped clavae and (10) longitudinal coxites of ovipositor.

**Description.** Body length = 10.5–13.0 mm. Elytra wider and longer than pronotum (width ratio elytra / pronotum = 1.1–1.2; length ratio elytra / the middle of pronotum = 2.4–2.9).

Dorsal side of head dull, with fine punctures (the intervals between the punctures are greater than the 2 diameters of the puncture). Frontoclypeal suture fine. Clypeal emargination relatively deep (clypeal emargination width / depth ratio = 5.5–5.7). Mentum with median part wide. Submentum with short base. Maxillary palp not widened (width of maxillary palp / length of 3rd antennomere = 1.0–1.2). Length of antennae slightly greater than pronotal length (ratio antenna / pronotum from tip of anterior pronotal angle to tip of posterior pronotal angle ca. 0.9). 3rd antennomere relatively long (length ratio of antennomere 3rd / 2nd = 3.2–3.5).

Pronotal disc transverse (middle of pronotum length / width ratio = 0.5–0.6); dull, with fine punctures (the intervals between the punctures are greater than the 3 diameters of the puncture). Lateral margins of pronotum narrowing towards apex. Apophyseal and basal depressions on pronotal disc present. Pronotal hypomera dull, without punctures.
Elytra oblong (elytra length / width ratio = 1.1–1.3). Elytral striae with fine punctures (the intervals between the punctures are greater than the 2 diameters of the puncture). Elytral intervals dull, non-convex, without punctures of with very fine punctuation. Elytral base slightly sinusoidal. Elytral humeri rounded, not protruding laterad. Wings absent. Scutellum triangular.

Intercoxal process of prosternum bellied. Metaventrite reduced (length ratio cavity of hind coxa / metaventrite between the insertions of mid and hind coxae ca. 2), with longitudinal depression. In both sexes abdominal process without tubercles, relatively narrow (process of 1st abdominal ventrite / process of metaventrite = 2.1–2.2). 5th abdominal ventrite without bordering; punctures fine (the intervals between the punctures are greater than the 2 diameters of the puncture).

Legs. Protarsi narrow. Other leg segments simple.

Male genitalia. Parameres narrowing towards apex; length equal to the 0.2 of the rest of aedeagal tegmen. Clavae hook-shaped. Female genitalia. Paraproct equal to coxites. Coxites narrow and long. Bursa copulatrix without sclerites.

**Etymology.** The name is derived from the combination of *Eleo* (prefix indicating the genus *Eleodes* Eschscholtz, 1829 – a poster beetle genus of the Third International Tenebrionoidea Symposium in Tempe, Arizona) and *Selinus*. This genus is named to thank the Steering Committee of the Third International Tenebrionoidea Symposium: Aaron Smith (lead organizer), Rolf Aalbu, Patrice Bouchard, Kojun Kanda, Nico Franz, Warren Steiner and Quentin Wheeler.

**Distribution.** *Eleoselinus* gen. n. specimens have been collected in the following ecoregion of Central Africa (Republic of the Congo): Western Congolian forest-savanna mosaic (Fig. 42).

**Species included (2).** *Eleoselinus villiersi* (Ardoin, 1965), comb. n. and *E. ursynowiensis* (Kamiński, 2011), comb. n.

**Key to the species of *Eleoselinus* gen. n.**

1 Pronotal sides evenly narrowing towards apex. Elytral striae impressed on whole length (see Kamiński and Raś 2011: 651). Intercoxal process of prosternum strongly protruding towards mesosternum (see Kamiński and Raś 2011: 650) .................................................................................

   **Eleoselinus villiersi**

– Pronotal sides rounded. Elytral striae impressed only near the punctures (see Kamiński and Raś 2011: 651). Intercoxal process of prosternum slightly protruding towards mesosternum (see Kamiński and Raś 2011: 650) .................

   .................................................................................

   **Eleoselinus ursynowiensis**
Eleoselinus villiersi (Ardoin, 1965), comb. n.
http://species-id.net/wiki/Eleoselinus_villiersi
Fig. 58


Redescription. Habitus as in Fig. 58. Body length = 10.5–12.0 mm. Elytra wider and longer than pronotum (width ratio elytra / pronotum = 1.1–1.2; length ratio elytra / the middle of pronotum = 2.7–2.9).

Dorsal side of head dull, with fine punctures (the intervals between the punctures are greater than the 4 diameters of the puncture). Frontoclypeal suture fine. Clypeal emargination relatively deep (clypeal emargination width / depth ratio = 5.5–5.7). Mentum with median part wide. Submentum with short base. Maxillary palp not widened (width of maxillary palp / length of 3rd antennomere = 1.0–1.2). Length of antennae slightly greater than pronotal length (ratio antenna / pronotum from tip of anterior pronotal angle to tip of posterior pronotal angle ca. 0.9). 3rd antennomere relatively long (length ratio of antennomere 3rd / 2nd = 3.2–3.5).

Pronotal disc transverse (middle of pronotum length / width ratio = 0.5–0.6), dull, with fine punctures (the intervals between the punctures are greater than the 3 diameters of the puncture). Anterior pronotal angles rounded and slightly protruding towards apex. Lateral margins of pronotal disc narrowing towards apex. Apophyseal and basal depressions on pronotal disc present. Pronotal hypomera dull, without punctures.

Elytra oblong (elytra length / width ratio = 1.1–1.3). Elytral striae with fine punctures (the intervals between the punctures are greater than the 4 diameters of the puncture). Elytral intervals dull, non-convex, without punctures. Elytral base slightly sinusoidal. Elytral humeri rounded, not protruding laterad. Wings absent. Scutellum triangular.

Intercoxal process of prosternum bellied. Metaventrite reduced (length ratio cavity of hind coxa / metaventrite between the insertions of mid and hind coxae ca. 2); with longitudinal depression. In both sexes abdominal process without tubercles; relatively narrow (process of 1st abdominal ventrite / process of metaventrite = 2.1–2.2). 5th abdominal ventrite without bordering; punctures fine (the intervals between the punctures are greater than the 2 diameters of the puncture).

Legs. Protarsi slightly narrow. Legs simple.

Male genitalia. Parameres narrowing towards apex; length equal to the 0.2 of the rest of aedeagal tegmen. Clavae hook-shaped. Female genitalia. Paraproct equal to coxites. Coxites narrow and long. Bursa copulatrix without sclerites.

Distribution. This species has been collected in the following ecoregion Central Africa (Republic of the Congo).
**Eleoselinus ursynowiensis** (Kamiński, 2011), comb. n.
http://species-id.net/wiki/Eleoselinus_ursynowiensis
Fig. 59


**Morphological data.** Because the original description (Kamiński and Raś 2011) of this species is relatively recent and consistent with the description style adopted in this study the morphology of this species was not redescribed.

**Distribution.** This species has been collected in the following ecoregion Central Africa (Republic of the Congo).

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**Genus Monodius** Koch, 1956, stat. r.


**Type species.** *Selinus convexipennis* Gebien, 1904; by original designation.

**Diagnosis.** The following character combination is unique for *Monodius* within the whole subtribe Platynotina: (1) antennomeres from 7 to 11 elongated (their length greater than the width), (2) anterior tentorial pit deep, clearly visible, (3) 5th abdominal ventrite strongly widened, (4) female protarsi widened, (5) penis wide, at least 4 times wider than clavae, (6) clavae long, their length more than half of the length of parameres, (7) apex of parameres fused and (8) bursa copulatrix with 2 additional sacs.

**Distribution.** *Monodius* specimens have been collected in the following ecoregions of West and Central Africa (Burkina Faso, Cameroon, Federal Republic of Nigeria, Ivory Coast, Republic of Benin, Republic of Ghana, Republic of Liberia, Republic of Niger, Sierra Leone, Togolese Republic): Cross-Sanaga-Bioko coastal forests, Atlantic Equatorial coastal forests, Central African mangroves, Eastern Guinean forests, Guinean forest-savanna mosaic, Mount Cameroon and Bioko montane forests, Northern Congolian forest-savanna mosaic, Northwestern Congolian lowland forests, West Sudanian savanna, Western Guinean lowland forests (Figs 42–43).

**Species included** (7). *Monodius convexipennis* (Gebien, 1904), *M. gravis* Koch, 1956, *M. laevistriatus* (Fairmaire, 1897), comb. n., *M. lamottei* (Gridelli, 1954), comb. n., *M. malaisei* Koch, 1956, *M. medius* (Fairmaire, 1897), *M. plicicollis* (Fairmaire, 1897), comb. n.
Key to the species of *Monodius*

1. Elytral surface dull. Margins of elytra in the basal part subparallel (elytral humeri slightly protruding outwards). Denticle at the apex of the inner face of male mesotibia large (Fig. 7). Apex of parameres emarginated at the apex (Figs 15, 17) .................................................................

2. Elytral surface shiny. Margins of elytra in the basal part rounded. Denticle at the apex of the inner face of male mesotibia small or absent (e.g. Fig. 29). Apex of parameres connected (Figs 14, 16) ............................................ *Monodius plicicollis*

3. Pronotal apophyseal depressions coarse. Male mesofemorae with a denticle (similar to the one in *E. laevisstriatus*, Fig. 40). Parameres strongly emarginated at the apex (Fig. 15) ........................................ *Monodius plicicollis*

4. Pronotal apophyseal depressions fine. Male mesofemorae without denticles. Parameres slightly emarginated at the apex (Fig. 17)........................................ *Monodius medius*

5. Male protibiae with median dilatation on the inner face (similar to the one in *M. convexipennis*, Fig. 37) ................................................ *Monodius medius*

6. Male protibiae almost straight (Fig. 38) ........................................ *Monodius medius*

7. Body size: 16.0–19.0 mm. Elytral intervals with fine punctures (Fig. 26). Male protibiae as in Fig. 30 ........................................ *Monodius medius*

8. Body size: 12.0–14.5 mm. Elytral intervals with conspicuous punctures. Male protibiae as in Fig. 37 ........................................ *Monodius medius*

9. Pronotal disc with two circular depressions in the middle. Aedeagal tegmen as in Fig. 19 .................................................... *Monodius laevisstriatus*

10. Pronotal disc without circular depressions. Aedeagal tegmen as in Fig. 16, 18... *Monodius convexipennis*

11. Elytral intervals with conspicuous punctures. Elytral apex as in Fig. 51. Aedeagal tegmen as in Fig. 16 ........................................ *Monodius convexipennis*

12. Elytral intervals with very coarse punctures (Fig. 28). Elytral apex rounded. Aedeagal tegmen as in Fig. 18 ........................................ *Monodius lamottei*

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*Monodius convexipennis* (Gebien, 1904)
http://species-id.net/wiki/Monodius_convexipennis
Figs 10, 16, 37, 42, 50, 51


Redescription. Habitat as in Fig. 50. Body length = 13.0–14.5 mm. Elytra wider and longer than pronotum (width ratio elytra / pronotum = 1.1–1.2; length ratio elytra / the middle of pronotum = 2.4–2.6).

Dorsal side of head dull, with punctures (the intervals between the punctures are smaller than the diameter of the puncture). Frontoclypeal suture fine. Clypeal emargination relatively deep (clypeal emargination width / depth ratio = 7.0–7.5). Mentum with median part wide. Submentum with short base. Maxillary palp not widened (width of maxillary palp / length of 3rd antennomere = 1.1–1.2). Length of antennae greater than pronotal length (ratio antenna / pronotum from tip of anterior pronotal angle to tip of posterior pronotal angle = 1.2–1.3). 3rd antennomere relatively long (length ratio of antennomere 3rd / 2nd = 2.8–2.9).

Pronotal disc transverse (middle of pronotum length / width ratio = 0.5–0.6), dull, with fine punctures (the intervals between the punctures are smaller than the diameter of the puncture). Anterior pronotal angles sharp and strongly protruding towards front. Lateral margins of pronotal disc subparallel at their basal half. Apophyseal and basal depressions on pronotal disc present; apophyseal depressions trapezoidal. Pronotal hypomera dull; without punctures.

Elytra oblong (elytra length / width ratio = 1.1–1.2). Elytral striae with fine punctures, impressed on the whole length. Elytral intervals shiny, non-convex, with conspicuous punctures (the intervals between the punctures are smaller than the diameter of the puncture). Elytral base slightly sinusoidal. Elytral humeri rounded, not protruding laterad. Wings absent. Scutellum rounded.

Intercoxal process slightly protruding towards mesoventritle. Metaventrite reduced (length ratio cavity of hind coxa / metaventrite between the insertions of mid and hind coxae ca. 2). In both sexes abdominal process without tubercles, relatively narrow (process of 1st abdominal ventrite / process of metaventrite = 2.1–2.3). 5th abdominal ventrite without bordering; punctures fine (the intervals between the punctures are greater than the 2 diameters of the puncture).

Male legs. Protarsi slightly widened. Protibiae as in Fig. 37. Mesofemorae with a small denticle at the apex. Metatibiae and Metafemorae with an hair fringe. Female legs. Protarsi slightly widened. Other leg parts simple.
Male genitalia. Parameres narrowing towards apex; length equal to the 0.3 of the rest of aedeagal tegmen (Fig. 16). Clavae straight (Fig. 16). Female genitalia. Paraproct equal to coxites. Bursa copulatrix with two sacs. Spermatheca with narrow ducts.

**Distribution.** This species has been collected in the following ecoregions of Central Africa (Cameroon): Atlantic Equatorial coastal forests, Central African mangroves, Cross-Sanaga-Bioko coastal forests, Mount Cameroon and Bioko montane forests, Northern Congolian forest-savanna mosaic, Northwestern Congolian lowland forests (Fig. 42).

**Monodius gravis** Koch, 1956
http://species-id.net/wiki/Monodius_gravis
Figs 14, 24, 26, 29, 30, 42, 52

**Monodius gravis** Koch, 1956: 184.


**Redescription.** Habitus as in Fig. 52. Body length = 16.0–19.0 mm. Elytra wider and longer than pronotum (width ratio elytra / pronotum = 1.1–1.2; length ratio elytra / middle of pronotum = 2.2–2.4).

Dorsal side of head dull, with fine punctures (the intervals between the punctures are greater than the 2 diameters of the puncture). Frontoclypeal suture fine. Clypeal emargination relatively deep (clypeal emargination width / depth ratio = 7.1–7.5). Mentum with median part wide. Submentum with short base. Maxillary palp not widened (width of maxillary palp / length of 3rd antennomere = 1.1–1.2). Length of antennae greater than pronotal length (ratio antenna / pronotum from tip of anterior pronotal angle to tip of posterior pronotal angle = 1.2–1.3). 3rd antennomere relatively long (length ratio of antennomere 3rd / 2nd = 2.8–2.9).

Pronotal disc transverse (middle of pronotum length / width ratio = 0.5–0.6), dull, with fine punctures (the intervals between the punctures are greater than the 3 diameters of the puncture). Anterior pronotal angles sharp and strongly protruding toward the front. Lateral margins of pronotal disc rounded. Apophyseal and basal depressions on pronotal disc present; apophyseal depressions trapezoidal. Pronotal hypomera dull; without punctures.

Elytra oblong (elytra length / width ratio = 1.1–1.2). Elytral striae with fine punctures; impressed on the whole length. Elytral intervals shiny, non-convex, with fine punctures (the intervals between the punctures are smaller than the diameter of the
Figures 22–24. Female genitalia. Ovipositor of *M. plicicollis* (22); bursa copultrix of *M. medius* (23), spermatheca of *M. gravis* (24).


Intercoxal process slightly protruding towards mesoventrite. Metaventrite reduced (length ratio cavity of hind coxa / metaventrite between the insertions of mid and
hind coxae ca. 2). In both sexes abdominal process without tubercles; relatively narrow (process of 1st abdominal ventrite / process of metaventrite = 2.1–2.3). 5th abdominal ventrite without bordering; punctures fine (the intervals between the punctures are greater than the 2 diameters of the puncture).

Male legs. Protarsi widened. Protibiae as in Fig. 30. Mesofemorae with a small denticle at the apex. Metafemorae with an hair fringe. Female legs. Protarsi slightly widened. Other leg parts simple.

Male genitalia. Parameres narrowing towards apex; length equal to the 0.3 of the rest of aedeagal tegmen (Fig. 14). Clavae straight (Fig. 14). Female genitalia. Paraproct equal to coxites. Bursa copulatrix with two sacs. Spermatheca with narrow ducts (Fig. 24).

**Distribution.** This species has been collected in the following ecoregions of West Africa (Republic of Benin, Togolese Republic): Guinean forest-savanna mosaic (Fig. 42).

*Monodius laevistriatus* (Fairmaire, 1897), comb. n.

http://species-id.net/wiki/Monodius_laevistriatus

Figs 19, 40, 42, 53


**Redescription.** Habitus as in Fig. 53. Body length = 12.0–14.0 mm. Elytra wider and longer than pronotum (width ratio elytra / pronotum = 1.1–1.2; length ratio elytra / the middle of pronotum = 2.2–2.4).

Dorsal side of head dull, with fine punctures (the intervals between the punctures are smaller than the diameter of the puncture). Frontoclypeal suture fine. Clypeal emargination relatively deep (clypeal emargination width / depth ratio = 7.1–7.5). Mentum with median part wide. Submentum with short base. Maxillary palp not widened (width of maxillary palp / length of 3rd antennomere = 1.1–1.2). Length of antennae greater than pronotal length (ratio antenna / pronotum from tip of anterior pronotal angle to tip of posterior pronotal angle = 1.2–1.3). 3rd antennomere relatively long (length ratio of antennomere 3rd / 2nd = 2.8–2.9).

Pronotal disc transverse (middle of pronotum length / width ratio = 0.5–0.6); dull, with fine punctures (the intervals between the punctures are greater than the 2 diameters of the puncture); with two circular depressions in the middle. Anterior pronotal angles sharp and strongly protruding towards front. Lateral margins of pronotal
disc rounded. Apophyseal and basal depressions on pronotal disc present; apophyseal depressions trapezoidal. Pronotal hypomera dull; without punctures.

Elytra oblong (elytra length / width ratio = 1.1–1.2). Elytral striae with fine punctures; impressed on the whole length. Elytral intervals shiny, non-convex, with conspicuous punctures (the intervals between the punctures are smaller than the diameter of the puncture). Elytral base slightly sinusoidal. Elytral humeri rounded, not protruding laterad. Wings absent. Scutellum rounded.

Intercoxal process not protruding towards mesoventrite. Metaventrite reduced (length ratio cavity of hind coxa / metaventrite between the insertions of mid and hind coxae ca. 2). In both sexes abdominal process without tubercles, relatively narrow (process of 1st abdominal ventrite / process of metaventrite = 2.1–2.3). 5th abdominal ventrite without bordering; punctures fine (the intervals between the punctures are greater than the 2 diameters of the puncture).

Figure 25. Phylogeny of the species of Ectateus and Selinus sensu Iwan 2002. Most parsimonious tree (L=57, CI=74, RI=90). Black circles represent single, non-homoplasious character state transformations, and white circles represent multiple, homoplasious character state transformations. The numbers above and below each circle correspond to character numbers and states, respectively. Additional numbers displayed at the top of branches represent Jackknife values (support below 50 was not illustrated). * – type species.
Male legs. Protarsi slightly widened. Protibiae as in *M. convexipennis*. Mesofemorae with a large denticle at the apex, mesotibia with a small denticle at the apex. Metafemorae with a hair fringe. Female legs. Protarsi slightly widened. Other leg parts simple.

Male genitalia. Parameres strongly narrowed toward apex; length equal to the 0.5 of the rest of aedeagal tegmen (Fig. 19). Clavae straight (Fig. 19). Female genitalia. Paraproct equal to coxites. Bursa copulatrix with two sacs. Spermatheca with narrow ducts.

**Distribution.** This species has been collected in the following ecoregions of West Africa (Sierra Leone): Western Guinean lowland forests (Fig. 42).

*Monodius lamottei* (Gridelli, 1954), comb. n.
http://species-id.net/wiki/Monodius_lamottei
Figs 18, 28, 42, 54


**Monodius laevistriatus** (Gridelli, 1954).– Ardoin 1963: 222; Iwan 2002b: 266.


**Redescription.** Habitus as in Fig. 54. Body length = 12.0–14.5 mm. Elytra wider and longer than pronotum (width ratio elytra / pronotum = 1.1–1.2; length ratio elytra / the middle of pronotum = 2.2–2.4).

Dorsal side of head dull, with fine punctures (the intervals between the punctures are smaller than the diameter of the puncture). Frontoceypeal suture fine. Clypeal emargination relatively shallow (clypeal emargination width / depth ratio = 10.0–11.5). Mentum with median part wide. Submentum with short base. Maxillary palp not widened (width of maxillary palp / length of 3\textsuperscript{rd} antennomere = 1.1–1.2). Length of antennae greater than pronotal length (ratio antenna / pronotum from tip of anterior pronotal angle to tip of posterior pronotal angle = 1.2–1.3). 3\textsuperscript{rd} antennomere relatively long (length ratio of antennomere 3\textsuperscript{rd} / 2\textsuperscript{nd} = 2.8–2.9).

Pronotal disc transverse (middle of pronotum length / width ratio = 0.5–0.6), dull, with fine punctures (the intervals between the punctures are smaller than the diameter of the puncture). Anterior pronotal angles sharp and strongly protruding towards
Figures 26–30. Elytral disc (26, 27, 28); male mesotibia (29); male protibia (30). *M. gravis* (26, 29, 30), *E. calcaripes* (27), *E. lamottei* (28).

Front. Lateral margins of pronotal disc rounded. Apophyseal and basal depressions on pronotal disc present; apophyseal depressions trapezoidal. Pronotal hypomera dull; without punctures.
Elytra oblong (elytra length / width ratio = 1.1–1.2). Elytral striae with fine punctures, impressed on the whole length. Elytral intervals shiny, non-convex, with coarse punctures (the intervals between the punctures are smaller than the diameter of the puncture). Elytral base slightly sinusoidal. Elytral humeri rounded, not protruding laterad. Wings absent. Scutellum rounded.

Intercoxal process protruding towards mesoventrite. Metaventrite reduced (length ratio cavity of hind coxa / metaventrite between the insertions of mid and hind coxae ca. 2). In both sexes abdominal process without tubercles, relatively narrow (process of 1st abdominal ventrite / process of metaventrite = 2.1–2.3). 5th abdominal ventrite without bordering; punctures fine (the intervals between the punctures are greater than the 2 diameters of the puncture).


Male genitalia. Parameres extended towards apex; length equal to the 0.5 of the rest of aedeagal tegmen (Fig. 18). Clavae straight (Fig. 18). Female genitalia. Paraproct equal to coxites. Bursa copulatrix with two sacs. Spermatheca with narrow ducts.

**Distribution.** This species has been collected in the following ecoregions of West Africa (Ivory Coast, Republic of Liberia): Eastern Guinean forests, Western Guinean lowland forests (Fig. 42).

**Monodius malaisei** Koch, 1956
http://species-id.net/wiki/Monodius_malaisei
Figs 9, 17, 38, 43, 55

**Monodius malaisei** Koch, 1956: 188.


Redescription. Habitus as in Fig. 55. Body length = 13.0-14.0 mm. Elytra wider and longer than pronotum (width ratio elytra / pronotum = 1.2–1.3; length ratio elytra / the middle of pronotum = 2.2–2.4).

Figures 37–40. Male protibiae (37–39); male mesofemora (40). M. convexipennis (37), M. malaisei (38), S. planus (39), E. laevistriatus (40).
Dorsal side of head dull, with fine punctures (the intervals between the punctures are smaller than the diameter of the puncture). Frontoclypeal suture fine. Clypeal emargination relatively shallow (clypeal emargination width / depth ratio = 10.0–11.5). Mentum with median part wide. Submentum with short base. Maxillary palp not widened (width of maxillary palp / length of 3rd antennomere = 1.1–1.2). Length of antennae greater than pronotal length (ratio antenna / pronotum from tip of anterior pronotal angle to tip of posterior pronotal angle = 1.2–1.3). 3rd antennomere relatively long (length ratio of antennomere 3rd / 2nd = 2.8–2.9).

Pronotal disc transverse (middle of pronotum length / width ratio = 0.5–0.6), dull, with fine punctures (the intervals between the punctures are smaller than the diameter of the puncture). Anterior pronotal angles sharp and strongly protruding towards front. Lateral margins of pronotal disc rounded. Apophyseal and basal depressions on pronotal disc present; apophyseal depressions trapezoidal. Pronotal hypomera dull, without punctures.

Elytra oblong (elytra length / width ratio = 1.1–1.2). Elytral striae with fine punctures; impressed on the whole length. Elytral intervals dull, non-convex, with fine punctures (the intervals between the punctures are greater than the 4 diameters of the puncture). Elytral base slightly sinusoidal. Elytral humeri slightly protruding laterad. Wings absent. Scutellum rounded.

Intercoxal process protruding towards mesoventrite. Metaventrite reduced (length ratio cavity of hind coxa / metaventrite between the insertions of mid and hind coxae ca. 2). In both sexes abdominal process without tubercles, relatively narrow (process of 1st abdominal ventrite / process of metaventrite = 2.1–2.3). 5th abdominal ventrite without bordering; punctures fine (the intervals between the punctures are greater than the 2 diameters of the puncture).
Male legs. Protarsi slightly widened. Protibiae as in Fig. 38. Mesotibiae with a large denticle at the apex. Metafemorae with an hair fringe. Female legs. Protarsi slightly widened. Other leg parts simple.

Male genitalia. Parameres extended towards apex; length equal to the 0.2 of the rest of aedeagal tegmen (Fig. 17). Clavae straight (Fig. 17). Female genitalia. Paraproct equal to coxites. Bursa copulatrix with two sacs. Spermatheca with narrow ducts.

**Distribution.** This species has been collected in the following ecoregions of West Africa (Republic of Ghana, Ivory Coast, Burkina Faso, Federal Republic of Nigeria, Republic of Niger): Eastern Guinean forests, Guinean forest-savanna mosaic, West Sudanian savanna (Fig. 43).

**Key to the subspecies of Monodius malaisei**

1  
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Male metatibiae curved and slightly dilated on distal half ........................................  
................................................................................. *Monodius malaisei malaisei* Koch, 1956  
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Male metatibiae straight........... *Monodius malaisei nigeriensis* Koch, 1956

*Monodius medius* (Fairmaire, 1897)  
http://species-id.net/wiki/Monodius_medius  
Figs 7, 23, 43, 56

*Monodius medius* (Fairmaire, 1897).—Koch 1956: 185; Girard 1975: 342.  


**Redescription.** Habitus as in Fig. 56. Body length = 12.0–15.0 mm. Elytra wider and longer than pronotum (width ratio elytra / pronotum = 1.2–1.3; length ratio elytra / the middle of pronotum = 2.2–2.4).

Dorsal side of head dull, with fine punctures (the intervals between the punctures are smaller than the diameter of the puncture). Frontoclypeal suture fine. Clypeal emargination relatively shallow (clypeal emargination width / depth ratio = 10.0–11.5). Mentum with median part wide. Submentum with short base. Maxillary palp
not widened (width of maxillary palp / length of 3rd antennomere = 1.1–1.2). Length of antennae greater than pronotal length (ratio antenna / pronotum from tip of anterior pronotal angle to tip of posterior pronotal angle = 1.2–1.3). 3rd antennomere relatively long (length ratio of antennomere 3rd / 2nd = 2.8–2.9).

Pronotal disc transverse (middle of pronotum length / width ratio = 0.5–0.6); dull, with fine punctures (the intervals between the punctures are greater than the 2 diameters of the puncture). Anterior pronotal angles sharp and strongly protruding towards front. Lateral margins of pronotal disc rounded. Apophyseal and basal depressions on pronotal disc present; apophyseal depressions trapezoidal. Pronotal hypomera dull, without punctures.

Elytra oblong (elytra length / width ratio = 1.1–1.2). Elytral striae with fine punctures, impressed on the whole length. Elytral intervals dull, non-convex, with fine punctures (the intervals between the punctures are greater than the 4 diameters of the puncture). Elytral base slightly sinusoidal. Elytral humeri slightly protruding laterad. Wings absent. Scutellum rounded.

Intercoxal process not protruding towards mesoventrite. Metaventrite reduced (length ratio cavity of hind coxa / metaventrite between the insertions of mid and hind coxae ca. 2). In both sexes abdominal process without tubercles, relatively narrow (process of 1st abdominal ventrite / process of metaventrite = 2.1–2.3). 5th abdominal ventrite without bordering; punctures fine (the intervals between the punctures are greater than the 3 diameters of the puncture).
Male legs. Protarsi slightly widened. Protibiae as in *M. convexipennis*. Mesotibiae with a large denticle at the apex. Metafemorae with a hair fringe. Female legs. Protarsi slightly widened. Other leg parts simple.

Male genitalia. Similar as in *M. malaisei*. Female genitalia. Paraproct equal to coxites. Bursa copulatrix with two sacs (Fig. 23). Spermatheca with narrow ducts.

**Distribution.** This species has been collected in the following ecoregions of West Africa (Republic of Ghana, Ivory Coast): Eastern Guinean forests, Guinean forest-savanna mosaic (Fig. 43).

**Monodius plicicollis** (Fairmaire, 1897), **comb. n.**
http://species-id.net/wiki/Monodius_plicicollis
Figs 4, 13, 15, 22, 43, 57


**Redescription.** Habitus as in Fig. 57. Body length = 13.0–18.0 mm. Elytra wider and longer than pronotum (width ratio elytra / pronotum = 1.2–1.3; length ratio elytra / the middle of pronotum = 2.2–2.4).

Dorsal side of head dull, with fine punctures (the intervals between the punctures are smaller than the diameter of the puncture). Frontoclypeal suture fine. Clypeal emargination relatively shallow (clypeal emargination width / depth ratio = 10.0–11.5). Mentum with median part wide. Submentum with short base. Maxillary palp not widened (width of maxillary palp / length of 3rd antennomere = 1.1–1.2). Length
of antennae greater than pronotal length (ratio antenna / pronotum from tip of anterior pronotal angle to tip of posterior pronotal angle = 1.2–1.3). 3rd antennomere relatively long (length ratio of antennomere 3rd / 2nd = 2.8–2.9).

Pronotal disc transverse (middle of pronotum length / width ratio = 0.5–0.6); dull, with fine punctures (the intervals between the punctures are greater than the 2 diameters of the puncture). Anterior pronotal angles sharp and strongly protruding towards front. Lateral margins of pronotal disc rounded. Apophyseal and basal depressions on pronotal disc present; apophyseal depressions trapezoidal; very coarse. Pronotal hypomera dull; without punctures.

Elytra oblong (elytra length / width ratio = 1.1–1.2). Elytral striae with fine punctures; impressed on the whole length. Elytral intervals dull, non-convex, with fine punctures (the intervals between the punctures are greater than the 4 diameters of the puncture). Elytral base slightly sinusoidal. Elytral humeri slightly protruding laterad. Wings absent. Scutellum rounded.

Intercoxal process not protruding towards mesoventrite. Metaventrite reduced (length ratio cavity of hind coxa / metaventrite between the insertions of mid and hind coxae ca. 2). In both sexes abdominal process without tubercles; relatively narrow (process of 1st abdominal ventrite / process of metaventrite = 2.1–2.3). 5th abdominal ventrite without bordering; punctures fine (the intervals between the punctures are greater than the 3 diameters of the puncture).


Male genitalia. Parameres extended towards apex; length equal to the 0.2 of the rest of aedeagal tegmen (Fig. 15). Clavae straight (Fig. 15). Female genitalia. Paraproct equal to coxites (Fig. 22). Bursa copulatrix with two sacs. Spermatheca with narrow ducts.

**Distribution.** This species has been collected in the following ecoregions of West Africa (Togolese Republic, Republic of Benin, Federal Republic of Nigeria): Eastern Guinean forests, Guinean forest-savanna mosaic, West Sudanian savanna (Fig. 43).

**Genus Selinus Mulsant & Rey, 1853**
http://species-id.net/wiki/Selinus


**Type species.** *Opatrum planum* Fabricius, 1792; designated by Gebien (1938).

**Diagnosis.** The following character combination is unique for *Selinus* within the whole subtribe Platynotina: (1) anterior tentorial pit deep, clearly visible, (2) antennomeres from 7 to 11 elongated (their length greater than the width), (3) pronotum wid-
A cladistically based reinterpretation of the taxonomy of two Afrotropical tenebrionid genera... 123

Distribution. Specimens of this genus have been collected in the following ecoregions of West Africa (Ivory Coast, Republic of Benin, Republic of Ghana, Republic of Guinea, Republic of Mali, Togolese Republic): Eastern Guinean forests, Guinean forest-savanna mosaic, West Sudanian savanna, Western Guinean lowland forests (Fig. 44).

Species included (2). Selinus planus (Fabricius, 1792) and S. striatus (Fabricius, 1794).

Key to the species of Selinus

1 Body size: 12.0–14.0 mm. Pronotal sides evenly narrowing towards apex. Pronotal and elytral surface with fine punctures (the intervals between the punctures are greater than the 3 diameters of the puncture). Male protibiae as in Fig. 39 ......................................................... Selinus planus

– Body size: 10.0–11.0 mm. Pronotal sides parallel in their basal half. Pronotal and elytral surface with conspicuous punctures (the intervals between the punctures are smaller than the diameter of the puncture). Male protibiae with very shallow dilatation near the middle............. Selinus striatus

Selinus planus (Fabricius, 1792)
http://species-id.net/wiki/Selinus_planus
Figs 1, 6, 39, 44, 60


Figures 50–54. Body habitus: *Monodius convexipennis* (50), *M. gravis* (52), *M. laevistriatus* (53) and *M. lamottei* (54). Apex of elytra of *M. convexipennis* (51).

**Redescription.** Habitus as in Fig. 60. Body length = 12.0–14.0 mm. Elytra wider and longer than pronotum (width ratio elytra / pronotum = 1.1–1.2; length ratio elytra / the middle of pronotum = 2.7–3.0).

Dorsal side of head dull, with punctures (the intervals between the punctures are smaller than the diameter of the puncture). Frontoclypeal suture fine. Clypeal emargination relatively deep (clypeal emargination width / depth ratio = 4.0–4.5). Mentum with median part wide. Submentum with short base. Maxillary palp not widened (width of maxillary palp / length of 3rd antennomere = 1.0–1.1). Length of antennae greater than pronotal length (ratio antenna / pronotum from tip of anterior pronotal angle to tip of posterior pronotal angle = 1.2–1.3). 3rd antennomere relatively long (length ratio of antennomere 3rd / 2nd = 2.8–3.0).

Pronotal disc transverse (middle of pronotum length / width ratio = 0.4–0.5); dull, with fine punctures (the intervals between the punctures are greater than the 3 diameters of the puncture). Anterior pronotal angles sharp and slightly protruding towards apex. Lateral margins of pronotum narrowing towards apex. Apophyseal and basal depressions on pronotal disc present; apophyseal depressions trapezoidal. Pronotal hypomera dull; without punctures.

Elytra oblong (elytra length / width ratio = 1.1–1.2). Elytral striae with fine punctures (sometimes absent). Elytral intervals shiny, non-convex; with conspicuous punctures (the intervals between the punctures are greater than the 3 diameters of the puncture). Elytral base slightly sinusoidal. Elytral humeri rounded, not protruding laterad. Wings absent. Scutellum triangular.

Intercoxal process protruding towards mesoventrite. Metaventrite reduced (length ratio cavity of hind coxa / metaventrite between the insertions of mid and hind coxae ca. 2). In both sexes abdominal process without tubercles; relatively narrow (process of 1st abdominal ventrite / process of metaventrite = 2.1–2.2). 5th abdominal ventrite with complete bordering; punctures fine (the intervals between the punctures are greater than the 2 diameters of the puncture).

Male legs. Protarsi slightly widened. Protibiae as in Fig. 39. Metafemorae with an hair fringe. Female legs. Protarsi slightly widened. Other leg parts simple.

Male genitalia. Parameres narrowing towards apex; length equal to the 0.2 of the rest of aedeagal tegmen. Clavae straight. Female genitalia. Paraproct longer than coxites. Spermatheca with narrow ducts.

**Distribution.** This species has been collected in the following ecoregions of West Africa (Ivory Coast, Republic of Benin, Republic of Ghana, Republic of Guinea, Togolese Republic): Eastern Guinean forests, Guinean forest-savanna mosaic, West Sudanian savanna (Fig. 44).


**Selinus striatus** (Fabricius, 1794)
http://species-id.net/wiki/Selinus_striatus
Figs 11, 21, 44, 61


**Redescription.** Habitus as in Fig. 61. Body length = 10.0–11.0 mm. Elytra wider and longer than pronotum (width ratio elytra / pronotum = 1.1–1.2; length ratio elytra / the middle of pronotum = 2.7–2.9).

Dorsal side of head dull, with punctures (the intervals between the punctures are smaller than the diameter of the puncture). Frontoclypeal suture fine. Clypeal emargination relatively deep (clypeal emargination width / depth ratio = 4.0–4.4). Mentum with median part wide. Submentum with short base. Maxillary palp not widened (width of maxillary palp / length of 3rd antennomere = 1.1–1.3). Length of antennae greater than pronotal length (ratio antenna / pronotum from tip of anterior pronotal angle to tip of posterior pronotal angle = 1.2–1.3). 3rd antennomere relatively long (length ratio of antennomere 3rd / 2nd = 2.8–3.0).

Pronotal disc transverse (middle of pronotum length / width ratio = 0.4–0.5); dull, with fine punctures (the intervals between the punctures are smaller than the diameter of the puncture). Anterior pronotal angles sharp and slightly protruding towards apex. Lateral margins of pronotal disc narrowing towards apex. Apophyseal and basal depressions on pronotal disc present; apophyseal depressions trapezoidal. Pronotal hypomera dull; without punctures.

Elytra oblong (elytra length / width ratio = 1.1–1.2). Elytral striae with fine punctures (sometimes absent). Elytral intervals shiny, non-convex, with conspicuous punctures (the intervals between the punctures are smaller than the diameter of the puncture). Elytral base slightly sinusoidal. Elytral humeri rounded, not protruding laterad. Wings absent. Scutellum triangular.
Intercoxal process protruding towards mesoventrite. Metaventrite reduced (length ratio cavity of hind coxa / metaventrite between the insertions of mid and hind coxae ca. 2). In both sexes abdominal process without tubercles; relatively narrow (process of 1st abdominal ventrite / process of metaventrite = 2.1–2.2). 5th abdominal ventrite with complete bordering; punctures fine (the intervals between the punctures are greater than the 2 diameters of the puncture).

Male legs. Protarsi slightly widened. Male protibiae with very shallow dilatation near the middle. Metafemorae with an hair fringe. Female legs. Protarsi slightly widened. Other leg parts simple.

Male genitalia. Parameres narrowing towards apex; length equal to the 0.2 of the rest of aedeagal tegmen (Fig. 21). Clavae straight (Fig. 21). Female genitalia. Paraproct longer than coxites. Spermatheca and bursa copulatrix as in S. planus.

**Distribution.** This species has been collected in the following ecoregions of West Africa (Ivory Coast, Republic of Ghana, Republic of Guinea, Republic of Mali): Eastern Guinean forests, Guinean forest-savanna mosaic, West Sudanian savanna, Western Guinean lowland forests (Fig. 44).

**Acknowledgments**

I am grateful to Laurent Soldati (France), Patrice Bouchard (Kanada) and the anonymous reviewer and for the valuable comments to the previous versions of this manuscript.
References


Integrative taxonomy of New Caledonian beetles: species delimitation and definition of the *Uloma isoceroides* species group (Coleoptera, Tenebrionidae, Ulomini), with the description of four new species

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§ http://zoobank.org/D0ABC503-75A3-4DB4-94FF-6F308124A1E1
¶ http://zoobank.org/12A8478C-2759-4C03-9532-F0C28B8B5CEB
#

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Academic editor: P. Bouchard | Received 15 November 2013 | Accepted 3 March 2014 | Published 12 June 2014


Abstract

New Caledonia is an important biodiversity hotspot with much undocumented biodiversity, especially in many insect groups. Here we used an integrative approach to explore species diversity in the tenebrionid genus *Uloma* (Coleoptera, Tenebrionidae, Ulomini), which encompasses about 150 species, of which 22 are known from New Caledonia. To do so, we focused on a morphologically homogeneous group by

* These authors have contributed equally and are considered joint first authors

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comparing museum specimens with material collected during several recent field trips. We also conducted molecular phylogenetic analyses based on a concatenated matrix of four mitochondrial and three nuclear genes for 46 specimens. The morphological study allowed us to discover and describe four new species that belong to the group of interest, the *Uloma isoceroides* group. Molecular analyses confirmed the species boundaries of several of the previously described species and established the validity of the four new species. The phylogenetic analyses also provided additional information on the evolutionary history of the group, highlighting that a species that was thought to be unrelated to the group was in fact a member of the same evolutionary lineage. Molecular species delimitation confirmed the status of the sampled species of the group and also suggested some hidden (cryptic) biodiversity for at least two species of the group. Altogether this integrative taxonomic approach has allowed us to better define the boundaries of the *Uloma isoceroides* species group, which comprises at least 10 species: *Uloma isoceroides* (Fauvel, 1904), *Uloma opacipennis* (Fauvel, 1904), *Uloma caledonica* Kaszab, 1982, *Uloma paniei* Kaszab, 1982, *Uloma monteithi* Kaszab, 1986, *Uloma robusta* Kaszab, 1986, *Uloma clamensae* sp. n., *Uloma condaminei* sp. n., *Uloma jourdani* sp. n., and *Uloma kergoati* sp. n. We advocate more studies on other New Caledonian groups, as we expect that much undocumented biodiversity can be unveiled through the use of similar approaches.

**Keywords**
Biodiversity hotspot, New Caledonia, New species, Phylogenetics, Taxonomy, Systematics, Tenebrionidae, *Uloma*

**Introduction**

New Caledonia, situated in the southwestern part of the Pacific region, is an old oceanic island that is considered as an important biodiversity hotspot (Myers et al. 2000; Lowry et al. 2004). As such it harbours a high concentration of endemic species, especially in evergreen forests that are endangered by nickel mining, human-caused wildfires and biological invasions (Lowry et al. 2004). To counter these threats more surveys are needed, to gain a better knowledge of the species richness and its distribution, which is desperately needed to support the establishment of relevant conservation policies (Bouchet et al. 1995; Mittermeier et al. 1996; Gargominy et al. 1996; Bouchet et al. 1998; Pascal et al. 2008).

Through the advent of molecular systematics, taxonomists have increased species discoveries and documented unsuspected cryptic biodiversity on biodiversity hotspots (Pons et al. 2006; Monaghan et al. 2009; Vieites et al. 2009). For New Caledonia, several phylogenetic studies have been carried out on various endemic groups (e.g. Swenson et al. 2001; Bartish et al. 2005; Murienne et al. 2005; Robillard and Desutter-Grandcolas 2006; Balke et al. 2007a; Smith et al. 2007; Espeland et al. 2008; Murienne et al. 2008; Sharma and Giribet 2009; Espeland and Johanson 2010; Cruaud et al. 2012; Heads 2013). New Caledonian biodiversity is thought to be very ancient and slow accumulating, as attested by local relicts such as tree ferns, conifers (e.g. *Agathis* and *Araucaria*), early angiosperm lineages (e.g. *Amborella*), more derived angiosperms (e.g. *Nothofagus*, palm trees, *Proteaceae*), unique birds (*Rhynochetos*), or harvestman invertebrates (*Troglosironidae*). Though the presence of these lineages is often interpreted as an indication of old vicariance events (Ladiges and Cantrill 2007; Heads 2008,
Integrative taxonomy of New Caledonian beetles: species delimitation and definition...

numerous studies have indicated that the contribution of recent dispersals events is more likely (see Grandcolas et al. 2008; Keppel et al. 2009; Espeland and Murienne 2011; Cruaud et al. 2012; Pillon 2012 for reviews or meta-analyses). The geological evidence also emphasizes a dynamic recent history (Cluzel et al. 2001; Pelletier 2006; Schellart et al. 2006 but see Ladiges and Cantrill 2007; Heads 2013). The fact that most clades appear to have recently diversified implies that the morphological differentiation between species may be shallow and hard to detect even for specialists, which argues in favour of more integrative taxonomic approaches mixing molecular, morphological, ecological, and geographic data (Padial et al. 2010; Schlick-Steiner et al. 2010).

Because New Caledonia is still subjected to numerous threats (biological invasions, mining, forest logging and burning), a particular effort must be undergone to discover, document and protect its unique biodiversity. Although its categorization as a biodiversity hotspot is based on estimates of diversity on vascular plants and vertebrate groups, it likely also applies to other groups such as insects (Stork and Habel 2014). The insect fauna of New Caledonia included about 4000 known species in 1993 with an estimated total of 16,000 (Chazeau 1993). Specific surveys of various groups of New Caledonian insects have underlined very high proportions of endemics species (e.g. Balke et al. 2007b; Kuschel 2008; Espeland and Johanson 2010), which parallel those of plants (Novotny et al. 2006). Other factors such as environmental filtering (e.g. role of ultramafic soils; Ladiges and Cantrill 2007; Espeland et al. 2008; Pillon et al. 2010) may also be invoked to explain this pattern. An example of recent increase in taxonomic knowledge through both morphology and molecular studies is in caddisflies (Trichoptera), for which 132 species were initially recorded from New Caledonia (of which 130 are endemic) (see also Balke et al. 2007b). Fifty-eight more species were recently discovered using a combination of data (Malm and Johanson 2007; Espeland and Johanson 2008a,b; Johanson and Keijser 2008; Malm and Johanson 2008a,b; Oláh and Johanson 2008), and more than 200 undescribed species so far are present in the collections at the Swedish Museum of Natural History (Espeland et al. 2008). Altogether this demonstrates the need for a more complete biodiversity inventory in order to set more adequate conservation priorities for the future.

In the darkling beetle family (Coleoptera, Tenebrionidae), the proportion of New Caledonian species that are endemic is extremely high (215 out of 234 species; Kaszab 1982, 1986). The species richness of New Caledonian tenebrionids is also likely underestimated, because few studies (and no molecular-based studies) have been conducted on this group since Kaszab’s monographic works on the archipelago (Kaszab 1982, 1986). In this study we chose to focus on Uloma (Tenebrioninae, Ulomini), a genus with a worldwide distribution that encompasses at least 150 species (Matsumoto and Nishikawa 1986), of which 22 are endemic to New Caledonia (Kaszab 1982, 1986). Most of these species cannot be reliably assigned to a homogeneous species group (Kaszab 1982, 1986). The only exception is a group of five species (U. caledonica, U. isoceroides, U. monteithi, U. paniei and U. robusta), which share the following combination of characters: (i) head short and broad; (ii) male with clypeus and frons located in the same plane, not impressed along the frontoclypeal suture, flat, with a shagreened dull surface; (iii) metathorax very short; (iv) flightless.
Here we aim at exploring species diversity in this group by comparing the specimens we collected through several field missions in New Caledonia with material from several collections and museums. We also use molecular phylogenetics that allows us to: (i) reconstruct the evolutionary history of the group; (ii) assess species boundaries within the group and confirm the existence of potential new species.

Material and methods

Sampling of specimens

Specimens were collected during several biodiversity surveys undergone between March 2008 and November 2011 in New Caledonia (project ANR BIONEOCAL). Most specimens were caught by hand through a careful examination of fallen branches, rotten logs and standing trees (either unhealthy or dead). In addition, we used headlamps at night to find and collect specimens where they were most active. For this study we tentatively included all specimens that possibly belonged to the group of interest. We also included specimens from *Uloma opacipennis*, as preliminary analyses conducted on a larger molecular dataset indicate that this species is potentially a member of the group of interest. Morphological examinations of specimens allowed us to determine that the sampled specimens likely corresponded to seven distinct morphospecies (see Table 1 and the Taxonomy results), of which four could not be assigned to any known species. As outgroups, we also used two morphologically unrelated species of *Uloma* that are not distributed in New Caledonia (*Uloma freyi* endemic to the Fiji Islands, and *Uloma rufa* widespread in Europe). *Uloma rufa* was used to root the tree based on the results of Kergoat et al. (2014).

DNA extraction and sequencing

Total DNA of 46 specimens was extracted following the non-invasive protocol of extraction of Gilbert et al. (2007). Four mitochondrial gene fragments were sequenced, namely 687 bp of the cytochrome oxidase I (COI), 458 bp of the cytochrome b (Cyt b), 380 bp of the ribosomal 12S RNA (12S), and 532 bp of the ribosomal 16S RNA (16S). Three nuclear gene regions were sequenced, namely 746 bp of the domain D2-D3 of the 28S ribosomal DNA (28SD2-D3), 459 bp of wingless (Wg), and 1881 bp of the 18S ribosomal DNA (18S). All these genes were chosen because they are known to be informative in phylogenetic analyses of tenebrionid beetles (Papadopoulou et al. 2009, 2010; Condamine et al. 2013) or in other coleopteran groups (McKenna et al. 2009; Kergoat et al. 2011; Deuve et al. 2012). Polymerase chain reaction amplifications were performed with standard settings for primer sequences and thermocycler procedures (see Belshaw and Quicke 2002; Kergoat et al. 2004, 2005; Wild and Maddison 2008 for additional information).

The PCR products were processed by the French sequencing centre Genoscope using a BigDye 3.1 sequencing kit and Applied 3730xl sequencers. The resulting
Table 1. Taxon sampling. All specimens are from New Caledonia with the exception of the individuals of *Uloma freyi* and *Uloma rufa*.

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‘Monts Koghis’
Uloma kergoati sp. n.
LSOL.01122
‘Monts Koghis’
Uloma kergoati sp. n.
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Uloma kergoati sp. n.
LSOL.01805
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LSOL.01806
‘Monts Koghis’
Uloma opacipennis (Fauvel, 1904)
LSOL.01020
‘Mont Do’
Uloma opacipennis (Fauvel, 1904)
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Uloma opacipennis (Fauvel, 1904)
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LSOL.02236
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Uloma opacipennis (Fauvel, 1904)
LSOL.02251
‘La Guen, Panié’
Uloma opacipennis (Fauvel, 1904)
LSOL.02260
‘Dawenia, Panié’
Uloma opacipennis (Fauvel, 1904)
LSOL.02261
‘Dawenia, Panié’
Uloma rufa (Piller & Mitterbacher, 1783)
U.rufa.1
(France)
12S
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KJ510076
KJ510077
KJ510078
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KJ510081
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GenBank accession No.
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18S
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KJ510156
KJ510157
KJ510158
KJ003714

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sequences of complementary strands were further edited and reconciled using Ge-
neious 5.1 (available at: www.geneious.com). All the sequences generated in this
study were deposited in GenBank (KJ509982-KJ51017, see Table 1 for details). For
all protein-coding genes (COI, Cyt b and Wg), we used Mesquite 2.75 (available at:
www.mesquiteproject.org) to check coding frames for possible errors or stop codons.
Alignment of non-coding genes (12S, 16S, 28SD2-D3, and 18S) was carried out us-
ing Muscle (Edgar 2004) with default option settings. The combination of the seven
gene fragments resulted in a matrix of 46 taxa and 5143 aligned characters.

Phylogenetic analyses

Maximum likelihood (ML) analyses were performed with the raxmlGUI package v1.3
(Silvestro and Michalak 2012), which relies on RAxML v.7.4.2 executables (Stamatakis
2006). We used partitioned analyses (Nylander et al. 2004) with one partition for the
mitochondrial genes and one partition for the nuclear genes. For each partition, we com-
bined a general time reversible (GTR) substitution model with a CAT (category) model,
which optimizes the evolutionary rate of individual sites using a fixed number of rate
categories. To account for by the fact that numerous sites were invariable we also added an
additional parameter to the model (+I; proportion of invariable sites). Then we conducted
100 independent runs with corresponding GTR +CAT +I models. Support of trees was
assessed using 1000 non-parametric bootstrap replicates. Nodes supported by bootstrap
values (BV) ≥ 70% were considered as strongly supported following Hillis and Bull (1993).

To determine putative molecular species clusters on our dataset we then use Pois-
son tree processes (PTP) models (Zhang et al. 2013). Because this approach does not
require ultrametrization of trees (and its associated biases), it constitutes an elegant
alternative to other species delineation models such as the General mixed Yule coales-
cent model of Pons et al. (2006). With the PTP model, speciation or branching events
are modelled in terms of number of substitutions (represented by branch lengths), so
it only requires a phylogenetic input tree. Corresponding analyses were conducted on
the web server for PTP (available at http://species.h-its.org/ptp/) using the best ML
tree resulting from the raxmlGUI analysis.

Morphological study

Specimens examined for this study are deposited in the following institutions and col-
lections (all collection codes follow Evenhuis (2008)):

BMNH The Natural History Museum, London, United Kingdom.
BPBM Hawai‘i, Bernice P. Bishop Museum, Honolulu, USA.
CBGP Centre de Biologie pour la Gestion des Populations, Montferrier-sur-Lez, France.
Specimens were glued on glue boards, then pinned, labelled and dry stored in insect boxes. The glue used (Cléopâtre™ ref. AD110P) to secure the specimens on the glue boards is water soluble and completely reversible. Male genitalia were also dissected and glued on the same glue board that their respective specimens. Pictures of specimens were taken by L. Soldati using the focus stacking system Entovision™ on the imaging platform of the CBGP. Morphological terms used in this study follow the terminology of Matthews and Bouchard (2008) and Matthews et al. (2010).

Results

Molecular phylogenetics

The ML analyses yield a best ML tree with a likelihood score of -11607.44 (Fig. 1). All the nodes that lead to putative taxa (i.e. morphospecies) are well-supported (BV ≥ 70%). All members of the group of interest are recovered in a well-supported clade (BV of 92%). Within this clade, the representatives of the *Uloma jouldani* sp. n. are in a sister position to all remaining NC representatives. Then, two major clades can be distinguished, each of them corresponding to three morphospecies. In the first, the two representatives of *U. isoceroides* are sisters to *U. clamensae* sp. n. and *U. condaminei* sp. n. In the second *U. kergoati* sp. n. is sister to a clade encompassing representatives of *U. caledonica* and *U. opacipennis*. At the intraspecific level it is also worth highlighting the fact that representatives of *U. jouldani* sp. n. are clustered into two well-differentiated clades (respectively supported by a BV of 77% and 96%). Regarding molecular species delimitation, the PTP analyses recover nine putative species clusters (see Fig. 1) for the seven sampled morphospecies belonging to the group of interest. Additional species clusters were found in *U. isoceroides* (two distinct clusters encompassing one individual each) and *U. jouldani* sp. n. (two distinct clusters encompassing six and four specimens, respectively).

Taxonomy

The *Uloma isoceroides* species group is named after *Uloma isoceroides*, the first described species of the group (page 182 in Fauvel 1904). This constitutes 10 species, four of
which are new. All but one (*U. opacipennis*) can be characterized by the following combination of characters: (i) head short and broad; (ii) male with clypeus and frons located in the same plane, not impressed along the frontoclypeal suture, flat, with a shagreened dull surface; (iii) metathorax very short. Though *Uloma opacipennis* is morphologically distinct from the other members of the group (see the corresponding diagnosis section) its inclusion is fully supported by the results of the molecular analyses.
**Uloma caledonica** Kaszab, 1982
http://species-id.net/wiki/Uloma_caledonica
Figs 2A, 3A–B


**Type locality.** Saint Louis, Forêt de Thi.

**Type specimens.** Holotype male (BPBM). Paratypes: 11 males and 10 females (BPBM), two males and one female (USNM), three males (IRSNB), none examined; one male, original label: “Nouvelle-Calédonie, 1893, Coll. Ed. Fleutiaux” (MNHN); one male, original label: “Nouvelle-Calédonie” (HNHM), both examined.

**Diagnosis.** *Uloma caledonica* is one of the four species of the group in which the mentum of the male is completely glabrous and flat. It differs from these three species (*U. jourdani*, *U. isoceroides* and *U. kergoati*) by the longer metaventrite (between meso- and metacoxae approximately as long as a meso-coxa), the humeri slightly developed, the elytral striae of punctures strongly marked and developed to apex, and the pronotal punctuation barely visible. The shape of the aedeagus is also unique among the New Caledonian *Uloma* species, with the parameres bottleneck-shaped and triangularly notched at the apex.

**Distribution.** Kaszab (1982: 87) cited this species from the following localities: Saint-Louis (Forêt de Thi), Rivière Bleue (Yaté), La Couèle-Yaté Rd., Mt Koghi, Nouméa, Île des Pins. “Neukaledonien (Grande Terre SO, Île des Pins)”.


**Uloma clamensae** L. Soldati, sp. n.
http://zoobank.org/D693C69B-FC2C-43D0-9BDC-93D7D95D26F5
http://species-id.net/wiki/Uloma_clamensae
Figs 3C–D, 4A, B, C, D

**Type specimens.** Holotype male, pinned, with genitalia glued on the same card as the specimen itself. Original label: “Nouvelle-Calédonie, Putchaté, Atéu, 23.IV.2009, E. Baby leg. / 20°59.39’S, 164°54.04’E, ca 370 m alt.” / *Uloma clamensae* m. n. sp. L. Soldati det. 2013, HOLOTYPE ♂ (red printed label) (MNHN); Paratypes, same data as Holotype: one female (MNHN), one male (CS).

**Diagnosis.** *Uloma clamensae* is closely related to *Uloma condaminei* sp. n. The two species are so similar that the only reliable way to separate them is to compare their male genitalia. *Uloma clamensae* and *U. condaminei* can also be distinguished from all the other *Uloma* species of New Caledonia by the unique structure of the mentum in the male: the mentum pilosity is reduced to two apical hair tufts on each side (Fig. 6F–G).
In the case of isolated females, the geographic distribution may distinguish *U. clamensae* from *U. condaminei*.

**Description.** Length 9.0–9.5 mm; width 3.2–3.5 mm. Shining, pitchy dark brown. Antennae, mouthparts, legs and elytra reddish-brown.

Head (Fig. 3E).

Male: Transverse, genae straight in front of the eyes, then continuous in curved line with the clypeus. Frontoclypeal suture superficially impressed. Frons and clypeus fused, with shagreened dull surface, covered with extremely fine, sparse and barely visible punctures. Vertex convex, shining and separated from the frons by a transverse depression that extends behind the eyes. Tempora (densely) and vertex (sparsely) coarsely punctured.

Female: in contrast to male, frontoclypeal area finely and quite densely punctate over a shining background. Frontoclypeal suture shallowly impressed.
Figure 4. *Uloma clamensae*: A habitus (dorsal view) B habitus (lateral view) C habitus (ventral view) D anterior tibia (upper face) E head (dorsal view). Scale bar: 5 mm.
Antennae (Fig. 4E) gradually becoming transverse and expanded from antennomere 5. Antennomeres 5–9 flattened with apices more or less protruding in middle, especially 7th.

Mentum of the male (Fig. 4C) cordate, with two oblique lateral grooves near the base and two apical dense hair tufts, all arranged symmetrically in relation to midline; disc slightly concave longitudinally, unpunctured and shining. Male mentum of *U. clamensae* is similar to the one of *U. condaminei* (see Fig. 6F–G). Female mentum cordate but narrower, not transverse, with the two oblique lateral grooves merging at base to form a U-shape in between, disc flat, smooth and shining, without punctuation.

Pronotum: about 1.2 times wider than long, sides subparallels, widest around the middle. Rim on the anterior margin at middle usually obliterated, sometimes slightly visible; base unmargined, with exception of two very short folds located at the level of the two concave curves of external margin. Anterior angles 90° but smooth at the top and slightly protruding forward, posterior angles obtuse. Lateral rims becoming progressively thinner from the base toward the anterior angles. Whole upper surface of the pronotum very finely punctate, sparser on the disc but denser on the sides.

Male: antero-median depression of pronotum well impressed, not reaching half of pronotal length, its posterior edge arcuate and delimited by four very faint elevations. The lateral bumps anterolaterally bordering the depression low and not projecting to anterior edge. Interior of depression somewhat more strongly punctate than rest of pronotal surface.

Female: pronotum regularly convex, without antero-median depression and overall finely punctate.

Prosternal process in lateral view obliquely bent beneath procoxae.

Elytra quite convex, humeral angles of lateral margin protruding. Lateral margin barely visible in dorsal view except around middle. Each elytron bears nine grooved and punctured striae and a faint scutellary striole. Strial punctures slightly wider than grooves. Elytral intervals nearly flat on disc and becoming slightly convex laterally and toward apex, covered with fine and superficial punctuation.

Metaventrite short, length between meso- and metacoxae less than half the length of mesocoxa.

Abdomen. Abdominal ventrites 1-4 (Fig. 4C) finely and superficially punctate on a narrow median longitudinal strip. On each side of this longitudinal strip, punctation becomes progressively larger and sparser toward the sides and the integument’s surface is slightly striate longitudinally. The apical ventrite covered with fine scattered punctation, its outer margin without rim.

Legs. Anterior tibiae (Fig. 4D) without carina on their upper face and strongly notched at the base of nearly half the length of inner side.

Aedeagus: tergal face (Fig. 3C), with basal two-thirds of parameres bottleneck-shaped, then abruptly enlarged and securiform at the apex. In lateral view (Fig. 3D), parameres bisinuate and narrowed toward apex.

**Etymology.** This new species is named after A.-L. Clamens, biologist and member of the “All Blaps” team.

**Distribution.** *Uloma clamensae* is currently only known only from its type locality in New Caledonia.
Uloma condaminei L. Soldati, sp. n.

http://zoobank.org/8EEBB1B0-79AD-4FEB-930F-FAF3C358805C
http://species-id.net/wiki/Uloma_condaminei
Figs 3E–F, 5A, B, C, D, E, 6F–G


**Diagnosis.** As underlined beforehand, Uloma condaminei is morphologically closely related to Uloma clamensae sp. n. It is also morphologically related to Uloma paniiei Kaszab, 1982 and Uloma robusta Kaszab, 1986 with whom it shares a similar type of aedeagus. Uloma condaminei can be distinguished from the former two by looking at the pilosity of the mentum. In U. condaminei, mentum’s pilosity is reduced to two apical hair tufts on each sides (Fig. 6F–G) while in U. paniiei and in U. robusta the sides of the mentum are completely fringed, from the lateral grooves to the anterior edge. Furthermore, the basal notch at the inner side of the anterior tibiae is larger and deeper (more than one-third of the inner side total length). The average size of U. condaminei is also smaller (8.0–10.0 mm instead of 10.5–12.2 mm).

**Description.** Length 8.0–10 mm; width 3.2–4.0 mm. Shining, pitchy dark brown. Antennae, mouthparts, legs and sometimes elytra reddish-brown.

Head: (Fig. 5E) Male: Transverse, genae rounded and continuous in curved line with the clypeus. Frontoclypeal suture not grooved. Frons and clypeus fused in a flat shagreened and dull surface covered with extremely fine, sparse and barely visible punctures. Vertex convex and separated from the frons by a light transverse depression that links the tempora together behind the eyes. Tempora (densely) and vertex (sparsely) coarsely punctured. Female: contrary to the male, the frontoclypeal area is finely punctate and shining and, at the location of the suture, there is a slight curved depression.

Antennae (Fig. 5E) gradually becoming transverse and expanded from antennomere 5. Antennomeres 5–7 flattened with the apical edges more or less lobate and dull.
Figure 5. *Uloma condaminei*: **A** habitus (dorsal view) **B** habitus (lateral view) **C** habitus (ventral view) **D** anterior tibia (upper face) **E** head (dorsal view). Scale bar: 5 mm.

Mentum (Figs. 6F–G) similar to *U. clamensae*, cordate, flat, with two oblique lateral grooves near the base and two apical dense hair tufts (Fig. 6F), all arranged symmetrically in relation to midline; disc unpunctured and shining. In the female,
Figure 6. *Uloma condaminei*: F forebody (lateral view) G forebody (ventral view). The arrows show the apical hair tufts on the mentum.
the mentum’s shape is rounder, the two oblique lateral grooves are closer, longer and deeper so that the midline appears to be convex and the anterior emargination very light.

Pronotum: about 1.2 times wider than long, sides weakly arcuate, widest around the middle. Rim on the anterior margin disappears completely on a short length in the middle; base unrimmed, with exception of two short folds located at the level of the two concave curves of external margin. Anterior angles 90° but smooth at the top and slightly protruding forward, posterior ones obtuse. Lateral rims becoming progressively thinner from the base toward the anterior angles. Whole upper surface of the pronotum finely and densely punctate, sparser on the disc but denser on the sides.

Male: antero-median depression of pronotum well impressed, not reaching half of pronotal length, its posterior edge arcuate and delimited by four very faint elevations. The lateral bumps anterolaterally bordering the depression low and not projecting to anterior edge. Interior of depression somewhat more strongly punctate than rest of pronotal surface.

Female: pronotum regularly convex, without antero-median depression and overall punctate.

Prosternal process in lateral view obliquely bent beneath procoxae.

Elytra quite convex, humeral angles of lateral margin protruding. Lateral margin barely visible in dorsal view except in the middle. Each elytron bears nine grooved striae of punctures and a faint scutellary striole. Strial punctures are slightly wider than grooves. Elytral intervals nearly flat on disc and becoming slightly convex laterally and toward apex, covered with fine and superficial punctuation.

Metaventrite short (Fig. 5C), between meso- and metacoxae about as long as the length of a mesocoxa.

Abdominal ventrites 1–4 (Fig. 5C) finely and densely punctate on a narrow median longitudinal strip. On each side of this longitudinal strip, punctuation becomes progressively larger and sparser toward the sides and the integument’s surface is slightly striate longitudinally. The anal ventrite finely and sparsely punctate, its outer margin without rim, except a very short fold on both sides, just in front of the base.

Anterior tibiae (Fig. 5D) with only a faint trace of carina on their upper surface and strongly notched at base of at least one-third of the length of the inner side.

Aedeagus: on tergal face (Fig. 3E), the basal two-third of the parameres are bottleneck-shaped, then suddenly enlarged and truncate at the apex. In lateral view (Fig. 3F), parameres are bisinuate and narrowed toward apex.

Etymology. This new species is named after our friend and colleague Dr. F.L. Condamine who was a PhD student at the time we prospected in New Caledonia. He is also a member of the “All Blaps” team.

Distribution. Uloma condaminei is currently known only from New Caledonia where it is endemic.
Uloma isoceroides (Fauvel, 1904)
http://species-id.net/wiki/Uloma_isoceroides
Figs 2B, 3G–H


Type locality. Baie du Prony, Mont Mou, Ourail, Kanala.

Type specimens. Lectotype male and paralectotypes (designated by Kaszab 1982) males and females of Melasia isoceroides Fauvel (IRSNB), none examined.

Diagnosis. Uloma isoceroides is one of the four species of the group in which the mentum of the male is completely glabrous and flat. It can be separated from U. calcedonica by the shorter metaventrite, (between meso- and metacoxae hardly longer than half of the length of a mesocoxa) and the humeri not developed. It differs from U. jourdani by the outer margin of terminal ventrite (anal sternite) regularly arcuate, without lateral sinuosities, the mentum as long as broad or longer, not cordate. Moreover, all the male antenomeres are shining and the aedeagus is different. It differs also from U. kergoati by the elytral striae of punctures normally marked and developed to the apex, the pronotum quite densely and sharp punctate, and the different aedeagus. Its size is also smaller in average (7.0-8.8 mm). Aedeagus (Fig. 3G, H) similar to the one of U. calcedonica (with the parameres bottleneck-shaped) but truncate (not notched) at the apex.

Distribution. Kaszab (1982: 86) cited this species from the following localities: Baie du Prony, Mt Mou, Ourail, Mt Rembai, Mt Do, Kanala [Canala], Plaine des Lacs, Pic du Pin, Rivière Bleue, Mt Koghi, Nouméa. “Neukaledonien (Grande Terre, Zentral Massiv und SW”.


Discussion: As underlined by the results of the PTP molecular species delimitation analyses, there is potentially some level of cryptic diversity for this species. One putative species corresponds to the material collected in the Plateau de Dogny, whereas the other putative species corresponds to material collected in the Tchamba forest mountain range. Further studies based on a larger sampling from additional localities should clarify this finding and possibly discern one or more cryptic species.
Uloma jourdani L. Soldati, sp. n.
http://zoobank.org/390037E3-3B06-48F9-A784-0A23B2117BC8
http://species-id.net/wiki/Uloma_jourdani
Figs 3I–J, 7A, B, C, D, E


Diagnosis. The completely glabrous and flat mentum of U. jourdani males is also found in U. caledonica, U. isoceroides and U. kergoati. Uloma jourdani can be distinguished from U. caledonica by its shorter metaventrite (the part between meso- and metacoxae hardly longer than half of the length of a mesocoxa), by the reduced humeri and also by different male aedeagus. It differs from U. isoceroides and U. kergoati by the shape of the terminal ventrite (anal sternite), by the presence of a dull shagreened patch on the upper face of male antennomeres 5–7 and also by differences in male aedeagus.

Description. Length 8.0–9.0 mm; width 4.0–4.2 mm. Shining, pitchy dark brown, elytra often brighter, dark red-brown. Antennae, mouthparts, legs and elytra reddish-brown.
Head (Fig. 7E).
Male: Transverse, genae straight just in front of the eyes, then continuous in curved line with the clypeus. Frontoclypeal suture shallowly impressed. Frons and clypeus fused in a shagreened and dull surface covered with extremely fine, sparse and barely visible punc-
tures. Vertex convex, shining and separated from the frons by a deep transverse impression that extends behind the eyes. Tempora and vertex (more sparsely) coarsely punctured.

Female: contrary to the male, the frontoclypeal area is finely and densely punctate over a shining background. The frontoclypeal junction is slightly convex and there are two feebly impressed oblique lateral lines at the place of the clypeo- genal suture. In between, the transversal line of the suture is barely visible.

Antennae (Fig. 7E) gradually becoming transverse and expanded from antennomere 5. Antennomeres 5–9 flattened with the apical edges more or less protruding in the middle, especially the 7th. In the males, antennomeres 5-7 are dull and shagreened on their upper face only.

Mentum (Fig. 7C) transverse, cordate, flat, with two oblique lateral grooves arranged symmetrically in relation to midline; disc flat, covered with a dense, extremely fine and horizontally confluent punctation. In the female, the mentum is similar to the male's one, but the punctation is less dense and distinct.

Pronotum: about 1.3 times wider than long. Sides narrow in light curve from rear to front, widest just in front of the base. Rim on the anterior margin obliterates completely in the middle; base unrimmed, with exception of two very short folds located at the level of the two concave curves of external margin. Anterior angles 90° but smooth at the top and slightly protruding forward, posterior ones obtuse. Lateral rims becoming progressively thinner from the base toward the anterior angles. Whole upper surface of the pronotum finely punctate, sparser on the disc but denser on the sides.

Male: antero-median depression of pronotum well impressed, quite broad, not reaching half of pronotal length, its posterior edge arcuate and delimited by four very faint elevations. The lateral bumps anterolaterally bordering the depression’s sides forward are low.

Female: pronotum regularly convex, without antero-median depression and overall finely punctate, but denser on the sides.

Prosternal process in lateral view in steep slope beneath procoxae.

Elytra convex, slightly oval, sides not subparallel. Humeral angles of lateral margin feebly protruding and generally covered by the posterior angles of pronotum. Lateral margin invisible in dorsal view, except at the level of the humeral angles and at the rear of elytra. Each elytron bears nine grooved striae of punctures and a faint scutellary striole. Strial punctures are slightly wider than grooves. Elytral intervals flat on disc and becoming very slightly convex laterally - but not at the apex - covered with fine and superficial punctuation.

Metaventrite short, between meso- and metacoxae, about half the length of a mesocoxa.

Anterior tibiae (Fig. 7D) with only a faint trace of carina on their upper surface and strongly notched at base of at least one-fourth of the length of the inner side.

Aedeagus: on tergal face (Fig. 3I), the basal two-third of the parameres are bottleneck-shaped, then slightly enlarged and securiform at the apex. In lateral view (Fig. 3J), parameres are bisinuate and narrowed toward apex.

**Etymology.** This new species is named after our friend Dr. H. Jourdan (IRD Nouméa) great connoisseur of New Caledonia. He is also a member of the “All Blaps” team.
Distribution. At present, *Uloma jourdani* is only known from the surroundings of Dawenia, in a valley situated at the foot of the western slopes of Mount Colnett in New Caledonia.

Discussion. As underlined by the results of the PTP molecular species delimitation analyses, there is potentially some level of cryptic diversity for this species. One putative species correspond to the material collected in Dawenia (in the Panié mountain range), whereas the other putative species correspond to material collected in La Guen and Wewec (in the Panié mountain range). Both groups are apparently morphologically indistinguishable, but we cannot exclude the possibility that future studies may find some morphological differences between the two. To avoid complicating possible future taxonomic revisions, we chose to only select specimens from one of the two putative groups (i.e. the specimens collected in Dawenia) as reference for all the type material.

*Uloma kergoati* L. Soldati, sp. n.
http://zoobank.org/A06836E0-2321-44B0-8828-8049C9EA7AAD
http://species-id.net/wiki/Uloma_kergoati
Figs 3K–L, 8A, B, C, D, E


Diagnosis. The completely glabrous and flat mentum of *U. kergoati* males is also found in *U. caledonica*, *U. isoceroides* and *U. jourdani*. It differs from *U. caledonica* by its shorter metaventrite (hardly longer than half of the length of a mesocoxa), by the reduced humeri and also by differences in male aedeagus. It can easily be distinguished from *U. jourdani* by the shining surface of the upper face of all male antennomeres and the aedeagus. It also differs from *U. isoceroides* by the elytral striae of punctures that become finer and blurred toward apex; in addition, the male aedeagus of these two species are also very distinctive.

Description. Length 8.0–11 mm; width 3.8–4.2 mm. Shining, pitchy dark brown. Antennae, mouthparts, legs and elytra reddish-brown.

Head (Fig. 8E).

Male: Transverse, genae straight in front of the eyes, then continuous in curved line with the clypeus. Frontoclypeal suture faintly impressed. Frons and clypeus fused in a flat shagreened and dull surface covered with extremely fine, sparse and barely

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visible punctures. Vertex separated from the frons by a superficial transverse impression. Tempora coarsely punctured. Vertex with very fine and obsolescent punctures, the background dull like the frontoclypeal area.

Figure 8. *Uloma kergoati*: A habitus (dorsal view) B habitus (lateral view) C habitus (ventral view) D anterior tibia (upper face) E head (dorsal view). Scale bar: 5 mm.
Female: contrary to the male, the frontoclypeal area is finely punctate and shining and, at the location of the suture, there is a shallow curved depression.

Antennae (Fig. 8E) gradually becoming transverse and expanded from antennomere 5. Antennomeres 5–9 flattened with the apical edges more or less protruding.

Mentum (Fig. 8E) cordate, flat, with two oblique divergent lateral grooves near the base. In the female, the mentum is narrower, the two oblique lateral grooves are closer, larger and less oblique (i.e. more parallel), the anterior margin is truncate.

Pronotum. Male: about 1.2 times wider than long, sides nearly straight in the basal half, then regularly arcuate toward the anterior angles, widest in front of the middle. Rim on the anterior margin disappears in the middle at level of the antero-median depression; at the same place, the anterior margin is emarginate and concave. Base without rim, except two very short folds located at the level of the two concave curves of external margin. Anterior angles 90°, posterior ones slightly obtuse. Whole upper surface of the pronotum densely punctate, sparser on the disc but denser and finer on the sides. Antero-median depression of pronotum quite deep, not reaching half of pronotal length, its posterior edge arcuate with a slight median impression. Interior of antero-median depression more coarsely punctate than rest of pronotal surface, the ground dull and shagreened.

Female: regularly convex, without antero-median depression and overall sharply and densely punctate, the punctures finer on the sides. Pronotum widest at base, then narrowed toward the front; the anterior edge tri-sinuate.

Prosternal process in lateral view obliquely bent beneath procoxae.

Elytra. Elytra quite convex transversally, humeri reduced. Humeral angles of lateral margin protruding and divergent (especially in the males); sides subparallel on one-third of the basal part, then regularly acuminate. Lateral margin visible in dorsal view except at level of ventrites 1-2. Each elytron bears nine grooved striae of punctures that tend to obliterate at the apex and a scutellary striole. Strial punctures are slightly wider than grooves. Elytral intervals nearly flat, covered with fine punctuation on a shining ground.

Metaventrite short, between meso- and metacoxae about as long as half the length of a mesocoxa.

Abdomen. Abdominal ventrites 1–4 (Fig. 8C) finely and densely punctate on a narrow median longitudinal strip. On each side of this longitudinal strip, the punctuation becomes progressively larger and sparser toward the sides before mixing up with longitudinal striae, except on the 4th ventrite where the striae are less developed. The anal ventrite finely punctate, sparsely toward the sides, its outer margin without rim.

Legs. Anterior tibiae (Fig. 8D) without carina on their upper surface and strongly notched at base of about one fourth of the inner side length.

Aedeagus. On tergal face (Fig. 3K), basal two-third of the parameres are bottle-neck-shaped, then suddenly enlarged and arcuate at the apex, with two lateral teeth on each side. In lateral view (Fig. 3L), parameres are bisinuate and narrowed toward apex.

**Etymology.** This new species is named after Dr. G.J. Kergoat researcher at the CBGP, member of the “All Blaps” team and one of the “survivors” of the Kouakoué expedition.

**Distribution.** *Uloma kergoati* is currently known only from New Caledonia where it is endemic.
**Uloma monteithi** Kaszab, 1986
http://species-id.net/wiki/Uloma_monteithi
Figs 2C, 3M–N


**Type locality.** Aoupinié, 20 km NE Poya.

**Type specimens.** Holotype male. Original label: “NEW CALEDONIA, Aoupinié, 20 km NE Poya, 650 m, 18–19 May 1984, G. Monteith & D. Cook / Queensland Museum, Brisbane, Reg. N°T.10111 / Holotypus 1986 ♂ *Uloma monteithi* Kaszab” (QM); Paratypes (same data as Holotype): one female (QM) and one male (HNHM), all examined.

**Diagnosis.** Among the *Uloma isoceroides* species group, *Uloma monteithi* can easily be distinguished by the mentum which is concave along the longitudinal axis (flat in all the other species of this group), shining, unpunctured. Male anterior tibiae strongly notched at base up to nearly half of the length of the inner face, then they extend straight to the apex. Pronotum upper surface finely punctate, sparser on the disc and denser on the sides. Elytra sharply striate-punctate, distinctly shallower at the apex. Elytral intervals quite flat, covered with extremely fine punctures, the background smooth and shining. Humeri not developed, metaventrite short like in *isoceroides*, wings reduced, flightless. Aedeagus (Fig. 3M–N). Length: 8.2-9.0 mm.

**Distribution.** So far, only known from the type locality.

**Uloma opacipennis** (Fauvel, 1904)
http://species-id.net/wiki/Uloma_opacipennis
Figs 2D, 3O–P


**Type locality.** Baie du Prony, Nouméa.

**Type specimens.** Lectotype male of *Melasia opacipennis* Fauvel (IRSNB); Paralectotypes: two females of *Melasia opacipennis* Fauvel (IRSNB), none examined. Lectotype and Paralectotypes designated by Kaszab (1982).

**Diagnosis.** *Uloma opacipennis* can be distinguished morphologically from all other New Caledonian species by the structure of its elytra, the integument of which is dull and shagreened, by the presence of a tooth on the underside of the head capsule on the postgenal margin, by the glabrous mentum of the male whose disc is convex between the two lateral subparallel grooves which are long and nearly reach the anterior edge, and by its characteristic aedeagus (Fig. 3O, P). Elytral striae crisp. Striae 1-3 thinner
Uloma opacipennis is morphologically unrelated to the other species of the Uloma isoceroides group. That said, molecular phylogenetic analyses indicate that it is a member of the same evolutionary lineage, hence its inclusion in the species group. On a morphological point of view, all the species of the Uloma isoceroides group, except U. opacipennis, share the following characters: Head short and broad. Male with clypeus and frons located in the same plane, not impressed along the clypeofrontal suture, flat, with a shagreened dull surface covered with extremely fine, sparse and barely visible punctuation. Metaventrite short, between median and posterior coxae approximately as long as or hardly longer than half of the length of a median coxa. Humeri slightly developed or reduced. Flightless species. On the contrary, in U. opacipennis the male head is normal, i.e. impressed along the clypeofrontal suture, not flattened and its surface is distinctly punctate. Metaventrite long, between median and posterior coxae longer than a median coxa. Humeri developed. Fully winged.

**Distribution.** Kaszab (1982: 95) cited this species from the following localities: Mt Panié, 250 m; Houadou (Karovin, Houailou) Riv.; Col d’Amieu, 500 m; Montagne des Sources; Rivière Bleue; Mt Koghi, 450–600 m; Îles Loyauté: Lifou, Wu. “Neukaledonien (Grande Terre von NW bis SO); Loyauté (Lifou)”.


**Uloma paniei** Kaszab, 1982

http://species-id.net/wiki/Uloma_paniei

Fig. 2E

**Uloma paniei** Kaszab, Folia Entomologica Hungarica 18: 84.

**Type locality.** Mont Ignambi.
**Type specimens.** Holotype male: “Nouvelle-Calédonie, Mt Ignambi, 2100 ft, 7.VIII.1914, leg. P. D. Montague” (BMNH); Paratypes: Mt Panie, 1911, P. D. Montague (one male and one female, BMNH); Ignambi Gipfel, 1300 m, 15.IV.1911, leg. F. Sarasin & J. Roux (one male, MTD); Panie Wald, 500 m, 27.VI.1911, leg. F. Sarasin & J. Roux (one female, MTD); Mt Panier [misspelled], 1200 m, 9.X.1967, leg. J. & M. Sedlacek (two females, BPBM). None examined.

**Diagnosis.** Within the *Uloma isoceroides* species group, *Uloma paniei* and *Uloma robusta* are the only species whose mentum of the male is adorned with two peripheral hair fringes along the sides and the front edge, leaving the disc glabrous. Both species have the male anterior tibiae shortly notched at base, maximum one third of the length of inner face. Size large (10.5-12.2 mm). *Uloma paniei* may be separated from *U. robusta* by the male anterior tibiae strongly and deeply notched at base of the inner face (up to one third of the inner side length), the disc of the mentum smooth and shining between the peripheral hair fringes in the males, the elytral surface shining, the striae deeper and expanded to the apex. The male aedeagus is similar in both species. It is unfortunately impossible to identify the females on the basis of morphological characters.

**Distribution.** Kaszab (1982: 84) cited this species from the following localities: Mt Ignambi, Mt Panié, “Neukaledonien (Grande Terre NW)”.

**Additional localities.** Mt Panié, 450–950 m, 14 May 1984, G. Monteith & D. Cook (QM).

*Uloma robusta* Kaszab, 1986
http://species-id.net/wiki/Uloma_robusta
Figs 2F, 3Q–R

*Uloma robusta* Kaszab, Annales Historico-Naturales Musei Nationalis Hungarici 78: 159.

**Type locality.** Mont Panié.

**Type specimens.** Holotype male. Original labels: “NEW CALEDONIA, Mt Panié, 1300–1600 m, 15 May 1984, G. Monteith & D. Cook / Queensland Museum, Brisbane, Reg. N°T.10108 / Holotypus 1986 ♂ *Uloma robusta* Kaszab” (QM); (QM); Paratypes (same data as Holotype): three females (QM) and one male (HNHM), all examined.

**Diagnosis.** *Uloma robusta* closely resembles *Uloma paniei* and both species occur in the same area of the northeastern mountain range of New Caledonia. However, in *U. robusta* the male anterior tibiae are less strongly notched at base of the inner face (about one-fifth of the inner side length), the disc of the mentum is coarsely punctate between the peripheral hair fringes, except on a narrow mid-longitudinal strip, the elytral surface is shagreened and dull and the striae shallower with a tendency to obliterate toward apex (especially striae 2, 3, 6 and 7). In *U. paniei*, on the contrary, the disc of the mentum is smooth and shining between the peripheral hair fringes, the elytral surface shining, the striae deeper and clearly visible up to the apex. The male aedeagus is similar in both species. It is unfortunately impossible to identify the females on the basis of morphological characters.
Distribution. *Uloma robusta* is probably endemic to the Panié mountain range.

Discussion. *Uloma robusta* is possibly a junior synonym of *Uloma paniei*. However, it was not possible for us to test this hypothesis based on the material we examine.

Discussion

Integrative taxonomy

The use of a combined approach based on morphology and on molecular data allowed us to better circumscribe the boundaries within a morphologically homogeneous group of species and to define the characteristics of the *Uloma isoceroides* species group. Without the results of molecular phylogenetic analyses, it would have been impossible to determine that *U. opacipennis* is a member of the same evolutionary lineage. The fact that *U. opacipennis* is in a derived position within the group also allow us to hypothesize that this taxon secondarily developed unique attributes of its own (elytra and head structures, shape of the aedeagus). The analyses of molecular species delimitation also provide more evidence to support the species status of the newly described species. It is especially the case for *Uloma clamensae* and *U. condaminei*, two species that are morphologically very close. In addition, the PTP analyses suggest some unsuspected cryptic biodiversity for two species (*U. jourdani* and *U. isoceroides*). For *U. isoceroides*, the fact that only two specimens were sequenced does not really allow us to confirm this hypothesis because of possible geographical sampling biases (Bergsten et al. 2012). On the contrary the sampling for *U. jourdani* is denser and the results are likely not artefactual. The two potential species *U. jourdani* clusters also have a disjunct distribution: members of the largest molecular group (six individuals) were only collected in Dawenia (in the Panié mountain range) while the members of the smallest cluster (four individuals) were collected in La Guen and Wewec (also in the Panié mountain range, separated by less than 10 km). Because members of both clusters are completely morphologically indistinguishable (even the males) we did not chose to describe two species. That said – as underlined in the results section – in the description of *U. jourdani* we chose to only use representatives of one cluster (the one from Dawenia) to provide type material. Alternatively we could have followed the views of several authors (e.g. Jörger and Schrödl 2013) who propose to use DNA sequence information as a line of evidence to describe cryptic diversity. Though we agree that this approach is another way of describing diversity, we prefer to remain conservative, pending the eventual discovery of diagnostic morphological characters.

Conclusions

The tenebrionid fauna of New Caledonia is rich and diverse with a level of high endemism: of the 238 species (including the four new species described here), 219 (92%) are unique to New Caledonia. By applying our integrative approach to a
broader sampling of *Uloma* or to other tenebrionid genera, we expect to discover new species in the genus *Uloma* but also in the well-diversified genera *Isopus* Montrouzier, 1860 (Cnodalonini, 35 described species, Kaszab 1982, 1986) and *Callismilax* F. Bates, 1874 (Titaenini, 51 described species, Kaszab 1982, 1986). Such a high level of taxonomic endemism is not uncommon for several clades that diversified in New Caledonia; e.g. 94% of the New Caledonian cricket fauna is endemic to the archipelago (Robillard and Desutter-Grandcolas 2008). In addition to the high endemism, the genus *Uloma* is of particular interest for the New Caledonian archipelago because it harbours a species diversity that is comparable to Australia (Australia has 27 species of *Uloma* while New Caledonia has now 26 species). In New Caledonia, despite the fact that most of *Uloma* species are wingless, they have been able to colonize very distinct lowland and mountainous ecosystems (cloud forest, dry forests, evergreen forests, maquis). Some *Uloma* species appear to have allopatric distributions but sympatric distributions seem to be the predominant pattern (Kaszab 1982, 1986). Personal observations during fieldwork confirmed that up to four species could live in the same rotten trunk. The distribution pattern for *Uloma* spp. can be qualified as microendemic because single mountains or specific mountain ranges usually harbour typical species communities. This is best shown in the Mont Panié range where at least five species are known to live sympatrically (potentially six). Although the factors that have promoted such an extraordinary pattern of microendemism are still to be determined, we think that future phylogenetic-based analyses coupled with biogeographic and diversification inferences may bring answers to this issue (see for instance the study Condamine et al. 2013 on another group of darkling beetles).

**Acknowledgements**

We wish to thank the associate editor Patrice Bouchard, Chris Reid and one anonymous reviewer for their constructive comments on a preliminary version of the manuscript. We thank the Environmental Managements (DENV) of Province Sud and Province Nord in New Caledonia for providing us with collecting permits and assistance in New Caledonia. Field collection in New Caledonia was also possible thanks to direct support from the IRD center of Nouméa and the help of Christian Mille (Institut Agronomique néo-Calédonien). Otto Merkl (HNHM), Chris Burwell and Geoff Thompson (QM), Antoine Mantilleri and Olivier Monteuil (MNHN) provided priceless assistance with the Coleoptera collections. Partial funding for this study was obtained through the program “ANR Biodiversité” of the French National Agency for Research (Project BIONEOCAL 2008-2012) and by proper funds from INRA for GJK and IRD for HJ. Part of the sequencing was also supported by the program “Bibliothèque du Vivant” (Project CIAM) supported by a joint CNRS, INRA and MNHN consortium. No conflicts of interest were discovered.
References


Oláh J, Johanson KA (2008) Generic review of Hydropsychinae, with description of Schmidopsyche, new genus, 3 new genus clusters, 8 new species groups, 4 new species clades,


The genus *Alphitobius* Stephens (Coleoptera, Tenebrionidae, Alphitobiini) in Africa and adjacent islands

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Academic editor: P. Bouchard | Received 5 November 2013 | Accepted 27 January 2014 | Published 12 June 2014


Abstract

All species of the genus *Alphitobius* Stephens, 1829 (Alphitobiini Reitter, 1917, subfamily Tenebrioninae Latreille, 1802) from Africa and adjacent islands are revised. New species: *Alphitobius capitaneus* sp. n. from Kenya. New synonyms: *Cryptops ulomoides* Solier, 1851, syn. n. of *Alphitobius diaperinus* (Panzер, 1796); *Alphitobius rufus* Ardoin, 1976, syn. n. of *Alphitobius bobohmi* Koch, 1953; *Peltoides* (*Micropeltoidea*) *crypticoides* Pic, 1916, syn. n. of *Peltoides* (*Micropeltoidea*) *opacus* (Gerstaecker, 1871), comb. n. Homonym: *Alphitobius ulomoides* Koch, 1953 = *Alphitobius arnoldi* nom. n. New combinations from *Alphitobius*: *Ulomoides basilewskyi* Ardoin, 1969, comb. n.; *Peltoides* (*Micropeltoidea*) *opacus* (Gerstaecker, 1871), comb. n. Figures of all examined species are added and a species key is compiled.

Keywords

Tenebrionidae, Alphitobiini, *Alphitobius*, taxonomy, new species, new synonym, new combination, Africa, species key
Introduction

Two species of the genus *Alphitobius* Stephens, 1829 (Alphitobiini Reitter, 1917, subfamily Tenebrioninae Latreille, 1802), namely *A. diaperinus* (Panzer, 1796) and *A. laevigatus* (Fabricius, 1781), have a cosmopolitan synanthropic distribution. All the other species were described from mature habitats in Africa south of the Sahara, so probably this is also the native area of both synanthropic species. Gebien (1921) presented the first key of the African species, including species of the genus *Diaclina* Jacquelin du Val, 1861. Additional species were added by Koch (1953), Ardoin (1958, 1963a, 1969, 1976), Ferrer (1983), and Bremer (1985). The goal of the present paper is a taxonomic revision of the African species, including the description of a new species, the recognition of new synonymies, a new name for a homonym, the transfer of two species from *Alphitobius* to *Ulomoides* and *Peltoides* respectively, providing also figures of all examined species, and compiling of a species key as well. Unfortunately, two taxa (*A. grands* Fairmaire, 1897 and *A. limbalis* Fairmaire, 1901) from Madagascar remained unknown to the authors.

The separation of *Alphitobius* from *Diaclina* was doubtful for a long time. Gebien (1921) separated both by the width of the genal canthus (wider than eyes in *Alphitobius*, narrower or as wide as eyes in *Diaclina*). However, some taxa described under *Alphitobius* have the canthus not broader than eyes (for example *A. lamottei* Ardoin, 1963, see also in species key of Bremer and Girard 1996). Only recently, Matthews and Bouchard (2008) defined the Alphitobiini, separated this tribe from the Diaperini, and discussed also a few differences between *Alphitobius* and *Diaclina*.

Some additional taxa were originally described under *Alphitobius*, but were assigned in the meantime to other genera, and are therefore not included herein. *Ulomoides cinctellus* (Fairmaire, 1902) (Madagascar), *Diaclina parallela* (Thomson, 1858) (Guinea), *Micropedinus pullulus* (Boheman, 1858) (Hongkong), *Menimus nitidulus* (Motschulsky, 1859) (Sri Lanka), *Menimus punctulatus* (Motschulsky, 1859) (Sri Lanka), *Ulomoides suffusus* (Wollaston, 1867) (Cape Verde), *Uloma sulcipennis* (Thomson, 1858) (Gabon), and *Ulomoides xamiaphilus* (Carter, 1920) (Australia). *Alphitobius distinguendus* Fairmaire, 1869 turned out to be a synonym of *Cenoscelis pulla* (Erichson, 1843). Herein, we transfer one additional species from *Alphitobius* to *Ulomoides*: *U. basilewskyi* (Ardoin, 1969), comb. n., and one from *Alphitobius* to *Peltoides* (Micropeltoides): *P. opacus* (Gerstaecker, 1871), comb. n.

Depositories

**CNC**  Canadian National Collection of Insects, Ottawa, Canada
**CRA**  Collection Dr. Rolf Aalbu, Dorado Hills, USA/California
**CRG**  Collection Dr. Roland Grimm, Neuenbürg, Germany
**MNB**  Museum für Naturkunde, Berlin, Germany
The genus *Alphitobius* Stephens (Coleoptera, Tenebrionidae, Alphitobiini) in Africa...

**MNHN**  Muséum National d’Histoire Naturelle, Paris, France
**MRAC**  Musée Royal de l’Afrique Centrale, Tervuren, Belgium
**NHMB**  Naturhistorisches Museum, Basel, Switzerland
**NMP**  National Museum, Department Entomology, Prague, Czech Republic
**SMNS**  Staatliches Museum für Naturkunde, Stuttgart, Germany
**TMSA**  Ditsong National Museum of Natural History, Pretoria, South Africa
**ZSM**  Zoologische Staatssammlung, Munich, Germany

The African species of *Alphitobius*

*Alphitobius acutangulus* Gebien, 1921
http://species-id.net/wiki/Alphitobius_acutangulus
Figs 12, 18

**Type specimens examined.** Senegal, no further data, holotype NHMB (sex not examined).

**New material.** Sudan, Dilling, 20.–22.III.1914, leg. Ebner, 1 ex. NHMB. – Sudan, N Darfur Prov., El Geneina, 4.–18.VI.1979, leg. I. Abuzinid, 8 ex. TMSA, 1 ex. CRG, 1 ex. MNB, 1 ex. SMNS (det. Bremer). – Burkina Faso (labelled as Ob. Volta), Pundu, Olsufiew, no further data, 4 ex. TMSA. – Chad, Massaguet, without date, leg. H. Franz, 1 ex. NHMB. – Chad, Deressia, near Lai, without date, leg. H. Franz, 1 ex. NHMB.

**Type locality.** “Senegal”.

**Distribution.** Senegal (Gebien 1921, Koch 1953); Sudan (Bremer and Girard 1996); Burkina Faso, Chad (new records).

*Alphitobius arnoldi* nom. n.
Figs 4, 19

*Alphitobius ulomoides* Koch, 1953 (homonym, not *Cryptops ulomoides* Solier, 1851, syn. n.)

**Type specimens examined.** Zimbabwe (labelled as S Rhodesia), Bulawayo, leg. G. Arnold, holotype TMSA (sex not examined).


**Type locality.** “Bulawayo”.

**Remarks.** *Cryptops ulomoides* Solier, 1851 from Chile is a junior synonym of *Alphitobius diaperinus* (Panzer, 1796) (see below). Thus *A. ulomoides* Koch, 1953 is a homonym and must have a new name, *arnoldi* nom. n.
Etymology. The new name is derived in honor of George Arnold (1881–1963), former curator in the “Rhodesia Museum” (now Natural History Museum of Zimbabwe, Bulawayo), specialist of African Hymenoptera, and collector of the holotype.

Distribution. Zimbabwe, Congo (Koch 1953); Somalia, Kenya, Tanzania (new records).
The genus Alphitobius Stephens (Coleoptera, Tenebrionidae, Alphitobiini) in Africa...

Alphitobius capitaneus sp. n.
http://zoobank.org/C18D8875-7C0A-46B4-8195-313B8DE1A2BE
http://species-id.net/wiki/Alphitobius_capitaneus
Figs 16, 20


Diagnosis. Alphitobius capitaneus sp. n. is distinguished from its congeners by size and shape of body. A similar body shape, especially the shape of pronotum has A. lamottei Ardoin, 1963, but this species is smaller (body length ≤ 7.0 mm) and differs by the reddish colour, by much finer punctation of dorsal surface, by longer and less distinct serrate antennae with basal antennomeres more elongated, and by the somewhat more stretched and apically narrowed apicale of aedeagus.

Description. Body length 8.8 mm, width at widest point behind middle of elytra 3.6 mm. Elongate, blackish brown, matt; borders of pronotum, lateral borders of elytra, subteral interval, and scutellum paler reddish brown. Complete dorsal surface with very fine and dense punctation, punctures bearing a minute seta. Head sub-trapezoidal; outline continuous, not interrupted between clypeus and frons; apical margin of epistome shallowly emarginate in the middle; fronto-clypeal suture complete and linearly impressed. Eyes large, constricted by genal canthus, dorsal part smaller than ventral part. Genal canthus hardly projecting beyond contours of eyes, with the outlines nearly continuous with the outlines of the latter. Tempora strongly narrowed towards neck. Antennae thickened, not reaching the base of pronotum, with the seven distal antennomeres forming a kind of club; 2nd antennomere wider than long; 3rd elongate, one and a half times as long as wide; 4th only slightly, 5th to 10th distinctly wider than long and distinctly serrate; distal antennomere rounded, as wide as long. Pronotum transverse, width/length ratio 1.7; transverse convex, widest at base, shallowly arcuate narrowing to apex. Anterior margin shallowly emarginate, basal margin bisinuate, all margins finely bordered; lateral margins separated from discal convexity by a narrow submarginal depression. Anterior and posterior corners rectangular. Propleura densely covered with small seta bearing tubercles, only along outer margins nearly smooth. Prosternum rugosely punctured, prosternal apophysis bent down behind procoxae. Elytra convex, elongate oval with subparallel sides and densely punctured striae; scutellar striole absent; intervals much broader than striae, nearly flat on disc, becoming more and more convex laterally and distally; lateral margins in dorsal view visible nearly over entire length, only concealed around apex; base as wide as base of pronotum; humeral angles obtuse, distinct. Scutellum large, triangular. Mesoventrite roughly punctured, with shiny median carina in basal part; triangular apophysis raised upwards and excavate. Metaventrite shiny, with fine median sulcus, finely punctured on disc, somewhat more coarsely punctured laterally. Abdominal ventrites with very dense and fine punctuation throughout, basally and laterally longitudinally wrinkled. Tibiae gradually and faintly dilated towards apex, without modifications. Aedeagus as in Fig. 20.

Etymology. Capitaneus (Latin) means conspicuous by greatness, refers in this case to the body size.
Alphitobius crenatus (Klug, 1834)
http://species-id.net/wiki/Alphitobius_crenatus
Figs 1, 21

Phaleria crenata Klug, 1834
Cataphronetis luctuosa Fairmaire, 1869, syn.


Type locality. “Madagascar” (crenata), “Nossi-Bé” (luctuosa).

Distribution. Madagascar (type locality), eastern Africa, Comores, Seychelles, Aldabra Islands (Koch 1953).

Alphitobius diaperinus (Panzer, 1796)
http://species-id.net/wiki/Alphitobius_diaperinus
Figs 15, 22

Tenebrio diaperinus Panzer, 1796
Tenebrio ovatus Herbst, 1799, syn.
Uloma opatroides Brullé, 1838, syn.
Cryptops ulomoides Solier, 1851, syn. n. (not homonym Alphitobius ulomoides Koch, 1953, arnoldi nom. n.)
Crypticus longipennis Walker, 1858, syn.
Phaleria rufipes Walker, 1858, syn.
Proselytus caffer Fåhraeus, 1870, syn.

Type specimens examined. Chile (labelled as Chili), Valparaiso, Gay 15-43, 1 syntype of Cryptops ulomoides Solier, 1851, MNHN, designated herewith as lectotype.

The genus Alphitobius Stephens (Coleoptera, Tenebrionidae, Alphitobiini) in Africa...


**Type locality.** “Germanica” (*diaperinus*); “Valparaiso” (*ulomoides*).

**Synonymy.** Examination of the syntype of Cryptops ulomoides Solier, 1851, shows a complete correspondence with Alphitobius diaperinus. The genus Cryptops was considered as synonym of Alphitobius since a long time (for example in the world catalogue of Gebien 1940), but the species ulomoides Solier, 1851 was not formally synonymised with diaperinus Panzer, 1796, so far. In consequence, Alphitobius ulomoides Koch, 1953 is a homonym and needs a new name, arnoldi nom. n. (see above).

**Distribution.** Cosmopolitan.
Alphitobius grandis Fairmaire, 1897
http://species-id.net/wiki/Alphitobius_grandis

**Remarks.** Material of this taxon is unknown to the authors. The type is said to be 9 mm long (Fairmaire 1897), the antennae are relatively short (“assez courtes et robustes”), the anterior corners of the pronotum are rectangular (“presque droit”), and the elytra have weak striae with large punctures (“stries assez peu profondes, mais fortement ponctués”).

**Type locality.** “Madagascar”.

**Distribution.** Madagascar.

Alphitobius hobohmi Koch, 1953
http://species-id.net/wiki/Alphitobius_hobohmi
Figs 5, 23

Alphitobius rufus Ardoin, 1976, syn. n.

**Type specimens examined.** Namibia (labelled as SWA), Abachaus, XII.1946, leg. G. Hobohm, holotype, 1 paratype *hobohmi* TMSA (sex not examined). – Tanzania, Mts. Uluguru, Morogoro Campus Fac. Agriculture, 600 m, V./VI.1971, leg. J. Debecker. ♀ holotype *rufus* MRAC.


**Type localities.** “Abachaus, Otjiwarongo” (*hobohmi*), “Morogoro” (*rufus*).

**Synonymy.** The Type specimens examined of *A. hobohmi* and *A. rufus*, as well as several non-type specimens from Namibia and adjacent Angola (near type locality of *hobohmi*), and from Tanzania and Kenya (near type locality of *rufus*) show no distinct external differences. The aedeagi of type specimens can not be compared, because the holotype of *rufus* is a female. Nevertheless, *A. rufus* is considered as a junior synonym of *A. hobohmi*. 
The genus *Alphitobius* Stephens (Coleoptera, Tenebrionidae, Alphitobiini) in Africa...

**Figures 5–8.** Dorsal view of African species of the genus *Alphitobius*. 5 *A. hobohmi*, non-type Angola, SMNS 6 *A. leleupi*, paratype, TMSA 7 *A. rugosulus*, non-type Tanzania, SMNS 8 *A. viator*, non-type RSA, SMNS. Scale: 2 mm.
Remarks. In some localities (for example Modimolle and Magudu) *A. hobohmi* was collected together with *A. viator*.

**Distribution.** Namibia (Koch 1953, Ferrer 2004); Tanzania, Kenya (Ardoin 1976); Ethiopia, Angola, South Africa (new records).

*Alphitobius karrooensis* Koch, 1953
http://species-id.net/wiki/Alphitobius_karrooensis
Figs 13, 24

**Type specimens examined.** Eastern Cape, Willowmore, 20.III.1919, leg. H. Brauns, holotype, 3 paratypes TMSA.


**Type locality.** “Willowmore”.

**Distribution.** South Africa (Koch 1953); Tanzania, Zambia, Botswana, Namibia (new records).

*Alphitobius kochi* Ardoin, 1958
http://species-id.net/wiki/Alphitobius_kochi
Figs 9, 25

**Type specimens examined.** Cameroon, N’Kongsamba, XI.1956, leg. J. Cantaloube, 4 paratypes TMSA, 2 paratypes NHMB, 1 paratype MNB, 1 paratype ZSM.

**New material.** Cameroon, Bambui, 9 miles NE Bamenda, 1450 m, 29.X.1966, leg. E. S. Ross & K. Lorenzen, 1 ex. CRA. – Cameroon, Doala, 10 m, 20.X.1966, leg. E. S. Ross & K. Lorenzen, 7 ex. CRA, 2 ex. SMNS, 1 ex. CRG. – Ivory Coast, 10
The genus Alphitobius Stephens (Coleoptera, Tenebrionidae, Alphitobiini) in Africa...

Figures 9–13. Dorsal view of African species of the genus Alphitobius. 9 A. kochi, non-type Togo, SMNS 10 A. lucasorum, paratype, TMSA 11 A. parallelipennis, non-type Angola, SMNS 12 A. acutangulus, non-type Sudan, SMNS 13 A. karrooensis, non-type RSA, TMSA. Scale: 2 mm.


Type locality. “N’Kongsamba”.

Distribution. Cameroon (type locality), Ivory Coast (Ardoin 1969, Bremer and Girard 1996); Liberia, Togo, Ghana (new records).
Alphitobius laevigatus (Fabricius, 1781)
http://species-id.net/wiki/Alphitobius_laevigatus
Figs 14, 26

Opatrum laevigatus Fabricius, 1781
Tenebrio mauritanicus Fabricius, 1792, syn.
Helops picipes Panzer, 1794, syn.
Helops piceus Olivier, 1795, syn.
Alphitobius granivorus Mulsant & Godart, 1868, syn.
Cataphronetis striatulus Fairmaire, 1869, syn.
Microphyes rufipes MacLeay, 1873, syn.
Alphitobius ruficolor Pic, 1925, syn.


Type locality. “Noua Zelandia”.

Distribution. Cosmopolitan.

Alphitobius lamottei Ardoin, 1963
http://species-id.net/wiki/Alphitobius_lamottei
Fig. 2

The genus *Alphitobius* Stephens (*Coleoptera, Tenebrionidae, Alphitobiini*) in Africa...

Figures 14–17. Dorsal view of African species of the genus *Alphitobius*. 14 *A. laevigatus*, non-type Germany, SMNS 15 *A. diaperinus*, non-type Germany, SMNS 16 *A. capitaneus* sp. n., holotype, CRG 17 *A. limbalis*, doubtful cotype, NHMB. Scale: 2 mm.
**Type locality.** “Mt. Nimba”.

**Distribution.** Guinea (type locality); Senegal (Ardoin 1963a); Ivory Coast (Ardoin 1969, Bremer and Girard 1996); The Gambia (Grimm 2002); Central African Republic (new record).

*Alphitobius leleupi* Koch, 1953
http://species-id.net/wiki/Alphitobius_leleupi
Figs 6, 27

**Type specimens examined.** Congo, Massif de Kundelungu, 14.XII.1949, leg. N. Leleup, 29 paratypes TMSA, 2 paratypes SMNS, 1 paratype CRG, 1 paratype ZSM.

**New material.** Congo, 57 miles N Popokabaka, 3.VIII.1957, leg. E. S. Ross & R. E. Leech, 2 ex. CRA, 1 ex. SMNS.

**Type locality.** “Kundelungu”.

**Remarks.** Among the type series in TMSA, the missing holotype of *A. parallelipennis* was found, see remarks under that species.

**Distribution.** Congo, Kenya (Koch 1953).
The genus Alphitobius Stephens (Coleoptera, Tenebrionidae, Alphitobiini) in Africa...

**Alphitobius limbalis** Fairmaire, 1901
http://species-id.net/wiki/Alphitobius_limbalis
Fig. 17

**Type specimens examined.** Without any data, 1 female “cotype” NHMB (Gebien collection).

**Remarks.** It seems doubtful to the authors, if the above listed female (body length 6 mm) without any data is really a type specimen. Other material of this taxon is unknown to the authors. The species is said to be similar to *A. luctuosus* (synonym of *Alphitobius crenatus* (Klug, 1833) (Fairmaire 1901), but is characterised by larger body size (6 mm), rounder pronotum and larger punctures in elytral striae.

**Type locality.** “Bélumbé”.

**Distribution.** Madagascar.

---

**Alphitobius lucasorum** Bremer, 1985
http://species-id.net/wiki/Alphitobius_lucasorum
Figs 10, 28

**Type specimens examined.** Sudan, N Darfur Prov., El Geneina, 7.–15.VI.1978, leg. I. Abuzinid, 1 paratype SMNS, 1 paratype TMSA, 1 paratype ZSM. – Ghana, Northern Prov., Nyankpala, 15 km W Tamale, 1.–30.IV.1970, leg. S. Endrödy-Younga, 2 paratypes TMSA.

**Type locality.** “El Geneina”.

**Distribution.** Cameroon, Nigeria, Ghana, Senegal, Sudan (type locality) (Bremer and Girard 1996); Chad (Bremer 1985).

---

**Alphitobius niger** Ferrer, 1983
http://species-id.net/wiki/Alphitobius_niger

**Type specimens examined.** None, see remarks.

**Remarks.** Unfortunately, this species was overlooked during the study, and was added here only during the review process. The species is said to be similar to *A. ulomoides*, for diagnosis and figures see Ferrer (1983). Genal canthus projecting outwards beyond contours of eyes, pronotum widest near base, aedeagus with acute apicale, body length 8 mm.

**Type locality.** “Lake Manyara”.

**Distribution.** Tanzania (type locality).
**Alphitobius parallelipennis** Koch, 1953
http://species-id.net/wiki/Alphitobius_parallelipennis
Figs 11, 29

**Type specimens examined.** Congo, Lulua, Tshibamba, XII.1931, leg. G. F. Overlaet, holotype MRAC. – Congo, Elisabethville, 7.XI.1923, leg. C. Seydel, 1 paratype TMSA.


**Type locality.** “Lulua, Tshibamba”.

**Remarks.** Bremer (1985) already assumed, that some specimens of the type series of *A. leleupi* and *A. parallelipennis* in TMSA are mislabelled, and that the actual depository of the holotype of *A. parallelipennis* seems unknown, at least it is not present in MRAC as published in the original description. De Meyer (VII.2013 in an email to the senior author) confirmed, that the holotype is lacking in MRAC with the remark “non renvoyé par Koch”. During the last visit of the senior author in TMSA, the mixture of locality and type labels could be confirmed, and also corrected. The holotype of *A. parallelipennis* could be recognised without any doubts among the type series of *A. leleupi*, although mislabelled, and was transferred with correct secondary labels from TMSA to MRAC.

**Distribution.** Congo (Koch 1953); Angola, Zambia, northeastern South Africa (new records).

**Alphitobius rugosulus** Koch, 1953
http://species-id.net/wiki/Alphitobius_rugosulus
Figs 7, 30

**Type specimens examined.** None, not in TMSA.

**New material.** Ethiopia, Oromia, 6.5 km SE Chichilla, 1550 m, 17.V.2012, leg. F. Wachtel, 1 ex. CRG. – Tanzania, Dodoma Prov., 15 km N Dodoma, 1550 m,
The genus Alphitobius Stephens (Coleoptera, Tenebrionidae, Alphitobiini) in Africa...

19.XII.2006, leg. F. Kantner, 1 ex. SMNS. – Tanzania, Dodomo Prov., 70 km N Dodoma, 1350 m, 17.XII.2006, leg. F. Kantner, 1 ex. SMNS.

**Type locality.** “Campi Simba”.

**Distribution.** Kenya (Koch 1953); Ethiopia, Tanzania (new records).

---

**Alphitobius viator** Mulsant & Godart, 1868
http://species-id.net/wiki/Alphitobius_viator
Figs 8, 31

**Uloma rufula** Fairmaire, 1883, syn.


**Type locality.** “Marseille, importée” (*viator*), “Abyssinie” (*rufula*).

**Remarks.** We could not clear, if *rufula* Fairmaire, 1883 is a synonym of *viator* Mulsant & Godart, 1868 (as listed in all catalogues), or of *hobohmi* Koch, 1953 (with *rufus* Ardoin, 1976, syn. n.). In some localities (for example Modimolle and Magudu) *A. viator* was collected together with *A. hobohmi*.

**Distribution.** Tropical and southern Africa, the holotype was imported to Marseille in southern France (Mulsant and Godart 1868).

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**Key to the species of African *Alphitobius***

Unfortunately, the taxonomic status of *Alphitobius grandis* Fairmaire, 1897 and *Alphitobius limbalis* Fairmaire, 1901 from Madagascar could not be enlightened by the authors, thus both taxa are not included herein. Also not included is *Alphitobius niger* Ferrer, 1983, which was overlooked during the study and included herein only during the review process. Compare also Figs 1–17.

1. Genal canthus not distinctly projecting outwards beyond contours of eyes.... 2
   – Genal canthus projecting outwards beyond contours of eyes......................... 5
2. Body length 8.8 mm, pronotum widest in posterior third.... *capitaneus* sp. n.
   – Body length ≤ 7.0 mm, pronotum widest near posterior angles ................. 3
3. Lateral margins of pronotum distinctly rounded towards anterior angles (Fig. 2) ......................................................................................................................... *lamottei*
   – Lateral margins of pronotum nearly straight or slightly sinuate narrowing towards anterior angles, thus shape of pronotum conical (Figs 4, 5)........... 4
4. Lateral margins of pronotum nearly straight, pronotal disc with punctures of similar size .......................................................................................................... *arnoldi* nom. n.
   – Lateral margins of pronotum slightly sinuate, pronotal disc with large and small punctures of different size ................................................................................. 6
5. Lateral margins of pronotum rounded towards posterior angles, pronotum widest in the middle or shortly behind the middle............................... 10
   – Lateral margins of pronotum subparallel, pronotum widest near base........ 6
6. Elytra without distinct punctural rows, only laterally with traces of punctural rows, elytra with fine microsetation.................................................. *acutangulus*
   – Elytra completely with distinct punctural rows, elytra bare or with fine microsetation........................................................................................................ 7
The genus *Alphitobius* Stephens (Coleoptera, Tenebrionidae, Alphitobiini) in Africa...

7 All elytral intervals distinctly convex, nearly keel-like (Figs 7, 9), elytra with fine microsetation .................................................................
8 All elytral intervals flat or only external intervals slightly convex, but not keel-like, elytra bare..................................................
9 Body length 3–4 mm, apicale of aedeagus with rounded tip (Fig. 25) .... *kochi*
10 Body length above 5 mm, apicale of aedeagus with triangular acute tip (Fig. 3) ............................................................
9 Internal punctural rows of elytra not impressed, last 5 antennomeres forming a separated club ...........................................
11 All punctural rows of elytra impressed, last 5 antennomeres not separated from the remaining basal ones .....................
11 Elytra long and narrow, parallel-sided (Figs 10, 11) .....................
12 Elytra shorter and broader, ovate (Figs 6, 8, 13, 15) ..................
13 Lateral margins of pronotum regularly rounded, anterior corners not prominent, apicale of aedeagus with rounded tip (Fig. 28) .... *lucasorum*
14 Lateral margins of pronotum parallel in basal part, anterior corners prominent, apicale of aedeagus triangular with acute tip (Fig. 29) .... *parallelipennis*
12 Lateral margins of pronotum straight and parallel in basal part, pronotum widest near base ...........................................................
13 Lateral margins of pronotum rounded towards posterior angles, pronotum widest in middle ..................................................................
14 Dorsal side blackish and shining, base of pronotum unbordered in the middle, apicale of aedeagus shorter (Fig. 22) ............... *diaperinus*
15 Dorsal side brownish and dull, base of pronotum completely bordered, apicale of aedeagus longer (Fig. 31) ....................... *viator*
14 Pronotum convex with rough and confluent punctuation, without slight transverse impression (Fig. 13) ....................... *karroensis*
15 Pronotum more flat and with finer separate punctuation, with a feeble transverse impression (Fig. 6) .................................

New combinations

*Ulomoides basilewskyi* (Ardoin, 1969), comb. n.
http://species-id.net/wiki/Ulomoides_basilewskyi
Figs 3, 32

*Alphitobius basilewskyi* Ardoin, 1969

Type specimens examined. Ivory Coast, Bingerville, VI.1962, leg. J. Decelle, male holotype MRAC. – Same locality and collector as holotype, but IV.1962–III.1963, 3 paratypes MRAC.

Type locality. “Bingerville”.
Remarks. Ulomoides basilewskyi (Ardoin, 1969) possesses distinctly crenulated outer margin of all tibiae (see Ardoin 1969), which is characteristic for some species of Ulomoides Blackburn, 1888 (Hinton 1947, under Martianus Fairmaire, 1893), but not for Alphitobius. In the structure of tibiae, the shape of body, eyes, and antennae U. basilewskyi resembles U. dermestoides (Chevrolat, 1878). The striking long apicale of the aedeagus (Fig. 32) resembles those of some Ulomoides, but differs distinctly from those of the Alphitobius species (Figs 18–31).

Distribution. Ivory Coast.

**Peltoides (Micropeltoides) opacus** (Gerstaeker, 1871), comb. n.
http://species-id.net/wiki/Peltoides_opacus

Alphitobius opacus Gerstaeker, 1871
Diaclina opaca (Gerstaeker, 1871) sensu Gebien (1940)
Peltoides (Micropeltoides) crypticoides Pic, 1916, syn. n.

**Type specimens examined.** Ugano, leg. v. d. Decken, no. 56752, no further data, holotype of *opacus* MNB. – Fort Crampel, no further data, holotype of *crypticoides* MNHN.


**Type localities.** “Ugano-Berge” (*opacus*), “Fort Crampel (Kaga Bandora)” (*crypticoides*).

**Remarks.** The examination of the type of *Alphitobius opacus* Gerstaeker, 1871 shows, that the original assignment to *Alphitobius* is wrong and that this species must be transferred to the genus *Peltoides* Laporte, 1832, subgenus *Micropeltoides* Pic, 1916, because of entirely different body shape, different shape of antennomeres, and different shape of male genitalia with the base of basale not asymmetrical as in Alphitobiini. The type of *Peltoides (Micropeltoides) crypticoides* Pic, 1916 fully coincide with *opacus*, and is thus a junior synonym.

**Distribution.** Tanzania (type locality *opacus*), Central African Republic (type locality of *crypticoides*); Senegal (Ardoin 1963b), Ivory Coast (Ardoin 1969), Mali, The Gambia (Grimm 2002, all under *P. (M.) crypticoides*); Benin, Cameroon, Guinea, Uganda, Angola, Zambia (new records).

Acknowledgements

For the trustful loan of specimens from the collections under their care, we cordially thank Rolf Aalbu (Dorado Hills, California), Michael Balke (München), François Gé-
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The genus *Alphitobius* Stephens (*Coleoptera, Tenebrionidae, Alphitobiini*) in Africa...

The photographs were taken by Johannes Reibnitz (Stuttgart) with a Leica DFC320 digital camera on a Leica MZ16 APO microscope and subsequently processed by him with Auto-Montage (Syncroscopy) software. The referees Julio Ferrer (Haninge) and Luboš Purchart (Brno) improved the manuscript by their comments.

### References


A preliminary phylogenetic analysis of the New World Helopini (Coleoptera, Tenebrionidae, Tenebrioninae) indicates the need for profound rearrangements of the classification

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Academic editor: P. Bouchard | Received 20 December 2013 | Accepted 19 April 2014 | Published 12 June 2014


Abstract

Helopini is a diverse tribe in the subfamily Tenebrioninae with a worldwide distribution. The New World helopine species have not been reviewed recently and several doubts emerge regarding their generic assignment as well as the naturalness of the tribe and subordinate taxa. To assess these questions, a preliminary cladistic analysis was conducted with emphasis on sampling the genera distributed in the New World, but including representatives from other regions. The parsimony analysis includes 30 ingroup species from America, Europe and Asia of the subtribes Helopina and Cylindrinotina, plus three outgroups, and 67 morphological characters. Construction of the matrix resulted in the discovery of morphological character states not previously reported for the tribe, particularly from the genitalia of New World species. A consensus of the 12 most parsimonious trees supports the monophyly of the tribe based on a unique combination of characters, including one synapomorphy. None of the subtribes or the genera of the New World represented by more than one species (Helops Fabricius, Nautes Pascoe and Tarpela Bates) were recovered as monophyletic. Helopina was recovered as paraphyletic in relation to Cylindrinotina. One Nearctic species of Helops and one Palearctic species of Tarpela (subtribe Helopina) were more closely
related to species of Cylindrinotina. A relatively derived clade, mainly composed by Neotropical species, was found; it includes seven species of *Tarpela*, seven species of *Nautes*, and three species of *Helops*, two Nearctic and one Neotropical. Our results reveal the need to deeply re-evaluate the current classification of the tribe and subordinated taxa, but a broader taxon sampling and further character exploration is needed in order to fully recognize monophyletic groups at different taxonomic levels (from subtribes to genera).

**Keywords**
External morphology, Holarctic genera, Neotropical clade, Neotropical genera, male and female genitalia, polyphyly, polytomy, paraphyletic Helopini

**Introduction**

The tribe Helopini Latreille, 1802 currently contains two subtribes (Cylindrinotina and Helopina), 42 genera, and 686 species (Gebien 1943, Blackwelder 1946, Nabozhenko and Löbl 2008). A significant part of this richness is concentrated in the Palearctic Region, for which a recent catalogue is available (Nabozhenko and Löbl 2008) and where taxonomic work has been relatively constant. In contrast, only four genera are recognized for the New World, three of which are Holarctic: *Helops* Fabricius, 1775; *Tarpela* Bates, 1870; *Odocnemis* Allard, 1876, and one is exclusively Neotropical: *Nautes* Pascoe, 1876. *Odocnemis* is currently classified in the subtribe Cylindrinotina, *Helops* and *Tarpela* in the subtribe Helopina, and *Nautes* has not been classified in a subtribe because it is not included in the catalogue of Nabozhenko and Löbl (2008) as it is not present in the Palearctic region.

*Helops*, the type genus of the tribe, was described by Fabricius (1775) based on a few cephalic structures, such as the maxillary and labial palps, the labium, and the antennae of a European species, *H. caeruleus* Linnaeus, 1758. In the following centuries more than two hundred Palearctic species were added to this genus, but subsequent regional taxonomic revisions transferred most of them to other genera, leaving *Helops* with nine species in the region (Reitter 1922, Nabozhenko and Löbl 2008). With one exception, no such revisions have taken place for the American component of the tribe, currently composed of 150 species. In the first synoptic work for the family in North America, Horn (1870) listed 23 species of *Helops* and *Stenotrichus rufipes* LeConte, 1851, which was placed in Amphidorini, but later synonymized with *Helops* (Bouchard et al. 2005). Allard (1876, 1877), author of the only world revision of the tribe, recognized *Helops opacus* LeConte, 1859 and reassigned the remaining species among the following genera: *Diastixus* Allard, 1876 and *Coscinoptilix* Allard, 1877 with exclusively American distribution, and *Stenomax* Allard, 1876, *Nesotes* Allard, 1876 and *Catomus* Allard, 1876, with Palearctic distributions. The *Stenomax* subgenus *Omaleis* Allard, 1877, which included three species from California, was recently synonymized with *Odocnemis* Allard, 1876 by Nabozhenko (2001a). Allard included three other genera for the continent: *Hegemona* Laporte de Castelnau, 1840, *Nautes*, and *Tarpela*, which were described from Neotropical species. *Hegemona* was later transferred to Stenochiinae...
A preliminary phylogenetic analysis of the New World Helopini...

(Doyen 1987). Twenty-six species of *Nautes* are Neotropical (Blackwelder 1946, Papp 1961, Steiner 2006) while *Tarpela* currently contains three Nearctic species (Gebien 1943, Papp 1961), 51 Neotropical species (Blackwelder 1946) and 15 species from Asia, mainly from Japan (Nabozhenko and Löbl 2008).

In the monumental *Biologia Centrali-Americana*, Champion (1887, 1893) described approximately half of the current Helopini species known from North and Central America. Even though he was aware of the heterogeneity of the group, he synonymized Allard’s five genera with *Helops*. In his opinion, retaining Allard’s names for the species originally placed in *Helops* would have required him to propose generic names for the species in *Nautes* and *Tarpela*. Unlike *Helops*, the genera *Tarpela* and *Nautes* have more detailed taxonomic descriptions and were thought to be closely related (Bates 1870). The configuration of the prosternum and mesosternum were the main characters proposed to differentiate the two genera (Bates 1870). Champion (1887) considered these characters to be inconsistent, changing Allard’s classification by transferring two species from *Nautes* to *Helops* and *Tarpela*: *N. färctus* (LeConte, 1858) and *N. eximia* (Bates, 1870), respectively. More recently, Doyen (1988) described two Mexican species of the tribe: *Helops scintillatus* and *H. noguerai*, but had problems assigning them to this genus because they shared characters with some species currently placed in *Nautes*.

In short, this diverse tribe includes two subtribes and multiple genera with worldwide distributions (Gebien 1943) and with different and conflicting circumscriptions, at least in the Holarctic and Neotropical components, considering from three (Champion 1887, 1893) to seven genera (Allard 1877). For the reasons detailed above, an evaluation of the recent classification seems necessary. A phylogenetic approach including all taxa is at this moment unrealistic, but a well design taxon sampling could shed light upon the naturalness of the genera and provide a basis for further research strategies aiming to translate phylogenetic hypotheses into natural classifications. The goals of this work are to explore and codify the morphological variation observed within the Neotropical helopines, for the first time test the monophyly of the subtribe Helopina and of three of the four genera present in the New World (two genera belonging in subtribe Helopina plus *Nautes* that is currently unassigned), and highlight issues in the current classification to provide guidance for future studies.

**Methods**

**Phylogenetic data: taxon sampling (Table 1)**

The subtribes Cylindrinotina and Helopina (Nabozhenko and Löbl 2008) were represented in the dataset by three and 20 species respectively. Taxa from three biogeographic regions were included in the sample: six Nearctic species of *Helops sensu* Champion (1887, 1893), one Nearctic species of *Odocnemis sensu* Nabozhenko (2001a), one Palearctic species from each of the following genera representing both subtribes: *Entomogonus* Solier, 1848; *Helops*, *Nalassus* Mulsant, 1854; *Probaticus* Seidlitz, 1896;
Raiboscelis Allard, 1876; Stenomax Allard, 1876; Tarpela, and seven Neotropical species of Nautes and Tarpela according to Champion (1887, 1893). This sampling also takes into account morphological variation and tries to include all genera recognized at some point for the Neotropics. Helops occidentalis (Allard, 1876), H. sumptuosus (Allard, 1877) and H. seriatus (Allard, 1877) are not included because of lack of material. Two species of the tribe Ulomini: Uloma mexicana Champion, 1886 and Hypogena biimpressa Champion, 1886, as well as Tenebrio molitor Linnaeus, 1758 from the tribe Tenebrionini were incorporated as outgroups.

### Table 1. Taxon sampling.

<table>
<thead>
<tr>
<th>Tribe</th>
<th>Subtribe</th>
<th>Species</th>
<th>Geographic distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Helopini</td>
<td>Cylindrinotina</td>
<td><em>Nalassus plebejus</em> Küster, 1850</td>
<td>Europe, Asia</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Odocnemis californicus</em> (Mannerheim, 1843)</td>
<td>Mexico, U.S.A.</td>
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<tr>
<td></td>
<td></td>
<td><em>Stenomax aeneus</em> Scopoli, 1763</td>
<td>Europe</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Entomogonus peryronis</em> Reiche, 1861</td>
<td>Asia</td>
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<td></td>
<td></td>
<td><em>Helops aereus</em> Germar, 1824</td>
<td>U.S.A.</td>
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<td><em>H. cisteloides</em> Germar, 1824</td>
<td>U.S.A.</td>
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<td><em>H. farctus</em> LeConte, 1858</td>
<td>U.S.A.</td>
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<td><em>H. inanis</em> Allard, 1877</td>
<td>Mexico</td>
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<td></td>
<td><em>H. insignis</em> Lucas, 1846</td>
<td>North of Africa</td>
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<td></td>
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<td><em>H. perforata</em> Horn, 1880</td>
<td>Mexico, U.S.A.</td>
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<td><em>H. punctipennis</em> LeConte, 1870</td>
<td>U.S.A.</td>
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<td><em>H. rosii</em> Germar, 1817</td>
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Specimens were kindly loaned by curators at the following national and international institutions:

**AMNH** American Museum of Natural History, New York, NY, USA (Lee Herman)

**BNHM** The Natural History Museum, London, U. K. (Max Barclay)

**CASC** California Academy of Sciences, San Francisco, CA, USA (Dave Kavanaugh)

**CNIN** Colección Nacional de Insectos, Instituto de Biología, UNAM, Mexico City, Mexico (Santiago Zaragoza Caballero)

**EMEC** Essig Museum of Entomology, University of California, Berkeley, CA, USA (Peter T. Oboyski)

**FMNH** Field Museum of Natural History, Chicago, IL, USA (James Boone)

**HNHM** Hungarian Natural History Museum, Budapest, Hungary (Otto Merkl)

**IEXA** Colección entomológica, Instituto de Ecología, A. C., Xalapa, Veracruz, Mexico (Miguel Ángel Morón & Delfino Hernández)

**MNHN** Museum National d’Histoire Naturelle, Paris, France (Antoine Mantilleri)

**LACM** Natural History Museum of Los Angeles County, Los Angeles, CA, USA (Weiping Xie)

**NMNH** National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (Warren Steiner & David Furth)

**OSUC** C. A. Triplehorn Insect Collection, Ohio State University, Columbus, OH, USA (Charles A. Triplehorn & Luciana Musetti)

**SBMNH** Santa Barbara Museum of Natural History, Santa Barbara, CA, USA (Michael Caterino)

**TAMU** Texas A & M University Insect Collection, College Station, TX, USA (Edward Riley)

**UCDC** Bohart Museum, University of California, Davis, CA, USA (Steve Heydon)

**ZMHB** Museum für Naturkunde der Humboldt-Universitat, Berlin, Germany (Bernd Jaeger)

**Phylogenetic data: characters**

Two hundred eighty-one specimens were examined with an Olympus SZH10 stereomicroscope (magnification: 17.5–350×) equipped with an ocular graticule for length measurements, and a drawing tube. Morphological characters were measured as follows: width of the head was measured across the vertex, length of the last antennomere in the female was measured along its longest edge; width was measured across its widest point; length of pronotum was measured along the midline from its anterior edge to its posterior edge; width was measured across its widest point. Puncture density follows modified conventions used by Paulsen (2005) and Smith et al. (2011): either confluent (separated by one or less than a puncture diameter), moderate (separated by 2–3 puncture diameters), or sparse (separated by 4 or more puncture diameters). Nomenclature and interpretation of female genital tract follows Tschinkel and Doyen (1980) and Doyen (1994).
Thirty-two characters correspond to external morphology; characters used in generic descriptions (Pascoe 1866, Bates 1870) or in previous phylogenetic studies (Doyen and Tschinkel 1982) were included (Figs 1, 2). The remaining 35 are based on male and female genitalia. Internal characters (Figs 3–6) were coded according to previous works (Antoine 1947, Doyen 1994, Flores 1996, Nabozhenko 2001a, Aalbu 2005, Rosas et al. 2011) independent of the fact that some were used to investigate other families as they are considered to be useful in Tenebrionidae as well (Rosas et al. 2011). Two characters (35, 43) plus two character states (67: 1, 2) were used for the first time. Female genitalia were dissected, cleared and stained following Tschinkel and Doyen (1980), replacing NaOH with KOH. Photographs were taken using a Leica microscope equipped with a camera Leica Z16 APO A. The imaging software used was Leica Application Suite 2.8.1.

In total, 44 binary and 23 multistate characters were coded and treated as non-additive. Individual consistency and retention indices (ci, ri) are provided for all characters from the consensus tree (synapomorphies have a value of 1 for both indices). Four additional characters (listed and explained at the end of the character list) were initially explored but removed from the final analysis due to their high homoplasy, assessed by a character removal methodology (see below).

1. Shape of union between clypeus and frons: (0) clypeus slightly depressed, weak fronto-clypeal suture (Fig. 1C); (1) clypeus strongly depressed, evident fronto-clypeal suture (ci= 0.25; ri= 0.80).
2. Length of antennae (male): (0) short, slightly over posterior margin of pronotum; (1) long, clearly surpassing posterior margin of pronotum (ci= 0.33; ri= 0.50).
3. Shape of antennae: (0) filiform (Fig. 1B); (1) submoniliform (synapomorphy).
4. Length of third antennomere: (0) longer than apical antennomeres (Fig. 1A); (1) shorter than or as long as apical antennomeres (Fig. 1B) (ci= 0.14; ri= 0.57).
5. Size of last antennomere (female): (0) almost as long as wide or wider than long (Fig. 1A); (1) 2.5 or more times as long as wide; (2) 1.5-2 times as long as wide (Fig. 1B) (ci= 0.30; ri= 0.30).
6. Head width (Fig. 2C): (0) 1.5 times width of intraocular space; (1) less than 1.5 times width of intraocular space (ci= 0.25; ri= 0).
7. Length of inner edge of maxillary palp (male): (0) 1-1.5 times length of posterior edge; (1) 1.6-2.5 times length of posterior edge; (2) 2.6-2.9 times length of posterior edge (Fig. 1C) (ci= 0.18; ri= 0.25).
8. Pronotum disk surface: (0) gibbous (Fig. 2C); (1) not gibbous (ci= 0.33; ri= 0.50).
9. Density of pronotum punctures: (0) very dense or confluent; (1) moderately dense; (2) sparse (ci= 0.25; ri= 0.40).
10. Depth of pronotum punctuation: (0) deep (more than 20 μm) (Fig. 2C); (1) medium (10-20 μm); (2) shallow (less than 10 μm) (ci= 0.25; ri= 0.64).
11. Setae of head and pronotum (observed at a magnification up to 140X): (0) present; (1) not evident (ci= 0.50; ri= 0.60).
12. Width of lateral carinae of pronotum: (0) lateral carinae 2-5 times width of anterior carina; (1) lateral carinae less than 2 times width of anterior carina (ci= 0.33; ri= 0.50).

13. Shape of anterior angles of pronotum: (0) acute; (1) blunt or slightly acute; (2) straight (ci= 0.25; ri= 0.40).

14. Lateral sides of pronotum: (0) with crenate carinae; (1) with smooth carinae; (2) without conspicuous carinae (ci= 0.40; ri= 0.40).

15. Shape of posterior angles of pronotum: (0) straight; (1) acute; (2) blunt; (3) obtuse (ci= 0.40; ri= 0.40).

16. Projection of posterior angles of pronotum: (0) strong; (1) weak (Fig. 2C) (ci= 0.50; ri= 0.50).
17. Posterior margin of pronotum: (0) convex; (1) straight; (2) bisinuate (Fig. 2C) (ci= 0.40; ri= 0.66).

18. Pronotum shape: (0) rectangular (its width 1.5 times or more its length) (Fig. 2C); (1) almost square (its width less than 1.5 its length) (ci= 0.50; ri= 0.92).

19. Propleura texture: (0) strongly rugose or punctated; (1) smooth or slightly rugose or punctated (ci= 0.20; ri= 0.33).

20. Elytra shape in lateral view: (0) strongly arcuate; (1) slightly arcuate; (2) more evident towards the middle and posteriorly (ci= 0.33; ri= 0.42).

21. Pronotum tegument: (0) smooth; (1) chagrined (ci= 0.16; ri= 0.28).

22. Elytra punctures: (0) in grooves; (1) in rows (ci= 0.12; ri= 0.50).

23. Shape of elytral interstriae: (0) convex; (1) flat; (2) acute (ci= 0.16; ri= 0.09).

24. Elytral tegument: (0) lustrous; (1) dull (ci= 0.14; ri= 0.33).

25. Metathoracic wings: (0) brachypterous or not evident; (1) fully developed (Figs 2A–B) (ci= 0.11; ri= 0.38).

26. Size of recurrent cell: (0) reduced (due to the approximation of the radial cross-vein to the recurrent radius) (Fig. 2A); (1) wide (due to the separation of the radial cross-vein to the recurrent radius) (Fig. 2B) (ci= 0.50; ri= 0.75).

27. Shape of prosternal process apex in ventral view: (0) strongly projected (Fig. 1F); (1) weakly, or not projected (Fig. 1E) (ci= 0.25; ri= 0.40).

**Figure 2.** Examples of non-traditional external characters in Helopini: A reduced recurrent cell (rc) (26:0) in fully developed wing (25:1) of *Helops californicus* Mannerheim B wide recurrent cell (rc) (26:1) in fully developed wing (25:1) of *Tarpela aerifera* Allard C head width and interocular width (6:0) and pronotum width and length (18:0) in *Tarpela costata* Champion 1887, showing a gibbous pronotum disk surface (8:0), with very dense (9:0) and very deep (10:0) pronotum punctures.
28. Shape of prosternal process apex in lateral view: (0) straight; (1) declivous (ci= 0.14; ri= 0.25).

29. Density of leg punctures: (0) femur punctures sparser than tibia punctures; (1) density of femur and tibia punctures similar (ci= 0.14; ri= 0.53).

30. Shape of third tarsomere: (0) lobate (Fig. 1D); (1) not lobate (ci= 0.16; ri= 0.54).

31. Size of fourth tarsomere: (0) shorter than third tarsomere (Fig. 1D); (1) as long as third tarsomere (ci= 0.20; ri= 0.66).

32. Density of punctures and pubescence of abdominal ventrites (male): (0) high towards middle of ventrites 1-3; (1) homogeneous on ventrites 1-5; (2) high towards middle of ventrites 1-5 (ci= 0.15; ri= 0.42).

33. Shape of inner sternite VIII (female): (0) blunt and narrow (Fig. 3D); (1) trapeziform or blunt and wide (Fig. 3E) (ci= 0.33; ri= 0).

Figure 3. Internal morphological characters (female genitalia) in Helopini: A length of paraproct (pp) three or more times length of coxite (cx) (39:0) illustrated from the ovipositor of Helops cisteloides Germar B long gonostyles (gt) (37:1) with wide apex (38:1), represented by the ovipositor of Odocnemis exaratus Germar, not included in the analysis C reduced gonostyles (37:0), with base as wide as apex (38:0) represented by the ovipositor of Tarpela micans (Fabricius), not included in the analysis D blunt, narrow apex of eighth sternite (33:0), not evident arms (34:1) and not dilated distal end of the spiculum ventrale (sv) (35:1) illustrated from H. cisteloides E trapeziform apex of eighth sternite (33:1), evident arms (34:0) and dilated distal end of spiculum ventrale (35:0), represented by sclerite of O. exaratus.
34. Arms of spiculum ventrale (female): (0) evident (Fig. 3E); (1) not evident (Fig. 3D) (ci= 0.20; ri= 0.33).
35. Shape of distal end of stalk of spiculum ventrale (female): (0) round or oval and dilated (Fig. 3E); (1) round but not dilated (Fig. 3D) (ci= 0.50; ri= 0.80).
36. Length/width ratio of gonostyles (female): (0) length twice or more its width; (1) length less than twice its width (ci= 0.25; ri= 0.25).
37. Relative length of coxites (female): (0) 8 or more times gonostyle length (Fig. 3C); (1) less than 8 times gonostyle length (Fig. 3B) (ci= 0.33; ri= 0.33).

Figure 4. Internal morphological characters (female genitalia) representing the different morphological types found in our sample of Helopini ag= accessory gland, sp= spermatheca, st= spermathecal tube(s), cd= common duct of accessory gland and spermatheca, v= vagina, ov= oviduct: A infundibular vagina (40:0), single spermatheca branched near its base (41:0, 42:0) and accessory gland in the common duct (49:1) illustrated from Helops insignis Germar representing the helopiod type (Nabozhenko 2001b, 2002a, 2002b, 2005) B vagina strongly curved and narrowed before the apex (40:1), single spermatheca not branched near the base (41:0, 42:1) illustrated from Nalassius plebejus Küster representing the nalassoid type (Nabozhenko 2001b, 2002a, 2002b) C female genital tract with three serial spermathecal tubes (41:1) close to each other (43:0) and terminal accessory gland (49:2) in Helops farctus LeConte, illustrating the pattern previously reported for some Pimeliinae species (Doyen 1994), here reported for the first time in Tenebrioninae D distant spermathecal tubes (43:1) in Helops perforatus Horn with terminal accessory gland (49:2), illustrating a pattern described here for the first time. Total length of the accessory gland is not represented in A and B.
38. Shape of gonostyles (female): (0) apex as wide as base (Fig. 3C); (1) with apex wider than base (Fig. 3B) (ci = 0.25; ri = 0.62).
39. Relative length of paraproct (female): (0) three or more times coxite length (Fig. 3A); (1) two times coxite length; (2) as long as coxites; (3) less than coxite length (ci = 0.37; ri = 0.50).
40. Shape of vagina (female): (0) infundibular or saciform, curved or not at the apex (i.e., at the connection with the spermatheca or common duct) (Fig. 4A–C); (1) saciform and strongly narrowed and curved before the apex (Fig. 4B) (synapomorphy).
41. Number of spermathecal tubes: (0) one (Fig. 4A-B); (1) more than one (Fig. 4C–D) (synapomorphy).
42. Spermathecal tubes structure: (0) branched near the base (Fig. 4A); (1) not branched, branched at the base (looking like a fascicule of tubes), or branched far from the base (Fig. 4B–D) (ci = 0.33; ri = 0.77).
43. Spermathecal tubes arrangement: (0) near to each other (Fig. 4C); (1) distant from each other (Fig. 4D) (ci = 0.50; ri = 0.50).
44. Common duct: (0) present; (1) absent (ci = 0.16; ri = 0).
45. Length of common duct of spermatheca and accessory gland: (0) long (Fig. 4D); (1) short (Fig. 4C); (2) intermediate (Fig. 4B) (ci = 0.20; ri = 0.27).
46. Position of common duct (female): (0) apical to vagina (Fig. 4A-D); (1) anterior to vagina apex (ci = 0.33; ri = 0).
47. Width of spermathecal tube(s) (female): (0) increases distally; (1) homogeneous width or gradually decreasing (ci = 0.50; ri = 0.66).
48. Texture of spermathecal tubes: (0) smooth; (1) annulate (synapomorphy).
49. Position of accessory gland: (0) emerging directly from the vagina, far from the spermatheca; (1) in the common duct (Fig. 4A-B); (2) terminal to the spermathecal tubes and common duct (Fig. 4C-D) (synapomorphy).
50. Arrangement of pleural rods of gastric spicula (male): (0) close towards the middle of their length (Fig. 5B); (1) close towards the proximal third; (2) close only at the end (Fig. 5A) (ci = 0.50; ri = 0.66).
51. Shape of pleural rods of gastric spicula (male): (0) straight of slightly curved (Fig. 5B); (1) strongly curved (Fig. 5A) (ci = 0.33; ri = 0.33).
52. Depth of notch of eighth sternite (male) measured as the ratio of sternite length (SL) and notch length (NL): (0) deep (SL/NL <3) (Fig. 5C); (1) shallow (SL/NL >3) (Fig. 5D); (2) without notch (ci = 0.50; ri = 0.81).
53. Width of notch of eighth sternite (male): (0) wide; (1) narrow (ci = 0.33; ri = 0).
54. Shape of lobes of eighth sternite (male): (0) notably and anteriorly wide (Fig. 5D); (1) narrow and acute or slightly blunt (Fig. 5C) (ci = 0.20; ri = 0.66).
55. Relative length of basal piece (male): (0) three or more times the length of parameres; (1) less than three times the length of parameres (Fig. 5E–F) (ci = 0.16; ri = 0).
56. Shape of parameres in lateral view (male): (0) sinuate (Fig. 6A); (1) straight or slightly curved (Fig. 6B-C) (ci = 0.25; ri = 0.57).
57. Setae on parameres (male): (0) present (Fig. 6D-E); (1) not evident (observed at a magnification up to 140X) (Fig. 6F) (ci = 0.25; ri = 0.66).
58. Distribution of evident setae on parameres (male): (0) covering apical half of parameres (Fig. 6D); (1) covering more than two thirds of parameres (Fig. 6E) (synapomorphy).

59. Sides of parameres in ventral view (male): (0) convergent to the apex, with a fusiform space in between (Fig. 6F); (1) not convergent (Fig. 6D–E) (ci= 0.50; ri= 0.92).

60. Constriction of the apex of parameres (male): (0) present (Fig. 6E); (1) absent (ci= 0.25; ri= 0.70).

61. Constriction of the apex of parameres (male): (0) strong; (1) weak (Fig. 6E) (ci= 0.33; ri= 0).

62. Shape of the apex of parameres (male): (0) blunt or straight (Fig. 6D); (1) acute (Fig. 6F); (2) fan shaped (ci= 0.50; ri= 0.80).

Figure 5. Internal morphological characters (male genitalia) representing the different morphological types found in our sample of Helopini: A pleural rods of gastral spicula close only at the end (50:2), representing the nalassoid type (Nabozhenko 2001b, 2002a), illustrated from Stenomax aeneus (Scopoli) B pleural rods of gastral spicula close towards the middle of their length (50:0), representing the helopiod type (Nabozhenko 2001b, 2002a, 2005), illustrated from Tarpela micas (Fabricius), not included in the analysis C narrow and acute lobes of eighth sternite (54:1) and deep notch (52:0) in Helops farctus LeConte D broad lobes of eighth sternite (54:0) and shallow notch (52:1) in S. aeneus E projected anterior part of basal piece (basal piece “J” shaped) in Odoncemis californicus Mannerheim (67:0) F anterior part of basal piece not projected in Nautes fervidus Pascoe (67:1), character state used for the first time in this study.
A preliminary phylogenetic analysis of the New World Helopini...

Figure 6. Aedeagal characters (male genitalia) representing the different morphological types found in or sample of Helopini: A evident setae (57: 0) representing the helopiod type (Nabozhenko 2001b, 2002a, 2005), distributed over half of the parameres (58: 0), illustrated from Helops caeruleus (Linnaeus), not included in the analysis (lateral view) B evident setae (57:0); representing the catomoid type (Nabozhenko 2006), distributed over two thirds of parameres (58:1) in Nautes fervidus Pascoe C not evident setae over parameres (57:1) representing the nalassoid type (Nabozhenko 2001b, 2002a, 2002b), illustrated from Odocnemis californicus Mannerheim D parameres not convergent (59:1), with blunt apex (62:0) in H. caeruleus (ventral view) E parameres not convergent (59:1) with weakly constricted apex (61:1) in N. fervidus F parameres convergent (59:0), with acute (60:1) not constricted apex (62:1) in O. californicus.

63. Apical projection of parameres in ventral direction (lateral and ventral view): (0) present; (1) absent (ci= 0.33; ri= 0.33).

64. Apical compression of parameres view laterally as a dorsal or dorso-ventral projection or keel: (0) present; (1) not evident (observed at a magnification up to 140X) (synapomorphy).

65. Width of parameres (male) at the middle: (0) narrower than basal piece (Fig. 6D); (1) as wide as basal piece (Fig. 6E–F) (ci= 0.25; ri= 0.57).

66. Shape of apex of median lobe (male): (0) blunt or with an inconspicuous notch; (1) lobate; (2) constricted (ci= 0.33; ri= 0.73).

67. Shape of anterior part of basal piece (male): (0) projected, basal piece “J” shaped (Fig. 5E); (1) not projected (Fig. 5F); (2) projected, basal piece “C” shaped (ci= 0.66; ri= 0.92).
**Removed characters:**

1. Width of pronotum: (0) widest towards the middle; (1) widest before middle; (2) widest at posterior margin or from middle to posterior margin.
2. Length of pronotum setae: (0) long (more than 100 μm); (1) short (less than 50 μm).
3. Projection of anterior angles of pronotum: (0) strong; (1) weak or absent.
4. Diameter of elytra punctures: (0) reduced (less than 200 μm); (1) large (more than 200 μm).

**Phylogenetic analysis**

The matrix was compiled using WinClada (Nixon 2002). Heuristic searches were conducted through NONA (Goloboff 1999) with multiple Tree Bisection and Reconnection (TBR) using 1,000 initial Wagner trees (mult*1000), holding 20 trees per replication (hold/20) and expanding the memory for a final TBR to completion with up to 10,000 trees (max*10000). The cladograms were rooted with *Uloma mexicana*. All most parsimonious trees (MPTs) found were collected, and ambiguously supported branches were collapsed in WinClada. Identical trees were then removed and a consensus was calculated using the option “Strict” in WinClada.

A simple sequential character removal analysis (modified after Davis et al. 1993) was carried out as implemented in WinClada (Nixon 2002), using the same search parameters as explained. The length of the resulting 71 consensus trees (one for each matrix resulting from the progressive removal of the 71 characters) was compared to determine the influence of each character in the topology of the consensus of the MPTs. In this way, four characters (listed above) were detected to particularly introduce conflict in the analysis due to high homoplasy values and were removed from the matrix. When removing each of these characters, the length of the consensus decreased by more than 30 steps and the resolution of the topology greatly improved. The final 67-character matrix (character listed and explained above) was then analyzed with the parameters described in the previous paragraph. These characters are mapped onto the consensus only if their optimization was not ambiguous and if they were present among all the MPTs. This was assessed using the option “Map Common synapomorphies” on the sub-menu “Synapomorphies” menu “Optimize” of TNT (Goloboff et al. 2003). The consensus was used to map homoplasy at the level of characters in WinClada; a metafile was created and the tree was edited using Corel Draw X6 (Corel Corporation 2012).

To evaluate statistical branch support, a bootstrap analysis was conducted with NONA (Goloboff 1999) through WinClada (Nixon 2002). For this analysis 1,000 replicates were conducted for each using 100 initial trees holding 20 trees and expanding the memory up to 1,000 trees (mult*100 hold/20 max*1000). Frequencies were calculated on the consensus of the 67-character matrix and only values above 50% are shown.
Results

The 67-character matrix (Table 2) yielded 12 most parsimonious trees with 301 steps (length = L), a consistency index (ci) of 0.29, and a retention index (ri) of 0.59. The strict consensus (L=314; ci=0.28; ri=0.56) is presented in Figure 7. Six out of seven characters retrieved as synapomorphies are from internal morphology. Four synapomorphies correspond to the female genitalia: vagina strongly curved in the apex (character 40: state 1), more than one spermathecal tube (41:1), smooth texture of spermathecal tube (48:0), and terminal position of the accessory gland (49:2). Two synapomorphies correspond to the male genitalia: distribution of evident setae on the parameres (58:1), and presence of a dorsal projection or keel on the parameres (64:0). One synapomorphy corresponds to external morphology: the filiform shape of the antennae: (3:0). Although only six clades had bootstrap values over 50%, most clades are supported by a unique combination of at least two characters.

The consensus shows that the monophyly of the tribe Helopini is supported by one synapomorphy: the filiform antennae (3:0). In contrast, none of the subordinated taxa within Helopini is supported as monophyletic: neither the subtribes (Cylindrinotina and Helopina) nor the genera represented by more than one species: Helops, Nautes, or Tarpela. Cylindrinotina is nested within Helopina and Tarpela cordicollis (Marseul, 1824) plus Helops aereus Germar, 1824 (Helopina) are in turn nested within Cylindrinotina. Helops and Tarpela are polyphyletic, while Nautes is paraphyletic (Helops farctus LeConte, 1858, at some point transferred to Nautes, and Tarpela aerifera Allard, 1876 share a common ancestor with it).

From the sampled Palearctic Helopina, only Helops rossii Germar, 1817 and H. insignis Lucas, 1846 constitute a clade that is sister to the rest of the tribe, and is supported by the pubescent ventrites with homogeneous punctures (32:1).

An heterogeneous clade formed by three genera of Cylindrinotina, Stenomax aeneus, Scopoli, 1763, Odocnemis californicus (Mannerheim, 1843) and Nalassus plebejus Küster, 1850 plus two species of Helopina: Tarpela cordicollis and Helops aereus is supported by the following internal characters: evident arms of the spiculum ventrale (34:0), dilated distal end of stalk of the spiculum ventrale (35:0), parameres without evident setae (57:1), and parameres with a keel (64:0), the last recovered as a synapomorphy. Helops aeneus was placed in Stenomax by Allard (1876) before Champion’s synonymization.

A large clade of mostly Neotropical species from the genera Helops, Nautes and Tarpela, plus two Nearctic species of Helops, was recovered with support from three characters: clypeus slightly depressed (1:0), more than one spermathecal tube (41:1) (retrieved as synapomorphy), and an accessory gland terminal to the spermathecal tubes (49:2) (retrieved as synapomorphy). Helops punctipennis LeConte, 1870 and H. rufipes (LeConte, 1851), both Nearctic, are supported as sister to this mostly Neotropical clade by two internal characters: the deep notch of the eighth sternite (52:0) and the lobate shape of the median lobe (66:1). The earlier divergent lineage within this mostly Neotropical species is a clade formed by Tarpela contigua Champion, 1887 and
### Table 2.
Matrix for the cladistics analysis of the tribe Helopini (Coleoptera, Tenebrioninae, Tenebrionini); "-" represents inapplicable character states, "?" represents not observed data.

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even the type (*N. fervidus* Pascoe, 1866). The internal clade containing the type species of *Tarpela* also includes *T. reticulata* Champion 1887 and *T. costata* Champion 1887, and is supported by three characters of the pronotum: the gibbous surface of the disk (8:0), the crenate carinae of the lateral sides (14:0), and the acute anterior angles (15:1), plus one internal female character: the relative length of the paraproct (39:0). The mostly *Nautes* clade also includes *Tarpela aerifera* and *Helops farctus*. This group is supported by the short size of the fourth tarsomere (31:0) and the constriction of the apex of the parameres (60:0).

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### Discussion

#### Taxonomic implications

Although supported by our results, the monophyly of the tribe still requires a more rigorous test including a wider sample of species from more tribes including species from other closely related tribes (e.g. Triboliini, Blaptini). The only synapomorphy supporting the tribe, the filiform shape of the antennae, could be an artifact of our sampling, as the antenna have also been reported as moniliform or gradually clavate. 
within the tribe (Aalbu et al. 2002). Based on our examination of many additional species, we know of no Helopini with moniliform or submoniliform antennae, nevertheless gradually clavate antennae are present in some species, such as *Nautes antennatus* Champion, 1887, *N. varians* Champion, 1887, *Helops durangoensis* Champion, 1887, and *H. rufipes*.

The fact that Cylindrinotina is nested within Helopina implies that there is no justification for the recognition of two subtribes: either no subtribes should be recognized or more subtribes should be recognized. A denser sampling of Palearctic species

<table>
<thead>
<tr>
<th>Taxon/character</th>
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</tr>
</thead>
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<tr>
<td><em>Uloma mexicana</em></td>
<td>1 2 1 1 1 2 2</td>
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<tr>
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<tr>
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</tr>
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<td><em>Helops insignis</em></td>
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<tr>
<td><em>Helops cisteloides</em></td>
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</tr>
<tr>
<td><em>Nautes enoplopoides</em></td>
<td>- 0 1 1 1 1 1</td>
</tr>
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<td><em>Helops perforatus</em></td>
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<tr>
<td><em>Nautes striatipennis</em></td>
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<td><em>Helops farctus</em></td>
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<tr>
<td><em>Tarpela torrida</em></td>
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<tr>
<td><em>Nautes magnificus</em></td>
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<tr>
<td><em>Tarpela depressa</em></td>
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<tr>
<td><em>Nautes varians</em></td>
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</tr>
<tr>
<td><em>Tarpela contigua</em></td>
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</tr>
<tr>
<td><em>Nautes belti</em></td>
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</tr>
<tr>
<td><em>Nautes fervidus</em></td>
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<td><em>Nalassus plebejus</em></td>
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<tr>
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<tr>
<td><em>Odocnemis californicus</em></td>
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<tr>
<td><em>Stenomax aeneus</em></td>
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<tr>
<td><em>Tarpela cordicollis</em></td>
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</tr>
<tr>
<td><em>Hypogena biimpressa</em></td>
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</tr>
<tr>
<td><em>Tenebrio biimpressa</em></td>
<td>- 0 1 1 1 0 0</td>
</tr>
</tbody>
</table>
Figure 7. Strict consensus of 12 most parsimonious trees (L= 314; ci=0.28; ri=0.56). Characters are mapped onto the consensus only if their optimization is not ambiguous and if they are present among all the MPTs. The consensus is used to map homoplasy at the level of characters. Black rectangles represent single, non-homoplasious character state transformations, and white rectangles represent multiple, homoplasious character state transformations. The number depicted above each rectangle represents the character and the number below the rectangle represents the character state. The bigger number below the branches corresponds to Bootstrap values over 50%. The combination of characters for each terminal is not shown. Three important synapomorphies are illustrated in the cladogram: the filiform antennae (3:0), as the single synapomorphy of the tribe, and the number of spermathecal tubes (41:1) plus the terminal position of the accessory gland (49:2), as the synapomorphies supporting a mostly Neotropical clade. These character states are reported for the first time for the tribe. Two shades of gray in the cladogram indicate the subtribe to which the terminals belong (except Nautes). Colors in the terminals indicate their geographic distribution. Below seven terminals the former classification (genus or subgenus) is shown. An asterisk indicates the type species included in the analysis: Tarpela browni and Nautes fervidus.
could help reveal which of these alternatives is better supported. According to the current sampling, it is possible that the Palearctic *Helops* remain as an independent earlier divergent lineage within the tribe, including the type species (*H. caeruleus*), which is morphologically similar to the sampled Palearctic species. If this was the case, *Helops* would have to be re-circumscribed to include only the Palearctic species and new generic names would be necessary for the New World lineages.

Further earlier divergent lineages may be revealed as sampling of *Entomogonus*, *Raiboscelis* and *Probaticus* is improved, as well as other genera not included in our sampling (e.g. *Catomus* Allard, 1876, *Hedyphanes* Fischer von Waldheim, 1820, and *Nesotes* Allard, 1876). The unresolved position of *Helops cisteloides* Germar, 1824 indicates the possibility that other New World lineages could be identified as sampling is increased. If subtribes are to be recognized, Cylindrinotina would need to be expanded to include Asian species of *Tarpela* (as *T. cordicollis*) and Nearctic *Helops* (as *H. aereus*). This subtribe would also have to include several Holartic genera (besides *Odocnemesis*). The Holartic region has an intricate history (Brown and Lomolino 1998), with dispersion of groups taking place in several moments of the Tertiary (Sanmartín et al. 2001). The geographic heterogeneity of the cylindrinotine clade shows the importance of using a phylogenetic approach in which the morphological diversity of the taxa is represented, regardless of their present geographic distribution.

The polyphyletic nature of *Helops* and *Tarpela* render Champion’s classification (1887, 1893) and those of previous authors like Horn (1870) artificial. In contrast to Champion’s conservative classification, Allard’s classification (1876, 1877) was more natural in the sense that he recognized several lineages in the New World, some of them with Holartic distribution. Allard’s placement of *H. aereus* in cylindrinotine is supported by our results; nevertheless our results suggest that it should be classified in *Nalassus*, not in *Stenomax*. However, further analyses including more genera from the subtribe are necessary before taxonomic changes are made. This is also the case of the Asiatic *Tarpela cordicollis*, which was classified in a different subgenus (*Lamperos*) by Allard (1877). Allard (1876) proposed the genus *Lamperos* to comprise some *Tarpela* species from North America and Japan, but later reduced it to subgenus (Allard, 1877), including *T. cordicollis*. Aside from this species of *Tarpela*, all the others, including the type (*T. browni*) are placed in a different lineage formed mostly by Neotropical species. This lineage, nevertheless, also includes species of *Nautes*.

The paraphyletic nature of *Tarpela* with respect to *Nautes*, could imply different outcomes as a wider taxon sampling (including more Nearctic species of *Helops*, *Nautes* and mainly *Tarpela*) and character (e.g. from DNA or fine structures revealed using SEM) is considered. Either several lineages could be recognized as different genera or all the species could be lumped in a single larger genus (*Nautes* due to nomenclatural priority, or if applicable, a conserved name *Tarpela*). Even if *Nautes* was supported as a different genus, taxonomic rearrangements seem to be likely. According to the current sampling, *Helops farctus* and *Tarpela aerifera* would need to be reassigned to *Nautes*.
Morphology

Female genitalia have been used as a source of characters to study the relationships among suprageneric taxa in Tenebrionidae (Tschinkel and Doyen 1980, Doyen and Tschinkel 1982, Doyen 1994). Nabozhenko (2006) recognized four morphological patterns for the female genitalia that he associated to lineages from Helopina and Cylindrinotina, two patterns within each subtribe. In our sampling we only observed two of these patterns (Fig. 4A, B), but we also observed two patterns not previously reported for the tribe (Fig. 4C, D). Nevertheless, one of these patterns (Fig. 4C) was previously described for species belonging to Pimeliinae (Doyen 1994). These two patterns newly reported for Tenebrioninae were only seen in the mostly Neotropical clade. Most of the members of this clade share the pattern previously reported for Pimeliinae (Fig. 4C) and the pattern that we report here for the first time (Fig. 4D) was present only in the earlier divergent group of this clade (*Helops perforatus*—*Tarpela contigua*) as well as in *T. depressa*.

Nabozhenko (2001b, 2002a, 2002b, 2005) describes the morphological patterns for the female genitalia tubes of the helopiod type as follows: basal spermathecal duct distinct; spermatheca consisting of two ducts of different length, without additional reservoirs and short processes; basal duct about as long as duct between place of running of gland and branching of spermatheca (Fig. 4A). The female genital tubes of the nalassoid type consist of a short and simple spermatheca, without lateral processes, reservoirs, and branching; gland short, about as long as spermatheca (Nabozhenko 2001b, 2002a, 2002b, Fig. 4B). The pattern shared with some Pimeliinae (Doyen 1994) consists of several spermathecal tubes close to each other or united at the base as a fascicle, always originating near or at the vagina apex, hence without a basal spermathecal duct (Fig. 4C). The newly documented pattern presents several spermathecal tubes distant from each other (Fig. 4D). In both cases, the accessory gland emerges from the common duct (if it is present), always in a terminal position with respect to the spermathecal tubes (Doyen 1994).

Due to its high variation, male genitalia have also been used to explore the relationships among species and higher taxonomic groups (e.g. Doyen and Tschinkel 1982, Aalbu 2005). As in the case of the female genitalia, Nabozhenko (2006) also recognized four morphological patterns for the male genitalia in lineages of the subtribes Helopina and Cylindrinotina. In contrast to the female genitalia, the morphological patterns found among the sampled species fit three of the previously described patterns by Nabozhenko (2006), only with what we consider a minor variation in the catomoid type. The patterns that we recognize correspond to Nabozhenko’s helopiod, nalassoid and catomoid types. According to Nabozhenko (2001b, 2002a, 2005) the helopiod male genitalia type in the broad sense (Fig. 5B) has, among other characters: heavily sclerotized parameres, covered with elongate punctures; baculiform sclerites of spiculum gastrale approximate, not curved outwards in dorsal view. The nalassoid male genitalia type (Figs 5A, E, and 6C, F) is characterized by: an aedeagus weakly sclerotized, semitransparent; parameres elongate, produced apically into compressed keel (Nabozhenko 2001b, 2002a). The catomoid male genitalia type is only present in the mostly Neotropical clade and is characterized by: penis with two or three apices,
rounded in apical part; phallobase very long in comparison with short parameres; parameres with elongate aspirate punctuation and inconspicuous short hairs (Fig. 6B, E) (Nabozhenko 2006). The variation we found for all the species with respect to the catomoid aedeagus type is a lobate apical part of the penis and a shorter basal piece (relative to the length of the parameres) (Fig. 5F).

The recognition of the female and male genitalia types is translated into several homology hypotheses reflected in the matrix as characters 33 to 67 and their corresponding character states (see the list of phylogenetic data: characters above).

Although widely used as a taxonomic character, the keel on the parameres (64) has been reported as not always present through the subtribe (Nabozhenko 2001a). Nevertheless, this could be an artifact of the observation tools, as small keels can be detected when using a scanning electron microscope (SEM) (results not shown). For this reason we prefer to code this condition as “not evident” (see character 64) (in contrast to lacking). This is the same for the “absence” of setae on the parameres, here coded as “not evident” (see character 57).

Other diagnostic or traditionally used characters of the clypeus, antennae, prosternum, wings and tarsi were homoplastic but generally informative, contributing to the overall resolution of the tree. Only four characters from the original matrix introduced high levels of conflict, resulting in a lack of resolution in the consensus. These characters were all continuous and without a more refine codification, e.g., using statistical or morphometric tools, they only obscured the relationships posed by the remaining characters. On the other extreme, the shape of the antenna, generally considered to be a homoplastic character, was recovered as synapomorphic for the tribe. However, this synapomorphy needs to be tested with a broader taxon sampling.

**Conclusions**

Although supported by our results, the monophyly of the tribe still requires a more rigorous test in terms of the taxon sampling from related tribes.

None of the subtribes or the analyzed subordinate genera of Helopini sampled by more than one species was corroborated as monophyletic. A wider taxon sampling is required to circumscribe them in a natural way.

*Helops* and *Tarpela* are polyphyletic, while *Nautes* is paraphyletic, and hence it is expected that further taxon and character sampling in a cladistic context will provide evidence for further splitting of *Helops* and *Tarpela* and a re-circumscription of *Nautes* including some *Helops* and *Tarpela*.

Our results show that in order to achieve a natural classification of Helopini, sampling of taxa should not be based on geographic distribution, although there might be some geographically correlated lineages. This approach has shown that there is a derived New World clade that is mainly composed by Neotropical species. Future efforts should also concentrate on increased sampling within this clade, to reveal other lineages or to corroborate the current ones, so that taxonomic changes can be concordantly proposed.
Acknowledgments

The authors would like to thank the steering committee of the Third International Tenebrionoidea Symposium for the invitation to present our results, especially to Dr Aaron Smith, for his help and useful comments. We are also grateful to the curators of the collections mentioned in the materials and methods section for loaning the specimens used in this work. We greatly appreciate the revision and valuable comments by Dr E. Nearns and Dr M. Zurita-García, as well as those by two anonymous reviewers and most particularly to the associate editor, Dr Patrice Bouchard, who not only provided relevant comments, but was also very understanding and helpful during the publication procedure. We would like to thank S. Guzmán (IBUNAM) for her help with the use of the Leica equipment. The first author thanks the Posgrado en Ciencias Biológicas, UNAM, for its support and the fund of the “Programa de Apoyo para Estudios de Posgrado” provided to visit the entomology collections at the Natural History Museum (BMNH) and the Muséum National d’Histoire Naturelle (MNHN). This study was funded with a doctoral fellowship from the Consejo Nacional de Ciencia y Tecnología (CONACYT 202666) to the first author.

References


Pascoe FP (1866) Notices of new or little known genera and species of Coleoptera. Journal of Entomology 2: 475.


Larvae of the genus *Eleodes* (Coleoptera, Tenebrionidae): matrix-based descriptions, cladistic analysis, and key to late instars

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Academic editor: P. Bouchard | Received 2 July 2013 | Accepted 10 October 2013 | Published 12 June 2014


Abstract

Darkling beetle larvae (Coleoptera, Tenebrionidae) are collectively referred to as false wireworms. Larvae from several species in the genus *Eleodes* are considered to be agricultural pests, though relatively little work has been done to associate larvae with adults of the same species and only a handful of species have been characterized in their larval state.

Morphological characters from late instar larvae were examined and coded to produce a matrix in the server-based content management system mx. The resulting morphology matrix was used to produce larval species descriptions, reconstruct a phylogeny, and build a key to the species included in the matrix.

Larvae are described for the first time for the following 12 species: *Eleodes anthracinus* Blaisdell, *Eleodes carbonarius* (Say), *Eleodes caudiferus* LeConte, *Eleodes extricatus* (Say), *Eleodes goryi* Solier, *Eleodes hispilabris* (Say), *Eleodes nigripolosus* LeConte, *Eleodes pilosus* Horn, *Eleodes subnitens* LeConte, *Eleodes tenuipes* Casey, *Eleodes tribulus* Thomas, and *Eleodes wheeleri* Aalbu, Smith & Triplehorn. The larval stage of *Eleodes arnatus* LeConte is redescribed with additional characters to differentiate it from the newly described congeneric larvae.

Keywords

Tenebrionidae, larvae, matrix-based descriptions, Eleodes
Introduction

Species of the genus *Eleodes* are among the most iconic and recognizable insects of the western United States. Flightless, almost always black in color, and medium to large sized (~10-50 mm), *Eleodes* are perhaps most closely associated with head-stands. While this behavior, linked to the exudation or squirting of a concoction of noxious defensive chemicals from paired reservoirs near the tip of the abdomen, is not unique to *Eleodes*, it has been the source of common names for the genus such as stink or circus beetles.

Larvae of the family Tenebrionidae are known as false wireworms. Feeding on seeds, roots, and subterranean stems, a number of them are considered agricultural pests, including *Eleodes extricatus* (Say, 1824), *Eleodes hispilabris* (Say, 1824), *Eleodes obsoletus* (Say, 1824), *Eleodes opacus* (Say, 1824), and *Eleodes suturalis* (Say, 1824) (Calkins and Kirk 1975). A summary of species considered agricultural pests and the crops they attack is given by Allsopp (1980). In spite of ecological and agricultural interest in false wireworms, and their potential contribution of a whole suite of characters for phylogenetic and taxonomic studies, knowledge of their morphology, development, and habits remain limited. Doyen (1988) estimated that approximately 240 genera and 300 species of darkling beetle larvae had been described which, as far as we know, remains a reasonable approximation. Of the 190+ currently valid *Eleodes* species, only seven have been previously described in the larval stages.

Taxonomic history

Relatively few *Eleodes* larvae have been described or characterized (Table 1). Gissler (1878) provided the first larval descriptions in the genus for *Eleodes dentipes* Eschscholtz, 1833 and *Eleodes giganteus* (Mannerheim, 1843). Hyslop (1912) described the larvae of *Eleodes vandykei* Blaisdell, 1909 (then listed as a subspecies of *Eleodes letcheri*) and *Eleodes pimelioides* Mannerheim, 1843 from the Pacific Northwest. McCulloch (1918) described *Eleodes tricostatus* (Say), 1824. Wade and St. George (1923) described *Eleodes suturalis* (Say, 1824), followed closely by illustrations, without additional descriptions, of the pygidia of *Eleodes carbonarius* (Say, 1824), *Eleodes opacus* (Say, 1824), and *E. tricostatus* by St. George (1924). Blaisdell (1909) redescribed the larvae of *E. dentipes* in greater detail and described the pupa of *Eleodes clavicornis* Eschscholtz, 1833. The most recent larval description was provided by Thomas (1984) for *Eleodes armatus* LeConte, 1851. In most cases, these descriptions are insufficient to reliably diagnose *Eleodes* larvae to species.

Matrix-based taxonomy

A number of modern taxonomic works on insects have produced descriptions based on matrices of morphological characters, including Winterton (2009), Yoder et al. (2009),
Larvae of the genus Eleodes (Coleoptera, Tenebrionidae)...

Talmas et al. (2011), and Mullins et al. (2012) to name a few. The advantages of this methodology include a structured and explicit differentia between the character states exhibited by each species or other taxonomic units, the ability to score new species into the matrix, an option to further utilize the matrix for phylogenetic analyses, and the capability to turn a matrix into a multi-entry key or link it to other data sources, such as an anatomy ontology. The present work is intended as a first step to describe the larvae of the genus Eleodes, define important characters for species and subgeneric differentiation, provide a first glimpse into evolutionary relationships within the genus, and provide a platform to link character states to the developing Coleoptera Anatomy Ontology (ColAO).

**Methods and Materials**

**Morphological parameters.** Measurements were taken using either digital calipers, an optical micrometer attached to a Nikon SMZ 1500 stereomicroscope, or measurement scales set in Photoshop specific to the camera and lens used to take measurements from images. Total length (TL) was measured from the anterior edge of the clypeus to the dorsomedial apex of abdominal segment IX. Prothoracic width (PW) and length (PL) were measured dorsally across the widest and longest points on the segment respectively, head capsule width (HW) was measured dorsally across the widest portion of the head (generally near the apex of the cranial stem). Terminology primarily follows Lawrence (1991). Dissections were performed using fine forceps and a sharpened #0 insect pin.

**Table 1.** Previous publications describing or illustrating Eleodes larvae.

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<thead>
<tr>
<th>Species</th>
<th>Publication</th>
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<tr>
<td>Eleodes armatus (LeConte), 1851</td>
<td>Thomas 1984</td>
<td>egg, larva, and pupa described, larva and pupa imaged</td>
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<td>Eleodes dentipes (Eschscholtz), 1833</td>
<td>Gissler 1878; Blaisdell 1909</td>
<td>Larva briefly described in Gissler (1878); larva redescribed and illustrated in Blaisdell (1909)</td>
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<tr>
<td>Eleodes giganteus (Mannerheim), 1843</td>
<td>Gissler 1878</td>
<td>egg and larva characterized; larva illustrated</td>
</tr>
<tr>
<td>Eleodes opacus (Say), 1824</td>
<td>St. George 1924</td>
<td>pygidium imaged; no description</td>
</tr>
<tr>
<td>Eleodes pimeloides (Mannerheim), 1843</td>
<td>Hyslop 1912</td>
<td>egg, larva, and pupa described; pygidium of larva imaged</td>
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<tr>
<td>Eleodes suturalis (Say), 1824</td>
<td>Wade and St. George 1923</td>
<td>egg, larva, and pupa described; larval natural history discussed, egg and pupa imaged</td>
</tr>
<tr>
<td>Eleodes tricostatus (Say), 1824</td>
<td>McCulloch 1918; St. George 1924</td>
<td>egg, larva, and pupa briefly characterized, larval natural history discussed; right mandible and pygidium of larva imaged in St. George (1924)</td>
</tr>
<tr>
<td>Eleodes vandykei Blaisdell, 1909</td>
<td>Hyslop 1912</td>
<td>egg, larva, and pupa described, egg, larva, and pupa imaged; species listed as E. letcheri vandykei</td>
</tr>
</tbody>
</table>
Photographs of specimens or characters were taken using a BK Plus or Passport Imaging system (R. Larimer, www.visionarydigital.com). Montaged images were assembled using Zerene Stacker (zerenesystems.com/stacker/) and backgrounds were cleaned up in Adobe Photoshop CS5. Confocal laser images were taken on a Zeiss LSM 710.

**Rearing.** Adult *Eleodes* specimens were hand collected from throughout the southwestern United States. Specimens were maintained in separate plastic containers for each species, locality, and collecting event on a substrate of sand. Every one to two weeks, containers were sifted for eggs and larvae. Larvae were reared on a sand/food substrate in plastic containers, with either plaster of Paris at the bottom watered though a vinyl tube to maintain a moisture gradient (Brown 1973) or with daily watering. A study detailing rearing regimes, instar numbers, and life histories for the reared species is forthcoming (Dornburg, Smith & Wheeler, in preparation).

**Matrix-based descriptions.** To allow for easier direct comparisons between larvae of different species and provide a framework for the addition of larvae from more *Eleodes* species in the future, descriptions were produced from a morphological character matrix and edited for traditional telegraphic description format. The character matrix was built in mx (Yoder et al. 2010), based on 86 morphological characters (Appendices 1 and 2). Mx was also used to produce the initial descriptions. Single state characters included in the descriptions, were also included in the matrix. All specimens scored in the matrix were classified as late (7th–11th) instar larvae based on their size or observed number of molts. The one exception was *Eleodes caudiferus*, in which only third instar larvae were available.

**Phylogeny.** A modified subset of the morphology matrix consisting of 48 characters scored for 13 species of *Eleodes* larvae, plus two outgroup species (*Tenebrio molitor* Linnaeus and *Zophobas morio* (Fabricius)), was exported to TNT (Goloboff et al. 2008) and Winclada-NONA (Nixon 2002, Goloboff 1999) for phylogenetic analyses. Invariant characters and characters judged to be potentially highly variable between specimens (e.g. many characters involving color) were excluded from the analyses. Some character states were reordered and/or combined in the matrix used for analyses (Appendices 3 and 4) to reflect outgroup scoring and to clarify discrete parsimony-informative states. Characters and states from Appendices 3 and 4 are abbreviated in the text as (character:state).

Traditional searches were run with 10,000 random additions and TBR branch swapping. New technology searches were also performed using a variety of settings for the Sectorial Search, Rachet, Drift, and Tree fusing functions. Standard bootstrap (10,000 replicates) and Bremer support were assessed in TNT.

**Results**

The phylogenetic analyses returned one most parsimonious tree (Fig. 1). The genus *Eleodes* was relatively strongly supported (BS=87, Bremer=8). *Eleodes extricatus* was placed at the base of the genus with the rest of the *Eleodes*, excluding a reversal in *E.*
Larvae of the genus *Eleodes* (Coleoptera, Tenebrionidae)...

The backbone of the clade had little support, several groupings were supported in the analyses. *Eleodes carbonarius* + *E. anthracinus*, representing the only members of the subgenus *Melaneleodes* in the analyses, was well supported (BS=99, Bremer=10). The presence of four long setae on the ligula (18:4, Fig. 11A) and a trapezoidal hypopharyngeal sclerome (19:1; Fig. 12A) may represent synapomorphies for the subgenus.

*Eleodes armatus* + (*E. tenuipes* + *E. hispilabris*) was supported (BS=60, Bremer=3), and represents most of the members of the nominate subgenus *Eleodes* in the analyses. The three species share two synapomorphies within the species sampled. One, the arrangement of anterior sensory papillae (16:1, Fig. 9B‒C); and two, the presence of a distinct apical tooth on the pygidium (42:1, Fig. 14A). *Eleodes caudiferus*, another species currently in the nominate subgenus, is lacking both characters and was (BS=64, Bremer=4) supported in a sister relationship with *Eleodes pilosus* from the subgenus *Tricheleodes*. Both *E. caudiferus* and *E. pilosus* adults are found on sand dunes, and the two larval synapomorphies the species share in the matrix (8:1 and 26:1) are based on the presence of dense setation, a common adaptation to living on sand. Hence, it is possible these character codings represent convergence based on larval habitat. *Eleodes caudiferus* also had one unusual autapomorphy in the presence of longitudinal tomen-
tose bands of setae along the margins of the abdominal sternites (Fig. 13A), which may also be an adaptation for living primarily on unconsolidated dunes. *Eleodes tribulus* was suggested as a member of the nominate subgenus (Triplehorn and Aalbu 1987), but also lacks the two synapomorphies found in other species of the subgenus. It was weakly supported in a relationship with *E. goryi + E. subnitens* from the subgenus *Protomerus*. Determining whether *E. caudiferus* and *E. tribulus* belong in the subgenus *Eleodes* requires further analyses of additional data.

**Larval descriptions**

Larvae are described or redescribed to include differential characters to separate species within the genus. Verbatim locality label data are listed with “/” indicating line breaks on the label.

*Eleodes* Eschscholtz, 1829

http://species-id.net/wiki/Eleodes

**Material examined.** Over 1,400 larval *Eleodes* specimens were examined for this study from 14 *Eleodes* species. In addition, historical descriptions and *Eleodes* specimens for which the species could not be confirmed due to a lack of positive association between adults and larvae also conform to the generic description provided.

**Description.** Integument strongly sclerotized, light tan to nearly black in color; setose, with hair-like setae throughout and spinose setae on legs and abdominal tergite IX. Thoracic and abdominal segments subcylindrical, surface coriaceous (Figs 2A‒D, 3A‒D, 4A‒C, 5A‒C, 6A‒C).

**Head.** Prognathous or slightly declined (Fig. 7A‒C), weakly dorsoventrally flattened, strongly constricted before occipital foramen. Epicranial stem one-fourth to one third head capsule length; frontal arms U-shaped or sinuate, occasionally obscured by sculpturing. Frons and dorsal portion of epicranial plates weakly to moderately rugose; punctate, punctures minute, lacking setae. Ventrolateral portions of epicranial plates setose; setae golden, erect; two stemmata present on each plate, pigmented spots often faded. Clypeus trapezoidal, often weakly transversely raised medi ally. Labrum with two transverse rows of six to fourteen erect setae present medially and subapically; anterior margin straight or weakly emarginate. Epipharynx (Fig. 8, 9A‒D, 10A‒D) with stout spiniform setae along anterior margin, an anterior cluster of four to six variably arranged spinules, a subanterior transverse row of four small spinules subtended by two spinose setae and posterior cluster of six to eight small spinules; tormae symmetrical or asymmetrical. Mandible apex bidentate, mola concave. Ligula small, setation variable (Fig. 11A‒C). Hypopharyngeal sclerome pentagonal or trapezoidal (Fig. 12A‒B). Gula distinct, trapezoidal, widest in basal half. Antenna three segmented, cylindrical.
Larvae of the genus Eleodes (Coleoptera, Tenebrionidae)...

Thorax. Prothoracic tergum 1.2× or more length of meso- or metaterga (Figs 2A–D, 3A–D); anterior transverse striated band present, generally darker than protergal disc; lateral margins with granulated band either distinct or barely visible (Fig. 7A–C). Posterior transverse striated band present on all thoracic tergites. Meso- and metathoracic tergites wider than long. Mesothoracic spiracle simple, ovate, approximately 1.5× size of abdominal spiracles; reduced metathoracic spiracle visible, less than one-fourth size of mesothoracic spiracle. Legs. Prothoracic leg slightly longer, much thicker than meso- and metathoracic legs; prothoracic tarsungulus strongly sclerotized, sickle-shaped; dorsal surface of prothoracic femur with faintly indicated basal sclerotized band; dorsal surface of prothoracic tibia slightly more sclerotized than ventral surface.

Abdomen. Abdominal tergites and sternites I–VIII with transverse striated bands present along posterior margins. Abdominal sternite I setose (Fig. 13A–B). Abdominal segment IX (pygidium) triangular in dorsal view, gradually reflexed to apex, urogomphi absent, apical tooth present or absent (Fig. 14A–B); marginal row of socketed spines present around posterior two-thirds to one half of segment. Abdominal segment X located ventrally; pygopods short, subconical, each with erect setae.

Variation. Eleodes larvae can vary greatly in pigmentation, size, number of spines on the legs and pygidium, and the overall degree of sclerotization. Characters in the matrix relating to general integument coloration (6, 24, 45, 46, 47, 69) can vary greatly between specimens depending on age of specimen, length of time since last instar, and preservation method. There may also be genetic variation, though specimens from our populations were generally homogeneous.

Diagnosis. All known Eleodes larvae share the following combination of characters: head capsule weakly dorsoventrally flattened, strongly constricted before occipital foramen; prothoracic tergum 1.2× or more length of meso- or metaterga, anterior transverse striated band present, lateral margins with granulated band either distinct or barely visible; prothoracic leg slightly longer and much thicker than meso- and metathoracic legs; 8–38 socketed spines on the pygidial margin, pygopods short, subconical, each with erect setae. However, the known Eleodes larvae cannot yet be separated from other Amphidorini larvae due to a lack of specimens.

Subgenus Blapylis Horn, 1870

Eleodes (Blapylis) nigropilosus (LeConte, 1851)
http://species-id.net/wiki/Eleodes_nigropilosus
Figure 4A

Material examined. Larval E. nigropilosus specimens were reared from adults with the following collecting information: “USA: CA: San Diego Co. / Oceanside beach / 33.1865, -117.3778 / 14.May.2011, ADSmith”. A total of 29 eggs and larvae were reared and examined for this study, of which 34 survived to the 2nd instar or beyond. The following description is based on a detailed examination of three 8-11th instar specimens.
Figure 2. Dorsal habitus of four *Eleodes* species: A. (*Caverneleodes*) *wheeleri*; B. (*Eleodes*) *armatus* C. (*Eleodes*) *caudiferus* D. (*Eleodes*) *tribulus*. Scale bar = 5 mm.
Figure 3. Dorsal habitus of four Eleodes species: A. (Litheleodes) extricatus B. (Melaneleodes) anthracinus C. (Melaneleodes) carbonarius D. (Tricheleodes) pilosus. Scale bar = 5 mm.
Description. TL: 12–15.9 mm, HW: 1.0–1.1 mm, PL: 1.3–1.5 mm, PW: 1.0–1.2 mm.

Head. Prognathous or weakly declined; weakly dorsoventrally flattened; width nearly equal to prothorax; sides rounded; strongly constricted before occipital foramen; color light to dark tan, same or nearly the same as body segments; punctuation minute, moderately dense, separated by 2–4 puncture diameters. Epicranial suture stem length approximately one-third head capsule length; frontal arms sinuate, not obscured by sculpturing. Frons faintly rugose. Epicranial plates weakly rugose dorsally; lateral portions moderately setose; ventral portion of each plate with row of four to five long setae along anterior margin near buccal cavity, not confluent with setae on lateral portions of plates, and a patch of short setae medially, forming a triangular pattern with its base near the anterior margin. Two stemmata present on each epicranial plate, pigmented spots often faded. Clypeus trapezoidal, not swollen, darker medially in basal half, minutely punctate, punctuation moderately dense, separated by 2–4 puncture diameters. Labrum not swollen, sides rounded, basal half more darkly pigmented, medial setal row with six to seven erect setae subapical setal row with seven to eight erect setae, anterior margin straight to weakly emarginate. Epipharynx anterior setal row with six stout spiniform setae, anterolateral margins with micro-setation; six anterior sensory papillae present, arranged in two irregular diagonal rows; four subanterior sensory papillae present, arranged as transverse row subtended by two spinose setae; eight posterior sensory papillae present, arranged in an irregular cluster. Tormae asymmetric, left torma smaller. Ligula apex and subapical dorsal surface densely micro-setose, two long subapical setae present ventrally. Hypopharyngeal sclerome pentagonal, tricuspidate. Gula distinct, trapezoidal, widest in basal half, length subequal or greater than maximum width. Antenna three segmented, cylindrical, length of first segment subequal to second.

Thorax. Thoracic tergites light tan, prothoracic sternite anterior to legs medium brown, thoracic sternites posterior to prolegs light brown. Prothoracic tergum subquadrate, 1.5× length of meso- or metaterga; anterior transverse striated band present, darker than protergal disc; lateral margins with distinct granulated band, darker than protergal disc. Posterior transverse striated band present on all thoracic tergites, forming a gradient from darker brown anteriorly to lighter brown along posterior border. Meso- and metathoracic tergites wider than long, each with a faintly indicated sclerotized transverse line present on anterior fifth. Thoracic tergites sparsely setose on dorsal surfaces, lateral margins more densely setose. Mesothoracic spiracle simple, ovate, approximately 1.5× size of abdominal spiracles; reduced metathoracic spiracle visible, less than one-fourth size of mesothoracic spiracle. Legs. Prothoracic leg slightly longer, much thicker than meso- and metathoracic legs; prothoracic tarsungulus strongly sclerotized, sickle-shaped; prothoracic trochanter with two stout spines ventromedially; prothoracic femur with ventromedial row of three spines, dorsal surface with faintly indicated basal sclerotized band; prothoracic tibia with ventromedial row of three to four spines, dorsal surface slightly more sclerotized than ventral surface. Mesotibia with two ventromedial spines.
Abdomen. Abdominal tergites and sternites light tan with darker transverse striated bands present along posterior margins of segments I–VIII, forming near contiguous band around segments, bands dark along anterior edge, fading to segment color posteriorly. Abdominal sternite I sparsely clothed in long erect setae from anterior margin.

Figure 4. Lateral habitus of three Eleodes species: A. E. (Blapylis) nigropilosus B. E. (Caverneleodes) wheeleri C. E. (Eleodes) armatus. Scale bar = 5 mm.
to near midline. Abdominal laterotergites with lateral margins distinctly pigmented. Abdominal segment IX (pygidium) triangular in dorsal view, gradually reflexed to apex, urogomphi absent, apex not forming a distinct tooth, moderately clothed in short and mid length erect setae, sclerotized uniformly throughout, lacking maculations; marginal row of 14–18 socketed spines present, arranged as single row around posterior two-thirds to one half of segment. Abdominal sternites I–VIII lacking longitudinal tomentose bands along lateral margins. Pygopods short, subconical, each with 9–12 erect setae.

**Diagnosis.** *Eleodes nigropilosus* larvae can be separated from the other currently known *Eleodes* species by having the posterior pigmented band around the abdominal segments forming a color gradient from dark along anterior edge and fading to the color of the rest of the segment posteriorly.

**Subgenus Caverneleodes Triplehorn, 1975**

*Eleodes (Caverneleodes) wheeleri* Aalbu, Smith, & Triplehorn, 2012

http://species-id.net/wiki/Eleodes_wheeleri

Figures 2A, 4B

**Material examined.** Larval *E. wheeleri* specimens were reared from adults with the following collecting information: “USA: Arizona: Gila Co. / Tonto Natural Bridge SP / N34.3214, W111.4569 / 11.IX.2010, ADSmith”. A total of 15 eggs and larvae were reared and examined for this study, with all surviving until the 2nd instar or beyond. The following description is based on a detailed examination of five 8-11th instar specimens.

**Description.** Measurements: TL: 18.0–23.9 mm, PL: 1.6–2.1 mm, PW: 2.1–2.7 mm, HW: 1.8–2.3 mm.

**Head.** Prognathous or weakly declined; weakly dorsoventrally flattened; width nearly equal to prothorax; sides rounded; strongly constricted before occipital foramen; color light tan, same or nearly the same as body segments; punctation minute, dense, separated by 1–2 puncture diameters. Epicranial suture stem length approximately onethird head capsule length; frontal arms sinuate, not obscured by sculpturing. Frons weakly rugose. Epicranial plates weakly rugose dorsally; lateral portions sparsely setose; ventral portion of each plate with row of six or more long setae along anterior margin near buccal cavity confluent with setae on lateral portions of plates, and a patch of short setae medially, forming a triangular pattern with its base near the anterior margin. Two stemmata present on each epicranial plate, pigmented spots often faded. Clypeus trapezoidal, swollen, darker medially in basal half, minutely punctate, punctation moderately dense, separated by 2–4 puncture diameters. Labrum swollen, sides rounded, basal half more darkly pigmented, medial setal row with six to seven erect setae, subapical setal row with seven to eight erect setae, anterior margin straight to weakly emarginate. Epipharynx anterior setal row with six stout spiniform setae, ante-
Larvae of the genus Eleodes (Coleoptera, Tenebrionidae)...

rolateral margins with micro-setation; four anterior sensory papillae present, arranged in two irregular longitudinal rows; four subanterior sensory papillae present arranged as a transverse row subtended by two spinose setae; eight posterior sensory papillae present, arranged in an irregular cluster. Tormae asymmetric, left torma smaller. Ligula apex lacking microsetae, two long subapical setae present ventrally, eight or more subapical setae present dorsally. Hypopharyngeal sclerome pentagonal, tricuspidate. Gula distinct, weakly trapezoidal, nearly rectangular. Antenna three segmented, cylindrical, first segment length subequal to second.

**Thorax.** Thoracic tergites light tan, prothoracic sternite anterior to legs light brown, thoracic sternites posterior to prolegs light tan to brown. Prothoracic tergum wider than long, 1.2× or more length of meso- or metaterga; anterior transverse striated band present, darker than protergal disc; lateral margins with very faint granulated band, nearly concolorous with protergal disc. Posterior transverse striated band present on all thoracic tergites, unicolorous brown. Meso- and metathoracic tergites wider than long, each with a faintly indicated sclerotized transverse line present on anterior fifth. Thoracic tergites sparsely setose on dorsal surfaces, lateral margins more densely setose. Mesothoracic spiracle simple, ovate, approximately 1.5× size of abdominal spiracles; reduced metathoracic spiracle visible, less than one-fourth size of mesothoracic spiracle. Legs. Prothoracic leg slightly longer, much thicker than meso- and metathoracic legs; prothoracic tarsungulus strongly sclerotized and sickle-shaped; prothoracic trochanter with two stout spines ventromedially; prothoracic femur with ventromedial row of four spines, dorsal surface with faintly indicated basal sclerotized band; prothoracic tibia with ventromedial row of five to six spines, dorsal surface slightly more sclerotized than ventral surface. Mesotibia with four to five ventromedial spines.

**Abdomen.** Abdominal tergites and sternites light tan with slightly darker transverse striated bands present along posterior margins of segments I–VIII, forming near contiguous unicolorous band around segments. Abdominal sternite I sparsely clothed in long erect setae along anterior margin. Abdominal laterotergites concolorous with tergites, lacking distinct pigmented margins. Abdominal segment IX (pygidium) triangular in dorsal view, gradually reflexed to apex, urogomphi absent, apex forming a small tooth, sparsely clothed in short and mid length erect setae, sclerotized uniformly throughout, lacking maculations; marginal row of 14–18 socketed spines present, arranged as single row around posterior two-thirds to one half of segment. Abdominal sternites I–VIII lacking longitudinal tomentose bands along lateral margins. Pygopods short, subconical, each with 11–15 erect setae.

**Diagnosis.** Eleodes wheeleri larvae can be separated from the other currently known Eleodes species by the pentagonal hypopharyngeal sclerome, the lack of a distinct apical tooth on the pygidium, the presence of two long subapical ventral setae on the ligula with eight or more setae present dorsally, and the lateral margins of the protergum with a very faint granulated band, nearly concolorous with protergal disc.

**Remarks.** Eleodes wheeleri was recently described (Aalbu et al. 2012) from Tonto Natural Bridge Caverns in Arizona and is known only from the type locality.
Subgenus *Eleodes* Eschscholtz, 1829

*Eleodes* (*Eleodes*) *armatus* LeConte, 1851
http://species-id.net/wiki/Eleodes_armatus
Figures 2B, 4C, 9B, 11B

**Material examined.** Larval *E. armatus* specimens were reared from adults with the following collecting information: “USA: CA: Riverside Co. / Palm Desert, 38th Ave / off Washington St. / N33.7721, W116.3071 / 10.X.2010, ADSmith”; “USA: AZ: Maricopa Co. / Phoenix, E. Eugie Ave / & 7th St. N33°36.665’ / W112°03.849’, 418 m., / 25 May 2011, R.Dornburg.” A total of 1805 eggs and larvae were reared and examined for this study, with 128 persisting to the 2nd instar or later. The following description is based on a detailed examination of fifteen 8-11th instar specimens

**Description.** TL: 21.0‒35.0 mm, HW: 2.4‒3.8 mm, PL: 2.4‒3.4 mm, PW: 2.9‒4.6 mm.

**Head.** Prognathous or weakly declined; weakly dorsoventrally flattened; width nearly equal to prothorax; sides rounded; strongly constricted before occipital foramen; color ferruginous, more heavily pigmented than body segments; punctuation minute, dense, separated by 1–2 puncture diameters. Epicranial suture stem length approximately one-fourth head capsule length; frontal arms sinuate, not obscured by sculpturing. Frons weakly rugose. Epicranial plates weakly rugose dorsally; lateral portions moderately setose; ventral portion of each plate with row of six or more long setae along anterior margin near buccal cavity confluent with setae on lateral portions of plates, and a patch of short setae medially, forming a triangular pattern with its base near the anterior margin. Two stemmata present on each epicranial plate, pigmented spots often faded. Clypeus trapezoidal, swollen, darker medially in basal half, minutely punctate, punctuation moderately dense, separated by 2–4 puncture diameters. Labrum swollen, sides rounded, basal half more darkly pigmented, medial setal row with seven to eight erect setae, subapical setal row with seven to eight erect setae, anterior margin straight to weakly emarginate. Epipharynx (Fig. 9B) anterior setal row with six stout spiniform setae, anterolateral margins with micro-setation; six anterior sensory papillae present, arranged in two irregular rows, each with two posterior papillae and one near the anterior margin; four subanterior sensory papillae present, arranged as a transverse row subtended by two spinose setae; eight posterior sensory papillae present, arranged in an irregular cluster. Tormae asymmetric, left torma smaller. Ligula apex lacking microsetae, two long subapical setae present ventrally, eight or more subapical setae present dorsally. Hypopharyngeal sclerome pentagonal, tricuspidate. Gula distinct, trapezoidal, widest in basal half, length less than maximum width. Antenna three segmented, cylindrical, first segment longer than second.

**Thorax.** Thoracic tergites light tan to ferruginous, prothoracic sternite anterior to legs ferruginous, thoracic sternites posterior to prolegs light brown. Prothoracic tergum wider than long, 1.2× or more length of meso-, metaterga; anterior transverse striated band present, darker than protergal disc; lateral margins with distinct granc-
Larvae of the genus *Eleodes* (Coleoptera, Tenebrionidae)...

Larvae of the genus *Eleodes* (Coleoptera, Tenebrionidae)...

lated band, darker than protergal disc. Posterior transverse striated band present on all thoracic tergites, unicolorous brown. Meso- and metathoracic tergites wider than long, each with a heavily sclerotized transverse line present on anterior fifth. Thoracic tergites sparsely setose on dorsal surfaces, lateral margins more densely setose. Mesothoracic spiracle simple, ovate, approximately 1.5× size of abdominal spiracles; reduced metathoracic spiracle visible, less than one-fourth size of mesothoracic spiracle. Legs. Prothoracic leg slightly longer, much thicker than meso- and metathoracic legs; prothoracic tarsungulus strongly sclerotized, sickle-shaped; prothoracic trochanter with two stout spines ventromedially; prothoracic femur with ventromedial row of six to ten spines, dorsal surface with faintly indicated basal sclerotized band; prothoracic tibia with ventromedial row of eight to eleven spines or spine setae, dorsal surface slightly more sclerotized than ventral surface. Mesotibia with five to seven ventromedial spines.

**Abdomen.** Abdominal tergites and sternites light tan to ferruginous, with slightly darker transverse striated bands present along posterior margins of segments I–VIII, forming near contiguous unicolorous band around segments. Abdominal sternite I moderately clothed in long erect setae from anterior margin to near midline. Abdominal laterotergites with lateral margins distinctly pigmented. Abdominal segment IX (pygidium) triangular in dorsal view, gradually reflexed to apex, urogomphi absent, apex forming a distinct tooth, sparsely clothed in short and mid length erect setae, sclerotized uniformly throughout, lacking maculations; marginal row of 22–24 socketed spines present, arranged as single row around posterior two-thirds to one half of segment. Abdominal sternites I–VIII lacking longitudinal tomentose bands along lateral margins. Pygopods short, subconical, each with 11–15 erect setae.

**Diagnosis.** *Eleodes armatus* larvae can be separated from the other currently known *Eleodes* species by presence of an apical tooth on the pygidium and the absence of stout spiniform setae on the anterolateral margins of the epipharynx.

**Eleodes** (*Eleodes*) *caudiferus* LeConte, 1858

http://species-id.net/wiki/Eleodes_caudiferus

Figures 2C, 5A, 13A

**Material examined.** Larval *E. caudiferus* specimens were reared from adults with the following collecting information: “USA: Arizona: Navajo Co. / dunes ~4mi N Chilchinbito / off route 59, el. 1738m / N36.58143, W110.06973 / 26.August.2010, ADSmith”. A total of 85 eggs and larvae were reared and examined for this study, of which 53 survived until the 2nd instar or later. The following description is based on a detailed examination of eleven 3-5th instar specimens.

**Description.** TL: 7.8–12.8 mm, HW: 1.0–1.4 mm, PL: 1.0–1.8 mm, PW: 1.3–1.7 mm.

**Head.** Prognathous or weakly declined; weakly dorsoventrally flattened; width narrower than prothorax; sides rounded; strongly constricted before occipital foramen; color dark tan, same or nearly the same as on body segments; punctuation minute,
moderately dense, separated by 2–4 puncture diameters. Epicranial suture stem length approximately one-fourth to one-third head capsule length; frontal arms sinuate, not obscured by sculpturing. Frons rugose. Epicranial plates rugose dorsally; lateral portions densely setose; ventral portion of each plate with row of six or more long setae along anterior margin near buccal cavity confluent with setae on lateral portions of plates, and a patch of short setae medially, forming a triangular pattern with its base near the anterior margin. Two stemmata present on each epicranial plate, pigmented spots often faded. Clypeus trapezoidal, swollen, darker medially in basal half, minutely punctate, puncta-
Larvae of the genus *Eleodes* (Coleoptera, Tenebrionidae)...

Larvae of the genus *Eleodes* (Coleoptera, Tenebrionidae)...

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...tion moderately dense, separated by 2–4 puncture diameters. Labrum swollen, sides rounded, basal half more darkly pigmented, medial setal row with 10–14 erect setae, subapical setal row with 10–14 erect setae, anterior margin straight to weakly emarginate. Epipharynx anterior setal row with eight or more stout spiniform setae, anterolateral margins with micro-setation; six anterior sensory papillae present, arranged in two irregular rows; four subanterior sensory papillae present arranged as a transverse row subtended by two spinose setae; eight posterior sensory papillae present, arranged in an irregular cluster. Tormae symmetrical or weakly asymmetric. Ligula apex densely microsetose, two long subapical setae present ventrally. Hypopharyngeal sclerome pentagonal, tricuspidate. Gula distinct, trapezoidal, widest in basal half, length less than maximum width. Antenna three segmented, cylindrical, first segment subequal to second.

**Thorax.** Thoracic tergites ferruginous, prothoracic sternite anterior to legs ferruginous, thoracic sternites posterior to prolegs light brown. Prothoracic tergum subquadrate, 1.5× length of meso- or metaterga; anterior transverse striated band present, darker than protergal disc; lateral margins with distinct granulated band, darker than protergal disc. Posterior transverse striated band present on all thoracic tergites, unicolorous brown. Meso- and metathoracic tergites wider than long, with sclerotized transverse line on anterior fifth absent, dense transverse band of short setae present near anterior margins of both tergites. Mesothoracic spiracle simple, ovate, approximately 1.5× size of abdominal spiracles; reduced metathoracic spiracle visible, less than one-fourth size of mesothoracic spiracle. Legs. Prothoracic leg slightly longer, much thicker than meso- and metathoracic legs; prothoracic tarsungulus strongly sclerotized, sickle-shaped; prothoracic trochanter with two stout spines ventromedially; prothoracic femur with ventromedial row of five to six spines, dorsal surface with faintly indicated basal sclerotized band; prothoracic tibia with ventromedial row of five to six spines or spinose setae, dorsal surface slightly more sclerotized than ventral surface. Mesotibia with row of three ventromedial spines.

**Abdomen.** Abdominal tergites and sternites light tan to ferruginous, with slightly darker transverse striated bands present along posterior margins of segments I–VIII, forming near contiguous unicolorous band around segments. Abdominal sternite I tomentose in anterior third, setae denser along near lateral margins. Abdominal laterotergites with lateral margins distinctly pigmented. Abdominal segment IX (pygidium) triangular in dorsal view, gradually reflexed to apex, urogomphi absent, apex attenuated and sclerotized, rarely forming a small tooth, sparsely clothed in short and mid length erect setae, sclerotized uniformly throughout, lacking maculations; marginal row of 28–38 socketed spines present, forming two or three irregular rows around posterior two-thirds to one half of segment, narrowing to single row around apex. Abdominal sternites I–VIII with longitudinal tomentose bands present along lateral margins. Pygopods short, subconical, each with 17–24 erect setae.

**Diagnosis.** *Eleodes caudiferus* larvae can be separated from the other currently known *Eleodes* species by the presence of longitudinal tomentose bands along the lateral margins of abdominal sternites I–VIII.
Eleodes (Eleodes) hispilabris (Say, 1824)
http://species-id.net/wiki/Eleodes_hispilabris
Figures 9C, 14A

Material examined. Larval E. hispilabris specimens were reared from adults with the following collecting information: “USA: TX: El Paso County / El Paso, sand dunes off / Hwy 180/Montana Ave. / N31.82327, W106.13234 / 21-22.VIII.2010, ADSmith”. A total of 46 eggs and larvae were reared and examined for this study, with 36 surviving until the 2nd instar or beyond. The following description is based on a detailed examination of five 8–11th instar specimens.

**Description.** TL: 21.0–32.0 mm, PL: 2.6–3.2 mm, PW: 3.0–3.7 mm, HW: 2.4–3.1 mm.

**Head.** Prognathous or weakly declined; weakly dorsoventrally flattened; width narrower than prothorax; sides rounded; strongly constricted before occipital foramen; color ferruginous, more heavily pigmented than body segments; punctation minute, dense, separated by 1–2 puncture diameters. Epicranial suture stem length approximately one-fourth head capsule length; frontal arms sinuate, not obscured by sculpturing. Frons rugose. Epicranial plates rugose dorsally; lateral portions moderately setose; ventral portion of each plate with row of four to five long setae along anterior margin near buccal cavity, not confluent with setae on lateral portions of plates, with a patch of short setae medially, forming a triangular pattern with its base near the anterior margin. Two stemmata present on each epicranial plate, pigmented spots often faded. Clypeus trapezoidal, swollen, darker medially in basal half, minutely punctate, punctation dense, separated by 1–2 puncture diameters. Labrum swollen, sides rounded, basal half more darkly pigmented, medial setal row with six to seven erect setae, subapical setal row with 10–14 erect setae, anterior margin straight to weakly emarginate. Epipharynx (Fig. 9C) anterior setal row with eight or more stout spiniform setae, anterolateral margins with stout spinose setae; six anterior sensory papillae present, arranged in two irregular rows, each with two posterior papillae and one near the anterior margin; four subanterior sensory papillae present, arranged as a transverse row subtended by two spinose setae; seven to eight posterior sensory papillae present, arranged in an irregular cluster. Tormae strongly asymmetric, left torma larger. Ligula apex lacking microsetae, two long subapical setae present ventrally, eight or more subapical setae present dorsally. Hypopharyngeal sclerome pentagonal, tricuspidate. Gula distinct, trapezoidal, widest in basal half, length less than maximum width. Antenna three segmented, cylindrical, first segment longer than second.

**Thorax.** Thoracic tergites light tan, prothoracic sternite anterior to legs light tan to ferruginous, thoracic sternites posterior to prolegs light brown. Prothoracic tergum wider than long, 1.2× or more length of meso- or metaterga; anterior transverse striated band present, darker than protergal disc; lateral margins with distinct granulated band, darker than protergal disc. Posterior transverse striated band present on all thoracic tergites, unicolorous brown. Meso- and metathoracic tergites wider than long, each with a heavily sclerotized transverse line present on anterior fifth. Thoracic tergites sparsely
Larvae of the genus Eleodes (Coleoptera, Tenebrionidae)...

setose on dorsal surfaces, lateral margins more densely setose. Mesothoracic spiracle simple, ovate, approximately 1.5× size of abdominal spiracles; reduced metathoracic spiracle visible, less than one-fourth size of mesothoracic spiracle. Legs. Prothoracic leg slightly longer, much thicker than meso- and metathoracic legs; prothoracic tarsus strongly sclerotized, sickle-shaped; prothoracic trochanter with one or two stout ventromedially spines; prothoracic femur with ventromedial row of six to ten spines, dorsal surface with faintly indicated basal sclerotized band; prothoracic tibia with ventromedial row of eight to eleven spines or spinose setae, dorsal surface slightly more sclerotized than ventral surface. Mesotibia with four to five ventromedial spines.

**Abdomen.** Abdominal tergites and sternites light tan, with slightly darker transverse striated bands present along posterior margins of segments I–VIII, forming near contiguous unicolorous band around segments. Abdominal sternite I sparsely clothed in long erect setae from anterior margin to near midline. Abdominal laterotergites with lateral margins distinctly pigmented. Abdominal segment IX (pygidium) triangular in dorsal view, gradually reflexed to apex, urogomphi absent, apex forming a distinct tooth, sparsely clothed in short and mid length erect setae, sclerotized uniformly throughout, lacking maculations; marginal row of 17–23 socketed spines present, arranged as single row around posterior two-thirds to one half of segment. Abdominal sternites I–VIII lacking longitudinal tomentose bands along lateral margins. Pygopods short, subconical, each with 9–12 erect setae.

**Diagnosis.** *Eleodes hispilabris* larvae can be separated from the other currently known *Eleodes* species by the presence of an apical tooth on the pygidium, stout spiniform setae on the anterolateral margins of the epipharynx, and a row of 6–10 ventromedial spines on the prothoracic femur.

**Eleodes (Eleodes) tenuipes** Casey, 1890
http://species-id.net/wiki/Eleodes_tenuipes

**Material examined.** Larval *E. tenuipes* specimens were reared from adults with the following collecting information: “USA: TX: El Paso County / El Paso, sand dunes off / Hwy 180/Montana Ave. / N31.82327, W106.13234 / 21-22.VIII.2010, ADSmith”. A total of five eggs and larvae were reared and examined for this study. The following description is based on a detailed examination of one late instar specimen.

**Description.** Measurements: TL: 39.0 mm, HW: 4.1 mm, PL: 4.0 mm, PW: 4.8 mm.

**Head.** Prognathous or weakly declined; weakly dorsoventrally flattened; width nearly equal to prothorax; sides rounded; strongly constricted before occipital foramen; color ferruginous, more heavily pigmented than body segments; punctation minute, dense, separated by 1–2 puncture diameters. Epicranial suture stem length approximately one-fourth head capsule length; frontal arms sinuate, not obscured by sculpturing. Frons rugose. Epicranial plates rugose dorsally; lateral portions moderately setose; ventral portion of each plate with row of six or more long setae along anterior margin near buccal cavity confluent with setae on lateral portions of plates, and a patch of short setae medially,
forming a triangular pattern with its base near the anterior margin. Two stemmata present on each epicranial plate, pigmented spots often faded. Clypeus trapezoidal, swollen, darker medially in basal half, minutely punctate, punctuation dense, separated by 1–2 puncture diameters. Labrum swollen, sides rounded, basal half more darkly pigmented, medial setal row with six to seven erect setae, subapical setal row with 10–14 erect setae, anterior margin straight to weakly emarginate. Epipharynx anterior setal row with eight or more stout spiniform setae, anterolateral margins with stout spinose setae; six anterior sensory papillae present, arranged in two irregular rows, each with two posterior papillae and one near the anterior margin; four subanterior sensory papillae present, arranged as a transverse row subtended by two spinose setae; eight posterior sensory papillae present, arranged in an irregular cluster. Tormae strongly asymmetric, left torma smaller. Ligula apex lacking microsetae, two long subapical setae present ventrally, eight or more subapical setae present dorsally. Hypopharyngeal sclerome pentagonal, tricuspidate. Gula distinct, trapezoidal, widest in basal half, length less than maximum width. Antenna three segmented, cylindrical, first segment longer than second.

**Thorax.** Thoracic tergites light tan, prothoracic sternite anterior to legs ferruginous, thoracic sternites posterior to prolegs light brown. Prothoracic tergum wider than long, 1.2× or more length of meso- or metaterga; anterior transverse striated band present, darker than protergal disc; lateral margins with distinct granulated band, darker than protergal disc. Posterior transverse striated band present on all thoracic tergites, unicolorous brown. Meso- and metathoracic tergites wider than long, each with a heavily sclerotized transverse line present on anterior fifth. Thoracic tergites sparsely setose on dorsal surfaces, lateral margins more densely setose. Mesothoracic spiracle simple, ovate, approximately 1.5× size of abdominal spiracles; reduced metathoracic spiracle visible, less than one-fourth size of mesothoracic spiracle. Legs. Prothoracic leg slightly longer, much thicker than meso- and metathoracic legs; prothoracic tarsungulus strongly sclerotized, sickle-shaped; prothoracic trochanter with one stout ventromedially spine; prothoracic femur with ventromedial row of 13–14 spines, dorsal surface with faintly indicated basal sclerotized band; prothoracic tibia with ventromedial row of eight to eleven spines or spinose setae, dorsal surface slightly more sclerotized than ventral surface. Mesotibia with five to seven ventromedial spines.

**Abdomen.** Abdominal tergites and sternites light tan, with slightly darker transverse striated bands present along posterior margins of segments I–VIII, forming near contiguous unicolorous band around segments. Abdominal sternite I sparsely clothed in long erect setae from anterior margin to near midline. Abdominal laterotergites with lateral margins distinctly pigmented. Abdominal segment IX (pygidium) triangular in dorsal view, gradually reflexed to apex, urogomphi absent, apex forming a distinct tooth, sparsely clothed in short and mid length erect setae, sclerotized uniformly throughout, lacking maculations; marginal row of 27 socketed spines present, arranged as single row around posterior two-thirds to one half of segment. Abdominal sternites I–VIII lacking longitudinal tomentose bands along lateral margins.

**Diagnosis.** *Eleodes tenuipes* larvae can be separated from the other currently known *Eleodes* species by the presence of an apical tooth on the pygidium, stout spiniform se-
Larvae of the genus *Eleodes* (Coleoptera, Tenebrionidae)...

tae on the anterolateral margins of the epipharynx, and a row of 13–14 ventromedial spines on the prothoracic femur. It is further differentiated from *E. hispilabris* by having a row of three ventromedial spines on the mesotarsus and having the ventral portion of the epicranial plates with a row of six or more long setae along anterior margin near buccal cavity, confluent with setae on lateral portions of plates.

**Remarks.** Five eggs or early instar larvae were initially placed in a rearing chamber on 25 September 2010, though by the first sifting only one specimen was found. The last specimen thrived until 27 January 2011 when it was preserved for this study.

**Eleodes (Eleodes) tribulus** Thomas, 2005

http://species-id.net/wiki/Eleodes_tribulus

Figures 2D, 5B, 9D

**Material examined.** Larval *E. tribulus* specimens were reared from adults with the following collecting information: “USA: AZ: Pinal Co. / I-10W Rest Area, mm183 / 33.029288, -111.771716 / 02 May 2011, ADSmith”. A total of 824 eggs and larvae were reared and examined for this study, of which 134 survived until the 2nd instar or later. The following description is based on a detailed examination of ten 8-11th instar specimens.

**Description.** TL: 13.0–19.0 mm, HW: 1.5–2.2 mm, PL: 1.2–2.7 mm, PW: 1.3–2.7 mm.

**Head.** Prognathous or weakly declined; weakly dorsoventrally flattened; width nearly equal to prothorax; sides angular; strongly constricted before occipital foramen; color light tan to medium brown, more heavily pigmented than body segments; punctation minute, moderately dense, separated by 2–4 puncture diameters. Epicranial suture stem length approximately one-third head capsule length; frontal arms sinuate, not obscured by sculpturing. Frons rugose. Epicranial plates weakly rugose dorsally; lateral portions moderately setose; ventral portion of each plate with row of six or more long setae along anterior margin near buccal cavity confluent with setae on lateral portions of plates, and a patch of short setae medially, forming a triangular pattern with its base near the anterior margin. Two stemmata present on each epicranial plate, pigmented spots often faded. Clypeus trapezoidal, swollen, darker medially in basal half, minutely punctate, punctuation moderately dense, separated by 2–4 puncture diameters. Labrum swollen, sides rounded, basal half more darkly pigmented, medial setal row with six to seven erect setae subapical setal row with six to seven erect setae, anterior margin straight to weakly emarginate. Epipharynx (Fig. 9D) anterior setal row with six stout spiniform setae, anterolateral margins with micro-setation; five to six anterior sensory papillae present, arranged in two irregular longitudinal rows or an irregular cluster; four subanterior sensory papillae present, arranged as a transverse row subtended by two spinose setae; seven to eight posterior sensory papillae present, arranged in an irregular cluster. Tormae asymmetric, left torma larger. Ligula apex and subapical dorsal surface densely micro-setose, two long subapical setae present ventrally. Hypopharyngeal sclerome pentagonal, tricuspidate. Gula distinct, trapezoidal,
widest in basal half, length subequal or greater than maximum width. Antenna three segmented, cylindrical, first segment length subequal to second.

**Thorax.** Thoracic tergites light tan, prothoracic sternite anterior to legs medium brown, thoracic sternites posterior to prolegs light brown. Prothoracic tergum sub-quadrate, 1.5× length of meso- or metaterga; lateral margins with distinct granulated band, darker than protergal disc; anterior transverse striated band present, darker than tergal disc. Posterior transverse striated band present on all thoracic tergites, unicolorous brown. Meso- and metathoracic tergites wider than long, each with a faintly indicated sclerotized transverse line present on anterior fifth. Thoracic tergites sparsely setose on dorsal surfaces, lateral margins more densely setose. Mesothoracic spiracle simple, ovate, approximately 1.5× size of abdominal spiracles; reduced metathoracic spiracle visible, less than one-fourth size of mesothoracic spiracle. Legs. Prothoracic leg slightly longer, much thicker than meso- and metathoracic legs; prothoracic tarsungulus strongly sclerotized, sickle-shaped; prothoracic trochanter with two stout spines ventromedially; prothoracic femur with ventromedial row of two spines and three to five longer setae, dorsal surface with faintly indicated basal sclerotized band; prothoracic tibia with ventromedial row of three to four spines, dorsal surface slightly more sclerotized than ventral surface. Mesotibia with three ventromedial spines.

**Abdomen.** Abdominal tergites and sternites light tan with darker transverse striated bands present along posterior margins of segments I–VIII, forming near contiguous unicolorous band around segments. Abdominal sternite I moderately clothed in long erect setae from anterior margin to near midline. Abdominal laterotergites with lateral margins distinctly pigmented. Abdominal segment IX (pygidium) triangular in dorsal view, gradually reflexed to apex, urogomphi absent, apex not forming a distinct tooth, moderately clothed in short and mid length erect setae, sclerotized uniformly throughout, lacking maculations; marginal row of 8–14 socketed spines present, arranged as single row around posterior two-thirds to one half of segment. Abdominal sternites I–VIII lacking longitudinal tomentose bands along lateral margins. Pygopods short, subconical, each with 11–15 erect setae.

**Diagnosis.** *Eleodes tribulus* larvae can be separated from the other currently known *Eleodes* species based on the pentagonal hypopharyngeal sclerome, lack of a caudal tooth on the pygidium, presence of 8–14 marginal spines on the pygidium, and the angular, nearly straight sides of the head capsule.

**Subgenus Litheleodes Blaisdell, 1909**

*Eleodes (Litheleodes) extricatus* (Say, 1823)  
http://species-id.net/wiki/Eleodes_extricatus  
Figures 3A, 5C, 7B, 10A, 12B, 13B

**Material examined.** Larval *E. extricatus* specimens were reared from adults with the following collecting information: “USA: TX: El Paso County / El Paso, sand dunes
Larvae of the genus Eleodes (Coleoptera, Tenebrionidae)...

Approximately 219 eggs and larvae were reared and examined for this study, with 150 surviving until the second instar or beyond. The following description is based on a detailed examination of thirteen 8–11th instar specimens.

**Description.** Measurements: TL: 15.4–33.3 mm, PL: 2.4–3.8 mm, PW: 2.2–3.8 mm, HW: 2.0–3.0 mm.

**Head.** Prognathous or weakly declined; weakly dorsoventrally flattened; width nearly equal to prothorax; sides rounded; strongly constricted before occipital foramen; color light tan, same or nearly the same as body segments; punctuation minute, dense, separated by 1–2 puncture diameters. Epicranial suture stem length approximately one-third head capsule length; frontal arms sinuate, not obscured by sculpturing. Frons faintly rugose. Epicranial plates faintly rugose dorsally; lateral portions moderately setose; ventral portion of each plate with row of six or more long setae along anterior margin near buccal cavity confluent with setae on lateral portions of plates and a patch of short setae medially, forming a triangular pattern with its base near the anterior margin. Two stemmata present on each epicranial plate, pigmented spots often faded. Clypeus trapezoidal, swollen or not, unicolorous, minutely punctate, punctuation dense, separated by 1–2 puncture diameters. Labrum swollen, sides rounded, basal half more darkly pigmented, medial setal row with six to seven erect setae, subapical setal row with six to seven erect setae, anterior margin straight to weakly emarginate. Epipharynx (Fig. 10A) anterior setal row with six stout spiniform setae, anterolateral margins with micro-setation; six anterior sensory papillae present, arranged in two irregular rows; four subanterior sensory papillae present, arranged as a transverse row subtended by two spinose setae; eight posterior sensory papillae present, arranged in an irregular cluster. Tormae symmetrical or weakly asymmetrical with left torma smaller. Ligula apex densely microsetose, two long subapical setae present ventrally. Hypopharyngeal sclerome pentagonal, tricuspidate. Gula distinct, trapezoidal, widest in basal half, length less than maximum width. Antenna three segmented, cylindrical, first segment longer than second.

**Thorax.** Thoracic tergites light tan, prothoracic sternite anterior to legs ferruginous, thoracic sternites posterior to prolegs light brown. Prothoracic tergum subquadrat, 1.5× length of meso- or metaterga; anterior transverse striated band present, darker than protergal disc; lateral margins with distinct granulated band, darker than protergal disc. Posterior transverse striated band present on all thoracic tergites, unicolorous brown. Meso- and metathoracic tergites wider than long, each with a heavily sclerotized transverse line present on anterior fifth. Thoracic tergites sparsely setose on dorsal surfaces, lateral margins more densely setose. Mesothoracic spiracle simple, ovate, approximately 1.5× size of abdominal spiracles; reduced metathoracic spiracle visible,
less than one-fourth size of mesothoracic spiracle. Legs. Prothoracic leg slightly longer, much thicker than meso- and metathoracic legs; prothoracic tarsungulus strongly sclerotized, sickle-shaped; prothoracic trochanter with two stout ventromedially spines; prothoracic femur with ventromedial row of two spines and three to five longer setae, dorsal surface with faintly indicated basal sclerotized band; prothoracic tibia with ventromedial row of three to four spines or spinose setae, dorsal surface slightly more sclerotized than ventral surface. Mesotibia with four to five ventromedial spines.

**Abdomen.** Abdominal tergites and sternites light tan, with slightly darker transverse striated bands present along posterior margins of segments I–VIII, forming near contiguous unicolorous band around segments. Abdominal sternite I sparsely clothed in long erect setae from anterior margin to near midline. Abdominal laterotergites with lateral margins distinctly pigmented. Abdominal segment IX (pygidium) triangular in dorsal view, gradually reflexed to apex, urogomphi absent, apex lacking a distinct tooth, sparsely clothed in short and mid length erect setae, sclerotized uniformly throughout, lacking maculations; marginal row of 17–23 socketed spines present, arranged as single row around posterior two-thirds to one half of segment. Abdominal sternites I–VIII lacking longitudinal tomentose bands along lateral margins. Pygopods short, subconical, each with 11–15 erect setae.

**Diagnosis.** *Eleodes extricatus* larvae can be separated from the other currently known *Eleodes* species based on the pentagonal hypopharyngeal sclerome, small or absent apical tooth on the pygidium, lateral margins of prothoracic tergum with a distinct granulated band, and having antennal segment I longer than antennal segment II.

**Remarks.** *Eleodes extricatus* is a widespread species found on dunes and at high elevations. Specimens from Arizona and Texas showed no population differences in the larval stage. Adults varied in the presence or prominence of muricate tubercles on the elytra.

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**Subgenus Melaneleodes Blaisdell, 1909**

*Eleodes (Melaneleodes) anthracinus* Blaisdell, 1909

http://species-id.net/wiki/Eleodes_anthracinus

Figures 3B, 6A, 7A, 8

**Material examined.** Larval *E. anthracinus* specimens were reared from adults with the following collecting information: “USA: AZ: Maricopa Co. / Eugie Ave & 7th St. / 25 Oct. 2011, R. Dornburg.” A total of 28 eggs and larvae were reared and examined for this study, of which all survived until the 3rd instar or later. The following description is based on a detailed examination of four 8–11th instar specimens.

**Description.** TL: 23.8–28.1 mm, HW: 2.3–2.4 mm, PL: 2.0–2.4 mm, PW: 2.5–2.8 mm.

**Head.** Prognathous or weakly declined; weakly dorsoventrally flattened; width nearly equal to prothorax; sides rounded; strongly constricted before occipital fo-
Larvae of the genus *Eleodes* (Coleoptera, Tenebrionidae)...

ramen; color medium brown to brown-grey, nearly as on body segments; minute punctuation moderately dense dorsally. Epicranial stem approximately one-third head capsule length; frontal arms U-shaped, not obscured by sculpturing. Frons and dorsal portion of epicranial plates faintly rugose; lacking non-primary setae.

**Figure 6.** Lateral habitus of three *Eleodes* species: **A** *E. (Melaneleodes) anthracinus* **B** *E. (Melaneleodes) carbonarius* **C** *E. (Tricheleodes) pilosus*. Scale bar = 5 mm.
Figure 7. Lateral habitus of the head and thoracic segments of three *Eleodes* species: **A** *E. (Melaneleodes) anthracinus*  **B** *E. (Litheleodes) extricatus*  **C** *E. (Promus) subnitens*. Scale bar = 5 mm.
Larvae of the genus *Eleodes* (Coleoptera, Tenebrionidae)...

Lateral portions of epicranial plates moderately setose; setae golden, erect, length equal to or longer than antennal segment 2; ventral portions of epicranial plates with a row of four long setae along anterior margin near buccal cavity with a patch of short setae medially forming a triangular pattern with its base near the anterior margin; two stemmata present on each plate, pigmented spots often faded. Clypeus trapezoidal; not swollen, moderately punctate, darker medially in basal half. Labrum not swollen, basal half more darkly pigmented; sides rounded; two transverse rows of seven to eight erect setae present medially and subapically; anterior margin straight. Epipharynx (Fig. 3) anterior setal row with six stout spiniform setae, anterolateral margins with micro-setation; six anterior sensory papillae present, arranged in two irregular diagonal rows; four subanterior sensory papillae present, arranged as a transverse row subtended by two spinose setae; eight posterior sensory papillae present, arranged in two irregular rows. Tormae asymmetrical, left torma smaller. Ligula with four long setae near apex. Hypopharyngeal sclerome trapezoidal. Gula distinct, trapezoidal, widest in basal half. Antenna three segmented, cylindrical; first segment longer than second.

**Thorax.** Grey-brown to medium brown dorsally and anterior to legs on prothoracic sternite, tan on rest of sternites; lighter transverse striated band present along anterior fourth of prothoracic tergum; thin darkly sclerotized transverse line present on anterior fifth of meso- and metathoracic tergites; striated bands present along posterior 5th of all thoracic tergites, color forming a gradient from darker brown anteriorly to lighter brown along posterior border. Eight evenly arranged setae present on dorsal surface of each thoracic terga, lateral margins more densely setose. Prothoracic tergum subquadrated, 1.5× length of meso- or metaterga; lateral margins lacking pigmented band. Meso- and metaterga wider than long, lacking pigmented bands along lateral margins; mesothoracic spiracle simple, ovate, approximately 1.5× size of abdominal spiracle; reduced metathoracic spiracle visible, less than one-fourth size of mesothoracic spiracle. Prothoracic leg slightly longer, much thicker than meso- and metathoracic legs; prothoracic tarsungulus strongly sclerotized, sickle-shaped; trochanter with row of two stout spines and two longer setae ventromedially, tibia with ventromedial row of two spines and four to five longer setae, tarsus with ventromedial row of four spines. Dorsal surface of protibia (at rest) with faintly indicated basal sclerotized band; dorsal surface of protarsus slightly more sclerotized than ventral surface.

**Abdomen.** Tergites grey-brown to medium brown dorsally, lightening towards lateral margins, sternites light to dark tan; transverse striated bands not visible on abdominal sternites, barely visible on posterior 5th of terga I–VIII, nearly concolorous with rest of tergites. Abdominal sternite I sparsely clothed in long erect setae from anterior margin to near midline, abdominal segments II–VIII each with two sparse transverse bands of long erect setae, posterior margin of segment 8 denser setal band. Abdominal laterotergites concolorous with tergites, lacking distinct pigmented margins. Abdominal segment IX (pygidium) triangular in dorsal view, gradually reflexed to apex, sparsely clothed in short and mid length erect setae, dorsally more sclerotized in apical two-thirds with faint maculations; marginal row of 14–18 socketed spines...
present apical half, apex not forming distinct sclerotized projection. Pygopods short, subconical, each with 11–15 erect spines.

**Variation.** Little variation was observed between specimens beyond the number of spines on the legs and pygidium, and the overall degree of sclerotization.

**Diagnosis.** *Eleodes anthracinus* larvae can be separated from most currently known *Eleodes* species based on their darker dorsal coloration on all segments, the absence of pigmented bands along the lateral margins of the thoracic terga, and the lack of a distinct sclerotized tooth at the apex of the pygidium. They can be distinguished from *E. carbonarius* larvae by their lighter ventral segments and lack of distinct posterior pigmented bands on the abdominal terga. Larvae of *Eleodes tricostatus* (Say), another species in the subgenus *Melaneleodes*, are mentioned as being “nearly black” by McColloch (1918). However, no other diagnostic characters are mentioned that would separate them from the other *E. anthracinus* or *E. carbonarius*.

**Figure 8.** *Eleodes (Melaneleodes) anthracinus*, epipharynx. asp = anterior spines, msp = medial spines, mst = microsetae, pap = sensory papillae, tor = tormae. Scale bar = 1 mm.
Larvae of the genus *Eleodes* (Coleoptera, Tenebrionidae)...

*Eleodes* (*Melaneleodes*) *carbonarius knausii* Blaisdell

Figures 3C, 6B, 9A, 11A, 12A

**Material examined.** Larval *E. carbonarius* specimens were reared from adults with the following collecting information: “USA: CO: Montezuma Co. / Ute RA off Hwy 160 / 37.3535, -108.44385 / 05 Jun 2011, ADSmith”. A total of 129 eggs and larvae were reared and examined for this study, with 45 surviving until the 2nd instar or later. The following description is based on a detailed examination of five 8–11th instar specimens.

**Description.** TL: 15.5–26 mm, HW: 2.3–3.0 mm, PL: 1.9–2.5 mm, PW: 3.0–3.5 mm.

**Head.** Prognathous, weakly flattened, narrower than prothorax; sides rounded, strongly constricted before occipital foramen; color ferruginous to dark brown, nearly as on body segments; minute punctation moderately dense dorsally. Epicranial stem approximately one-third head capsule length; frontal arms U-shaped, not obscured by sculpturing. Frons and dorsal portion of epicranial plates faintly rugose; lacking non-primary setae. Lateral portions of epicranial plates moderately setose; setae golden, erect, length equal to or longer than antennal segment 2; ventral portions of epicranial plates with a row of four to five long setae along anterior margin near buccal cavity and a patch of short setae medially forming a triangular pattern with its base near the anterior margin; two stemmata present on each plate, pigmented spots often faded. Clypeus trapezoidal; not swollen, moderately punctate, darker medially in basal half. Labrum not swollen, basal half more darkly pigmented; sides rounded; two transverse rows of six to seven erect setae present medially and subapically; anterior margin straight to weakly emarginate. Epipharynx (Fig. 9A) anterior setal row with six stout spiniform setae, anterolateral margins with micro-setation; six anterior sensory papillae present, arranged in two irregular diagonal rows; four subanterior sensory papillae present, arranged as a transverse row subtended by two spinose setae; eight posterior sensory papillae present, arranged in an irregular cluster. Tormae asymmetrical, left torma larger. Hypopharyngeal sclerome trapezoidal. Ligula with four long setae near apex. Gula distinct, trapezoidal, widest in basal half. Antenna three segmented, cylindrical; first segment longer than second.

**Thorax.** Dark brown to ferruginous dorsally and anterior to legs on prothoracic sternite, lighter brown on rest of sternites; distinct longitudinally striated band present along anterior fourth of prothoracic tergum; thin darkly sclerotized transverse line present on anterior fifth of meso- and metathoracic tergites; striated bands present along posterior 6th of all thoracic tergites, darker than rest of surface. Eight evenly arranged setae present on dorsal surface of each thoracic terga, lateral margins more densely setose. Prothoracic tergum wider than long, 1.5× length of meso- or metaterga; lateral margins lacking pigmented band. Meso- and metaterga wider than long, lacking pigmented bands along lateral margins; mesothoracic spiracle simple, ovate, approximately 1.5× size of abdominal spiracle; reduced metathoracic spiracle visible, less than one-fourth size of mesothoracic spiracle. Prothoracic leg slightly longer, much thicker than meso- and metathoracic legs; prothoracic tarsungulus strongly sclerotized, sickle-
shaped; trochanter with two stout spines ventromedially, tibia with ventromedial row of three to four spines and four to five longer setae, tarsus with ventromedial row of five spines. Dorsal surface of protibia (at rest) with basal sclerotized band; dorsal surface of protarsus more sclerotized than ventral surface.

**Abdomen.** Tergites dark brown to ferruginous, concolorous or lightly lighter than tergites; longitudinally striated bands not visible on abdominal sternites, distinct on posterior 5th of terga 1–8. Abdominal sternite I sparsely clothed in long erect setae from anterior margin to near midline, abdominal segments 2–8 each with two sparse transverse bands of long erect setae, posterior margin of segment 8 denser setal band. Abdominal laterotergites concolorous with tergites, lacking distinct pigmented margins. Abdominal segment IX (pygidium) triangular in dorsal view, gradually reflexed to apex, sparsely clothed in short and mid length erect setae, apical two-thirds with faint maculations; marginal row of 18–20 socketed spines present apical half, apex not forming distinct sclerotized projection. Pygopods short, subconical, each with 9–12 erect spines.

![Figure 9. Epipharynges of four *Eleodes* species: A. *Melaneleodes* carbonarius B. *Eleodes* armatus C. *Eleodes* hispilabris D. *Eleodes* tribulus. Scale bars = 1 mm.](image-url)
Variation. Little variation was observed between specimens beyond the number of spines on the legs and pygidium, and the overall degree of sclerotization.

Diagnosis. *Eleodes carbonarius* larvae can be separated from most currently known *Eleodes* species their darker dorsal coloration on all segments, the absence of pigmented bands along the lateral margins of the thoracic terga, and the lack of a distinct sclerotized tooth at the apex of the pygidium. They can be further distinguished from *E. anthracinus* larvae as outlined in that species diagnosis.

Remarks. *Eleodes carbonarius* adult morphology is notoriously variable across the species range and even within populations. Nine subspecies are currently recognized (Triplehorn and Thomas 2011). The specimens examined were all reared from a few females of *E. carbonarius knausi* Blaisdell collected at a single locality. Larval characters showed little variation; however, this may change as more specimens are reared from other localities and subspecies.

Subgenus *Promus* LeConte, 1862

*Eleodes* (*Promus*) *goryi* Solier, 1848

http://species-id.net/wiki/Eleodes_goryi

Figures 10B, 11C

Material examined. Larval *E. goryi* specimens were reared from adults with the following collecting information: “USA: TX: Hidalgo County / Bentsen-Rio Grande Valley / State Park, fm2062 Mission / N26°10.37’, W098°22.93’ / 02.Sept.2011, Aaron Smith”. A total of 460 eggs and larvae were reared and examined for this study, with 25 surviving until the 2nd instar or beyond. The following description is based on a detailed examination of three 8–11th instar specimens.

Description. TL: 25.0–25.4 mm, HW: 2.0–2.1 mm, PL: 2.0–2.1 mm, PW: 2.2–2.4 mm.

Head. Prognathous or weakly declined; weakly dorsoventrally flattened; width nearly equal to prothorax; sides rounded; strongly constricted before occipital foramen; color ferruginous to dark brown, more heavily pigmented than body segments; punctation minute, moderately dense, separated by 2–4 puncture diameters. Epicranial suture stem length approximately one-third head capsule length; frontal arms U-shaped, not obscured by sculpturing. Frons faintly rugose. Epicranial plates faintly rugose dorsally; lateral portions moderately setose; ventral portion of each plate with row of six or more long setae along anterior margin near buccal cavity confluent with setae on lateral portions of plates, and a patch of short setae medially, forming a triangular pattern with its base near the anterior margin. Two stemmata present on each epicranial plate, pigmented spots often faded. Clypeus trapezoidal, swollen, darker medially in basal half, minutely punctate, punctuation moderately dense, separated by 2–4 puncture diameters. Labrum swollen, sides rounded, basal half more darkly pigmented, medial setal row with six to seven erect setae, subapical setal row with six...
to seven erect setae, anterior margin straight to weakly emarginate. Epipharynx (Fig. 10B) anterior setal row with six stout spiniform setae, anterolateral margins with micro-setation; six anterior sensory papillae present, arranged in two irregular rows; four subanterior sensory papillae present, arranged as a transverse row subtended by two spinose setae; eight posterior sensory papillae present, arranged in an irregular cluster. Tormae strongly asymmetrical with left torma larger. Ligula apex densely microsetose, two long subapical setae present ventrally. Hypopharyngeal sclerome pentagonal, tricuspidate. Gula distinct, trapezoidal, widest in basal half, length subequal or greater than maximum width. Antenna three segmented, cylindrical, first segment subequal to second.

**Thorax.** Thoracic tergites light tan, prothoracic sternite anterior to legs ferruginous to medium brown, thoracic sternites posterior to prolegs medium brown. Prothoracic tergum wider than long, 1.2× or more length of meso- or metaterga; anterior transverse striated band present, darker than protergal disc; lateral margins with distinct
Larvae of the genus *Eleodes* (Coleoptera, Tenebrionidae) are characterized by a granulated band, darker than protergal disc. Posterior transverse striated band present on all thoracic tergites, unicolorous brown. Meso- and metathoracic tergites wider than long, each with a heavily sclerotized transverse line present on anterior fifth. Thoracic tergites sparsely setose on dorsal surfaces, lateral margins more densely setose. Mesothoracic spiracle simple, ovate, approximately 1.5× size of abdominal spiracles; reduced metathoracic spiracle visible, less than one-fourth size of mesothoracic spiracle. Legs. Prothoracic leg slightly longer, much thicker than meso- and metathoracic legs; prothoracic tarsungulus strongly sclerotized, sickle-shaped; prothoracic trochanters with two stout ventromedially spines; prothoracic femur with ventromedial row of two spines and three to five longer setae, dorsal surface with faintly indicated basal sclerotized band; prothoracic tibia with ventromedial row of three to four spines or spinose setae, dorsal surface slightly more sclerotized than ventral surface. Mesotibia with three ventromedial spines.

**Abdomen.** Abdominal tergites and sternites 1–7 light tan, with slightly darker transverse striated bands present along posterior margins of segments I–VIII, forming near contiguous unicolorous band around segments. Abdominal tergite 8 more darkly pigmented than preceding segments. Abdominal sternite I moderately clothed in long erect setae from anterior margin to near midline. Abdominal laterotergites with lateral margins distinctly pigmented. Abdominal segment IX (pygidium) triangular in dorsal view, gradually reflexed to apex, urogomphi absent, apex lacking a distinct tooth, moderately clothed in short and mid length erect setae, dorsally more sclerotized in apical two-thirds with faint maculations; marginal row of 18–20 socketed spines present, arranged as single row around posterior two-thirds to one half of segment. Abdominal sternites I–VIII lacking longitudinal tomentose bands along lateral margins. Pygopods short, subconical, each with 11–15 erect setae.

**Diagnosis.** *Eleodes goryi* larvae can be separated from the other currently known *Eleodes* species based on the darkly pigmented eighth and ninth abdominal tergites. It is further distinguished by the pentagonal hypopharyngeal sclerome, lack of a caudal tooth on the pygidium, and the presence of 3–4 ventromedial spines on the protibia.

*Eleodes (Promus) subnitens* LeConte, 1851

http://species-id.net/wiki/Eleodes_subnitens

Figures 7C, 10C

**Material examined.** Larval *E. subnitens* specimens were reared from adults with the following collecting information: “USA: Arizona: Gila Co. / Tonto Natural Bridge SP / N34.3214, W111.4569 / 11.IX.2010, ADSmith”. A total of 7 eggs and larvae were reared and examined for this study, of which four survived until the 2nd instar or later. The following description is based on a detailed examination of two 8–11th instar specimens.

**Description.** TL: 23.1–30.8 mm, HW: 2.0–3.0 mm, PL: 2.0–2.9 mm, PW: 2.2–3.1 mm.
Head. Prognathous or weakly declined; weakly dorsoventrally flattened; width nearly equal to prothorax; sides rounded; strongly constricted before occipital foramen; color ferruginous, more heavily pigmented than body segments; punctuation minute, moderately dense, separated by 2–4 puncture diameters. Epicranial suture stem length approximately one-third head capsule length; frontal arms sinuate, not obscured by sculpturing. Frons faintly rugose. Epicranial plates faintly rugose dorsally; lateral portions moderately setose; ventral portion of each plate with row of six or more long setae along anterior margin near buccal cavity confluent with setae on lateral portions of plates and a patch of short setae medially, forming a triangular pattern with its base near the anterior margin. Two stemmata present on each epicranial plate, pigmented spots often faded. Clypeus trapezoidal, swollen, darker in apical half, minutely punctate, punctuation moderately dense, separated by 2–4 puncture diameters. Labrum swollen, sides rounded, basal half more darkly pigmented, medial setal row with six to seven erect setae, subapical setal row with seven to eight erect setae, anterior margin straight to weakly emarginate. Epipharynx (Fig. 10C) anterior setal row with six stout spiniform setae, anterolateral margins with micro-setation; six anterior sensory papillae present, arranged in two irregular rows; four subanterior sensory papillae present, arranged as a transverse row subtended by two spinose setae; eight posterior sensory papillae present, arranged in an irregular cluster. Tormae asymmetrical with left torma smaller. Ligula apex densely microsetose, two long subapical setae present ventrally. Hypopharyngeal sclerome pentagonal, tricuspidate. Gula distinct, trapezoidal, widest in basal half, length subequal or greater than maximum width. Antenna three segmented, cylindrical, first segment subequal to second.

Thorax. Thoracic tergites light tan, prothoracic sternite anterior to legs ferruginous, thoracic sternites posterior to prolegs light brown. Prothoracic tergum wider than long, 1.2× or more length of meso- or metaterga; anterior transverse striated band present, darker than protergal disc; lateral margins with distinct granulated band, darker than protergal disc. Posterior transverse striated band present on all thoracic tergites, uni-

Figure 11. Ligulas of three Eleodes species: A E. (Melaneleodes) carbonarius B E. (Eleodes) armatus C E. (Promus) goryi. Scale bars = 200 μm.
Larvae of the genus Eleodes (Coleoptera, Tenebrionidae)...

colorous brown. Meso- and metathoracic tergites wider than long, each with a heavily sclerotized transverse line present on anterior fifth. Thoracic tergites sparsely setose on dorsal surfaces, lateral margins more densely setose. Mesothoracic spiracle simple, ovate, approximately 1.5× size of abdominal spiracles; reduced metathoracic spiracle visible, less than one-fourth size of mesothoracic spiracle. Legs. Prothoracic leg slightly longer, much thicker than meso- and metathoracic legs; prothoracic tarsungulus strongly sclerotized, sickle-shaped; prothoracic trochanter with two stout ventromedially spines; prothoracic femur with ventromedial row of two spines and three to five longer setae, dorsal surface with faintly indicated basal sclerotized band; prothoracic tibia with ventromedial row of five to six spines or spinose setae, dorsal surface slightly more sclerotized than ventral surface. Mesotibia with four to five ventromedial spines.

**Abdomen.** Abdominal tergites and sternites I–VIII light tan, with slightly darker transverse striated bands present along posterior margins, forming near contiguous unicolorous band around segments. Abdominal sternite I moderately clothed in long erect setae to posterior pigmented band. Abdominal laterotergites with lateral margins distinctly pigmented. Abdominal segment IX (pygidium) triangular in dorsal view, gradually reflexed to apex, urogomphi absent, apex lacking a distinct tooth, moderately clothed in short and mid length erect setae, dorsally sclerotization uniform throughout, lacking maculations; marginal row of 18–20 socketed spines present, arranged as single row around posterior two-thirds to one half of segment. Abdominal sternites 1–8 lacking longitudinal tomentose bands along lateral margins. Pygopods short, subconical, each with 17–24 erect setae.

**Diagnosis.** Eleodes subnitens larvae can be separated from the other currently known Eleodes species by the pentagonal hypopharyngeal sclerome, prothoracic tergum wider than long, 8th and 9th abdominal tergites not darker than proceeding segments, lack of a caudal tooth on the pygidium, and the presence of 5–6 ventromedial spines on the protibia.

**Figure 12.** Hypopharyngeal scleromes of two Eleodes species: A E. (Melaneleodes) carbonarius B E. (Litheleodes) extricatus. Scale bars = 200 μm.
**Subgenus** *Tricheleodes* Blaisdell, 1909

*Eleodes (Tricheleodes) pilosus* Horn, 1870
http://species-id.net/wiki/Eleodes_pilosus
Figures 3D, 6C, 10D, 14B

**Material examined.** Larval *E. pilosus* specimens were reared from adults with the following collecting information: “NEVADA: Washoe Co. / N39°16.427', W119°47.070' / November 14, 2011 / P. Skelley, sifting lakeside dunes”. A total of 208 eggs and larvae were reared and examined for this study, of which 94 survived until the 2nd instar or later. The following description is based on a detailed examination of nine 8–11th instar specimens.

**Description.** TL: 14.2–26.0 mm, PW: 1.7–3.3 mm, PL: 1.4–3.4 mm, HW: 1.6–2.6 mm.

**Head.** Prognathous, weakly flattened, narrower than prothorax; sides rounded, strongly constricted before occipital foramen; color nearly as in body segments. Epicranial stem short, one-fourth head capsule length; frontal arms U-shaped, partially obscured by sculpturing. Frons and dorsal portion of epicranial plates rugose; sparsely setose; densely punctate, punctures minute, lacking setae. Ventrolateral portions of epicranial plates densely setose; setae golden, erect, most longer than antennal segment 2, interspersed with shorter setae; two stemmata present on each plate, pigmented spots often faded. Clypeus trapezoidal; swollen, weakly transversely raised medially; moderately punctate, rugose in basal half. Labrum slightly swollen, basal fourth darkly pigmented; sides rounded, minutely tomentose; two transverse rows of six to eight erect setae present medially and subapically; anterior margin straight. Epipharynx (Fig. 10D) anterior setal row with six stout spiniform setae, anterolateral margins with micro-setation; seven
Larvae of the genus Eleodes (Coleoptera, Tenebrionidae)...  

anterior sensory papillae present, arranged in two irregular longitudinal rows; four sub-anterior sensory papillae present, arranged as a transverse row subtended by two spinose setae; seven posterior sensory papillae present, arranged in an irregular cluster. Tormae asymmetrical, left side torma smaller with or without a small spine near emergent edge. Hypopharyngeal sclerome pentagonal, tricuspidate. Gula distinct, trapezoidal, widest in basal half. Antenna three segmented, cylindrical; first segment longer than second.

**Thorax.** Light to dark tan, darker longitudinally striated bands present on anterior margin of prothoracic tergum and posterior 5th of all thoracic tergites. Sparsely setose along dorsal margins of terga near striated bands, lateral margins more densely setose. Prothoracic tergum subquadrate, 1.5× length of meso- or metaterga; lateral margins with pigmented band along entire length. Mesothoracic spiracle simple, ovate, approximately 1.5× size of abdominal spiracle; reduced metathoracic spiracle visible, less than one-fourth size of mesothoracic spiracle. Prothoracic leg slightly longer, much thicker than meso- and metathoracic legs; tarsungulus strongly sclerotized, sickle-shaped; trochanter with two stout spines ventromedially, tibia and tarsus each with a ventromedial row of four to seven spines, number of spines often differing between prolegs. Dorsal surface of protibia (at rest) with basal sclerotized band; dorsal surface of protarsus sclerotized.

**Abdomen.** Light to dark tan, darker longitudinally striated bands present on posterior 5th of segments I–VIII. Abdominal sternite I moderately clothed in long erect setae, sparser medially, extending to posterior pigmented band, abdominal tergite I and segments II–VIII sparsely clothed in short to mid length setae. Lateral margins of abdominal laterotergites I–VIII darkly pigmented, ventral margin with two pigmented bands. Abdominal segment IX (pygidium) triangular in dorsal view, moderately clothed in long erect setae; marginal row of 10–20 socketed spines present apical half, apex not forming distinct sclerotized projection. Pygopods short, subconical, each with 16–20 erect spines.

*Figure 14.* Pygidia of two *Eleodes* species: **A**. *E. (Eleodes) hispilabris* **B**. *E. (Tricheleodes) pilosus.* Scale bar = 1 mm.
Diagnosis. *Eleodes pilosus* larvae can be separated from the other currently known *Eleodes* species by the pentagonal hypopharyngeal sclerome, lack of a caudal tooth on the pygidium, presence of 8–14 marginal spines on the pygidium, subquadrate prothoracic tergum, and having abdominal sternite I moderately clothed in long erect setae to posterior pigmented band.

Key to the late instar larvae of 13 *Eleodes* species

1. Lateral margins of abdominal sternites I–IX pigmented, with golden tomentose setae (Fig. 13A)...................................................................................... *Eleodes caudiferus* LeConte
2. Apex of pygidium attenuated and sclerotized, forming a distinct projection (Fig. 14A).....................................................................................................
3. Anterolateral margins of epipharynx with micro-setation (Fig. 8, 9A–B,D, 10A–D), lacking stout setae ........................................... *Eleodes armatus* LeConte
4. Mesotarsus with row of three ventromedial spines; ventral portion epicranial plates with row of six or more long setae along anterior margin near buccal cavity, confluent with setae on lateral portions of plates; prothoracic femur with ventromedial row of 13–14 spines ...................... *Eleodes tenuipes* Casey
5. Granulated band along lateral margins of protergum faint, concolorous with protergal disc (Fig. 7A) .................................................................
6. Hypopharyngeal sclerome pentagonal, tricuspidate (Fig.12B); ligula apex lacking microsetae, two long subapical setae present ventrally, eight or more subapical setae present dorsally (Fig.11B); pigmented band present along posterior margin of abdominal sterna, integument usually tan................................. *Eleodes wheeleri* Aalbu, Smith, & Triplehorn
7. Terga dark brown, nearly black, throughout; prothoracic tergum wider than long, 1.2× or more length of meso- or metaterga; posterior pigmented band
on abdominal terga I–VIII darker than rest of segment; abdominal sternites nearly concolorous with tergites.*Eleodes carbonarius* (Say)  
7’ Terga medium brown, lighter towards margins; prothoracic tergum subquadrate, 1.5× length of meso- or metaterga; posterior pigmented band on abdominal terga I–VIII concolorous with rest of segment; abdominal sternites lighter than tergites.*Eleodes anthracinus* (Blaisdell)  
8 (5’) Pigmented band around posterior margin of abdominal segments dark along anterior edge, fading to segment color posteriorly (Fig. 4A) .................................................................*Eleodes nigropilosus* (LeConte)  
8’ Pigmented band around posterior margin of abdominal segments unicolorous, darker than rest of segment throughout..................................................................................................................9  
9 (8’) Abdominal sternite I moderately clothed in long erect setae to posterior pigmented band; seven anterior sensory papillae present on epipharynx in all specimens examined.*Eleodes pilosus* (Horn)  
9’ Abdominal sternite I with sparsely setose on at most anterior half; six anterior sensory papillae present on epipharynx in all specimens examined ......................10  
10 (9’) Antennal segment I longer than antennal segment II (Fig. 7A–B); gula length less than maximum width ..................................................*Eleodes extricatus* (Say)  
10’ Antennal segment I subequal to antennal segment II (Fig. 7C); gula length subequal or greater than maximum width ....................................................................................11  
11 (10’) Pygidium with marginal row of 8–14 socketed spines; prothoracic tergum subquadrate, 1.5× length of meso- or metaterga.*Eleodes trilbusus* Thomas  
11’ Pygidium with marginal row of 18–20 socketed spines; prothoracic tergum wider than long, 1.2× or more length of meso- or metaterga.........................12  
12 (11’) Eighth and ninth abdominal tergites more darkly pigmented than preceding segments, protibia with ventromedial row of 3–4 spines.*Eleodes goryi* Solier  
12’ Eighth and ninth abdominal tergites with same pigmentation as preceding segments; protibia with ventromedial row of 5–6 spines ......................................................................................................................*Eleodes subniten* LeConte

**Notes on additional species**

*Eleodes spinipes* (Solier). One specimen of *Eleodes spinipes ventricosus* (TB08942) was reared to a late instar, 9th or 10th, in the lab. However, the specimen apparently died in its rearing container while molting and suffered some damage, thus obscuring many characters. What could be seen of the epipharynx, ligula, and abdominal segment IX, including the presence of an apical tooth on the pygidium, place it with *Eleodes armatus*, *E. hispilabris*, and *E. tenuipes* in the subgenus *Eleodes*. The presence of spinose setae along the anterolateral margins of the epipharynx placed it closest to *E. hispilabris*, and *E. tenuipes*. 


Previously described species

**Eleodes dentipes** Eschscholtz. Little comparative data to separate the species can be drawn from Gissler (1878). Blaisdell (1909) provides a more detailed description, but likewise does not include many characters currently necessary to differentiate the species.

**Eleodes giganteus** Mannerheim. Little comparative data to separate this species from the other currently described *Eleodes* larvae can be drawn from Gissler (1878).

**Eleodes pimelioides** (Mannerheim). Little comparative data to separate this species from the other currently described *Eleodes* larvae can be drawn from Hyslop (1912).

**Eleodes suturalis** (Say). The thorough description in Wade and St. George (1923) easily places this species within the subgenus *Eleodes* based on the epipharynx and the apical tooth on the pygidium. It also appears to have spinose setae on the anterolateral margins of the epipharynx, as in *E. hispilabris*, *E. spinipes*, and *E. tenuipes*.

**Eleodes tricostatus** (Say). McColloch (1918) describes the larvae as black in color after the first instar. The larvae of *E. carbonarius* and *E. anthracinus*, the only other *Melaneleodes* larvae known, are similarly dark. The picture provided by McColloch (plate 5, image B), also looks similar to *E. carbonarius* in gestalt.

**Eleodes vandykei** Blaisdell. Little comparative data to separate this species from the other currently described *Eleodes* larvae can be drawn from Hyslop (1912).

Discussion

As adult morphology in many *Eleodes* species may be heavily influenced by participation in mimicry rings with co-occurring species (Doyen and Somerby 1974), the addition of characters from larval morphology may help produce a more accurate phylogeny based on morphological data than one using adult morphology alone. The presented phylogeny (Fig. 1) demonstrates the utility of larval morphology in resolving at least some relationships within the genus *Eleodes*. The subgenus *Melaneleodes* was well supported based on several synapomorphies present in the two included species. The subgenus *Eleodes* showed two synapomorphies supporting a relationship for three of the included species, but did not recover a clade containing all of the current or presumed species from the nominate subgenus. Both *E. tribulus* and *E. caudiferus* are somewhat unusual members of the subgenus based on adult morphology as well; hence further research is needed to accurately place them within the subgeneric classification. The inclusion of more taxa should increase phylogenetic accuracy and help illuminate the currently unresolved relationships between the *Eleodes* subgenera (Heath et al. 2008). It is likely that extensive modifications to the matrix and key will be needed as more larvae become known. It is also possible that some species, particularly closely related ones, cannot be separated based on larval characters alone.

By producing matrix-based descriptions within mx, we are creating a growing repository of digital morphological and specimen data, already available through the tenebro-
Larvae of the genus *Eleodes* (Coleoptera, Tenebrionidae)... nidbase.org portal, including an online multi-entry key (http://tenebrionidbase.org/public clave) to the currently known *Eleodes* larvae. Characters and states from the matrix and key will also be linked to the developing Coleoptera Anatomy Ontology project (ColAO).

**Acknowledgements**

We would like to thank the following people for collecting or helping to rear specimens for this project: Paul Skelley, Stephanie Delgado, Soon Flynn, Amanda Smith, Jazmine Mayberry, Tiffany Gruna, Erik Posch, and Wade Wilber. James Thostenson and Andrew Johnston provided technical and operational assistance with the CLSM at the American Museum of Natural History. Rolf Aalbu, Nico Franz, and David Grimaldi provided insightful comments and suggestions to improve the manuscript. Funding was provided by the International Institute for Species Exploration at Arizona State University and the NSF ARTS program (DEB-1258154).

**References**


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Appendix 1

1. Head – orientation: (0) prognathous or weakly declined; (1) hypognathous
2. Head – shape: (0) rounded; (1) weakly dorsoventrally flattened; (2) strongly dorsoventrally flattened
3. Head – width: (0) narrower than prothorax; (1) nearly equal to prothorax; (2) wider than prothorax
4. Head – sides: (0) rounded; (1) angular
5. Head – constriction: (0) strongly constricted before occipital foramen; (1) weakly constricted before occipital foramen
6. Head – color: (0) medium brown; (1) brown–grey; (2) ferruginous; (3) dark brown; (4) light tan; (5) dark tan
7. Head – color vs body color: (0) same or nearly the same as body segments; (1) more heavily pigmented than body segments
8. Head – punctuation: (0) impunctate; (1) minute; (2) moderate
9. Head – punctuation density: (0) impunctate; (1) sparse, separated by more than 4 puncture diameters; (2) moderate, separated by 2–4 puncture diameters; (3) dense, separated by 1–2 puncture diameters; (4) nearly confluent, separated by less than a puncture diameter; (5) confluent, at least some punctures merged
10. Epicranial suture – stem length: (0) approximately one–third head capsule length; (1) approximately one–fourth head capsule length
11. Epicranial suture – frontal arms: (0) U–shaped, not obscured by sculpturing; (1) U–shaped, partially obscured by sculpturing; (2) V–shaped, not obscured by sculpturing; (3) V–shaped, obscured by sculpturing
12. Frons – sculpturing: (0) smooth; (1) faintly rugose; (2) rugose
13. Epicranial plates – dorsal sculpturing: (0) smooth; (1) faintly rugose; (2) rugose
14. Frons – non–primary setae: (0) absent; (1) present
15. Lateral portions of epicranial plates: (0) sparsely setose; (1) moderately setose; (2) densely setose
16. Ventral portions of epicranial plates – setation 1: (0) with row of four to five long setae along anterior margin near buccal cavity, not confluent with setae on lateral portions of plates; (1) with row of six or more long setae along anterior margin near buccal cavity confluent with setae on lateral portions of plates; (2) with two long setae along anterior margin near buccal cavity, not confluent with setae on lateral portions of plates
17. Ventral portions of epicranial plates – setation 2: (0) patch of short setae medially forming a triangular pattern with its base near the anterior margin
18. Stemmata: (0) two present on each epicranial plate, pigmented spots often faded
19. Clypeus – shape: (0) trapezoidal
20. Clypeus – inflation: (0) not swollen; (1) swollen
21. Clypeus – punctuation density: (0) impunctate; (1) sparse, separated by more than 4 puncture diameters; (2) moderate, separated by 2–4 puncture diameters;
(3) dense, separated by 1–2 puncture diameters; (4) nearly confluent, separated by less than a puncture diameter; (5) confluent, at least some punctures merged

22. Clypeus – pigmentation: (0) unicolorous; (1) darker medially in basal half; (2) basal half darker; (3) apical half darker

23. Labrum – inflation: (0) not swollen; (1) swollen

24. Labrum – pigmentation: (0) unicolorous; (1) basal half more darkly pigmented

25. Labrum – sides: (0) rounded; (1) straight

26. Labrum – medial setal row: (0) absent; (1) six to seven erect setae; (2) seven to eight erect setae; (4) ten to fourteen erect setae; (5) four erect setae; (6) two erect setae

27. Labrum – subapical setal row: (0) absent; (1) six to seven erect setae; (2) seven to eight erect setae; (4) ten to fourteen erect setae

28. Labrum – anterior margin: (0) straight to weakly emarginate; (1) medially emarginate

29. Epipharynx – anterior setal row: (0) absent; (1) with six stout spiniform setae; (2) with eight or more stout spiniform setae

30. Epipharynx – anterolateral margins: (0) with stout spinose setae; (1) with microsetation; (2) lacking setation

31. Epipharynx – anterior sensory papillae (spinule) number: (0) six; (1) seven; (2) eight; (3) four; (4) five

32. Epipharynx – anterior sensory papillae (spinule) arrangement: (0) two irregular diagonal rows; (1) two irregular longitudinal rows; (2) two irregular rows, each with two posterior papillae and one near the anterior margin; (3) irregular cluster

33. Epipharynx – subanterior sensory papillae: (0) transverse row of four small sensory papillae subtended by two spinose setae

34. Epipharynx – posterior sensory papillae number: (0) six; (1) seven; (2) eight

35. Epipharynx – posterior sensory papillae arrangement: (0) two irregular rows; (1) irregular cluster

36. Tormae: (0) strongly asymmetric; (1) weakly asymmetric

37. Tormae 2: (0) symmetrical; (1) asymmetrical, left torma smaller; (2) asymmetrical, left torma larger; (3) asymmetrical, left torma smaller, with or without small spine near emergent edge

38. Ligula – setae: (0) apex glabrous, four long subapical setae present, two ventrally and two dorsally; (1) apex densely microsetose, two long subapical setae present ventrally; (2) apex lacking microsetae, two long subapical setae present ventrally, eight or more subapical setae present dorsally; (3) apex with fringe of 6–10 long setae, medially with longitudinal row of short stout setae; (4) apex with median longitudinal row of microsetae dorsally, two long subapical setae present ventrally

39. Hypopharyngeal sclerome: (0) trapezoidal; (1) pentagonal, tricuspidate; Shape of hypopharyngeal sclerome

40. Gula: (0) distinct, hexagonal, widest near middle; (1) distinct, weakly trapezoidal, nearly rectangular; (2) trapezoidal, widest at base

41. Gula – fusion: (0) sutures visible throughout; (1) sutures fused, not visible in basal half

42. Gula – length: (0) less than maximum width; (1) subequal or greater than maximum width
Larvae of the genus *Eleodes* (Coleoptera, Tenebrionidae)...

43. Antenna: (0) three segmented, cylindrical, first segment longer than second; (1) three segmented, cylindrical, first segment subequal to second; (2) three segmented, cylindrical, first segment shorter than second

44. Antenna – segment 2 sensorium: (0) forming a single incomplete ring around the base of segment 3; (1) consisting of many small rounded sensoria around base of segment 3

45. Thoracic tergites – color: (0) grey–brown; (1) medium brown; (2) ferruginous; (3) dark brown; (4) light tan

46. Prothoracic sternite – color anterior to legs: (0) grey–brown; (1) medium brown; (2) ferruginous; (3) dark brown; (4) light brown

47. Thoracic sternite color – posterior to prolegs: (0) tan; (1) light brown; (2) medium brown

48. Prothoracic sternum – anterior transverse striated band: (0) absent; (1) present along anterior fourth, lighter than tergal disc; (2) present along anterior fourth, darker than tergal disc

49. Thoracic tergites – posterior transverse band: (0) absent; (1) present along posterior 5th of all thoracic tergites, striated; (2) present along posterior 6th of all thoracic tergites, striated; (3) present along posterior 4th of all thoracic tergites, striated; (4) present, not striated

50. Thoracic tergites – posterior striated band color: (0) absent; (1) forming a gradient from darker brown anteriorly to lighter brown along posterior border; (2) unicolorous, brown, darker midtergite

51. Mesothoracic tergite – sclerotized transverse line: (0) absent; (1) present on anterior fifth, heavily sclerotized; (2) present on anterior fifth, faint

52. Metathoracic tergite – sclerotized transverse line: (0) absent; (1) present on anterior fifth, heavily sclerotized; (2) present on anterior fifth, faint

53. Thoracic tergites – setae: (0) absent; (1) eight evenly arranged setae present on dorsal surface of each thoracic tergite, lateral margins more densely setose; (2) more than eight dorsal setae present, pattern variable; (3) dense transverse band of short setae near anterior margins of meso– and metatergites

54. Prothoracic tergum – shape: (0) subquadrate, 1.5× or more length of meso– or metaterga; (1) wider than long, 1.2× or more length of meso– or metaterga

55. Prothoracic tergum – lateral margins: (0) granulated band faint, concolorous with protergal disc; (1) granulated band distinct, darker than protergal disc; (2) granulated band absent

56. Meso– and metaterga – shape: (0) wider than long

57. Meso– and metaterga – lateral margin: (0) lacking pigmented bands; (1) pigmented bands present

58. Mesothoracic spiracle: (0) simple, ovate, approximately 1.5× size of abdominal spiracles

59. Prothoracic legs: (0) slightly longer and much thicker than meso– and metathoracic legs; (1) slightly longer and slightly thicker than meso– and metathoracic legs

60. Prothoracic legs – tarsungulus: (0) strongly sclerotized and sickle–shaped; (1) strongly sclerotized, attenuated and slightly hooked
61. Prothoracic legs – trochanter: (0) with row of two stout spines and two longer setae ventro–medially; (1) with row of two stout spines ventro–medially; (2) one stout ventro–medial spine present

62. Prothoracic legs – femur: (0) with ventro–medial row of two spines and three to five longer setae; (1) with ventro–medial row of three to four spines and four to five longer setae; (2) with ventro–medial row of five to six spines; (3) with ventro–medial row of six to ten spines; (4) with ventro–medial row of 13 to 14 spines; (5) with ventro–medial row of three spines; (6) with ventro–medial row of four spines

63. Prothoracic legs – tibia: (0) with ventro–medial row of three to four spines; (1) with ventro–medial row of five to six spines; (2) with ventro–medial row of eight to eleven spinose setae; (3) with eight or more spines ventro–medially, not forming a regular row

64. Prothoracic legs – femur dorsal surface (at rest): (0) with faintly indicated basal sclerotized band; (1) lacking basal sclerotized band

65. Prothoracic legs – tibia dorsal surface (at rest): (0) slightly more sclerotized than ventral surface

66. Mesotibia – posterior surface: (0) row of three spines; (1) row of two spines; (2) row of four to five spines; (3) row of five to seven spinose setae; (4) four spines in 2×2 pattern

67. Abdominal tergites 1–7 – color: (0) light tan; (1) grey–brown; (2) medium brown; (3) ferruginous; (4) dark brown

68. Abdominal tergites 1–7 – color gradation: (0) unicolorous; (1) lightening towards lateral margins; (2) darkening towards lateral margins

69. Abdominal sternites – color: (0) light tan; (1) dark tan; (2) ferruginous

70. Abdominal tergites 1–8 – transverse striated bands: (0) absent; (1) barely visible on posterior 5th of segments; (2) distinct on posterior 5th of segments

71. Abdominal sternites 1–8 – transverse striated bands: (0) absent; (1) barely visible on posterior 5th of segments; (2) distinctly visible, forming near contiguous band with tergal band

72. Abdominal sternite I – setae: (0) absent; (1) sparsely clothed in long erect setae from anterior margin to near midline; (2) moderately clothed in long erect setae to posterior pigmented band; (3) moderately clothed in long erect setae from anterior margin to near midline; (4) tomentose in anterior third, denser along near lateral margins; (5) sparsely clothed in long erect setae along anterior margin

73. Abdominal segments 2–8 – setae: (0) absent; (1) each segment with two sparse transverse bands of long erect setae; (2) each segment with two sparse transverse bands of long erect setae, posterior margin of segment 8 denser setal band; (3) otherwise

74. Abdominal tergites 1–8 – posterior margin color gradation: (0) dark along anterior edge, fading to segment color posteriorly; (1) unicolorous, darker than rest of segment throughout

75. Abdominal tergite 8 – pigmentation: (0) more darkly pigmented than preceding segments; (1) same pigmentation as preceding segments
76. Abdominal tergite 9 – pigmentation: (0) more darkly pigmented than preceding segments; (1) same pigmentation as preceding segments; (2) lighter than preceding segments

77. Abdominal laterotergites: (0) concolorous with tergites, lacking distinct pigmented margins; (1) lateral margins distinctly pigmented

78. Abdominal segment IX, pygidium – dorsal aspect: (0) triangular in dorsal view, gradually reflexed to apex, apex not forming a distinct tooth; (1) triangular in dorsal view, gradually reflexed to apex, apex attenuated and sclerotized, forming a distinct tooth; (2) triangular in dorsal view, gradually reflexed to apex, apex attenuated and sclerotized, rarely forming a small tooth in some specimens; (3) triangular in dorsal view, gradually reflexed to apex, apex with distinct urigomphi

79. Abdominal segment IX, pygidium – setae: (0) absent; (1) sparsely clothed in short and mid length erect setae; (2) moderately clothed in short and mid length erect setae; (3) few primary setae

80. Abdominal segment IX, pygidium – dorsal sculpturing: (0) dorsally more sclerotized in apical two-thirds with faint maculations; (1) sclerotization uniform throughout, lacking maculations

81. Abdominal segment IX, pygidium – marginal row of socketed spines: (0) 14–18 spines; (1) 18–20 spines; (2) 17–23 spines; (3) 22–24 spines; (4) 8–14 spines; (5) 27 spines; (6) 28–38 spines; (7) four spines

82. Abdominal segment IX, pygidium – marginal row of socketed spines 2: (0) forming a single row around posterior two-thirds to one half of segment; (1) forming two or three irregular rows around posterior two-thirds to one half of segment, narrowing to single row around apex; (2) four distinct, regular spines

83. Abdominal sternites I–VIII, longitudinal tomentose bands along lateral margins: (0) present; (1) absent

84. Abdominal segment X – pygopods: (0) short, subconical; (1) longer, tip inverted

85. Abdominal segment X – pygopod setation: (0) each with 9–12 erect setae; (1) each with 11–15 erect setae; (2) each with 17–24 erect setae; (3) each with 10 or more erect setae on more heavily sclerotized posterior face

86. Urogomphi: (0) absent; (1) present, connected at base or complex; (2) present, paired
## Appendix 2

### Descriptive Character Codings

Characters with “{ }” indicate polymorphic codings

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## Appendix 3

**Cladistic Morphological Character Matrix**

1. **Head – width:** (0) nearly equal to prothorax; (1) narrower than prothorax
2. **Head – color vs body color:** (0) more heavily pigmented than body segments; (1) same or nearly the same as body segments
3. **Head – punctation density:** (0) impunctate-nearly confluent, separated by less than a puncture diameter; (1) sparse, separated by more than 4 puncture diameters; (2) moderate, separated by 2-4 puncture diameters; (3) dense, separated by 1-2 puncture diameters
4. **Epicranial suture – stem length:** (0) approximately one third head capsule length; (1) approximately one fourth head capsule length
5. **Epicranial suture – frontal arms:** (0) sinuate; (1) U shaped
6. **Frons – sculpturing:** (0) distinctly rugose; (1) faintly rugose
7. **Epicranial plates – dorsal sculpturing:** (0) distinctly rugose; (1) faintly rugose
8. **Lateral portions of epicranial plates:** (0) sparse to moderately setose; (1) densely setose
9. **Ventral portions of epicranial plates – setation:** (0) with row of four to five long setae along anterior margin near buccal cavity, not confluent with setae on lateral portions of plates; (1) with row of six or more long setae along anterior margin near buccal cavity, confluent with setae on lateral portions of plates; (2) with two long setae along anterior margin near buccal cavity, not confluent with setae on lateral portions of plates
10. **Clypeus – shape:** (0) swollen; (1) not swollen
11. **Clypeus – punctation density:** (0) dense, separated by 1-2 puncture diameters; (1) moderate, separated by 2-4 puncture diameters
12. **Labrum – inflation:** (0) swollen; (1) not swollen
13. **Labrum – subapical setal row:** (0) six to seven erect setae; (1) seven to eight erect setae; (2) ten to fourteen erect setae
14. **Epipharynx – anterior setal row:** (0) with six stout spiniform setae; (1) with eight or more stout spiniform setae
15. **Epipharynx – anterolateral margins:** (0) lacking setation; (1) with stout spinose setae; (2) with micro-setation
16. **Epipharynx – anterior spinule arrangement:** (0) two semi uniform rows or irregular cluster; (1) two rows, each with two posterior papillae and one near the anterior margin
17. **Tormae:** (0) weakly asymmetric, more irregularly shaped and somewhat acute; (1) strongly asymmetric, broadly triangular and acute
18. **Ligula – setae:** (0) apex with fringe of 6-10 long setae medially with longitudinal row of short stout setae; (1) apex with median longitudinal row of microsetae dorsally two long subapical setae present ventrally; (2) apex densely microsetose two long subapical setae present ventrally; (3) apex lacking microsetae, two long subapical setae present ventrally, eight or more subapical setae present dorsally; (4) apex glabrous, four long subapical setae present two ventrally and two dorsally
19. **Hypopharyngeal sclerome:** (0) pentagonal, tricuspidate; (1) trapezoidal
20. Gula: (0) trapezoidal, widest at base; (1) distinct, hexagonal to nearly rectangular, widest near middle
21. Gula – length: (0) equal to or less than maximum width; (1) greater than maximum width
22. Antennae: (0) three segmented, cylindrical, first segment shorter than second; (1) three segmented, cylindrical, first segment longer than second; (2) three segmented, cylindrical, first segment subequal to second
23. Prothoracic tergum – anterior transverse striated band: (0) present along anterior fourth, darker than tergal disc; (1) present along anterior fourth, lighter than tergal disc
24. Mesothoracic tergite – sclerotized transverse line: (0) absent; (1) present on anterior fifth, heavily sclerotized; (2) present on anterior fifth, faintly indicated
25. Metathoracic tergite – sclerotized transverse line: (0) absent; (1) present on anterior fifth, heavily sclerotized; (2) present on anterior fifth, faintly indicated
26. Thoracic tergites – setae: (0) eight evenly arranged setae present on dorsal surface of each thoracic tergite, lateral margins more densely setose; (1) more than eight dorsal setae present, pattern variable
27. Prothoracic tergum – shape: (0) subquadrate, 1.5× length of meso- or metaterga; (1) wider than long, 1.2× or more length of meso- or metaterga
28. Prothoracic tergum – lateral margins: (0) granulated band faint, concolourous with protergal disc; (1) granulated band distinct, darker than protergal disc; (2) granulated band absent
29. Meso- and metaterga – lateral margin: (0) pigmented bands present; (1) lacking pigmented bands
30. Prothoracic legs: (0) slightly longer and slightly thicker than meso- and metathoracic legs; (1) slightly longer and much thicker than meso- and metathoracic legs
31. Prothoracic legs – tarsungulus: (0) strongly sclerotized, attenuated and slightly hooked; (1) strongly sclerotized and sickle shaped
32. Prothoracic legs – tibia: (0) with ventro–medial row of three to four spines; (1) with ventro–medial row of five to six spines; (2) with ventro–medial row of eight to eleven spinose setae; (3) with eight or more spines ventro–medially not forming a regular row
33. Prothoracic legs – femur dorsal surface at rest: (0) with faintly indicated basal sclerotized band; (1) lacking basal sclerotized band
34. Abdominal sternites – color: (0) light tan; (1) dark tan; (2) ferruginous
35. Abdominal sternites I–VIII – transverse striated bands: (0) barely visible on posterior 5th of segments; (1) distinctly visible, forming near contiguous band with tergal band
36. Abdominal sternite I – setae: (0) sparsely clothed in long erect setae along anterior margin; (1) sparsely clothed in long erect setae from anterior margin to near midline; (2) moderately clothed in long erect setae to posterior pigmented band; (3) moderately clothed in long erect setae from anterior margin to near midline; (4) tomentose in anterior third, denser along near lateral margins
37. Abdominal segments II-VIII – setae: (0) absent; (1) each segment with two sparse transverse bands of long erect setae; (2) each segment with two sparse transverse bands of long erect setae, posterior margin of segment 8 denser setal band; (3) otherwise

38. Abdominal tergites I-VIII – posterior margin color gradation: (0) dark along anterior edge, fading to segment color posteriorly; (1) unicolorous darker than rest of segment throughout

39. Abdominal tergite VIII – pigmentation: (0) more darkly pigmented than preceding segments; (1) same pigmentation as preceding segments

40. Abdominal tergite IX – pigmentation: (0) more darkly pigmented than preceding segments; (1) same pigmentation as preceding segments; (2) lighter than preceding segments

41. Abdominal laterotergites: (0) lateral margins distinctly pigmented; (1) concolorous with tergites, lacking distinct pigmented margins

42. Abdominal segment IX (pygidium) – shape: (0) triangular in dorsal view, gradually reflexed to apex, apex not forming a distinct tooth; (1) triangular in dorsal view, gradually reflexed to apex, apex attenuated and sclerotized forming a distinct tooth; (2) triangular in dorsal view, gradually reflexed to apex, apex attenuated and sclerotized rarely forming a small tooth in some specimens; (3) triangular in dorsal view, gradually reflexed to apex, apex with distinct urigomphi

43. Abdominal segment IX (pygidium) – setae: (0) few primary setae; (1) sparsely clothed in short and mid-length erect setae; (2) moderately clothed in short and mid-length erect setae

44. Abdominal segment IX (pygidium) – dorsal sculpturing: (0) dorsally more sclerotized in apical two thirds, with faint maculations; (1) sclerotization the same throughout, lacking maculations

45. Abdominal segment IX (pygidium) – marginal row of socketed spines: (0) four; (1) eight or more

46. Abdominal segment IX (pygidium) – marginal row of socketed spines 2: (0) four distinct regular spines; (1) forming a single row around posterior two thirds to one half of segment; (2) forming two or three irregular rows around posterior two thirds to one half of segment, narrowing to single row around apex

47. Abdominal segment X – pygopods: (0) longer, tip inverted; (1) short, subconical

48. Abdominal segment X – pygopod setation: (0) each 16 or less setae; (1) each with 17 or more setae
### Appendix 4

Cladistic Character Codings

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New species and records of Charisius Champion from Mexico and Central America (Coleoptera, Tenebrionidae, Alleculinae)

J. M. Campbell

Canadian National Collection of Insects, Arachnids and Nematodes, Agriculture and Agri-Food Canada, Ottawa, Ontario, K1A 0C6

http://zoobank.org/A0F2D6F3-B44B-4ED2-9B1E-3BDC39ED8C50

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Academic editor: P. Bouchard | Received 13 December 2013 | Accepted 12 March 2014 | Published 12 June 2014

http://zoobank.org/E9AB764D-FADB-45E2-B9B2-B4CF782CB3AD


Abstract

The species of the genus Charisius Champion, from Mexico and Central America are reviewed. The flightless genus Narses Champion, with one included species, N. subalatus Champion, is placed in synonymy with the genus Charisius. Four new species are described and illustrated, C. granulatus and C. punctatus (from Guatemala) and C. apterus and C. howdenorum (from Mexico). Charisius subalatus (Champion) is redescribed and illustrated. The species C. interstitialis Champion is placed in synonymy with C. zunilensis Champion. The genus is redescribed to include the four new species and N. subalatus. New distributional records are presented for all other species of the genus and a revised key is presented for identification of all the species of the genus.

Keywords

Coleoptera, Tenebrionidae, Alleculinae, Narses, Charisius, Mexico, Central America, Systematics, New synonymy, New species, New Combination
Introduction

The purpose of this paper is to record and describe the new species and distributional records of the genus *Charisius* Champion that have accumulated since my previous revision of the genus. I have placed the genus *Narses* Champion in synonymy with *Charisius* and have redescribed its only included species, *N. subalatus*. The classification and arrangement of the species described in the earlier paper is followed except for the addition of the subalatus group to include the two flightless species. The four new species and *Narses subalatus* are described and illustrated.

Methods

All measurements were made with an ocular micrometer mounted in a Leitz stereoscopic microscope. Measurements were made of the overall length from the anterior margin of the labrum to the apex of the elytra; the ocular index (OI) of both males and females; the lengths of the third and fourth antennomeres; the length and width of the tenth antennomere and the pronotal index (PI). The photographs were made with a Leica Digital DC500 Imaging Workstation using Zerene Stacker software and retouched with Adobe Photoshop software.

The terminology used in this paper is that recommended by Lawrence et al (2010). Other terms were described in my previous paper (1965) except the terms ocular index and pronotal index. The ocular index is the ratio of the distance between the eyes to the greatest distance across the eyes times 100. The pronotal index is the measurement of the width of the pronotum at its widest divided by the length of the pronotum along the midline times 100. My previous paper (1965) should be consulted for full descriptions and illustrations of all the previously described species.

Material was examined from the following collections:

**AMNH** American Museum of Natural History, New York, NY.
**CASC** California Academy of Sciences, San Francisco, CA
**CMNC** Canadian Museum of Nature, Alymer, Quebec, Canada
**CNCI** Canadian National Collection of Insects, Ottawa, Ontario, Canada
**EGRC** E. G. Riley Collection, Texas A & M University, College Station, TX.
**JEWC** J. E. Wappes Collection, San Antonio, TX.
**USNM** United States National Museum, Washington, DC.
**UNMO** University of Montana, Bozeman, MON.

Holotypes are deposited in the Canadian National Collection of Insects, Ottawa (CNCI), and the Collection of the University of Montana (UMON).

The dorsal habitus of all species are illustrated to show the various color patterns of each species and the male terminalia of all the new species and *C. subalatus* are illustrated with photographs.
Systematics

Charisius Champion
http://species-id.net/wiki/Charisius

Charisius Champion (1888: 421); Champion (1893: 565); Campbell (1965: 43).

Description. Body narrowly elongate (Figs 1–6, 9–12) (broader in subalatus group, Figs 7–8); glabrous dorsally; color ranging from light to dark reddish-brown, often with yellow and/or piceous markings on elytra. Surface varying from smooth, shining, with very fine microsculpture (visible only under high magnification) to dull with dense, moderately fine, visible microsculpture. Length 6-13 mm.

Head moderately sparsely to moderately densely, evenly punctate on vertex; punctures separated by average distance equal to or slightly greater than diameter of a puncture. Eyes moderate in size, separated by distances ranging from equal to or slightly greater than diameter of eye (OI ranging from 30 to 47); with distinct, well-developed nuchal-constriction (Figs 2, 4). Maxillary palpus (Fig. 16) with apical segment broadly securiform; apex subequal in length to outer side; mandible with apex shallowly notched medially. Antennae narrowly elongate (Figs 1–6); antennomere 2 very short, antennomere 3 much longer than 2, slightly shorter than to slightly longer than 4; 4–10 each elongate, at least two times longer than wide; sides only slightly widened from base to apex; antennal sensoriae small, visible only under high magnification, evenly distributed on segments 4–11.

Pronotum with base distinctly narrower than base of elytra (Figs 1–10); sides variable, ranging from evenly narrowed from base to near apex to widest near middle and curved both anteriad and posteriad; width greater than length (PI ranging from 67 to 95); anterior margin truncate to slightly convex; anterior angles distinct, narrowly rounded. Basal foveae small, moderately deeply impressed, connected across base of pronotum by distinct transverse, prebasal groove. Prosternum elongate (Figs 17–18), horizontal anteriad of procoxae, prosternal process evenly rounded, abruptly declivous anteriad and posteriad of procoxae. Mesoventrite elongate (Fig. 17), distinctly more elongate than mesocoxal cavities except in species of subalatus group (Fig. 18); with shallow to moderately deep, V-shaped mesosventral cavity; intercoxal process gradually sloped to prosternum. Metaventrite with surface finely, sparsely to moderately coarsely punctate; disc distinctly more elongate between coxae than length of mesocoxal cavities (except in species of subalatus group). Third and fourth segments of anterior and intermediate tarsi and penultimate segment of posterior tarsi lobed ventrally, in addition, basal two segments of protarsus lobed ventrally in male (except C. salvini).

Elytra elongate (Figs 1–6, 9–12); sides parallel for basal half; then evenly narrowed to apex except C. apterus and C. subalatus (Figs 7–8); striae moderately shallowly impressed near base, becoming more deeply impressed approaching apex (striae unimpressed between strial punctures in C. howdenorum (Fig. 19); strial interstices usually
convex or rarely flat; impunctate or with a row of fine, median punctures visible only under high magnification. Elytral epipleurae ending just before apex of elytra; evenly arched from base to apex. Ventrites finely, sparsely punctate or impunctate.

Male: Eighth sternite divided into two large, well developed lobes (Figs 21–24); apex of each lobe appearing glabrous, actually bearing small, densely placed, dentiform setae which extend along inner margin to near base (visible only under high magnification). Ninth sternite bilobed; lobes small, not joined medially, reaching only to base of eighth sternal lobes. Apicale of aedeagus variable (Figs 25–28); ranging from 2.8 to 3.5 times as long as basale (apicale very short in salvini group, basale 6.9 to 7.9 times longer than apicale).

**Type species.** I previously designated *Charisius fasciatus* Champion as the type species of the genus (Campbell 1965: 45). The type species of *Narses* is *N. subalatus* Champion, by monotypy (Champion 1888: 423).

**Remarks.** Champion (1888 and 1893) described the genus *Charisius* to include five species and the genus *Narses* to include only *N. subalatus*. Subsequently, I revised the genus *Charisius* (1965) and included one additional species, *C. mexicanus*. In this paper, based on additional material, I have placed one species, *C. interstitialis* Champion, in synonymy with *C. zunilensis* Champion and have described an additional four new species. Species of *Charisius* occur in moderate to high elevations from central Mexico south to the highlands of Nicaragua. Records cited in this paper extend the known ranges of several species from Guatemala south to El Salvador and Honduras. One specimen of *C. salvini* was collected in Nicaragua.

Adults of *Charisius* are easily distinguished from all other Mexican and Central American members of the tenebrionid subfamily Alleculinae (Tribe Alleculini) by the combination of having the body glabrous dorsally; by the deep, prebasal transverse groove connecting the basal foveae of the pronotum; by having the elytral interstices impunctate except for a median row of minute punctures visible only under high magnification; by their elongate, almost filiform antennae, with the subapical antennomeres at least two times longer than wide; by their narrow and elongate shape (see Figs 1–12), and by the broadly securiform shape of the apical segments of the maxillary palpi (Fig. 16). Adults of seven of the ten species now known differ from those of all other species of Mexican and Central American Alleculina in having distinctive yellow and/or black markings on the elytra.

Champion distinguished the genus *Narses* from *Charisius* based only on the presence of reduced wings, stating that the genera are similar in all other respects. The discovery of a second flightless species, *C. apterus* and an examination of the male terminalia of all the species confirm that *Narses* and *Charisius* are congeneric.

I have retained the same species groups that I established in my previous paper except that I have added an additional group for the two flightless species.

**Bionomics.** Adults of *Charisius* are found primarily throughout the rainy season. In Guatemala and southern Mexico the rainy season normally begins in March or April and the season ends usually in November. Adults are usually collected by beating dead leaves of thick, mixed vegetation. Apparently, there is no plant host specificity involved since I have collected specimens from the leaves of oaks, dead vines, tree
ferns, and a number of different deciduous trees. I collected and reared one larva of *C. fasciatus* from rotting detritus from inside a hollow log. A pupa and one adult were collected from pupal cells about a meter above ground level in soft, decaying wood of a dead, standing oak.

**Fasciatus Group**

Species of this group may be easily distinguished in having the wings fully developed, in having yellow, transverse markings on the elytra, by their larger size, in having the male anterior tibiae distinctly widened on the inner side near the middle (except *C. granulatus*), the male fifth visible ventrite not impressed medially and the apicale of the aedeagus elongate (Fig. 25). The basale of the aedeagus varies from 2.5 to 3.5 times longer than the apicale.

1. *Charisius fasciatus* Champion

http://species-id.net/wiki/Charisius_fasciatus

Figs 1–3, 13, 17

*Charisius fasciatus* Champion (1888: 421, pl. 19, Figs 12, 12a, 13); Campbell (1965: 67, Figs 3, 9, 15, 16).

**Type.** Lectotype, male, Quiché Mountains, Guatemala (Campbell 1965: 47). The specimen is in the BMNH.

**Distribution and records.** *Charisius fasciatus* was previously known from six specimens collected from the highlands of Guatemala. The following records extend the known range of this species into the state of Chiapas in southern Mexico, Honduras and El Salvador. It has been collected between the elevations of 1500 to 2750 meters.

**EL SALVADOR:** Cerro Verde, 2000 m, 1.V.1971, HF Howden (CMNC) 1.

**GUATEMALA:** El Progresso: 28-29 km N San Augustin, 7000–8500 ft, 17–21. IV.1990, JE Wappes (JEWC) 1. Jalapa: Miramundo, 8400 ft., 3.VII.1986, JMC (CNCI, JMCC) 4. Quetzaltenango: Santa María, Los Pirineos, 4500 ft, 15.VI. 1966, JMC (JMCC) 1; Santa María, 5,000 ft, 18.V.1966, JMC (JMCC) 1; Santa María, 6,000 ft, 10.VII.1965, JMC (JMCC) 1; 4 km W Santa María, 5000 ft, 27.III.1966, JMC (JMCC) 1; 3 km SE Zunil, Tzanjoyan, 2400 m, 1.XI.1965, JMC (JMCC) 2; 12 km SE Zunil, NW face Cerro Zunil, Fuentes Georginas, 2700 m, 17.VI.1993, R Anderson (CMNC) 1. Quiché: Nebaj, 6000 ft, 9.VIII.1947, C & P Vaurie (AMNH) 1. Suchitepéquez: 5 km S Santiago Atitlan, 1500 m, 13.IX.1965, JMC (JMC) 1; Zunil, 2 km N Finca Colimas, 6000 ft, 28.IV.1966, JMC (JMCC) 2. Zacapa: 3 km NE San Lorenzo, Sierra de las Minas, 1800 m, 6.VII.1986, JMC (CNCI) 1; 6 km NE San Lorenzo, 6500 ft, 17.VI.1993, JMC (CNCI, JMCC) 2; 8 km NE San Lorenzo, Sierra de las Minas, 2100 m, 10.VII.1986 and 18.VII.1986, JMC (CNCI) 2.
Figures 1–6. Dorsal habitus of species of *Charisius*: 1 *C. fasciatus*, from Tinijapa, 8 mi NE San Cristobal de las Casas, Chiapas, Mexico 2 *C. fasciatus*, from 8 km NE San Lorenzo, Zacapa, Guatemala 3 *C. fasciatus*, from Santa María, Quezaltenango, Guatemala 4 *C. picturatus*, from Route 190, 33.0 miles NW Oaxaca, Oaxaca, Mexico 5 *C. mexicanus*, from 8 km S Suchixtepec, Oaxaca, Mexico 6 *C. granulatus*, from 29 km N San Augustín, El Progresso, Guatemala.

MEXICO: Chiapas: Cerro Huitepec (Pico), ca 5 km W San Cristóbal de las Casas, 2750 m, 23.IX.1991, R Anderson (CMNC) 1; 5 km W San Cristóbal, 3.V.1969, HF Howden (CMNC) 1; 6 km E San Cristóbal, 9.V.1969, HF Howden (JMCC) 1; 8 km NE San Cristóbal, 17.V.1969, HF Howden (CMNC) 1; 8 mi S Simojovel, 10.VI.1969, JMC (CNCI) 1; San Cristóbal de las Casas, 26.VII.1969, LA Kelton (CNCI) 2; 5 mi W San Cristóbal, 28.VI.1969, JMC, (CNCI, JMCC) 5; 8 mi NE San Cristóbal, 5.V.1969, HF Howden (CMNC) 2; 11 mi NE San Cristóbal, 18.V.1969, HF Howden (CMNC) 2; Tinijapa, 8 mi NE San Cristóbal 26.V.1969 and 18.V.1969, JMC (CNCI, JMCC) 12; Rte. 190, 16.8 mi SE Teopisca, 6700 ft., 2.IX.1967, Ball, TL Erwin, RE Leech (CNCI) 1.

**Remarks.** This species is the most variable in color of any species of the genus. It closely resembles *C. picturatus*, *C. mexicanus*, and *C. granulatus* in some of its color patterns. No differences were noted in the structure of the aedeagus and the male seventh and eighth sternites between the males of these color forms. In my earlier revision I recognized two distinct color forms, one with three yellow, transverse bands across the elytra (from Totonicapán and the Quiché Mountains of Guatemala) and the second form with only two transverse bands (from Cerro Zunil, near Quezaltenango and Calderas, near Antigua in Guatemala). A long series of specimens from a number of areas near San Cristóbal de las Casas in Chiapas and a number of different localities in Guatemala are intermediate between these two previously recognized color forms, so I am unable to distinguish various color forms based on geographical variation.

Adults of *C. fasciatus* may be distinguished from those of *C. mexicanus* by differences in the structure of the male eighth sternal lobes and by the distinctly finer and sparser punctuation of the pronotum (Figs 13, 14). Adults of *C. fasciatus* differ from those of *C. picturatus* (Fig. 4) by having the yellow regions of the elytral bands (Figs 1–3) less irregular and the basal band larger, extending to near the sutural margin. Some of the specimens from San Cristóbal are virtually indistinguishable in color from those of *C. mexicanus*. They may be distinguished only by dissection of the male eighth sternal lobes and by the distinctly finer punctuation of the pronotum. Adults of *C. granulatus* closely resemble the other species of the fasciatus group in the color patterns, however adults of this species may be easily distinguished from all other species of this group by the more coarsely punctate pronotum, by having the surface between the punctures coarsely granulate and not shining and by the narrow apicale having the sides distinctly sinuate before the apex (Fig. 25).

I have provisionally assigned one specimen from El Salvador to this species, but it differs in having the apical two yellow bands reduced to small spots and in having the elytral striae completely unimpressed between the strial punctures on the apical fourth of the elytra. No other differences were noted.

Adults were collected by beating dead leaves in a pine-oak forest, from a Malaise trap set in an oak forest and from dead leaves alongside a logging road in the Sierra de las Minas, Guatemala. I reared adults from larvae and pupae collected from wood in hollow logs and from dead wood found in a tree hole.
2. **Charisius picturatus** Champion

http://species-id.net/wiki/Charisius_picturatus

Fig. 4

*Charisius picturatus* Champion (1893: 565, pl, 23, fig. 21); Campbell (1965: 48, Figs 10, 17).

**Type.** Lectotype, male, Omilteme, Guerrero, Mexico 8000 ft (Campbell 1965: 48). The specimen is in the BMNH.

**Distribution and records.** This species was described from one male and one female from Omiltemi, Guerrero, Mexico. I have provisionally assigned two additional females to this species.

**Remarks.** These specimens agree in all respects with those previously described by Champion except that the overall coloration is a darker reddish-brown. The specimen from Oaxaca was collected from an oak forest.

3. **Charisius mexicanus** Campbell

http://species-id.net/wiki/Charisius_mexicanus

Figs 5, 14

*Charisius mexicanus* Campbell (1965: 49, Figs 4, 8, 11, 18).

**Type.** Holotype, male, 5.2 miles west Acultzingo (Veracruz), Puebla, Mexico (Campbell 1965: 49). The specimen is in the BMNH.

**Distribution and records.** This species was previously known from Mexico in the states of Morelos and Puebla. The species has been collected at elevations ranging from 1800 to 2700 m. The following new records are cited.

**Remarks.** These specimens agree in all respects with those previously described by Champion except that the overall coloration is a darker reddish-brown. The specimen from Oaxaca was collected from an oak forest.
Remarks. There is little variation in the color pattern of this species (see Fig 5). As previously mentioned, males of *C. fasciatus* from the state of Chiapas in Mexico may be distinguished from those of *C. mexicanus* with certainty only by examination of the male eighth sternal lobes. The adults of *C. mexicanus* can usually be distinguished by the distinctly coarser punctation of the pronotum (Fig. 14) and by the shorter apicale of the aedeagus (apicale 2.5–2.9 as long as basale).

Most adults were collected by beating dead leaves of oak trees. The specimens collected by EL Sleeper were taken in a boreal forest and an oak-pine woodland. All known records of *C. mexicanus* are from north of the Isthmus of Tehuantepec and those of *C. fasciatus* are from south of the Isthmus.

This species was previously known only from the highlands of central Mexico. These are the first records of the species from the Mexican states of Guerrero and Oaxaca.

4. *Charisius granulatus* sp. n.
http://zoobank.org/9DA0E160-6B50-440E-ACAF-BBDB641D6F5E
http://species-id.net/wiki/Charisius_granulatus
Figs 6, 15

Description. Dark reddish-brown; elytra yellow with broad basal, large medial, and smaller V-shaped piceous markings (Fig. 6). Length 9.9–10.9 mm.

Head coarsely, densely, evenly punctate; punctures separated by average distance less than diameter of a puncture. Eyes moderate in size, mean ocular index of 5 specimens 35.4 (30–40).

Pronotum distinctly wider than long, mean pronotal index of 5 specimens 82.6, ranging from 81 to 84; surface microsculpture densely, coarsely granulate, opaque; punctures coarse (Fig. 15), moderately dense, separated on center of disc by average distance equal to or slightly greater than diameter of a puncture, punctures becoming finer and distinctly more widely separated on sides of disc; sides straight, subparallel from base to apical fourth then convexly narrowed to apex; transverse groove broad, moderately deeply impressed, disc shallowly, but distinctly impressed along midline. Prosternum and hypomeron with a few widely scattered, moderately coarse punctures. Metaventrite normally elongate, length between meso- and metacoxae distinctly longer than length of mesocoxal cavity; surface finely, moderately sparsely punctate medially, punctures becoming coarser approaching sides. Ventrites with punctures fine; last two ventrites slightly more coarsely and densely punctate. Elytra with striae moderately impressed basally, becoming deeply impressed towards apex; strial interstices convex.

Male. Anterior tibiae not sexually modified; anterior tarsal claws each with 7–9 teeth. Ventrite five not impressed medially. Lobes of eighth sternum (Fig. 21) broad, slightly curved medially, apices broadly, evenly rounded; apical and inner margins with row of very fine, short, dentiform setae; viewed laterally, lobes only slightly deflexed. Lobes of ninth sternum short, moderately broad, with apices evenly convex. Aedeagus with apicale (Fig. 25) narrow, with sides narrowed from base to narrowly rounded apex; sides moderately strongly sinuate just before apex.
Female. Anterior tarsal claws each with 7 teeth. Elytra with sutural margin and apex entire.

**Types.** Holotype, male, with labels as follows: GUAT., Zac., 8 km N San Lorenzo, 10.VI.1993, 6700’, J. M. Campbell/ HOLOTYPE _ Charisius granulatus, desig. 2013, J.M.Campbell. The specimen is deposited in the CNCI.

Paratypes: two males and two females deposited in the collections of JEWC and JMCC.

**Distribution and records.** This species is known only from the Departamentos of El Progresso and Zacapa in Guatemala.


**Etymology.** The species name granulatus is derived from the unique granulate microsculpture on the pronotal disc.

**Remarks.** Adults of the species _Charisius granulatus_ may be easily distinguished from those of all other species of _Charisius_ in having the pronotum moderately densely, coarsely punctate with the surface between the punctures coarsely, densely granulate, opaque. The color pattern of the elytra (Fig. 6) will readily distinguish adults of _C. granulatus_ from those of _C. mexicanus_ and the Chiapas population of _C. fasciatus_. Males differ from those of all other species of the fasciatus group in lacking any trace of an expansion on the inner surface of the anterior tibiae.

**Subalatus Group**

Species of this group may be easily distinguished from those of other species groups of _Charisius_ by having the wings greatly reduced, shorter than the elytra and the functionally related shortening of the metaventrite (Fig. 18). In addition, the species are moderately large in size (7.6–9.8 mm in length), the male anterior tibiae are slightly, convexly widened on the inner margin, and the male fifth visible ventrite is not impressed medially. Males of _C. apterus_ are unknown.

This species group contains two flightless species, one _C. subalatus_, formerly placed in the genus _Narses_, and the new species _C. apterus_.

**5. Charisius apterus sp. n.**

http://zoobank.org/C6B07DD8-B980-4E47-9D7E-D2AE5FC1F67C
http://species-id.net/wiki/Charisius_apterus
Figs 7, 20

**Description.** Dark reddish-brown; elytron yellow with extensive brunneous markings as follows: moderately broad, transverse bands across basal fourth and across middle; narrow, jagged band across apical fourth and extreme apical portion; suture brunneous (Fig. 7). Length 9.8 mm.
New species and records of Charisius Champion from Mexico and Central America...

Figures 7–12. Dorsal habitus of species of Charisius. 7 C. apterus, from 2 mi. S Cerro Pelon, Oaxaca, Mexico 8 C. subalatus, from Miramundo, Jalapa, Guatemala 9 C. zunilensis, from 6 mi N San Lorenzo, Zacapa, Guatemala 10 C. howdenorum, from Tinijapa, 8 mi. NE San Cristobal de las Casas, Chiapas, Mexico 11 C. salvini, from Finca Florencia, Sacatepequez, Guatemala 12 C. punctatus, from San Lorenzo, Zacapa, Guatemala.
Head coarsely, densely punctate, punctures separated by distance distinctly less than diameter of a puncture. Eyes small, widely separated dorsally, ocular index of female holotype 47. Pronotum slightly wider than long, PI of holotype 88; surface with microsculpture finely, uniformly granulate, not shining; moderately densely and coarsely punctate, punctures separated by distance slightly greater than diameter of a puncture; punctures evenly distributed except becoming sparser on narrow band at anterior lateral angles of pronotum; sides distinctly convex, widest at apical third, distinctly narrowed towards base; transverse groove broad, shallowly impressed; midline broadly, shallowly impressed on basal half.

Prosternum and hypomeron sparsely, finely punctate; postcoxal extension of sides of pronotum with row of coarse, moderately shallow impressions. Metaventrite short, length between meso- and metacoxae subequal in length to length of mesocoxal cavity; moderately coarsely and densely, evenly punctate. Abdomen with basal three ventrites with a few scattered, fine punctures; apical two ventrites more densely punctate with punctures separated by distance approximately two to three times diameter of puncture. Elytra 3.2 times longer than pronotum (in unique holotype)
New species and records of Charisius Champion from Mexico and Central America...

with striae shallowly, evenly impressed throughout; strial punctures coarse, narrowly separated along striae; intervals slightly convex. Wings reduced, flightless.

Male. Unknown.

Female. Anterior tarsal claws each with 6 teeth. Elytra with sutural margin near apex and apex emarginate as in Fig. 20. Fifth visible sternite broadly, shallowly impressed medially.

Type. Holotype, female with labels as follows: MEX. OAXACA, 2 mi. S Cerro Pelon, 03 JUL 1982, 8-9000 ft. MA Ivie colr./ Holotype __, Charisius apterus, desig. 2013, JM Campbell. The holotype is deposited in the collection of the University of Montana.

Distribution and records. Charisius apterus is known only from the type locality in Oaxaca, Mexico.

Etymology. The species name apterus is derived from the species having the flight wings reduced to short stubs.

Remarks. Adults of this remarkable flightless species can be easily distinguished from those of all other species of Charisius except C. subalatus by having the wings shorter than the elytra and the associated reduction in length of the metaventrite. The female holotype differs from specimens of C. subalatus by the distinctive elytral markings (Fig. 7) and by the unusual modifications of the elytral apices (Fig. 20). Other than the reduced wings and modified elytral apices of the female, the species is readily assigned to Charisius by the fact that the body is completely glabrous dorsally, the pronotum has a distinct, transverse depression across the base, and the antennae are elongate with the apical segments at least 2 times longer than wide.

6. Charisius subalatus (Champion), comb. n.

http://species-id.net/wiki/Charisius_subalatus

Figs 8, 18, 22, 26

Narses subalatus Champion (1888: 424, pl. 19, Figs 15, 16a, 16b).

Description. Uniformly reddish-brown; without elytral markings (Fig. 8). Length 7.6–8.7 mm.

Head coarsely, densely, evenly punctate on vertex; punctures separated by average distance less than diameter of a puncture. Eyes moderate in size, widely separated dorsally; mean OI of 9 specimens 45.2 (range 42–48). Pronotum slightly wider than long, average PI of 9 specimens 90.5 (range 87–96); with surface very finely granulate, opaque; finely, shallowly, sparsely punctate, punctures separated by average distance at least two times diameter of a puncture; punctures evenly distributed over most of disc except becoming nearly impunctate near sides; sides distinctly curved, widest across middle; with midline shallowly impressed in basal half. Prosternum and hypomeron with a few widely scattered, moderately coarse punctures; postcoxal extension of sides of pronotum with a few coarse, moderately shallow impressions. Metaventrite (Fig. 18)
short, length between meso- and metacoxae shorter than length of mesocoxal cavity; moderately coarsely, densely, contiguously punctate medially in males, punctures becoming coarser and sparser approaching sides; coarsely punctate medially in female with

punctures distinctly separated, punctures becoming coarser approaching sides. Ventrites finely, moderately sparsely punctate. Elytra 3.1–3.3 times longer than pronotum; striae shallowly, evenly impressed throughout (in specimens from Miramundo, Guatemala and El Salvador striae completely unimpressed between punctures); strial punctures coarse, narrowly separated along striae; intervals flat. Wings reduced, distinctly shorter than elytra; flightless.

Male. Anterior femora with patch of fine, dense pubescence on middle of ventral margin. Anterior tibiae slightly widened near middle on inner margin. Fifth ventrite unimpressed medially. Eighth sternal lobes (Fig. 22) broad, only slightly curved medially and distinctly curved ventrally near apices; apices of lobes narrowly rounded; viewed laterally, apices of lobes distinctly deflexed. Lobes of ninth sternum short, broad, with apices almost truncate. Aedeagus with apicale (Fig. 26) moderately narrow, with sides converging from base to near apex and distinctly constricted just before apex; apex narrowly rounded; viewed laterally, apicale slightly curved dorsally with apex very narrowly rounded; basale 2.8 to 2.9 times longer than apicale.

Female. Elytra with sutural margin and apex entire.

**Type.** Not designated. The species was described by Champion from Totonicapán, 8,500–10,500 feet and the Quiché Mountains, 8,000 ft, both in Guatemala. The type series is in the BMNH.

**Distribution and records.** The following records extend the known range of this species from Chiapas in southern Mexico to El Salvador.

- **EL SALVADOR:** Chalatenango; El Pital, 13.1 km N San Ignacio, 2650 m, 28.VIII.1994, R Anderson (CMNC) 1.

**Remarks.** Charisius subalatus and C. apterus are the only known flightless species of the genus. Adults of C. subalatus may be easily distinguished from those of C. apterus by the lack of markings on the elytra, by the much finer and sparser punctuation of the head and pronotum, and by the lack of emarginations on the suture and apex of the female elytra. The close similarity of the male terminalia of C. subalatus, particularly with the species of the fasciatus group, provides additional confirmation for placing this genus in synonymy with the genus Charisius.

This species is known only from high elevations. It has been collected from bromeliads, from a Berlese sample of leaf litter in a cloud forest, and by beating herbaceous vegetation along the edge of a forest.

**Zunilensis Group**

Species of this group (Figs 9, 10) are distinguished by lacking any trace of elytral markings, by having the wings fully developed, in lacking any trace of a swelling on

the inner margin of the male protibia, in lacking impressions on the male fifth visible ventrite, and in having the apicale of the aedeagus elongate.

This species group contains two species, one of which, C. howdenorum, is described as new. One species, C. interstitialis Champion, is placed in synonymy.
**7. Charisius zunilensis** Champion
http://species-id.net/wiki/Charisius_zunilensis

Fig. 9

*Charisius zunilensis* Champion (1888: p. 422, pl. 19, fig. 14); Campbell (1965: p. 50, Figs 6, 12).

*Charisius interstitialis* Champion (1888: p. 422); Campbell (1965: p. 50) [**Syn. n.**].

*Charisius floridanus* Linell (1901: p. 184); Campbell (1965: p. 51).

**Types.** Lectotype, male, Cerro Zunil, 4,000–5000 feet, Guatemala (Campbell 1965, p. 50). The type of *C. interstitialis* is a lectotype, male, from Jalapa, Mexico. These lectotypes are in the collection of the BMNH. The holotype of *C. floridanus* is type 4174 in the USNM.

**Distribution and records.** The species is now known from the Mexican state of Veracruz south to Honduras. It is common and widely distributed in the highlands of Guatemala and southern Mexico. The species has been collected at elevations ranging from 1500 to 2500 m.

GUATEMALA: Baja Verapaz: km 4.1 Chilasco Rd., 4.VI.1993, JMC (JMCC) 1; 6.5 km W Chilasco, 1600 m, 22.V.1991, R Anderson (CMNC) 6; 6.5 km W Chilasco, 19.VI.1993, 1800 m, JMC (JMCC) 2; 7.8 km W Chilasco, 1700 m, 24.V.1991, H & A Howden (CMNC) 2; 8.6 km W Chilasco, 1500 m, 24.V.1991, R Anderson (CMNC) 3; 8 km S Purulhá, 1600 m, 25 & 29.V.1991, H & A Howden (CMNC) 2; 127.6 km S Purulhá, 1500 m, 21.V.1991, R Anderson (CMNC) 1; border of departments of Chimaltenango and Sololá, near Los Robles, 6000 ft, 12.IX.1965, JMC (JMCC) 1. Guatemala: Guatemala City, Cerro Alux, 2200 m, 9.VI.1991, R Anderson (CMNC) 1. Quezaltenango: Santa María, 18.V.1966, 5,000 ft, JMC (JMCC) 1; 2 km N Santa María, near tunnel, 5500 ft, 10.VII.1965, 25–27, VIII.1965, 24.X.1965, JMC (CNCI, JMCC) 5; Volcán de Chicabal, 2100 m, 25.VIII.1965, JMC (CNCI) 1; 5.4 km SE Zunil, 2200 m, 19.VI.1993, R Anderson (CMNC) 1. Sacatepequez: Finca Florencia, 24.VI.1993, JMC (JMCC) 1. San Marcos: 20 km. W San Marcos, 2200 m, 3.X.1965, JMC (JMCC) 2; 8 km NE San Rafael Pie de la Cuesta, 2000 m, 4.VI.1966, JMC (CNCI, JMCC) 2. Suchitepequez: 5 km S Santiago Aritlan, 1500 m, 29.VIII.1965, JMC (JMCC) 1; Zunilito, 2 km N Finca Colimas, 6000 ft, 28.IV.1966, JMC (CNCI, JMCC) 7; 10 km NE Yepocapa, 8000 ft, 29.V.1966, JMC (JMCC) 1. Zacapa: San Lorenzo, Sierra de las Minas, 1740 m, 9–17.VII.1986, JMC (CNCI) 17; same locality, 7.VII.1986, L LeSage (CNCI) 1; same locality, 17–18.VI.1993, JMC (CNCI, JMCC) 7; 3 km NE San Lorenzo, Sierra de las Minas, 1800 m, 6.VII.1986, JMC (CNCI) 7; 5–8 km N San Lorenzo, 1900–2000 m, 10.VI.1993, H & A Howden (CMNC) 1; 5 mi N San Lorenzo, 12.VII.1986, JMC (JMCC) 3; 6 km N Lorenzo, 17.VI.1983, 6500 ft, JMC (CNCI, JMCC) 6; 8 km NE San Lorenzo, 2100 m, 18.VII.1986, JMC (CNCI, JMCC) 3; 8 km N San Lorenzo, 10.VI.1993, 6700 ft, JMC (CNCI, JMCC) 11.
Figures 25–28. Apicale of aedeagus of species of *Charisius*: left, ventral view; right, lateral view 25 *C. granulatus* 26 *C. subalatus* 27 *C. howdenorum*; 28 *C. punctatus*. 
HONDURAS: Francisco Morazán: 30 km E Tegucigalpa, Cerro Uyuca, 1800 m, 19.V.1994, H & A Howden (CMNC) 3; La Tigra Nat. Pk., NE Tegucigalpa, 1900 m, 4.VI.1994, H & A Howden (CMNC) 2; 10 km W Zamorano, Cerro Uyuca, 1950 m, 18.VIII.-2.IX.1994, S & J Peck (CMNC) 2.


Remarks. *Charisius zunilensis* was previously known from only a few specimens collected on the Cerro Zunil near Quetzaltenango, Guatemala and *C. interstitialis* was known only from a few specimens collected at Jalapa, Veracruz, Mexico. In my previous revision of the genus (1965), I suggested that the two species could by synonyms, but delayed placing one of them in synonymy until additional material was available. Based on the new records cited below, there is little doubt that only one species is at hand.

There is considerable variation in the development of the microsculpture on the head and pronotum of this species ranging from almost completely lacking to moderately coarsely and densely granulate, and in the density and coarseness of punctation between the eyes and on the center of the pronotum. However, all degrees of variation can be found in specimens from throughout the range so there is no justification for recognizing more than one species. Most adults of this species were collected by beating dead leaves, particularly of oak trees and coffee shade trees.

8. *Charisius howdenorum* sp. n.
http://zoobank.org/771CBAF4-8CED-41A2-B9FD-62783030C62D
http://species-id.net/wiki/Charisius_howdenorum
Figs 10, 19, 23, 27

Description. Dark reddish-brown to dark brown (Fig. 10); antennae and legs slightly paler than body; elytra without markings. Length 6.5–8.6 mm.

Head moderately coarsely, densely, evenly punctate on vertex; punctures separated by average distance less than diameter of a puncture. Eyes moderate in size, mean OI of 10 specimens 43.9 (range 41–47). Pronotum distinctly wider than long, mean PI of 10 specimens 82.6, ranging from 77 to 86; surface with microsculpture moderately coarse, granulate, only slightly shining; punctures moderately coarse, moderately dense, separated on center of disc by average distance equal to or slightly greater than diameter of a puncture, punctures finer, distinctly sparser on sides; sides straight or slightly sinuate on basal two-thirds, then evenly, convexly narrowed to apex; con-
vex, widest near middle then evenly narrowed to base and apex; disc often faintly impressed along midline. Prosternum and hypomeron moderately sparsely, coarsely, irregularly punctate; punctures separated by distance greater than diameter of a puncture. Metaventrite finely, moderately densely punctate medially in male; punctures becoming coarser approaching sides; finely and sparsely punctate medially in female. Abdomen with fine, scattered punctures on basal three ventrites, last two visible ventrites more coarsely and slightly more densely punctate. Elytra (Fig. 19) with striae unimpressed; strial interstices flat.

Male. Anterior tibia not widened on inner side. Fifth ventrite unimpressed medially. Lobes of eighth sternum (Fig. 23) broad, straight, apices evenly convex; viewed laterally, lobes slightly deflexed apically. Lobes of ninth sternum short, moderately broad, with apices broadly convex. Aedeagus with apicale (Fig. 27) moderately narrow; sides narrowed from base to near middle then subparallel to evenly convex apex; viewed laterally, apicale straight, basale 3.2–3.3 times longer than apicale.

Female. Elytra with sutural margin and apex entire.

**Types.** Holotype, male, with labels as follows: MEX., Tinijapa, 8 km NE San Cristobal, Chis., V.26.1969, J. M. Campbell/ HOLOTYPE _, Charisius howdenorum, desig. 2013, J.M.Campbell. The specimen is deposited in the CNCI.

Paratypes, 23 in the CNCI the CMNC and JMCC.

MEXICO: Chiapas: 5 mi W San Cristobal, Chis., V.26.1969, JMC (CNCI) 1; 8 mi NE San Cristobal, 26–28.VI.1969, JMC (CNCI, JMCC) 5; 11 mi NE San Cristobal, 18.V.1969, HF Howden (CMNC) 1; Tinijapa, 8 mi NE San Cristobal, 26.V.1969 JMC (CNCI, JMCC) 11; nr. Tinijapa, 8 km NE San Cristobal, 18.V.1969, JMC (CMNC, JMCC) 6.

**Etymology.** This species is named in honor of Dr. Henry and Anne Howden, Canadian Museum of Nature, Alymer, Quebec, Canada who have facilitated several of my trips to Mexico and Guatemala; and have collected many of the specimens described in this paper.

**Remarks.** Adults of *C. howdenorum* are similar to those of *C. zunilensis*, but differ most noticeably in having the elytral striae unimpressed between the strial punctures (Fig. 19). They also differ in being somewhat darker in color, in having the pronotum less shining with the microsculpture distinctly more coarsely and densely granulate, and, in the males, the metaventrite is finely, but distinctly more densely punctate medially. There is little difference between the male terminalia of the two species.

**Salvini Group**

Species of this group may be easily distinguished by having the wings fully developed, in having at least the apex of the elytra piceous to black, in being moderately large in size (length 7.9–10.9 mm), in having the male anterior tibiae distinctly widened on the inner margin, in having the male fifth ventral segment deeply impressed medially, and the short apicale of the aedeagus (Fig. 28).
The species group contains two species, one of which is described as new. *Charisius salvini* differs from *C. punctatus* and all other species of the genus in having only the two basal segments of the male protarsus lobed ventrally.

9. *Charisius salvini* Champion

http://species-id.net/wiki/Charisius_salvini

Figs 11, 16

*Charisius salvini* Champion (1888: p. 423, pl. 19, fig. 15); Campbell (1965: 52, Figs 5, 14).

**Type.** Lectotype, male, Calderas, Guatemala (Campbell 1965: 52). The specimen is in the BMNH.

**Distribution and records.** *Charisius salvini* was previously known from the highlands of southeastern and southcentral Guatemala. The species is now known to be widespread in Guatemala and is reported from El Salvador, Honduras and Nicaragua at elevations between 1340 and 1830 meters in elevation.

**EL SALVADOR:** Cerro Verde, 2000 m, 1.V. and 4.V.1971, HF Howden (CMNC, JMCC) 3.


**NICARAGUA:** Cerro Chimbórazo, 13°02‘N, 85°56’W, 20.XI.1971, H Stockwell (CNCI) 1.

**Remarks.** Specimens of *C. salvini* may be distinguished from those of all other species of *Charisius* by being uniformly reddish-brown dorsally with only the extreme apex of the elytra piceous to black and in having only the basal two segments of the male protarsus lobed ventrally. They also differ from all other species except the following in having the pronotum coarsely, moderately densely, evenly punctate and by the very distinctive shape of the male eighth sternal lobes and aedeagus (see Campbell 1965, Fig. 5).
I have provisionally assigned one male from Nicaragua to this species. It agrees well with all the characters of *C. salvini* except the male anterior tibiae are slightly sinuate on the inner margin and it has a piceous, transverse band across the apical third of the elytra. This record extends the known range of species of *Charisius* south to Nicaragua.

Most specimens were collected by beating clumps of dead branches and leaves in shrubs and low hanging trees. Adults were collected from coffee shade trees near the upper limits of coffee growing zones.

10. *Charisius punctatus* sp. n.

http://zoobank.org/27045083-198A-4614-B95A-7786EDDA7842
http://species-id.net/wiki/Charisius_punctatus
Figs 12, 24, 28

**Description.** Body reddish-brown; elytra testaceus with each elytron having piceous markings as follows (Fig. 12): a small circle near middle, a narrow, crescent-shaped band at apical fourth and extreme apex piceous to black (Fig. 12). Length 7.0–10.9 mm.

Head moderately coarsely punctate on vertex; punctures separated by distance subequal to diameter of a puncture. Eyes moderately small, mean OI of 5 males 32.7 (range 30–35) and of five females 38.6 (range 37–40). Pronotum distinctly wider than long, mean PI of 11 specimens 84.6 (range 83 to 88); surface smooth, shining; punctures coarse, moderately densely, evenly distributed, separated by average distance distinctly greater than diameter of a puncture; sides sinuate near base, widest near middle than evenly convex to just before apex; disc evenly convex in cross section. Prosternum and hypomeron coarsely, densely punctate; punctures separated by distance less than diameter of a puncture. Metaventrite finely, sparsely punctate medially, punctures becoming coarser and denser approaching sides. Ventrites with punctures moderately fine, sparsely distributed; last two visible ventrites more coarsely and densely punctate. Elytra with striae moderately deeply, evenly impressed throughout; strial interstices moderately convex.

Male. Anterior tibia triangularly widened on inner side near middle. Fifth ventrite broadly, deeply, triangularly impressed medially. Lobes of eighth sternum (Fig. 24) broad, with apical third broadly expanded, apices obliquely truncate; viewed laterally, distinctly deflexed apically. Lobes of ninth sternum short, moderately broad, with apices evenly convex. Aedeagus with apicale (Fig. 28) short, moderately narrow; sides narrowed from base to narrowly, evenly convex apex, slightly constricted medially; viewed laterally, apicale strongly curved dorsally; basale 7.1–7.9 times longer than apicale.

Female. Elytra with sutural margin and apex entire.

**Type.** Holotype, male, with labels as follows: GUAT. Depto. Zacapa, San Lorenzo, 1740 m, Sierra de las Minas, 18.VII.1986, J.M.Campbell/ beating mixed vegetation in pine-oak forest/ HOLOTYPE _. Charisius punctatus, desig. 2013, J.M. Campbell. The specimen is deposited in the CNCI.

Paratypes, 44 in the CNCI, CMNC, JMCC, and the JEWC.
New species and records of *Charisius* Champion from Mexico and Central America...

**Distribution and records.** This species is known only from Guatemala between 1400 and 1740 meters in elevation.


**Etymology.** The species name punctatus refers to the coarse punctation of the pronotum.

**Remarks.** Adults of *C. punctatus* are very similar to those of *C. salvini*, but may be easily distinguished by the additional piceous markings on the elytra (Fig. 9). Males may also be distinguished by having the basal four segments of the anterior tarsi lobed ventrally, by having a triangular expansion on the inner margin of the anterior tibia; by the broader and deeper median impression of the fifth abdominal ventrite, and by the more broadly expanded apical portion of the eighth sternal lobes (Fig. 24) which are obliquely truncate.

The species has been collected beating mixed dead and herbaceous vegetation in a pine-oak forest.

**Key to species of Charisius Champion**

1. Wings reduced, flightless species, metaventrite short (Fig. 18) ....................2
   - Wings fully developed, metaventrite normal in length (Fig. 17) ..................3
2. Elytra with transverse yellow bands; apex of female elytron emarginate (Figs 7, 20) .................................................................5. *C. apterus* sp. n.
   - Elytra uniform in color (Fig. 8), apex of elytra in female entire .................6. *C. subalatus* (Champion)
3. Elytra with distinct, yellow, transverse markings (Figs 1–6) ......................4
   - Elytra uniform in color or with piceous to black markings (Figs 9–12) ......8
4. Pronotum with surface microsculpture densely, coarsely granulate, opaque; punctures coarse, moderately densely distributed (Fig. 15) ..................
   - Pronotum with surface microsculpture fine, visible only under high magnification (64×), shining; punctures fine, sparsely distributed (Figs 13, 14) .....5
5. Elytra with basal yellow band greatly expanded, basal band interrupted only by elytral suture (Figs 1, 5–6) .................................6
   - Elytra with basal yellow band reduced to oval spot or absent, not reaching suture (Figs 2, 3, 5) .........................................................7
6 Male eighth sternal lobes narrow (see Campbell 1965, p. 55), evenly curved medially; known from south of the Isthmus of Tehuantepec in Mexico... 1. *C. fasciatus* Champion (in part)

– Male eighth sternal lobes broad, (see Campbell 1965, p. 55) only slightly curved medially; known from north of the Isthmus of Tehuantepec of Mexico...

3. *C. mexicanus* Campbell

7 Basal yellow spot extending from sides to middle of each elytron (Fig. 4); sides of pronotum parallel for basal half... 2. *C. picturatus* Champion

– Basal yellow spot of elytra either absent (Fig. 2) or represented by a large, oval spot placed in- middle of each elytral disc (Fig. 3)... 1. *C. fasciatus* (in part)

8 Elytra with at least apex piceous to black (Figs 9, 11); last visible sternite of male deeply impressed medially ................................................................. 9

– Elytra uniform in color (Figs 9, 10) ; last visible sternite of male not im-

9 pressed ........................................................................ 10

9 Elytra with only apex piceous to black (Fig. 11); male protarsus with only bas-

sal two segments lobed ventrally; male anterior tibiae at most slightly sinuate on internal margin ................................................................. 9. *C. salvini* Champion

– Each elytron with a median piceous spot and a narrow, crescent-shaped band at apical fourth (Fig. 12); male protarsus with basal four segments lobed ventrally; male anterior tibiae with distinct, triangular swelling on inner margin.......................... 10. *C. punctatus* sp. n.

10 Elytra with striae distinctly impressed between strial punctures from base to apex (Fig. 9)................................. 7. *C. zunilensis* Champion

– Elytra with striae completely unimpressed between strial punctures (Fig. 19)...

Conclusions

Species of *Charisius* are widely distributed at moderately high to high elevations from central Mexico south to Nicaragua. Elevations have been recorded from 1340 meters to 2800 meters. Species of the genus have several characters normally associated with higher elevations. All species of the genus are glabrous dorsally and two of the species (*C. apterus* and *C. subalatus*) have the flight wings reduced and are flightless.

The close similarity of the male eighth sternal lobes of *C. subalatus* with the species of the fasciatus group (compare Figs 21 and 22) are additional justification for placing *Narses* in synonymy with *Charisius* as previously suggested by Champion (1888, p. 423).

The species of the genus were previously unknown from south of Guatemala, however, additional collecting has extended their known range south to Nicaragua.
Acknowledgements

I would like to thank Lee Hermann, (AMNH), DH Kavanaugh (CASC), Robert Anderson, (CMNC). Patrice Bouchard and Anthony Davies (CNCI); Warren Steiner, (USNM), J.E. Wappes, (JEWC), EG Riley (EGRC), and Mike Ivie (UMON), for the loan of specimens used in this study. I also thank George Ball, University of Alberta and H. F. Howden for their gifts of specimens to the Canadian National Collection of Insects (CNCI), the Canadian Museum of Nature or to my personal collection (JMCC).

Much of the material listed in this paper was collected during the time I was employed by the University of Kentucky on a two year contract with the Asociacion Nacional de Cafe of Guatemala and subsequent collecting trips while employed at the CNC. For brevity, I have used only my initials in the records of each species to indicate the material collected by me during these periods. I gratefully acknowledge the assistance of Jack Schuster, Universidad del Valle, Guatemala City and to the CanaColl Foundation, Ottawa for logistic and financial support for the Canadian National Collection’s expedition to Guatemala in 1986. The manuscript was reviewed by Patrice Bouchard and to two anonymous reviewers whose comments are greatly appreciated. I would especially like to thank Mr. Anthony Davies for his generous and much needed assistance in preparing the photographs.

References


An unusual suite of sexual characters in three new species of *Hymenorus* (Coleoptera, Tenebrionidae, Alleculinae) from Guatemala and Mexico

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† http://zoobank.org/A0F2D6F3-B44B-4ED2-9B1E-3BDC39ED8C50

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Academic editor: P. Bouchard | Received 20 November 2013 | Accepted 12 March 2014 | Published 12 June 2014

http://zoobank.org/B6BEFE0B-5A97-4049-93B5-7D358EC5B99C


Abstract

Two species, *Hymenorus bifurcatus*, and *H. excavatus* are described as new from Guatemala and the new species *H. balli* from both the state of Chiapas in southern Mexico and Guatemala. These three species are unique among the species of *Hymenorus* Mulsant, 1851 in the unusual and highly modified fifth ventrites of the male and the modified shape of the female ninth tergites. The unusual sexual characters of the males and females are illustrated with photographs. The usage of the generic names *Hymenorus* Mulsant versus *Hymenophorus* Mulsant is discussed.

Keywords

Coleoptera, Tenebrionidae, Alleculinae, *Hymenophorus, Hymenorus*, Guatemala, Chiapas, taxonomy, new species

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Introduction

The genus *Hymenorus* Mulsant 1851 is the largest, but least studied genus of Alleculinae from North and Central America. The species of Mexico and Central America were studied by Champion (1888, 1893) who included 39 species of which all but two were described as new. Fall (1931) reviewed the species of Canada, Baja California and the United States including 100 species; Marshall (1970) transferred two species from the Southwestern United States to the genus *Alethia* Champion & Campbell described one new species from California (1982), two species from Panama (1962), and 16 species from the West Indies (1971). These are the only recent studies of the New World species of the genus. I am currently revising the species of Alleculinae of Costa Rica which, when published, will add an additional eight species to the Central American fauna. In going through my collection for this study, three highly unusual species were discovered from Guatemala and Chiapas in southern Mexico. None of these resemble any of the species previously known from Central America or Mexico.

Species of *Hymenorus* may be readily distinguished from those of other genera of Alleculinae occurring in Mexico and Central America by the generic key provided by Champion (1888) in the Biologia Centrali-Americana. In North and Central America the genus has never been adequately described. Instead, any species of Alleculinae with unusual or unique characters have been removed to other genera. The remaining species are left in *Hymenorus*. In southern Mexico and Guatemala any small (less than 10 mm), light to dark brown, pubescent Alleculinae with at least some of the tarsal segments lobed that have the apical segment of the maxillary palpus secuiiform and the antennae moderately elongate (antennomeres four through ten from just over one to approximately two times longer than wide) have been assigned to *Hymenorus*.

Methods

All measurements were made with an ocular micrometer mounted in a Leitz stereoscopic microscope. Measurements were made of the overall length from the anterior margin of the labrum to the apex of the elytra; the ocular index (OI) of both males and females (the distance between the eyes dorsally divided by the greatest distance across the eyes multiplied by 100); and the lengths of the third and fourth antennomeres and the length and width of the tenth antennomere. Measurements of the tenth antennomere are used for comparison because their length is less variable than those of the ultimate segment. The pronotal index (PI) is a measurement of the length of the pronotum divided by the greatest width of the pronotum multiplied by 100. The photographs were made with a Leica Digital DC500 Imaging Workstation using Zerene Stacker software and retouched with Adobe Photoshop software.
The terminology used in this paper is the same as that recommended by Lawrence et al (2010). All material included in this paper were collected by the author except for the long series of *H. balli* from Chiapas collected by George Ball and two specimens of *H. excavatus* collected by WB. Warner (WBWC). All holotypes are deposited in the Canadian National Collection of Insects, Ottawa (CNCI). Paratypes are deposited in the CNCI, my personal collection, JM Campbell, Ottawa, Canada (JMCC) and the WB Warner collection, Chandler, Arizona, USA (WBWC).

**Systematics**

Usage of the generic name *Hymenorus* Mulsant and the name *Hymenophorus* Mulsant has been confused. Mulsant (1851) described *Hymenophorus* with the type species the new species *Hymenophorus doublieri*. In the emendanda section of a later paper (1852, p. 188) Mulsant changed the name to *Hymenorus* based on his belief that the name *Hymenophorus* was a junior homonym of *Hymenophora* Laporte (1843) [Hemiptera]. Mulsant (1856b, p. 20) later added a second new species to the genus, *Hymenorus rugicollis*. Subsequent papers, both from the Nearctic and Palearctic Regions have consistently used the name *Hymenorus* until recent papers by Novák (2006, 2007) and the publication of the catalogue of the Palaearctic Coleoptera (Novák and Petterrsson 2008). In recent checklists or catalogues of regions of the Palaearctic fauna, following the publication of this catalogue, the name *Hymenopohorus* has been adopted. Nearctic workers have used the name *Hymenorus* consistently since the genus was first recorded from North America (LeConte 1866) and the name *Hymenorus* has continued to be used by North American workers. The type species of both names is *H. doublieri* Mulsant, 1851.

In this paper I have followed the usage adopted by Bouyon (2011) who follows the International Code of Zoological Nomenclature (ICZ, 1999, Article 35.2.3.1) in recognizing the generic name *Hymenorus* as the valid name. Because the emendation of *Hymenophorus* to *Hymenorus* is in prevailing usage and attributed to the original author and date, it is deemed to be a justified emendation (ICZ, 1999 Article 33.2.3.1) and the name thus corrected retains the authorship and date of the original spelling (ICZ, 1999, Article 33.2.2). *Hymenorus* continues to be consistently used in all recent publications of the New World species of the genus.

*Hymenorus Mulsant, 1851*  
http://species-id.net/wiki/Hymenorus

**Hymenorus** Mulsant, 1852, p. 188 [emendation]; Mulsant (1856a: 17, 33); Jacquelin du Val (1861: 344, 356); LeConte (1866: 137); LeConte and Horn (1883: 390); Champion (1888: 386, 424); Seidlitz (1896: 49); Casey (1891: 72, 83); Blatchley (1910: 1271, 1273); Reitter (1911: 351, 352); Fall (1931: 161); Chagnon and Robert (1962: 325); Campbell (1962: 92); Arnett (1962: 703); Hatch (1965: 183); Campbell (1971: 68); Campbell (1982: 31; Campbell (1984: 296); Downie and Arnett (1996:1099); Aalbu et al. (2002, 480, 499); Steiner (2004: 739); Althoff et al. (2005: 905); Bouyon (2011: 191); Kanda (2013: 587).

**Description.** A full description of the New World species of *Hymenorus* is not possible at this time pending modern revisions of the more than 170 North and Central American species of the genus. However, the following brief description will readily distinguish these three species from all other New World species of *Hymenorus*.

Body narrowly elongate-oval (Fig. 1); length 7.5–10.0 mm. Eyes large, moderately separated dorsally; OI of males varying from 18 to 27, females slightly more widely separated, OI varying from 18–33. Antennae narrowly elongate, antennomeres four through ten narrowly elongate, approximately two times longer than wide. Pronotum (Fig. 2) wider than long, width at base slightly narrower than width of base of elytra; PI ranging from 62 to 78; disc with fine, dense microsculpture between punctures; punctures coarse, dense, narrowly separated, evenly distributed over disc; each puncture obliquely impressed. Metaventrite moderately densely punctate medially, punctures becoming sparser laterally; without median patches of dense, elongate setae. Like all *Hymenorus* species, the third and fourth segments of the pro- and mesotarsi and the penultimate segment of the metatarsi have a distinct membranous lobe on the ventral margins.

Male. *Hymenorus excavatus* and *H. bifurcatus* have the second segment of the anterior tarsus with a small, rudimentary lobe and a densely pubescent pad on the venter of the basal segment; only the third and fourth segments of the protarsi are lobed in *H. balli*. The anterior tarsal claws of the three species each have at least 20 teeth (Fig. 3). The fifth abdominal ventrite is highly modified, in one species (*H. excavatus*) (Figs 10, 11), the ventrite is deeply, triangularly excavate from the apical margin to the anterior third; in *H. balli* (Figs 4–5) and *H. bifurcatus* (Figs 7–8) the ventrites have a distinct, bifurcate process projecting ventrally from the middle of the disc. Lobes of eighth sternite of each species are highly modified (Figs 19–21), unlike any other species of the genus.

Female. The ninth tergite (Figs 6, 9, 12) of each species is highly modified and completely unlike any other known species of the genus. In most species of the genus the apical margin of the tergite is evenly convex and the length of the tergite varies from short to elongate.

**Remarks.** I have not provided a key to distinguish these species. Other than sexual characters they are very similar. The modifications of the male fifth abdominal ventrite and lobes of the eighth sternite and the shape of the female ninth tergite will readily distinguish the species. In most series a few of the sexual characters are readily visible without dissections.
Hymenorus balli sp. n.
http://zoobank.org/29D2A338-1174-4BD0-9152-E8D0ADF06A1F
http://species-id.net/wiki/Hymenorus_balli
Figs 1, 4–6, 13–14, 19

Description. Body light to dark brown; legs light brown to testaceous; narrowly elongate-oval (Fig. 1). Length 7.5–10.0 mm. Setae short, subrecumbent; uniformly reddish-brown. Eyes moderately separated dorsally (OI of male 19–25 and of female 25–33). Vertex coarsely, densely, punctate; punctures separated by distance approximately half diameter of a puncture. Antennae narrowly elongate, antennomeres 3–11 slightly and evenly widened from base to apex. Apex of sixth antennomere extending posteriad to base of pronotum; antennomeres 3 and 4 subequal in length; tenth antennomere approximately two times longer than wide.

Pronotum distinctly wider than long, PI index 62–71; sides evenly, gradually narrowed from base to apical fourth then evenly curved to continuously curved apical margin; basal angles rectangular; base slightly, but distinctly narrower than base of elytra; basal margin slightly bisinuate; basal foveae small, shallowly impressed, separated by broad, shallow, median impression; midline unimpressed; sides at basal angles slightly reflexed. Disc with fine, dense microsculpture between punctures; punctures coarse, dense, narrowly separated, evenly distributed over disc; each puncture obliquely impressed.

Hypomeron finely, densely, evenly punctate to lateral margins. Basal three abdominal ventrites moderately densely, evenly punctate; punctures each with a short, recumbent seta. Elytra with striae evenly, shallowly impressed; strial punctures circular, almost contiguous along striae; strial interstices slightly convex; interstices moderately densely punctate; punctures randomly distributed, approximately 2 or 3 punctures wide across interval. Metatarsus with basal segment subequal in length to segments 2–4 combined.

Male. Second segment of anterior tarsus without rudimentary lobe on ventral margin. Tibiae not modified. Posterior femora with ventral margin flattened, glabrous, with outer margin of glabrous area distinctly carinate. Anterior tarsal claws each with more than 20 teeth. Metaventrite finely, densely punctate medially; punctures becoming coarser, sparser laterally; median punctures each bearing an elongate, posteriorly directed seta. Fifth abdominal ventrite highly modified (see Figs 4, 5) with large, broad, bifurcate process projecting ventrally from middle of disc; bifurcate process densely setate on outer margins; disc broadly, moderately deeply impressed behind bifurcate process; apical margin of ventrite broadly truncate. Lobes of eighth sternite (Fig. 19) highly modified; narrowed medially with apex broadly widened, inner anterior angle of apical enlargement triangularly narrowed; base of lobes with a moderately long, less heavily sclerotized lobe projecting medially. Lobes of ninth sternite (Fig. 19) short, strongly curved medially, apex broadly rounded. Apicale (Figs 15–16) moderately broad with sides slightly narrowed from base to broadly truncate apex; penis narrowly elongate with sides evenly narrowed from base to apex.
Figure 1–6. 1 dorsal habitus of *Hymenorus balli* 2 head and pronotum of *H. excavatus* 3 protarsal claws of *H. excavatus* 4 and 5 male fifth ventrite of *H. balli* 4 ventral view 5 lateral oblique view 6 dorsal view of female ninth tergite of *H. balli*. 
Female. Anterior tarsus without rudimentary lobes or setaceous pads on basal two segments. Anterior tarsal claws each with 9–10 teeth. Metaventrite moderately coarsely punctate medially; punctures becoming slightly coarser, sparser laterally; median punctures each bearing a short, appressed seta. Apical portion of fifth ventrite broadly impressed. Ninth tergite (Fig. 6) with apical margin broadly, evenly convex; with narrow, evenly sclerotized band completely around sides and apex of tergite.

**Type.** Holotype, male, with labels as follows: “GUAT, 22 km S San Marcos, 5000’, IX.3–1965, JM.Campbell/ HOLOTYPE ♂ Hymenorus balli, desig. 2013, JM Campbell”. The holotype is deposited in the CNCI.

Paratypes. Males 12, females 19.


**Etymology.** This species is named in honor of George Ball, University of Alberta, Edmonton in recognition of his many contributions to the study of Coleoptera (particularly Carabidae). Dr. Ball collected a long series of this species from Chiapas, the only record of any of the three species described in this paper from Mexico.

**Remarks.** The modifications of the male fifth ventrite (Figs 4, 5) are the most unusual of any species of Alleculinae known to me from the New World. In addition to the bizarre modifications of the fifth ventrite, the shape of the male lobes of the eighth and ninth sternites (Fig. 19) and the shape of the apicale (Figs 13, 14) of the aedeagus will readily distinguish the species. The lobe attached to the base of the inner side of each lobe of the eighth sternite is unknown from any other species of the genus. Females are easily distinguished by examination of the eighth tergite (compare Figs 6, 9, 12).

This species was collected by beating arboreal bromeliads and from under moss and bromeliads on tree trunks.

**Hymenorus bifurcatus sp. n.**

http://species-id.net/wiki/Hymenorus_bifurcatus
Figs 7–9, 15, 16, 20

**Description.** This species is almost indistinguishable from *H. balli* and *H. excavatus* based on non-sexual characters. Only the slight variations in non-sexual characters are described below; full descriptions are given for the male and female characters.

Length 7.9–8.8 mm. Eyes moderately separated dorsally; OI 23 to 27 and of female 28 to 31. PI 72 to 78; basal fovea of pronotum slightly more elongate than in *H.*
Figure 7–12. 7 and 8 male fifth ventrite of *H. bifurcatus* 7 ventral view 8 lateral oblique view 9 dorsal view of female ninth tergite of *H. bifurcatus* 10 dorsal view of female ninth tergite of *H. bifurcatus* 11 and 12 male fifth ventrite of *H. excavatus* 11 ventral view 12 lateral oblique view.
An unusual suite of sexual characters in three new species of Hymenorus...

balli and H. excavatus, extending from base to near middle of disc. Pronotal punctures angularly impressed throughout.

Metatarsus with basal segment subequal to or slightly longer than segments 2–4 combined.

Male. Anterior tarsus with rudimentary lobe on venter of second segment and pubescent pad on venter of first segment. Posterior femora evenly convex on ventral margin; without carina on outer side of ventral margin. Anterior tarsal claws each with more than 20 teeth (Fig. 3). Fifth ventrite highly modified (see Figs 7, 8), with small, evenly curved process projecting ventrally from middle of disc; apex of process shallowly bifurcate; disc broadly, shallowly impressed behind median process; apical margin broadly convex. Lobes of eighth sternite (Fig. 20) broad, strongly sinuate and curved medially; apex of lobes narrowly rounded; inner sides of lobes broadly, deeply, concavely impressed. Lobes of ninth sternite (Fig. 20) short, narrow, with apical margin moderately narrowly rounded. Apicale (Figs 15, 16) triangular with sides evenly narrowed from base to narrowly rounded apex; penis as in H. balli.

Female. Anterior tarsal claws each with 7–10 teeth. Apical portion of fifth abdominal ventrite narrowly impressed. Ninth tergite (Fig. 9) broad, almost arrowhead shaped with sides widened from truncate apical margin, then abruptly narrowed to base.

Types. Holotype, male, with labels as follows: GUAT, Border of depts. of Sololá and Chimaltenango, nr. Los Robles, IX-12–1965, 6000’, JM Campbell/ HOLO-TYPE, ♂ Hymenorus bifurcatus, desig. 2013, JM.Campbell The specimen is deposited in the CNCI.

Paratypes. Males 16, females, 17.


Etymology. This species is named bifurcatus in recognition of the small, bifurcate process near the middle of the male fifth ventrite.

Remarks. This species is almost identical to the sympatric species H. balli in all external characters except for the lack of a carina on the venter of the posterior femora of the males. The process on the male fifth visible ventrite (Figs 7–8) is somewhat similar to that of H. balli except that it is much smaller and the apical margin of the bifurcate lobes is narrow and shallowly impressed. The lobes of the male eighth sternite (Fig. 20) are very different from those of H. balli; each lobe is broad, spoon-shaped with the apical margin narrowly convex. The deep, concave impression on the inner side of each lobe is unique within the genus. Females may be distinguished by the very different shape of the ninth tergite (compare Figs 6, 9, and 12).

This species was collected by beating dead leaves of recently cut trees, by beating composit shrubs, and from an arboreal bromeliad.
Figure 13–18. 13–14 ventral (left) and lateral (right) views of aedeagus of *H. balli* 15–16 ventral (left) and lateral (right) views of aedeagus of *H. bifurcatus* 17–18 ventral (left) and lateral (right) views of aedeagus of *H. excavatus*. 
**Hymenorus excavatus** sp. n.

http://zoobank.org/268BC875-B177-4E86-A494-2E65EEBC9B3A

http://species-id.net/wiki/Hymenorus_excavatus

Figs 2–3, 10–12, 17–18, 21

Description. This species is almost indistinguishable from *H. balli* and *H. bifurcatus* based on non-sexual characters. Only the slight variations in non-sexual characters are described below; full descriptions are given for the male and female characters.

Length 8.0–9.7 mm. Eyes moderately separated (OI of male 18 to 24 and of female 18 to 28).

PI index 66 to 73; sides narrowed from base to apical fourth then evenly curved to slightly concave to truncate anterior margin; median basal fovea more elongate than in *H. balli*, extending from base to near middle of disc.

Elytra with punctures of intervals slightly denser than in *H. balli* and *H. bifurcatus* with 3 or 4 punctures across each interval. Metatarsus with basal segment distinctly longer than segments 2–4 combined.

Male: Venter of anterior tarsi with rudimentary lobes on apex of second segment and densely pubescent pad on basal segment. Posterior femora evenly convex on ventral margin, without carina on outer side. Anterior tarsal claws each with more than 20 teeth. Fifth abdominal ventrite highly modified (Figs 11, 12), broadly, deeply, triangularly impressed from apical margin to basal third; sides of impression sharply carinate. Lobes of eighth sternite (Fig. 21) broadly spoon-shaped, curved medially; outer sides evenly convex, apex of lobes narrowly triangular; inner side of lobes each with short tooth near base. Lobes of ninth sternite (Fig. 21) very short, not extending beyond base of lobes of eighth sternite. Apicale (Figs 17, 18) broad, with sides slightly concave medially; apex truncate; penis narrowly triangular.

Female: Anterior tarsal claws each with 7–10 teeth. Apical third of fifth abdominal ventrite broadly, shallowly, concavely impressed; apical margin broadly convex. Ninth tergite (Fig. 12) with apical margin broadly convex; laterally, slightly truncate mediately; heavily sclerotized area covering all of tergite except small, triangular, membranous section mediately at base.

Types. Holotype, male, with labels as follows: 22 km S San Marcos, 5000’, IX-3–1965, JM Campbell/ HOLOTYPE ♂, Hymenorus excavatus, desig. 2013, JM.Campbell The specimen is deposited in the CNCI.

Paratypes: 13 males, 11 females.


Etymology. This species is named excavatus in recognition of the deeply excavate fifth visible male ventrite.
Remarks. *Hymenorus excavatus* is similar in external appearance to the two preceding species. Males may be readily identified by the unique sexual modifications of the male fifth abdominal ventrite (Figs 10–11), the eighth and ninth sternites (Fig. 21) and the aedeagus (Figs 17–18). Females are difficult to distinguish externally, but can easily be distinguished by the unique shape (somewhat like an arrowhead) of the ninth tergite (compare Figs 6, 9, and 12). Females can be provisionally distinguished from those of *H. balli* by the shallower and broader impression of the fifth abdominal ventrite.

Discussion

These three species are extremely similar to each other except for the very different sexual modifications of the male fifth ventrite and terminalia and the shape of the female ninth tergite (Figs 6, 9, 12). In addition to the unique modifications of the male sexual characters (particularly the modification of the male fifth abdominal ventrite), all three species may be readily distinguished from all other species of *Hymenorus* from southern Mexico and Central America by the combination of their relatively larger size (7.5–10 mm), by having in excess of 20 teeth on the male anterior tarsal claws (Fig. 3), by the more narrowly elongate shape of the body (Figs 1, 2) (most *Hymenorus* species are more broadly elongate). The males of *H. bifurcatus* and *H. excavatus* each have a rudimentary tarsal lobe on the second segment and a densely pubescent pad on the venter of the basal tarsal segment of the anterior tarsi (most *Hymenorus* have only the third and fourth anterior tarsal segments lobed ventrally with the basal two segments not modified); the lobes of the eighth sternite of the male of all three species are glabrous (most *Hymenorus* have fine setae on the apex).
A number of species of *Hymenorus* from both North and Central America have an unusual modification of the male posterior femora in which the ventral margin is glabrous, either flattened or concavely impressed with the outer margin distinctly carinate. All of the species having this character also have the male anterior tarsal claws with at least 20 teeth (this character is shared with a few other species having the ventral margin evenly convex and pubescent). Of the three species described as new, *H. balli* and *H. excavatus* both have the male posterior femora modified, but *H. bifurcatus* has the ventral margin evenly convex and pubescent.

The fact that these three species are sympatric in distribution and so similar in non sexual characters and so dissimilar in sexual characters brings to question how and for what selective advantage did these species evolve in such close proximity and what is the purpose of the extreme modifications of the sexual characters?

**Acknowledgements**

Special thanks to Anthony Davies for assisting in the preparation of the photographic images and arranging the plates. I also thank Patrice Bouchard and Mr. Davies for their many helpful comments during and after preparation of the manuscript. Yes Bousquet and Patrice Bouchard gave valuable advice of the proper usage of the names *Hymenorus* Mulsant versus *Hymenophorus* Mulsant. Two anonymous reviewers gave very constructive comments which significantly improved the quality of the manuscript.

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An unusual suite of sexual characters in three new species of Hymenorus...

Larvae and pupae of two North American darkling beetles (Coleoptera, Tenebrionidae, Stenochiinae), *Glyptotus cribratus* LeConte and *Cibdelis blaschkei* Mannerheim, with notes on ecological and behavioural similarities

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Academic editor: P. Bouchard  |  Received 20 December 2013  |  Accepted 4 February 2014  |  Published 12 June 2014

http://zoobank.org/412C5EF5-6C9F-4D3F-B040-4D92DFA15C80


Abstract

This study describes and illustrates the larvae and pupae of two North American darkling beetles (Coleoptera: Tenebrionidae) in the subfamily Stenochiinae, *Glyptotus cribratus* LeConte from the southeastern United States, and *Cibdelis blaschkei* Mannerheim from California. Both species inhabit forested regions where adults and larvae occur in soft rotten dry wood of dead branches on living trees or in sections recently fallen from them. Species identity was confirmed by rearing of adults and pupae and the discovery of both in pupal cells with associated exuvia. Specimen label data and notes on habitats are provided. Antipredator defense structures and behaviour are noted for larvae and pupae of both species.

Keywords

Antipredator defense, identification, immature stages, North America, pinching organs, rotten wood, saproxylic insects, urogomphi
Introduction

The Stenochiinae (Coleoptera: Tenebrionidae) are a large, diverse group of darkling beetles (Matthews et al. 2010), but even in areas with faunas considered to be well known, immature stages of many common species remain undescribed, especially the ephemeral pupae. Stenochine larvae often possess distinctive apical abdominal armature, presumed to be defensive. Known pupal structures inspire equal curiosity and provide good characters for analysis of generic relationships (Bouchard and Steiner 2004). Larvae and pupae of *Glyptotus cribratus* LeConte from the southeastern United States and *Cibdelis blaschkei* Mannerheim from California – the type-species of their respective genera – are described in this study for the first time, with the intent of contributing to characterization of features useful for future identification and studies of phylogeny. Both species inhabit forested regions where adults, larvae and pupae have been found in soft rotten dry wood of dead branches on living trees or in sections recently fallen from them. The discovery and recognition of this particular niche should facilitate collection of these and other tenebrionid larvae occupying forest habitats.

Materials and methods

Larval specimens were preserved in 80% ethanol; prior to this, some were killed either with hot water or by fumigation in ethyl acetate. Pupal specimens were similarly preserved as described earlier (Steiner 1995). Specimen label data below are given verbatim, with commas inserted for clarity, and breaks between labels are separated by a forward slash. Numbers of specimens bearing those data follow in parentheses, indicated as (L) larva, (P) pupa, or adult with associated exuvia. All specimens are deposited in the United States National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC, USA.

Systematics

*Glyptotus cribratus* LeConte

http://species-id.net/wiki/Glyptotus_cribratus

Background. A single larva from southern Florida, USA, presumed to be *G. cribratus*, was reported by St. George (1924), who provided some key characters though the specimen’s identity has remained uncertain. New associated adult and larval material, including one larva reared to an adult and another providing the first known pupal specimen (described herein), shows that the larva from St. George’s account was not that of *Glyptotus*, as discussed below. The specimen, presumably in USNM, could not be located.

Three mature larvae, found in wood products from Mexico, 1982–84, were identified as “*Glyptotus* sp.” by T. J. Spilman, but it is uncertain what material he used
Larvae and pupae of two North American darkling beetles...

...to make this determination; these larvae are considered in the present study to be *G. cribratus*, identical to specimens from USA; the species is known from southern Texas and thus its occurrence in north-eastern Mexico is feasible.

**Description of mature larva.** (Figures 1, 3–5, 9–12).

**Body.** Length 23–30 mm; elongate-cylindrical, pale yellowish-white with light brown dorsal bands at posterior edges of terga and anterior edge of prothoracic tergum; mandible apices and bases, claws of tarsunguli, and apices of urogomphi and associated processes blackish to brown, heavily sclerotized; cuticle otherwise lightly sclerotized, surfaces shining, finely rugose, with scattered fine setae; abdominal tergum VIII slightly darker yellow-brown with scattered large circular punctures.

**Head.** Prognathous, head slightly declined, globular but slightly flattened dorsoventrally. Head capsule width 3.4–3.5 mm. Epicranial stem about one fifth head capsule length; frontal arms widely V-shaped, fine and obscure. Each half of head capsule with 10–13 scattered, long erect setae positioned dorsally and laterally. Stemmata five on each side closely posterior to antenna base, variably pigmented; anterior row of three closely spaced and usually darker than offset pair behind them. Clypeus convex, transverse, weakly trapezoidal, about two times wider than long, with one long seta on each side of disc and three smaller setae at lateral edges. Labrum transverse, convex, with two long discal setae, two anterior setae near midline, and four smaller, fine setae along each side of anterior edge. Epipharynx with three relatively stout setae along each side of anterior margin and two very short, stout medial spines, the pair slightly offset to left; with a cluster of 8–9 small round sensory papillae anterior to spines; tormae slightly asymmetrical. Antenna three segmented with membranous base globular, wider than long; first segment longest, cylindrical, wider toward apex, 2.5× longer than wide; second segment ovoid, two thirds as long as first, 2× longer than wide, with apical sensoria flat, kidney-shaped, partly encircling base of third segment; third segment very small, cylindrical, 1.5× longer than wide, with a single fine seta apically. Mandibles asymmetrical, apices tridentate, left mandible with a fourth feeble tooth dorsally along sharp incisor edge; left mola concave, with a prominent premolar tooth and three transverse, sclerotized ridges; right mola convex, with a transverse fossa surrounded by irregularly prominent ridges. Ligula with four fine apical setae; prementum, mentum, submentum each with a pair of long setae near base. Hypopharyngeal sclerome well developed, tridentate, with smooth concavity in middle; median tooth carinate, with Y-shaped arms to prominent, conical, lateral teeth; basal transverse ridge asymmetrical.

**Thorax.** Prothorax as long as wide; meso- and metathorax wider than long; terga with 9–12 fine setae on each side, more closely spaced laterally. Mesothoracic spiracle simple, ovate, slightly larger and narrower than abdominal spiracles; metathoracic spiracle visible, very small, nearly circular. Prothoracic leg slightly larger than mid- and hindlegs; all legs with trochanter elongated, with anterior and posterior rows of setae on ridges; femur and tibia bearing scattered, shorter setae; tarsungulus with two pre-basal setae; claw simple, sharp, curved apically, two thirds the length of tarsungulus.

**Abdomen.** Abdominal segments I–VII similar, nearly as long as wide, gradually slightly wider posteriorly; terga with sparse setae as on thoracic terga; spiracles annular,
broadly ovate; sterna on each side with an anterior group of 4–5 setae of varying sizes and a pair of setae posteriorly. Tergum VII with a field of circular, deep punctures across anterior two thirds of middle. Tergum VIII as long as wide, abruptly narrowing posteriorly, with an extensive field of large, deep, circular punctures across anterior half and expanding on sides and dorsally with 7–8 scattered fine setae on each side; sloped posterior bearing two somewhat sclerotized, umbonate bullae on each side, large lateral one with a long seta arising from anterior of base of umbo; small umbo posterior to larger one and closer to midline, connected to larger by a feeble ridge, the four bullae forming a trapezoidal arrangement in posterior view, immediately anterior to a broad membranous apical area which opposes a similar dorsal membrane at anterior of tergum IX. Tergum IX short, about two thirds the width of tergum VIII and hinged to it, allowing curved urogomphi to come forward to oppose and contact bullae of tergum VIII; lateral hinge joint with a sclerotized, tooth-like, anterior process; urogomphi long, gradually tapered, divergent and curved dorsally with sharp apices pointing anteriorly, nearly round in cross-section, darkly sclerotized in apical half, each with three other sclerotized, tooth-like projections near base, as follows: large
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lateral claw-like process with apex pointed upward, forward and angled laterally, with a single dorsal seta below apex; small dorsal cone-like process bearing a single seta near apex; smaller, mesal, short, pointed to button-like process closely opposing other on opposite urogomphus. Other setae on tergum IX long, scattered; urogomphus with three setae on ventral (posterior) side; hinge process with a single seta near base; lateral and ventral surface with 7–8 scattered setae. Abdominal segment X small, ventral, transverse, semi-circular, convex, 3× wider than long, with a row of six fine setae across width; pygopods absent.

**Description of pupa.** (Figures 17–20, 25, 27).

**Body.** Length (from anterior edge of pronotum to tips of urogomphi) 15.1 mm, width of pronotum 3.9 mm; body color white with brownish surface setae, apices of urogomphi and spines on lateral processes; body very sparsely setose except pronotum with numerous fine discal and marginal setae, more dense anteriorly. Lateral processes of middle abdominal segments well developed, wing-like, bearing anterior and posterior smooth teeth and two smaller setigerous lateral spines between them; urogomphi long, smooth, gradually tapered to divergent, upturned apices.

**Head.** Hypognathous; surface smooth but with transverse wrinkles across frons; projection above antennal insertion rounded, not prominent; a few fine setae on frons, near eye, on clypeus and labrum; single seta on left mandible, near middle on outer curve; row of four setae on right mandible, from base to near middle on outer curve; single very small seta on outer edge of maxillary palpus, at base of last segment.

**Thorax.** Pronotum broadly shield-shaped, slightly wider than long, smooth with subtle transverse wrinkles; anterior angles and apex broadly rounded, posterior margin narrowly sinuate with posterior angles slightly pointed posteriorly. Pronotal surfaces with many short, fine setae except anterior margin and part of disc bare and setae more sparse in posterior part of disc; setae most closely spaced along margin of anterior angle, with some setae 2× longer than adjacent ones, fine and often curved; hypomeron smooth, with a few widely spaced fine setae; meso- and metatergite transverse, smooth, with very few fine setae; mesonotum produced and elevated posteriorly at middle (scutellar umbo); metanotum about 2× longer mesonotum, nearly 2× longer than abdominal tergite 1. Elytral sheath smooth with broad, shallow wrinkles; metathoracic wing sheath slightly shorter apically; meso- and metaventrite smooth. Legs and tarsi smooth, with a few scattered fine setae; femora with 5–7 setae from mid-length to near apex; tibiae with 3–5 setae along mid-length; protarsii with 3–4 setae on apical tarsomeres ventrally and laterally; apical tarsomeres of meso-and metatarsi with 1–2 setae laterally.

**Abdomen.** All surfaces smooth, bearing scattered fine setae; spiracles annular, vertically ovate to reniform, barely pigmented, visible on segments 2–6. Tergite 1 short, with five discal setae on each side, lateral process with single small posterior tooth and two small lateral spines with a wide, U-shaped emargination between them; smallest spine near base of tooth and bearing an apical seta, largest (anterior) sharply pointed, with a sub-apical seta. Tergites 2–5 of similar form, quadrate, transverse, with 4–5 discal setae on each side; lateral processes each with anterior and slightly smaller posterior...
teeth, stout but pointed at sclerotized, curved apices; lateral spines with sharp, sclerotized tips; larger of lateral spines near midpoint between teeth, bearing a sub-apical seta on posterior side, smaller spine arising from mid-length of posterior tooth, bearing a sub-apical seta on anterior side. Ventrites 2–6 smooth, convex, with 4–7 small fine setae on each side. Lateral process of tergite 6 with posterior tooth absent, both spines with sub-apical seta on posterior side. Tergite 7 narrower than preceding tergites, with four small fine setae on each side, with lateral process positioned and directed ventrally, not in same plane as preceding processes, anterior tooth reduced to a rounded lobe and posterior tooth absent, two posteriorly curved spines with sub-apical setae on posterior sides; sternite 7 roughly semicircular, transversely rugose apically, with three small discal setae on each side, the pair of larger setae along apical margin, with two smaller ones between them. Tergite 8 narrower than tergite 7, narrowing to broadly rounded apex, with lateral process reduced to a narrow ridge with two posteriorly curved spines only, posterior spine very reduced; spines with sub-apical setae on posterior sides; sternite 8 semicircular, with three small discal setae on each side, posterior most pair at sides of a transverse, raised area near apex. Tergite 9 short, bearing large divergent urogomphi, each gradually tapered and more sclerotized toward upturned, very sharp apices; cleft between urogomphi V-shaped with a narrowly rounded apex; base of uro-
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Glyptotus cribratus larval, pupal and reared adult material examined.  

Specimens collected in USA. “FLORIDA: Highlands Co., Archbold Biol. Sta., S of Lake Placid, S. side of Lake Annie, 27°12’35”N, 81°21’W, 19 April 2003 / In soft rotten dry wood of low dead branch on live Quercus virginiana; W. E. Steiner, J. M. Swearingen et al. collectors” (3 L); Same data except “Reared from larva; emerged October 2003, larval exuvia not recovered” (1 A); “FLORIDA: Highlands Co., Archbold Biol. Sta., S. of Lake Placid, forest tract, NE part, 27°12’N, 81°20’W, 19 April 2003 / W. E. Steiner & J. M. Swearingen collectors / In pithy rotten wood of dead standing oak branch, mixed scrub forest burned ca 1 year ago” (2 L); “FLORIDA: Highlands Co., Archbold Biol. Sta., S. of Lake Placid, hill area E of Station, 27°11’N, 81°20’30”W / 31 December 2006, W. E. Steiner, J. M. Swearingen, A. W. & B. B. Norden, collectors / In dry rotten wood of recently fallen dead branch of live oak” (1 L); “FLORIDA: Highlands Co., 2 km N. Cornwell at Kissimmee River, 1 March 1984 / In rotting wood of log of live oak / W. E. Steiner, A. G. Gerberich, J. E. Lowry collectors” (1 L); “GEORGIA: Camden County, Little Cumberland Island, 30°58’N, 81°25’W, 30 November 1997 / In dry soft rotten wood of hanging branch Quercus virginiana in maritime forest / W. E. Steiner, J. M. Swearingen, W. A. Dix, C. Wells collectors” (1 L); same data except “25 November 1998 / In dry soft rotten wood of dead branch in canopy of Quercus virginiana in maritime forest” (2 L); same data except “In pithy rotten wood of dead branch recently fallen from live oak, Quercus virginiana” (1 L); same data except “28 November 1998 / Associated with adult Glyptotus cribratus in dry soft rotten wood of small low branch on live Quercus virginiana in maritime forest” (1 L); “NORTH CAROLINA: Dare County, Kill Devil Hills, 35°59’33”N, 75°39’11”W, 23 February 2007, coll. W. E. Steiner & J. M. Swearingen / In dry rotten wood of recently fallen dead branch of s. red oak (Quercus falcata)” (1 L); same data except “28 November 1998 / Associated with adult Glyptotus cribratus in dry soft rotten wood of small low branch on live Quercus virginiana in maritime forest” (1 L); “SOUTH CAROLINA: Dillon Co.; Fork; Little Pee Dee S.P., sand area, 34°19’10”N, 79°17’06”W, 16 April 2012 / In dry soft rotten wood of dead branch of live Quercus laevis in open pine-oak sand scrub; colls. J. C. Ciegler, W. E. Steiner, J. M. Swearingen” (1 L); “SOUTH CAROLINA: Georgetown County; Huntington Beach, near Murrells Inlet, 33°30’51”N, 79°03’09”W, 15 April 2012 / In dry soft rotten wood of dead lower branch Quercus virginiana in maritime forest; colls. J. C. Ciegler, W. E. Steiner, J. M. Swearingen” (1 L); “TEXAS: Comal County, Espinazo del Diablo, 9 km SW Wimberley, 29°55’30”N, 98°09’05”W, 17 November 2013 / In dry pithy wood of recently fallen branch of living Quercus virginiana fusiformis / Colls. W. E. Steiner, J. M. Swearingen, J. R. Ott, E. Silverfine” (1 L); “TEXAS: Hays County, Driftwood, at Dutchman Vineyards,
30°06′09″N, 98°0′51″W, 15 November 2013 / In dry pithy wood of dead low branches on large living *Quercus virginiana fusiformis* / Colls. W. E. Steiner, J. M. Swearingen, J. R. Ott, E. Silverfine” (4 L); “TEXAS: Hays County, Freeman Ranch, NW of San Marcos, 29°56′23″N, 98°0′44″W, 15 November 2013 / In dry pithy wood of dead low branch on large living *Quercus virginiana fusiformis* / Colls. W. E. Steiner, J. M. Swearingen, J. R. Ott, E. Silverfine” (1 L); same data except second label “In dry pithy wood of recently fallen branch of large living *Quercus virginiana fusiformis*” (1 L); “TEXAS: Hays County, Rutherford Ranch area NW of Kyle; oak grove near pond, 30°02′49″N, 97°57′56″W, 16 November 2013 / In dry pithy wood of recently fallen branch of large living *Quercus virginiana fusiformis* / Colls. W. E. Steiner, J. M. Swearingen, J. R. Ott, E. Silverfine” (1 L); same data except “(Preserved 11 Dec. 2013) / In dry pithy wood of dead low branch on large living *Quercus virginiana fusiformis*” (2L); “TEXAS: Hays County, Rutherford Ranch area NW of Kyle; near old ranch house ruins, 30°04′0″N, 97°56′37″W, 16 November 2013 / In dry pithy wood of recently fallen branch of large living *Quercus virginiana fusiformis* / Colls. W. E. Steiner, J. M. Swearingen, J. R. Ott, E. Silverfine” (1 L); “TEXAS: San Patricio Co., 12 km NE Sinton, Welder Wildlife Refuge, 8 December 1984, W. Steiner, B. Gill & D. Whitehead collrs. / In rotting wood of *Celtis* / larva coll. 8 Dec. 84, pupated 25 Apr. 85, eclosed 14 May 85, preserved 1 June” (1 adult pinned with larval and pupal exuvia); “VIRGINIA: City of Va. Beach,
Larvae and pupae of two North American darkling beetles

First Landing S. P., beach campground, 36°55.4’N, 76°2.8’W, 16 June 2007 / In pithy rotten wood of dead branch recently fallen from live oak, Quercus virginiana / W. E. Steiner, J. M. Swearingen et al. collectors” (1 L).

**Specimens intercepted from MEXICO.** “Glyptotus sp. det. T.J. Spilman 1982, ex Mexico, at Hidalgo 4194, in Prosopis sp. stem, at Brownsville, #11491, 22v82, 82-6571” (1 L); “Glyptotus sp. det. T.J. Spilman 1983, ex Reynosa, Mexico, 8iiii83, at Hidalgo 4194, on stem Prosopis juliflora” (1 L); “Glyptotus sp. det. T.J. Spilman 1984, ex Mexico, at Laredo, 17843, in rotting log, 4xii83, 84-549” (1 L).

*Cibdelis blaschkei* Mannerheim

http://species-id.net/wiki/Cibdelis_blaschkei

**Background.** *Cibdelis blaschkei* is a very common beetle throughout much of California, with large series of adults represented in collections, but surprisingly, no specimens of its larvae or pupae could be found in museum holdings, nor are there any records of immature stages in the literature. The discovery of aerial dead wood larval habitats on trees in eastern USA localities led to the examination of similar wood in California, resulting in the collections listed below. Several other *Cibdelis* species have been described, all from California; the genus needs revision (Aalbu et al. 2002).

**Description of mature larva.** Figures 2, 6–8, 13–16.

**Body.** Length 24–29 mm; elongate-cylindrical, pale yellowish-white with light brown dorsal bands at posterior edges of terga and anterior edge of prothoracic tergum; mandible apices and bases, claws of tarsunguli, and apices of urogomphi and associated processes blackish to brown, heavily sclerotized; abdominal terga VIII and IX dorsally slightly darker yellow-brown; prothoracic sternum in front of leg more sclerotized, light brown; cuticle otherwise lightly sclerotized, surfaces shining, finely rugose and obscurely punctate, with scattered fine setae.

**Head.** Prognathous, slightly declined, globular but slightly flattened dorsoventrally. Epicranial stem about one third head capsule length; frontal arms sinuate, lyre-shaped, fine and obscure. Each half of head capsule dorsally and laterally with 13–17 scattered, long erect setae. Stemmata five on each side closely posterior to antenna base, variably pigmented; anterior row of three contiguous and very close to offset pair behind them. Clypeus convex, transverse, weakly trapezoidal, about two times wider than long, with one long seta on each side of disc and three smaller setae at lateral edges. Labrum transverse, convex, with two long discal setae, two short anterior setae near midline arising from dark punctures, and four smaller fine setae along each side of anterior edge. Epipharynx with three relatively stout setae along each side of anterior margin and two very short, stout medial spines, the pair closely spaced and slightly offset to left; with a cluster of 7–8 small round sensory papillae anterior to spines; tormae slightly asymmetrical. Antenna three segmented with membranous base globular; first segment longest, cylindrical, narrower near middle, 3× longer than wide; second segment cylindrical, two thirds as long as first, 2× longer than wide, widest near apex, with apical sensoria flat, kidney-shaped, partly encir-
clinging base of third segment; third segment very small, cylindrical, 1.5× longer than wide, with a single fine seta apically. Mandibles asymmetrical, the right slightly smaller than left; right mandible with apex tridentate, palmate, left mandible with three broad apical teeth and a fourth pointed, thin, on sharp dorsal incisor edge; left mola concave, with a prominent premolar tooth and three transverse, sclerotized ridges; right mola convex, with two transverse fossae surrounded by irregularly prominent ridges. Ligula with six small apical setae arranged in two rows; prementum, mentum, submentum each with a pair of long setae near base. Hypopharyngeal sclerome well developed, tridentate, with smooth concavity in middle; median tooth with V-shaped carinae, arms forming a bridge to prominent crest of lateral teeth; basal transverse ridge symmetrical, concave across middle.

Thorax. Prothorax as long as wide; meso- and metathorax about 2× wider than long; protergum with 11–15 fine setae of varying size on each side, sparsely arranged in two bands; meso- and metaterga with 6–7 similar scattered setae. Mesothoracic spiracle simple, irregularly ovate, slightly larger and narrower than abdominal spiracles; metathoracic spiracle not visible. Prothoracic leg slightly larger than mid- and hindlegs; all legs with trochanter elongated, with anterior and posterior ridges bearing a few fine setae; femur and tibia bearing scattered, shorter setae; tarsungulus with two pre-basal setae; claw simple, sharp, curved apically, two thirds the length of tarsungulus.
Abdomen. Abdominal segments I-VII similar, slightly wider than long, successive segments gradually slightly wider posteriorly; terga with sparse long setae as on thoracic terga, 9–10 on each side; spiracles annular, broadly ovate; sterna on each side with an anterior row of three fine setae and a pair of setae posteriorly. Tergum VIII nearly as long as wide, slightly narrowed posteriorly, dorsally with 9–10 scattered fine setae on each side, those nearest dorsal process arising from circular, pigmented punctures and in a moderately sclerotized area with smaller scattered punctures; dorsal outline in lateral view straight from base to apex of pointed, posterior process, one on each side, the close pair in dorsal view forming a V-shaped cleft at midline; pointed apices divergent, darkly sclerotized, joined to rounded mola-like process ventral and mesal to them; dorsum behind processes abruptly sloped downward to a broad membranous apical area that opposes a similar dorsal membrane at anterior of tergum IX. Tergum IX short, about two thirds the width of tergum VIII and hinged to it, allowing curved urogomphi to come forward to oppose and straddle pair of processes of tergum VIII; lateral hinge joint obscure, without sclerotized, tooth-like, anterior process; urogomphi robust, gradually tapered, slightly divergent and curved dorsally with sharp apices pointing anteriorly, nearly round in cross-section, darkly sclerotized in apical half, each with sclerotized, tooth-like projections near base, as follows: small dorsolateral conical process without associated seta; dorsomedial process bearing a single small seta between larger pointed mesal tooth and feeble lateral tooth, the mesal teeth closely opposing each other between urogomphi. Other setae on tergum IX long, scattered, those on and near base of urogomphus arising from large, circular, pigmented punctures; urogomphus with a lateral seta near mid-length, two on ventral (posterior) side; lateral and ventral surface with 9–12 scattered setae of varying size. Abdominal segment X small, ventral, transverse, semi-circular, convex, 2.5× wider than long, with a row of 6 fine setae across width; pygopods absent.

Description of pupa. (Figures 21–24, 26, 28).

Body. Length (from anterior edge of pronotum to tips of urogomphi) 15.7–18.5 mm, width of pronotum 4.8–5.0 mm; body color white with brownish surface setae, apices of urogomphi and spines on lateral processes; body very sparsely setose. Lateral processes of middle abdominal segments well developed, wing-like, bearing anterior and posterior curved teeth and two smaller setigerous lateral spines between them; urogomphi long, wrinkled at base, gradually tapered to divergent, sharp apices.

Head. Hypognathous; surface with dense shallow punctures and between eyes with faint transverse wrinkles; projection above antennal insertion absent; a few fine setae on frons, near eye, on clypeus and labrum; a row of four setae on each mandible from base to apical one-third along outer curve; single very small seta on outer edge of maxillary palpus, at base of last segment.

Thorax. Pronotum broadly shield-shaped, slightly wider than long, smooth with a mixture of fine shallow punctures and subtle transverse wrinkles; anterior margin broadly rounded, lateral margin slightly explanate with thick bead, posterior margin nearly straight with posterior angles narrowly rounded, not produced posteriorly. Pronotal surfaces with sparse, fine setae along anterior and lateral margin, much smaller across middle; most of disc bare except for widely spaced setae, three on each side an-
teriorly, two posteriorly, and 1–3 very small setae laterally; hypomeron smooth, with a few widely spaced fine setae, some larger immediately under lateral margin; meso- and metanotum transverse, smooth, with 1–2 fine setae on each side; mesonotum produced and slightly elevated posteriorly at middle (scutellar umbo); mesonotum, metanotum, and abdominal tergite 1 short, roughly equal in length. Elytral sheath smooth with feeble, longitudinal furrows and sub-apical raised bulla; metathoracic wing sheath of thin membrane and shorter than elytral sheath, not visible beneath elytral sheath (unless dissected or observed in bloated specimens); meso- and metasternum short, smooth. Legs and tarsi smooth, with a few scattered fine setae; femora with 7–10 setae from mid-length to near apex; tibiae with 3–5 setae along mid-length; protarsi with 5–6 setae on apical tarsomeres ventrally and laterally; apical tarsomeres of meso- and metatarsi with 3–4 setae laterally.

**Abdomen.** All surfaces smooth, bearing scattered fine setae; spiracles annular, rounded, barely pigmented, visible on segments 2–6. Tergite 1 short, with 4–5 discal setae on each side, lateral process with anterior tooth reduced to a small conical projection bearing an apical seta; posterior tooth with sharp, sclerotized apex abruptly directed posteriorly; lateral spine near base of each tooth small, narrowly conical, lightly sclerotized, directed slightly to anterior, with a broad, shallow emargination between them; anterior spine with seta directed posteriorly; posterior spine with seta directed

**Figures 25–28.** Right lateral abdominal processes of tergites 1–4, pupa of *Glyptotus cribratus* (25) and *Cibdelis blaschkei* (26), *Glyptotus cribratus*, live pupa (dorsolateral view) and associated larval exuvia, Kill Devil Hills, North Carolina (27), *Cibdelis blaschkei*, live pupa (lateral view) and associated larval exuvia in pupal cell of oak wood, Angwin, California (28). Length of pupae 15–16 mm.
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anteriorly. Tergites 2–6 of similar form, quadrate, transverse, with 4–5 discal setae on each side; lateral processes each with prominent anterior and slightly smaller posterior teeth, strongly curved and gradually tapered to sharp, sclerotized apices; anterior tooth with small serrations along curve on anterior side; each tooth with associated lateral spine arising near base between them and with apex curved posteriorly; spines bearing a long seta on dorsal side, arising from a sclerotized elevated base; a broad, shallow emargination between spines with a very small setiferous accessory spine along length, usually closer to anterior spine; anterior spine with seta directed posteriorly; posterior spine with seta directed anteriorly in most examples. Ventrites 2–6 smooth, convex, with 1–7 small fine setae on each side, basal ventrites with fewer setae. Tergite 7 narrower than preceding tergites, with 3–4 small fine setae on each side, anterior tooth small, posterior tooth absent, posterior spine very small, accessory spine absent; sternite 7 semicircular, with 3–4 small discal setae on each side, the larger setae paired near apical margin. Tergite 8 narrower than tergite 7, narrowing to broadly rounded apex, with lateral process reduced to a narrow ridge with 2 posteriorly directed setae only; discal setae 3–4 on each side; sternite 8 semicircular, with 2 small discal setae on each side near apical margin. Tergite 9 small, narrow, bearing large, divergent, posteriorly directed urogomphi, each gradually tapered and more sclerotized toward sharp apices, with irregular crenulate surface along mid-length; cleft between urogomphi V-shaped with a narrowly rounded apex; base of urogomphus laterally with a single prominent seta arising from a sclerotized, raised base; 7–8 other fine setae present ventrally on base of urogomphus and ventrolateral side of tergite 9; sternite 9 in male pupae small, narrowly transverse, with 2 setae on each side; sternite 9 in female pupae not visible. Genital segment in male pupae small, recessed, smooth, convex, slightly wider than long, with rounded apical lobes separated with a small median notch; in female pupae large, produced, smooth, roughly trapezoidal, with two divergent papillae bearing a single small seta laterally, papillae separated by a sinuate apical margin.

_Cibdelis blaschkei_ larval, pupal and reared adult material examined. “CALIFORNIA: Contra Costa Co., Tilden Park NE of Berkeley, 37°53’24”N, 122°14’13”W, 23 June 2012, colls. W. E. Steiner, J. M. Swearingen et al. / Under bark of fallen pine branch in mixed forest grove” (1 P); “CALIFORNIA: Napa Co., Angwin, near airport, 38°34’13”N, 122°25’50”W, 29 June 2012, coll. W. E. Steiner & J. M. Swearingen, In rotten dry wood of fallen oak branch in mixed forest” (5 L); same data except: “preserved 2 July 2012” (1 P); “preserved 4 July 2012” (2 P); “preserved 9 July 2012” (2 P); “CALIFORNIA: Napa County, St. Helena, 16 Feb. 2003, W. E. Steiner, J. M. Swearingen et al. collectors / In dry rotten wood of recently fallen dead branch of oak” (2 L); same data except “21 Dec. 2003” (2 L); “CALIFORNIA: Napa County, 7 km NW St. Helena, 38°32’N, 122°31’W / 15 Dec. 2003, W. E. Steiner & J. M. Swearingen collectors / In dry rotten wood of recently fallen dead branch of oak” (2 L); “CALIFORNIA: Napa Co., Silverado area, 5 km NE of Napa, 38°20’N, 122°15’W / 18 Feb. 2003, W. E. Steiner, J. M. Swearingen collectors / In pithy dry wood of fallen oak branch ca. 8 cm diameter on ground, open hills with oak groves (3 L); same data except “25 April 2004” and “branch ca. 5 cm.” (1 L); “CALIFORNIA: Napa Co., Skyline Park area, 5 km SE of Napa, 38°16’N, 122°15’W
Both *Glyptotus cribratus* and *Cibdelis blaschkei* are beetles of forested areas, their larvae being dependent on dead, rotten wood for survival. They tend to be more common in forest edge habitats or at single trees or groves in open areas, where wood dries out more rapidly and is slower to decay than in mesic forest interiors. These species may be avoiding attack by fungal, bacterial, or other pathogens and/or avoiding competition from insects inhabiting more damp wood in shaded situations. Furthermore, larvae are rarely if ever found in rotten wood on the ground, with the exception of recently fallen branches; these beetles appear to be specialists in dead wood involving mostly smaller branches, on living, usually old trees. Specimen data and observations indicate that if inhabited branches happen to fall, older, nearly full-grown larvae may be able to complete development. Adults probably breed commonly in canopy-level wood; an opportunity to observe *G. cribratus* on dead canopy branches of oak (Little Cumberland Island, Georgia) led to collection of adults and larvae in exposed, rotten branches several meters above ground. The dead oak branches in which *Glyptotus* and *Cibdelis* have been found were usually covered with lichens, which possibly serve as food for adults.

Adult beetles are nocturnal, often found on bark at night, but hide during the day in hollow dead branches as well as under the bark of dead branches or main trunks. Adults and larvae of both species are active throughout the year, but pupation seems to be restricted to spring and summer. Larvae tunnel in moderately soft dry wood, consuming it (and probably fungal tissue within) and depositing pelleted frass in the
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burrow; they can occur immediately under the bark or in the branch interior. Most larvae have been collected in smaller branches, 3–15 cm diameter, with wood that is easily broken apart by hand. Pupation occurs in the same wood. In one instance, the pupal period lasted 19 days for a Texas specimen of *Glyptotus*, reared at 22–26°C; no comparable pupal data are available for *Cibdelis*, but the period is likely similar. Except for one record of a pupa beneath bark of an undetermined pine species, *C. blaschkei* is typically associated with oaks.

*Glyptotus cribratus* occurs from coastal Virginia to Texas (Hoffman et al. 2002) where it is often associated with live oak, *Quercus virginiana* Mill., which has a similar distribution, but other species of *Quercus*, as well as *Celtis* and *Prosopis* spp., are recorded hosts. Beetles are most common in maritime oak forests and sandhill habitats of the coastal plain but also occur in middle elevations of the southern Appalachians. This species is common as well in the elevated karst areas of central Texas (Edwards Plateau), which have a distinct oak flora.

**Observations on defense structures and behaviour. Larval characters.** In larvae of both *Cibdelis* and *Glyptotus*, the manner in which the long, upcurved urogomphi oppose the raised areas and posterior projections of tergite 8 appear to form a pinching structure, as seen in occasional specimens preserved in the “closed” position (Figures 11, 12, 15, 16). The opportunity to observe pinching behavior was offered by the recent collections of larvae on several occasions. When larvae are removed from the burrow in dead wood, they appear incapable of rapid evasive movement but do writhe in a circular movement when held at the middle by forceps or fingers, and the hinged urogomphi can be seen to open and close against segment 8 when the end of the abdomen is touched. Inserting a stiff hair, fine piece of grass, or insect pin tip in the dorsal gap between tergites 8 and 9 usually prompted the larva to pinch; occasionally, the larva will hold on and can be lifted off the substrate for several seconds before releasing the pinch. When full-grown larvae of *Glyptotus* were first exposed and restrained, pinches were observed and felt on fingertips; the larvae also appeared to be trying to bite with mandibles. These actions could possibly defend the larvae from attack by small lizards and other predators. When approached in the wood tunnel by a potential predatory insect, either end could be capable of some defense.

Pointed, upturned urogomphi are present in many tenebrionid larvae, but few possess opposing processes on tergite 8 and the hinge-like joint between segments. Long tactile setae, “trigger hairs,” are associated with processes on tergite 8 and occupy the space between the sloped dorsum of tergite 8 and the urogomphi at rest. The paired processes seen in *Cibdelis* larvae are of unique form, previously unknown, but the hinge-like joint is not apparent. The raised bullae of tergite 8 and other features of the pinching assembly in *Glyptotus* are very similar to those of the related stenochiine larva, *Haplandrus fulvipes* (Herbst) (St. George 1924, Figures 38-39). In the same work, a larva identified as *Glyptotus* from Florida was described in the key with “Pygidium with transverse row of strong, hook-shaped, seta-bearing spines anterior to cerci” but was not illustrated. This larva could not have been *Glyptotus* because these different features are all on tergum 9; no modifications of tergum 8 were noted.
Larvae of Helopini, also described from dead wood, have abdominal apices very similar to those of *Glyptotus*, for example *Helops caeruleus* L. (Schiödte 1878, Figures 20–21, Plate 11) and *Deretus spinicollis* Schawaller (Purchart and Nabozhenko 2012, Figures 9–10). The pinching ability of these larvae is probably comparable to that of *Glyptotus*.

**Pupal characters.** Like known pupae of other stenochiines, those of *Cibdelis* and *Glyptotus* are armed with lateral abdominal gin traps that pinch between the posterior and anterior curved teeth, with lateral projecting spines and associated tactile hairs. Use of these structures and associated body movements have been studied in other pupae (Bouchard and Steiner 2004 and papers cited within) and the live pupae observed in this study displayed these actions. Pupal cells in the soft wood (Figure 28), formed by the mature larva before pupation, offer a large space in which pupae can actively rotate the body and use pinching organs. As noted in other stenochiine pupae, gin trap teeth of opposing lateral processes have the “posterior is ventral to anterior” closure type (Steiner 1995, Figure 104) in the pinched position.

Pupae of *G. cribratus*, a winged species, possess fully formed wing sheaths beneath the elytral sheaths. Conversely, *C. blaschkei* is wingless, with elytra partially fused, though pupae still retain empty wing sheaths of nearly full length—a condition noted by Spilman (1979) in which a long sheath with vestigial or absent wing development indicates occasional flightlessness within groups otherwise characterized by flight. This is the case among Stenochiinae, where flightlessness appears to have evolved multiple times within a large clade of mostly winged species (Matthews et al. 2010).

**Acknowledgments**

Assistance in fieldwork, access to natural areas, and hospitality on travel over several decades has been given by many: Jil, John and Helen Swearingen, Carole Russell, Rolf and Denise Aalbu, Jan Ciegler, Art Evans, Andy Gerberich, Will Dix, Cyd Wells, Elaine Nakash, Don Whitehead, Bruce Gill, Mark Deyrup, Arnold and Beth Norden, Jim Ott and Eva Silverfine. Photographs of specimens were contributed by Eugenio Nearns (Figures 1–2) and Jil Swearingen (Figure 28). Review of the manuscript by James Dunford and Trip Lamb greatly improved the prose and presentation.

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Note on brachypterous Stenochiini from China (Coleoptera, Tenebrionidae) with description of a new species

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Academic editor: P. Bouchard | Received 30 September 2013 | Accepted 29 January 2014 | Published 12 June 2014


Abstract
A checklist of 29 brachypterous species in the tenebrionid tribe Stenochiini is given for China and neighboring countries. A new species is described and illustrated under the name of Strongylium liangi sp. n. (CHINA: Yunnan). Also, some new distribution data is provided for S. claudum (Gebien, 1914), and a distribution map of all Strongylium species in the checklist is presented.

Keywords
Tenebrionidae, Stenochiini, Strongylium, new species, China

Introduction
The East Asian brachypterous species of the tenebrionid tribe Stenochiini, including 14 species/subspecies in four genera, were revised by Masumoto (1999). Later, more species and genera were added or transferred to this group by Ando (2003), Masumoto
(2006), Yuan and Ren (2006), Masumoto et al. (2007), Löbl et al. (2008), Ando and Nakahama (2009), and Masumoto et al. (2013). This group currently includes six genera and 28 species/subspecies, of which 13 species/subspecies in four genera are known to occur in China. In the present study, a new brachypterous species of *Strongylium* from Yunnan, China is described, *Strongylium liangi* sp. n. The checklist of the brachypterous species of the tribe Stenochiini from China and neighboring countries is updated and a distribution map of the *Strongylium* species is provided, including new distribution data for *S. claudum* (Gebien, 1914).

**Material and methods**

Specimens were examined and illustrated under a Nikon (SMZ800) dissecting microscope (equipped with a camera lucida), illustrations were processed using the software (CorelDRAW X3). Measurements were taken using a Leica (M205 A) dissecting microscope. Habitus photographs were taken with a Nikon (D 300S) camera. The distribution data in Figure 1 are derived from examined specimens and literature records. The holotype of *Strongylium liangi* sp. n. is deposited in the Institute of Zoology, Chinese Academy of Sciences, Beijing, China (IZCAS). All other materials are in the Museum of Hebei University, Baoding, China (MHBU).

The following measurements are used in the text, with all measurements in millimeters: body length: length of the body from the anterior edge of the clypeus to elytral apex; body width: length of the maximal elytral width; pronotal length: length of the pronotum along the midline; pronotal width: maximum width of the pronotum; elytral length: length of the elytra from the base of the scutellum to the elytral apex along the suture.

**Taxonomy**

*Strongylium liangi* sp. n.
http://zoobank.org/A0C3D887-33D1-46F5-8123-CD3CA1901276
http://species-id.net/wiki/Strongylium_liangi
Figs 2–10

**Type specimen.** Holotype male: China, Yunnan, Lushui county, Pianma town, Yakou, 19.v.2005, Hong-Bin Liang leg. (IZCAS).

**Diagnosis.** The new species is similar to *S. tanakai* Ando, 2003, from Japan because their humeri are more developed than other brachypterous species of *Strongylium*, such as *S. claudum* (Fig. 11) and *S. wuyishanense*, but can be distinguished from the latter by its stouter body, the distance between the eyes being narrower than the transverse diameter of an eye, and the shape of the aedeagus, that is obliquely narrowed apically in dorsal view, slightly curved in lateral view.

**Etymology.** Named in honor of Dr. Hong-Bin Liang, collector of the holotype.
Note on brachypterous Stenochiini from China (Coleoptera, Tenebrionidae)...

Description. Male (Figs 2–10). Body length 14.4 mm, elongate, slightly wider posteriorly. Colour dark brownish black, pronotum reddish, antennae and legs dark reddish brown, tarsi slightly lighter; head, antennae and pronotum almost dull, elytra shining; body surface almost glabrous except antennae, tarsi and ventral surface. Head (Fig. 2) subhexagonal, densely punctate; clypeus transverse, slightly and gradually declined forward in basal part, strongly bent ventrad in apical part, truncate at anterior edge; fronto-clypeal suture deeply depressed; genae obliquely raised, with outer margins obtusely produced; frons somewhat widely T-shaped, steeply inclined anteriorly, slightly, longitudinally impressed in middle, surface irregularly and finely punctate, punctures often fused with one another, distance between eyes 0.66 times as wide as transverse diameter of an eye in dorsal view. Eyes medium-sized, rather protruding. Antennae (Fig. 4) subfiliform, reaching basal 1/5 of elytra, ratio of the length of antennomeres II–XI as 0.31: 1.02: 0.76: 0.58: 0.63: 0.65: 0.56: 0.53: 0.54: 0.67. Maxillary palpomere IV (Fig. 5) moderately expanded. Pronotum (Fig. 3) 1.06 times as wide as long, widest before the middle; anterior margin bordered, border tapering laterad; posterior margin bisinuate, bordered; both sides steeply inclined downwards, lateral margins arcuate anteriorly, obliquely narrowed at posterior one-third, bordered along entire length; anterior angles rounded, posterior angles subrectangular; disc moderately convex, shallowly impressed near anterior margin, densely covered with confluent, ocellate punctures. Scutellum triangular, densely and rugosely punctate. Elytra elongate ovoid, slightly dilated posteriorly, 2.11 times as long as wide, widest at apical one-third, 3.68 times as long as and 1.62 times as wide as pronotum; disc slightly convex, striae fine, strial punctures circular and fine anteriorly, be-

Figure 1. Distribution of brachypterous species of the genus Strongylium Kirby from China and neighbouring countries: 1 S. becvarianum Masumoto 2 S. claudum (Gebien) 3 S. habashanense habashanense Masumoto 4 S. habashanense lijiangense Masumoto 5 S. jizushanense Masumoto 6 S. liangi sp. n. 7 S. marseuli marseuli Lewis 8 S. marseuli watanabei Nomura & Yamazaki 9 S. marseuli nigripes Nomura & Yamazaki 10 S. masatakai Masumoto, Lee & Akita 11 S. tanakai Ando 12 S. wuyishanense Yuan & Ren.
coming finer and nearly disappearing apically; intervals slightly convex, flattened apically, sparsely covered with microscopic granules at posterior 1/4; humeri moderately swollen, hind wings reduced, reaching basal 3/4 of elytra. Prosternum narrow, strongly raised between coxal cavities, impressed in middle, prosternal process strongly declined to roundly produced and protruding at apex. Abdominal ventrites (Fig. 7) covered with microscopic punctures and setae, ventrite V with dense punctures and setae, setae longer than those on I–IV. Legs slender, simple, length ratio of metatarsomeres I–IV as 2.01: 1.03: 0.68: 1.44. Aedeagus 2.48 mm long, 0.5 mm wide (Figs 8–9).

Female: unknown.

*Strongylium claudum* (Gebien, 1914)
http://species-id.net/wiki/Strongylium_claudum

Fig. 11

*Crosocelis clauda* Gebien, 1914: 53
*Strongylium claudum*: Masumoto, 1999: 121.
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Distribution. China: Taiwan.

Strongylium wuyishanense Yuan & Ren, 2006
http://species-id.net/wiki/Strongylium_wuyishanense

Strongylium wuyishanense Yuan & Ren, 2006: 852.

Type material examined. Holotype: 1♂ (MHBU), China, Fujian, Mt. Wuyi, Huanggangshan, 21.v.2004, Cai-Xia Yuan & Jing Li leg.

A checklist of brachypterous species of the tribe Stenochiini from China and neighbouring countries

**Eucrossoscelis** Nakane, 1963 [Type species: *Eucrossoscelis broscosomoides* Nakane, 1963]
2. *broscosomoides* Nakane, 1963: 29, Japan (Amami-Oshima Is.)
3. *hastatus* Yuan & Ren, 2006: 851, China (Guizhou)
4. *michioi* Chûjô, 1978: 78, Japan (Okinawa-jiama)
5. *maruyamai* Masumoto, 1999: 121, Japan (Ryukyu Islands)

**Saitostrongylium** Masumoto, 1996 [Type species: *Saitostrongylium acco* Masumoto, 1996]

**Stenochinus** Motschulsky, 1860 [Type species: *Stenochinus reticulatus* Motschulsky, 1860]
7. *akiyamai* Masumoto, Akita & Lee, 2013: 266, China (Taiwan)
8. *amplus* (Gebien, 1914: 8), China (Taiwan) [Originally in *Dicraeosis*]
9. *bacillus* (Marseul, 1876: 103), Japan (Nagasaki (type locality), Honshu, Shikoku, Kyushu, Okinoshima Is., Kochi Pref. and Yushima Is.) [Originally in *Dicraeosis*]
10. *datangla* (Merkl, 1992: 273), Vietnam (Lam Dong) [Originally in *Dicraeosis*]
11. *furcifer* (Shibata, 1980: 73), China (Taiwan) [Originally in *Dicraeosis*]
12. *mysticus* Masumoto, Akita & Lee, 2013: 268, China (Taiwan)
13. *unicornis* (Shibata, 1980: 68), China (Taiwan) [Originally in *Dicraeosis*]

**Strongylium** Kirby, 1819 [Type species: *Strongylium chalconotum* Kirby, 1819]
14. *becvarianum* Masumoto, 1999: 119, Thailand (Mae Hong Son)
15. *claudum* (Gebien, 1914: 53), China (Taiwan) [Originally in *Crossoscelis*]
16. *habashanense habashanense* Masumoto, 1999: 114, China (Yunnan)
17. *habashanense lijiangense* Masumoto, 1999: 115, China (Yunnan)
18. *jizushanense* Masumoto, 1999: 116, China (Yunnan)
19. *liangi* sp. n., China (Yunnan)
22. *marseuli watanabei* Nomura & Yamazaki, 1960: 15, Japan (Shikoku)
23. *masatakai* Masumoto, Lee & Akita, 2007: 156, China (Taiwan)
24. *tanakai* Ando, 2003: 79; Ando & Nakahama, 2009: 37 (male), Japan (Hyogo (type locality), Yamaguchi)
25. *wuyishanense* Yuan & Ren, 2006: 852, China (Fujian)
Note on brachypterous Stenochiini from China (Coleoptera, Tenebrionidae)

**Uenomisolampidius Masumoto, 1996** [Type species: *Uenomisolampidius shunichii* Masumoto, 1996]
(26) *shunichii* Masumoto, 1996: 36, Vietnam (Ha Tay)

**Uenostrongylium Masumoto, 1999** [Type species: *Cryptobates laosensis* Pic, 1928]
(27) *becvari* Masumoto, 2006: 70, China (Guizhou)
(28) *hunanense* Masumoto, 2006: 72, China (Hunan)
(29) *laosensis* (Pic, 1928: 26), Laos (type locality), Vietnam

**Acknowledgements**

We are grateful to Dr. Hong-Bin Liang (IZCAS) for collecting the holotype of *Strongylium liangi*, Mrs. Xi-Juan Yang (MHBU) for her help in operating the GIS and Dr. Yu-Xia Yang (College of Life Sciences, Hebei University) for her suggestions in improving our manuscript. Thanks are also due to Dr. Ottó Merkl (Hungarian Natural History Museum), editor and an anonymous reviewer for their important comments and corrections. The study is supported by the National Natural Foundation of China (No. 31093430) and the High-level university construction projects funded projects of Shaanxi Province (No. 2012SXTS03).

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