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

Edited by

Patrice Bouchard & Aaron D. Smith

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2014

ZooKeys 415 (Special Issue)

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

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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

Contents

ZooKeys 415: 1–8 (2014)
doi: 10.3897/zookeys.415.7113
www.zookeys.org

EDITORIAL

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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

Citation: Smith AD, Aalbu RL, Bouchard P (2014) Editorial: Third International Tenebrionoidea Symposium. In: Bouchard P, Smith AD (Eds) Proceedings of the Third International Tenebrionoidea Symposium, Arizona, USA, 2013. ZooKeys 415: 1–8. doi: 10.3897/zookeys.415.7113

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.

Figure 1. August 7th, before the first talk.

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,

Figure 2. Pre-meeting sightseeing stop at Zion National Park, Utah. Left to right: Wolfgang Schawaller, René Fouquè, Gustavo Flores.

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.

Figure 5. Post meeting dinner. Left to right, back row: Bill Warner, Rich Cunningham, Pat Bouchard, Wolfgang Schawaller, Aaron Smith, Milton Campbell, Andrew Johnston, Marcin Kamiński; front row: Ron Somerby, Gael Kergoat, Roland Grimm, Rolf Aalbu, Rebecca Dornburg, René Fouquè, Gustavo Flores, Paulina Cifuentes Ruiz.

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 Guodong 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

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Rolf L. Aalbu (USA)
Jason T. Botz (USA)
Patrice Bouchard (Canada)
Milton Campbell (Canada)
Alejandro Castro Tovar (Spain)
Paulina Cifuentes Ruiz (Mexico)
Adriana Li Colinas (Spain)
Shanshan Liu (China)
James Pflug (USA)
Guodong Ren (China)
Wolfgang Schawaller (Germany)
Aaron D. Smith (USA)
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Rebecca Dornburg (USA)
Gustavo E. Flores (Argentina)
Rene Fouque (Czech Republic)
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Andrew Johnston (USA)
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Kojun Kanda (USA)
Gael J. Kergoat (France)
Larry Stevens (USA)
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Charles A. Triplehorn (USA)
Bill Warner (USA)
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ZooKeys 415: 9–22 (2014)
doi: 10.3897/zookeys.415.6523
www.zookeys.org

RESEARCH ARTICLE

A peer-reviewed open-access journal
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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

Citation: Aalbu RL, Smith AD (2014) The Tenebrionidae of California: A Time Sensitive Snapshot Assessment. In: Bouchard P, Smith AD (Eds) Proceedings of the Third International Tenebrionoidea Symposium, Arizona, USA, 2013. ZooKeys 415: 9–22. doi: 10.3897/zookeys.415.6523

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

Introduction

The state of California is part of the California Floristic Province, one of 34 global biodiversity hotspots identified by Conservation International[1]. 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[2]. 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[3]. 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].

2 See http://www.conservation.org/WHERE/PRIORITY_AREAS/HOTSPOTS/NORTH_CENTRAL_AMERICA/CALIFORNIA-FLORISTIC-PROVINCE/Pages/default.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), Amphidorini (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 subspecies[5]; 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 Herbarium[6] (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.

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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.

6 Geographic subdivisions of California, Jepson Flora Project (eds.) [2013] Jepson eFlora, http://ucjeps.berkeley.edu/IJM.html [accessed on December 9, 2013].

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 edrotines) 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 Phrenapatinae (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 Nyctoporini, 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.

Table 1. Status Groups and Endemicity. Group 0: Known new but undescribed species; Group 1: currently projected valid species and subspecies; Group 2: most likely synonyms, but synonymy not determined without further study; and Group 3: known but unpublished synonyms.

Status group	Non endemic species	Endemic species	Total
0	2	8	10
1	249	155	404
2	6	27	33
3	22	17	39
	279	207	486

Table 2. California Species, Described vs Realistic. Species counts for the state and % endemicity based on current valid species (A) and a realistic estimation of actual species counts (B).

Category	Status groups	Species	Endemics	Total	% Endemic
A: Described	1, 2 & 3	277	199	476	41.81%
B: Realistic	0, 1, & 2	257	190	447	42.51%

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

Region	Number of species	Number of endemics	% Endemism	Area (km²)	Species diversity per 1000 km²
California*	447**	190	43%	423970	1.05
USA***	1184	?	>60%	9827000	0.12
Mexico***	1340	723	54%	1973000	0.68
Baja California***	404	225	56%	73909	5.47

* Bordered by 3 states and Baja California.

** 34% of all U.S. species.

*** 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* (*Melaneleodes*) *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 form 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.

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.

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

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

Floristic Region	All Endemics	Non Endemic	All Species
Desert Areas	37	94	131
California Floristic Province	124	81	205
Both Areas	16	60	76
Unknown California locality, cosmopolitan or introduction	13	22	35

Figures

California Tenebrionidae (January 2014)

#	Endemic CA	Status group	Species	Distribution
Pimeliinae Cnemeplatiini				
1	✓	1	Alaudes alternata Fall, 1928	5
2		3	Alaudes fallax Fall, 1928	5
3	✓	0	Alaudes n.sp. Colorado Desert	3 4 5
4	✓	0	Alaudes n.sp. Fresno	5 7
5	✓	0	Alaudes n.sp. Mojave	2 3
6		1	Alaudes setigera Blaisdell, 1919	5 6 7 8 BC
7		1	Alaudes singularis Horn, 1870	2 3 4 5 6 8 NV AZ ID
8		3	Alaudes testacea Blaisdell, 1919	8
9	✓	0	Lepidocnemeplatia n.sp.	4
10		1	Lepidocnemeplatia sericea (Horn), 1870	6 7 9 5 8 AZ OR ID ME NV UT +
Pimeliinae Stenosini				
11	✓	1	Araeoschizus andrewsi Papp, 1981	4
12		1	Araeoschizus armatus Horn, 1870	3 2 NV
13	✓	1	Araeoschizus costipennis LeConte, 1851	5 4
14	✓	1	Araeoschizus doyeni Papp, 1981	5
15	✓	1	Araeoschizus exiguus Casey, 1907	5
16	✓	1	Araeoschizus hardyi Papp, 1981	4
17	✓	1	Araeoschizus hystrix Papp, 1981	4
18	✓	1	Araeoschizus kaszabi Papp, 1981	5 3
19	✓	1	Araeoschizus lariversi Papp, 1981	3
20	✓	1	Araeoschizus simulans Casey, 1907	U type only
21	✓	1	Araeoschizus sulcicollis disjunctus Papp, 1981	8
22		1	Araeoschizus sulcicollis sulcicollis Horn, 1870	3 NV
23	✓	1	Typhleusechus chemehuevii Aalbu & Andrews, 1985	3
24	✓	1	Typhleusechus singularis Linell, 1897	5 7 8
Pimeliinae Cryptoglossini				
25		1	Asbolus laevis LeConte, 1851	4 BC AZ
26		1	Asbolus mexicanus angularis (Horn), 1894	4 BC AZ
27	✓	1	Asbolus papillosus (Triplehorn), 1964	3 4
28		1	Asbolus verrucosus LeConte, 1851	7 8 3 4 5 2 AZ NV ME
29		1	Cryptoglossa muricata (LeConte), 1851	7 5 3 4 AZ NV ME
30		1	Cryptoglossa spiculifera (LeConte), 1861	4 ME
31		1	Schizillus laticeps Horn, 1874	2 3 4 5 7 BC
32		1	Schizillus nunenmacheri Blaisdell, 1921	2 3 NV AZ UT
Pimeliinae Nyctoporini				
33		1	Nyctoporis aequicollis Eschscholtz,1831	5 6 7 9 8 NV
34		1	Nyctoporis carinatus LeConte, 1851	6 9 8 7 5 BC
35	✓	1	Nyctoporis cristata Eschscholtz,1831	6 7 8 9
36		3	Nyctoporis maura Casey, 1907	6
37		3	Nyctoporis pullata Casey, 1907	9
38	✓	1	Nyctoporis sponsa Casey, 1907	9 7 6
39		3	Nyctoporis tetrica Casey, 1907	7
40	✓	1	Nyctoporis vandykei Blaisdell, 1931	6 7 5 8
Pimeliinae Asidini				
41		1	Microschatia championi Horn, 1893	4 BC
42		1	Microschatia inaequalis LeConte, 1851	5 BC
43		1	Philolithus actuosus (Horn) 1870	3 4 AZ NV
44		1	Philolithus carinatus LeConte, 1851	3 AZ
45	✓	2	Philolithus jaegeri (Papp), 1961	3
46	✓	1	Philolithus opimus Casey, 1912	3
47		3	Philolithus porcatus (Papp), 1961	3
48		3	Philolithus rugosus (Papp), 1961	3
49		1	Stenomorpha (Asidina) confluens (LeConte), 1851	3 AZ
50		1	Stenomorpha (Asidina) parallela (LeConte), 1851	3 4 AZ
51		1	Stenomorpha (Asidina) semilaevis (Horn), 1870	3 4 NV AZ ME
52		1	Stenomorpha (Asidina) wickami (Horn), 1894	4 AZ
53	✓	1	Stenomorpha (Pycnomorpha) angulata (LeConte), 1851	5 8
54		1	Stenomorpha (Pycnomorpha) californica (Motschulsky), 1870	5 BC
55		1	Stenomorpha (Pycnomorpha) cressoni (Blaisdell), 1933	4 AZ
56		1	Stenomorpha (Pycnomorpha) gibicollis (LeConte), 1851	5 BC
57	✓	3	Stenomorpha (Stenomorpha) amplicollis (Casey), 1912	6 7 8
58	✓	1	Stenomorpha (Stenomorpha) captiosa (Horn), 1870	6 7 8
59	✓	3	Stenomorpha (Stenomorpha) compressa (Horn), 1870	7
60	✓	3	Stenomorpha (Stenomorpha) crassa (Casey), 1912	6 7 8
61	✓	3	Stenomorpha (Stenomorpha) deceptor (Casey), 1912	6 7 8
62	✓	3	Stenomorpha (Stenomorpha) evanescens (Casey), 1912	2 3 4 9 7
63	✓	3	Stenomorpha (Stenomorpha) gravidipes (Casey), 1912	6 7 8
64	✓	3	Stenomorpha (Stenomorpha) integer (Casey), 1912	6 7 8
65	✓	3	Stenomorpha (Stenomorpha) lecontei (Horn), 1866	2 3 4 9 7
66	✓	3	Stenomorpha (Stenomorpha) lecontella Blaisdell, 1936	2 3 4 9 7
67		1	Stenomorpha (Stenomorpha) marginata (LeConte), 1851	3 AZ NM
68	✓	3	Stenomorpha (Stenomorpha) maritima (Casey), 1912	6 7 8
69	✓	1	Stenomorpha (Stenomorpha) mckittricki (Pierce), 1944	7
70	✓	3	Stenomorpha (Stenomorpha) neutralis (Casey), 1912	2 3 4 9 7
71	✓	3	Stenomorpha (Stenomorpha) speculata Blaisdell, 1936	2 3 4 9 7
72	✓	3	Stenomorpha (Stenomorpha) spurcans (Casey), 1912	2 3 4 9 7
73	✓	3	Stenomorpha (Stenomorpha) subelegans (Casey), 1912	6 7 8
74	✓	3	Stenomorpha (Stenomorpha) tularensis (Casey), 1912	6 7 8
75		3	Stenomorpha (Stethasida) adumbrata Casey, 1912	5 BC AZ
76		3	Stenomorpha (Stethasida) angustula (Casey), 1890	5 BC
77		3	Stenomorpha (Stethasida) brevipes Casey, 1912	5 BC AZ
78		3	Stenomorpha (Stethasida) convergens Casey, 1912	5 BC AZ
79		3	Stenomorpha (Stethasida) discreta Casey, 1912	5 BC AZ
80	✓	3	Stenomorpha (Stethasida) laevigatus (Papp), 1961	5
81		3	Stenomorpha (Stethasida) longula Casey, 1912	5 BC AZ
82		1	Stenomorpha (Stethasida) muricatula (LeConte), 1851	5 BC
83		1	Stenomorpha (Stethasida) obsoleta (LeConte), 1851	5 BC AZ
84		3	Stenomorpha (Stethasida) pertinax Casey, 1912	5 BC
85		3	Stenomorpha (Stethasida) socors Casey, 1912	5 BC
86		3	Stenomorpha (Stethasida) stricta Casey, 1912	5 BC
87		3	Stenomorpha (Stethasida) tarsalis Casey, 1912	5 BC AZ
88		3	Stenomorpha (Stethasida) tenax Casey, 1912	5 BC
89		3	Stenomorpha (Stethasida) torpida Casey, 1912	5 BC AZ
90		1	Stenomorpha (Stethasida) unica Casey, 1912	5 BC AZ
91		3	Stenomorpha (Stethasida) vergrandis Casey, 1912	5 BC
92		1	Stenomorpha (Trichiasida) acerba (Horn), 1878	3 4 AZ UT
93	✓	1	Stenomorpha (Trichiasida) hirsuta (LeConte), 1851	4
94		1	Stenomorpha (Trichiasida) hispidula (LeConte), 1851	3 4 AZ UT
95		1	Stenomorpha (Trichiasida) impetrata (Horn), 1894	4 AZ
96	✓	3	Stenomorpha (Trichiasida) lineatopilosa Casey, 1912	4
97	✓	1	Stenomorpha (Trichiasida) luctata (Horn), 1870	5
Pimeliinae Coniontini				
98		1	Coelus ciliatus Eschscholtz, 1829	5 8 9 OR WA CA
99		1	Coelus globosus LeConte, 1851	5 8 BC
100	✓	1	Coelus gracilis Blaisdell, 1939	7
101	✓	1	Coelus pacificus Fall, 1897	5
102	✓	1	Coniontis abdominalis LeConte, 1859	5 8
103	✓	1	Coniontis affinis LeConte, 1851	8 9 6
104		1	Coniontis blaisdelli Casey, 1908	6 7 8 9 AZ

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).

California Tenebrionidae (January 2014)

#	Endemic CA	Status group	Species	Distribution
105		1	Coniontis callida Casey, 1908	6 9 CA WA OR NV
106	✓	2	Coniontis catalinae Casey, 1908	5
107	✓	2	Coniontis costulata Casey, 1908	8
108	✓	1	Coniontis elliptica Casey, 1884	4 5 6 7
109	✓	1	Coniontis elongata Casey, 1890	4 5 6 7 8 9 1
110	✓	1	Coniontis eschscholtzi Mannerheim, 1840	U
111		1	Coniontis extricata Casey, 1908	5 8 9 OR
112	✓	1	Coniontis farallonica Casey, 1895	8
113	✓	1	Coniontis genitiva Casey, 1890	9
114	✓	1	Coniontis globulina Casey, 1895	5
115	✓	1	Coniontis hoppingi Blaisdell, 1918	6
116	✓	1	Coniontis integer Casey, 1908	5 7
117	✓	1	Coniontis lamentabilis Blaisdell, 1924	5 8 7
118		1	Coniontis lassenica Casey, 1908	9 1 5 NV ID
119	✓	1	Coniontis lata LeConte, 1866	8
120		1	Coniontis microsticta Casey, 1908	8 ID
121	✓	2	Coniontis musculus Blaisdell, 1918	U
122		1	Coniontis nemoralis Eschscholtz, 1840	8 5 6 7 OR
123		1	Coniontis obesa LeConte, 1851	1 2 5 6 9
124		1	Coniontis opaca Horn, 1870	2 NV WA
125		1	Coniontis ovalis LeConte, 1851	1 2 6 7 9 AZ CA CO ID NV OR WA UT
126	✓	1	Coniontis pallidicornis Casey, 1890	5
127	✓	1	Coniontis parallela Casey, 1890	U
128		1	Coniontis parviceps Casey, 1890	5 8 7 BC
129	✓	1	Coniontis pectoralis Casey, 1908	U
130	✓	1	Coniontis puncticollis LeConte, 1851	5 6 7 8 9
131	✓	1	Coniontis remnans Pierce, 1945	5
132	✓	1	Coniontis robusta Horn, 1870	5 6 7 8
133	✓	1	Coniontis sanfordi Blaisdell, 1895	6 8 9
134	✓	1	Coniontis santarosae Blaisdell, 1921	5
135		1	Coniontis setosa Casey, 1890	6 OR WA CA ID UT
136		1	Coniontis subpubescens LeConte, 1851	8 3 5 6 9 OR BC
137	✓	1	Coniontis timida Casey, 1908	8
138	✓	1	Coniontis vandykei Blaisdell, 1921	5
139	✓	1	Coniontis viatica Eschscholtz, 1929	8
140		1	Eusattus costatus Horn, 1870	5 BC
141		1	Eusattus difficilis LeConte, 1851	3 4 5 7 ME AZ NV
142		1	Eusattus dilatatus LeConte, 1851	4 3 AZ ME
143		1	Eusattus dubius arizonensis Doyen, 1984	3 4 AZ NV
144		1	Eusattus dubius dubius LeConte, 1851	3 4 2 NV AZ UT
145		1	Eusattus muricatus muricatus LeConte, 1851	1 2 3 4 9 5 AZ NM TX CO UT NV ID OR WA
146		1	Eusattus phreatophilus Doyen, 1984	3 2 NV
147	✓	1	Eusattus politus Horn, 1883	5
148		1	Eusattus productus LeConte, 1858	4 ME
149		1	Eusattus reticulatus (Say), 1824	4 AZ
150	✓	1	Eusattus robustus LeConte,1866	5
Pimeliinae Edrotini				
151	✓	1	Auchmobius angelicus Blaisdell. 1934	5
152	✓	1	Auchmobius parvicollis Blaisdell. 1934	8
153	✓	1	Auchmobius picipes Blaisdell. 1934	8
154	✓	1	Auchmobius sanfordi Blaisdell. 1934	5
155	✓	1	Auchmobius slevini Blaisdell. 1934	8
156	✓	1	Auchmobius subboreus Blaisdell. 1934	8
157	✓	1	Auchmobius sublaevis LeConte, 1851	2
158		1	Chilometopon abnorme (Horn), 1870	3 4 AZ NV ME
159		1	Chilometopon brachystomum Doyen, 1982	3 4 NV BC
160		1	Chilometopon helopoides Horn, 1874	2 3 4 AZ ID NV NM UT BC
161	✓	1	Chilometopon microps MacLachlan & Olson, 1990	3 4
162		1	Chilometopon pallidum Casey, 1890	3 4 AZ NV NM TX ME BC
163		1	Cryptadius inflatus LeConte, 1851	5 BC
164		1	Edrotes arens La Rivers, 1947	5 AZ
165		1	Edrotes ventricosus LeConte, 1851	3 4 5 AC BC ME ID NV
166	✓	1	Eurymetopon ochraceum Eschscholtz,1831	U type only
167		1	Eurymetopon rufipes Eschscholtz, 1831	U type only
168	✓	1	Hylocrinus blaisdelli Casey, 1890	7 6
169		1	Hylocrinus depressulus Casey, 1907	U
170	✓	1	Hylocrinus filitarsis Casey, 1907	5 4 8
171		1	Hylocrinus longulus LeConte, 1851	5 6 3 5 8 AZ
172		1	Hylocrinus oblongulus Casey, 1907	4 BC
173	✓	1	Hylocrinus piceus Casey, 1890	5
174		2	Melanastus aequicollis Casey,1907	9 NV
175	✓	1	Melanastus ater (LeConte), 1851	9 8
176		2	Melanastus crassicornis (Casey), 1907	9 OR
177	✓	2	Melanastus exoletus Casey,1907	5
178	✓	2	Melanastus lucidulus Casey,1907	8
179		2	Melanastus moestus Casey,1907	8 UT
180		1	Melanastus obesus (LeConte), 1851	5 8 7 BC
181	✓	1	Melanastus obtusus (LeConte), 1866	5 8 7
182	✓	2	Melanastus otiosus Casey,1907	8
183	✓	2	Melanastus sterilis Casey,1907	3
184	✓	2	Melanastus thoracicus (Casey), 1907	5
185	✓	1	Melanastus vergrandis Casey,1907	6
186		1	Metoponium abnorme LeConte, 1851	4 ME
187		1	Metoponium bicolor Horn, 1870	7 3 AZ
188	✓	2	Metoponium concors Casey,1907	3
189		2	Metoponium convexicolle LeConte, 1851	7 5 3 AZ
190	✓	2	Metoponium cylindricum Casey, 1890	3
191	✓	2	Metoponium dubium Casey, 1884	4
192	✓	2	Metoponium edax Casey,1907	5
193	✓	2	Metoponium egregium Casey,1907	4
194	✓	2	Metoponium extensum Casey,1907	U
195	✓	2	Metoponium faustum Casey,1907	3 4
196		2	Metoponium fusculum Casey, 1890	4 AZ
197	✓	2	Metoponium gravidum Casey,1907	3
198	✓	2	Metoponium gulosum Casey,1907	7
199		2	Metoponium hebes Casey,1907	4 AZ
200	✓	2	Metoponium insulare Casey,1907	5
201	✓	2	Metoponium integer Casey,1907	4
202	✓	2	Metoponium molestum Casey,1907	4
203	✓	2	Metoponium opacipenne Casey,1907	3 4
204	✓	2	Metoponium probatum Casey,1907	5
205	✓	2	Metoponium tersum Casey,1907	5
206	✓	2	Metoponium testaceum Casey,1907	3
207		1	Micromes maritimus (Casey), 1891	5 BC
208		1	Micromes ovipennis (Horn), 1870	5 BC
209	✓	0	Oxygonodera n.sp.	2
210	✓	2	Stibia blairi Blaisdell, 1936	U type only (BMNH)
211		1	Stibia imperialis Blaisdell, 1936	4 BC
212		1	Stibia puncticollis Horn, 1870	5 BC
213		3	Stibia tanneri Blaisdell, 1936	6
214	✓	1	Telabis fidelis Casey, 1907	4

Figure 1. Continue.

California Tenebrionidae (January 2014)

#	Endemic CA	Status group	Species	Distribution
215		1	Telabis incisa Casey, 1907	4 NV
216	✓	1	Telabis opacella Casey, 1907	5
217		1	Telabis punctulata LeConte, 1866	3 AZ
218		1	Telabis serrata (LeConte), 1866	3 4 BC ME AZ UT NV
219		1	Telabis sodalis Horn, 1870	3 4 AZ
220		1	Triorophus laevis LeConte, 1851	3 4 AZ NV ME UT BC
221		1	Triorophus rugiceps LeConte, 1851	2 3 7 8 6 5 NV
222		1	Triphalopsis californicus Doyen, 1982	4 BC
Pimeliinae Epitragini				
223		1	Bothrotes plumbeaus tenebriosus Casey, 1907	5 AZ
224		1	Metopoloba pruinosa pruinosa (Horn), 1870	3 4 AZ NV ME BC
225		1	Polemiotus submetallicus (LeConte), 1854	4 AZ ME
Pimeliinae Anepsiini				
226		1	Anchomma costatum LeConte, 1858	3 5 6 7 NV
227		1	Anepsius delicatulus LeConte, 1851	8 5 7 2 3 4 BC AZ UT NV
228	✓	1	Batuliodes obesus Doyen, 1987	3 4
229		1	Batuliodes rotundicollis (LeConte), 1851	3 4 BC AZ
230		1	Batuliodes spatulatus Doyen, 1987	3 4 BC AZ
231		1	Batuliodes wasbaueri Doyen, 1987	4 BC
232		1	Batuliomorpha comatus Doyen, 1987	3 BC
233	✓	1	Batuliomorpha imperialis Doyen, 1987	4
234		1	Batulius setosus LeConte, 1851	3 4 BC AZ
Pimeliinae Vacronini				
235		1	Alaephus gracilis Fall, 1905	8 5 3 AZ
236	✓	1	Alaephus longicornis Casey, 1924	5
237		1	Alaephus macilentus Casey, 1891	3 ME NM AZ
238	✓	1	Alaephus maderensis Casey, 1924	5
239		1	Alaephus pallidus Horn, 1870	7 6 2 UT
240		1	Alaephus puberulus Fall, 1907	5 UT
241		1	Eupsophulus castaneus Horn, 1870	3 4 ME BC AZ
Pimeliinae Cnemodini				
242		1	Cnemodinus testaceus Horn, 1870	3 4 AZ
Lagriinae Lagriini				
243	✓	1	Statira dumalis Parsons,1973	4
244		1	Statira latitator Parsons,1973	4 BC
245		1	Statira pluripunctata Horn, 1888	4 AZ NM TX ME
Lagriinae Goniaderini				
246	✓	0	Eschatoporis n.sp. Aalbu m.s.	9
247	✓	1	Eschatoporis nunenmacheri Blaisdell, 1906	8
Lagriinae Laenini				
248	✓	1	Eschatomoxys andrewsi Aalbu & Thomas, 2007	4
249		1	Eschatomoxys wagneri Blaisdell, 1935	3 4 AZ UT
Phrenapatinae Penetini				
250		1	Clamoris americana (Horn), 1874	9 4 OR
Diaperinae Phaleriini				
251		1	Phaleria debilis LeConte, 1866	4 ME
252		1	Phaleria rotundata LeConte,1851	5 8 BC
253		1	Phaleromela globosa (LeConte), 1857	8 9 CA OR WA
254		1	Phaleromela humeralis (Laporte), 1840	3 ASIA
255		1	Phaleromela prohumeralis Triplehorn, 1961	U OR
256		1	Phaleromela variegata Triplehorn, 1961	9 4 CA OR WA
Diaperinae Diaperini				
257		1	Alphitophagus bifasciatus (Say), 1824	C
258		1	Cynaeus angustus (LeConte), 1851	5 AZ UT ME
259		1	Cynaeus depressus Horn, 1870	5 AZ BC
260	✓	1	Diaperis californica Blaisdell, 1929	6
261	✓	1	Pentaphyllus californicus Horn, 1870	6
262		1	Platydema americanum Laporte & Brulle, 1831	6 AZ ID CA NM TX UT WA +
263	✓	1	Platydema neglectum Triplehorn, 1965	1 6 5 2
264		1	Platydema oregonense LeConte, 1857	5 6 7 9 CA OR WA
265		1	Sitophagus hololeptoides Laporte, 1840	C
Diaperinae Crypticini				
266		1	Gondwanocrypticus platensis (Fairmaire), 1883	C 5 SA
Diaperinae Myrmechixenini				
267		1	Myrmechixenis lathridioides Crotch, 1873	6 8 TX +
Diaperinae Hypophloeini				
268		1	Corticeus hatchi Boddy, 1957	9 OR
269		1	Corticeus opaculus (LeConte), 1878	8 5 AZ
270		1	Corticeus praetermissus (Fall), 1926	1 2 4 5 6 7 8 9 AZ BC NM UT NV ID OR WA CA +
271		1	Corticeus strublei Blaisdell, 1934	3 6 9 WA ID UT AZ NM +
272		1	Corticeus substriatus (LeConte), 1852	1 2 3 5 6 7 8 9 ME AZ NM UT NV ID WA OR CA +
273		1	Corticeus tenuis (LeConte), 1878	6 OR WA CA AZ ID +
Tenebrioninae Bolitophagini				
274		1	Eleates explanatus Casey, 1890	6 7 9 OR WA CA ID
275		1	Eleates occidentalis Casey. 1886	6 8 WA
276		1	Megeleates sequoiarum Casey,1895	9 6 7 5 3 BC OR
Tenebrioninae Opatrini				
277		1	Blapstinus brevicollis LeConte, 1851	2 3 4 5 6 7 8 AZ
278		1	Blapstinus castaneus Casey, 1890	5 AZ
279		3	Blapstinus coronadensis Blaisdell, 1892	5
280		1	Blapstinus dilatatus LeConte, 1851	2 3 4 5 6 7 8 AZ NV UT
281		1	Blapstinus discolor Horn, 1870	9 8 7 6 5 4 3 2 1 NV OR ID UT WA CA
282		1	Blapstinus histricus Casey, 1890	4 5 7 8 AZ NV
283	✓	1	Blapstinus lecontei Mulsant & Rey, 1859	5
284		1	Blapstinus pimalis Casey, 1885	5 8 AZ NM TX CO UT NV
285		1	Blapstinus pulverulentus Mannerheim, 1843	9 OR WA
286		1	Blapstinus substriatus Champion, 1885	1 9 6 AR NV NM TX CO UT WY ID OR WA MT CA
287		1	Blapstinus sulcatus LeConte, 1851	2 3 4 5 6 7 8 AZ NV
288		1	Blapstinus vandykei Blaisdell, 1942	2 3 4 5 AZ
289		1	Cheirodes californica (Horn), 1870	2 3 4 7 AZ NV
290		1	Conibiosoma elongatum Horn, 1870	3 5 7 4
291		0	Conibius n.sp.	7 OR
292		1	Conibius seriatus LeConte, 1851	3 4 5 7 8 BC
293		1	Gonocephalum sp.	5 OW
294		1	Mecysmus angustus (LeConte), 1851	3 4 5 8 BC
295		1	Mecysmus tenuis Casey,1890	5 BC
296		1	Nocibiotes crassipes (Casey), 1890	4 BC
297		1	Nocibiotes granulatus (LeConte), 1851	3 4 AZ

Figure 1. Continue.

California Tenebrionidae (January 2014)

#	Endemic CA	Status group	Species	Distribution
298	☐	1	Notibius laticeps Casey, 1890	4 AZ BC
299	☐	1	Notibius puberulus LeConte, 1851	3 4 AZ
300	☐	1	Notibius puncticollis LeConte, 1851	7 5 3 NV
301	☐	1	Opatroides punctulatus Brullé, 1832	7 OW
302	☐	1	Tonibius sulcatus LeConte, 1851	3 5 BC
303	☐	1	Trichoton sordidum (LeConte), 1851	4 AZ BC ME NM
304	☐	1	Ulus crassus LeConte, 1851	8 5 7 BC ME ZA NM TX

Tenebrioninae Amphidorini

#	Endemic CA	Status group	Species	Distribution
305	☑	1	Eleodes (Blapylis) aristatus Somerby 1977	2
306	☑	1	Eleodes (Blapylis) bishopensis Somerby & Doyen 1976	5
307	☐	1	Eleodes (Blapylis) blanchardii Blaisdell 1909	5 6 AZ
308	☐	1	Eleodes (Blapylis) brunnipes Casey 1890	6 9 AZ NM CO UT NV OR WA ID WY
309	☐	1	Eleodes (Blapylis) caseyi Blaisdell 1909	2 5 NV
310	☑	1	Eleodes (Blapylis) clavicornis Eschscholtz 1833	5 8
311	☑	1	Eleodes (Blapylis) consobrinus LeConte 1851	5 6 8
312	☑	1	Eleodes (Blapylis) cooperi Somerby & Doyen 1976	6
313	☐	1	Eleodes (Blapylis) cordatus Eschscholtz 1863	9 6 8 5 OR
314	☑	1	Eleodes (Blapylis) fuchsii Blaisdell 1909	5 8
315	☐	1	Eleodes (Blapylis) hoppingi Blaisdell 1909	6 2 NV AR
316	☑	1	Eleodes (Blapylis) hornii Blaisdell 1909	6 2 1
317	☑	1	Eleodes (Blapylis) incultus LeConte 1861	5
318	☑	1	Eleodes (Blapylis) kaweanus Blaisdell 1933	6
319	☑	1	Eleodes (Blapylis) lariversi Somerby & Doyen 1976	6
320	☑	1	Eleodes (Blapylis) littoralis Eschscholtz 1831	5 6 7 8
321	☐	1	Eleodes (Blapylis) neotomae Blaisdell 1909	5 5 BC
322	☐	1	Eleodes (Blapylis) nigropilosa (LeConte) 1851	5 8 BC
323	☑	1	Eleodes (Blapylis) panamintensis Somerby 1977	3
324	☑	1	Eleodes (Blapylis) parvicollis Eschscholtz 1829	6
325	☐	1	Eleodes (Blapylis) pimelioides Mannerheim 1843	1 3 5 8 CA AZ CO ID OR UT WA WY
326	☐	1	Eleodes (Blapylis) propinquus Blaisdell 1918	1 OR
327	☑	1	Eleodes (Blapylis) scabripennis LeConte 1859	5 6
328	☑	1	Eleodes (Blapylis) scabriventris Blaisdell 1933	6 7 8
329	☐	1	Eleodes (Blapylis) scabrosus Eschscholtz 1833	8 9 OR WA
330	☑	1	Eleodes (Blapylis) schlingeri Somerby & Doyen 1976	6
331	☑	1	Eleodes (Blapylis) spilmani Somerby & Doyen 1976	9
332	☑	1	Eleodes (Blapylis) subtestitus Blaisdell 1939	5
333	☐	1	Eleodes (Blapylis) tenebrosus (Horn) 1870	1 2 6 NV UT OR ID
334	☐	1	Eleodes (Blapylis) versatilis Blaisdell 1921	9 OR
335	☐	1	Eleodes (Blapylis) volcanensis Somerby 1977	9 OR
336	☑	1	Eleodes (Caverneleodes) microps Aalbu et al., 2012	2
337	☐	1	Eleodes (Cratidus) osculans (LeConte) 1851	5 8 BC
338	☑	1	Eleodes (Discogenia) marginatus Eschscholtz 1833	6 5 8
339	☐	1	Eleodes (Discogenia) scabriculus LeConte 1858	6 7 OR NV
340	☐	1	Eleodes (Eleodes) acuticaudus LeConte 1851	8 5 BC
341	☐	1	Eleodes (Eleodes) armatus LeConte 1851	7 8 2 3 4 5 AZ NV BC ME BC
342	☐	1	Eleodes (Eleodes) dentipes Eschscholtz 1833	9 8 7 6 1 5 OR
343	☐	1	Eleodes (Eleodes) gracilis LeConte 1858	5 3 8 2 4 NV AZ NM TX UT CO
344	☐	1	Eleodes (Eleodes) grandicollis Mannerheim 1843	8 5 4 BC
345	☐	1	Eleodes (Eleodes) hispilabris Say 1824	9 8 7 AR CA NM TX UT WA OR NV CO ID +
346	☐	1	Eleodes (Eleodes) moestus Blaisdell 1921	5 BC
347	☐	1	Eleodes (Eleodes) obscurus Say 1824	1 2 AZ ME CO ID NV OR TX UT WA +
348	☐	1	Eleodes (Eleodes) subcylindricus Casey 1890	2 3 4 NV
349	☑	1	Eleodes (Litheleodes) corvinus Blaisdell 1921	1
350	☐	1	Eleodes (Litheleodes) granulatus LeConte 1857	9 OR
351	☐	1	Eleodes (Litheleodes) letcheri Blaisdell 1909	1 2 NV ID
352	☑	1	Eleodes (Litheleodes) papillosus Blaisdell 1917	9
353	☐	1	Eleodes (Litheleodes) vandykei Blaisdell 1909	1 9 OR WA NV AR
354	☐	1	Eleodes (Melaneleodes) carbonarius (Say) 1823	3 4 5 ME AR UT NV BC TX NM ID
355	☐	1	Eleodes (Melaneleodes) humeralis LeConte 1857	9 CA WA OR NV CO U
356	☑	1	Eleodes (Melaneleodes) quadricollis Eschscholtz 1833	8
357	☐	1	Eleodes (Melaneleodes) rileyi Casey 1891	2 NV AZ UT NM ID OR
358	☑	1	Eleodes (Metablapylis) aalbui Triplehorn 2007	2
359	☐	1	Eleodes (Metablapylis) californicus Blaisdell 1929	3 5 AZ
360	☐	1	Eleodes (Metablapylis) dissimilis Blaisdell 1909	3 ME NV AZ
361	☑	0	Eleodes (Metablapylis) n.sp.	5
362	☐	1	Eleodes (Metablapylis) nigrinus LeConte 1858	1 2 CA AZ CO ID MT NV NM OR UT WA WY
363	☐	1	Eleodes (Pseudeleodes) granosus LeConte 1866	2 3 4 NV ID
364	☐	1	Eleodes (Pseudeleodes) inyoensis Tanner 1961	2 NV
365	☑	1	Eleodes (Steneleodes) gigantea Mannerheim 1843	6 7 8 9
366	☐	1	Eleodes (Tricheleodes) hirsutus LeConte 1861	2 3 NV
367	☐	1	Eleodes (Tricheleodes) obesus Doyen 1985	9 1 OR
368	☐	1	Eleodes (Tricheleodes) pilosus Horn, 1870	1 2 3 9 NV UT
369	☑	1	Eleodimorpha bolcan Blaisdell, 1909	5
370	☐	1	Embaphion depressum LeConte, 1858	4 3 AZ
371	☐	1	Embaphion elongatum Horn, 1870	2 NV
372	☐	0	Lariversius n.sp.	3 NV
373	☐	1	Lariversius tibialis Blaisdell, 1947	2 NV
374	☐	1	Neobaphion elongatum Blaisdell, 1933	2 NV
375	☐	1	Trogloderus costatus LeConte, 1879	3 2 NV
376	☐	1	Trogloderus costatus mayhewi Papp, 1961	3 NV
377	☑	2	Trogloderus costatus pappi Kulzer, 1960	3

Tenebrioninae Cerenopini

#	Endemic CA	Status group	Species	Distribution
378	☐	1	Cerenopus concolor LeConte, 1851	3 4 ME AZ

Tenebrioninae Eulabini

#	Endemic CA	Status group	Species	Distribution
379	☑	1	Apsena barbarae Blaisdell, 1932	5
380	☑	1	Apsena crassicornis (Casey), 1890	5
381	☑	1	Apsena grossa (LeConte), 1866	5
382	☑	1	Apsena laticornis (Casey), 1891	5
383	☑	1	Apsena leachi Blaisdell, 1932	6
384	☐	1	Apsena pubescens (LeConte),1851	5 BC
385	☑	1	Apsena rufipes rufipes (Eschscholtz), 1829	5 6 7 8
386	☑	1	Apsena rufipes simplex Blaisdell, 1932	8
387	☐	1	Argoporis apicalis californica Berry, 1851	4 AZ ME
388	☐	1	Argoporis bicolor (LeConte), 1851	3 4 AZ
389	☐	1	Epantius obscurus LeConte, 1851	5 8 9 BC
390	☑	1	Eulabis bicarinata Eshscholtz, 1829	8 9 6 7

Tenebrioninae Ulomini

#	Endemic CA	Status group	Species	Distribution
391	☐	1	Uloma longula LeConte, 1861	5 9 6 7 OR

Tenebrioninae Helopini

#	Endemic CA	Status group	Species	Distribution
392	☑	1	Helops angustus LeConte, 1859	5
393	☐	1	Helops attenuatus (LeConte),1851	3 4 NV AZ
394	☑	1	Helops bachei LeConte, 1861	5
395	☐	1	Helops blaisdelli Casey, 1891	5 BC
396	☑	1	Helops californicus Mannerheim, 1843	9 8 6 7
397	☐	1	Helops confluens (Casey), 1924	5 BC
398	☑	1	Helops discipula Casey, 1891	3 4 5

Figure 1. Continue.

California Tenebrionidae (January 2014)

#	Endemic CA	Status group	Species	Distribution
399		1	Helops edwardsi Horn, 1870	3 5 OR
400	✓	1	Helops fresnoensis Blaisdell, 1931	7
401		1	Helops laetus LeConte, 1857	8 WA
402	✓	1	Helops obtusangula Blaisdell, 1921	5 8
403	✓	1	Helops opacus LeConte, 1859	1 9 6 5 7
404	✓	1	Helops punctipennis LeConte, 1866	6
405		1	Helops rufipes (LeConte), 1851	5 BC
406	✓	1	Helops rugicollis LeConte, 1866	5
407	✓	1	Helops rugulosus LeConte, 1866	5 7 9 6
408	✓	1	Helops simulator Blaisdell, 1921	6
409		1	Helops spretus Horn, 1880	2 NV
410	✓	1	Helops stenotrichoides Blaisdell, 1895	6 8
411	✓	1	Helops strigicollis Horn, 1885	3 4
412		1	Helops tumescens LeConte, 1866	3 4 AZ

Tenebrioninae Triboliini

#	Endemic CA	Status group	Species	Distribution
413		1	Gnathocerus cornutus (Fabricius) 1801	C
414		1	Gnathocerus maxillosus (Fabricius) 1801	C
415		1	Latheticus oryzae Chittenden, 1880	C
416		1	Latheticus prosopis Chittenden, 1904	C
417		1	Lyphia tetraphylla (Fairmaire,1856)	C
418		1	Mycotrogus angustus Horn, 1870	4 AZ
419		1	Mycotrogus piceus Horn, 1870	4 BC
420		1	Palorus ratzeburgii (Wissnmann), 1848	C
421		1	Palorus subdepressus Wollaston, 1864	C
422		1	Tharsus seditiosus LeConte, 1866	C
423		1	Tribolium audax Uyttenboogsart, 1933	C
424		1	Tribolium brevicorne (LeConte), 1859	C
425		1	Tribolium castaneum Herbst, 1797	C
426		1	Tribolium confusum Jacquelin du Val, 1868	C
427		1	Tribolium destructor Uyttenboogsart, 1933	C
428		1	Tribolium madens (Charpentier), 1825	C

Tenebrioninae Apocryphini

#	Endemic CA	Status group	Species	Distribution
429	✓	1	Apocrypha anthicoides Eschscholtz, 1831	9 8 5 7 6
430		1	Apocrypha clivinoides Horn, 1870	2 NV
431	✓	1	Apocrypha setosa Doyen & Kityama, 1980	8

Tenebrioninae Alphitobiini

#	Endemic CA	Status group	Species	Distribution
432		1	Alphitobius diaperinus (Panzer), 1797	C
433		1	Alphitobius laevigatus Fabricius, 1781	C
434		1	Metaclisa marginalis Horn, 1870	5 6 8 1 7 9 BC
435		1	Bius estriatus LeConte, 1851	7 8 2 NV BC
436	✓	0	Neatus n.sp.	6 8
437		1	Tenebrio molitor Linnaeus, 1758	C
438		1	Tenebrio obscurus Fabricius,1792	C

Tenebrioninae Centronopini

#	Endemic CA	Status group	Species	Distribution
439		1	Scotobaenus parallelus LeConte,1859	9 6 OR
440	✓	1	Scotobaenus punctatus (Blaisdell), 1933	6
441	✓	1	Scotobaenus simplex (Blaisdell), 1937	6
442	✓	1	Scotobaenus wagneri (Blaisdell), 1933	6

Alleculinae Alleculini

#	Endemic CA	Status group	Species	Distribution
443		1	Hymenorus apacheanus Casey, 1891	3 4 AZ
444	✓	1	Hymenorus discrepans Casey, 1891	5
445		1	Hymenorus exiguus Casey, 1891	4 AZ
446	✓	1	Hymenorus fusculus Casey, 1891	5 6
447	✓	1	Hymenorus fusicornis Casey, 1891	5
448	✓	1	Hymenorus infuscatus Casey, 1891	5
449	✓	1	Hymenorus inquilinus Casey, 1891	6
450	✓	1	Hymenorus irritus Fall, 1931	5 8
451	✓	1	Hymenorus jacobinus Fall, 1931	U
452	✓	1	Hymenorus montivagus Fall, 1931	U
453	✓	1	Hymenorus parvus Fall, 1931	3
454		1	Hymenorus protibialis Fall, 1931	3 4 AZ
455		1	Hymenorus punctatissimus LeConte, 1866	3 4 NM TX UT AZ
456	✓	1	Hymenorus punctulatus (LeConte), 1859	6
457	✓	1	Hymenorus rufohumeralis Campbell, 1982	8
458		1	Hymenorus sinuatus Fall, 1931	9 OR
459		1	Hymenorus thoracicus Fall, 1931	4 AZ
460	✓	1	Hymenorus ulomoides Fall, 1931	U
461	✓	1	Hymenorus uniseriatus Casey, 1891	U
462		1	Isomira comstocki Papp, 1956	7 6 9 8 5 1 CA ME ID OR UT WA
463	✓	1	Isomira damnata Marshall, 1970	6 7
464	✓	1	Isomira luscitiosa Casey, 1891	5 8 6
465	✓	1	Isomira monticola Casey, 1891	U
466	✓	1	Isomira variabilis (Horn),1875	8 9 6 5
467	✓	1	Mycetochara marshalli Campbell, 1978	7
468		1	Mycetochara procera Casey, 1891	9 6 CA AZ ID OR WA
469	✓	1	Mycetochara pubipennis (LeConte), 1878	5
470	✓	1	Pseudocistela opaca LeConte, 1859	9 8 6 5 3
471		1	Pseudocistela pacifica Hopping, 1933	9 CA OR WA
472		1	Pseudocistela pinguis LeConte, 1866	5 WA CA OR
473		1	Stenochidius cyanescens LeConte, 1859	9 8 6 OR ID
474	✓	1	Stenochidius gracilis LeConte, 1851	6 5 8
475	✓	1	Stenochidius robustus Schaeffer, 1911	8 9 7 6

Stenochiinae Cnodalonini

#	Endemic CA	Status group	Species	Distribution
476		1	Alobates pennsylvanicus (DeGeer), 1775	5 BC
477	✓	1	Cibdelis bachei LeConte, 1861	9 8 7 6
478	✓	1	Cibdelis blaschkei Mannerheim, 1843	8
479		1	Coelocnemis californica Mannerheim, 1843	5 8 9 6 CA ME ID NV OR UT
480	✓	1	Coelocnemis lucia Doyen, 1973	8
481		1	Coelocnemis magna LeConte, 1851	5 8 9 6 2 AZ NM
482		1	Coelocnemis punctata LeConte, 1855	1 2 3 NV UT AZ
483		1	Coelocnemis rugulosa Doyen, 1973	1 OR
484		1	Coelocnemis sulcata Casey, 1895	2 3 NV AZ UT
485		1	Iphthiminus laevissimus (Casey), 1890	5 6 9 3 1 OR
486		1	Iphthiminus serratus Mannerheim, 1843	1 9 6 5 AZ WY WA UT OR NM MT ID CO

Figure 1. Continue.

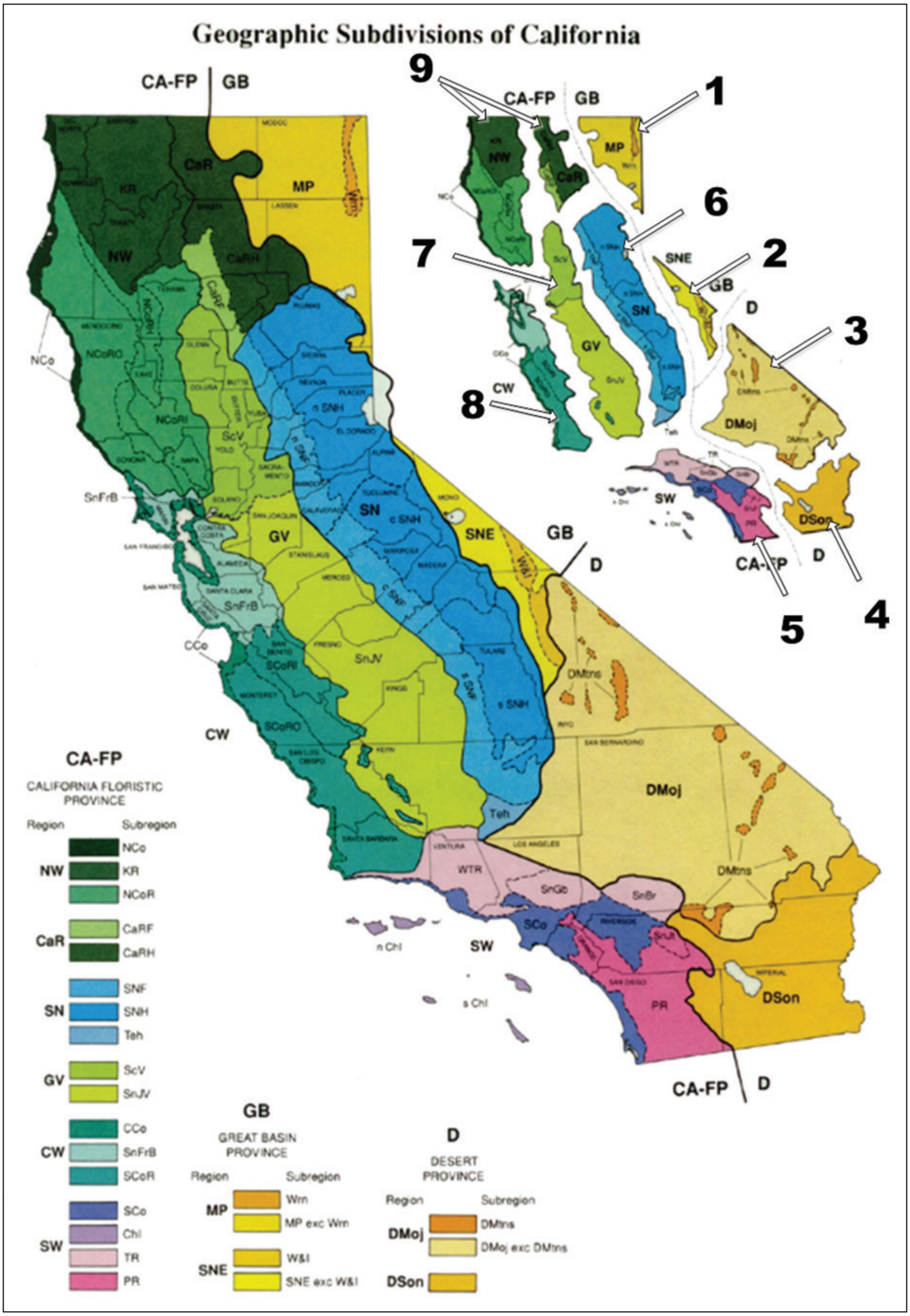

Figure 2. Geographic subdivisions of California from http://ucjeps.berkeley.edu/cguide.html#Map with Unit Boundaries with regions 1–9 outlined.

Regional Endemic California Tenebrionidae (January 2014)

REGION — Species present, Percent endemic

1: The Northern Great Basin Province — 29: 3.45%

including the Warner Mountains and Modoc Plateau

1 Eleodes (Litheleodes) corvinus Blaisdell 1921

2: The Southern Great Basin Province — 55: 9.09%

including the White and Inyo Mountains and intermountain valleys east of the Sierras Nevada's and White Mountains

1 Auchmobius sublaevis LeConte, 1851
2 Eleodes (Blapylis) aristatus Somerby 1977
3 Eleodes (Caverneleodes) microps Aalbu et al., 2012
4 Eleodes (Metablapylis) aalbui Triplehorn 2007
5 Oxygonodera n.sp.

3: The Mojave Desert — 112: 10.71%

and associated desert mountains

1 Araeoschizus lariversi Papp, 1981
2 Eleodes (Blapylis) panamintensis Somerby 1977
3 Hymenorus parvus Fall, 1931
4 Melanastus sterilis Casey,1907
5 Metoponium concors Casey,1907
6 Metoponium cylindricum Casey, 1890
7 Metoponium gravidum Casey,1907
8 Metoponium testaceum Casey,1907
9 Philolithus jaegeri (Papp), 1961
10 Philolithus opimus Casey, 1912
11 Trogloderus costatus pappi Kulzer, 1960
12 Typhleusechus chemehuevii Aalbu & Andrews, 1985

4: The Sonoran (Colorado) Desert — 113: 11.50%

and associated desert mountains

1 Araeoschizus andrewsi Papp, 1981
2 Araeoschizus hardyi Papp, 1981
3 Araeoschizus hystrix Papp, 1981
4 Batuliomorpha imperialis Doyen, 1987
5 Eschatomoxys andrewsi Aalbu & Thomas, 2007
6 Lepidocnemeplatia n.sp.
7 Metoponium dubium Casey, 1884
8 Metoponium egregium Casey,1907
9 Metoponium integer Casey,1907
10 Metoponium molestum Casey,1907
11 Statira dumalis Parsons,1973
12 Stenomorpha (Trichiasida) hirsuta (LeConte), 1851
13 Telabis fidelis Casey, 1907

5: The South Coast — 170: 24.12%

including the Transverse and Peninsular Ranges and Channel Islands

1 Alaephus longicornis Casey, 1924
2 Alaephus maderensis Casey, 1924
3 Alaudes alternata Fall, 1928
4 Apsena barbarae Blaisdell, 1932
5 Apsena crassicornis (Casey), 1890
6 Apsena grossa (LeConte), 1866
7 Apsena laticornis (Casey), 1891
8 Araeoschizus doyeni Papp, 1981
9 Araeoschizus exiguus Casey, 1907
10 Auchmobius angelicus Blaisdell. 1934
11 Auchmobius sanfordi Blaisdell. 1934
12 Blapstinus lecontei Mulsant & Rey, 1859
13 Coelus pacificus Fall, 1897
14 Coniontis catalinae Casey, 1908
15 Coniontis globulina Casey, 1895
16 Coniontis pallidicornis Casey, 1890
17 Coniontis remnans Pierce, 1945
18 Coniontis santarosae Blaisdell, 1921
19 Coniontis vandykei Blaisdell, 1921
20 Eleodes (Blapylis) bishopensis Somerby & Doyen 1976
21 Eleodes (Blapylis) incultus LeConte 1861
22 Eleodes (Blapylis) subtestitus Blaisdell 1939
23 Eleodes (Metablapylis) n.sp.
24 Eleodimorpha bolcan Blaisdell, 1909
25 Eusattus politus Horn, 1883
26 Eusattus robustus LeConte,1866
27 Helops angustus LeConte, 1859
28 Helops bachei LeConte, 1861
29 Helops rugicollis LeConte, 1866
30 Hylocrinus piceus Casey, 1890
31 Hymenorus discrepans Casey, 1891
32 Hymenorus fusicornis Casey, 1891
33 Hymenorus infuscatus Casey, 1891
34 Melanastus exoletus Casey,1907
35 Melanastus thoracicus (Casey), 1907
36 Metoponium edax Casey,1907
37 Metoponium insulare Casey,1907
38 Metoponium probatum Casey,1907
39 Metoponium tersum Casey,1907
40 Mycetochara pubipennis (LeConte), 1878
41 Stenomorpha (Trichiasida) luctata (Horn), 1870
42 Telabis opacella Casey, 1907

6: The Sierra Nevada Mountains — 100: 16.00%

1 Apsena leachi Blaisdell, 1932
2 Diaperis californica Blaisdell, 1929
3 Eleodes (Blapylis) cooperi Somerby & Doyen 1976
4 Eleodes (Blapylis) kaweanus Blaisdell 1933
5 Eleodes (Blapylis) lariversi Somerby & Doyen 1976
6 Eleodes (Blapylis) parvicollis Eschscholtz 1829
7 Eleodes (Blapylis) schlingeri Somerby & Doyen 1976
8 Helops punctipennis LeConte, 1866
9 Helops simulator Blaisdell, 1921
10 Hymenorus inquilinus Casey, 1891
11 Hymenorus punctulatus (LeConte), 1859
12 Melanastus vergrandis Casey,1907
13 Pentaphyllus californicus Horn, 1870
14 Scotobaenus punctatus (Blaisdell), 1933
15 Scotobaenus simplex (Blaisdell), 1937
16 Scotobaenus wagneri (Blaisdell), 1933

7: The Central Valley — 76: 6.58%

1 Coelus gracilis Blaisdell, 1939
2 Helops fresnoensis Blaisdell, 1931
3 Metoponium gulosum Casey,1907
4 Mycetochara marshalli Campbell, 1978
5 Stenomorpha (Stenomorpha) mckittricki (Pierce), 1944

8: The Central Coast — 110: 18.18%

including the San Francisco Bay area and Coast Ranges

1 Apocrypha setosa Doyen & Kityama, 1980
2 Apsena rufipes simplex Blaisdell, 1932
3 Araeoschizus sulcicollis disjunctus Papp, 1981
4 Auchmobius parvicollis Blaisdell. 1934
5 Auchmobius picipes Blaisdell. 1934
6 Auchmobius slevini Blaisdell. 1934
7 Auchmobius subboreus Blaisdell. 1934
8 Cibdelis blaschkei Mannerheim, 1843
9 Coelocnemis lucia Doyen, 1973
10 Coniontis costulata Casey, 1908
11 Coniontis farallonica Casey, 1895
12 Coniontis hoppingi Blaisdell, 1918
13 Coniontis lata LeConte, 1866
14 Coniontis timida Casey, 1908
15 Coniontis viatica Eschscholtz, 1929
16 Eleodes (Melaneleodes) quadricollis Eschscholtz 1833
17 Eschatoporis nunenmacheri Blaisdell, 1906
18 Hymenorus rufohumeralis Campbell, 1982
19 Melanastus lucidulus Casey,1907
20 Melanastus otiosus Casey,1907

9: The Northern Coast — 73: 5.48%

including the Cascade and Klamath Ranges as well as the Northern Coast Ranges

1 Coniontis genitiva Casey, 1890
2 Eleodes (Blapylis) spilmani Somerby & Doyen 1976
3 Eleodes (Litheleodes) papillosus Blaisdell 1917
4 Eschatoporis n.sp. Aalbu m.s.

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

Aalbu RL (2005) The pimeliine tripe Cryptoglossini: classification, biology and inferred phylogeny (Coleoptera: Tenebrionidae). Annales Zoologici 55: 677–756.

Aalbu RL, Smith AD, Triplehorn CA (2012) A Revision of the *Eleodes* Subgenus *Caverneleodes* with new species and notes on cave breeding *Eleodes* (Tenebrionidae: Amphidorini). Annales Zoologici (Warszawa) 62(2): 199–216. doi: 10.3161/000345412X652729

Aalbu RL, Kanda K, Steiner WE Jr. (2009) *Opatroides punctulatus* Brullé now esablished in California (Coleoptera: Tenebrionidae). Pan-Pacific Entomol. 85(2):38–42. doi: 10.3956/2008-24.1

Aalbu RL, Triplehorn CA, Campbell JM, Brown KW, Somerby R, Thomas DB (2002) 106. Tenebrionidae. In: Volume 2 of Arnett R et al. The Beetles of the United States. CRC press, New York, 463–509.

Brown KW, Doyen JT (1991) Review of the genus *Microschatia* (Solier) (Tenebrionidae: Coleoptera). J. New York. Entomol. Soc. 99: 539–582.

Doyen JT (1973) Systematics of the Genus *Coelocnemis*: A Quantitative Study of Variation. Univ. of Calif. publications in entomology 73: 1–110.

Doyen JT (1984) Systematics of *Eusattus* and *Conisattus* (Coleoptera; Tenebrionidae; Coniontini; Eusatti). Occ. Pap. Calif. Acad. Sci. No. 141, 104 pp.

Doyen JT (1987) Review of the tenebrionid tribe Anepsiini (Coleoptera). Proceedings of the California Academy of Sciences 44: 343–371

Geographic subdivisions of California, Jepson Flora Project (Eds) [2013] Jepson eFlora, http://ucjeps.berkeley.edu/IJM.html [accessed on December 9, 2013]

Pape RB, Aalbu RL, Thomas DB (2007) A Revision of the Genus *Eschatomoxys* Blaisdell (Tenebrionidae: Pimeliinae: Edrotini)) with notes on the biology of a new species. Coleop. Bull. 61(4): 519–540. doi: 10.1649/0010-065X(2007)61[519:AROTGE]2.0.CO;2

Papp CS (1981) Revision of the genus *Araeoschizus* LeConte (Coleoptera: Tenebrionidae). Ent. Arb. Mus. Frey 29: 273–420.

Smith AD (2013) Phylogenetic revision of the North American Asidini (Coleoptera: Tenebrionidae). Sys. Entomol.

Thomas DB (2005) Blaisdell's formae and homonyms in the genus *Eleodes* Eschscholtz (Coleoptera; Tenebrionidae: Embaphionini). Annales Zoologici 55(4): 549–560.

Triplehorn CA (2007) New species of *Eleodes* (Coleoptera: Tenebrionidae). Proc. Entomol. Soc. Wash. 109(3): 628–642.

Triplehorn CA, Thomas DB (2011) Studies in the Genus *Eleodes* Eschscholtz with a Revision of the Subgenus *Melaneleodes* Blaisdell and *Omegeleodes*, new subgenus (Coleoptera: Tenebrionidae). Trans. American Entomol. Soc. 137(3+4): 251–281.

ZooKeys 415: 23–51 (2014)
doi: 10.3897/zookeys.415.6524
www.zookeys.org

RESEARCH ARTICLE

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

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

http://zoobank.org/EAADCDB3-4F61-4973-AEE3-998216B2307C

Citation: Bousquet Y, Bouchard P (2014) Review of the species of *Paratenetus* Spinola inhabiting America, north of Mexico (Coleoptera, Tenebrionidae). In: Bouchard P, Smith AD (Eds) Proceedings of the Third International Tenebrionoidea Symposium, Arizona, USA, 2013. ZooKeys 415: 23–51. doi: 10.3897/zookeys.415.6524

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 Eatton 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.
AMNH	American Museum of Natural History, New York, New York. Lee H. Herman.
BMNH	The Natural History Museum, London, United Kingdom. Maxwell Barclay.
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.

GMNH Georgia Museum of Natural History, The University of Georgia, Athens, Georgia. E. Richard Hoebeke.
GHC Gerard J. Hilchie Collection, Edmonton, Alberta.
JBWM Wallis-Roughley Museum of Entomology, University of Manitoba, Winnipeg, Manitoba. Robert E. Roughley.
JCC Janet Ciegler Collection, West Columbia, South Carolina.
LEMM Lyman Entomological Museum and Research Laboratory, McGill University, Sainte-Anne-de-Bellevue, Quebec. Stéphanie Boucher.
LSAM Louisiana State Arthropod Museum, Louisiana State University, Baton Rouge, Louisiana. Matthew L. Gimmel.
MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts. Philip Perkins.
MRSN Museo Regionale di Scienze Naturali, Torino, Italy. Luca Picciau.
NFC Northern Forestry Centre, Edmonton, Alberta. Greg R. Pohl.
RAM Royal Alberta Museum, Edmonton, Alberta. Mark Steinhilber.
RBCM Royal British Columbia Museum, Victoria, British Columbia. Claudia Copley.
RLAC Rolf L. Aalbu Collection, Sacramento, California.
RSM Royal Saskatchewan Museum, Regina, Saskatchewan. Ronald R. Hooper.
RWC Reginald P. Webster Collection, Charters Settlement, New Brunswick.
SEMC Snow Entomological Museum, University of Kansas, Lawrence, Kansas. Zachary Falin.
TAMU Texas A&M University, College Station, Texas. Edward G. Riley.
UASM Strickland Museum, University of Alberta, Edmonton, Alberta. Danny Shpeley.
UBC Spencer Entomological Museum, University of British Columbia, Vancouver, British Columbia. Karen Needham.
USNM National Museum of Natural History, Smithsonian Institute, Washington, DC. Warren E. Steiner.
ZMMU Zoological Museum, Moscow University, Moscow, Russia. Nikolay B. Nikitsky.

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

Paratenetus Spinola, 1844: 116. Type species: *Paratenetus punctatus* Spinola, 1844 designated by Lucas (1920: 483).
Storthephora Mäklin, 1875: 658. Type species: *Storthephora denticollis* Mäklin, 1875 by present designation. Synonymy established by Champion (1893: 47).

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 palpomeres.

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) placed the genera of Heterotarsini (except *Heterotarsus*) in the lagriine subtribe Lupropina of the tribe Adeliini. Parsons (1976: 211) listed *Paratenetus* in the lagriid subfamily Lupropinae. Doyen and Tschinkel (1982: 183) indicated that the genus may belong to the belopines, currently a valid lagriine tribe. Campbell (1991: 261) listed *Paratenetus* in the lagriid subfamily Goniaderinae and Aalbu et al. (2002a: 509; 2002b: 484) retained also the genus in the lagriine tribe Goniaderini. On the other hand, Ferrer and Ødegaard (2005: 648) included it in the lagriine tribe Lupropini following Ardoin (1961) and Parsons (1976).

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 Goniaderini 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**

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 .... ***P. exutus*** **Bousquet & Bouchard**

– 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 **4**

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.

Species	Distribution
P. antennalis Kulzer, 1958	Brazil
P. atricolor Pic, 1934	Brazil
P. auritus (Mäklin, 1875)	Brazil
P. bicoloricollis Pic, 1939	Brazil
P. bordoni Marcuzzi, 1994	Venezuela
P. brevipennis Champion, 1886	Panama
P. cicatricosus Motschulsky, 1868	Brazil
P. constrictus Champion, 1893	Mexico, Central America
P. corticarioides Champion, 1886	Mexico, Central America
P. corumbanus Pic, 1934	Brazil
P. crenulatus Champion, 1886	Panama
P. denticollis (Mäklin, 1875)	Venezuela
P. denticulatus Champion, 1886	Panama
P. discoidalis Pic, 1939	Brazil
P. donckieri Pic, 1925	Brazil
P. ensellatus Pic, 1934	Brazil
P. epitragoides Berg, 1889	Argentina
P. exutus Bousquet & Bouchard, sp. n.	Canada, U.S.A.
P. foveithorax Ferrer & Ødegaard, 2005	Panama
P. freyi Kulzer, 1958	Brazil
P. fuscus LeConte, 1850	Canada, U.S.A.
P. germaini Pic, 1926	Bolivia
P. gibbipennis Motschulsky, 1868	Canada, U.S.A.
P. gounellei Pic, 1920	Brazil
P. grandicornis Motschulsky, 1868	Nicaragua, Panama
P. grandis Pic, 1920	Brazil
P. helgae Kulzer, 1958	Trinidad
P. huequensis Marcuzzi, 1994	Venezuela
P. humeralis Pic, 1934	Brazil
P. inaequalis Pic, 1925	Brazil
P. inermis Champion, 1893	Guatemala
P. koltzei Pic, 1939	Mexico
P. laticollis Pic, 1925	Brazil
P. latipennis Pic, 1920	Peru
P. lebasi Spinola, 1844	Columbia
P. limbaticollis Pic, 1921	Brazil
P. lithophiloides Pic, 1921	Brazil
P. longicornis Pic, 1925	Guadeloupe
P. luridus Motschulsky, 1868	Brazil
P. mexicanus Pic, 1925	Mexico
P. nigricornis Champion, 1893	Mexico, Central America
P. obovatus Champion, 1893	Central America
P. punctatus Spinola, 1844	Canada, U.S.A.
P. punctulatus Champion, 1893	Mexico, Central America
P. ruficornis Champion, 1886	Panama
P. sexdentatus Champion, 1893	Central America
P. sparsepunctatus Pic, 1939	Argentina

Species	Distribution
P. suturalis Pic, 1921	Brazil
P. testaceicornis Pic, 1925	Brazil
P. testaceipes Pic, 1934	Bolivia
P. testaceus Pic, 1920	Costa Rica
P. texanus Bousquet & Bouchard, n.sp.	U.S.A., Mexico
P. tibialis Champion, 1893	Mexico, Central America
P. tropicalis Motschulsky, 1868	Mexico, Central America
P. tuberculatus Champion, 1886	Panama
P. vianai Pic, 1939	Argentina
P. villosus Champion, 1886	Mexico, Central America

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 subquadrate or very slightly 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. **Manitoba**. "Tp.2, Rge. 15, E. 1 Mer." (CNC). Rennie (CNC). Brandon (RBCM). Telford (NFC). Winnipeg (RBCM). **Ontario**. "Jonction Hwy 17 & 71" (CNC). Bainsville (LEMM). Prince Edward Co. (CNC, CUIC, MCZ, CAS, USNM). Lancaster (LEMM). Chaffeys Locks Biol. Station (CNC). Alfred (CNC). Long Sault (CNC). 10 km W North Gower (CNC). Nepean (CNC). Belleville (CUIC). Thwartway Island, St. Lawrence Is. Nat. Park (CNC). Point Pelee (CNC). 2 km SE Spencerville (CNC). 4 km SW Kanata (CNC). Ottawa (CNC). Constance Bay (CMN). 4 km N of Westport (CNC). Campden (CNC). Rondeau Prov. Park (CNC). Arnprior (CNC). Erieau (CNC). 7 km W. Carleton Place (CNC). Blackburn (CNC). Normandale (CNC). Pelee Island (CNC). Hamilton (CNC). Flint Hill, nr Kemptville (CNC). Trenton (CNC). Toronto (CUIC, MCZ, USNM). Milton (CNC). **Quebec**. Montreal (CNC). Rigaud (CNC). Gatineau (CNC, CAS). Blind Lake, Gatineau Park (CNC). Gatineau Park (DENH). Hudson Heights (CNC). Oka (CNC). Ormstown (CNC). United States of America. **Alabama**. *Mobile Co.*: Mt. Vernon (CUIC). *Monroe Co.*: Haines Island Park, 3.5 mi. W Franklin (FSC). **Connecticut**. *Fairfield Co.*: Westport (AMNH). *Litchfield Co.*: Torrington (DENH); Canaan (TAMU); Cornwall (CUIC, AMNH). **Georgia**. *Clarke Co.*: 5 mi W Athens (GMNH); Whitehall Forest (GMNH). *Rabun Co.*: Tally Mill Crk. at Hwy 28 (CNC); Satolah (CNC). **Illinois**. "N. Ill." (MCZ). "Ill." (USNM). **Maine**. *Cumberland Co.*: Portland (CNC). *Kennebec Co.*: Monmouth (MCZ). *Oxford Co.*: Paris (MCZ). **Massachusetts**. "Mass." (USNM). *Bristol Co.*: Swansea (MCZ); Somerset (MCZ); Dighton (MCZ); Fall River (MCZ). *Hampshire Co.*: Mount Tom (MCZ). *Middlesex Co.*: Waverly (USNM); Framingham (CNC, CUIC, MCZ); Lowell (MCZ); Sherborn (CUIC, AMNH); Hopkinton (CUIC); Cambridge (MCZ, USNM); Newton (MCZ). *Norfolk Co.*: Brookline (CUIC, MCZ, AMNH); Sharon (CUIC). **Michigan**. *Marquette Co.*: Marquette (USNM). *Oakland Co.* (CUIC). *Wayne Co.*: Detroit (MCZ, USNM). **Minnesota**. *Crow Wing Co.*: Brainerd (CNC). *Hennepin Co.*: Lake Minnetonka (CUIC). **Missouri**. *Saint Charles Co.*: St. Charles (MCZ). **Nebraska**. *Cuming Co.*: West Point (USNM). **New Hampshire**. *Grafton Co.*: Franconia (MCZ, AMNH); 0.5 mi S Rumney (DENH); Hanover (DENH). *Rockingham Co.*: Hampton (DENH, USNM); Odiorne Point State Park (DENH). *Strafford Co.*: Somersworth (DENH); Durham (DENH); 3 mi. E Durham (DENH). **New Jersey**. *Union Co.*: Union (CUIC, AMNH); Roselle (USNM);

Elizabeth (USNM). **New York**. "S[taten] I[sland]" (MCZ). *Dutchess Co*.: Bulls Head (AMNH). *Oswego Co*.: North Pond (CUIC); Oswego (CUIC). *Queens Co*.: Flushing, L.I. (CUIC). **North Carolina**. *Haywood Co*.: Round Knob (USNM). *Henderson Co*.: 14 mi NW Hendersonville (SEMC). *Macon Co*.: 3 mi NW Highlands (DENH). *Montgomery Co*.: 2 mi S Eldorado (DENH). *Yancey Co.*: Black Mountains (AMNH). **North Dakota**. *Richland Co*.: Mirror Pool (USNM). **Ohio**. "Ohio" (MCZ). **Pennsylvania**. "Penn" (MCZ). *Allegheny Co*.: Allegheny (USNM). **Rhode Island**. "R.I." (USNM). **South Carolina**. *Calhoun Co*.: Wannamaker NP, St. Matthews (JCC). *Chester Co*.: Leeds (JCC). *Edgefield Co*.: Sumter Nat. For. (DENH). *Lexington Co*.: West Columbia (JCC). *Newberry Co*.: Billy Dreher Island State Park (JCC). *Pickens Co*.: Nine Times (JCC). *Union Co*.: Sedalia (JCC). **Tennessee**. "Chilhowee Mountain" (CMN). *Blount Co*.: Rt. 129 just below rd. at The Narrows Overlook, GSMNP (LSAM); Ace Gap, GSMNP (LSAM). *Cocke Co*.: Gabes Mtn., GSMNP (LSAM). *Sevier Co*.: 0.5 mi W Laurel Falls Trailhead, GSMNP (LSAM); Twin Creeks, GSMNP (LSAM); Grapeyard Ridge (LSAM). **Texas**. *Blanco Co*.: Cypress Mill (USNM). **Virginia**. *Giles Co*.: Bald Knob, Mountain Lake (USNM); 9 km N Mountain Lake (USNM). *Lee Co*.: Pennington Gap (USNM). **Wisconsin**. *Bayfield Co*.: Bayfield (USNM). *Dane Co*.: Madison (TAMU). *Shawano Co*.: Tilleda (FSC).

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).

Records. We have seen 305 specimens from the following localities. CANADA. **Alberta**. "Tp. 74, Rge. 25, W. 5 Mer." (CNC). "Tp. 11, Rge. 1, W. 5 Mer." (CNC). Waterton Park (CNC). Calgary (CNC, ENMU, CAS, GHC). Castor (UASM). Edmonton (CUIC, UASM). Stettler (CNC). Cochrane (CNC). 30 km W Cochrane (CNC). Cypress Hills (CNC). Waiparous (CNC). Jumpingpound Creek (CNC). Sundre (CNC). Elkwater (CNC). **British Columbia**. North Pine (UBC). Pouce Coupe (UBC). **Manitoba**. "Tp. 9, Rge. 16, W. 1 Mer." (CNC). Aweme (CNC, JBWM, RAM). Brandon (RBCM). Sandilands (JBWM). Birds Hill Prov. Park (ENMU). Husavik (CNC). **Northwest Territories**. Louise Falls, Hay River (CNC). Simpson (CAS). **Ontario**. Prince Edward Co. (CNC, USNM). Pelee Island (CNC). Ottawa (CNC). Constance Bay (CMN). Trenton (CNC). Arnprior (CNC). **Quebec**. Chelsea (CNC). Rigaud (CNC). Sainte-Croix-de-Lotbiniere (LEMM). Cap Rouge (CNC). **Saskatchewan**. Lac La Ronge (CNC). Morse (RSM). Rosefield (RSM). Oxbow (USNM). UNITED STATES OF AMERICA. **Colorado**. *Boulder Co*.: Boulder (CNC, USNM). *Custer Co*. (USNM). *Douglas Co*.: Castle Rock (CNC). *El Paso Co*.: Colorado Springs (USNM). *Jefferson Co*.: Lookout Mountain (CUIC). **Connecticut**. *Fairfield Co*.: Westport (AMNH). **District of Columbia**. "DC" (CNC, USNM). **Illinois**. "N. Ill." (MCZ). *Champaign Co*.: Urbana (USNM). **Iowa**. "Iowa" (MCZ, AMNH). *Johnson Co*.: Iowa City (USNM, AMNH). *Story Co*.: Ames (USNM). **Kansas**. "Ks" (USNM). "Kans" (USNM). *Douglas Co*.: Lawrence (CNC). *Shawnee Co*.: Topeka (USNM). **Maryland**. "Md." (CNC). *Anne Arundel Co*.: 6 km ESE Laurel (USNM). **Massachusetts**. "Mass" (USNM). *Essex Co*.: Lynn (MCZ, USNM); Salem (USNM). *Middlesex Co*.: Sherborn (MCZ, USNM); Tyngsboro (MCZ). *Norfolk Co*.: Brookline (MCZ). **Michigan**. *Marquette Co*.: Marquette (USNM). **Montana**. "Mont." (CUIC).

"Montana" (USNM). *Dawson Co*.: Glendive (USNM). *Powder River Co*.: Fort Howes (USNM). *Rosebud Co*.: Colstrip (USNM). **Nebraska**. "Neb." (USNM). *Red Willow Co*.: McCook (MCZ). **New Mexico**. "N. Mex." (USNM). *San Miguel Co*.: Trout Spring (MCZ). **New York**. "N.Y." (CUIC, MCZ). *Westchester Co*.: Peekskill (CUIC). *New York Co*.: Central Park, L.I. (USNM). **North Dakota**. *Richland Co*.: Mirror Pool (USNM). **Rhode Island**. "R.I." (USNM). **South Dakota**. *Jackson Co*.: Cottonwood (RLAC). **Tennessee**. "Tenn." (MCZ). **Vermont**. "Vt." (MCZ). **Wisconsin**. "Wis" (MCZ). *Sauk Co*.: Spring Green (USNM). **Wyoming**. *Converse Co*.: 11 mi N Douglas (CNC). *Laramie Co*.: Cheyenne (USNM).

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).

Paratenetus punctatus Spinola, 1844: 118. Type locality: «Etats-unis de l'Amérique septentrionale» (original citation). Synonymy established by LeConte (1859: 325).

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 punctation 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. Parameres 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. **Manitoba**. "Tp. 3, Rge. 17, E.1 Mer." (CNC). Victoria Beach (JBWM). **New Brunswick**. Jackson Falls, Carleton Co. (RWC). 10 km NW New River Beach, Charlotte Co. (AFC). 12 km SSE Upper Napan, Northumberland Co. (RWC). Cranberry Lake Protected Natural Area, Queens Co. (AFC). Acadia Research Forest, Sunbury Co. (AFC, RWC). Charters Settlement, York Co. (RWC). Canterbury, York Co. (RWC). 15 km W Tracy, York Co. (RWC). 14 km WSW Tracy, York Co. (AFC). **Ontario**. Ottawa (CNC). Constance Bay (CMN). Flint Hill, nr Kemptville (CNC). Ad & Lennox Co. (CNC, FSC, AMNH). Pelee Island (CNC). Leamington (CNC). Hastings Co. (CNC). Walsingham (CNC). Prince Edward Co. (CNC, USNM). Point Pelee (CNC). Rondeau Prov. Pk. (CNC). Arnprior (CNC). Chaffeys Locks (CNC). Northumberland Co. (CNC). Sudbury (CNC). Hamilton (CNC). Gordon Island (St. Lawrence Is. Nat. Pk.) (CNC). 13 km W of Mattawa (CNC). Toronto (CUIC). 2–5 km W Mallorytown Landing (CMN). **Quebec**. Rouville (CNC). Fort Coulonge (CNC). Parc Provincial d'Oka (CNC). Berthierville (CNC). Parc de la Gatineau (CNC). Laniel (CNC). Ile-du-Grand-Calumet (Pontiac) (CNC). Rigaud (CNC). Montreal

(CNC). Parc de la Yamaska (CNC). United States of America. **Arkansas**. *Garland Co*.: 3 mi W Crystal Springs (SEMC). **Connecticut**. *Fairfield Co*.: Westport (AMNH). *Litchfield Co*.: Litchfield (AMNH). *New Haven Co*.: Middlebury (USNM); Hamden (CUIC). **District of Columbia**. "D.Col." (USNM). Takoma Park (USNM). Washington (USNM). **Florida**. "Fla" (USNM). *Alachua Co*.: Gainesville (FSC); Newnans Lake (RLAC). *Duval Co*.: Jacksonville (USNM). *Escambia Co*.: Pensacola (FSC). *Hillsborough Co*.: Tampa (USNM). *Indian River Co*.: south of Vero Beach (FSC). *Levy Co*.: 4 mi SW Archer (FSC). *Marion Co*.: Juniper Springs (FSC); Rainbow Springs (FSC); Ocala National Forest (CMN, FSC). *Palm Beach Co*.: Lake Worth (CUIC). *Polk Co*.: Lake Marion Creek (GMNH). *Putnam Co*.: 2.5 mi NE Florahome (FSC); Crescent City (USNM); Welaka Exp. Sta. (DENH, LSAM). *Saint Johns Co*.: St. Augustine (MCZ). *Santa Rosa Co*.: 4 mi N Munson (LSAM). *Seminole Co*.: Lake Mary (MCZ). *Volusia Co*.: South Daytona (CNC); Daytona (USNM). **Georgia**. *Charlton Co*.: 2.8 mi N Saint George (FSC). *Johnson Co*.: 1 mi E Kite (FSC); Suwanee Canal Rec. Area (FSC). *Montgomery Co*.: 5 mi W Uvalda (GMNH). *Rabun Co*. (MCZ); Clayton (MCZ). *Tattnall Co*. (FSC). *Union Co*.: "Herbert Reece Park" (GMNH). **Illinois**. *Knox Co*.: Galesburgh (MCZ). *Macon Co*. (FSC). **Indiana**. *Allen Co*.: "Schoaf Park" (USNM). *Howard Co*.: "NW Howard Co." (LSAM). *Jasper Co*.: Jasper/Pulaski St. Forest (USNM). *LaPorte Co*.: Michigan City (USNM). *Monroe Co*.: Bloomington (FSC, USNM). *Porter Co*.: Dunes St. Pk. (RLAC). *Tippecanoe Co*. (CUIC, USNM, AMNH); "McCormick Woods" (USNM). **Iowa**. "Iowa" (USNM). *Johnson Co*.: Iowa City (USNM). *Polk Co*.: "Brown WDS Psv" (CUIC); W. Saylorville Lake (CUIC, USNM). **Kansas**. "Kans" (USNM). *Cherokee Co*.: 2 mi S Galena (SEMC). *Crawford Co*.: Pittsburg (SEMC); 2 mi W Pittsburg (SEMC). *Douglas Co*.: 2 mi NW of Baldwin (SEMC). *Jackson Co*.: 6.5 km W Mayetta (SEMC). *Jefferson Co*.: 1 km SW Perry State Park (SEMC). *Johnson Co*.: Overland Park Arboretum (SEMC). *Labette Co*.: Big Hill Reservoir (SEMC). *Neosho Co*.: 2 mi SE Erie (SEMC). *Sedgwick Co*.: 0.5 mi S of Derby (SEMC). *Shawnee Co*.: S of intersection Woodring Rd & 69th St (SEMC). **Kentucky**. "Ky" (USNM). *Marshall Co*. (FSC). **Louisiana**. *Caddo Parish*: Jacobs Nature Park (LSAM). *Claiborne Parish*: Corney Lake (CNC). *East Feliciana Parish*: Idlewild Exp. Station (LSAM). *Livingston Parish*: Livingston (LSAM). *Natchitoches Parish*: Kisatchie Nat. For. (LSAM). *West Feliciana Parish*: Saint Francisville (CMN); Tunica Hills, 0.5 mi W Weyanoke (LSAM). **Maine**. *Androscoggin Co*.: Wales (MCZ). *Cumberland Co*.: Casco (CUIC). *Franklin Co*.: Dead River (USNM); Farmington (USNM). *Kennebec Co*.: Augusta (DENH); Monmouth (MCZ). *Oxford Co*.: Rumford (USNM); Bethel (AMNH). *Penobscot Co*.: Lee (DENH); Passadumkeag (CUIC). *Piscataquis Co*.: Greenville (USNM). *Washington Co*.: Beddington (USNM). *York Co*.: West Lebanon (DENH). **Maryland**. *Allegany Co*.: Piclic Ridge, 5 km SE Pratt (USNM); Fifteen Mile Creek (RLAC). *Anne Arundel Co*.: 8 km ESE Laurel (USNM); 6 km ESE Laurel (USNM); Edgewater (USNM); 6 km S Edgewater (USNM); 3 km WSW Bristol at Jug Bay (USNM); Odenton (CUIC, USNM). *Baltimore Co*.: 4 km SW Cockeysville (USNM); Catonsville (USNM). *Calvert Co*.: Plum Point (USNM). *Carroll Co*.: Eldersburgh (USNM). *Cecil Co*.: Pleasant Hill (USNM); Port Deposit

(USNM). *Frederick Co*.: 2 mi W Thurmont (USNM). *Garrett Co*.: Rock Lodge, 4 km SW Bittinger (USNM); 7 mi N Oakland (USNM). *Montgomery Co*.: Kensington (USNM); Potomac (USNM); Rockville (USNM); Plummers Island (USNM); Great Falls (USNM); Hughes Hollow area, 5 km W Seneca (USNM). *Prince Georges Co*.: Cheverly (USNM); Bladensburg (USNM); Takoma Park (USNM); Laurel (USNM); Priest Bridge (USNM); Oxon Hill (USNM); Beltsville (USNM); Greenbelt (Park) (USNM); Bowie (USNM). *Somerset Co*.: Shelltown (USNM). *Talbot Co*.: 3 km SE Easton (USNM); Wittman (USNM); McDaniel (USNM). *Worcester Co*.: Assateague Island (USNM). **Massachusetts**. *Barnstable Co*.: Cape Cod (CNC). *Bristol Co*.: Dartmouth (MCZ). *Essex Co*.: Nahant (MCZ). *Hampden Co*.: Springfield (USNM). *Middlesex Co*.: Lincoln (MCZ); Sherborn (MCZ); Framingham (MCZ); Hopkinton (MCZ); Tyngsboro (MCZ); Natick (MCZ); Cambridge (MCZ). *Norfolk Co*.: Brookline (MCZ). *Plymouth Co*.: Marion (USNM). *Suffolk Co*.: Boston (MCZ); Jamaica Plain (CUIC). **Michigan**. *Shiawassee Co*.: Rose Lake Wldlf. Exp. Station (USNM). *Wayne Co*.: Detroit (USNM). **Minnesota**. *Hennepin Co*.: Minneapolis (CNC). *Houston Co*.: Winnebago Cr. Vy., 3–4 m NE Eitzen (USNM). *Saint Louis Co*.: Duluth (MCZ). **Mississippi**. *George Co*.: Lucedale (CUIC). *Greene Co*.: Leakesville (CUIC). *Lauderdale Co*.: Marion (MCZ). **Missouri**. *Barry Co*.: Mark Twain Nat. For. (FSC). *Boone Co*.: Ashland Wildlife Ar. (TAMU). *Clay Co*.: Cooley Lake (FSC). *Greene Co*.: near James River (TAMU). *Jackson Co*.: Raytown (FSC). *Oregon Co*.: Mark Twain Nat. For. (FSC). *Randolph Co*.: 1 mi E Moberly (TAMU). **New Hampshire**. "N.H." (USNM). *Coos Co*.: Gorham (CNC); Mt. Washington (DENH, MCZ, AMNH). *Grafton Co*.: Mt. Moosilauke (MCZ); Bedell Bridge St. Pk. (DENH); Bath (DENH). *Hillsborough Co*.: Antrim (MCZ). *Merrimack Co*.: Concord (DENH). *Strafford Co*.: 1 mi SW Durham (DENH); Dover (DENH). **New Jersey**. "N.J." (AMNH). *Atlantic Co*.: Buena (MCZ). *Bergen Co*.: Fort Lee (AMNH). *Burlington Co*.: Wharton State Forest (TAMU); Pemberton (USNM); 7 mi E Batsto (USNM). *Cumberland Co*.: Rutgers Exp. Sta. (USNM). *Essex Co*.: South Orange (MCZ); Eagle Rock (USNM); Montclair (USNM). *Gloucester Co*.: Malaga (USNM). *Monmouth Co*.: Highlands (USNM). *Monroe Co*.: Delaware Water Gap (USNM). *Morris Co*.: Boonton (USNM). *Ocean Co*.: Lakehurst (CUIC, CUIC, USNM). *Orange Co*.: Greenwood Lake (CUIC, USNM). **New York**. "S.I." (USNM). *Albany Co*.: Delmar (CUIC); Rensselaerville (USNM). *Clinton Co*.: vic. Taylor Pond Campground (GMNH). *Erie Co*.: Buffalo (MCZ, USNM). *Essex Co*.: New Russia (CUIC); Whiteface Mt. (USNM). *Orange Co*.: Greenwood Lake (CUIC); Fort Montgomery (CUIC); West Point (USNM). *Putnam Co*.: Brewster (CUIC). *Rockland Co*.: Nyack (CUIC). *Saint Lawrence Co*.: Rossie (USNM). *Seneca Co*.: Willard (USNM). *Suffolk Co*.: Huntington, Long Island (DENH); Southold, L.I. (CUIC); Wyandanch, L.I. (USNM); Bellport (USNM); Yaphank (USNM). *Tompkins Co*.: Ithaca (CUIC, FSC, USNM); Dryden (CUIC). *Yates Co*.: Seneca Lake (USNM). **North Carolina.** "N.C." (MCZ). "Round Knob" (USNM). *Brunswick Co*.: Southport (FSC). *Buncombe Co*.: 6 mi S Asheville (SEMC). *Burke Co*.: Linville Falls (CNC). *Columbus Co*.: Lake Waccamaw (USNM). *Gates Co*.: 6 km ENE Corapeake (USNM). *Haywood Co*.: Cove Creek (JCC); Cataloochee Divide (LSAM, MCZ); 9 mi W Waynesville (SEMC). *Henderson Co*.: Fletcher (FSC). *Jackson Co*.: Balsam (USNM). *Macon Co*.: Nantahala Gap (CUIC); Highlands (CMN, CNC). *Mitchell Co*. (USNM). *Moore Co*.: Southern Pines (USNM). *New Hanover Co*.: Wilmington (USNM). *Swain Co*.: 2.5 mi NNE Cherokee, GSMNP (SEMC); Andrews Bald, GSMNP (LSAM); Ekaneetlee Gap, GSMNP (LSAM). *Transylvania Co*.: Lake Toxaway (AMNH). *Watauga Co*.: 3 mi NW Blowing Rock (TAMU). *Yancey Co*.: Black Mountains (USNM, AMNH). **Ohio**. *Ashland Co*.: Mohican St. Pk. (FSC). *Champaign Co*.: Cedar Swamp (FSC). *Ottawa Co*.: Fishery Bay, S. Bass Isl. (CUIC). *Union Co*. (CUIC). **Oklahoma**. *Latimer Co*. (FSC, TAMU); 5 mi W Red Oak (CNC, TAMU). **Pennsylvania**. "Pen" (CNC, UASM). *Allegheny Co*.: Allegheny (CUIC). *Dauphin Co*.: Dauphin (CUIC). *Lehigh Co*.: Lehigh Gap (USNM). *Luzerne Co*.: Hazleton (MCZ). *Montgomery Co*.: Abington (MCZ). *Philadelphia Co*.: Frankford (USNM). *Pike Co*.: Twin Lakes (USNM). **South Carolina**. "S.C." (MCZ). "Shiloh" (JCC). *Georgetown Co*.: Sandy Island (JCC). *Richland Co*.: Pontiac (JCC). **Tennessee**. "Chimney Camp, Gt. Smoky Mts." (CUIC). *Blount Co*.: Cades Cove, GSMNP (LSAM, SEMC). *Cocke Co*.: Davenport Gap, GSMNP (LSAM). *Sevier Co*.: Goshen Prong, GSMNP (LSAM); Chimney Tops Picnic Nature Trail, GSMNP (LSAM); Roaring Fork, GSMNP (LSAM); Brushy Mnt., GSMNP (LSAM). **Texas**. *Brazos Co*.: College Station (TAMU). **Vermont**. *Bennington Co*.: Manchester (MCZ). *Chittenden Co*.: Burlington (USNM). *Orange Co*.: 12 mi E Chelsea (TAMU). **Virginia**. "Middletown" (MCZ). "Franklin Park" (USNM). *Arlington Co*.: Glencarlyn (USNM). *Fairfax Co*.: Vienna (USNM); Black Pond (USNM); Great Falls (USNM); Great Falls N.P. near Clay Pond (USNM); Great Falls N.P. near quarry site (USNM). *Giles* Co.: Mountain Lake, Univ. Va. Biological Sta. (USNM). *Lee Co*.: Pennington Gap (MCZ). *Loudoun Co*.: Middleburg (USNM). *Louisa Co*.: Gum Spring (USNM). *Montgomery Co*.: Blacksburg (CUIC). *Nelson Co*. (USNM). *Page Co*.: Skyland (CUIC, MCZ). *Rockbridge Co*.: Natural Bridge (USNM). *Shenandoah Co*.: New Market (USNM). *Warren Co*.: 7 km NNE Linden, summit of Blue Mt. (USNM). Alexandria (USNM). **West Virginia**. *Greenbrier Co*.: W. Sulphur (USNM). *Jefferson Co*.: Harpers Ferry (USNM); Shepherdstown (USNM). *Pocahontas Co*.: Cranberry Glades (USNM). *Preston Co*.: Aurora (USNM). **Wisconsin**. "Wis" (MCZ). *Bayfield Co*.: Bayfield (USNM). *Douglas Co*.: Bennett (USNM). *Sauk Co*.: Sauk City (GMNH). *Shawano Co*.: Tilleda (FSC). *Wood Co*.: Griffith State Nursery (USNM). **Wyoming**. *Weston Co*.: Newcastle (USNM).

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.

Paratypes from the following localities: **Manitoba**. Ninette, 31-V-1958, J.F. McAlpine (2, CNC); same locality, 30-V-1958, R.B. Madge (1, CNC). **New Brunswick**. Tabusintac, 19-VI-1939, W.J. Brown (2, CNC); same data but 20-VI. 1939 or 22-VI-1939 (4, CNC). York Co., 14 km WSW of Tracy, S of Rt 646, 45.6741°N, 66.8161°W, 26 April-10 May 2010, R. Webster & C. MacKay coll. (2, RWC). York Co., 15 km W of Tracy off Rt. 645, 45.6848°N, 66.8821°W, 19–25 May 2009, R. Webster & M.-A. Giguère coll. (3, RWC). York Co., New Maryland Charters Settlement, 45.8430°N, 66.7275°W, 12 July 2005, R. P. Webster coll. (1, RWC); same locality but 45.8340°N, 66.7450°W, 30 April 2005 (1, RWC). Queens Co., Cranberry Lake P.N.A., 46.1125°N, 65.6075°W, 24 April-5 May 2009, R. Webster & M.-A. Giguère coll. (1, RWC); same locality but 3–13 May 2011, M. Roy & V. Webster coll. (1, RWC). Carleton Co., Jackson Falls, "Bell Forest", 46.2200°N, 67.7231°W, 28.April-9 May 2009, R. Webster & M.-A. Giguère coll. (1, RWC). Carleton Co., Wakefield Meduxnekeag Valley Nature Preserve, 46.1890°N, 67.6766°W, 8 June 2005, M. Giguère & R. Webster coll. (1, RWC); same locality but 46.1935°N 67.6825°W, 19 April 2995 (1, RWC). Albert Co., Shepody N.W.A., Germantown Section, 45.7101°N 64.7542°W, 30 July 2004, R.P. Webster coll. (1, RWC). Sunbury Co., Acadia Research Forest, 45.9866°N, 66.3841°W, 8–13 May 2009, 13–19 May 2009, 19–25 May 2009, 16–24 June 2009, R. Webster & M.-A. Giguère coll. (10, RWC). **Nova Scotia**. St. Peters, 25-VII-1930, M.L. Prebble (1, CNC). **Ontario**. Alfred bog, 16.VI.1981, A. Davies (1, CNC). **Quebec**. Sainte-Catherine Portneuf, 29-VIII-1971, Claude Chantal (1, CNC). D[ivision de] R[ecensement] Bellechasse, St-Nérée, 10.VII.1976, J.F. Landry (3, CNC). Cascapedia, 11.VI.1933, W.J. Brown (1, 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 spinelike 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 mesotibia.

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

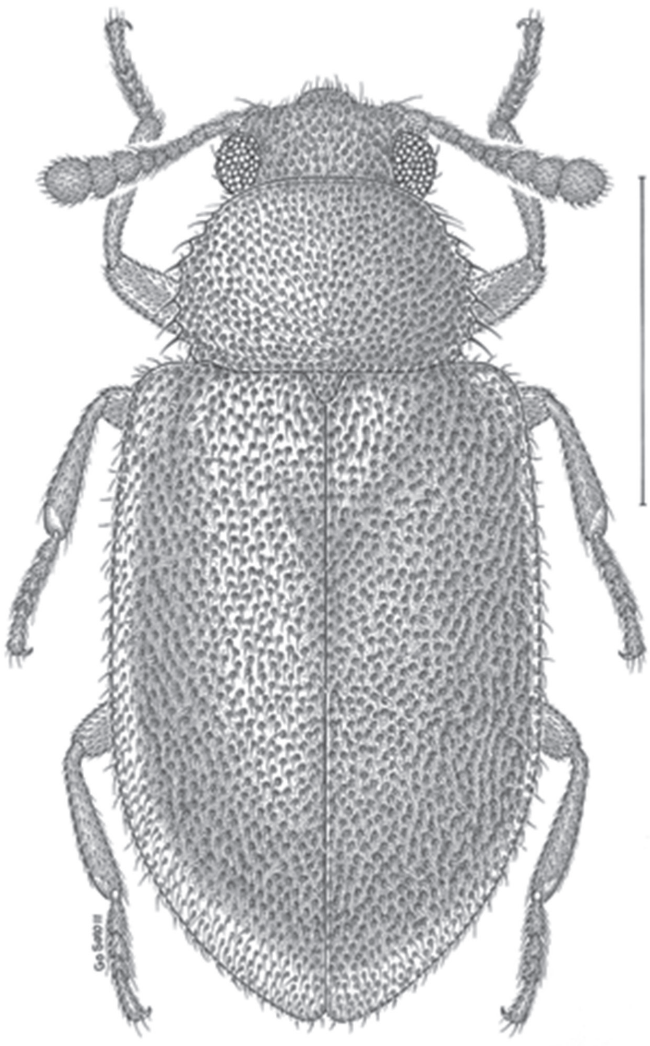


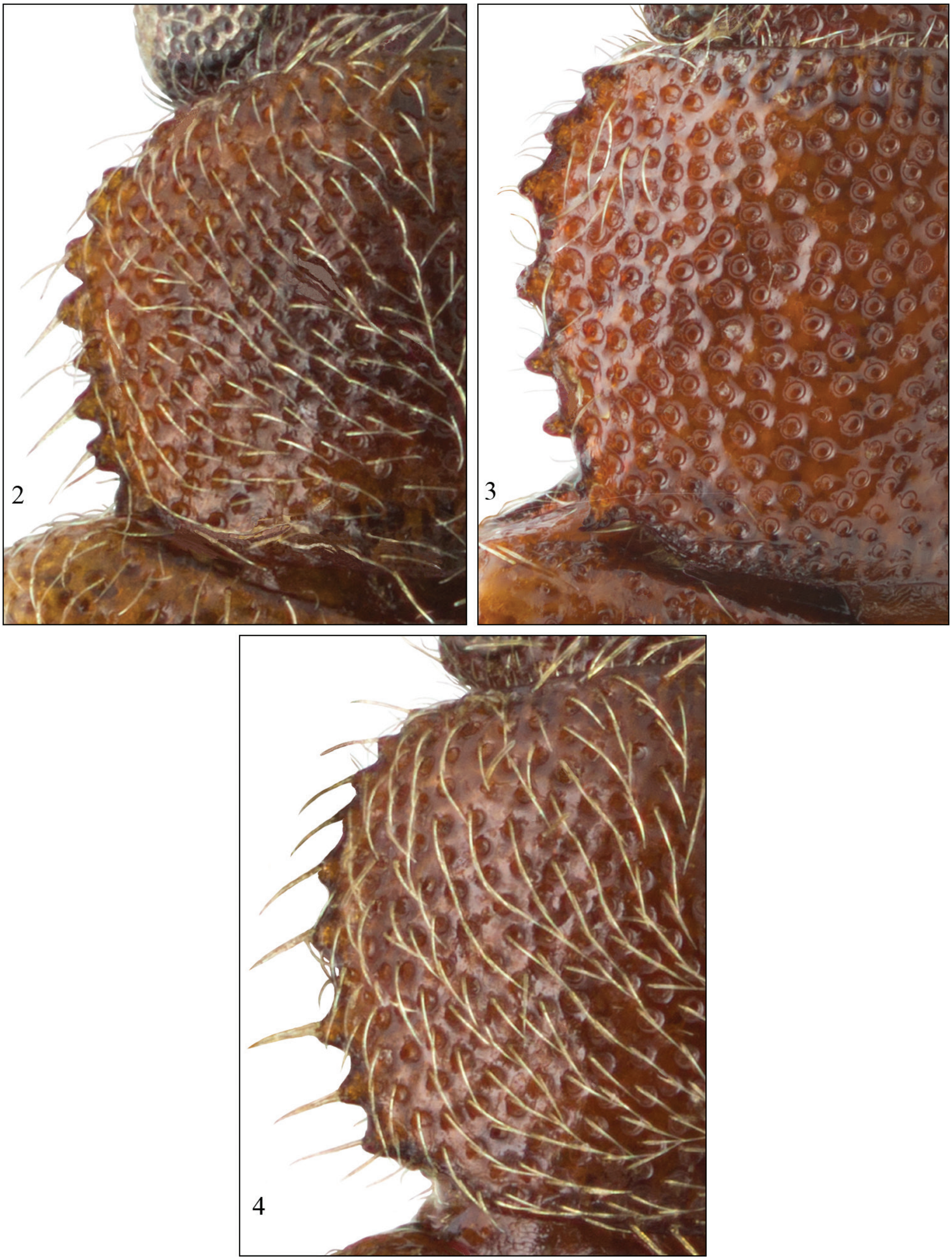
Figure 1. Dorsal habitus drawing of *Paratenetus exutus*.

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 subcontiguous 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.

Distribution. This species ranges from Cape Breton Island to northwestern Alberta, south to east-central Texas, southern Alabama, and southern Florida (Fig. 13).

Records. We have seen 416 specimens, including the type material, from the following localities. Canada. **Alberta**. "Tp. 73, Rge. 17, W. 4" (CNC). Peace River (NFC). **Manitoba**. Aweme (CNC). **New Brunswick**. Fredericton (CNC). **Nova Scotia**. Kentville (CNC). Annapolis Royal (CNC). Portapique (MCZ). St. Peter's (AFC). Cape Breton (CNC, AFC). Grand River (CNC, AFC). Woodside (AFC). White Point Beach, Queens Co. (JCC). **Ontario**. Ridgeway (MCZ). Trenton (CNC). Prince Edward Co. (CNC). La Rose Forest, near Bourget (CNC). **Quebec**. Hull [= Gatineau] (CAS). Lac Duparquet (LEMM). Lac Labyrinthe [Abitibi] (LEMM). Laniel (CNC). Valcartier (CNC). **Saskatchewan**. Red Earth (RSM). Somme (RSM). United States of America. **Alabama**. *Conecuh Co*.: 19 km NE Evergreen (USNM). **Arkansas**. *Newton Co*.: 12 mi. W Jasper (SEMC). **Connecticut**. *Litchfield Co*.: Cornwall (RLAC, CUIC). **District of Columbia**. Washington (USNM). **Florida**. "Fla" (USNM). "Haulover" (USNM). *Alachua Co*.: Cross Creek (FSC); Gainesville (RLAC); nr. Paynes Prairie St. Pk. (FSC). *Brevard Co*.: Hatbill St. Pk. (FSC). *Dade Co*.: Everglades Nat. Pk. "Royal Palm Pk." (CMN); Everglades Nat. Pk., Royal Palm Hammock (FSC). *Highlands Co*.: Archbold Biological Station (TAMU). *Lake Co*.: Camp McQuarrie (FSC). *Liberty Co*.: Torreya St. Pk. (FSC). *Putnam Co*.: 2 mi. SW Interlachen (FSC). *Volusia Co*.: Enterprise (USNM). **Illinois**. *Lake Co*.: Grayslake (SEMC). **Indiana**. *Monroe Co*.: Bloomington (FSC). **Iowa**. *Buchanan Co*.: Independence (USNM). *Polk Co*.: Walnut Woods St. Pk. (CUIC, USNM). **Kansas**. *Bourbon Co*.: 9 mi SW Ft. Scott (SEMC). *Crawford Co*.: 3 mi NE Pittsburg (SEMC). *Jefferson Co*.: 1 km SW Perry State Park (SEMC); University of Kansas Field Station, Nelson Ravine Forest (SEMC); The Falin Property, 1.5 km N jct. 94th St. & Kingman Rd. (SEMC). *Marshall Co*.: Alcove Springs State Park (SEMC). *Neosho* Co.: 2 mi SE Erie (SEMC). *Osage Co*.: Melvern Lake Project, Outlet Park (SEMC); Pomona Lake, Outlet Park (SEMC). *Pottawatomie Co*.: St. George (SEMC). *Wabaunsee Co*.: 10 mi SW Alma (SEMC). **Kentucky**. "Ky" (USNM). **Lousiana**. *East Baton Rouge Parish*: LA 37 at Comite River (LSAM). *East Feliciana Parish*: Boy Scout Camp Avondale, E of Clinton (LSAM); 1.2 mi S Central (LSAM). **Maine**. *Aroostook Co*.: St. Francis (DENH); Crystal (USNM); Howe Brook (USNM); Portage (USNM); Clayton Lake (USNM); Ashland (USNM). *Cumberland Co*.: South Portland (CUIC). *Franklin Co*.: Oquossoc (DENH). *Hancock Co*.: Blue Hill (DENH); E. Orland (USNM). *Kennebec Co*.: Vassalboro (USNM); Augusta (USNM). *Knox Co*.: Friendship (USNM). *Lincoln Co*.: New Harbor (USNM); Bristol (USNM); Boothbay Harbour (USNM). *Oxford Co*.: Peru (CUIC, MCZ). *Penobscot Co*.: Lee (USNM); Springfield (USNM). *Piscataquis Co*.: Kokadjo (DENH); Dover-Foxcropt (DENH); Chesuncook (USNM). *Somerset Co*.: Caratunk (DENH, USNM); Embden (USNM); Bingham (USNM); Brighton (DENH); Rockwood (USNM); Seboomook (DENH). *Waldo Co*.: Palermo (USNM). *Washington Co*.: Princeton (DENH, USNM); Wesley (DENH, USNM); Steuben (CNC). *York Co*.: West Lebanon (DENH). **Maryland**. *Carroll Co*.: Finksburg (USNM). *Somerset Co*.: Shelltown (USNM). *Talbot Co*.: Wittman (USNM); 3 km SE Easton (USNM). **Michigan.** *Marquette Co*.: Marquette (USNM). *Wayne Co*.:



Figures 2–4. Left half of pronotum. **2** *Paratenetus exutus* **3** *P. punctatus* **4** *P. texanus.*

Detroit (USNM). **Minnesota**. *Becker Co*.: Itasca St. Pk. area (USNM). *Crow Wing Co*.: Lake Hubert (CNC). *Sherburne Co*.: Elk River (CNC). **Mississippi**. *George Co*.: Lucedale (CUIC). *Greene Co*.: Leakesville (CUIC). **Missouri**. *Greene Co*.: nr. James River (TAMU). *Randolph Co*.: 1 mi E Moberly (TAMU). **New Jersey**. *Atlantic Co*.:

5 mi. N Hammonton (RLAC). *Cape May Co*.: Anglesea (USNM). *Ocean Co*.: Lakehurst (CUIC). *Salem Co*.: Lake Hudson, near Deepwater (RLAC). *Union Co*.: Elizabeth (USNM). **New York**. *Suffolk Co*.: Yaphank, L.I. (USNM). *Ulster Co*.: West Park (CUIC); Slide Mt. (CUIC). **North Carolina**. *Buncombe Co*.: Oteen (USNM); 6 mi S Asheville (SEMC). *Haywood Co*.: 9 mi. W Waynesville (SEMC); Cataloochee, GSMNP (LSAM); Purchase Knob, GSMNP (LSAM). *Henderson Co*.: Fletcher (FSC). *Swain Co*.: Andrews Bald, GSMNP (LSAM); Clingmans Dome, GSMNP (LSAM). *Yancey Co*.: Black Mountains (AMNH). **North Dakota**. *Richland Co*.: Mirror Pool (USNM). **Ohio.** *Fairfield Co*.: Barnebey Center (RLAC). *Franklin Co*.: Worthington (RLAC). *Hamilton Co*.: Cincinnati (USNM). *Highland Co*. (FSC). *Hocking Co*.: Ward Township (RLAC). *Pike Co*.: Jackson Lake (RLAC). *Preble Co*.: Hueston Woods (RLAC). *Ross Co*.: Tar Hollow St. Pk. (FSC). *Trumbull Co*.: Phalanx (CUIC). **Oklahoma**. *Latimer Co*.: Red Oak (FSC, TAMU). **Pennsylvania**. *Fayette Co*.: 5 mi. W. Ohiopyle (USNM). **Tennessee**. *Cocke Co*.: Albright Grove (LSAM). *Sevier Co*.: Ramsey Cascade Trail, GSMNP (LSAM); Goshen Prong, GSMNP (LSAM); Indian Gap, GSMNP (LSAM). *Swain Co*.: near Charlies Bunion, GSMNP (FSC). **Texas**. *Colorado Co*.: Columbus (USNM). *Victoria Co*.: Victoria (USNM). **Virginia**. "Ft. Monroe" (USNM). Covington (FSC). *Bath Co*.: 9.6 km N Clifton Forge (CNC). *Lee Co*.: Pennington Gap (MCZ). *Loudoun Co*.: 3 km SE Lovettsville (USNM). *Montgomery Co*.: Caldwell Fields (FSC, TAMU). **West Virginia**. *Mingo Co*.: Justice (CUIC). *Pocahontas Co*.: Cranberry Glades (USNM). **Wisconsin**. *Bayfield Co*.: Bayfield (USNM). *Wood Co*.: Griffith State Nursery (USNM).

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.

Figures 5–9. Parameres (dorsal view). **5** *Paratenetus gibbipennis* **6** *P. fuscus* **7** *P. exutus* **8** *P. punctatus* **9** *P. texanus.*

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.

Paratypes from the following localities: **Texas**. Port Isabel, 17.X.1982, 20.X.1982, 30.III.1987, BF&JL Carr (6, CNC). 18 mi. E of Hebbronville, 25.III.1987, BF&JL Carr (10, CNC). Cameron Co., Brownsville, 19 July 1981, W.E. Steiner (2, USNM). Cameron Co., Palmito Hill Hist. Site, Hwy. 4 east of Brownsville, 12-X-1993, S.M. Clark (2, RLAC). Cameron Co., 11 mi. W Boca Chica, 28 Sept. 1976, R. Turnbow (3, FSC). Hidalgo Co., Mission, Bentsen State Park, 17 (or 18) July 1981, W.E. Steiner (2, USNM). Hidalgo Co., Anzalduas Co. Pk., 19 Oct. 1985, Wappes & Downie (2, FSC). Bee Co., Beeville, 19 June 1974, W.E. Steiner (1, USNM).

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

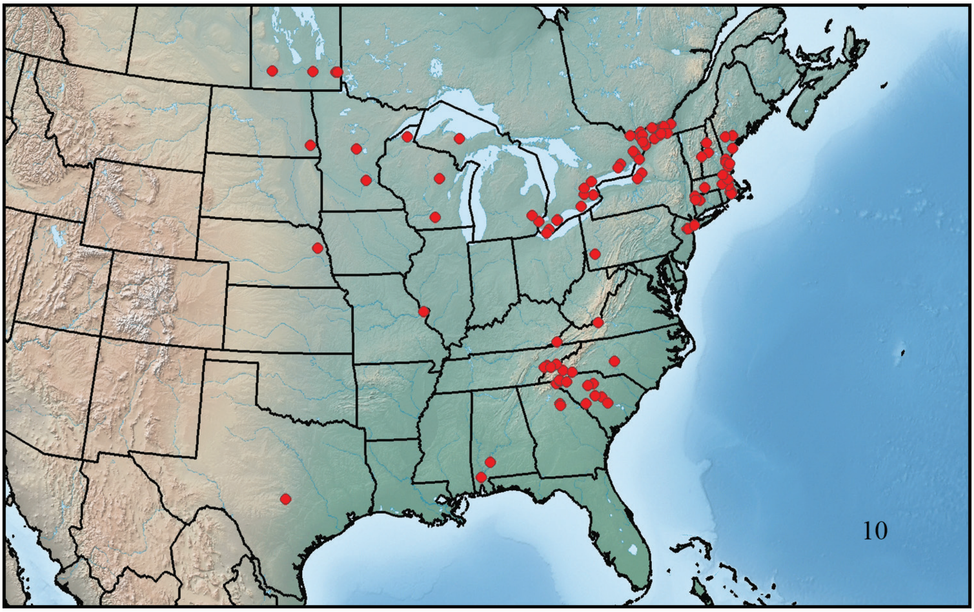
Diagnosis. Members of this species can be distinguished from those of *P. punctatus* and *P. exutus* in having the punctures on the pronotum sparser, not subcontigous even on the lateral half. They can also be distinguished from most adults of *P. punctatus* by their smaller size and from most adults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

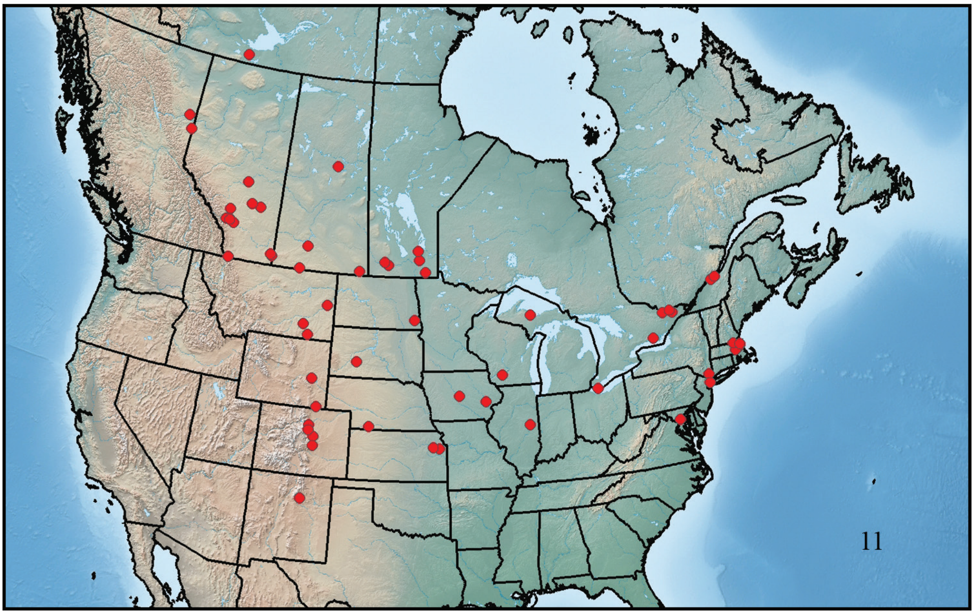
Description. Body dorsally yellow to pale reddish brown, with the pronotum and head usually slightly darker than elytra and legs; antennal club slightly darker than antennomeres 1–8 in many specimens, often reddish brown to partially piceous, yellowish and as pale as legs in some specimens; metaventrite 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





Figures 10–11. Maps showing collection localities in North America. **10** *Paratenetus gibbipennis* **11** *P. fuscus*.

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

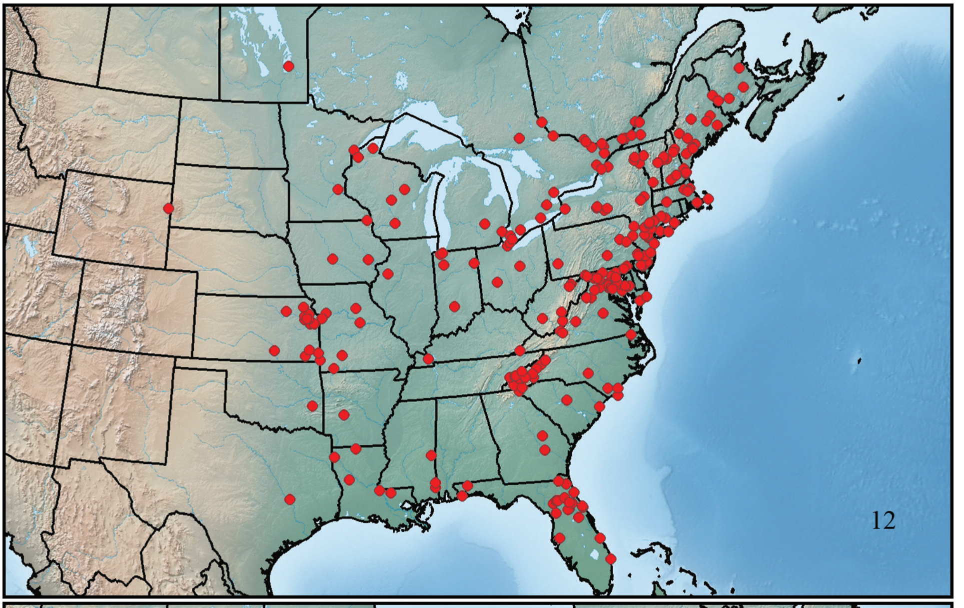
W Boca Chica Beach (TAMU); Brownsville (CNC, CUIC, MCZ, TAMU, USNM); 4 mi ESE Brownsville (TAMU); 6 mi E Brownsville (TAMU); 10 mi E Brownsville (RLAC, LSAM); 12.5 mi E Brownsville (TAMU); 13.5 mi E Brownsville (TAMU); W of Harlingen (TAMU); Main Reservoir near Brownsville (RLAC); Resaca de las Palomas 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 (CMN); 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 m 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).

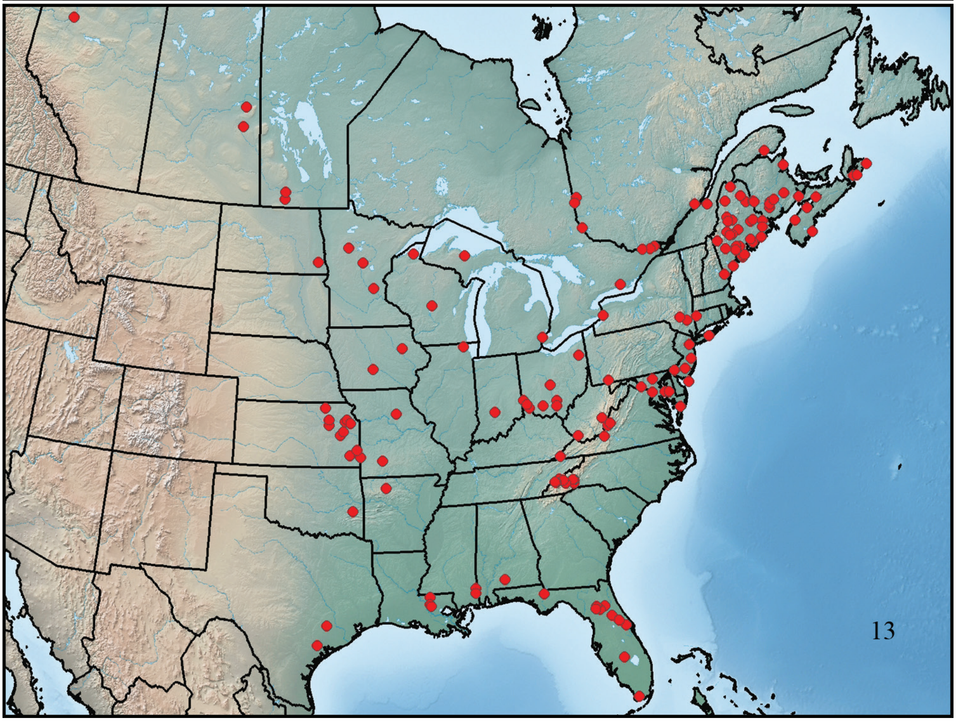
Remarks. The two specimens from Miami in Florida externally agree perfectly with those from Texas. One is a male and its genitalia are identical to those of specimens from Texas.

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).





Figures 12–13. Maps showing collection localities in North America. **12** *Paratenetus punctatus* **13** *P. exutus*.

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*,

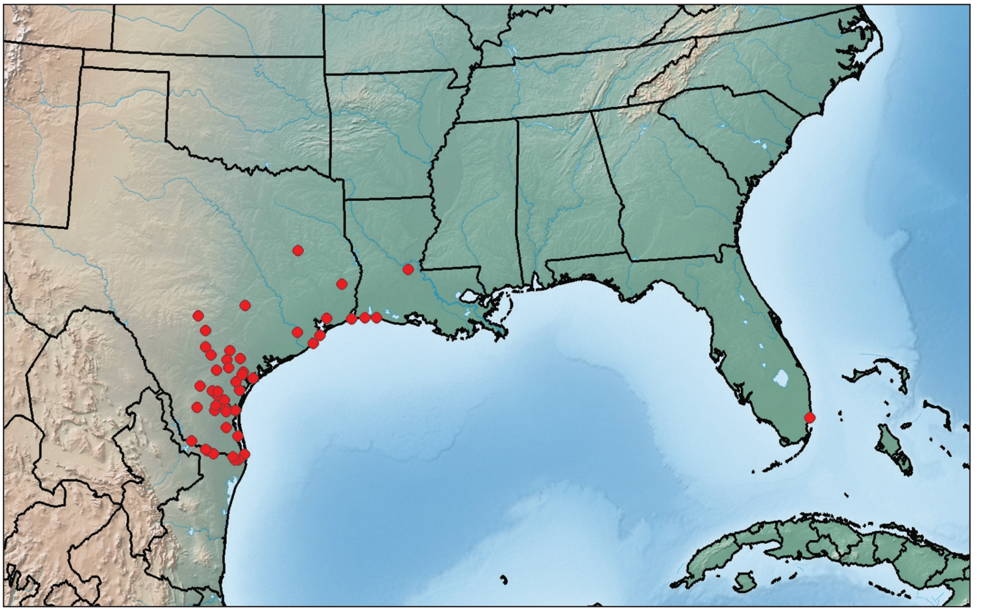


Figure 14. Map showing collection localities in America (north of Mexico) of *Paratenetus texanus*.

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.

References

Aalbu RL, Flores GE, Triplehorn CA (2002a) Tenebrionidae. In: Llorente Bousquets J, Morrone JJ (Eds) Biodiversidad, taxonomía y biogeografía de arthrópodos de México: Hacia una síntesis de su conocimiento. Volumen III. Universidad Nacional Autónoma de México, Mexico, 499–512.

Aalbu RL, Triplehorn CA, Campbell JM, Brown KW, Somerby RE, Thomas DB (2002b) 106. Tenebrionidae Latreille 1802. In: Arnett RH Jr, Thomas MC, Skelley PE, Frank JH (Eds)

American Beetles. Volume 2. Polyphaga: Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, 463–509.

Agassiz L (1846) Nomenclator zoologicus, continens nomina systematica generum animalium tam viventium quam fossilium, secundum ordinem alphabeticum disposita, adjectis auctoribus, libris in quibus reperiuntur, anno editionis, etymologia et familiis ad quas pertinent, in variis classibus. Fasciculus XI. Continens Coleoptera. Jent et Gassmann, Soloduri, xii + 170 pp.

Ardoin P (1961) Contribution à l'étude des Tenebrionides malgaches. Deux nouveaux genres d'Adeliini malgaches. Bulletin de l'Académie Malgache (n.s.) 37 [1959]: 31–38.

Arnett RH Jr (1962) The beetles of the United States (a manual for identification). Part V. Suborder Polyphaga (Cont.). Series Cucujiformia (Cont.). Tenebrionoidea. Cucujoidea. The Catholic University of America Press, Washington D.C., 645–850.

Blatchley WS (1910) An illustrated descriptive catalogue of the Coleoptera or beetles (exclusive of the Rhynchophora) known to occur in Indiana. With bibliography and descriptions of new species. The Nature Publishing Co., Indianapolis, 1386 pp. doi: 10.5962/bhl.title.56580

Böving AG, Craighead FC (1931) An illustrated synopsis of the principal larval forms of the order Coleoptera. Entomologica Americana (new series) 11 [1930]: 1–80.

Campbell JM (1991) Family Lagriidae – lagriid beetles. In: Bousquet Y (Ed) Checklist of beetles of Canada and Alaska. Agriculture Canada, Ottawa, 261–262.

Champion GC (1893) Note on the genus *Storthephora*, Mäklin. The Entomologist's Monthly Magazine 29: 47.

Downie NM, Arnett RH Jr. (1996) The beetles of northeastern North America. Volume II: Polyphaga: series Bostrichiformia through Curculionoidea. The Sandhill Crane Press, Gainesville (FL), x + 891–1721.

Doyen JT, Tschinkel WR (1982) Phenetic and cladistic relationships among tenebrionid beetles (Coleoptera). Systematic Entomology 7: 127–183. doi: 10.1111/j.1365-3113.1982.tb00129.x

Fall HC (1907) Descriptions of new species. In: Fall HC, Cockerell TDA. The Coleoptera of New Mexico. Transactions of the American Entomological Society 33: 218–272.

Ferrer J, Ødegaard F (2005) New species of darkling beetles from Central America with systematic notes (Coleoptera: Tenebrionidae). Annales Zoologici 55: 633–661.

Gebien H (1911) Coleopterorum Catalogus auspiciis et auxilio W. Junk editus a S. Schenkling. Pars 28: Tenebrionidae III. W. Junk, Berlin, 355–585.

Gebien H (1941) Katalog der Tenebrioniden. Teil II. Mitteilungen der Münchener Entomologischen Gesellschaft 31: 803–834.

Horn GE (1870) Revision of the Tenebrionidae of America, north of Mexico. Transactions of the American Philosophical Society (Series 2) 14: 253–404.

LeConte JL (1850) General remarks upon the Coleoptera of Lake Superior. In: Agassiz JLR. Lake Superior: its physical character, vegetation, and animals, compared with those of other and similar regions. With a narrative of the tour, by J. Eliott Cabot. And contributions by other scientific gentlemen. Gould, Kendall and Lincoln, Boston, 201–242.

LeConte JL (1859) The complete writings of Thomas Say on the entomology of North America. Edited by John L. Le Conte, M.D. with a memoir of the author, by George Ord. In two volumes. Vol. II. Ballière Brothers, New York, iv + 814 pp.

LeConte JL (1862) Classification of the Coleoptera of North America. Prepared for the Smithsonian Institution. Smithsonian Miscellaneous Collections [no] 265. Smithsonian Institution, Washington [D.C.], 209–286.

Leng CW (1918) Notes on some changes in the list of Coleoptera. Journal of the New York Entomological Society 26: 201–211.

Leng CW (1920) Catalogue of the Coleoptera of America, north of Mexico. John D. Sherman, Jr., Mount Vernon (NY), x + [1] + 470 pp.

Lucas R (1920) Catalogus alphabeticus generum et subgenerum Coleopterorum orbis terrarum totius (famil., trib., subtr., sect. incl.). Pars I. Nicolai, Berlin, xxxi + 696 pp.

Mäklin FW (1875) Neue *Statira*-Arten und einige mit der genannten Gattung verwandte Formen. Acta Societatis Scientiarum Fennicae 10: 633–660.

Melsheimer FE (1853) Catalogue of the described Coleoptera of the United States. Revised by S.S. Haldeman and J.L. LeConte. Smithsonian Institution, Washington D.C., xvi + 174 pp.

Motschulsky V (1868) Énumération des nouvelles espèces de Coléoptères rapportés de ses voyages. 6-ième article. Bulletin de la Société Impériale des Naturalistes de Moscou 41: 170–201.

Parsons CT (1976) A key to Nearctic *Statira* and *Arthromacra* (Lagriidae). The Coleopterists Bulletin 29 [1975]: 211–226.

Say T (1826) Descriptions of new species of coleopterous insects inhabiting the United States. Journal of the Academy of Natural Sciences of Philadelphia 5: 237–284.

Spinola MM (1844) Essai monographique sur les clérites insectes coléoptères. Tome second. Ponthenier, Gênes, 216 pp.

Steiner WE, Jr (1995) Structures, behaviour and diversity of the pupae of Tenebrionidae (Coleoptera). In: Pakaluk J, Ślipiński SA (Eds) Biology, phylogeny, and classification of Coleoptera: papers celebrating the 80th birthday of Roy A. Crowson. Volume 1. Muzeum i Instytut Zoologii PAN, Warszawa, 504–539.

Tschinkel WR, Doyen JT (1980) Comparative anatomy of the defensive glands, ovipositors and female genital tubes of tenebrionid beetles (Coleoptera). International Journal of Insect Morphology and Embryology 9: 321–368. doi: 10.1016/0020-7322(80)90009-4

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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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Academic editor: *P. Bouchard* | Received 20 November 2013 | Accepted 19 March 2014 | Published 12 June 2014

http://zoobank.org/C620B268-3075-4659-8C90-62866DF93193

Citation: Flores GE, Pizarro-Araya J (2014) Towards a revision of the South American genus *Praocis* Eschscholtz (Coleoptera, Tenebrionidae), with estimation of the diversity of each subgenus. In: Bouchard P, Smith AD (Eds) Proceedings of the Third International Tenebrionoidea Symposium, Arizona, USA, 2013. ZooKeys 415: 53–80. doi: 10.3897/zookeys.415.6656

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.**, *Orthogonoderes* 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 *Praocida*: *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.

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).

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

MNHN	Muséum National d'Histoire Naturelle, Paris, France
MNHUB	Museum fur Naturkunde der Humboldt Universitat, Berlin, Germany
MNNC	Museo Nacional de Historia Natural, Santiago, Chile
NHMB	Natural History Museum, Basel, Switzerland

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).

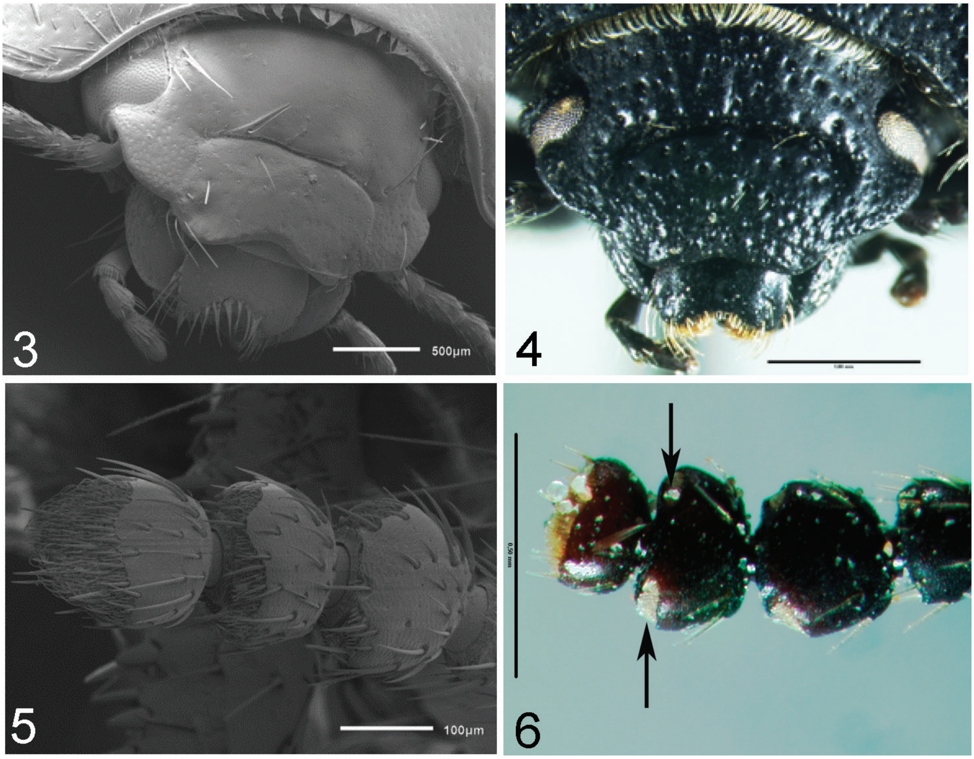
The remaining five names of the subgenera proposed by Kulzer (1958): *Mesopraocis*, *Postpraocis*, *Hemipraocis*, *Praonoda*, and *Praocida* are unavailable because Kulzer (1958) did not designate type species for these subgenera. To be available, every new genus-group name published after 1930 must, 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



Figures 3–6. 3 *Praocis* (*P.*) *subaenea*, head in dorsal view **4** *Praocis* (*Orthogonoderes*) *rotundata*, head in frontal view **5** *Praocis* (*P.*) *bicentenario*, antennomeres 9–11 in dorsal view **6** *Praocis* (*Orthogonoderes*) *rotundata*, antennomeres 9–11 in dorsal view (Figs **3** and **5** scanning electron micrographs previously published in Flores and Pizarro-Araya 2012, Zootaxa 3336: Figs **1** and **2**; copyright Magnolia Press, reproduced with permission).

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 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 quadrisulcata* 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); *Praocis bicentenario* Flores & Pizarro-Araya, 2012; *Praocis medvedevi* Flores & Pizarro-Araya, 2012; *Praocis bicostata* Philippi & Philippi, 1864 (type lost, assigned to (*Praocis*) 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 Limarí, 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).

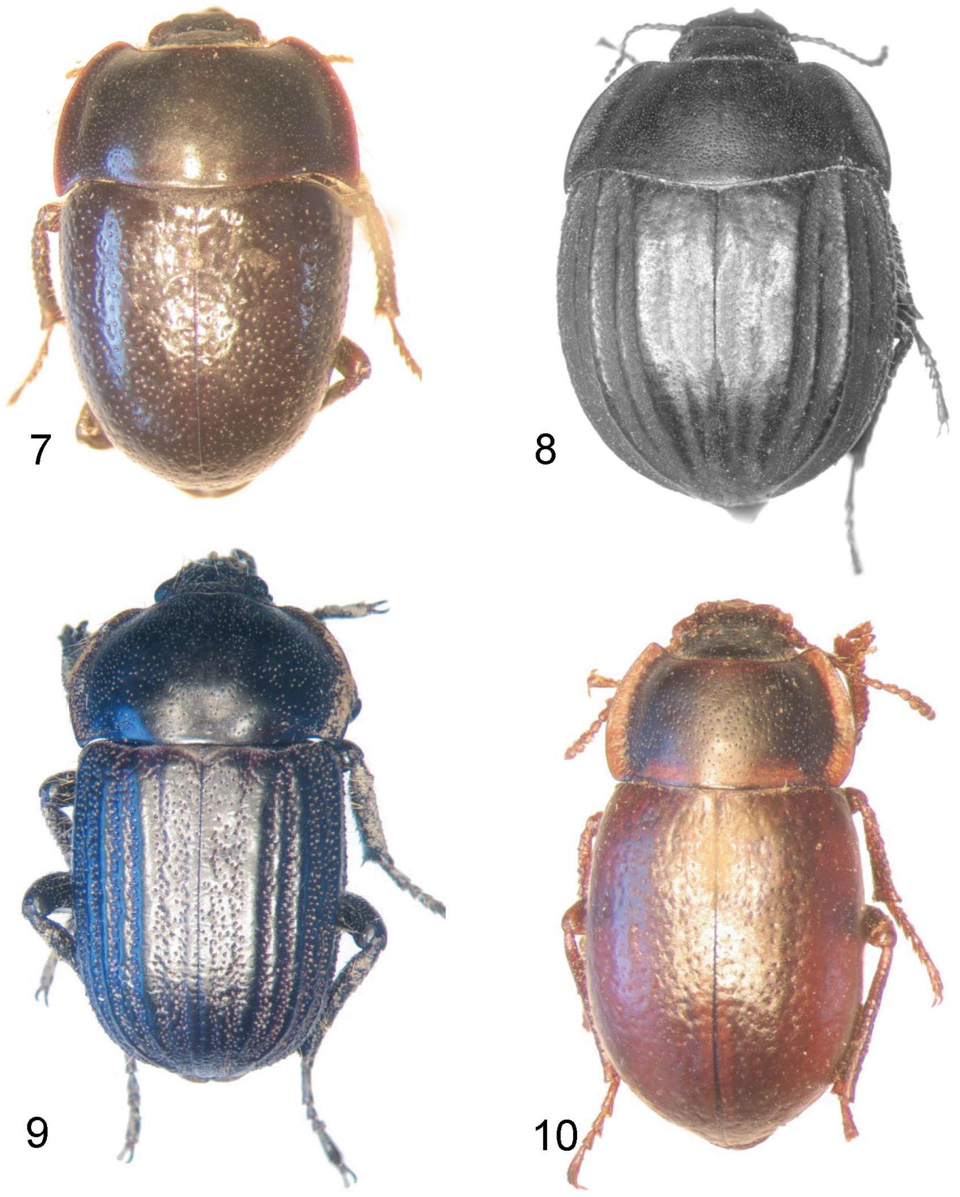
Habitat. The distribution range of the subgenus extends from sea level to an altitude of ~1325 m. All *Mesopraocis* species are associated with coastal dunes stabilized with vegetation or paleodunes in the transitional coastal desert of Chile and have nocturnal habits, remaining during the day under 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.



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*) *chevrolatii nigra* **10** *Praocis* (*Filotarsus*) *peltata*.

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 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 Enquelga, 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, Prepuna and Monte (Morrone 2006) (Fig. 19).

New records. We present new records of *Praocis* (*Postpraocis*) *pentachorda* 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).

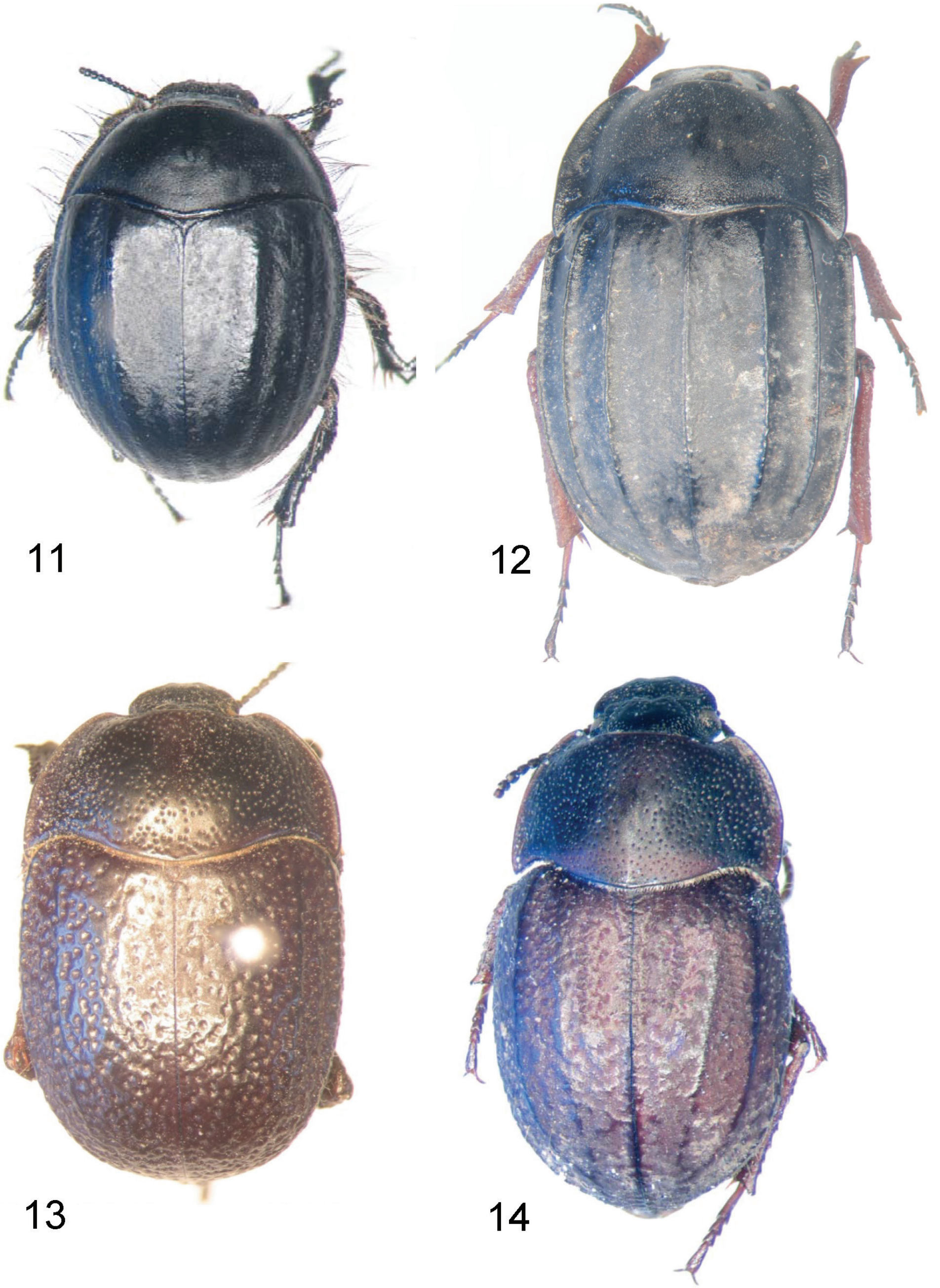
Species included. *Praocis curtisii* Solier, 1851; *Praocis costatula* Gay & Solier in Solier, 1840 (= *Praocis angulifera* Philippi & Philippi, 1864, synonymy by Kulzer 1958); *Praocis pubescens* Philippi & Philippi, 1864; *Praocis pentachorda* Burmeister, 1875 (= *Praocis larraini* Marcuzzi, 2001, synonymy by Flores 2009); *Praocis pentachorda 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



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* (*Praocida*) *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 semiarid 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).

Species included. *Praocis chevrolatii* Guérin-Méneville, 1834 (= *Praocis gayi* Solier, 1840, synonymy by Kulzer 1958) (= *Praocis hispidula* Philippi & Philippi, 1864, synonymy by Kulzer 1958) (= *Praocis laticollis* Philippi & Philippi, 1864, synonymy by Kulzer 1958); *Praocis chevrolatii subcostata* Gay & Solier in Solier, 1840 (= *Praocis chevrolatii coquimboana* Kaszab, 1969, synonymy by Flores 2007); *Praocis chevrolatii nigra* Kulzer, 1958; *Praocis hirtuosa* Gay & Solier in Solier, 1840 (= *Praocis pubens* Philippi & Philippi, 1864, synonymy by Kulzer 1958); *Praocis nuda* Kulzer, 1958.

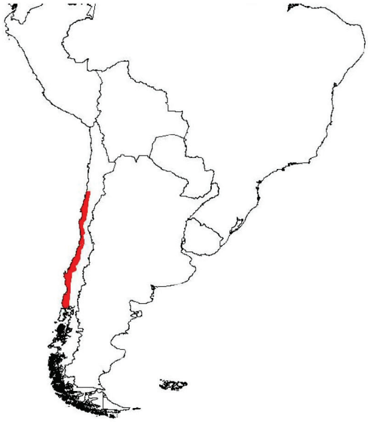
(5) Subgenus *Praocis* (*Filotarsus*) Gay & Solier in Solier, 1840

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, estern 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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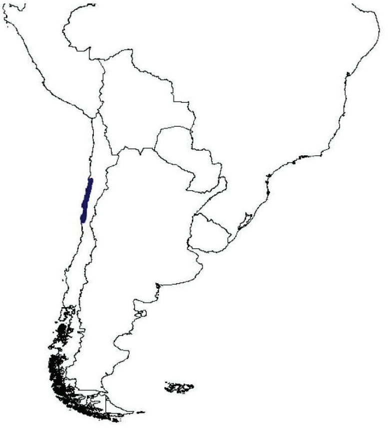

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Figures 15–18. 15 Distribution area of the subgenus *Praocis* (*Praocis*) **16** Punta de Choros (Coquimbo Region, Chile), habitat of *Praocis* (*Praocis*) *spinolai* **17** Distribution area of the subgenus *Praocis* (*Mesopraocis*) **18** Chañaral 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 forsteri* 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.

(6) Subgenus *Praocis* (*Hemipraocis*) Flores & Pizarro-Araya, subgen. n.

http://zoobank.org/1EF65CCD-D4C2-4B9F-BB5B-7BB98170599D
Figs 11, 25–26

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.

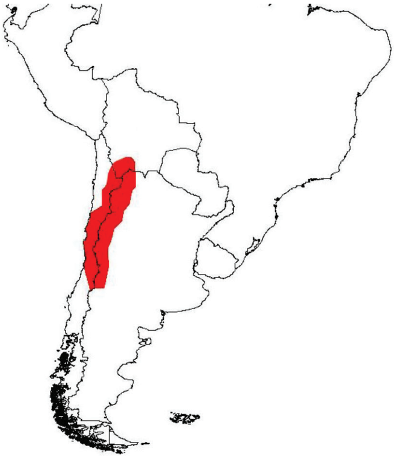
Distribution. The species of *Praocis* (*Hemipraocis*) occur from central Argentina (southern Mendoza 36°S and coastal Buenos Aires 36°S), to southern Argentina and Chile (northern Magellan Strait 52°S), in the biogeographic provinces of Patagonia, Monte and Pampa (Morrone 2006) (Fig. 25).

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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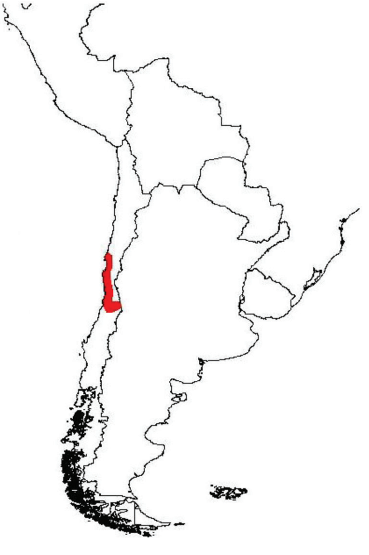

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Figures 19–22. 19 Distribution area of the subgenus *Praocis* (*Postpraocis*) **20** Totoralillo Norte (Coquimbo Region, Chile), habitat of *Praocis* (*Postpraocis*) *curtisii* **21** Distribution area of the subgenus *Praocis* (*Anthrasomus*) **22** Socos (Coquimbo Region, Chile), habitat of *Praocis* (*Anthrasomus*) *chevrolatii subcostata*.

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).

(7) 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, protibiae 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).

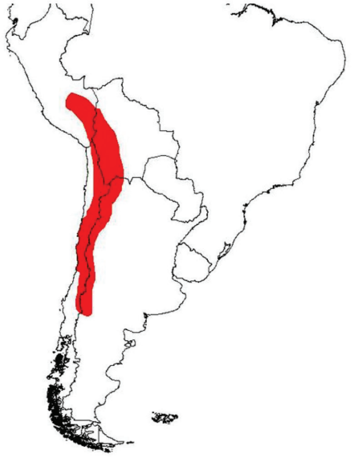
Species included. *Praocis bicarinata* Burmeister, 1875 (= *Praocis silphomorpha* Fairmaire, 1883a, synonymy by Berg 1884); *Praocis molinari* Kulzer, 1958.

(8) Subgenus *Praocis* (*Orthogonoderes*) Gay & Solier in Solier, 1840
Figs 13, 29–30

= *Aulacus* Gray, 1832: 783. Type species: *Aulacus chilensis* Gray, 1832, monotypy. Synonymy by Kulzer (1958).
= *Eurygona* Laporte, 1840: 187. Type species: *Aulacus chilensis* Gray, 1832, monotypy. Synonymy by Kulzer (1958).

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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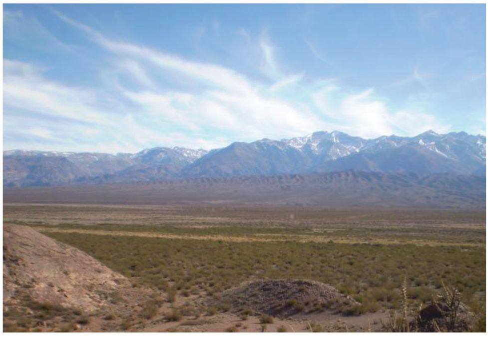

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Figures 23–26. 23 Distribution area of the subgenus *Praocis* (*Filotarsus*) **24** Uspallata Valley (Mendoza, Argentina), habitat of *Praocis* (*Filotarsus*) *oblonga* **25** Distribution area of the subgenus *Praocis* (*Hemipraocis*) **26** Peninsula 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).

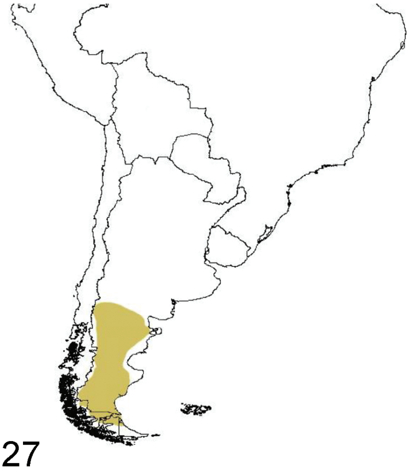
Species included. *Praocis cribrata* Gay & Solier in Solier, 1840; *Praocis adspersa* Germain, 1855; *Praocis depressicollis* Germain, 1855; *Praocis ecostata* Kulzer, 1958; *Praocis subreticulata* Gay & Solier in Solier, 1840; *Praocis dentipes* Germain, 1855; *Praocis pleuroptera* Gay & Solier in Solier, 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 picipes* Germain, 1855 (= *Praocis consobrina* Philippi & Philippi, 1864, synonymy by Kulzer 1958) (= *Praocis rotundicollis* Philippi & Philippi, 1864, synonymy by Kulzer 1958); *Praocis costipennis* Solier, 1851; *Praocis rugata* Gay & Solier in Solier, 1840; *Praocis punctata* Gay & Solier in Solier, 1840; *Praocis rotundata* Lacordaire, 1830 (= *Praocis soror* Kulzer, 1958, synonymy by Flores and Pizarro-Araya 2010); *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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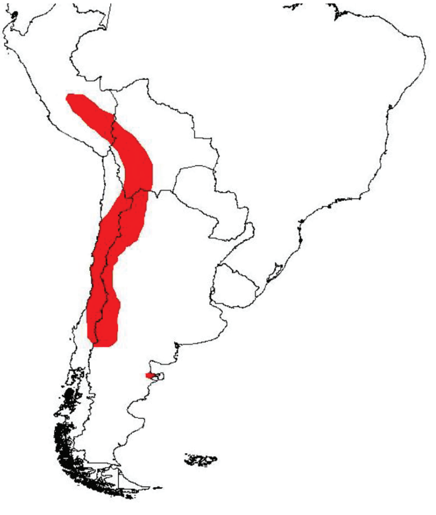

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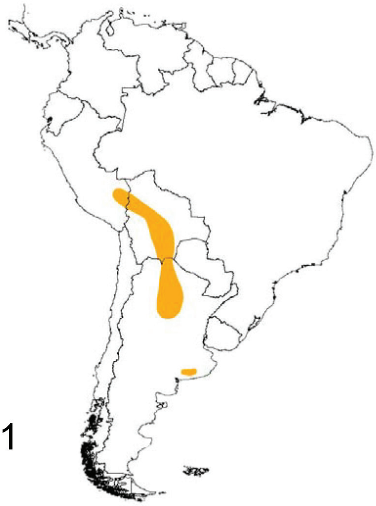
Figures 27–30. 27 Distribution area of the subgenus *Praocis* (*Praonoda*) **28** Southern Santa Cruz (Argentina), habitat of *Praocis* (*Praonoda*) *bicarinata* **29** Distribution area of the subgenus *Praocis* (*Orthogonoderes*) **30** Choros Bajos, (Coquimbo Region, Chile), habitat of *Praocis* (*Orthogonoderes*) *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;



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Figures 31–32. 31 Distribution area of the subgenus *Praocis* (*Praocida*) **32** Capilla del Monte (Córdoba, Argentina), habitat of *Praocis* (*Praocida*) *teniucosta* (Photo by Liliana Arguello).

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* Marcuzzi, 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.

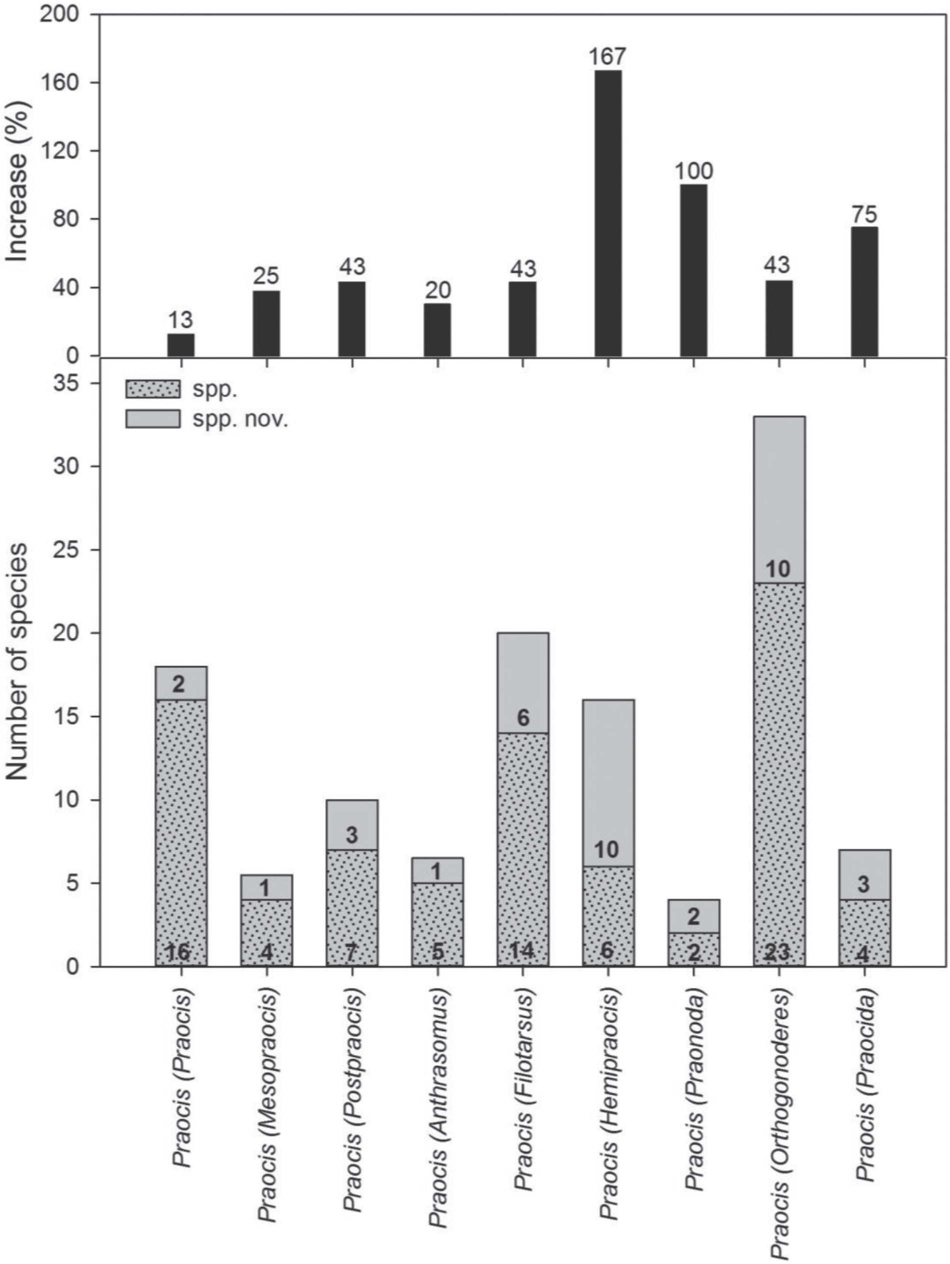

Figure 33. Diversity of the subgenera of *Praocis*. Current number of species (dotted); number of species to be described or recently described (grey) and percentage of increasing of species for each subgenus (black).

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 antennomere 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 antennomere 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 antennomere 10; antennomere 11 equal length as antennomere 10; apical tomentose sensory patches on antennomere 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; antennomere 9 longer than antennomere 10 (Fig. 3); antennomere 11 longer than antennomere 10 (Fig. 3); apical tomentose sensory patches on antennomere 11 on distal half (Fig. 3); ventral surface of profemora lacking a row of setae on anterior edge	**5**
5	Apical tomentose sensory patches on antennomere 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 antennomere 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 antennomere 11 on distal half (Fig. 3)	7
–	Apical tomentose sensory patches on antennomere 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 antennomere 10; clypeal suture as a horizontal groove covered by frons (Figs 4, 13)	***Orthogonoderes* Gay & Solier**
–	Antennomere 11 longer than antennomere 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*.

Characters	Character states	Subgenera								
		Praocis s. str.	***Mesopraocis***	***Postpraocis***	***Anthrasomus***	***Filotarsus***	***Hemipraocis***	***Praonoda***	***Orthogonoderes***	***Praocida***
1) Clypeus, anterior margin	A) extending beyond to lateral expansion of frons	×	×	×	×	×	×	×	×	×
	B) at same level as lateral expansion of frons					×				
2) Clypeus, width of anterior margin	A) not exceeding half the interocular width	×	×	×	×	×	×	×	×	×
	B) same width as interocular distance					×				
3) Clypeal suture	A) as horizontal groove				×	×	×	×	×	×
	B) as vertical groove	×	×	×		×				
4) Antennomere 9	A) longer than antennomere 10	×		×	×	×	×	×	×	×
	B) equal in length to antennomere 10		×							
5) Antennomere 11	A) Longer than antennomere 10	×		×	×	×	×	×		×
	B) shorter than antennomere 10								×	
	C) equal in length to antennomere 10		×							
6) Apical tomentose sensory patches on antennomere 10	A) in two areas subequal in size		×	×	×		×	×	×	×
	B) in a dorsally continuous semicircle	×				×				
7) Apical tomentose sensory patches on antennomere 11	A) on distal third		×						×	×
	B) on distal half	×		×	×	×	×	×		
8) Prosternum	A) with a narrow edge on anterior margin	×	×	×	×	×				
	B) without edge on anterior margin						×	×	×	×
9) Lateral margin of elytron	A) well defined	×		×			×	×	×	×
	B) not defined		×		×	×				
10) Ventral surface of profemora	A) with a row of setae on anterior edge	×	×							
	B) without a row of setae on anterior edge			×	×	×	×	×	×	×
11) Protibiae	A) explanate	×	×			×	×	×	×	×
	B) not explanate			×	×					

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 organizators of the Third International Symposium on Tenebrionoidea 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-Juñent (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).

References

Alfaro FM, Pizarro-Araya J, Flores GE (2009) Epigean tenebrionids (Coleoptera: Tenebrionidae) from the Choros Archipelago (Coquimbo Region, Chile). Entomological News 120: 125–130. doi: 10.3157/021.120.0201

Arnett RH, Samuelson GA, Nishida GM (1993) The Insect and Spider Collections of the World. 2nd edition. Sandhill Crane Press, Gainesville, Florida, 310 pp.

Berg C (1884) (Synonymies). Bulletin de la Société Entomologique de France 1884: 98–99.

Berg C (1889) Quadraginta Coleoptera nova Argentina (Tenebrionidae). Anales de la Universidad de Buenos Aires 4: 127–145.

Burmeister H (1875) Melanosoma Argentina. Stettiner Entomologische Zeitung 36: 457-500.

Cortés-Contreras M, Pizarro-Araya J, Alfaro FM, Cepeda-Pizarro J (2013) Coleópteros epigeos (Insecta: Coleoptera) asociados a ecotopos dunarios de la cordillera de la costa de Chile. IDESIA (Chile) 31: 95–101. doi: 10.4067/S0718-34292013000400013

Curtis J (1845) Descriptions of the insects collected by Captain P.P. King, in the survey of the Straits of Magellan. Transactions of the Linnean Society of London 19: 41–476. doi: 10.1111/j.1096-3642.1842.tb00371.x

Erichson WF (1834) Coleoptera. In: Meyen FJF. Beiträge zur Zoologie, gesammelt auf einer Reise um die Erde. Nova Acta Physico-Medica Academiae Caesareae-Leopoldino-Carolinae, Naturae Curiosorum 16 (Suppl. 1): 219–276. Bonn.

Eschscholtz JF (1829) Zoologischer Atlas, enthaltend Abbildungen und Beschreibungen neuer Theirarten, während des Flottcapitains von Kotzebue zweiter Reise um die Welt, auf der Russisch-Kaiserlichen Kriegsschlupp Predpriaetië in the Jahren 1823–1826. Drittes Heft, G. Reimer, Berlin, 18 pp, pls. 11–15.

Fairmaire L (1883a) Note sur quelques Coléoptères de Magellan et de Santa Cruz. Annales de la Société Entomologique de France ser. 6, vol. 3: 483–506.

Fairmaire L (1883b) Description de quelques Coléoptères de la Patagonie et de la République Argentine. Annales de la Société Entomologique de France ser. 6, vol. 3: 507–516.

Fairmaire L (1902) Diagnosis de Coléoptères hétéromères recueillis par M.G.A. Baer au Pérou. Bulletin de la Société Entomologique de France 7: 148–151.

Ferrú MA, Elgueta M (2011) Lista de Coleópteros (Insecta: Coleoptera) de las Regiones de Arica y Parinacota y de Tarapacá, Chile. Boletín del Museo Nacional de Historia Natural, Chile 60: 9–61.

Fischer von Waldheim G (1844) Spicilegium Entomographiae Rossicae. Bulletin de la Société Impériale des Naturalistes de Moscou 17: 3–144.

Flores GE (2007) New synonymies and lectotype designations in the Neotropical tribes Nycteliini, Praocini, and Scotobiini (Coleoptera: Tenebrionidae). Annales Zoologici 57: 409–426.

Flores GE (2009) Revision of some types of the South American tribes Nycteliini, Praocini, and Scotobiini (Coleoptera: Tenebrionidae), with new synonymies. Zootaxa 1985: 21–33.

Flores GE, Chani-Posse M (2005) *Patagonopraocis*, a new genus of Praocini from Patagonia (Coleoptera: Tenebrionidae). Annales Zoologici 55: 575–581.

Flores GE, Pizarro-Araya J (2006) The Andes mountain range as a vicariant event in the Pimeliinae (Coleoptera: Tenebrionidae) in southern South America. Cahiers Scientifiques 10: 95–102.

Flores GE, Pizarro-Araya J (2010) Two new synonymies in the genus *Praocis* (Coleoptera: Tenebrionidae). Zootaxa 2386: 65–68.

Flores GE, Pizarro-Araya J (2012) Systematic revision of the South American genus *Praocis* Eschscholtz, 1829 (Coleoptera: Tenebrionidae). Part 1: Introduction and subgenus *Praocis* s. str. Zootaxa 3336: 1–35.

Flores GE, Carrara R, Cheli GH (2011) Three new Praociini (Coleoptera: Tenebrionidae) from Peninsula Valdés (Argentina), with zoogeographical and ecological remarks. Zootaxa 2965: 39–50.

Gajardo R (1994) La vegetación natural de Chile. Clasificación y distribución geográfica. Editorial Universitaria, Santiago, Chile, 165 pp.

Germain P (1855) Descripción de Coleópteros de diversas especies que no se hallan en la obra del señor Gay. Anales de la Universidad de Chile 12: 386–407.

Gray GR (1832) Notices of new genera and species. Insecta. In: Griffith E, Pigdeon E (Eds) The Animal Kingdom arranged in conformity with its organization by the Baron Cuvier, member of the institute of France, with supplementary additions to each order. Whittaker, Treacher, and Co., London. Volume 15: 1–796.

Guérin-Méneville FE (1834) Matériaux pour une classification des Mélasomes. Magazine de Zoologie 3e. année: 1–39.

ICZN (1999) International Code of Zoological Nomenclature. Fourth Edition. Adopted by the International Union of Biological Sciences. International trust for Zoological Nomenclature, London, xxix + 306 pp.

Kaszab Z (1964) The zoological results of Gy. Topáls collectings in South Argentina. 13. Coleoptera-Tenebrionidae. Annales Historico-Naturales Musei Nationalis Hungarici (Pars Zoologica) 56: 353–387.

Kaszab Z (1969) The scientific results of the Hungarian soil Zoological Expeditions to South America. 17. Tenebrioniden aus Chile (Coleoptera). Opuscula Zoologica Budapest 9 (2): 291–337.

Kulzer H (1958) Monographie der südamerikanischen Tribus Praocini (Col.) (16 Beitrag zur Kenntnis der Tenebrioniden). Entomologische Arbeiten aus dem Museum George Frey 9: 1–105.

Kulzer H (1962) Neue Tenebrioniden aus Südamerika (Col.) (23 Beitrag zur Kenntnis der Tenebrioniden). Entomologische Arbeiten aus dem Museum George Frey 13: 79–100.

Lacordaire JT (1830) Mémoire sur les habitudes des insectes coléoptères de l'Amérique méridionale (Hétéromères). Annales de Sciences Naturelles 20: 274–291.

Lacordaire JT (1859) Histoire Naturelle des Insectes. Generades Coléoptères ou exposé méthodique et critique de tous les genres proposés jusqu'ìci dans cet ordre d'insectes. Tome cinquième. Contenant les familles des Ténébrionides, Cistélides, Nilionides, Pythides, Mélandryides, Lagriides, Pédilides, Anthicides, Pyrochroides, Mordellides, Rhipiphorides, Stylopides, Meloïdes et Oedémérides. Librairie Encyclopédique de Roret, Paris, Première partie ([1] + 1–400), Deuxième partie, [1] + 401–750.

Laporte FLNC (Comte de Castelnau) (1840) Historie naturelle des insectes, vol. 2. P. Duménil, Paris, 564 pp.

Marcuzzi G (1977) Nuove specie di tenebrionidi dell'Argentina (Coleoptera). Memorie della Societá Entomologica Italiana 55: 139–152 (1976).

Marcuzzi G (2001) New species of tenebrionid beetles from Central and South America (Col. Heteromera). Annali del Museo Civico di Storia Naturale Giacomo Doria 93: 269–291 (2000).

Molinari HJ (1969) Tenebriónidos nuevos de Jujuy (República Argentina). Revista de la Sociedad Entomológica Argentina 31(1–4): 133–140.

Morrone JJ (2006) Biogeographic areas and transition zones of Latin America and the Caribbean islands based on panbiogeographic and cladistics analyses of the entomofauna. Annual Review of Entomology 51: 467–494. doi: 10.1146/annurev.ento.50.071803.130447

Motschulsky V (1845) Remarques sur la collection des coléoptères Russes de Victor Motschoulsky. 1er article. Bulletin de la Société Impériale des Naturalistes de Moscou 18: 1–127.

Peña LE (1966) Catálogo de los Tenebrionidae (Coleoptera) de Chile. Entomologische Arbeiten aus dem Museum George Frey 17: 397–453.

Philippi RA, Philippi FH (1864) Beschreibung einiger neuen Chilenischen Käfer. Stettiner Entomologische Zeitung 25 (10–12): 313–406.

Solier AJJ (1840) Essai sur les Collaptèrides. 11e Tribu. Praocites. Annales de la Société Entomologique de France 9: 207–370.

Solier AJJ (1851) Fauna chilena: Coleópteros. In: Gay C. Historia Física y Política de Chile. Zoología, Vol. 5. Imprenta de Maulde et Renou, Paris, 183–204.

ZooKeys 415: 81–132 (2013)
doi: 10.3897/zookeys.415.6406
www.zookeys.org

RESEARCH ARTICLE

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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

http://zoobank.org/372DF48D-D163-4742-AABF-5D7E4913050C

Citation: Kamiński MJ (2013) A cladistically based reinterpretation of the taxonomy of two Afrotropical tenebrionid genera *Ectateus* Koch, 1956 and *Selinus* Mulsant & Rey, 1853 (Coleoptera, Tenebrionidae, Platynotina). In: Bouchard P, Smith AD (Eds) Proceedings of the Third International Tenebrionoidea Symposium, Arizona, USA, 2013. ZooKeys 415: 81–132. doi: 10.3897/zookeys.415.6406

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 laevistriatus* (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 distincly 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:

BMNH	Natural History Museum, London, Great Britain
HNHM	Hungarian Natural History Museum, Budapest, Hungary
JFCS	Julio Ferrer Collection, Haninge, Sweden
MHNG	Muséum d'histoire naturelle de la Ville de Genève, Geneva, Switzerland
MIIZ	Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, Poland
MNB	Museum für Naturkunde, Germany, Berlin
MNHN	Muséum National d'Histoire naturelle, Paris, France
MHNL	Centre de Conservation des Collections, Muséum d'Histoire Naturelle, Lyon, France
MRAC	Royal Museum for Central Africa, Tervuren, Belgium
RBINS	Royal Belgian Institute of Natural Sciences, Brussels, Belgium
TMNH	Ditsong National Museum of Natural History, Pretoria, Republic of South Africa
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
ZMAS	Zoological Museum, Academy of Sciences, Sankt Petersburg, Russia

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 a 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* Ardoin, 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 punctatostriatus* (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. Anntenna: (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).

Taxon / character	1	6	11	16	21	26	31	36
Zidalus latipes	00000	00000	01000	10000	00000	00100	00000	00000
Lechius abacoides	00000	10000	01000	00000	00000	00000	00000	00000
Pseudoselinus punctatostriatus	00000	01000	01000	00101	00000	01100	00000	00000
Upembarus upembaensis	00000	01000	01000	00100	00000	00100	00000	00000
Ectateus crenatus	00111	00110	10211	10011	11100	00001	00100	10001
Ectateus curtulus	0?010	00100	10211	00011	10100	00???	?????	??000
Ectateus ghesquierei	00111	00110	10211	00011	11100	00001	00100	10001
Ectateus laevistriatus	01001	10000	00101	10001	00000	10110	01011	01100
Ectateus lamottei	01001	10000	00101	00001	00000	10110	01011	01100
Ectateus modestus	01111	00110	10211	10011	10100	00001	00100	10000
Ectateus ursynowiensis	10000	00000	00100	01000	00101	00001	00100	00000
Ectateus villiersi	10000	00001	00100	01000	00001	00001	00100	00000
Selinus calcaripes	01111	00110	10211	10011	10000	00001	00100	10000
Selinus convexipennis	01001	10000	00101	00001	00000	10110	01010	01100
Selinus gravis	01000	10000	00100	00001	00000	10110	01010	01100
Selinus malaisei	01000	10000	00100	00000	00010	10110	11010	02100
Selinus medius	01000	10000	00100	00000	00010	10110	11010	02100
Selinus palnus	01000	10001	00100	00001	00000	01100	00010	00010
Selinus plicicollis	01000	10000	00100	00000	00010	10110	11010	02100
Selinus striatus	01000	10001	00100	00001	00000	01100	00010	00010

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 (Raś and Kamiński 2013, Kamiński 2013c).
12. Ratio of prothorax width (tw) and pronotal disc height (dh): (0) < 5; (1) > 6 (Raś 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 Raś 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) impressed 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 longitudinal depression.

Abdomen (characters 26–27)

26. 5^{th} abdominal ventrite: (0) relatively narrow; (1) strongly widened (Fig. 10).
27. 5^{th} 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 absent; (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 retention 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 synonimized with *Selinus* 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

Ectateus Koch, 1956: 230.– Iwan 2001b: 352, 2002a: 66, 2002b: 265, 2004a: 541, 2004b: 739; Iwan and Banaszkiewicz 2007: 725; Kamiński and Raś 2011: 647; Kamiński 2013a: 85; Raś and Kamiński 2013: 381.

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 protibia 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) **3**

– Body size: 11.5–14.0 mm. Antennomeres form 7 to 11 elongated. Elytral striae with superficial punctures; intervals flat (Fig. 27) **4**

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) .... ***Ectateus crenatus***

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

Selinus calcaripes Gebien, 1904: 3.– Gebien 1910: 277, 1938: 297; Koch 1956: 238; Kulzer 1963: 425, Iwan 2002b: 265.

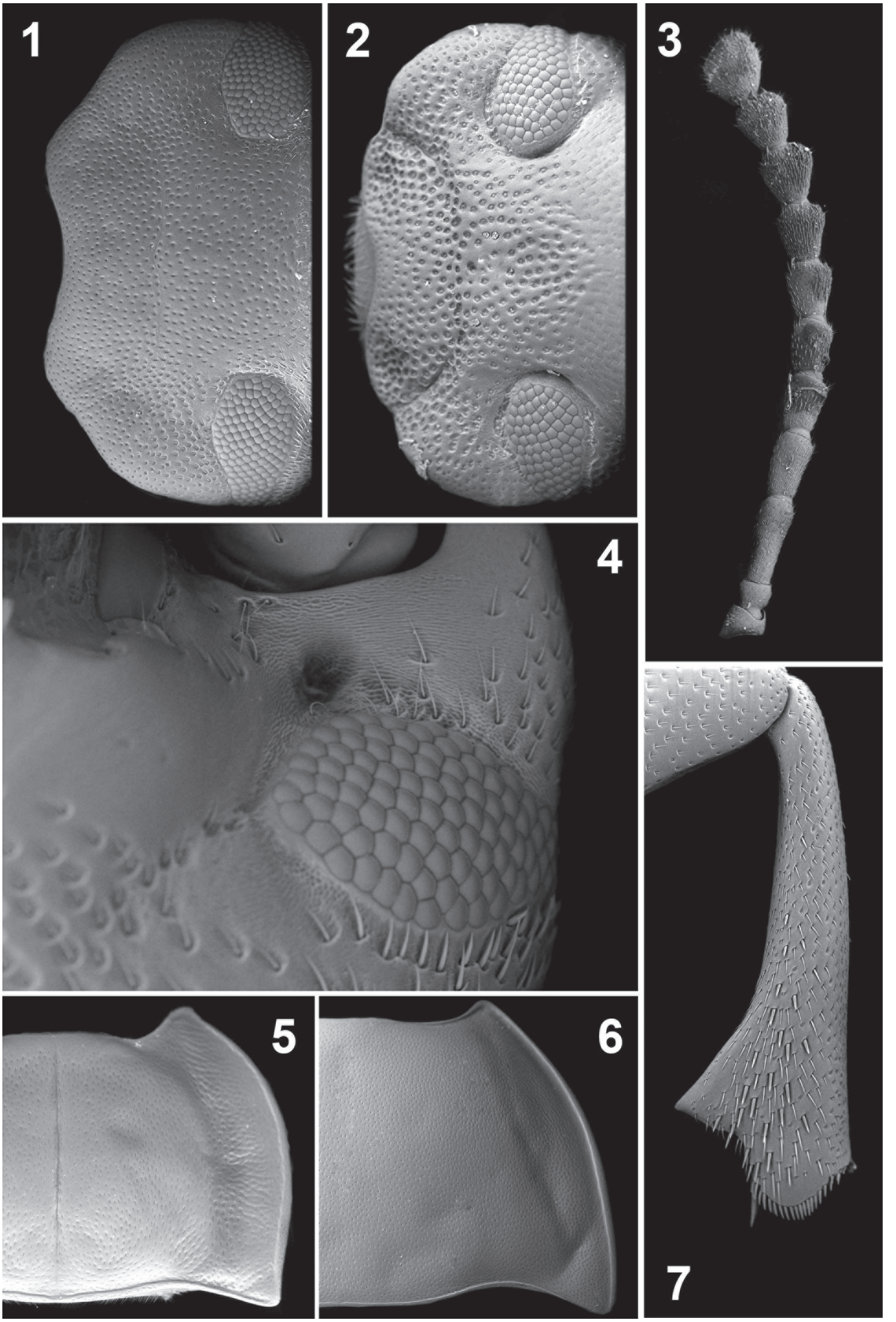
Notes. The types of *Selinus calcaripes* seems to be lost. According to the information provided by Iwan (2002b) they should be deposited in Naturhistorisches Museum collection (Basel, Switzerland). Unfortunately, the curators do not confirm this statement. Additionally, during the preparation of my 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 menaged 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 differers 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 a independent species – not as a synonym of *Ectateus curtulus*.

Studied material. Neotype designated here, male (MNHN): "Rep. Centrafric., La Maboke, 2.IX.1967, L. Matile rec.". **Other material**: male (MNHN): "Musée du Congo, Haut-Uele: Yebo moto, VII-1926, L. Burgeon", male (MRAC): "Musée du Congo, Haut-Uele: Yebo moto, V-1926, L. Burgeon", male (MRAC): "Musée du Congo, Bambesa, 15-X-1933, J. V. Leroy", male and 3 females (MRAC): "Coll. Mus. Tervuren, Oubanghi-Chari: Bangui I/III.1968, ex. coll. Breuning", male and female (RBINS): "R.I.Sc.Nat. Belg.,I.G. 16.364", 4 females (MNHN): "Calcaripes, Geb., det. Dr. Kaszab", male and female (MNHN): "Boukoko, Rep. Centr Afric.",



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**).

male and female (MNHN): "La Maboke, Rep. Centr Afric.", 2 males and female (MNHN): "Lamaboké, 10.XI.1965", male and female (MNHN): "Lamaboké, 20-21.XI.1966", male (MNHN): "Lamaboké, 18.XI.1965", 2 females (HNHM): "Cameroon, Dja Reserve, Ekom, 21-26.XII. 1996, G. Hácz & G. Köszegi", 3 males (MNB): "Kamerun Buea, 1-7.III.1912, v. Rothkirch S.G.", female (MNB): "Kamerun, Brea 1000m, 2. - 7. III- 1912; v. Rothkirch S.G.", female (MNB): "Kamerun, Soppo 25. II. 1912, v. Rothkirch S.G.", 2 males (MNHN): "Lamaboké, Rep. Centrafric., V-1964, J. Carayon", female (MNHN): "1968-69, La Maboké, Rép. Centre Afr., P. Teochhi leg.", male (MNHN): "21.VIII.1969, La Maboké, Rép. Centre Afr., P. Teochhi leg.", female (RBINS): "Coll. R. I. Sc. N. B., congo belge Beni, crottes d' éléphants, 18-I-1952 Ch. Verbeke", female (MNHN): "Muséum Paris, La Maboké, Rép. Centrafric.", male (MRAC): "Musée du Congo, Région de Sassa, 1895-96, Colmant", male and female (MNHN): "Cameroun, Dr. G. Nonveiller", female (MNHN): "Muséum Paris, Congo Moyen, Rég. de M`Baiki, (D Fidao), Pitard 1919", male (MNHN): "Uganda Prot., Mabira Forest, Chagwe., 3,500-3,800 ft.", female (MNHN): "Uganda, Nimuli to, Murchison Falls", male (MNB): "Neu-Kamerun, No. 3360-71, Tessmann S.G."

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 crenatus Fairmaire, 1897: 121.– Gebien 1910: 277, 1938: 297.

Ectateus crenatus (Fairmaire, 1897).– Koch 1956: 235, Iwan 2002b: 265; Iwan and Banaszkiewicz 2007: 728.

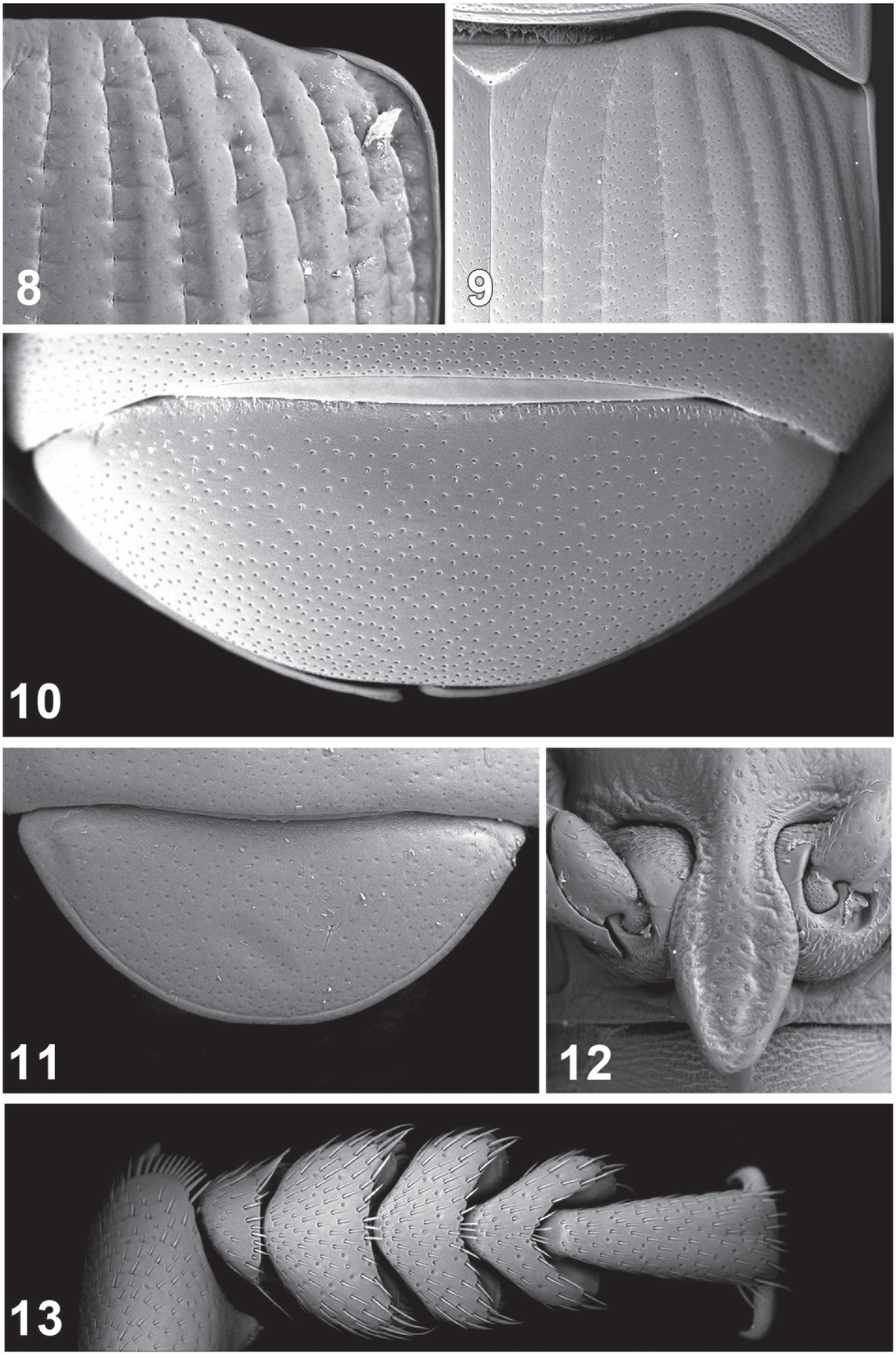
Selinus monardi Kaszab, 1951: 2 (syn. nov.)

Ectateus latipennis Koch, 1956: 234 (syn. nov.).– Iwan 2002a: 67, 2002b: 266.

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 synonim 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*.

Studied material. Three specimens with "type" labels are available. Fairmaire (1897) do not specify the number of individuals on which he described this species. Lectotype designation is needed to fix the taxonomic status of the genus and the species. **Lectotype** designated here, male (MNHN): "TYPE", "Museum Paris, 1906, Coll. L. Fairmaire", "*Selinus crenatus*"; **Paralectotypes**, male (MNHN), female (MNHN): "TYPE", "Museum Paris, 1906, Coll. L. Fairmaire", "*Selinus crenatus* Farim 1896, Congo", female (MNHN): "*Selinus crenatus* Fm n. sp.", "TYPE", "Museum Paris, 1906, Coll. L. Fairmaire", "Congo". **Other material**: male (MRAC): "Musée du Congo, Barumbu - VIII-1925, (J. Ghesquière), S.A.R. Prince Léopold" (Holotype of *Ectateus latipennis* Koch, 1956), female (RBINS): "Ibembo, Itimbiri" (Allotype of *Ectateus latipennis* Koch, 1956), male (MNHN): "Kamerun, Joko"



Figures 8–13. Elytral disc (**8, 9**); 5th abdominal ventrite (**10, 11**), intercoxal process of prosternum (**12**), male protarsi (**13**). *E. crenatus* (**8, 12**), *M. convexipennis* (**10**), *M. malaisei* (**9**), *M. plicicollis* (**13**), *S. striatus* (**11**).

(Holotype of *Selinus monardi* Kaszab, 1951), male and female (MNHN): "Joko, Kamerun" (Paratype and allotype of *Selinus monardi* Kaszab, 1951), male and female (MNHN): "Cameroun, Dr. G. Nonveiller", male and female (MNHN): "Muséum Paris, Cameroun, B. de Miré", 3 males and 2 females (MNHN): "Ogodué, Lambaréné, R. Ellenberger 1913", male (MNHN): "Congo Français, region D' ouesso, Bassin N`Gokko-Sanga, Dr. J. Gravot 1906", male (MNHN): "Congo Français, Talagouga Prés N`Jolé, legit R. Ellenberger, E. Haug 1906", male and female (MNHN): "Ogooué, Sam-Kita", 3 females (MNHN): "Congo, Ogooué, Sam Kita, R. Ellenberger 1910", 2 males and 2 females (MNHN): "Gabon, Libreville et env.", male and female (MNB): "Span. Guinea, Nkolentangan, XI. 07-V.08, G. Teßmann S.G.", female (MNHN): "Benito, Congo Franc.", female (MNHN): "Gabon, Tholon", male and female (MNHN): "XII.1970, Mbalmayo, CAMEROUN, Mbarga leg.", female (MNHN): "Congo belge Centr., Kassai, Edm. Taymans, 1904", male (MHNG): "CAMEROUN VII.83, Etoubi Assok, à la lumière, F. Notari", female (MNB): "Neu-Kamerun, No. 3337-52, Tessmann S.G.", female (MRAC): "Coll. Mus. Congo, Mayumbe: Terr. Tshela, rég. de Mabuba VI-1958, Dr R. Laurent", male (MRAC): "Mus. Roy. Afr. Centr., Guinée Esp: Bata, Rév. P. Basilio", male (MNHN): "Kuilu, Fr. Congo., Mocquerys, 1892", male (RBINS): "Chutes de Samlia, Riv N. Gamie, Mocquereys".

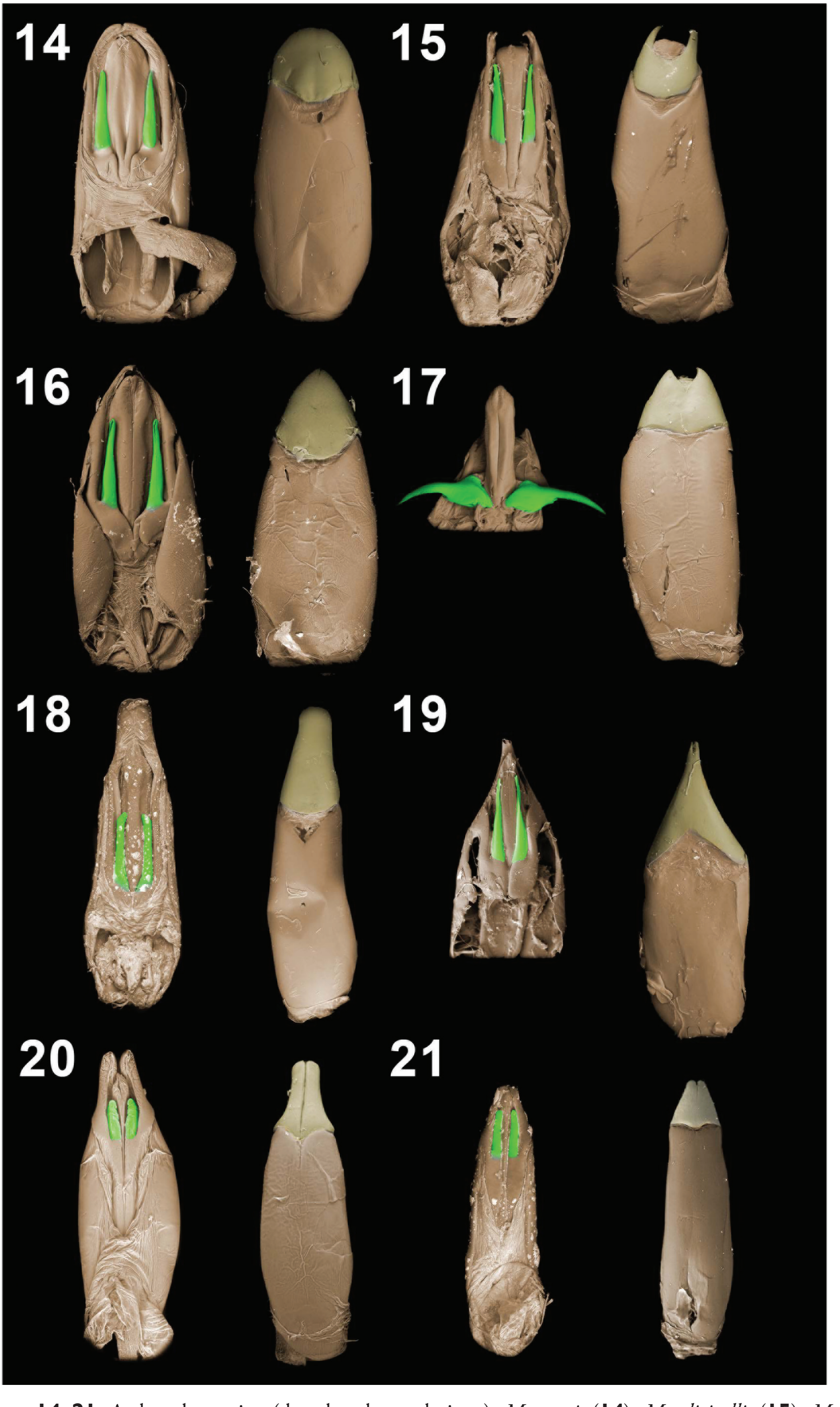
Redescription. Habitus as in Fig. 46. Body length = 7.0–9.0 mm. Elytra wider and longer than pronotum (width ratio elytra / pronotum = 1.1–1.2; length ratio elytra / the middle of pronotum = 2.4–2.6).

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 puncturation (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



Figures 14–21. Aedeagal tegmina (dorsal and vental views). *M. gravis* (**14**), *M. plicicollis* (**15**), *M. convexipennis* (**16**), *M. malaisei* (**17**), *M. lamottei* (**18**), *M. laevistriatus* (**19**), *E. calcaripes* (**20**), *S. striatus* (**21**).

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

Selinus curtulus Fairmaire, 1893: 143.– Gebien 1910: 277, 1938: 297.
Ectateus curtulus (Fairmaire, 1893).– Koch 1956; Iwan 2002a: 67, 2002b: 265.

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 hypomera 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 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.

Female genitalia. Paraproct equal to coxites. Bursa copulatrix without sclerites. Spermatheca unknown.

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.

Ectateus ghesquierei Koch, 1956

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

Figs 5, 33, 41, 48

Ectateus ghesquierei Koch, 1956: 232.– Iwan 2002a: 67, 2002b: 265.

Studied material. Six syntypes of *Ectateus ghesquierei* are available. Lectotype designation is needed to fix the taxonomic status of the genus and the species. **Lectotype** designated here, (MRAC): "Musée du Congo Belge, Kasai: Kondué, E. Luja"; **Paralectotypes**, 3 females (MRAC): same data, 2 females (MRAC): "Coll. Mus. Congo, Mayidi, 1943, Rév. P. Van Eyen". **Other material**: female (MNHN): "Voka Congo, X.1977", male and female (MNHN): "2.11.1963., No 78, sifted litter, leg. Endrőy-Younga" "Soil-Zoological Exp., Congo-Brazzaville, Kindamba, Méya, Louolo river".

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 punctures are 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. Metafemorae 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

Anchophthalmus modestus Fairmaire, 1887: 282.– Gebien 1910: 278, 1938: 298.
Ectateus modestus (Fairmaire, 1887).– Koch 1956: 241; Ardoin 1965: 964; Iwan 2001b: 359, 2002a: 67, 2002b: 266, 2003: 181, 2004a: 548; Kamiński and Raś 2011: 648.

Studied material. Lectotype (designated by Kamiński in Kamiński and Raś 2011), male (MNHN): “Type”, “Muséum Paris, 1906, Coll. L. Fairmaire”; **Paralectotype**, female (MNHN): “Type”, “Muséum Paris, 1906, Coll. L. Fairmaire”, “*Anchophthalmus modestus* (Fairmaire) 1887 [unreadable]”. **Other material**: male and females (MNHN): “Kangu, Mayombe, Congo Belge Dr. Peregl”, 2 males and 2 females (MNHN): “Sibiti, Congo, XI-1963”, 2 males (MNHN): “Franz. Congo”, male and female (MNHN): “2.11.1963., No 78, sifted litter, leg. Endrődy-Younga” “Soil-Zoological Exp., Congo-Brazzaville, Kindamba, Méya, Louolo river”, 2 females (MRAC): “Musée du Congo, Mayumbe: Luali, -IX-1937, Dr. Dartevelle”, female (MRAC): “Coll. Mus. Congo, Mayidi, 1942, Rév. P. Van Eyen”, male (MNHN): “Muséum Paris, Loango, Rochut & Perraudin, 161-96”, male (JFCS):“Luvulu, Kouilau, Congo”, female (JFCS): “Luvulu, Kipanga, Kouilau”, 3 females (JFCS): “Congo, Luvulu, Kipanga, Kouilau”, male (MNHN): “9.XI.1974, Voka près Boko, Rép. Pop. CONGO, Fr. Giov. Onore”, male (MNHN): “10-15.XI.1974, Voka près Boko, Rép. Pop. CONGO, Fr. Giov. Onore”, female (MNHN): "X.1976, Voka près Boko, Rép. Pop. CONGO, Fr. Giov. Onore", male (RBINS): "Kuimba-Diambo, 15-XI-25, A. Collart", male (RBINS): "I.R.Sc.N.B. I.G. 25.041, Coll. & det. J. Delève", 2 females (MRAC): "Coll. Mus. Congo, Mayumbe: T. Kipanzu, de, Singa à Mbomba V/VI-58, Dr R. Laurent", female (MNHN): label unreadable, male (MRAC): "Coll. Mus. Tervuren, Angola: Benguela, ex. coll. Breuning", male (SMNS): "Kongo, Voka, XI. 1974, W. Heinkel", male (MNHN): "Tschiloengo, Congo", male (RBINS): "R. I. Sc. Nat. Belg., I.G. 16.364".

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 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 = 8.0–8.4). 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 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. 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. 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 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. 2.0. 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 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 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.

Diagnosis. The presence of the basal depressions on the pronotal disc place *Eleoselinus* near to (Kamiński 2013c): *Anchophthalmops* Koch, 1956, *Anchophthalmus* Gerstaecker, 1854, *Kochogaster* Kamiński & Raś, 2011, *Ectateus*, *Glyptopteryx* Gebien, 1910, *Microselinus* Koch, 1956, *Monodius*, *Nesopatrum* Gebien, 1920, *Phallocentrion* Koch, 1956, *Phymatoplata* Koch, 1956, *Platykochius* Iwan, 2002, *Platymedvedevia* Iwan & Banaszkiewicz, 2007, *Quadrideres* Koch and *Selinus*.

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) anntenna 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

Ectateus villiersi Ardoin, 1965: 964.– Iwan 2002b: 266; Iwan and Banaszkiewicz 2007: 729; Kamiński 2011: 648 (in Kamiński and Raś 2011).

Studied material. Holotype, male (MNHN): "Brazzaville, Congo, V-1963", "Muséum Paris, Mission A. Descarpentries et A. Villers, 1963-1964". **Other specimens**, female (MNHN): "Allotype" same data as holotype, 7 males and 9 females (MNHN): "Juil 1959, Brazzaville, Congo. L. Vincent", male "Kimpoko, Kongo", female (MNHN): "Muséum Paris, Congo, Brazzaville, Mission Chari-Tchad, Dr J. Decorse 1904".

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

Ectateus ursynowiensis Kamiński, 2011: 648 (in Kamiński and Raś 2011).

Studied material. Holotype, male (MNHN): "Juil 1959, Brazzaville, Congo. L. Vincent", male "Kimpoko, Kongo"; **Paratypes**, 10 males and 9 females (MNHN and MIIZ): same data as holotype; female (MNHN): "Muséum Paris, Congo et Oubanghi, Decaux 1896"; male (MNHN): "Muséum Paris, Congo Franc., Env. De Brazzaville, E. Roubaud et A. Weiss, 1907".

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).

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

Monodius Koch, 1956: 181.– Iwan 2001b: 352, 2002a: 100 (syn. with *Selinus*).

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)	**4**
2	Pronotal apophyseal depressions coarse. Male mesofemorae with a denticle (similar to the one in *E. laevistriatus*, Fig. 40). Parameres strongly emarginated at the apex (Fig. 15)	***Monodius plicicollis***
–	Pronotal apophyseal depressions fine. Male mesofemorae wihout denticles. Parameres slightly emarginated at the apex (Fig. 17)	**3**
3	Male protibiae with median dilatation on the inner face (similar to the one in *M. convexipennis*, Fig. 37)	***Monodius medius***
–	Male protibiae almost straight (Fig. 38)	***Monodius malaisei***
4	Body size: 16.0–19.0 mm. Elytral intervals with fine punctures (Fig. 26). Male protibiae as in Fig. 30	***Monodius gravis***
–	Body size: 12.0-14.5 mm. Elytral intervals with conspicuous punctures. Male protibiae as in Fig. 37	**5**
5	Pronotal disc with two circular depressions in the middle. Aedeagal tegmen as in Fig. 19	***Monodius laevistriatus***
–	Pronotal disc wtihout circular depressions. Aedeagal tegmen as in Fig. 16, 18	**6**
6	Elytral intervals with conspicuous punctures. Elytral apex as in Fig. 51. Aedeagal tegmen as in Fig. 16	***Monodius convexipennis***
–	Elytral intervals with very coarse punctures (Fig. 28). Elytral apex rounded. Aedeagal tegmen as in Fig. 18	***Monodius lamottei***

***Monodius convexipennis* (Gebien, 1904)**

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

Figs 10, 16, 37, 42, 50, 51

Selinus convexipennis Gebien, 1904: 2.– Gebien 1910: 277, 1938: 297; Iwan 2001b: 360, 2002a: 101, 2002b: 302.

Monodius convexipennis (Gebien, 1904).– Koch 1956: 181; Iwan 1990: 430.

Studied material. 45 males and 41 females (MIIZ): "Mus. Zool. Polonicum Warszawa 12/45", "Kamerun, Barombi, Conradt", "Selinus convexipennis H. Gebien 1939", 20 males and 12 females (MNHN): "Muséum Paris", "Kamerun, L. Conradt, 1898-1899", 3 males and female (MRAC): "Coll. Mus. Tervuren Cameroun, Mt Balmayo (M. Barga), XII 1972, Ex. Coll. Breuning", female (MRAC): "Coll. Mus. Tervuren, Oubanghi-

Chari", "ex. Coll. Breuning", 4 females (MNHN): "Muséum Paris, 1952, coll. R. Oberthur", "Afriq Occid, Johann-Albrechts Höhe, Station Kamerun, L.Conradt, 1896", male (MNHN): "Muséum Paris, coll. P. Ardoin, 1978", "Cameroun Yaoundé Vadon!", 3 males and 4 females (MNB): "Kamerun, John.Albreschtshöhe, 8.11.1898-10.3.1899, leg Conradt", 6 males and 4 females (MNB): "N.W.Kamerun, Moliwe b. Victoria, 10-20.12.07, Frfr. v. Maltzan G.", male and 6 females (MNB): "N.-Kamerun, Joh.-Albrechtshöhe, III.96, L.Conradt S. ", 2 males (MNB): "S.-Kamerun, Bipindi, IX.1898 ‚Zenker S. V.", 2 females (MNB): "Kamerun, Bascho, Adamatz S.G.", male and females (MNB): "Kamerun, Nokundange, 16-30 VI 05, G. Leßmann S. G.", "1908-09.", male (MNB): "Neu-Kamerun, Dengdeng Station, 26.III.1914, Mildbraed S.G.", male (MNB): "Kamerun, Duala, Schäfer S.G.", 3 males (MNHN): "Muséum Paris ex. Coll. P. Ardoin 1978", "Duala Bothkiych", 3 males and female (SMNS): "Malimba Pahl 91".

Redescription. Habitus 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 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. 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.
Selinus gravis (Koch, 1956).– Iwan 2002a: 101, 2002b: 302.

Studied material. Female (MNHN): "Schantung, Tsingtau, Miss. Mus. Steyl", 3 males and 2 females (MNHN): "Muséum Paris, Bas Dahomey, Torricada E. Poisson 1902", "Novembre", female (MNB): "Süd Togo zw. Haho u. Shioftuss Laadschaften Gamme u. Gaohe Smend S.", 2 females (MIIZ): "Museum Zool. Polonicum, Warszawa, 12/45", "Selinus n.sp. H. Gebien det. 1939", "Guinea", male (MNHN): "Wydah R. P. Ménager".

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**).

puncture). Elytral base slightly sinusoidal. Elytral humeri rounded, not protruding laterad. Wings absent. Scutellum rounded.

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

Selinus laevistriatus Fairmaire, 1897: 122. – Gebien 1910: 278, 1921: 21, 1938: 297.
Ectateus laevistriatus (Fairmaire, 1897).– Koch 1956: 237; Ardoin 1969: 143, 1971: 284; Iwan 2002a: 67, 2002b: 265.

Studied material. Holotype, female (MNHN): "TYPE", "Sierra-Leone", "Selinus laevistriatus Frm [unreadable] Type", "Muséum Paris, 1906, Coll. L. Fairmaire". **Other material**: males and 2 female (MNHN): "Fort Camp, 1070m, 26-V-1963", "Mission ENS-IFAN, aux Monts LOMA, Sierra Leone", "Muséum Paris, coll. P. Ardoin, 1978", "*Monodius laevistriatus*, Fairm., P. Ardoin det. 1966".

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

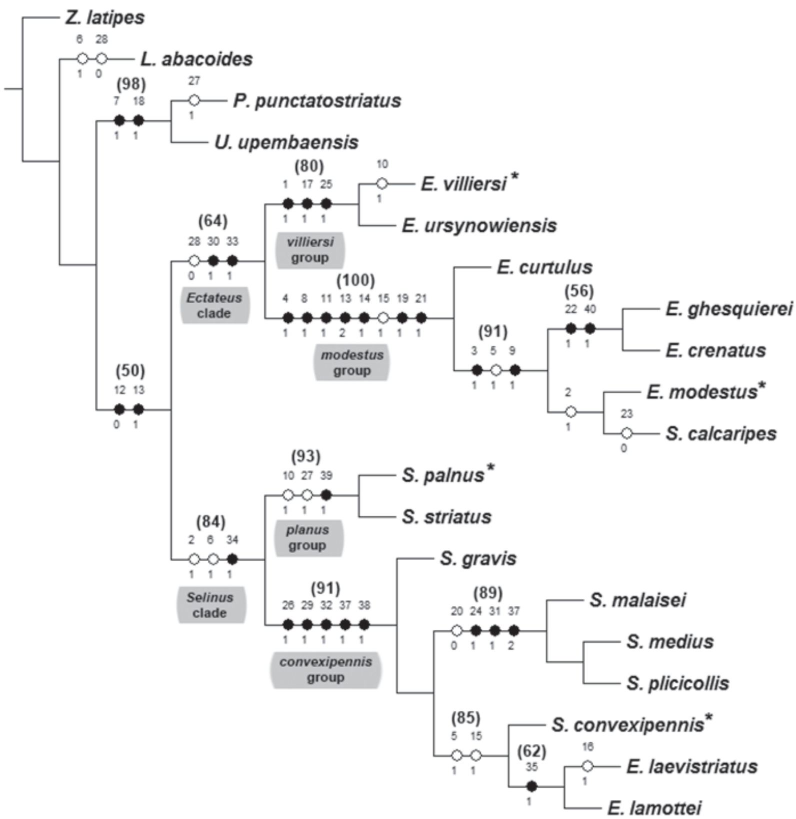


Figure 25. Phylogeny of the species of *Ectateus* and *Selinus sensu* Iwan 2002. Most parsimonious tree (L=57, CI=74, RI=90). Black circles represent single, non-homoplasious character state transformations, and white circles represent multiple, homoplasious character state transformations.The numbers 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.

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).

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 an 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

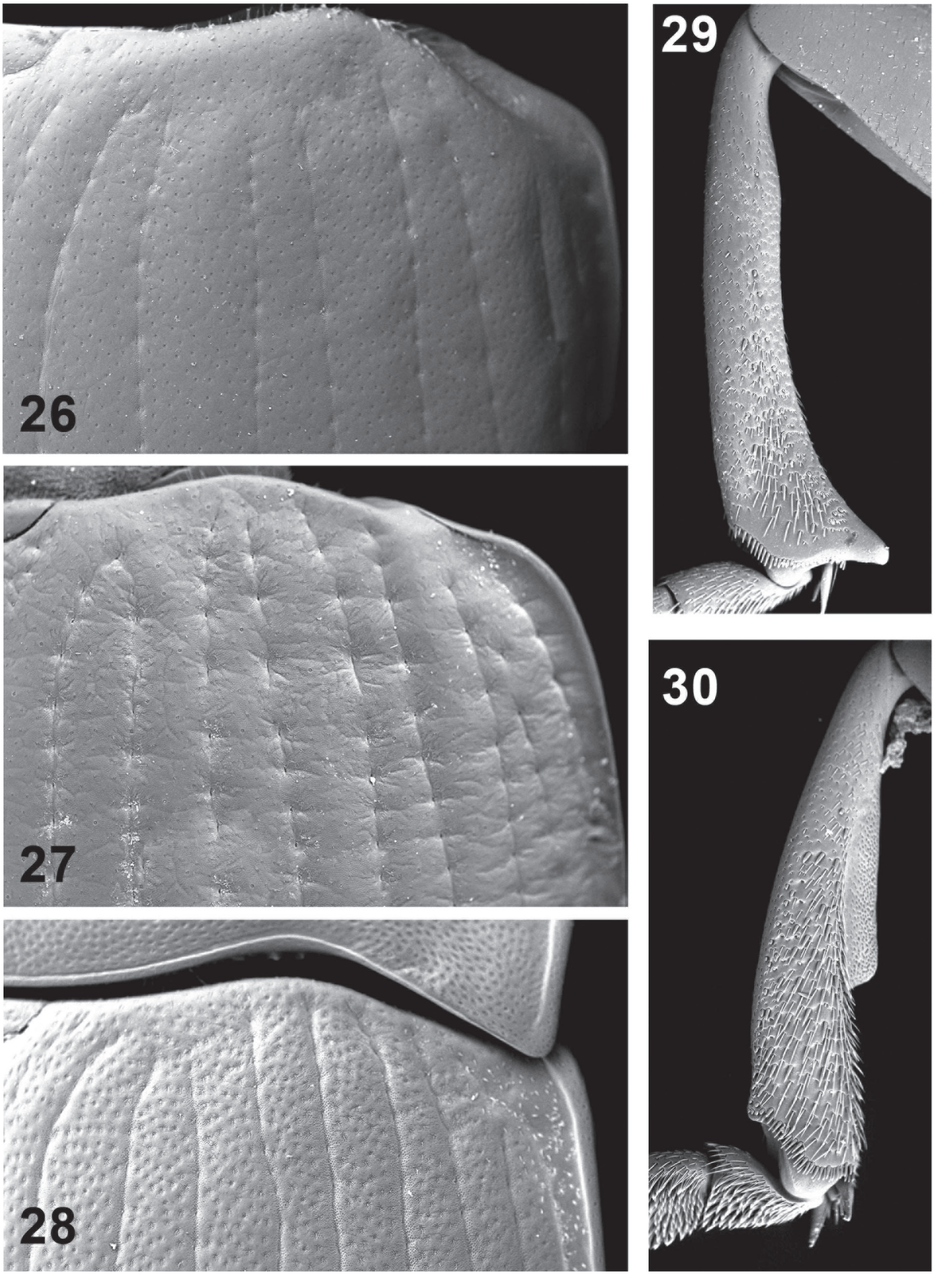
Selinus lamottei Gridelli, 1954: 127.
Ectateus lamottei (Gridelli, 1954).– Ardoin 1963: 222; Iwan 2002b: 266.

Studied material. Holotype, male (MNHN): "Muséum Paris, Nimba (Guinée), M. Lamotte II. VI. 42", "Typus", "Keoulenta"; **Paratypes**, male and female (MNHN): same data as holotype. **Other material**: 3 females (MNHN): "Muséum Paris, Côte d'Ivoire, Réserve du Banco, R. Paulian & C. Delamare", 2 males and 2 females (MNHN): "Coll Mus. Tervuren, Côte d'Ivoire: Bingervillie, X.1961, J. Decelle", "Muséum Paris Coll. P. Ardoin, 1978", female (MRAC): "Coll Mus. Tervuren, Côte d'Ivoire: Korea, S. de Daloa, J. Decelle, VII / IX.1962", "*Ectateus laevistriatus*, det. Ardoin 1965", female (MRAC): "Coll Mus. Tervuren, Côte d'Ivoire: Adlapoté, 80 km. W. Abidjan, J. Decelle, II-1962", "*Ectateus laevistriatus*, det. Ardoin 1965", males (TMNH): "Adiopodoumé, B. Côte d'Ivoire, Ledoux", female (MNHN): "Côte d'Ivoire", "Muséum Paris Coll. P. Ardoin, 1978".

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). 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



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 legs. Protarsi slightly widened. Protibiae as in *M. convexipennis*. Mesotibiae with a small 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 0.5 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.

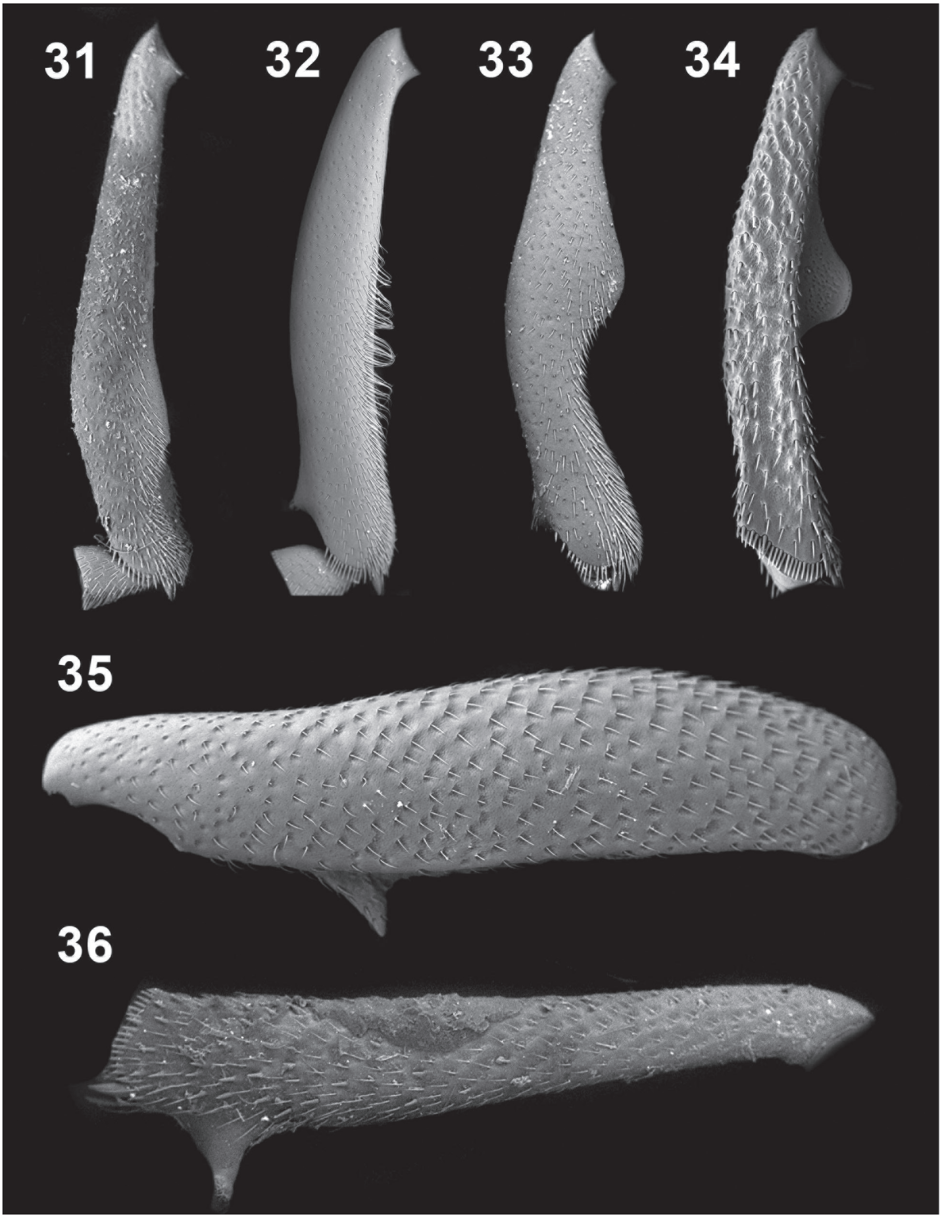
Distribution. This species has been collected in the following ecoregions of West Africa (Ivory Coast, Republic of Liberia): Eastern Guinean forests, Western Guinean lowland forests (Fig. 42).

Monodius malaisei Koch, 1956

http://species-id.net/wiki/Monodius_malaisei
Figs 9, 17, 38, 43, 55

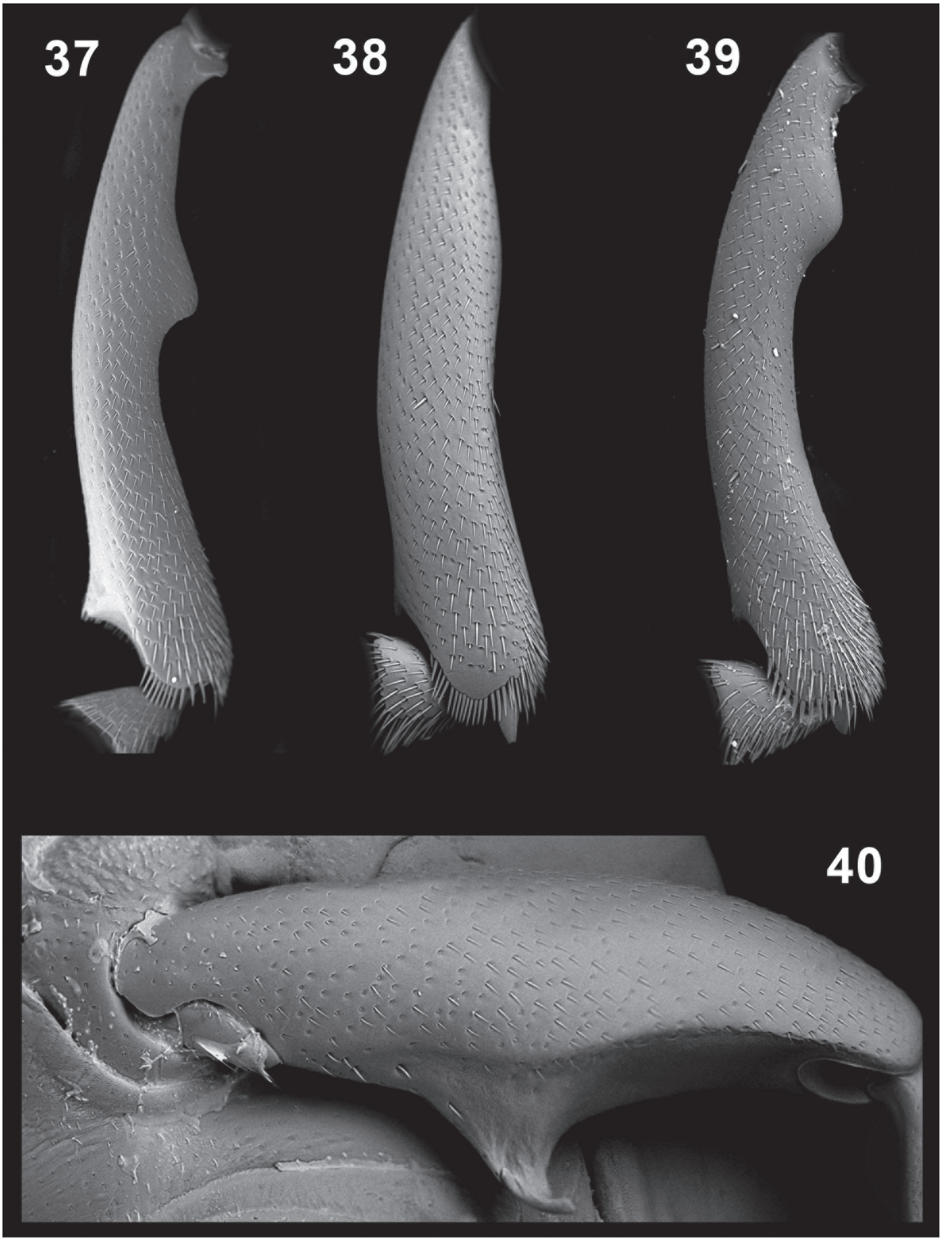
Monodius malaisei Koch, 1956: 188.
Selinus malaisei (Koch, 1956).– Iwan 2002a: 101, 2002b: 302.

Studied material. Twelve syntypes of *Monodius malaisei malaisei* are available. Lectotype designation is needed to fix the taxonomic status of the species and the subspecies. **Lectotype** designated here, male (TMNH): “Paratype No: 3224, *Monodius malai-*, *sei* Koch”, “Ob. Volta, Pundu, Olsufiew”; **Paralectotypes**, male (TMNH): same data as holotype, except the number referring to paratype (3226, 3227). **Other material**: 12 males and 15 females (MNHN): “Muséum Paris, Haute Volta, Gaoua, H. Labouret 1924”, 2 males and 2 females (ZMAS): “Poundou, Hante, Volta, Afr. Occ. Fr., Олсуфъев 927”, male and female (ZMAS): “Ouagadougou, Afrique Occ. Fr. Олсуфъев VII. VIII 927”, 3 males and 4 females (MRAC): “Coll. Mus. Tervuren, Haute Volta: Bobo-Dioulasso, 10.V.1964, R. Siffointe”, 2 males (MNHN): “Oyo Yoruba P. François”, “Muséum Paris, Coll. L. Fairmaire”, 2 males (MNHN): “Abétifi, Côte d’Ivoire”, “Muséum Paris”, 2 males (MNHN): “Tortiya, Cte Ivoire, II.59, R. Villemain”, “Muséum Paris”, 2 males (MNB): “Togo, Station Ho, Schroder S.”, male (MNHN): “Muséum Paris Soudan Franc Région Volta Sikasso- Bobo-San A.



Figures 31–36. Male protibiae (**31–34**); male mesofemora (**35**); male mesotibia (**36**). *E. calcaripes* (**31**), *E. modestus* (**32**), *E. ghesquierei* (**33**), *E. crenatus* (**34–36**).

Chevalier 1900", "Mai-Juin", 2 males (MNHN): "Muséum Paris coll. P.Ardoin 1978", "Monodius Selinus malaisei Koch ssp. nigeriensis Koch P. Ardoin det.1972", "Niamey-Niger Leg. Loups", 2 males and 2 females (MNHN): "Muséum Paris, Coll. P. Ardoin, 1978", "IX.1971, Pabré, Haute Volta, R.P. Fernandez".



Figures 37–40. Male protibiae (**37–39**); male mesofemora (**40**). *M. convexipennis* (**37**), *M. malaisei* (**38**), *S. planus* (**39**), *E. laevistriatus* (**40**).

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).

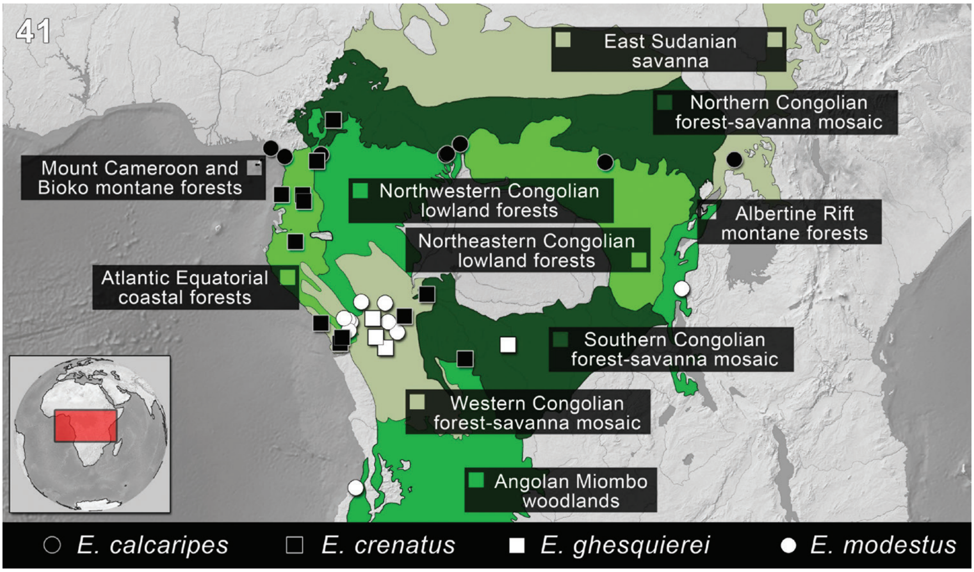


Figure 41. Distribution of the species of *Ectateus sensu novum*. The division of Afrotropical Realm into ecoregions was adopted after Olson et al. 2001. Different colors were used to distinguish the adjacent ecoregions.

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

– Male metatibiae straight..........***Monodius malaisei nigeriensis* Koch, 1956**

***Monodius medius* (Fairmaire, 1897)**

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

Figs 7, 23, 43, 56

Selinus medius Fairmaire, 1897: 122.– Gebien 1910: 278, 1938: 297; Iwan 2001b: 360, 2002a: 101, 2002b: 303.

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

Selinus angulatipes Gebien, 1921: 21.– Gebien 1938: 297; Koch 1956: 185 (syn); Kulzer 1963: 425.

Studied material. Holotype, male (MNHN): "Type", "Muséum Paris, Paris, Collection Leon Fairmaire, 1906", "Selinus medius Fm guinea, Acut. det.". **Other material**: 6 males and 2 females (RBINS): "*Selinus*, *angulatipes*, det. H. Gebien 1913, n. sp.", "Type", "Asenté Akem, (Ashanti), Guineé" (Syntypes of *Selinus angulatipes* Gebien, 1921), 11 males and 6 females (MNHN): "Lamto, Pacobo, V. 1968", "Côte d'Ivoire, CL. Girard Col.", male (MRAC): "Coll. Mus. Tervuren, Côte d'Ivoire, Kossou 18.2.1975, R. Jocqué", 2 males (MRAC): "Coll. Mus. Tervuren, Côte d'Ivoire: Bouaké, VII-, 1977, P. M. Elsen", male and female (MRAC): "Coll. Mus. Tervuren, Togo: Missahoué 650 m., VI.1963, Mme Y. Schach".

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

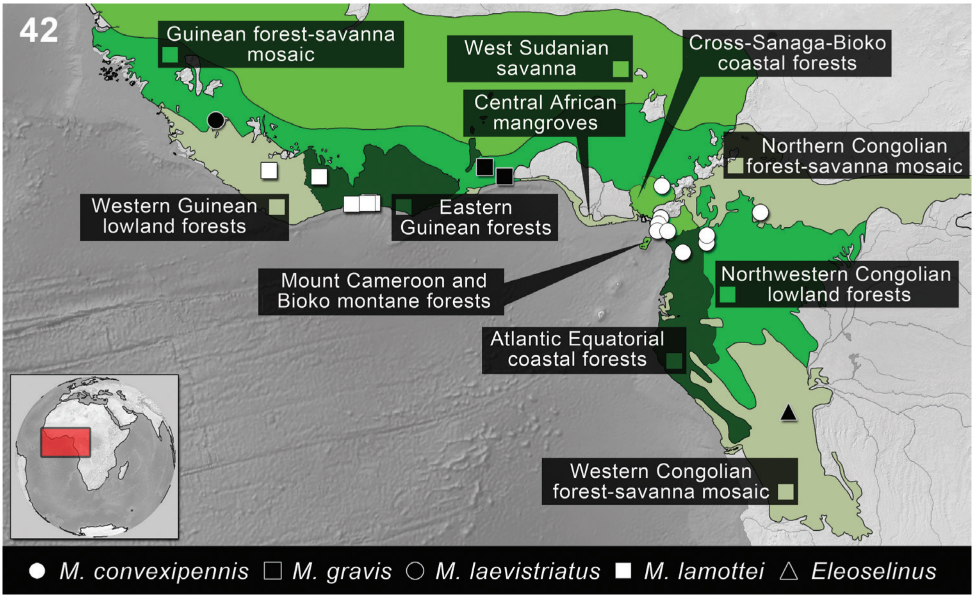


Figure 42. Distribution of the species of *Monodius convexipennis*, *M. gravis*, *M. laevistriatus*, *M. lamottei* and *Eleoselinus* gen. n. The division of Afrotropical Realm into ecoregions was adopted after Olson et al. 2001. Different colors were used to distinguish the adjacent ecoregions.

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).

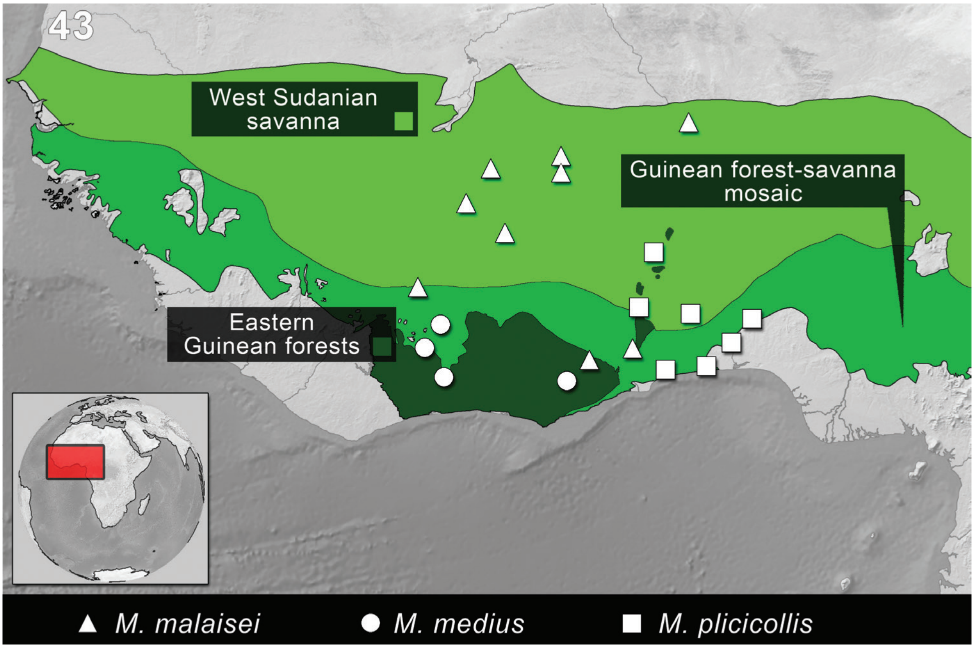


Figure 43. Distribution of the species of *Monodius malaisei*, *M. medius* and *M. plicicollis*. The division of Afrotropical Realm into ecoregions was adopted after Olson et al. 2001. Different colors were used to distinguish the adjacent ecoregions.

Male legs. Protarsi slightly widened. Protibiae as in *M. convexipennis*. Mesotibiae with a large denticle at the apex. Metafemorae with an 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

Selinus plicicollis Fairmaire, 1897: 123.– Gebien 1910: 278, 1938: 297; Koch 1956: 244; Iwan 2002a: 101, 2002b: 303.

Studied material. Holotype, male (MNHN): "*Selinus plicicollis*, Fairm, Togo", "Togoland L. Conradt 1892-1893", "Muséum Paris, 1906, Coll. L. Fairmaire"; **Paratype**, male (MNHN): same data as holotype. 11 males and 10 females

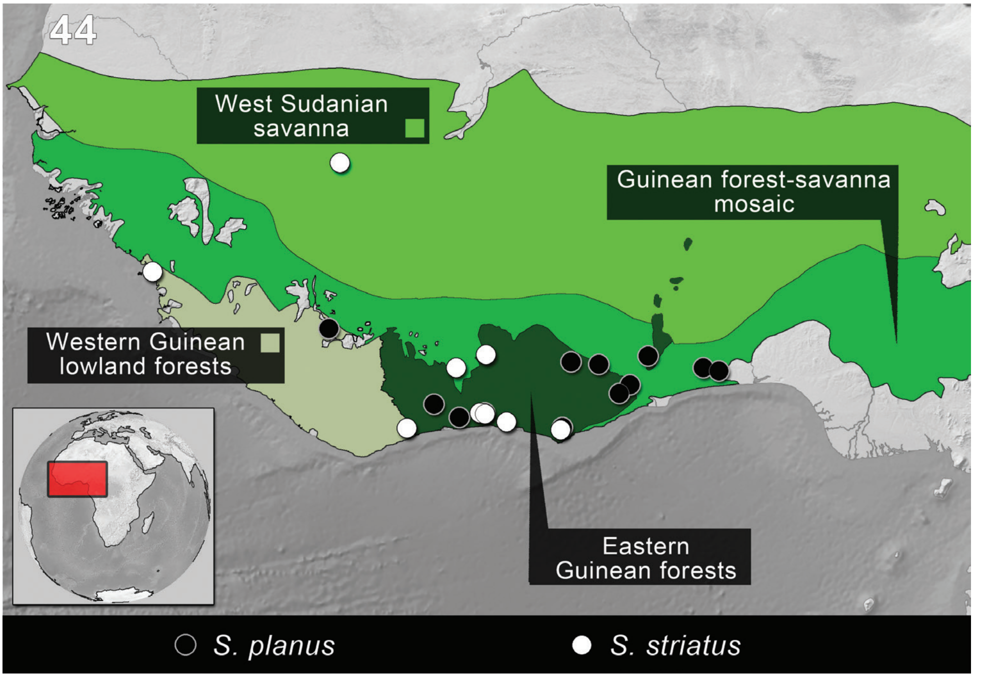


Figure 44. Distribution of the species of *Selinus sensu novum*. The division of Afrotropical Realm into ecoregions was adopted after Olson et al. 2001. Different colors were used to distinguish the adjacent ecoregions.

(MRAC): "Coll. Mus. Tervuren Togo: Niamtougou, 21/24-VII-1969, F. Puylaert", female (MIIZ): "Mus. Zool. Polonicum Warszawa 12/45", "*Selinus plicicollis* H.Gebien det.1939", "Dahomey", male and female (MNHN): "Museum Paris, Moyen-Dahomey, Plateau de Zaguanado, Saison des Drages te. Des Tornades P. Ducorps 1910", female (MNB): "Togo Bismarckburg, 12-14.IV.93, L. Conradt S.", male and female (MNHN): "Abboekuta, P. Francois", "Museum Paris, Coll. Ch. Alluaud, coll. L.Fairmaire 1906", female (TMNH): "Oyo Yoruba P. François", "*Selinus plicicollis*", 7 males and 10 females (MNHN): "Togoland L. Conradt 1892-1893", "Muséum Paris, 1906, Coll. L. Fairmaire", 2 females (MNHN): "26. XII.1975, Akoumapé, Togo, J-Cl. Martin", "Museum Paris, coll. P. Ardoin, 1978", 6 males and 7 females (MNHN): "Museum Paris Dahomey env. De Porto-Novo, Waterlot 1910".

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 legs. Protarsi slightly widened. Protibiae straight. Mesotibiae and mesofemorae 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. 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).

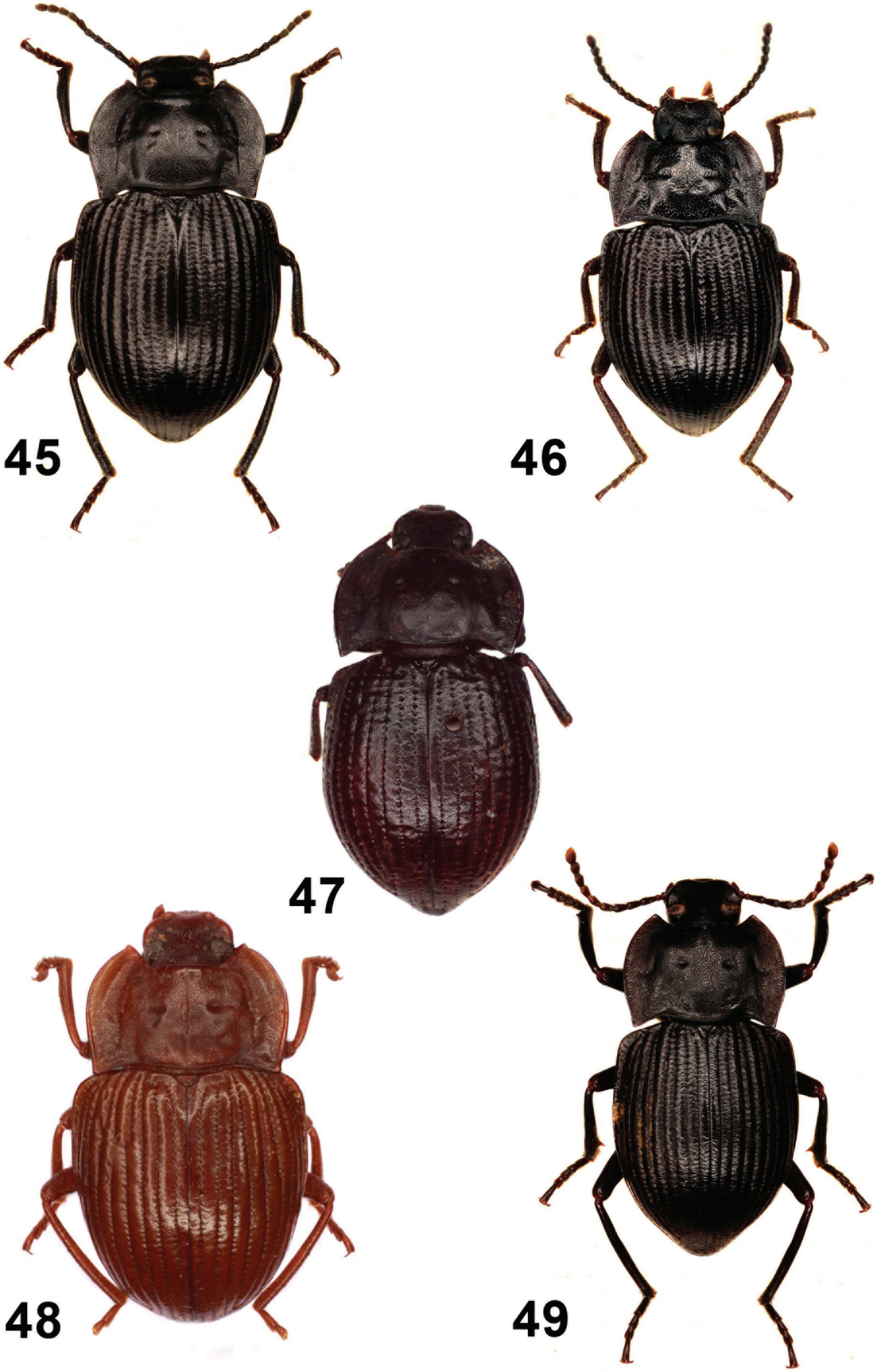
Genus *Selinus* Mulsant & Rey, 1853

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

Selinus Mulsant & Rey, 1853a: 322.– Lacordaire 1859: 241, Gemminger and de Harold 1870: 1915; Gebien 1910: 277, 1938: 297; Koch 1956: 242; Iwan 2001b: 352, 2002a: 100, 2002b: 302, 2004a: 541, 2004b: 739, 2005: 615; Iwan and Banaszkiewicz 2005: 603, 2007: 725.

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-



Figures 45–49. Body habitus: *Ectateus calcaripes* (**45**), *E. crenatus* (**46**), *E. curtulus* (**47**), *E. ghesquierei* (**48**) and *E. modestus* (**49**).

est at the base, (4) 5th abdominal ventrite bordered, (5) paraproct longer than coxites, (6) clavae long, their length more than half of the length of parameres.

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)

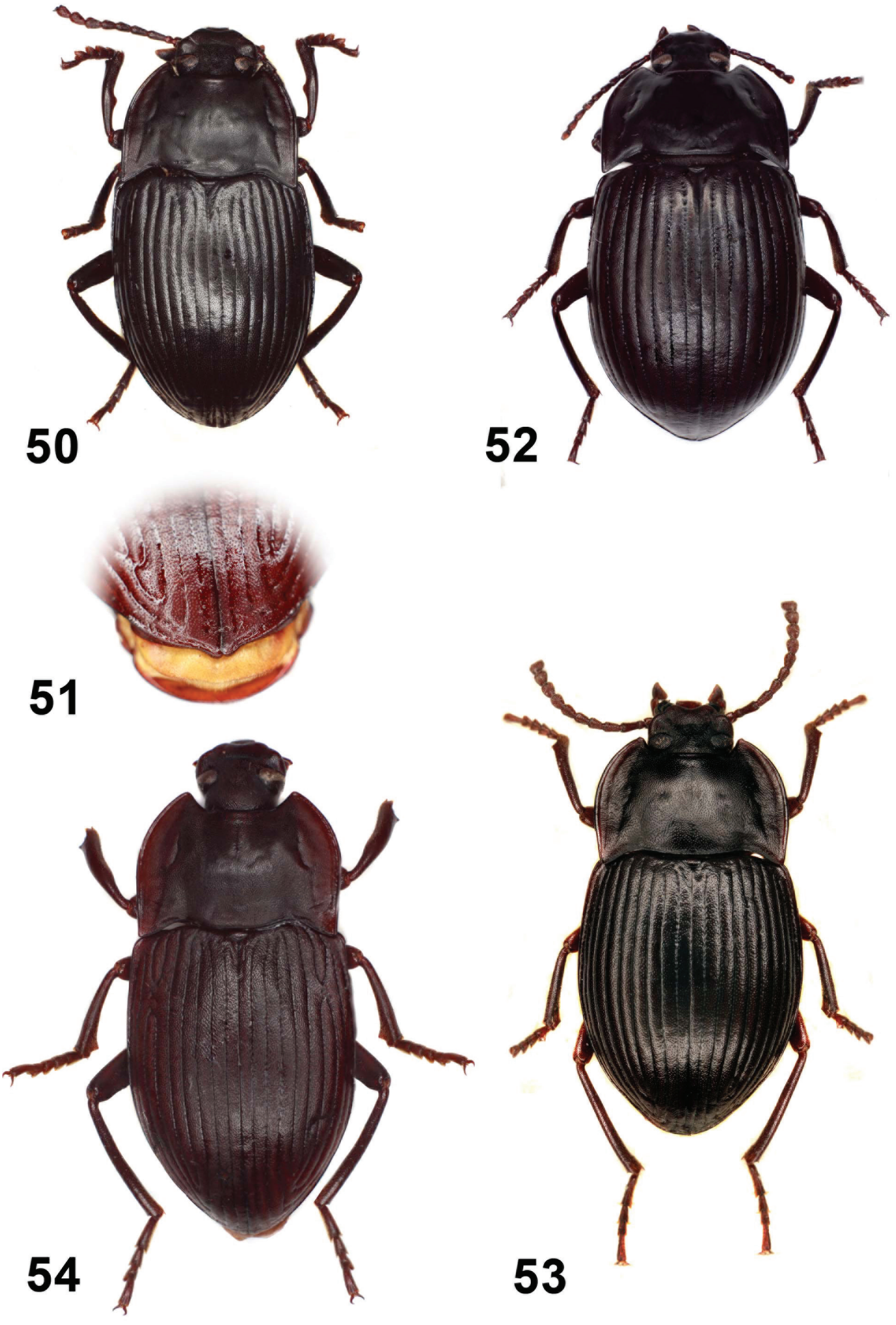
http://species-id.net/wiki/Selinus_planus

Figs 1, 6, 39, 44, 60

Opatrum planum Fabricius, 1792: 118.– Herbst 1793: 215; Fabricius 1801: 90.

Selinus planus (Fabricius, 1792).– Mulsant and Rey 1853a: 324; Gemminger and de Harold 1870: 1915; Péringuey 1892: 56; Gebien 1906: 211, 1910: 278, 1938: 297; Koch 1956: 251; Iwan 1990: 430, 2001b: 360, 2002a: 101, 2002b: 303; Iwan and Banaszkiewicz 2005: 605.

Studied material. Paratype, female (MNHN): "Guinée, coll. R. Oberthür, ex coll. Deyrolle". **Other material**: 10 males and 9 females (MNHN): "Muséum Paris, Bas Dahomey, Torricada E. Poisson 1902", "Novembre", 6 males and 5 females (MNHN): "Muséum Paris Dahomey env. De Porto-Novo, Waterlot 1910", 3 males (MNHN): "Muséum Paris coll. P. Ardoin 1978", "15/20.X.1967, Takoradi, Ghana, Cl. Besnard leg.", "♂", female (MNHN): "Ashanti", "Muséum Paris, (Coll. Ch. Alluaud), coll. L.Fairmaire 1906", 2 males and 3 females (MNB): "Togo Amedzowe", 2 males and female (MRAC): "Coll. Mus Tervuren, Togo: Missahoué 650 m., VI.1963, Mme Y. Schach", female (MNHN): "Under log, river bank", "Akuse, Gold Coast, 23-II-29", "Museum Paris", male (MNHN): "Abétifi, Côte d'Ivoire", "Muséum Paris", 2 females (MRAC): "Coll. Mus. Tervuren, Ghana: Volta River, 12.VII.1964, G. Marlier", 2 males (MNHN): "Togo, Palime, Forêt de Klouto, 20-24-IV-74 S. Vit", female (MRAC): "Coll. Mus. Tervuren,



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**).

Côte d'Ivoire: Eremankono, S. de Divo, J. Decelle VII-1962", male and female (MNHN): "Goldküste, Ostertag", 2 males (MNHN): "Addah.", "Muséum Paris", male (MNHN): "Gold Coast", "Koumassi", 3 males and female (MNHN): "Dahomey, Athieme, J. M. Renou 1898", female (BMNH): "Aburi, Gold Coast, W. H. Patterson., 1914-29", female (MNHN): "Talanzoa", "Muséum Paris, Nimba (Guinée), M. Lamotte II. VI. 42".

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.

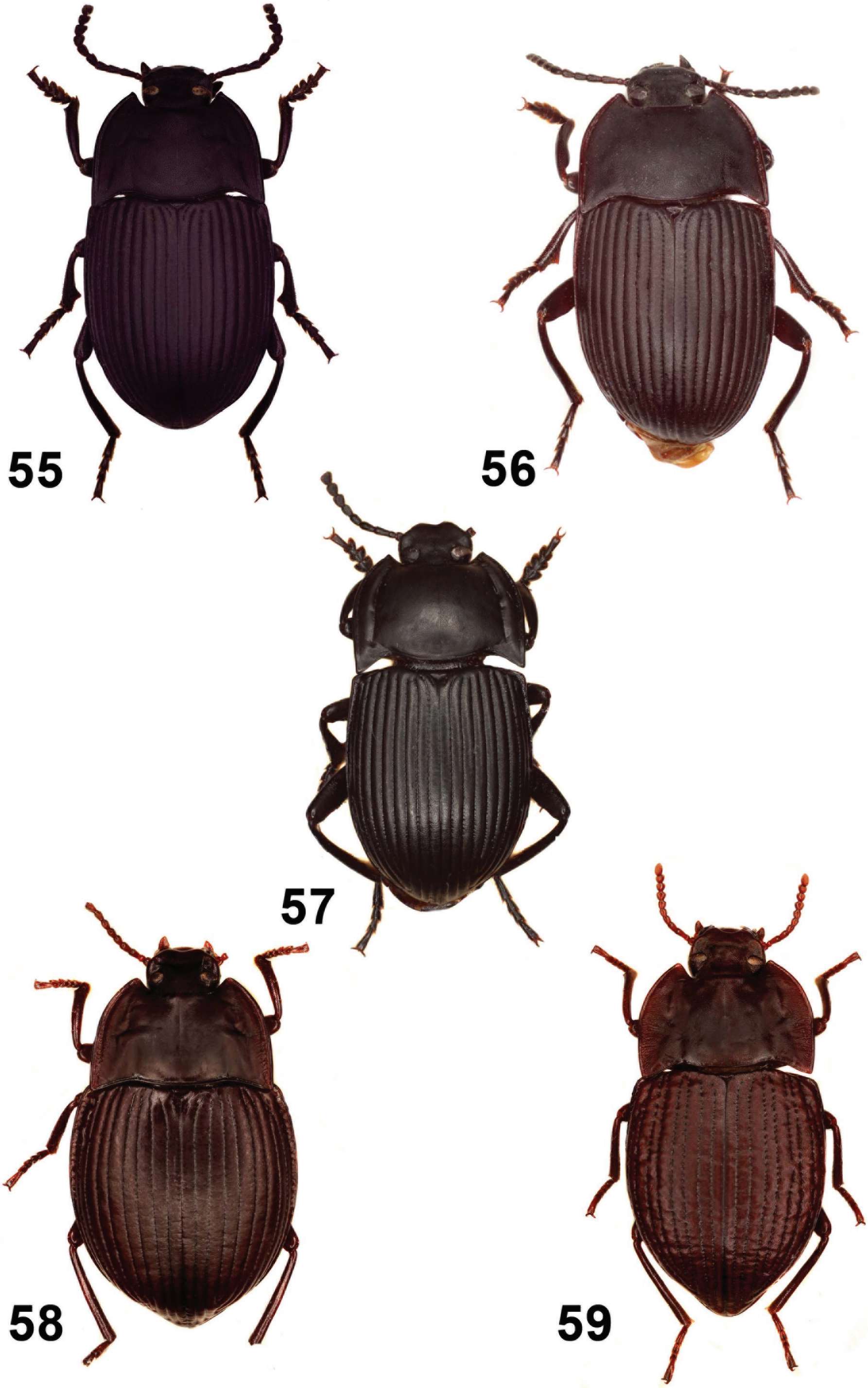
Elytra oblong (elytra length / width ratio = 1.1–1.2). Elytral striae with fine punctures (sometimes absent). Elytral intervals shiny, non-convex; with conspicuous punctures (the intervals between the punctures are greater than the 3 diameters of the puncture). Elytral base slightly sinusoidal. Elytral 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).



Figures 55–59. Body habitus: *Monodius malaisei* (**55**), *M. medius* (**56**), *M. plicicollis* (**57**), *Eleoselinus villiersi* (**58**) and *E. ursynowiensis* (**59**).

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

Helops striatus Fabricius, 1794: 440.– Fabricius 1801: 161.
Selinus striatus (Fabricius, 1794).– Gebien 1906: 211, 1910: 278, 1938: 298; Koch 1956: 254; Ardoin 1963: 223, 1969: 143; Iwan 2002b: 303.

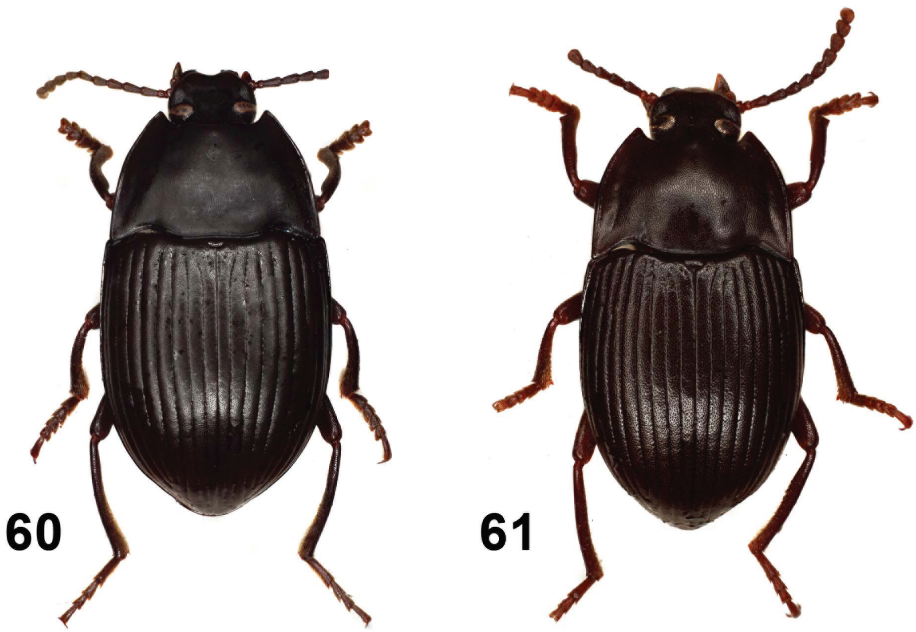
Studied material. 3 females (MNHN): "Muséum Paris, Côte d'Ivoire, Reserve du Banco, R. Paulian & C. Delamare", 2 males and female (MNHN): "Muséum Paris (coll. Ch. Alluaud) coll. L. Fairmaire 1906", "Assinie Côte occid. Afrique Ch. Alluaud 1886", male and female (MNHN): "Coll Mus. Tervuren, Côte d'Ivoire: Bingervillie, X.1961, J. Decelle", "Muséum Paris Coll. P. Ardoin, 1978", female (MRAC): "Cerole de Sassandra, Cote d'Ivoire 4.1962, J.Hamon Orstom Rec.", "*Selinus striatus* Fab. P. Ardoin det.1963", "♀", female (MRAC): "Coll. Mus. Tervuren Côte d'Ivoire: Amanikro, 50 km. N.W. Abengourou J.Decelle V/VI.1961, "Récolté sur cacaoyer", "Selinus striatus Fab. P.Ardoin det.1965", male and female (MNHN): "Muséum Paris (coll. Ch.Alluaud) coll. L. Fairmaire 1906", "Rhobomp, Sierra Leone", male (MNHN): "Muséum Paris, Iles se Los, Tamara, J. Serand 1913", male (MHNL): "Dimbokru, Côte d'Ivoire, G. Skibiski, Lyon", male (MNHN): "Muséum Paris coll. P. Ardoin 1978", "3.V.1967, Takoradi, Ghana, Cl.Besnard leg.", "♂".

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.



Figures 60–61. Body habitus: *Selinus planus* (**60**) and *S. striatus* (**61**).

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 slightly widened. Male protibiae with very shallow dilatation near the mddle. 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

Ardoin P (1963) La réserve naturelle intégrale du Mont Nimba. III. Coleoptera Tenebrionidae. Mémoires de l'Institut Français d'Afrique Noire 66: 221–267.

Ardoin P (1965) Contribution à la faune du Congo (Brazzaville) (Mission A. Villers et A. Descarpentries). VIII. Coléoptères Ténébrionides. Bulletin de l'Institut Français d'Afrique Noire, Série A, 27: 963–1015.

Ardoin P (1969) Contribution à la connaissance de la Faune Entomologique de la Côte–D'Ivoire (J. Decelle, 1961–1964), Deuxième Partie 37 – Coleoptera, Tenebrionidae. Musée Royal de l'Afrique Centrale, Annales – Serie IN-8° - Sciences Zoologiques 175: 139–285.

Ardoin P (1971) Le massif des Monts Loma (Sierra Leone). XII. Coleoptera Tenebrionidae. Mémoires de l'Institut Français d'Afrique Noire 86: 283–290.

Banaszkiewicz M (2006) Comparative study of female genitalia in Pedinini (*sensu* Iwan 2004) (Coleoptera: Tenebrionidae: Pedinini), with notes on the classification. Annales Zoologici 56: 59–77.

Bouchard P, Lawrence JF, Davies A, Newton AF (2005) Synoptic classification of the world Tenebrionidae (Insecta: Coleoptera) with a review of family-group names. Annales Zoologici (Warszawa) 55(4): 499–530.

Bouchard P, Bousquet Y, Davies AE, Alonso-Zarazaga MA, Lawrence JF, Lyal CHC, Newton AF, Reid CAM, Schmitt M, Ślipiński SA, Smith ABT (2011) Family-group names in Coleoptera (Insecta). ZooKeys 88: 1–972. doi: 10.3897/zookeys.88.807

Fabricius JC (1792) Entomologia Systematica emendata et aucta. Secundum classes, ordines, genera, species adjectis synonimis, locis, observationibus, descriptionibus. Hafniae, 1, pars 1, XX+330 pp.

Fabricius JC (1794) Entomologia systematica emendata et aucta adjectis synonymis, loci, observationibus, descriptionibus, Vols. 1–4. Hafniae.

Fabricius JC (1801) Systema Eleutheratorum secundum ordines, genera, species adiectis synonymis, locis, observationibus, descriptionibus. Kiliae, 1, XXIV+506 pp.

Fairmaire L (1887) Coléoptères des Voyages de M. G. Revoil chez les Somalis et dans l'intérieur du Zanguebar. Annales de la Société Entomologique de France 7: 227–368.

Fairmaire L (1893) Coléoptères de l'Oubanghi, recueillis par Crampel. Annales de la Société Entomologique de France 62: 135–146.

Fairmaire L (1897) Coléoptères nouveaux de l'Afrique intertropicale et australe. Annales de la Société Entomologique de France 66: 109–152.

Farris JS (1989) The retention index and the rescaled consistency index. Cladistics 5: 417–419. doi: 10.1111/j.1096-0031.1989.tb00573.x

Gebien H (1904) Beiträge zur Kenntnis der Insektenfauna von Kamerun. No 28. Verzeichnis der von Professor Dr. Yngve Sjöstedt in Kamerun gesammelten Tenebrioniden. Arkiv Fur Zoologi 2: 1–31.

Gebien H (1906) Über die von Fabricius beschreiben Typen von Tenebrioniden in den Museen von Kopenhagen und Kiel. Deutsche Entomologische Zeitschrift 1: 209–237.

Gebien H (1910) Tenebrionidae I. In: W. Junk, S. Schenkling, Coleopterorum Catalogus, Berlin 18: 167–354.

Gebien H (1921) Die Tenebrioniden West–Afrikas. Archiv für Naturgeschichte 86: 1–256.

Gebien H (1938) Katalog der Tenebrioniden. Teil II. Mitteilungen der Muncher Entomologischen Gesellschaft 28: 49–80, 283–428 [370–465].

Gemminger M, Harold E (1870) Catalogus Coleopterorum hucusque descriptorum synonymicus et systematicus. Tenebrionidae, Nilionidae, Pythidae, Melandryidae, Lagriidae, Pedilidae, Anthicidae, Pyrochroidae, Mordellidae, Thipidophoridae, Cantharidae, Oedemeridae 7: 1801–2668.

Girard C (1975) Étude des peuplements de Coléoptères Ténébrionides de la savane de Lamto (Côte D'Ivoire). Annales de la Société Entomologique de France, (Nouvelle série) 2: 335–381.

Goloboff PA, Farris J, Nixon K (2003) T.N.T. Tree Analysis Using New Technology. http://www.zmuc.dk/public/phylogeny/tnt

Gridelli E (1954) La réserve naturelle intégrale du mont Nimba. Coléoptères Ténébrionides. Mémoires de l'Institut Français d'Afrique Noire 40: 123–146.

Herbst JFW (1793) Natursystem aller bekannten in– und ausländischen Insecten, als eine Fortsezung der von Büffonschen Naturgeschichte. Der Käfer, Berlin, 5, XV+392 pp., 16 pls.

Hijmans RJ, Guarino L, Mathur P (2012) DIVA-GIS. Version 7.5. A geographic information system for the analysis of species distribution data. http://www.diva-gis.org

Iwan D (1990) Platynotini (Coleoptera, Tenebrionidae, Platynotini) of the Natural History Museum in Geneva. Revue suisse de zoologie 97: 427–434.

Iwan D (2000) Oviviparity in tenebrionid beetles of the melanocratoid Platynotina (Coleoptera: Tenebrionidae: Platynotini) from Madagascar with notes on the viviparous beetles. Annales Zoologici 50: 15–25.

Iwan D (2001a) A revision of *Phallocentrion* Koch, 1956 from Africa (Coleoptera: Tenebrionidae: Platynotini). Annales Zoologici 51: 53–63.

Iwan D (2001b) Comparative study of male genitalia in Opatrinae *sensu* Medvedev (1968) (Coleoptera: Tenebrionidae), with notes on the tribal classification. Part I. Annales Zoologici 51: 351–390.

Iwan D (2002a) Generic classification of the tribe Platynotini (Coleoptera: Tenebrionidae), with notes on phylogeny. Annales Zoologici 52: 1–149.

Iwan D (2002b) Catalogue of the World Platynotini (Coleoptera: Tenebrionidae). Genus 13: 219–323.

Iwan D (2003) *Synquadrideres*, new genus of Platynotini from Kenya (Coleoptera: Tenebrionidae). Annales Zoologici 53: 181–187.

Iwan D (2004a) Revision of African *Ectateus* group (Coleoptera: Tenebrionidae: Platynotini). Part I. Introduction and genus *Nesopatrum* Gebien, 1920. Annales Zoologici 54: 541–552.

Iwan D (2004b) A comparative study of male genitalia in Opatrinae *sensu* Medvedev (1968) (Coleoptera: Tenebrionidae), with notes on the reinterpreted tribal classification. Part II. Annales Zoologici 54: 735–765.

Iwan D (2005) Revision of African *Ectateus* group (Coleoptera: Tenebrionidae: Platynotina). Part III. Genus *Platykochius* Iwan, 2002. Annales Zoologici 55: 615–624.

Iwan D, Banaszkiewicz M (2005) Revision of African *Ectateus* group (Coleoptera: Tenebrionidae: Platynotina). Part II. Genus *Pseudoselinus* Iwan, 2002. Annales Zoologici 55: 603–613.

Iwan D, Banaszkiewicz M (2007) *Platymedvedevia*, a new genus of *Ectateus* group from Tropical Africa (Coleoptera: Tenebrionidae: Platynotina). Annales Zoologici 57: 725–731.

Iwan D, Kamiński MJ (2012) Revision of the Malagasy genus *Lechius* Iwan, 1995 (Coleoptera: Tenebrionidae: Pedinini). Zootaxa 3399: 23–34.

Kamiński MJ, Raś M (2011) New status of the genus *Ectateus* Koch, 1956 with taxonomic notes on the *Ectateus* generic group (Coleoptera: Tenebrionidae: Platynotina). Annales Zoologici 61: 647–655. doi: 10.3161/000345411X622507

Kamiński MJ, Raś M (2012) Catalogue of the melanocratoid Platynotina (Tenebrionidae: Pedinini). Annales Zoologici 62: 227–243. doi: 10.3161/000345412X652756

Kamiński MJ (2012) Taxonomy of the Afrotropical genera *Angolositus* Koch, 1955 and *Pseudoselinus* Iwan, 2002 with a key to species (Coleoptera: Tenebrionidae: Pedinini). Zootaxa 3500: 49–60.

Kamiński MJ (2013a) Two new species of the Afrotropical genus *Quadrideres* Koch, 1956 (Coleoptera: Tenebrionidae: Pedinini), with notes on the *interioris* species-group. Annales Zoologici 63: 85–94. doi: 10.3161/000345413X666129

Kamiński MJ (2013b) Taxonomy and distribution of the Afrotropical genus *Anchophthalmops* Koch, 1956 with a key to species (Coleoptera: Tenebrionidae: Pedinini). Zootaxa 3709: 501–523. doi: 10.11646/zootaxa.3709.6.1

Kamiński MJ (2013c) A new genus and species of the Afrotropical Platynotina from Tanzania (Coleoptera: Tenebrionidae: Pedinini). Acta Entomologica Musei Nationalis Pragae 53: 703–714.

Kamiński MJ, Iwan D (2013) Taxonomy of the genus *Kochogaster* Kamiński et Raś, 2011 (Coleoptera: Tenebrionidae: Pedinini), with description of a second known species. Zootaxa 3669: 027–036.

Kaszab Z (1951) Tenebrionides. In: Monard A. Résultats de la Mission zoologique suisse au Cameroun. Institut Français d'Afrique Noire-Centre du Cameroun, 1–3.

Koch C (1956) Exploration du Parc National de l'Upemba. II. Tenebrionidae (Coleoptera, Polyphaga), Opatrinae, First part: Platynotini, Litoborini and Loensini. Bruxelles, 472 pp.

Kulzer H (1963) Verzeichnis des Typenmaterials der Tenebrionidensammlung des Museums G. Frey. Entomologischen Arbeiten aus dem Museum G. Frey 14: 375–434.

Lacordaire M (1859) Histoire naturelle des Insectes. Genera des Coléoptères ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes. Tribu XXV. Pédinides. Paris, 5: 1–400 [226–243].

Maddison WP, Maddison DR (2011) Mesquite: a modular system for evolutionary analysis. Version 2.75.

Matthews EG, Lawrence JF, Bouchard P, Steiner WE, Ślipiński SA (2010) 11.14 Tenebrionidae Latreille, 1802. In: Leschen RAB, Beutel RG, Lawrence JF (Eds) Handbook of Zoology. A Natural History of the Phyla of the Animal Kingdom.Volume IV- Arthropoda: Insecta. Part 38. Coleoptera, Beetles. Volume 2: Systematics (Part 2). Walter de Gruyter, Berlin, 574–659.

Mulsant E, Rey C (1853) Essai d'une division des derniers mélanosomes. Mémoires de la Société Agriculturale de Lyon (Ser. 2), 2: 226–329.

Nixon KC (2002) WinClada, Version 1.00.08. http://www.cladistics.com

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'Amico JA, Itoua I, Strand HW, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P, Kassem KR (2001) Terrestrial Ecoregions of the World: A new map of life on Earth (PDF, 1.1M). BioScience 51: 933–938. doi: 10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Péringuey ML (1892) Third contribution to the South African coleopterous fauna. Transactions of the South African Philosophical Society 6: 1–94. doi: 10.1080/21560382.1889.9526255

Raś M, Kamiński MJ (2013) X-ray microtomography as a tool for taxonomic investigations: prothoracic skeletal structure in some Tenebrionidae (Coleoptera). Annales Zoologici 63: 381–391. doi: 10.3161/000345413X669649

ZooKeys 415: 133–167 (2014)
doi: 10.3897/zookeys.415.6623
www.zookeys.org

RESEARCH ARTICLE

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

http://zoobank.org/6DB22FE6-1042-4E38-BA18-8174028FA452

Citation: Soldati L, Kergoat GJ, Clamens A-L, Jourdan H, Jabbour-Zahab R, Condamine FL (2014) 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. In: Bouchard P, Smith AD (Eds) Proceedings of the Third International Tenebrionoidea Symposium, Arizona, USA, 2013. ZooKeys 415: 133–167. doi: 10.3897/zookeys.415.6623

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

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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,

2013) 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 Keijsner 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*.

Systematics			GenBank accession No.						
Species	**Voucher No.**	**Locality**	**12S**	**16S**	**Cyt b**	**COI**	**28SD2-D3**	**Wingless**	**18S**
Family Tenebrionidae Latreille, 1802									
Subfamily Tenebrioninae Latreille, 1802									
Tribe Ulomini Blanchard, 1845									
Uloma caledonica Kaszab, 1982	**LSOL.01828**	'Parc de la Rivière bleue'	KJ510053	-missing-	-missing-	-missing-	-missing-	-missing-	-missing-
Uloma caledonica Kaszab, 1982	**LSOL.02085**	'Parc de la Rivière bleue'	KJ510054	-missing-	-missing-	-missing-	-missing-	-missing-	-missing-
Uloma clamensae sp. n.	**LSOL.01336**	'Putchaté, Atéu'	KJ510055	KJ510095	KJ510021	KJ509982	KJ510159	KJ510042	KJ510127
Uloma clamensae sp. n.	**LSOL.02021**	'Massif des Lèvres'	KJ510056	KJ510096	-missing-	KJ509983	KJ510160	-missing-	KJ510128
Uloma condaminei sp. n.	**LSOL.02108**	'Wayem, Panié'	-missing-	-missing-	-missing-	KJ509984	-missing-	-missing-	-missing-
Uloma condaminei sp. n.	**LSOL.02126**	'Wayem, Panié'	KJ510057	-missing-	-missing-	KJ509985	-missing-	-missing-	-missing-
Uloma condaminei sp. n.	**LSOL.02127**	'Wayem, Panié'	KJ510058	KJ510097	-missing-	KJ509986	-missing-	-missing-	-missing-
Uloma condaminei sp. n.	**LSOL.02129**	'Wayem, Panié'	KJ510059	KJ510098	-missing-	KJ509987	-missing-	-missing-	-missing-
Uloma condaminei sp. n.	**LSOL.02130**	'Wayem, Panié'	KJ510060	KJ510099	-missing-	KJ509988	KJ510161	-missing-	KJ510129
Uloma condaminei sp. n.	**LSOL.02131**	'Wayem, Panié'	-missing-	KJ510100	-missing-	-missing-	-missing-	KJ510043	-missing-
Uloma condaminei sp. n.	**LSOL.02142**	'Wayem, Panié'	KJ510061	-missing-	-missing-	KJ509989	-missing-	-missing-	-missing-
Uloma condaminei sp. n.	**LSOL.02147**	'Wayem, Panié'	KJ510062	KJ510101	-missing-	KJ509990	KJ510162	-missing-	KJ510130
Uloma freyi Kulzer, 1960	**LSOL.00996**	(Fiji islands)	KJ510063	KJ510102	KJ510022	KJ509991	KJ510163	KJ510044	KJ510131
Uloma isoceroides (Fauvel, 1904)	**LSOL.01144**	'Plateau de Dogny'	KJ510064	KJ510103	-missing-	KJ509992	KJ510164	-missing-	KJ510132
Uloma isoceroides (Fauvel, 1904)	**LSOL.01250**	'Massif de la Tchamba'	KJ510065	KJ510104	KJ510023	KJ509993	KJ510165	-missing-	KJ510133
Uloma jourdani sp. n.	**LSOL.02158**	'Wewec, Panié'	KJ510066	KJ510105	KJ510024	KJ509994	-missing-	-missing-	KJ510134
Uloma jourdani sp. n.	**LSOL.02209**	'La Guen, Panié'	KJ510067	-missing-	-missing-	KJ509995	-missing-	-missing-	-missing-
Uloma jourdani sp. n.	**LSOL.02242**	'La Guen, Panié'	KJ510068	KJ510106	KJ510025	KJ509996	KJ510166	-missing-	KJ510135
Uloma jourdani sp. n.	**LSOL.02243**	'La Guen, Panié'	KJ510069	KJ510107	KJ510026	KJ509997	-missing-	-missing-	KJ510136
Uloma jourdani sp. n.	**LSOL.02201**	'Dawenia, Panié'	KJ510070	KJ510108	-missing-	KJ509998	KJ510167	-missing-	KJ510137
Uloma jourdani sp. n.	**LSOL.02202**	'Dawenia, Panié'	KJ510071	KJ510109	-missing-	KJ509999	KJ510168	-missing-	KJ510138
Uloma jourdani sp. n.	**LSOL.02263**	'Dawenia, Panié'	KJ510072	KJ510110	KJ510027	KJ510000	-missing-	KJ510045	KJ510139
Uloma jourdani sp. n.	**LSOL.02265**	'Dawenia, Panié'	KJ510073	KJ510111	-missing-	KJ509101	-missing-	-missing-	KJ510140
Uloma jourdani sp. n.	**LSOL.02292**	'Dawenia, Panié'	KJ510074	KJ510112	-missing-	KJ509102	KJ510169	KJ510046	KJ510141

Systematics			GenBank accession No.						
Species	Voucher No.	Locality	12S	16S	Cyt b	COI	28SD2-D3	Wingless	18S
Uloma jourdani sp. n.	**LSOL.02294**	'Dawenia, Panié'	KJ510075	KJ510113	KJ510028	KJ509103	-missing-	KJ510047	KJ510142
Uloma kergoati sp. n.	**LSOL.01012**	'Monts Koghis'	KJ510076	-missing-	-missing-	KJ509104	-missing-	-missing-	KJ510143
Uloma kergoati sp. n.	**LSOL.01122**	'Monts Koghis'	KJ510077	-missing-	-missing-	-missing-	-missing-	-missing-	KJ510144
Uloma kergoati sp. n.	**LSOL.01587**	'Monts Koghis'	KJ510078	KJ510114	KJ510029	KJ509105	KJ510170	-missing-	KJ510145
Uloma kergoati sp. n.	**LSOL.01805**	'Monts Koghis'	KJ510079	-missing-	KJ510030	KJ509106	-missing-	-missing-	KJ510146
Uloma kergoati sp. n.	**LSOL.01806**	'Monts Koghis'	KJ510080	-missing-	KJ510031	KJ509107	-missing-	-missing-	KJ510147
Uloma opacipennis (Fauvel, 1904)	**LSOL.01020**	'Mont Do'	KJ510081	-missing-	-missing-	KJ509108	-missing-	-missing-	KJ510148
Uloma opacipennis (Fauvel, 1904)	**LSOL.01360**	'Parc de la Rivière bleue'	KJ510082	KJ510115	KJ510032	-missing-	-missing-	-missing-	KJ510149
Uloma opacipennis (Fauvel, 1904)	**LSOL.02144**	'Wayem, Panié'	KJ510083	-missing-	-missing-	KJ510009	KJ510171	-missing-	-missing-
Uloma opacipennis (Fauvel, 1904)	**LSOL.02184**	'Dawenia, Panié'	KJ510084	KJ510116	KJ510033	KJ510010	KJ510172	KJ510048	-missing-
Uloma opacipennis (Fauvel, 1904)	**LSOL.02185**	'Dawenia, Panié'	KJ510085	KJ510117	KJ510034	KJ510011	KJ510173	-missing-	-missing-
Uloma opacipennis (Fauvel, 1904)	**LSOL.02193**	'Dawenia, Panié'	KJ510086	KJ510118	KJ510035	KJ510012	KJ510174	KJ510049	KJ510150
Uloma opacipennis (Fauvel, 1904)	**LSOL.02206**	'Dawenia, Panié'	KJ510087	-missing-	-missing-	KJ510013	-missing-	-missing-	-missing-
Uloma opacipennis (Fauvel, 1904)	**LSOL.02224**	'La Guen, Panié'	KJ510088	KJ510119	KJ510036	-missing-	-missing-	-missing-	KJ510151
Uloma opacipennis (Fauvel, 1904)	**LSOL.02225**	'La Guen, Panié'	KJ510089	KJ510120	KJ510037	KJ510014	-missing-	-missing-	KJ510152
Uloma opacipennis (Fauvel, 1904)	**LSOL.02236**	'La Guen, Panié'	KJ510090	KJ510121	-missing-	KJ510015	-missing-	KJ510050	KJ510153
Uloma opacipennis (Fauvel, 1904)	**LSOL.02237**	'La Guen, Panié'	KJ510091	KJ510122	-missing-	KJ510016	-missing-	KJ510051	KJ510154
Uloma opacipennis (Fauvel, 1904)	**LSOL.02250**	'La Guen, Panié'	KJ510092	KJ510123	KJ510038	KJ510017	KJ510175	KJ510052	KJ510155
Uloma opacipennis (Fauvel, 1904)	**LSOL.02251**	'La Guen, Panié'	KJ510093	KJ510124	KJ510039	KJ510018	-missing-	-missing-	KJ510156
Uloma opacipennis (Fauvel, 1904)	**LSOL.02260**	'Dawenia, Panié'	-missing-	KJ510125	KJ510040	KJ510019	-missing-	-missing-	KJ510157
Uloma opacipennis (Fauvel, 1904)	**LSOL.02261**	'Dawenia, Panié'	KJ510094	KJ510126	KJ510041	KJ510020	-missing-	-missing-	KJ510158
Uloma rufa (Piller & Mitterbacher, 1783)	**U.rufa.1**	(France)	KC160347	KC160424	-missing-	-missing-	-missing-	-missing-	KJ003714

sequences of complementary strands were further edited and reconciled using Geneious 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 using 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 combined 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 Poisson 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 coalescent 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 collections (all collection codes follow Evenhuis (2008)):

BMNH The Natural History Museum, London, United Kingdom.
BPBM Hawaii, Bernice P. Bishop Museum, Honolulu, USA.
CBGP Centre de Biologie pour la Gestion des Populations, Montferrier-sur-Lez, France.

CS	Collection Soldati, Montpellier, France.
HNHM	Hungarian Natural History Museum, Budapest, Hungary.
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium.
MNHN	Muséum National d'Histoire Naturelle, Paris, France.
MTD	Museum für Tierkunde, Dresden, Germany.
QM	Queensland Museum, Brisbane, Australia.
USNM	National Museum of Natural History, Washington D.C., USA.

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 jourdani* 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. jourdani* 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. jourdani* 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

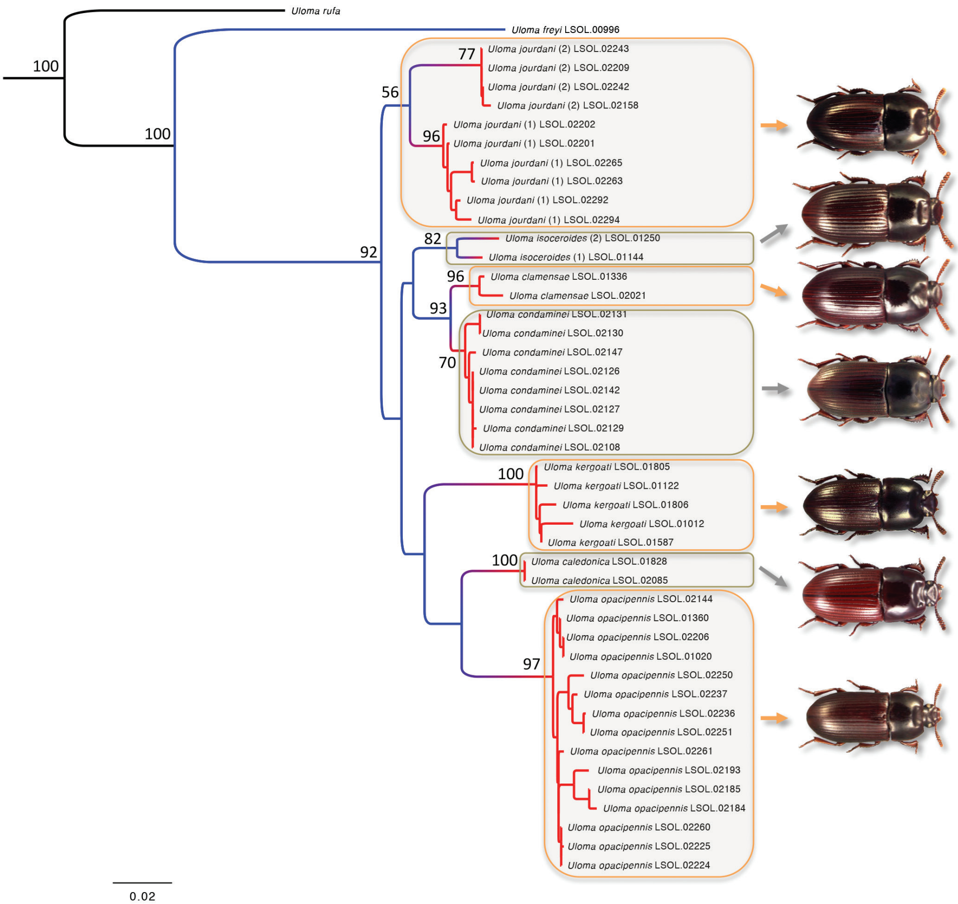

Figure 1. Maximum likelihood tree resulting from the analysis of the combined dataset. Support of major nodes is provided by BV (only BV ≥ 50% are figured). For the group of interest we used coloured frames to highlight the seven sampled morphospecies (*Uloma caledonica*, *U. clamensae*, *U. condaminei*, *U. isoceroides*, *U. jourdani*, *U. kergoati* and *U. opacipennis*). On the right, corresponding male habitus are also included for illustrative purpose. Results of the PTP analysis are provided using coloured branches. Putative molecular species are indicated using transitions between blue-coloured branches to red-coloured branches. For the two cases (for *U. isoceroides* and *U. jourdani*) in which two distinct putative species clusters are inferred we added numbers into brackets to indicate the assignation of specimens to a specific species cluster.

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

Uloma caledonica Kaszab, Folia Entomologica Hungarica 18: 87.

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 mesocoxa), the humeri slightly developed, the elytral striae of punctures strongly marked and developed to apex, and the pronotal punctation 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)".

Additional localities. Mont Do (21°45.63'S, 166°00.15'E, ca 940 m) 6.III.2008, L. Soldati, G.J. Kergoat & H. Jourdan rec. (CBGP); Parc Provincial de la Rivière Bleue, Refuge des Ornithologues (22°08.04'E, 166°39.19'S, ca 190 m) 4.XI.2008, L. Soldati, G.J. Kergoat, F.L. Condamine & H. Jourdan rec. (CBGP).

***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, E

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).

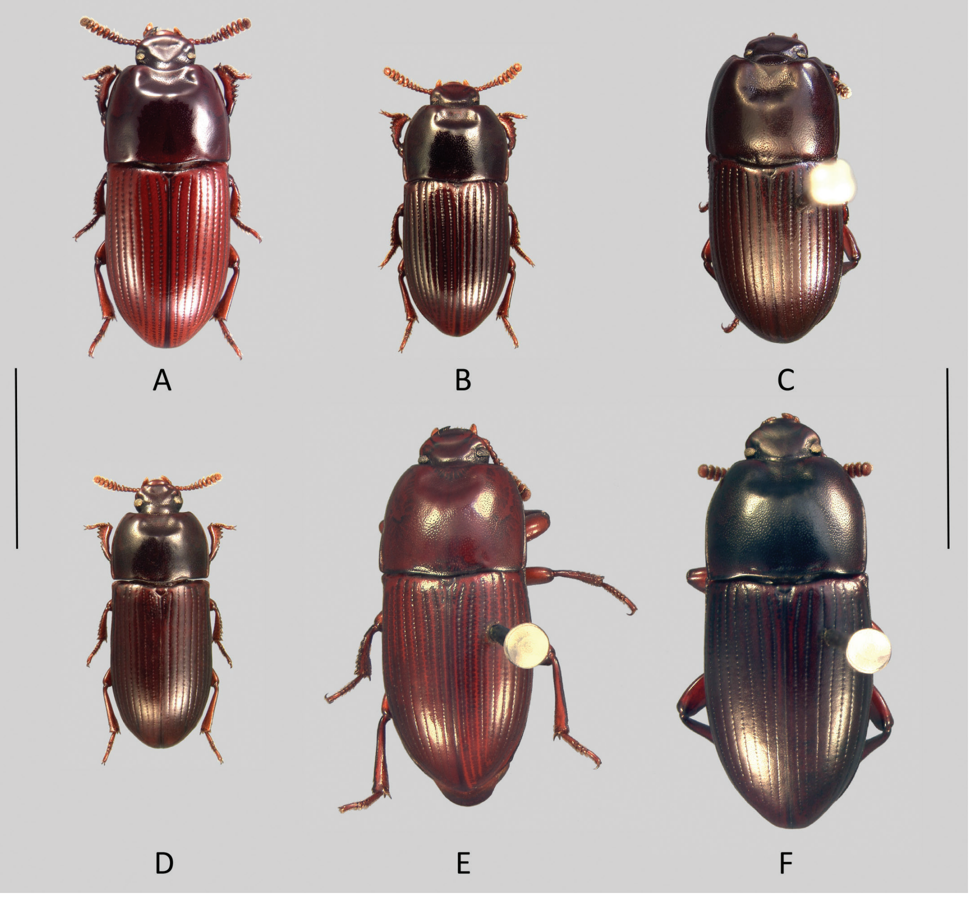

Figure 2. Habitus (dorsal view): **A** *Uloma caledonica* **B** *Uloma isoceroides* **C** *Uloma monteithi* **D** *Uloma opacipennis* **E** *Uloma paniei* **F** *Uloma robusta*. Scale bar: 5 mm.

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 3. Aedeagus (tergal face and lateral view): **A–B** *Uloma caledonica* **C–D** *Uloma clamensae* **E–F** *Uloma condaminei* **G–H** *Uloma isoceroides* **I–J** *Uloma jourdani* **K–L** *Uloma kergoati* **M–N** *Uloma monteithi* **O–P** *Uloma opacipennis* **Q–R** *Uloma robusta*.

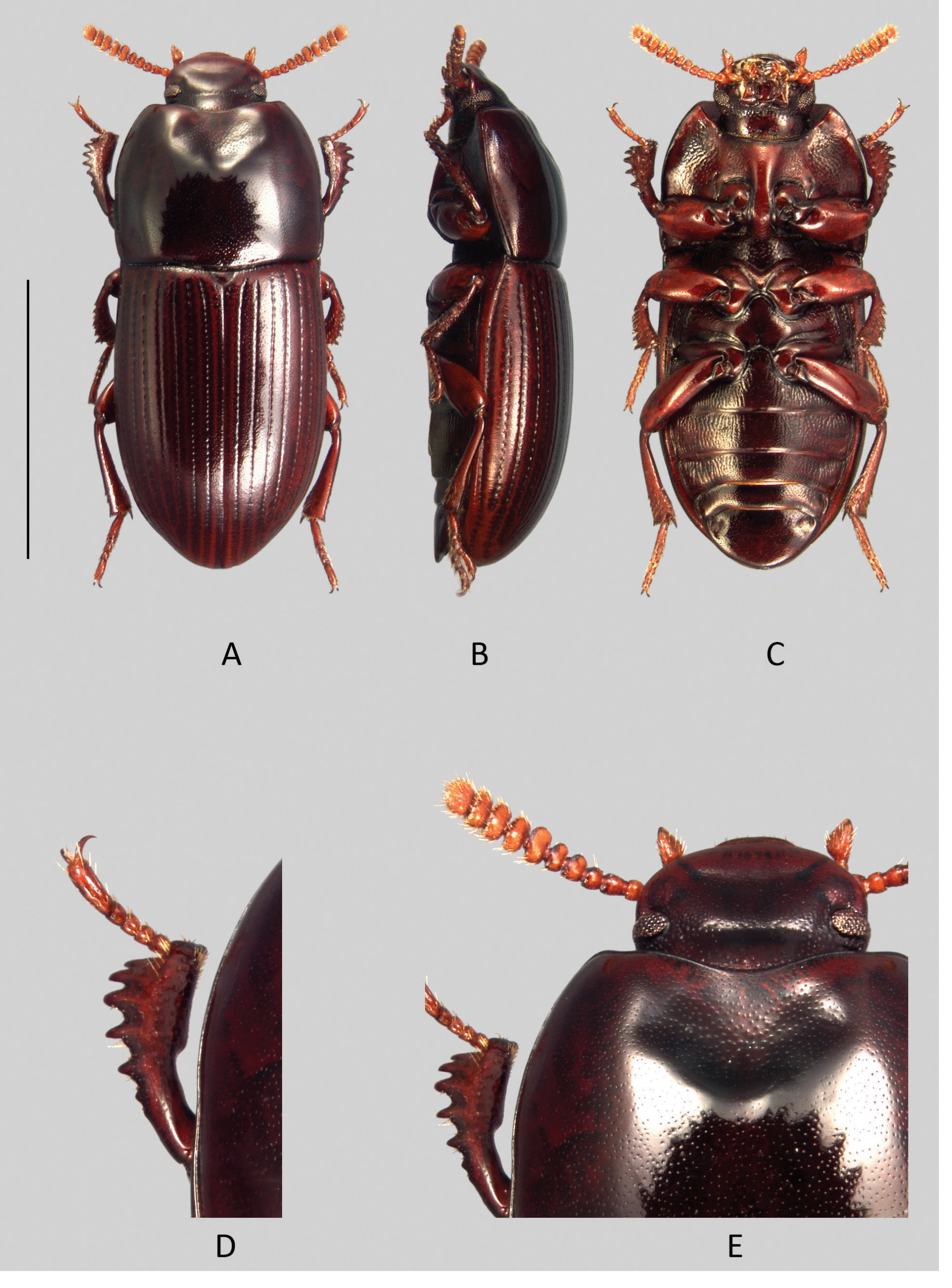

Figure 4. *Uloma clamensae*: **A** habitus (dorsal view) **B** habitus (lateral view) **C** habitus (ventral view) **D** anterior tibia (upper face) **E** head (dorsal view). Scale bar: 5 mm.

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 punctation.

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 punctation.

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

Type specimens. Holotype male, pinned, with genitalia glued on the same card as the specimen itself. Original label: "Nouvelle-Calédonie, Roches de Ouaième, 2.XI.2010, H. Jourdan & C. Mille leg. / 20°38.333'S, 164°52.092'E ca 680 m alt." / *Uloma condaminei* m. n. sp. L. Soldati det. 2013, HOLOTYPE ♂ (red printed label) (MNHN); Allotype female. Original label: "Nouvelle-Calédonie, Roches de Ouaième, 2.XI.2010, H. Jourdan & C. Mille leg. / 20°38.283'S, 164°52.010'E, ca 700 m alt." / *Uloma condaminei* m. n. sp. L. Soldati det. 2013, ALLOTYPE ♀ (red printed label) (MNHN); Paratypes: one male (MNHN), one male and one female (CS): "Nouvelle-Calédonie, Roches de Ouaième, 4.XI.2010, H. Jourdan & C. Mille leg. / 20°38.567'S, 164°51.607'E, ca 800 m alt." / *Uloma condaminei* m. n. sp. L. Soldati det. 2013; Paratypes: one male (CS), one male (HNHM) one female (CBGP), "Nouvelle-Calédonie, Roches de Ouaième, 4.XI.2010, H. Jourdan & C. Mille leg. / 20°38.333'S, 164°51.947'E, ca 750 m alt."/ *Uloma condaminei* m. n. sp. L. Soldati det. 2013; Paratype: one male (CBGP) "Nouvelle-Calédonie, Roches de Ouaième, 1.XI.2010, H. Jourdan & C. Mille leg. / 20°38.400'S, 164°52.285'E ca 600 m alt." / *Uloma condaminei* m. n. sp. L. Soldati det. 2013.

Diagnosis. As underlined beforehand, *Uloma condaminei* is morphologically closely related to *Uloma clamensae* sp. n. It is also morphologically related to *Uloma paniei* 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. paniei* 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.

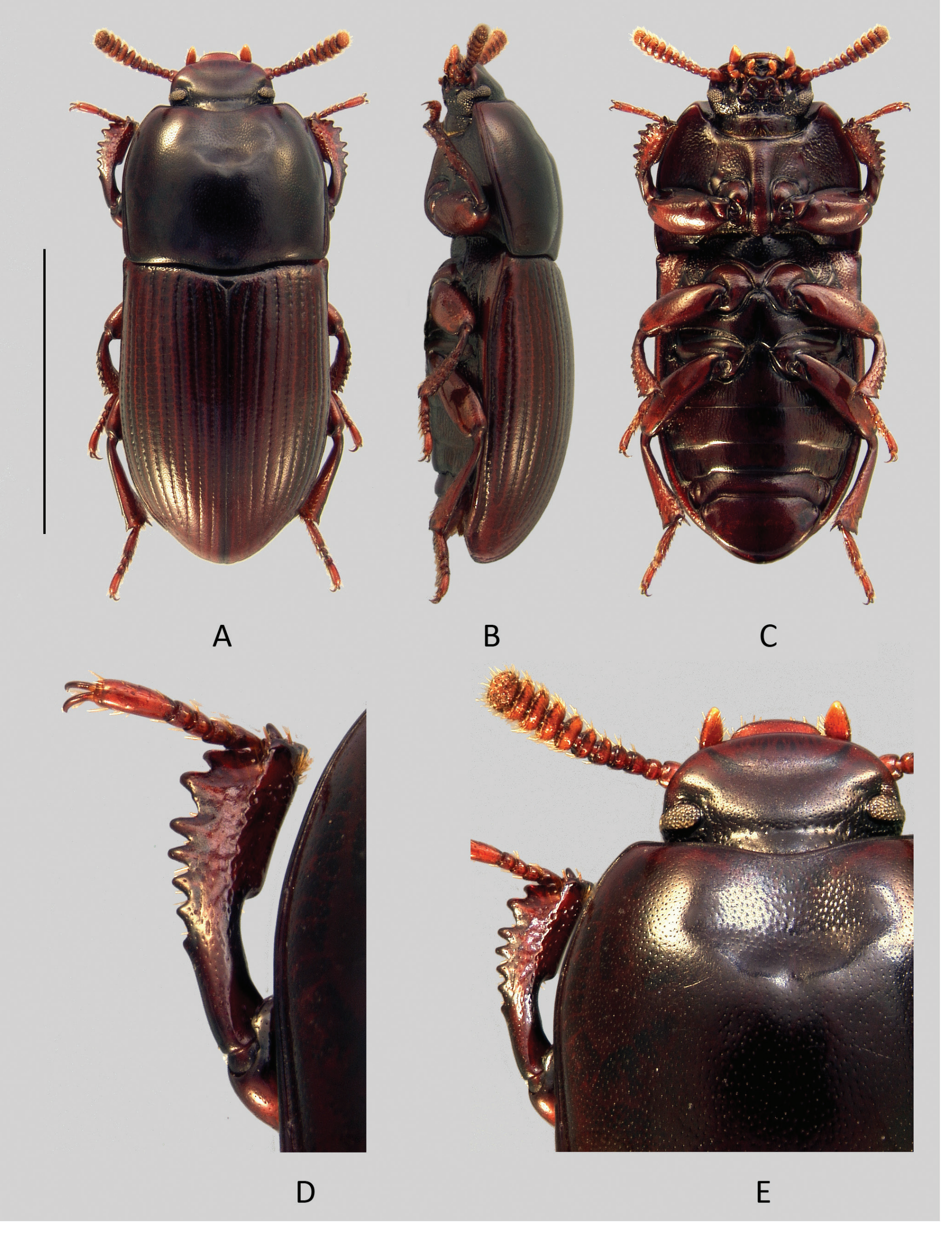

Figure 5. *Uloma condaminei*: **A** habitus (dorsal view) **B** habitus (lateral view) **C** habitus (ventral view) **D** anterior tibia (upper face) **E** head (dorsal view). Scale bar: 5 mm.

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 punctation.

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, punctation 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

Melasia isoceroides Fauvel, Revue d'Entomologie 23: 180, 182.
Uloma isoceroides Fauvel, Gebien H. 1911, Tenebrionidae III. In: Schenkling S (Ed) *Coleopterorum Catalogus*. Vol.18: 402.

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. caledonica* 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. caledonica* (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)".

Additional localities. Monts Koghis (22°10.63'S, 166°30.49'E, ca 460 m) 4.III.2008, L. Soldati, G.J. Kergoat & H. Jourdan rec. (CBGP); Réserve Botanique de Bois du Sud (22°10.41'S, 166°45.83'E, ca 210 m) 8.III.2008, L. Soldati, G.J. Kergoat & H. Jourdan rec. (CBGP); Plateau de Dogny (21°37.03'S, 165°53.05'E, ca 920 m) 29.X.2008, L. Soldati, G.J. Kergoat & F.L. Condamine rec. (CBGP); Massif forestier de la Tchamba (21°00.71'S, 165°15.58'E, ca 200 m) 8.IV.2009, L. Soldati, G.J. Kergoat, H. Jourdan & F.L. Condamine rec. (CBGP).

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

Type specimens. Holotype male, pinned, with genitalia glued on the same glue board as the specimen itself. Original label: "Nouvelle-Calédonie, Massif du Panié, Dawenia, 13.XI.2010, Jourdan & Mille rec. / 20°32.268'S, 164°40.903'E, ca 640 m NC130-2a'" / Uloma jourdani m. n. sp. L. Soldati det. 2013, HOLOTYPE ♂ (red printed label) (MNHN); Allotype female, pinned. Original label: "Nouvelle-Calédonie, Massif du Panié, Dawenia, 14.XI.2010, H. Jourdan & C. Mille / 20°32.290'S, 164°40.967'E, ca 620 m NC139-2a'" / Uloma jourdani m. n. sp. L. Soldati det. 2013, ALLOTYPE ♀ (red printed label) (MNHN); Paratypes: one male (MNHN) and one female (CBGP): "Nouvelle-Calédonie, Massif du Panié, Dawenia, 13.XI.2010, H. Jourdan & C. Mille / 20°32.268'S, 164°40.903'E, ca 630 m; Paratypes: two males (CBGP): "Nouvelle-Calédonie, Massif du Panié, Dawenia, 13.XI.2010, H. Jourdan & C. Mille / 20°32.268'S, 164°40.903'E, ca 640 m" ; Paratypes: one male (CS): "Nouvelle-Calédonie, Massif du Panié, Dawenia, 12.XI.2010, H. Jourdan & C. Mille / 20°32.265'S, 164°40.843'E ca 620 m" ; Paratypes: one male and one female (CS): "Nouvelle-Calédonie, Massif du Panié, Dawenia, 14.XI.2010, H. Jourdan & C. Mille / 20°32.262'S, 164°41.092'E ca 620 m"; Paratype: one female (CS): "Nouvelle-Calédonie, Massif du Panié, Dawenia, 14.XI.2010, H. Jourdan & C. Mille / 20°32.290'S, 164°40.967'E ca 620 m".

Other material. one male, Nouvelle-Calédonie, Massif du Panié, Wewec, forêt sur pente, 20°35.63'S, 164°43.66'E ca 420 m, 8.XI.2010, H. Jourdan & C. Mille rec.; one female, Massif du Panié, La Guen, 20°37.48'S, 164°46.83'E ca 580 m, 23.XI.2010, H. Jourdan & C. Mille rec.; one female, Massif du Panié, La Guen, 20°37.50'S, 164°46.83'E ca 590 m, 19.XI.2010, H. Jourdan & C. Mille rec.; two males and one female, Massif du Panié, La Guen, 20°37.50'S, 164°46.83'E ca 590 m, 18-25.XI.2010, H. Jourdan & C. Mille rec.; one male, Massif du Panié, La Guen, 20°37.50'S, 164°46.92'E ca 570 m, 18.XI.2010, H. Jourdan & C. Mille rec.

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).

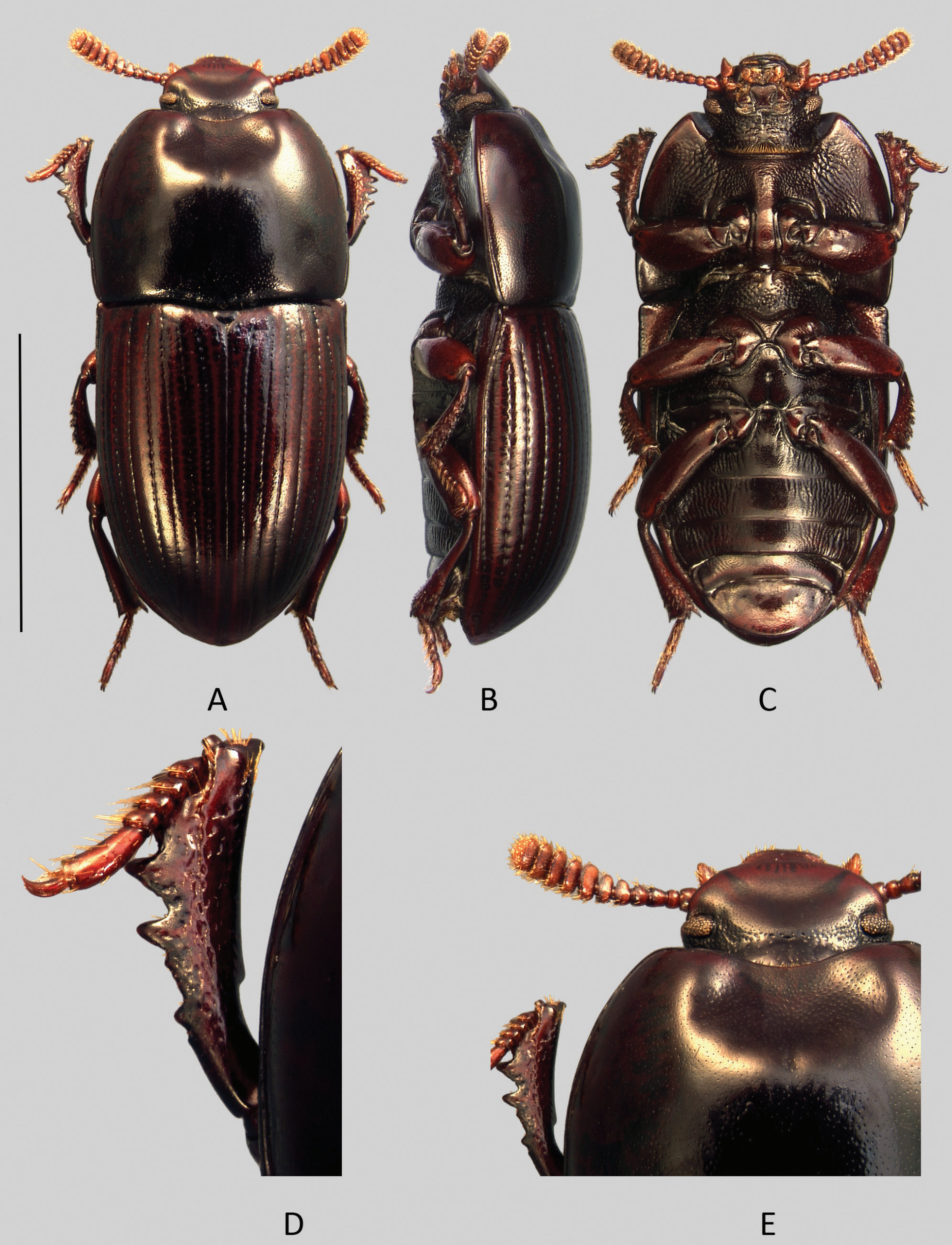

Figure 7. *Uloma jourdani*: **A** habitus (dorsal view) **B** habitus (lateral view) **C** habitus (ventral view) **D** anterior tibia (upper face) **E** head (dorsal view). Scale bar: 5 mm.

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 punctures. 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 clypeogenal 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

Type specimens. Holotype male, pinned, with genitalia glued on the same card as the specimen itself. Original label: "Nouvelle-Calédonie, Massif du Kouakoué, 17-23.III.2008, H. Jourdan, G. Kergoat & L. Soldati leg. / 21°57.427'S, 166°32.294'E, ca 1280 m alt. / *Uloma kergoati* m. n. sp. L. Soldati det. 2013, HOLOTYPE ♂" (red printed label) (MNHN); Allotype female, pinned. Original label: "Nouvelle-Calédonie, Massif du Kouakoué, 17-23.III.2008, H. Jourdan, G. Kergoat & L. Soldati leg. / 21°57.427'S, 166°32.294'E, ca 1280 m alt. NC16-2b" / *Uloma kergoati* m. n. sp. L. Soldati det. 2013, ALLOTYPE ♀ (MNHN); Paratypes, same data as holotype: one female (MNHN), one male (HNHM), two males (CBGP), three males and one female (CS).

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

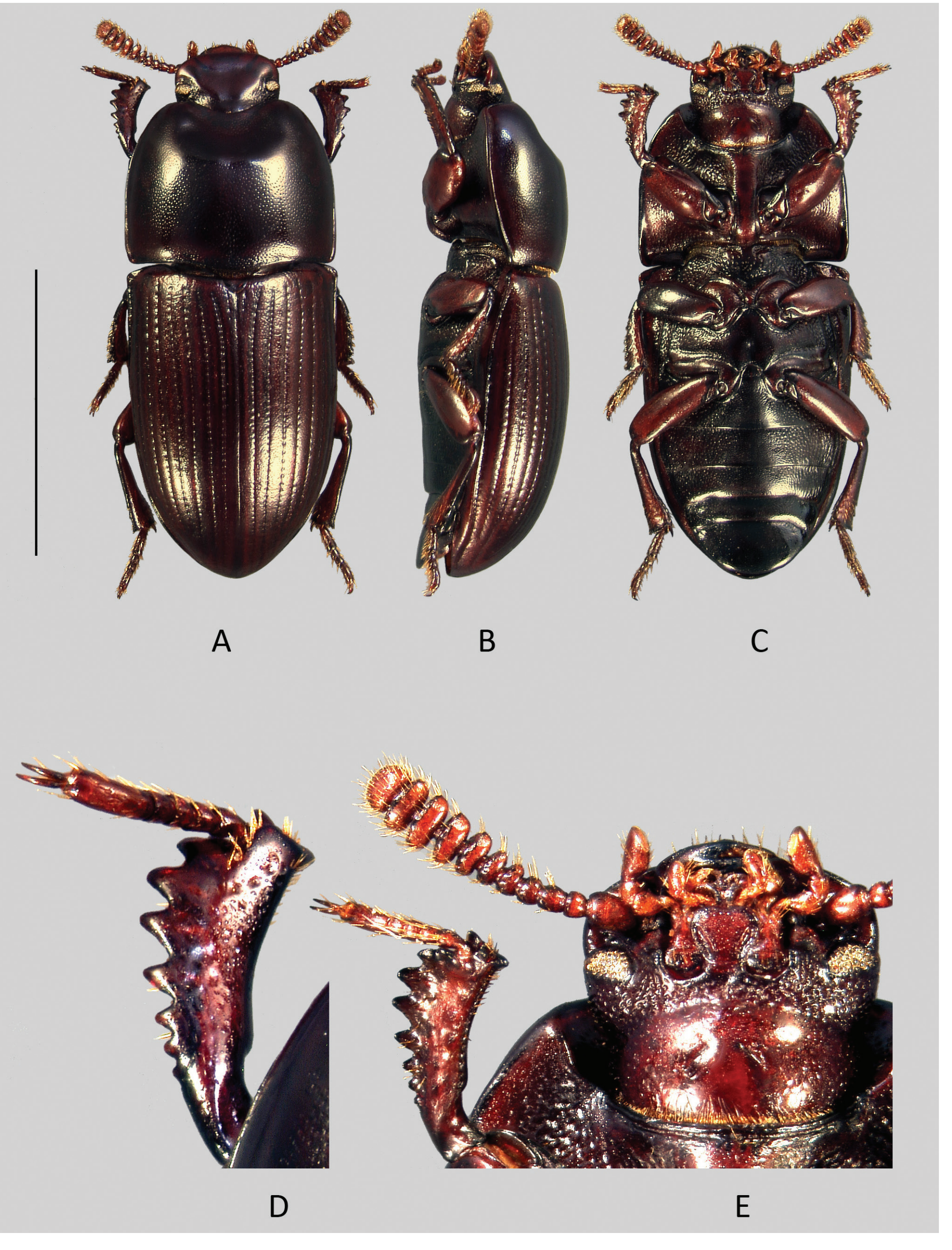

Figure 8. *Uloma kergoati*: **A** habitus (dorsal view) **B** habitus (lateral view) **C** habitus (ventral view) **D** anterior tibia (upper face) **E** head (dorsal view). Scale bar: 5 mm.

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.

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 punctation 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

Uloma monteithi Kaszab, Annales Historico-Naturales Musei Nationalis Hungarici, 78: 160.

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

Melasia opacipennis Fauvel, Revue d'Entomologie 23: 180, 182.
Uloma opacipennis Fauvel, Gebien H. 1911, Tenebrionidae III. In: Schenkling S (Ed) *Coleopterorum Catalogus*. Vol.18: 403.

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 and shallower on the apical declivity. Rows of punctures dense and slightly wider than the striae. Antero-median depression of the pronotum in the male small and rounded. Pronotum finely and sparcely punctate. Male anterior tibiae slightly notched at base on the internal face. Male antennae distinctly expanded from 5th antennomere. Average size small: 7.0–7.5 mm long.

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, sparce and barely visible punctation. 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)".

Additional localities. Mont Koghis (22°10.63'S, 166°30.49'E, ca 460 m alt.) 4.III.2008, L. Soldati, G.J. Kergoat & H. Jourdan rec. (CBGP); Mts Koghis, ca 400 m, 26 may 1984, G. Monteith & D. Cook (QM); Réserve botanique de Bois du Sud (22°10.41'S, 166°45.83'E, ca 210 m) 8.III.2008, L. Soldati, G.J. Kergoat & H. Jourdan rec. (CBGP); Parc des Grandes Fougères, Pic Vincent (21°36.16'S, 165°46.44'E, ca 690 m) 28.III.2008, L. Soldati, G. Kergoat & H. Jourdan rec. (CBGP); Réserve de Yaté Barrage (22°09.23'S, 167°53.51'E, ca 270 m) 23.X.2009, L. Soldati, G.J. Kergoat, F.L. Condamine & H. Jourdan rec. (CBGP); Roches de Ouaième (20°38.28'S, 164°52.01'E, ca 700 m) 2.XI.2010, H. Jourdan & C. Mille rec. (CBGP); Massif du Panié, La Guen (20°37.50'S, 164°46.83'E, ca 590 m) 18-25.XI.2010, H. Jourdan & C. Mille rec. (CBGP); Massif du Panié, La Guen (20°37.42'S, 164°46.85'E, ca 590 m) 20.XI.2010, H. Jourdan & C. Mille rec. (CBGP); Massif du Panié, Dawenia (20°32.26'S, 164°40.90'E, ca 630 m) 15.XI.2010, H. Jourdan & C. Mille rec. (CBGP).

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 Montreuil (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

Balke M, Pons J, Ribera I, Sagata K, Vogler AP (2007a) Infrequent and unidirectional colonization of hyperdiverse *Papuadytes* diving beetles in New Caledonia and New Guinea. Molecular Phylogenetics and Evolution 42: 5005–516.

Balke M, Alarie Y, Ribera I, Wewalka G (2007b) Molecular Phylogeny of Pacific Island Colymbetini: radiation of New Caledonian and Fijian species. Zoologica Scripta 36: 173–200. doi: 10.1111/j.1463-6409.2006.00265.x

Bartish IV, Swenson U, Munzinger J, Anderberg AA (2005) Phylogenetic relationships among New Caledonian Sapotaceae (Ericales): molecular evidence for generic polyphyly and repeated dispersal. American Journal of Botany 92: 667–673. doi: 10.3732/ajb.92.4.667

Belshaw R, Quicke DLJ (2002) Robustness of ancestral state estimates: evolution of life history strategy in ichneumonoid parasitoids. Systematic Biology 51: 450–477. doi: 10.1080/10635150290069896

Bergsten J, Bilton DT, Fujisawa T, Elliott M, Monaghan MT, Balke M, Hendrich L, Geijer J, Herrmann J, Foster GN, Ribera I, Nilsson AN, Barraclough TG, Vogler AP (2012) The effect of geographical scale of sampling on DNA barcoding. Systematic Biology 61: 851–869. doi: 10.1093/sysbio/sys037

Bouchet P, Jaffré T, Veillon J-M (1995) Plant extinction in New Caledonia: protection of sclerophyll forests urgently needed. Biodiversity and Conservation 4: 415–428. doi: 10.1007/BF00058425

Bouchet P, Jaffré T, Veillon J-M (1998) Threatened plants of New Caledonia: Is the system of protected areas adequate? Biodiversity and Conservation 7: 109–135.

Chazeau J (1993) Research on New Caledonian terrestrial fauna: achievements and prospects. Biodiversity Letters 1: 123–129. doi: 10.2307/2999756

Cluzel D, Aitchison JC, Picard C (2001) Tectonic accretion and underplating of mafic terranes in the Late Eocene intraoceanic fore-arc of New Caledonia (Southwest Pacific): geodynamic implications. Tectonophysics 340: 23–59. doi: 10.1016/S0040-1951(01)00148-2

Condamine FL, Soldati L, Clamens A-L, Rasplus J-Y, Kergoat GJ (2013) Diversification patterns and processes of wingless endemic insects in the Mediterranean Basin: historical biogeography of the genus *Blaps* (Coleoptera: Tenebrionidae). Journal of Biogeography 40: 1899–1913.

Cruaud A, Jabbour-Zahab R, Genson G, Ungricht S, Rasplus J-Y (2012) Testing the emergence of New Caledonia: fig wasp mutualism as a case study and a review of evidence. PLoS ONE 7: e30941. doi: 10.1371/journal.pone.0030941

Deuve T, Cruaud A, Genson G, Rasplus J-Y (2012) Molecular systematics and evolutionary history of the genus *Carabus* (Col. Carabidae). Molecular Phylogenetics and Evolution 65: 259–275. doi: 10.1016/j.ympev.2012.06.015

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acid Research 35: 1792–1797. doi: 10.1093/nar/gkh340

Espeland M, Johanson KA (2008a) Revision of the New Caledonian *Hydrobiosella* (Trichoptera: Philopotamidae) with description of five new species. In: Proceedings of the XIIth International Symposium of Trichoptera, 91–102.

Espeland M, Johanson KA (2008b) New species and descriptions of females of the New Caledonian endemic genus *Xanthochorema* (Trichoptera, Hydrobiosidae). In: Grandcolas P (Eds) Zoologia Neocaledonica 6, Systematics and Biodiversity in New Caledonia. Mémoires du Muséum National d'Histoire Naturelle 197: 79–97.

Espeland M, Johanson KA, Hovmöller R (2008) Early *Xanthochorema* (Trichoptera, Insecta) radiations in New Caledonia originated on ultrabasic rocks. Molecular Phylogenetics and Evolution 48: 904–917. doi: 10.1016/j.ympev.2008.06.006

Espeland M, Johanson KA (2010) The diversity and radiation of the largest monophyletic animal group on New Caledonia (Trichoptera: Ecnomidae: *Agmina*). Journal of Evolutionary Biology 23: 2112–2122. doi: 10.1111/j.1420-9101.2010.02072.x

Espeland M, Murienne J (2011) Diversity dynamics in New Caledonia: towards the end of the museum model? BMC Evolutionary Biology 11: 254. doi: 10.1186/1471-2148-11-254

Evenhuis N (2008) The insect and spider collections of the world website. http://hbs.bishopmuseum.org/codens/ [accessed on November 15, 2013]

Fauvel A (1904) Faune analytique des Coléoptères de la Nouvelle-Calédonie, 2[e] partie. Revue d'Entomologie 23: 164–208.

Gargominy O, Bouchet P, Pascal M, Jaffré T, Tourneur JC (1996) Conséquences des introductions d'espèces animales et végétales sur la biodiversité en Nouvelle-Calédonie. Revue d'Ecologie (Terre Vie) 51: 375–401.

Gilbert MTP, Moore W, Melchior L, Worobey M (2007) DNA extraction from dry museum beetles without conferring external morphological damage. PLoS ONE 2: e272. doi: 10.1371/journal.pone.0000272

Grandcolas P, Murienne J, Robillard T, Desutter-Grandcolas L, Jourdan H, Guilbert E, Deharveng L (2008) New Caledonia: a very old Darwinian island? Philosophical Transactions of the Royal Society of London B 363: 3309–3317. doi: 10.1098/rstb.2008.0122

Heads MJ (2008) Panbiogeography of New Caledonia, south-west Pacific: basal angiosperms on basement terranes, ultramafic endemics inherited from volcanic island arcs and old taxa endemic to young islands. Journal of Biogeography 35: 2153–2175. doi: 10.1111/j.1365-2699.2008.01977.x

Heads MJ (2013) Biogeography of Australasia: A Molecular Analysis. Cambridge University Press. doi: 10.1017/CBO9781139644464

Hillis DM, Bull JJ (1993) An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. Systematic Biology 42: 182–192.

Johanson KA, Keijsner M (2008) Phylogeny of the Helicophidae (Trichoptera), with emphasis on the New Caledonian species of *Helicopha*. Systematic Entomology 33: 451–483. doi: 10.1111/j.1365-3113.2008.00423.x

Jörger KM, Schrödl M (2013) How to describe a cryptic species? Practical challenges of molecular taxonomy. Frontiers in Zoology 10: 59. doi: 10.1186/1742-9994-10-59

Kaszab Z (1982) Die Tenebrioniden Neukaledoniens und der Loyauté-Inseln (Coleoptera). Folia Entomologica Hungarica 28: 1–294.

Kaszab Z (1986) Tenebrioniden (Coleoptera) aus Neukaledonien. Annales Historico-Naturales Musei Nationalis Hungarici 78: 151–175.

Keppel G, Lowe AJ, Possingham HP (2009) Changing perspectives on the biogeography of the tropical South Pacific: influences of dispersal, vicariance and extinction. Journal of Biogeography 36: 1035–1054. doi: 10.1111/j.1365-2699.2009.02095.x

Kergoat GJ, Delobel A, Silvain J-F (2004) Phylogeny and host-specificity of European seed beetles (Coleoptera, Bruchidae), new insights from molecular and ecological data. Molecular Phylogenetics and Evolution 32: 855–865. doi: 10.1016/j.ympev.2004.02.019

Kergoat GJ, Delobel A, Fédière G, Le Ru B, Silvain J-F (2005) Both host-plant phylogeny and chemistry have shaped the African seed-beetle radiation. Molecular Phylogenetics and Evolution 35: 602–611. doi: 10.1016/j.ympev.2004.12.024

Kergoat GJ, Le Ru BP, Genson G, Cruaud C, Couloux A, Delobel A (2011) Phylogenetics, species boundaries and timing of resource tracking in a highly specialized group of seed beetles (Coleoptera: Chrysomelidae: Bruchinae). Molecular Phylogenetics and Evolution 59: 746–760. doi: 10.1016/j.ympev.2011.03.014

Kergoat GJ, Soldati L, Clamens A-L, Jourdan H, Jabbour-Zahab R, Genson G, Bouchard P, Condamine FL (2014) Higher level molecular phylogeny of darkling beetle (Coleoptera: Tenebrionidae). Systematic Entomology. doi: 10.1111/syen.12065

Kuschel G (2008) Curculionoidea (weevils) of New Caledonia and Vanuatu: basal families and some Curculionidae. Zoologica Neocaledonica 6: 99–249.

Ladiges PY, Cantrill D (2007) New Caledonia-Australian connections: biogeographic patterns and geology. Australian Systematic Botany 20: 383–389. doi: 10.1071/SB07018

Lowry PP, Munzinger J, Bouchet P, Géraux J, Bauer AM, Langrand O, Mittermeier RA (2004) New Caledonia. In: Mittermeier RA, Robles Gil P, Hoffmann M, Pilgrim J, Brooks T, Mittermeier CG, Lamoreux JL, da Fonseca GAB (Eds) Hotspots revisited: earth's biologically richest and most threatened ecoregions. CEMEX, Mexico City, Mexico, 193–197.

Malm T, Johanson KA (2007) Three new species of *Symphitoneuria* Ulmer (Trichoptera: Leptoceridae) from New Caledonia. In: Proceedings of the XIIth International Symposium of Trichoptera, 181–190.

Malm T, Johanson KA (2008a) Revision of the New Caledonian endemic genus *Gracilipsodes* (Trichoptera: Leptoceridae: Grumichellini). Zoological Journal of the Linnean Society 153: 425–452. doi: 10.1111/j.1096-3642.2008.00403.x

Malm T, Johanson KA (2008b) Description of eleven New *Triplectides* species (Trichoptera: Leptoceridae) from New Caledonia. Zootaxa 1816: 1–34.

Matsumoto K, Nishikawa N (1986) A revisional study of the species of the genus *Uloma* from Japan, Korea and Taiwan (Tenebrionidae, Coleoptera). Insecta Matsumurana 34: 17–43.

Matthews EG, Bouchard P (2008) Tenebrionid beetles of Australia: description of tribes, keys to genera, catalogue of species. Australian Biological Resources Study, Canberra, 398 pp.

Matthews EG, Lawrence JF, Bouchard P, Steiner WE, Slipinski SA (2010) 11.14. Tenebrionidae Latreille, 1802. In: Leschen RAB, Beutel RG, Lawrence JF (Eds) Handbook of Zoology. A Natural History of the Phyla of the Animal Kingdom. Volume IV - Arthropoda: Insecta. Part 38. Coleoptera, Beetles. Volume 2: Systematics (Part 2). Walter de Gruyter, Berlin, 574–659.

McKenna D, Sequeira AS, Marvaldi AE, Farrell BD (2009) Temporal lags and overlap in the diversification of weevils and flowering plants. Proceedings of the National Academy of Sciences of the United States of America 106: 7083–7088. doi: 10.1073/pnas.0810618106

Mittermeier RA, Werner TB, Lees A (1996) New Caledonia – a conservation imperative for an ancient land. Oryx 30: 104–112. doi: 10.1017/S0030605300021487

Monaghan MT, Wild R, Elliot M, Fujisawa T, Balke M, Inward DJG, Lees DC, Ranaivosolo R, Eggleton P, Barraclough TG, Vogler AP (2009) Accelerated species inventory on Madagascar using coalescent-based models of species delineation. Systematic Biology 58: 298–311. doi: 10.1093/sysbio/syp027

Murienne J, Grandcolas P, Piulachs MD, Bellés X, D'Haese C, Legendre F, Pellens R, Guilbert E (2005) Evolution on a shaky piece of Gondwana: is local endemism recent in New Caledonia? Cladistics 21: 2–7. doi: 10.1111/j.1096-0031.2004.00042.x

Murienne J, Pellens R, Budinoff RB, Wheeler WC, Grandcolas P (2008) Phylogenetic analysis of the endemic New Caledonian cockroach *Lauraesilpha*. Testing competing hypotheses of diversification. Cladistics 24: 1–11. doi: 10.1111/j.1096-0031.2008.00204.x

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853–858. doi: 10.1038/35002501

Novotny V, Drozd P, Miller SE, Kulfan M, Janda M, Basset Y, Weiblen GD (2006) Why are they so many species of herbivorous insects in tropical rainforests? Science 313: 1115–1118. doi: 10.1126/science.1129237

Nylander JAA, Ronquist F, Huelsenbeck JP, Nieves-Aldrey JL (2004) Bayesian phylogenetic analysis of combined data. Systematic Biology 53: 47–67. doi: 10.1080/10635150490264699

Padial JM, Miralles A, De la Riva I, Vences M (2010) The integrative future of taxonomy. Frontiers in Zoology 7: 16. doi: 10.1186/1742-9994-7-16

Papadopoulou A, Anastasiou I, Keskin B, Vogler AP (2009) Comparative phylogeography of tenebrionid beetles in the Aegean archipelago: the effect of dispersal ability and habitat preference. Molecular Ecology 18: 2503–2517. doi: 10.1111/j.1365-294X.2009.04207.x

Papadopoulou A, Anastasiou I, Vogler AP (2010) Revisiting the insect mitochondrial molecular clock: the mid-Aegean trench calibration. Molecular Biology and Evolution 27: 1659–1672. doi: 10.1093/molbev/msq051

Pascal M, Richer de Forges B, Le Guyader H, Simberloff D (2008) Mining and other threats to the New Caledonia biodiversity hotspot. Conservation Biology 22: 498–499. doi: 10.1111/j.1523-1739.2008.00889.x

Pelletier B (2006) Geology of the New Caledonia region and its implications for the study of the New Caledonian biodiversity. Documents Scientifiques et Techniques de l'IRD II 7: 17–30.

Pillon Y, Munzinger J, Amir H, Lebrun M (2010) Ultramafic soils and species sorting in the flora of New Caledonia. Journal of Ecology 98: 1108–1116. doi: 10.1111/j.1365-2745.2010.01689.x

Pillon Y (2012) Time and tempo of diversification in the flora of New Caledonia. Botanical Journal of the Linnean Society 170: 288–298. doi: 10.1111/j.1095-8339.2012.01274.x

Pons J, Barroclough TG, Gomez-Zurita J, Cardoso A, Duran DP, Hazell S, Kamoun S, Sumlin WD, Vogler AP (2006) Sequence-based species delimitation for the DNA taxonomy of undescribed insects. Systematic Biology 55: 595–609. doi: 10.1080/10635150600852011

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, 12 new species clusters and 62 new species from the Oriental and Afrotropical regions (Trichoptera: Hydropsychidae). Zootaxa 1802: 1–248.

Robillard T, Desutter-Grandcolas L (2006) Phylogeny of the cricket subfamily Eneopterinae (Orthoptera, Grylloidea, Eneopteridae) based on four molecular loci and morphology. Molecular Phylogenetics and Evolution 40: 643–661. doi: 10.1016/j.ympev.2005.10.019

Robillard T, Desutter-Grandcolas L (2008) Systematics of *Matuanus* Gorochov (Grylloidea, Podoscirtidae, Podoscirtinae) from New Caledonia: new data and the analysis of venation diversity. In: Grandcolas P (Ed) Zoologia Neocaledonica 6, Systematics and Biodiversity in New Caledonia. Mémoires du Muséum National d'Histoire Naturelle 196: 273–289.

Schellart WP, Lister GS, Toy VG (2006) A Late Cretaceous and Cenozoic reconstruction of the Southwest Pacific region: Tectonics controlled by subduction and slab rollback processes. Earth-Science Reviews 76: 191–233. doi: 10.1016/j.earscirev.2006.01.002

Schlick-Steiner BC, Steiner FM, Seifert B, Stauffer C, Christian E, Crozier RH (2010) Integrative taxonomy: a multisource approach to exploring biodiversity. Annual Review of Entomology 55: 421–438. doi: 10.1146/annurev-ento-112408-085432

Sharma P, Giribet G (2009) A relict in New Caledonia: Phylogenetic relationships of the family Troglosironidae (Opiliones: Cyphophthalmi). Cladistics 25: 279–294. doi: 10.1111/j.1096-0031.2009.00252.x

Smith SA, Sadlier RA, Bauer AM, Austin CC, Jakman T (2007) Molecular phylogeny of the scincid lizards of New Caledonia and adjacent areas: Evidence for a single origin of the endemic skinks of Tasmantis. Molecular Phylogenetics and Evolution 43: 1151–1166. doi: 10.1016/j.ympev.2007.02.007

Stork N, Habel JC (2014) Do biodiversity hotspots protect more than tropical forest plants and vertebrates? Journal of Biogeography 41: 421–428. doi: 10.1111/jbi.12223

Stamatakis A (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22: 2688–2690. doi: 10.1093/bioinformatics/btl446

Silvestro D, Michalak I (2012) raxmlGUI: a graphical front-end for RaxML. Organisms Diversity and Evolution 12: 335–337. doi: 10.1007/s13127-011-0056-0

Swenson U, Backlund A, McLoughghlin S, Hill RS (2001) *Nothofagus* biogeography revisited with special emphasis on the enigmatic distribution of subgenus *Brassospora* in New Caledonia. Cladistics 17: 28–47. doi: 10.1111/j.1096-0031.2001.tb00109.x

Vieites DR, Wollenberg KC, Andreone F, Köhler J, Glaw F, Vences M (2009) Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. Proceedings of the National Academy of Science of the United States of America 106: 8267–8272. doi: 10.1073/pnas.0810821106

Wild AL, Maddison DR (2008) Evaluating nuclear protein-coding genes for phylogenetic utility in beetles. Molecular Phylogenetics and Evolution 48: 877–891. doi: 10.1016/j.ympev.2008.05.023

Zhang J, Kapli P, Pavlidis P, Stamatakis A (2013) A general species delimitation method with applications to phylogenetic placements. Bioinformatics 29: 2869–2876. doi: 10.1093/bioinformatics/btt499

ZooKeys 415: 169–190 (2014)
doi: 10.3897/zookeys.415.6676
www.zookeys.org

RESEARCH ARTICLE

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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

http://zoobank.org/23D45EAE-2FBE-42D2-9BA6-E3775704C29D

Citation: Schawaller W, Grimm R (2014) The genus *Alphitobius* Stephens (Coleoptera, Tenebrionidae, Alphitobiini) in Africa and adjacent islands. In: Bouchard P, Smith AD (Eds) Proceedings of the Third International Tenebrionoidea Symposium, Arizona, USA, 2013. ZooKeys 415: 169–190. doi: 10.3897/zookeys.415.6676

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* (Panzer, 1796); *Alphitobius rufus* Ardoin, 1976, **syn. n.** of *Alphitobius hobohmi* Koch, 1953); *Peltoides* (*Micropeltoides*) *crypticoides* Pic, 1916, **syn. n.** of *Peltoides* (*Micropeltoides*) *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* (*Micropeltoides*) *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. grandis* 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

MNHN	Muséum National d'Histoire Naturelle, Paris, France
MRAC	Museé 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

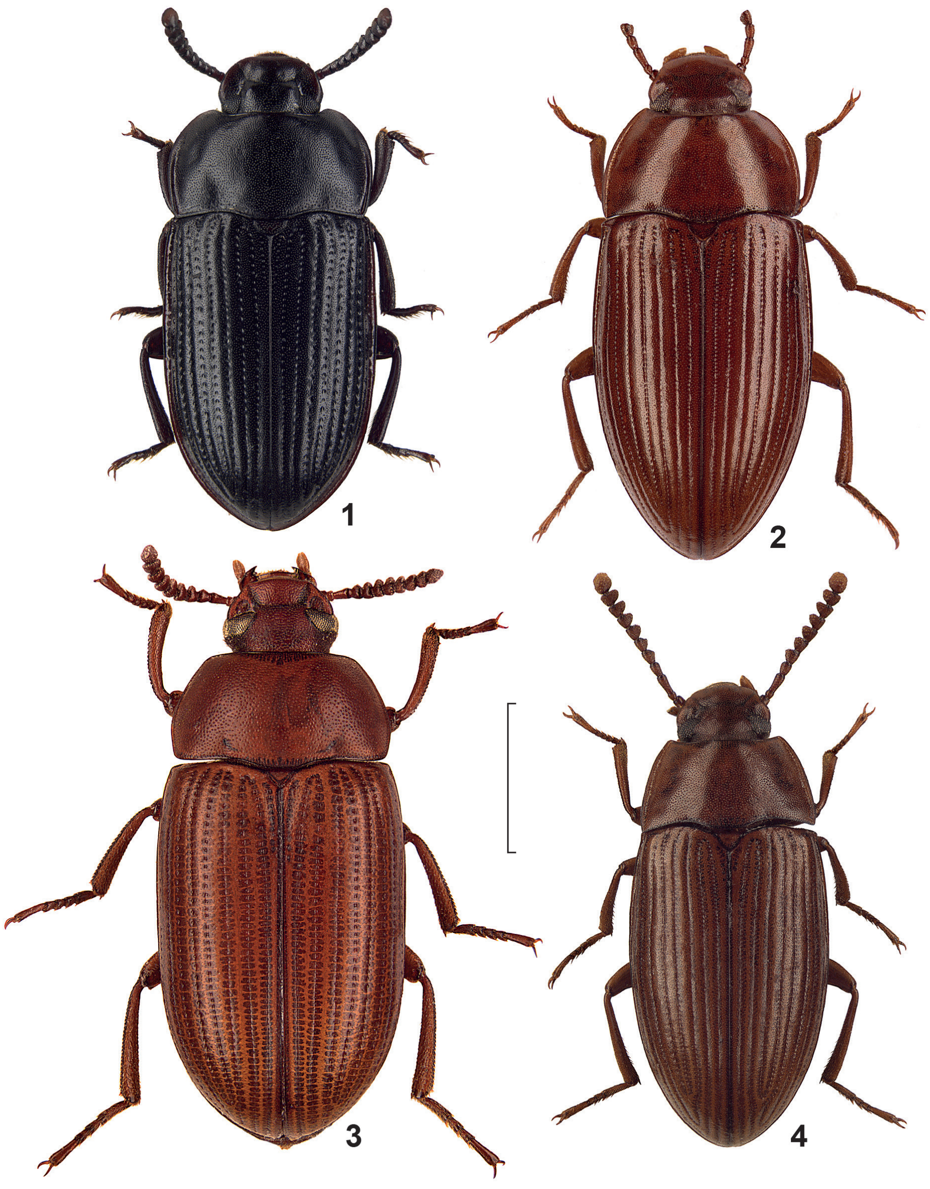
Alphitobius ulomoides Koch, 1953 (homonym, not *Cryptops ulomoides* Solier, 1851, syn. n.)

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

New material. Somalia, Car-Car Mts., IX.1959, leg. C. Koch, 2 ex. TMSA (det. Ferrer). – Somalia, Gardo, 810 m, 22.X.1957, leg. G. Scortecci, 1 ex. TMSA. – Kenya, Witu, Lamu, Wangi, without date, leg. G. Denhardt, 1 ex. ZSM, 3 ex. MNB (det. Bremer). – Tanzania, Mgorogoro Prov. 10 km N Mikumi, 11.I.2007, leg. F. Kantner, 1 ex. SMNS.

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.



Figures 1–4. Dorsal view of African species of the genus *Alphitobius* and *Ulomoides*. **1** *A. crenatus*, non-type Madagascar, SMNS **2** *A. lamottei*, non-type Central African Republic, SMNS **3** *Ulomoides basilewskyi* comb. n., holotype, MRAC **4** *A. arnoldi* nom. n., non-type Tanzania, SMNS. Scale: 2 mm.

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).

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

Type specimens. Holotype male: Kenya, Samburu Nature Reserve, Samburu River Lodge, 28.III.1988, leg. R. Grimm, CRG.

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, sutural 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 punctation 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.

New material. Madagascar, no further data, 2 ex. TMSA. – Madagascar, Ambaton, no further data, 1 ex. SMNS. – S Madagascar, Midongy, no further data, 3 ex. SMNS. – C Madagascar, Katsepy (Majunga), 24.–31.XII.1997, leg. P. Pacholátko, 1 ex. SMNS. – Madagascar, Antananarivo Distr., Moramanga, 12.II.1995, leg. I. Jeniš, 1 ex. ZSM. – Madagascar, Toliaro Prov., Andohahela NP, Forêt d'Ambohibory, 300 m, 16.–20.I.2002, leg. Fisher, Grifswold et al., 1 ex. CRA. – Madagascar, Toliaro Prov., Cap Sainte Marie, 200 m, 11.–15.II.2002, leg. Fisher, Grifswold et al., 3 ex. CRA. – Madagascar, Toliara Prov., Forêt de Tsinjoriaky, 70 m, 6.–10.III.2002, leg. Fisher, Grifswold et al., 1 ex. CRA. – Madagascar, Toliara Prov., Tsimanampetsotsa NP, 25 m, 18.–22.III.2002, leg. Fisher, Grifswold et al., 1 ex. CRA.

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.

New material. Somalia, Genale, 1935, leg. R. Ciferri, 3 ex. TMSA. – Sudan, Mt. Sangha, no further data, leg. Škulina, 1 ex. NMP. – Sudan, Wad Medani, 21.XII.1952, leg. W. Büttiker, 1 ex. TMSA. – Ghana, Ashanti Region, Kumasi, Nhiasu, 16.V.1987, leg. S. Endrödy-Younga, 1 ex. TMSA. – Nigeria, Ile-Ife, 7.VII.1988, leg. F.-T. Krell, 10 ex. SMNS. – Liberia, Bong Town, 23.III.1988, leg.

F.-T. Krell, 3 ex. SMNS. – Ivory Coast, Adiopodoumé, 11.V.1988, leg. F.-T. Krell, 8 ex. SMNS. – Cameroon, Buea, 11.II.1980, leg. H. Schmalfuss & M. Schlegel, 6 ex. SMNS. – Guinea, Kouroussa, 16.XI.1995, leg. U. Lange, 1 ex. SMNS. – Congo, Tshuapa, Flandria, 1946/1947, leg. P. Hulstaert, 3 ex. TMSA. – Uganda, Kampala, V.1927, leg. H. Hargreaves, 1 ex. TMSA (det. Bryant). – Kenya, no further data, leg. Škulina, 1 ex. NMP. – Kenya, Voi (Tsavo), 8.–10.XI.1996, leg. M. Snížek, 1 ex. CRG. – Zambia, 30 km NE Livingstone, 1.XI.2002, leg. F. Wachtel,1 ex. CRG. – Zambia, 30 km NW Sesheke, 13.I.2010, leg. P. Schüle, 1 ex. SMNS. – Zambia, Western Prov., 7.6 km S Ushaa, 1050 m, 2.XII.2010, leg. F. Génier, 1 ex. CNC. – Angola, Cunene Prov., 10 km N Humbe, 3.XI.2011, leg. P. Schüle, 1 ex. SMNS. – Angola, Oshikoto Prov., 9 km S Ondangwa Nakambale Museum, 25.XI.2012, leg. P. Schüle, 1 ex. SMNS. – Namibia, Abachaus, XII.1949, leg. G. Hobohm, 1 ex. TMSA. – Namibia, Kaokoveld, 13 km W Ehombe Mt., 11.II.1975, leg. S. Endrödy-Younga & Schulze, 1 ex. TMSA. – Namibia, Etosha NP, Halali, 16.–17.XII.1993, leg. M. Uhlig, 1 ex. MNB. – NW Namibia, Epupa Falls, 660 m, 11.–12,.IV.2005, leg. W. Schawaller, 1 ex. SMNS. – S Namibia, Naukluft Park East, 1500 m, 7.–10.II.2010, leg. W. Schawaller, 1 ex. SMNS. – Botswana, Okavango, Maxwee Lagoon, VIII.1976, leg. Russel-Smith, 1 ex. TMSA. – South Africa, Northern Cape, Pofadder, 760 m, 4.X.1990, leg. W. Wittmer, 1 ex. NHMB. – South Africa, Limpopo, Krüger NP, 18.VI.1990, leg. L. Braack, 3 ex. TMSA. – South Africa, Limpopo, Amatola Farm NE Vivo, 1000 m, 15.–17.XII.2003, leg. W. Schawaller, 4 ex. SMNS. – South Africa, Gauteng, Pretoria Distr, Roodeplat, 8.–10.X.1960, leg. Neubecker, 1 ex. TMSA. – South Africa, Gauteng, Ezemvelo NR, 26.I.2004, leg. TMSA staff, 3 ex. TMSA. – South Africa, KwaZulu-Natal, Hluhluwe, 29.XI.1992, leg. S. Endrödy-Younga, 1 ex. TMSA. – South Africa, KwaZuluNatal, Ndumo, 21.XI.2002, leg. J. Harrison & R. Müller, 1 ex. TMSA. – South Africa, KwaZulu-Natal, Kosi Bay NR, 11.–17.XI.2002, leg. W. Schawaller, 1 ex. SMNS. – South Africa, Free State, Farm Abel 52, 4 km E Parys, 12.–13.I.1992, leg. M. Krüger, 6 ex. TMSA. – South Africa, Northern Cape, 70 km S Olifantshoek, Witsand NR, 1200 m, 4.–7.II.2012, leg. W. Schawaller, 2 ex. SMNS. – Madagascar, Kirindy Forest, 21.XI.1998, leg. R. Müller, 2 ex. TMSA. – Madagascar, Tsaratanana, Antsirasira, Morwato West, 26.XI.–3.XII.2001, leg. V. Dolin, 1 ex. SMNS. – Rodrigues Island, Anse aux Anglais, Port Mathurin, 22.IX.1995, leg. R. Fricke, 4 ex. SMNS.

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

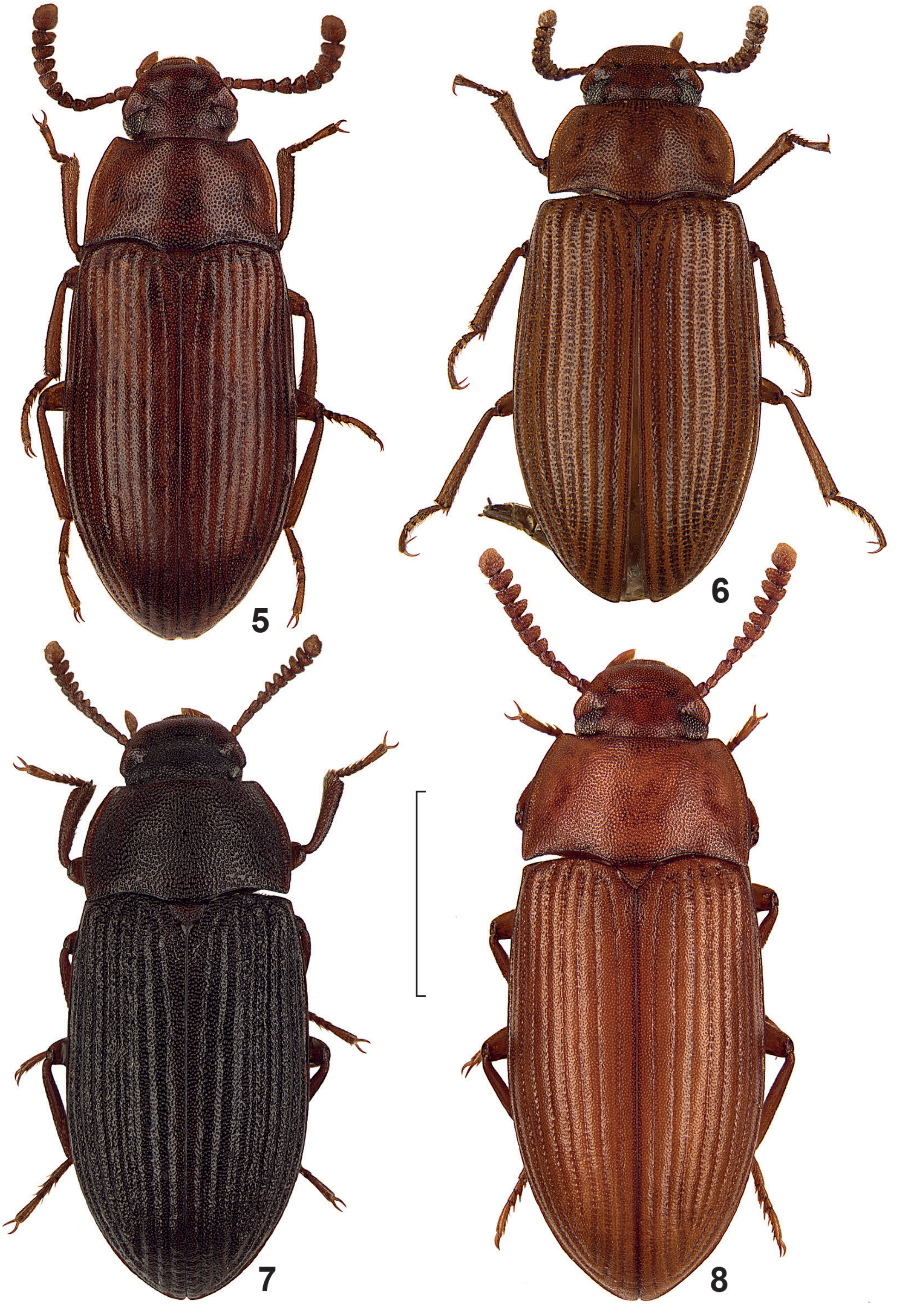
Alphitobius rufus Ardoin, 1976, syn. n.

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.

New material. Ethiopia, Hararge Prov., Bisidimo, 1500 m, V.–VII.1984, leg. V. Meyer, 2 ex. ZSM. – Kenya, Meru Distr., Materi (Mitunguu), 800 m, 8.IV.1987, leg. R. Mourglia, 1 ex. SMNS (*rufus* det. Bremer). – Kenya, Meru Distr., Mojwa, 1300 m, 3.IV.1987, leg. R. Mourglia, 1 ex. ZSM (*rufus* det. Bremer). – Tanzania, Moschi, no further data, 1 ex. ZSM. – Tanzania, Manyara Lake, XII.1961, leg. H. & B. Frey, 1 ex. NHMB. – Namibia, Windhuk, 1906, leg. F. Kunze, 1 ex. MNB (det. Ferrer). – Angola, Blé Prov., Chissamba Mission Station, 1440 m, 9.XI.2011, leg. R. Müller, 1 ex. TMSA. – Angola, Huila Prov., 10 km SW Cacula, 1550 m, 4.–6.XI.2011, leg. R. Müller & P. Schüle, 1 ex. TMSA, 3 ex. SMNS. – Angola, Huila Prov., 15 km S Caluquembe, 1620 m, 6.XI.2011, leg. R. Müller, 1 ex. TMSA. – Angola, Huila Prov., 3.5 km SW Negola, 8.XII.2012, leg. P. Schüle, 2 ex. SMNS, 2 ex. CRG. – South Africa, Limpopo, Naboomspruit, Torino Ranche, 15.I.1990, leg. S. Endrödy-Younga, 1 ex. TMSA. – South Africa, Limpopo, 10 km N Modimolle (Nylstroom), 1300 m, 10.XII.2008, leg. R. Müller, 1 ex. TMSA. – South Africa, Free State, Bothaville, Vaal River, 16.I.2003, leg. M. Snižek, 1 ex. SMNS. – South Africa, KwaZulu-Natal, SW Magudu, 4.–5.I.2009, leg. R. Müller & P. Schüle, 2 ex. SMNS, 2 ex. TMSA. – South Africa, KwaZulu-Natal, Ndumo NR, 100 m, 10.XII.2010, leg. R. Müller, 1 ex. TMSA.

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*.



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.

New material. Tanzania, Tabora, leg. Holtz, 1 ex. MNB (det. Bremer as *A. leleupi*). – Zambia, Western Prov., 3.8 km E Namushakende, 1100 m, 29.XI.2010, leg. F. Génier, 1 ex. CNC. – Zambia, Western Prov., 7 km S Mukokwa, 1100 m, 1.XII.2010, leg. F. Génier, 1 ex. CNC, 1 ex. SMNS. – Botswana, Okavango, Thamalakane, XII.1973, leg. P. Reavel, 1 ex. CRG. – Botswana, Chizwina, Francistown-Mosetse, 5.V.1995, leg. J. Harrison, 1 ex. SMNS. – Namibia (labelled as S. W. Africa), 3 miles NE Waterberg, 1420 m, 21.XII.1966, leg. E. S. Ross & K. Lorenzen, 1 ex. CRA. – Namibia (labelled as S. W. Africa), Okahandja, Farm Okaundua, 21.–29.XI.1933, leg. W. Krieg, 1 ex. NHMB. – South Africa, Northwest Prov., Bloemhof, 24.IV.1961, leg. F. Zumpt, 2 ex. NHMB. – South Africa, Kalahari Gemsbok Park, Nossob River, V.1956, TMSA Expedition, 12 ex. TMSA, 2 ex. SMNS. – South Africa, Kalahari Gemsbock Park, Mata-Mata, 18.XII.1974, leg. S. Endrödy-Younga, 1 ex. TMSA. – South Africa, Limpopo, Waterberg, Geelhoutbush Farm, 3.X.1995, leg. S. Endrödy-Younga & C. Bellamy, 2 ex. TMSA. – South Africa, Northern Cape, Garies, 14.XI.1948, leg. C. Koch, 1 ex. TMSA. – South Africa, Northern Cape, Witsand NR, 1160 m, 5.II.2012, leg. R. Müller, 1 ex. TMSA. – South Africa, Eastern Cape, Willowmore, I.1954, leg. F. Zumpt, 7 ex. NHMB, 2 ex. SMNS.

Type locality. "Willowmore".

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

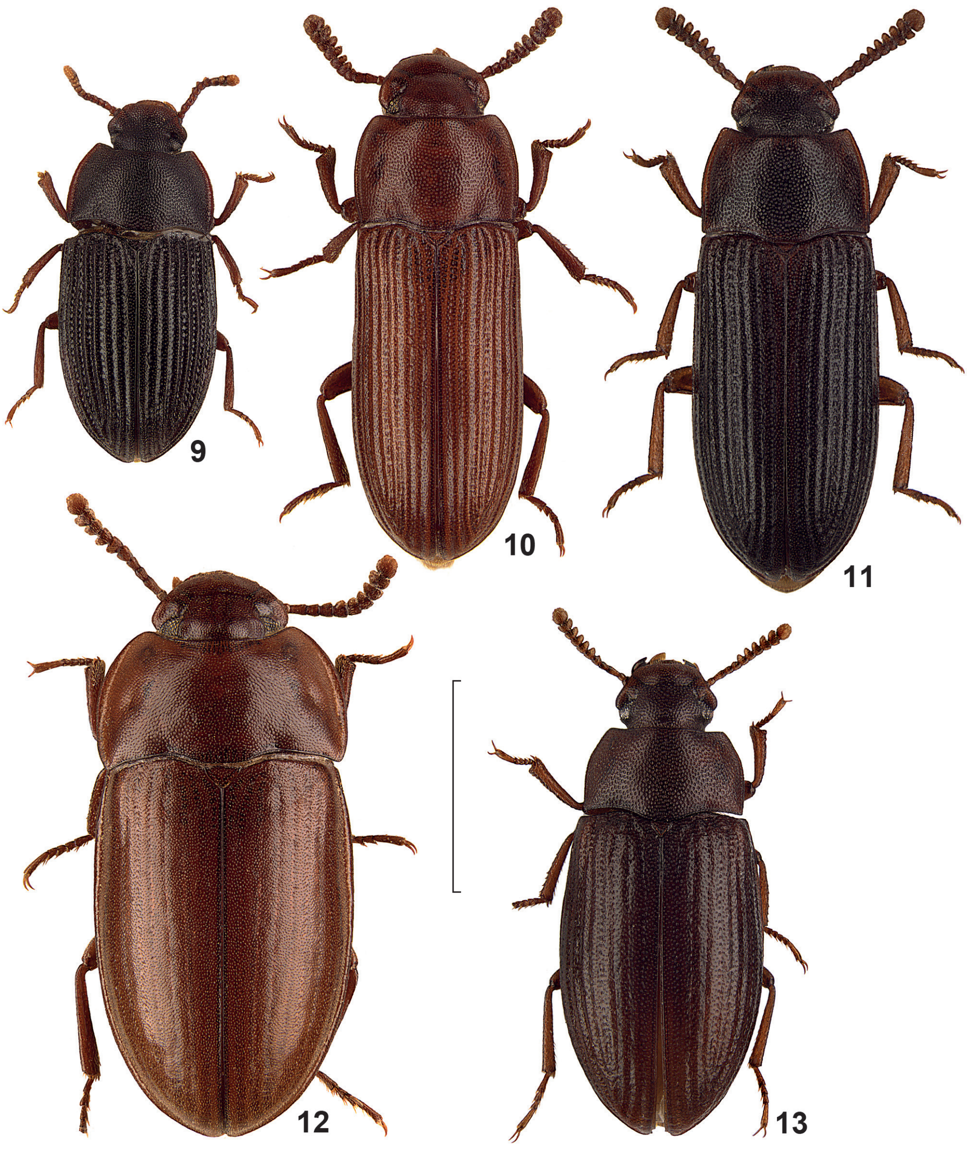
Alphitobius kochi Ardoin, 1958

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



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.

miles SE Touba, 420 m, 20.VIII.1966, leg. E. S. Ross & K. Lorenzen, 12 ex. CRA, 2 ex. SMNS. – Liberia, Cari Suakoko, 17.III.1988, leg. F.-T. Krell, 1 ex. SMNS. – Togo/ Ghana, border area, Brou fou, 27.X.1984, leg. K. Erber, 1 ex. SMNS.

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.

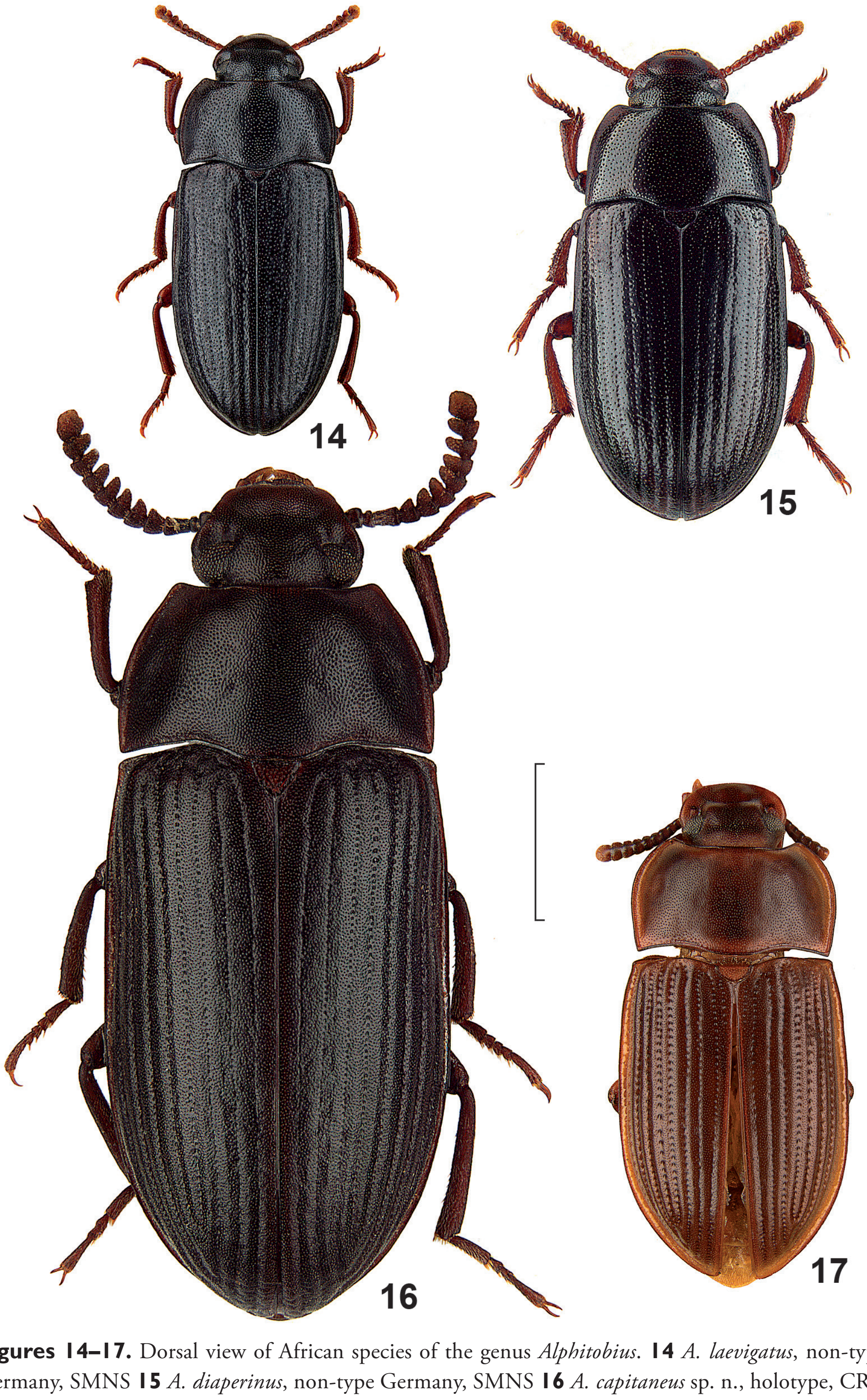
New material. Somalia, Eil (Nogal), III./IV.1938, leg. S. Venzo, 1 ex. TMSA. – Niger, Maradi, 5.–7.VIII.1981, leg. R. Grimm, 1 ex. CRG. – Niger, Niamey, 9. –14.VIII.1989, leg. R. Grimm, 2 ex CRG. – Ghana, Ashanti Region, Kumasi, Nhiasu, 16.V.1967, leg. S. Endrödy-Younga, 1 ex. TMSA. – Cameroon, Longji, 1905, leg. H. Paschen, 1 ex. MNB. – Cameroon, Sasse-Buea, IV.–V.1951, collector unknown, 1 ex. CRA. – Congo, Oubangui-Chari, no further data, leg. Škulina, 1 ex. NMP. – Kenya, no further data, leg. Škulina, 1 ex. NMP. – Tanzania, Daressalam, Pangani, about 1930, leg. R. Regner, 6 ex. MNB. – Tanzania, Pangani to Tanga, VI.1891, leg. Conradt, 2 ex. MNB. – Tanzania, Massa to Tanga, 14.VII.–6.VIII.1891, leg. Conradt, 3 ex. MNB. – Madagascar, Fianarantsoa Prov., Ranamafona, 29.XI.–2.XII.1995, leg. I. Jeniš , 1 ex. CRG. – Madagascar, Ambovombe Distr., Faux Camp, I.1956, leg. C. Koch, 2 ex. TMSA. – Namibia, Fish River Canyon, Ai-Ais, 250 m, 19.XI.1993, leg. M. Uhlig, 1 ex. MNB. – South Africa, Limpopo, Krüger NP, Skukuza, 29.I.1994, leg. S. Endrödy-Younga, 1 ex. TMSA. – South Africa, Limpopo, Krüger NP, Skukuza, 8.–22.XII.2009, leg. J. Harrison, 2 ex. TMSA. – South Africa, Limpopo, Krüger NP, Skukuza, VIII.1992, leg. L. Braack, 10 ex. TMSA. – South Africa, Gauteng, Pretoria, 28.XI.1999, leg. B. Dombrowsky, 1 ex. TMSA. – South Africa, Cape Town, 1965, leg. Dickson, 2 ex. TMSA.

Type locality. "Noua Zelandia".

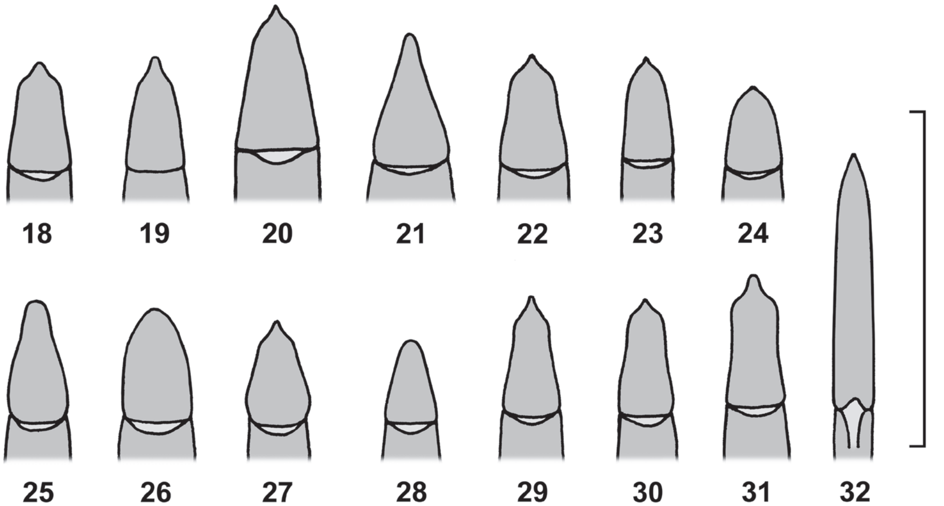
Distribution. Cosmopolitan.

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

New material. Ivory Coast, Bingerville, V.1962, leg. J. Decelle, 1 ex. NHMB. – Guinea, Gbakoré, XII.1983, leg. C. Girard, 2 ex. TMSA (det. Bremer). – Guinea, Mt. Nimba, Keoulenta, 12.I.1984, leg. C. Girard & M. Lamotte, 1 ex. TMSA (det. Bremer). – The Gambia, Kabafita Forest Park, 19.VII.2000, leg. R. Grimm, 1 ex. CRG. – Central African Republic, 35 km E Ndele, 450 m, 18.V.2009, leg. J. Halada, 1 ex. SMNS.



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.



Figures 18–32. Apicale of aedeagus of African species of the genus *Alphitobius* and *Ulomoides*. **18** *A. acutangulus*, non-type Sudan, SMNS **19** *A. arnoldi* nom. n., non-type Tanzania, SMNS **20** *A. capitaneus* sp. n., holotype, CRG **21** *A. crenatus*, non-type Madagascar, SMNS **22** *A. diaperinus*, non-type Zambia, SMNS **23** *A. hobohmi*, non-type Angola, SMNS **24** *A. karooensis*, non-type Botswana, SMNS **25** *A. kochi*, non-type Ivory Coast, SMNS **26** *A. laevigatus*, non-type Nepal, SMNS **27** *A. leleupi*, non-type Congo, SMNS **28** *A. lucasorum*, paratype, SMNS **29** *A. parallelipennis*, non-type Zambia, CRG **30** *A. rugosulus*, non-type Tanzania, SMNS **31** *A. viator*, non-type Zambia, CRG **32** *Ulomoides basilewskyi* comb. n., holotype, MRAC. Scale: 1 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).

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.

New material. Angola, Huila Prov., 75 km N Kaconda, 1640 m, 10.XI.2011, leg. R. Müller, 1 ex. TMSA. – Angola, Huila Prov., 10 km S Kacula, 1560 m, 12.–13. XI.2011, leg. R. Müller & P. Schüle, 1 ex. TMSA, 1 ex. SMNS. – Angola, Huila Prov., 15–20 km S Caluquembe, 6.–7.XI.2011, leg. R. Müller & P. Schüle, 2 ex. TMSA, 2 ex. SMNS. – Angola, Huila Prov., 3.5 km SW Negola, 8.XII.2012, leg. P. Schüle, 2 ex. SMNS. – Zambia, 150 km S Kasemba, 11.XI.2002, leg. F. Wachtel, 11 ex. CRG. – Zambia, 40 km NE Livingstone, Mabula Camp, 14.XI.2002, leg. F. Wachtel, 1 ex. CRG. – Zambia, Lusaka, Kafue River, 1200 m, 22.XI.–2.XII.1987, leg. R. Mourglia, 4 ex. ZSM. – Zambia, Northern Prov., Chipona Falls, 30 km S Chinsali, 5.–6. XII.2002, leg. F. & L. Kantner, 1 ex. SMNS. – Zambia, Copperbelt Prov., NW Kapiri Mposhi, 8.XII.2002, leg. F. & L. Kantner, 1 ex. SMNS. – Zambia, Central Prov., 25 km NE Lilemone, 1250 m, 5.XII.2010, leg. F. Génier, 6 ex. CNC. – Zambia, Lusaka Prov., 9 km E Mulalika, 1100 m, 24.XI.2010, leg. F. Génier, 1 ex. CNC. – South Africa, Limpopo, Krüger NP, Shingwedzi, 19.–20.XI.1961, leg. Vári & Rorke, 1 ex. TMSA. – South Africa, Limpopo (labelled as Transvaal), Manyeleti Game Reserve, 18.XI.1987, leg. T. van Viegen, 1 ex. 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, 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.

New material. Ethiopia, Ambo, 3.XI.1990, leg. L. Medvedev, 1 ex. SMNS. – Sudan, North Dafur, El Geneina, 10.VII.1978, leg. I. Abuzinid, 1 ex. ZSM (det. Kaszab). – Ivory Coast, Bingerville, 1962–1964, leg. J. Decelle, 6 ex. MRAC (det. Ardoin). – Ivory Coast, Kafolo/Comoé, 21.IV.1988, leg. F.-T. Krell, 1 ex. SMNS. – Burkina Faso (labelled as Haute Volta), Ouagadongou, no date, leg. Škulina, 1 ex. NMP. – Guinea, N'Zerekoré, 1.–15.XI.1951, leg. S. H. Olsen, 4 ex. NHMB. – Guinea Bissau, Bolama, VI.–XII.1899, leg. L. Fea, 1 ex. NHMB. – Congo, Tshiobo, N'Goy, 3.–4.VII.1926, leg. A. Collart, 2 ex. TMSA, 1 ex. SMNS. – Central African Republic, Uam, Bosum, IV.–VI.1914, leg. Tessmann, 11 ex. MNB. – Central African Republic, 40 km SW Bandoro, 530 m, 14.IV.2010, leg. Halada, 1 ex. SMNS. – Cameroon, Jaunde, X.1914, leg. Tessmann, 1 ex. MNB. – Kenya (labelled as Afr. or.), Ikutha, no further dates, 7 ex. MNB. – Kenya, Mt. Elgon, eastern slope, 2200 m, 23.–27.III.1988, leg. H. J. Bremer, 1 ex. ZSM. – Tanzania, 2 miles SE Mkomazi, 1500 ft. (460 m), 7.I.1970, leg. M. E. Irwin & E. S. Ross, 1 ex. CRA. – Malawi, Salima, 5.–6.I.2002, leg. J. Bezděk, 1 ex. SMNS. – Zambia (labelled as N Rhodesia), Lochinvar, near Monze, 13.–26.X.1962, leg. F. Zumpt, 3 ex. NHMB. – Zambia, Northern Prov., Chipona Falls, 30 km S Chinsali, 5.–6.XII.2002, leg. F. Kantner, 1 ex. SMNS. – Zambia, 150 km S Kasempa, 11.XI.2002, leg. F. Wachtel, 1 ex. CRG. – Zimbabwe, 60 km N Bulawayo, Maraposa Road, 3.XII.1998, leg. M. Snižek, 1 ex. ZSM. – Botswana, 10 km N Martin's Drift, 7.I.2010, leg. P. Schüle, 1 ex. SMNS. – Angola, Sá da Bandeira, 2.X.1949, leg. B. Malkin, 1 ex. CRA. – Angola, Huambo Prov., 75 km N Caconda near Cuima, 10.–11.XI.2011, leg. P. Schüle, 1 ex. SMNS. – South Africa, Limpopo, Manyeleti Game Reserve, 17.–19.XI.1987, leg. T. van Viegen, 2 ex. TMSA. – South Africa, Limpopo, Naboomspruit, Torino Ranche, 15.I.1990, leg. S. Endrödy-Younga, 1 ex. TMSA. – South Africa, Limpopo, Kruger NP, Skukuza Research Camp, 1.–16.XII.2010, leg. J. Harrison, 1 ex. TMSA. – South Africa, Limpopo, Amatola, Scott Farm, 26.I.1998, leg. R. Müller, 1 ex. TMSA. – South Africa, Limpopo, Thabazimbi, 16.XI.2002, leg. F. Wachtel, 4 ex. CRG. – South Africa, Limpopo, N Makopane (Potgietersrus), Thabaphaspha Farm, 1400 m, 13.–14.XII.2003, leg. R. Müller & W. Schawaller, 1 ex. SMNS, 1 ex. TMSA. – South Africa, Limpopo, Mapungubwe, Little Muck NR, 500 m, 6.–9.XII.2008, leg. W. Schawaller, 1 ex. SMNS. – South Africa, Limpopo, 10 km N Modimolle (Nylstroom), Kuthaba Bush Lodge, 1300 m, 10.–13.XII.2008, leg. W. Schawaller, 2 ex. SMNS. – South Africa, Limpopo, Waterberg, Geelhoutbosch Farm, 15.XII.1997, leg. C. L. Bellamy, 1 ex. TMSA. – South Africa, Limpopo, 15 km NE Klaserie, Guernsey Farm, 18.–30.XII.1985, leg. S. & J. Peck, 1 ex. TMSA. – South Africa, Mpumalanga, Booysendal Farm, 25.X.2000, leg. TMSA staff, 1 ex. TMSA. – South Africa, Gauteng, Tswaing, 17.II.2003, leg. TMSA staff, 1 ex. TMSA. – South Africa, Free State, Bothaville, 15.II.1898, leg. H. Brauns, 5 ex. TMSA. – South Africa, KwaZulu-Natal, SW Magudu, 4.–5.I.2009, leg. P. Schüle, 3 ex. SMNS.

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).

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	***hobohmi***
5	Lateral margins of pronotum rounded towards posterior angles, pronotum widest in the middle or shortly behind the middle	**6**
–	Lateral margins of pronotum subparallel, pronotum widest near base	**10**
6	Elytra without distinct punctural rows, only laterally with traces of punctural rows, elytra with fine microsetation	***acutangulus***
–	Eytra completely with distinct punctural rows, elytra bare or with fine microsetation	**7**

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**
8 Body length 3–4 mm, apicale of aedeagus with rounded tip (Fig. 25) .. ***kochi***
– Body length above 5 mm, apicale of aedeagus with triangular acute tip (Fig. 3) .... ***rugosulus***
9 Internal punctural rows of elytra not impressed, last 5 antennomeres forming a separated club .... ***laevigatus***
– All punctural rows of elytra impressed, last 5 antennomeres not separated from the remaining basal ones .... ***crenatus***
10 Elytra long and narrow, parallel-sided (Figs 10, 11).......... **11**
– Elytra shorter and broader, ovate (Figs 6, 8, 13, 15) **12**
11 Lateral margins of pronotum regularly rounded, anterior corners not prominent, apicale of adeagus with rounded tip (Fig. 28).......... ***lucasorum***
– 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**
13 Dorsal side blackish and shining, base of pronotum unbordered in the middle, apicale of aedeagus shorter (Fig. 22) ....***diaperinus***
– 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).......... ***karooensis***
– Pronotum more flat and with finer separate punctuation, with a feeble transverse impression (Fig. 6) .... ***leleupi***

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* (Gerstaecker, 1871), comb. n.

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

Alphitobius opacus Gerstaecker, 1871
Diaclina opaca (Gerstaecker, 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.

New material. Benin, Kokora, 52 km N Save, 21.VI.2001, leg. F. & L. Kantner, 1 ex. SMNS. – Uganda, Bwamba Forest, 2500 ft. (760 m), III.1948, leg. J. G. Williams, 1 ex. SMNS. – Angola, Huila Province, 20 km S Caluquembe, 6.–7.XI.2011, leg. P. Schüle, 1 ex. SMNS. – Guinea (labelled as French Guinea), Region Kindia, Ségueia, 10.V.1951, leg. J. Bechyné, 4 ex. NHMB, 1 ex. CRG. – SE Cameroon, Lolodorf, leg. L. Conradt, 1895, 1 ex. NHMB. – Tanzania (labelled as Deutsch Ostafrika), [residual label unreadable], 1 ex. NHMB. – Zambia, Ikengele, Nchila Reserve, 6.XI.2002, leg. F. Wachtel, 1 ex. CRG.

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

Remarks. The examination of the type of *Alphitobius opacus* Gerstaecker, 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 Génier (Gatineau, Québec), Claude Girard (Paris), Jiři Hájek (Prague), Bernd Jäger and Manfred Uhlig (Berlin), Antoine Mantilleri (Paris), Marc de Meyer (Tervuren), Ruth Müller (Pretoria), and Eva Sprecher (Basel). Harold Labrique (Lyon) and Martin Lillig (Saarbrücken) kindly sent copies of two old papers. 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

Ardoin P (1958) Nouvelles espèces africaines de Ténébrionides (Col.). Bulletin de la Société entomologique de France 63: 17–31.

Ardoin P (1963a) La réserve naturelle intégrale du Mont Nimba. VII. Coleoptera Tenebrionidae (Troisième note). Mémoirs de l'Institut français d'Afrique noire 66: 221–267.

Ardoin P (1963b) Contribution à l'étude de la faune de la basse Casamance (Sénégal) VI. Bulletin de l'Institut français d'Afrique noire (A) 25: 1374–1387.

Ardoin P (1969) Contribution à la connaissance de la faune entomologique de la Côte-d'Ivoire (J. Decelle, 1961–1964). XXXVII. Coleoptera Tenebrionidae. Annales du Musèe royale de l'Afrique centrale (série Zoologie) 175: 139–285, pls. I–XI.

Ardoin P (1976) Mission entomologique du Musée Royal de l'Afrique Central aux Monts Uluguru, Tanzanie (L. Berger, N. Leleup et J. Debecker, V–VIII.1971), 20. Coleoptera Tenebrionidae. Revue de Zoologie africaine 90: 723–768, pls. VII–X.

Bremer HJ (1985) Eine neue *Alphitobius*-Art (Coleoptera. Tenebrionidae, Ulomini). Entomologische Blätter 81: 62–66.

Bremer HJ, Girard C (1996) L'Entomofaune des Termitières mortes de *Macrotermes*. Occurrence of *Alphitobius lamottei* Ardoin in the chamber of dead termitaries (Coleoptera, Tenebrionidae, Alphitobiini). Revue française d'Entomologie (NS) 18: 135–137.

Fairmaire L (1897) Matériaux pour la faune coléoptèrique de la region malgache, 3e note. Annales de la Société Entomologique de Belgique 41: 92–119.

Fairmaire L (1901) Matériaux pour la faune coléoptèrique de la region malgache, 11e note. Revue d'Entomologie 20: 101–248.

Ferrer J (1983) Seven new species of Tenebrionidae from the Old World (Coleoptera). Entomologica scandinavica 14: 137–144. doi: 10.1163/187631283X00029

Ferrer J (2004) Tenebrionidae (Coleoptera) de Namibia, avec descriptions de 12 espèces nouvelles. Mitteilungen aus dem Museum für Naturkunde Berlin, Zoologische Reihe 80: 181–250. doi: 10.1002/mmnz.20040800204

Gebien H (1921) Die Tenebrioniden Westafrikas. Archiv für Naturgeschichte 86 (1920): 1–256.

Gebien H (1940) Katalog der Tenebrioniden. Teil II. Mitteilungen der Münchener Entomologischen Gesellschaft 30: 1061–1092.

Grimm R (2002) Tenebrionidae von Gambia (Insecta, Coleoptera). Entomofauna 23: 353–380.

Hinton HE (1947) On some new and little-known Indo-Australian Diaperini (Coleoptera, Tenebrionidae). The Annals and Magazine of natural History 14: 81–98.

Koch C (1953) The Tenebrionidae of Southern Africa. III. Tenebrionidae from a nest of *Tatera*. Revue de Zoologie et de Botanique Africaines 47: 1–30.

Matthews EG, Bouchard P (2008) Tenebrionid beetles of Australia. Descriptions of tribes. keys to genera. catalogue of species. Australian Biological Resources Study, Canberra, 398 pp.

Mulsant E, Godart A (1868) Description de deux espèces nouvelles d'*Alphitobius* (Coléoptères de la tribu des Latigenes, famille des Ulomiens). Annales de la Société Linnéenne de Lyon 16: 288–291.

ZooKeys 415: 191–216 (2014)
doi: 10.3897/zookeys.415.6882
www.zookeys.org

RESEARCH ARTICLE

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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

http://zoobank.org/CCC9E426-368A-4C1C-BFB6-8C8517B41E1B

Citation: Cifuentes-Ruiz P, Zaragoza-Caballero S, Ochoterena-Booth H, Morón MA (2014) A preliminary phylogenetic analysis of the New World Helopini (Coleoptera, Tenebrionidae, Tenebrioninae) indicates the need for profound rearrangements of the classification. In: Bouchard P, Smith AD (Eds) Proceedings of the Third International Tenebrionoidea Symposium, Arizona, USA, 2013. ZooKeys 415: 191–216. doi: 10.3897/zookeys.415.6882

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

(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. farctus* (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;

Table 1. Taxon sampling.

	Tribe	Subtribe	Species		Geographic distribution
Ingroup	Helopini	Cylindrinotina	*Nalassus plebejus*	Küster, 1850	Europe, Asia
			Odocnemis californicus	(Mannerheim, 1843)	Mexico, U.S.A.
			Stenomax aeneus	Scopoli, 1763	Europe
		Helopina	*Entomogonus peryronis*	Reiche, 1861	Asia
			Helops aereus	Germar, 1824	U.S.A.
			H. cisteloides	Germar, 1824	U.S.A.
			H. farctus	LeConte, 1858	U.S.A.
			H. inanis	Allard, 1877	Mexico
			H. insignis	Lucas, 1846	North of Africa
			H. perforatus	Horn, 1880	Mexico, U.S.A.
			H. punctipennis	LeConte, 1870	U.S.A.
			H. rossii	Germar, 1817	Europe
			H. rufipes	(LeConte, 1851)	Mexico, U.S.A.
			Probaticus tentyrioides	Küster, 1851	Asia, Europe
			Raiboscelis corvinus	Küster, 1850	Asia, Europe
			Tarpela aerifera	Allard, 1876	Mexico, Central America
			T. browni	Bates, 1870	Nicaragua
			T. contigua	Champion, 1887	Mexico
			T. cordicollis	Marseul, 1876	Japan
			T. costata	Champion, 1887	Mexico, Nicaragua
			T. depressa	Champion, 1887	Mexico
			T. reticulata	Champion, 1887	Honduras
			T. torrida	Champion, 1887	Mexico
		unassigned	*Nautes belti*	Allard, 1877	Central America
			N. enoplopoides	Champion, 1887	Guatemala
			N. fervidus	Pascoe, 1866	Mexico, Central America
			N. magnificus	Champion, 1887	Guatemala
			N. splendens	Champion, 1887	Panama
			N. striatipennis	Champion, 1887	Mexico
			N. varians	Champion, 1887	Mexico
Outgroup	Ulomini		*Uloma mexicana*	Champion, 1886	Mexico, Central America
			Hypogena biimpressa	Champion, 1886	Mexico, Central America, South America
	Tenebrionini		*Tenebrio molitor*	Linnaeus, 1758	global

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.

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, Intituto 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 punctation: (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).

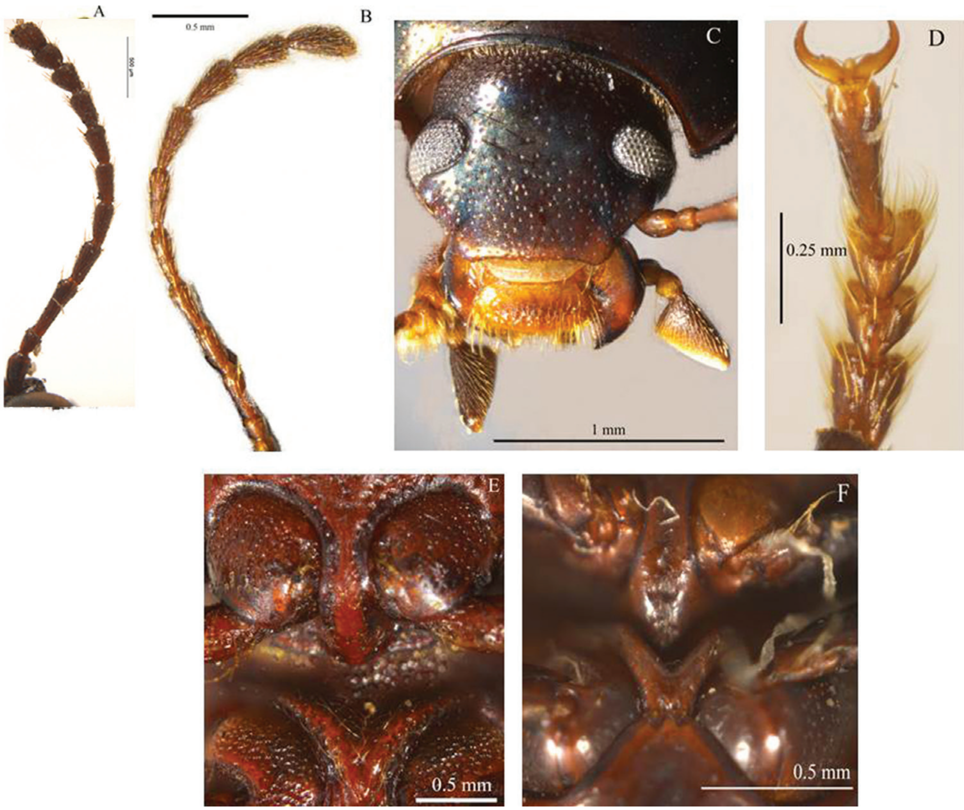

Figure 1. Examples of external characters (mainly diagnostic), traditionally used in *Helops*, *Tarpela* and *Nautes*, (number of character : character state): **A** broad apical antennomere (5:0), shorter than the third antennomere (4:0) illustrated from *Helops aereus* Germar **B** filiform apical antennomeres (5:2), as long as the third antennomere (4:1) illustrated from *Nautes fervidus* Pascoe **C** male maxillary palps with length of inner edge 2.6–2.9 times the length of posterior edge (7:2) illustrated from *Nautes chrysomeloides* Champion **D** third lobate segment of male tarsi (30:0) and short fourth tarsomere (31:0) illustrated from *N. fervidus* **E** not prominent prosternum (27:1) in *Helops cisteloides* Germar **F** prominent-acute prosternum (27:0) in *N. fervidus*.

12. Width of lateral carinae of pronotum: (0) lateral carinae 2-5 times width of anterior carinae; (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).

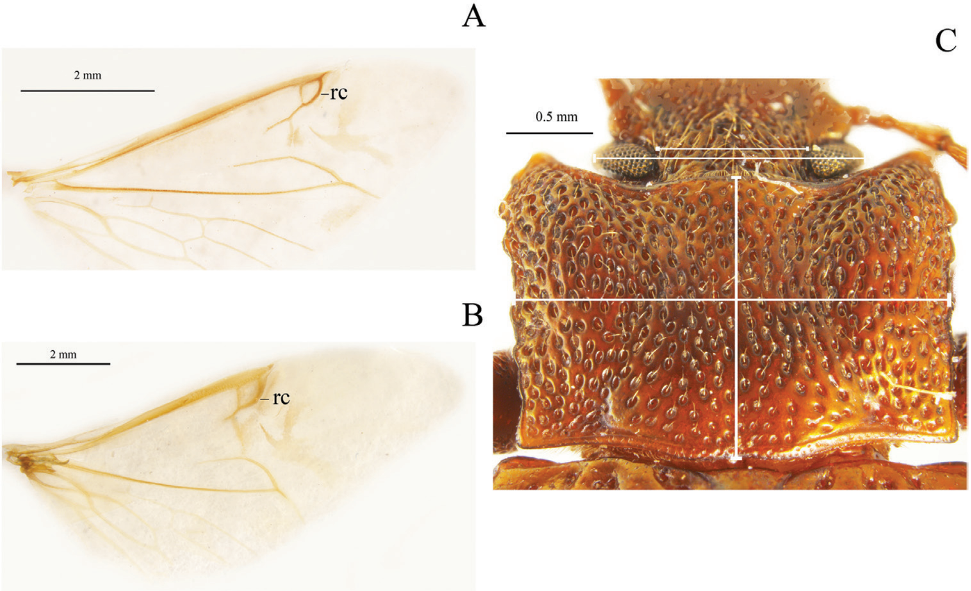

Figure 2. Examples of non-traditional external characters in Helopini: **A** reduced recurrent cell (rc) (26:0) in fully developed wing (25:1) of *Helops californicus* Mannerheim **B** wide recurrent cell (rc) (26:1) in fully developed wing (25:1) of *Tarpela aerifera* Allard **C** head width and interocular 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.

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).

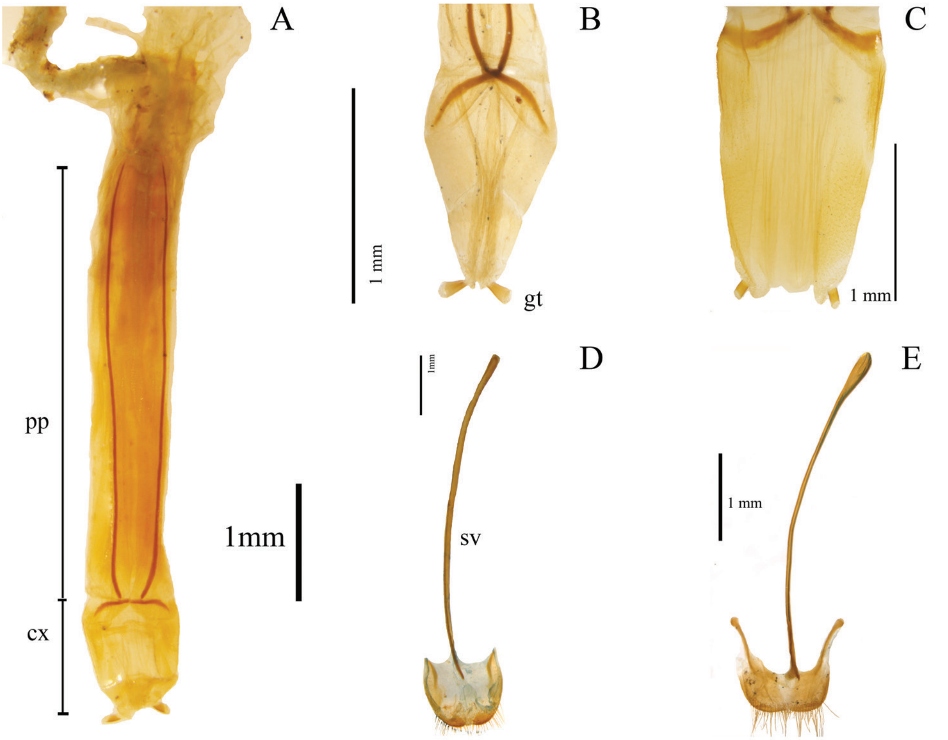

Figure 3. Internal morphological characters (female genitalia) in Helopini: **A** length of paraproct (pp) three or more times length of coxite (cx) (39:0) illustrated from the ovipositor of *Helops cisteloides* Germar **B** long gonostyles (gt) (37:1) with wide apex (38:1), represented by the ovipositor 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.*

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).

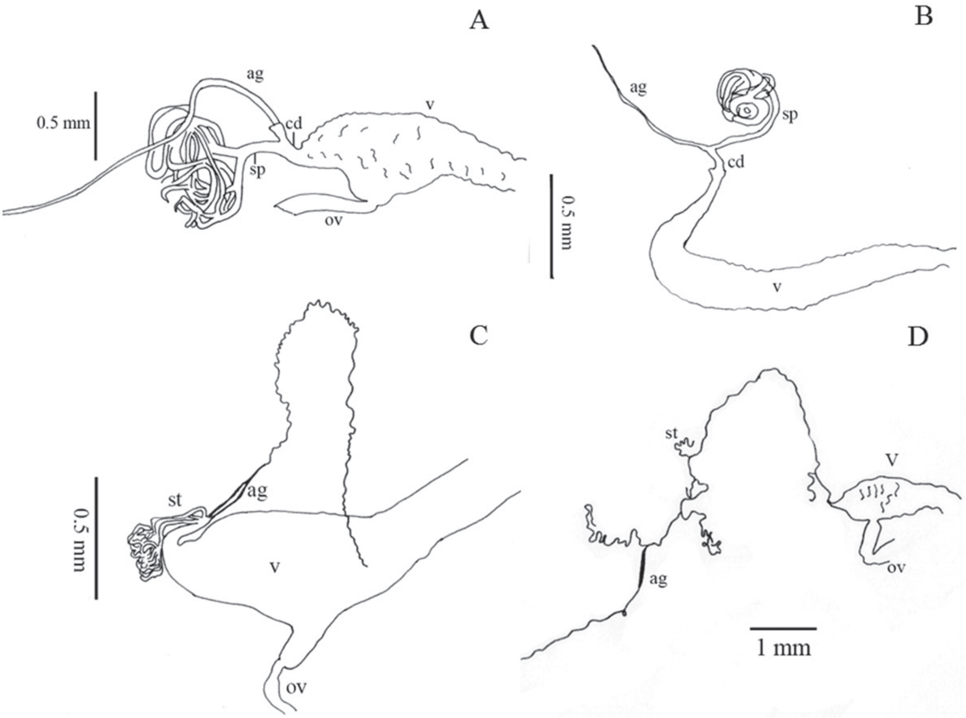

Figure 4. Internal morphological characters (female genitalia) representing the different morphological types found in our sample of Helopini ag= accessory gland, sp= spermatheca, st= spermathecal tube(s), cd= common duct of accessory gland and spermatheca, v= vagina, ov= oviduct: **A** infundibular 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 *Nalassus 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**.

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).

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 sacciform, curved or not at the apex (i.e., at the connection with the spermatheca or common duct) (Fig. 4A–C); (1) sacciform 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 gastral 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 gastral 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).

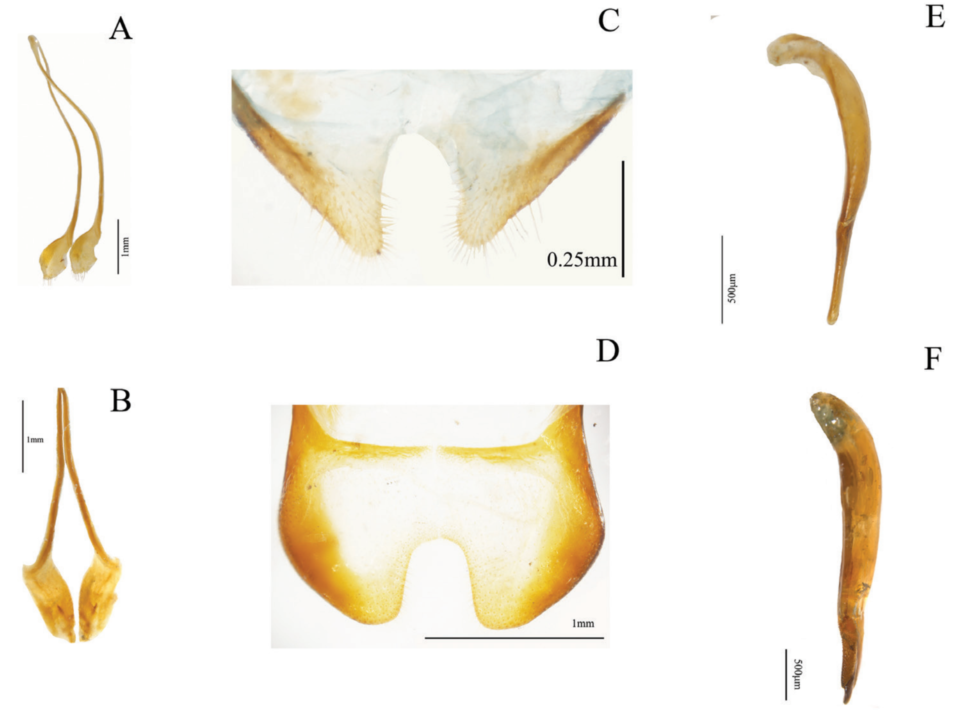

Figure 5. Internal morphological characters (male genitalia) representing the different morphological types found in our sample of Helopini: **A** pleural rods of gastral spicula close only at the end (50:2), representing the nalassoid type (Nabozhenko 2001b, 2002a), illustrated from *Stenomax aeneus* (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 micans* (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 *Odocnemis 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.

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).

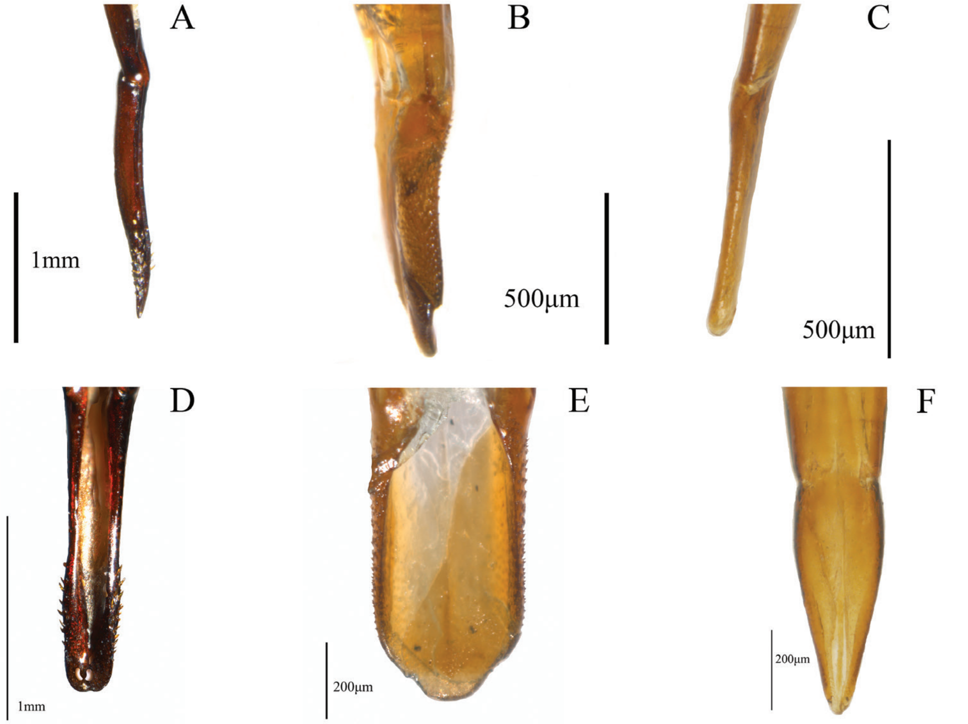

Figure 6. Aedeagal characters (male genitalia) representing the different morphological types found in or sample of Helopini: **A** evident setae (57: 0) representing the helopiod type (Nabozhenko 2001b, 2002a, 2005), distributed over half of the parameres (58: 0), illustrated from *Helops caeruleus* (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 "Synapomophies" 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 Neartic, 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.

Taxon/character					5					10					15					20
Uloma mexicana	1	0	1	1	0	0	0	1	1	0	1	1	1	1	0	1	2	1	0	1
Helops punctipennis	1	1	0	1	3	0	1	1	0	2	0	1	1	1	0	1	2	1	0	1
Entomogonus peyronis	1	1	0	0	0	0	?	1	0	0	0	1	1	2	0	1	0	1	0	1
Raiboscelis corvinus	0	1	0	0	3	0	1	1	0	0	0	1	1	1	3	1	0	1	0	1
Probaticus tentyrioides	1	1	0	0	2	0	2	1	0	1	0	1	1	1	3	1	0	1	0	0
Helops rossii	1	1	0	0	0	0	0	1	0	0	0	1	1	1	0	1	2	1	0	1
Helops insignis	1	1	0	0	3	0	0	1	0	0	0	1	1	1	0	1	2	1	0	1
Helops cisteloides	1	1	0	0	2	0	1	1	0	1	0	1	1	1	0	1	0	1	0	1
Nautes enoplopoides	0	1	0	1	?	0	1	1	2	-	0	1	2	1	0	1	2	0	1	0
Helops perforatus	0	1	0	0	2	0	1	1	0	1	0	1	1	1	0	1	1	1	0	1
Nautes striatipennis	0	1	0	1	1	0	1	1	0	1	0	1	0	1	0	1	2	0	0	1
Helops farctus	0	1	0	1	2	1	1	1	0	1	0	1	0	1	0	1	2	0	0	0
Nautes splendens	0	1	0	1	2	0	2	1	2	2	1	0	0	1	0	1	2	0	1	0
Tarpela browni	1	1	0	1	?	0	1	0	0	0	0	1	0	0	1	0	2	0	0	1
Tarpela torrida	0	1	0	1	2	0	2	1	0	0	1	1	0	1	0	1	2	0	1	1
Nautes magnificus	0	1	0	1	2	0	1	0	1	2	1	0	1	1	1	1	2	0	1	0
Tarpela depressa	0	1	0	0	?	0	1	1	1	2	0	1	1	1	0	1	2	0	1	1
Nautes varians	0	0	0	1	0	0	1	1	0	1	0	1	0	1	0	1	2	0	0	0
Tarpela contigua	0	0	0	1	2	0	2	1	0	1	0	1	1	1	0	1	0	1	0	1
Nautes belti	0	1	0	1	2	0	2	1	1	2	0	1	1	1	0	1	2	0	0	1
Nautes fervidus	0	1	0	1	2	0	?	1	2	2	1	0	0	1	0	1	2	0	1	0
Tarpela aerifera	0	1	0	0	2	0	2	1	1	2	0	1	1	0	0	0	2	0	0	1
Tarpela reticulata	1	1	0	1	2	0	1	0	0	0	0	0	1	0	1	0	2	0	0	1
Helops rufipes	1	1	0	0	0	1	1	1	0	1	0	1	2	2	3	1	0	1	0	1
Helops inanis	0	1	0	0	2	0	0	1	0	2	0	1	1	1	0	1	0	1	0	1
Tarpela costata	0	1	0	0	0	0	1	0	0	0	0	1	1	0	1	1	2	0	0	0
Nalassus plebejus	1	1	0	0	0	0	1	1	1	2	0	1	0	1	0	1	2	0	0	1
Helops aereus	1	1	0	0	0	0	1	1	0	2	0	1	0	1	0	1	2	1	0	1
Odocnemis californicus	1	1	0	0	2	0	1	1	0	2	0	1	1	1	0	1	0	1	0	1
Stenomax aeneus	1	1	0	0	2	0	2	1	0	1	0	1	1	1	0	1	0	1	0	2
Tarpela cordicollis	1	1	0	0	2	0	2	0	1	2	0	1	1	1	0	1	0	1	0	1
Hypogena biimpressa	1	0	1	0	2	1	2	1	1	0	2	0	0	1	0	1	2	1	0	1
Tenebrio molitor	0	0	1	1	0	1	0	1	1	2	1	1	1	2	0	1	2	1	1	1

Helops perforatus Horn, 1880, supported by two internal characters: paraproct three or more times longer than the coxite (39:0) and the presence of a ventral projection at the parameres apex (63:0). *Helops inanis* Allard, 1877 and *Tarpela depressa* Champion, 1887 form a grade with respect to the remaining mostly Neotropical species. There is then a polytomy that includes *Tarpela torrida* Champion 1887, a clade with three *Tarpela* species including the type (*T. browni* Bates, 1870), and another clade that is mostly composed of *Nautes* species and includes all the sampled species of this genus,

Table 2. Continue.

Taxon/character					25					30					35					40
Uloma mexicana	0	0	0	0	1	0	1	1	0	1	1	1	1	0	?	1	0	0	3	0
Helops punctipennis	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	2	0
Entomogonus peyronis	1	1	1	1	0	–	1	1	1	1	1	2	1	1	1	0	1	0	1	0
Raiboscelis corvinus	1	1	1	1	0	–	1	1	1	0	0	2	?	1	1	0	1	0	1	0
Probaticus tentyrioides	1	–	–	1	0	–	1	1	0	0	0	1	1	1	1	0	1	1	1	0
Helops rossii	1	0	1	0	0	–	1	1	1	1	1	1	1	1	1	0	1	0	1	0
Helops insignis	1	0	1	1	0	–	1	1	1	1	1	1	1	1	1	0	1	0	1	0
Helops cisteloides	1	1	1	0	0	–	1	1	0	0	0	2	0	1	1	1	1	0	0	0
Nautes enoplopoides	?	0	1	1	0	–	1	0	1	0	0	2	1	1	1	0	1	1	0	0
Helops perforatus	1	1	1	0	0	1	1	1	1	1	1	2	1	1	1	0	1	1	0	0
Nautes striatipennis	1	0	1	0	1	1	0	0	0	0	0	2	1	1	1	0	1	1	0	0
Helops farctus	1	0	0	0	0	–	1	1	0	0	0	0	1	1	1	0	1	1	1	0
Nautes splendens	0	1	1	0	1	1	0	0	0	0	0	0	1	1	1	?	?	?	1	0
Tarpela browni	?	1	1	0	1	1	1	1	0	0	1	0	1	1	1	0	1	1	0	0
Tarpela torrida	?	1	2	0	1	1	1	1	0	1	1	0	1	1	1	0	1	1	1	0
Nautes magnificus	1	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	1	1	0
Tarpela depressa	0	0	0	0	1	1	1	1	0	1	1	0	1	1	1	0	1	1	1	0
Nautes varians	1	0	0	0	1	1	1	1	0	0	–	0	1	1	1	0	1	1	0	0
Tarpela contigua	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	0	1	?	0	0
Nautes belti	1	0	1	0	1	1	0	0	0	1	0	0	1	1	0	0	1	1	1	0
Nautes fervidus	0	0	1	0	1	1	0	0	0	0	0	0	1	1	1	1	1	1	1	0
Tarpela aerifera	1	1	2	0	1	1	1	1	0	1	0	0	1	1	1	0	1	1	1	0
Tarpela reticulata	?	1	2	0	1	1	1	0	0	1	1	0	1	1	1	0	1	1	0	0
Helops rufipes	0	1	2	1	0	–	1	1	1	1	1	1	0	1	1	0	0	0	1	0
Helops inanis	1	1	1	1	0	–	1	1	1	1	1	1	1	0	1	0	1	1	1	0
Tarpela costata	0	1	2	0	1	1	0	0	1	1	1	2	1	1	1	0	1	1	0	0
Nalassus plebejus	1	0	0	0	1	0	1	1	0	1	1	2	1	0	0	0	1	1	1	1
Helops aereus	1	1	0	0	0	–	1	1	0	1	1	0	1	0	0	0	1	1	1	1
Odocnemis californicus	1	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	1	1	1	0
Stenomax aeneus	0	1	1	0	0	1	1	1	1	0	0	1	1	0	0	0	1	1	1	0
Tarpela cordicollis	1	0	1	0	1	0	1	1	0	1	1	2	1	1	0	0	1	1	1	0
Hypogena biimpressa	0	0	1	0	1	0	1	1	1	1	1	2	1	1	1	1	1	0	2	0
Tenebrio molitor	1	0	0	1	1	1	1	0	1	1	1	2	0	0	1	0	0	1	3	0

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).

Table 2. Continue.

Taxon/character					45					50					55					60
Uloma mexicana	0	0	–	0	1	1	0	1	1	2	0	2	–	–	0	0	1	–	0	0
Helops punctipennis	0	0	–	0	2	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0
Entomogonus peyronis	0	0	–	0	2	0	1	0	1	0	0	?	?	?	1	0	0	0	0	1
Raiboscelis corvinus	0	0	–	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	1
Probaticus tentyrioides	0	0	–	0	1	0	1	0	1	0	0	1	0	0	1	1	0	1	0	1
Helops rossii	0	0	–	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	1
Helops insignis	0	0	–	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	1
Helops cisteloides	0	0	–	0	2	0	1	0	1	0	0	1	0	1	0	0	0	1	0	1
Nautes enoplopoides	1	1	0	1	–	–	1	0	2	0	0	0	1	0	1	1	0	1	1	1
Helops perforatus	1	1	1	0	0	0	1	0	2	1	0	0	0	0	1	1	0	1	0	1
Nautes striatipennis	1	1	0	0	1	0	1	0	2	0	0	0	0	1	1	1	0	1	1	0
Helops farctus	1	1	0	0	1	0	1	0	2	0	0	0	0	1	1	1	0	1	1	0
Nautes splendens	1	1	0	0	1	0	1	0	2	0	0	0	0	1	1	1	0	1	1	0
Tarpela browni	1	1	0	0	1	0	1	0	2	0	0	0	0	0	1	1	0	1	1	1
Tarpela torrida	1	1	0	1	2	0	1	0	2	0	0	0	0	1	1	1	0	1	1	1
Nautes magnificus	1	1	0	0	1	0	1	0	2	0	0	0	0	1	1	1	0	1	1	0
Tarpela depressa	1	1	1	0	0	0	1	0	2	0	–	0	0	0	1	1	0	1	0	1
Nautes varians	1	1	0	0	1	0	1	0	2	0	0	0	0	1	1	1	1	1	1	0
Tarpela contigua	1	1	1	0	0	0	1	0	2	0	0	0	0	0	1	1	0	1	0	1
Nautes belti	1	1	0	0	2	1	1	0	2	0	0	0	0	1	1	1	0	1	1	0
Nautes fervidus	1	1	0	1	–	–	1	0	2	0	0	0	0	1	1	1	0	1	1	0
Tarpela aerifera	1	1	0	1	–	0	1	0	2	0	0	1	0	1	1	1	0	1	1	0
Tarpela reticulata	1	1	0	0	–	0	1	0	2	0	0	0	0	1	0	1	0	1	1	1
Helops rufipes	0	0	–	0	2	0	1	0	1	0	0	0	0	0	1	1	0	1	1	0
Helops inanis	1	1	0	0	1	0	1	0	2	0	0	0	0	1	1	1	1	1	0	1
Tarpela costata	1	1	0	0	1	0	1	0	2	0	0	0	0	1	1	1	0	1	1	1
Nalassus plebejus	0	1	–	0	1	0	0	0	1	1	0	1	0	0	1	1	1	–	0	1
Helops aereus	0	1	–	0	2	0	0	0	1	1	1	1	0	0	1	1	1	–	0	1
Odocnemis californicus	0	1	–	0	2	0	1	0	1	1	1	1	0	0	1	1	1	–	0	1
Stenomax aeneus	0	1	–	0	0	1	1	0	1	2	0	1	0	0	0	0	1	–	0	1
Tarpela cordicollis	0	1	–	0	2	0	0	0	1	1	1	1	1	0	1	1	1	–	0	1
Hypogena biimpressa	0	1	–	1	–	–	1	1	–	2	1	1	0	0	1	0	1	–	0	1
Tenebrio molitor	0	0	–	1	–	–	1	0	0	0	0	0	1	0	0	1	1	–	0	1

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

Table 2. Continue.

Taxon/character					65		
Uloma mexicana	1	2	1	1	1	2	2
Helops punctipennis	0	1	0	1	1	1	1
Entomogonus peyronis	–	0	1	1	0	?	0
Raiboscelis corvinus	–	0	1	1	0	0	0
Probaticus tentyrioides	–	0	1	1	0	0	0
Helops rossii	–	0	1	1	0	0	0
Helops insignis	–	0	1	1	0	0	0
Helops cisteloides	–	0	1	1	0	0	0
Nautes enoplopoides	–	0	1	1	1	1	1
Helops perforatus	–	1	0	1	1	1	1
Nautes striatipennis	1	0	1	1	1	1	1
Helops farctus	0	0	1	1	1	1	1
Nautes splendens	1	0	1	1	1	1	1
Tarpela browni	–	0	1	1	1	0	1
Tarpela torrida	–	0	1	1	1	1	1
Nautes magnificus	1	0	1	1	1	1	1
Tarpela depressa	–	1	0	1	1	1	1
Nautes varians	1	0	1	1	1	0	1
Tarpela contigua	–	1	0	1	1	1	1
Nautes belti	1	0	1	1	1	1	1
Nautes fervidus	1	0	1	1	1	1	1
Tarpela aerifera	1	0	1	1	1	0	1
Tarpela reticulata	–	0	1	1	1	1	1
Helops rufipes	1	1	1	1	1	1	0
Helops inanis	–	1	1	1	1	1	1
Tarpela costata	–	0	1	1	1	0	1
Nalassus plebejus	–	1	1	0	1	0	0
Helops aereus	–	1	1	0	1	0	0
Odocnemis californicus	–	1	1	0	1	0	0
Stenomax aeneus	0	1	1	0	0	0	0
Tarpela cordicollis	1	1	1	0	1	0	0
Hypogena biimpressa	–	0	1	1	0	2	2
Tenebrio molitor	–	0	1	1	1	0	0

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

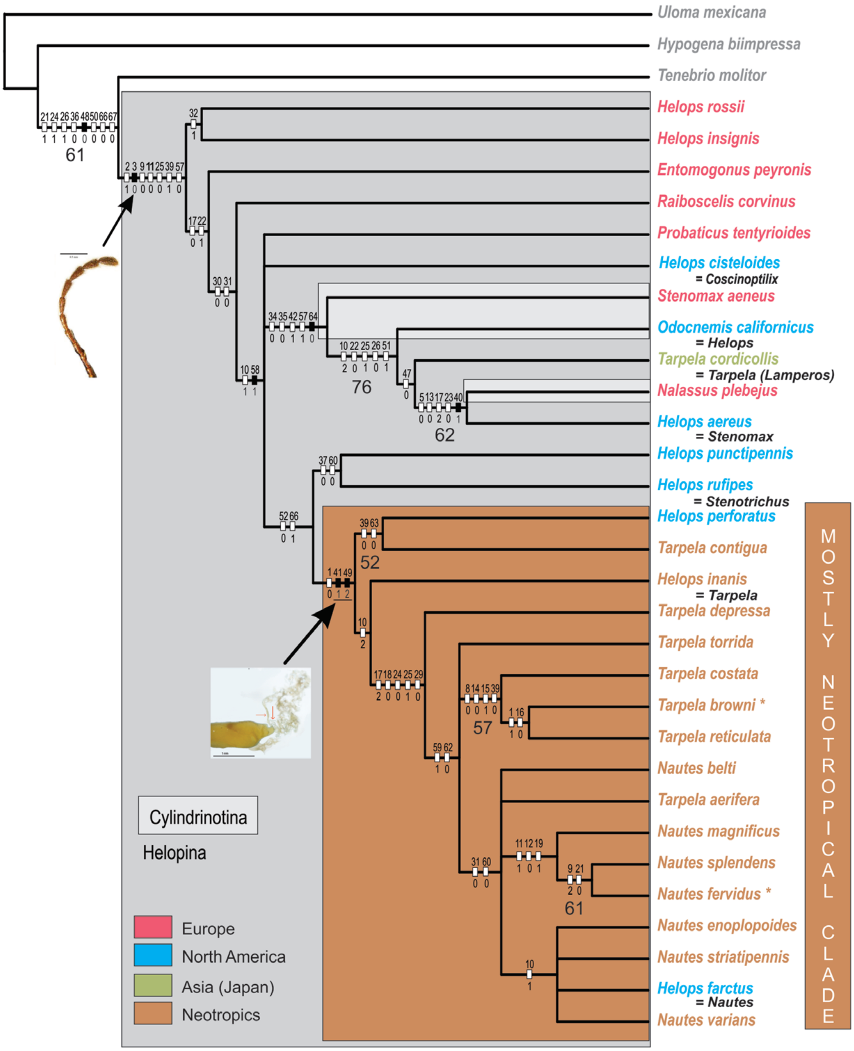

Figure 7. Strict consensus of 12 most parsimonious trees (L= 314; ci=0.28; ri=0.56). Characters are mapped onto the consensus only if their optimization is not ambiguous and if they are present among all the MPTs. The consensus is used to map homoplasy at the level of characters. Black rectangles represent 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 Paleartic 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 Neartic *Helops* (as *H.aereus*). This subtribe would also have to include several Holartic genera (besides *Odocnemis*). The Holarctic 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 Holarctic 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 helopioid, 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

Aalbu RL, Triplehorn CA, Campbell JM, Brown KW, Somerby RE, Thomas DB (2002) Tenebrionidae. In: Arnett RH Jr., Thomas MC (Eds) American Beetles: Polyphaga: Scarabaeoidea through Curculionoidea. Vol. 2. CRC Press, Boca Raton, 496.

Aalbu RL (2005) The pimeliine tribe Cryptoglossini: classification, biology and inferred phylogeny (Coleoptera: Tenebrionidae). Annales Zoologici 55(4): 677–756. http://www.miiz.waw.pl/periodicals/annales-zoologici/abstracts/AZ_55-4abs.pdf

Allard E (1876) Révision des hélopides vrais de Lacordaire. Abeille 14: 1–80.

Allard E (1877) Révision des hélopides vrais. Mittheilungen der Schweizerischen Entomologischen Gesellschaft 5: 13–268.

Antoine M (1947) Notes d'entomologie Marocaine. XLIV. Matériaux pour l'étude des Helopinae du Maroc (Col. Tenebrionides). Bulletin de la Société des Sciences Naturelles du Maroc 27: 123–162.

Bates F (1870) Description of new genera and species of Heteromera. Entomologist's Monthly Magazine 6: 272.

Blackwelder RE (1946) Checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America, Part 3. Bulletin of the United States National Museum 185: 343–550.

Bouchard P, Lawrence JF, Davies AE, Newton AF (2005) Synoptic classification of the world Tenebrionidae (Insecta:Coleoptera) with a review of family-group names. Annales Zoologici 55(4): 499–530. http://www.miiz.waw.pl/periodicals/annales-zoologici/abstracts/AZ_55–4abs.pdf

Brown JH, Lomolino MV (1998) Biogeography. Sinauer, 691 pp.

Champion GC (1887) Biologia Centrali-Americana. Insecta. Coleoptera (Tenebrionidae). Vol. 4, Part 1, 276–320.

Champion GC (1893) Biologia Centrali-Americana. Insecta. Coleoptera (Tenebrionidae). Vol. 4, Part 2, 551–558.

Corel Corporation (2012) CorelDRAW Graphics Suite X6 (v16).

Davis JI, Frohlich MW, Soreng RJ (1993) Cladistic characters and cladogram stability. Systematic Botany 18(2): 188–196. doi: 10.2307/2419396

Doyen JT, Tschinkel WR (1982) Phenetic and cladistic relationships among tenebrionid beetles (Coleoptera). Systematic Entomology 7: 127–183. doi: 10.1111/j.1365-3113.1982.tb00129.x

Doyen JT (1988) Tenebrionidae and Zopheridae of the Chamela Biological Station and vicinity, Jalisco, Mexico (Coleoptera). Folia Entomologica Mexicana 77: 211–276.

Doyen JT (1987) New and little known Tenebrionidae from Central America and Mexico, with remarks on their classification (Coleoptera). Pan-Pacific Entomologist 63(4): 301–318.

Doyen JT (1994) Cladistic relationships among Pimeliinae Tenebrionidae (Coleoptera). Journal of the New York Entomological Society 101(4): 443–514.

Fabricius JC (1775) Systema Entomologiae, sistens insectorum classes, ordines, genera, spcies, adiectis synonymis, locis, descriptionibus, observationibus. Officina Libraria Kortiii, Flensburg and Leipzig, Germany, 832 pp. doi: 10.5962/bhl.title.36510

Flores GE (1996) Estudio comparativo de las estructuras genitales en la tribu Nycteliini (Coleoptera: Tenebrionidae). Revista de la Sociedad Entomológica Argentina 55(1–4): 33–48.

Gebien H (1943) Katalog der Tenebrioniden. Teil III (part). Mitteilungen der Münchener Entomologischen Gesellschaft 33: 404–430.

Goloboff PA (1999) NONA, Version 2.0 (for Windows) http://www.cladistics.com [accessed on 21 October 2012]

Goloboff PA, Farris JS, Nixon KC (2003) T.N.T.: Tree Analysis Using New Technology. Program and documentation, available from the authors, and at http://www.zmuc.dk/public/phylogeny

Horn GH (1870) Revision of the Tenebrionidae of America, north of Mexico. Transactions of the American Philosophical Society 14: 64–404. doi: 10.2307/1005214

Nabozhenko MV (2001a) On the classification of the tenebrionid tribe Helopini, with a review of the genera *Nalassus* Mulsant and *Odocnemis* Allard (Coleoptera, Tenebrionidae) of the European part of CIS and the Caucasus. Entomological Review 81(8): 909–942. http://www.maik.ru/abstract/enteng/1/enteng0909_abstract.pdf

Nabozhenko MV (2001b) Taxonomic notes on the genus *Zophohelops* Reitter, 1901 with description of new species from Tadzhikistan and new genus *Pseudoprobaticus* gen. n. (Coleoptera: Tenebrionidae). Annales Zoologici 51(4): 113–117. http://www.miiz.waw.pl/periodicals/annales-zoologici/abstracts/51_4.pdf

Nabozhenko MV (2002a) Darkling beetles of the tribe Helopini (Coleoptera, Tenebrionidae) of European part of CIS and the Caucasus. PhD dissertation, Zoological Institute of Russian Academy of Sciences, St. Petersburg.

Nabozhenko MV (2002b) Taxonomic significance of the female genital tubes in the tribe Helopini (Coleoptera, Tenebrionidae). In: Proceedings of the XII Congress of the Russian Entomological Society, St. Petersburg (Russia), August 2002, 393 pp.

Nabozhenko MV (2005) Interstructural correlations in the evolution of tenebrionid beetles of the tribe Helopini (Coleoptera, Tenebrionidae). Caucasian Entomological Bulletin 1(1): 37–48. http://ssc-ras.ru/files/files/4_Nabozhenko.pdf

Nabozhenko MV (2006) A revison of the genus *Catomus* Allard, 1876 and the allied genera (Coleoptera, Tenebrionidae). Entomological Review 86(9): 1024–1072. http://www.maik.ru/abstract/enteng/6/enteng1024_abstract.pdf, doi: 10.1134/S0013873806090065

Nabozhenko MV, Löbl I (2008) Tribe Helopini. In: Löbl I, Smetana A (Eds) Catalogue of Palaearctic Coleoptera. Volume 5. Tenebrionoidea. Apollo Books, Stenstrup, 241–257.

Nixon KC (2002) WinClada ver. 1.00.08. http://www.cladistics.com [accessed 21 October 2012]

Papp CS (1961) Checklist of Tenebrionidae of America north of the Panama Canal. Opuscules Entomologiques 26: 97–140.

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

Paulsen MJ (2005) A revision of the southern South American stag beetles of the genus *Sclrerostomus* Burmeister (Coleoptera: Scarabaeoidea: Lucanidae). Zootaxa 1060: 1–26. http://www.mapress.com/zootaxa/2005f/zt01060p026.pdf

Reitter E (1922) Bestimmungstabelle der europäischen Coleopteren, Tenebrionidae, 17. Theil, Unterfamilie Helopinae: 2. Wiener Entomologische Zeitung 39: 113–171.

Rosas MV, Morrone JJ, Del Río MG, Lanteri AA (2011) Phylogenetic analysis of the *Pantomorus-Naupactus* complex (Coleoptera: Curculionidae: Entiminae) from North and Central America. Zootaxa 2780: 1–19. http://www.mapress.com/zootaxa/2011/f/z02780p019f.pdf

Sanmartín I, Enghoff H, Ronquist F (2001) Patterns of animal dispersal, vicariance and diversification in the Holarctic. Biological Journal of the Linnean Society 73: 345–390. doi: 10.1006/bijl.2001.0542

Smith AD, Miller KB, Wheeler QD (2011) A new species of *Stenomorpha* Solier (Coleoptera: Tenebrionidae: Pimeliinae: Asidini) from Cuatrociénegas, Mexico with a key to the *furcata* species group. Zootaxa 2909: 27–37. http://www.mapress.com/zootaxa/2011/f/z02909p037f.pdf

Steiner WE (2006) New species of darkling beetles (Coleoptera: Tenebrionidae) from San Salvador Island, Bahamas. Zootaxa 1158: 1–38. http://www.mapress.com/zootaxa/2006f/z01158p038f.pdf

Tschinkel WR, Doyen JT (1980) Comparative anatomy of the defensive glands, ovipositors and female genital tubes of tenebrionid beetles (Coleoptera). International Journal of Insect Morphology and Embryology 9: 321–368. doi: 10.1016/0020-7322(80)90009-4

ZooKeys 415: 217–268 (2014)
doi: 10.3897/zookeys.415.5887
www.zookeys.org

RESEARCH ARTICLE

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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

http://zoobank.org/287A4DC8-0EFC-42C6-AA55-DBB4D7A3441B

Citation: Smith AD, Dornburg R, Wheeler DD (2013) Larvae of the genus *Eleodes* (Coleoptera, Tenebrionidae): matrix-based descriptions, cladistic analysis, and key to late instar. In: Bouchard P, Smith AD (Eds) Proceedings of the Third International Tenebrionoidea Symposium, Arizona, USA, 2013. ZooKeys 415: 217–268. doi: 10.3897/zookeys.415.5887

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 nigropilosus* LeConte, *Eleodes pilosus* Horn, *Eleodes subnitens* LeConte, *Eleodes tenuipes* Casey, *Eleodes tribulus* Thomas, and *Eleodes wheeleri* Aalbu, Smith & Triplehorn. The larval stage of *Eleodes armatus* 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-standing. 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 subterreanean 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. McColloch (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),

Table 1. Previous publications describing or illustrating *Eleodes* larvae.

Species	Publication	Remarks
Eleodes armatus (LeConte), 1851	Thomas1984	egg, larva, and pupa described, larva and pupa imaged
Eleodes dentipes (Eschscholtz), 1833	Gissler 1878; Blaisdell 1909	Larva briefly described in Gissler (1878); larva redescribed and illustrated in Blaisdell (1909)
Eleodes giganteus (Mannerheim), 1843	Gissler 1878	egg and larva characterized; larva illustrated
Eleodes opacus (Say), 1824	St. George 1924	pygidium imaged; no description
*Eleodes pimelioides (*Mannerheim), 1843	Hyslop 1912	egg, larva, and pupa described; pygidium of larva imaged
Eleodes suturalis (Say), 1824	Wade and St. George 1923	egg, larva, and pupa described, larval natural history discussed, egg and pupa imaged
Eleodes tricostatus (Say), 1824	McColloch 1918; St. George 1924	egg, larva, and pupa briefly characterized, larval natural history discussed; right mandible and pygidium of larva imaged in St. George (1924)
Eleodes vandykei Blaisdell, 1909	Hyslop 1912	egg, larva, and pupa described, egg, larva, and pupa imaged; species listed as *E. letcheri vandykei*

Talamas 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.

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.*

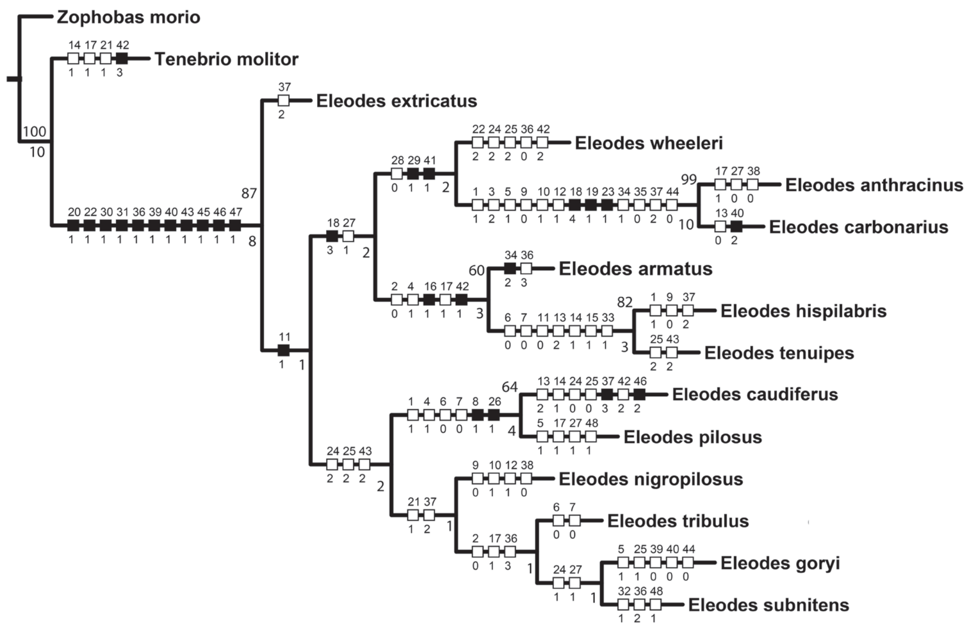

Figure 1. Most parsimonious tree (L=141, CI = 0.5, RI = .53) based on larval morphology. Numbers not associated with rectangles are bootstrap support values (above branches) and Bremer support values (below branches). Smaller numbers above rectangles on branches represent character number; numbers below rectangles represent character state. Black rectangles correspond to non-homoplasious character state changes. White rectangles correspond to homoplasious character state changes. All character states were unambiguously optimized on the tree.

hispilabris + *E. tenuipes*, having moderately punctate clypei (11:1). While 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 tomentose 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 *Promus*. 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 medially. 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.

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.

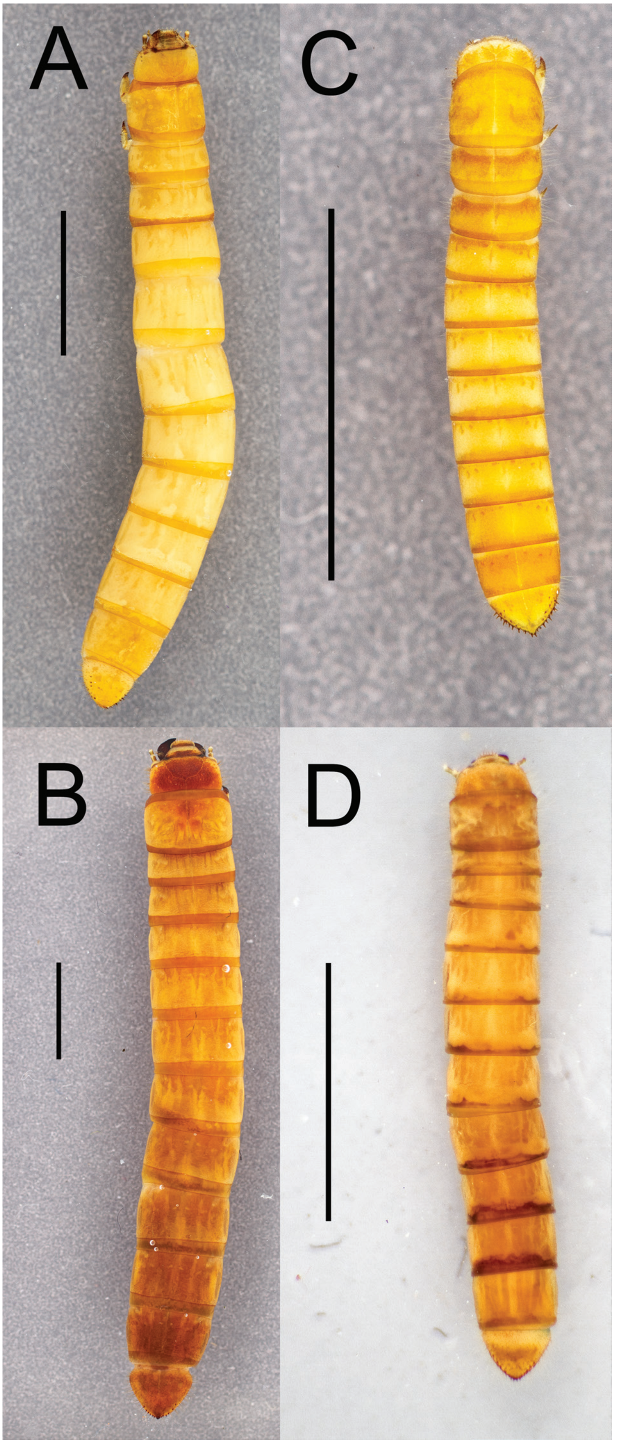

Figure 2. Dorsal habitus of four *Eleodes* species: **A** *E.* (*Caverneleodes*) *wheeleri*; **B** *E.* (*Eleodes*) *armatus* **C** *E.* (*Eleodes*) *caudiferus* **D** *E.* (*Eleodes*) *tribulus*. Scale bar = 5 mm.

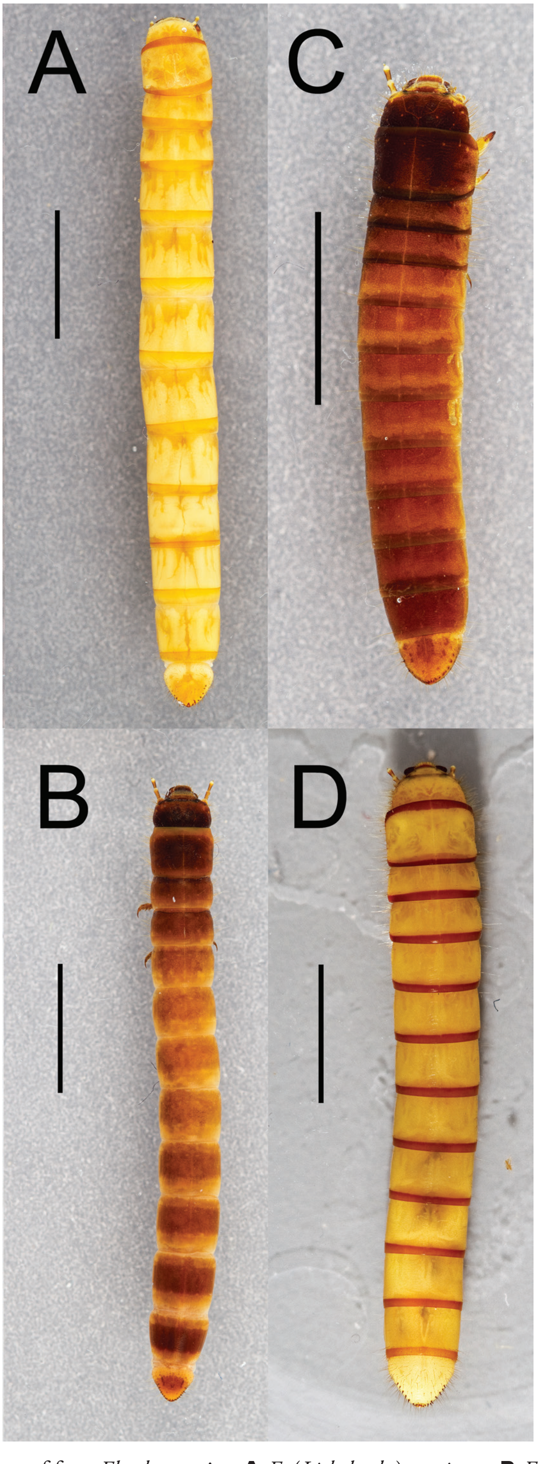

Figure 3. Dorsal habitus of four *Eleodes* species: **A** *E.* (*Litheleodes*) *extricatus* **B** *E.* (*Melaneleodes*) *anthracinus* **C** *E.* (*Melaneleodes*) *carbonarius* **D** *E.* (*Tricheleodes*) *pilosus*. Scale bar = 5 mm.

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; 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 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, punctation 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.

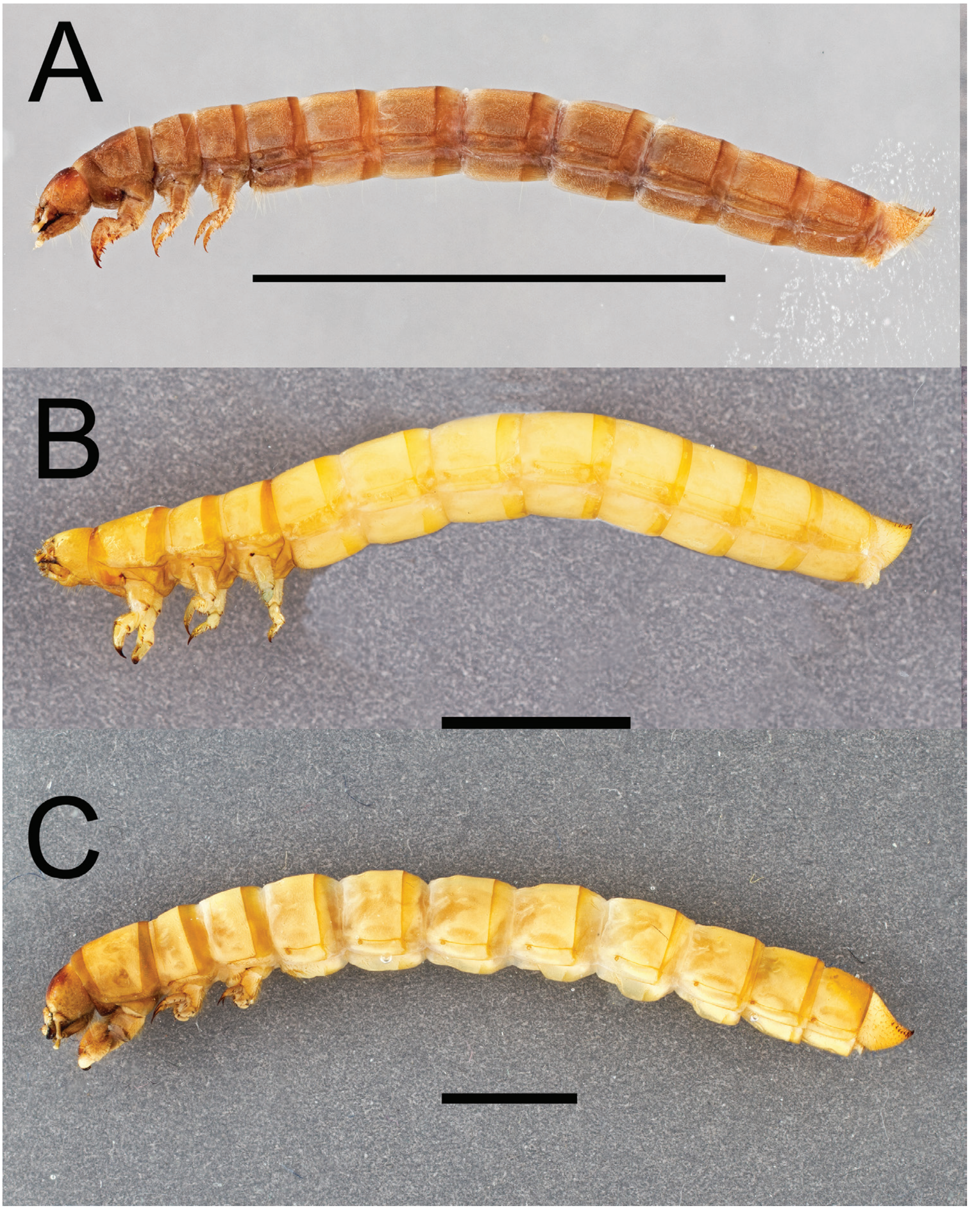

Figure 4. Lateral habitus of three *Eleodes* species: **A** *E.* (*Blapylis*) *nigropilosus* **B** *E.* (*Caverneleodes*) *wheeleri* **C** *E.* (*Eleodes*) *armatus*. Scale bar = 5 mm.

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 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, anterolateral 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; 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 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, punctation 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 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 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 spinose 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 epipharnyx.

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 untill 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; punctation minute,

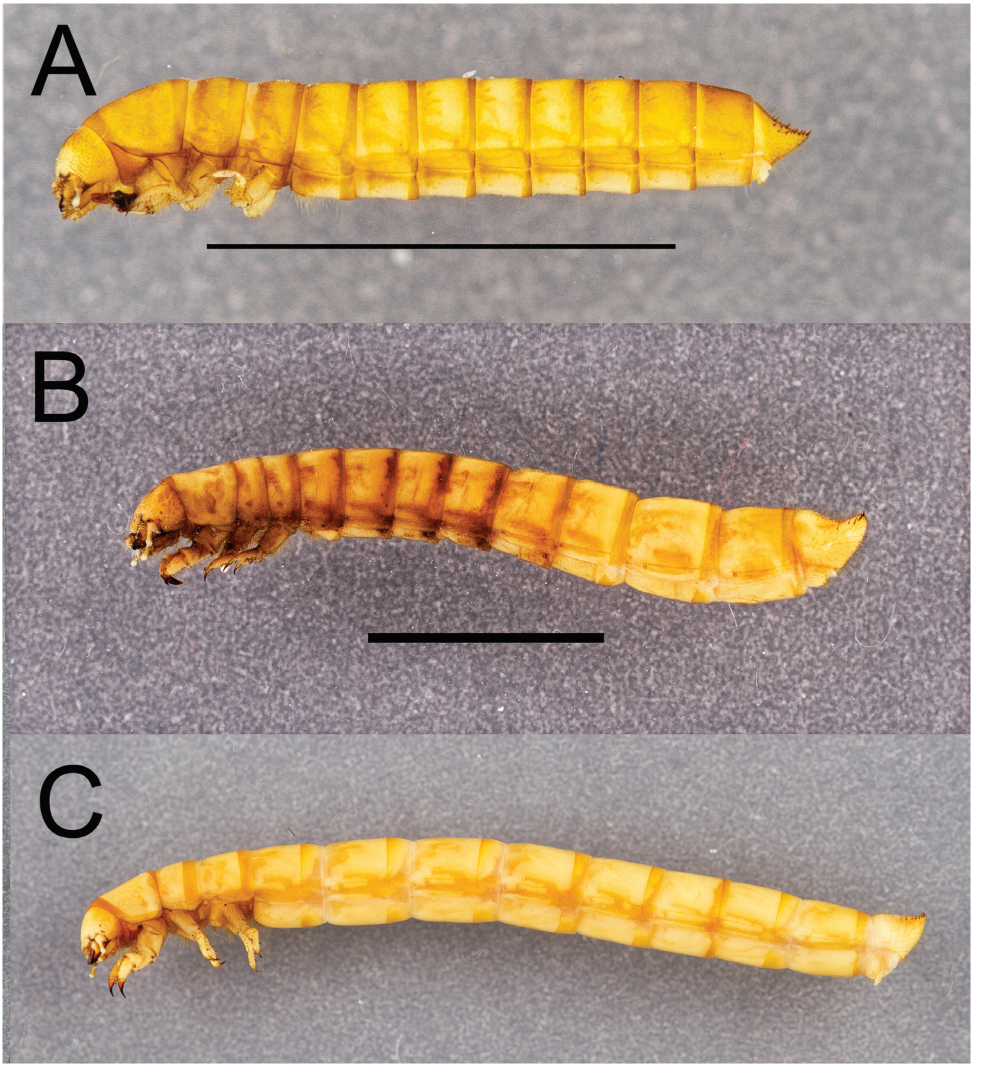

Figure 5. Lateral habitus of three *Eleodes* species: **A** *E.* (*Eleodes*) *caudiferus* **B** *E.* (*Eleodes*) *tribulus* **C** *E.* (*Litheleodes*) *extricatus*. Scale bar = 5 mm.

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, punctation 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 symetrical 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 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 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 epipharnyx, 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”. Atotal 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, 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 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 setae on the anterolateral margins of the epipharnyx, 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, 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 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 subquadrate, 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 off / Hwy 180/Montana Ave. / N31.82327, W106.13234 / 21–22.VIII.2010, ADSmith", "USA: Arizona: Navajo Co. / dunes ~4mi N Chilchinbito / off route 59, el. 1738m / N36.58143, W110.06973 / 26.August.2010, ADSmith", "USA: AZ: Graham Co. / Pinaleño Mnts, Hospital Flat Camp / N32°39'58.0", W109°52'30.9" / el.9000' 22.Aug.2010 / ADSmith", "USA: Arizona: Gila County / E. Verde River off NF-272 / N34.303, W111.3496 / 27.August.2010, ADSmith". 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; punctation 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, 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 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 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, 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.

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-

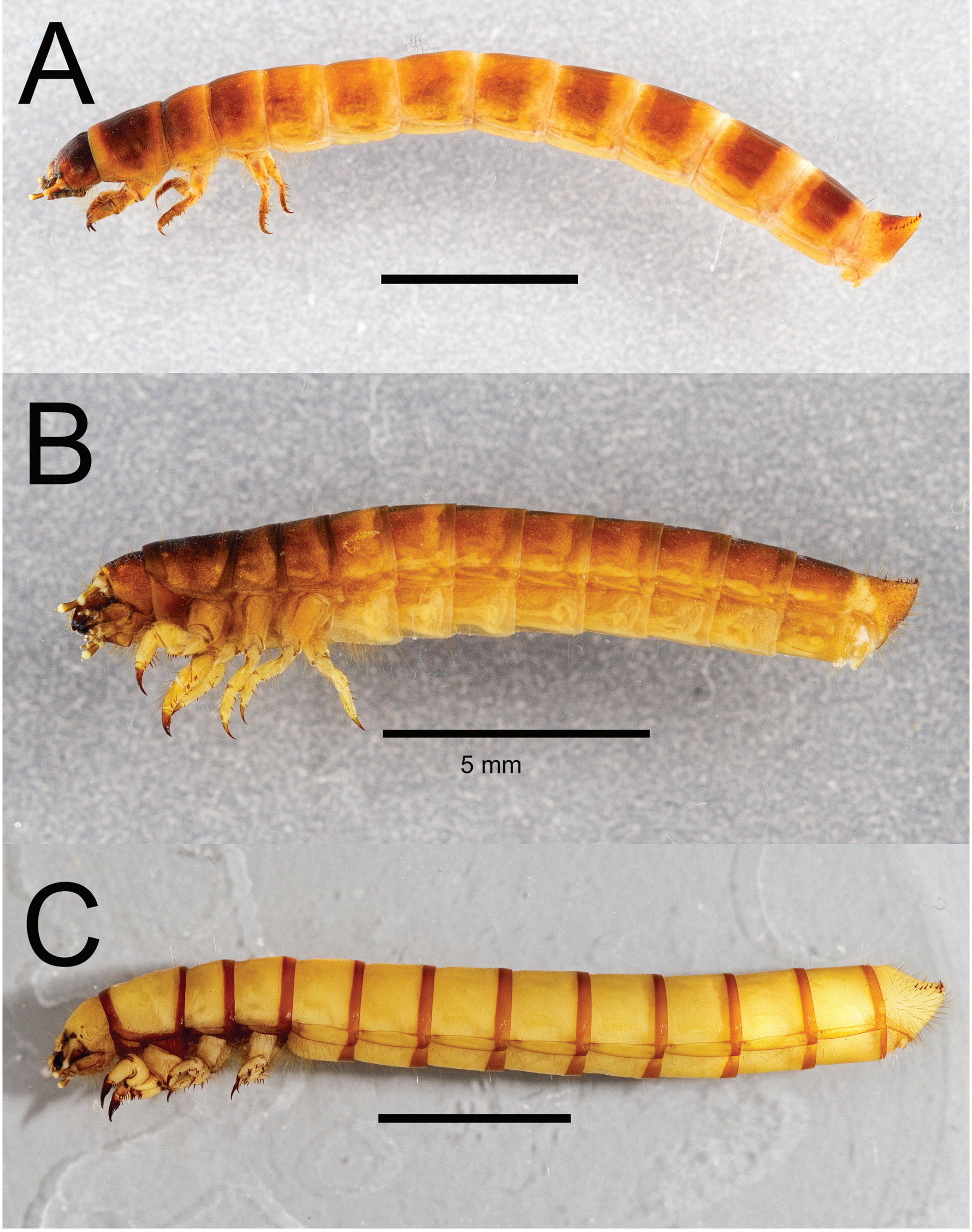

Figure 6. Lateral habitus of three *Eleodes* species: **A** *E.* (*Melaneleodes*) *anthracinus* **B** *E.* (*Melaneleodes*) *carbonarius* **C** *E.* (*Tricheleodes*) *pilosus*. Scale bar = 5 mm.

ramen; color medium brown to brown-grey, 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.

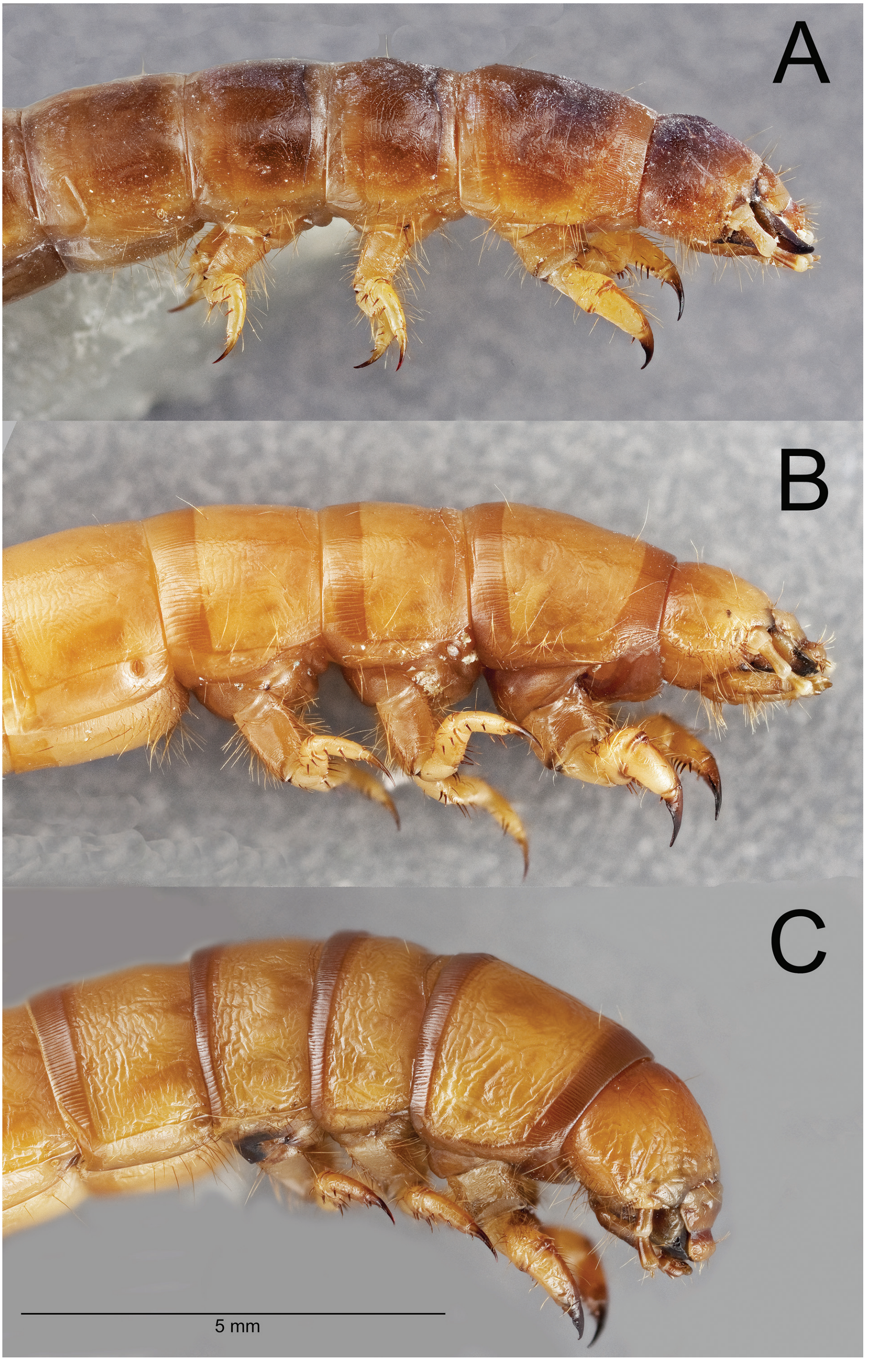

Figure 7. Lateral habitus of the head and thoracic segments of three *Eleodes* species: **A** *E.* (*Melaneleodes*) *anthracinus* **B** *E.* (*Litheleodes*) *extricatus* **C** *E.* (*Promus*) *subnitens*. Scale bar = 5 mm.

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 subquadrate, 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

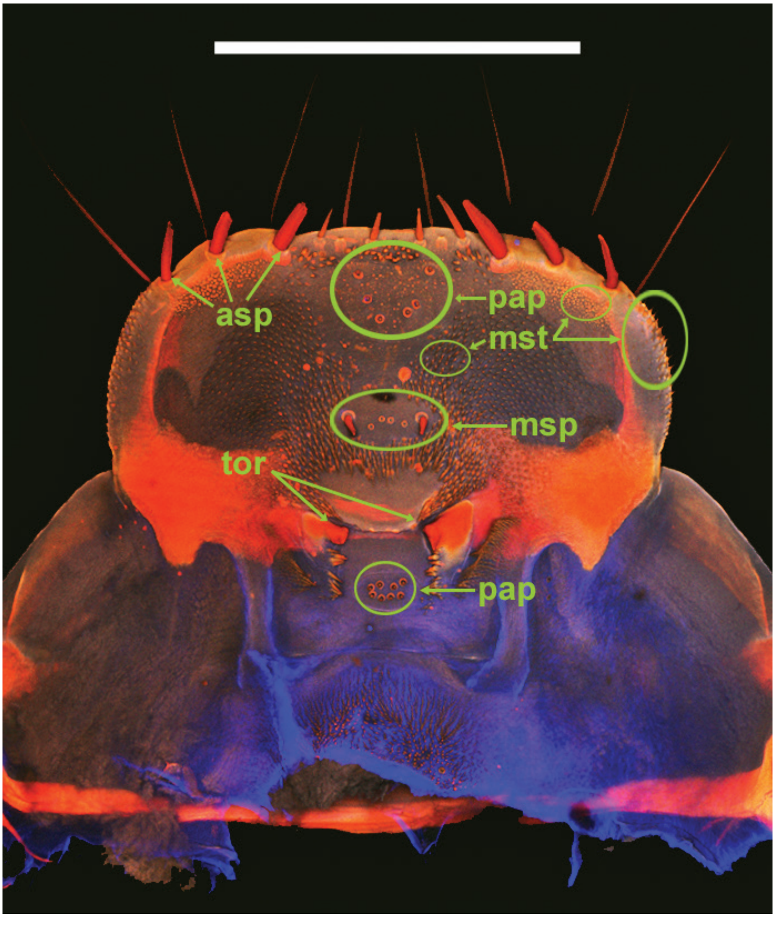

Figure 8. *Eleodes* (*Melaneleodes*) *anthracinus*, epipharnyx. asp = anterior spines, msp = medial spines, mst = microsetae, pap = sensory papillae, tor = tormae. Scale bar = 1 mm.

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*.

***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-

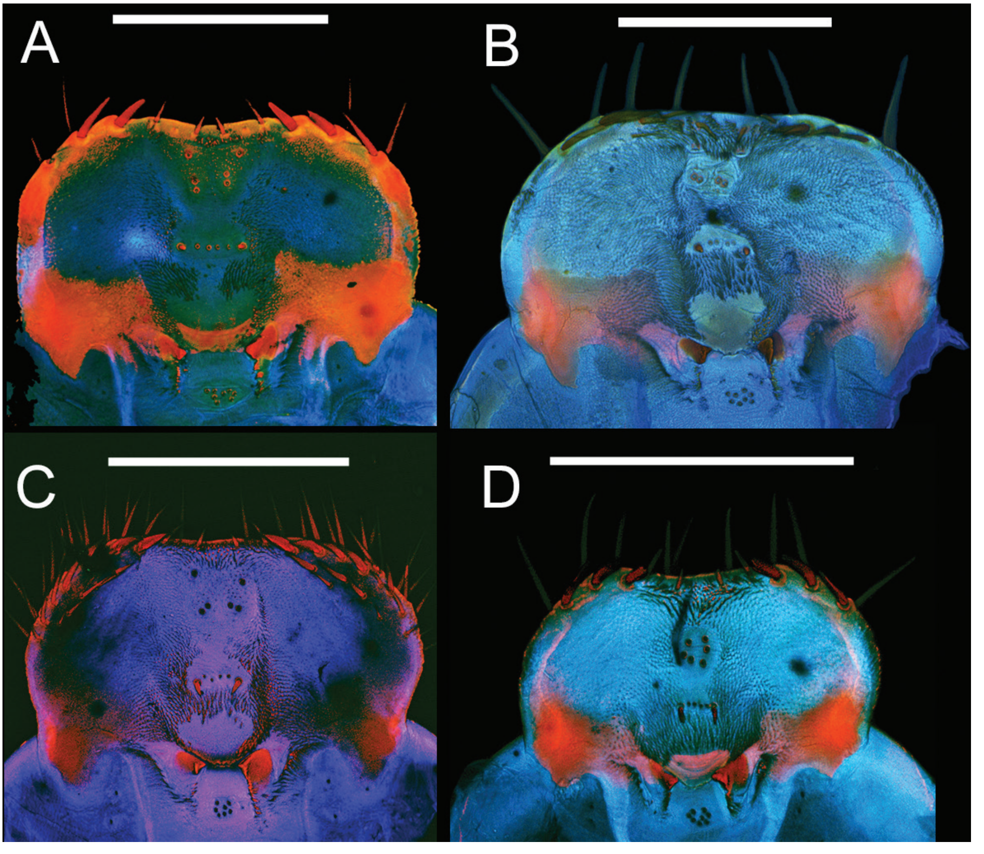

Figure 9. Epipharynges of four *Eleodes* species: **A** *E.* (*Melaneleodes*) *carbonarius* **B** *E.* (*Eleodes*) *armatus* **C** *E.* (*Eleodes*) *hispilabris* **D** *E.* (*Eleodes*) *tribulus*. Scale bars = 1 mm.

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.

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, 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 six

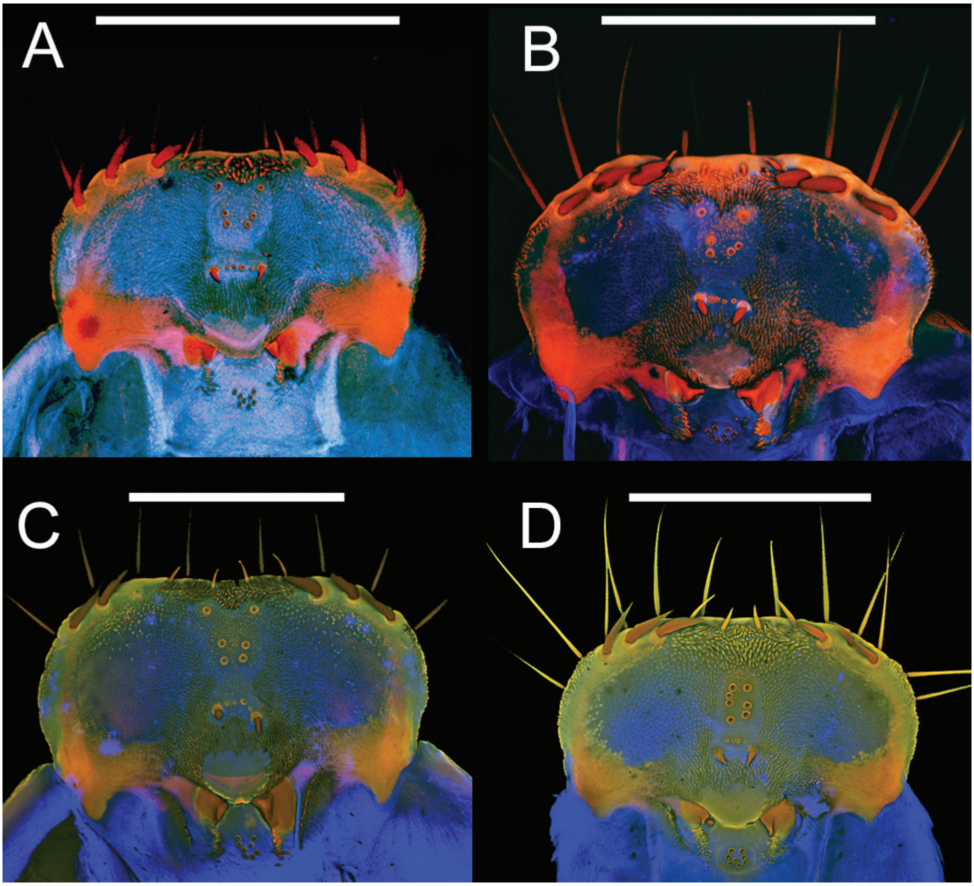

Figure 10. Epipharynges of four *Eleodes* species: **A** *E.* (*Litheleodes*) *extricatus* **B** *E.* (*Promus*) *goryi* **C** *E.* (*Promus*) *subnitens* **D** *E.* (*Tricheleodes*) *pilosus*. Scale bars = 1 mm.

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 asymetrical 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 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 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.

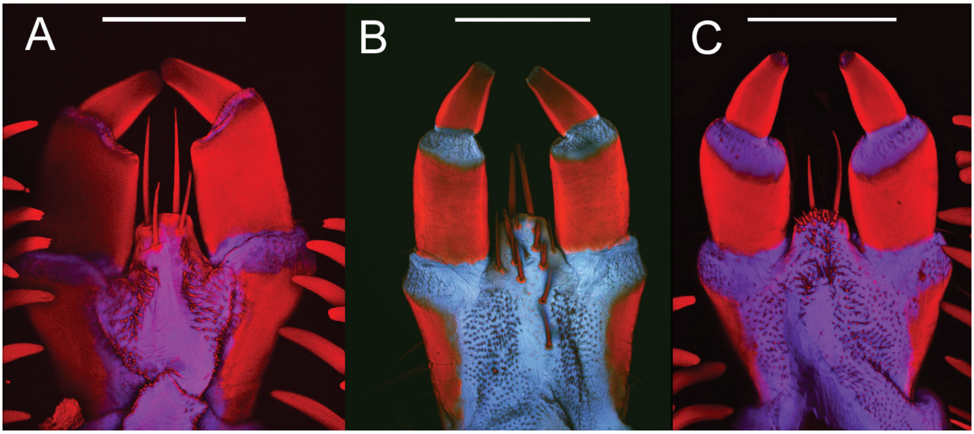

Figure 11. Ligulas of three *Eleodes* species: **A** *E.* (*Melaneleodes*) *carbonarius* **B** *E.* (*Eleodes*) *armatus* **C** *E.* (*Promus*) *goryi*. Scale bars = 200 µm.

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, 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, 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 (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 asymetrical 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-

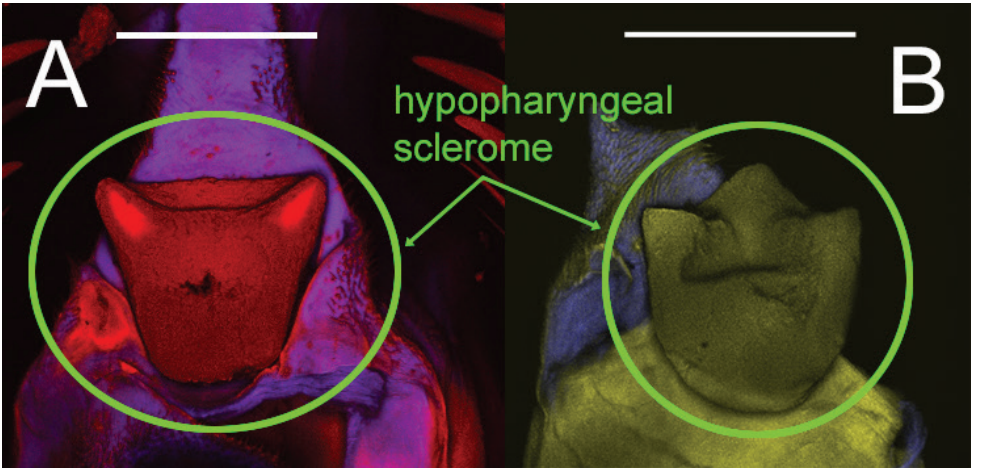

Figure 12. Hypopharyngeal scleromes of two *Eleodes* species: **A** *E.* (*Melaneleodes*) *carbonarius* **B** *E.* (*Litheleodes*) *extricatus*. Scale bars = 200 µm.

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 margins8, 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.

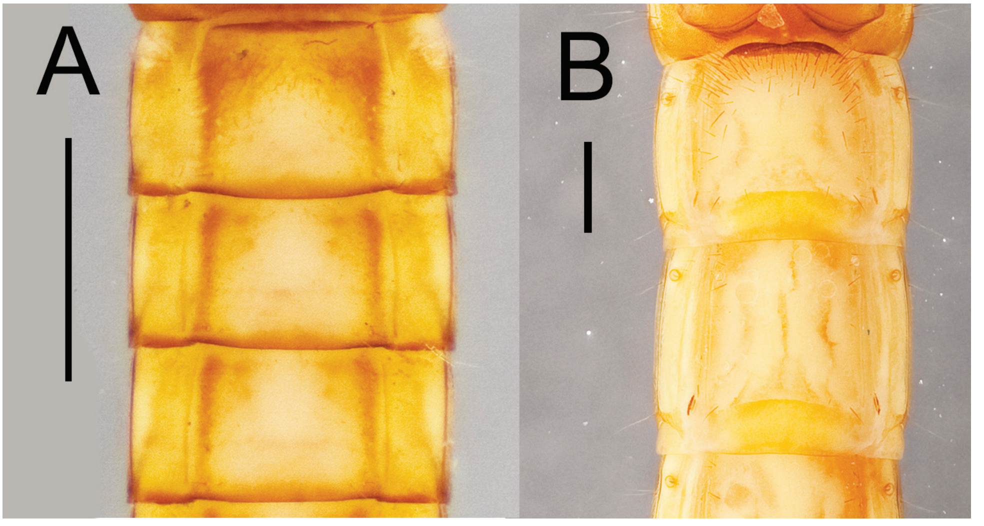

Figure 13. Abdominal sternites I and II for two *Eleodes* species: **A** *E.* (*Eleodes*) *caudiferus* **B** *E.* (*Litheleodes*) *extricatus*. Scale bars = 1 mm.

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: 1.4–3.4mm, HW: 1.6–2.6mm.

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

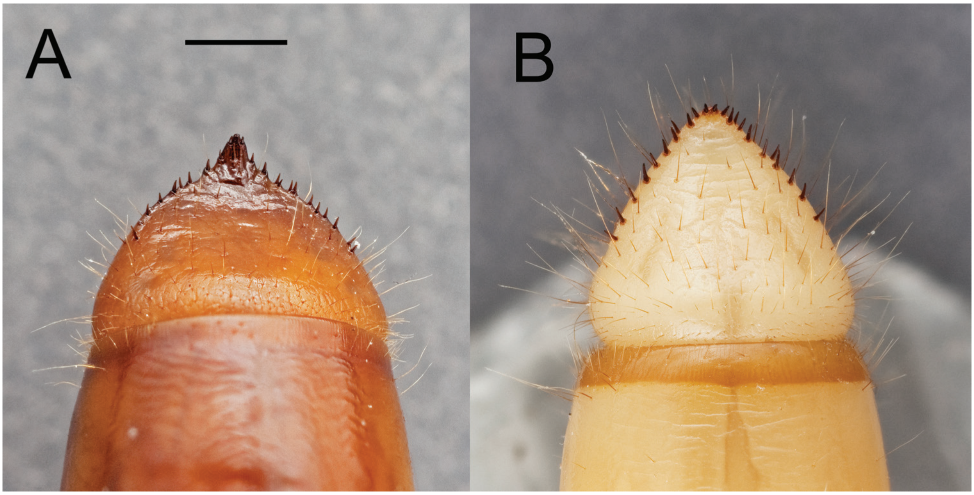

Figure 14. Pygidia of two *Eleodes* species: **A** *E.* (*Eleodes*) *hispilabris* **B** *E.* (*Tricheleodes*) *pilosus*. Scale bar = 1 mm.

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; 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.

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**

1' Lateral margins of abdominal sternites I–IX unpigmented, lacking tomentose setae (Fig. 13B) **2**

2 (1') Apex of pygidium attenuated and sclerotized, forming a distinct projection (Fig. 14A) **3**

2' Apex of pygidium somewhat attenuated, lightly or unsclerotized, not forming distinct projection (Fig. 14B) 5

3 (2) Anterolateral margins of epipharynx with micro-setation (Fig.8, 9A–B,D, 10A–D), lacking stout setae .... ***Eleodes armatus* LeConte**

3' Anterolateral margins of epipharynx with stout setae (Fig. 9C) **4**

4 (3) 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**

4' Mesotarsus with two ventromedial spines, ventral portion epicranial plates with row of four to five long setae along anterior margin, not confluent with setae on lateral portions of plates; prothoracic femur with ventromedial row of 6–10 spines.. ***Eleodes hispilabris* (Say)**

5 (2') Granulated band along lateral margins of protergum faint, concolorous with protergal disc (Fig. 7A) **6**

5' Granulated band along lateral margins of protergum distinct, darker than protergal disc (Fig. 7B–C) **8**

6 (5) 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**

6' Hypopharyngeal sclerome trapezoidal (Fig.12A); ligula apex glabrous, four long subapical setae present, two ventrally and two dorsally (Fig.11A); pigmented band absent along posterior margin of abdominal sterna, integument usually dark brown **7**

7 (6) 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 epipharnyx 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 epipharnyx 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 tribulus* 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 subnitens* 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 epipharnyx, 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 epipharnyx 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 epipharnyx and the apical tooth on the pygidium. It also appears to have spinose setae on the anterolateral margins of the epipharnyx, 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 tenebrionidbase.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

Aalbu RA, Smith AD, Triplehorn CA (2012) A revision of the *Eleodes* subgenus *Caverneleodes* with new species and notes on cave breeding *Eleodes* (Tenebrionidae: Amphidorini). Annales Zoologici 62: 199–216. doi: 10.3161/000345412X652729

Allsopp PG (1980) The biology of false wireworms and their adults (soil-inhabiting Tenebrionidae) (Coleoptera): a review. Bulletin of Entomological Research 70: 343–379. doi: 10.1017/S0007485300007628

Blaisdell FE (1909) A monographic revision of the Coleoptera belonging to the Tenebrionid tribe Eleodiini inhabiting the United States, lower California, and adjacent islands. Bulletin of the United States National Museum 63: 1–524. doi: 10.5479/si.03629236.63.1

Brown KW (1973) Description of immature stages of *Philolithus densicollis* and *Stenomorpha puncticollis* with notes on their biology (Coleoptera, Tenebrionidae, Tentyriinae). Postilla 162: 1–28.

Calkins CO, Kirk VM (1975) False wireworms of economic importance in South Dakota (Coleoptera: Tenebrionidae). South Dakota Agricultural Experiment Station Bulletin: 115–120.

Doyen JT (1988) Descriptions of some phylogenetically important larvae of Tenebrionidae (Coleoptera). Coleopterists Bulletin 42: 285–301.

Doyen JT, Somerby RE (1974) Phenetic similarity and Mullerian mimicry among darkling ground beetles (Coleoptera:Tenebrionidae). Canadian Entomologist 106: 759–772. doi: 10.4039/Ent106759-7

Gissler CF (1878) On coleopterous larvae of the family of Tenebrionidae. Bulletin of the Brooklyn Entomological Society 1: 18–19.

Goloboff PA (1999) NONA (NO NAME), version 2.0 (for Windows). Published by the author, Tucumán, Argentina.

Goloboff P, Farris J, Nixon K (2008) TNT: a free program for phylogenetic analysis. Cladistics 24: 774–786. doi: 10.1111/j.1096-0031.2008.00217.x

Heath TA, Hedtke SM, Hillis DM (2008) Taxon sampling and the accuracy of phylogenetic analyses. Journal of Systematics and Evolution 46: 239–257.

Hyslop JA (1912) The false fireworms of the Pacific Northwest. United States Bureau of Entomology Report 95: 73–87.

Lawrence JF (1991) Order Coleoptera. In: Stehr FW (Ed) Immature Insects, Vol. 2. Kendall/Hunt Publishing Co., Dubuque, Iowa, 144–298.

McColloch JW (1918) Notes on false fireworms with especial reference to Eleodes tricostata. Journal of Economic Entomology 11: 212–224.

Mullins PL, Kawada R, Balhoff JP, Deans AR (2012) A revision of *Evaniscus* (Hymenoptera, Evaniidae) using ontology-based semantic phenotype annotation. ZooKeys 223: 1–38. doi: 10.3897/zookeys.223.3572

Nixon KC (2002) WinClada ver. 1.00.08. Published by the author, Ithaca, NY.

Say T (1823–1824) Descriptions of coleopterous insects collected in the late expedition to the Rocky Mountains performed by order of Mr. Calhoun, Secretary of War, under the command of Major Long. Journal of the Academy of Natural Sciences of Philadelphia 3: 139–216 [1823]; 238–282, 298–331, 403–462 [1824].

St. George RA (1924) Studies of the Larvae of North American Beetles of the Subfamily Tenebrioninae with a description of the larva and pupa of *Merinus laevis* (Olivier). Proceedings of the Unites States National Museum 65: 1–22. doi: 10.5479/si.00963801.65-2514.1

Talamas EJ, Masner L, Johnson NF (2011) Revision of the Malagasy genus *Trichoteleia* Kieffer (Hymenoptera, Platygastroidea, Platygastridae). ZooKeys 80: 1–126. doi: 10.3897/zookeys.80.907

Thomas DB (1984) The life history and ecology of the pinacate beetle, *Eleodes armatus* LeConte (Tenebrionidae). Coleopterists Bulletin 38: 150–159.

Triplehorn CA, Aalbu RL (1987) Eleodes blaisdelli Doyen, a synonym of E. caudatus (Horn) (Coleoptera: Tenebrionidae). Coleopterists' Bulletin 41: 370–372.

Triplehorn CA, Thomas DB (2011) Studies in the genus *Eleodes* Eschscholtz with a revision of the subgenus *Melaneleodes* Blaisdell and *Omegeleodes*, new subgenus (Coleoptera: Tenebrionidae: Eleodini). Transactions of the American Entomological Society 137: 251–281.

Wade JA, St. George RA (1923) Biology of the false wireworm, Eleodes suturalis. Journal of Agricultural Research 36: 547–566.

Winterton SL (2009) Revision of the stiletto fly genus *Neodialineura* Mann (Diptera: Therevidae): an empirical example of cybertaxonomy. Zootaxa 2157: 1–33.

Yoder MJ, Valerio AA, Polaszek A, Masner L, Johnson N (2009) Revision of *Scelio pulchripennis* – group species (Hymenoptera, Platygastroidea, Platygastridae). In: Johnson N (Ed) Advances in the systematics of Hymenoptera. Festschrift in honour of Lubomír Masner. ZooKeys 20: 53–118. doi: 10.3897/zookeys.20.205

Yoder MJ, Mikó I, Seltmann KC, Bertone MA, Deans AR (2010) A Gross Anatomy Ontology for Hymenoptera. PLoS ONE 5(12): e15991. doi: 10.1371/journal.pone.0015991

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 – punctation: (0) impunctate; (1) minute; (2) moderate
9. Head – punctation 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 – punctation 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 micro–setation; (2) lacking setation

31. Epipharnyx – anterior sensory papillae (spinule) number: (0) six; (1) seven; (2) eight; (3) four; (4) five

32. Epipharnyx – 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. Epipharnyx – subanterior sensory papillae: (0) transverse row of four small sensory papillae subtended by two spinose setae

34. Epipharnyx – posterior sensory papillae number: (0) six; (1) seven; (2) eight

35. Epipharnyx – 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 longitidinal 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

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 tergum – 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 onmore 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

Eleodes_nigropilosus	01100501202110100000210101201100021111100110411211221010100015000100022120111021001000
Eleodes_tribulus	01110{04}112022201100012111011011{04}{03}0{12}1021100110411212221010100010000000022321111021401010
Eleodes_wheeleri	011004013021100100012111012011310211121100104 4{01}212221100000016100200022511110211001010
Eleodes_armatus	011002113121101100012111022011020210121000000{24}21212111110100013200 3{03}0{02}1{12}311111111301010
Eleodes_caudiferus	010005012{01}22202100012{01}110440210002110110001022121200301010001210 00{03}0022431111221610020
Eleodes_hispilabris	01000211312222010000131110140200 20{12}10221000004{24}121211111 01000{12}32102000221211111111201000
Eleodes_tenuipes	0{01}1002113122201100013{12}1101402002021012100000421212121110100024210300022111111121501 0?0
Eleodes_extricatus	0110040130211011000{01}30110110110002 11{01}11000004212121110101000100002000221211110112010 10
Eleodes_anthracinus	01000{01}0120011010000021010220110002001000 0000{01}{01}011111100000000000000{12}1{01}1{01}120110010{014.0}01010
Eleodes_carbonarius_ knausi	01000{23}01200110100000210101101100021120000000{23}{23}112211110000001110 02{34}0{01}20121120010101000
Eleodes_goryi	01100{23}1120011011000121110110110002102110011 04{12}22{23}2111110100010000000002232100102010 1010
Eleodes_subnitens	0110021120211011000123110120110002102110011042123212111010001010020000222211110211 01020
Eleodes_pilosus	01000{45}0131122121000120110{12}{12}01111011031100000412232222110100012100100022211111021201020
Tenebrio_molitor	0110020130211002000131100620200002101412012022223211101010111500040002251100133172 1132
Zophobas_morio	01100{23}1141222010000132110510120102111312102111224200100010111131023012150000103072 11?0

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. Epipharnyx – 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

Eleodes_nigropilosus	0120011001111020020112022001011000112011002111110
Eleodes_tribulus	0020000010100020120112022001011000132111002111110
Eleodes_wheeleri	0130011010101020030102022010111100101111121111110
Eleodes_armatus	0031011010101021130101011011011202131111011111110
Eleodes_caudiferus	1121000110102120020102000101011100143111022112110
Eleodes_hispilabris	1031000000002111130101011011011210112111011111111
Eleodes_tenuipes	003100001000211113010101201101121011111110121111?
Eleodes_extricatus	0130011010000020020101011001011000112111001111110
Eleodes_anthracinus	1120111001111020141101111000111001012011101011110
Eleodes_carbonarius_knausi	1120111001110020041101111010111101012112101011110
Eleodes_goryi	0020111010100020120112011011011000132100002011110
Eleodes_subnitens	0020011010101020120112012011011100122111002111111
Eleodes_pilosus	113110011010[01]020120101022111011100121111002111111
Tenebrio_molitor	0130011020001110110010011001000000101100030100000
Zophobas_morio	0001000000000000000000000000000311000000000000000

ZooKeys 415: 269–293 (2014)
doi: 10.3897/zookeys.415.6794
www.zookeys.org

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New species and records of *Charisius* Champion from Mexico and Central America (Coleoptera, Tenebrionidae, Alleculinae)

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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

Citation: Campbell JM (2014) New species and records of *Charisius* Champion from Mexico and Central America (Coleoptera, Tenebrionidae, Alleculinae). In: Bouchard P, Smith AD (Eds) Proceedings of the Third International Tenebrionoidea Symposium, Arizona, USA, 2013. ZooKeys 415: 269–293. doi: 10.3897/zookeys.415.6794

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).
Narses Champion (1888: 423). **Syn. n.**

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 mesoventral 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

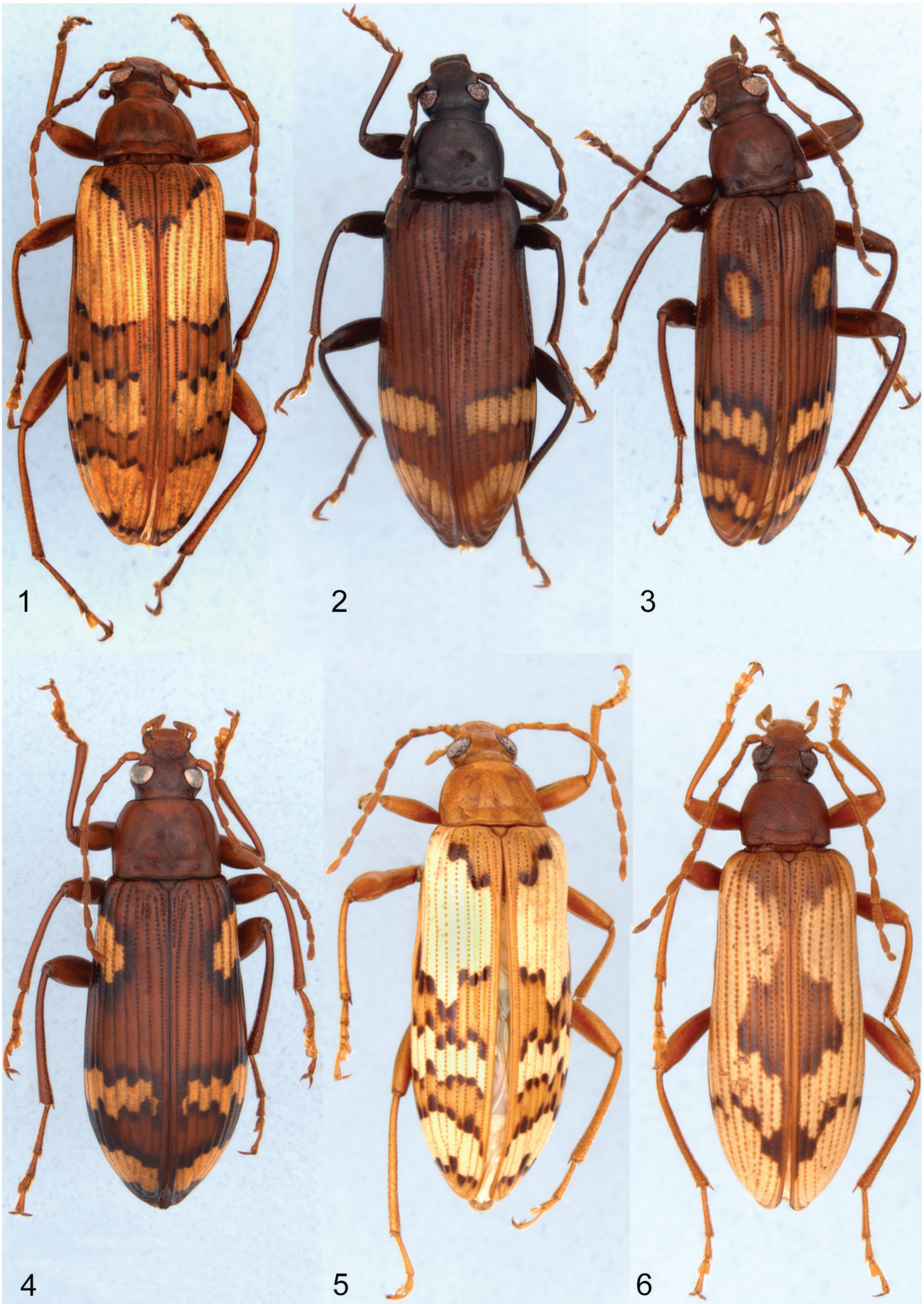
Charisius fasciatus Champion (1888: 421, pl. 19, Figs 12, 12a, 13); Campbell (1965: 67, Figs 3, 9, 15, 16).

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; Zunilito, 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.

HONDURAS: Francisco Morazán: 21.5 km N Tegucigalpa, PN La Tigra, 1950 m, 15.VIII–2.IX.1994, S&J Peck (CMNC) 1.

MEXICO: Chiapas: Cerro Huitepec (Pico), ca 5 km W San Cristobal de las Casas, 2750 m, 23.IX.1991, R Anderson (CMNC) 1; 5 km W San Cristobal, 3.V.1969, HF Howden (CMNC) 1; 6 km E San Cristobal, 9.V.1969, HF Howden (JMCC) 1; 8 km NE San Cristobal, 17.V.1969, HF Howden (CMNC) 1; 8 mi S Simojovel, 10.VI.1969, JMC (CNCI) 1; San Cristobal de las Casas, 26.VII.1969, LA Kelton (CNCI) 2; 8 mi NE San Cristobal, 28.VI.1969. JMC, (CNCI, JMCC) 5; same locality, 5.V.1969, HF Howden (CMNC) 2; 11 mi NE San Cristobal, 18.V.1969, HF Howden (CMNC) 3; Tinijapa, 8 mi NE San Cristobal 26.V.1969 and 18.V.1969, JMC (CNCI, JMCC) 12; 11 mi NE San Cristobal, 18.V.1969, HF Howden (CMNC) 2; 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 punctation 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 punctation 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.

MEXICO: Mexico: San Cayetana, Villa de Allende, 16.IX.1953, V Aquilar Vegs. (CNCI) 1. Oaxaca: Route 190, 33 mi NW Oaxaca, 4–5.IX.1967, G Ball, TL Erwin, RE Leech (CNCI) 1.

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. Holoype, 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.

MEXICO: Guerrero: 1.3 km SW Filo de Caballo, 2700 m, 17.VII.1992, RS Anderson (CMNC) 1; 3 mi SW Filo de Caballo, 17.VII.1984, Carroll, Schaffner, Friedlander (EGRC) 3; 18-20 km SW Filo de Caballo, 9000 ft, 17.IX.1989, E Giesbert & JE Wappes (JEWC) 2. Mexico: San Cayetano, Villa de Allende, 16.IX.1953, V. Aguilar Vegs. (JMCC) 1; 3.6 km W Villa Victoria, 1925/10002, 2,530 m, 15–16.VII.1979, EL & KW Sleeper (CASC) 1. Michoacan:: Cerro Estimbo, 15.9 km NW Quiraga, 1943/10148, 13-14.VII.1979, 2,225 m, EL & KW Sleeper (CASC) 1. Morelos: Tres Marías, Wickham (USNM) 3. Oaxaca: El Cerazal, 16 km NE Oaxaca, 2300 m, 12.VI1979, H & A Howden (CMNC) 2; 20 mi S Juchatengo, Route 131, 6,000 ft, HF Howden (JMCC) 1; Hwy 131, 70 km S Oaxaca, 2150 m, 17.VI.1979, H &A Howden (CMNC) 1; 14 km N San Juan del Estado, 2600 m, 4.VIII.1986, H & A Howden (CMNC, JMCC) 2; Hwy. 175, 3 mi N Suchixtepec, 9500 ft, 4.VI.1971, DE Bright (CNCI) 1; 8 km S Suchixtepec, 6.VIII.1986, H & A Howden (CMNC, JMCC) 4.

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.

GUATEMALA: El Progresso: above Los Albores, 8000 ft, 7–8.V.1991, E Giesbert (JMCC, JEWC) 2; 28–29 km N San Augustin, 7–8500 ft, 19–21.IV.1990, J. E. Wappes (JMCC, JEWC) 2. Zacapa: 8 km N San Lorenzo, 10.VI.1993, 6700 ft, JMC (CNCI) 1.

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.

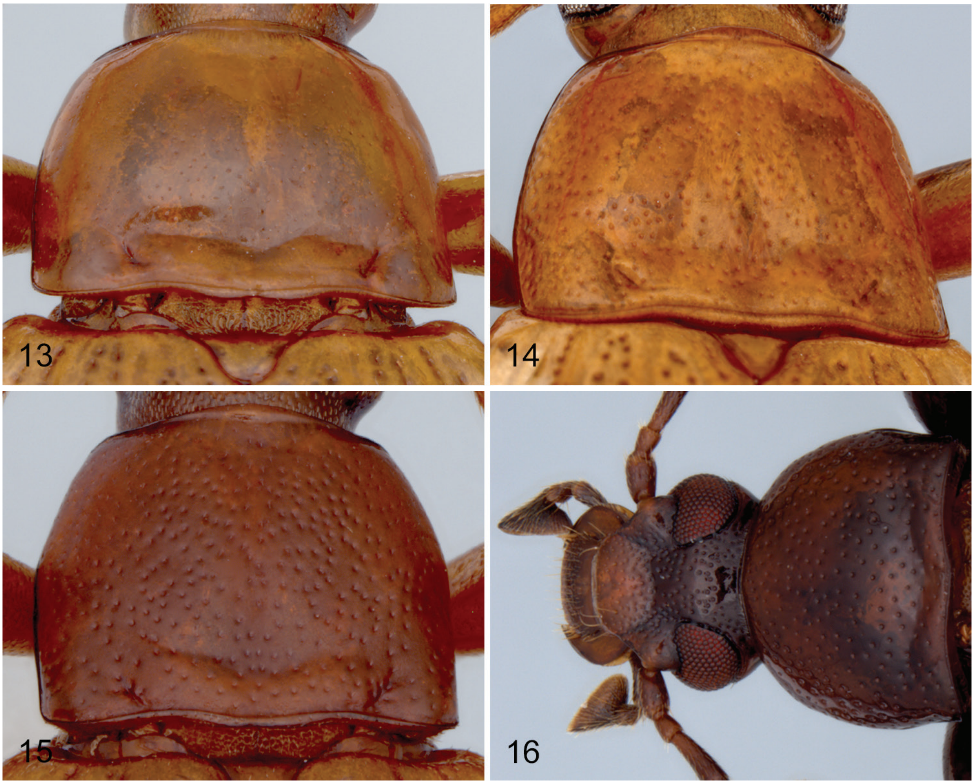
This species group contains two flightless species, one *C. subalatus*, formerly placed in the genus *Narses*, and the new species *C. apterus*.

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.

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.



Figures 13–15. Pronotum of species of *Charisius*: **13** *C. fasciatus* **14** *C. mexicanus* **15** *C. granulatus* **16** Head and pronotum of *C. salvini*.

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) 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.

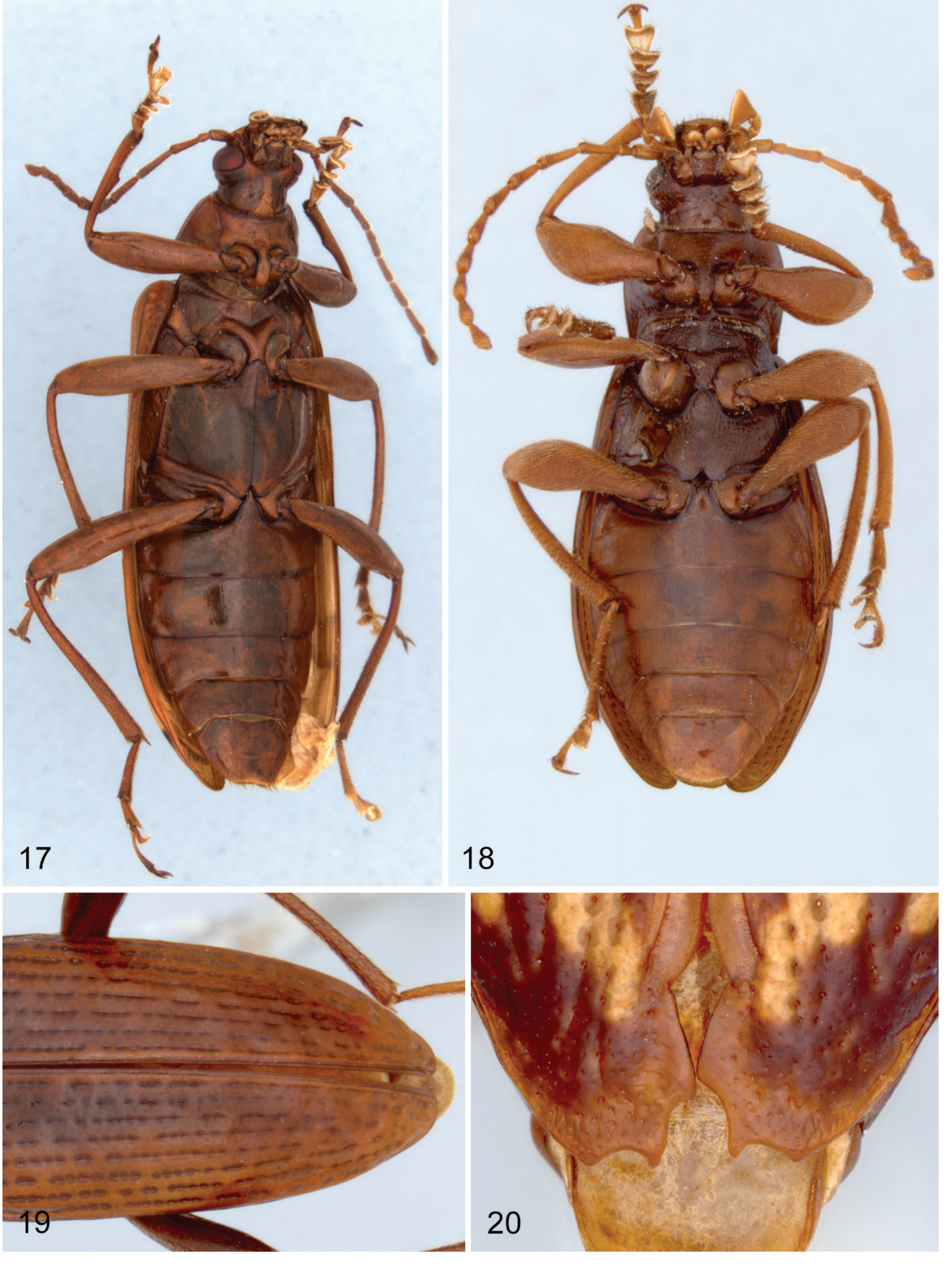
http://species-id.net/wiki/Charisius_subalatus

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)



Figures 17–20. Ventral view of species of *Charisius*: **17** *C. fasciatus* **18** *C. subapterus* **19** elytral striae of *C. howdenorum* **20** apex of female elytra of *C. apterus*.

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.

GUATEMALA: Jalapa: Miramundo, 8400 ft, 3.VII.1986, JMC (CNCI, JMCC) 3. Quetzaltenango: Balneario Georginas, 1920–2460 m, 19.VI.1993, F. Genier (CMNC) 2. San Marcos: Volcán Tacaná, SE slope, Rancho San Antonio, 9,000 ft, 27–28.VII.1972, GE Ball (CNCI) 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 punctation 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

Figures 21–24. Ventral view of lobes of male eighth and ninth sterna of species of *Charisius*: **21** *C. granulatus* **22** *C. subalatus* **23** *C. howdenorum* **24** *C. punctatus*.

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 Atitlan, 1500 m, 29.VIII.1965, JMC (JMCC) 1; Zunilito, 2 km N Finca Colimas, 6000 ft, 28.IV.1966, 6.V.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, JMC) 6; 8 km NE San Lorenzo, 2100 m, 18.VII.1986, JMC (CNCI) 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.

MEXICO: Chiapas: 20 km N Bochil, Yerba Buena, 5700 ft, 8.VI.1969, JMC (CNCI) 1; 5 mi SW El Bosque, 4.VII.1969, Campbell & Bright (CNCI) 1; San Cristobal de las Casas, 17.V.1990, H & A Howden (CMNC) 1; 5 mi W San Cristobal, 19.V.1969, JMC (CNCI) 1; 8 mi NE San Cristobal, Tinijapa, 18.V.1969, 26.V.1969, JMC (CNCI, JMCC) 16; 8 mi NE San Cristobal, 28.VI.1969, JMC (CNCI) 4; 11 mi NE San Cristobal, 8.V.1969, HF Howden (CMNC) 1; 15 km SE San Cristobal, 11.VI.1989, H Howden (CMNC) 1. Veracruz: 7 km E Huatusco, 22.VI-2.VII.1983, 1250 m, S Peck (CMNC) 1; Jalapa, JT Mason (AMNH) 1.

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; convex, 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 de las Casas, 19.V.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.

GUATEMALA: Baja Verapaz: 5 km above Ixpaco, 4300 ft, 22.VI.1983, JMC (CNCI) 1; 9 km S San Jeronimo, 4500 ft, 25.VI.1966 (JMCC) 2; 7.8 mi W Chilasco, 1700 m, 24.V.1991, H & A Howden (CMNC) 1. Chimaltenango: 7 km N Laguna de Calderas, 14.V.1966, JMC (CNCI, JMCC) 5. Esquintla: 3 km E San Vicente Pacayá, 5500 ft, 14.V.1966, JMC (CNCI, JMCC) 5; 4 km N Palin, 4500 ft, 21.VI.1966, JMC (JMCC) 1. Guatemala: Cerro Alux, 24.VI.1993, RS Anderson (CMNC) 1; 14.5 km SE Guatemala, Puenta Parada, 1790 m, 13.VI.1991, A Howden (CMNC, JMCC) 3. Sacatepequez: Antigua, IX.1959, NLH Krauss (USNM) 1; Finca Florencia, 24.VI.1993, JMC (CNCI, JMCC) 4; 1 km W Sta Lucia Milpas Altas, 3.VI.1993, JMC (CNCI) 1. Suchitepéquez: 2 km N Finca Colima, Zunilito, 6000 ft, 6.V.1966, JMC (JMCC) 1. Quezaltenango: 12.9 km SW Zunil, 1340 m, 18.VI.1993, RS Anderson (CMNC) 1.

HONDURAS: Cortez: 25 km N Cofradia, PN Cusucol, 1550 m, 19.IX–7.X.1994, S & J Peck (CMNC) 1. Francisco Morazán: 30 km E Tegucigalpa, Cerro Uyuca, 1800 m, 3.VI.1994, H & A Howden (CMNC) 1. Ocotepeque: 11 km E Ocotepeque, 1450 m, 16.VI. 1994, R Anderson (CMNC) 1.

NICARAGUA: Cerro Chimborazo, 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 acoss 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, JM Campbell. The specimen is deposited in the CNCI.

Paratypes, 44 in the CNCI, CMNC, JMCC, and the JEWC.

Distribution and records. This species is known only from Guatemala between 1400 and 1740 meters in elevation.

GUATEMALA: Alta Verapaz: Jnct. Rds. Coban & Purulhá, 5500 ft, 24.VI.1966, JMC (JMCC) 1. Baja Verapaz: Pantin Rd., 9 km N Salamá, 20–21.VI.1993, JMC (JMCC) 1; 6–9 km E Purulhá, 5000 ft, 15–24.IV.1990, E Geisbert (JEWC) 1. Chimaltenango: Yepocapa, 4600 ft, 10.V.1966, JMC (JMCC) 1. Zacapa: San Lorenzo, Sierra de las Minas, 1740 m, 8–11.1986, JMC (CNCI, JMCC) 10; same locality, 11.VII. and 17.VII.1986, L LeSage (CNCI) 2; same locality, 5200 ft, 17–19.VI.1986, JMC (CNCI, JMCC) 11; nr. San Lorenzo, 13.IV.1990, JE.Wappes (JEWC) 1; vic. San Lorenzo, 5800 ft, 10–15.VI.1991, E Geisbert (JEWC) 1; 13 km N Hwy, San Lorenzo Rd., 3000 ft, 17.VI.1993, JMC (CNCI) 1.

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) .... **4. *C. granulatus* sp. n.**
–	Pronotum with surface microsculpture fine, visible only under high magnfication (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 impressed **10**

9 Elytra with only apex piceous to black (Fig. 11); male protarsus with only basal 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)... ....**8. *C. howdenorum* sp. n.**

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 Café 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

Campbell JM (1965) A revision of the Genus *Charisius* (Coleoptera: Alleculidae). The Coleopterists Bulletin 19: 43–56.

Champion GC (1888) Family Cistelidae. In: Godman FD, Salvin O (Eds) Biologia Centrali-Americana. Insecta Coleoptera. Vol. IV, pt. 1, 385–465, pls 17–21.

Champion GC (1893) Heteromera. In: Godman FD, Salvin O (Eds) Biologia Centrali-Americana. Vol. IV, pt. 1, 477–572.

Lawrence JF, Beutel RG, Leschen RAB, Ślipiński SA (2010) 2. Glossary of Morphological Terms. In: Leschen RAB, Beutel RG, Lawrence JH (Eds) Coleoptera, Beetles, Morphology and Systematics. Vol. 2: 9–20.

Linell M (1901) Descriptions of some new species of North American heteromerous Coleoptera. Proceedings of the Entomological Society of Washington 4: 180–186.

ZooKeys 415: 295–309 (2014)
doi: 10.3897/zookeys.415.6662
www.zookeys.org

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An unusual suite of sexual characters in three new species of *Hymenorus* (Coleoptera, Tenebrionidae, Alleculinae) from Guatemala and Mexico

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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

Citation: Campbell JM (2014) An unusual suite of sexual characters in three new species of *Hymenorus* (Coleoptera, Tenebrionidae, Alleculinae) from Guatemala and Mexico. In: Bouchard P, Smith AD (Eds) Proceedings of the Third International Tenebrionoidea Symposium, Arizona, USA, 2013. ZooKeys 415: 295–309. doi: 10.3897/zookeys.415.6662

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

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 securiform 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 Zoolgical 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

Hymenophorus Mulsant, 1851, p. 201 [1852a, p. 68]; type species *Hymenophorus doublieri* Mulsant, 1851, by monotypy. Novák 2006, p. 317; Novák 2007; Novák and Petterrsson 2008, p. 322.

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 (1962:9 2); 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.

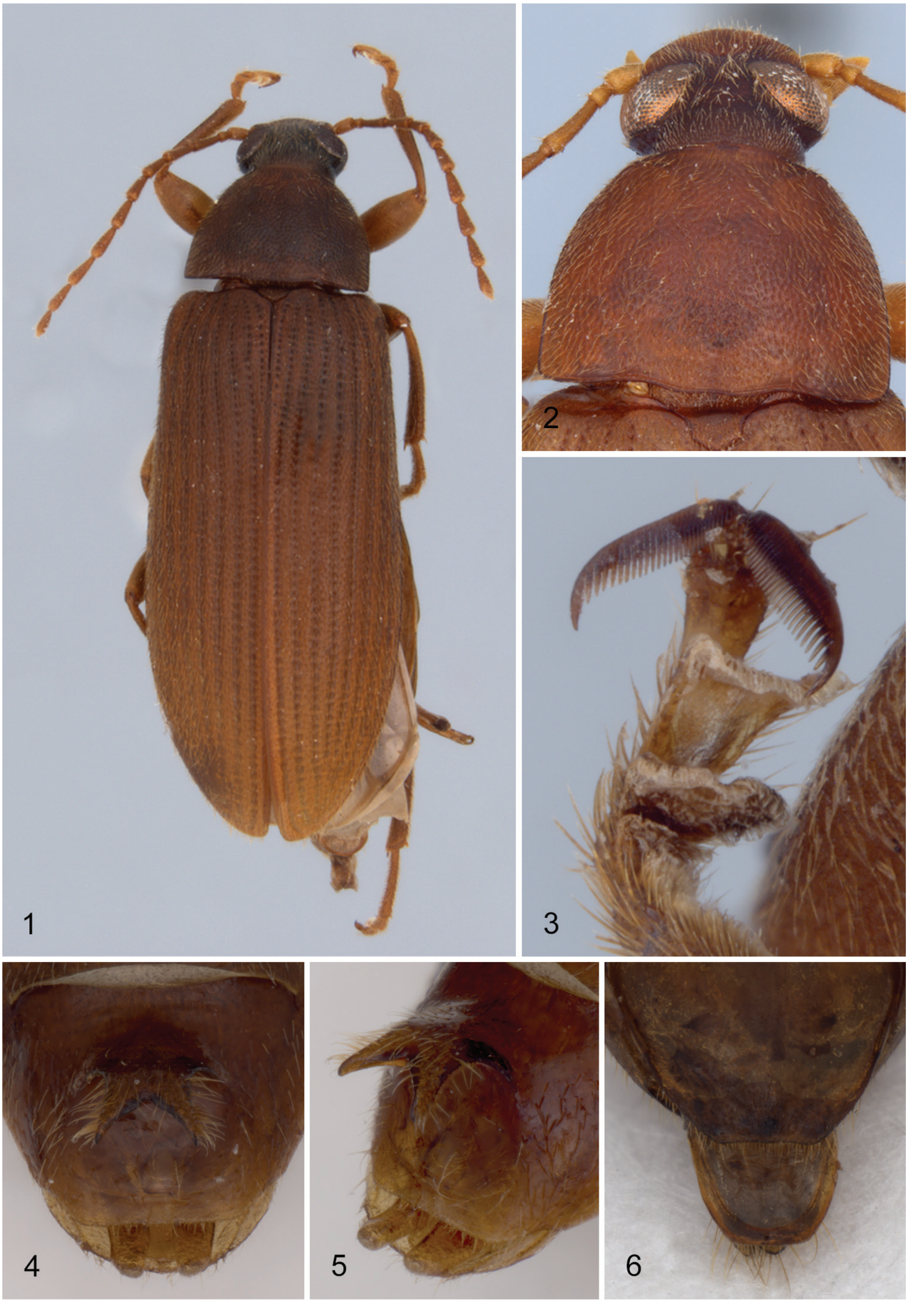

Figure 1–6. 1 dorsal habitus of *Hymenorus balli* **2** head and pronotum of *H. excavatus* **3** protarsal claws of *H. excavatus* **4** and **5** male fifth ventrite of *H. balli* **4** ventral view **5** lateral oblique view **6** dorsal view of female ninth tergite of *H. balli*.

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.

GUATEMALA: Sacatepequez: Finca Florencia, 24.VI.1993, JMC (CNCI) 1. Quezaltenango: nr. tunnel, 2 km N Santa María, 5500 ft, VII.10.1965, X.24.1965 JMC (JMCC) 3; 3 km N Santa María, 6000 ft, VIII.27.1965, JMC (JMCC) 1. San Marcos: 20 km S San Marcos, 4500 ft, IX.4.1964, JMC (CNCI) 2; 22 km S San Marcos, 5000 ft, IX.3.1965, X.2.1965, JMC (CNCI) 8.

MEXICO: Chiapas: Pico Gallo, NW Union Juarez, 5000–6000 ft, 1972, G. E. Ball (CNCI, JMCC) 16.

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://zoobank.org/66308321-E639-48B2-A240-B6F967101AEB
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.*

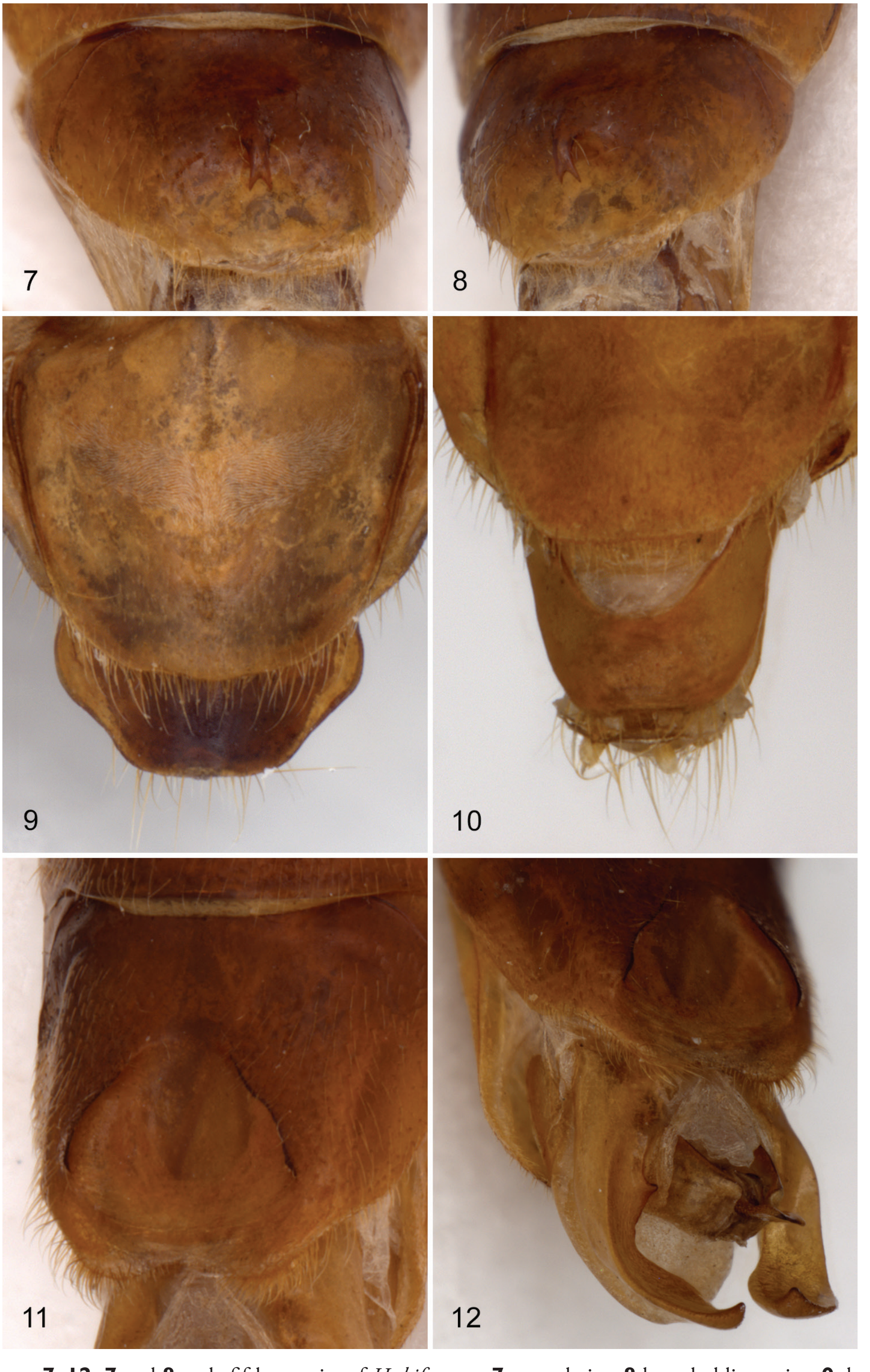

Figure 7–12. 7 and **8** male fifth ventrite of *H. bifurcatus* **7** ventral view **8** lateral oblique view **9** dorsal view of female ninth tergite of *H. bifurcatus* **10** dorsal view of female ninth tergite of *H. bifurcatus* **11** and **12** male fifth ventrite of H. excavatus **11** ventral view **12** lateral oblique view.

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/ HOLOTYPE, ♂ Hymenorus bifurcatus, desig. 2013, JM.Campbell The specimen is deposited in the CNCI.

Paratypes. Males 16, females, 17.

GUATEMALA: Quezaltenango: Tzanjoyan, 3 km SE Zunil, 2300 m, XI.1.1965, JMC (CNCI, JMCC) 5. Sacatepéquez: Finca Florencia, 24.VI.1993, JMC (JMCC) 2. San Marcos: 20 km S San Marcos, 4500 ft, IX.4.1964, JMC (JMCC) 1; 22 km S San Marcos, IX.3.1965, JMC (JMCC) 1. Border between Sololá and Chimaltenango: nr. Los Robles, IX.12.1965, 6000 ft, JMC (CNCI, JMCC) 27.

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 are 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 medially; heavily sclerotized area covering all of tergite except small, triangular, membranous section medially 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.

GUATEMALA: Esquintla: 3 km E San Vicente Pacayá, 5500 ft, V.14.1966, JMC (JMCC) 2. San Marcos: 10 km N La Reforma, 4500 ft, IX.4.1964, JMC (CNCI, JMCC) 7; 22 km S San Marcos, 5000 ft, VI.4.1966, X.2.1965, IX.3.1965, JMC (CNCI, JMCC) 11; 20 km S San Marcos, 4500 ft, IX.4.1964, JMC (JMCC) 2. Suchitepéquez: UVG Reserve, S side of Volcán Atitlán, 91°8.85W, 14°32.04N, X.9–11.2009, 1543 m, (WBWC) 2.

Etymology. This species is named excavatus in recognition of the deeply excavate fifth visible male ventrite.

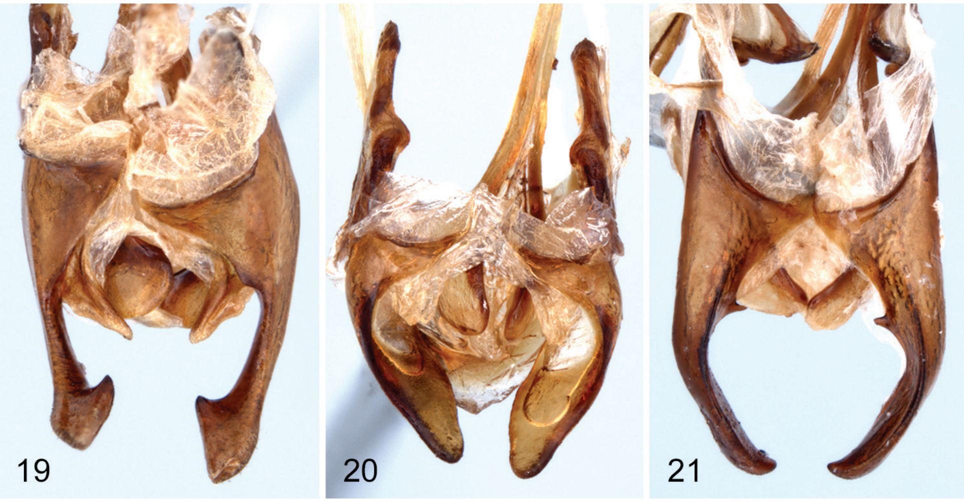

Figure 19–21. Ventral view of male eighth and ninth ventrites of **19** *H. balli* **20** *H. bifurcatus* **21** *H. excavatus.*

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 abdomnal 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.

References

Aalbu RL, Triplehorn CAS, Campbell JM, Brown KW, Somerby RE, Thomas DB (2002) 106. Tenebrionidae Latreille, 1802. In: Arnett RH, Thomas MC, Skelley PE, Frank JH (Eds) American Beetles, Vol. 2, Polyphaga, Scarabaeoidea through Curculionoidea. CRC Press, 463–509.

Althoff DM, Seagraves KA, Pellmyr O (2005) Community context of an obligate mutualism: Pollinator and florivore effects on *Yucca filamentosa*. Ecology 86(4): 905–913. doi: 10.1890/04-1454

Arnett RH, Jr. (1962) The beetles of the United States (A manual for identification). Part II. fasc. 75. The Catholic University of America Press, Washington, D.C., 701–706.

Blatchley WS (1910) An illustrated descriptive catalogue of the Coleoptera or beetles known to occur in Indiana. Bulletin Indiana Department of Geology and Natural Resources. No. 1, 1386 pp.

Bouyon H (2011) About the genera and the gender of genera in Alleculinae (Coleoptera, Tenebrionidae. Bulletin de la Société Entomologique de France 116(2): 191–193.

Campbell JM (1962) Two new species of *Hymenorus* (Coleoptera: Alleculidae) from Panama. The Coleopterists Bulletin 16: 92–96.

Campbell JM (1971) A revision of the Alleculidae (Coleoptera) of the West Indies. Memoir of the Entomological Society of Canada 81: 1–140. doi: 10.4039/entm10381fv

Campbell JM (1982) A new species of *Hymenorus* (Coleoptera: Alleculidae) from California. The Coleopterists Bulletin 36: 131–134.

Campbell JM (1984) *Onychomira floridensis*, a new genus and species from Florida with a revised key to the genera of North American Alleculidae. The Coleopterists Bulletin 38: 288–300.

Casey TL (1891) Coleopoterological notices. III. Annals of the New York Academy of Sciences 6: 69–170.

Chagnon G, Robert A (1962) Principaux Coléptères de la province de Quebéc. Les Presses de l'Université de Montréal, Montreal, Quebec, 440 pp.

Champion GC (1888) Family Cistelidae. In: Godman FD, Salvin O (Eds) Biologia Centrali-Americana. Insecta Coleoptera. Vol. IV, pt. 1, 385–465, pls 17–21.

Champion GC (1892–1893) Heteromera. In: Godman FD, Salvin O (Eds) Biologia Centrali-Americana. Insecta Coleoptera. Vol. IV, pt. 1, 477–572, pl. 23.

Downie NM, Arnett RH Jr (1996) The beetles of Northeastern North America. Vol. 2. Polyphaga: series Bostrichiformia through Curculionoidea. The Sandhill Crane Press, Gainesville, Florida. x: 871–1721.

Fall HC (1931) The North American species of *Hymenorus* (Coleoptera : Alleculidae). Transactions of the American Entomological Society 57: 161–247.

Hatch MH (1965) The beetles of the Pacific Northwest. Part IV: Macrodactyles, Palpicornes, and Heteromera, Vol. 16. University of Washington Publication in Biology, Seattle Washington, 268 pp.

Jacquelin du Val PNC (1861) In: Manuel entomologique. Généra des coléoptères d' Europe comprenant leur classification en familles naturelles, la description de tous les genres, des tableaux synoptiques destinés à faciliter l'étude, le catalogue de toutes les espèces, de nombreux dessins au trait de charactèrs et plus de treize cent types représentant un ou plusieurs insects de chaque genre dessinés et peints d'après nature avec le plus grand soin par M Jules Migneaux. Tome troisième. A. Deyrolle, Paris, 463 [1] pp.

Kanda K (2013) *Madreallecula mcclevei* Kanda (Coleoptera: Tenebrionidae: Alleculinae: Alleculini), new genus and new species of comb-clawed beetle from Arizona, USA. The Coleopterists Bulletin 67(4): 587–590. doi: 10.1649/0010-065X-67.4.587

Lawrence JF, Beutel RG, Leschen RAB, Ślipiński A (2010) 2. Glossary of Morphological Terms. In: Leschen RAB, Beutel RG, Lawrence JH (Eds) Coleoptera, Beetles, Morphology and Systematics. Vol. 2, 9–20.

LeConte JL (1866) New species of North American Coleoptera. Smithsonian Miscellaneous Collections 167: 87–177.

LeConte JL, Horn GH (1883) Classification of the Coleoptera of North America. Smithsonian Miscellaneous Collections 26 (4 [no. 507]): xxxviii + 567 pp.

Marshall JD (1970) North American Alleculidae (Coleoptera, Alleculidae): Miscellaneous papers I. Separating the genera *Alethia* Champion and *Hymenophorus* Mulsant with a new synonym and a new combination in *Alethia*. Biological Society of Nevada, Occasional Papers. No. 24: 1–7.

Mulsant É (1851) Description d'un genre et d'un coléoptère nouveau dans la famille des cisteliens. Mémoires de l'académie des Sciences de Lyon. ser. 2, vol. 1: 201–204.

Mulsant É (1852) Description d'un genre et d'un coléoptère nouveaux dans la familie des cisteliens. Opuscules Entomologique 1: 68–71.

Mulsant É (1856a) Histoire naturelle des coléoptères de France. Vol 6, Pectinipèdes. Maison, Paris, 96 pp.

Mulsant É (1856b) Notes relatives a quelque insectes Coléoptères de la tribu des Pectinipèdes. Famille des Cistéliens. Alléculates. Opuscules Entomologiques 7: 17–59.

Novák V (2006) *Hymenophorus evae* sp. nov. and *H. gerdae* sp. nov. (Coleoptera: Tenebrionidae: Alleculinae) from Iran. Acta Societatis Zoologicae Bohemicae 69: 317–325.

Novák V (2007) New Alleculidae (Coleoptera: Tenebrionidae) species from Nepal. Veroeffentlichungen des Naturkjundemuseums Erfut 26:233–240.

Novák V, Petterrsson R (2008) Alleculinae. In: Löbl I, Smetana A (Eds) Catalogue of Palearctic Coleoptera, Vol. 5, Tenebrionoidea. Stenstrup, Apollo Books, 319–339.

Reitter E (1911) Fauna Germanica. Die Käfer des Deutschen Reiches Nach der analytischen Methode bearbeitet. Band III. Lutz KG, Stuttgart, 436 pp. pls. 81–128.

von Seidlitz G (1896) Naturgeschichte der Insecten Deutschlands. Alleculidae. Abt. 1, Band 5 (2). Lief 1, Bogen, i-xviiii 304 pp.

Steiner WE Jr. (2004) New distribution records and recent spread of *Hymenorus farri* Campbell (Coleoptera: Tenebrionidae: Alleculinae) to Florida and in the Caribean region. Proceedings of the Entomological Society of Washington 106(4): 317–325.

ZooKeys 415: 311–327 (2014)
doi: 10.3897/zookeys.415.6891
www.zookeys.org

RESEARCH ARTICLE

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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

Citation: Steiner WE, Jr. (2014) 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. In: Bouchard P, Smith AD (Eds) Proceedings of the Third International Tenebrionoidea Symposium, Arizona, USA, 2013. ZooKeys 415: 311–327. doi: 10.3897/zookeys.415.6891

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. Stenochiine 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 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.

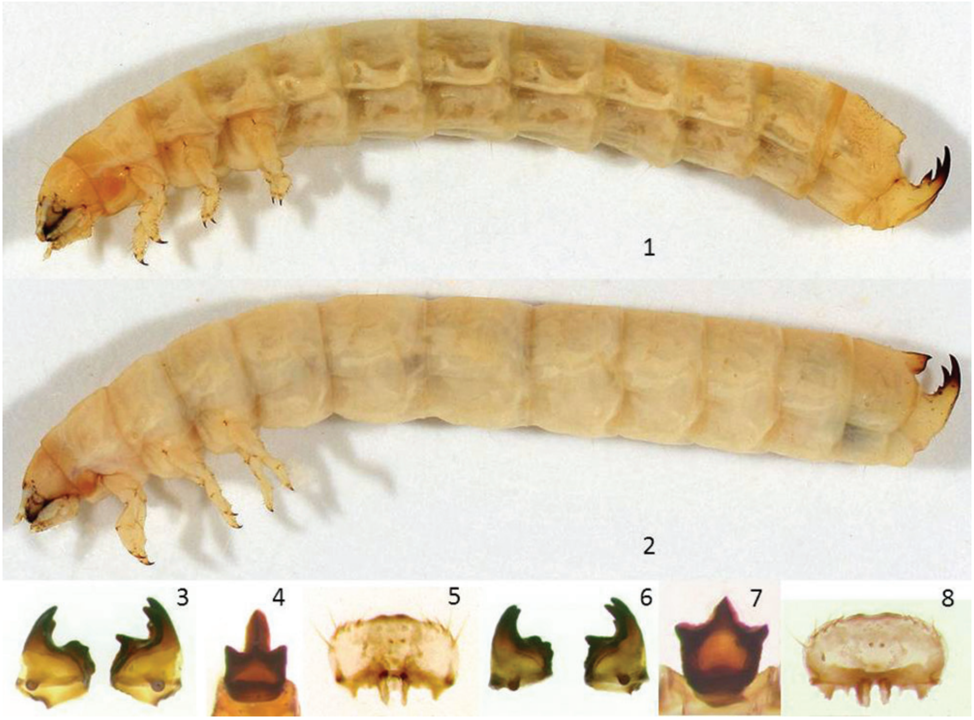
Description of mature larva. (Figures 1, 3–5, 9–12).

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 prebasal 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,



Figures 1–8. Mature larva of *Glyptotus cribratus*, lateral view, length 22 mm (**1**), mature larva of *Cibdelis blaschkei* lateral view, length 25 mm (**2**), *Glyptotus cribratus* larva, mandibles, ventral view, length 0.9–1.0 mm (**3**), epipharyngeal sclerome, length 0.4 mm (**4**), epipharynx, width 0.8 mm (**5**), *Cibdelis blaschkei* larva, mandibles, ventral view, length 0.7–0.8 mm (**6**), epipharyngeal sclerome, length 0.3 mm (**7**), epipharynx, width 0.7 mm (**8**).

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 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; protarsi with 3–4 setae on apical tarsomeres ventrally and laterally; apical tarsomeres of meso-and metatarsi with 1–2 setae laterally.

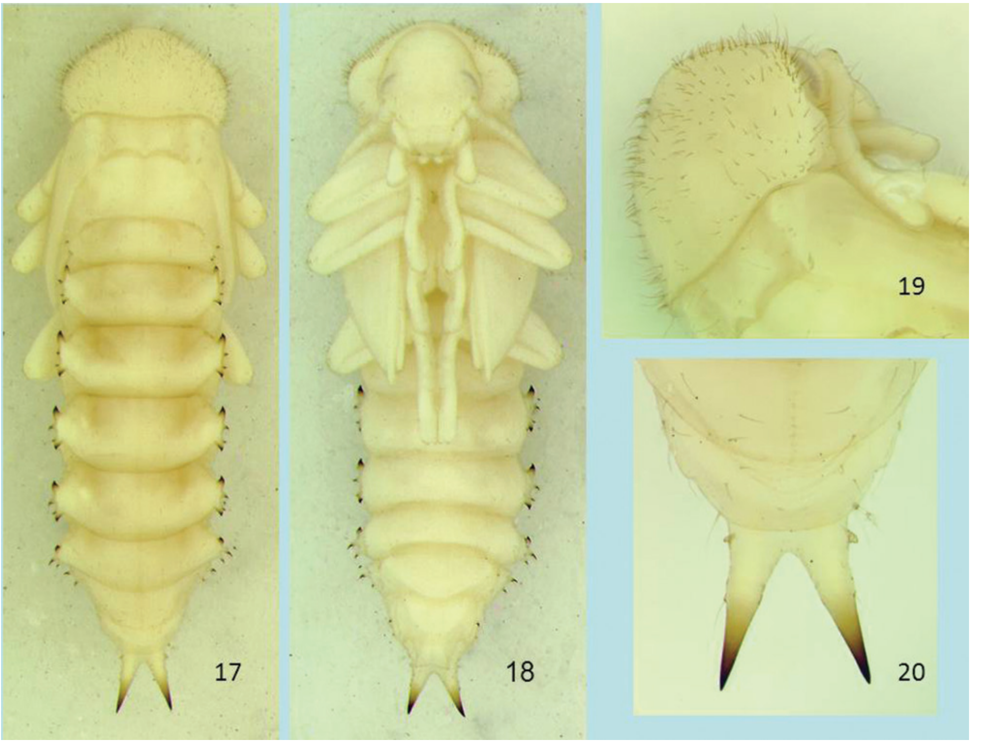
Abdomen. All surfaces smooth, bearing scattered fine setae; spiracles annular, vertically ovate to reniform, barely pigmented, visible on segments 2–6. Tergite 1 short, with five discal setae on each side, lateral process with single small posterior tooth and two small lateral spines with a wide, U-shaped 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

Figures 9–16. Abdominal apices of mature larvae of *Glyptotus cribratus* (**9–12**), dorsal (**9**) and lateral (**10**) view, urogomphi at rest, dorsal (**11**) and lateral (**12**) view, urogomphi raised, and abdominal apices of mature larvae of *Cibdelis blaschkei* (**13–16**), dorsal (**13**) and lateral (**14**) view, urogomphi at rest, dorsal (**15**) and lateral (**16**) view, urogomphi raised. Maximum widths of abdominal segments 3.3–3.5 mm.

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 urogomphus laterally with a single small, tooth-like protuberance, not heavily sclerotized, with a fine seta on mesal side near base; other long fine setae present on side of base of urogomphus and ventrolateral side of urogomphus to about mid-length, the latter arising from small protuberances. Genital segment (female pupa) roughly trapezoidal, smooth, with two divergent, protruding papillae bearing a single small seta laterally, papillae with a shallow V-shaped emargination between them.

***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 "Reared from larva in dry rotten wood of recently fallen dead branch of s. red oak (*Quercus falcata*); pupated 25 April, preserved 1 May 2007" (1 P with larval exuvia); "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,



Figures 17–20. Pupa of *Glyptotus cribratus*, dorsal view (**17**) and ventral view (**18**), pronotum, dorsolateral view (**19**), abdominal apex and urogomphi, dorsal view (**20**). Length of pupa 15.1 mm.

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 log 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, 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, 8iii83, 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

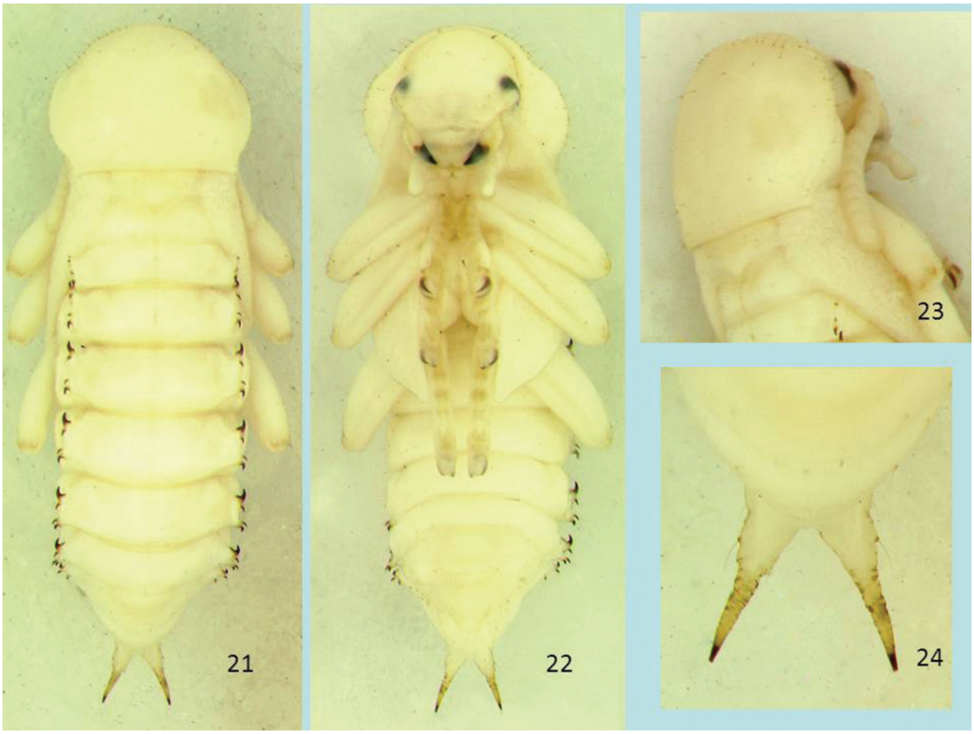
http://species-id.net/wiki/Cibdelis_blaschkei

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-



Figures 21–24. Pupa of *Cibdelis blaschkei*, dorsal view (**21**) and ventral view (**22**), pronotum, dorsolateral view (**23**), abdominal apex and urogomphi, dorsal view (**24**). Length of pupa 16.2 mm.

cling 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.

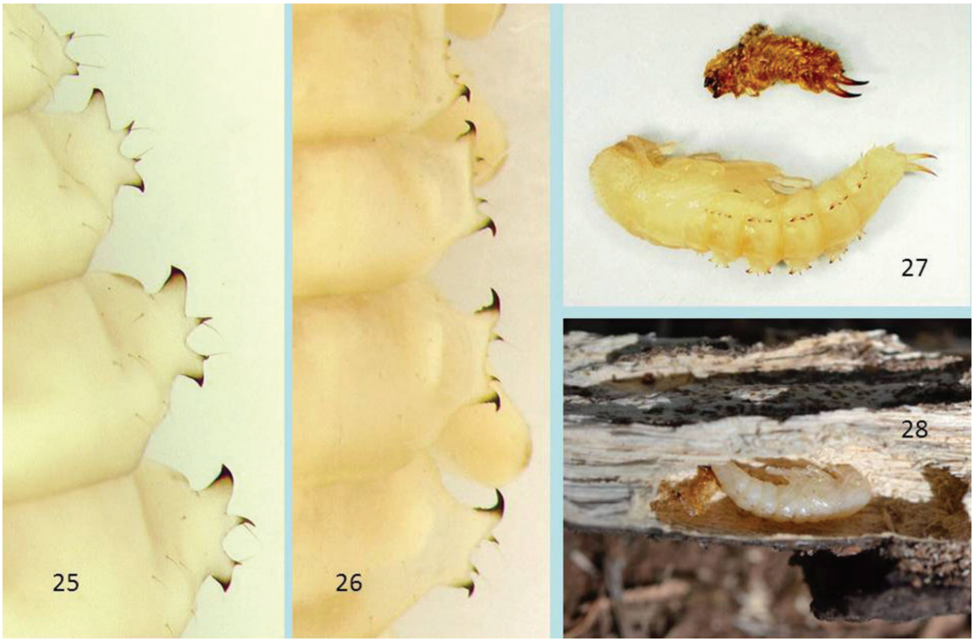
Abdomen. Abdominal segments I-VII similar, slightly wider than long, successive segments gradually slightly wider posteriorly; terga with sparse long setae as on thoracic terga, 9–10 on each side; spiracles annular, broadly ovate; sterna on each side with an anterior row of three fine setae and a pair 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-



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.

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 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

/ 8 Feb. 2003, W. E. Steiner, J. M. Swearingen collectors / In dry rotten wood of recently fallen dead branch of oak" (3 L); "CALIFORNIA: Napa Co., Soda Canyon Road at ravine, NE of Napa, 38°23'06"N, 122°16'51"W, 22 June 2012, In rotten dry wood of fallen oak branch, roadside in open forest" (1 P, partially eaten, larval exuvia not found); "CALIFORNIA: Napa Co., Soda Springs Road NE of Napa, 38°23'28"N, 122°17'07"W, 22 June 2012, coll. W. E. Steiner & J. M. Swearingen, In rotten dry wood of fallen oak branch, roadside in open forest" (1 L); same data except "28 June 2012" (1 L); "CALIFORNIA: Napa Co., Spanish Flat, near Lake Berryessa, 11 April 2008 / pupated 21 April, preserved 29 April 2008 / W. E. Steiner, J. M. Swearingen collectors, In rotten wood of fallen branch of oak on ground (larva)" (1 P); "CALIFORNIA: Napa Co., Yountville, 38°24'N, 122°22'W / 9 Feb. 2003, W. E. Steiner, J. M. Swearingen collectors / In rotten dry wood of fallen branch of *Quercus garryana* among vineyards" (1 L); same data except "In rotten dry wood of recently fallen dead branch of *Quercus garryana* / Reared from larva found 9 Feb. 2003, pupated 23 May (found), preserved 1 June 2003" (1 P); "CALIFORNIA: Napa Co., 3 km NW Yountville, 38°25'01"N, 122°23'58"W, 21 October 2010, coll. W. E. Steiner & J. M. Swearingen / In rotten dry wood of fallen branch *Quercus garryana* among vineyards" (1 L); same data except "38°25'05"N, 122°23'52"W, 25 June 2012 / Found in pupal cell in rotten dry wood of fallen branch *Quercus garryana* among vineyards; (1 P); same data except "preserved 19 July 2012" (3 teneral adults pinned with associated larval and pupal exuvia in gelatin capsule). "CALIFORNIA: Sonoma Co., 1 km N Wikiup, 38°31'33"N,122°45'41"W, 15 October 2009, coll. W. E. Steiner & J. M. Swearingen / In dry rotten wood of recently fallen dead branch of oak" (5 L).

Habitats and observations on life history. 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 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 posess 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.

References

Aalbu RL, Triplehorn CA, Campbell JM, Brown KW, Somerby RE, Thomas DB (2002) Tenebrionidae Latreille 1802. In: Arnett RH, Thomas MC, Skelley PE, Frank JH (Eds) American Beetles, Volume 2. CRC Press, Boca Raton, Florida, 463–509. doi: 10.1201/9781420041231.ch7

Bouchard P, Steiner WE (2004) First descriptions of Coelometopini pupae (Coleoptera: Tenebrionidae) from Australia, Southeast Asia and the Pacific region, with comments on phylogenetic relationships and antipredator adaptations. Systematic Entomology 29: 101–114. doi: 10.1111/j.1365-3113.2004.00230.x

Hoffman RL, Roble SM, Steiner WE (2002) Thirteen Additions to the Known Beetle Fauna of Virginia (Coleoptera: Scirtidae, Bothrideridae, Cleridae, Tenebrionidae, Melyridae, Callirhipidae, Cerambycidae, Chrysomelidae). Banisteria 20: 53–61.

Matthews EG, Lawrence JF, Bouchard P, Steiner WE, Ślipiński SA (2010) Tenebrionidae Latreille, 1802. In: Leschen RAB, Beutel RG, Lawrence JF (Eds) Handbook of Zoology. Volume IV, Arthropoda: Insecta. Part 39. Coleoptera, Beetles. Volume 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter de Gruyter, Berlin, 574–659.

Purchart L, Nabozhenko MV (2012) First description of larva and pupa of the genus *Deretus* (Coleoptera: Tenebrionidae) with key to the larvae of the tribe Helopini. In: Hájek J, Bezděk J (Eds) Insect biodiversity of the Socotra Archipelago. Acta Entomologica Musei Nationalis Pragae 52 (supplementum 2): 295–302.

Schiödte JC (1878) De metamorphosi Eleutheratorum observationes: bidrag til insekternes udviklingshistorie. Pars X. Tenebriones. Naturhistorisk Tidsskrift B 11: 497–598.

Steiner WE (1995) Structures, behavior and diversity of the pupae of Tenebrionidae (Coleoptera). In: Pakaluk J, Slipinski SA (Eds) Biology, phylogeny, and classification of Coleoptera: Papers celebrating the 80th birthday of Roy A. Crowson, 1. Muzeum i Instytut Zoologii PAN, Warsaw, 503–539.

St. George RA (1924) Studies on the larvae on North American beetles of the subfamily Tenebrioninae with a description of the larva and pupa of *Merinus laevis* (Olivier). Proceedings of the United States National Museum 65: 1–22. doi: 10.5479/si.00963801.65-2514.1

Spilman TJ (1979) Larvae and pupae of *Centronopus calcaratus* and *Centronopus suppressus* (Coleoptera: Tenebrionoidae) with an essay on wing development in pupae. Proceedings of the Entomological Society of Washington 81: 513–521.

ZooKeys 415: 329–336 (2014)
doi: 10.3897/zookeys.415.6349
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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

http://zoobank.org/A24B833D-C218-48BE-A63A-A9C1D5A3C5BD

Citation: Yuan C-X, Ren G-D (2014) Note on brachypterous Stenochiini from China (Coleoptera, Tenebrionidae) with description of a new species. In: Bouchard P, Smith AD (Eds) Proceedings of the Third International Tenebrionoidea Symposium, Arizona, USA, 2013. ZooKeys 415: 329–336. doi: 10.3897/zookeys.415.6349

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.

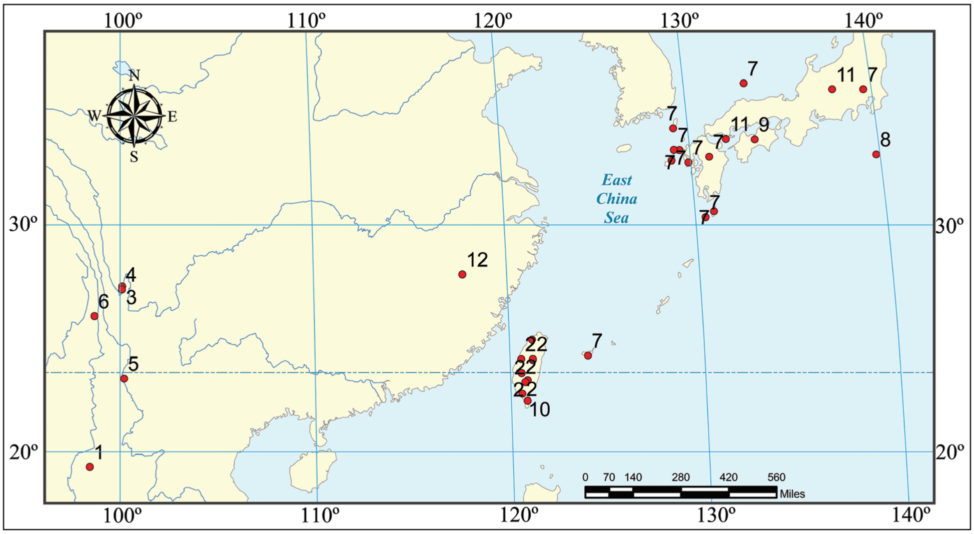
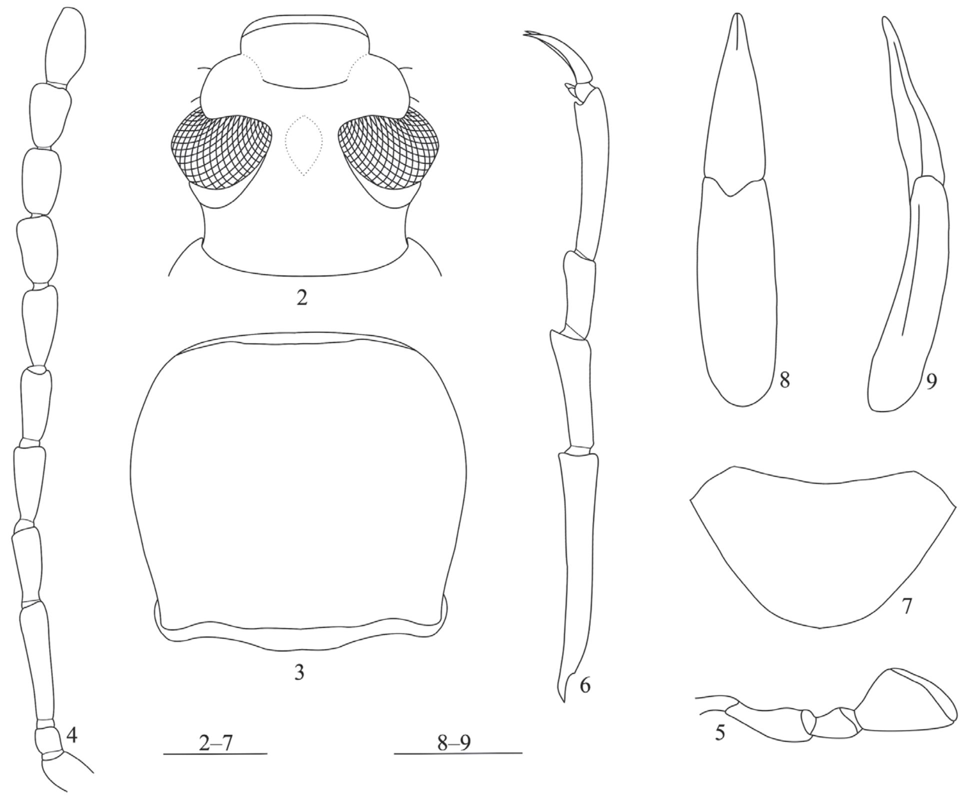


Figure 1. Distribution of brachypterous species of the genus *Strongylium* Kirby from China and neighbouring countries: **1** *S. becvarianum* Masumoto **2** *S. claudum* (Gebien) **3** *S. habashanense habashanense* Masumoto **4** *S. habashanense lijiangense* Masumoto **5** *S. jizushanense* Masumoto **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.

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; frontoclypeal 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-



Figures 2–9. *Strongylium liangi* sp. n. **2** head **3** pronotum **4** antennae **5** maxillary palp **6** hind tibia **7** abdominal ventrite V **8** aedeagus in dorsal view **9** aedeagus in lateral view. Scales: 1 mm.

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

Crossoscelis clauda Gebien, 1914: 53
Strongylium claudum: Masumoto, 1999: 121.

Figures 10–11. Habitus. **10** *S. liangi* sp. n. **11** *S. claudum* (Gebien, 1914).

Material examined. 1♂, Taiwan, Kaohsiung, Xiaoguanshan, 10.xii.1996, Wen-Yi Zhou leg.; 1♂, 1♀, Taiwan, Kaohsiung, Tengzhi, 1.xi.2008, Chang-Qing Chen leg.; 1♂, Taiwan, Pingtung, Erjituan, 5.iv.1997, Wen-Yi Zhou leg.; 1♀, Taiwan, Nantou, Ren'ai, qingjing, 1890 m, 7.v.1996, Wen-Yi Zhou leg.; 1♀, Taiwan, Taipei, Sanxia town, 24.v.1994, Wen-Yi Zhou leg.

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.

Distribution. China: Fujian.

A checklist of brachypterous species of the tribe Stenochiini from China and neighbouring countries

***Eucrossoscelis* Nakane, 1963** [Type species: *Eucrossoscelis broscosomoides* Nakane, 1963]
(1) *araneiformis* (Allard, 1876: 67), Japan (Nagasaki, Ryushu), (= *Strongylium helopioides* Lewis, 1894: 482) [Originally in *Helops*?; synonymized by Chûjô 1985: 65]
(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]
(6) *acco* Masumoto, 1996: 34, Vietnam (Lai Chau)

***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 Ysushima 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)
(20) *marseuli marseuli* Lewis, 1894: 481, Japan (Nagasaki (type locality), SW Honshu, Oki Is., Kyushu, Tsushima, Hirado-jima, Gotô Islands, Koshiki-jima Is., Tanegashima, Ôsumi-kuroshima, Yakushima), (= *apterum* Nomura & Yamazaki, 1960: 14) [synonymized by Nakane 1975: 162]
(21) *marseuli nigripes* Nomura & Yamazaki, 1960: 15, Japan (Hachijô-jima of the Izu Islands)
(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)

***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. Xiu-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).

References

Allard M (1876) Révision des hélopines vrais de Lacordaire. L'Abeille, Journal d'Entomologie 14: 1–80.

Ando K (2003) A new *Strongylium* species (Coleoptera: Tenebrionidae) occurring in Japan. Entomological Review of Japan 58(1): 79–81.

Ando K, Nakahama N (2009) Discovery of the male of *Strongylium tanakai* Ando (Coleoptera: Tenebrionidae). Entomological Review of Japan 64(1): 37–39.

Chûjô M (1978) Tenebrionidae of the Nansei Islands III (Coleoptera). Esakia 11: 63–80.

Chûjô M (1985) Notes on the Japanese Tenebrionidae (Coleoptera). Esakia 23: 61–66.

Gebien H (1914) Sauter's Formosa-Ausbeute. Tenebrionidae (Coleoptera). Archiv für Naturgeschichte A 79(9) [1913]: 1–58.

Lewis G (1894) On the Tenebrionidae of Japan. The Annals and Magazine of Natural History 6(13): 465–484. doi: 10.1080/00222939408677738

Löbl I, Merkl O, Ando K, Bouchard P, Lillig M, Masumoto K, Schawaller W (2008) Tenebrionidae. In: Löbl I, Smetana A (Eds) Catalogue of Palaearctic Coleoptera. Vol. 5. Apollo Books, Stenstrup, 105–352.

Marseul SA de (1876) Coléoptères du Japon recueillis par M. Georges Lewis. Énumération des Hétéromères avec la description des espèces nouvelles. Annales de la Société Entomologique de France (5) 6: 93–142.

Masumoto K (1996) New tenebrionid beetles of the tribes Strongyliini, Misolampini and Adeliini (Coleoptera) from northern Vietnam. Bulletin of the National Science Museum, Tokyo (A) 22: 33–43.

Masumoto K (1999) Study of Asian Strongyliini (Coleoptera, Tenebrionidae) VII. Brachypterous Strongyliines. Elytra, Tokyo 27(1): 113–125.

Masumoto K (2006) Two New Apterous Stenochiines Species from China (Coleoptera: Tenebrionidae: Stenochiini). Entomological Review of Japan 61(1): 69–74.

Masumoto K, Lee CF, Akita K (2007) New Tenebrionid beetles from Taiwan (2). Two new species dedicated to the late Dr. Masataka Satô. Elytra, Tokyo 35(1): 153–158.

Masumoto K, Akita K, Lee CF (2013) New tenebrionid (Coleoptera) beetles from Taiwan (8). Descriptions of six new species and new occurrence records of four species from Taiwan. Elytra, Tokyo, New Series 3(2): 255–273.

Merkl O (1992) Tenebrionidae (Coleoptera) from Laos and Vietnam, with reclassification of Old World "Doliema". Acta Zoologica Academiae Scientiarum Hungaricae 38(3–4): 261–280.

Motschulsky V de (1860) Insectes des Indes orientales, et de contrées analogue. Études Entomologiques 8[1859]: 25–118.

Nakane T (1963) New or little-known Coleoptera from Japan and its adjacent regions, XIX. Fragmenta Coleopterologica 6–7: 26–30.

Nakane T (1975) On the heteromerous Coleoptera occurring in Kyushu including Yakushima and Tanegashima. Memoirs of the National Science Museum 8: 161–172.

Nomura S, Yamazaki H (1960) A new species and two new subspecies of the genus *Strongylium* from Japan (Tenebrionidae). Entomological Review of Japan 12(1): 14–16.

Pic M (1928) Notes et descriptions. Mélanges Exotico-Entomologiques 51: 1–36.

Shibata T (1980) Notes on Tenebrionidae from Taiwan and Japan, III. (Coleoptera). Entomological Review of Japan 34 (1–2): 63–74.

Yuan CX, Ren GD (2006) A new record genus of Strongyliini (Coleoptera, Tenebrionidae) from China, with two new species and two new names. Acta Zootaxonomica Sinica 31(4): 851–854.