CANTHONINI (SCARABAEIDAE: SCARABAEINAE) OF GONDWANA: COMPARISON OF MALE GENITALIA, EVOLUTIONARY TRENDS AND PHYLOGENY

BY

CLAUDIA ALEJANDRA MEDINA URIBE

SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

DOCTOR OF PHILOSOPHY

(ENTOMOLOGY)

DEPARTMENT OF ZOOLOGY AND ENTOMOLOGY

FACULTY OF NATURAL AND AGRICULTURAL SCIENCES

UNIVERSITY OF PRETORIA

To my brother

Jesús Andrés Medina Uribe (1978 – 2012)

“Three things cannot be long hidden: the sun, the moon, and the truth”

Buddha

“Hay tres cosas que no pasan mucho tiempo ocultas: el sol, la luna y la verdad”

Buda

"The impassive skies were neutral, empty, still.
Then something in the inscrutable darkness stirred;
A nameless movement, an unthought Idea
Insistent, dissatisfied, without an aim,
something that wished but knew not how to be,
teased the Inconscient to wake Ignorance.
A throe that came and left a quivering trace,
gave room for an old tired want unfilled,
at peace in its subconscient moonless
caveto raise its head and look for absent light,
straining closed eyes of vanished memory,
like one who searches for a bygone self
and only meets the corpse of his desire"

Savitri Canto 1
The Book of Beginning
Sri Aurobindo

"Los cielos impasibles eran neutros, vacíos, inmóviles

entonces algo se movió en la tiniebla inescrutable;
un movimiento sin nombre, una Idea impensada,
insistente, insatisfecha, sin objeto,
algo que sin saber como anhelaba ser,
hostigo al Inconsciente para despertar la Ignorancia.
Una angustia que vino y dejó una trémula huella
dio lugar a que una vieja necesidad cansada e insatisfecha,
en paz en su caverna subconsciente sin luna,
alzara la cabeza y fuera en pos de una luz ausente,
esforzando los ojos cerrados de una memoria desvanecida,
como alguien que busca lo que fue en otro tiempo
y solo encuentra el cadáver de su deseo"

Savitri Canto 1
El libro de los comienzos
Sri Aurobindo

TABLE OF CONTENTS

Chapter II: Systematics of the southern African genus *Epirinus* Reiche (Coleoptera: Scarabaeinae: Canthonini): descriptions of new species and phylogeny (54–70)

Chapter III: Evolutionary trends and phylogeny of the tribe Canthonini (71–85)

ACKNOWLEDGMENTS

Even though the Acknowledgments appear at the beginning of the text, they have to be written at the end, after the work is done. I am very happy finally to say “thank you” to so many people who have made possible the culmination of this work.

I chose the long path to my Ph.D. My doctoral thesis went through many different stages over many years, and so many people encouraged, advised, and supported me physically and emotionally during this period of my life. The order in which I mention professors, colleagues, friends, family and institutions does not necessarily reflect the importance or quality of their help. The list is long, and I trust that I’ve left no one out.

First, I want to generously thank my director, Prof. Clarke Scholtz, mainly for his patience with a somehow difficult student like I was. From the beginning he was enthusiastic about the project and his agile and effective diligence made possible and eased my arrival to African lands. I am grateful for his confidence in the project, his advice and his unconditional support.

I also want to thank Prof. Chris Chimimba, Director of the Department of Zoology and Entomology of the University of Pretoria, for his crucial support in the completion of this thesis.

I also received decisive support from Juan Carlos Bello, Coordinator of the Gestión de Información y Conocimiento Program of the Alexander von Humboldt Institute; his absolute support was important in the culmination of my thesis.

Bruce Gill has been a very important influence on my evolving knowledge of dung beetles. When I finally came to realize the dimensions of my chosen thesis project, I understood why it was so difficult for me to convince him of my idea. He tried to persuade me to develop a more modest project, but Bruce! My stubbornness was stronger! Thanks for all your help!

The time I spent at the University of Pretoria was stimulating and meaningful in my career as an entomologist, thanks in large part to the interaction with Vasily Grebennikov. From him, I learned enormously about the traditionally European style of pinning insects and storing specimens. He taught me the genitalia cleaning technique and helped me to improve my sketches. Vasily was a good partner and friend during my stay in Pretoria. My research greatly benefitted from his experience. Thank you, Vasia, for the “tea club”, the pizza and the chocolates at the end of the day!

The interaction and friendship with Arturo González and Fredy Molano has been crucial to the development of my ideas about Canthonini tribe systematics. We shared many opinions and long working sessions. I am in debt to Arturo for his support during my leave of absence, and his valuable help in the revision and edition of the final draft of the thesis.

The persistence of Fernando Vaz de Mello in the study of tropical dung beetles provided me with inspiration for the progress of the thesis. We discussed the evolution of the subfamily and shared the discoveries of male genitalia sclerites. I thank him for his answers to my many questions, specimen donation, as well as for critical literature.

Ruth Müller, from the Transvaal Museum, supported my work in different ways; She made my stay at the collection easier and more pleasant and also facilitated the specimen loans. Ruth generously welcomed me to her home when I needed it; her hospitality was unlimited.

I express my gratitude to Riaan Stals (National Collection, South Africa), for the loan of specimens. For the same reason I am also in debt to G. Montheith (Queensland Museum, Australia), Enrico Barbero (Torino University, Italy), Roig-Nuñet (IADIZA, Argentina), Francois Génier (Canadian Museum of Nature, Canada), Estella Monteresinos (Río Cuarto, Argentina), Patricia González (Republic University, Uruguay), and Eric Matthews (South Australian Museum, Australia). Several of them also donated specimens for genitalia dissections.

I am very grateful to Prof. Mario Zunino with whom I shared ideas about the evolution of beetle's genitalia and for his help in reviewing the chapter on genitalia variation. I am also grateful to Keith Philips for his advice in cladistic analysis.

Experiences exchanged with Shaun Forgie, Catherine Sole, Christian Deschodt, Adrian Davis and Ute Kryger were very rewarding for my study. I would also like to thank Ingrid Vis, the secretary of the Department of Zoology and Entomology for her logistic support. Also I am in debt to Carmen Jacobs and Cathy Barnard for all her help with the final process of the thesis.

So many colleagues and friends helped me with this project in different ways. Thanks to: Alberto Ballerio, Xiomara Villalba, Johann Cárdenas, Diana Espitia, Astrid Pulido, Alejandro Lopera, Fernando Fernández, Mila Coca, and Rafael Miranda.

John Miles, an unconditional friend, has contributed enormously to my academic formation with good books and discussions about systematics and evolution. I want to thank him for his constant interest in my academic projects and his valuable help in the editorial review of the final document.

I am in debt to family -- my mother Rosa Matilde Uribe and my father Jairo Medina -- for their unconditional support. Their constant love and presence during my stay in South Africa stimulated me to persevere.

For a long period of time during my doctorate studies, I was a nomad, with no permanent place to call home, so I lived with relatives and friends; I am almost certain that old thesis files still remain in their computers. Thanks to my brothers and sisters and their families: Felipe, Cecilia, Lila, Carolina, Andres, Jhon Jairo and Juan David. Thanks to my grandmother Rosita and my aunt Paty, for all their love and constant support. To Clara Uribe and her family for their hospitality in Popayán. To Ledy Idarraga, Alexandra Medina and Alexandra Bruno for arranging places for me to stay in Cali and Bogotá. I am also grateful to my good friend Lucero Cortez for all her help.

I express gratitude to Guillermo González for his loving support at the end, and to Gloria Saffon and Angela Zuluaga for their friendship, care, and moral support.

Two very important people in my life were also part of this project; Natalia, my daughter, and Fernando Zapata. They supported in the first place my crazy idea of going to South Africa. Thank you Fer for all your help and support, and for letting me express my ideas and hypothesis about Canthonini evolution over lunch; that was probably very boring for you!. To Natica, for her patience and loving support during these years.

AGRADECIMIENTOS

Los Agradecimientos, aunque van al comienzo del texto, se escriben al final, por eso me siento feliz de llegar a esta parte agradable de dar gracias a tanta gente que hizo posible la culminación de este trabajo.

Escogí el camino largo para mi Ph.D. Fue así como la tesis doctoral pasó por diferentes etapas durante varios años, y así también fue mucha y variada la gente que me estimuló, asesoró, y apoyó física y emocionalmente durante esta etapa de mí vida. No necesariamente el orden en que menciono profesores, colegas, amigos, familia e instituciones, tiene que ver con la importancia o calidad de la ayuda. La lista de gente es larga, y espero nadie se quede por fuera.

Quiero dar gracias generosas a mi director profesor Clarke Scholtz, en especial por la paciencia que tuvo con una estudiante tan polémica y de cierta manera difícil, como yo. Desde el inicio tuvo mucho entusiasmo por el proyecto y su ágil y efectiva diligencia hizo posible y más fácil mi llegada a tierras africanas. Le agradezco enormemente la oportunidad que me dio, su confianza en el proyecto, su asesoría y respaldo incondicional.

Además quiero agradecer al Prof. Chris Chimimba, Director del Departamento de Zoología y Entomología de la Universidad de Pretoria, por su crucial apoyo para la culminación de la tesis. Sus mensajes alentadores fueron definitivos.

Recibí significativa colaboración de Juan Carlos Bello, coordinador del programa Gestión de Información y Conocimiento (GIC), del Instituto Alexander Von Humboldt, su apoyo total fueron definitivos en la culminación de la tesis.

Bruce Gill ha hecho parte importante de mi formación y conocimiento en escarabajos coprófagos. Cuando finalmente comprendí la dimensión de la tesis, entendí por que había sido tan difícil convencerlo de este proyecto en la sistemática de los Canthoninos. Él intento persuadirme para hacer un proyecto mas pequeño, pero no, ¡mi terquedad fue mas grande! ¡Gracias Bruce por toda tu ayuda!

La estadía en la Universidad de Pretoria fue estimulante y muy significativa en mi formación como entomóloga, gracias a la interacción con Vasily Grebennikov. De él aprendí mucho sobre el montaje y mantenimiento de especímenes al estilo tradicional europeo. Él me enseñó la técnica de limpieza de la genitalia, y ayudó a mejorar mis dibujos. Vasily fue un gran compañero y amigo durante mi estadía en Pretoria. Mi investigación se benefició mucho de su experiencia. ¡Gracias Vasia por el “tea club”, las pizzas y los chocolates al final del día!

La interacción y la amistad con Arturo González y Fredy Molano han sido cruciales en el desarrollo de las ideas sobre la sistemática de la tribu Canthonini, muchas opiniones y jornadas de trabajo hemos compartido juntos. Estoy en deuda con Arturo por su apoyo durante la licencia laboral y su valiosa ayuda en la edición y revisión de la última parte de la tesis.

La persistencia en el estudio de los escarabajos tropicales de Fernando Vaz de Mello siempre me dio una chispa de inspiración para el desarrollo de la tesis. Con él discutí sobre la evolución de la subfamilia, y compartí los hallazgos sobre los escleritos de la genitalia. Gracias a él por sus respuestas, donación de especímenes y envió de literatura.

Mi amiga Ruth Müller, del Museo de Transvaal, apoyó mi trabajo de diferentes maneras. Ella hizo más fácil y alegre mis estadías en la colección, así como facilitó el préstamo de especímenes. Ruth además me abrió la puerta de su casa cuando la necesite y su generosidad no tuvo límites.

Agradezco a Riaan Stals (Colección Nacional, Sur África) por facilitar el préstamo de especímenes. Por este mismo motivo estoy en deuda con G. Montheith (Museo de Queensland, Australia), Enrico Barbero (Universidad de Torino, Italia), Roig-Nuñet (IADIZA, Argentina), François Génier (Museo Canadiense de la Naturaleza, Canadá), Estella Monteresinos (Rio Cuarto, Argentina), Patricia González (Universidad de la República, Uruguay), y a Eric

Matthews (Museo de Australia, Australia), algunos quienes además donaron material para las disecciones.

Estoy agradecida con el profesor Mario Zunino con quien compartí ideas acerca de la evolución de la genitalia de los escarabajos y su ayuda en la revisión del capítulo sobre la variación de la genitalia. También con Keith Philips por su asesoría en los análisis cladísticos.

El intercambio con mis compañeros Shaun Forgie, Catherine Sole, Christian Deschodt, Adrian Davis and Ute Kryger fue muy productivo para mi doctorado. Agradezco también a Ingrid Vis, secretaria del Departamento de Zoología y Entomología de la Universidad de Pretoria, por todo la colaboración en lo logístico. Estoy en deuda además con Carmen Jacobs y Cathy Barnard for toda su ayuda en el proceso final de la tesis.

Muchos colegas y amigos participaron de alguna manera en la elaboración de la tesis, gracias a Alberto Ballerio, Xiomara Villalba, Johann Cárdenas, Diana Espitia, Astrid Pulido, Alejandro Lopera, Fernando Fernández, Mila Coca, y Rafael Miranda.

A Jhon Miles, amigo incondicional, que ha contribuido a mi formación con buenos libros y discusiones sobre sistemática y evolución, por su constante interés en mis proyectos académicos y por su valiosa ayuda en la revisión editorial del manuscrito final, le estoy muy agradecida.

Estoy en deuda con mi familia, mi madre Rosa Matilde Uribe y mi padre Jairo Medina, quienes me han apoyado totalmente; su constante amor y presencia durante mi estadía en Sur África fue muy estimulante.

Una fase de mi doctorado coincidió con una época nómada de mi vida; por largo tiempo no tuve un lugar fijo para vivir, así que lo hice en casas de familiares y amigos; en el computador de cada una de estas casas seguramente todavía reposa un borrador viejo de la tesis. Gracias a mis hermanos y a sus familias, Felipe, Cecilia, Lila, Carolina, Andrés, Jhon Jairo y Juan David. Agradezco a la abuelita Rosa y la tía Paty por todo su amor y constante apoyo. A Clara Uribe y familia por su hospitalidad en Popayán. A Ledy Idarraga, Alexandra Medina y Alexandra Bruno por proporcionarme sedes indefinidas en Cali y Bogotá. Tambien estoy agradecida con mi buena amiga Lucero Cortez por sus múltiples ayudas.

Agradezco a Guillermo González por su amoroso apoyo en la parte final de la tesis, asi como a Gloria Saffon y a Angela Zuluaga por su amistad, cuidados y respaldo.

Dos personas muy importantes en mi vida hicieron también parte de este proyecto: Natalia, mi hija y Fernando Zapata, ellos me acompañaron en la idea loca de ir a Sur África. Gracias Fer por toda tu ayuda y apoyo, y por dejarme aburrirte a la hora del almuerzo con las hipótesis sobre la evolución de los Canthonines. A Natica por su paciencia y su apoyo en estos años.

GENERAL SUMMARY

The current study is about the evolution and the morphology of dung beetles, subfamily Scarabaeinae. The study includes the systematics of the tribe Canthonini and an exhaustive analysis of the morphological variation of male genitalia including species from the 11 tribes of the subfamily, mainly Canthonini, Ateuchini, Scarabaeini and Coprini. With the aim to go deep in the phylogenetic relationships of the tribe Canthonini, the largest of the subfamily Scarabaeinae, with 91 genera and 875 species, a total of 109 genera, 327 species and 513 specimens were reviewed. The tribe Canthonini is mainly distributed in Gondwana, with species in America, Africa, Madagascar, Australia, New Zealand and the Oriental region. Species of the different regions were included in the detailed examination of male genitalia as well in the cladistic analysis using morphological characters.

Strong evidence of a need for sub-division of Canthonini in natural groups, morphologically and ecologically more solid groups, is one of the main results obtained. Three tribes are proposed, the tribe Byrrhidiini (*Byrrhidium*, *Dicranocara*, *Namakwanus*, and *Versicorpus*), tribe Circelliini (monotypic genus *Circellium*), and the tribe Canthonini, firstly with the American genera (*Canthon*, *Malagoniella*, *Megathopa*, *Megathoposoma*, *Eudinopus*, *Canthonidia*, *Tetraechma*, *Anisocanthon*, *Melanocanthon*, *Sylvicanthon*, and *Hansreia*), as well as the African genera *Gyronotus* and *Anachalcos*. Genera from Madagascar, Australia and the Oriental region should be treated in separate analyses, and probably the pre-established tribes such as Panelini, Epilissini and Mentophilini, could acquire validity in the context of a new classification for these groups currently in Canthonini.

The phylogeny of the genus *Epirinus* and description of six new species is also presented. *Epirinus* is a monophyletic group, although by morphological differences, is not considered under the tribe Canthonini. Equally the genus *Deltochilum* is not considered as part of the tribe Canthonini, since in the phylogenetic analysis of American genera, *Deltochilum* appear polyphyletic, and

this genus deserves a more detailed analysis of its systematics and classification.

Patterns of variation in the genitalia structures, mainly the sclerites, were useful in species separation and to define genera. However, the patterns were not so suitable in setting the limits of the tribes. To date, taxonomists have been trying to fit the whole range of variation in species and genera into a pre-established and limited Scarabaeinae tribal classification. Based on this study the recommendation for a better understanding of the evolutionary history, and to improve the taxonomic classification of the tribe Canthonini and the Scarabaeinae dung beetles, is to study in detail each group, in morphological, molecular and even ecological and biogeographical aspects. Information from these different approaches, will help to establish the borders for the tribes, and therefore to have more accurate classifications.

RESUMEN GENERAL

El presente estudio es acerca de la evolución y morfología de escarabajos coprófagos de la subfamilia Scarabaeinae. Incluye el estudio de la sistemática de la tribu Canthonini y un análisis exhaustivo de la variación morfológica del órgano genital masculino, incluyendo especies de las 11 tribus de la subfamilia; principalmente Canthonini, Ateuchini, Scarabaeini y Coprini. Un total de 109 géneros, 327 especies y 513 especímenes fueron revisados con el fin de profundizar en las relaciones filogenéticas de la tribu Canthonini, que con cerca de 91 géneros y 875 especies, es la más grande de la subfamilia Scarabaeinae. La tribu Canthonini se encuentra distribuida principalmente en lo que se denominó Gondwana, con especies en América, África, Madagascar, Australia, Nueva Zelanda y la región Oriental. Especies de las diferentes regiones fueron incluidas en la examinación detallada de la genitalia y en el análisis cladístico usando caracteres morfológicos.

De los resultados encontrados se evidencia la urgente necesidad de subdividir la tribu Canthonini en grupos naturales, morfológica y ecológicamente mas solidos. Se propone la tribu Byrrhidiini (*Byrrhidium*, *Dicranocara*, *Namakwanus*, y *Versicorpus*), la tribu Circelliini (género mono-típico *Circellium*), y la tribu Canthonini, inicialmente incluyendo los géneros americanos (*Canthon*, *Malagoniella*, *Megathopa*, *Megathoposoma*, *Eudinopus*, *Canthonidia*, *Tetraechma*, *Anisocanthon*, *Melanocanthon*, *Sylvicanthon*, y *Hansreia*), además de los géneros africanos *Gyronotus* y *Anachalcos*. Géneros de Madagascar, Australia y la región Oriental deben tratarse en análisis separados, y muy probablemente las tribus previamente establecidas como Panelini, Epilissini y Mentophilini podrían tener validez en el contexto de una nueva clasificación para estos grupos actualmente en Canthonini.

Se presenta además, la filogenia del género *Epirinus* con la descripción de seis nuevas especies. *Epirinus* es un grupo mono-filetico, sin embargo, no se considera parte de la tribu Canthonini por diferencias en la morfología. Igualmente el género *Deltochilum* no se considera como parte de la tribu

Canthonini, en el análisis filogenético de los géneros americanos, *Deltochilum* aparece poli-filetico, lo que amerita un análisis más detallado de su sistemática.

Patrones de variación en las estructuras de la genitalia, principalmente de los escleritos, mostraron ser útiles para separar especies y definir géneros. Sin embargo, no se observaron patrones de variación que soporten la delimitación de las tribus. Hasta ahora taxónomos han tratado de ajustar todo el rango de variación en especies y géneros dentro de una pre establecida y limitada clasificación de las diferentes tribus de la subfamilia. Basado en este estudio, la recomendación para un mejor entendimiento de la historia evolutiva y para mejorar la clasificación de la tribu Canthonini y de los escarabajos coprófagos Scarabaeinae en general, es estudiar en mas detalle cada grupo y entender la variación en sus aspectos morfológicos, moleculares y más aun ecológicos y biogeográficos. Información desde estas diferentes aproximaciones ayudará a establecer los bordes de las tribus y así tener clasificaciones mas acertadas.

GENERAL INTRODUCTION

Systematics, Ecological, and Evolutionary Background

The tribe Canthonini van Lansberge 1874, is the largest of the subfamily Scarabaeinae, with 45% of the genera. It contains 91 genera and approximately 875 currently described species. It is widely distributed in the regions that were part of Gondwana: South America, Africa, Australia, Madagascar, New Zealand, Indochina, New Caledonia, New Guinea, and Sumatra (Cambefort 1991). Under the tribe Canthonini have been grouped genera from all these geographical regions considered to be roller dung beetles that have somewhat similar morphology, i.e., mostly elongated medial and posterior legs. Nevertheless, the variation in leg morphology within and among all these genera is enormous. Furthermore, Canthonini, as a whole, cannot be considered to be a "roller dung beetle tribe". Only one group of genera are true rollers; others do not make or roll balls of dung. For most of the genera the feeding and nesting behaviour is still unknown.

The canthonines have diverse morphologies, reproductive strategies and feeding specializations. They are associated with different types of ecosystems, that include savannas, dry and humid tropical forest, deserts and relictual biomes. Furthermore, members of the tribe have different distributional and geographical patterns influenced by climate change and historical affects such as Mesozoic and Cenozoic events (Davis & Scholtz 2001, Davis *et al.* 2002).

All the climate changes and tectonic movements that occurred during the Cenozoic era have affected the evolution of dung beetles. Regression of forests, the expansion of grasslands and the movement of the continents with the separation of South America from Africa, the isolation of Australia, and connections and disconnections between Africa-Eurasia and Eurasia-North America are directly related to the evolutionary history of the subfamily Scarabaeinae (Cambefort 1991). The current distribution of the different groups of dung beetles somehow reflects this history. Two tribes, Canthonini and Ateuchini Castelnau 1840, (previously known as Dichotomiini Pereira 1954, see

Montreuil 1998) are mainly distributed in the southern hemisphere, more precisely in the continents that were part of Gondwana. These two groups have been considered sister groups and the oldest in the evolution of the subfamily (Cambefort 1991, Philips *et al.* 2004, Sole *et al.* 2011).

The beetles, in general, are an old group, arising nearly 250 million years ago (Cambefort 1991). The minimum age for a Scarabaeoidea, deduced from the fossil record, is 152 myr, and there is evidence for the origin of the family Scarabaeidae dating from the Upper Cretaceous (Krell 2000, 2006). Despite the large number of described fossils of Scarabaeoidea, 244 species (Krell 2000), there is insufficient information to elaborate the evolutionary history of the group from ancient times, especially from the mid Mesozoic to the Cenozoic era. As stated by Krell (2006), the ground plan for the basal Scarabaeinae is still a mystery, and their appearance and what prepared them morphologically for the explosive radiation of the group after the mammals´ expansion, is still unknown (Scholtz *et al.* 2009). The oldest Scarabaeinae fossil similar in appearance to a modern Scarabaeinae is *Prionocephale deplanate*, found in the Lanxi formation in Zhejian, China, (Krell 2006). Although the fossil resembles a modern Scarabaeinae dung beetle, according to Krell (2006), similar to an Onthophagini or a telecoprid, the age does not to agree with the evolutionary history of the group, as other fossils of similar age have a different body shape, not similar to those of extant dung beetles (Krell 2006, Scholtz *et al.* 2009). According to the fossil record, and from molecular estimates of divergence times, the indicated time for the origin of the dung beetle lineages, which include Scarabaeinae and the sister sub-family Aphodiinae, is 65 mya (Cambefort 1991, Krell 2000, Sole & Scholtz 2010).

Although some authors have proposed the association of dung beetles with dinosaur dung, which would mean that they were well established in the dinosaur era (Jeannel 1942, Chin & Gill 1996), most of the evidence shows dung beetles radiating in the Oligocene period, about 30 mya (Krell 2006, Scholtz *et. al.* 2009); it has been assumed that dung beetles evolved in association with the radiation of the large mammals in Africa (Sole & Scholtz 2010) in response to large quantities and diversity of mammalian dung (Davis *et al.* 2002, Scholtz *et al.* 2009). Different fossils of extant dung beetles such as *Anachalcos, Copris,* and *Metacatharsius,* have been recorded from the Miocene of Rusinga and Mfangano island in lake Victoria, Kenya (Kreel 2006). Sole & Scholtz (2010) indicated that the most recent dung beetle ancestor may have originated around 40 mya. For some groups such as the tribe Scarabaeini, a Miocene age was recorded (Forgie *et al.* 2006); the Madagascan tribe Helictopleurini, has been dated back to between 37 and 23 mya (Wirta *et al.* 2008); and to 56 mya for the origin of the ancient tribes Canthonini and Ateuchini (Sole & Scholtz 2010).

The first fossils related to an extant canthonine, fossil dung balls in a nest from a beetle similar to the genus *Megathopa* Eschscholtz 1822, dating from the lower Oligocene, were discovered in the Patagonian desert (Cambefort 1991). Also dung beetle fossil balls of different ichnospecies of *Coprinisphaera* have been recorded from trace fossils of South American Cenozoic (Genise *et al.* 2004, Laza 2006). A bispherical brood ball related to an extant species of *Canthon* Hoffmannsegg 1817, dating from the early Pleistocene, is described from Sanandresians Aridosols from the Pampean region in Argentina (Cantil *et al.* 2013).

Although it has been widely affirmed that tribes distributed in the southern hemisphere, such as Canthonini and Ateuchini, had a Gondwana origin (Philips *et al.* 2004, Monaghan *et al.* 2007), the separation of the continents of Gondwana began at the end of Cretaceous, long before dung beetles had become well established. Paulian (1987) proposed that Canthonini had colonized Madagascar during Cretaceus: However, Orsini *et al.* (2007), based on molecular distances, calculate a Miocene origin (13 mya) for the tribe in the island. As discussed by Scholtz *et al.* (2009), one or several dispersals, instead of vicariance events, could be the explanation for the presence of Canthonini and the absence of Ateuchini in the island. However, this is not consistent with the hypothesis of dung beetle fauna in Mesozoic Gondwana vicariance (Davis *et al.* 2002).

In spite of different questions around the evolutionary history of the subfamily Scarabaeinae having been investigated -- as whether the group has a late Mesozoic or a Cenozoic origin; whether the current geographical distribution of the different tribes corresponds to a more Gondwana origin; or whether distribution is due to a vicariance or to dispersal events -- there is no single explanation. All these matters have been addressed from different perspectives, including the fossil record (Halffter & Matthews 1966, Krell 2006), evolutionary trends in feeding habits (Scholtz & Chown 1995), biogeographical and distributional analysis (Davis & Scholtz 2001, Davis *et al*. 2002), and from molecular distances calculations (Orsini *et al*. 2007, Wirta *et al.* 2008, Sole & Scholtz 2010). However, at present, there is no generally accepted explanation of the historical evolution of such a complex group as the dung beetle subfamily Scarabaeinae. One plausible hypothesis for the origin and evolution of dung beetles is that it occurred in Africa together with the radiation and dispersal of mammal groups (Sole & Scholtz 2010), but possibly with a later further taxonomic radiation in each region. Nevertheless, more evidence is necessary to explain the whole process of origin and dispersal of the groups from Africa to the rest of the world.

The geological history, landscape, and climatic conditions differ among the continents and so do the groups. Tropical forests are vast in America, while savannas are more common in Africa and Australia. The groups we see today are the products of their evolutionary history, as influenced by the transformations of the regions and habitats where they are distributed. For the discussion of the antecedents of the tribe that follows, I will describe the particularities of the Canthonini beetles in each of the regions.

American Canthonines

The tribe Canthonini is the largest group of dung beetles in tropical America. It is highly heterogeneous with many atypical mono-specific genera and others with numerous species. There is also large variation in body size, with species 1.7 mm long to species 45 mm long. Morphological variation is also wide and includes species of the more typical Canthonini, with enlarged legs and more rounded body (e.g., such as *Canthon* and related genera) and species with flattened bodies and tubercles on the elytra and with different types of legs (e.g., *Eudinopus* Burmeister 1840 and *Scybalophagus* Martínez 1953).

The tribe occupies almost all of the different types of habitats in the Americas; species can be found in lowland forests, open grassland, and high (up to 4000 m) in the mountains, as is the case of *Scybalophagus*, distributed in the high Andes of Chile and Argentina (Ocampo & Molano 2011). *Malagoniella* Martínez 1961 and *Scybalocanthon* Martínez 1948 are widely distributed at low elevation in dry and humid forests of Central and South America. *Canthon* and *Deltochilum* Eschscholtz 1822, the two most abundant genera in the tribe are widely distributed in dry and moist forest; some species of *Canthon* also occupy open savannas, but most of the species are restricted to forest below 1800 m. Species of *Deltochilum* are widely distributed in low tropical forest, especially the *D. pairle* group; however, in montane forest, up to 2800 m, *D. hypponum* (Buquet 1844) can be found (Medina *et al.* 2002, González *et al.* 2009).

The tropical forests in America represent one of the largest extensions of forests in the world. They are considered to be the centre of evolution and diversification of some Scarabaeinae phyletic lines (Halffter 1991). Different genera of Canthonini, such as *Canthon*, *Deltochilum*, *Scybalocanthon*, and *Sylvicanthon* Halffter & Martínez 1977 are mainly associated with this ecosystem. Their strategy of dung search and behaviour directly reflects their association with and diversification into this habitat (Halffter 1991, Gill 1991, Padilla & Halffter 2007).

The groups of beetles associated with wet tropical forest ecosystems are mainly coprophagous dung beetles, but some necrophagous or even predatory species include some exceptional specializations. Species of *Canthon* are able to find and follow, either by visual or auditory cues, troops of monkeys, and some species that are consider arboreal make and roll balls of dung on leaves (Gill 1991, Castellanos *et al.* 1999). In species of *Canthon* (subgenus *Glaphyrocanthon* Martínez 1948), after rolling the ball on a leaf, they drop to the ground along with the ball (Gill 1991, Vaz de Mello 1999). Halffter & Matthews

(1966) reported that *C. subhyalinus* Harold 1867 have been collected from the anal hair of monkeys of the genera *Allouata* and *Callibaceus*. *Canthon politus* Harold 1868 and *Canthon columbianus* Schmidt 1920 have been observed in the mountains of Colombia rolling balls on the leaves with dung of howler monkeys *Allouata paliata* and *A. seniculus* (Medina *et al.* 2002). Gill (1991) describes how thousands of *Canthon angustatus* Harold 1867 formed a cloud of flying beetles under the tree attracted to the early morning defecation of a troop of *A. palliata*. This type of resource utilization is not exclusive to *Canthon*; different researches have documented the strategy of the utilization of dung from the canopy leaves. Vaz de Mello & Louzada (1997) reported four species of Canthonini from the genera *Canthon*, *Sylvicanthon*, and *Deltochilum* to be collected mostly in aerial traps.

Some species are scavengers, preferring carcasses to dung, as is the case with many species of the genera *Deltochilum* and *Canthon*. However, they do not feed exclusively on dung or carcasses; some species generally known to be scavengers can shift to feeding on dung when the availability of carrion is low. This kind of shift in feeding behaviour is more common in the tropical forest where food resources can be scarce, patchy, and ephemeral. Some species of *Deltochilum* are specialist predators on millipedes, and the predatory behaviour has been documented for *D. cupreicolle viridescens* Martínez 1948 in Brazil (Silva *et al.* 2012), in the *Deltochilum valgum* group in Guatemala (Cano 1998), and in *Deltochilum kolbei* Paulian 1938 (Halffter & Matthews 1966). Several species of *Canthon* from Brazil are reported to kill reproductive *Atta* ants and use them as carrion (Hertel & Colli 1998). Some other Canthonini, mainly the smaller ones are associated with vegetable debris (decaying fruit, rotten seeds, and dry fungi), e.g., *Canthon leechi* Martínez Halffter & Halffter 1964 and *Deltochilum fuscocupreum* Bates 1870, have been reported feeding on fungus (Halffter & Matthews 1966).

Other alternative food resources for dung beetles include non-mammalian vertebrate dung such as iguana and boa constrictor faeces; *S. moniliatus* (Bates 1887) were trapped on iguana dung on Barro Colorado Island (Young 1981). *C. lamprimus* Bates 1887 were collected on toad faeces (Gill

1991) and canthonines were reported by Halffter & Matthews (1966) using bird droppings.

The tribe in America has a large number of monotypic genera. Some of them have been considered isolated, not showing similarities with the rest of the genera of the tribe. One of the monotypic genera is *Eudinopus*, which lives in the Andean-Patagonian steppes in southern South America (Halffter & Martinez 1966). This species is considered rare, as it has been poorly collected. In addition, little is known of its biology and the species was believed to be extinct since it was not collected for more than 20 years (Monterresinos com. pers.). However, the species was observed and collected in the summer of 2002 in the prairies of Nihuil, Mendoza Province, Argentina (Medina & Scholtz personal observations) and has been recently reported from Bolivia (Vidaurre *et al.* 2009). Other monotypic genera include *Canthotrypes* Paulian 1939, *Xenocanthon* Martínez 1952, *Hansreia* Halffter & Martínez 1977, and *Streblopus* van Lansberge, 1874, but they are also, rarely collected, and poorly studied.

Genera with a large number of species such as *Canthon* and *Deltochilum*, with approximately 189 and 84 described species, respectively, have been better studied, although their taxonomy is also very complex and still not well understood (Medina *et al.* 2003). For the genus *Deltochilum*, which represents a more solid group than *Canthon,* some progress in its taxonomy had been achieved recently (González *et al.* 2009, Génier 2012).

The literature on the American Canthonini is vast. Researchers such as G. Halffter, A. Martinez, F. Pereira and others studied the tribe in America. They described species, genera and reviewed some groups within the tribe (Halffter 1958, 1961, Martínez 1948, 1950, 1952, 1954a, 1954b, Pereira 1953, Pereira & Martínez 1956, 1959). In 1966, Halffter and Martínez began what they called a “monographic revision of the American Canthonines”. In this work, which was subsequently published in four parts (1966, 1967, 1968, 1977), the authors proposed to standardize the criteria for delimiting the genera and subgenera of the subtribe Canthonina. More recently Medina *et al.* (2003) studied the systematics of the genus *Canthon*, the largest in the tribe in America and some other, related genera. In this work the authors revealed some systematics problems within the tribe and with some important genera, which appear not to be monophyletic groups of species.

More recently, some American genera have been studied: *Deltochilum* (González *et al.* 2009), *Scybalophagus* (Ocampo & Molano 2011), and new taxa have been described as new species in *Scybalocanthon* (Molano & Medina 2010, Silva 2011), *Deltochilum* (González *et al.* 2009, Genier 2012), and in *Cryptocanthon* Balthasar 1942 (Arias & Medina In Press). The phoretic land snails genus *Zonocopris* Arrow 1932, was reviewed by Vaz de Mello (2007), He found this genus related to the genera *Cryptocanthon*, *Paracryptocanthon* Howden & Cook 2002 and *Bdelyrus* Harold 1869. The species *Z. machadoi* Vaz de Mello 2007, was described in the same paper.

Genera considered as Canthonini were transferred to other tribes; *Sinapisoma* Boucomont 1928 is now part of the tribe Ateuchini (subtribe Ateuchina), and the genus *Holocanthon* Martinez & Pereira 1956 was transferred to Coprini Leach 1815, (Vaz de Mello 2008). In the same work, Vaz de Mello, based on a phylogenetic analysis, proposed the genera *Anomiopus* Westwood 1842, *Scatonomus* Erichson 1835, and *Hypocanthidium* Balthasar 1938 to be Canthonini and not Ateuchini. The most recently described genus included in Canthonini is *Tesseredoniella* (Vaz de Mello & Halffter 2006). This genus, with two species, is considered more similar to the Australian genera *Tesserodon* Hope 1837 and *Aptenocanthon* Matthews 1974, and not related to other new world Canthonini. It was provisionally placed in Canthonini.

African Canthonines

Contrary to what happened in America, where the tribe is widespread throughout the continent, the tribe in continental Africa has a relictual pattern. Except for the genus *Anachalcos* Hope 1837, which is widely distributed throughout the continent, most genera are restricted to the southernmost part of Africa (Scholtz & Howden 1987b, Davis *et. al.* 2001, Deschodt & Scholtz 2008, Deschodt *et al.* 2011). Competition between the canthonines and modern rollers, such as the tribes Scarabaeini, Gymnopleurini, and Sysyphini, and their inability to occupy the driest habitats have certainly caused the regression of canthonine beetles as such in Africa.

The tribe in Africa comprises 22 genera and 97 species, counting the taxa described in the last decade, including six flightless, newly described genera: *Dicranocara* Frolov & Scholtz 2003*, Aliuscanthoniola* Deschodt & Scholtz 2008*, Dwesasilvasedis* Deschodt & Scholtz 2008, *Parvuhowdenius* Deschodt & Scholtz 2008*, Nebulasilvius* Deschodt & Scholtz 2008, and *Versicorpus* Deschodt, Davis & Scholtz 2011, and new species in these and other genera were been described; *Anachalcos* (Josso & Prévost 2001), *Epirinus* Reiche 1841 (Medina & Scholtz 2005), *Namakwanus* Scholtz & Howden 1987, *Dicranocara* (Frolov & Scholtz 2005, Deschodt *et al.* 2007, 2011), and *Gyronotus* van Lansberge 1874 (Moretto & Perissonotto 2013).

In general, most of the genera of African canthonines are comprised of medium- to small-sized beetles. There are some genera of small beetles, such as *Odontoloma* Boheman 1857, *Bohepilissus* Paulian, 1975 *Outenikwanus* Scholtz & Howden 1987, *Endroedyolus* Scholtz & Howden 1987, and *Peckolus* Scholtz & Howden 1987, with species between 1.7–3.5 mm long. Other genera have medium-sized to large members, such *Gyronotus*, *Circellium* Latreille 1825, *Anachalcos*, and *Canthodimorpha* Davis Scholtz & Harrison 1999. Species of the genus *Epirinus* are small- to medium-sized beetles. Various genera have wingless members, and it is mainly the small Canthonines that have some features that distinguish them from the rest of the genera of the tribe. Some are hairy with a densely punctuate body surface. The aedeagus of most of them has asymmetrical parameres. The genera *Epirinus* and *Odontoloma* comprise numerous species: *Epirinus* with 29 (Medina & Scholtz 2005), and *Odontoloma* (Scholtz & Howden 1987b) with 21. Certainly after a careful revision of *Odontoloma* the number of described species will greatly increase, as in *Epirinus*. These two genera are mainly forest specialists, distributed in small forest patches. Other than these two genera, most of the African Canthonini are monotypic or with few species. Most of the remaining genera are forest specialists, distributed along the mountains and coastlines of southeastern Africa between the Western Cape Province in South Africa and the east Usambara mountains in Tanzania (Deschodt & Scholtz 2008, Mlambo *et al.* 2013).

Another group classified as Canthonini is the genera of flightless, specialized species, associated with rocky hyrax middens (*Procavia capensis*). They are distributed in the arid areas from the southwestern part of South Africa including Namaqualand and Namibia (Deschodt *et al.* 2007). These genera that include *Byrrhidium* Harold 1869, *Namakwanus, Dicranocara* and *Versicorpus*, share morphological and behavioural features that make them different from the other genera of the tribe Canthonini. Despites these species have been however classified as Canthonini, based in the results of the present analysis, I suggest this group placed in a separate tribe, because of differences in mouthparts and male genitalia, which make them the only Scarabaeinae beetles with these unique features and different from other Scarabaeinae dung beetles including *Coptorhina* Hope 1830. Also they are an ecologically functional group that occupies a specific habitat and niche (see Byrrhiidini, for further discussion). The other group is restricted to the patchy and relictual forest, distributed from the Cape peninsula in southwestern South Africa to Kwazulu-Natal in the east. It includes the small genera of African dung beetles more closely related to other tribes of the subfamily than the larger, typical roller Canthonini (Deschodt & Scholtz 2007).

With the exception of the monotypic genus *Circellium*, whose biology, distribution, and conservation status have been extensively documented in the last decade (Kryger *et al.* 2006), the biology and habits of most African Canthonines are not well known. *Circellium bacchus* (Fabricius, 1781) is the largest flightless roller dung beetle which is now restricted to a few isolated fragments in the Cape provinces in South Africa. The species has a preference for buffalo and elephant dung. It has the lowest fecundity recorded for a dung beetle, with the average of one progeny produced per year. Their conservation status is considered vulnerable as the species depends on dung of two large herbivores (elephant and buffalo), which are restricted to conservation areas (Kryger *et al.* 2006).

Cambefort (1978), Scholtz & Howden (1987a, 1987b), Davis *et al.* (1999), Medina & Scholtz (2005), and more recently Deschodt *et al.* (2007, 2008, 2011) have studied African Canthonini from a taxonomic perspective. Since the revisions of African Canthonini by Scholtz and Howden (1987a, 1987b) it has been said that the tribe in Africa is not a monophyletic group; rather that it is comprised of different ancient groups that probably gave origin to more modern groups of the tribe in other geographical regions.

Madagascar Canthonines

Madagascar is one of the hotspots of global biodiversity. It has a large number of endemic groups, even at higher taxonomic levels, mainly explained by its long isolation (Myers *et al.* 2000). It is a large island, of 587,000 km^2, which became separated from Africa 160 million years ago and from India 80 million years ago. The dung beetle fauna (Scarabaeinae) in Madagascar, endemic at subtribal and generic level (Lebis 1953, Paulian & Lebis 1960), is dominated by two taxonomic groups: Canthonini and Helictopleurini. Madagascar lacks native ungulates and dung beetles have coevolved with lemurs, the diverse group of primates endemic to the island (Goodman & Granzhorn 2004, Wirta *et al.* 2008). In contrast to Africa, where dung beetles are more associated with open grassland and use dung of large herbivores and omnivores, in Madagascar native dung beetles occur in forests, associated with lemur dung and carrion (Koivulehto 2004, Wirta *et al.* 2008).

There is a sound taxonomic knowledge of Malagasy canthonines. The taxonomy was revised in the 1950´s and 1960s´ by Lebis (1953), and Paulian (1975, 1976) and Paulian & Lebis (1960). Subsequent works of Paulian increased the number of described genera and species (Paulian & Cambefort 1991), and more recently the “Metapopulation Research Group” from the University of Helsinki, has sampled and studied the Malagasy dung beetle fauna from different points of view: taxonomic (Montreuil 2003a, 2003b, 2004, 2005a, 2005b, 2006, 2008a, 2008b), biological, ecological (Wirta 2009), and molecular (Orsini *et al.* 2007, Koivulehto 2004; Viljanen, 2004, Montreuil & Viljanen 2007, Wirta & Montreuil 2008, Viljanen *et al.* 2010).

The number of described species of canthonines in Madagascar is greater than in the whole of Africa: 13 genera and 191 species versus 22 genera and 95 species on the mainland. The community of Malagasy canthonines is made up of small- to medium-sized beetles (2-14 mm), more associated with wet forest than to open grassland (Wirta *et al.* 2010). As in the Americas, there are a few genera with large numbers of species, such as *Arachnodes* Westwood 1847 (71), *Epactoides* Olsoufieff 1947 (37), and *Nanos* Westwood 1847 (30), and others with few species. Species of these genera are typical roller dung beetles associated with the inner forest of Magadascar, using mainly lemur dung, carrion, and debris for subsistence (Viljanen *et al.* 2010). Similarities between the genera from the Americas and from Madagascar have been documented in relation to the food relocalization and breeding, as with the similarities reported for *Nanos viettei* (Paulian 1976) and *Canthon cyanellus* Leconte, 1859 (Viljanen 2009). One species of *Arachnodes*, *A. vicinus* (Castelnau 1840) has been observed gathering dung on leaves and dropping to the ground, as many species of *Canthon* in America do. Species of *Arachnodes* are mostly collected in traps set above the ground instead of ground traps, which suggests an association with the dung of animals in the canopy (Wirta *et al.* 2010).

The canthonines of Madagascar were divided into two groups according to the size of the first metatarsus in relation to the second. Hence, the groups were denominated brevitarsi and longitarsi (Paulian 1975, 1976). The longitarsi group is comprised of species with the first metatarsus longer than the second, and included five genera that were posteriorly synonymized with the genus *Epactoides* (Wirta & Montreuil 2008). This character is also present in the Oriental genus, *Ochicanthon* Vaz de Mello 2003, which suggests a probable relationship of this genus with the group longitarsi (Wirta & Montreuil 2008). The brevitarsi were integrated for the rest of the genera with the first metatarsus shorter that include *Epilissus* Reiche 1841, *Arachnodes*, *Cambefortantus* Paulian 1986, among others, that are a part what had been called the tribe Epilissini (Lansberge 1874). A systematic analysis using molecular data proposes three lineages for Malagasy canthonines: one is formed by *Epactoides*. Another formed by *Apotolampros* Olsoufieff 1947 and *Nanos*, where the morphologically similar genus *Cambefortantus* would also be included. The third group includes *Arachnodes* and *Epilissus* species (Wirta *et al.* 2010). The phylogenetic relationships of canthonines of Madagascar with the rest of Canthonini and with other tribes of Scarabaeinae remain unresolved. Although some relationships have been documented among the groups of Madagascar with the Australasian genera such as *Onthobium* Reiche 1860, *Lepanus* Balthasar 1966, *Panelus* Lewis 1895, and *Saphobius* Sharp 1873 (Montreuil 2008a).

Australian Canthonines

Currently in the Australian region 29 genera and 167 species are recognised, including the genus *Amphistomus* van Lansberge 1874, which was previously included in the tribe Sisyphini (Matthews 1974). The Australian canthonines were known as the Mentophilides, a name that Lansberge (1874) gave to differentiate Australian canthonines from the rest. Despite this suggestion, the category was dropped in Janssen's (1949) classification. Matthews (1974) suggested the taxon "Mentophilina" to classify the Australian genera that have the pseudoepipleura outside the seventh striae and have simple claws. The group also presents atypical features such as pronotal carinae, tubercles, and tibiae dilated distally. Some members of the group are flightless and unable to make balls. Other species, however, can roll marsupial, sheep, and rabbit pellets (Matthews 1974). This group includes the genus *Cephalodesmius* Westwood 1841, which process leaves and other plant materials to construct brood balls. This species has a particular mode of nidification, with biparental care and a division of labour by sex (Monteith & Storey 1981). The other group has simple elytra and dentate or subdentate claws, and have the external appearance of a "typical" canthonine. Members of this group make balls and their behaviour is more similar to the American groups (Matthews 1974).

Most of the Australian canthonines are small- to medium-sized beetles. The group includes many species with reduced wings, covering a whole range in wing reduction to completely atrophied anterior wings. Most of the species are distributed near the coastline in wetter and warmer areas, occupying different vegetation communities that include shrubs and closed and open coastal forest. The drier central part of Australia is mostly inhabited by Canthonini beetles; only a few species from the genera *Coproecus* Reiche 1841, *Mentophilus* Laporte de Castelnau 1840 and two species of *Tesserodon* Hope 1837 are the only species adapted to the dry areas in the central part of the continent (Matthews 1974).

In general, Australian canthonines are coprophagous, but species of *Boletoscapter* Matthews 1974, *Tesserodon*, and *Mentophilus* have been recorded under mushrooms, and the genus *Ignambia* Heller 1916 has been collected in leaf litter (Matthews 1974).

The taxonomy and systematics of the tribe Canthonini were studied by E. G. Matthews (1974). He extensively reviewed the Australian canthonines under the designation of subtribe Canthonina, subtribe of Scarabaeini. In this paper he described three genera and 52 species. Since he had studied the canthonines of the Antilles (Matthews 1966) he compared the canthonines of these two regions. He suggested that the canthonines must have been derived from ancestors that invaded Australia probably in the early Cretaceous, perhaps together with the early marsupials. He also thought that the Australian Canthonines are most closely related to the American taxa, rather than African or Madagascar ones. This extensive document (Matthews 1966) also includes species distributions and notes on the behaviour of Australian Canthonines, and has proved a good base for the later studies in the group.

Isolated works have dealt with individual genera such as *Aptenocanthon* (Storey 1984, Storey & Monteith 2000), *Aulacopris* White 1859 (Storey 1986), *Tesserodon* (Storey 1991), *Temnoplectron* Westwood 1841 (Reid & Storey

2000, Bell *et al.* 2004), and *Lepanus* (Matthews & Weir 2002).

Oriental Canthonines

Canthonines in the Oriental region are characterized by small and some flightless endemic species, most associated with relictual forest and low altitude montane forest. Species of *Ochicanthon* are moist forest dwellers with some wingless endemic species (Latha *et al.* 2011); for example, some species of *Ochicanthon* and *Panelus* Lewis 1895 had restricted distributions in the Western Gaths in India, an ecoregion catalogued as one of the hotspots of biodiversity in India and well known for high endemism and species richness (Sabu *et al.* 2011a, 2011b)

In the Oriental group of canthonines are some genera that have suffered successive taxonomic changes among the tribes Canthonini, Onthophagini, and Alloscelini, such as the genera *Cassolus* Sharp, 1875 and the genus *Haroldius* Boucomont 1914. *Haroldius* was left in Canthonini by Krikken & Huijbregts (2006), as proposed by Paulian (1985). Despite that *Haroldius* is a large genus, with more than 30 species, little is known about its biology and larvae are unknown. Adults are soil and litter occupants and some species have been reported associated with ants and termites. They have some morphological adaptations, i.e., the loricate structure and flattened tibiae to favour the association with social insects (Krikken & Huijbregts 2006).

Some other oriental genera have been studied; the genus *Falsignambia* Paulian 1987 species of *Anonthobium* Paulian 1984 were described from New Caledonia (Paulian 1987). One recently studied Oriental genus is *Ochicanthon* (Vaz de Mello 2003) [*Phacosoma* (Boucomont 1914)]. With 39 species, the genus is widely distributed in Sundalan (Krikken & Huijbregts 2007) and India (Latha *et al.* 2011). The genus *Haroldius* has been re-diagnosed and its relationships with related genera are discussed in Krikken & Huijbregts (2006). More recently Tarasov & Keith (2011) described one species of the genus *Parachorius* Harold, 1873, which they found to be close to the genus *Cassolus*. Despite these advances in the taxonomy and systematics of these genera, more comprehensive studied of the Oriental Canthonini is needed.

New Zealand Canthonines

The canthonines in New Zealand consist of two endemic genera of flightless beetles: *Saphobiamorpha* Brookes 1944 with only one species --*S. maoriana* Brookes 1944, larger in body size -- and the genus *Saphobius* Sharp 1873, smaller-bodied and with numerous species (14). Both genera are saprophagous and may be found in dung of introduced mammals (Cambefort 1991). Also present in New Zealand is *Epirinus aeneus* Wiedemann 1823, introduced from South Africa (Emberson & Matthews 1973).

The taxonomic status of the subfamily Scarabaeinae

The tribe Canthonini has received attention in different research fields such as ecology behaviour, and diversity (Davis *et al.* 2000, Koch *et al.* 2000, Larsen *et al.* 2009, Silva *et al.* 2012). Taxonomically the group has been studied in each region; monographs, generic revisions, and species descriptions are profuse from each continent. Many authors have stressed the taxonomic problems within the tribe (Scholtz & Howden 1987a, 1987b, Matthews 1974, Medina *et al.* 2003, Tarasov & Keith 2011) and it is widely acknowledged that the tribe is not monophyletic (Philips *et al.* 2004, Monaghan *et al.* 2007, Sole & Scholtz 2010). Nevertheless, a new classification, splitting the tribe into more accurate and functional taxonomic groups entails a large amount of remaining work.

The taxonomy and classification of the subfamily Scarabaeinae is poorly resolved, at least for the New World. Hundreds of dung beetles remain in local collections without taxonomic identification, and within the tribes with many taxonomic problems that still need attention (Medina *et al.* 2003, Vaz de Mello 2008). I consider three different issues as responsible for the current state of the taxonomy of dung beetle subfamily Scarabaeinae: One is related to the division of the subfamily into guilds of rollers and tunnelers. Despite the fact that these two guilds are the most common in the subfamily, neither is a monophyletic unit. It is clear that roller behaviour has appeared more than once in the evolutionary history of the tribe (Philips *et al.* 2004), and rolling also has been considered ancestral and probably lost in many groups. Many studies have used this division of the subfamily without considering that for many genera, behaviour is still unknown.

Second, choosing dung beetles as an indicator group for biological assessment, and the ease of collecting thousands of dung beetles, has meant that many new researchers focused on exhaustive collecting, without much effort in taxonomic identification. Thus, there are many ecological works, in comparison with relatively few papers containing species description, taxonomic revision, and phylogenies. The taxonomic incongruity, which has been evaluated for the Colombian Andes, is that in nearly 60 papers, 40 % lack specific identification (Cultid *et al.* 2012).

And third, dung beetles are a very plastic group that has evolved in relation to the efficient exploitation of the main source of food, mostly dung, which has produced multiple similar adaptations for the use of this ephemeral resource. Indeed, the many convergences that are detected among the groups has made it more difficult to trace evolutionary history based on ancestor-descendent relationships. In the tribal phylogenies produced so far, the constant pattern is the high level of homoplasic characters, and the difficulty to define the groups based on true synapomorphies (Medina *et al.* 2003, Philips *et al.* 2004).

Various studies have illustrated phylogenetic and taxonomic problems with the tribe; many genera do not fit well as Canthonini, or they show stronger relationships with members of other tribes (Matthews 1974, Tarasov & Keith 2011). The taxonomic monographs considering the tribe in different geographic areas (America, Africa, Australia, and Madagascar) have shown common difficulties in delimiting genera and elucidating relationships within groups. Different authors have stressed that some genera are morphologically isolated, having atypical characters, and some of them show no apparent relationship with any other member of the tribe in the same region. Other genera of

Canthonini show apparent relationships with genera that are very distant geographically, or show affinity to other taxa outside of the tribe Canthonini (Matthews 1974, Scholtz & Howden 1987b, Medina *et al.* 2003, Vaz de Mello 2008).

The objective of the present work is to contribute to a better understanding of the tribe Canthonini; beginning with the exploration of the variation in the structures of the internal male genitalia in the subfamily Scarabaeinae (Chapter I), a review of the African genus *Epirinus* (Chapter II) and a proposal to split the tribe based on phylogenetic analysis using morphological characters (Chapter III).

THESIS LAYOUT

In order to understand the limits and relationships of the tribe Canthonini, genera from other Subfamilies (Aphodiinae, Geotrupinae), and from other tribes, different from Canthonini, were included for extensive comparison. A total of 109 genera, 327 species and 513 specimens were examined for this thesis (see: Appendix 1. and Table 1. in Chapter II). The thesis includes a general introduction, general conclusions, and three separate chapters, each chapter in the form of a scientific publication, containing its own abstract, introduction, reference list, and appendices. The first chapter includes a comparative analysis of the internal male genitalia of the subfamily Scarabaeinae with emphasis on Canthonini. Sclerites and other structures of the internal sac are described and illustrated for a wide range of genera that includes 62 of Canthonini, 12 of Coprini, and 11 of Ateuchini among others (see: Table 1, Chapter I). Also the names used for the male genitalia including its internal structures are reviewed and a set of names for the parts of the male genitalia is proposed to ease comparisons (Medina *et al.* 2013). The second chapter is a review of the African genus *Epirinus*. It contains the descriptions of six new species, a key to the species, and a cladistic analysis based on the morphology of the 29 currently known species in the genus (Medina & Scholtz 2005). The third chapter presents a phylogenetic hypothesis of the tribe Canthonini based on two sets of taxa and morphological data for two different cladistic analyses: one includes 51 taxa of Canthonini worldwide and 152 character (Appendices 2 and 3), and the second includes 28 taxa mainly American and 90 characters (Appendices 4 and 5).

In the current document the name Canthonini (= Deltochilini Bouchard *et al.* (2011) is used. In chapter I, the tribe is denominated Deltochilini, as required for publication in Zootaxa.

References

Arias, J. & Medina, C.A. In press. Tres nuevas especies de *Cryptocanthon* Balthasar, 1942 (Coleoptera: Scarabaeidae: Scarabaeinae) para Colombia. Caldasia.

Bell, K.L., Yeates, D.K., Moritz, C., Monteith, G.B. 2004. Molecular phylogeny and biogeography of the dung beetle genus *Temnoplectron* Westwood (Scarabaeidae: Scarabaeinae) from Australia's wet tropics. Molecular Phylogenetics and Evolution. 31, 741–753.

Cambefort, Y., 1978. Canthonina nouveaux ou peu connus d'Afrique continentale Coleoptera: Scarabaeidae. Journal of the Entomological Society of Southern Africa. 412, 199–213.

Cambefort, Y. 1991. Biogeography and Evolution, pp 51-74. *In*: I. Hanski & Y. Cambefort. (Eds.) *Dung Beetle Ecology*. Princeton University Press, Princeton.

Cano, E.B. 1998. *Deltochilum valgum acropyge* Bates (Coleoptera: Scarabaeidae: Scarabaeinae): habits and distribution. The Coleopterists Bulletin. 52, 174–178.

Cantil, L.F., Sánchez, M.V., Bellosi, E.S., González, M.G., Sarzetti, L.C., Genise, J.F. 2013. *Coprinisphaera akatanka* isp. nov.: The first fossil brood ball attributable to necrophagous dung beetles associated with an Early Pleistocene environmental stress in the Pampean region (Argentina). Palaeogeography, Palaeoclimatology, Palaeoecology. 386, 541–554.

Castellanos, M.C., Stevenson, P.R., Escobar, F. 1999. Dung Beetles (Scarabaeidae: Scarabaeinae) attracted to woolly monkey (*Lagothrix lagothricha*) dung in Tinigua National Park, Colombia. Coleopterists Bulletin. 53, 155–159.

Chin, K., Gill, B.D. 1996. Dinosaurs, dung beetles, and conifers: Participants in a Cretaceous food web. Palaios. 11, 280.

Cultid, C.A., Medina, C.A., Martínez, B.G., Escobar, A. F., Constantino, L. M., Betancur, N. J. 2012. Escarabajos coprófagos (Scarabaeinae) del eje cafetero: Guía para el estudio ecológico. WCS Colombia, CENICAFE, Villa María, Caldas (Colombia), pp. 198.

Davis, A.J., Huijbregts, H., Krikken, J. 2000. The role of local and regional processes in shaping dung beetle communities in tropical forest plantations in Borneo. Global Ecology and Biogeography. 9, 281–292.

Davis, A.L., Scholtz, C.H., Harrison, J.D.G. 2001. Cladistic, phenetic and biogeographical analysis of the flightless dung beetle genus, *Gyronotus* van Lansberge (Scarabaeidae: Scarabaeinae), in threatened eastern Afrotropical forests. Journal of Natural History. 35, 1607–1625.

Davis, A.L.V., Aarde, R.J.V., Scholtz, C.H., Delport, J.H. 2002. Increasing representation of localized dung beetles across a chronosequence of regenerating vegetation and natural dune forest in South Africa. Global Ecology and Biogeography. 11, 191–209.

Davis, A.L.V., Scholtz, C.H. 2001. Historical vs. Ecological Factors Influencing Global Patterns of Scarabaeine Dung Beetle Diversity. Diversity and Distributions. 7, 161–174.

Davis, A.L.V., Scholtz, C.H., Harrison, J.D.G. 1999. New and threatened Afrotropical, dung beetle taxa in the Gondwanaland tribe Canthonini (Coleoptera: Scarabaeidae). African Entomology. 7, 77–84.

Deschodt, C.M., Davis, A.L.V., Scholtz, C.H. 2011. New dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae) taxa from arid South-western Africa. Insect Systematics and Evolution. 42, 277–294.

Deschodt, C.M., Kryger, U., Scholtz, C.H. 2007. New taxa of relictual Canthonini dung beetles (Scarabaeidae: Scarabaeinae) utilizing rock hyrax middens as refuges in South-western Africa. Insect Systematics and Evolution 38, 361–376.

Deschodt, C.M., & Scholtz, C.H. 2008. Systematics of South African forest-endemic dung beetles: new genera and species of small Canthonini (Scarabaeidae: Scarabaeinae). African Entomology. 16, 91–106.

Emberson, R.M., Matthews, E.G. 1973. Introduced Scarabaeinae (= Coprinae) (Coleoptera) in New Zealand. New Zealand Entomologist. 5, 346-350.

Frolov, A.V. 2005. A New Species of the Dung Beetle Genus *Namakwanus* (Coleoptera, Scarabaeidae) from Namibia. Pensoft Publishers Sofia 11, 245–247.

Frolov, A.V., Scholtz, C.H. 2003. A new genus and species of dung beetle from southern Namibia (Coleoptera: Scarabaeidae: Scarabaeinae). African Entomology. 11, 297–29.

Génier, F. 2012. A new species and notes on the subgenus *Deltochilum* (*Deltochilum*) Eschscholtz, 1822 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilini). Zootaxa. 3357, 25–36.

Genise, J.F., Bellosi, E.S., Gonzalez, M.G. 2004. An approach to the description and interpretation of ichnofabrics in palaeosols. Geological Society, London, Special Publications. 228, 355–382.

Gill, B.D. 1991. Dung beetles in tropical American forests, pp 211–229. *In*: I. Hanski & Y. Cambefort. (Eds.) *Dung Beetle Ecology*. Princeton University Press, Princeton.

González, F.A., Molano, F., Medina, C.A. 2009. The subgenera *Calhyboma*, *Hybomidium*, and *Telhyboma* (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilum) in Colombia. Revista Colombiana de Entomología. 35, 253–274.

Goodman, S.M., Ganzhorn, J.U. 2004. Biogeography of lemurs in the humid forests of Madagascar: the role of elevational distribution and rivers. Journal of Biogeography. 31, 47–55.

Halffter, G. 1958. Dos nuevos generos de Canthonini. Ciencia (Mexico) 17(10-12), 207–212.

Halffter, G. 1961. Monografía de las especies norteamericanas del genero *Canthon*. Ciencia. 20 (9-12), 225–320.

Halffter, G. 1991. Historical and ecological factors determining the geographical distribution of beetles (Coleoptera: Scarabaeidae: Scarabaeinae). Folia Entomologica Mexicana. 82, 195–238.

Halffter, G., Martínez, A. 1966. Revisión monográfica de los Canthonina americanos (Coleoptera, Scarabaeidae) (I. parte). Revista de la Sociedad Mexicana de Historia Natural. 27, 89-177.

Halffter, G., Martínez, A. 1967. Revisión monográfica de los Canthonina americanos (Coleoptera, Scarabaeidae) (II. parte). Revista de la Sociedad Mexicana de Historia Natural. 28, 79–116.

Halffter, G., Martínez, A. 1968. Revisión monográfica de los Canthonina americanos (Coleoptera, Scarabaeidae) (III. parte). Revista de la Sociedad Mexicana de Historia Natural. 29, 209–290.

Halffter, G., Martínez, A.1977. Revisión monográfica de los Canthonina americanos (Coleoptera, Scarabaeidae). (IV. parte) Clave para generos y subgeneros. Folia Entomológica Mexicana. 38, 29–107.

Halffter, G., Matthews, E.G. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). Folia Entomológica Mexicana. (12-14), 312.

Hertel, F., Colli, G.R. 1998. The use of leaf-cutter ants, *Atta laevigata* (Smith), (Hymenoptera: Formicidae), as a substrate for oviposition by the dung beetle *Canthon virens* Mannerheim (Coleoptera: Scarabaeidae) in Central Brazil. The Coleopterists Bulletin. 105–108.

Janssens, A. 1949. Contribution à l’étude des coleóptères lamellicornes, table synoptique et assai de classification pratique des coléoptères Scarabaeidae. Bulletin du Musee Royal d’Histoire Naturelle de Belgique. 25 (15), 1–30.

Jeannel, R. 1942. La genèse des faunes terrestres: éléments de biogéographie. Presses Universitaires de France, Paris.

Josso, J.F., Prévost, P. 2001. Contribution à la connaissance des Scarabaeidae africains: (Coleoptera, Scarabaeidae, Coprinae) Cahiers Magellanes. Association Magellanes.

Krell, F-T. 2006. Fossil record and evolution of Scarabaeoidea (Coleoptera: Polyphaga). pp 120-143. *In:* M.L. Jameson and B.C. Ratcliffe (Eds.). *Scarabaeoidea in the 21st Century: A Festschrift honoring Henry F. Howden.* Coleopterists Society Monograph. Number 5, 216 pp.

Koivulehto, H. 2004. Madagascar's dung beetles – rain forest species avoid open areas. (MSc.). University of Helsinki, Helsinki.

Krikken, J., Huijbregts, J. 2006. Miniature scarabs of the genus *Haroldius* on Sulawesi, with notes on their relatives (Coleoptera: Scarabaeidae). Tijdschrift voor Entomologie. 149, 167- 187.

Krikken, J., Huijbregts, J. 2007. Taxonomic diversity of the genus *Ochicanthon* in Sundaland (Coleoptera: Scarabaeidae: Scarabaeinae). Tijdschrift voor Entomologie. 150, 421.

Kryger, U., Tukker, R., Scholtz, C.H. 2006. Biology and ecology of *Circellium bacchus* (Fabricius 1781)(Coleoptera Scarabaeidae), a South African dung beetle of conservation concern. Tropical Zoology. 19, 185–207.

Lansberge, G.V. 1874. Observations sur la classification des lamellicornes coprophages. I. Ateuchides. Annales De La Société Entomologique De Belgique. 17, 177–193.

Larsen, T.H., Lopera, A., Forsyth, A., Génier, F. 2009. From coprophagy to predation: a dung beetle that kills millipedes. Biological Letters. 5, 152–155.

Laza, J.H. 2006. Dung-Beetle Fossil Brood Balls: The Ichnogenera *Coprinisphaera* Sauer and *Quirogaichnus* (Coprinisphaeridae). Ichnos. 13, 217–235.

Lebis, E. 1953. Révision des Canthoninae de Madagascar. Mémoires de l'Institut Scientifique de Madagascar. 3, 107–252.

Martínez, A. 1948. Un género nuevo y dos especies nuevas de Canthonini (Coleoptera. Scarabaeidae.) de Venezuela. Anales de la sociedad científica Argentina. CXLVI, 41–51.

Martínez, A. 1950. Contribución al conocimiento del género *Megathopa* Eschscholtz, 1822, en la Argentina. Revista Española de Entomología. XXVI, 167–269.

Martínez, A. 1952. Scarabaeidae nuevos o poco conocidos III (Coleoptera). Misión de Estudios de Patología Regional Argentina. 4, 159–172.

Martínez, A. 1954a. Insectos nuevos o poco conocidos XI. Revista de la Sociedad Entomológica Argentina. 17, 43–47.

Martínez, A. 1954b. *Pseudepillisus* (Coleoptera: Scarabaeidae). Neotropica I. 28.

Matthews, E.G. 1966. A taxonomic and zoogeographic survey of the Scarabaeinae of the Antilles: (Coleoptera: Scarabaeidae). American Entomological Society Memoirs. 21, 1-134.

Matthews, E.G, 1974. A revision of the Scarabaeine dung beetles of Australia. II. Tribe Scarabaeini. Australian Journal of Zoology Supplementary Series. 22, 1–211.

Matthews, E.G., Weir, T. 2002. Two new species of the genus *Lepanus* Balthasar from South Australia (Coleoptera: Scarabaeidae). Records of the South Australian Museum. 35(1), 79–84.

Medina, C.A., Scholtz, C. H. 2005. Systematics of the southern African genus *Epirinus* Reiche (Coleoptera: Scarabaeinae: Canthonini): descriptions of new species and phylogeny. Insect Systematics and Evolution. 36, 145–160.

Medina, C.A., Escobar, F., Kattan, G.H. 2002. Diversity and Habitat Use of Dung Beetles in a Restored Andean Landscape. Biotrópica 34, 181–187.

Medina, C.A., Molano, F., Scholtz, C.H. 2013. Morphology and terminology of dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) male genitalia. Zootaxa. 3626, 455–476.

Medina, C.A., Scholtz, C.H., Gill, B.D. 2003. Morphological variation and systematics of *Canthon* Hoffmansegg 1817, and related genera of New World Canthonini dung beetles (Coleoptera, Scarabaeinae). Deutsche Entomologische Zeitschrift. 50, 23–68.

Molano, F., Medina, C.A. 2010. Especie nueva de *Scybalocanthon* (Coleoptera: Scarabaeinae: Canthonini) y descripción de la variación del órgano genital masculino. Revista Mexicana de Biodiversidad. 81, 689–699.

Monteith, G.B., Storey, R.I. 1981. The biology of *Cephalodesmius*, a genus of dung beetles which synthesizes “dung” from plant material (Coleoptera: Scarabaeidae: Scarabaeinae). Memoirs of the Queensland Museum. 20 253-277.

Montreuil, O. 2008a. Révision du genre *Cambefortantus* Paulian, 1986 (Insecta, Coleoptera, Scarabaeidae). Zoosystema. 30, 641–650.

Montreuil, O. 1998. Analyse phylogénétique et paraphylie des Coprini et Dichotomiini (Coleoptera: Scarabaeidae). Scénario Biogéographique. Annales de la Société Entomologique de France. 34, 135–148.

Montreuil, O. 2003a. Contribution à l'étude des Canthonini malgaches: Description de deux Pseudarachnodes Lebis, 1953 (Coleoptera, Scarabaeidae). Revue Française d'Entomologie. 25, 113–116.

Montreuil, O. 2003b. Contribution à l'étude des Canthonini malgaches deuxième note: Description de deux nouveaux *Aleiantus* Olsoufieff, 1947 (Coleoptera, Scarabaeidae). Revue Française d'Entomologie. 25, 143–146.

Montreuil, O. 2004. Contribution à l'étude des Canthonini de Madagascar (3e note): Description de deux *Apotolamprus* Olsoufieff, et mises au point taxonomiques et nomenclaturales (Coleoptera, Scarabaeidae). Revue Française d'Entomologie. 26, 67–72.

Montreuil, O. 2005a. Contribution à l'étude des Canthonini de Madagascar (4e note): Deux nouveaux *Apotolamprus* Olsoufieff, 1947 (Coleoptera, Scarabaeidae). Revue Française d'Entomologie. 27, 1–4.

Montreuil, O. 2005b. Contribution à l'étude des Canthonini de Madagascar (5e note): Description de nouveaux *Aleiantus* Olsoufieff, 1947 (Coleoptera, Scarabaeidae). Revue Française d'Entomologie. 27, 153–160.

Montreuil, O. 2006. Contribution à l'étude des Canthonini de Madagascar (6e note): Mises au point taxonomiques et nomenclaturales et description de nouvelles espèces du genre *Arachnodes* Westwood, 1847 (Coleoptera, Scarabaeidae). Revue Française d'Entomologie. 28, 97–110.

Montreuil, O. 2008b. Contribution à l´étude des Canthonini de Madagascar (8e note): nouveax *Apotolamprus* Olsoufieff, 1947 (Coleoptera, Scarabaeidae). Revue Francaise d´Entomologie. 30, 27–37.

Montreuil, O., Viljanen, H. 2007. Contribution à l'étude des Canthonini de Madagascar (7e note): Mises au point taxonomiques et nomenclaturales dans le genre *Nanos* Westwood, 1847 (Coleoptera, Scarabaeidae). Revue Française d'Entomologie. 29, 1–10.

Moretto, P., Perissinotto, R. 2013. Description and ecology of two new species of *Gyronotus* van Lansberge, 1874 (Coleoptera, Scarabaeidae) from southern Africa. ZooKeys. 344, 73–82.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G.A.B., Kent. J. 2000. Biodiversity hotspots for conservation priorities. Nature. 403, 853–858.

Ocampo, F.C., Molano, F. 2011. Revisión y biogeografía del género neotropical de escarabajos estercoleros *Scybalophagus* (Coleoptera: Scarabaeidae). Revista de la Sociedad Entomológica Argentina. 70, 231–253.

Orsini, L., Koivulehto, H., Hanski, I. 2007. Molecular evolution and radiation of dung beetles in Madagascar. Cladistics. 23, 145–168.

Padilla, D.N., Halffter, G. 2007. Biogeography of the areas and Canthonini (Coleoptera: Scarabaeidae) of dry tropical forests in Mesoamerica and Colombia. Acta Zoológica Mexicana. 23, 73–108.

Paulian, R. 1975. Sur quelques Canthonina [Coléoptères Scarabéides] montagnards de Madagascar. Annales de la Société Entomologique de France (Nouvelle Série). 11, 221–252.

Paulian, R. 1976. Révision des Canthonina Longitarses [Coleoptera Scarabaeidae] de Madagascar. Annales de la Société Entomologique de France (Nouvelle Série). 12, 458–479.

Paulian, R. 1985. Notes sur les Coléoptères Scarabaeidae du Muséum de Genève. 2. Revue Suisse de Zoologie. 92(1), 189-203.

Paulian, R., 1987. Canthoninae néo-calédoniens nouveaux ou peu connus (Coleoptera: Scarabaeidae). Nouvelle Revue d'Entomologie. 4 (1), 247–253.

Paulian, R., Cambefort, Y.1991. Remarques sur le genre *Helictopleurus* et description de trois nouvelles espèces (Coleoptera Scarabaeidae). Revue Française d'Entomologie (Nouvelle Série). 13, 113–118.

Paulian, R., Lebis, E. 1960. Faune de Madagascar: Fasc. 11 - Insectes, Coléoptères Scarabaeidae, Scarabaeina et Onthophagini Helictopleurina. Muséum National d'Histoire Naturelle Faune de Madagascar. 11, 130.

Pereira, F. 1953. Notas Sinonímicas. Dusenia. 4, 387–402.

Pereira, F., Martínez, A. 1959. Tres nuevos géneros de Canthonini americanos (Coleoptera, Scarabaeidae). Acta Zoológica Lilloana Argentina. XVII, 163–184.

Philips, T.K., Pretorius, E., Scholtz, C.H. 2004. A phylogenetic analysis of dung beetles (Scarabaeinae: Scarabaeidae): unrolling an evolutionary history. Invertebrate Systematics. 18, 53–88.

Reid, C.A.M., Storey, R.I. 2000. Revision of the dung beetle genus *Temnoplectron* Westwood (Coleoptera: Scarabaeidae: Scarabaeini). Memoirs of the Queensland Museum. 46, 253–297.

Sabu, T.K., Nithya, S., Vinod, K.V. 2011a. Faunal survey, endemism and possible species loss of Scarabaeinae (Coleoptera: Scarabaeidae) in the western slopes of
the moist South Western Ghats, South India. Zootaxa. 2830: 29-38.

Sabu, T.K., Vinod, K.V., Latha, M., Nithya, S., Boby, J. 2011b. Cloud forest dung beetles (Coleoptera: Scarabaeinae) in the Western Ghats, a global biodiversity hotspot in southwestern India. Tropical Conservation Science. 4 (1), 12-24.

Scholtz, C.H., Howden, F.H. 1987a. A Revision of the southern African genus *Epirinus* Reiche (Coleoptera: Scarabaeidae: Scarabaeinae). Journal of Entomological Society of South Africa. 50, 121–154.

Scholtz, C.H., Howden, H.F. 1987b. A revision of the African Canthonina (Coleoptera: Scarabaeidae: Scarabaeinae). Journal of the Entomological Society of Southern Africa. 50, 75–119.

Scholtz, C.H., Davis, A.L.V., Kryger, U. 2009. Evolutionary biology and conservation of dung beetles. Pensoft. Sofia-Moscow.

Silva, F.A.B. 2011. A New Species of the Genus *Scybalocanthon* (Coleoptera: Scarabaeinae) from Southeast Brazil. PloS One. 6 (11), 1-5.

Silva, F.A.B., Vidaurre, T., Vaz de Mello, F., Louzada, J. 2012. Predatory behaviour in *Deltochilum*: convergent evolution or a primitive character within a clade? Journal of Natural History. 46, 1359–1367.

Sole, C.L., Scholtz, C.H. 2010. Did dung beetles arise in Africa? A phylogenetic hypothesis based on five gene regions. Molecular Phylogenetics and Evolution. 56, 631–641.

Sole, C.L., Wirta, H., Forgie, S.A., Scholtz, C.H. 2011. Origin of Madagascan Scarabaeini dung beetles (Coleoptera: Scarabaeidae): dispersal from Africa. Insect Systematics and Evolution 42, 29–40.

Storey, R.I. 1984. A new species of *Aptenocanthon* Matthews from North Queensland (Coleoptera: Scarabaeidae: Scarabaeinae). Memoirs of The Queensland Museum. 21, 387–390.

Storey, R.I. 1986. A new flightless species of *Aulacopris* White from north Queensland (Coleoptera: Scarabaeidae: Scarabaeinae). Memoirs of the Queensland Museum 22, 197–203.

Storey, R.I. 1991. New species and new records of *Tesserodon* Hope (Coleoptera: Scarabaeidae) from northern Australia. Memoirs of The Queensland Museum 30, 577–588.

Storey, R.I., Monteith, G.B. 2000. Five new species of *Aptenocanthon* Matthews (Coleoptera: Scarabaeidae: Scarabaeinae) from tropical Australia, with notes on distribution. Memoirs of the Queensland Museum. 49 (6), 349–358.

Tarasov, S., Keith, D. 2011. *Parachorius semsanganus* sp. n. (Coleoptera, Scarabaeidae, Scarabaeinae) from Laos and its significance in the phylogeny of Oriental Deltochilini. Zookeys. 51–57.

Vaz de Mello, F. 2003. *Ochicanthon*, a new name for *Phacosoma* Boucomont (Coleoptera, Scarabaeidae), preoccupied with *Phacosoma* Jukes-Browne (Mollusca). The Coleopterists Bulletin. 57, 25–26.

Vaz de Mello, F. 2007. Revision and phylogeny of the dung beetle genus *Zonocopris* Arrow, 1932 (Coleoptera: Scar- abaeidae: Scarabaeinae), a phoretic of land snails. Annales de la Société Entomologique de France. 43(2), 231–239.

Vaz de Mello, F. 2008. Synopsis of the new subtribe Scatimina (Coleoptera: Scarabaeidae: Scarabaeinae: Ateuchini), with descriptions of twelve new genera and review of *Genieridium*, new genus. Zootaxa. 1–75.

Vaz de Mello, F., Halffter, G. 2006. A new dung beetle genus with two new species from Chile (Coleoptera: Scarabaeidae: Scarabaeinae). Zootaxa. 1193, 59–68.

Vaz de Mello, F.Z. 1999. Scarabaeidae s. str. (Coleoptera: Scarabaeoidea) de um fragmento da Floresta Amazônica no estado do Acre, Brasil. 1. Taxocenose. Anais da Sociedade Entomológica do Brasil. 28, 439–446.

Vaz de Mello, F.Z., Louzada, J.N. 1997. Consideracoes sobre forrageio arboreo por Scarabaeidae (Coleoptera, Scarabaeoidea), e dados sobre sua ocorrencia em floresta tropical do Brasil. Acta Zoológica Mexicana. 55–61.

Vidaurre, T., Ledezma J., Vaz de Mello, 2009. Primer registro de *Eudinopus dytiscoides* (Schreibers, 1802)(Coleoptera: Scarabaeidae: Scarabaeinae: Canthonini) para Bolivia. Acta zoológica Mexicana. 25, 187–189.

Viljanen, H. 2004. Diet specialization among endemic forest dung beetles in Madagascar (MSc.). University of Helsinki, Finland.

Viljanen, H. 2009. Life history of *Nanos viettei* (Paulian, 1976) (Coleoptera: Scarabaeidae: Canthonini), a representative of an endemic clade of dung beetles in Madagascar. The Coleopterists Bulletin. 63, 265–288.

Viljanen, H., Wirta, H., Montreuil, O., Rahagalala, P., Johnson, S., Hanski, I. 2010. Structure of local communities of endemic dung beetles in Madagascar. Journal of Tropical Ecology. 26, 481–496.

Wirta, H. 2009. Complex phylogeographical patterns, introgression and cryptic species in a lineage of Malagasy dung beetles (Coleoptera: Scarabaeidae). Biological Journal of the Linnean Society. 96, 942–955.

Wirta, H., Montreuil, O. 2008. Evolution of the Canthonini Longitarsi (Scarabaeidae) in Madagascar. Zoologica Scripta. 37, 651–663.

Wirta, H., Orsini, L., Hanski, I. 2008. An old adaptive radiation of forest dung beetles in Madagascar. Molecular Phylogenetics and Evolution 47, 1076–1089.

Wirta, H., Viljanen, H., Orsini, L., Montreuil, O., Hanski, I. 2010. Three parallel radiations of Canthonini dung beetles in Madagascar. Molecular Phylogenetics and Evolution. 57, 710–727.

Young, O. P. 1981. The attraction of neotropical Scarabaeinae (Coleoptera: Scarabaeidae) to reptile and amphibian fecal material. The Coleopterists Bulletin. 35, 345–348.

CHAPTER I

MORPHOLOGY AND TERMINOLOGY OF DUNG BEETLES (COLEOPTERA: SCARABAEIDAE: SCARABAEINAE) MALE GENITALIA

Claudia A. Medina

Fredy Molano

Clarke H. Scholtz

Zootaxa 3626 (4): 455–476 (2013)

Zootaxa 3626 (4): 455–476
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3626.4.3
http://zoobank.org/urn:lsid:zoobank.org:pub:C715FA62-52CA-4CE8-81AD-B46E3277D756

Morphology and terminology of dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) male genitalia

CLAUDIA A. MEDINA[1,2], FREDY MOLANO[3] & CLARKE H. SCHOLTZ[1]

[1]*Department of Zoology & Entomology University of Pretoria, Pretoria, South Africa*

[2]*Current address: Programa de Gestión de Información y Conocimiento GIC-Colecciones Biológicas, Instituto Alexander von Humboldt. Boyacá, Colombia. E-mail: camedina@humboldt.org.co*

[3]*Laboratorio de Entomología, Museo de Historia Natural "Luis Gonzalo Andrade," Escuela de Ciencias Biológicas, Universidad Pedagógica y Tecnológica de Colombia. Boyacá, Colombia. E-mail: fredymol@gmail.com*

Abstract

The external and internal male genitalia of 327 species of 11 tribes of the subfamily Scarabaeinae, including species of Deltochilini, Scarabaeini, Gymnopleurini, Ateuchini, and Coprini, among others, were examined. Descriptions of the variations in the genital segment, the aedeagus, the internal sac, and its sclerites and raspules are presented. An exhaustive comparison of structures, names, and terminology used in literature for Scarabaeinae male genitalia are discussed. The internal sac of the aedeagus is divided in areas for an easer comparison of its internal structures; basal, submedial, medial, and apical areas are described in detail and compared. The variation of apical and medial sclerites, as well as the raspules of the submedial area, are described and compared in detail among all the taxa studied.

Key words: Scarabaeinae, male genitalia, aedeagus, internal sac, sclerites

Resumen

Se examinó la genitalia externa e interna de machos de 327 especies de 11 tribus de la subfamilia Scarabaeinae incluyendo especies de Deltochilini, Scarabaeini, Gymnopleurini, Ateuchini, y Coprini, entre otras. Descripciones de la variación del segmento genital, el edeago, el saco interno, sus escleritos y raspulas, son presentadas. Una comparación exhaustiva de las estructuras del órgano genital masculino de los Scarabaeinae, sus nombres y terminologia usada en la literatura es expuesta. El saco interno es dividido en áreas para facilitar la comparación de sus estructuras; se describen y comparan detalladamente el área basal, submedial, medial y apical. La variación de los escleritos apicales y mediales, así como las raspulas del area submedial son descritas y comparadas en detalle entre todos los taxones estudiados.

Introduction

In Coleoptera, the internal male genitalia have been poorly studied, and the functioning of internal male structures is not yet well understood. However, morphological structures within male genitalia have been widely used for taxonomic and systematics purposes. Genitalia provide, in many cases, taxonomically useful characters for distinguishing organisms at the species level, usually where no other morphological traits will suffice. Therefore, in differentiating species, genitalia of beetles have been widely documented. Using the technique of inflating the internal sac, the internal structures have been studied in Carabidae: Cicindelinae (Matalin 1998, 1999), Chrysomelidae (Berti & Mariau 1999), and Cerambycidae (Rubenyan 2002, Anichtchenko & Verdugo 2004). In groups such as Carabidae (Matalin 1999, Roig-Junent 2000), Staphylinidae (Márquez 2001), and Curculionidae (Thompson 1988), among others, external and internal male genitalia have important structures that have been used to define taxonomic groups and to produce phylogenetic hypothesis of the evolution of the taxa.

Accepted by A.B.T. Smith: 11 Feb. 2013; published: 15 Mar. 2013

Within the superfamily Scarabaeoidea, male genitalia characters have been limited to a more taxonomic than a phylogenetic use. Diagnostic characters from external and internal male genitalia are widely used in different groups: Geotrupidae (Bovo & Zunino 1983), Aphodiinae (Kral 2000), Melolonthinae (Coca-Abia & Martín-Piera 1998). A comparative study of external genitalia in 12 families of Scarabaeidae was prepared by D'Hotman & Scholtz (1990), and descriptions for internal structures were prepared for some genera of Ochodaeidae (Carlson & Ritcher 1974, Carlson 1975).

Scarabaeinae male genitalia have been used in many cases to differentiate species (*i.e*., *Microcopris* Balthasar, 1958 in Ochi & Masahiro [1996] and *Onthophagus* Latreille, 1802 in Stefano & Ivo [2001]). The internal male genitalia of beetles are frequently used in review and revisions (Martínez & Pereira 1956, Matthews 1974, Ochi *et al*. 1997, Reid 2000), compared to *Eurysternus* Dalman, 1824 and *Sisyphus* Latreille, 1807 (López-Guerrero 1999), and described as in the genus *Phanaeus* MacLeay, 1819 (Price 2005). However, sclerites or other structures from the internal sac of the aedeagus of Scarabaeinae beetles are rarely described in detail, catalogued, or used in phylogenetic studies: Barbero *et al*. (1991) used the accessorial lamellae (here referred to as sclerites) to differentiate groups of genera in the tribe Sisyphini; Martín-Piera (1987) used the copulatrix lamina (here referred as basal sclerite) to construct the phylogeny of the *Chironitis* Lansberge, 1875*;* variation in the lateral sinus of the structure determined an apomorphy for the group with respect to other genera such as *Bubas* Mulsant, 1842 and *Onitis* Fabricius, 1798.

Mario Zunino has thoroughly studied and described in detail the structures of the male genitalia (including the aedeagus and the internal sac) of different groups of dung beetles, mainly in the tribe Onthophagini (Zunino 1978). He has included internal male genitalia in the descriptions of species (Zunino 1981), in the reviews of species groups (Zunino 1979, 1985; Zunino & Halffter 1987), and he produced the first phylogenetic hypothesis of the subfamily Scarabaeinae based on morphological characters of the male genitalia (Zunino 1983). Following the proposal of analyzing and homologizing the internal structures of the internal sac, Medina *et al*. (2003) described in detail the sclerites of the internal sac of the genus *Canthon* Hoffmannsegg, 1817 and other New World genera of Deltochilini; they found that some subgenera of *Canthon* shared the same type of sclerites, but they also recognized the enormous variation in the sclerites even within one genus. Medina & Scholtz (2005) used the structures of the internal sac in the cladistic analysis of the genus *Epirinus* Reiche, 1841, and more recently Tarasov & Solodovnikov (2011) did a comparative study of endophalic sclerites of an extended group of the tribe Onthophagini, including homologized characters in the pyhologenetic analysis of this group, finding a high number of informative characters.

Internal male genitalia have been used in different taxonomic generic studies; *i.e*., *Ateuchus* Weber, 1801 (Génier 2000, Kolhmann 2000), *Coptodactyla* Burmeister, 1846 (Reid 2000), *Temnoplectron* Westwood, 1841 (Reid & Storey 2000), *Macroderes* Westwood, 1842 (Frolov & Scholtz 2004), *Epirinus* (Medina & Scholtz 2005), *Dichotomius* Hope, 1838 (López-Guerrero 2005), *Phanaeus* (Price 2005), *Ochicanthon* Vaz-de-Mello, 2003 (Krikken & Huijbregts 2007), *Coptorhina* Hope, 1835 (Frolov *et al*. 2008), *Copris* Geoffroy, 1762 (López-Guerrero *et al*. 2009), Scatimina (Vaz-de-Mello 2008), *Deltochilum* Eschscholtz, 1822 (González *et al*. 2009), and *Scybalocanthon* Martínez, 1948 (Molano & Medina 2010). González *et al*. (2009) described and illustrated the internal sac and the sclerites of the 13 species of three subgenera of *Deltochilum* (*Calhyboma, Hybomidium*, and *Telhyboma;* (now *Deltochilum sensu stricto* Génier 2012) of Colombia, in South America. They classified the sclerites as in Medina *et al*. (2003), and at least three types of apical sclerites, the aedeagus, and the segment genital, are illustrated for each of these species.

House & Simmons (2003, 2005) studied the genital morphology and internal fertilization in the species *Onthophagus taurus* (Schreber, 1759). They characterized the internal sclerites as important structures in the sexual selection of this species. Werner & Simmons (2008) also studied in detail the evolution and function of the genitalia of this species.

Internal male genitalia of dung beetles have numerous structures that vary greatly among the groups. If the variation in the structures of the internal male genitalia is well understood, it will give useful information in different fields of research, including morphology, systematics, sexual selection, and evolution. In this paper, the wide variation of the structures and terminology of the internal sac of the Scarabaeinae dung beetles is presented and discussed. The genital segment, the aedeagus, the internal sac, and its internal structures are described in detail and compared within a large number of genera of Scarabaeinae dung beetles.

Methods and material

Specimen preparation. Dissections of internal male genitalia of the taxa selected were performed. Dry specimens were carefully cleaned and softened by immersion in hot water for 30–60 minutes, depending on specimen size. Dissections were performed under a stereomicroscope using forceps and needles. In large beetles the aedeagus was removed through the opening of the pygidium, while in small specimens (less than 5 mm) the whole abdomen was removed. The genital segment and the aedeagus was removed and heated in KOH 5% in small glass jars until the internal structures were soft. The internal sac was drawn out by gently pulling the outer portion of the sac from the inside of the sclerotized capsule of the aedeagus. Holding the temones with the forceps, the other extreme of the sac was pulled until the complete sac was stretched. If the sac still looked dirty or unclear, it was heated again for another few minutes until the sac was clear and the structures inside were visible enough. Once the sac was completely clean, it was rinsed with 70% ethyl alcohol.

The structures were prepared on microscope slides in liquid glycerine. Preparations on microscope slides were labeled with the corresponding species name and a number corresponding to the dry specimen on a pin.

Material examined. To have a broad outline of the variation in the internal male genitalia of the subfamily Scarabaeinae, a total of 327 species from 11 tribes from the different regions were dissected. A total of 397 male genitalia were examined, including taxa from the different tribes (Table 1). To examine the intraspecific variation, depending on the availability of material in some genera, large series of more than 10 specimens of the same species were also dissected.

TABLE 1. Number of taxa examined for the study. Classification followed as in Bouchard *et al*. 2011.

Subfamily /tribe	Genera	Species	Specimens
Aphodiinae Leach, 1815	4	6	9
Geotrupinae Latreille, 1802	1	1	1
Scarabaeinae Latreille, 1802	104	320	503
Ateuchini Perty, 1830	11	17	27
Coprini Leach, 1815	12	25	28
Deltochilini Lacordaire, 1856	62	229	387
Eucraniini Burmeister, 1873	3	4	4
Gymnopleurini Lacordaire, 1856	2	3	3
Oniticellini Kolbe, 1905	1	2	2
Onitini Laporte, 1840	1	2	2
Onthophagini Burmeister, 1846	4	7	10
Phanaeini Hope, 1838	1	1	1
Scarabaeini Latreille, 1802	6	28	37
Sysiphini Mulsant, 1842	1	2	2
Total	109	327	513

The following institutions provided material to the study:

BDGC	Bruce D. Gill, private collection, Ottawa, Canada
BMNH	The Natural History Museum, London, UK
CMNC	Canadian Museum of Nature, Ottawa, Canada
ECC	Colección Escarabajos Coprófagos de Colombia, Bogotá, Colombia
CEMT	Seção de Entomologia da Coleção Zoológica, Departamento de Biologia e Zoologia, Instituto de Biociências, Universidade Federal de Mato Grosso. Cuiabá, Brasil
IAVH	Colección Entomológica, Instituto Alexander von Humboldt, Villa de Leyva, Colombia
IAZA	Colección de Entomología del Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza, Argentina

NCSA	National Collection, Pretoria, South Africa
MUJ	Museo Javeriano de Historia Natural Lorenzo Uribe, Pontificia Universidad Javeriana, Bogotá, Colombia
QCAZ	Pontificia Universidad Católica del Ecuador, Insects collection Quito, Ecuador
SAMC	South African Museum, Cape Town, South Africa
SAMN	South Australian Museum, North Terrace, Adelaide, Australia
TMSA	Transvaal Museum, Pretoria, South Africa
UPSA	University of Pretoria Scarabs Collection, Pretoria, South Africa
UPTC	Universidad Pedagogica y Tecnológica de Colombia, Tunja, Colombia
URCM	Universidad de La República, Montevideo, Uruguay
URCA	Universidad de Río Cuarto, Río Cuarto, Argentina

Results and discussion

The first papers describing dung beetle male genitalia appeared in the mid 20th century. Pereira (1941) and Pereira & D´Andretta (1955) drew the first internal sac of the aedeagus for the genus *Deltochilum*. Then Pereira & Martínez (1956, 1960), Martínez & Pereira (1956), Binaghi *et al*. (1969), Zunino (1972), and Matthews (1974) also included drawings of internal sac of the aedeagus in its descriptions, but it was until the work of Zunino (1978) was published that the foundations for the preparation and study of internal male genitalia of Scarabaeinae dung beetles were established. Since then, multiple investigations regarding male genitalia have been published. After an intensive literature search, all these papers are listed in Table 2; in the first row, we included the names for the structures as defined here. Also, all the structures have been compared and analyzed regarding their position and shape. One of the first sclerites of the internal sac, which has been studied in detail, is the lamelle copulatrix ("lamela copuladora principal") in the genus *Onthophagus* (Zunino & Halffter 1988), here called the medial sclerites. D´Hotman & Scholtz (1990) studied in detail the male genitalia of the subfamily Scarabaeinae and established a nomenclature for these structures, which it is still followed. After that, multiple papers have included internal male genitalia, generally the apical sclerites. Table 2 summarizes the different studies and the names used for the structures in the male genitalia of dung beetles. After a large revision of a large number of individuals, the variation of dung beetles genitalia has been widely known. Here we describe all the internal and external structures of male genitalia. Comparing with the existing literature, we defined names for the homologous structures. Table 2 shows the names we have assigned to each structure and below the other author's names used for the same structure, this comparison permit us to unify all the names and to have a more comprehensive knowledge of the structures. In the following sections, we present a description of all the structures in the internal male genitalia of dung beetles (Scarabaeinae).

Morphology of male genitalia in Scarabaeinae

The male genitalia in Scarabaeinae are formed by the genital segment, the aedeagus, and the internal sac of aedeagus (Figs. 1–4). In the following, we describe the general morphology of these three main structures of male genitalia, discussing the terminology most commonly used in literature, and establishing homologies for the main parts of these structures.

Genital segment. The genital segment is derived from the ninth abdominal segment (D´Hotman & Scholtz 1990). It is connected to the pygidium and surrounds and supports the aedeagus. It is a membranous capsule with ventral and lateral sclerotized plates, which varies in position, orientation, shape, and degree of sclerotization. The variation in the shape of the genital segment among dung beetles is enormous and it has not been described in detail for the group. D´Hotman & Scholtz (1990) described the structure for the subfamily Scarabaeinae; Philips *et al*. (2004) included three characters of this structure in their tribal systematic analysis of the subfamily Scarabaeinae; Philips *et al*. (2002) used it in their analysis of phylogeny of Eucraniini, and Medina & Scholtz (2005) included the genital segment for analysis of the genus *Epirinus*.

TABLE 2. List of references and names of structures used for the internal male genitalia of dung beetles (Scarabaeinae).

Reference	**STRUCTURES**							
Medina & Molano (as proposed here)	**Aedeagus**	**Internal sac**	**Apical sclerites**	**Basal sclerite**	**Plate sclerite**	**Elongate sclerite**	**Medial sclerite**	**Raspules**
Matthews (1974)	Genital capsule or aedeagus	Internal sac	Sclerotized elements	Virgular sclerite	Flagelar sheath	Flagellum or spicule		Spinulose field
Zunino & Halffter (1988)	Edeago	Saco interno	Lamelas accesorias				Lamela copuladora	Cinta espinosa lamelar
D´Hotman & Scholtz (1990)	Edeagus	Internal sac	Internal sac armature					
Barbero *et al.* (1991)	Falloteca	Endophallo	Lamelle accessorie basali				Lamella copulatrice	
Génier (1996)	Aedeagus	Internal sac	Accessory sclerites	Lambda sclerite	Sigmoideo sclerite	Flagella		
Barbero *et al.* (1998)	Aedeagus	Endophallus		Lateral structure	Apical structure	Apical structure		Basal structure
Montreuil (1998)		Sac interne	Pièces sclérifiées	Pièces intermédiaires	Pièces intermédiaires	Pièces intermédiaires	Lamelle copulatrice	
López-Guerrero (1999)	Aedeagus	Endofallus	Accesory laminae	Copulative laminae (*Eurysternus*)	Copulative laminae (*Sisyphus*)	Flagelum		Rapulas
Kohlmann (2000)	Aedeagus	Internal sac	Apical lamellae				Hooks	Spines
Reid (2000)		Ejaculatory sac	Basal sclerites	Ring sclerite	Basal sclerites	Flagelum		
Reid & Storey (2000)	Aedeagus	endofallus	Endophallic sclertites	Ring sclerite	Basal sclerites	Flagelum	"median" sclerite	
Medina *et al.* (2003)	Aedeagus	Internal sac	Sclerites	Circular sclerite	Plate-shaped sclerite	Elongated sclerite		Brushes
House & Simmons (2003)	Aedeagus	Endophallus	Genital sclerites	Sclerite 1	Sclerite 5	Sclerites 2 and 3	Sclerite 4	
Frolov & Scholtz (2004)	Aedeagus	Internal sac		Sclerite	Sclerite			
Medina& Scholtz (2005)	Aedeagus	Internal sac	Sclerites	Sclerite "X"	Sclerite "Y"	Sclerite "Z"		
López-Guerrero (2005)	Edeago	Saco interno	Lamelas accesorias	Segunda lamela accesoria	Tercera lamela accesoria	Primera lamela accesoria	Lamela copulatriz	Ráspulas
Price (2005)	Genital capsule	Internal sac	Sclerites	Sclerite II	Sclerite III	Sclerites IV, V, VI	Sclerite I	Spinulate pocket
Frolov *et al.* (2008)	Aedeagus	Internal sac						
Werner & Simmons (2008)	Aedeagus	Endophallus	Endophallus sclerites	Sclerite 1	Sclerite 5	Sclerites 2 and 3	Sclerite 4	
López-Guerrero *et al.* (2009)	Aedeagus		Accessory lamella	Parietal accessory lamella	Conical accessory lamellae	Conical accessory lamellae		Raspula
Tarasov & Kabakov (2010)	Aedeagus	Internal sac					Lamella copulatrix	
Tarasov & Solodovnikov (2011)	Aedeagus	Endophallus	Endophallic sclerites	Superior right peripheral sclerite	Fronto-lateral peripheral sclerite	Axial sclerite and subaxial sclerite	Lamella copulatrix	

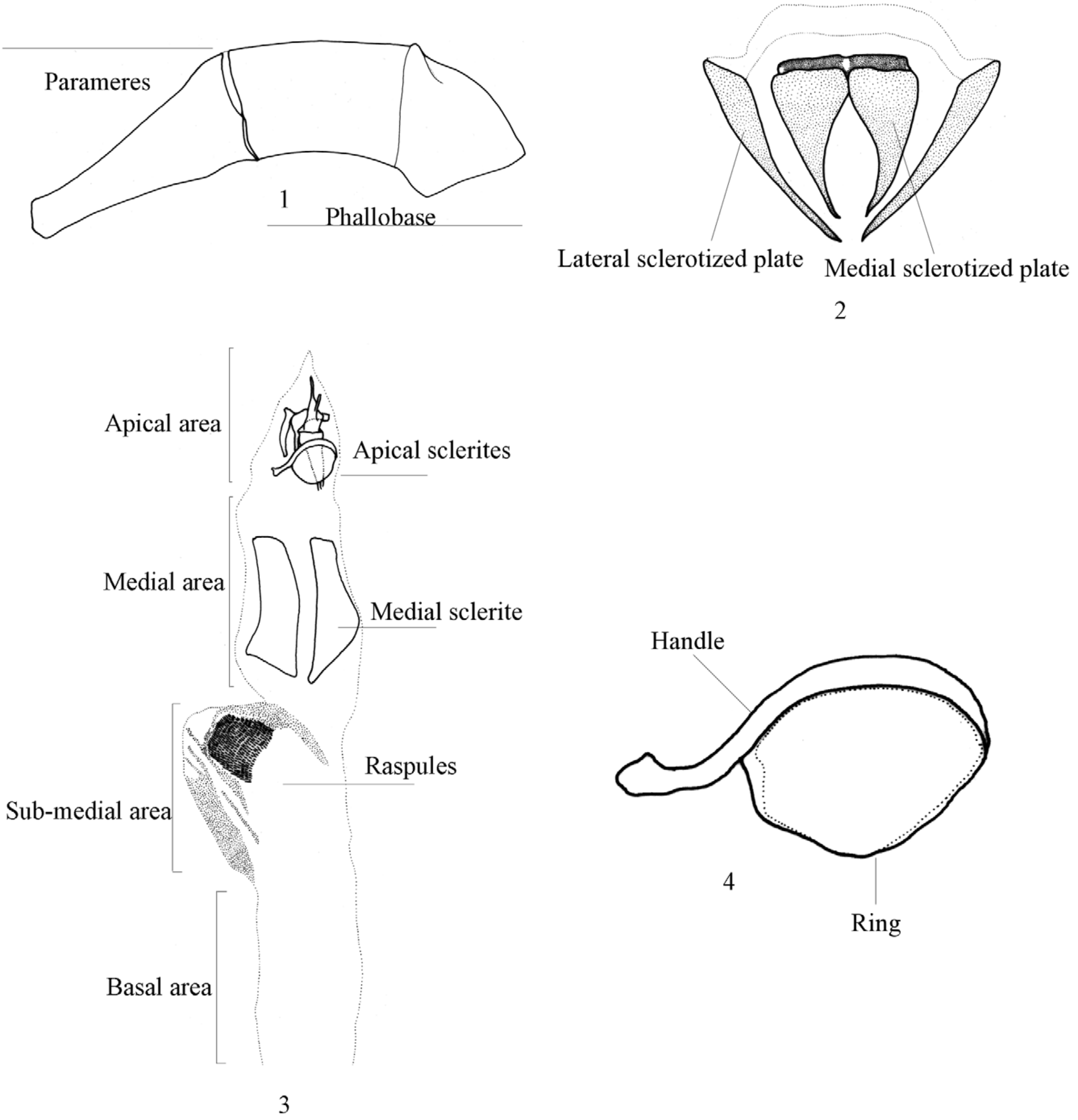


PLATE 1. Figures 1–4. 1. Aedeagus. 2. Genital segment. 3. Internal sac of the aedeagus. 4. Basal sclerite.

The genital segment has two main shapes among the Scarabaeinae studied; it can be triangular or quadrangular depending on the position and orientation of the lateral plates; as these can be longitudinally or obliquely located. In the triangular-shape genital segment, the lateral plates converge to the center, varies in grade of sclerotization, and the plates could be fused in the middle or not. The variation consist in the shape and grade of thickness of the lateral plates; some slender as in *Arachnodes splendidus* (Fairmaire, 1889) (Fig. 5) and *Onitis* sp1. (Fig. 6), and thicker as in *Gyronotus fimetarius* Kolbe, 1894 (Fig. 7). In a few genera, the plates are fused in the middle and are projected in a filament that can vary in length (Fig. 8). This is seen in *Coptorhina excavata* Frolov, Akhmetova & Scholtz, 2008 and *Dicranocara* Frolov & Scholtz, 2003.

In the genital segment, which has a more quadrangular shape, the lateral plates are longitudinally located (Figs. 9, 10); in some species the extreme basal of the lateral plate can be curved as in *Canthon quinquemaculatus* Laporte, 1840 (Fig.11) and *Anachalcos procerus* Gerstaecker, 1874 (Fig.12). Most species of *Canthon* and

Hansreia Halffter & Martínez, 1977 (Fig. 13) have a part of the lateral plate longitudinally straight, and the rest is oblique (Figs. 14–16).

The capsule of the genital segment has a medial sclerotized plate that varies greatly within the subfamily (Figs. 2, 10, 17–26, 33). The medial plate can be entirely formed by a medial quitinized portion (Figs. 10, 18, 19, 20–22), complete with two projections (Figs. 7, 11, 27–30), or completely divided into two lateral quitinized plates (Figs. 31, 32, 34–39). In most species of the *Canthon* examined, these lateral plates resemble a reverse half moon (Figs. 9, 14, 15, 36–42).

The large Deltochilines from the New World (*Deltochilum, Malagoniella* Martínez, 1961, *Megathopa* Eschscholtz, 1822, *Eudinopus* Burmeister, 1840), from Africa (*Anachalcos* Hope, 1837), and from Australia (*Aulacopris* White, 1859) present a quadrangular genital segment with thick and quitinous transversal folds (Fig. 43). Genera from South Africa and Afro-Oriental Australia (*i.e.*, *Aphengoecus* Péringuey, 1901, *Panelus* Lewis, 1895) and the genera from New Zealand (*Saphobiamorpha* Brookes, 1944 and *Saphobius* Sharp, 1873) lack the sclerotized lateral arms.

Aedeagus. The aedeagus is formed both by an external quitinous capsule, and the internal sac. The aedeagus externally is formed by the phallobase; a cylindrical piece that contains the internal sac and the parameres. The aedeagus is attached to the genital segment by membranes at the point of articulation of the phallobase and the parameres. The parameres are a pair of sclerotized plates that articulate with the distal end of the phallobase. In most of the genera, they are capable of opening and closing and form a tubular structure through which the internal sac is everted. The internal sac contains different sclerotized structures, spines and setae in different areas, which form part of the sensory system of this group (Fig. 3).

In the subfamily Scarabaeinae, the angle between the phallobase and the parameres show an important variation. In Coprini, Onitini, and Eucraniini, the aedeagus is almost straight through the phallobase, and the parameres form a broad angle of more than 110º, almost reaching 180º (*Copris* spp. Figs. 44–46, *Dichotomius bos* (Blanchard, 1846) Fig. 47, *Ontherus sanctaemartae* Génier, 1996 Fig. 48, *Oxysternon palaemon* Laporte, 1840 Fig. 49, *Garreta unicolor* Fahraeus, 1857 Fig. 50, *Gymnopleurus* sp. Fig. 51, *Anomiopsoides heteroclyta* (Blanchard, 1845) Fig. 52, *Ennearabdus lobocephalus* Harold, 1868 Fig. 53, *Eucranium* sp. Fig. 54). In the rest of the tribes and majority of species studied, the phallobase and the parameres form an angle between 90 and 110º (Figs. 55–59). However, some genera of Deltochilini present an unusual aedeagus. In the New World genus *Canthonella* Chapin, 1930 the parameres are reduced and the basal piece is transformed to an elongate, slender, and curved tube with the parameres highly reduced. The genus *Canthochilum* Chapin, 1934 also has the parameres reduced and fused in the middle.

The parameres can be symmetrical or asymmetrical. Most of the genera of African and Australian deltochilines and the tribe Scarabaeini have asymmetrical parameres (Figs. 60–64). In some genera, the left paramere is larger and broad; but in many genera the left paramere has a bizarre shape compared to the right paramere. In the genus *Circellium* Latreille, 1825, the tip of the left paramere is curved forming a hook (Fig. 60) and asymmetrical parameres are evident in *Anachalcos procerus, Epirinus validus* Péringuey, 1901, and *Gyronotus fimetarius* (Figs. 61–63). In Scarabaeini the right paramere has a small spine at the base of the paramere (Figs. 78–80). In *Canthonosoma castelnaui* (Harold, 1868) and *Streblopus opatroides* Lansberge, 1874 (Figs. 64, 65), the differences are observed in the apex of the paramere forming an extension as a hook. In *Temnoplectron reyi* Paulian, 1934 (Fig. 66) the difference between parameres is less evident.

New World Deltochilini does not typically have asymmetrical parameres, with the exception of the genus *Scybalocanthon* (Fig. 67, Molano & Medina 2010), and some species of the genera *Deltochilum* and *Canthon; i.e.*, *Deltochilum* (*Deltochilum*) *orbiculare* Lansberge, 1874 (González *et al*. 2009), and *C. cyanellus* LeConte, 1859, *C. quinquemaculatus*, *C. aberrans* (Harold, 1868), *C. angularis* Harold, 1868, *Canthon* sp. (Figs. 68–72).

In the ventral view of the parameres, an extension with the shape of a quitinous small plate is observed in the species of the tribe Coprini (*Copris dracunculus* Ferreira, 1959, *C. incertus* Say, 1835, *C. mesacanthus* Harold, 1878, *Dichotomius bos*, and *Ontherus sanctaemartae* (Figs. 44–48); this extension sometimes covers part of the following paramere (*O. sanctaemartae* Fig. 48). In the tribes Gymnopleurini and Onitini a similar structure has been observed. In other species a quitinous lobule between the parameres ventrally was observed. This structure is present in the species of large New World deltochilines as *Eudinopus dytiscoides* (Schreibers, 1802), *Malagoniella astyanax columbica* Harold, 1867, *M. a. punctatostriata* (Blanchard, 1845), *M. puncticollis* (Blanchard, 1845) and *Megathoposoma candezei* Harold, 1873 (Figs. 73–77).

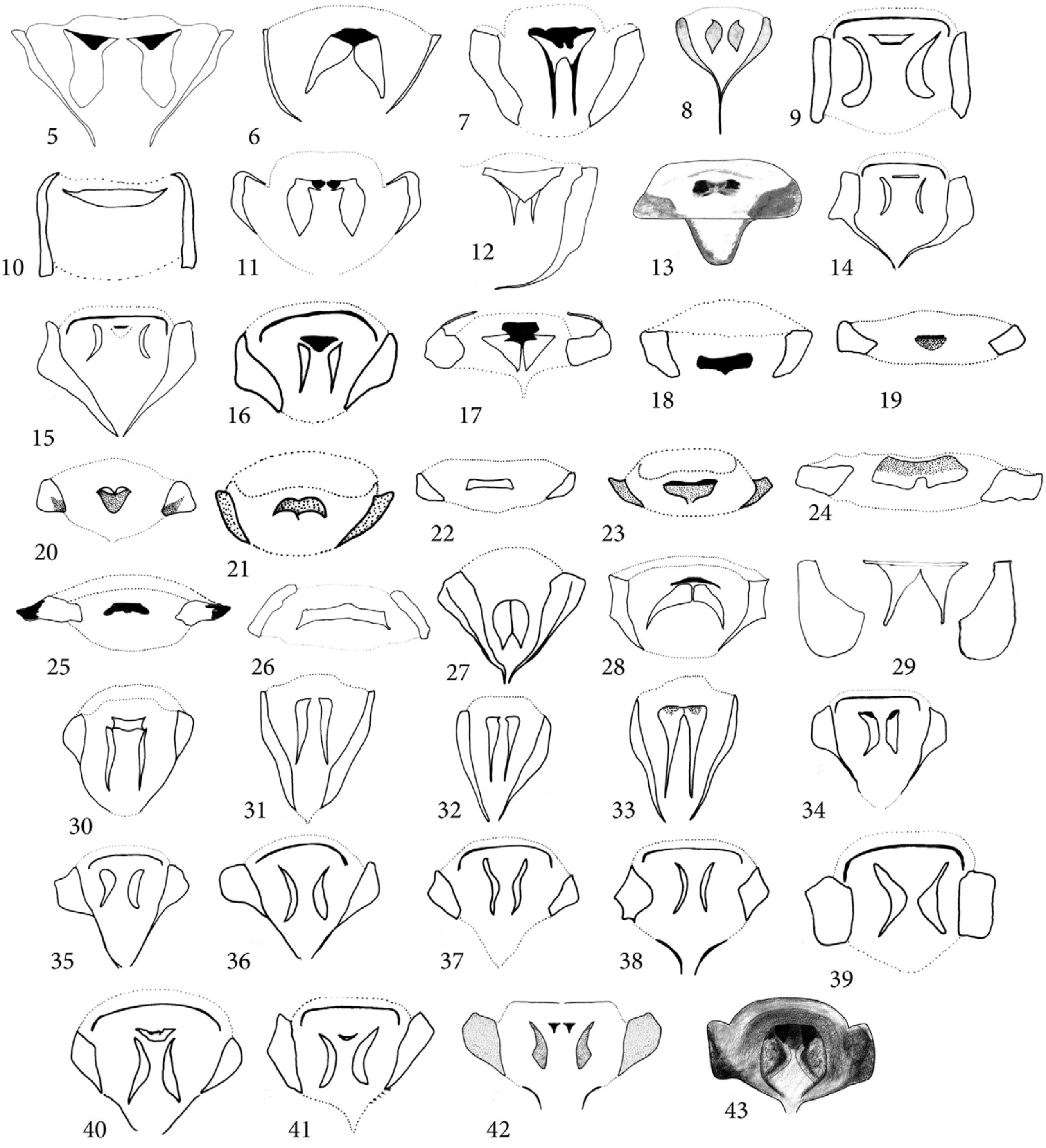


PLATE 2. Figures 5–43. Genital segment. 5. *Arachnodes splendidus* (Fairmaire, 1889). 6. *Onitis* sp. 1. 7. *Gyronotus fimetarius* Kolbe, 1894. 8. *Coptorhina excavata* Frolov, Akhmetova, & Scholtz, 2008. 9. *Canthon cyanellus* LeConte, 1859. 10. *Amphistomus inermis* Matthews, 1974. 11. *Canthon quinquemaculatus* Laporte, 1840. 12. *Anachalcos procerus* Gerstaecker, 1874. 13. *Hansreia affinis* (Fabricius, 1801). 14. *Canthon septemmaculatus* (Latreille, 1812). 15. *Canthon triangularis* (Drury, 1773). 16. *Canthon melancholicus* Harold, 1868. 17. *Ateuchus* sp. 18. *Uroxys coarctatus* Harold, 1867. 19. *Dichotomius bos* (Blanchard, 1845). 20. *Coptodactyla glabricollis* (Hope, 1842). 21. *Digitonthophagus gazella* (Fabricius, 1787). 22. *Onthophagus mirabilis* Bates, 1886. 23. *Proagoderus brucei* Reiche, 1847. 24. *Scarabaeus* (*Pachysoma*) sp. 25. *Sceliages adamastor* (LePeletier & Serville, 1828). 26. *Eudinopus dytiscoides* (Schreibers, 1802). 27. *Ontherus sanctaemartae* Génier, 1996. 28. *Onitis* sp. 2. 29. *Malagoniella astyanax punctatostriata* (Blanchard, 1845). 30. *Anomiopus* sp. 31. *Copris dracunculus* Ferreira, 1959. 32. *Copris incertus* Say, 1835. 33. *Copris mesacanthus* Harold, 1878. 34. *Canthon* sp. 35. *Canthon lamproderes* Redtenbacher, 1867. 36. *Canthon aequinoctialis* Harold, 1868. 37. *Canthon unicolor* Blanchard, 1846. 38. *Canthon fortemarginatus* Balthasar, 1939. 39. *Canthon humectus* (Say, 1832). 40. *Canthon virens* Mannerheim, 1829. 41. *Canthon indigaceus* LeConte, 1866. 42. *Canthon chalcites* (Haldeman, 1843). 43. *Deltochilum* (*Deltohyboma*) sp.

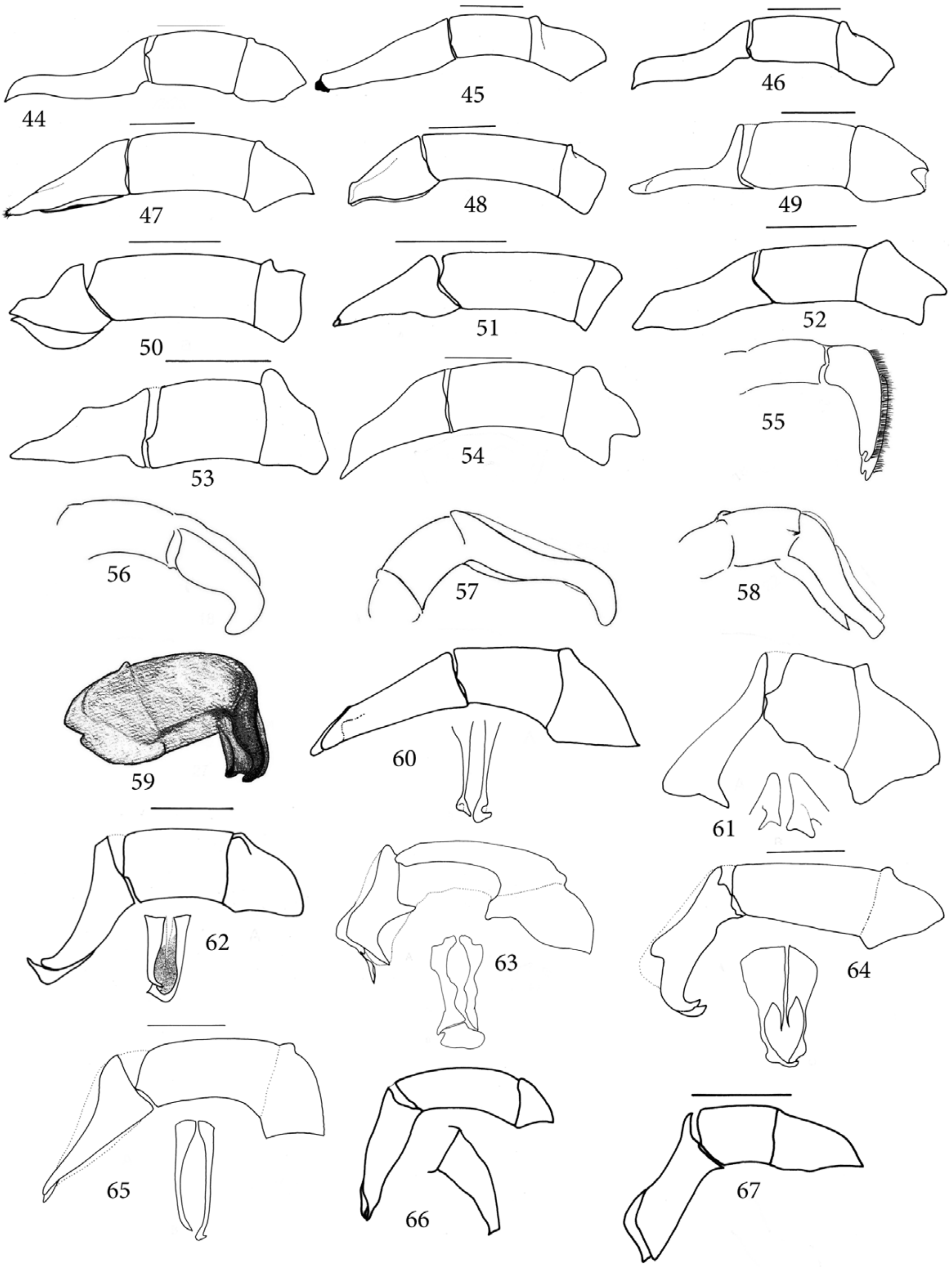


PLATE 3. Figures 44–67. Aedeagus. 44. *Copris dracunculus* Ferreira, 1959. 45. *Copris incertus* Say, 1835. 46. *Copris mesacanthus* Harold, 1878. 47. *Dichotomius bos* (Blanchard, 1846). 48. *Ontherus sanctaemartae* Génier, 1996. 49. *Oxysternon palaemon* Laporte, 1840. 50. *Garreta unicolor* Fahraeus, 1857. 51. *Gymnopleurus* sp. 52. *Anomiopsoides heteroclyta* (Blanchard, 1845). 53. *Ennearabdus lobocephalus* Harold, 1868. 54. *Eucranium* sp. 55. *Namakwanus irishi* Scholtz & Howden, 1987. 56. *Namakwanus* sp. 57. *Epirinus mucrodentatus* Scholtz & Howden, 1987. 58. *Epirinus relictus* Scholtz & Howden, 1987. 59. *Diorygopyx tibialis* (MacLeay, 1871). 60. *Circellium bacchus* (Fabricius, 1781). 61. *Anachalcos procerus* Gerstaecker, 1874. 62. *Epirinus validus* Péringuey, 1901. 63. *Gyronotus fimetarius* Kolbe, 1894. 64. *Canthonosoma castelnaui* (Harold, 1868). 65. *Streblopus opatroides* Lansberge, 1874. 66. *Temnoplectron reyi* Paulian, 1934. 67. *Scybalocanthon moniliatus* (Bates, 1887).

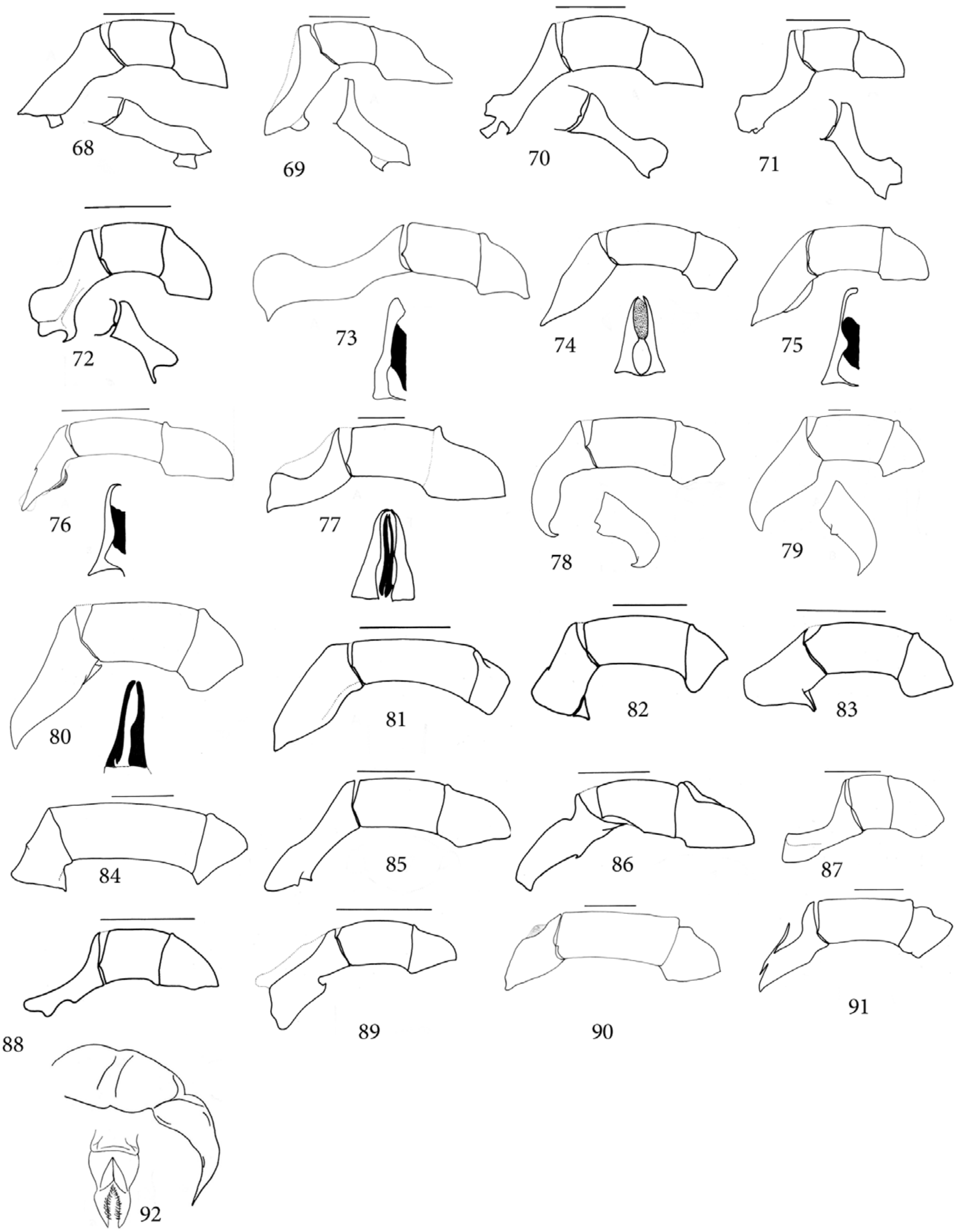


PLATE 4. Figures 68–92. Aedeagus. 68. *Canthon cyanellus* LeConte, 1859. 69. *Canthon quinquemaculatus* Laporte, 1840. 70. *Canthon aberrans* (Harold, 1868). 71. *Canthon angularis* Harold, 1868. 72. *Canthon* sp. 73. *Eudinopus dytiscoides* (Schreibers, 1802). 74. *Malagoniella astyanax columbica* Harold, 1867. 75. *Malagoniella astyanax punctatostriata* (Blanchard, 1845). 76. *Malagoniella (Megathopomima) puncticollis* (Blanchard, 1845). 77. *Megathoposoma candezei* Harold, 1873. 78. *Scarabaeus (Pachysoma)* sp. 79. *Scarabaeus zambezianus* Péringuey, 1901. 80. *Sceliages adamastor* (LePeletier & Serville, 1828). 81. *Sisyphus schaefferi* (Linnaeus, 1758). 82. *Digitonthophagus gazella* (Fabricius, 1787). 83. *Onthophagus mirabilis* Bates, 1886. 84. *Proagoderus brucei* Reiche, 1849. 85. *Coptodactyla glabricollis* (Hope, 1842). 86. *Coptorhina excavata* Frolov, Akhmetova, & Scholtz, 2008. 87. *Anisocanthon villosus* (Harold, 1868). 88. *Anomiopus* sp. 89. *Sylvicanthon bridarollii* (Martínez, 1949). 90. *Deltochilum (Deltohyboma)* sp. 1. 91. *Deltochilum* (*Deltohyboma*) sp. 2. 92. *Dicranocara deschodti* Frolov & Scholtz, 2003.

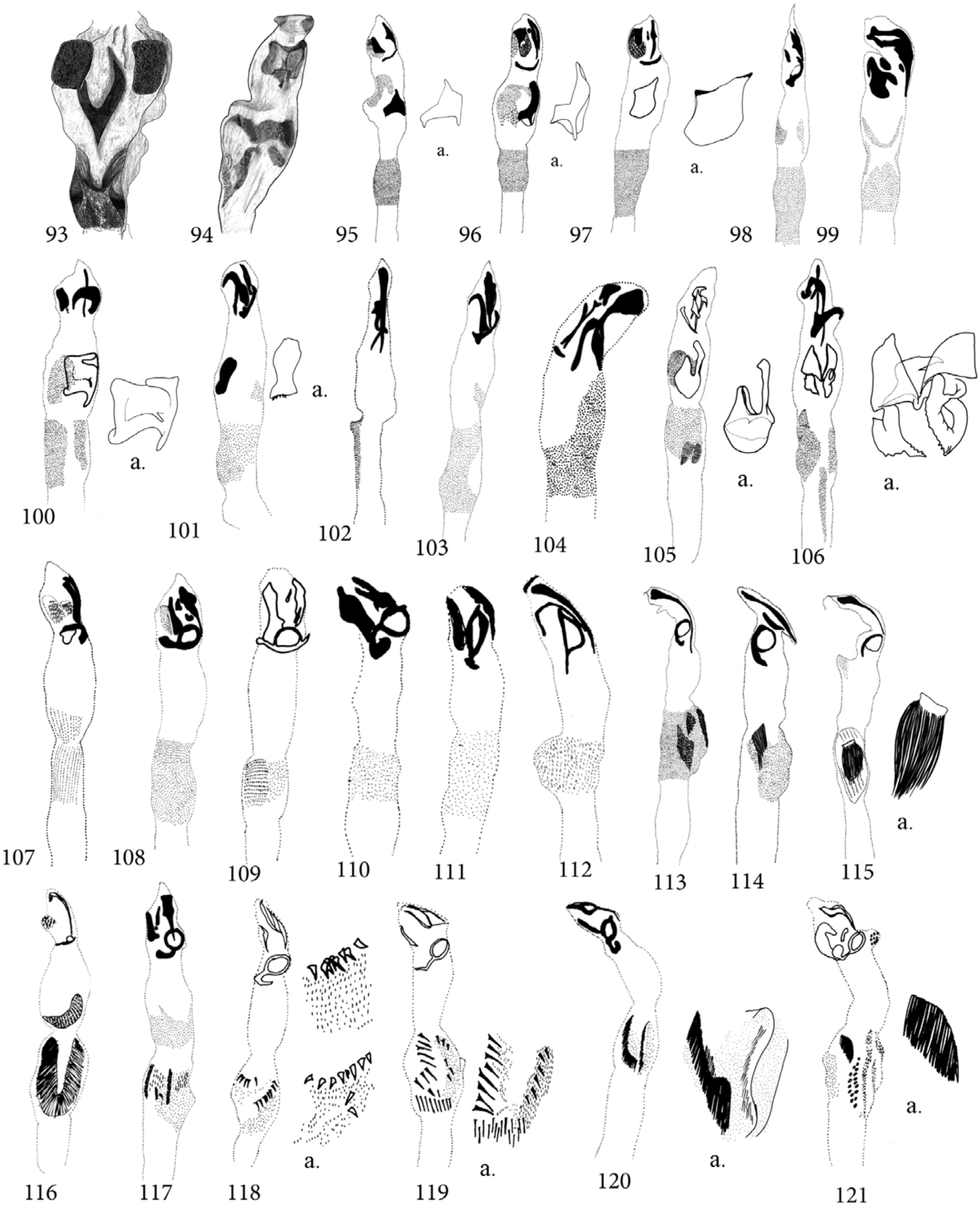


PLATE 5. Figures 93–121. Internal sac. 93. *Ataenius* sp. 94. *Byrrhidium convexum* Scholtz & Howden, 1987. 95. *Anomiopsoides heteroclyta* (Blanchard, 1845). 96. *Ennearabdus lobocephalus* Harold, 1868. 97. *Eucranium* sp. 98. *Bdelyrus* sp. 99. *Coptorhina excavata* Frolov, Akhmetova, & Scholtz, 2008. 100. *Dichotomius bos* (Blanchard, 1846). 101. *Copris dracunculus* Ferreira, 1959. 102. *Copris incertus* Say, 1835. 103. *Copris mesacanthus* Harold, 1878. 104. *Digitonthophagus gazella* (Fabricius, 1787). 105. *Onthophagus mirabilis* Bates, 1886. 106. *Proagoderus brucei* Reiche, 1847. 107. *Malagoniella astyanax columbica* Harold, 1867. 108. *Anomiopus* sp. 109. *Canthon angularis* Harold, 1868. 110. *Canthon* sp. 111. *Canthon lamproderes* Redtenbacher, 1867. 112. *Canthon auricollis* Redtenbacher, 1867. 113. *Scarabaeus (Pachysoma)* sp. 114. *Scarabaeus zambezianus* Péringuey, 1901. 115. *Sceliages adamastor* (LePeletier & Serville, 1828). 116. *Circellium bacchus* (Fabricius, 1781). 117. *Sylvicanthon bridarollii* (Martínez, 1949). 118. *Canthon unicolor* Blanchard, 1846. 118a. Raspule. 119. *Canthon fortemarginatus* Balthasar, 1939. 119a. Raspule. 120. *Canthon humectus* (Say, 1832). 120a. Raspule. 121. *Canthon virens* Mannerheim, 1829. 121a. Raspule.

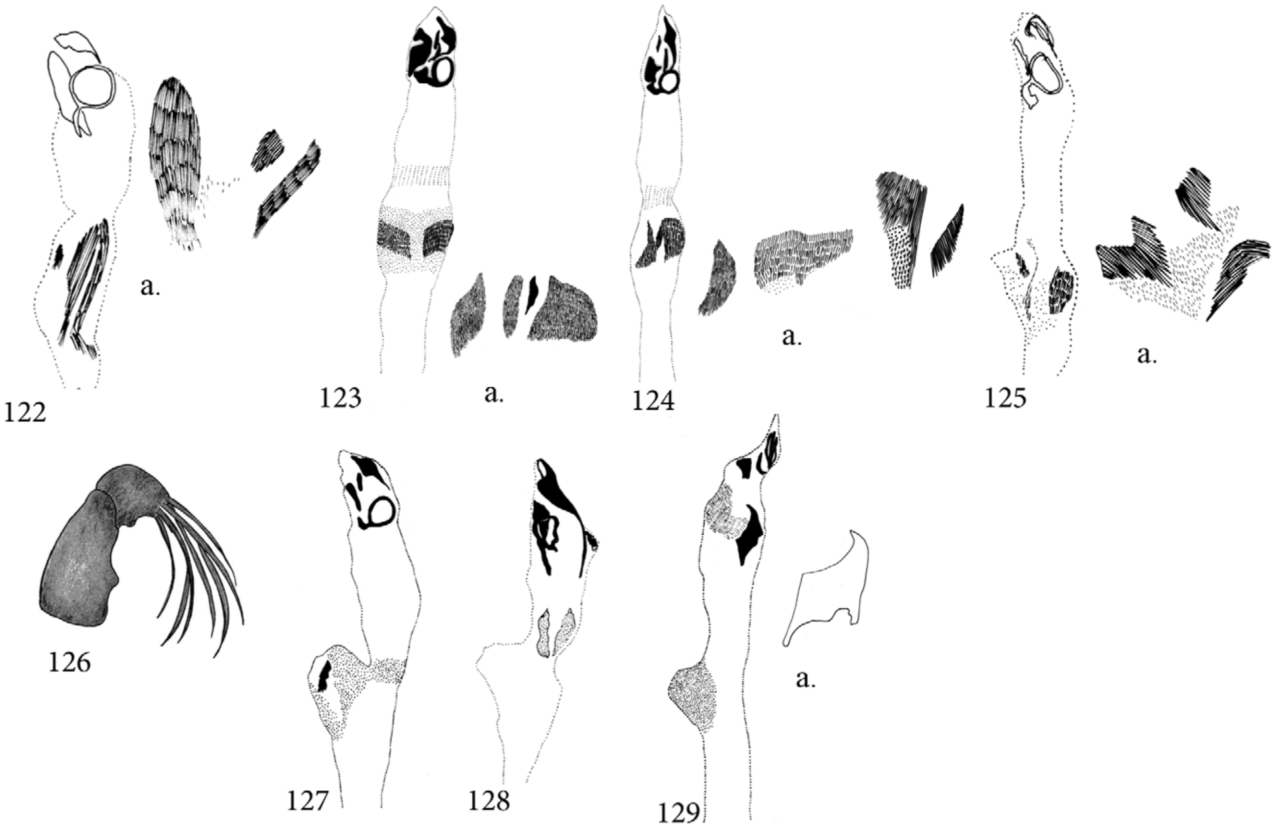


PLATE 6. Figures 122–129. Internal sac. 122. *Canthon cyanellus* LeConte, 1859. 122a. Raspule. 123. *Canthon quinquemaculatus* Laporte, 1840. 123a. Raspule. 124. *Canthon septemmaculatus* (Latreille, 1812). 124a. Raspule. 125. *Canthon triangularis* (Drury, 1773). 125a. Raspule. 126. *Scarabaeus canaliculatus* Fairmaire, 1888 (Raspule). 127. *Scybalocanthon moniliatus* (Bates, 1887). 128. *Canthon fulgidus* Redtenbacher, 1867. 129. *Oxysternon palaemon* Laporte, 1840.

The variation in the shape of the parameres can be quite large in genera with a large number of species, such as *Canthon* and *Deltochilum*. In *Canthon*, four different types of aedeagus by the shape of the parameres are recognized (Medina *et al*. 2003). The triangular shape is the most common among the species studied, although with variations especially on the ventral face, which has some sinuosities, *i.e*., in the tribe Scarabaeini (Figs. 78–80) and in *Sisyphus schaefferi* (Linnaeus, 1758) (Fig. 81), or can be very narrow as in *Oxysternon palaemon* (Fig. 49), or with evident variation in the apex of each paramere (*Copris* spp. Figs. 44–46), *Dichotomius bos,* and *O. sanctaemartae* (Figs. 47, 48). The rectangular shape is observed in species of Onthophagini with some small teeth in the apex seen in the ventral view (Figs. 82–84). In *Coptodactyla glabricollis* (Hope, 1842) and *Coptorhina excavata* (Figs. 85, 86), the rectangular shape is also observed in *Anisocanthon villosus* (Harold, 1868), *Anomiopus* sp., *Sylvicanthon bridarollii* (Martínez, 1949), and in different species of *Canthon* (Figs. 87–89) the parameres are more enlarged and with a notch in the ventral side of each paramere (Medina *et al*. 2003).

In the genus *Deltochilum*, the variation observed is even larger than in *Canthon*. Different types of aedeagus were observed within only one group of species belonging to one *Deltochilum* subgenus; a large variation was found in the *D. spinipes* group (subgenus *Deltohyboma*), which has species distributed in the New World tropics. Different species from the same group collected from different localities in the Andean cordillera in Colombia, presented different types of aedeagus. These species are very similar in external morphology but vary greatly in male genitalia, including the shape of the parameres of the aedeagus. It looks as if every species examined had a very distinct type of aedeagus (Figs. 90, 91).

In other small genera, where more than one species of the genus were dissected, differences in the aedeagus were also observed. In the genus *Namakwanus* Scholtz & Howden, 1987 two extremely different aedeagus were observed (Figs. 55, 56). Species of the African genus *Gyronotus* van Lansberge, 1874 presented two different recognizable types of aedeagus, as was also observed in the genus *Anachalcos*. Larger species of *Anachalcos* presented a truncate border different to those in smaller species. On the contrary, genera such as *Odontoloma* Boheman, 1857 and *Epirinus* have a constant pattern in the shape of the parameres of the aedeagus. For the genus *Epirinus,* where all the species were observed (Medina & Scholtz 2005), small variation among the species could be detected, but the general pattern in the shape of the aedeagus is constant. *Epirinus* is a monophyletic genus and taxonomically well defined, and that may be the reason for the small variation in the shape of the parameres (Figs. 57, 58).

Other important features observed in the aedeagus are the presence of setae. In general, the aedeagus in Scarabaeinae are glabrous, but in species of *Byrrhidium* Harold, 1869*, Dicranocara*, and *Namakwanus* setae are evident. In *Namakwanus streyi* Frolov, 2005, a row of long setae along the side of the parameres is present (Figs. 56, 92), which was also noticed in one species of *Canthochilum* setae in the tip of the parameres, and in some species of the genus *Uroxys* Westwood, 1842.

Internal sac of the aedeagus. The internal sac of the aedeagus in Scarabaeinae beetles is an elongate, membranous, and transparent bag encased within the quitinous capsule of the aedeagus. For a better understanding of the structures in each part of the sac, the extended sac has been divided in four parts (regions): basal, submedial, medial, and apical (Fig. 3). The basal area is continuous to the temones, and is generally free of sclerotized structures. In the submedial area, located just after the basal area, the raspules is present in some groups. In the medial area, there are from zero up to three sclerotized structures present; called the medial sclerites, or also called copulatrice lamellae (Zunino 1979). The apical area is where the main quitinized structures are located; the apical sclerites, also called accessory lamellae or accessory sclerites by various authors (see Table 2).

Most of the genera of Scarabaeinae have a basic type of internal sac: an elongate and tubular bag with apical sclerites, with folds or/and brushes in the submedial part and the temones on the other extreme (basal part). A group of genera including *Byrrhidium*, *Dicranocara*, *Namakwanus*, and *Sarophorus* Erichson, 1847 have a shorter sac with weaken defined apical sclerites and temones in the other extreme, different from the appearance of the sac in the rest of the Scarabaeinae genera examined; the sac in these four genera is more similar to the sac found in the Aphodiinae examined (Figs. 93, 94). In the rest of the Scarabaeinae dung beetles, the four anteriorly described areas are present. As follows, we describe the variation in the submedial, medial and apical area where quitinous structures are present.

Submedial area. In most of the genera examined, the submedial area of the sac is tubular, without deformations; however in some species, a lateral and pronounced extension forming a lobule was observed: in the genus *Scybalophagus* Martínez, 1953 (Ocampo & Molano 2011), in most species of the genus *Scybalocanthon* (Fig. 127, Molano & Medina 2010); in some subgenera of *Deltochilum* (González *et al*. 2009); and in some species of *Canthon; C. auricollis* Redtenbacher, 1867 (Fig. 112)*, C. fulgidus* Redtenbacher, 1867 (Fig. 128), and *C. bicolor* Laporte, 1840 (Medina *et al*. 2003). This lateral projection is also present in *O. palaemon* (Fig. 129).

The submedial area can be covered by small or large spines or setae that can be arranged in structures that have the appearance of brushes with thick and long spikes, or are formed by large scales or bristles. These structures are known as raspules (Zunino 1972), or brushes of the internal sac (Medina *et al*. 2003). The raspules are present indistinctly in many groups and tribes within the subfamily, and they are not exclusive of any tribe or groups of genera. The function of these structures is unknown.

In *Anomiopsoides heteroclyta*, *Ennearabdus lobocephalus*, *Eucranium* sp., and (Figs. 95–97), *Bdelyrus* sp. (Fig. 98), the raspules form a band of small scales that cover the whole area, while in other genera the area is partially covered by scales (*C. excavata* Fig. 99), *D. bos* (Fig. 100), *Copris* spp. (Figs. 101–103), *Digitonthophagus gazella* (Fabricius, 1787) (Fig. 104), *Onthophagus mirabilis* Bates, 1886 (Fig. 105), *Proagoderus brucei* Reiche, 1847 (Fig. 106), *M. astyanax columbica* (Fig. 107), *Anomiopus* sp. (Fig. 108), and some species of *Canthon* (Figs. 109–112). Spines of larger size forming defined areas are also present in *Scarabaeus* (*Pachysoma*) sp., *S. zambezianus* Péringuey, 1901, *Sceliages adamastor* (LePeletier & Serville, 1828) (Figs. 113–115). In *Circellium bacchus* (Fabricius, 1781) the raspule has a U shape (Fig. 116). In *S. bridarollii* (Fig. 117), there are different sizes of scales and spines as well in various species of *Canthon* (*C. unicolor* Blanchard, 1846, Fig. 118*; C. fortemarginatus* Balthasar, 1939, Fig. 119). Some species of *Canthon* have a clump of setae as in (*C. humectus* (Say, 1832), Fig. 120*; Canthon virens* Mannerheim, 1829, Fig. 121*; C. cyanellus*, Fig. 122*; C. quinquemaculatus*, Fig. 123*; C. septemmaculatus* (Latreille, 1812), Fig. 124*;* and *C. triangularis* (Drury, 1773) Fig. 125).

In other groups, the raspules are well defined in a more solid structure that varies in number and shapes.

Genera have three, two, or one defined raspule. The raspules could be elongate or oval, with long and thin spikes or with short and wide spines. In the genus *Scarabaeus*, the raspule is formed by a quitinous base with seven elongate filaments (Fig. 126). In all the species examined of this genus, the same type of raspule was observed with the same number of filaments.

Medial area. In the medial area, sclerotized structures may or may not be present. In some genera, the medial sclerites are always present as in the case of *Deltochilum, Onthophagus, Canthidium* Erichson, 1847, *Dichotomius, Oxysternon* Laporte, 1840 and *Uroxys* and in the tribes Eucraniini and Onitini. The number of sclerites is variable from one and three, but generally there is one sclerite and the shape varies depending of the species. These medial sclerites are never present in the tribe Deltochilini, with the exception of the genus *Deltochilum*.

Apical area. A group of apical sclerites are located in the apical area (Fig. 3). Most species have three sclerites: the basal sclerite, which is transverse and basally located; the elongate sclerite, usually larger and with long filaments, and the plate sclerite, which has different shapes but is generally broad and flat. In some genera, a scaly area is present in this region; in Aphodinae it has larger scaly areas, and in some Scarabaeinae species a remanent of this scaly area it is still observed.

Apical sclerites. Detailed descriptions of the internal sac's sclerites of mostly American Deltochilini were presented in Medina *et al*. (2003). They recognized three main different types of sclerites: the circular sclerite (here called basal sclerite), an elongate sclerite and a plate-like sclerite. These three types of sclerites are generally constant in the internal male genitalia of Scarabaeinae dung beetles, but there is a large variation among them. Despite the fact that the variation in the shape of these sclerites is enormous, it has been possible to recognize these structures as homologues after the dissection of larger amount of specimens, allowing an exhaustive comparison among a large amount of genera of the subfamily Scarabaeinae.

Basal sclerite. This is a particularly common and constant sclerite in the internal sac of Scarabaeinae dung beetles (Fig. 4). It is located at the base of the apical area and its transversly located regarding the other sclerites. In Medina *et al*. (2003), it was called circular sclerite since part of the sclerite is a circular shape. After dissecting a large number of genera within the subfamily Scarabaeinae, a large variation in the basal sclerite was observed. In most of the groups, the basal sclerite is always present, well developed, with a circular complete part (the ring). In others, the circular part is open; in others this sclerite is extremely reduced, and in other groups it does not have a circular part at all. According to the position with respect to otherones, this sclerite has been called basal sclerite; it is always in the same position, it is surrounded with a membranous layer of the sac and it is basal to the other sclerites.

The basal sclerite is known in the literature as a lateral structure (Barbero *et al*. 1998), ring sclerite (Reid 2000, Reid & Storey 2000), virgular sclerite (Forgie 2002) and circular sclerite (Medina *et al*. 2003, see Table 2).

The variation of the basal sclerite with a circular shape for New World Deltochilini was described in detail by Medina *et al*. (2003). Some terms, used for the descriptions of the circular sclerites in Medina *et al*. (2003) are used again here. For example, the ring is used to describe the circular part of the sclerites, when present, and the "handle" is used when the circular part is accompanied by an enlarged and quitinous extension (Figs. 130–132).

The variation of the basal sclerite can be enormous, but the shape is constant within the same genera or some group of species as it is the case in some groups of *Canthon* and subgenera of *Deltochilum*. Three main forms of basal sclerite have been noticed among the taxa studied: basal sclerite with circular shape; basal sclerite as a hook without the circular part, which looks as if the circular part were lost; and a basal sclerite extremely reduced, but with the circular part still visible.

Circular-shape basal sclerite. This type of sclerite is the most common form found among the Scarabaeinae taxa studied as many different genera of the subfamily have a basal sclerite with a circular part. The variation amount this circular-shape basal sclerite is enormous. Most genera of Deltochilini have a typical and well-developed circular sclerite; in the large New World Deltochilini, most of the genera have a very similar basal circular sclerite. The most usual and noticeable basal circular sclerite are present in the genera *Canthon* and *Scybalocanthon* that share a very similar sclerite with a well-delimited, large, open ring and a defined handle. *Hansreia*, *Sylvicanthon* Halffter & Martínez, 1977, and *Anisocanthon* Martínez & Pereira, 1956 also have a similar circular sclerite (Figs. 133–138, 140). Genera such as *Scatonomus* Erichson, 1835 and *Anomiopus* Westwood, 1842 now proposed as Deltochilini (Vaz-de-Mello 2008), have a similar circular sclerite as present in *Canthon*. The same has been observed in the genus *Garreta* Janssens, 1940 and *Gymnopleurus* Illiger, 1803 (tribe Gymnopleurini).

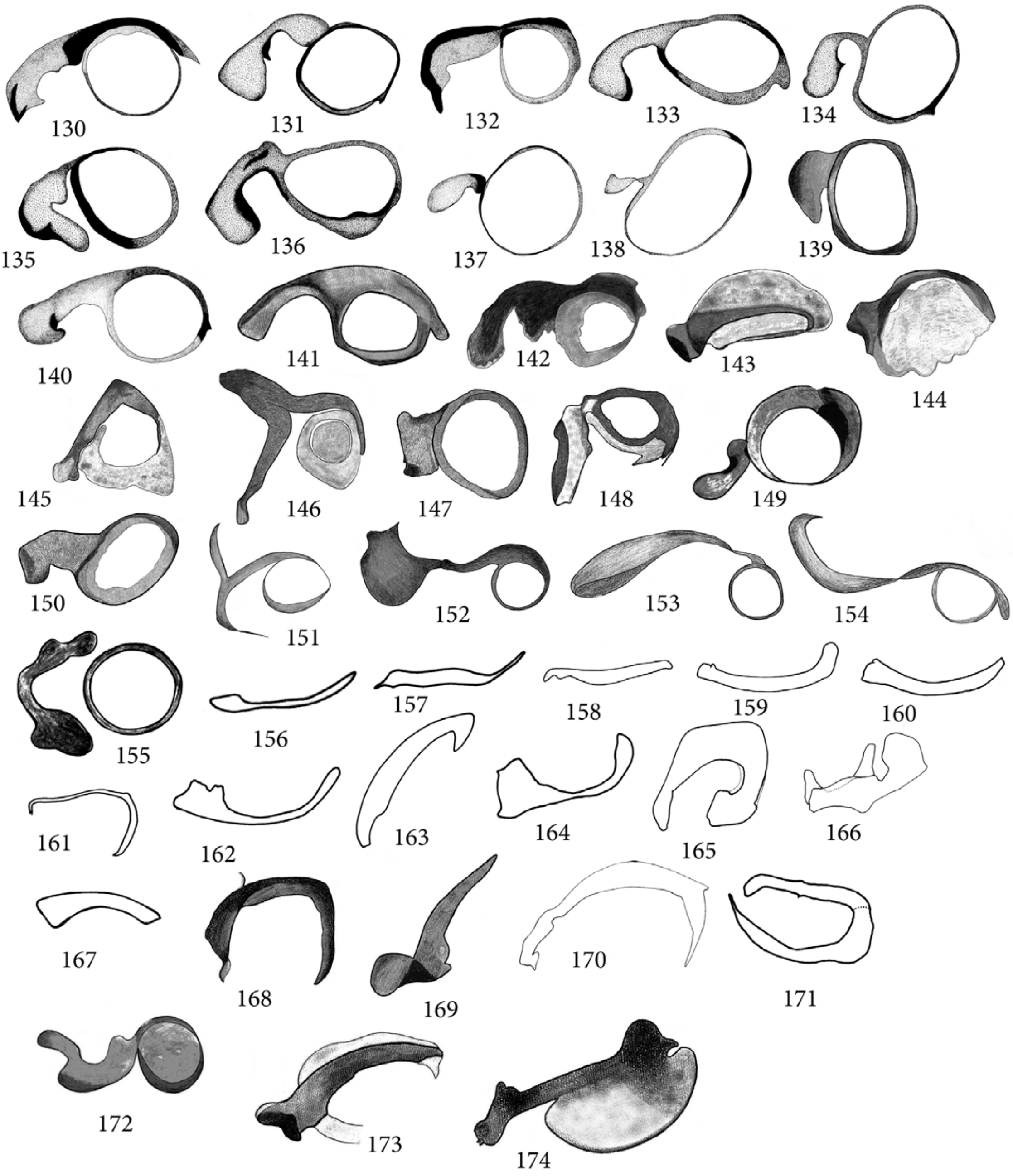


PLATE 7. Figures 130–174. Basal sclerite. 130. *Canthon tetraodon* Blanchard, 1846. 131. *Sylvicanthon bridarollii* (Martínez, 1949). 132. *Melanocanthon bispinatus* (Robinson, 1941). 133. *Canthon humectus* (Say, 1832). 134. *Canthon triangularis* (Drury, 1773). 135. *Canthon quinquemaculatus* Laporte, 1840. 136. *Canthon pilularius* (Linnaeus, 1758). 137. *Canthon violaceus* (Olivier, 1789). 138. *Canthon bicolor* Laporte, 1840. 139. *Aulacopris maximus* Matthews, 1974. 140. *Scybalocanthon moniliatus* (Bates, 1887). 141. *Eudinopus dytiscoides* (Schreibers, 1802). 142. *Circellium bacchus* (Fabricius, 1781). 143. *Bohepilissus subtilis* (Boheman, 1857). 144. *Diorygopyx tibialis* (MacLeay, 1871). 145. *Cryptocanthon newtoni* Howden, 1976. 146. *Paracanthon* sp. 147. *Demarziella interrupta* (Carter, 1936). 148. *Coptodactyla lesnei* Paulian, 1933. 149. *Thyregis kershawi* Blackburn, 1904. 150. *Pedaria* sp. 151. *Janssensantus pauliani* Scholtz & Howden, 1987. 152. *Caccobius megaponerae* Brauns, 1914. 153. *Canthidium perceptibile* Howden & Young, 1981. 154. *Bdelyropsis bowditchi* (Paulian, 1939). 155. *Uroxys rugatus* Boucomont, 1928. 156. *Digitonthophagus gazella* (Fabricius, 1787). 157. *Onthophagus mirabilis* Bates, 1886. 158. *Anomiopsoides heteroclyta* (Blanchard, 1845). 159. *Ennearabdus lobocephalus* Harold, 1868. 160. *Eucranium* sp. 161. *Canthidium* sp. 162. *Copris dracunculus* Ferreira, 1959. 163. *Copris incertus* Say, 1835. 164. *Copris mesacanthus* Harold, 1878. 165. *Dichotomius bos* (Blanchard, 1846). 166. *Ontherus sanctaemartae* Génier, 1996. 167. *Oxysternon palaemon* Laporte, 1840. 168. *Anachalcos convexus* Boheman, 1857. 169. *Tesserodon novaehollandiae* (Fabricius, 1775). 170. *Arachnodes* sp. 171. *Eurysternus cyanescens* Balthasar, 1939. 172. *Temnoplectron bornemisszai* Matthews, 1974. 173. *Mentophilus hollandiae* Laporte, 1840. 174. *Nanos clypeatus* (Laporte, 1840).

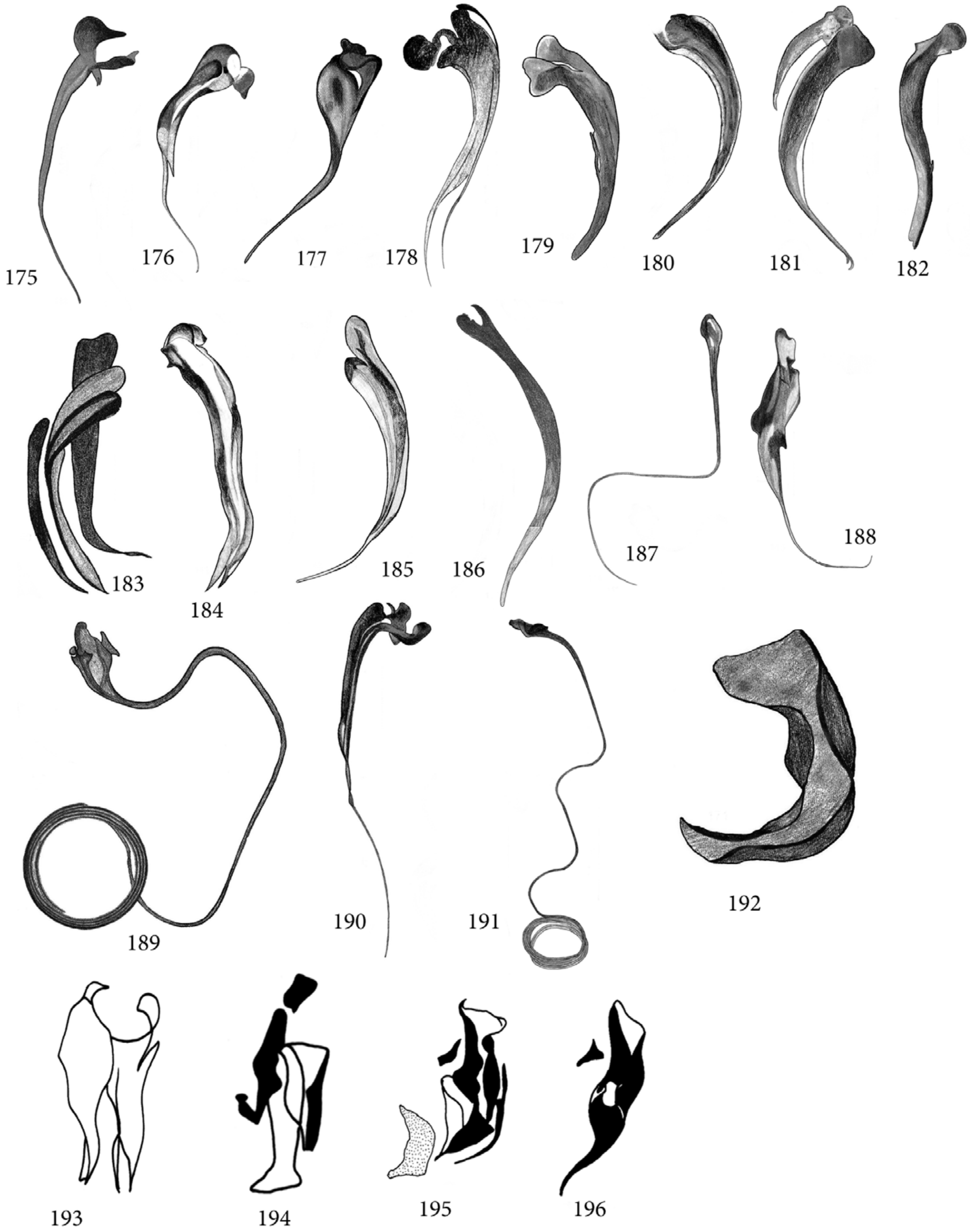


PLATE 8. Figures 175–196. Elongate sclerite. 175. *Gyronotus carinatus* Felsche, 1911. 176. *Demarziella interrupta* (Carter, 1936). 177. *Mentophilus hollandiae* Laporte, 1840. 178. *Epirinus mucrodentatus* Scholtz & Howden 1987. 179. *Aulacopris maximus* Matthews, 1974. 180. *Circellium bacchus* (Fabricius, 1781). 181. *Eudinopus dytiscoides* Schreibers, 1802. 182. *Tesserodon novaehollandiae* (Fabricius, 1775). 183. *Scarabaeus canaliculatus* Fairmaire, 1888. 184. *Pedaria* sp 185. *Bohepilussus subtilus* (Boheman, 1857). 186. *Thyregis kershawi* Blackburn, 1904. 187. *Arachnodes nitidus* (Laporte, 1840). 188. *Epilissus splendidus* Fairmaire, 1889. 189. *Paracanthon* sp. 190. *Anachalcos convexus* Boheman, 1857. 191. *Nanos clypeatus* (Laporte, 1840). 192. *Epirinus ngomae* Medina & Scholtz 2005. 193. *Malagoniella astyanax columbica* Harold, 1867. 194. *Canthon melancholicus* Harold, 1868. 195. *Canthon aequinoctialis* Harold, 1868. 196. *Canthon aberrans* (Harold, 1868).

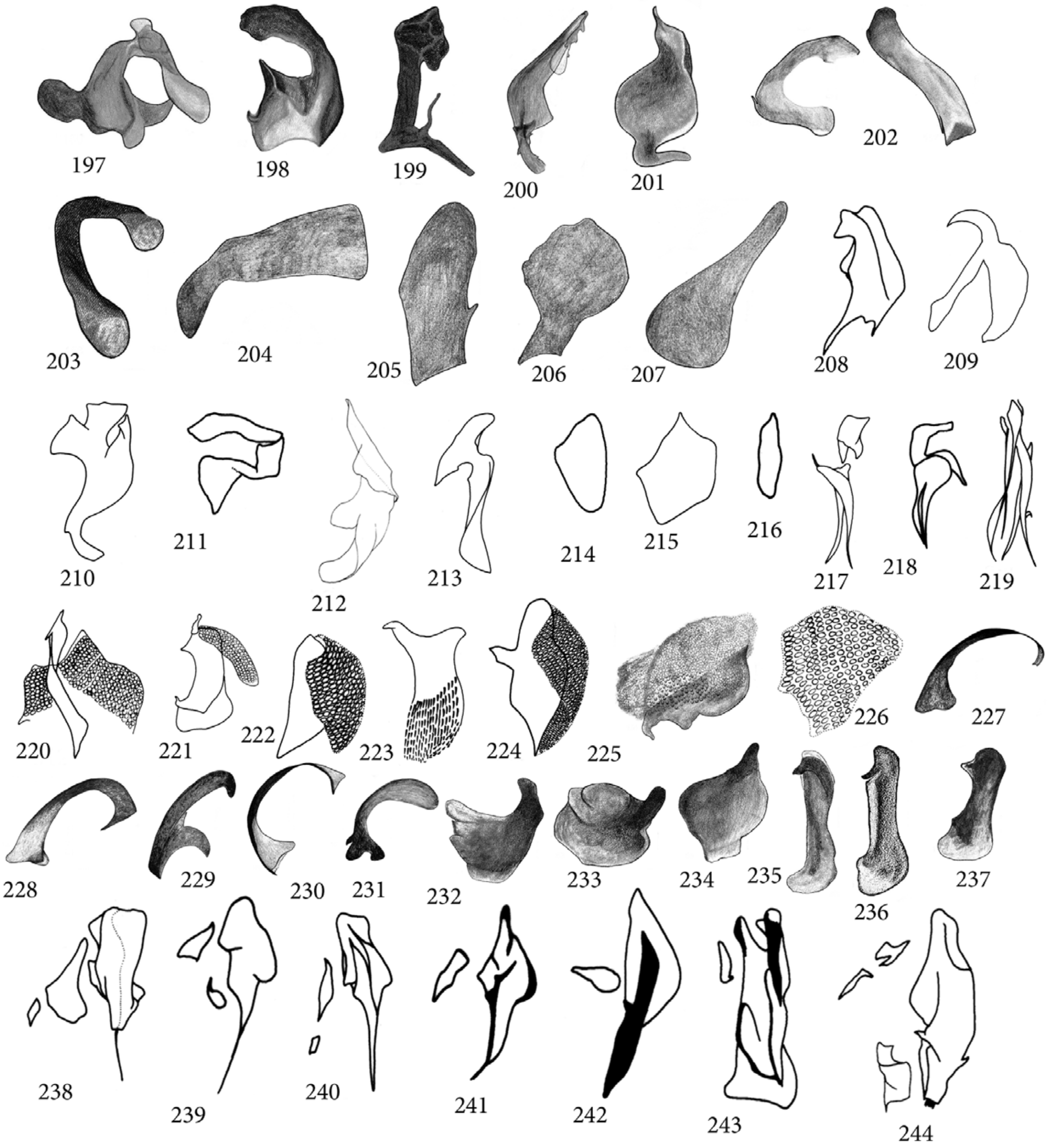


PLATE 9. Figures 197–244. Plate sclerite. 197. *Diorigopyx tibialis* (MacLeay, 1871). 198. *Gyronotus carinatus* Felsche, 1911. 199. *Arachnodes nitidus* (Laporte, 1840). 200. *Epilissus splendidus* (Fairmaire, 1889). 201. *Eudinopus dytiscoides* Schreibers, 1802. 202. *Pedaria* sp. 203. *Hansreia affinis* (Fabricius, 1801). 204. *Deltochilum mexicanum* Burmeister, 1848. 205. *Cryptocanthon newtoni* Howden, 1976. 206. *Deltochilum gibbosum* (Fabricius, 1775). 207. *Anisocanthon villosus* (Harold, 1868). 208. *Canthidium* sp. 1928. 209. *Copris dracunculus* Ferreira, 1959. 210. *Copris incertus* Say, 1835. 211. *Coptodactyla glabricollis* Hope, 1842. 212. *Arachnodes* sp. 213. *Onitis* sp. 214. *Coptorhina excavata* Frolov, Akhmetova & Scholtz, 2008. 215. *Oxysternon palaemon* Laporte, 1840. 216. *Bdelyrus* sp. 217. *Digitonthophagus gazella* Fabricius, 1787. 218. *Onthophagus mirabilis* Bates, 1886. 219. *Proagoderus brucei* Reiche, 1849. 220. *Canthon aberrans* (Harold, 1868). 221. *Canthon* sp. 222. *Anomiopsoides heteroclyta* (Blanchard, 1845). 223. *Ennearabdus lobocephalus* Harold, 1868. 224. *Eucranium* sp. 225. *Diorigopyx tibialis* (MacLeay, 1871). 226. *Circellium bacchus* (Fabricius, 1781). Basal sclerite. 227. *Epirinus ngomae* Medina & Scholtz 2005. 228. *Epirinus hluhluwensis* Medina & Scholtz, 2005. 229. *Epirinus pseudorugosus* Medina & Scholtz, 2005. 230. *Epirinus punctatus* Scholtz & Howden, 1987. 231. *Epirinus relictus* Scholtz & Howden, 1987. 232. *Canthon rubrescens* Blanchard, 1846. 233. *Canthon femoralis* (Chevrolat, 1834). 234. *Canthon angustatus* Harold, 1867. 235. *Canthon dives* Harold, 1868. 236. *Canthon latipes* Blanchard, 1846. 237. *Canthon rutilans* Laporte, 1840. 238. *Anisocanthon villosus* (Harold, 1868). 239. *Anomiopus* sp. 240. *Sylvicanthon bridarollii* (Martínez, 1949). 241. *Scybalocanthon moniliatus* (Bates, 1887). 242. *Canthon gemellatus* Erichson, 1847. 243. *Canthon* sp. 244. *Canthon lamproderes* Redtenbacher, 1867.

Larger Deltochilini from the New World such as *Eudinopus*, *Scybalophagus*, and *Megathoposoma* and the genus *Circellium* from Africa, have a basal circular sclerite with defined ring and handle. Other genera of Deltochilini from Africa (*Bohepilissus* Paulian, 1975), Australia (*Canthonosoma* MacLeay, 1871, *Aulacopris*, and *Diorygopyx* Matthews, 1974) and from New Zealand (*Saphobiamorpha* and *Saphobius*) also have a basal circular sclerite (Figs. 139, 141–144).

In the New World genus *Cryptocanthon* Balthasar, 1942 two different types of circular sclerite were observed. In *C. newtoni* Howden, 1976 the ring in the circular sclerites is formed by a continuation of the handle; the extreme of the handle looks as if it is folded over itself forming the ring structure; the ring is not completely a circular shape and it has a more triangular appearance instead (Fig. 145). In *C. foveatus* Cook, 2002 the sclerite has a similar shape but the ring is complete and differentiable from the handle; no other genera showed similar sclerites to those. In the genus *Paracanthon* Balthasar, 1938 the ring has a membranous filling (Fig. 146).

In *Malagoniella* and *Megathopa* the "handle" is well developed and ticks, generally with a noticeable process; the ring is membranous and an irregularly shape, and in some cases so translucent it is barely visible.

Basal sclerite circular is also present in the Australian genera *Demarziella* Balthasar, 1961, *Thyregis* Blackburn, 1904 and *Coptodactyla* (Figs. 147–149), and in the genus *Pedaria* Laporte, 1832 from Africa (Fig. 150). The whole internal male genitalia in these four genera of tunnelers (*Coptodactyla*, *Thyregis*, *Demarziella*, and *Pedaria*) are more similar to Deltochilini genera than to other Coprini genera.

In the African genus *Janssensantus* Paulian, 1976, the circular sclerite is well formed with a conspicuous handle, which has a lateral projection (Fig. 151). The species *Caccobius megaponerae* Brauns, 1914 (Onthophagini) has a circular sclerite with a ring similar to this, though the handle in this species ends in a large flattened plate (Fig. 152). In the species *Bdelyropsis bowditchi* (Paulian, 1939), and *Canthidium perceptibile* Howden & Young, 1981 (Coprini) a similar basal sclerite was found with a conspicuous ring and enlarged "handle" (Figs. 153, 154). A perfect circular ring completely separated from the handle was also observed in *Uroxys rugatus* Boucomont, 1928 (Ateuchini, Fig. 155) and in *Amphistomus inermis* Matthews, 1974.

Basal sclerite without ring. A very different type of basal sclerite was observed in genera from different tribes, including Deltochilini, Onthophagini (Figs. 156, 157), Eucraniini (Figs 158–160), Coprini (Figs. 162–166), and Phanaeini (Fig. 167). The sclerite has a simple structure as a slender bar without a ring. It can be in the shape of a hook (Coprini), resembling the handle of the circular sclerite described previously; even in some genera it is possible to notice the process of the handle, typical of a circular sclerite. This sclerite is present in the Deltochilini genera *Anachalcos*, *Gyronotus*, and *Canthodimorpha* Davis, Scholtz, & Harrison, 1999 from Africa (Fig. 168), *Tesserodon* from Australia (Fig. 169) and *Arachnodes* Westwood, 1847 from Madagascar (Fig. 170). The genus *Macroderes* a typical African tunneller beetle, has a very similar basal sclerite as the deltochilines. This type of sclerite is also present in the genera *Onthophagus*, *Eurysternus*, and *Canthidium* (Figs. 161, 171).

Basal sclerite reduced. In most genera of Australian Deltochilini (*Aptenocanthon* Matthews, 1974, *Monoplistes* van Lansberge, 1874, *Onthobium* Reiche, 1860, *Temnoplectron*, *Boletoscapter* Matthews, 1974, *Tesserodon* Hope, 1837, and *Menthophilus* Laporte, 1840) the basal sclerite is extremely reduced, it has a circular part that is solid and well sclerotized (Figs.172, 173). The genus *Nanos* Westwood, 1847 from Madagascar also has an atypical sclerite with a solid circular part (Fig. 174). Similar reduced basal sclerite was observed in the African genus *Hammondantus* Cambefort, 1978.

Various species of the genus *Uroxys* (*U. cuprescens* Westwood, 1842*; U. microcularis* Howden & Young, 1981*; U. boneti* Pereira & Halffter, 1961; and *U. brachialis* Arrow, 1933) have a basal sclerite similar to circular sclerite, but extremely reduced in size compared to the rest of sclerites in the sac.

Elongate sclerite. This structure is also known as flagellum, virga, or ligulla (Snodgrass 1935). This sclerite is present in most of the tribes of Scarabaeinae dung beetles. It is formed of different superimposed, sclerotized plates, which can be highly fused forming a solid structure, or the plates can be loose, with membranous regions among the sclerotized plates. Generally the sclerite is easily recognizable by its elongate shape, with the superior extreme enlarged and thick, and the other slender and elongate. In the species studied, this sclerite is located between the basal sclerite and the plate sclerite.

The variation in this sclerite is enormous, with differences in general shape, grade of sclerotization, and presence or absence of filaments (Figs. 175–191). In some genera, the sclerite may end in long filaments of different grade of thickness and length. As with the basal sclerite, the elongate sclerite can be constant or highly variable within determinated groups. For species of *Canthon,* Medina *et al*. (2003) found a high variation and not a constant pattern in the elongate sclerites. On the contrary, the same type of elongate sclerite was observed in all the species of the genus *Epirinus* (Fig. 192). Generally the sclerite has short filaments; nonetheless, in some cases the filaments can be well developed as in *Paracanthon, Nanos* (Fig. 189, 191), and *Cryptocanthon*. The filaments can also be absent as in *Malagoniella* (Fig. 193), *Saphobiamorpha*, and *Tesserodon*, and in different species of *Canthon* (Figs. 194–196).

In the genera *Paracanthon* and *Nanos*, the filament is elongate forming a string-like circle shape and does in fact seem to be rolled in a perfect circle (Figs. 189, 191). It is surprising that these unusual sclerites with that such long flagellum are present in two genera so distant geographically.

Tarasov & Solodovnikov (2011) described this sclerite as a complex of sclerites, denominated by these authors as axial and subaxial sclerites, which in Onthophagini dung beetles are formed by three different subaxial sclerites. From this structure, seven different characters were coded for the cladistic analyses of 54 taxa of Onthophagini, with the result of important informative chacracteres in the phylogeny of the group.

The plate-shape and other sclerites. The plate-shape sclerite is a constant structure in the internal sac of Scarabaeinae beetles, with a large range of variation (Figs. 197–207). This structure generally can be recognized by its lateral position to the handle side of the basal sclerite, and laterally to the elongate sclerite. Usually this sclerite has a flattened shape with deformations in the extremes.

The different variations of the plate sclerite are more difficult to describe, as the structure can take diverse shapes in the various genera. Some patterns were found in small groups of species; in most species it is a flat structure with some folds and upgrowings ending in tips (*Canthidium* sp. *Copris dracunculus*, *Copris incertus*, *Coptodactyla glabricollis* (Figs. 208–211)*, Arachnodes* sp. (Fig. 212)*, Onitis* sp1. (Fig. 213)*,* and *E. dytiscoides* (Fig. 201); in other species it can be a simple structure (*Coptorhina excavata,* Fig. 214)*, O. palaemon* (Fig. 215)*, Bdelyrus* sp. (Fig. 216), or be formed by various superimposed elongate plates (Onthophagini, Figs. 217–219). In some species it is observed that this sclerite is accompanied by a membranous area formed by small and large scales as in the tribe Eucraniini (Fig. 222–224); the genera *Sarophorus* and *Menthophilus*; and in some species of *Canthon* (Figs. 220–221). This sclerite is absent in *C. bacchus* (Fig. 226)*, M. astyanax columbica, M. astyanax punctatostriata, M. punticollis,* and *Streblopus opatroides*. In *Mentophilus hollandiae* Laporte, 1840, the sclerite is absent but the scaly area is present (Fig. 225).

The variation in the plate sclerite is similar to what was found for elongate and basal circular sclerites. In some well-defined groups of species, the same type of plate sclerite was observed. This was observed in *Epirinus* (Figs. 227–231), and in some species of *Canthon* (Figs. 232–237). In some genera where more than one species was examined, the same type of plate was found as in *Gyronotus*, *Scybalophagus*, and in some species of *Scybalocanthon*, but not in all the genera that were examined.

Other sclerites. In some species there are some small accessory sclerites in addition to the main apical sclerites already described. The number can vary from one and three, and in general they are small quitinous pieces that are closer to the plate and elongate sclerite. These sclerites vary in shape and size within the genera, but the same type can be seen in species of the same genus as *Epirinus* (Figs. 227–231). In the genus *Anisocanthon*, *Anomiopus*, *Canthon*, *Scybalocanthon*, and *Sylvicanthon* these types of sclerites are also common (Figs. 238–244).

Conclusions

The use of novel morphological characters is necessary for a better understanding of phylogenetic relationships within the subfamily Scarabaeinae. The study of the morphological variation of the sclerites of the internal sac has uncovered important information needed to solve problems and eluicidate evolutionary relationships among the groups, as the sclerites are highly informative in cladistic analyses (Medina & Scholtz 2005, Tarasov & Solodonikov 2011). However, since there are multiples studies of the internal male genitalia of Scarabaeinae dung beetles, it is important to homologize the structures and unify the names for future and larger comparisons.

Historically, some classical names have been used for the sclerotized structures in the internal sac; a summary of used names for each structure is presented in Table 2. A common name for the sclerotized structures is lamellae, and the structure located in the medial area of the sac has been called lamella copulatrice. The term sclerite is defined as a hardened body part, and for arthropods has been used to design sclerotized structures of segmental origin; it has also been used to name sclerotized pieces of the body. In recent literature regarding internal male genitalia, the word sclerite has been widely used to name the sclerotized structures of the internal sac instead of lamellae. After a careful revision of the names used for male genitalia structures, we have synthesized the names as proposed in Table 2. We hope that this revision of names will help unify the nomenclature for future comparisons of genitalia structure in studies of functional anatomy, taxonomy, and systematics.

Despite of the progress made by different phylognetic analysis within the subfamily Scarabaeinae (Montreuil 1998, Philips *et al*. 2004, Monaghan *et al*. 2007), an accurate tribal classification, according to the evolutionary history of the whole subfamily, is still necessary. We hope that future dung beetle systematists will use the morphological features of internal male genitalia discussed in this paper to improve dung beetle phylogenetics and classification.

Acknowledgments

We wish to thank the curators and colleagues of different institutions that provided the specimens for the study: Alejandro Lopera, Bruce Gill, Enrico Barbero, Eric Matthews, Estela Monteresinos, Fernando Vaz-de-Mello, Francois Génier, Geoff Monteith, Giovanny Fagua, Keith Philips, Riann Stals, Ruth Muller, and Sergio Roig. Thanks to Professor Mario Zunino, who not only has been an inspiration for the evolutionary studies in dung beetles male genitalia, but also also read the manuscript and gave us important suggestions. We also thank Arturo González for his help in the organization of the figures and his comments on the final manuscript. Thanks to the two anonymous reviewers who helped improved the manuscript. This study is part of the doctoral thesis of the first author, who is grateful to the team of dung beetle researchers at the University of Pretoria for all their support. We give a special thanks to Vasily Grebennikov for his advice and mentorship. Part of this study was funded by National Research Foundation (NRF) and the University of Pretoria studentship to the first author.

References cited

Anichtchenko, A. & Verdugo, A. (2004) *Iberodorcadion (Hispanodorcadion) zenete,* nueva especie Ibérica de cerambícido (Coleoptera, Cerambycidae, Lamiinae) procedente de Sierra Nevada (Andalucía, España). *Boletín de la Sociedad Andaluza de Entomología,* 11, 31–42.

Barbero, E., Palestrini C. & Zunino M. (1991) Filogenesi, biogeografia e sistematica generica dei Sisyphini (Coleoptera: Scarabaeidae), pp. 837–844. *Atti XVI Congresso Nazionale Italiano di Entomologia Bari-Martina Franca (TA), 23/28 settembre*. Verona, Italy.

Barbero, E., Palestrini, C. & Roggero, A. (1998) Phylogenetic relationships in the genus *Scarabaeus* Linnaeus. Atti 1. Colloquio Nazionale di Sistematica Cladistica. *Memorie del Museo civico di storia naturale di Verona*, 13, 87–96.

Berti, N. & Mariau, D. (1999) *Coelaenomenodera lameensis* n. sp., ravager du palmier à huile (Coleoptera, Chrysomelidae). *Nouvelle Revue d'Entomologie,* 16, 253–267.

Binaghi, G., Dellacasa, G. & Poggi, R. (1969) Nuovi Caratteri diagnostici per la determinazione degli *Onthophagus* del gruppo *ovatus* (L.) e geonemia controllata delle specie Italiane del grupo. *Memorie de lla Società Entomologica Italiana*. Genova, 48, 29–46.

Bouchard, Y., Davies, A.E., Alonso-Zarazaga, M.A., Lawrence, J.F., Lyal, C.H.C., Newton, A.F., Reid, C.A.M., Schmitt, M., Ślipiński, S.A. & Smith, A.B.T. (2011) Family-group names in Coleoptera (Insecta). *Zookeys*, 88, 1–972. http://dx.doi.org/10.3897/zookeys.88.807

Bovo, B. & Zunino, M. (1983) Nouvi generi di Geotrupini (Coleoptera, Scarabaeoidea: Geotrupidae) asiatici. *Bullettino del Museo Regionale di Scienze Naturali. Torino,* 1, 397–416.

Carlson, D.C. (1975) Taxonomic characters of the genus *Ochodaeus* Serville with descriptions of two new species in the *O. pectoralis* Leconte species complex (Coleoptera: Scarabaeidae). *Bulletin Southern California Academy of Sciences,* 74, 49–65.

Carlson, D.C. & Ritcher, P.O. (1974) A new genus of Ochodaeidae and a description of the larvae of *Pseudochodaeus estriatus* (Schaeffer) (Coleoptera: Scarabaeidae). *The Pan-Pacific Entomologist,* 50, 99–110.

Coca-Abia, M. & Martín-Piera, F. (1998) Revisión taxonomica del género *Rhizotrogus* Berthold, 1827 (Coleoptera, Scarabaeidae, Melolonthidae). *Coleopterological Monographs. Asociación Europea de Entomología,* 2, 1–140.

D'Hotman, D. & Scholtz, C.H. (1990) Comparative morphology of the male genitalia of derived groups of Scarabaeoidea (Coleoptera). *Elytron,* 4, 3–39.

Forgie, S.A., Grebennikov, V.V. & Scholtz, C.H. (2002) Revision of *Sceliages* Westwood, a millipede-eating genus of southern Africa dung beetles (Coleoptera: Scarabaeidae). *Invertebrate Systematics*, 16, 931–955. http://dx.doi.org/10.1071/IT01025

Frolov, A.V. & Scholtz, C.H. (2004) Revision of the southern African genus *Macroderes* Westwood (Coleoptera: Scarabaeidae: Scarabaeinae). *Annales de la Société Entomologique de France*, 40, 373–393.

Frolov, A.V., Akhmetova, L.A. & Scholtz, C.H. (2008) Revision of the obligate mushroom-feeding African "dung beetle" genus

Coptorhina Hope (Coleoptera: Scarabaeidae: Scarabaeinae). *Journal of Natural History,* 42, 1477–1508. http://dx.doi.org/10.1080/00222930802002535

Génier, F. (1996) A revision of the Neotropical genus *Ontherus*. *Memoirs of the Entomological Society of Canada,* 170, 1–169. http://dx.doi.org/10.4039/entm128170fv

Génier, F. (2000) New North American *Ateuchus* Weber (Coleoptera: Scarabaeidae, Scarabaeinae). *The Coleopterists Bulletin,* 54, 341–346. http://dx.doi.org/10.1649/0010-065X(2000)054[0341:ANNAAW]2.0.CO;2

Génier F. (2012) A new species and notes on the subgenus *Deltochilum* (*Deltochilum*) Eschscholtz, 1822 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilini). *Zootaxa,* 3357, 25–36.

González, A., Molano, F., & Medina, C.A. (2009) Los subgéneros *Calhyboma* Kolbe 1893, *Hybomidium* Shipp 1897 y *Telhyboma* kolbe 1893 de *Deltochilum* (Coleoptera: Scarabaeidae: Scarabaeinae) en Colombia. *Revista Colombiana de Entomología,* 35, 253–274.

House, C.M. & Simmons, L.W. (2003) Genital morphology and fertilization success in the dung beetle *Onthophagus taurus:* an example of sexual selected male genitalia. *Proceedings the Royal Society London,* 270, 447–455. http://dx.doi.org/10.1098/rspb.2002.2266

House, C.M. & Simmons, L.W. (2005) The evolution of male genitalia: patterns of genetic variation and covariation in the genital sclerites of the dung beetle *Onthophagus taurus*. *Journal of Evolutionary Biology,* 18, 1281–1292. http://dx.doi.org/10.1111/j.1420-9101.2005.00926.x

Kohlmann, B. (2000) New species and distribution records of Mesoamerican *Ateuchus* (Coleoptera: Scarabaeidae). *Revista de Biología Tropical,* 48, 235–246.

Kral, D. (2000) A review of Chinese *Aphodius* species (Coleoptera: Scarabaeidae). Part 2: revision of the subgenus *Brachiapodius*. *Acta Societatis Zoologicae Bohemicae,* 64, 65–92.

Krikken, J. & Huijbregts, J. (2007) Taxonomic diversity of the genus *Ochicanthon* in Sundaland (Coleoptera: Scarabaeidae: Scarabaeinae). *Tijdschrift voor Entomologie,* 150, 421–479. http://dx.doi.org/10.1163/22119434-900000241

López-Guerrero, I. (1999) Morphological comparison of the male genitalia of *Eurysternus* Dalman and *Sisyphus* Latreille (Coleoptera, Scarabaeidae, Scarabaeinae). *The Coleopterists Bulletin,* 53, 201–207.

López-Guerrero, I. (2005) Los *Dichotomius* (Coleoptera: Scarabaeidae: Dichotomiinae) de la Fauna de México. *Boletín de la Sociedad Entomológica Aragonesa,* 36, 195–209.

López-Guerrero, I., Zunino, M., & Halffter, G. (2009) Taxonomic use of the characters in Mexican *Copris* (Coleoptera: Scarabaeidae, Scarabaeinae): the case of *Copris klugi sierrensis* Matthews and the *C. armatus* species complex. *The Coleopterists Bulletin,* 63, 203–212. http://dx.doi.org/10.1649/1145.1

Márquez, J. (2001) Systematic review of *Heterolinus* Sharp (Coleoptera: Staphylinidae: Xantholinini). *The Coleopterists Bulletin,* 55, 317–329. http://dx.doi.org/10.1649/0010-065X(2001)055[0317:SROHSC]2.0.CO;2

Martín-Piera, F. (1987) Revision of the genus *Chironitis* Lansberge 1875. *Entomologische Arbeiten aus dem Museum Georg Frey,* 35/36, 203–245.

Martínez, A. & Pereira, F.S. (1956) Dois generos novos de Deltochilini Americanos. *Papéis Avulsos do departamento de Zoologia*, 12, 363–388.

Matalin, A.V. (1998) The tiger-beetles of "*hybrida*"-species group (Coleoptera, Carabidae, Cicindelinae). III. A taxonomic review of the Iberian *Cicindela lagunensis* Gautier, 1872 complex. *Graellsia,* 54, 75–96. http://dx.doi.org/10.3989/graellsia.1998.v54.i0.346

Matalin, A.V. (1999) The tiger-beetles of the *hybrida* species-group. II. A taxonomic review of subspecies of *Cicindela sahlbergii* Fischer von Waldheim, 1824 (Coleoptera Carabidae Cicindelini). *In*: A.Zamotajilov & R. Sciaky (eds.), *Advances in Carabidology.* Muiso publishers, Krasnodar, Russia, pp. 1–473.

Matthews, E.G. (1974) A revision of the Scarabaeine dung beetles of Australia II. Tribe Scarabaeini. *Australian Journal of Zoology, Supplementary Series*, 24, 1–211. http://dx.doi.org/10.1071/AJZS024

Medina, C. A., Scholtz, C. & Gill, B. D. (2003) Morphological variation and systematics of *Canthon* Hoffmannsegg 1817, and related genera of new world Deltochilini dung beetles (Coleoptera, Scarabaeidae). *Deutsche Entomologische Zeitschrift,* 50, 23–68. http://dx.doi.org/10.1002/mmnd.20030500105

Medina, C.A. & Scholtz, C. (2005) Systematics of the southern African genus *Epirinus* Reiche (Coleoptera: Scarabaeinae: Deltochilini): descriptions of new species and phylogeny. *Insects Systematic and Evolution,* 36, 145–160. http://dx.doi.org/10.1163/187631205788838500

Molano, F. & Medina, C.A. (2010) Especie nueva de *Scybalocanthon* (Coleoptera: Scarabaeinae: Deltochilini) y descripción de la variación del órgano genital masculino. *Revista Mexicana de Biodiversidad,* 81, 689–699.

Monaghan, M.T., Inward, D. J.G., Hunt, T. & Vogler, A.P. (2007) A molecular phylogenetic analysis of the Scarabaeinae (dung beetles). *Molecular Phylogenetics and Evolution*, 45, 674–692. http://dx.doi.org/10.1016/j.ympev.2007.06.009

Montreuil, O. (1998) Analyze phylogénétique et paraphylie des Coprini et Dichotomiini (Coleoptera: Scarabaeidae). Scénario biogéographique. *Annales de la Société Entomologique de France* (N.S.), 34, 135–148.

Ocampo, F.C. & Molano, F. (2011) Revision and Biogeography of the Neotropical dung beetle genus *Scybalophagus* (Coleoptera: Scarabaeidae). *Revista de la Sociedad Entomológica Argentina,* 70 (3-4), 231–253.

Ochi, T. & Masahiro, K. (1996) Studies on the coprophagous scarab beetles from East Asia: IV. (Coleoptera, Scarabaeidae). *Giornale*

Italiano di Entomologia, 8, 17–28.

Ochi, T., Masahiro, K. & Kikuta, T. (1997) Studies of the family Scarabaeidae (Coleoptera) from Borneo. The genera *Paragymnopleurus* and *Sisyphus*. *Giornale Italiano di Entomologia,* 8, 239–250.

Pereira, F. (1941) *Pinotus* de la república de Argentina (Col. Lam. Copridae). *Anales de la Sociedad Científica Argentina*, 131, 262–267.

Pereira, F.S. & D´Andretta, M.A.V. (1955) The species of *Deltochilum* of the subgenus *Calhyboma* Kolbe. *Revista Brasileira de Entomologia*, 4, 7–50.

Pereira, F.S. & Martínez, A. (1956) Os generos de Canthonini Americanos (Col. Scarabaeidae). *Revista Brasiliera Entomologica*, 6, 91–192.

Pereira, F. S. & Martínez, A. (1960) Notas escarabeidológicas – II. *Revista Brasileira de Entomologia*, 9, 37–55.

Philips, T.K., Scholtz, C.H. & Ocampo, F.C. (2002) A phylogenetic analysis of the Eucraniini (Coleoptera: Scarabaeidae: Scarabaeinae). *Insects Systematic and Evolution,* 33, 241–252.
http://dx.doi.org/10.1163/187631202X00145

Philips, K., Pretorius, E. & Scholtz, C.H. (2004) A phylogenetic analysis of dung beetles (Scarabaeinae: Scarbaeidae) unrolling an evolutionary history. *Invertebrate Systematics,* 18, 53–88.
http://dx.doi.org/10.1071/IS03030

Price, D.L. (2005) Descriptions of the male and female genitalia of *Phanaeus* (MacLeay) (Scarabaeidae: Scarabaeinae): The *vindex* species group. *The Coleopterists Bulletins,* 59, 197–203. http://dx.doi.org/10.1649/743

Reid, C.A.M. (2000) A complex of cryptic species in the genus *Coptodactyla* Burmeister (Coleoptera: Scarabaeidae: Coprini). *Memoirs of the Queensland Museum,* 46, 231–251.

Reid, C.A.M. & Storey, R.I. (2000) Revision of the dung beetle genus *Temnoplectron*. *Memoirs of the Queensland Museum,* 46, 253–297.

Roig-Juñent, S. (2000) The subtribes and genera of the tribe Broscini (Coleoptera, Carabidae): cladistic analysis, taxonomic treatment, and biogeographical considerations. *Bulletin of the American Museum of Natural History,* 255, 1–90.
http://dx.doi.org/10.1206/0003-0090(2000)255%3C0001:TSAGOT%3E2.0.CO;2

Rubenyan, A.A. (2002) A method for making preparations of the endophallus sack in beetles of the family *Cerambycidae*. *Entomological Review,* 82, 376–377.

Snodgrass, R.E. (1935) *Principles of Insect Morphology*. McGraw-Hill, New York, 667 pp.

Stefano, Z. & Ivo, G. (2001) A survey of the *Onthophagus* (s.l.) species occurring in Syria (Coleoptera Scarabaeidae Scarabaeinae). *Memories de lla Societa Entomologica Italiana*, 80, 87–105.

Tarasov, S.I. & Kabakov, O.N. (2010) Two new species of *Onthophagus* (Coleoptera: Scarabaeidae) from Indochina, with a discussion of some problems with the classification of *Serrophorus* and similar subgenera. *Zootaxa*, 2344, 17–28.

Tarasov, S.I. & Solodovnikov, A.Y. (2011) Phylogenetic analyses reveal reliable morphological markers to classify mega-diversity in Onthophagini dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae). *Cladistics,* 27, 1–39.
http://dx.doi.org/10.1111/j.1096-0031.2011.00351.x

Thompson, R.T. (1998) Revision of the weevil genus *Leptostethus* Waterhouse, 1853 (Coleoptera, Curculionidae, Entiminae). *Cimbebasia Memoir*, 7, 1–80.

Vaz-de-Mello, F. (2008) Synopsis of the new subtribe Scatimina (Coleoptera: Scarabaeidae: Scarabaeinae: Ateuchini), with descriptions of twelve new genera and review of *Genieridium,* new genus**.** *Zootaxa,* 1955, 1–75.

Werner, M & Simmons, L.W. (2008) The evolution of male genitalia: functional integration of genital sclerites in the dung beetle *Onthophagus taurus*. *Biological Journal of the Linnean Society,* 93, 257–266.
http://dx.doi.org/10.1111/j.1095-8312.2007.00924.x

Zunino, M. (1972) Revisione delle specie paleartiche del genere *Onthophagus*. I.Il sottogenere *Euonthophagus*. *Bollettino del Museo di Zoologia dell'Università di Torino,* 1, 1–28.

Zunino, M. (1978) La posizione sistematica del "*Caccobius* (*Caccophilus*) *anomalus*" (Coleoptera, Scarabaeoidea). *Bollettino del Museo di Zoologia dell"Università di Torino*, 3, 9–14.

Zunino, M. (1979) Gruppi artificiali e gruppi naturali negli *Onthophagus* (Coleoptera Scarabaeoidea. *Bollettino del Museo di Zoologia dell'Università di Torino,* 1, 1–18.

Zunino, M. (1981) Note su alcuni *Onthophagus* americani e descrizione di nuove specie (Coleoptera. Scarabaeidae). *Bollettino del Museo di Zoologia dell'Università di Torino,* 6, 75–86.

Zunino, M. (1983) Essai préliminaire sur 1´evolution des armures genitales des Scarabaeinae, par rapport à la taxonomie du groupe et à 1´évolution du comportement di nidification. *Bulletin de la Societé Entomologique de France,* 88, 531–542.

Zunino, M. (1985) Las relaciones taxonómicas de los Phanaeina (Coleoptera, Scarabaeinae) y sus implicaciones biogeográficas. *Folia Entomologica Mexicana,* 64, 101–115.

Zunino, M. & Halffter, G. (1987) Sobre *Onthophagus* Latreille, 1802 Americanos (Coleoptera: Scarabaeidae: Scarabaeinae). *Elytron,* 11, 157–178.

Zunino, M. & Halffter, G. (1988) Análisis taxonómico, ecológico y biogreográfico de un grupo americano de *Onthophagus*. *Museo Regionale di Scienze Naturale Torino Monografia,* 9, 1–211.

CHAPTER II

SYSTEMATICS OF THE SOUTHERN AFRICAN GENUS *EPIRINUS* REICHE (COLEOPTERA: SCARABAEINAE: CANTHONINI): DESCRIPTIONS OF NEW SPECIES AND PHYLOGENY

Claudia A. Medina

Clarke H. Scholtz

Insect Systematics and Evolution 36:2 (2005)

Systematics of the southern African genus *Epirinus* Reiche (Coleoptera: Scarabaeinae: Canthonini): descriptions of new species and phylogeny

CLAUDIA A. MEDINA and CLARKE H. SCHOLTZ

Insect Syst.Evol.

Medina, C. A. and Scholtz, C. H.: Systematics of the southern African genus *Epirinus* Reiche (Coleoptera: Scarabaeinae: Canthonini): descriptions of new species and phylogeny. *Insect Syst. Evol.* 36: 145-160. Copenhagen, June, 2005. ISSN 1399-560X.

The genus *Epirinus* is reviewed. It consists of 29 species, including six new ones described in this paper: *E. aquilus*, *E. hluhluwensis*, *E. minimus*, *E. ngomae*, *E. pseudorugosus* and *E. sebastiani*. A key to all the species of *Epririnus* is provided as are distribution map and illustrations of the most important morphological features to distinguish the species. Phylogenetic relationships within the genus are investigated, using cladistic analysis of 79 morphological characters including male and female genitalia. Various synapomorphies support the genus *Epirinus* as a monophyletic group of species. They are: shape of the internal border of the eye, genital segment with short projections, and presence of sclerite "X" in the internal male genitalia. There is no support for the flightless species to be treated as a separate genus, as has been proposed in the past.

C. A. Medina and C. H. Scholtz: Department of Zoology & Entomology, University of Pretoria, Pretoria 0002, South Africa

Introduction

The genus *Epirinus* represents a southern African group of 29 species of Scarabaeinae dung beetles. The species are mainly associated with herbivore dung, but some are known to feed on carrion. Some of the larger species have been observed rolling balls of dung, while some of the smaller ones have been collected in leaf litter (Scholtz & Howden 1987a). The genus is predominantly relictual in distribution, with species occurring in lowland and mountain forests along the eastern coast of South Africa, temperate forests of the southern Cape and in Namaqualand on the west coast of South Africa. Few species are widespread in the region.

Epirinus was last revised by Scholtz & Howden (1987a). In that paper they provided a key to species as well as descriptions and distribution maps for all the species then known (23).

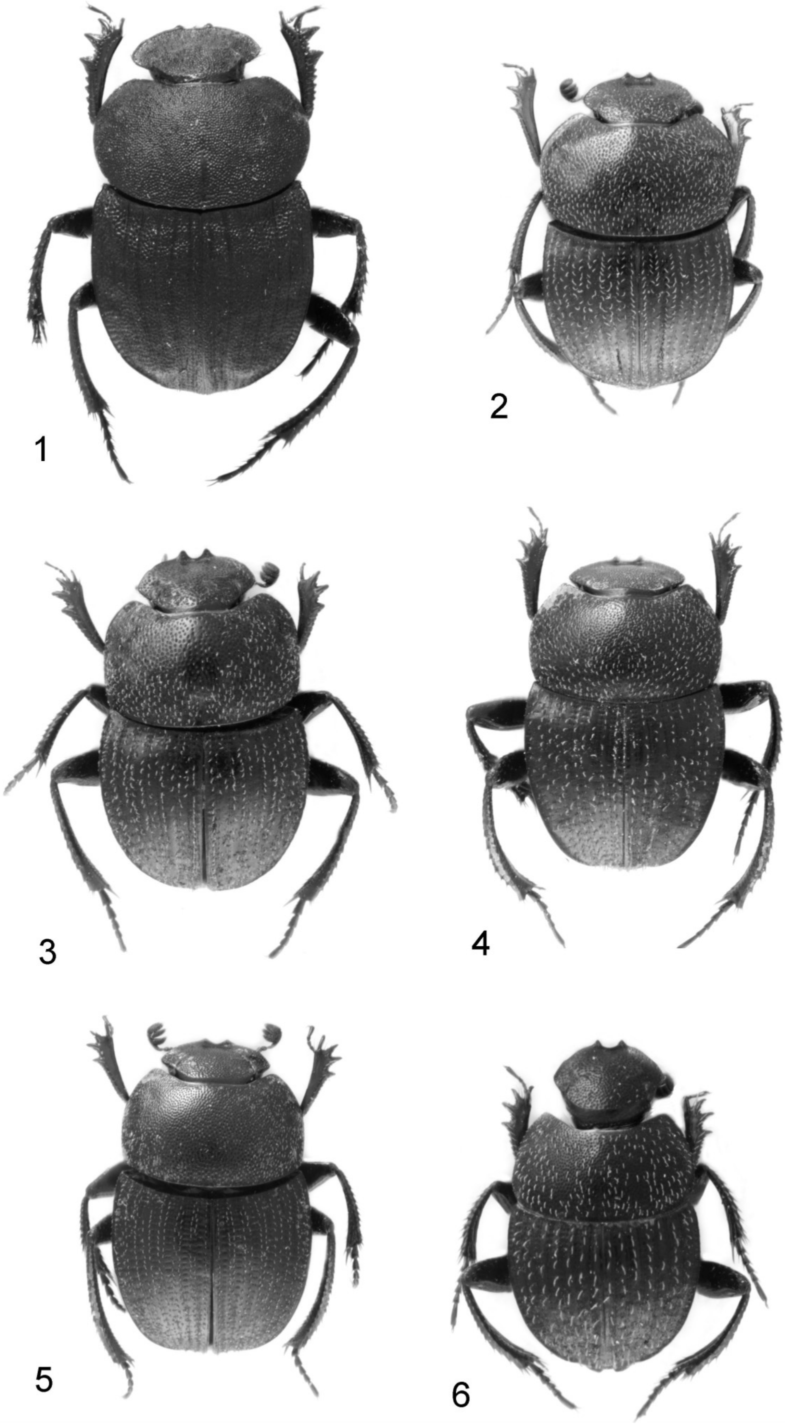
Two main groups can be recognized in the genus on the basis of the presence of complete and developed membranous wings or the reduced state of those. Those with reduced membranous wings, and without a visible umbone, were accorded generic status, [as *Endroedyantus*] by Cambefort, (1978). However, it was synonymised with *Epirinus* (Scholtz & Howden 1987a).

Since Scholtz & Howden's study a large amount of material has accumulated in South African museums, including new species, so one of the aims of this project was to review the new material and to describe the new species. A second aim was to taxonomically and phylogenetically re–assess the characters considered in the past to support the distinction of the species into two genera and to investigate previously unstudied ones, which could possibly provide unequivocal support for one or two genera.

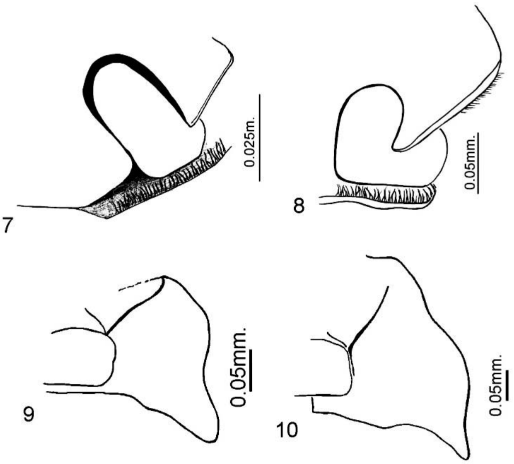
Descriptions of six undescribed species (Figs. 1–6) and a key for the identification of all the species are provided. Also the phylogenetic relationships within the genus *Epirinus* are investigated and discussed.

Materials and Methods

Institutions which provided material and in which types are deposited are as follows:



Figs 1–6. Habitus: 1. *Epirinus pseudorugosus* sp.n. 2. *E. hluhluwensis* sp. n. 3. *E. ngomae* sp.n. 4. *E. aquilus* sp. n. 5. *E. sebastiani* sp.n. 6. *E. minimus* sp. n.



Figs 7–10. Eye, dorsal view and proepisterna. 7. *E. validus* Péringuey 8. *Anachalcos convexus* Boheman 9. *E. validus* Péringuey 10. *E. flagellatus* Fabricius.

BMNH	The Natural History Museum, London, England
MNHN	Museum National d'Histoire Naturelle, Paris, France
NCSA	National Collection, Pretoria, South Africa
TMSA	Transvaal Museum, Pretoria, South Africa
SAMC	South African Museum, Cape Town, South Africa
ZISP	Zoological Institute, Saint Petersburg, Russia
ZMHB	Zoologisches Museum, Berlin, Germany
UPSA	University of Pretoria Scarabs Collection, Pretoria, South Africa

Specimen preparation

A total of 2266 specimens of 29 species of *Epir.–inus* was examined. Dry specimens were softened by immersion in hot water for 20 min. Male and female genitalia were removed, cleaned in a hot water solution of KOH, and studied on microscope slides in glycerol.

Dissections of genitalia were prepared in 57 males and 49 females for detailed examination. All specimens identified to species during this study bear an identification label.

The illustrations were made using a dissecting microscope; they were scanned into a computer file as bitmap images and modified with image analysis software (Paint Shop Pro).

Genus *Epirinus* Reiche

Epirinus Reiche, 1841: 212; Lacordaire 1856: 81; Péringuey 1901: 89; Gillet 1911:03; Ferreira 1964: 3; Ferreira 1969: 136; Scholtz &Howden 1987a.
Type–Species: *Scarabaeus flagellatus* Fabricius, by subsequent designation, Janssens, 1938.
Endroedyantus Cambefort, 1978: 201; Scholtz & Howden 1987a.

Colour. – Mostly dull black but also bronze, metallic green or bicolourous black and green.

Length. – 2.8–13.5 mm.

Head. – Clypeus bidentate, teeth barely protruding to large, pointed or rounded; median indentation deep to barely visible to distinct; surface densely punctate; internal border of eye oblique and carinated (Fig. 7).

Pronotum. – Surface sparsely to densely punctate, with or without setae; median longitudinal line visible or obsolete, or fovea present; lateral margin evenly rounded to oblique for anterior one–third; anterior angle round to slightly pointed.

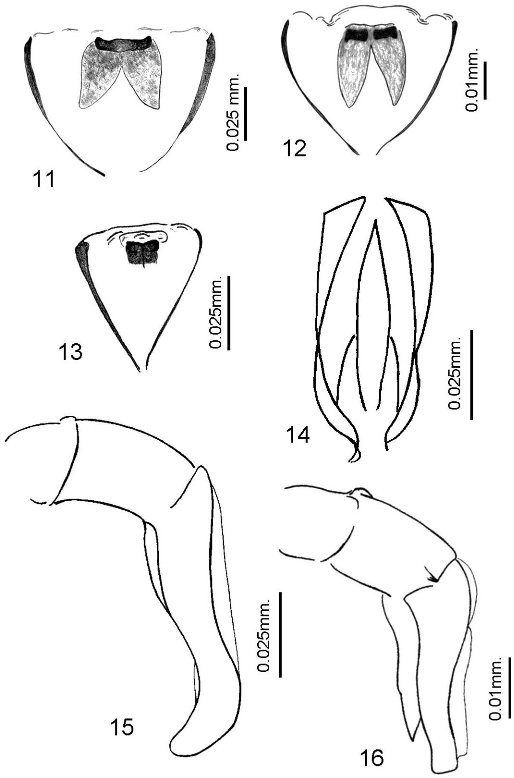
Elytra. – Antero–lateral region with humeral keel (umbone) present or absent, when present usually small but distinct; striae very pronounced to barely visible and may be distinctly and deeply punctured to barely so; interstriae variable from flat without sculpture to tectiform with large granules, or setose; dorsal margin of epipleura from narrow to wide; apical callosity barely raised to large; episternal sides glabrous to striate, setose or granulate or in combination.

Venter. – Metasternum and abdominal sternites sparsely to densely punctate, with or without setae; pygidium punctate, setose, granulate or in combination, or distinctly tuberculate or costate; episternal carina either clearly reaches anterior pronotal margin or ends just short of margin.

Legs. – Metatibiae dimorphic to similar in the sexes with degree of crenulation of the inner surface and curvature varying.

Genitalia. – Parameres asymmetrical, but similar in all species; internal sac of the aedeagus with a plate–shaped sclerite (sclerite X; Figs. 17–27).

Distribution. – All species occur south of 23°S in southern Africa.



Figs 11–16. Genital segment. 11. *E. mucrodentatus* Scholtz & Howden12. *E. relictus* Scholtz & Howden 13. *E. hluhluwensis* sp. n. 14–16. aedeagus. 14–15. Parameres *E. relictus* Scholtz & Howden 14. Frontal view. 15 Lateral view. 16. *E. mucrodentatus* Scholtz & Howden

Key to the species of *Epirinus* (modified from Scholtz & Howden 1987a)

1. Antero-lateral regions of the elytra with a developed humeral keel (winged species)......... 2

– Antero-lateral region of the elytra without humeral keel (flightless species)...................... 20

2. (1) Pygidium with tubercles, protuberances or raised costae.. 3

– Pygidium without tubercles, protuberances or raised costae 4

3. (2) Length less than 5 mm............................... .... *punctatus* Scholtz & Howden

– Length greater than 6 mm.......................... .... *relictus* Scholtz & Howden

4. (2) Proepisternal carina reaching anterior margin of pronotum (Fig. 9).................................. 5

– Proepisternal carina not reaching anterior margin of pronotum (Fig 10).......................... 14

5. (4) Apex of anterior angle of pronotum with slight lateral indentation 6

– Apex of anterior angle of pronotum without indentation 9

6. (5) Body length less than 12 mm 7

– Body length greater than 12 mm 8

7. (6) Elytral striae parallel-sided; elytral interstriae with distinct rows of regularly-spaced granules; abdominal sternites densely punctured; specimens black ... *bentoi* Ferreira

– Elytral striae with punctures broader than rest of the elytra; elytral interstriae with very small, irregularly-spaced granules; abdominal sternites sparsely punctured; specimens often green or partly so................. .... *aeneus* (Wiedemann)

8. (6) Elytral interstriae uneven, with deep punctures and irregularly arranged granules...... .... *sulcipennis* Bohemann

– Elytral striae flat, with up to four rows of regular granules .... *validus* Péringuey

9. (5) Length of elytra not more than twice length of pronotum; specimens brown, often with curved pronotal and elytral setae .... *gratus* Péringuey

– Length of elytra not more than twice pronotal length.. 10

10. (9) Striae with distinct, deep punctures; interstrial surface uneven, punctate, with widely spaced granules... 11

– Striae continuous, without distinct punctures; interstrial surface with small shiny-black granules close together.................... .... *granulatus* Scholtz & Howden

11. (9) Elytra with lateral deformations.................... 12

– Elytra without deformations; interstriae with small granules mainly in the anterior half; large pronotum and short elytra......... .... *drakomontanus* Scholtz & Howden

12. (11) Interstriae with abundant, long and curved setae and distinct round interstrial punctures................................... *comosus* Péringuey

– Interstriae without abundant long setae 13

13. (12) Elytral interstriae with deep, irregular punctures; body length smaller than 6 mm .... *pseudorugosus* sp. n.

– Elytral interstriae with small shiny tubercles; without deep, irregular punctures; body length larger than 6 mm................... .... *rugosus* Scholtz & Howden

14. (4) Elytral interstriae with large, round, shiny protuberances ....*flagellatus* (Fabricius)

– Elytral interstriae without shiny protuberances, with granules, at most 15

15. (14) Seventh interstria distinctly raised, with larger granules......................... *asper* Péringuey

– Seventh interstria not distinctly raised, not with larger granules...................................... 16

16. (15) Elytral interstriae with distinct granules 17

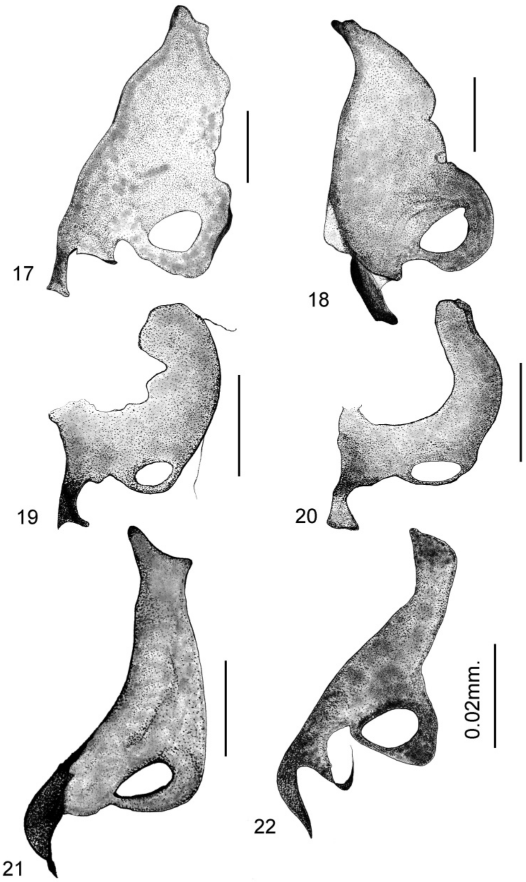
– Elytral interstriae without raised granules, at most with very small shiny spots.......... .... *mucrodentatus* Scholtz & Howden

17. (15) Strial punctures rounded considerably wider than the rest of the striae................. .... *pygidialus* Scholtz & Howden

– Strial punctures barely wider than the rest of the striae.. 18

18. (17) Clypeus with pointed teeth; pygidium without punctures; indentation of clypeo-

genal suture wide .... *scrobiculatus* Harold
– Clypeus with rounded teeth; pygidium punctate 19
19. (18) Abdominal sternites with large punctures on anterior hal......... *striatus* Scholtz & Howden
– Abdominal sternites with small punctures over most of surface.............. *obtusus* Boheman
20 (1). Pygidium with distinct tubercles or costa 21
– Pygidium without distinct tubercles or costa; epipleural margins distinctly raised .... *silvestris* Cambefort
21. (20) Punctures on pronotal surface with diameter less than distance between them; body length larger than 5 mm ....*montanus* Scholtz & Howden
– Punctures on pronotal surface with diameter as large or greater than distance between them; body length smaller than 5 mm.. 22
22. (21) Pronotum with distinct latero-medial foveae and medial depression 23
– Pronotum without foveae and medial depression.. 25
23. (22) Pronotum with medial depression and two pronounced lateral foveae 24
– Pronotum with medial depression, without lateral foveae; metasternum very sparsely punctate.................... *davisi* Scholtz & Howden
24. (23) Clypeal teeth well developed, pointing upward, with narrow medial indentation .... *hluhluwensis* sp. n.
– Clypeal teeth smaller with wide indentation; broad pronotum.................... *ngomae* sp. n
25. (22) Interstriae with a single row of setae 27
– Interstriae from second or third to eighth with more than one row of setae.................... 28
27. (26) Interstriae with a medial row of small granules with associated setae; metasternal punctures with diameter less than distance between them; body length larger than 3 mm.. *hilaris* Péringuey
– Body length less than 3 mm; interstriae with long, straight and sparse setae .... *minimus* sp. n.
28. (26) Second elytral interstria, with two parallel rows of setae, setae short, interstriae punctate .... *sebastiani* sp. n.
– Second elytral interstria with only one row of setae, setae longer, interstriae smooth and glossy.. 29
29. (28) Humeral area of elytra with a flattened depression; setae long; elytra black glossy .... *aquilus* sp. n.
– Humeral area of elytra convex; setae short, broad with sharp recurved point .... *convexus* Scholtz & Howden



Figs 17–22. Sclerite « X » from the internal male genitalia. 17. *E. sulcipennis* Boheman 18. *E. asper* Péringuey 19. *E. aeneus* (Wiedemann) 20. *E. bentoi* Ferreira 21. *E. flagellatus* Fabricius 22. *E. pseudorugosus* sp. n.

***Epirinus pseudorugosus* sp. n.**

(Figs 1, 22, 38, 40)

Diagnosis. – This species is most similar to *E. rugosus* from which it can be differentiated by its size and the elytra densely punctate with deep and irregular punctures, which are absent in *E. rugosus*. This latter also has the elytra covered with small tubercles, which are absent in *E. pseudorugosus*. Sclerites of the internal sac of the aedeagus and female genitalia are also diagnostic for this species (Figs. 22, 38, 40).

Description of holotype. –Male, 5.5 mm., pronotal width 3.3 mm., elytral width 3.3 mm.
Head: – Clypeal teeth small, pointed, widely separated; lateral indentation of clypeo–genal suture faint; surface densely punctured;
Pronotum: Surface densely punctated with deep round and oval punctures; medial longitudinal line visible posteriorly; anterior angle slightly pointed.

Elytra: Humeral umbone distinct; striae distinct, with irregular, deep punctures; deformations in the humeral area and towards lateral margins; third and fifth elytral striae raised; with sparse setae; apical tubercles conspicuous.

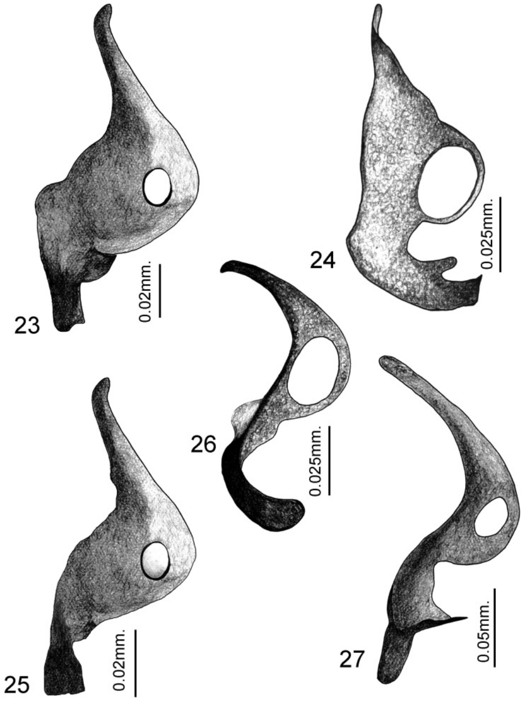
Venter: Proepisternal carina not reaching anterior pronotal margin; metasternum very densely punctate, with setae posteriorly; abdominal sternites densely punctured; sixth and seventh sternite with a medial row of short golden setae; pygidium with sparse setae.

Male genitalia: Genital segment with sclerotized rectangular area, internal sac with four defined apical sclerites; sclerite X with secondary process ending in a long filament (Fig. 22).

Female genitalia: Sensorial plates thick and well sclerotized (Fig. 40)

Entomology. – The name *pseudorugosus* is derived from its similarity to *E. rugosus*.

Remarks. – Body length in this species varies from 4.5 – 5.5 mm.



Figs 23–27. Sclerite « X » from the internal male genitalia. 23. *E. sebastiani* sp. n. 24. *E. hluhluwensis* sp. n. 25. *E. aquilus* sp. n. 26. *E. ngomae* sp. n. 27. *E. minimus* sp. n.

Material examined. – Holotype. S. Africa, SW Cape West Coast N. Park 33.10S – 18.08E 3. VII. 1987, ex cattle dung baited pitfall in pasture, leg. ALV Davis (NCSA). Paratypes same data as holotype (3 TMSA, 2 NCSA); Langebaan, C.P. 12 km farm Geelbek 27. VIII.1977 leg. A. L. V. Davis (2 NCSA).

Epirinus hluhluwensis sp. n.

(Figs 2, 24, 29, 47)

Diagnosis. – This species is most similar to *E. ngomae*, and *E. davisi*. It can be differentiated from *E. davisi* by the presence of two lateral foveae and a medial depression in the pronotum. From *E. ngomae*, it can be differentiated by the shape of the clypeal teeth; they are bigger and point upward, with a narrower indentation. Shape of the sclerites of the internal sac of the aedeagus (Fig. 24, 29) and female genitalia (Fig. 47) are also diagnostic for this species.

Description. Holotype. – Male. 3.4 mm., pronotal width 1.9 mm., elytral width 1.9 mm.

Head: Clypeal teeth prominent, pointed upward, with grouped setae at base; with distinct median indentation; lateral margin without indentation; surface densely punctate, associated with setae; eyes narrower posteriorly.

Pronotum: Surface densely punctate with round and oval punctures associated with setae; medial depression with a median longitudinal line and two lateral foveae.

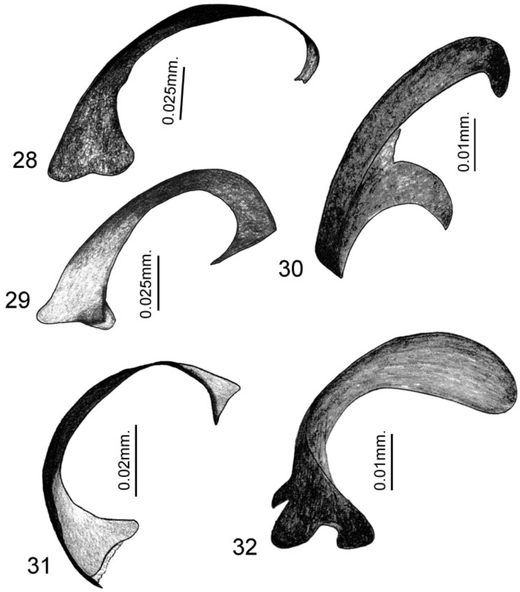
Elytra: Striae distinct, with large, oval punctures; interstriae glossy; second to eighth interstria with two well– defined rows of setae; first and last interstria with one row of setae; setae broad, golden with recurved points; margin raised and darkly sclerotized; apical tubercles inconspicuous.

Venter: Proepisternal carina reaching anterior pronotal margin; abdominal sternites with a median row of large punctures, each with adjacent seta; pygidium with one medial tubercle.

Male genitalia: Genital segment with sclerotized rectangular, central plate, and with a longitudinal sclerotized projection; internal sac with five defined apical sclerites; sclerite X as in fig 27; secondary process reduced; primary process well sclerotized; sclerite Y as in fig (29).

Female genitalia: Sensorial plates elongated; spermatheca elongated, terminal portion straight (Fig 47).

Etymology. – The name *hluhluwensis* is derived from the name of the game reserve where this species occurs.



Figs 28–32. Sclerite « Y » from the internal male genitalia. 28. *E. ngomae* sp. n. 29. *E. hluhluwensis* sp. n. 30. *E. pseudorugosus* sp. n. 31. *E. punctatus* Scholtz & Howden 32. *E. relictus* Scholtz & Howden.

Remarks. – Body length varies in this species from 2.7–3.9 mm.

Material Examined. – Holotype. S. Afr. Zululand, Hluhluwe Game Res. 28.05S – 32.04E, 20.11.1992; E–Y: 2837, ground traps with feces bait for 8 days, leg. Endrödy–Younga (TMSA). Paratypes same data as holotype (64 TMSA,10 NCSA, 4 BMNH, 4 MNHN, 4 SAMS, 2 ZMHB, 4 UPSA, 2 ZISP).

Epirinus ngomae sp. n.

(Figs 3,26, 28, 37, 48)

Diagnosis. – This species can be distinguished by the broad pronotum and the shape of the clypeal teeth, which are smaller and with wider indentation than in *E. hluhluwensis*. Differences in the sclerites of the internal sac of the aedeagus (Fig. 26, 28), and female genitalia (Fig. 48) are also diagnostic for the species.

Holotype. – Male. Body length 4.1 mm., pronotal width 1.9 mm., elytral width 1.9 mm.

Head: Clypeal teeth small, pointed, and with grouped setae at base; with distinct median indentation; lateral margin without indentation; surface densely punctate, associated with setae; eyes narrower posteriorly.

Pronotum: Robust; lateral border forming a pronounced angle; surface densely punctate with round and oval punctures associated with setae; medial depression with a medial longitudinal line, and two lateral foveae.

Elytra: Striae distinct, with large, oval punctures; interstriae glossy; second to eighth interstriae with two well– defined rows of setae, first and last interstriae with one row of setae; setae broad, golden with recurved points; margin raised and darkly sclerotized; apical tubercles inconspicuous.

Venter: Proepisternal carina reaching anterior pronotal margin; abdominal sternites with a medial row of large punctures, each with adjacent seta; pygidium with two medial tubercles.

Male genitalia: Genital segment with rectangular sclerotized central plate, and with a longitudinal sclerotized projection; internal sac with five defined apical sclerites; sclerite X as in fig. 26; secondary apophysis reduced, primary apophysis well sclerotized; sclerite Y as in fig. 28. Sclerite V present as in fig. 37.

Female genitalia: As in fig. 48.

Etymology. – The name *ngomae* is derived from the name of the forest were this species occurs.

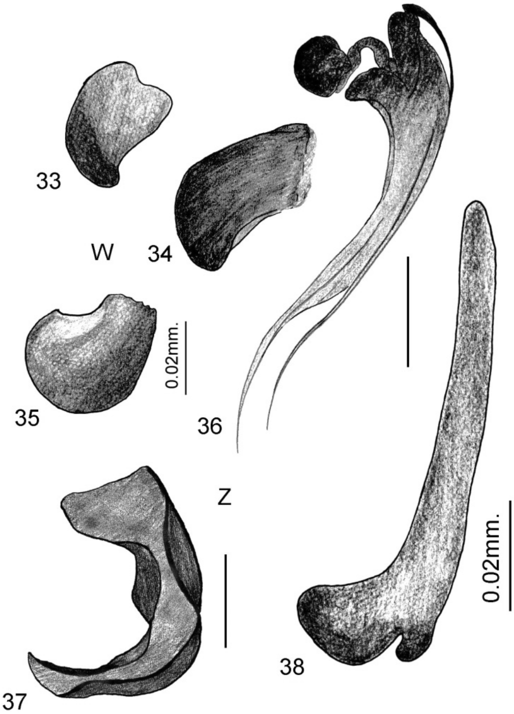
Remarks. – Body length varies in this species from 3.0 – 4.3 mm.

Material Examined. – Holotype. S. Afr. KZN Ngome State Forest 27.49S – 31.25E pitfall trap, indigenous forest 17.11.1992– 6.01.93 1100m, leg. M.v. de Merwe (NCSA). Paratypes. same as holotype (18 NCSA, 2 UPSA); S. Afr. Zulu Drakensberg Ngome For. Sta. 27.49. S – 31.25E 24.2. 1997; E–Y: 3283, ground traps with faeces bait, leg. Endrödy–Younga. (64 TMSA, 6 NCSA, 4 BMNH, 4 MNHN, 8 SAMS, 4 UPSA, 2 ZISP). South Africa: KZN Ngome State Forest 27.49.5S – 31.25.2E ca. 1130m 15. 02. 1997, leg. C.H. Scholtz & R. Stals (24 pinned specimens and 53 in alcohol NCSA). South Africa K. Zulu Natal Ngome State Forest 1100m 27.49S – 31.25E Pitfall Trap with dung bait 7.III.2003 Frolov & Deschodt leg. (specimens in alcohol 50 ZISP, 662 TMSA).

Epirinus aquilus sp. n.

(Figs 4, 25, 34, 46)

Diagnosis. – This species is noticeably darker and glossier than the other small, flightless species of *Epirinus*. It is more similar to *E. convexus* from which it can be differentiated by a flattened depression in the humeral area of the elytra, longer elytral setae, and elytral borders raised and sclerotized. Shape of the sclerites of the internal sac of the aedeagus (Figs 25, 34) and female genitalia (Fig. 46) are also diagnostic for this species.



Figs 33–38. Sclerite « Y » from the internal male genitalia. 33. *E. minimus* sp. n. 34. *E. aquilus* sp. n. 35. *E. sebastiani* sp. n. 36. *E. mucrodentatus* Scholtz & Howden 37. *E. ngomae* sp. n. 38. *E. pseudorugosus* sp. n.

Holotype. – Male. Body length 3.4 mm., pronotal width 2.1 mm., elytral width 2.2 mm.

Head: Clypeal teeth small, with a wide medial indentation; lateral margin without indentation; clypeo–genal suture not visible; surface densely punctate; eyes narrower posteriorly.

Pronotum: Surface densely punctate with round and oval punctures associated with setae.

Elytra: Striae distinct, with large, oval punctures; interstriae glossy; second to eighth interstriae with two well– defined rows of setae, first and last interstriae with one row of setae; setae broad, golden with recurved points; margin raised; apical tubercles inconspicuous.

Venter: Proepisternal carina reaching anterior pronotal margin; abdominal sternites punctate in the anterior half, with a median row of large punctures, each with adjacent long seta; pygidium with two reduced medial tubercles.

Male genitalia: Genital segment with rectangular central plate, more sclerotized towards the extremes; internal sac with four defined apical sclerites; sclerite X with the medial hole reduced; secondary process as a long filament; primary process well sclerotized (Fig. 25) sclerite W as in fig 34.

Female genitalia: Sensorial plates reduced to two small circular sclerites (Fig. 46).

Etymology. – The name *aquilus* is derived from the dark, glossy coloration of the body of this species.

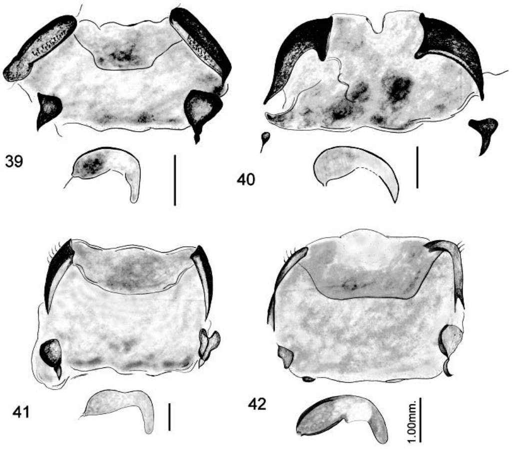
Remarks. – Body length varies in this species from 3.0 – 3.8 mm.

Material examined. – Holotype. S. Afr. Eastern Cape Pr. Grahamstown, hill slope with forest, PFT (pig dung) 18–19–01 2002, leg. A. Frolov (TMSA). Paratypes. Same data as holotype (3 TMSA, 2 ZISP); S. Afr; SE Cape Prov. Alexandria For. St. 33.43 S – 26.23 E leg. Endrödy–Younga (15 TMSA, 4 NCSA, 1 BMNH, 1 MNHN, 2 SAMS, 4 UPSA, 2 ZMHB)

Epirinus sebastiani sp. n.

(Figs 5, 23, 35, 44)

Diagnosis. – This species can be differentiated from the other small flightless species by the interstriae punctate and slightly rough; second interstria with two parallel and well defined rows of whitish setae; clypeal teeth small; pronotum with setae only laterally. Shape of the sclerites of the internal sac of the aedeagus (Figs 23, 35) and female genitalia (Fig. 44) are also diagnostic for this species.



Figs 39–42. Female genitalia. 39. *E. striatus* Scholtz & Howden 40. *E. pseudorugosus* sp. n. 41. *E. mucrodentatus* Scholtz & Howden 42. *E. bentoi* Ferreira.

Holotype. – Female. Body length 3.4 mm., range 3.0 – 3.8, pronotal width 2.1 mm., elytral width 2.2 mm.

Head: Clypeal teeth small, with a wide medial indentation; lateral margin without indentation; clypeo–genal suture not visible; surface densely punctate; eyes narrower posteriorly.

Pronotum: Surface densely punctated, with round and oval punctures associated with setae.

Elytra: Striae distinct, with large, oval punctures, interstriae glossy; third to eighth interstriae with two well– defined rows of setae; first, second and last interstriae with one row of setae; setae broad, golden with recurved points; margin raised; apical tubercles inconspicuous.

Venter: Proepisternal carina reaching anterior pronotal margin; abdominal sternites punctate in the anterior half, with a median row of large punctures, each with adjacent long seta; pygidium with two reduced medial tubercles.

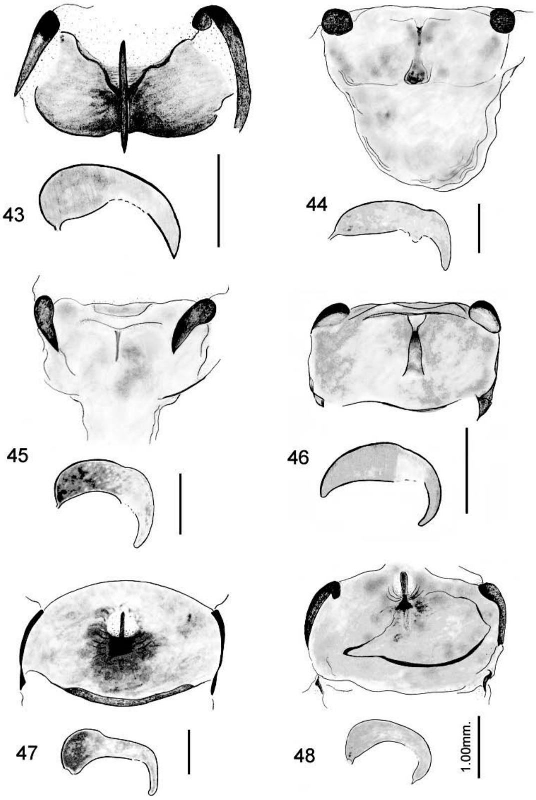
Male genitalia: Genital segment with rectangular central plate, more sclerotized towards the extremes; internal sac with four defined apical sclerites; sclerite X with the medial hole reduced (Fig. 23); sclerite W as in fig 35.

Female genitalia: Sensorial plates reduced to two small circular sclerotized plates (Fig. 44).

Etymology. – This species is named for the late Dr. Sebastian Endrödy–Younga of the Transvaal Museum, Pretoria, who collected large series of *Epirinus* material.

Remarks. – It is very likely that the specimen selected as the Holotype and the majority of the paratypes are incorrectly labeled. The specimens are labeled as "probably Uitsoek" [Mpumalanga Province], but it is most likely that the species is actually distributed in the Eastern Province, where other specimens of this species have also been collected. Other species of beetles that were part of the same mixed samples have been confidently placed as east coast species and not from central parts of the country at all, so the Uitsoek locality is almost certainly wrong (J. Harrison, R. Müller, TMSA, personal communication).

Material examined. – Holotype, S. Afr.; E Transvaal [probably Uitsoek]. Leg. Endrödy–Younga, ground trap with faeces bait (TMSA). Paratype same data as the holotype (22 TMSA, 6 NCSA, 4 BMNH, 4 MNHN, 4 SAMS, 4 UPSA); S. Afr. Ciskei Amatole, Pirie For. 32.43 S – 27.17 E. 8.12 1987; indig. forest litter Leg. Endrödy–Younga. (3 TMSA), S. Afr; Cape, Amatole Isidenge, block A1 32.41 S – 27.17E. 14.11 1987; indig. forest litter. leg. Endrödy–Younga (2TMSA).



Figs 43–48. Female genitalia. 43. *E. punctatus* Scholtz & Howden 44. *E. sebastiani* sp. n 45. *E. minimus* sp. n. 46. *E. aquilus* sp. n. 35. 47. *E. hluhluwensis* sp. n. 48. *E. ngomae* sp. n.

Epirinus minimus sp. n.

(Figs 6, 27, 33, 45)

Diagnosis. – This species is the smallest of all the species of *Epirinus*. It is more similar to *E. convexus* but can be differentiated from the latter species by the body size and the elytral setae. The elytral setae in *E. minimus* are longer and generally straight, although some may be recurved at their points but not as much as in *E. convexus* or *E. aquilus*. The setae are not arranged in two rows as in the majority of the small flightless species. Sclerite X with secondary process not as long as in *E. aquilus*. Sensorial plates in female genitalia comma–shaped (Fig. 45).

Holotype. – Male, body length 2.1 mm., pronotal width 1.4 mm., elytral width 1.5 mm.

Head: Clypeal teeth small, with a wide medial indentation; lateral margin without indentation; clypeo–genal suture not visible; surface densely punctate; eyes narrower posteriorly.

Pronotum: Surface densely punctate with round and oval punctures associated with setae; medial posterior depression present.

Elytra: Striae distinct, with large, oval punctures, interstriae glossy; first interstria with a row of broadly spaced setae; the rest of the interstriae usually with a single row of setae and some other setae not organized in rows; setae broad, golden, usually straight or with slightly recurved points; apical tubercles inconspicuous.

Venter: Proepisternal carina reaching anterior pronotal margin; abdominal sternites punctate in the anterior half, with a median row of large punctures, each with adjacent long seta; pygidium with two medial tubercles.

Male genitalia: Genital segment with rectangular sclerotized central plate; internal sac with four defined apical sclerites; sclerite X elongated and with secondary process developed (Fig. 27); sclerite W as in fig 33.

Female genitalia: Sensorial plates comma–shaped (Fig. 45).

Etymology. – The name *minimus* is derived from the small size of this species.

Remarks. – Body length varies in this species from 1.9 – 2.6mm.

Material examined. – Holotype. S. Afr. Cape Prov. Alexandria For. St. 33.43S – 26.23E. 5.12.1987; E–Y: 2550; indig. forest litter, leg. Endrödy–Younga (TMSA). Paratypes same data as holotype (35 TMSA, 4 NCSA, 2 BMNH, 2 SAMC, 3 UPSA).

Phylogenetic analysis of the genus *Epirinus*

Methods. – The putative relationships of the genus *Epirinus* with other genera of Canthonini are still imprecise. *Epirinus* seems to be very isolated in its phylogenetic relationships although its species share some external features with other large African canthonines such as *Circellium*, *Anachalcos*, and *Gyronotus*, and with the genera *Streblopus* and *Eudinopus* from America (Medina, C.A. in preparation). However, there is no clear indication of the sister group of the genus so far. We have used *Circellium bacchus* for outgroup comparisons, assuming *Circellium* to be an old African element, which *Epirinus* might be related to. Together with all 29 species of *Epirinus*, two species of *Anachalcos*, (*A. convexus* and *A. spectabilis*), and *Gyronotus carinatus* were also included as terminals in the analysis for a total of 33 taxa.

Seventynine morphological characters were used for the cladistic analysis. Fortysix binary and 33 multistate characters were coded. Seven characters were run as additive and the rest as non–additive. The most parsimonious cladograms were found using the commands ‘hold 20000’, ‘mult* 3000’, and ‘max*’ in the program Nona (Goloboff 1995). Character state distributions were examined using the program Clados (Nixon 1995) and Winclada (Nixon 1999). Branch support values (Bremer 1994) were calculated to examine character support throughout the cladogram. Support values were calculated using Nona by reading in the consensus of the most parsimonious cladogram and using commands ‘hold 60000’ ‘sub–optimal 9’ and ‘bsupport 9’. The results were saved to an output file for posterior viewing.

For some species we were unable to get specimens of both sexes, so the genitalia were not studied. In such cases the unobservable character is treated as “?”. Inapplicable states were coded when a morphological structure was not present in determined taxa, then the information about this structure does not apply to those taxa. No autapomorphies for terminals were included in the analysis, except those character states, which are autapomorphies in multistate characters.

Characters. – **Male Genitalia:** In *Epirinus* the genital segment is triangular with external borders slightly sclerotized that confluence towards the middle without touching one another. The sclerotized superior plate varies in shape and in degree of sclerotization among the species (Figs 11–13). The parameres of the aedeagus are asymmetrical, with the right paramere longer than the left and curved across the latter (Figs. 14–16). The shape of the aedeagus is very similar in all the species, except for *E. relictus*, which has more elongated parameres, but asymmetrical in the same way as the rest of the species in the genus.

The internal sac of the aedeagus has three to five apical sclerites. The elongated sclerite (Fig. 36) that is present in most Scarabaeinae beetles (Medina, et al. 2003) is present in four main types in the species of *Epirinus*. One type that is present in the larger species of *Epirinus* is a well sclerotized semicolon–shaped sclerite with elongated filaments (Fig. 36). Another type of elongated sclerite is present in a group of flightless species (Node B, character 68). In this group the elongated sclerite is less sclerotized and formed by different small and close sclerites. A third type of elongated sclerite is comma–shaped and with fused but short filaments. This type is shared by the species at node E. Different elongated plates without fused filaments form the fourth type of elongated sclerite, which is present in *E. hluhluwensis*, *E. ngomae*, *E. punctatus,* and *E. relictus*.

The sclerite X is the main synapomorphy for the genus *Epirinus*. We have examined the variation in the sclerites of the internal sac in 58 genera of Canthonini and in 35 genera from other tribes of Scarabaeinae, and no other genera have a similar sclerite (Medina, C. A. in preparation). This sclerite is exclusively present in the genus *Epirinus* and represents a good synapomorphy for the group. The structure is an elongated plate with a medial lateral hole, which can vary in size, but it is present in all the species of *Epirinus*. The different types and variations of this sclerite are shown in the figures 17–27.

Female genitalia: The female genitalia in *Epirinus* vary considerably among groups of species, especially in the presence and shape of the external plates (hemisternites; Lindroth & Palmén 1970). Some species have large and well sclerotized superior plates as in *E. striatus* and *E. pseudorugosus* sp.n (Figs 39–40). These plates may also have setae. In other species the plates are situated laterally and longitudinally instead of superiorly and transversely; they may also be reduced to thinner, elongated lateral plates as present in *E. bentoi*, and *E. gratus* (Fig. 42). In one group of flightless species the plates are modified as two sclerotized, round plates (node B, Figs 44–46). In some of the small flightless species the central area of the vagina has dark spots and lines spreading from the core (Figs 47–48).

The spermatheca also varies in shape, and species can be differentiated accurately by the shape and degree of curvature of the posterior end.

List of characters and their states used in the cladistic analysis

Consistency index and retention index on the consensus tree (Fig. 49) are indicated for each character. Observed character states are given in Appendix 1.

1. Clypeus dorsally: (0) without defined teeth; (1) with defined small teeth; with prominent teeth; (CI = 0.28, RI = 0.16)
2. Medial part of the clypeus: (0) forming a wide U; (1) slightly wide U; (2) a narrow U; (3) very narrow U; (CI = 0.42, RI = 0.33)
3. Clypeal teeth, externally; (0) continuous; (1) not continuous; (2) separated abruptly; (CI = 0.33, RI = 0.00)
4. Anterior cephalic border: (0) with setae; (1) glabrous; (CI = 0.50, RI = 0.50)
5. Anterior cephalic border: (0) with setae but no keel; (1) with setae on a keel; (CI = 0.16, RI = 0.64)
6. Setae: (0) running along the clypeus; (1) just at the base of the teeth; (CI = 0. 20, RI = 0.66)
7. Setae at the base of the clypeal teeth: (0) on a line; clumped (1); (CI = 0.25, RI = 0.72)
8. Setae at the base of the teeth: (0) reduced to a few, less than 10; (1) more than 10; (CI = 0.20, RI = 0.71)
9. Gena: (0) notched; (1) slightly notched; (2) entire; (CI = 0.30, RI = 0.68)
10. Clypeo–genal suture: (0) visible; (1) not visible; (CI = 0.33, RI = 0.00)
11. Internal border of the eye: (0) straight (Fig 8); (1) oblique (Fig 7); (CI = 1.00, RI = 1.00) (Figs. 7–8)
12. Internal border of the eye: (0) not carinated; (1) carina just in the eye; (2) carina running posteriorly; (CI = 1.00, RI = 1.00)
13. Posterior length of dorsal eye: (0) larger than 15 ommatidia; (1) between 10–15; (2) between 5–10; (3) between 3–5; (4) 2 or less; (CI = 0.36, RI = 0.78)
14. Pro–episternal keel: (0) absent; (1) incomplete (Fig. 10); (2) complete (Fig. 9); (CI = 0.40, RI = 0.70)
15. Apex of anterior angle of pronotum: (0) without any indentation; (1) with indentation; (CI = 0.50, RI = 0.75)
16. Pronotum: (0) without medial depression; (1) with medial depression; (CI = 0.33, RI = 0.66)
17. Pronotum: (0) without lateral foveae; (1) with 2 lateral foveae; (CI = 0.50, RI = 0.66)
18. Pronotum: (0) without medial line; (1) with medial line; (CI = 0.16, RI = 0.64)
19. Pronotum: (0) smooth (minute punctures); (1) small punctures; (2) medium sized punctures; (3) large punctures; (CI = 0.23, RI = 0.44)
20. Pronotum: (0) without umbilical punctures; with umbilical punctures; (CI = 0.14, RI = 0.53)

21. Pronotum: (0) space between punctures less than diameter of the puncture; (1) equal to diameter; (2) larger than the diameter; (CI = 0.22 RI = 0.22)
22. Pronotum: (0) not granulated; (1) granulated; (CI = 0.25, RI = 0.00)
23. Pronotum: (0) rounded punctures; (1) elongated punctures; (CI = 0.50, RI = 0.00)
24. Elytral strial line: (0) faint; (1) marked; (CI = 0.33, RI = 0.53)
25. Space between strial lines: (0) narrow; (1) wide; (CI = 0.5, RI = 0.85)
26. Elytral striae: (0) continuous; (1) interrupted; (CI = 0.12, RI = 0.36)
27. Elytral striae: (0) without visible punctures; (1) with punctures; (CI = 0.33, RI = 0.00)
28. Elytral striae: (0) with large punctures; (1) just interrupting the strial line; (2) small not interrupting the strial line; (CI = 0.2, RI = 0.66)
29. Strial punctures: (0) spaced equal to the diameter of the puncture or more; (1) spaced less than the diameter; (2) not spaced; (CI = 0.5, RI = 0.66)
30. Elytra: (0) not hairy; (1) with few setae; (2) slightly hairy; (3) very hairy; (CI = 0.27, RI = 0.66)
31. Setae on elytra: (0) short; (1) long; (CI = 0.33, RI = 0.71)
32. Setae on elytra: (0) straight; (1) curved; (CI = 0.33, RI = 0.77)
33. First interstria; (0) setae not on a row; (1) with one row of setae; (2) with two rows of setae; (CI = 0.50, RI = 0.33)
34. Second interstria: (0) setae not on a row; (1) with one row of setae; with two rows of setae; (CI = 0.18, RI = 0.35)
35. Interstriae: (0) smooth (without protuberances); (1) with small protuberances; (2) with medium sized protuberances; (3) with large protuberances; (CI = 0.27, RI = 0.50)
36. Elytra: (0) without waves at base; (1) wavy at base;(2) with deformations over the whole elytra; (CI = 0.50, RI = 0.87)
37. Elytra; (0) without lateral waves; (1) with lateral waves; (CI = 0.50, RI = 0.00)
38. Elytral interstriae: (0) not raised; (1) first raised; (2) three and four raised; (3) seven raised; (CI = 0.42, RI = 0.20)
39. Anterior wings (0) well developed; (1) reduced; (2) absent; (CI = 0.66, RI = 0.90)
40. Elytra: (0) with apical tubercles; (1) without apical tubercles; (CI = 0.50, RI = 0.87)
41. Elytral border; (0) not raised; (1) strongly raised; (CI = 0.50, RI = 0.00)
42. Epipleura: (0) reduced; (1) as a thin band; (2) ample; (CI = 0.50, RI = 0.81)
43. Epipleura: (0) without striae on first half of the elytra; (1) with faint striae; (2) with a well marked stria in the first half; (CI = 0.25, RI = 0.53)
44. Mesosternum: (0) triangular; (1) a thin band; (2) reduced; (CI = 0.33, RI = 0.60)
45. Metasternum: (0) smooth; (1) punctate; (2) densely punctate; (CI = 0.28, RI = 0.54)
46. Pygidium: (0) without tubercles; (1) with two lateral tubercles; (2) with one central tubercle; (CI = 0.33, RI = 0.55)
47. Pygidium; (0) glabrous; (1) setose; (CI = 1.00, RI = 1.00)
48. Parameres of the aedeagus: (0) symmetrical; (1) asymmetrical; (CI = 0.50, RI = 0.50)
49. Central plate of genital segment projections: (0) long projections; (1) short projections; (2) no projections; (CI = 1.00, RI = 1.00)
50. Central plate: (0) darkly sclerotized and with elongated filaments; (1) with two separated rectangular sclerotized areas (Fig. 12); with two separated comma–shaped sclerotized areas (C); (3) sclerotized areas fused in the middle, lateral areas reduced; (4) sclerotized areas rectangular not fused medially and with lateral areas with straight tips; (5) sclerotized areas fused medially and lateral areas with pointing lateral tips; (6) lateral areas reduced medially; (CI = 0.85, RI = 0.93)
51. Number of sclerites of the internal sac: (0) five; (1) four; (2) three; (CI = 1.00, RI = 1.00)
52. Sclerite X (*Epirinus* type): (0) absent; (1) present; (CI = 1.00, RI = 1.00)
53. Sclerite X: (0) as in *E. relictus*; (1) as in *E. davisi* group figs 26–27; (2) as in fig. 19; (3) as in fig 18; (4) as in fig 21; (5) as in fig. 27; (6) as in *E. silvestris*; (CI = 0.75, RI = 0.85)
54. Sclerite X: (0) handle not folded; (1) folded; (CI = 1.00, RI = 1.00)
55. Sclerite X: (0) without filament; (1) with filament (CI = 0.50, RI = 0.83)
56. Sclerite filament: (0) short; (1) long; (CI = 0.33, RI = 0.66)
57. Sclerite X hole: (0) diameter greater than the distance to the external border; (1) diameter equal; (2) diameter shorter than the distance from the border; (CI = 0.33, RI = 0.20)
58. Sclerite X hole: (0) diameter greater than the

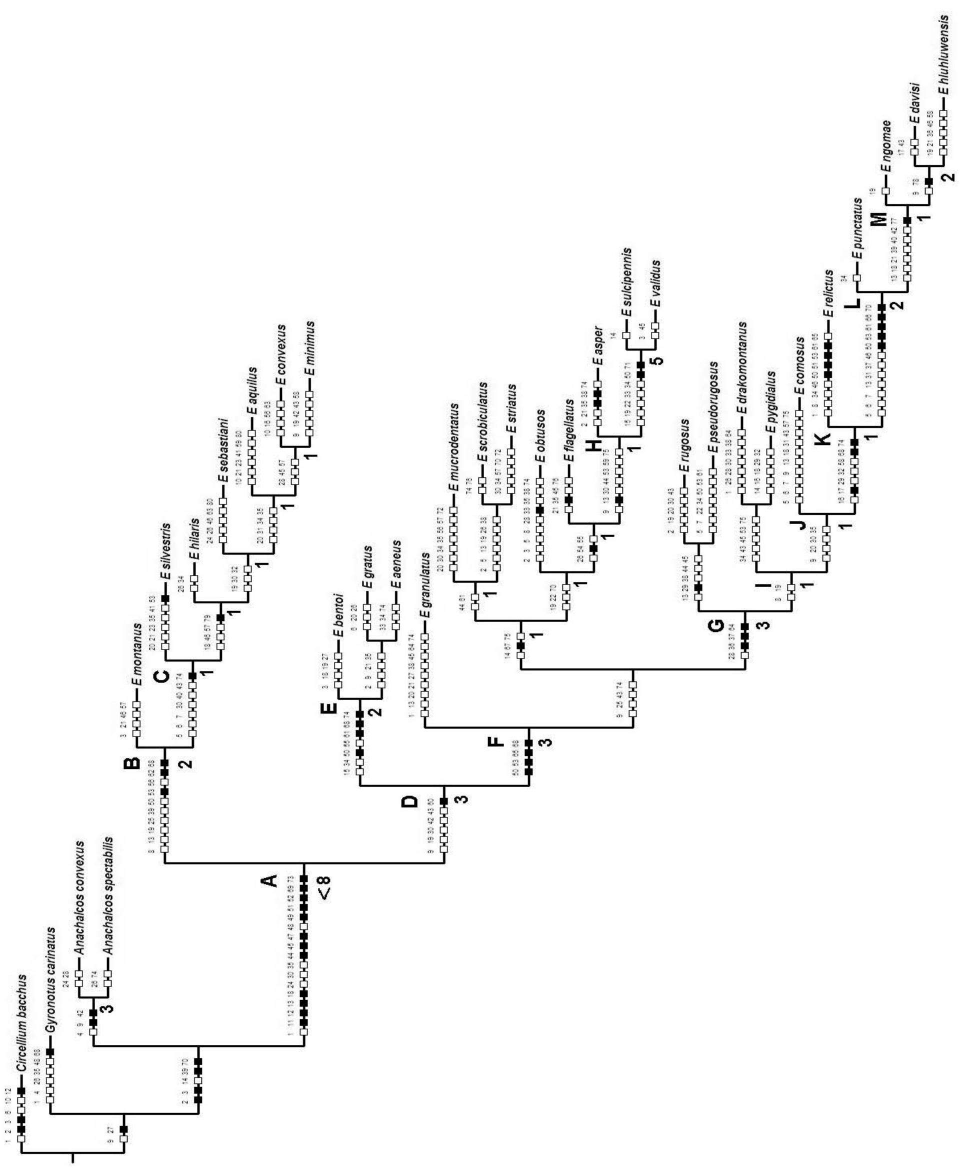


Fig. 49. Strict consensus tree (Deltran optimized) from 3 cladograms (331 steps, CI = 40, RI = 67). Numbers below branches correspond to Bremer–support values. Letters above nodes are to distinguish them for discussion in the text. Black hatchmarks indicating changes without homoplasy, white hatchmarks indicating changes with homoplasy.

distance to the internal border; (1) smaller; (CI = 0.33, RI = 0.33)

59. Distance from the hole to the internal border; (0) less than two times the diameter of the hole; (1) more than 2 times; (CI = 0.50, RI = 0.66)
60. Sclerite Y (half–moon, Figs 28–32): (0) absent; (1) present; (CI = 1.00, RI = 1.00)
61. Sclerite Y: (0) as in *E. relictus* (Fig 32); (1) as in *E. ngomae* sp. n. (Figs. 28–31); (2) as in *E. granulatus*; (3) as in *E. aeneus*; (4) as in *E. pseudorugosus* (Fig. 30); (CI = 0.66, RI = 0.71)
62. Sclerite W (Figs 33–35): (0) absent; (1) present; (CI = 1.00, RI = 1.00)
63. Sclerite W as E: (0) oval; (1) rounded; (CI = 0.50, RI = 0.00)
64. Sclerite Y as C: (0) base as a half circle; (1) as 1/4 of a circle; (2) as 1/8 of a circle; (CI = 0.66, RI = 0.75)

65. Sclerite Z (Figs 37–38): (0) absent; (1) present; (CI = 0.50, RI = 0.92)
66. Sclerite Z: (0) curved as in *E. punctatus* (Fig. 37); (1) straight (Fig 38); (CI = 1.00, RI = 1.00)
67. Sclerite Z straight: (0) as in *E. validus*; (1) as in *E. comosus*; (CI = 1.00, RI = 1.00)
68. Sclerite elongated: (0) as in *Anachalcos*; as in *Gyronotus* (1); as in *E. relictus* (2); as in *E. aeneus* (3); as in *E. validus* (4); as in *E. montanus* (5); (CI = 1.00, RI = 1.00)
69. Elongate sclerite: (0) fused flagella; (1) free flagella; (CI = 1.00, RI = 1.00)
70. Elongate sclerite: (0) without the oval sclerite on top; (1) with reduced oval sclerite on top; (2) with small oval sclerite; (3) with large oval sclerite; (CI = 0.60, RI = 0.75)
71. Female genitalia: (0) without sclerotized spots; with sclerotized spots; (CI = 1.00, RI = 1.00)
72. Lateral plates of female genitalia: (0) without a sharp point; (1) with a sharp point; (CI = 0.50, RI = 0.00)
73. Central plate: (0) absent; (1) present; (CI = 1.00, RI = 1.00)
74. Lateral plates (hemisternites): (0) large and strongly sclerotized; (1) as two thick rectangular blocks (Fig. 39); (2) as two thin plates (Fig. 41); (3); thin and elongated plates (Fig. 42); (4) small–round plates (Figs 44–46); (5) reduced and thin (Figs 47–48); (CI = 0.50, RI = 0.68)
75. Lateral and superior plates: (0) glabrous; (1) setose; (CI = 0.25, RI = 0.57)
76. Setae on lateral plates: (0) few less than 7; (1) more than 7; (CI = 0.50, RI = 0.00)
77. Plate with lateral projections: (0) absent; (1) present; (CI = 1.00, RI = 1.00)
78. Internal border of spermatheca; (0) curved (Fig. 43); (1) forming a straight angle (Fig 47); (CI = 1.00, RI = 1.00)
79. Internal duct: (0) absent; (1) present; (CI = 1.00, RI = 1.00)

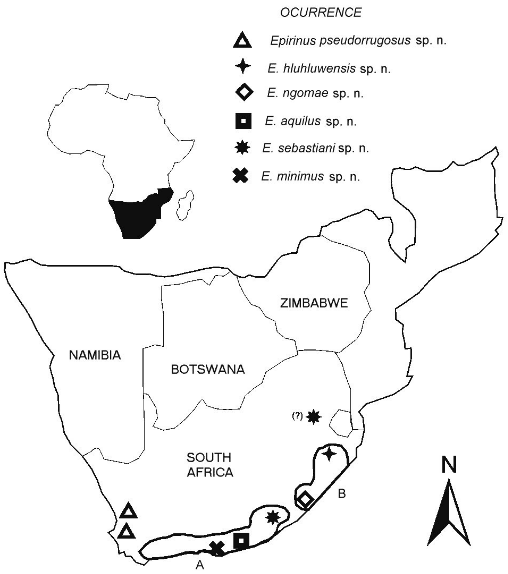


Fig. 50. Distribution map of the new species of *Epirinus*. Circled areas distinguish between the distribution areas of the major groups. The circle A borders the group distributed from Western Cape to Transkei area (Node B; Fig. 49), while the circle B borders the more forest restricted group (Node K; Fig. 49).

Results of cladistic analysis

The analysis of 79 characters resulted in three most parsimonious cladograms of 322 steps (CI = 41, RI = 68). The highest Bremer value in the tree topology supports the genus *Epirinus* (Fig. 49, Node A). The genus is unequivocally a monophyletic group of species, based on the following synapomorphies: shape of the internal border of the eye, genital segment with short projections; and presence of sclerite X in the internal sac.

Despite the morphological differences between the winged species and the flightless species, which are mainly related to body size, and differences associated with the presence or absence of wings, there is no support for the flightless species to be considered as a separate genus. All the flightless species share with the others all the synapomorphies for the genus.

One group of flightless species appears basal and separated from the rest of the *Epirinus* species, with synapomorphic characters from the shape of the sclerites of the internal sac of the aedeagus (Node B). This group includes forest species distributed from the Western Cape area to Transkei (Fig. 50). A subgroup from this clade (Node C) shares the presence of two, sclerotized, and ball–shaped plates in the female genitalia.

The intermediate nodes in the cladogram include most of the large and winged species. These species are more widespread in southern Africa and are associated with other non–forest habitats (e.g. Namaqualand, Karoo, and southern Kalahari). An exception is the species in node H, which are amongst the largest species of *Epirinus*; they have widely separated eyes and are restricted to high–lying areas of the eastern escarpment (Scholtz & Howden, 1987a).

The most derived group in the cladogram includes two species of winged *Epirinus* (*E. relictus* and *E. punctatus*), which are related to the rest of the small flightless species (Node K). The pronotum with lateral fovea, shape of the elongated sclerite of the internal sac of the aedeagus, and shape of the lateral plates of the female genitalia are shared by these species. These species are distributed in northern Kwa–Zulu Natal, mainly in small patches of relict forest (Fig. 50).

The tribe Canthonini is currently distributed in the continents that were part of Gondwana, mainly Africa, America and Australia. The tribe has a common history that goes back to more than 75 million years, probably before the separation of Gondwana into the continents that we see today. African genera of Canthonini have apparent relationships with the American genera rather than those from Australia (Medina, C. A. in preparation). In Africa, in the middle Eocene forest and bush gradually changed into grassland and the savanna habitat spread as the grazing mammals diversified (Cambefort, 1991). Large ball–rolling dung beetles (Scarabaeini) diversified in such open habitats, while small canthonines were left to occupy the forest relicts, probably associated with the dung of small mammals.

A few genera of Canthonini are widely distributed in Africa (i.e. *Anachalcos*); the others are more restricted to the southern regions (Scholtz & Howden 1987b). Although some species of *Epirinus* are widespread in South Africa in different types of habitats that include open grasslands, savannas, and the Nama–Karoo, some have a close association with forest. As with other small African genera, currently classified as canthonines, such as *Odontoloma*, *Janssensantus*, *Outenikwanus*, *Bohepilissus*, among others, *Epirinus* could be part of an ancient group of forest dung beetles. What we see today is a mixed group, formed by one group of species that had adapted to different habitats and types of excrement, and two other groups of species, which have retained their relictual associations and with two possible separated origins. For the "*davisi*" group (Node M) we can assume, on the base of its various characters shared with winged species (i.e. *E. punctatus* and *E. relictus*), that its origin is derived from a winged species. The other group of flightless species appears basal in the cladogram, and its origin could be either from a winged or wingless beetle.

As some species of *Epirinus* have very localized and restricted forest distribution, it is advisable to consider their conservational status. Small patches of forest maintain unique populations of species as in the case of *E. ngomae* sp.n, *E. hluhluwensis* sp.n. and *E. davisi*. These species should be considered endangered, as they will be vulnerable to habitat transformation or destruction.

Acknowledgements

We are grateful to curators of the Institutions from which specimens were borrowed, especially to Ruth Muller (TMSA), and Riaan Stals (NCSA). Adrian Davis provided us with material and valuable suggestions on the project. Alberto Ballerio helped us with Latin names for the new species, and Andrey Frolov kindly helped with the habitus images. This project was funded by an operating grant from the South African National Research Foundation to CHS, and by NRF and University of Pretoria studentships to CAM.

References

Bremer, K. (1994) Branch support and tree stability. *Cladistics* 10: 295–304.

Cambefort, Y. (1978) Canthonina nouveaux ou peu connus d'Afrique continentale (Coleoptera: Scarabaeidae). *Journal of the Entomological Society of Southern Africa*. 41(2): 199–213.

Cambefort, Y. (1991) Biogegraphy and evolution. Pp. 51–67, *in* Hanski, I & Cambefort, Y.: *Dung Beetle Ecology*, Princeton (Princeton University Press). 481 pp.

Goloboff, P. (1995) *NONA, Version 2.0.* – Fundación e Instituto Miguel Lillo, Tucumán, Argentina.

Lindroth C.H. & E. Palmén. (1970) 16. Coleoptera Pp. 80–88, *in* Tuxen S.L.: *Taxonomist's glossary of genitalia in insects*. 359 pp. Scandinavian University Books, Denmark.

Medina, C.A., C. Scholtz, & B.D. Gill. (2003) Morphological variation and systematics of *Canthon* Hoffmansegg 1817, and related genera of new world Canthonini dung beetles (Coleoptera, Scarabaeinae). *Deutsche Entomologische Zeitschrift*. 50 (1): 23–68.

Nixon, K.C. (1995) *CLADOS, Version 1.9.4.* – Cornell University, Ithaca, NY.

Nixon, K. C. (1999) *Winclada (BETA)* ver. 0.9.9. – Published by the author, Ithaca, NY.

Scholtz, C. H. & H.F. Howden. (1987) A revision of the southern African genus *Epirinus* Reiche (Coleoptera: Scarabaeidae: Scarabaeinae). *Journal of the Entomological Society of Southern Africa*. 50(1): 121–154.

Scholtz, C. H. & H.F. Howden. (1987) A revision of the African Canthonina (Coleoptera: Scarabaeidae: Scarabaeinae). *Journal of the Entomological Society of Southern Africa*. 50(1): 75–119.

Accepted for publication January 2005

Appendix 1. Data matrix for 33 taxa including all the species of *Epirinus* used in the cladistic analysis (description of characters satates are included in the text).

	111111111222222222233333333334444444444555555555566666666667777777777 1234567890123456789012345678901234567890123456789012345678901234567890123456789
Circellium bacchus	232011011101000000000000–0000––0––––000020020000000020–––––––0–0––0––00000000–000
Gyronotus carinatus	0001––––2000000000000–0011100––––1000200200000100 20–––––––0–0––0––10000000–000
Anachalcos convexus	1111––––3000020000000001001000––––00000000000000000020–––––––0–0––0––00200000–000
A. spectabilis	1111––––3000020000000000011100––––00000000000000000020–––––––0–0––0––00200010–000
Epirinus drakomontanus	1110100000122200013000111110 0––00111200012120112511301001012 0–2111412001110000
Epirinus pygidialus	2110100000122101003000110101201101110000121201125113010010120–1111412001110000
Epirinus punctatus	2110011010123201113100011010131111010000011111112311110100 0–110––10–2110015 0–000
Epirinus relictus	0110100110122201113100011010130111011000011112112101001000–100––0––21200150–000
Epirinus bentoi	2100100110122210001000010 00––200111000000121101122112 00–010130––0––31200130–000
Epirinus gratus	2210110100122210012120010111020011000000012110112211200–010130––0––31200130–000
Epirinus aeneus	2210100100122210012020010011020000000000012110112211200–010130––0––31200120–000
Epirinus sulcipennis	2110100110121210012000011111010000100000011210112611310–011120–0110413 10110–000
Epirinus validus	2100100110121110012000011111010000100000011220112611310–011120–01104131 0110–000
Epirinus granulatus	1110100110123200012110010 00––2001210010001212011251140100101 20–2111412 00120–000
Epirinus comosus	2110011020123200003100011010031012011000010110112511401011012 0–1111412001110000
Epirinus flagellatus	2110100100122100011011011111020012300000011120112511410–010120–0110413001111000
Epirinus asper	2210100110121100011011011111010012200300011210112511310–011120–0110413001200000
Epirinus rugosus	2010100100123200011100011010230012111200010220112511401001012 0–1111412?????????
Epirinus scrobiculatus	2010000100123100013000011111020012100100011210112511401001014 0––110412001211000
Epirinus striatus	2010000100123100013000011111010010100100011210112511401011014 0––110413011110000
Epirinus obtusos	2000000000122100011001011010020022000100011110112511401001012 0–0110413001210000
Epirinus mucrodentatus	2110100100122100012100011011010011000000011210112511401121014 0––110412011110000
Epirinus pseudorugosus	2110001100123200012001011010220010111200011220112411301001014 0–1111412001 10–000
Epirinus silvestris	2110011020124200011110111011020012000011121110112411601101 00–10–0––51200140–000
Epirinus montanus	2100100020124200011010011011010012100010020112112411501121 00–10–0––512?????????
Epirinus davisi	21100110201242010031200110101311120100110201111 1??????????????????????00150–110
Epirinus convexus	2110011021124201002100011010031111000011021121112411501001 00–11–0––51200140–001
Epirinus hilaris	2110011020124200001000011111020011100011021111112411501121 00–10–0––51200140–001
Epirinus hluhluwensis	2110011020124201102110011010131112000011021112112311101001011 0––10–21100150–110
Epirinus sebastiani	2110011020124200002000001111030112100011021112112411501121 00–11–0––51200140–001
Epirinus minimus	2110011010124200001100011010031111000011010121112411501100–0–10–0––51200140–001
Epirinus ngomae	2110011010124201102120011010131112010011021111112311101000–110––10–21100150–100
Epirinus aquilus	2110011021124200002110111011031111000011121111112411501121 10–10–0––51200140–001

CHAPTER III

EVOLUTIONARY TRENDS AND PHYLOGENY OF THE TRIBE CANTHONINI

Abstract

The phylogeny of the tribe Canthonini, the largest of the subfamily Scarabaeinae, is examined. Two different sets of characters and taxa (matrix for phylogenetic analysis) were used to approach the tribe as it is currently classified (see: appendices 2-5). One matrix includes genera of most of the regions where the tribe is distributed (America, Africa, Madagascar and Australia), and the second matrix includes mainly American genera. The main result of the analysis is strong evidence of a need for sub-division in the tribe. A large division separates the large-bodied and more typical roller beetles of America and Africa from the small and not necessarily roller beetles from all the regions. Although a more detailed taxonomic study will be necessary to define taxonomic and nomenclatural issues in the tribe Canthonini and close relatives from the result of the current analysis, three tribes are proposed: Byrrhidiini (*Byrrhidium*, *Dicranocara*, *Namakwanus*, and *Versicorpus*) Circelliini (including the monotypic genus *Circellium*), and Canthonini, initially including mainly the American genera *Canthon*, *Malagoniella*, *Megathopa*, *Megathoposoma*, *Eudinopus*, *Canthonidia*, *Tetraechma*, *Anisocanthon*, *Melanocanthon*, *Sylvicanthon*, and *Hansreia*, and the African *Gyronotus* and *Anachalcos*. Genera from Madagascar and the Australiasian region should be addressed separately. Relationships of some groups of species indicate that the previously established tribes Panelini, Epilissini, and Mentophilini could be valid for these groups, and in the context of a new tribal classification.

INTRODUCTION

The tribe Canthonini includes about 873 species belonging to 91 recognized genera, equivalent to 40% of the entire subfamily Scarabaeinae. One of the basic characteristics that has been used to classify dung beetles as Canthonini is the shape of the legs. Most species of Canthonini have been classified as such, based on the presence of elongated middle and posterior legs, and in most cases the roller condition was assumed for these species. Historically dung beetles were divided into two main guilds, rollers and tunnelers. Typical tunnelers have robust, short and triangular-shaped medium and posterior legs, while typical rollers have slender, elongated and curved medium and posterior legs. These two morphological traits match with the basic behaviour of rolling and tunnelling. Unfortunately, dividing a whole subfamily of nearly 6000 species according to the behaviour of rolling or tunnelling has been insufficient. Most, but not all, dung beetles can be classified in one of these two categories, and the creation of these two guilds has forced hundreds of species to fit in these categories with the result a classification that does not correspond with all the variations among currently described dung beetles. Genera from different regions and with extreme morphological features were classified under the tribe Canthonini, and recent morphological and molecular analyses have documented the polyphyletic character of the tribe Canthonini (Philips, *et al.* 2004, Monaghan *et al.* 2007, Sole & Scholtz 2010).

The current classification of the tribe has a long history of taxonomic and nomenclatural changes, and the status and names of the tribes have been affected by the changes in the classification of the whole subfamily. For that reason it is important to look at the history of these changes in the tribe Canthonini.

Historical aspects of the division and classification of the tribe Canthonini

To understand the nomenclatural history of the dung beetles currently classified as subfamily Scarabaeinae it is necessary to go back to the "Systema Natura" of Linnaeus (1758), with his description of the genus *Scarabaeus* Linnaeus 1758. After Linnaeus, other authors, such as Fabricius 1775, Degeer 1783, and Olivier 1789 increased the number of Coleopteran genera. But it was Latreille (1796) who gave the level of families to the recognised groups of beetles similar to what we have currently. He recognized two families of Scarabaeidae beetles: “Familie primièr” including the genus *Lucanus* and others, and “Fam 2.” including genera such as *Trox* Fabricius 1775, *Geotrupes* Latreille 1796, *Copris* Geoffroy 1762, and *Scarabaeus*, among others. Since then, different systems of classification, such as that of Janssens (1949) and Paulian (1988), have been proposed, but there is still no consensus among authors on the classification of the family Scarabaeidae and subfamily Scarabaeinae (Grebennikov & Scholtz 2004, Scholtz *et al.* 2009). Some authors still consider that the true dung beetles (subfamily Scarabaeinae) should be recognised at the family level. A recent, detailed description of the nomenclatural history for the superfamily Scarabaeoidea is presented by Kohlmann & Moron (2003).

For the tribe Canthonini, which concerns the present work, it is necessary to go back to Lacordaire (1856), who divided Coprides into two main groups: Copris vrais (Scatonomides, Onthophagides, Coprides, and Onitides) and Ateuchides (Ateuchides vrais, Deltochilides, Gymnopleurides, and Menthophilides). This was the first classification scheme that provides an idea of the different groups of dung beetles that resemble the different tribes relevant to the current classification. Later, Lansberge (1874) described the tribe Canthonides with three sections: Section 1, the true Canthonides, including mainly American genera; Section 2, the Mentophilides, divided into Epilissides and Epirinides, includes mainly African and Australian genera; and Section 3, Ateuchides, where the genus *Circellium* Latreille 1825 was placed. Kolbe (1905) was the first to use “Canthoninae”, the latinized form of “Canthonides”. Arrow (1931) described the tribe Panelini to include some Oriental (Asiatic) genera. Janssens (1946) included a key to the identification of the groups of Scarabaeinae similar to those in the current classification. This included the tribe Scarabaeini with the subtribes Canthonides, Sisyphides, Gymnopleurides, Scarabaeides, Eucranides, and Alloscelides. Later the same author included the suffix “ina” for the subtribes, and since then began the use of the name “Canthonina” for the tribe Canthonini (Janssens 1949). Lebis (1953) considered the tribe Epilissini valid for the Malagasy genera. Balthasar (1963) followed Janssens´ classification, and this system was also followed by Halffter &

Matthews (1966). The latter authors, in their publication on the natural history of the subfamily Scarabaeinae, included a list of all genera of the subfamily Scarabaeinae, arranged in the tribes in the sense of Janssens (1949). Matthews (1974) studied Australian Canthonina, and he mentioned that it would be convenient to use Mentophilina for a group of Australian genera.

Taxonomic changes in recent decades include the transfer of some genera from Ateuchini to Coprini (Montreuil 1998), a change that is included in Smith´s (2006) review of family names. In the revision of the family group names, Bouchard *et al.* (2011) validate the name Deltochilini Lacordaire 1856 for the tribe Canthonini. However, the name Deltochilini has not been universally recognized. In a previous publication Smith (2006) alleged that: “Although Deltochilini has priority over Canthonini the latter is in prevailing usage at the tribal level and must not be displaced by the older name (Article 35.5)”. So under this assumption, I consider the name Canthonini should remain valid.

Despite some phylogenetic studies of groups that include Canthonini species based on morphology (Zunino 1983, Montreuil 1998, Medina *et al.* 2003 Philips *et al.* 2004, Vaz de Mello 2008), or DNA (Villalba *et al.* 2002, Ocampo & Hawks 2006, Monaghan *et al.* 2007, Orsini *et al.* 2007, Wirta *et al.* 2008, Sole & Scholtz 2010), these have been insufficient in relation to the number of genera and species in the tribe, the variation and complexity of the groups, and the high levels of homoplasious characters in the phylogenies. The current scenario is that, despite the past efforts, a better understanding of the evolution of the tribe and its phylogenetic relationships needs more decisive and collaborative work, as well as the implementation of new techniques or combined analyses.

Methods

Two sets of morphological data were organized to evaluate the phylogenetic relationships of the tribe Canthonini, in two separate analyses. The first includes representative species of Canthonini from the different regions were the tribe is distributed, and some additional species from the tribe Ateuchini with various genera from Demarziellini, in the sense of Vaz de Mello (2008). Genera of Ateuchini were included for the following reasons: firstly, owing to similarities in the morphology of the internal male genitalia that species of this tribes show with some genera of Canthonini (see Medina *et al.* 2013); secondly, recent cladistic analyses have shown these two tribes to be phylogenetically related and additional evidence of their relationships is needed. In this study two different genera of the subfamily Aphodiinae, *Aphodius* Illiger 1798 and *Ataenius* Harold 1867, were used for outgroup comparison and to root the tree. The cladistic analysis included 152 morphological characters and 51 taxa (Appendices 2. and 3.).

The second analysis included genera that were together in the main clade in the first analysis. This analysis included mainly American genera plus one genus from Africa (*Anachalcos* Hope 1837). Species from different subgenera of *Canthon* (9) and *Deltochilum* (4) were included, for a total of 28 taxa; 90 characters were coded (Appendices 4. and 5.). The genus *Coptorhina* Hope 1830, which appears basal in other phylogenies, and has been proposed as basal to the subfamily Scarabaeinae (Philips *et al.* 2004, Monaghan *et al.* 2007), was used for outgroup comparisons.

The specimens were dissected and soft parts (mouthparts and internal male genitalia) were heated in a solution of 5 % KOH in small jars until the structures were soft and clear. Structures were prepared on microscope slides with glycerine for comparisons.

The two cladistic analyses were performed using the program Nona (Goloboff 1993) and cladograms were examined with Clados (Nixon 1995) and Winclada (Nixon 2002). The characters were run under the Fitch parsimony, unordered and weighted equally (Goloboff 1993). The search for the most parsimonious cladograms was replicated 10000 times using multiple TBR (mult* and max* in Nona). Branch support values and Bremmer support were calculated.

Results and Discussion

The first analysis, of 152 characters and 51 taxa, resulted in a single most parsimonious cladogram of 1181 steps (Ci = 26, Ri = 52). This topology shows three main clades (Figure 1.). One clade is formed by the southern African taxa *Dicranocara*, *Byrrhidium*, and *Namakwanus*. The second large node (clade 3 Figure 1.), includes mainly the medium-sized to larger, true roller dung beetles from America and Africa, and the third clade is formed by genera of Canthonini plus Ateuchini mainly from Australia, Madagascar, and Africa. It also includes some American genera, such as *Agamopus* Bates 1887, *Cryptocanthon*, *Canthonella* Chapin 1930, *Canthochilum* Chapin 1934, and *Paracanthon* Balthasar 1939, as well as the genus *Sinapisoma*, transferred from Canthonini to the tribe Ateuchini (Vaz de Mello 2008).

Clade 1. Tribe Byrrhidiini new tribe

The genera *Namakwanus* Scholtz & Howden 1987 and *Byrrhidium* Harold 1869 were considered under the tribe Canthonini by the presence of three or fewer teeth in the outer margin of the fore tibiae, and parallel or slightly oblique mesocoxae (Scholtz & Howden 1987a). Recently two genera related to *Namakwanus* and *Byrrhidium* were discovered: *Dicranocara* Frolov & Scholtz 2003, and *Versicorpus* Deschodt, Davis & Scholtz 2011. These four genera have the same geographical distribution and occupy similar ecological niches. Comparisons of internal male genitalia and characters from the mouthparts, mainly the epipharynx, show that this group is a different phyletic line from the rest of African genera of Canthonini, and differs morphologically from the other groups in Scarabaeinae. I consider this group more basal and outside of the tribe Canthonini or Ateuchini; the sclerotized mouthparts and differences in the male genitalia separate it from other genera of Ateuchini, including *Coptorhina*; for that reason I consider it valid to classify the genera as members of a new tribe, Byrrhidiini. Also In the molecular analyses of Sole & Scholtz (2010), the group appear as a distinct basal clade.

Byrrhidiini, new tribe

Diagnosis: The tribe Byrrhidiini can be differentiated from other tribes in the subfamily Scarabaeinae mainly by characters in the mouthpart and male genitalia; well sclerotized labrum and epipharynx, maxillae and mandible with sclerotized portions. Internal sac short, apical area with sclerotized superimposed structures.

Description: The external appearance of the body in the species included in Byrrhidiini is ovoid dull dark, smooth surface with sparse punctures. Clypeus with two distinct obtuse upward teeth excessively developed in *Dicranocara*; eyes narrow, surrounded by a defined band, with opistoma oblique, forming a smaller 90-degree angle with the posterior margin. Gula with a distinct thin band of fine setae; epipharynx with a well sclerotized plate, medial process of the epipharynx solid, without setae and tapered towards the apex; lateral combs fused completely; comb of the molar lobe of the mandible with a few thick projections; distal comb reduced. Pronotum strongly convex, proepimeron excavated, with a complete proepisternal keel. Mesosternum with a well developed deep and wide sulcus. Elytra fused along sutural margins, without humeral umbones, with feebly marked striae, elytral interval flat, sparsely punctate. Metathoracic wing reduced. Pygidium slightly convex without keels. Fore tibiae with three or two teeth, two in species of the genera *Byrrhidium* and *Dicranocara*; fore tarsus generally short or reduced. Mid-coxae slightly oblique, located totally in the metasternum. Meso- and metatibiae slender, laterally compressed and with bristles along the inner and outer surface. Aedeagus with symmetrical parameres; most species with tapered parameres and with setae along the borders. Internal sac short, without defined basal plate, or enlarged sclerites. The male of *Versicorpus* is unknown, so genitalia have not been examined.

Type genus: *Byrrhidium* Harold 1869

Distribution: The tribe is distributed in arids regions of Southern Africa, in the narrow coastal strip between the Atlantic Ocean and the Great Escarpment. The genera in this group have been mainly collected associated with dung middens of hyrax (*Procavia capensis*) between large boulders on river banks (Frolov & Scholtz 2003, Deschodt *et al.* 2011).

Remarks: The genera included in the tribe are: *Byrrhidium* Harold 1869, *Namakwanus* Scholtz & Howden 1987, *Dicranocara* Frolov & Scholtz 2003 and *Versicorpus* Deschodt, Davis & Scholtz 2011.

Clade 2. Circelliini new tribe

The monotypic genus *Circellium* (*C. bacchus*) appears basal and outside of the main clade (Fig 1.). This genus has traditionally been classified within Canthonini, although some authors classified it as Scarabaeini (= Scarabaeina in Halffter & Matthews 1966). *Circellium* shares some characters with the tribe Scarabaeini, i.e. opistoma dividing the eye totally; medial and posterior coxae oblique, as well as characters from the mouthparts, i.e. anterior border of labium entire, and forming an angle > to 90 degrees with the lateral edge. This monospecific genus has unique characters (see the diagnosis below), enough to differentiate it from the related tribes Scarabaeini and Canthonini; it should be classified as a separate tribe, consequently Circelliini. In an analysis of 200 morphological characters, Philips *et al.* (2004) show *Circellium* as more closely related to the Scarabaeini. Based on molecular data, the tribal analysis by Monaghan *et al.* (2007) shows that *Circellium* is not related to other Canthonini from Africa or America. In their Bayesian tree, *Circellium*, together with two species of *Ateuchus* (*A. ecuadorense* [Boucomont 1928] and *A. chrysopyge* [Bates 1887]), are linked to the tribe Scarabaeini. In the consensus phylogram, using mitochondrial and nuclear gene data, Sole & Scholtz (2010) found *Circellium* sharing a clade with the genus *Pedaria* (Ateuchini) but having no relationship to the other African genera included in their analysis.

Circelliini, new tribe

Diagnosis: The tribe is distinguished from other tribes in the subfamily Scarabaeinae by the following combination of characters: opistoma closed posteriorly, dividing the eye completely; epipharynx narrowly indented in the middle; fore tarsus absent, medial and posterior coxae oblique.

Description: Very large beetles, black, oval and strongly convex, pronotum and elytra of similar size. Clypeus wrinkled, with two well-developed rounded teeth; eye small, surrounded by a slender carena; canthus closed posteriorly dividing the eye completely; opistoma transversal, forming a 90 degree angle with the posterior margin. Gula with a thick line of setae. Epipharynx narrowly indented in the middle; medial process of the epipharynx running longitudinally and reaching the anterior border, with coarse setae at the apex, lateral combs fused at the transverse suture. Pronotum large and convex; surface finely punctate with minute punctures widely separated, lateral margin rounded, without a pronounced angle; proepimerom not excavated; proespisternal keel absent.

Mesosternum with a band of uniform setae running transversally. Elytra without marked umbone; striae feebly marked; elytral intervals flat. Membranous wings absent. Pygidium without depressions in the middle. Fore tibiae with three teeth; mid-coxae slightly oblique, with less than 50% located in the mesosternum; mid-tibiae triangular, with longitudinal margins in dorsal face; with transversal carenas with setae; posterior femur with distal part not enlarged; posterior tibiae slender, not enlarged apically. Aedeagus with asymmetrical parameres; left paramere curved upwards; internal sac well developed with well defined basal and elongated sclerite; plate sclerite not well sclerotized and formed by large scales; raspule well developed and u-shaped.

Type genus: *Circellium* Latreille 1825

Distribution: The tribe is restricted to a few fragments of semi arid-bush along the south and east coast of South Africa.

Remarks: The tribe is formed by the monotypic genus *Circellium*, with the only species described *C. bacchus*. No close relatives of *C. bacchus* are known, and the tribe should be seen as an old lineage, that carries unique phylogenetic information, and which consequently deserves significant conservation strategies.

Clade 3. Tribe Canthonini

The other large clade in the cladogram (node 3, Figure 1.) which includes *Anachalcos, Deltochilum* (*Deltohyboma*), *Deltochilum* (*Euhyboma*), *Epirinus*, *Megathoposoma*, *Malagoniella*, *Megathopa*, *Scybalophagus*, *Eudinopus*, *Hansreia*, *Melanocanthon*, *Canthon* (*Francmonrosia*), *Anisocanthon*, *Sylvicanthon*, *Canthon* (*Glaphyrocanthon*), *Scybalocanthon*, *Canthonidia*, and *Tetraechma* is what should be considered as the tribe Canthonini. An exception is *Epirinus*, which has been found to be more closely related to other tribes in other, different phylogenetic analyses (Philips *et al.* 2004, Monaghan *et al.* 2007, Sole & Scholtz 2010). This group of genera shares characters from the proespisternal keel, the meso-metasternal suture, and characters from the membranous wings (see Appendix 2. list of characters: 44, 55, 83).

The genus *Gyronotus* van Lansberge 1874 is basal to the previous clade, between *C. bacchus* and node 3 (Figure 1.). This genus, as well as *Epirinus*, will deserve more detailed analysis, including more species of the genus, plus other African genera, to confirm its tribal position.

Clade 4. Other tribes

The large third clade of the cladogram includes mainly the small-bodied genera of American and African Canthonini mixed with genera from Madagascar and the Australasian region (Figure 2.). Higher support values (> 4) are concentrated in some pairs of genera that appear related in the cladogram, i.e. the Madagascan genera *Nanos* Westwood 1947 and *Arachnodes*, the Australian genera *Canthonosoma* MacLeay 1871 and *Cephalodesmius* Westwood 1841, and the American genera *Cryptocanthon* and *Paracanthon*.

Some of the groups in this part of the cladogram show roughly what may be a new tribal classification for the non-Canthonini genera, considering the previously used tribes such as Epilissini, Mentophilini, Panelini, and some part of the Ateuchini. Clade 5, *Nanos* plus *Arachnodes*, and including *Epillisus* and other genera from Madagascar could be viewed as part of Epilissini. Most Australasian genera, plus *Saphobiamorpha* from New Zealand integrate clades 6 and 7, in part, so should probably be classified as tribe Mentophilini. The last two clades (8 and 9) mostly contain genera considered related to Ateuchini and Coprini. The genus *Panelus* in the Monaghan *et al.* (2007) molecular analysis appears related to genera in the tribe Coprini, (*Copris* Muller 1764, *Microcopris* Balthasar, 1958, and *Heliocopris* Hope, 1837). *Zonocopris*, a monophyletic American genus, has been found to be related to *Cryptocanthon*, *Bdelyrus* and *Canthochilum*, genera currently considered insertae sedis (Vaz de Mello 2008).

To evaluate the relationships of all the genera that have been excluded from the tribe Canthonini in this analysis, a separate and specific analysis including more genera from Madagascar and the Australasian region, and using a set of characters focused on the morphology particular to these groups, will be needed. Also, it will be important to determine if the tribes Panelini, Epilissini, and Mentophilini could be validated in the new scheme of tribal classification.

Canthonini and Deltochilini: Are they different tribes?

The second analysis resulted in eight most parsimonious cladograms. (L = 472, Ci= 32, Ri = 47). The consensus tree collapsed at three nodes (Ci = 31 Ri = 46) yielding an interesting topology. The genus *Streblopus* is basal in the cladogram and can be viewed as being outside of the tribe Canthonini. This genus is morphologically atypical, and does not show a relationship with other members of the group of American or African Canthonini. *Streblopus* has similar asymmetrical parameres to *Canthonosoma* (Medina *et al.* 2013), and may be related to the Australian genera in Mentophilini. The genus *Deltochilum* is basal in the cladogram and polyphyletic, as is the genus *Canthon*.

Based on the results of the two analyses, what should be classified as the tribe Canthonini is mostly defined by inclusion of the genera; *Anachalcos, Gyronotus*, *Malagoniella*, *Megathopa*, *Eudinopus*, *Megathoposoma*, *Melanocanthon*, *Canthon*, *Hansreia*, *Anisocanthon*, *Sylvicanthon*, *Canthonidia*, *Tetraechma*, and *Scybalocanthon*. The synapomorphies supporting the clades are mainly related to the epipharynx, proepisternum, genital segment, and structures of the internal sac. In this group, the genus *Anachalcos* is included; however, a more detailed analysis including more species of *Anachalcos, Gyronotus*, and the genus *Canthodimorpha* would be necessary to define whether these genera are part of the tribe Canthonini or if Canthonini should be composed by only the American genera.

The situation of the genus *Epirinus* needs to be deeply reviewed. Although in the first analysis the genus appears in the group of Canthonini, *Epirinus* has too many differences to be thus classified. Despite that, *Epirinus* is a true African roller dung beetle (Mlambo *et al.* 2011); it seems to be basal to all the African roller genera, and is probably one of the more ancient linages. In other analyses (Philips *et al.* 2004, Monaghan *et al.* 2007), *Epirinus* appears related to other tribes and not with the Canthonines. In the morphological analysis of Philips *et al.* (2004), the genus shows relationships with genera of the tribe Coprini. In the molecular phylogeny of Monaghan *et al.* (2007), *Epirinus* appears in the same clade with Sysyphini, Onitini, Oniticellini, and Onthophagini, and far from the other Canthonini used in the analysis. Based on a molecular analysis, including mostly African genera, *Epirinus* forms a distinct lineage separated from the rest of African genera (Sole & Scholtz 2010).

The two largest genera of the Canthonini in America, *Canthon* and *Deltochilum*, are not closely related, and both genera need to be deeply reviewed; and the taxonomy and nomenclature need to be defined. In the second cladogram (Figure 2.), species of *Deltochilum* are basal and not clustered together, indicating a deep revision of the group and its classification is necessary. Scant support is observed for the rest of the cladogram. Two groups are supported: one formed by *Tetraechma* Blanchard 1843 and *Canthonidia* Paulian 1938, based on a character from the mandible, and the other group includes species of *Canthon*, *Anisocanthon, Scybalocanthon*, *Sylvicanthon*, and *Hansreia*, supported by characters from sculpturation of the head surface and from the male genitalia. Other genera that show affinity are *Malagoniella* and *Megathopa*, as well as the pair of *Tetraechma* and *Canthonidia*, which appear together in both analyses.

The genus *Canthon*, with 189 species, has a long nomenclatural history with many changes in the classification and in its internal organization into subgenera, groups, and phyletic lines (Halffter & Martínez 1977). The genus is clearly not monophyletic, although some groups could be natural groups of species, as, in part, the subgenera *Francmonrosia* Pereira & Martínez 1959 and *Glaphyrocanthon* Martínez 1948 in part (Medina *et al.* 2003). After careful examination, some genera that were classified within *Canthon*, such as: *Geocanthon, Nesocanthon, Goniocanthon* (Pereira & Martínez 1956), and *Boreocanthon* (Halffter 1961), could acquire generic status. In a recent study, by Villalba (2013), using morphology of the internal sac and general external morphology, the *femoralis* group of the subgenus *Glaphyrocanthon* integrated by 12 species, showed to be a solid group and could be validated as the genus *Geocanthon sensu* Pereira & Martinez (1956).

The genus *Deltochilum* is a more robust group than *Canthon*, with particular morphology and characters, which, in general, differentiate the group clearly from the other canthonine genera. One feature that is widely shared by species of *Deltochilum* is the presence of two medial sclerites of the internal sac (see Figure 1. in Chapter I., Medina *et al.* 2013), and external features from the elytra sculpturation (González *et al.* 2009). However, large variation among the subgenera has been documented in male genitalia, in the aedeagus, and in the internal sac, including the apical sclerites and the lateral lobule (Medina *et al.* 2013), as well as in the external morphology (González *et al.* 2009). Eight subgenera are currently recognized in *Deltochilum* (Génier 2012), some of them well differentiated, mainly in specific characters from external morphology (A. González personal communication). Some groups can be differentiated by dissimilarities in basal and elongated sclerites sufficient to be classified as different genera. *Deltochilum* species do not share many characters with other genera of American or African Canthonini; the differences mentioned may be sufficient to split *Deltochilum* into several genera and to classify the group as a different tribe, separate from Canthonini. In this sense, both tribes -- Canthonini and Deltochilini -- will be valid.

Conclusions

The main result of these analyses is that the tribe Canthonini, as currently classified, should be divided to have more robust species groups sharing morphological features, as well as to reflect evolutionary and biogeographical history. It has been widely documented that the origin and radiation of the main groups within Scarabaeinae beetles occurred in Africa, and from there, different processes of dispersion and colonization to other regions have occurred (Davis *et al.* 2002, Sole & Scholtz 2010). The polyphyletic tribes Canthonini and Ateuchini, with predominant southern hemisphere distributions, have been mainly classified according to rolling or tunnelling behaviour. However, as has been documented, rolling and tunnelling behaviours arose and were lost independently in the history of these groups (Philips *et al.* 2004). From the results of recent analyses, including the present morphological and cladistic study, the tribe Canthonini is essentially a tropical group with some elements that reflect a Gondwana ancestry. It is mostly comprised of roller dung beetles, with a large, more recent diversification of some genera in connection to the rapid expansion of tropical ecosystems, including tropical humid forest, as most of these genera are closely associated with the inner tropical forest. Groups such as *Canthon*, *Deltochilum*, *Scybalocanthon*, *Sylvicanthon*, among others, are mainly tropical forest specialists, while other genera, with fewer species, such as *Malagoniella*, *Megathopa*, *Eudinopus*, *Scybalophagus*, among others, are more closely related to old linages with more temperate distributions.

Other genera, such as the Australian *Amphistomus*, should not be classified as Canthonini. Although I have not included this genus in the cladistic analysis, from the morphological comparison, I consider that this genus should be omitted from the tribe. The internal male genitalia are completely different from those of the rest of the genera considered here, such as of Canthonini. Nor does the external morphology match with the basic features of the tribe. Also the African genera *Janssensantus* Paulian 1976, *Pycnopanelus* Arrow, 1931, *Aphengoecus* Peringuey 1901, and *Hammondatus* Cambefort 1978, and probably the other small-bodied African genera not included in the current analysis, should be considered as different tribes based in the degree of differences with the rest of the larger rollers of Africa.

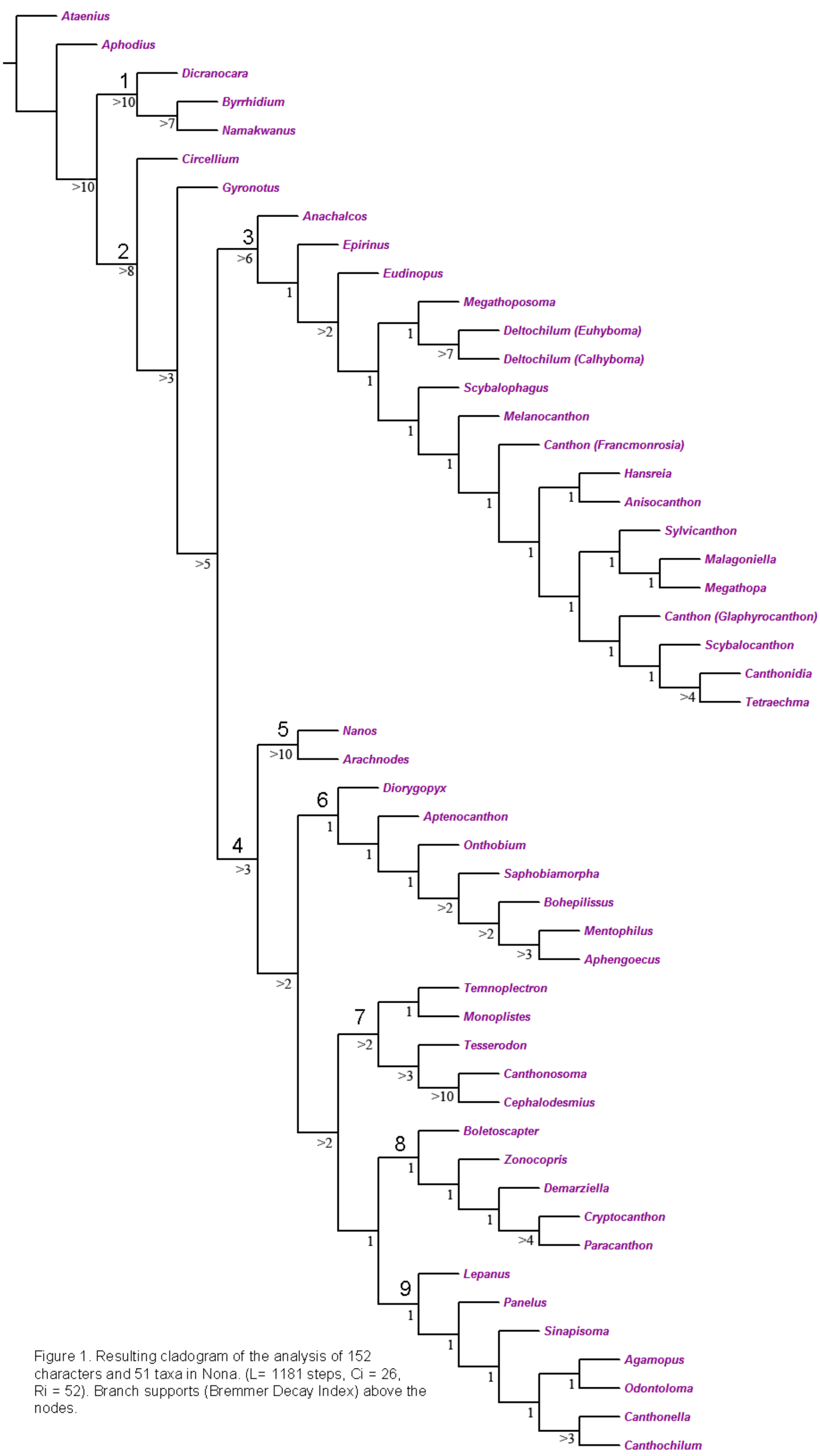


Figure 1. Resulting cladogram of the analysis of 152 characters and 51 taxa in Nona. (L= 1181 steps, Ci = 26, Ri = 52). Branch supports (Bremmer Decay Index) above the nodes.

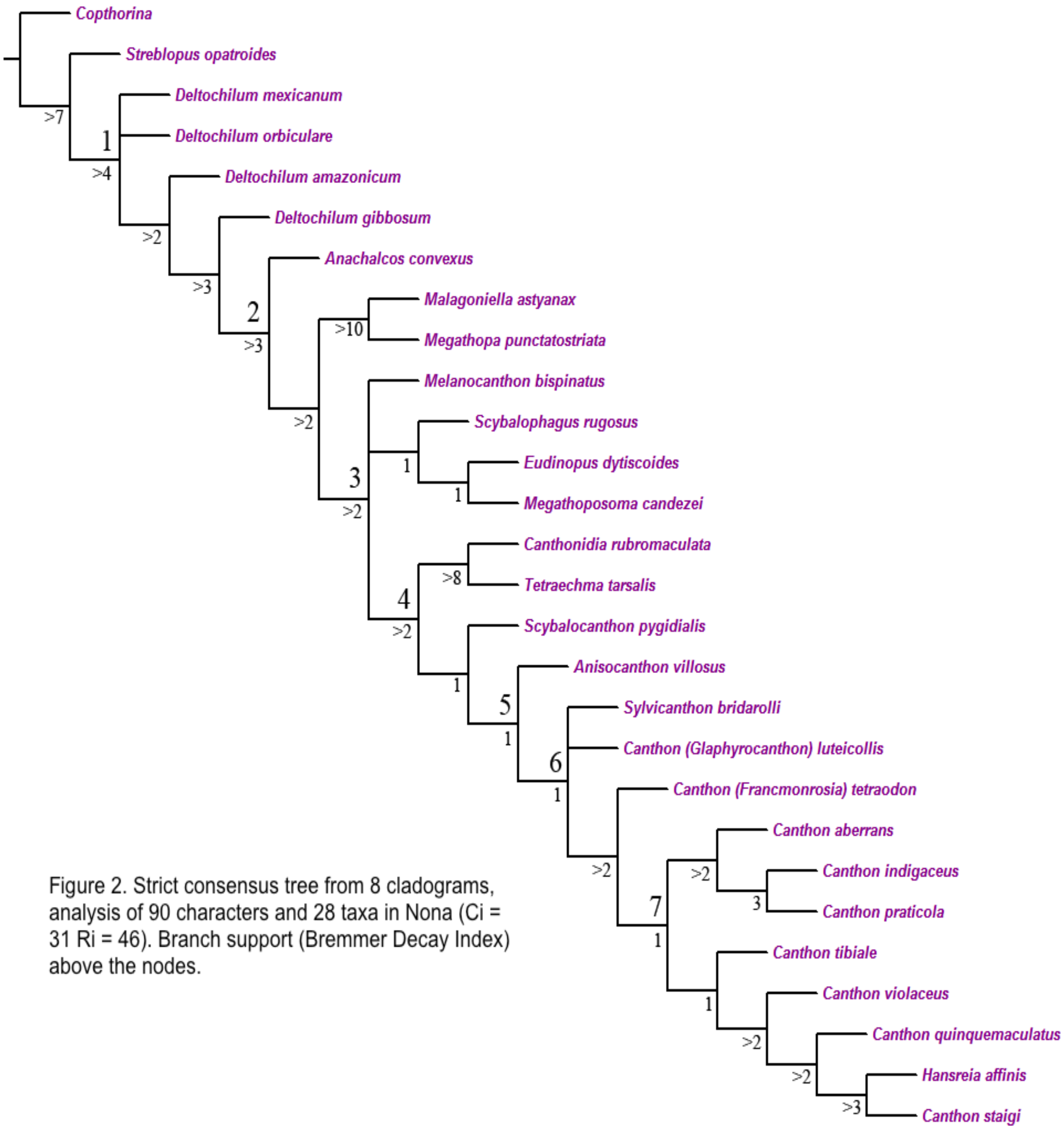


Figure 2. Strict consensus tree from 8 cladograms, analysis of 90 characters and 28 taxa in Nona (Ci = 31 Ri = 46). Branch support (Bremmer Decay Index) above the nodes.

GENERAL CONCLUSIONS

The taxonomy and systematics of dung beetles, although at first glance appearing an easy matter, has generally resulted in contradictory analyses and frustrating discoveries. Large patterns of variation in morphology have been detected in groups of structures as in male genitalia (Tarasov & Solodovnikov 2011, Medina *et al.* 2013) horn variation (Emlen *et al.* 2005, Emlen & Simmons 2005), elytral sculpturation (González *et al.* 2009) hindwing articulation sclerites (Browne & Scholtz 1995, 1998). Efforts to understand the evolutionary relationships of the whole subfamily using different approaches, morphological (Philips *et al.* 2004, Vaz de Mello 2008), molecular (Monahagan *et al.* 2007, Ocampo & Hawks 2006, Orsini *et al.* 2007, Wirta *et al.* 2008, Sole & Scholtz 2010) have been pursued. But to know the true evolutionary history and the radiation of the whole subfamily Scarabaeinae, much information is still missing.

The subfamily Scarabaeinae is a complex group of beetles that have been called dung beetles, but embrace such a large diversity of other feeding habits, that perhaps the term “dung beetle” needs to be replaced by a more generic name. Also the names “roller”, “dweller”, and “tunneler” do not account for all the diverse behaviours and specializations displayed by the different species of the subfamily. As the groups are better studied, more differences are detected. In morphology, the variation within the groups is enormous; intraspecific variation could be larger and includes body size gradients and morphological differences. For Scarabaeinae beetles, especially the males of horned species, the terms “major” or “minor”, referring to larger or smaller beetles, with larger or smaller horns has been addressed. This enormous variation has been observed and widely documented in various species of *Onthophagus* and *Oxysternon*, where three different forms (trimorphism) have been detected (Rowland & Emlen 2009). In the horned species of *Onthophagus* and *Dichotomius*, hornless male individuals have been observed, (Medina C. A. unpublished data). Similar types of variation have been reported for species of the genus *Uroxys*, which present sexual dimorphism and extreme intraspecific body size variation, which makes species differentiation so difficult (Cultid *et al.* 2012). Slight differences in the morphology of some species of *Canthon* have produced erroneous species identifications that dramatically change the distribution of large data sets of these species in Colombia (González & Medina in preparation). Similar morphological difficulties have been documented for the Malagasy dung beetles, where some genera have been synonymized (Wirta & Montreuil 2008). And in different taxonomic papers complexes of species, and cryptic species are reported (Reid 2000, Wirta 2009). The difficulties in species differentiation are widely documented (Tarasov & Keith 2011).

The patterns of variation in morphology, observed for numerous groups within the subfamily Scarabaeinae, change at different levels. For example, for some genera the internal sac sclerites have a constant arrangement, but associated with normal variation in the structures within the species, as is the case in the genus *Epirinus* described in Chapter II. For other genera, mainly those with larger numbers of species, the variation can be greater and some patterns in subgroups can be detected, as is observed in *Canthon* and *Deltochilum*. These patterns of variation, observed for the genera are not applicable to the tribes, and the tribes, which are a supra-generic organization, need a combination of morphological characters and maybe more information on geographic distribution, natural and evolutionary history, in order to achieve a more accurate classification.

More recently, with increasing use of molecular analysis techniques using mitochondrial and nuclear gene information, different phylogenetic studies have documented the systematics and taxonomic incongruities in different groups across the continents in more detail (Orsini *et al.* 2007, Sole & Scholtz 2010). More effort in combined analyses and new techniques to better understand the characters that best reflect ancestry-descendent relationships are urgently needed. The different groups that comprise Canthonini and Ateuchini in the various regions have experienced different evolutionary strategies and different processes of expansion, colonization and radiations, so the efforts to understand these processes should include various forms of analysis including not just an exhaustive morphological study but reinforced molecular, ecological and distributional analysis.

A better approach to understand the evolutionary history, and to improve the taxonomic classification of Scarabaeinae dung beetles, is to study in detail each group, instead of broader analyses with just a few taxa represented. Understanding the morphological and genetic variation within each genus and in relation to the related genera, would help to define the borders of the groups and from that to build the scheme of classification for larger supra-generic groups; tribes, subtribes, or even subfamilies. To date the approach to classification has been doing the opposite, trying to fit the whole range of variation in species and genera into a pre-established and limited tribal classification. To advance towards the goal of a better scheme of classification for the subfamily Scarabaeinae, the first step is to recognize the true dimension of the group. Compared with other groups of beetles, the Scarabaeinae dung beetles is not the largest, but the morphological diversity and complexity of behaviours and specializations deserve a wiser way of looking.

References

Arrow, G. J. 1931. The fauna of British India including Ceylon and Burma. Coleoptera, Lamellicornia. III. Coprinae. Taylor and Francis, London.

Balthasar, V. 1963. Monographie der Scarabaeidae und aphodiidae der palaearktischen und orientalischen region. Coleoptera: Lamellicornia. Verlag der Tschechoslowakischen Akademie der Wissenschaften. Praga.

Bouchard, P., Bousquet, Y., Davies, A., Alonso-Zarazaga, M., Lawrence, J., Lyal, C., Newton, A., Reid, C., Schmitt, M., Slipinski, A., Smith, A. 2011. Family-group names in Coleoptera (Insecta). ZooKeys. 88, 1–972.

Browne, D.J., Scholtz, C.H. 1995. Phylogeny of the families of Scarabaeoidea (Coleoptera) based on characters of the hindwing articulation, hindwing base and wing venation. Systematic Entomology. 20, 145–173.

Browne, J., Scholtz, C.H. 1998. Evolution of the scarab hindwing articulation and wing base: a contribution toward the phylogeny of the Scarabaeidae (Scarabaeoidea: Coleoptera). Systematic Entomology. 23, 307–326.

Cultid, C.A., Medina, C.A., Martínez, B.G., Escobar, A.F., Constantino L. M., Betancur, N.J. 2012. Escarabajos coprófagos (Scarabaeinae) del eje cafetero: Guía para el estudio ecológico. WCS Colombia, CENICAFE, Villa María, Caldas (Colombia).

Davis, A.L.V., Aarde, R.J.V., Scholtz, C.H., Delport, J.H. 2002. Increasing representation of localized dung beetles across a chronosequence of regenerating vegetation and natural dune forest in South Africa. Global Ecology and Biogeography. 11, 191–209.

Degeer, C. 1783. Genera et Species Insectorum. Lipsiae.

Emlen, D.J., Hunt, J., Simmons, L.W. 2005. Evolution of sexual dimorphism and male dimorphism in the expression of beetle horns: phylogenetic evidence for modularity, evolutionary liability, and constraint. American Naturalist. 166 (4), 42–68.

Emlen, D.J., Marangelo, J., Ball, B., Cunningham, C.W. 2005. Diversity in the weapons of sexual selection: horn evolution in the beetle genus *Onthophagus* (Coleoptera: Scarabaeidae). Evolution. 59, 1060–1084.

Fabricius, J. 1775. Systema Entomologiae. Flensburg y Lipsiae.

Génier, F. 2012. A new species and notes on the subgenus *Deltochilum* (*Deltochilum*) Eschscholtz, 1822 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilini). Zootaxa. 25–33.

Goloboff, P.A. 1993. Nona. Sierra Madre de Tucuman, Argentina.

González, F.A., Molano, F., Medina C.A. 2009. The subgenera *Calhyboma*, *Hybomidium*, and *Telhyboma* (Coleoptera: Scarabaeidae: Scarabaeinae: *Deltochilum*) in Colombia. Revista Colombiana de Entomología. 35, 253–274.

Grebennikov, V.V., Scholtz, C.H. 2004. The basal phylogeny of Scarabaeoidea (Insecta: Coleoptera) inferred from larval morphology. Invertebrate Systematics. 18, 321-348.

Halffter, G., Martínez, A. 1966. Revisión monográfica de los Canthonina Americanos (Coleoptera, Scarabaeidae) (I. parte). Revista de la Sociedad Mexicana de Historia Natural. 27, 89–177.

Halffter, G., Martínez, A. 1977. Revisión monográfica de los Canthonina Americanos (Coleoptera, Scarabaeidae). (IV. parte) Clave para generos y subgeneros. Folia Entomológica Mexicana 38, 29–107.

Halffter, G., Matthews, E. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). Folia Entomológica Mexicana. (12-14), 312.

Janssens, A. 1946. Contribution a l'étude des Coléopteres Lamellicornes coprophages, XI. Bulletin du Musée Royal d'Histoire Naturelle de Belgique. 22, 1–13.

Janssens, A. 1949. Contribution à l'étude des coleóptères lamellicornes, Table synoptique et assai de classification pratique des coléoptères Scarabaeidae. Bulletin du Musee Royal d'Histoire Naturelle de Belgique. 25(15), 1–30.

Kohlmann, B., Morón, M.A. 2003. Análisis histórico de la clasificación de los Coleoptera Scarabaeoidea o Lamellicornia. Acta Zoológica Mexicana (n. s.). 90, 175–280.

Kolbe, J. H. 1905. Über die Lebensweise und die geographische Verd-breitung der coprophagen Lamellicornier. Zoologischen Jarrbhern supplement VIII. 475–594.

Lacordaire, J. T. 1856. Histoire Naturelle des Insectes. Genera des Coléoptères. Librairie Encyclopédique de Roret. Paris.

Lansberge, G.V. 1874. Observations sur la Classification des Lamellicornes Coprophages. I. Ateuchides. Annales de la Société Entomologique de Belgique. 17, 177–193.

Latreille, P. A. 1796. Précis des caractères génériques des insectes, disposés dans un ordre naturel. Prèvôt, Paris.

Lebis, E. 1953. Révision des Canthoninae de Madagascar. Mémoires de l'Institut scientifique de Madagascar. 3, 107–252.

Linnaeus, C. 1758. Systema Naturae per Regna Tria Naturae Secundum Classes, Ordines, Genera, Synonymis, Locis., 10a ed. Laurentii Salvii. Stockholm.

Matthews, E.G. 1974. A revision of the Scarabaeine dung beetles of Australia. II. Tribe Scarabaeini. Australian Journal of Zoology Supplementary Series. 22, 1–211.

Medina, C.A., Molano, F., Scholtz, C.H. 2013. Morphology and terminology of dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) male genitalia. Zootaxa. 3626, 455–476.

Medina, C.A., Scholtz, C.H., Gill, B.D. 2003. Morphological variation and systematics of *Canthon* Hoffmansegg 1817, and related genera of New World Canthonini dung beetles (Coleoptera, Scarabaeinae). Deutsche Entomologische Zeitschrift. 50, 23–68.

Mlambo, S., Sole, C.L., Scholtz, C.H. 2011. Phylogeny of the African ball-rolling dung beetle genus *Epirinus* Reiche (Coleoptera: Scarabaeidae: Scarabaeinae). Invertebrate Systematics. 25, 197–207.

Monaghan, M.T., Inward, D.J.G., Hunt, T., Vogler, A.P. 2007. A molecular phylogenetic analysis of the Scarabaeinae (dung beetles). Molecular Phylogenetics and Evolution. 45, 674–692.

Montreuil, O. 1998. Analyse phylogénétique et paraphylie des Coprini et Dichotomiini (Coleoptera: Scarabaeidae). Scénario biogéographique. Annales de la Société Entomologique de France. 34, 135–148.

Nixon, K. C., 1995. CLADOS. Ithaca, New York.

Nixon, K. C., 2002. WINCLADA. Ithaca, New York.

Ocampo, F.C., Hawks, D.C. 2006. Molecular phylogenetics and evolution of the food relocation behaviour of the dung beetle tribe Eucraniini (Coleoptera : Scarabaeidae : Scarabaeinae). Invertebrate Systematics. 20, 557–570.

Olivier, A. G. 1789. Encyclopedique méthodique. Histoire naturelle. Insectes. Vol. 4, Panckoucke, Paris.

Orsini, L., Koivulehto, H., Hanski, I. 2007. Molecular evolution and radiation of dung beetles in Madagascar. Cladistics 23, 145–168.

Paulian, R. 1988. Biologie des Coléoptères. Lechevalier, Paris.

Philips, T.K., Pretorius, E., Scholtz, C.H. 2004. A phylogenetic analysis of dung beetles (Scarabaeinae: Scarabaeidae): unrolling an evolutionary history. Invertebrate Systematics. 18, 53–88.

Reid, C.A.M. 2000. A complex of cryptic species in the genus *Coptodactyla* Burmeister (Coleoptera: Scarabaeidae: Coprini). Memoirs of the Queensland Museum. 46, 231–251.

Rowland, J.M., Emlen, D.J. 2009. Two thresholds, three male forms result in facultative male trimorphism in beetles. Science. 323, 773–776.

Scholtz, C.H., Howden, F.H. 1987a. A revision of the southern African genus *Epirinus* Reiche (Coleoptera: Scarabaeidae: Scarabaeinae). Journal of Entomological Society of South Africa. 50, 121–154.

Smith's, A.B.T. 2006. A review of the family-group names for the superfamily Scarabaeoidea (Coleoptera) with corrections to nomenclature and a current classification. The Coleopterists Bulletin. 60, 144–204.

Sole, C.L., Scholtz, C.H. 2010. Did dung beetles arise in Africa? A phylogenetic hypothesis based on five gene regions. Molecular Phylogenetic and Evolution. 56, 631–641.

Tarasov, S.I., Solodovnikov, A.Y. 2011. Phylogenetic analyses reveal reliable morphological markers to classify mega-diversity in Onthophagini dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). Cladistics. 27, 490–528.

Tarasov, S., Keith, D. 2011. *Parachorius semsanganus* sp. n. (Coleoptera, Scarabaeidae, Scarabaeinae) from Laos and its significance in the phylogeny of Oriental Deltochilini. Zookeys. 51–57.

Vaz de Mello, F. 2007. Revision and phylogeny of the dung beetle genus *Zonocopris* Arrow, 1932 (Coleoptera: Scar- abaeidae: Scarabaeinae), a phoretic of land snails. Annales de la Société Entomologique de France. 43(2), 231–239.

Vaz de Mello, F. 2008. Synopsis of the new subtribe Scatimina (Coleoptera: Scarabaeidae: Scarabaeinae: Ateuchini), with descriptions of twelve new genera and review of *Genieridium*, new genus. Zootaxa 1–75.

Villalba-C, X. 2013. Curaduría y sistematización de la colección general de referencia de escarabajos coprófagos con énfasis en *Canthon* Hoffmannseg, 1817: grupo femoralis (Scarabaeidae: Scarabaeinae) del Instituto de Investigación en Recursos Naturales Alexander von Humboldt. (Pregrado). Universidad Pedagógica y Tecnológica de Colombia, Tunja.

Villalba, S., Lobo, J.M., Martín-Piera, F., Zardoya, R. 2002. Phylogenetic relationships of Iberian dung beetles (Coleoptera: Scarabaeinae): insights on the evolution of nesting behavior. Journal of Molecular Evolution. 55, 116–126.

Wirta, H. 2009. Complex phylogeographical patterns, introgression and cryptic species in a lineage of Malagasy dung beetles (Coleoptera: Scarabaeidae). Biological Journal of the Linnean Society. 96, 942–955.

Wirta, H., Montreuil, O. 2008. Evolution of the Canthonini Longitarsi (Scarabaeidae) in Madagascar. Zoologica Scripta. 37, 651–663.

Wirta, H., Orsini, L., Hanski, I. 2008. An old adaptive radiation of forest dung beetles in Madagascar. Molecular phylogenetics and evolution. 47, 1076–1089.

Zunino, M. 1983. Essai préliminaire sur l’évolution des armures génitales des Scarabaeinae, par rapport à la taxonomie du groupe et à l’évolution du comportement de nidification (Coleoptera, Scarabaeidae). Bulletin de la Société Entomologique de France. 88, 531–542.

Appendix 1. List of species examined.

Subfamily/Tribe	**Genera**	**Subgenera**	**Species**	**Specimens**
GEOTRUPIDAE	*Athyreus*		*unicornis*	1♂
APHODINAE	*Aphodius*		*fimetarius*	1♀
			sp.	3♀
			sp.	1♀
	Ataenius		*sp*	1♂
	Colobopterus			1♂
	Teuchetes		*sp.*	1♂, 1♀
SCARABAEINAE ATEUCHINI	*Agamopus*		*sp.*	1♀
			viridis	2♂, 1♀
	Ateuchus		*sp.*	1♂
	Bdelyropsis		*howditchi*	1♂
	Bdelyrus		*sp.*	1♂
	Coptorhina		*excavata*	2♂
	Demarziella		*interrupta*	1♂
			sp.	1♂
	Pedaria		*sp.*	1♂
	Pseudocoptorhina		*gomezi*	1♂
	Sarophorus		*costatus*	1♂, 1♀
	Sinapisoma		*minuta*	1♂
	Uroxys		*bidentis*	1♂
			brachialis	2♂, 1♀
			caucanus	3♂,1♀
			microcularis	2♂
			rugatus	1♂
SCARABAEINAE COPRINI	*Canthidium*		*gr. Centrale*	2♂
			perceptibile	1♂
			sp1.	1♂
			sp2	1♂
			sp3	1♂
			sp4	1♂
			sp5	1♂
			sp6	1♂
	Chalcocopris		*hesperum*	1♂
	Copris		*dracunculus*	1♂
			incertus	1♂
			mesecanthus	1♂

	Coptodactyla		*glabricollis*	1♂
			lesnei	1♂
	Dichotomius		*bos*	1♂
			quinquedens	1♂
			quinquelobatus	1♂
			satanas	1♂
	Heliocopris			1♂
	Holocanthon		*mateui*	1♂
	Macroderes		*sp.*	2♂, 1♀
	Metacatharsius		*opacus*	1♂
	Ontherus		*sanctaemartae*	1♂
	Synapsis		*temolus*	1♂
	Thyregis			1♂
SCARABAEINAE CANTHONINI	*Amphistomus*		*complanatus*	1♂
			inermis	1♂
			sp.	1♂
			squalidus	1♂
	Anachalcos		*convexus*	2♂, 2♀
			procerus	1♂
			sp-1	1♂
			sp-2	1♂, 1♀
			spectabilis	1♂
	Anisocanthon		*pigmaeus*	1♂
			villosus	1♂
	Anomiopus		*panamensis*	1♂
	Anonthobium		*sp.*	1♂, 1♀
	Aphengoecus		*multiserratus*	1♂, 2♀
	Aptenocanthon		*sp.*	1♂
			winyar	1♀
	Arachnodes		*nitidus*	1♂
			sp.	1♂
			splendidus	1♂, 1♀
	Aulacopris		*maximus*	1♂
	Bohepilissus		*subtilis*	2♂, 1♀
	Bolestocarper		*cornutus*	2♂
	Byrrhidium		*convexum*	3♂
	Canthochilum		*oackleyi*	1♂
			taino,	1♂,1♀
	Canthodimorpha		*lawrencei*	1♂
	Canthon	*(Boreocanthon)*	*ebenus*	1♂

			lecontei	1♂
			praticola	1♂, 1♀
		(Canthon)	aberrans	3 ♂
			aequinoctialis	4♂
			chalcites	1♂
			cyanellus	1♂,1♀
			humectus	1♂
			imitador	2♂
			indigaceus	3♂, 1♀
			pilularius	2♂
			virens	1♂, 1♀
		(Francmonrosia)	dives	1♂
			lamproderes	1♂
			latipes	2♂
			rutilans	1♂
			tetraodon	1♂
		(Glaphyrocanthon)	angustatus	2♂
			columbianus	1♂
			halleri	1 ♂
			luteicollis	4♂, 1♀
			politus	5♂, 1♀
			rubrescens	2♂
			viridis vasquezae	1♂, 1♀
		(Goniocanthon)	fulgidus	1♀
			smaragdulus	1♂
		(Nesocanthon)	violaceus	1♂
		(Peltecanthon)	staigi	1♂, 1♀
		(Psedepilissus)	sp-1	1♂
			sp-2	1♂, 1♀
			lunatus tibiale	1♂
			angularis	1♂
			auricollis	1♂
			denticulatus	1♂
			fortemarginatus	1♂
			gemellatus	1♂
			melancholicus	1♂
			monilifer	1♂, 1♀
			perseverans	1♂
			quinquemaculatus	2♂, 1♀
			septemmaculatus	1♂

			sp.	1♂, 1♀
			sp. (unicolor group)	1♂, 1♀
			triangularis	1♂
			unicolor	1♂
	Canthonella		*gomezi*	1♂
			silphoides	2♂, 1♀
	Canthonidia		*rubromaculata*	1♂, 2♀
	Canthonosoma		*castelnaui*	3♂, 2♀
			macleayi	1♂
	Cephalodesmius		*laticollis*	1♂
			quadridens	2♂
	Circellium		*bacchus*	3♂, 2♀
	Cryptocanthon		*foveatus*	1♂
			newton	1♂
			sp.	1♂, 1♀
	Deltochilum	*(Aganhyboma)*	*cupreicolle*	1♂
			trisignatum	1♂
		(Calhyboma)	*carinatum*	1♂
			cristinae	1♂
			elevatum	1♂
			hypponum	1♂
			luederwaldti	1♂
			mexicanum	1♂
			riehli	1♂
			robustus	1♂
			tessellatum	1♂
			variolosum	1♂
			verruciferum	1♂
		(Deltochilum)	*dentipes*	1♂
			enceladus	1♂
			orbiculare	1♂
			rosamarie	1♂
			scabriusculum	1♂
		(Deltohyboma)	*aff. Aequinoctiale*	1♂
			aff. Valgum	1♂
			parile	1♂
			pseudoparile	1♂
			sp1	1♂
			sp2	1♂
			sp3	1♂
			sp4	1♂

			sp5	1♂
			violetae	2♂
		(Euhyboma)	*brasilense*	1♂
		(Hybomidium)	*icarus*	1♂
			lobipes	1♂
			loperae	1♂
			orbignyi	1♂
			panamensis	1♂
			pseudoicarus	1♂
			sp.	1♂
			sublaeve	1♂
		(Parahyboma)	*furcatum*	1♂
			granulosum	1♂
		(Rubrohyboma)	*rubripenne*	1♂
			sp. (barbipes group)	1♂
	Dicranocara		*deschodti*	2♂, 1♀
	Diorygopyx		*incomptus*	2♂
			tibialis	1♂
	Dwesasilvasedis		*medinae*	1♂
	Epilissus		*prasinus*	1♂
	Epirinus		*aeneus*	3♂, 1♀
			aquilus	2♂, 3♀
			asper	1♂,1♀
			bentoi	1♂, 1♀
			comosus	1♂, 1♀
			convexus	2♂, 4♀
			davisi	1♀
			drakomontanus	1♂, 1♀
			flagellatus	2♂, 2♀
			granulatus	1♂, 1♀
			gratus	1♂, 3♀
			hilaris	3♂, 3♀
			hluhluwensis	2♂, 4♀
			minimus	1♂, 1♀
			montanus	1♂
			mucrodentatus	2♂, 1♀
			ngomae	3♂, 2♀
			obtusus	1♂, 1♀
			pseudorugosus	2♂, 1♀
			punctatus	1♂, 2♀

			pygidialus	1♂,1♀
			relictus	3♂, 1♀
			rugosus	1♂
			scrobiculatus	1♂, 1♀
			sebastiani	2♂, 3♀
			silvestres	3♂, 1♀
			striatus	1♂, 1♀
			sulcipennis	1♂, 1♀
			validus	3♂, 1♀
	Eudinopus		*dytiscoides*	1♂, 1♀
	Gyronotus		*carinatus*	3♂, 1♀
			fimetarius	3♂
			mulangensis	1♂
			pumilus	3♂, 1♀
	Hammondantus		*psammophilus*	1♂
	Hansreia		*affinis*	1♂
	Ignambia		*fascicullata*	1♂
	Janssensantus		*pauliani*	1♂, 1♀
	Lepanus		*ustulatus*	2♂
			villosus	1♂
	Malagoniella		*astyanax*	2♂
			magnifica	2♂
			villosa	1♂
	Megathopa		*bicolor*	1♂, 1♀
			punctatostriata	1♂
	Megathoposoma		*candezei*	1♂
	Melanocanthon		*bispinatus*	2♂
			nigricornis	1♀
	Mentophilus		*hollandiae*	1♂, 1♀
	Monoplistes		*curvipes*	1♂
			leai	1♂, 1♀
	Namakwanus		*irishi*	1♂
			sp.	2♂
	Nanos		*clypeatus*	1♂
			sp.	1♂
	Odontoloma		*endroedyi*	1♂, 1♀
			peckorum	1♂
			pygidiale	2♂
	Onthobium		*cooki*	1♂
	Outenikwanus		*sp.*	1♂, 1♀
	Panelus		*parvulus*	1♂

	Paracanthon		*pereirai*	1♀
			sp.	1♀
			sp-01	1♂
			sp-02	1♂
			sp-03	1♀
			trichonotulus	1♂
	Pararacanthon		*sp-04*	1♀
	Paronthobium		*simples*	1♀
	Pseudocanthon		*iuanaloi*	1♂
			perplexus	2♂,1♀
	Pycnopanelus		*kirkkeni*	3♀
	Saphobiamorpha		*sp.*	1♂
	Saphobius		*sp.*	1♂
	Scatonomus		*fasciculatus*	1♂
	Scybalocanthon		*aff. imitans*	1♂
			aff. kelleri	1♂
			aff. nigriceps	1♂
			aff. pygidialis	1♂
			arcabuquensis	1♂
			darlingtoni	1♂
			maculatus	1♂
			moniliatus	1♂
			pygidialis	1♂
			sexpilotus	1♀
			trimaculatus	1♂
	Scybalophagus		*cf. rugosus*	1♂
			plicatipennis	1♂, 1♀
			rugosus	3♂
			sp.	1♂
	Streblopus		*opatoides*	1♂
	Sylvicanthon		*bridarollii*	1♂
			forviventre	1♂
	Temnoplectron		*bornemisszai*	1♀
				1♂
			politulum	2♂
			reyi	1♂
	Tesserodon		*novaehollandiae*	1♂
	Tetraechma		*tarsalis*	2♂, 1♀
	Vulcanocanthon		*seminulum*	1♂
	Zonocopris		*sp.*	1♂
SCARABAEINAE	*Anomiopsoides*		*carifrons*	1♂

EUCRANIINI				
			heteroclyta	1♂
	Ennerabdulus		*lobocephalus*	1♂
	Eucranium		*sp.*	1♂
SCARABAEINAE GYMNOPLEURINI	*Garreta*		*nitens*	1♂
			unicolor	1♂
	Gymnopleurus		*flagellatus*	1♂
SCARABAEINAE ONITICELLINI	*Eurysternus*		*caribaeus*	1♂
			cyanescens	1♂
SCARABAEINAE ONITINI	*Onitis*		*sp1*	1♂
SCARABAEINAE ONTHOPHAGINI	*Caccobius*		*near megaporenae*	2♂, 1♀
			sp.	1♂,
	Digitonthophagus		*gazella*	1♂
	Onthophagus		*curvicornis*	1♂
			miriabilis	1♂
			paloma	1♂, 1♀
	Proagoderus		*brucei*	1♂
SCARABAEINAE SCARABAEINI	*Mnematidium*		*multidentatum*	1♂
			ritchei	1♂
			silenus	1♂
	Pachylomerus		*femoralis*	1♂,1♀
	Pachysoma		*bennigseni*	1♂
			denticolle	1♂
			gariepinum	2♂
			hippocrates	2♂
			rodriguesi	1♂
			striatum	1♂
	Scarabaeolus		*bohemani*	1♂
			flavicornis	1♂
			rubripenis	2♂
	Scarabaeus		*(gr) caniculatus*	1♂
			canaliculatus	1♂
			galenus	1♂
			goryi	1♂
			lamark	1♂
			nigroaeneus	3♂
			proximus	2♂

			rugosus	1♂
			rusticus	1♂
			satyrus	1♂
			westwoodi	1♂
			zambesianus	2♂, 1♀
	Scarrabaeus		*subaeneus*	1♂
	Sceliages		*adamastor*	1♂
			hippias	1♂
SISYPHINI	*Sisyphus*		*schaefferi*	1♂
	Sysiphus		*sp.*	1♂

Appendix 2. List of morphological characters used for the phylogenetic analysis one.

0. Clypeus: wrinkled = 0, punctuate = 1, granulate = 2, smooth = 3.

1. Number of clypeal teeth: none = 0, two poorly developed = 1, two well developed = 2, four with the two external poorly developed = 3, four well developed = 4, five teeth = 5.

2. Clypeal teeth ventral: no U shaped and without setae = 0, U shaped covered by setae = 1.

3. Clypeus ventrally: without a longitudinally aligned ridge, transverse ridge or tooth = 0, with a distinctive tooth = 1, with a longitudinally ridge = 2, transverse ridge = 3.

4. Gena lateral edge: entire = 0, with a notch = 1, completely divided = 2.

5. Eye in dorsal view: without a canthus over the surface of the head, eye seen laterally = 0, with defined canthus open posteriorly = 1, with canthus closed posteriorly = 2, eyes not seen dorsally = 3.

6. Eye canthus: not dividing eye into upper and lower halves = 0, dividing the eye = 1.

7. Eye: opistoma straight longitudinal = 0, opistoma transversal = 1, opistoma oblique = 2.

8. Eye dorsally: without any carina or surrounded by a wide band = 0, surrounded by a defined band = 1, surrounded by a strong carina = 2.

9. Eye dorsally: open widely = 0, narrow but the same opening anteriorly and posteriorly = 1, wide anteriorly and narrow posteriorly = 2, narrow almost closed posteriorly = 3.

10. Eye position in relation with the head posterior border: forming an angle of 90 degrees = 0, forming angle smaller than 90 degrees = 1.

11. Gula: with a tick line of setae = 0, with a triangular area covered with setae = 1, with a distinct fine band of fine setae = 2.

12. Gula proximal margin: with setae along the anterior border, abundant at the extremes = 0, with setae along the anterior border and in the extremes = 1, with a few setae at the extremes = 2, without setae = 3.

13. Epipharynx: without an anterior sclerotized plate = 0, with a well sclerotized plate = 1.

14. Anterior border excluding the process if projecting: slightly pointed = 0, narrowly indented at the middle = 1, broadly indented at the middle = 2, approximately truncate = 3, broadly rounded = 4.

15. Process of the epipharynx: reduced to a small apical process = 0, present running longitudinally until suture transverse = 1, running longitudinally passing the suture transverse,

but no reaching = 2, running longitudinally and reaching the anterior border = 3, running longitudinally and passing the anterior border = 4.

16. Process of the epipharynx apically in ventral view: solid and tapered towards the apex = 0, formed by two bars joined at the apex = 1, bell-shaped = 2, lance-shaped = 3

17. Process of the epipharynx posteriorly: solid and fused to the tormae = 0, with an opened area in the middle = 1.

18. Process of the epipharynx at the level of the transverse suture: oblique = 0, parallel = 1.

19. Apex of anterior dorsal process of the epipharynx associated with: coarse setae = 0, relatively fine setae = 1, not setae = 2.

20. Process of the epipharynx posteriorly: solid without setae = 0, forming and arch with setae = 1, forming an arch without setae = 2, diamond area = 3.

21. Lateral combs: double row, both formed by a single row of setae = 0, double row, the external formed by a band of setae = 1, double row the internal one covering just the anterior part = 2, single row running in the anterior part = 3.

22. Lateral combs: not fused = 0, fused anteriorly of the suture transverse = 1, fused at the suture transverse = 2, fused posteriorly the suture transverse = 3, fused all = 4.

23. Cavity on dorsal side of the proximal: present = 0, absent = 1.

24. Cavity of the proximal epipharynx: not reaching the suture transverse = 0, reaching the suture transverse = 1.

25. Cavity: reduced = 0, ample = 1.

26. Tormal arm: reduced = 0, present as a short projection and covered by a fine layer of setae = 1.

27. Mentum anterior border: shallow depressed = 0, entire = 1, divided = 2.

28. Shape of the first labial palpomere: quadrangular = 0, cylindrical = 1, triangular = 2, trapezoidal = 3.

29. Shape of the second palpomere: quadrangular = 0, cylindrical = 1, lamellated = 2, triangular = 3, rounded = 4.

30. Second palpomere: smaller than the first one = 0, larger = 1.

31. Third palpomere: larger than the second = 0, smaller than the second = 1, reduced = 2.

32. Mentum anterior in relation with the lateral edge: concave = 0, distinctly notched to slightly concave = 1, forming a straight angle < 90 degrees = 2, forming an angle > 90 degrees = 3.

33. Mentum: length about equal to width = 0, transverse = 1.

34. Mentum: without setae = 0, with a few setae = 1, with abundant long setae = 2.

35. Paraglossal lobes: without rounded scales = 0, with rounded scales in the external border = 1.

36. Mentum: without a depression on the middle = 0, with a longitudinal depression in the middle = 1, with a triangular-shaped depression = 2, with a round-shaped depression = 3.

37. Comb of the molar lobe: absent = 0, with a few tick projections = 1, with projections thinner than in state 1, and thicker than the fine hairs = 2, with very fine hairs = 3.

38. Distal comb: absent = 0, reduced a small portion = 1, developed = 2.

39. Proepimeron: no excavated = 0, excavated = 1.

40. Proepisternal keel: absent = 0, incomplete = 1, complete = 2.

41. Proepeisternal keel in the external border: straight = 0, curved = 1.

42. Anterior border of the basisternum: without a notch = 0, with a notch = 1.

43. Longitudinal keel of proepisternum: absent = 0, present = 1.

44. Mesosternum anterior border carena: absent = 0, present as defined band = 1, present as a slender carena = 2, present as a raised carena = 3.

45. Mesosternun anterior transverse sulcus: absent = 0, well developed deep and wide = 1, deep but not wide = 2, well developed, and broaden laterally = 3, a very fine sulcus = 4, just indicated but not deep = 5.

46. Mesosternun anterior transverse sulcus: not interrupted in the middle = 0, interrupted by a half part of its extension = 1, interrupted by a band = 2, interrupted by a very fine line = 3, interrupted with a longitudinal sulcus = 4 interrupted by a triangular solid area = 5, interrupted partially = 6.

47. Mesosternum in the middle: larger than laterally = 0, narrower than laterally = 1, similar length than laterally = 2.

48. Mesosternum band of setae: absent = 0, a band of uniform setae normal size running transversally = 1, a band of very long setae = 2.

49. Mesosternum posterior border: as a simple suture = 0, a deep sulcus = 1, a broad suture = 2.

50. Mesosternum region posterior to the anterior carena in the middle: larger than the anterior region = 0, the same length = 1, reduced = 2.

51. Mesosternun posterior band of setae: absent = 0, present as defined band of contiguous seta = 1, present as a defined of very long setae = 2, scattered setae laterally = 3, a row of setae laterally = 4.

52. Meso-metasternal suture: straight or slightly curved = 0, forming a strong arc = 1, straight in the middle, but forming 90 degrees angles laterally = 2, sinuated = 3.

53. Middle coxae: totally located in metasternum = 0, more than 50 % of coxae in the mesosternum = 1, less than 50% of coxae in the mesosternum = 2.

54. Coxae orientation: parallel = 0, slightly oblique 25 degrees = 1, strongly oblique 45 degrees = 2.

55. Middle coxae separation posteriorly: much less the distance half of the coxae = 0, nearly as half of the coxae = 1, larger than half of the coxae = 2, as larger as the length of the coxae = 3, larger than the length of the coxae = 4.

56. Metathorax area: without tubercles, or raised area = 0, with a defined protuberance = 1, with one raised area = 2, with two raised areas = 3.

57. Metathorax longitudinal line: present = 0, absent = 1.

58. Thorax fovea lateral: absent = 0, present as rounded puncture = 1, present as clump of punctures = 2.

59. Thorax surface: without tubercles or carenas = 0, tubercles = 1.

60. Thorax portion lateral of pronotum: without depressions = 0, with depressions = 1.

61. Thorax sculpture: with small rounded punctures = 0, with large rounded punctures = 1, with minute punctures wide separated = 2, with punctures associated with a setae = 3, smooth = 4, with small granules = 5.

62. Number of teeth on fore tibia: two = 0, three = 1, four = 2.

63. Micro teeth in anterior tibiae between second and third teeth: absent = 0, more than one micro teeth present = 1.

64. Apex of the tibiae: not enlarged = 0, enlarged towards the internal border = 1.

65. Trochanter-femoral pit: absent = 0, present = 1.

66. Membranous wings: present, full developed = 0, present but not functional = 1, vestigial = 2, absent = 3.

67. Costal setae: absent in basal plate = 0, present in basal plate = 1.

68. Setae along of the costal margin: reduced just few small setae = 0, moderate amount, from costal vein to half distance towards base = 1, large amount of joined setae extending over the costae = 2.

69. Setae along the margin costae: present passing the fold = 0, not passing the fold = 1.

70. Radial vein at its base: without row of setae = 0, with setae = 1.

71. Costal margin: with internal visible channels = 0, without visible channels = 1.

72. Shape of cell: as a triangular shaped plate = 0, reduced a very thin plate = 1, absent = 2.

73. R1 and R2: free, not fused to C = 0, fused to C = 1.

74. R1 and R2: distinctly visible as two separated parallel veins = 0, distinctly visible as two separated veins but not parallel veins = 1, visible as "single" vein formed by two veins juxtaposed = 2.

75. Margin of the wing in anal region: with a notch = 0, without notch = 1.

76. Veins 3A and 2A: not forming a cell = 0, forming a cell = 1.

77. Posterior margin in the anal area: without a row of small spines = 0, with spines = 1.

78. Jugal vein 1: absent = 0, present = 1, fused to J2 = 2.

79. Jugal vein 2: absent = 0, present = 1, forming a cell = 2.

80. Jugal vein 3: absent = 0, present = 1, fused to anal vein = 2.

81. Tibiae: completely triangular without longitudinal margins in dorsal face = 0, triangular but with longitudinal margins in dorsal face = 1 rectangular at the base, but enlarged apically = 2, rectangular, not enlarged apically = 3.

82. Tibiae: with transversal carenas with setae = 0, with one carena with setae = 1, without transversal carena with setae = 2.

83. Tibiae with longitudinal carenas with setae: without longitudinal margins with setae = 0, with row of setae, but without defined margin = 1, with longitudinal margins with setae running just half of the tibiae = 2, with longitudinal margins with setae running along the whole tibiae = 3, with margin and just a few clumps of setae, but no row of setae = 4.

84. Posterior femur: distal part not enlarged = 0, distal part enlarged = 1.

85. Posterior tibiae: completely triangular, tubular = 0, triangular, but with longitudinal margins with setae developed = 1, sinuated = 2, slender at the base and enlarged apically = 3, the whole tibiae slender not enlarged apically = 4.

86. Region media of the tibiae: without a small transversal carena with setae = 0, with a small transversal carena with setae = 1, with a full developed transversal carenas = 2.

87. Tibiae: without longitudinal margins with setae = 0, with longitudinal margins but the external covering just half of the = 1, with longitudinal margins covering the complete tibiae = 2, with longitudinal margins interrupted by clumps of setae = 3.

88. Tibial spur: two = 0, one = 1.

89. Internal face of the tibiae: not flat = 0, flat = 1.

90. Distal tibiae: without lateral projection = 0, with lateral projection = 1.

93. Anterior margin: straight = 0, slightly depressed = 1, slightly convex = 2.

94. Anterior process: absent = 0, small conical process = 1, medium size = 2, larger = 3.

95. Transverse intrascutal suture: absent = 0, present = 1.

96. Transverse intrascutal suture: Without lateral process = 0, with a coma-shaped lateral process = 1.

97. Prescutum: without longitudinal suture = 0, with longitudinal suture just in the anterior half = 1, with longitudinal suture covering the whole prescutum = 2.

98. Prescutum ventral ridge: absent = 0, developed = 1.

99. Prescutum central depression: longitudinal, with parallel sides, open posteriorly = 0, pear-shaped more or less rounded but the posterior margin open = 1, wider anteriorly forming a triangular area = 2.

100. Prescutum depression: without setae = 0, with setae = 1.

101. Prescutum depression: with a longitudinal central suture = 0, without central suture = 1.

102. Shape: elongated, rectangular more than twice longer than wider = 0, more quadrangular, not more than twice longer = 1.

103. Anterior area of the elytra: seen dorsally, in a transversal plane = 0, not seen dorsally in a perpendicular plane = 1.

104. Posterior edge of the elytra: without keels = 0, with keels = 1.

105. External border of the elytra: with a row of setae = 0, without a row of setae = 1.

106. Number of elytral striae: nine = 0, eight = 1, ten = 2.

107. Pseudoepipleura: absent = 0, out seventh striae = 1, out eighth striae = 2, out ninth striae = 3, out tenth striae = 4.

108. Epipleura: without setae on the carena = 0, with a raised carena with setae = 1.

109. Epipleura: reduced = 0, as a thin band = 1, a wide band = 2.

110. Humeral striae: not carinated = 0, carinated = 1.

111. Humeral area: not tuberculated = 0, tuberculated = 1.

112. Metatarsal claws tooth: absent = 0, with small basal teeth = 1, with a well developed teeth = 2.

113. Scutellum dorsally: visible = 0, not visible = 1.

115. Antero- groove: absent = 0, faintly visible = 1, present with complete lateral edges throughout = 2.

116. Antero- groove: V shaped = 0, nearly parallel sided = 1, distinctly parallel sided = 2.

117. prepygidium: reduced to a thin band = 0, a wide band = 1, a wide band with basal sulcus = 2.

118. Transverse ridge: absent = 0, slightly pronounced = 1, pronounced = 2.

119. Posterior margin of the prepygidium: straight = 0, with anterior projection = 1.

120. Dorsal surface of the pygidium: flat without depression in the middle = 0, with transversal depression = 1, with basal depression = 2, with a shallow depression = 3.

121. Prepygidium: not forming a straight angle with the pygidium = 0, forming a straight angle with the pygidium = 1.

122. Sternites: not constraint in the middle = 0, constraint in the middle = 1.

123. First ventrite: reduced a thin line in the middle = 0, distinctly visible and widen in the middle = 1, occupying a large part of the sternites = 2.

124. Genital segment; lateral border: with sclerotized arms oblique and fused posteriorly = 0, with sclerotized arms oblique toward inside but not fused = 1, with sclerotized arms nearly parallel = 2, with sclerotized arms oblique toward outside = 3, with sclerotized arms parallel anteriorly and oblique posteriorly = 4, without sclerotized arms = 5.

125. Genital segment; lateral borders: fused medially with an elongated tip = 0, fused medially without the elongated tip = 1, not fused medially = 2.

126. Genital segment; ventral plate: as a triangular-shaped central darkened area = 0, as a heart-shaped darkened area = 1, as a rectangular area = 2, with two separated triangular areas = 3, two triangular areas joined and anteriorly = 4, a large well-chitinized plate with two long filaments = 5.

127. Parameres: shorter than the lobule = 0, larger than the lobule = 1, reduced = 2.

128. Parameres: symmetrical = 0, asymmetrical left paramere larger = 1, asymmetrical with left paramere forming an expanded plate = 2, asymmetrical with right paramere larger = 3.

129. Parameres with respect of the basal piece: not angulated = 0, forming an angle larger than 90 degrees = 1, forming an angle of 90 degrees = 2.

130. Parameres: with a row of setae in the internal border = 0, without setae = 1.

131. Parameres lateral view: distinctly tapered to a point = 0, narrower posteriorly but not ending as a point = 1, blunt or truncate = 2, divided in the middle forming two projections = 3.

132. Internal sac: as tubular bag, without deformations = 0, with a lateral projection in the part = 1.

133. Internal sac: not fully developed, no basal area = 0, full developed with all areas developed = 1.

134. Apical area of the internal sac: with a sclerotized structure attached to a membranous part = 0, one big plate with elongated projection fused in the middle = 1, sclerites elongated and plate fused = 2, sclerites well formed basal, plate, and elongated = 3, sclerites present but reduced = 4.

135. Apical area of the internal sac; basal sclerite: absent = 0, well formed circular shaped = 1, circular shaped reduced = 2, curved without ring = 3.

136. Apical area of the internal sac; basal sclerite: without process = 0, with process moderate size = 1, with process as a long projection = 2.

137. Basal circular sclerite projection (handle) insertion to the ring: enclose most of the ring = 0, enclose partially the ring and forming a 90 degrees angle = 1, enclose partially the ring forming a wider than 90 degrees angle = 2, not enclosing the ring = 3.

138. Basal circular sclerite projection (handle): slender = 0, expanded distally = 1.

139. Basal circular sclerite projection (handle): short = 0, elongated = 1.

140. Apical area, basal sclerite circular: without a developed apical process = 0, with a triangular-shaped process = 1, with an irregular-shaped process = 2.

141. Apical area, basal circular sclerite: tick ring = 0, slender ring = 1.

142. Apical area covered by scales inside of the internal sac: present as two large square apical areas = 0, present as a small oval or rounded area = 1, absent = 2.

143. Apical area: without sclerotized structures = 0, with a sclerotized sclerite = 1 with two sclerites = 2.

144. Sclerite on top of the internal sac of the aedeagus: absent = 0, present = 1.

145. Basal circular sclerite: absent = 0, Type A = 1, Type B = 2, Type C = 3, Type D = 4, Type E = 5, Type F = 6, Type G = 7, Type H = 8.

146. Basal circular sclerite Type B: with prominent handle process = 0, with small handle process = 1.

147. Elongated sclerite: absent = 0, fused to a plate = 1 without filament = 2, with short filaments = 3, with long filaments at the end = 4, with a very long filament rolled up = 5.

148. Plate of the internal sac with basal projections forming a comb: absent = 0, present = 1.

149. Half-moon sclerite: absent = 0, present = 1.

150. Plate sclerite: absent = 0, with undulated borders = 1, with the superior extreme tapered and curved = 2, elongated shaped and joined to the elongated sclerite = 3, elongated shaped and fused to the elongated sclerite = 4, more or less quadrangular, and concave = 5, rectangular shaped = 6, C-shaped = 7.

151. Raspules: as two defined lateral structures = 0, present as many different irregular shaped structures = 1, one round or oval raspule = 2, one v-shaped upside-down = 3, 2 raspules = 4, a quitinous base with seven elongated filaments = 5, absent = 6.

Appendix 3. Matrix used for phylogenetic analysis one.

Ataenius

000000000000000000--0-0000000000000001000000-0000-000000010-00000100000-10000000000
1000000000000011000000000000000000000-0000000000000000000------0000-00000

Aphodius

000000000000000010000000000001000001000100-0000-000000000-00000100000-10000000000
1000000000000011000011000000000000000-0000000000000000000------0000-000—

Circellium

000002110000000130010112001013101301003200-00322210100211-0000210003-------------
10404131001----------11010100000112210000101251211101211211102002040042

Deltochilum (Euhyboma)

11000102100100342010112001023401102003200-10102110201213-00011110000201011101
02222230402 100011310112111110201110112010100124241011111310201002203-30026

Deltochilum (Calhyboma)

11000102100110342010112001023401102003202110252110201213-100111100002010111010
22222304021000113101121111110201110112010100114240011111310201002201-30026

Scybalophagus

2303010213100033301111300102340111201320000113122220213 101005100000200001101
0222002012 11000103101021111010201110110-10100103241021011310211002001-20022

Byrrhidium

0211210213123101011201400110210110110111210021301000001301100100003-------------
222020111010000----0111012402000111-0000010003131100010------2010-11001

Namakwanus

0211010213123101011201400110210110110111210021301000001301100210003-------------
222020111010000----0111012402000111-0000010003102000010------2010-11001

Dicranocara

1200010213123101001201400110210110110111210021301000001201100200003-------------
22202011101??????-???11012402000111-0000010003101000010------2010-11000

Canthonella

3102010200023033110133010003112000032121010240100002020100041100010001101010000
12313021100100101001011011101002112010000100103001-0140------2000-----6

Agamopus

110201020101201301013141—0111012010032121010200100002020100021100010001101
1110110123010211 0002110001111101120100011211102010011000110130------2100-20076

Canthochilum

341001020202303311013101-000311200002212100024010001102010004110001000111
0101000012313021100102100011111011101000112110000105-23001-01310000002000-30056

Odontoloma

150001022312200201013001—0020122010032121000240100011120100011000010001
011110000012101021 1 00002100000011111201110112221010100010001201 30------2000-20026

Epirinus

01101102111000333010 12-001003001002003212000112212103213010001100001100001101
1011211401021000121102011111011-01010111-10000111241111101310001002017-40026

Anachalcos

110001020001002430111130010234011020032120102121100032130110021000002010212010111
21230402100010110102111010101000112210000101251111111330-----2002140046

Gyronotus

100001020001003430101130010031011010032 00-10232010000112010011100 03--------------
1230402100100210002011101010100011221000010125121100133 0-----2002030026

Eudinopus

220001022111003333010113001023201102003202000335122223212311005210000200021201011
2314041210001031021211111103010101 10-1100010322101110131020110200 1-30026

Megathoposoma

211002120110003333010112001023201102003200100351102422122110001100012010011010222
12204021000113101121111010201010112010100102251011111310211001001-20026

Malagoniella

03121102001010333010211001023201112003201-1021511121222101100411000120001110
1000232404031000103101021111010001100112010100102240001011311211001002120016

Megathopa

031311020010103330102110010232011120032 01-
10315110211221011002110001100011111000232 4
04031000103101021111010001100112010100102240011001311211001002120014

Canthonidia

02100102021220343011113000020100112002200-0021221000021301100311000010001 1111
01121230403100010310102111101000100011 0-10-0011424102120131021000 2001-20066

Tetraechma

141011021112203430111130010231001120022 00-
00212210000213211003110000100111110000012 304031 000102101021111010001000110-10-
00112-310111013102100 02001-30026

Hansreia

11121102111120423001113001003401202023201-
103112102002130110041100001001002100 0003
23040210001231110211110102010101120101001042210212013103100 12001-30023

Anisocanthon

111011020111302430111130010231011120132121002152101002130110131100001001011110000
32304021000111100021111110401010110-10-001042410211013103100 12001-30066

Scybalocanthon

311001020212303430111130000231011120132 00-
0004211000020301000411000010011111100023 23 0402100010210102111010401000110-
1010010424111121131031000 2001-20026

Sylvicanthon

3100110200123033301111300102310111201321210021521020000301000411000019100121 1000
01230402100010311102111101040100011201010010123102120131121 1111001-20162

Melanocanthon

23111102211120333011111001023201112003210-00225210103223210005110000200011101
000032304021000102101021111010301010110-10000104241021111311211102001-30061

Canthon (Francmonrosia)

23101102120130343010112001023101102013200-
00225210100213011004110000200111101000211 30102110010310212111101040101011 0-
1010010424102130131121110 2001-30025

Canthon (Glaphyrocanthon)

331201021312303430111120010231011020132121002152101002030110041100001001112 11000
2123010210001021000211110104010001 10-1010010424101120131021120 2001-20021

Sinapisoma

0100011201010000014000100130 0-----2000-200540201100411010100012000000001130
102100010211102 11110111010001120101000001400010 01300-----2000-20054

Lepanus

01001112011130101201111101320300002004-3002402010004110001000010001000010304
021000102 110011111011001001112011130101201111101320300002004-30024

Mentophilus

12110112112101101211111001320001001001-30104010110131000 1-------------00401021001--
00---10111010112110112112101101211111001320001001001-30104

Aptenocanthon

1102010200023042010132-000001101101003212100---------- 0--1000211013-------------
12301021101002100010111012101000112210100101221221001320---002004-20026

Diorygopyx

3202110200023023010132-0100011011020032121010140100002 1101000211101-------------
12311021101011102010111010301002112012100100011321001320---002004-30024

Temnoplectron

3202110200023023111132-0100003011020032121002140100001020100041100011011000110111
32314021010102100011111010301002112010100102-10011101320---002006-40054

Monoplistes

1202110202112023010132-
01000110110200321210021401000011201000311100100010000101111230
40210101021100111110103 01001112012100102-11001001320---002004-40044

Boletoscapter

1202010211113023111112-0110001011010032121000140100000020111031101010000000
11000012301021000001110011111012101000112111121100040021001320---002005-30011

Aphengoecus

1400200221121004010022-0000011010010032121000100100002 1400200221121004010022-
000001101001003212100010010000202000112110000105-11111001320---002004-20034

Canthonosoma

1211010210113033310002-010011101202003200-1003401000021201011310002-------------
32304021001111100021111010102000112010100102-10021001310300002000-30034

Cephalodesmius

1211021200113033310002-010011101202003200-0003401000021201001310002-------------
32304021001111100021111010102000112010100102-10011001310300002000-30034

Bohepilissus

1200010201121034301133-00000230110000321210002400000021201000011003-------------
123140210010--10--10111011002002112010100101-20001001320---002005-30004

Panelus

32000102021210241100032-010000112100003212100014010001202010001110001001110001
00002030402100010110001111010101001112010100105-10301101320---002000-20004

Demarziella

130211020302302430111100000023122010032121010540110011020020041101010001101100111
12100201100102100011111112101012112111000101110111001310310002008-30002

Tesserodon

1212010212123023111132-010001101001003212100010112000202010013110101000000110
1111030402100010210001111101210101011201200010???1111301320---001000-00004

Onthobium

1212010202022023001112100000110120100321210001011200021201000311113-------------
122010210010100---00111012100001112010131101201121101320---002004-20026

Saphobiamorpha

1102010202111032001132-00000110110100321210001401000121001101311113-------------
12303021001010100020101012112000112010100105-11121311320001002002120044

Zonocopris

1202010200011002501221401100000200100321210002201000020201101310010100002001100
0012301021100111100010111012101000112111000101210011001320---002008-30004

Cryptocanthon

110213020-02303311013101--00010220000221210001400000111401001311013-------------
123030211010000----0111012102012112010000100000011101310000002103-30120

Paracanthon

010110031101010010101110000000030211000021100201110122010110031101010010101110000
00003021100002110020111012202010112010100100011021101322001002103-50014

Nanos

311201020002102300011210010110011010032121000160110001120110010010010000101011111
123040210001011010211110113020001120101001000011200013?0001002001-50024

Arachnodes

1201100211100100001010111111240403100010110102111101131201100211100100001010111111
2404031000101101021111011301000112010130101201011211330-----2004-30016

Appendix 4. List of morphological characters used for the phylogenetic analysis two.

0. Clypeus dorsally: wrinkled = 0, punctuated = 1, smooth = 2.

1. Dorsal clypeal teeth number: none = 0, two poorly developed = 1, two well developed = 2, four with the two external poorly developed = 3, four well developed = 4.

2. Space between the teeth: the same or less than the wide of the base of one teeth = 0, wider than the length of the base of the teeth = 1.

3. Space between the teeth: forming a U = 0, forming a V = 1, broadly opened = 2.

4. Clypeus ventral, longitudinal carena: absent = 0, present = 1.

5. Clypeus ventrally: without a longitudinally aligned ridge, transverse ridge or tooth = 0, with a distinctive tooth = 1, with a longitudinal ridge = 2, transverse ridge = 3.

6. Clypeal teeth ventral: no U shaped and without setae = 0, U shaped covered by setae = 1.

7. Anterior cephalic border: with setae = 0, glabrous = 1.

8. Anterior cephalic border: with setae on a keel = 0, with setae no on a keel = 1, without setae = 2.

9. Anterior border of the clypeus with keel with setae: running along the clypeus = 0, just at the base of the teeth = 1.

10. Gena lateral edge: entire = 0, with notch = 1, completely divided = 2.

11. Opistoma: transversal = 0, oblique = 1.

12. Internal border of canthus posteriorly: triangular shaped = 0, parallel = 1.

13. Eye dorsal: narrow almost closed posteriorly = 0, narrow but the same opening anteriorly and posteriorly = 1, wide anteriorly and narrow posteriorly = 2, open widely = 3.

14. Internal margin of the eye: forming an angle larger of 90 degrees = 0, forming an angle smaller of 90 degrees = 1, forming an angle of 90 degrees = 2.

15. Eye dorsally: without any carina or surrounded by a wide band = 0, surrounded by a band = 1, surrounded by a carena = 2.

16. Gula: with a triangular area covered with setae = 1, with a distinct fine band of fine setae = 2, with a tick line of setae = 3, with a line of setae with a small projection in the middle = 4.

17. Gula proximal margin: with setae along anterior border and abundant at the extremes = 0, with setae along anterior border and in the extremes = 1, a few setae at the extremes = 2, without setae = 3.

18. Anterior border of the epipharynx: not continuous = 0, continuous = 1.

19. Anterior border of the epipharynx excluding the process if projecting: broadly convex = 0, narrowly concave in the middle = 1, broadly concave in the middle = 2, straight = 3.

20. Apex of anterior dorsal process of the epipharynx associated with: coarse setae = 0, relatively fine setae = 1, not setae = 2.

21. Process of the epipharynx ventral view: solid and tapered towards the apex = 0, forming by two bars joined at the apex = 1, bell shaped = 2 lanced shaped = 3.

22. Process of the epipharynx posteriorly: solid and fused to the tormae = 0, with an opened area in the middle = 1.

23. Process of the epipharynx: running longitudinally passing the suture transverse but not reaching = 2, running longitudinally and reaching the anterior border = 3, running longitudinally and passing the anterior border = 4.

24. Process of the epipharynx: no reaching the anterior border = 0, reaching the anterior border = 1.

25. Process of the epipharynx: surpassing the anterior border = 0, not surpassing the anterior border = 1.

26. Process of the epipharynx: with a chitinous overgrow = 0, without a chitinous overgrow = 1.

27. Posterior end of the process: solid = 0, divided = 1.

28. Hairs of the anterior border of the epipharynx: shorter = 0, longer = 1.

29. Internal lateral comb of the epipharynx: surpassing the suture transverse = 1, up to anterior border = 2.

30. Process posteriorly: solid without setae = 0, forming an arch with setae = 1, forming and arch without setae = 2, forming a diamond area = 3.

31. Lateral combs of the epipharynx: fused = 0, not fused = 1.

32. Lateral combs of the epipharynx: fused completely = 0, fused anteriorly = 1, fused at the transverse suture = 2, fused posteriorly = 3, not fused = 4.

33. Cavities of the epipharynx: reduced = 0, ample = 1.

34. Paraglossal strut at proximal apex: bifurcate = 0, no bifurcate = 1.

35. Mentum apical edge marginally: shallow depressed = 0, narrow U-shaped = 1, Wide U-shaped = 2, straight = 3, divided = 4.

36. Mentum apical margin near the lateral edge: rounded = 0, distinctively notched to slightly concave = 1, forming a straight angle = 2, with a concave depression = 3.

37. Mentum: length about equal to wide = 0, transverse = 1.

38. Mentum: without a depression on the middle = 0, with a long longitudinally depression in the middle = 1, with a triangular-shaped depression = 2.

39. Shape of the first palpomere labial: quadrangular = 0, cylindrical = 1, triangular = 2, trapezoidal = 3.

40. First palpomere attached to the labium: without stalk = 0, with stalk = 1.

41. Shape of the second palpomere: quadrangular = 0, cilindrical = 1, lamellate = 2, triangular = 3, rounded = 4.

42. Third palpomere: large than the second = 0, smaller than the second = 1, reduced = 2.

43. Comb of the molar lobe: with tick hair = 0, with very fine hair = 1.

44. Proepimeron: no excavated = 0, excavated = 1.

45. Proepisternal suture: absent = 0, incomplete = 1, complete = 2.

46. Anterior border of the basisternum: without notch = 0, with notch = 1.

47. Proepimeron: oblique = 0, horizontal = 1.

48. proepisternal keel: complete = 0, incomplete = 1, insinuated = 2.

49. Posterior area of the proepisterno: with parallel keel = 0, without keel = 1.

50. Proepisterno: with setae = 0, glabrous = 1.

51. Proesternum: with row of setae = 0, without row of setae = 1.

52. Row of hair trough: thorax ventral = 0, only proepimero = 1.

53. Cavities mesocoxales: oblique = 0, parallel = 1.

54. Mesosternun: well developed = 0, reduced = 1.

55. Anterior border of the mesosternun: complete = 0, interrupted in the middle = 1.

56. Anterior border of the mesosternun: curved = 0, straight = 1.

57. Anterior part, near to the border of the mesosternun: flat = 0, with a depression = 1.

58. Anterior border of the mesosternun: forming a sharp tip = 0, straight = 1.

59. Male genitalia, genital segment, lateral border: as two sclerotized arms completely oblique = 0, as two sclerotized arms anteriorly parallel and posteriorly oblique = 1, as two sclerotized arms completely parallel = 2, with two parallel arms anteriorly and two oblique posteriorly = 3.

60. Male genitalia, genital segment ventral plate: as a heart-shaped darkened area = 1, as a rectangular area = 2, with two separated triangular areas = 3, two triangular areas joined and anteriorly = 4, a large well-chitinized plate with two long filaments = 5.

61. Male genitalia, parameres of the aedeagus: shorter than the lobule = 1, larger than the lobule = 2.

62. Male genitalia, parameres of the aedeagus: asymmetric = 0, symmetric = 1.

63. Male genitalia, parameres of the aedeagus: symmetrical = 0, asymmetrical left paramere larger = 1, asymmetrical with left paramere forming an expanded plate = 2.

64. Male genitalia, parameres of the aedeagus, posterior border of the parameres: notched = 0, divided = 1, with pointed tip = 2.

65. Male genitalia lobule and parameres of the aedeagus: forming a right angle = 0 not forming a right angle = 1.

66. Male genitalia, parameres of the aedeagus in relation to the lobe: larger = 0, the same length = 1, shorter = 2.

67. Male genitalia internal sac of the aedeagus: as a tubular bag, without deformations = 0, with a lateral projection in the part = 1.

68. Male genitalia sclerite: absent = 0, present indistinctly shaped = 1, present as two elongated bars = 2.

69. Male genitalia scales forming a rounded area apical within internal sac: absent = 0, present = 1.

70. Male genitalia, handle of basal circular sclerite: large = 0, short = 1.

71. Male genitalia, ring of basal circular sclerite: thickened = 0, partially thickened = 1, thinner = 2.

72. Male genitalia, ring of basal circular sclerite: with protuberance = 0, without protuberance = 1.

73. Male genitalia, ring of basal circular sclerite: with deformations in the external border = 0, without deformations in the external border = 1.

74. Male genitalia, ring of basal circular sclerite: not well chitinized = 0, partially chitinized = 1, completely chitinized = 2.

75. Male genitalia, ring of basal circular sclerite: oval shaped = 0, circular shaped = 1, not well defined = 2.

76. Male genitalia, handle of basal circular sclerite: with medial process = 0, without process = 1.

77. Male genitalia, handle of basal circular sclerite: thickened on the base = 0, not thickened on the base = 1.

78. Male genitalia, handle of basal circular sclerite: wide = 0, narrow = 1.

79. Male genitalia, elongated sclerite: with filament = 0, without filament = 1.

80. Male genitalia, elongated sclerite: with short filament = 0 with elongated filament = 1.

81. Male genitalia, plate sclerite: absent = 0, with undulated borders = 1, with the superior extreme tapered and curved = 2, more or less quadrangular, and concave = 3, elongated shaped and fused to the elongated sclerite = 4, rectangular shaped = 5.

82. Male genitalia, accessory sclerite: absent = 0, present = 1.

83. Male genitalia, chitinous structure in the part of the sac: present = 0, absent = 1.

84. Male genitalia, scale area: present = 0, absent = 1.

85. Male genitalia, raspules: present as many different irregular shaped structures = 0, one round or oval raspule = 1, one v-shaped = 2, 2 raspules = 3, forming a band surrounding the sac = 4, absent = 5.

86. Male genitalia, raspules: with elongated hair = 0, with short hair = 1.

87. Teeth of fore tibiae: two = 0, three = 1, four = 2, five = 3.

88. Position of teeth of fore tibiae: proximal = 0, first distal = 1, second distal 2, and third distal = 3.

89. Position of teeth of fore tibiae: lateral = 0, one towards front = 1, all towards front = 2

Appendix 5. Matrix used for phylogenetic analysis two.

Copthorina

020000012-011120110110141101020000131002002102010011-100-0003110212000---------1-
201101001

Anachalcos convexus

111100001?
0113201002130410010210311200031411121101000001000152112101001100000010040115-011

Eudinopus dytiscoides

120100012?
0101101013030310101130311200030211020021000011010122102100000011201000020--5-331

Megathoposoma candezei

1200001???00----101303031010--1-21120003021100102100011100015210210101001120 0--1-
20--5-331

Scybalophagus rugosus

020011000111000210131303010012313102001304110000010000110003421020010 0?20120---1-
20--1-130

Streblopus opatroides

1012031120000320111103041011023101010000041101000010110010121110212001021122---1-
01--0-130

Malagoniella astyanax

0201001001011320111303031111122011103103021101111101011100241102111010100000001-
10115-011

Megathopa punctatostriata

0201001001011320111303031111122011123103021101111100011100241102100010100000001-
101131010

Canthonidia rubromaculata

020100100101121022131304101102113112100011000001-11001110001421021000012012111 01-
20115-001

Anisocanthon villosus

110100100101111043121304111112113112001301111201 0111-010-
0014210110000120110111015 00 15-011

Hansreia affinis

220102100111111121013020-1112103010202314110200110 01111100322100100001211111111-21112-021

Scybalocanthon pygidialis

21010010010112101313130411111210301200030111000 1-111-1110001420111010011011011 01-20115-021

Sylvicanthon bridarolli

220110000101132043131303 0-111210311200130111120001 11-110-010320011000110011111 01-211010020

Melanocanthon bispinatus

0300111000011111121313031111021111121003021110 01-1000010-0114210210100110110000015 0110-000

Tetraechma tarsalis

1401001000211111221313041011021131141003010000 01-1100110-0023210210000120111110 1-21115-000

Canthon (Francmonrosia) tetraodon

030100100011122123130304111112112112001301110001211 1-110-0014210110000010110000 1-21105-011

Canthon (Glaphyrocanthon) luteicollis

2301120001011301231313041111121121120013011102010111-110-00142102100001201101100120100-01100-011

Canthon staigi

210103100111131213130304011112-031120023031102011111-110-0012? 100100001211111101201141011

Canthon quinquemaculatus

230103000111111223130304111112-031120012130102012110 0110-0013? 1011000010112110001200001021

Canthon violaceus

01010??00001131223130304111112-131121001000??201-1100110-00???10210?0012111111 11-21014-011

Canthon tibiale

2101030000011112231????101102-131120020000-020121100111100??? 10110?001101101101-201100011

Canthon indigaceus

011-01000001132223130013111112-13112001000010201-1100110-01???10110?001101200000120104?010

Canthon praticola

030102000001112221131014111102-131120020000?0201-1000010-01???10110?001101100000120114?000

Canthon aberrans

210002100111122223112013111112-031110011000?020111101111000???02000?011101100000120104?011

Deltochilum mexicanum

111002012?010220121210-41000120141112002041-12110111101111104 11021012011012111101-00?5?120

Deltochilum gibbosum

121000001?01132010130204100002-12112000314110011-111-0111001421021012012001000000-0015-021

Deltochilum amazonicum

121000012?011320131302041001012141122012041-0011-11-1000101?421001212012111010000-00???120

Deltochilum orbiculare

111000112?011320120212041101112141112012041-0011-11110101010410001212011112101000-00???100