INSTITUTO DE
ECOLOGIA. A.C.

REVISIÓN TAXONÓMICA Y ANÁLISIS FILOGENÉTICO DE LA TRIBU ATEUCHINI (Coleoptera: Scarabaeidae: Scarabaeinae)

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REVISIÓN TAXONÓMICA Y ANÁLISIS FILOGENÉTICO DE LA TRIBU ATEUCHINI (Coleoptera: Scarabaeidae: Scarabaeinae)

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"... a gente quer passar um rio a nado, e passa; mas vai dar na outra banda é num ponto muito mais embaixo, bem diverso do em que primeiro se pensou. Viver nem não é muito perigoso?"
(Guimarães Rosa: Grande Sertão: Veredas, 1956)

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"Ah, vai vir um tempo, em que não se usa mais matar gente..."
(Guimarães Rosa: Grande Sertão: Veredas, 1956)

RECHAZO PARA FINES DE NOMENCLATURA ZOOLÓGICA

Este trabajo, en su actual presentación (tésis de grado), no debe considerarse como una publicación válida para fines de nomenclatura zoológica. Este es el *disclaim* / *dénégation* mencionado en el Código Internacional de Nomenclatura Zoológica (edición 1999), capítulo tres, artículos 8.2 y 8.3.

A mi familia (presente y ausente), por todo.

DECLARACIÓN

Excepto cuando es explícitamente indicado en el texto, el trabajo de investigación contenido en esta tesis fue efectuado por Fernando Zagury Vaz de Mello como estudiante de la carrera de Doctorado en Ciencias (Sistemática) entre agosto de 2003 y julio del 2007, bajo la supervisión del Dr. Gonzalo Halffter Salas.

Las investigaciones reportadas en esta tèsis no han sido utilizadas anteriormente para obtener otros grados académicos, ni serán utilizadas para tales fines en el futuro.

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RESÚMEN GENERAL

El presente trabajo es un estudio de los Scarabaeinae (Coleoptera: Scarabaeidae) pertenecientes a la tribu Ateuchini. Con base en estudios filogenéticos morfológicos, se delimita la tribu Ateuchini como grupo monofilético y monotético, y se ubican los géneros que quedan fuera de la tribu en otras tribus. Se propone la división de Ateuchini en tres subtribus monofiléticas y monotéticas, una de las cuales es revisada en nivel de género, con la descripción de doce géneros nuevos. Para las otras dos subtribus de Ateuchini, se presentan sinopsis de los géneros en forma de claves, incluyendo a tres géneros nuevos de Ateuchini y un género nuevo de Coprini que incluye especies previamente asignadas a un género de Ateuchini. Se proponen una nueva tribu y cuatro nuevas subtribus que incluyen especies previamente consideradas en Canthonini y Ateuchini, así como la revalidación de las tribus Coptodactylini y Demarziellini, ésta última propuesta como grupo-hermano de Ateuchini. Se revisan los géneros *Tesserodoniella* Vaz-de-Mello & Halffter y *Zonocopris* Arrow a nivel de especie. Las consecuencias de una nueva división de Scarabaeinae en tribus son discutidas desde el punto de vista de los estudios de evolución del comportamiento de nidificación, y se plantean estudios aún necesarios para crear una nueva clasificación más estable desde el punto de vista taxonómico y útil desde el punto de vista evolutivo.

"O diabo na rua, no meio do redemunho..."
(Guimarães Rosa: Grande Sertão: Veredas, 1956)

PRESENTACIÓN

Este trabajo se divide en seis partes (capítulos):

En el capítulo uno presento un análisis histórico de la división supragenérica de los Scarabaeinae y análisis previos de las relaciones entre los grupos. Dicho análisis evidencia la necesidad de estudios de las tribus Ateuchini, Coprini y Canthonini, y propone un estudio de la primera.

En el capítulo dos, presento la descripción de una subtribu de Ateuchini (Scatimina); defino a la subtribu Ateuchina; ubico a los géneros excluidos de estas dos tribus en otras tribus (Coprini y Canthonini) o los considero como *incertae sedis*; y presento herramientas de identificación de los géneros de Scatimina, doce de los cuales son nuevos, listando sus especies y abundante material examinado. Dicho trabajo está sometido a la revista Zootaxa.

En el capítulo tres, presento un análisis filogenético de los géneros de Scarabaeinae ya ubicados en Ateuchini, y varios otros de Canthonini considerados en literatura o previamente por mí como emparentados con aquellos. A partir de este análisis ubico a los géneros dejados como *incertae sedis* en el capítulo anterior en tribus monofiléticas, una de las cuales es nueva. La nueva tribu incluye cuatro nuevas subtribus, tres de las cuales están integradas por géneros anteriormente en Ateuchini y una por géneros previamente en Canthonini. Las tribus Coptodactylini y Demarziellini son consideradas válidas, la primera incluyendo a géneros antes en Coprini y uno previamente en

Ateuchini, y la segunda incluyendo a varios géneros anteriormente en Ateuchini y varios otros en Canthonini. Presento la hipótesis de la tribu Demarziellini como grupo-hermano de la tribu Ateuchini. Propongo una tercera subtribu para Ateuchini, que incluye a géneros previamente en Ateuchini y en Canthonini, y presento claves para los géneros que componen dicha subtribu (incluyendo a dos nuevos, con especies previamente ubicadas en *Uroxys*) y Ateuchina (con un género nuevo, con especies previamente ubicadas en *Ateuchus, Canthidium* y *Agamopus*). Un grupo de especies previamente pertenecientes al género *Ateuchus* es ubicado en un nuevo género perteneciente a la tribu Coprini.

En el capitulo cuatro, presento la descripción de un nuevo género (con dos especies nuevas) perteneciente a la tribu Demarziellini como fue definida en el capítulo tres y antes ubicado provisionalmente en Canthonini, y comento sus relaciones con otros géneros del grupo. El trabajo está publicado en Zootaxa (Vaz-de-Mello & Halffter, 2006).

En el capítulo cinco reviso al género *Zonocopris*, hasta entonces con un historial de transferencias entre Canthonini y Ateuchini, y propongo su ubicación cercana a géneros tanto de Canthonini como de Ateuchini, en el grupo que formaría la tribu Demarziellini. El trabajo está publicado en los Annales de la Société Entomologique de France (Vaz-de-Mello, 2007).

En el capítulo seis presento consideraciones generales sobre los resultados de este trabajo, con sus implicaciones para el conocimiento de la evolución de los Scarabaeinae y su clasificación, sugiriendo estudios futuros.

Capítulo I

Introducción General

"Vergebens, daß Ihr ringsum wissenschaflich schweift,
Ein jeder lernt nur, was er lernen kann"

(Mephisto al alumno, Goethe: Faust, primera parte, 1806)

La superfamilia Scarabaeoidea Latreille, 1802, frecuentemente llamada Lamellicornia, incluye a un grupo de coleópteros cuya identidad ya estaba reconocida por Linnaeus (1758) bajo el género *Scarabaeus* Linnaeus, 1758. Aunque formen un grupo cohesivo y sin mayores divergencias desde entonces, su clasificación interna fue y es todavía sujeta a intenso debate, resumido por Kohlmann & Morón (2003).

Muestra de la falta de consenso sobre su taxonomía interna, es el hecho de que la superfamília Scarabaeoidea sea dividida en un número de familias que varía de tres a veinte y nueve, de acuerdo con distintos autores (ej. Janssens, 1949 – tres familias; Paulian, 1988 – veinte y nueve famílias). Así, el nombre Scarabaeidae Latreille, 1802, es empleado para designar varios grupos distintos más o menos excluyentes, que contienen al género *Scarabaeus*. Considero que los grupos de escarabajos estercoleros más comúnmente referidos como Scarabaeinae (o Scarabaeidae de otros autores) – los escarabajos estercoleros “verdaderos” y Aphodiinae (Aphodiidae de otros autores) deben formar parte de una única familia. Así, en adelante me referiré a los escarabajos del estiércol sobre los cuales trato y que comprenden un grupo caracterizado muy bien y desde hace mucho tiempo, como Scarabaeinae.

La larga y confusa historia de la taxonomía supragenérica de los Scarabaeinae

Un excelente recuento histórico de la clasificación de la superfamilia Scarabaeoidea lo presentan Kohlmann & Morón (2003), así que solamente voy a abordar lo pertinente a la subfamilia Scarabaeinae de la familia Scarabaeidae.

Como ya fue dicho, Linnaeus (1758) consideró a un solo género dentro de lo que llamamos hoy Scarabaeoidea. Fue Geoffroy, en 1762, quien pasó al género *Copris* Geoffroy, 1762, las especies de *Scarabaeus* que no presentaran escutelo visible, carácter que comparten casi todos los grupos hoy conocidos de Scarabaeinae. Fabricius (1798) consideró a los géneros *Copris* y *Onitis* Fabricius, 1798, incluyendo a especies hoy consideradas como Scarabaeinae. Weber (1801) describió el género *Ateuchus* Weber, 1801, para incluir a una especie norteamericana, *Ateuchus histeroides* Weber, 1801. Fabricius (1801) tomó el género *Ateuchus*, pero sin incluir en él a la especie de Weber, y dándole un sentido y composición muy distintos del de este autor, por lo que no queda claro si es un homónimo secundario, o una cita errónea (véase capítulo III). Latreille (1802), describe el género *Onthophagus*; Illiger, en 1803, el género *Gymnopleurus*. A partir de entonces, varios géneros nuevos son descritos, fragmentando a los hasta entonces conocidos, o basados en especies previamente desconocidas. Leach, en 1815, llamó Coprides al grupo que incluye a los presentes Scarabaeinae, y Aphodida a los Aphodiinae.

La primera división supragenérica de los presentes Scarabaeinae, fue la de Castelnau, quien, en 1840, dividió su tribu Coprophages en cuatro grupos: los Aphodiides, largamente equivalente a los modernos Aphodiinae; los Onitides, comprendiendo a los géneros de Scarabaeinae modernos con escutelo expuesto o “indicado”; los Coprites, incluyendo los Scarabaeinae de escutelo no expuesto y con tibias medianas y posteriores expandidas apicalmente; y los Ateuchites, que incluían a los Scarabaeinae con escutelo no expuesto y tibias medianas y posteriores no expandidas apicalmente. Queda claro por su descripción y especies incluidas, que Castelnau consideró a *Ateuchus* en el sentido de Fabricius, y no en el de Weber. Aunque Castelnau cita a los dos como autores de *Ateuchus*, la especie de Weber no es incluída en ninguno de los géneros, y el género *Choeridium* Le Peletier & Serville, 1828, es incluido en los Coprides, aunque bajo dicho género se comprendía el nombre de una especie que es hoy considerada sinónimo de *Ateuchus histeroides*.

Mulsant (1842) agrega a esa división los Sisyphaires, grupo definido para incluir al género *Sisyphus* Latreille, 1807. Burmeister (1846), considerando ya a Aphodiinae excluido del grupo a que pertenecen los Scarabaeinae, no incluye a los Sisyphaires en su arreglo supragenérico del grupo, pero introduce ahí a los Onthophagidae, caracterizados por la extrema reducción o ausencia del tercer segmento de los palpos labiales.

Erichson (1847) consideró solamente dos divisiones: Ateuchini, para los anteriormente agrupados en Ateuchides y Sisyphaires, y Coprini, para los Coprides, Onitides y Onthophagidae. Lacordaire (1856) consideró esta misma división como primaria, pero dividió a los Ateuchides en Ateuchides *vrais* (los hoy llamados Scarabaeini), Gymnopleurides (Sisyphini, Gymnopleurini y parte de Canthonini), Deltochilides (parte de Canthonini) y Minthophilides (*sic* - parte de Canthonini); y los Coprides en Coprides *vrais* (parte de Coprini, Phanaeini, parte de Ateuchini), Scatonomides (los presentes Ateuchini y parte de Coprini), Onitides (Onitini) y Onthophagides (Eurysternini, Onthophagini y Oniticellini). Harold, en 1867, describe a Choeridiidae, separándolo de

Scatonomidae por el hipómero anteriormente excavado, e incluyendo en este último a *Canthidium* Erichson, 1848, que Lacordaire y Erichson habían considerado en Coprides. Burmeister, en 1873, describe a Eucraniadae, para un grupo de géneros endémicos de Argentina hasta entonces considerados en Ateuchidae.

En 1874, van Lansberge presenta un corto estudio de los Ateuchides, agrega a los Ateuchides *vrais* el género *Gymnopleurus* (considerando así a Gymnopleurides como sinónimo de Ateuchides *vrais*) y a los Eucraniadae; describe la tribu Canthonides, incluyendo ahí casi la totalidad de los géneros hasta recientemente considerados en la tribu Canthonini; mantiene la tribu Sisyphides de Mulsant, agregando a los *Eurysternus* y al género australiano *Amphistomus* Lansberge, 1874, y considera a *Drepanocerus* como un género de transición entre éstos y los Onthophagides. Considera la tribu Canthonides integrada por dos grupos: los Canthonides *vrais* y los Menthophilides, el segundo grupo dividido en Epilissides y Epirinides, este último incluyendo al género *Menthophilus*. El mismo van Lansberge, en 1875, presenta una clave para identificación de los grupos de Coprides, en su monografía de los Onitides. Dicha clave divide el grupo entre Ontophagides y Coprides. Los Onthophagides se dividen en Onitides y Onthophagides, de los cuales sólo Onitides es dividido, entre Onitides propiamente dichos y Drepanocerides (grupo que había sido considerado “de transición” bajo los Sisyphides el año anterior – Lansberge, 1874).

Kolbe (1905), en un magnífico trabajo que resume el conocimiento de entonces sobre el comportamiento y la distribución geográfica de los escarabajos coprófagos, considera a éstos en un sentido mucho más amplio, incluyendo a los actuales Geotrupidae (incluso Bolboceratidae), Pleocomidae, Taurocerastinae (de Geotrupidae), Orphnidae, Chironidae y Aphodiinae con estatus de subfamilias de Scarabaeidae, que además incluye a las siguientes subfamilias compuestas de géneros hoy en Scarabaeinae: Onthophaginae (con las tribus Onthophagini, Oniticellini, Drepanocerini y Onitini); Pinotinae, incluyendo a todos los modernos Ateuchini y a algunos géneros hoy en Onthophagini y en Coprini; Coprinae, incluyendo a parte de lo hoy considerado como Coprini; Phanaeini, ya en su concepto volumétrico (en el sentido empleado por Kluge [1999]) moderno; Eucraniinae; Canthoninae, en el concepto de van Lansberge; Sisyphinae, también siguiendo a van Lansberge; Gymnopleurinae, incluyendo solamente a *Gymnopleurus*; y Scarabaeinae, en un concepto muy similar al de los Ateuchides/ Ateuchites citados hasta entonces basados en el concepto fabriciano de *Ateuchus*, para ese momento ya considerado sinónimo de *Scarabaeus*.

Gillet (1911) y Boucomont & Gillet (1927), en el Coleopterorum Catalogus, llaman Coprinae a los modernos Scarabaeinae, y consideran una división muy similar a la de Kolbe, excepto que incluyen a Gymnopleurides, Canthonides, Eucranides, y Sisyphides como subtribus de Scarabaeini; Pinotides y Phanaeides como subtribus de Coprini; y Onitides y Drepanocerides como subtribus de Onitini en 1911, transfiriendo Drepanocerides a Oniticellini en 1927.

Arrow (1931) describió la tribu Panelini para incluir a algunos géneros orientales hasta entonces en Pinotini o Canthonini. Paulian (1933a), describió a la tribu Coptodactylini, para incluir a dos géneros australianos con número de estrías elitrales mayor que en los Coprini.

Janssens (1946) presenta una clave de identificación de los grupos de Scarabaeidae Laparosticti, considerando a los Scarabaeinae en su sentido actual, divididos en los siguientes grupos: tribu Scarabaeini, incluyendo a las subtribus Canthonides, Sisyphides, Gymnopleurides, Scarabaeides, Eucranides y Alloscelides; tribu Oniticellini con las subtribus Drepanocerides, Oniticellides y Helictopleurides; tribu Onthophagini, sin subdivisiones; tribu Onitini, sin subdivisiones; tribu Coprini, con las subtribus Pinotides, Coptodactylides, Coprides y Phanaeides. En 1949, el mismo autor extendió la clave a todos los Scarabaeidae, con nomenclatura modernizada (subfijo –ina para las subtribus).

En 1951, Martínez sinonimizó el género *Pinotus* Erichson, 1847 con *Dichotomius* Hope, 1838, y siguiendo el código de nomenclatura entonces vigente, propuso a Ateuchini como nombre sustitutivo para Pinotini (que entonces incluía al género *Ateuchus* Weber). En 1954, Pereira propone el nombre Dichotomiini como sustitutivo para el mismo grupo. Ferreira (1953) propuso la subtribu Pachysomides para dos géneros africanos de Scarabaeina; Lebis (1953) consideró como válida a la tribu Epilissini, incluyendo ahí a todos los géneros de Madagascar entonces y después considerados como Canthonina. Pereira & Martínez (1956) proponen la subtribu Ennearabdina (en Coprini, según la propuesta de Janssens) para el género *Ennearabdus*. Vulcano *et al.* (1961), presentando un estudio sobre el género *Eurysternus* Dalman, 1824, lo excluyen de los Sisyphina, proponiendo la tribu Eurysternini para él solo, transfiriendo el género *Amphistomus*, entonces en Sisyphina, a Canthonina.

Balthasar, en 1961, describe, en Aphodiinae, la nueva tribu Demarziellini, con un solo género descrito en el mismo trabajo, que después fue transferido a Scarabaeinae y desde entonces considerado como parte de los Dichotomiini o Ateuchini (Matthews & Stebnicka, 1986). Balthasar (1963) consideró la misma clasificación usada por Janssens (1949).

Halffter & Matthews (1966) listaron los géneros entonces conocidos de Scarabaeinae, ubicándolos en sus tribus correspondientes según Janssens (1949), con las modificaciones propuestas por autores posteriores, y considerando a Coptodactylina como sinónimo de Coprina. Matthews (1971), tratando taxonómicamente a los Canthonini de Australia, habla de la conveniencia de reconsiderar a Menthophilina como grupo válido. Edmonds (1972) excluyó a tres géneros de la subtribu Phanaeina, considerándolos como *incerta sedis*. Edmonds & Halffter (1978) transfirieron dos géneros de Coprina a Dichotomiina. Mostert & Holm (1982) sinonimizaron a *Pachysoma* con *Scarabaeus*, estableciendo así, indirectamente, Pachysomina como sinónimo objetivo de Scarabaeina. Halffter & Edmonds (1982) listaron los géneros de Scarabaeinae con clasificación similar a la adoptada por Halffter & Matthews (1966), con la única diferencia de pasar a Dichotomiina los géneros excluidos por Edmonds de Phanaeina, que fueron enseguida tomados por Zunino (1983a; 1985) que los consideró formando su nueva subtribu Gromphina, en la tribu Onitini, que incluiría también a Phanaeina y Eucraniina, poniendo a Ennearabdina (subjetivamente) como sinónimo de ésta última.

Branco (1991) transfirió de Dichotomiina a Onthophagini un grupo de géneros afrotropicales; el mismo autor, en 1997, sinonimizó a la subtribu Alloscelina con la tribu Onthophagini. Montreuil (1998) tranfirió a varios géneros de Ateuchini (incluyendo a *Dichotomius*) a Coprini. Philips *et al.* (2004a) consideraron a Gromphina como sinónimo de Phanaeini.

El cuadro 1. presenta los géneros-tipo de distintas entidades supragenéricas de Scarabaeinae y su posición en distintas clasificaciones. Un historial más específico de la tribu Ateuchini se presenta en el capítulo III.

La corta y decepcionante historia de los estudios filogenéticos de relaciones entre las tribus de Scarabaeinae

Aunque Paulian (1933b), presentó un trabajo sobre la filogenia de los escarabajos coprófagos (Fig. 1.), no es hasta el trabajo de Zunino (1983b) que se puede hablar realmente de filogenia en el sentido más moderno. Dicho autor presenta una filogenia basada sobre todo en caracteres genitales, en que señala claramente la hipótesis de no-monofilia de las tribus Scarabaeini y Coprini como entonces estaban consideradas (Fig. 2.; Fig. 3.: mismo árbol erróneamente interpretado por Philips *et al.* [2004b]). Zunino (1983a, 1985) presentó un análisis específico para la ubicación de Phanaeina y Gromphina en Onitini y Eucraniini como grupo-hermano de éstos. El siguiente análisis filogenético publicado conteniendo distintas tribus y subtribus de Scarabaeinae, fue el de Montreuil (1998) (Fig. 4.; Fig. 5.: datos reanalizados por Philips *et al.* [2004b] con la exclusión de un género), que es el que define a las tribus Coprini y Ateuchini como se consideran en el presente trabajo. En este artículo, Montreuil (1998) transfiere varios géneros de Dichotomiini a Coprini, incluso a *Dichotomius*, lo que trae consigo que que el grupo hasta entonces generalmente llamado Dichotomiini fuera denominado Ateuchini, lo que, por alguna razón no justificada fue sistemáticamente ignorado.

Villalba *et al.* (2002) presentaron un análisis basado en datos moleculares de los géneros de Scarabaeinae de la Península Ibérica (Fig. 6.), en el que la tribu Coprini aparece anidada entre tres grupos tradicionalmente ubicados en la tribu Scarabaeini. Philips *et al.* (2004b) realizan el análisis más amplio publicado hasta entonces, con datos morfológicos de representantes de todas las tribus entonces consideradas válidas por ellos, llegando a un resultado que evidencia la no-monofilia de las tribus Coprini, Dichotomiini y Canthonini, y la cercanía filogenética de las tribus Onthophagini, Oniticellini, Onitini y Eurysternini (Fig. 7.). Dicho trabajo presenta además una interpretación novedosa de la evolución del comportamiento de rodaje, proponiendo en términos filogenéticos la hipótesis de su aparición múltiple.

Ocampo & Hawks (2006) presentaron un análisis molecular, confirmando la relación estrecha entre Eucraniini y Phanaeini (propuesta por Zunino en 1983 y 1985), así como la polifilia de Canthonini y Dichotomiini. Dicho análisis, aunque dirigido al clado Phanaeini-Eucraniini, también apoya la hipótesis del surgimiento múltiple del rodaje.

Los otros pocos trabajos con filogenias en Scarabaeinae tratan solamente de relaciones entre géneros en tribus hasta ahora consideradas monofiléticas (Scarabaeini, Eucraniini, Phanaeini, Onthophagini) o relaciones entre especies dentro del mismo género.

Problemas nomenclaturales

No son pocos los problemas nomenclaturales serios que involucran nombres del grupo família (superfamília, família, subfamilia, tribu y subtribu) en los Scarabaeinae. Para comenzar, el propio género *Scarabaeus* es discutido, ya que Lacordaire, en 1856, designó como tipo a *S. hercules* Linnaeus, 1758, que es la especie-tipo del género tipo de la subfamilia Dynastinae (considerada por muchos autores como parte de la familia Melolonthidae). El caso, por someterse a la Comisión Internacional de Nomenclatura Zoológica (Branco, 2007), ha llevado a actitudes extremas como la de Adám (2003), quien tomó al sinónimo más antiguo de *Scarabaeus* como tipo para proponer la utilización de Actinophorini como nombre sustituto para Scarabaeini.

Un buen resumen de los nombres del grupo de la familia en Scarabaeoidea es presentado por Smith (2006), habiendo sido omitidas (probablemente por descuido) tres cosas relativamente importantes sobre los Scarabaeinae: 1. la tribu Demarziellini Balthasar (que debería, por los criterios utilizados, haber sido puesta entre los sinónimos de Ateuchini); 2. la autoría de Paulian para Coptodactylini (ahí atribuida a Janssens, quién la citó trece años después); y 3. La latinización de Mentophilini Lacordaire, 1856 por Matthews (1974), que la haría disponible, aunque por los criterios usados por el autor, como sinónimo de Canthonini.

El otro problema nomenclatural serio involucra a Ateuchini. El nombre Ateuchites fue propuesto por Castelnau en 1840 sobre *Ateuchus* Fabricius (no Weber), y usado sin latinizarse apenas a lo largo del siglo XIX. En 1951, Martínez propuso el nombre Ateuchini, basado en *Ateuchus* Weber, como nuevo. La primera latinización de Ateuchites Castelnau debería considerarse como la de Smith (2006). El ICZN establece que cuando un nombre del grupo de la familia se propone sobre un género que es un homónimo posterior, el nombre no debe ser considerado disponible, a no ser que esté efectivamente en uso (ICZN, 1999: art. 39). Ahora bien, el problema es saber si Ateuchini Martínez es un homónimo o no, ya que como Ateuchites Castelnau no fue latinizado hasta 2006, no debería ser considerado válido hasta entonces. Actualmente estoy preparando en colaboración con Tristão Branco una solicitud a la Comisión de que el nombre Ateuchites/ Ateuchini Castelnau sea considerado no disponible, quitando así el fantasma del homónimo sobre el nombre de Martínez.

Objetivos del presente trabajo

Mis objetivos en este trabajo son:

1. Delimitar la tribu Ateuchini basada en un criterio de monofilia
2. Determinar las relaciones de la tribu Ateuchini con otros grupos de Scarabaeinae
3. Presentar herramientas para la identificación de las subtribus y géneros de Ateuchini
4. Ubicar en tribus más adecuadas los géneros considerados hasta ahora en Ateuchini y que no pertenecen a esta tribu como grupo monofilético
5. Sentar las bases para el estudio futuro más detallado de los grupos a que pertenecen dichos géneros.

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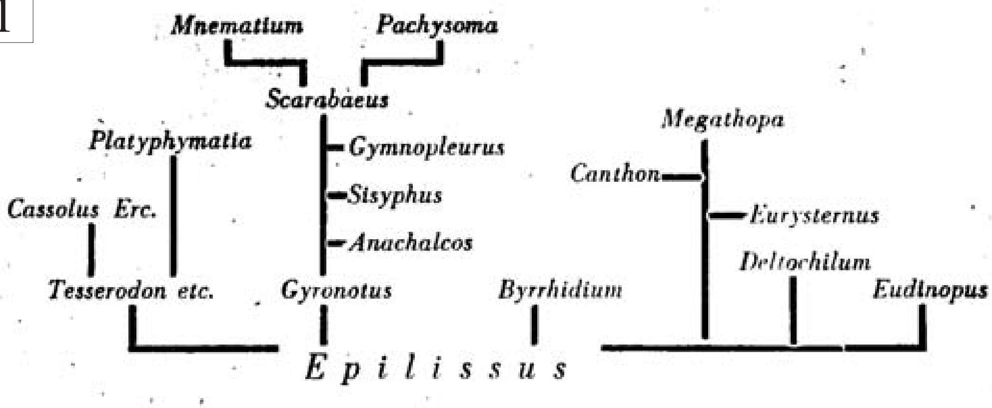
Cuadro 1. Géneros-tipo de taxones del grupo de la família en Scarabaeinae y su ubicación taxonómica según distintas síntesis.

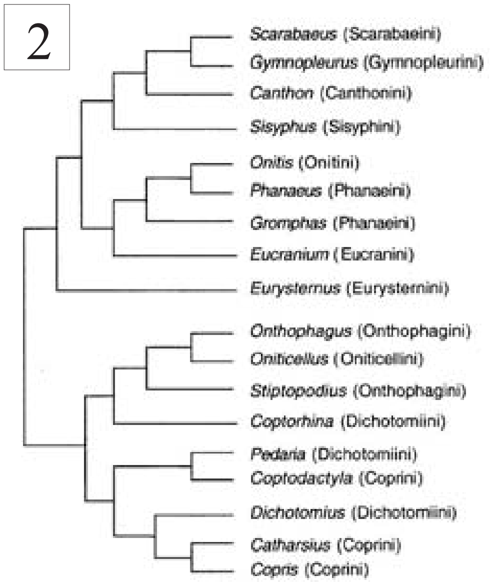
Género (nombre actual)	Castelnau (1840)	Lacordaire (1856)	Kolbe (1905)	Coleopterorum Catalogus	Janssens (1949)	Halffter & Matthews (1966)	Halffter & Edmonds (1982)	Acumulado hasta el presente trabajo
Alloscelus	-	-	-	-	Scarabaeini-Alloscelina	Scarabaeini-Alloscelina	Scarabaeini-Alloscelina	Onthophagini
Ateuchus	Coprites	Coprides-Scatonomides	Pinotinae	Coprini-Pinotides	Coprini-Pinotina	Coprini-Dichotomina	Coprini-Dichotomina	Ateuchini
Canthon	Ateuchites	Ateuchides-Gymnopleurides	Canthoninae	Scarabaeini-Canthonides	Scarabaeini-Canthonina	Scarabaeini-Canthonina	Scarabaeini-Canthonina	Canthonini
Copris	Coprites	Coprides-Coprides	Coprinae	Coprini-Coprides	Coprini-Coprina	Coprini-Coprina	Coprini-Coprina	Coprini
Coptodactyla	-	-	Coprinae	Coprini-Coprides	Coprini-Coptodactylina	Coprini-Coprina	Coprini-Coprina	Coprini
Deltochilum	Ateuchites	Ateuchides-Deltochilides	Canthoninae	Scarabaeini-Canthonides	Scarabaeini-Canthinina	Scarabaeini-Canthonina	Scarabaeini-Canthonina	Canthonini
Demarziella	-	-	-	-	-	-	Coprini-Dichotomina	Ateuchini
Dichotomius	-	-	Pinotinae	Coprini-Pinotides	Coprina-Pinotina	Coprini-Dichotomina	Coprini-Dichotomina	Coprini
Drepanocerus	-	Coprides-Onthophagides	Onthophaginae-Drepanocerini	Onitini/Oniticellini-Drepanocerides	Oniticellini-Drepanocerina	Oniticellini-Drepanocerina	Oniticellini-Drepanocerina	Oniticellini-Drepanocerina
Ennearabdus	-	-	Pinotinae	Coprini-Pinotides	Coprini-Pinotina	Coprini-Ennearabdina	Coprini-Ennearabdina	Eucraniini
Epilissus	-	-	Canthoninae	Scarabaeini-Canthonides	Scarabaeini-Canthonina	Scarabaeinae-Canthonina	Scarabaeinae-Canthonina	Canthonini
Eucranium	-	Ateuchides-Ateuchides	Eucraniinae	Scarabaeini-Eucranides	Scarabaeini-Eucraniina	Scarabaeini-Eucraniina	Scarabaeini-Eucraniina	Eucraniini
Eurysternus	Onitides	Coprides-Onthophagides	Sisyphinae	Scarabaeini-Sisyphides	Scarabaeini-Sisyphina	Scarabaeini-Eurysternina	Eurysternini	Eurysternini
Gromphas	-	Coprides-Coprides	Phanaeinae	Coprini-Phanaeides	Coprini-Phanaeina	Coprini-Phanaeina	Coprini-Dichotomina	Phanaeini
Gymnopleurus	Ateuchites	Ateuchides-Gymnopleurides	Gymnopleurinae	Scarabaeini-Gymnopleurides	Scarabaeini-Gymnopleurina	Scarabaeini-Gymnopleurina	Scarabaeini-Gymnopleurina	Gymnopleurini
Helictopleurus	-	-	-	Oniticellini	Oniticellini-Helictopleurina	Oniticellini-Helictopleurina	Oniticellini-Helictopleurina	Oniticellini-Helictopleurina

Género (nombre actual)	Castelnau (1840)	Lacordaire (1856)	Kolbe (1905)	Coleopterorum Catalogus	Janssens (1949)	Halffter & Matthews (1966)	Halffter & Edmonds (1982)	Acumulado hasta el presente trabajo
Menthophilus	Ateuchites	Ateuchides-Minthophilides	Canthoninae	Scarabaeini-Canthonides	Scarabaeini-Canthonina	Scarabaeini-Canthonina	Scarabaeini-Canthonina	Canthonini
Oniticellus	Onitides	Coprides-Onthophagides	Onthophaginae-Oniticellini	Oniticellini	Oniticellini-Oniticellina	Oniticellini-Oniticellina	Oniticellini-Oniticellina	Oniticellini-Oniticellina
Onitis	Onitides	Coprides-Onitides	Onthophaginae-Onitini	Onitini-Onitides	Onitini	Onitini	Onitini	Onitini
Onthophagus	Coprites	Coprides-Onthophagides	Onthophaginae-Onthophagini	Onthophagini	Onthophagini	Onthophagini	Onthophagini	Onthophagini
Pachysoma	Ateuchites	Ateuchides-Ateuchides	Scarabaeinae	Scarabaeini-Scarabaeides	Scarabaeini-Scarabaeina	Scarabaeini-Scarabaeina	Scarabaeini-Scarabaeina	Scarabaeini
Panelus	-	-	Canthoninae	Scarabaeini-Canthonides	Scarabaeini-Canthonina	Scarabaeini-Canthonina	Scarabaeini-Canthonina	Canthonini
Phanaeus	Coprites	Coprides-Coprides	Phanaeinae	Coprini-Phanaeides	Coprini-Phanaeina	Coprini-Phanaeina	Coprini-Phanaeina	Phanaeini
Scarabaeus	Ateuchites	Ateuchides-Ateuchides	Scarabaeinae	Scarabaeini-Scarabaeides	Scarabaeini-Scarabaeina	Scarabaeini-Scarabaeina	Scarabaeini-Scarabaeina	Scarabaeini
Scatonomus	Ateuchites	Coprides-Scatonomides	Pinotinae	Coprini-Pinotides	Coprini-Pinotina	Coprini-Pinotina	Coprini-Dichotomina	Ateuchini
Sisyphus	Ateuchites	Ateuchides-Gymnopleurides	Sisyphinae	Scarabaeini-Sisyphides	Scarabaeini-Sisyphina	Scarabaeini-Sisyphina	Scarabaeini-Sisyphina	Sisyphini

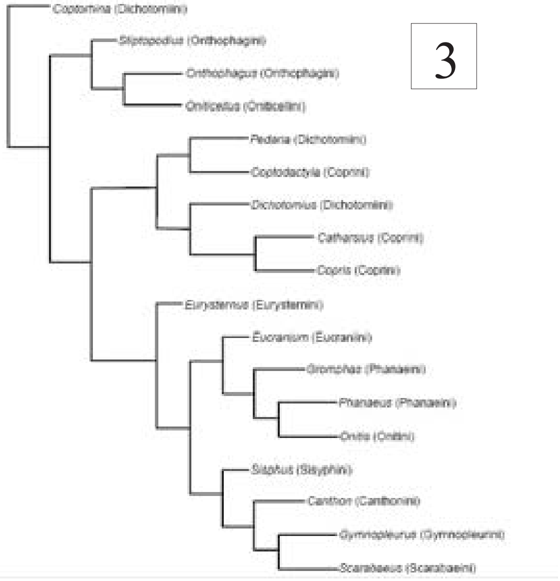
1

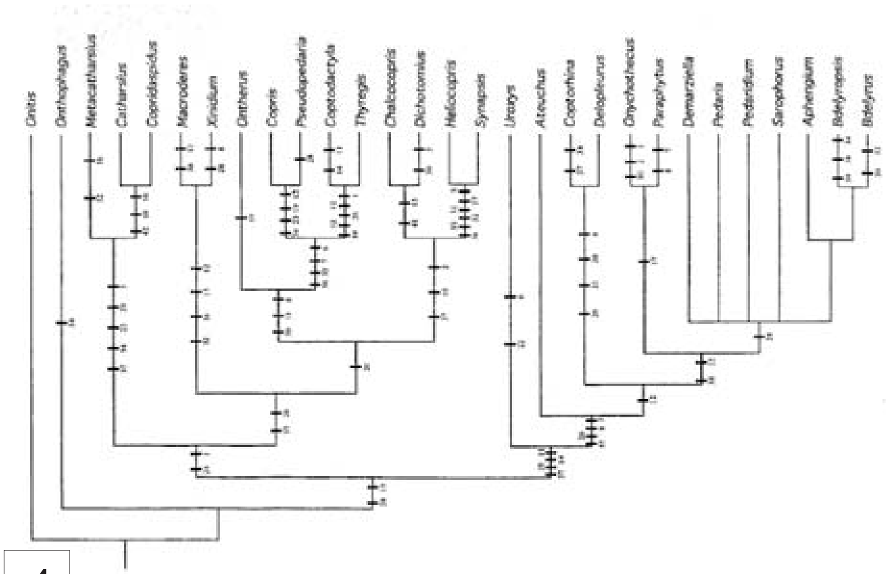

Mnematium
Pachysoma
Scarabaeus
Platyphymatia
Gymnopleurus
Sisyphus
Anachalcos
Cassolus Erc.
Tesserodon etc.
Gyronotus
Byrrhidium
Megathopa
Canthon
Eurysternus
Deltochilum
Eudinopus
Epilissus

2


Scarabaeus (Scarabaeini)
Gymnopleurus (Gymnopleurini)
Canthon (Canthonini)
Sisyphus (Sisyphini)
Onitis (Onitini)
Phanaeus (Phanaeini)
Gromphas (Phanaeini)
Eucranium (Eucranini)
Eurysternus (Eurysternini)
Onthophagus (Onthophagini)
Oniticellus (Oniticellini)
Stiptopodius (Onthophagini)
Coptorhina (Dichotomiini)
Pedaria (Dichotomiini)
Coptodactyla (Coprini)
Dichotomius (Dichotomiini)
Catharsius (Coprini)
Copris (Coprini)

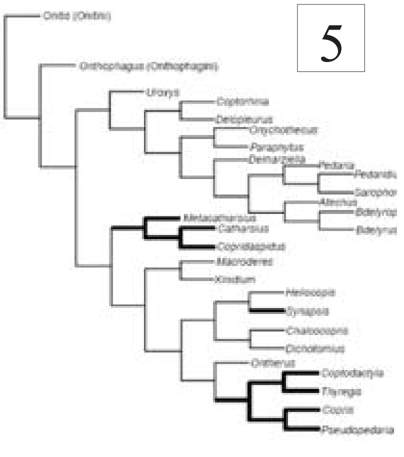
3


Coptorhina (Dichotomiini)
Stiptopodius (Onthophagini)
Onthophagus (Onthophagini)
Oniticellus (Oniticellini)
Pedaria (Dichotomiini)
Coptodactyla (Coprini)
Dichotomius (Dichotomiini)
Catharsius (Coprini)
Copris (Coprini)
Eurysternus (Eurysternini)
Eucranium (Eucranini)
Gromphas (Phanaeini)
Phanaeus (Phanaeini)
Onitis (Onitini)
Sisphus (Sisyphini)
Canthon (Canthonini)
Gymnopleurus (Gymnopleurini)
Scarabaeus (Scarabaeini)

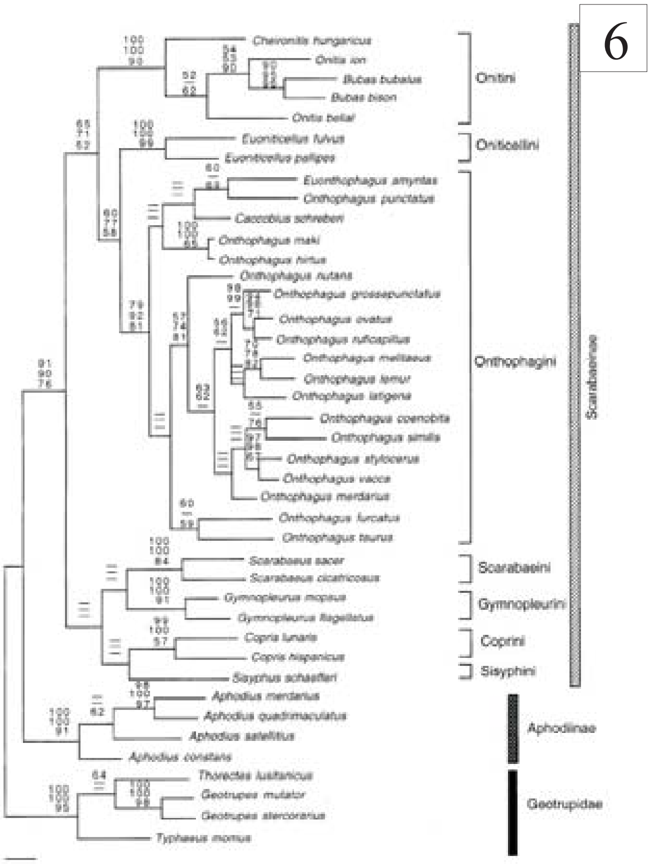

Onitis
Onthophagus
Metacatharsius
Catharsius
Copridaspidus
Macroderes
Xinidium
Ontherus
Copris
Pseudopedaria
Coptodactyla
Thyregis
Chalcocopris
Dichotomius
Heliocopris
Synapsis
Uroxys
Ateuchus
Coptorhina
Delopleurus
Onychothecus
Paraphytus
Demarziella
Pedaria
Pedaridium
Sarophorus
Aphengium
Bdelyropsis
Bdelyrus

4

5


Onitis (Onitini)
Onthophagus (Onthophagini)
Uroxys
Coptorhina
Delopleurus
Onychothecus
Paraphytus
Demarziella
Pedaria
Pedaridium
Sarophorus
Ateuchus
Bdelyropsis
Bdelyrus
Metacatharsius
Catharsius
Copridaspidus
Macroderes
Xinidium
Heliocopris
Synapsis
Chalcocopris
Dichotomius
Ontherus
Coptodactyla
Thyregis
Copris
Pseudopedaria

6


Cheironitis hungaricus
Onitis ion
Bubas bubalus
Bubas bison
Onitis belial
Euoniticellus fulvus
Euoniticellus pallipes
Euonthophagus amyntas
Onthophagus punctatus
Caccobius schreberi
Onthophagus maki
Onthophagus hirtus
Onthophagus nutans
Onthophagus grossepunctatus
Onthophagus ovatus
Onthophagus ruficapillus
Onthophagus melitaeus
Onthophagus lemur
Onthophagus latigena
Onthophagus coenobita
Onthophagus similis
Onthophagus stylocerus
Onthophagus vacca
Onthophagus merdarius
Onthophagus furcatus
Onthophagus taurus
Scarabaeus sacer
Scarabaeus cicatricosus
Gymnopleurus mopsus
Gymnopleurus flagellatus
Copris lunaris
Copris hispanicus
Sisyphus schaefferi
Aphodius merdarius
Aphodius quadrimaculatus
Aphodius satellitius
Aphodius constans
Thorectes lusitanicus
Geotrupes mutator
Geotrupes stercorarius
Typhaeus momus
Onitini
Oniticellini
Onthophagini
Scarabaeini
Gymnopleurini
Coprini
Sisyphini
Scarabaeinae
Aphodiinae
Geotrupidae
100
100
93
91
90
76
65
71
62
100
100
99
60
77
58
79
92
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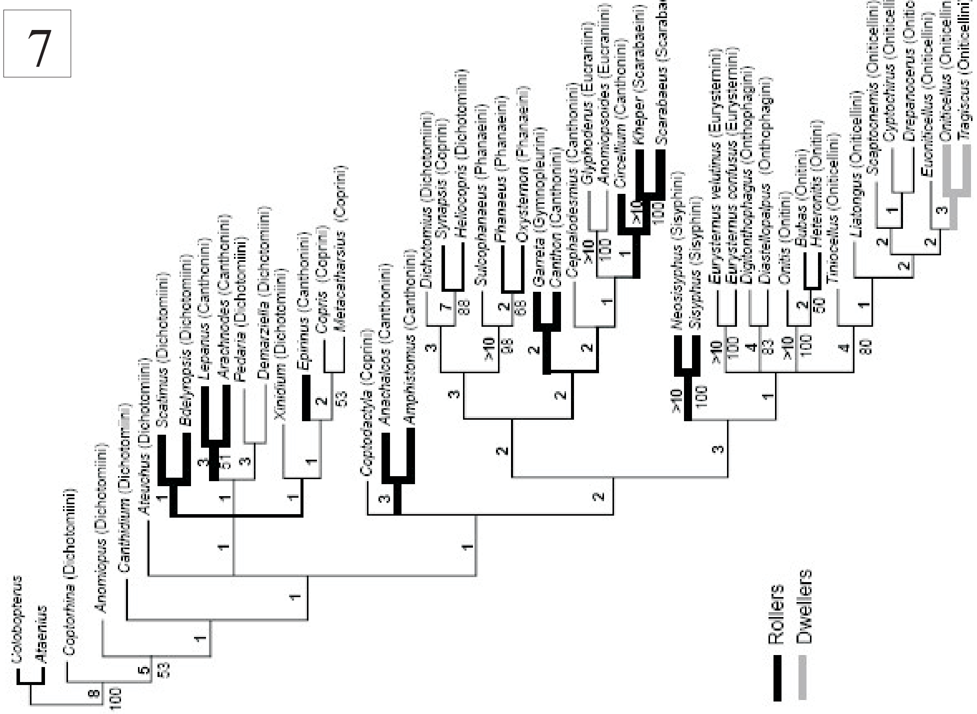
91
100
100
95
64

7


Colobopterus
Ataenius
Coptorhina (Dichotomiini)
Anomiopus (Dichotomiini)
Canthidium (Dichotomiini)
Ateuchus (Dichotomiini)
Scatimus (Dichotomiini)
Bdelyropsis (Dichotomiini)
Lepanus (Canthonini)
Arachnodes (Canthonini)
Pedaria (Dichotomiini)
Demarziella (Dichotomiini)
Xinidium (Dichotomiini)
Epirinus (Canthonini)
Copris (Coprini)
Metacatharsius (Coprini)
Coptodactyla (Coprini)
Anachalcos (Canthonini)
Amphistomus (Canthonini)
Dichotomius (Dichotomiini)
Synapsis (Coprini)
Heliocopris (Dichotomiini)
Sulcophanaeus (Phanaeini)
Phanaeus (Phanaeini)
Oxysternon (Phanaeini)
Garreta (Gymnopleurini)
Canthon (Canthonini)
Cephalodesmius (Canthonini)
Glyphoderus (Eucraniini)
Anomiopsoides (Eucraniini)
Circellium (Canthonini)
Kheper (Scarabaeini)
Scarabaeus (Scarabaeini)
Neosisyphus (Sisyphini)
Sisyphus (Sisyphini)
Eurysternus velutinus (Eurysternini)
Eurysternus confusus (Eurysternini)
Digitonthophagus (Onthophagini)
Diastellopalpus (Onthophagini)
Onitis (Onitini)
Bubas (Onitini)
Heteronitis (Onitini)
Tiniocellus (Oniticellini)
Liatongus (Oniticellini)
Scaptocnemis (Oniticellini)
Cyptochirus (Oniticellini)
Drepanocerus (Oniticellini)
Euoniticellus (Oniticellini)
Oniticellus (Oniticellini)
Tragiscus (Oniticellini)
Rollers
Dwellers
8
100
5
53
1
1
1
1
1
1
3
51
3
1
2
53
1
3
2
2
3
3
7
88
>10
98
2
88
2
2
2
1
>10
100
1
>10
100
>10
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>10
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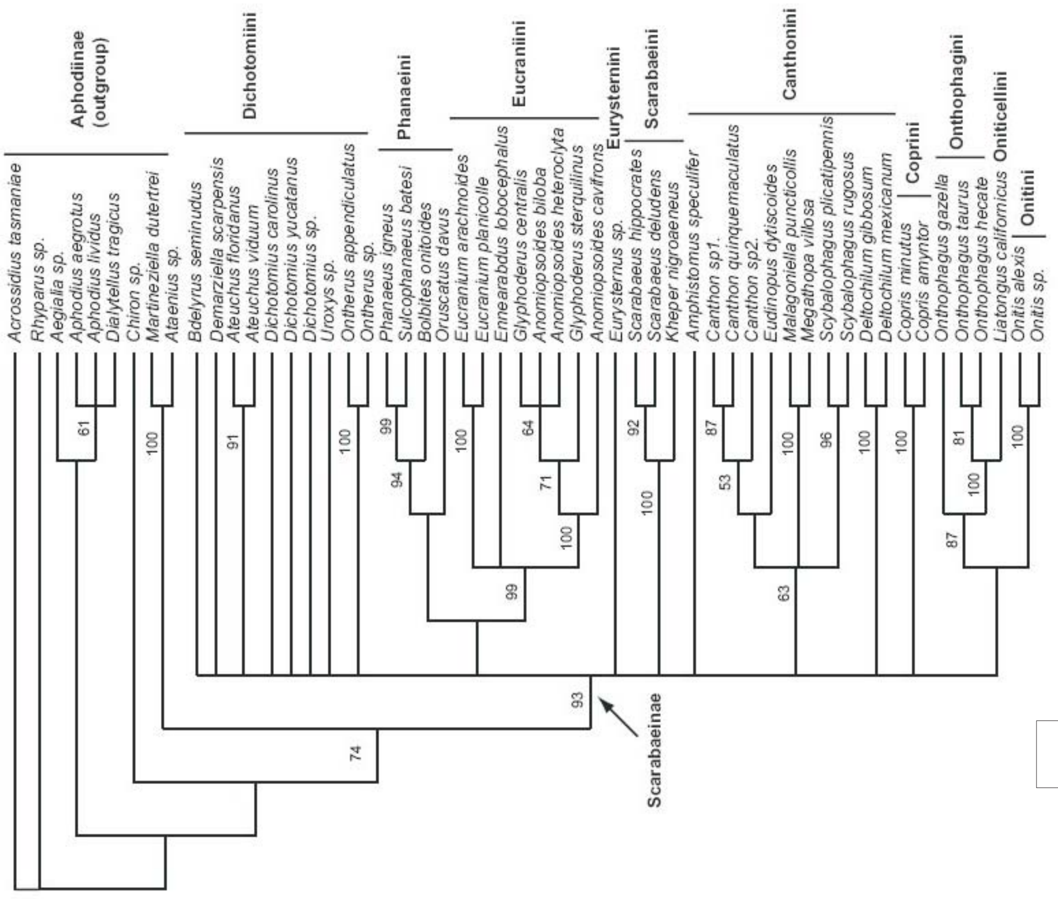
4
80
1
2
1
2
2
3


Acrossidius tasmaniae
Rhyparus sp.
Aegialia sp.
Aphodius aegrotus
Aphodius lividus
Dialytellus tragicus
Chiron sp.
Martinezziella dutertrei
Ataenius sp.
Aphodiinae (outgroup)
Bdelyrus seminudus
Demarziella scarpensis
Ateuchus floridanus
Ateuchus viduum
Dichotomius carolinus
Dichotomius yucatanus
Dichotomius sp.
Uroxys sp.
Ontherus appendiculatus
Ontherus sp.
Dichotomiini
Phanaeus igneus
Sulcophanaeus batesi
Bolbites onitoides
Oruscatus davus
Phanaeini
Eucranium arachnoides
Eucranium planicolle
Ennearabdus lobocephalus
Glyphoderus centralis
Anomiopsoides biloba
Anomiopsoides heteroclyta
Glyphoderus sterquilinus
Anomiopsoides cavifrons
Eucraniini
Eurysternus sp.
Eurysternini
Scarabaeus hippocrates
Scarabaeus deludens
Kheper nigroaeneus
Scarabaeini
Amphistomus speculifer
Canthon sp1.
Canthon quinquemaculatus
Canthon sp2.
Eudinopus dytiscoides
Malagoniella puncticollis
Megathopa villosa
Scybalophagus plicatipennis
Scybalophagus rugosus
Deltochilum gibbosum
Deltochilum mexicanum
Canthonini
Copris minutus
Copris amyntor
Coprini
Onthophagus gazella
Onthophagus taurus
Onthophagus hecate
Onthophagini
Liatongus californicus
Oniticellini
Onitis alexis
Onitis sp.
Onitini
61
100
74
91
100
99
94
100
64
71
100
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63
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87
81
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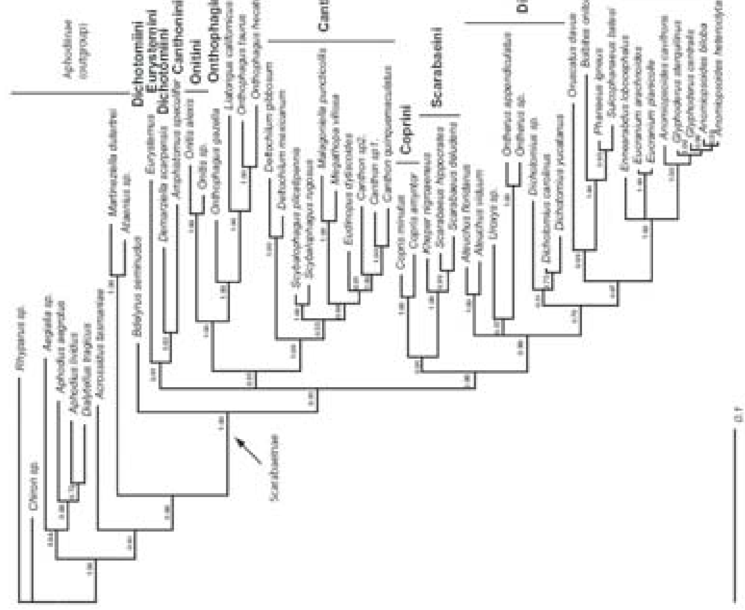
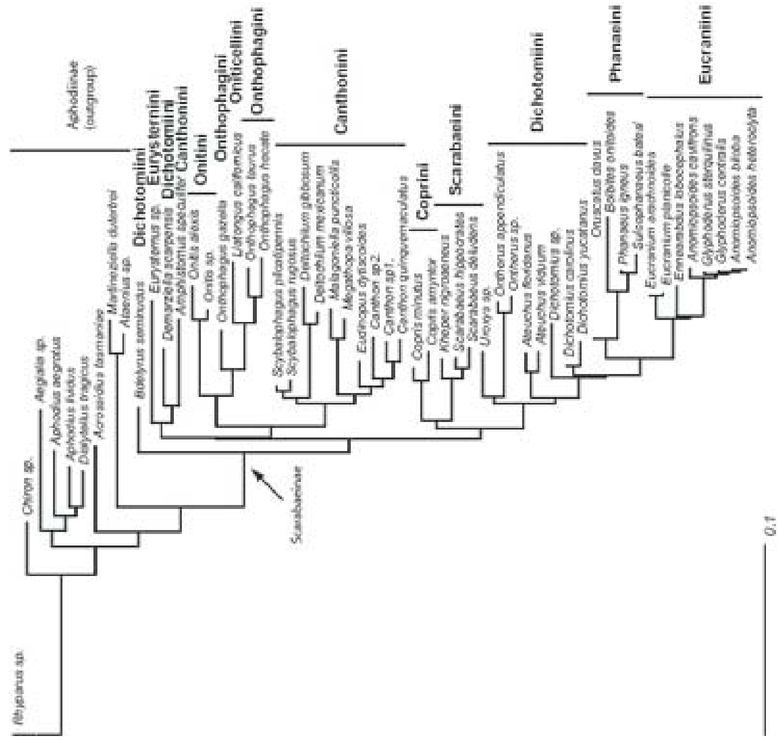
100
Scarabaeinae

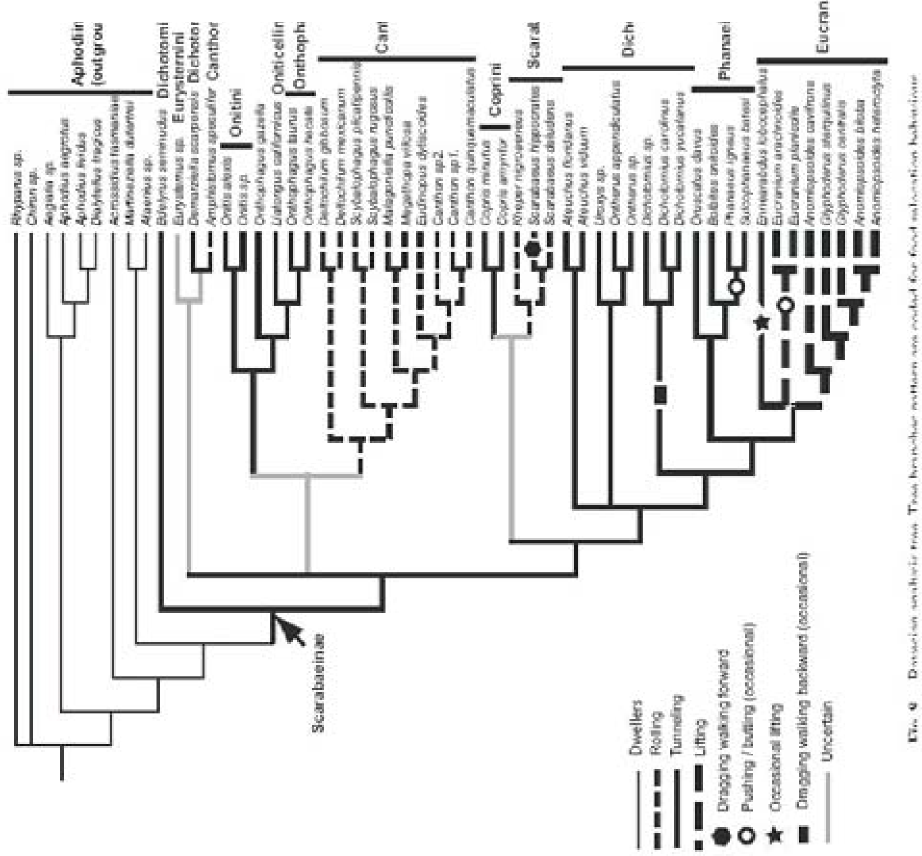
8

9


Aphodiinae (outgroup)
Dichotomiini
Eurysternini
Dichotomiini
Canthonini
Onitini
Onthophagini
Oniticellini
Onthophagini
Canthonini
Coprini
Scarabaeini
Dichotomiini
Phanaeini
Eucraniini
Scarabaeinae
0.1


Aphodiinae (outgroup)
Dichotomiini
Eurysternini
Dichotomiini
Canthonini
Onitini
Onthophagini
Oniticellini
Onthophagini
Canthonini
Coprini
Scarabaeini
Dichotomiini
Phanaeini
Eucraniini
Scarabaeinae
0.1

10


Aphodiini (outgroup)
Dichotomiini
Eurysternini
Onitini
Oniticellini
Coprini
Phanaei
Eucraniini
Scarabaeinae
Dwellers
Rolling
Tunnelling
Lifting
Dragging walking forward
Pushing / butting (occasional)
Occasional lifting
Dragging walking backward (occasional)
Uncertain

11

Capítulo II

Synopsis of the new subtribe Scatimina (Coleoptera: Scarabaeidae: Scarabaeinae: Ateuchini), with descriptions of twelve new genera

Fernando Z. Vaz-de-Mello

Enviado a Zootaxa en abril de 2007

"Enfim, cada um o que quer aprova, o senhor sabe: pão ou pães, é questão de opiniães..."
(Guimarães Rosa: Grande Sertão: Veredas, 1956)

Synopsis of the new subtribe Scatimina (Coleoptera: Scarabaeidae: Scarabaeinae: Ateuchini), with descriptions of twelve new genera

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Abstract: The **new subtribe** Scatimina (part of the tribe Ateuchini Castelnau) is described, and includes the genera *Scatimus* Erichson; *Scatrichus* Génier & Kohlmann, 2003; *Trichillum* Harold, 1868; *Pedaridium* Harold, 1868; *Eutrichillum* Martínez, 1969, **new status**; *Besourenga*, **new genus** (type species *Trichillum minutum* Saylor); *Bradypodidium*, **new genus** (type-species *Trichillum bradyporum* Boucomont); *Degallieridium*, **new genus** (type-species *Degallieridium lilliputanum*, **new species**); *Feeridium*, **new genus** (type species *Feeridium woodruffi*, **new species**); *Genieridium*, **new genus** (type species *Pedaridium bidens* Balthasar); *Leotrichillum*, **new genus** (type species *Pedaridium louzadaorum* Vaz-de-Mello & Canhedo); *Martinezidium*, **new genus** (type species *Pedaridium galileoae* Génier & Vaz-de-Mello); *Nunoidium*, **new genus** (type species *Pedaridium argentinum* Arrow); *Onoreidium*, **new genus** (type species *Trichillum cristatum* Arrow); *Pereiraidium*, **new genus** (type species *Pedaridium almeidai* Pereira); *Silvinha*, **new genus** (type species *Silvinha unica*, **new species**); and *Trichillidium*, **new genus** (type species *Pedaridium quadridens* Arrow). The subtribe Ateuchina Castelnau is here defined and includes *Ateuchus* Weber, *Deltorhinum* Harold, *Aphengium* Harold and *Sinapisoma* Boucomont (transferred from Canthonini). The genera *Scatonomus* Erichson, *Anomiopus* Westwood and *Hypocanthidium* Balthasar are transferred from Ateuchini to Canthonini, and the genera *Canthidium* Erichson, *Parachorius* Harold (formerly Ateuchini) and *Holocanthon* Martínez & Pereira (formerly Canthonini) are transferred to Coprini. The genera *Bdelyropsis* Pereira, Vulcano & Martínez, *Bdelyrus* Harold, *Coptorhina* Hope, *Delopleurus* Erichson, *Demarziella* Balthasar, *Onychothecus* Boucomont, *Paraphytus* Harold, *Pedaria* Laporte, *Pleronyx* Lansberge, *Pseuduroxys* Balthasar, *Sarophorus* Erichson and *Uroxys* Westwood are considered as *incerta sedis* in the Ateuchini, not fitting nor Ateuchina nor Scatimina. A key is presented to the genera of Scatimina, and another for species of the genus *Genieridium* that are also diagnosed. Each genus of Scatimina is diagnosed and has comprising species listed, with remarks on affinities, composition and distribution. All genera except *Scatimus* and *Scatrichus* are (re)described, and examined material of already or here described species is listed. The following three **new species** are described: *Degallieridium lilliputanum*, **new species**; *Feeridium woodruffi*, **new**

species and *Silvinha unica*, **new species**. The following 32 **new combinations** are stablished (original genus in parenthesis): *Besourenga minutus* (Saylor) (*Trichillum*)**;** *B. vejdovskyi* (Balthasar) (*Trichillum*); *B. amarillai* (Aguilar) (*Pedaridium*); *B. horacioi* (Martínez) (*Trichillum*); *Bradypodidium adisi* (Ratcliffe) (*Trichillum*); *B. bradyporum* (Boucomont) (*Trichillum*); *B. venezuelense* (Ferreira & Galileo) (*Pedaridium*); *Eutrichillum arcus* (Solís & Kohlmann) (*Trichillum*); *E. hirsutum* (Boucomont) (*Trichillum*); *E. hystrix* (Arrow) (*Trichillum*); *Genieridium bidens* (Balthasar) (*Pedaridium*); *G. bordoni* (Martínez) (*Pedaridium*); *G. cryptops* (Arrow) (*Pedaridium*); *G. margareteae* (Génier & Vaz-de-Mello) (*Pedaridium*); *G. medinae* (Gill & Vaz-de-Mello) (*Pedaridium*); *G. paranense* (Arrow) (*Pedaridium*); *G. zanunciorum* (Vaz-de-Mello & Canhedo) (*Pedaridium*); *Leotrichillum louzadaorum* (Vaz-de-Mello & Canhedo) (*Pedaridium*); *Martinezidium fulgens* (Arrow) (*Pedaridium*); *M. galileoae* (Génier & Vaz-de-Mello) (*Pedaridium*); *M. martinsi* (Ferreira & Galileo) (*Pedaridium*); *M. maya* (Vaz-de-Mello, Halffter & Halffter) (*Pedaridium*); *Nunoidium argentinum* (Arrow) (*Pedaridium*); *Onoreidium bottimeri* (Howden & Young) (*Pedaridium*); *O. cristatum* (Arrow) (*Trichillum*); *O. howdeni* (Ferreira & Galileo) (*Pedaridium*); *O. ohausi* (Arrow) (*Trichillum*); *Pereiraidium almeidai* (Pereira) (*Pedaridium*); *Trichillidium brevisetosum* (Howden & Young) (*Pedaridium*); *T. caingua* (Martínez) (*Pedaridium*?); *T. pilosum* (Robinson) (*Trichillum*); *Trichillidium quadridens* (Arrow) (*Pedaridium*). Distribution maps are presented for the newly described species, for *Pereiraidium almeidai*, and for every species of *Genieridium*.

Resúmen: Se describe a la **nueva subtribu** Scatimina (parte de la tribu Ateuchini Castelnau), que incluye a los géneros *Scatimus* Erichson; *Scatrichus* Génier & Kohlmann, 2003; *Trichillum* Harold, 1868; *Pedaridium* Harold, 1868; *Eutrichillum* Martínez, 1969, **n. status**; *Besourenga*, **n. g.** (especie-tipo *Trichillum minutum* Saylor); *Bradypodidium*, **n. g.** (especie-tipo *Trichillum bradyporum* Boucomont); *Degallieridium*, **n. g.** (especie-tipo *Degallieridium lilliputanum*, **n. sp.**); *Feeridium*, **n. g.** (especie-tipo *Feeridium woodruffi*, **n. sp.**); *Genieridium*, **n. g.** (especie-tipo *Pedaridium bidens* Balthasar); *Leotrichillum*, **n. g.** (especie-tipo *Pedaridium louzadaorum* Vaz-de-Mello & Canhedo); *Martinezidium*, **n. g.** (especie-tipo *Pedaridium galileoae* Génier & Vaz-de-Mello); *Nunoidium*, **n. g.** (especie-tipo *Pedaridium argentinum* Arrow); *Onoreidium*, **n. g.** (especie-tipo *Trichillum cristatum* Arrow); *Pereiraidium*, **n. g.** (especie-tipo *Pedaridium almeidai* Pereira); *Silvinha*, **n. g.** (especie-tipo *Silvinha unica*, **n. sp.**); y *Trichillidium*, **n. g.** (especie-tipo *Pedaridium quadridens* Arrow). La subtribu Ateuchina Laporte es diagnosticada y incluye a *Ateuchus* Weber, *Deltorhinum* Harold, *Aphengium* Harold y *Sinapisoma* Boucomont (transferido desde Canthonini). Se transfiere a los géneros *Scatonomus* Erichson, *Anomiopus* Westwood y *Hypocanthidium* Balthasar de Ateuchini a Canthonini, y los géneros *Canthidium* Erichson, *Parachorius* Harold (Ateuchini) y *Holocanthon* Martínez & Pereira (Canthonini) a Coprini. Los géneros *Bdelyropsis* Pereira, Vulcano & Martínez, *Bdelyrus* Harold, *Coptorhina* Hope, *Delopleurus* Erichson, *Demarziella* Balthasar, *Onychothecus* Boucomont, *Paraphytus* Harold, *Pedaria* Laporte, *Pleronyx* Lansberge, *Pseuduroxys* Balthasar, *Sarophorus* Erichson y *Uroxys* Westwood se consideran como *incerta sedis* en Ateuchini. Se presenta una clave para los géneros de Scatimina, y otra para las especies del género *Genieridium*, que son también diagnosticadas. Se diagnostica a cada género de Scatimina y sus especies ya descritas son enlistadas, con observaciones sobre afinidades, composición y distribución. Todos los géneros, con la excepción de *Scatimus* y *Scatrichus*, son (re)descritos, y se enlista todo el material examinado de cada especie ya descrita. Se describen a las siguientes tres **nuevas** especies: *Degallieridium lilliputanum*, **n. sp.**; *Feeridium woodruffi*, **n. sp.** y *Silvinha unica*, **n. sp.**. Se establecen las siguientes 32 **nuevas** combinaciones (género original entre paréntesis): *Besourenga minutus* (Saylor) (*Trichillum*)**;** *B. vejdovskyi* (Balthasar) (*Trichillum*); *B. amarillai* (Aguilar) (*Pedaridium*); *B. horacioi* (Martínez) (*Trichillum*); *Bradypodidium adisi* (Ratcliffe) (*Trichillum*); *B. bradyporum* (Boucomont) (*Trichillum*); *B. venezuelense* (Ferreira & Galileo) (*Pedaridium*); *Eutrichillum arcus* (Solís & Kohlmann) (*Trichillum*); *E. hirsutum* (Boucomont) (*Trichillum*); *E. hystrix* (Arrow) (*Trichillum*); *Genieridium bidens* (Balthasar) (*Pedaridium*); *G. bordoni* (Martínez) (*Pedaridium*); *G. cryptops* (Arrow) (*Pedaridium*); *G. margareteae* (Génier & Vaz-de-Mello) (*Pedaridium*); *G. medinae* (Gill & Vaz-de-Mello) (*Pedaridium*); *G. paranense* (Arrow) (*Pedaridium*); *G. zanunciorum* (Vaz-de-Mello & Canhedo) (*Pedaridium*); *Leotrichillum louzadaorum* (Vaz-de-Mello & Canhedo) (*Pedaridium*); *Martinezidium fulgens* (Arrow) (*Pedaridium*); *M. galileoae* (Génier & Vaz-de-Mello) (*Pedaridium*); *M. martinsi* (Ferreira & Galileo) (*Pedaridium*); *M. maya* (Vaz-de-Mello, Halffter & Halffter) (*Pedaridium*); *Nunoidium argentinum* (Arrow) (*Pedaridium*); *Onoreidium bottimeri* (Howden & Young) (*Pedaridium*); *O. cristatum* (Arrow) (*Trichillum*); *O. howdeni* (Ferreira & Galileo) (*Pedaridium*); *O. ohausi* (Arrow) (*Trichillum*); *Pereiraidium almeidai* (Pereira) (*Pedaridium*); *Trichillidium brevisetosum* (Howden & Young) (*Pedaridium*); *T. caingua* (Martínez) (*Pedaridium*?); *T. pilosum* (Robinson) (*Trichillum*); *Trichillidium quadridens* (Arrow) (*Pedaridium*). Se presentan mapas de distribución para las especies nuevas, para *Pereiraidium almeidai*, y para cada especie de *Genieridium*.

Resumo: A **nova subtribo** Scatimina (parte da tribo Ateuchini Castelnau) é descrita, e inclui os gêneros *Scatimus* Erichson; *Scatrichus* Génier & Kohlmann, 2003; *Trichillum* Harold, 1868; *Pedaridium* Harold, 1868; *Eutrichillum* Martínez, 1969, **n. status**; *Besourenga*, **n. g.** (espécie-tipo *Trichillum minutum* Saylor); *Bradypodidium*, **n. g.** (espécie-tipo *Trichillum bradyporum* Boucomont); *Degallieridium*, **n. g.** (espécie-tipo *Degallieridium lilliputanum*, **n. sp.**); *Feeridium*, **n. g.** (espécie-tipo *Feeridium woodruffi*, **n. sp.**); *Genieridium*, **n. g.** (espécie-tipo *Pedaridium bidens* Balthasar); *Leotrichillum*, **n. g.** (espécie-tipo *Pedaridium louzadaorum* Vaz-de-Mello & Canhedo); *Martinezidium*, **n. g.** (espécie-tipo *Pedaridium galileoae* Génier & Vaz-de-Mello); *Nunoidium*, **n. g.** (espécie-tipo *Pedaridium argentinum* Arrow); *Onoreidium*, **n. g.** (espécie-tipo *Trichillum cristatum* Arrow); *Pereiraidium*, **n. g.** (espécie-tipo *Pedaridium almeidai* Pereira); *Silvinha*, **n. g.** (espécie-tipo *Silvinha unica*, **n. sp.**); y *Trichillidium*, **n. g.** (espécie-tipo *Pedaridium quadridens* Arrow). A subtribo Ateuchina Castelnau é diagnosticada e inclui *Ateuchus* Weber, *Deltorhinum* Harold, *Aphengium* Harold e *Sinapisoma* Boucomont (transferido de Canthonini). Os gêneros *Scatonomus* Erichson, *Anomiopus* Westwood y *Hypocanthidium* Balthasar são transferidos de Ateuchini a Canthonini, e os gêneros *Canthidium* Erichson, *Parachorius* Harold (Ateuchini) e *Holocanthon* Martínez & Pereira (Canthonini) a Coprini. Os gêneros *Bdelyropsis* Pereira, Vulcano & Martínez, *Bdelyrus* Harold, *Coptorhina* Hope, *Delopleurus* Erichson, *Demarziella* Balthasar, *Onychothecus* Boucomont, *Paraphytus* Harold, *Pedaria* Laporte, *Pleronyx* Lansberge, *Pseuduroxys* Balthasar, *Sarophorus* Erichson e *Uroxys*

Westwood são considerados *incerta sedis* em Ateuchini. É apresentada uma chave para os gêneros de Scatimina, e outra para as espécies de *Genieridium*, que são também diagnosticadas. Cada gênero de Scatimina é diagnosticado e é acompanhado por uma lista de suas espécies já descritas, com observações sobre afinidades, composição e distribuição. Todos os gêneros, exceto *Scatimus* e *Scatrichus*, são (re)descritos, e todo o material examinado das espécies já descritas é listado. As seguintes três **novas espécies** são descritas: *Degallieridium lilliputanum*, **n. sp.**; *Feeridium woodruffi*, **n. sp. e** *Silvinha unica*, **n. sp.**. As seguintes 32 **novas combinações** são estabelecidas: (gênero original entre parênteses): *Besourenga minutus* (Saylor) (*Trichillum*)**;** *B. vejdovskyi* (Balthasar) (*Trichillum*); *B. amarillai* (Aguilar) (*Pedaridium*); *B. horacioi* (Martínez) (*Trichillum*); *Bradypodidium adisi* (Ratcliffe) (*Trichillum*); *B. bradyporum* (Boucomont) (*Trichillum*); *B. venezuelense* (Ferreira & Galileo) (*Pedaridium*); *Eutrichillum arcus* (Solís & Kohlmann) (*Trichillum*); *E. hirsutum* (Boucomont) (*Trichillum*); *E. hystrix* (Arrow) (*Trichillum*); *Genieridium bidens* (Balthasar) (*Pedaridium*); *G. bordoni* (Martínez) (*Pedaridium*); *G. cryptops* (Arrow) (*Pedaridium*); *G. margareteae* (Génier & Vaz-de-Mello) (*Pedaridium*); *G. medinae* (Gill & Vaz-de-Mello) (*Pedaridium*); *G. paranense* (Arrow) (*Pedaridium*); *G. zanunciorum* (Vaz-de-Mello & Canhedo) (*Pedaridium*); *Leotrichillum louzadaorum* (Vaz-de-Mello & Canhedo) (*Pedaridium*); *Martinezidium fulgens* (Arrow) (*Pedaridium*); *M. galileoae* (Génier & Vaz-de-Mello) (*Pedaridium*); *M. martinsi* (Ferreira & Galileo) (*Pedaridium*); *M. maya* (Vaz-de-Mello, Halffter & Halffter) (*Pedaridium*); *Nunoidium argentinum* (Arrow) (*Pedaridium*); *Onoreidium bottimeri* (Howden & Young) (*Pedaridium*); *O. cristatum* (Arrow) (*Trichillum*); *O. howdeni* (Ferreira & Galileo) (*Pedaridium*); *O. ohausi* (Arrow) (*Trichillum*); *Pereiraidium almeidai* (Pereira) (*Pedaridium*); *Trichillidium brevisetosum* (Howden & Young) (*Pedaridium*); *T. caingua* (Martínez) (*Pedaridium*?); *T. pilosum* (Robinson) (*Trichillum*); *Trichillidium quadridens* (Arrow) (*Pedaridium*). Mapas de distribuição são apresentados para as espécies novas, para *Pereiraidium almeidai*, e para cada espécie de *Genieridium*.

Introduction

The tribe Ateuchini, as defined by Montreuil (1998), includes most genera of Scarabaeinae with apically expanded meso-and metatibiae not assignable to the other tribes with similarly expanded tibiae: namely Coprini, Phanaeini, Oniticellini, Onitini and Onthophagini. All genera presently included in Ateuchini are tropical, and the tribe is presently defined mostly on the absence of the defining characters of the remaining paracoprid (tunneler) tribes. In other words, Ateuchini as presently comprised, lacks a unique set of defining characters (synapomorphies).

My purpose is to define a new subtribe for some Neotropical genera now included in Ateuchini. It is a contribution toward an ongoing study of the suprageneric classification of the tribe by me and François Génier.

History of the genus *Pedaridium* Harold, 1868 and relatives

The genus *Pedaria* was erected by Laporte (1832), for a single African species, *P. nigra*, from Senegal. In 1859, Harold described the first non-African species of this genus, *Pedaria hirsuta*, based on a number of specimens from Brazil from his own and Sturm's collections.

In 1868, Harold erected a new scarab genus, *Trichillum*, including in it, *T. heydeni* Harold, 1868, and established in his key the genus *Pedaridium* for the American species of *Pedaria*. He distinguished it from *Trichillum* by the shorter hind basitarsomere and unexpanded epipleuron. He did not designate a type species for *Pedaridium*; however, as only *Pedaria hirsuta* was described from the Americas, it can be considered an implicit designation (monotypy). Harold (1869a) made, finally, the combination *Pedaridium hirsutum*, and Preudhomme de Borre (1880) described a second species of *Trichillum*.

Arrow (1913) described three more species of *Pedaridium,* Boucomont (1928) described two more species of *Trichillum*. Arrow (1931) revised the genus *Trichillum* and described three new species, not mentioning species described in 1928 by Boucomont. The same author, one year later (Arrow, 1932) described two more species of *Pedaridium* and gave an updated key for the genus *Pedaridium* and comments about Boucomont's (1928) descriptions of *Trichillum*. Saylor (1935) described three more species of *Trichillum*.

Paulian (1936) described the homonymous *T. arrowi* based on a single specimen from Pará, Brazil, giving a new key for the species known in this genus, except for those of Saylor (1935). Balthasar (1938) described one more species of *Pedaridium* and presented a key for all species of *Pedaridium* known at that time. The same author (Balthasar, 1939a) reviewed the genus *Trichillum* and described two new species, and later (Balthasar, 1942) one more species of *Trichillum*. Pereira (1946) described another species of *Pedaridium*. Robinson (1948) described one more *Trichillum*. Martínez (1951) described another *Pedaridium.*

Martínez (1969) erected the subgenus *Eutrichillum* for *Trichillum*, transferred *T. bradyporum*, *T. ohausi* and *T. elongatum* to *Pedaridium*, hypothesized that *T. hirsutum* could also be a *Pedaridium*, and considered the last and *T. cristatum* as *incertae sedis*. In the same paper the author reviewed the subgenus *Trichillum*, describing three new species in it and one new species without stated subgenus. The same author (Martínez, 1974) described "*Pedaridium* (?) *caingua"*, and stated that this new species, together with *P. quadridens*, should constitute a new taxon under study by him.

Ratcliffe (1980) described adults, larvae and pupae of a new species of *Trichillum*, gave both keys for subgenera of *Trichillum* and for species in the subgenus *Eutrichillum*, including *T. hirsutum* Boucomont, 1928. The same author (Ratcliffe, 1981) redescribed the type of *Trichillum hirsutum*.

Howden & Young (1981) described two species of *Pedaridium* from Panama, assigned *Trichillum pilosus* Robinson, 1948 to *Pedaridium*, based on characters used by Paulian (1936) and Martínez (1969) to distinguish these genera, and commented on the confusion regarding distinguishing characters between *Trichillum* and *Pedaridium*, and the need of comprehensive revisions of both.

Martínez (1992) described a Venezuelan species of *Pedaridium*, and in the abstract of this paper, in both Spanish and English, mentioned an undescribed species from Mexico.

Ferreira & Galileo (1993) revised the genus *Pedaridium*, excepting for *P. bordoni* Martínez, 1992, that was probably not known to them. In this revision, they transferred one species of *Trichillum* to *Pedaridium*, described six new species, and chosed to enphasize the shape of pseudepipleuron (then called epipleuron) to distinguish *Trichillum* and *Pedaridium*. It is important to point out that the authors did not examine most of the type specimens, which are in European museums.

Verdú & Galante (1997) described a new species of *Trichillum* from Uruguay, and gave a new key for species in the subgenus *Trichillum.*

Montreuil (1998), in a paper on phylogenetic relations between Ateuchini and Coprini, examined *Pedaridium* (the type species and, possibly, some additional species not stated), and placed it in an unsolved clade including *Demarziella*, *Pedaria, Sarophorus* Erichson, 1847, and the clade *Bdelyrus* Harold, 1869 + *Bdelyropsis* Pereira, Vulcano & Martínez, 1960. This paper did not include *Trichillum*.

Vaz-de-Mello & Canhedo (1998) described two more *Pedaridium* species, and included those and *P. bordoni* Martínez, 1992 in the Ferreira & Galileo (1993) key for species. In 2001, Aguilar described a new Paraguayan *Pedaridium*. The author did not mention the revision by Ferreira & Galileo (1993), and stated that the new species had sinuate epipleura *(sic)*, a character that would place the species in *Trichillum* according to Ferreira & Galileo (1993).

Verdú & Galante (2001) described larvae and breeding behavior of two species of *Pedaridium,* and concluded that the genus seems to be polyphyletic based on larval morphological characters. A short comment was made on *Trichillum externepunctatum* corroborating Ohaus' (1909) and their own data on *Pedaridium*, that those genera do not present nesting behavior.

Génier & Vaz-de-Mello (2002) diagnosed and designated lectotypes for those species described by Arrow in both *Trichillum* and *Pedaridium*, synonymizing three previously described species, and described two new species for species previously erroneously identified. Solís & Kohlmann (2003) described a species of *Trichillum (Eutrichillum);* Gill & Vaz-de-Mello (2003) and Vaz-de-Mello *et al.* (2004) described two other *Pedaridium* species. Vaz-de-Mello (2003) presented a preliminary overview of the entire group, without nomenclatorial validity (this work contains a disclaim), but containing an exhaustive review of literature and specimens. Finally, Vaz-de-Mello & Génier (2005) synonymized three previously described species in *Trichillum* and *Pedaridium*, and described three new previously misidentified species in the genus *Trichillum*.

Since very early, both *Trichillum* and *Pedaridium* have been placed near *Ateuchus* (as *Choeridium*, for instance by Harold (1869a)). Morphological differences between *Pedaridium* and *Pedaria* have never been pointed out in literature, since the only commented difference between them is the geographical distribution.

Differences between the genera *Trichillum* and *Pedaridium* have been discussed in many papers. In original description of the genera (for *Pedaridium*, in key), Harold (1868) stated that they do differ by shape of "epipleuron" and length of the hind basitarsomere. After that, only the second character was taken into account for assigning new species to each of those genera (Arrow, 1913, 1931, 1932;

Balthasar, 1939; Martínez, 1969). Howden & Young (1981) used the unique or double setose puncture rows in the interstriae to differentiate genera, resulting in the placement of all Panamanian species in *Pedaridium*. Ferreira & Galileo (1993) used just the shape of epipleuron, pointing out that Pereira (1946) had described a *Pedaridium* with hind basitarsomere longer than the second tarsomere. During the 20th century, some species described in *Trichillum* have been transferred to *Pedaridium* by subsequent authors, so did Martínez (1969), with three species, Howden & Young (1981), with one species, and Ferreira & Galileo (1993), who tranferred another species.

Verdú & Galante (2001), citing larval morphology of three species of the genus *Pedaridium*, and mentioning information provided by Vaz-de-Mello *in litteris* on adult morphology, considered that genus to be probably a polyphyletic group.

All the confusion regarding generic assignments indicates that the two genera are not reciprocal monophyletic groups, and that a global revision of this group is necessary in order to establish consistent genus-level taxa. Moreover, the enormous variability in external characters such as dorsal hairs, punctures, legs and clypeal form, also indicate that other characters must be used in order to reach a more accurate generic system for this group.

Vaz-de-Mello (2003) proposed the division of the group, based on an extensive morphological phylogenetic analysis, in twenty groups with generic status, without formally describing them. This classification, with many modifications based on posterior unpublished analyses is very similar to the one adopted here.

Up to now (excluding the present paper), the genus *Pedaridium* has included 28 valid species. The genus *Trichillum* includes two subgenera. The nominotypical subgenus contains ten valid species names, and *Trichillum (Eutrichillum)*, contains six valid species names. One species name is considered as *incerta sedis*, without subgeneric placement.

The former genus *Scatimus* Erichson, 1847

Erichson (1847) erected the genus for the new species *Scatimus cucullatus* which he distinguished from *Choeridium* Serville (= *Ateuchus* Weber) based primarily on the presence in *Scatimus* of carinae on the outer edge of the meso- and metatibiae. Other species have been added to the genus by Harold (1862; 1869), Preudhomme de Borre (1886), Balthasar (1939), Martínez (1988), and Kohlmann and Solís (1996). The phylogenetic position of this genus has been debated, some considering it to be a close relative of *Ateuchus* (Erichson, 1848; Lacordaire, 1856, Harold, 1867; Bates, 1887; Balthasar, 1939a; Edmonds & Halffter, 1978; Halffter & Edmonds, 1982); and others placing it closer to *Copris* Geoffroy (Lüderwaldt, 1931; Pereira, 1954); and yet others as a “bridge” between *Ateuchus* and *Copris* (Martínez, 1988).

Scatimus was first reviewed by Balthasar (1939). Génier and Kohlmann (2003) split the genus, creating *Scatrichus* for *S. bicarinatus* Harold, 1869 and two new species, while in *Scatimus* two species have been synonymized and four described as new, both genera being taxonomically reviewed. Génier and Kohlmann also proposed the phylogenetic sisterhood between (*Scatimus* + *Scatrichus*) and *Pedaridium*.

Materials and Methods

This study is based on examination of about fifteen thousand specimens belonging to more than one hundred species (many yet undescribed) from the following collections (institutional curators' names in parenthesis):

ABC: Alberto Ballerio personal collection, Brescia, Italy.
AMBC: Ayr M. Bello personal collection, Rio de Janeiro, RJ, Brazil.
BDGC: Bruce D. Gill personal collection, Woodlawn, Ontario, Canada.
BMNH: The Natural History Museum, London, England (Malcolm Kerley).
BRBA: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires (A. Bachmann).
CAMC: Claudia A. Medina personal collection, Cali, Colombia.
CMNC: Canadian Museum of Nature, Ottawa, Canada (Henry Howden and François Génier).
CNCI: Canadian National Collection of Insects, Ottawa (Antony Davies and Patrice Bouchard).
EMOC: Enrique Montes de Oca personal collection, Xalapa, Mexico.
EMRL: Entomolog7y Museum and Research laboratory, McGill University, Montreal, Canada.
ESAP: Escola Superior de Agricultura "Luiz de Queirós", Universidade de São Paulo, Piracicaba, SP, Brazil (Roberto A. Zucchi).
FEIS: Faculdade de Engenharia de Ilha Solteira da Universidade Estadual Paulista, Ilha Solteira, SP, Brazil (Carlos A. H. Flechtmann).
FMLT: Fundación Miguel Lillo, San Miguel de Tucumán, Argentina (A. Terán).
FMNH: Field Museum of Natural History, Chicago, USA (Alfred Newton)
FVMC: Fernando Vaz-de-Mello personal collection, Lavras, MG, Brazil.
FZRS: Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, RS, Brazil (Maria Helena M. Galileo).
GVHC: Gonzalo and Violeta Halffter personal collection, Coatepec, México.
IAHC – Instituto Alexander von Humboldt, Villa de Leyva, Colombia (Fernando Fernández).
IBSP: Coleção Entomológica "Adolph Hempel", Instituto Biológico, São Paulo, SP, Brazil (Sergio Ide).
IEX: Instituto de Ecología, A.C., Xalapa, México (Miguel Ángel Morón).
IRSN: Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium (Marcel Cludts).
LDC: Leonardo Delgado personal collection, México, DF, México.
MAMC: Miguel A. Morón personal collection, Xalapa, México.
MAPA: Museu Anchieta, Porto Alegre, RS, Brazil (Fernando R. Meyer).
MEUA: Museo Entomológico, Universitad d'Alicant, Spain (José Verdú and Eduardo Galante).
MNHN: Muséum National d'Histoire Naturelle, Paris (Yves Cambefort and Olivier Montreuil).

MNRJ: Museu Nacional da Universidade Federal do Rio de Janeiro, RJ, Brazil (Miguel A. Monné and Paulo R. Magno).
MTMB: Magyar Természettudomány Muzéum, Budapest, Hungary (Otto Merkl).
MZSP: Museu de Zoologia da Universidade de São Paulo, SP, Brazil (Ubirajara R. Martins, Cleide Costa, Carlos Campaner, Sergio Ide and Sonia Casari).
NHMB: Naturhistorisches Museum, Basel, Switzerland (Eva Sprecher).
NMM: Natuurhistorisch Museum Maastricht, The Netherlands (F. Dingemans-Backels and Alexey Tishechkin).
NMP: Narodní Muzeum, Prague (NMP – Josef Jelínek).
PSC: Paul Schoolmeesters private collection, Herent, Belgium.
PUCE: Pontifícia Universidad Católica del Ecuador, Quito, Ecuador (Giovanni Onore and Carlos Carpio).
TAMU: Texas A&M University, Austin (Ed Riley via Dave Edmonds).
UNSM: University of Nebraska State Museum, Lincoln, NE, USA (Brett Ratcliffe and Mary Liz Jameson).
URRJ: Universidade Federal Rural do Rio de Janeiro, Seropédica, RJ, Brazil (Francisco Racca Filho and Paschoal Grossi)
USNM: United States National Museum, Washington, USA (Nancy Adams)
UVG: Universidad del Valle de Guatemala (Enio Cano and Jack Schuster).
WDEC: W.D. Edmonds personal collection, Marfa, USA.
ZMHB: Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (Hella Wendt).

Species already described (except for *Scatimus* and *Scatrichus*, for which the excellent paper by Génier and Kohlmann [2003] is referred) and those described in the present paper have a mention of the material examined up to date, which will be referred in subsequent papers.
As for geographical distributions, I reffer to the excellent paper by Morrone (2006).
SEM photos have been taken with a LEO XXX variable pressure scanning electron microscope, at NAP-MEPA (ESALQ, USP).

Results and Discussion

Scatimina, new subtribe

Diagnosis: The subtribe Scatimina can be separated readily from all remaining Scarabaeinae by the following combination of characters: Trochantofemoral pit present; hypomeron anteriorly deeply excavated, excavation bordered posteriorly by transverse carina; pseudoepipleuron present lateral to 8th elytral stria, delimited by folding or convexity of 9th interstria, and separated from epipleuron by stria distinctly visible at least basally (Fig. 5-11).

Description: Clypeus centrally with an emargination, or two or more teeth, or both, never simply rounded; external genal angle clearly obtuse; clypeal ventral process a transverse carina, sometimes angled or tuberculated in middle, united to transversal supraepipharyngeal ridge by angle or short longitudinal carina. Separation between submentum and gula simply curved to obtusely V-shaped, sometimes indistinct, gula laterally glabrous, and anteriorly slightly pointed. Antennae with nine segments, first segment of club completely tomentose. Mentum apically not emarginated, or only slightly so, with medial dorsal, pointed prolongation (serving as "base" for membranous dorsally-positioned ligulae). Labial palpus three-segmented, third much narrower and smaller than second. Side of pronotal disk with indistinct to distinct callosity, without longitudinal sulcus or distinct fovea; centrally without elevations, sulci, or tubercles, simply convex. Posterior pronotal border unbeaded. Hypomeron anteriorly deeply excavated, excavation separated from posterior part by transverse carina. Mesosternum anteriorly with transverse sulcus. Metasternum anteriorly with transverse sulcus parallel and very close to (often coincident with) middle of meso-metasternal suture, prolonged parallel to middle coxa laterally.

Protibial apex mesally truncated in straight angle, except for mesal apical tooth in some males; apical protibial border straight, continuous (i. e., without angle) with anterior border of apical tooth, such that two margins (protibial body and apical tooth) lie in straight line (Fig. 1-4). Protibia with three or fewer teeth, with tarsal insertion near the mesal apical border. Protrochantofemoral pit present. Middle coxal axis very slightly angled, almost parallel to longitudinal body axis. Mesotibial apex obliquely truncated (mesal angle acute). Metatibial apex entire below tarsal insertion. Meso- and metatibiae with longitudinal external carina indicated on disc, and dorso-external longitudinal carina well defined, while ventro-external one is absent or indicated by row of setae. Meso-and metatibial apical fimbriae alternate in size and thickness, with short, thick setae comingled with long, narrow setae (sparse short ,thick setae also present on the external surface of meso and metatibiae). Elytra with nine striae. Pseudoepipleuron present lateral to 8th elytral stria, delimited by fold or convexity of 9th interstria and separated from epipleuron by epipleural stria well defined at least in basal half (Fig. 5-11).

Sixth abdominal ventrite never shortened medially. Basal pygidial sulcus present. Male genitalia with genital segment transverse, conformed of a central rounded plate and a lateral rectangular elongated plate at each side. Paramera almost symmetrical at least in size and shape of sides. Transverse parietal lamella of internal sac (lupe-shaped lamella of authors) with basal arc very reduced, so that one side of the circle is obliterated or completely absent. Female genitalia with coxites present, sometimes fused ventrally. Spermathecal base simply rounded or pointed, never bilobed or expanded; apex simply pointed.

Type genus: *Scatimus* Erichson, 1847

Remarks

The new subtribe includes the following Neotropical genera: *Scatimus* Erichson; *Scatrichus* Génier & Kohlmann, 2003; *Trichillum* Harold, 1868; *Pedaridium* Harold, 1868; *Eutrichillum* Martínez, 1969, **new status**; *Besourenga*, **new genus**; *Bradypodidium*, **new genus**; *Degallieridium*, **new genus**; *Feeridium*,

new genus; *Genieridium*, **new genus**; *Leotrichillum*, **new genus**; *Martinezidium*, **new genus**; *Nunoidium*, **new genus**; *Onoreidium*, **new genus**; *Pereiraidium*, **new genus**; *Silvinha*, **new genus**; and *Trichillidium*, **new genus**.

Besides the characters mentioned above, the following are apomorphies supporting Scatimina (Vaz-de-Mello, in preparation): the presence of a pit in the external face of first and second antennal lamellae (these pits appear to have been secondarily lost in *Scatrichus*), the presence of an anterior transverse carina on mesoepimeron (lost in the group formed by *Trichillum*, *Besourenga*, *Degallieridium*, *Feeridium* and *Eutrichillum*, and in most species of *Scatimus*), the spatulate form of the protibial spur in males (modified in one species of *Trichillum* and at least some species of *Scatimus*), the sinuate form of middle tibial spurs, the absence of a basal raspula and the presence of an elongated flagelliform sclerite in the internal sac.

The Scatimina are distributed in the entire Neotropical region as defined by Morrone (2006), except for the Antillean Dominion, as well as in the entire Mexican Transition Zone, a province of the Nearctic Region (Sonora), and part of the South American Transition Zone (Monte and – maybe - Prepuna provinces).

The throchanterofemoral pit is not unique to the new subtribe but is also present in other former ateuchines, commented below:

Although *Pedaria* and *Demarziella* have been regarded as relatives of *Trichillum* and *Pedaridium* (based on the presence of dorsal setae and fused abdominal sternites), they present the following important differences: Elytra with ten striae (as opposed to nine in the Scatimina – the ninth and tenth striae are often partially fused in the middle but well differentiated both anteriorly and posteriorly); paramera distinctly asymmetrical; and the well developed lupe-shaped lamella in the internal sac. These characters of *Pedaria* and *Demarziella* are shared with *Coptodactyla* Burmeister, 1846, *Thyregis* Blackburn, 1904 and *Microcopris* Balthasar, 1958, now formally in the tribe Coprini, which lack fused abdominal sternites. These genera might well be regarded as a separate tribe (Coptodactylini Paulian, 1933), but that is out of the scope of the present paper. I presently regard them as *incertae sedis*.

The temptation to include the genus *Uroxys* in Scatimina is great, but the heterogeneity and presumed polyphyletic origin of the genus (Halffter & Matthews, 1966; Halffter & Edmonds, 1982; Martínez, 1988) and various taxonomic and nomenclatorial difficulties make it inadvisable at the present time. One difficulty is the uncertain position of the type-species of *Uroxys*. Some species presently in *Uroxys* or assignable to it are here excluded from Scatimina because of the presence of a longitudinal sulcus on each side of the pronotum and the complete lupe-shaped sclerite in the internal sac. It seems that at least one of the species-groups now placed in *Uroxys* belongs or is very close to Scatimina.

Finally, *Bdelyropsis* Pereira, Vulcano & Martínez 1960 presents pseudoepipleuron originating from a fold in the 8th interstria, and appears to be related to a group of genera currently in the Canthonini, that includes *Zonocopris* and *Cryptocanthon*, among others (Vaz-de-Mello, in press; see below on *Bdelyrus*).

A new diagnosis for the tribe Ateuchini greatly depends on the reassignment of the genera here considered as *incertae sedis* to other tribes and will be presented in a subsequent paper. The proposal of a new subtribe subtribe in Ateuchini results in the recognition of the subtribe Ateuchina Castelnau, which is provisionally diagnosed as follows: medial part of clypeal surface concave, clypeal ventral process in form of a transverse carina; front throcantofemoral pit absent; front tibia with anterior border completely straight (as in Scatimina), except for male's antero-apical tooth, nine elytral striae (with pseudoepipleuron delimited by a fold or convexity in the 9th interstria); pronotum simply convex, at most with discal longitudinal sulcus; lateral pronotal pit well defined; hypomeron anteriorly deeply excavated and with a transverse carina (as Scatimina); paramera symmetrical; internal sac sclerites represented by few small flagelliform lamellae, all apical in position.

As here defined, the subtribe Ateuchina is Neotropical and Nearctic and includes the following genera: *Ateuchus* Weber, 1801 (with the exclusion of some species to be assigned to other genera in the near future), *Deltorhinum* Harold, 1869, *Aphengium* Harold, 1868, and *Sinapisoma* Boucomont, 1928 (formerly placed in Canthonini), as well as taxa yet to be described.

Most other ateuchine genera (all lacking throcantofemoral pit) are here considered to be Ateuchini *incertae sedis*.

The genera *Canthidium* Erichson, 1847 (based on examination of *Canthidium lentum* Erichson, 1847, type species) and *Parachorius* Harold, 1873 have ten elytral stria, the 9th one being easily discernable of the 8th only at elytral apex, and both have hypomera very feebly excavated anteriorly, although the transverse carina is present, and an angle between the anterior borders of the apical protibial teeth and the mesal apical margin of tibia (that is, anterior tibial border as a whole is not straight). Those characters point to a close relationship between them and *Holocanthon* Martínez & Pereira, 1956 (today placed in the Canthonini), and justify their inclusion in the tribe Coprini, where the most closely related group would be the one composed of *Dichotomius* Hope, 1838, and its allies. The subgenus *Eucanthidium* Martínez & Halffter, 1986 (based on examination of *Canthidium cupreum* Blanchard, 1845, type species), shares all those characters except that only 9 elytral striae are present; *Eucanthidium* may later turn out to be a taxonomic isolate.

Bdelyrus Harold, 1868, has a double pseudoepipleuron, originated from folds in both 8th and 9th interstriae, lacks the developed trochantofemoral pit, and has a very peculiar assemblage of internal sac sclerites. However, its unusual abdominal shape is similar to that of *Paracryptocanthon*, and the supraunguicular spines found otherwise only in *Zonocopris* appears to relate *Bdelyrus* to the yet unnamed group that includes those genera (Vaz-de-Mello, in press, see above also on *Bdelyropsis*).

Onychothecus Boucomont, 1912 and *Paraphytus* Harold, 1877 both possess ten elytral striae. *Scatonomus* Erichson, 1835 and *Anomiopus* Westwood, 1842 (and the related *Hypocanthidium* Balthasar, 1938) appear to be true Canthonini, in fact closely related to *Canthon*. This has been yet suggested by Canhedo (2006), who didn’t make any formal assignment, and I here assign them to that tribe.

Finally, *Sarophorus*, *Coptorhina*, *Frankenbergerius* and *Delopleurus* present a unique lateral sinuosity on elytra, a longitudinal groove on gula, a very simple internal sac, in some cases lacking sclerites, and a very distinctive spermatheca with flat basal paired lobes found otherwise only in some Canthonini; these genera should be considered as a group distinct from Ateuchini (Zunino, 1983; Frolov & Scholtz, 2003; Frolov & Scholtz, 2005).
A summary of the subtribal or tribal position of genera commented on above as stated by this work is presented on Table 1.

The present necessity to fragment two previously very heterogenous genera, *Trichillum* and *Pedaridium*, into 15 is yet another consequence of the tremendous increase in data and material during the remarkable surge in field and museum work on dung beetles during the past 30 or so years. The number of new species known by me in these two groups alone has increased by about 80 (200%) in the last decade; while some are described here, many will be described in subsequent papers. Likewise, in this paper and elsewhere, the recent increase in the number of new taxonomic characters has permitted taxonomic and cladistic studies of higher resolution. Other recent cases of severe splitting of previously heterogenous genera are those of *Panelus* Lewis, 1895 (Scholtz & Howden, 1987; Ochi *et al*., 1998; Paulian, 1976; 1985; Matthews, 1974), *Epilissus* Reiche, 1841 (Olsoufieff, 1935; 1947; Paulian, 1939), and the " group" *Stiptopodius* Harold, 1871 (Branco, 1989; 1990; 1991; 1992a; 1992b; 1992c). My personal opinion is that, if those cited genera (including those treated here) were of larger size and with more diversity in collections (it must be said that most collections are very poor in representatives of the diversity of those groups, most having a very small number of species of few subgroups of it), then they would have been splitted (or independently described one by one) much earlier.

Key to the genera of Scatimina (partly taken from Génier & Kohlmann, 2003)

1. Length of last abdominal sternite (measured along midline) about equal to lengths of other sternites or not longer than two of them together … 2
-. Last abdominal sternite very long (measured along midline), extending from pygidium to metacoxae; remaining sternites clearly discernable only laterally … 3

2. Head with two parallel transverse carinae. Lateral edge of pronotum crenulate, with setose punctures. Apical declivity of elytron with setiferous punctures on interstriae. Throchantofemoral pit of anterior leg oval, transverse. Lateral declivity of pronotum with accessory setiferous punctures. Southeastern and central Brazil … **14. *Scatrichus* Génier & Kohlmann, 2003**
-. Head with one transverse carina, or with one conical tubercle. Lateral edge of pronotum simple, lacking setose punctures. Apical declivity of elytron lacking setiferous punctures on interstriae. Throchantofemoral pit of anterior leg rounded. Lateral declivity of pronotum lacking setiferous punctures. Northern South America up to northwestern Mexico … **13 *Scatimus* Erichson, 1847**

3. Elytral pseudoepipleuron forming two sinuosities, the posterior one (near metacoxa) partially covering true epipleuron, and sometimes angled (Fig. 5, 9) … 4

- Elytral pseudoepipleuron at most forming one long sinuosity in its anterior half that does not fold over true epipleuron (sometimes true epipleuron with excavation near metacoxa) (Fig. 6-8, 10-11) … 5

4. Clypeal teeth clearly arising from below dorsal clypeal margin (Fig. 91). Pseudoepipleuron without anterior longitudinal carina in the basal half; posterior pseudoepipleuron sinuosity bent over anteriorly, posterior half of pseudoepipleuron not distinguishable from true epipleuron (that is, epipleural stria shaded off in the posterior half) (Fig. 9). Male with apical segment of anterior tarsi excavated dorsally to receive claws, and paramera strongly divergent in the middle and convergent apically (Fig. 92). Southeastern Brazil … **15. *Silvinha* new genus**

-. Clypeal teeth continuous with dorsal clypeal margin (Fig. 98, 100, 102). Pseudoepipleuron with a sharp anterior longitudinal carina extending up to the posterior pseudoepipleuron sinuosity, which is bent over true epipleuron and angled; posterior half of pseudoepipleuron completely distinguishable posteriorly from true epipleura by epipleural stria (Fig. 5). Male with apical segment of anterior tarsi not modified; paramera flattened, truncated apically, without external lobes. South America east of the Andes excluding southern Argentina … **17. *Trichillum* Harold, 1868**

5. Pseudoepipleuron posteriorly abruptly narrowed from near metacoxa, margin forming an angle (Fig. 10)… 6

-. Pseudoepipleuron gradually reduced in width, margin straight near metacoxa (Fig. 6, 8, 11) ... 7

6. Clypeo-genal suture clearly visible, extending from fronto-clypeal suture to clypeo-genal border. Clypeo-genal border incised, with clypeus and gena separately rounded, clypeus evenly rounded between clypeal teeth and clypeo-genal suture (Fig. 49). Northern Argentina, central and southeastern Brazil, Paraguay, eastern Bolivia, Amazonia (except north), one isolated species in Costa Rica … 4**. *Eutrichillum* Martínez, 1969, new status**

-. Clypeo-genal and fronto-clypeal sutures indistinct. Clypeal margin lateral to clypeal teeth strongly curved or angled, becoming straight anteriorly to clypeo-genal border, itself straight or slightly sinuate (Fig. 39, 41). Paraguay, eastern Bolivia, central Brazil and western Amazonia … **1. *Besourenga* new genus**

7. Head with two horns (males) (Fig. 88) or two feeble separate convexities (females) (Fig. 90) on frontoclypeal region; anterior margin of pronotum beaded. Southern Brazil … **12. *Pereiraidium*, new genus**

-. Head without horns or tubercles on frontoclypeal region, anterior margin of pronotum unbeaded … 8

8. Front tibia with two or three lateral teeth which together occupy one-half or less of length of tibia; middle tibia not strongly widened apically, apico-lateral area ventrally covered by very long setae … 9

-. Front tibia with three lateral teeth together occupying at least apical three-fifths of length of tibia; if occupying less than three-fifths of tibial length, then middle tibia with strong lateroventral tooth and apex abruptly extended laterally, and with sparse apical ventral setae … 10

9. Head flat to very feebly evenly convex, lacking evident shallow concavities in front of eyes; clypeus laterally straight to slightly curved outwardly, gena not protruding beyond clypeus (Fig. 43, 45). Body elongated (Fig. 17), elytral striae non-moniliform (strial punctures small and well separated). Claws and apical segment of front tarsi of males strongly modified (Fig. 46). Costa Rica to southeastern Brazil … 2**. *Bradypodidium*, new genus**

-. Head evenly convex centrally, with distinct shallow concavities in front of eyes; clypeal margin laterally curved inwardly, gena protruding beyond clypeus (Fig. 93, 95, 97). Body strongly rounded (Fig 35-36), striae moniliform at least in the apical half (strial punctures twice width of stria, punctures weakly separated or contiguous in posterior half). Claws and tarsomeres of male not modified. Nicaragua to Ecuador; Brazil, Argentina, Paraguay, Bolivia … **16. *Trichillidium*, new genus**

10. Sides of pronotum (in dorsal view) sinuous (Fig. 29, 87). Elytra distinctly tectiform, sutural (first) interstriae distinctly elevated and disc flat at each side (Fig. 29). Southern Brazil … **11. *Pedaridium* Harold, 1868**

-. Sides of pronotum, in dorsal view, not sinuated. Elytra at most slightly tectiform; sutural (first) interstria not distinctly elevated; elytral surface evenly convex … 11

11. Eyes dorsally as wide as long; dorsal interocular distance less than two times width of one eye (Fig. 20, 52); pronotum separated from hypomeron by row of punctures, not by carina. Amazon river border and French Guyana … **5. *Feeridium,* new genus**

-. Dorsal interocular distance at least five times width of a single eye; pronotum separated of hypomeron by sharp longitudinal carina or at least weak carina between punctures (Fig. 59) … 12

12. Clypeal teeth upturned and widely separated, area between teeth shallow, very widely U-shaped; head central surface strongly convex, sometimes with a transverse carina. Clypeal teeth separated by a distance at least as wide as a half of interocular width, generally much more (Fig. 79, 82-83). Middle (and to lesser degree hind) tibiae, in ventral view, with strong tooth near middle of lateral border, tooth bearing a very thick and short seta (this structure is similar to structures that interrupt the ventral transverse apical carina of the same tibia) (Fig. 81). Body strongly convex, oval (Fig. 27-28). Ecuador, Panama and Costa Rica … **10. *Onoreidium*, new genus**

-. Head flat or anterior margin in the middle concave, or clypeal emargination distinct, if teeth absent then emargination widely V-shaped (strongly curved in the middle). Middle and hind tibiae with very reduced external ventral tooth in the middle, and apically with transverse carina bearing long setae … 13

13. Pseudoepipleuron glabrous, with longitudinal fold making it approximately vertical in anterior half, and horizontal in posterior half. Width of eye (view dorsally) greater than one-half length (Fig. 47, 72). Length under 2.8 mm ... 14
-. Pseudoepipleuron all the same plane, with distinct row of setae along most of length (rarely lacking in anterior third only). Width of eye (view dorsally) equal to or less than one half length. length exceeding 2.8 mm … 15

14. Hypomeron with posterior longitudinal carina. Elytral interstriae uniformly flat, not distictly more convex apically; discal interstriae with single row of setose punctures. Central Brazil, Paraguay, Argentina … **7. *Leotrichillum*, new genus**
-. Hypomeron posteriorly without longitudinal carina. Elytral interstriae more convex apically than on disc; discal interstriae with two rows of punctures and one row of setae. Central Brazil … **3. *Degallieridium*, new genus**

15. Middle and hind tibiae slender, length at least four times apical width. Mexico, Guatemala, Argentina, western Paraguay … **8. *Martinezidium*, new genus**
-. Middle and hind tibia strongly widened posteriorly, length at most three times apical width (in some cases hind tibia strongly modified laterally) ... 16

16. Males with modified claws (Fig. 60, 62), length of meso- and metatibiae more than three times apical width. Eyes dorsally minute or absent; when present separated by more than 10 times their width (Fig. 55, 57, 60, 62, 64, 68, 70). Base of pronotum unbeaded, laterally with weak carina between punctures separating pronotal disk from hypomeron. Pygidium inclinated in ~45 degrees from vertical, in ventral view its horizontal projection ocupying at least 2/5 of abdominal length, generally more. Colombian Andes, southern Venezuela, Bolivia, Paraguay, Brazil and Argentina … **6. *Genieridium*, new genus**
-. Males with claws unmodified, meso-and metatibiae less than three times as long as wide at apex. Eyes dorsally oval and well developed, separated by seven to eight times their width (Fig. 77) . Pronotum beaded basally, separated of hypomeron by strong, smooth carina. Pygidium almost vertical, its horizontal projection ocupying less than 1/5 of abdominal length. Central Argentina … **9. *Nunoidium*, new genus**

1. *Besourenga* **new genus**

Diagnosis: Size small (2-3.5 mm); clypeus with two teeth separated by narrow U- or V-shaped emargination; clypeo-genal edge straight or sinuate, with lateral border of clypeus angled or strongly curved lateral to clypeal teeth (Fig. 39, 41); elytra with only one row of setose punctures on each discal interstria; pseudoepipleuron with an angle near metacoxa, resulting from the very strong reduction of width of pseudoepipleuron from there to the apex (Fig. 10).

Description: Size small, body oval (Fig. 15-16), color grey or brown to black, always lacking metallic sheen. Clypeus anteriorly bearing two strong teeth, separated by narrow U- or V-shaped emargination. Clypeo-genal and fronto-clypeal sutures indistinct. Clypeal margin externally to clypeal teeth strongly curved or angled, becoming straight anteriorly to clypeo-genal border, which is straight or slightly sinuate. Genal margin straight or slightly curved between clypeus and lateral angle (Fig 39, 41). Anterior pronotal border unbeaded. Pronotal disc laterally with a glabrous indistinct callosity, centrally covered by large setose punctures. Hypomeron posteriorly with longitudinal caria. Mesoepimeron with a transverse anterior carina. Metasternon with setigerous punctures on the disc. Elytra with discal interstriae with single row of setigerous punctures, mesal striae slightly to strongly widened and deepened at apical declivity. Pseudoepipleuron with an angle near metacoxa, resulting from the very strong reduction of width from there to the apex; with setigerous punctures present only at base. Front tibiae with three strong lateral teeth, occupying apical four fifths of tibial length; ventrally with scale-like setae on teeth. Parameres shorter than one half of the length of the phallobase, simply elongated and flattened (Fig. 40). Coxites symmetrical well separated. Spermatheca spiral-shaped.

Secondary sexual characters: Males bear a digitiform prolongation of mesal apical angle of protibia, and apical tarsomere of front tarsi excavated dorsally to receive front claws that are strongly curved in the middle, forming an angle (Fig 42). Metasternal disc is somewhat concave in males, and very flat in females.

Type species: *Trichillum minutum* Saylor, 1935 (present designation) = *Besourenga minutus* (Saylor, 1935), **new combination**.

Etymology: Masculine combination of *besouro* (Brazilian Portuguese word for “beetle”), and *Alvarenga*, proper name, in honor to Moacyr Alvarenga, good friend and amateur coleopterist responsible for collecting much of the material analized here and specialist in the taxonomy of the family Erotylidae. *Besourenga* was his nickname in the Brazilian Air Force, where his passion for collecting beetles was widely celebrated.

Distribution: Bolivia east of the Andes, southern Amazonia in Bolivia, Peru and Brazil, eastern Paraguay and central Brazil including western parts of São Paulo, Minas Gerais and Bahia. That distribution comprises the Pantanal and Tapajós-Xingu provinces of the Amazonian subregion, and the Cerrado and Chaco provinces of the Chacoan subregion (Morrone, 2006).

Remarks: A clade comprising *Trichillum*, *Besourenga*, *Degallieridium*, *Feeridium* and *Eutrichillum* is supported by the absence of the transvese carina on mesoepimeral disc, while the sisterhood of *Besourenga* to *Trichillum* is supported by the spiral spermathecal shape and the form of clypeal border sides. The monophyly of the genus is supported by the slight expansion of the lateral genal angle in relation to other groups closely related, the smaller size, and the absence of a lateral pronotal callosity. The presence of setigerous punctures in the pronotal disc (also present in one species of *Trichillum*) and the modification of front claws in males are character states whose optimizations are ambiguous and could be merely symplesiomorphies. Except for *B. horacioi* from forests in southern Amazonia, all species of *Besourenga* are from open habitats in the Chaco and Cerrado biomes. Specimens of this genus are usually collected with flight intercept traps, at light, or more rarely with dung-baited pitfall traps.

Composition: Besides the type species, the new genus includes *Besourenga vejdovskyi* (Balthasar, 1939), **new combination** (described as *Trichillum*), *Besourenga amarillai* (Aguilar, 2001), **new combination** (described as *Pedaridium*), *Besourenga horacioi* (Martínez, 1969), **new combination**, and several new species currently under study.

Material examined:

1.1. *Besourenga minutus* (Saylor, 1935), **new combination**
Trichillum minutum Saylor, 1935: 207; Balthasar, 1939: 13, 20, 24; Blackwelder, 1944: 204; Hamel *et al.*, 2006: 12.
Trichillum (Eutrichillum) minutum; Martínez, 1969: 120-121; Ratcliffe, 1980: 341

Type series: Holotype f#: **PARAGUAY**: **Concepción:** Horquetá (USNM).
Non-type material examined: **BOLIVIA**: **Santa Cruz:** Ichilo, Buenavista, Tacu, III-1951, Martínez (1 CMNC); **PARAGUAY**: **Concepción:** Horquetá, IV-1934, Schultze (2 CMNC, 1 FVMC), Horquetá, 4-XII-1934 (1 CMNC).

1.2. *Besourenga vejdovskyi* (Balthasar, 1939), **new combination**
Trichillum vejdovskyi Balthasar, 1939: 20, 23-24; Martínez, 1947: 110; Hamel *et al.*, 2006: 12.
Trichillum (Eutrichillum) vejdovskyi; Martínez, 1969: 120-121; Ratcliffe, 1980: 341

Type series: Holotype m#: **BOLIVIA**: **Santa Cruz:** Umg. Buenavista, 450 m, Steinbach (NMP).
Non-type material examined: **BOLIVIA**: **Santa Cruz:** Gutiérrez, Portachuelo, II-1950, Martínez (1 CMNC); Río Piray, XI-1950, Martínez (1 CMNC); Santa Cruz, XI-1955, Zischka (1 FVMC).

1.3. *Besourenga amarillai* (Aguilar, 2001), **new combination**
Pedaridium amarillai Aguilar, 2001: 1-3

Type series: Holotype f# not seen (Museo de História Natural del Paraguay, Asunción).

Non-type material examined: **BRAZIL**: **Distrito Federal:** RECOR-IBGE, XII-1999, M Milhomem, campo sujo (2 FVMC); **Goiás:** Goiânia, 21-XII-1984, MJ Ferreira (2 FVMC); Jataí, Faz. Nova Orlândia, I-1964, Martins, Morgante & Silva (1 IBSP).

1.4. *Besourenga horacioi* (Martínez, 1969), **new combination**

Trichillum (?) *horacioi* Martínez, 1969: 142-145

Trichillum horacioi; Hamel *et al.*, 2006: 12.

Type series: Holotype f#: **BOLIVIA**: **Santa Cruz:** Sara, Nueva Moka, XII-1960, A Martínez (BRBA).

Non-type material examined: **BRAZIL**: **Pará:** Serra Norte, Piste N1 km 22, 1-XI-1984 (2 CMNC); Redenção, XI-1999, P Scheffler (2 FVMC); X-1998, P&T Scheffler (10 FVMC); **Rondônia:** 62 km SW Ariquemes, nr Faz. Rancho Grande, 8-20-XI-1994, J Eger, C O'Brien, black light (4 BDGC); **PERU**: **Madre de Dios:** Río Palma Real Grande, Limon Camp, 220 m, X-1999, T Larsen (10 CMNC).

2. *Bradypodidium*, **new genus**

Diagnosis: Small oval to elongate species (Fig. 17), hairs very fine, clypeus with none, two or four teeth (Fig. 43, 45), elytral striae deeper and wider posteriorly, front tibial teeth concentrated in the apical one-half of tibia; males with front claws and last tarsomere strongly modified (Fig. 46); lacking apico-mesal tooth in front tibia; paramera elongated, flat and wider at apex, always with mesal apexes superposed (Fig. 44).

Description: Size 2.3-3.7 mm. Body oval, with elytra clearly wider than protorax (Fig. 17); color tan to black, rarely with traces of metallic sheen. Clypeus with none, two or four teeth (interspecific and sexual differences in the number of teeth exist in at least some species associated with a wide variety of general head forms: transverse, rounded, or triangularly elongated). Clypeal border lateral to teeth straight to feebly rounded, continuous with genal border. Clypeo-frontal and clypeo-genal sutures indistinct, head dorsally flat except for anteromedian part of clypeus. Eyes (seen from above) dorsally oval, interocular space 8 to 10 times wider than one eye width (Fig. 43, 45). Pronotum without anterior bead, lateral callosity ill-defined. Disc centrally with setose punctures. Hypomeron laterally separated from pronotal disk by strong carina and bearing a strong posterior longitudinal carina parallel to the pronoto-hypomeral delimitation. Mesoepimeron with anterior transverse carina. Metasternum with setose punctures present on the disk. Elytral interstriae almost flat, each with two well separated rows of setose punctures; striae wider and deeper on the posterior declivity. Pseudoepipleuron gradually narrowed from the anterior third to end of elytron, with setigerous punctures all along. Front tibia with three teeth, the basal one frequently reduced; teeth concentrated in the apical two-fifths of tibia; lateral tibial margin denticulate between base and basal tooth; ventral scale-like setae of tibial teeth absent. Middle and hind tibiae elongate, much longer than five times their apical width. Metatarsus with first segment longer than second flattened and oval. Paramera blade-like, tips slightly overlapped, apically wider than at middle (Fig. 44), about as long as half the fallobase or shorter. Coxites present, large and symmetrical, Spermatheca C-shaped, gradually narrowed posteriorly, basally globous and strongly modified in conical point at duct insertion.

Secondary sexual characters: Apical tarsomere of front tarsi of male excavated dorsally to receive front claws; claws strongly curved in the middle, forming an angle (Fig. 46). Metasternal disc is somewhat concave in males, and very flat in females. Front tibial teeth much wider and robust in females; males frequently with very reduced basal tooth. In species with variable clypeal shape, males often with more elongated clypeus when teeth are present, and reduced or absent lateral clypeal teeth, while females almost always present transverse or rounded head with four well developed clypeal teeth. Pygidium much more transverse and vertical in females than in males.

Type species: *Trichillum bradyporum* Boucomont, 1928 (present designation) = *Bradypodidium bradyporum* (Boucomont, 1928), **new combination**.

Etymology: Combination of *Bradypus* (genus name of the most common sloths [Mammalia: Edentata: Bradypodidae], in reference to phoretic relation the beetles have with sloths); and *Pedaridium*, genus name; gender neuter.

Distribution: Widely co-distributed with sloths in the Neotropical region from Costa Rica to southeastern Brazil.

Remarks: Collection records suggest an obligatory relationship with sloths. *Bradypodidium* is closely related to *Trichillidium*, sharing with this genus front tibial teeth concentrated in the apical half of tibia, slender dorsal setae, among many other characters. Monophyly of *Bradypodidium* is supported by the relatively slender male tibia in relation to female, laminate overlapped paramera, relatively elongated body, transverse pygidium in females, and the association with sloths. See under *Onoreidium* for more remarks on *Trichillidium-Bradypodidium*.

Composition: Besides the type species, the genus *Bradypodidium* includes *B. adisi* (Ratcliffe, 1980), **new combination**, *B. venezuelense* (Ferreira & Galileo, 1993), **new combination**, and at least three new species presently under study.

Material examined:

2.1. *Bradypodidium adisi* (Ratcliffe, 1980), **new combination**

Trichillum (Eutrichillum) adisi Ratcliffe, 1980: 337-341

Pedaridium adissi; (*sic*) Ferreira & Galileo, 1993: 28-29

Pedaridium adisi; Vaz-de-Mello & Canhedo, 1998: 100; Vaz-de-Mello, 2000: 194; Verdú & Galante, 2001: 601-602

Type series: Holotype not seen (Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil).

Paratypes: **BRAZIL**: **Amazonas:** Ilha do Curari, 25-I-1978, R Best, Br tridactylus (8 CMNC, 2 CNCI); Manaus, 2-VI-1977, J Adis, *B. tridactylus* (1 BDGC, 1 CMNC, 1 CNCI, 3 FVMC, 2 FMNH); Paricatuba nr. Manaus, 14-VI-1977, J. Adis, col. from *Brad. tridactylus* (1 FMNH).

Non-type material examined: **BRAZIL**: **Amazonas:** Ilha do Curari, 2-VI-1977, J Adis, Sloth (1 CMNC, 1 FVMC); **Pará:** Ilha de Marajó, distr. Caldeirão, II-1924, Wilh. Ehrhardt ("Typus" *Pedaridium setulosum* Balthasar *i. litt.* NMP); **PERU**: **Loreto:** R Yaropa, Puerto Miguel, 200 m, 16-23-XII-1994, T Hácz & G Holzinger (2 HMNH); Río Ucayali, Yarinacocha, 27-V-1945, J Schunke, pele de preguiça (1 CMNC, 1 FVMC).

2.2. *Bradypodidium bradyporum* (Boucomont, 1928), **new combination**

Trichillum bradyporum Boucomont, 1928: 188; Balthasar, 1939: 15-17, 26; Blackwelder, 1944: 204; Costa-Lima, 1953: 22

Pedaridium bradyporum; Martínez, 1969: 119; Ferreira & Galileo, 1993: 36; Vaz-de-Mello *et al.*, 2002: 676; Solís & Kohlmann, 2003: 9-11

Type series: Holotype not sexed: **COSTA RICA**: **Limón:** Hamburgfarm, Reventazón, Ebene Limón, 21-VIII-1925, F Nevermann, am Affer im Pelz von 3 zeilig Faulfier (MNHN).

Non-type material examined: **COSTA RICA**: **Cartago:** Catie, 3 km SE Turrialba, 600 m, 13-16-V-1985, J Doyen (1 BDGC); Turrialba, Catie, 600 m, 16-V-1979, H&A Howden (1 CMNC); Turrialba, III-1952, A Trejos, on *Bradypus griseus* (1 CNCI); **Limón:** Hamburgfarm, Reventazón, Ebene Limón, 27-X-1931, Nevermann, am anus von *Bradypus infuscatus* (1 BDGC, 1 CMNC, 1 MZSP, 7 NHMB, 3 FVMC); 1936 (1 CMNC); 1936-39 (1 CNCI); **ECUADOR**: **Esmeraldas:** La Chiquita, 5 m, 11 km SE San Lorenzo, 3-16-VI-1975, S&J Peck (1 CMNC).

2.3. *Bradypodidium venezuelense* (Ferreira & Galileo, 1993), **new combination**

Pedaridium venezuelensis Ferreira & Galileo, 1993: 27-28

Type series: Holotype not seen.

Paratype: **VENEZUELA**: **Carabobo:** San Esteban, 100 m, 01-VII-1975, Martínez (1 FZRS).

Non-type material examined: **VENEZUELA**: **Aragua:** Rancho Grande 1100 m, 16-V-1967, H&A Howden (1 CMNC); 18-19-II-1971, H&A Howden (1 CMNC); 24-25-II-1971, 800 m (1 FVMC).

3. *Degallieridium* **new genus**

Diagnosis: Body short, oval, convex (Fig. 18) and very small size (length 2.0 mm or less). Dorsum brown, dorsal setae thick, as wide as lateral elytral striae. Clypeus with two teeth, laterally rounded; eyes dorsally as long as twice their width (Fig. 47). Hypomeron without lateral longitudinal carina. Elytral interstriae with two rows of punctures, only one of them bearing setae. Pseudoepipleuron medially inflexed, but gradually narrowed posteriorly (Fig. 11). Paramera strongly divergent apically (Fig. 48).

Description: Length 1.8-2.0; body short (Fig. 18), oval, bright brown, with no traces of metallic sheen. Clypeus with two triangular teeth separated by V-shaped emargination, laterally simply rounded and continuous with genal border. Clypeo-frontal and clypeo-genal sutures indistinct. Eyes (seen dorsally) twice as long as wide, separated by four eye–widths (Fig. 47). Pronotum lacking bead on anterior margin; lateral callosity present, elongated and darker than remaining parts of pronotum; disk centrally with large setose punctures. Pronotum and hypomeron separated by simple complete carina, with its posterior two thirds placed ventrally (anterior third lateral). Hypomeron laterally lacking longitudinal carina; mesoepimeron anteriorly lacking transverse carina. Metasternum with small glabrous punctures on the disk. Elytral interstriae with two rows of punctures on disc, inner one bearing setae; interstriae flat on disk, apically convex; striae apically clearly wider and deeper than on disk. Pseudoepipleuron medially inflexed (posteriorly almost in a transverse plane in relation to anterior part), but without sharp angle and gradually narrowed posteriorly (Fig. 11), completely glabrous. Front tibia laterally with three strong teeth, occupying the apical 70%, not denticulate basally, and ventrally lacking scale-like setae on teeth. Width of apices of middle and hind tibiae about one-third length of tibia. Length of parameres shorter than one-half that of phallobase, right angled in relation to phallobase axis, apically flattened and strongly divergent with sharp lateral apical angles (Fig. 48). Internal sac with a long helicoidal pseudoflagellum occupying most of phallobase length, and a secondary pseudoflagellum flattened all along. Coxites small and well defined, glabrous. Spermatheca C-shaped, strongly narrowed apically, basally somewhat bulbous; spermathecal duct not sclerotized.

Secondary sexual characters: Males have front claws strongly bent in the middle and last tarsomere hollowed to receive them, an apical mesal tooth in protibia directed downward, and less transverse pygidium compared to females.

Type species: *Degallieridium lilliputanum* **new species** (monotypy).

Composition: Besides the type species, the genus contains at least one new species currently being described.

Etymology: After Nicolas Degallier, friend, histeridologist and collector of part of the type-series of the species described below. Gender neuter.

Distribution: Central Brazil (Minas Gerais and Distrito Federal) and Bolivia, corresponding to scattered localities in Cerrado and Chaco provinces of the Chacoan subregion.

3.1. *Degallieridium lilliputanum* **new species**

Type series: Holotype m#: BRAZIL: **Distrito Federal:** Brasilia, 1100 m, XI-2001, N. Degallier (MZSP ex-FVMC).

Paratypes: BRAZIL: **Distrito Federal:** Brasilia, 1100 m, XI-1999 (1 CMNC); X-2000, N. Degallier (1 FVMC); **Minas Gerais:** Paracatu, XII-1996, S. Lourenço (2 FVMC).

Description: Holotype m#. Size 1.9 mm. Color tan to light brown, dorsal setae claviform, pale yellow. Head as long as wide, gently and regularly curved from the rounded genal lateral angle to clypeal teeth. Clypeal teeth triangular, short, separated by wide V-shaped emargination with rounded bottom. Head covered by round simple punctures separated by 1.5 to two diameters; punctures variable in size, with smaller punctures concentrated in the anterior half of head and larger ones on the posterior half; larger punctures up to 1.5 times as large as smaller ones, some bearing a seta (Fig. 47). Pronotum evenly covered by large oval setose punctures, separated by less than one to one and one-half diameters. Some punctures bearing a seta. Posterior two thirds of pronotal lateral margin bent ventrally and hidden from dorsal view; anterior third visible from above. Prosternum and mesosternum covered by oval, ocellated, glabrous punctures, separated by less than one half of their diameter; hypomeron with similar but slightly smaller and more rounded punctures, more sparse anteriorly. Meso-metasternal suture in middle rounded but in a stronger arc than laterally, giving to metasternal lobe a wide rounded triangular shape. Posterior two thirds of anterior metasternal lobe with sides nearly parallel; slightly divergent; lobe and metasternal disk covered by simple punctures, with very sparse ocellate punctures posteriorly and laterally, similar to those of metasternal sides, where glabrous ocellated punctures are much smaller and sparser than in pro- and mesosternon. Elytral mesal striae with regular punctures separated by about three diameters, each puncture as wide as 1.5 strial widths on disk; striae in the posterior fourth much deeper and wider, with punctures nearly confluent. Interstrial setae wider and denser laterally than mesally. Length of apical tooth of front tibia about as long as 3 that of basal tooth, and 1.5 times that of middle tooth; spur triangular, flattened dorsally. Length of middle and hind femora about three times their maximum width. Hind basitarsus rectangular, length about 1.25 times that of second tarsomere. Abdominal sternites covered by punctures similar to those of lateral metasternal lobes. Pygidium about 1.5 times as wide as long, with very sparse simple punctures; basal punctures setiferous. Length of parameres slightly less than one-half that of phallobase, with latero-apical angles directed downward (Fig. 48). Internal sac with helicoidal pseudoflagellum occupying most of phallobase length, base of which strongly curved; length of secondary pseudoflagellum two thirds that of primary one.

Variation: Paratypes vary only in sexual features (females lack modifications in front tarsi and claws, lack the meso-apical tooth of front tibia, have the differencves in size of protibial teeth less pronounced, and have more transverse pygidium and abdominal strenites more convex and with longer disk) and slightly in size (1.8-2.0 mm).

Etymology: Reference to Lilliput, the island of small people, the Lilliputians, in Jonathan Swift's 1726 novel, *Gulliver's Travels*.

Distribution: Central Brazil (northwestern Minas Gerais and Distrito Federal), corresponding to the central part of the Cerrado province in the Chacoan subregion (Fig. 103).

Remarks: This genus appears closely related to *Feeridium*, with which it shares the absence of the hypomeral lateral longitudinal carina, pseudoepipleural longitudinal fold, and parameral and spermathecal general form. It is most easily distinguishable by size (*Feeridium* is about five times longer) and body form (very elongated in *Feeridium*), although many other differences do exist, for instance, *Feeridium* lacks modification in male front claws. Both genera belong to the clade that includes also *Trichillum, Eutrichillum* and *Besourenga* (see discussion under that later). An strong overall similarity exists between *Degallieridium* and *Leotrichillum*, and the relationships of this last to other genera are confuse.

4. *Eutrichillum* Martínez, 1969 **new status**

Trichillum (Eutrichillum) Martínez, 1969: 121; Ratcliffe, 1980: 340-341; Martínez, 1989: 60; Solís & Kohlmann, 2003: 10, 12.
Trichillum (Eutrichillum) Martínez, 1967 (sic): Vaz-de-Mello, 2000: 195.

Diagnosis: Head with clypeo-genal margin strongly incised (so clypeus and gena separately rounded) and clypeo-genal suture strongly marked, in some cases joining the clypeo-frontal suture and forming a very feeble acute pseudocarina, mostly effaced in the middle (Fig. 49). Pseudoepipleuron strongly narrowed posteriorly.

Description: Length 2.7-4.6 mm, body short oval (Fig. 19), color grey to black with feeble metallic sheen, or completely metallic green to red. Clypeus with two strong teeth, separated by narrow U-shaped emargination, mesal border of tooth almost parallel; clypeus external to teeth regularly rounded, separated of genal border by incision, genal border being separately strongly and regularly curved. Clypeo-frontal and clypeo-genal sutures strongly indicated and anastomosed, being frequently cariniform at least near junction. Eyes dorsally as wide as one third to one fifth of its length, separated by 8-12 widths dorsally (Fig. 49). Anterior pronotal bead absent, lateral pronotal callosity well defined and elongate; disk centrally with uniform elongate setose punctures; pronotum separated of hypomeron by complete carina. Hypomeron with strong lateral longitudinal carina; mesoepimeron anterior transverse carina present;

metasternal disk with round simple setose punctures. Elytral interstria with only one row of setose punctures, situated laterally in interstriae one and two, and mesally in the remaining interstriae; interstriae flat all along, slightly deeper and widened posteriorly. Pseudoepipleuron strongly narrowed posteriorly from about metacoxa, with an strong marginal angle there; glaborus all along. Front tibia with three very strong teeth, distributed along apical three fifths, denticulate basally, with ventral scale-like setae. Middle and hind femurs as wide as one third to one fourth of their length, tibiae apically as wide as one third to one fouth of their length. Metatarsus with basitarsomere longer than second tarsomere. Parameres with apex strongly deflexed, forming a strong conjoint hub in the apical third, with strong apico-external subquadrate flat lobes downward directed (Fig. 50); internal sac with pseudoflagellum highly sclerotized, positioned in helicoid inside phallobase, but straighted when extruded, with a wide triangular base with one to three strong teeth, and a pointed apex, with the entire body canaliculate longitudinally, and with a large triangular plate accessory lamella; coxites not heavily sclerotized, large; spermatheca C-shaped, sinuate in the middle, but with strongly narrowed and spiral-shaped base and apex (Fig. 14), duct very long, spirally shaped and not sclerotized..

Secondary sexual characters: Males have front claws strongly bent medially, and last tarsite modified in order to receive them (Fig. 51); front tibial apico-mesal tooth present in males and apically directed; abdominal disk flatter than in females, pygidium less transverse, and metasternum flatter than in females (that have it slightly convex).

Type species: *Trichillum boucomonti* Saylor, 1935 = *T. hirsutum* Boucomont, 1928 (original designation) = *Eutrichillum hirsutum* Boucomont, 1928, **new combination**.

Distribution: A group of species (of which two already described) inhabit South American lowlands, east of the Andes as far south as Buenos Aires in Argentina; one species in Costa Rica. This corresponds to a very disjunct distribution, comprisin in one side the entire Chacoan, Parana and Amazonian subregions, and in the other some localities in Eastern Central America province of the Caribbean subregion.

Remarks: Species of this genus are mostly necrophagous and frequently attracted to lights. The genus belongs to the clade that includes *Feeridium, Degallieridium, Besourenga* and *Trichillum* (see under *Besourenga*), and is characterized by the following synapomorphies: clypeus and gena separately rounded; clypeo-genal and clypeo-frontal sutures strongly indicated; parameres forming dorsal hump on the apical third; pseudoflagellum compressed (as a resort) in the internal sac in helicoid form and straighted when extruded; spermatheca with base and apex strongly narrowed and spirally.

Composition: Apart of the type species, the genus contains *Eutrichillum hystrix* (Arrow, 1931), **new combination** (described as *Trichillum*)**,** *E. arcus* (Solís & Kohlmann, 2003), **new combination** (described as *Trichillum*), and at least five new species currently being described.

Material examined:

4.1. *Eutrichillum arcus* (Solís & Kohlmann, 2003), **new combination**
Trichillum (Eutrichillum) arcus Solís & Kohlmann, 2003: 10, 12-14

Type series: Holotype not seen (Instituto Nacional de Biodiversidad, San José, Costa Rica).
Paratypes: COSTA RICA: **Alanjuela:** Sect. San Ramón de los Ríos, 1.5 km NO Hda. Nueva Zelandia, 620 m, 12-21-VI-1996, FA Quesada (3 FVMC); **Guanacaste:** Est. Pitilla, 9 km S Sta. Cecilia, P.N. Guanacaste, 700 m, V-1994, C Moraga (2 FVMC); **Heredia:** Est. Biol. La Sielva, 21-VI-1998, C Carlton & A Tishechkin (1 FVMC).

4.2. *Eutrichillum hirsutum* (Boucomont, 1928), **new combination**
Trichillum hirsutum Boucomont, 1928: 187; Arrow, 1932: 226; Paulian, 1936: 206-207; Balthasar, 1939: 13, 19, 22-23; Pessôa & Lane, 1941: 447; Blackwelder, 1944: 204; Martínez, 1969: 119; Vaz-de-Mello & Génier, 2005: 44-45; Hamel *et al.*, 2006: 12.
Trichillum boucomonti Saylor, 1935; Balthasar, 1939: 13, 18, 22; Blackwelder, 1944: 204
Trichillum (Eutrichillum) boucomonti; Martínez, 1969: 120-121; Ratcliffe, 1980: 341; (*pars*) Ratcliffe, 1981: 185; Martínez, 1987: 60; Monteresino *et al*., 1996: 107; Vaz-de-Mello, 2000: 195; Génier & Vaz-de-Mello, 2002: 189
Trichillum (Eutrichillum) hirsutum; Ratcliffe, 1980: 341; (*pars*) Ratcliffe, 1981: 183-184; Vaz-de-Mello, 2000: 195.

Type series:
Trichillum hirsutum Boucomont, 1928: Holotype f#: BRAZIL: **São Paulo:** no locality (MNHN).
Trichillum boucomonti Saylor, 1935: Holotype f#: PARAGUAY: **Concepción:** Horquetá (USNM).

Non-type material examined: ARGENTINA: **Corrientes:** Sto Tomé, XI-1945, Martínez (2 CMNC); **Misiones:** PN Iguazu, 180 m, XII-1990-I-1991, S Peck (2 CMNC); BOLIVIA: **Ichilo:** Buenavista, XI-XII-1948, L. Peña (1 FMNH); **Santa Cruz:** Gutiérrez, Portachuelo, II-1950, Martínez (2 CMNC); Santa Cruz, XI-1955, Zischka (5 CMNC); BRAZIL: **Bahia:** Barreiras, XII-1991 (1 FVMC); Encruzilhada, XII-1980, Alvarenga & Martínez (2 CMNC, 1 FVMC); Encruzilhada, 980 m, XI-1972, Alvarenga (3 MZSP); **Distrito Federal:** Brasília 1100 m, II-2001, N Degallier (2 FVMC); X-2000 (4 FVMC); XI-1999 (1 CMNC); XII-1997, P. Grossi (1 FVMC); Est. Florestal Cabeça do Veado, 1100 m, 27-X-1971, EG, I & EA Munroe (1 CNCI); RECOR-IBGE, 27-V-1997, I Diniz (1 FVMC); XI-1999, M Milhomem, campo sujo (1 FVMC); XII-1999 (1 FVMC); **Espírito Santo:** Pque Sooretama, Linhares, 12-27-X-1962, FS Pereira (1 MZSP); Venda Nova do Imigrante, X-1998, Falqueto & Vaz-de-Mello (2 FVMC); **Goiás:** Bom Jardim de Goiás, II-1997, FZ Vaz-de-Mello (2 FVMC); Goiânia, 03-XII-2001, SS Silva (3 FVMC); Jataí, Faz Nova Orlândia, I-1964, Martins, Morgante & Silva (2 MZSP, 1 IBSP); Jataí, I-1955 (2 CMNC, 10 MZSP); Rio Verde, II-1998, J Carlos (1 AMBC); **Mato Grosso do Sul:** Costa Rica, 17-XII-1993, S Ide (5 MZSP); Nova Andradina, II-1996, Louzada & Vaz-de-Mello (1 FVMC); Selvíria, UNESP farm:01-IV-1999, CAH Flechtmann, ex black light, Brachiaria decumbens pasture (1 FEIS); 20-I-1999 (1 FEIS); **Mato Grosso:** Barra do Tapirapé, 2-16-I-1966, B Malkin (1 IBSP); XI-1964, Malkin (1 CMNC); Diamantino, Alto Rio Arinos, XI-1998, E Furtado (1 FVMC); Pq Nac. Xingu, Jacaré, XI-1961, Alvarenga & Bokermann (116 MZSP); Xingu:XI-1947 (1 MNRJ); XI-1961 Alvarenga & Werner (89 MZSP); XI-1961, Alvarenga (3 CMNC); **Minas Gerais:** Açucena, II-1952, Pereira (1 CMNC); Águas Vermelhas, XII-1998, Bello & Vaz-de-Mello (1 FVMC); Belo Horizonte, X-1950 (1 MZSP); Buritis (Rib. Confins), X-1964, Exp. Dep. Zool. (1 CMNC); Caxambu, 02-XII-1990, Bello (1 FVMC); Cordisburgo, Faz Pontinha, I-1992, FZ Vaz-de-Mello (1 FVMC); Ipatinga, XI-1994, E Grossi (1 FVMC); Martinho Campos, X-1991(1 FVMC); Montes Claros, I-2000, JNC Louzada (3 FVMC); Nova Era, I-1993 (1FVMC); Paracatu, II-1997, S Lourenço (2 FVMC); XII-1996 (3 FVMC); Vespasiano, I-1952, Pe. Pereira (1 BDGC, 6 CMNC); XII-1945, Pereira (4 CMNC); XII-1951 (1 MZSP); Viçosa, mata do Paraíso, I-1995, JNC Louzada (1 FVMC); I-1996, Louzada, Sperber & Vaz-de-Mello (2 FVMC); Viçosa, 02-II-1994, JNC Louzada (1 FVMC); 03-II-1994 (4 FVMC); 04-I-1994 (3 FVMC); 07-I-1994 (2 FVMC); 10-I-1992, Lopes & Louzada (1 FVMC); 10-I-1994, JNC Louzada (2 FVMC); 12-I-1992, Lopes & Louzada (1 FVMC); 21-XI-1991, Lopes & Louzada (1 FVMC); 25-I-1994, JNC Louzada (1 FVMC); **Paraná:** Curitiba, II-1944, Hatsbach (1 MZSP); Londrina, :XI-1998, J Lopes (3 AMBC); XI-XII-1998, IM Medri (1 FVMC); Vila Velha, II-1945 (1 MZSP); **Rio de Janeiro:** 17 km E Nova Friburgo, 750 m, 21-I-2000, Génier & Ide (1 CMNC); Itatiaia, 20-I-1993, CL Godinho Jr (1 FVMC); Nova Friburgo, 1000 m, I-2002, P&E Grossi (2 FVMC); I-2001 (1 AMBC); III-1998, P Grossi (1 FVMC); XI-1996, FZ Vaz-de-Mello (1 FVMC); **Rio Grande do Sul:** Near Cachoeira, Henninger (1 CMNC); **São Paulo:** no locality, Mráz leg. (2 NHMB); Aclimação, XII-1958 (1 CMNC); Barueri, 22-II-1956, K. Lenko (1 MZSP); XII-1955 (1 CMNC); Botucatu, 22-II-1955, Werner (3 MZSP); Cerqueira César, XII-1999, J Carlos (1 AMBC); Cidade, Ipiranga, XII-1958, A Martínez (3 BDGC, 5 CMNC); XII-1962, Martínez (2 CMNC); Itu, Faz. Pau d' Alho, 12-15-XI-1960, Martins (1 MZSP); II-1969, Martins (1 MZSP); Mogi Guaçu, Faz. Campininhas, I-8-I-1970, JM & BA Campbell (2 CNCI); Pirassununga, Usina – luz, 9-XI-1945, Schubart (2 MZSP); XI-1952 (2 MZSP); Pirassununga, XI-1952 (1 CMNC); XI-1956, Martínez (3 CMNC); Ribeirão Preto (Fac. Medicina), I-1955, Barretto (1 MZSP); Rio Claro, XII-1942, Claretiano (17 MZSP); São Paulo, Ipiranga (1 MZSP); Ypiranga, XI-1929, Spitz (1 MZSP); PARAGUAY: **Do.?:** Chaco, XII-1934, Schultze (1 CMNC); **Alto Paraná:** Limoy, XI-1990, G Arriágada (3 FVMC); RB Itabo, X-1989, G Arriágada (2 FVMC); **Canindeyú:** Est. Pozuelo, XII-1990, G Arriágada (3 FVMC); **Central:** Asunción, IX-1944 (5 MZSP); XI-1944 (1 CMNC); **Concepción?:** Mariscal Estigarribia, I-1990, G Arriágada (1 FVMC); **Concepción:** Horquetá, I-1934, Schultze (1 CMNC); I-1943 (1 CMNC); IV-1934 (1 CMNC); **Guayrá:** Villarrica, X-1934, Köller (1 MNHU); XI-1955, Schade (2 CMNC); **Paraguary:** Naranjo, 09-14-XII-1998 (1 FVMC); Sapucay, 05-XI-1991, U Drechsel (12 ABC); **San Pedro:** Río Ypané, Cororó, XI-1979, Martínez (17 CMNC); **San Pedro?:** Peribebuy, XI-1946 (1 CMNC).

4.3. *Eutrichillum hystrix* (Arrow, 1931) , **new combination**

Trichillum hystrix; Arrow, 1931: 609-610; Arrow, 1932: 226; Paulian, 1936: 206, 207; Balthasar, 1939: 13, 21, 25; Blackwelder, 1944: 204; Martínez, 1959: 64.
Trichillum (Eutrichillum) hystrix; Martínez, 1969: 120-121; Ratcliffe, 1980: 341; Martínez, 1987: 60; Génier & Vaz-de-Mello, 2002: 188-190.

Type series: Lectotype m# (designated by Génier & Vaz-de-Mello, 2002): ARGENTINA: Santa Fé: Estancia la Noria, Rio San Javier, G.E. Bryant, 27.XII.1911 (BMNH). Paralectotypes: Same data as lectotype except: XII.1911 (1m#, 1f# BMNH), 10.XII.1911 (1f# CMNC), 14.XII.1911 (1m# BMNH), 20.XII.1911 (2f#f# BMNH), 23.XII.1911 (2f#f# BMNH), 3.I.1912 (1m# BMNH).

Non-type material examined: ARGENTINA: **Buenos Aires:** Belgrano, XII-1941 (1 CMNC); Capital Federal, Villa Devoto, XII-1925, Bridarolli (2 CMNC); Gral. Sarmiento, JC Paz, I-1952, Martínez (5 CMNC); San Isidro, Casa, I-1960, Martínez (2 CMNC); Tigre, V-1945, MJ Viana (2 CMNC, 1 FVMC); Buenos Aires, Richter (3 IRSN); **Córdoba:** Cruz Alta; II-1946; JP Duret (4 CMNC); **Santa Fé:** Do. Capital, Piquete; I-1942; Martínez (2 CMNC); Estancia La Noria, Río San Javier, 23-XII-1911, GE Bryant (1 NHMB); **Santa Fé?:** Carcarana (10 UNSM, 4 FVMC); PARAGUAY: **Alto Paraná:** Puerto Stroessner; 6-I-1966; Hungarian Soil-Zool. Exp. (1 HMNH); **San Pedro?:** Peribebuy:V-1946, Williener (1 CMNC); NO DATA (4 FMLT).

5. *Feeridium* **new genus**

Diagnosis: Size large (4.5-5.2 mm), very elongated (Fig. 20). Middle and posterior femora very strong and rounded (Fig. 54), eyes extremely large dorsally, interocular space narrower than two eye widths (Fig. 52). Eytral intervals sparsely punctate, with setae only at apex and sides, in a single row.

Description: Length 4.5-5.2 mm, body very elongated, with subparallel sides (Fig. 20); color brown, opaque, with no trace of metallic sheen. Clypeus with two strong teeth, separated by narrow U-shaped emargination, clypeus laterally and gena continuously rounded. Clypeo-frontal and clypeo-genal sutures not discernable. Eyes dorsally enormous, al long as wide, separated by less then 1.5 eye widths (Fig. 52). Anterior pronotal bead absent, lateral pronotal callosity rounded and darkened. Pronotal disk covered by simple strong punctures, but withou setae; separated of hypomeron by row of punctures, without carina. Hypomeron without lateral longitudinal carina; mesoepimeron anterior transverse carina strong and distinct; metasternal disk with minute impressed punctures. Elytral interstriae flat, with unorganized punctures on disk, sparse setae present only apically and laterally, in a single row; striae feebly deeper posteriorly, not widened. Pseudoepipleuron gradually narrowed posteriorly, with slight longitudinal fold near metacoxa, completely glabrous. Front tibia with three very strong teeth, distributed in apical three fifths, basally not denticulate, lacking ventral scale-like setae. Middle femur wider than one third of its length, hind femur about as wide as one half of its length (Fig. 54); middle tibia apically wider than one third of its length, hind tibia apically quite as wide as one half of its length (Fig. 54). Hind tarsi with basitarsomere as long as 1.5 times the following tarsite. Parameres as long as two thirds of phallobase, flattened and truncate, apically divergent (Fig. 53). Internal sac with pseudoflagellum relativelly short and bent in the middle, rounded by a flat large acessory lamella. Coxites triangular, very sclerotized and pointed. Spermateca C-shaped, bulbous basally (with a narrow point in the duct insertion), drastically narrowed apically, with duct short and not sclerotized.

Secondary sexual characters: Males have central part of the last abdominal sternite flat to slightly concave, pygidium more elongated, and a front tibial apico-mesal tooth, downward directed.

Type species: *Feeridium woodruffi* **new species** (monotypy).

Composition: Monobasic.

Distribution: French Guyana and Amazonian Brazil. Known from Humid Guiana, Roraima and Varzea provinces of the Amazonian subregion.

Etymology: After François Feer, who collected and sent me the first specimens I saw of this genus. Gender neutral.

5.1. *Feeridium woodruffi* **new species**

Type series: Holotype m#: BRAZIL: **Amazonas:** Tabatinga, XI-1956, FM Oliveira (BRBA).
Paratypes: BRAZIL: **Amazonas:** 70 km N Manaus, Fazenda Esteio, 07-VI-1986, B Klein, human dung, nature forest, AM (1 FVMC); Tabatinga, XI-1956, FM Oliveira (1 BRBA); FRENCH GUYANA: **Cayenne:** Nouragues, III-1997, F Feer (1 FVMC); V-1995 (1 FVMC).

Description: Holotype m#. length 5.0 mm. Body elongated, aphodiiform (Fig. 20). Head wider than long, clypeus with two rounded triangular teeth, slightly rounded laterally, with margin continuous to that of gena. Head convex, concave anteriorly and transversely concave anteriorly to each eye, forming a diagonal lump at each side, indicating the place of the indinstinct clypeo-genal suture. Head surface with mixed simple setose and simple smaller glabrous punctures, the setose ones denser on clypeus. Eyes separated by about 1.3 eye widths, about as wide as long (Fig. 52). Pronotal disk convex, covered by simple glabrous punctures separated by 1-3 diameters, setae present only on each side of anterior margin, and at pronotal sides. Hypomeral posterior punctures larger but more sparse than at pronotal disk. Mesosternon covered by large almost coalescent ocellate diagonally elongated punctures. Meso-metasternal suture strongly angled with a rounded tip, metasternal anterior lobe clearly narrower posteriorly, romboid. Metasternum with disk with rhomboid, feebly delimited concavity, covered by sparse glabrous simple punctures. Lateral metasternal lobes with diagonally elongated ocellated glabrous punctures, separated by about one diameter. Elytra with discal striae sinuate-punctate, punctures indistinct and almost contiguous or separated by less than one diameter. Discal interstriae with unorganized small punctures, separated by two to four diameters; setae present only apically, and in one well delimited row in the eighth interstria, mesally. Front tibiae with apico-mesal tooth short, triangular and downward directed; spur flattened, ogival with acute tip. Meso- and metatibiae with apex with apical carina accompanied by row of very dense and long setae, longer than basitarsite (Fig. 54). Metatibial basitarsite flattened and trapeziform. Abdomen with rouded ocellate punctures on disk, separated by about 2 diameters, with one lateral row of setose punctures posteriorly in the last sternite. Pygidium with simple sparse setose punctures. Parameres as in figure 53.

Variation: Paratypes vary in size (4.5 – 5.2 mm) and in sexual features: females lack the protibial apico-mesal tooth and the metasternal disk concavity.

Etymology: After Dr. Robert Woodruff, scarabeidologist. Although that name was already *i. litt.* in Martínez' material in BRBA, I extend my own homage to Dr. Woodruff.

Distribution: French Guyana and Brazil (Amazonas), as for the genus (Fig. 103).

Remarks: The condition of the parameres and pseudepipleuron relates this genus to *Degallieridium*. However, it superficially rensembles both *Genieridium* and *Nunoidium*, from which it is immediately distinguished by the condition of pseudepipleuron, head and elytra. Synapomorphies defining this genus include lack of row-organized elytral disk punctation, absence of pronoto-hypomeral carina, lack of sexual differences in front tarsi, size of eyes and psammophiliform development of legs.

6. *Genieridium* **new genus**

Diagnosis: Moderate to large-sized species (only rare specimens of *G. cryptops* measure less than 3.7 mm), oval-elongate shape (Fig. 21-22); clypeal teeth two (Fig. 55, 60, 62, 64, 70) or none, in latter case clypeus widely emarginated (Fig. 57, 68). Eyes dorsally absent or very small, separated by more than 12 eye widths. Pronotum separated from hypomeron by weak carina (Fig. 59). Elytra convex at least in the anterior half. Length of middle and hind tibiae at least three times width at apex. Males with mesal apical teeth in protibiae, and all claws modified, bent (middle and hind claws less modified than front claws), last tarsomere of front legs modified to receive claws. Length of last abdominal sternite along midline equal to or less than medial width of metafemur; pygidium, in ventral view, ocuppying more than 2/5 of abdominal horizontal length.

Description: Length 3.5-6.5 mm, body oval elongated, convex (Fig. 21-22), color grey to black, brown in teneral specimens, shining or opaque, lacking any traces of metallic sheen. Clypeus with two teeth or none, always with a central anterior concavity coincident with emargination, that is present also in toothless species (Fig. 57, 68). Clypeus laterally regularly rounded, continuous with genal border. Clypeo-frontal and clypeo-genal sutures indistinct, head lacking any traces of carinae or tubercles. Eyes dorsally absent or very small, when present elongated, more than three times as long as their width, and separated by at least 12 eye widths (Fig. 55, 57, 60, 62, 64, 68, 70). Anterior and posterior pronotal beads lacking, pronotum simply convex, with lateral callosities feebly distinguished only by lack of punctation. Pronotal disk covered by simple setose punctures and separated of hypomeron by weak but distinct carina interrupted by regular setose punctures. Hypomeron ventrally with strong lateral longitudinal carina, mesoepimeron with transverse anterior carina stronger mesally. Metasternum with simple setose punctures on disk. Elytra with one or two rows of setose punctures, discal interstriae flat all along; striae apically deeper and slightly wider than on disk. Pseudoepipleuron gradually narrowed posteriorly, superiorly with a complete row of setose punctures all along. Front tibia with three strong teeth occupying at least the apical three fifths, basally denticulate, with ventral scale-like setae. Middle and hind tibiae strongly widened apically, apical width more than one third of tibial length. Paramera flattened, right-angled in relation to phallobase, shorter than half of phallobase length. Spermatheca simply C-shaped, in one case (*G.* cryptops) with elongated base and apex. Coxites triangular and symmetrical.

Secondary sexual characters: Males have front claws bent in the middle, and middle and hind claws also modified, either bent in the middle or larger than in females and with stronger basal angle; front tarsus with last tarsomere modified to receive claws; metasternal disc strongly concave (less concave or flat in females), pygidium narrower than in females, and each tibia with apico-mesal tooth, sometimes modified in laminate anteriorly directed apodeme in hind tibia.

Type species: *Pedaridium bidens* Balthasar, 1942 (present designation) = *Genieridium bidens* (Balthasar, 1942), **new combination**.

Etymology: After François Génier, good friend and scarabeidologist, companion in so many works and ideas. Gender neutral.

Distribution: Colombia, Venezuela, non-Amazonian Brazil, eastern Bolivia, Paraguay, and northeastern Argentina. The genus presents a disjunct distribution, with one nucleus in the Caribbean subregion (Northwestern South American dominion), occupying the Cauca, Maracaibo, Venezuelan Coast and Venezuelan Llanos provinces, and the other in the Chacoan, Parana and Amazonian subregions, occupying the Pantanal, Caatinga, Cerrado, Chaco, Brazilian Atlantic Forest, Parana Forest, and *Araucaria angustifolia* Forest provinces (Fig. 104-107).

Remarks: This genus forms a trichotomy with *Pedaridium* and *Nunoidium*, and presents as main external synapomorphies the elongation and inclined orientation of pygidium, and the punctation interrupting the pronoto-hypomeral carina. Main differences with *Pedaridium*, apart from characters mentioned as synapomorphies of *Genieridium,* include the much shorter phallobase, differently shaped internal sac sclerites (*Pedaridium* lacks all but the pseudoflagellum), lack of basal "tooth" in the spermatheca, elytra conjointly convex (*Pedaridium* has clearly tectiform elytra, separately flattened) and absence of longer setae on the anterior part of pronotum and of a pronotal lateral expansion. From *Nunoidium* it is readily distinguished by the lack of a posterior pronotal bead, reduction of lateral bead, reduced eyes, and presence of sexually dimorphic claws. This genus includes two clearly delimited monophyletic, biogeographically-defined groups: species from Venezuela and Colombia are characterized by strong modification of male hind legs –with flattened, blade-like apico-mesal tooth– and southern species by the reduction of the seventh elytral stria.

Composition: Besides the type species, the genus contains at least *G. cryptops* (Arrow, 1913), **new combination**; *G. paranense* (Arrow, 1932), **new combination**; *G. bordoni* (Martínez, 1992), **new combination**; *G. zanunciorum* (Vaz-de-Mello & Canhedo, 1998), **new combination**; *G. margareteae* (Génier & Vaz-de-Mello, 2002), **new combination**; and *G. medinae* (Gill & Vaz-de-Mello, 2003), **new combination** (all described as *Pedaridium*). As no new species of this genus is known to me, I present a small synopsis below.

Key to the species of *Genieridium*

1. Eyes hidden dorsally (Fig. 64). Central Colombia … 6.5. *G. medinae* (Gill & Vaz-de-Mello, 2004)
-. Eyes small but visible dorsally … 2

2. Clypeal teeth lacking (Fig. 57, 68) … 3
-. Two clypeal teeth present … 4

3. Elytral striae without evident punctures. Venezuela … 6.2. *G. bordoni* (Martínez, 1992)
-. Elytral striae with ocellated punctures. Southern Brazil … 6.6. *G. paranense* (Arrow, 1932)

4. Clypeal teeth very acute, sides almost parallel in the apical part (Fig. 60, 70)… 5
-. Clypeal teeth obtuse, short, equilaterous (Fig. 55, 62)… 6

5. Clypeal teeth arising from below clypeal margin (Fig. 60). Central Brazil, Northern Argentina, Paraguay and Bolivia … 6.3. *G. cryptops* (Arrow, 1913)
-. Clypeal teeth in the same plane as clypeal margin (Fig. 70). Southeastern Brazil … 6.7. *G. zanunciorum* (Vaz-de-Mello & Canhedo, 1998)

6. Elytral striae straight, without punctures. Central Brazil and Paraguay … 6.1. *G. bidens* (Balthasar, 1938)

-. Elytral striae marked by inconspicuous punctures that make striae appear sinuated. Northeastern and Central Brazil … 6.4. *G. margareteae* (Génier & Vaz-de-Mello, 2002)

Material examined:

6.1. *Genieridium bidens* (Balthasar, 1938), **new combination**

Pedaridium bidens Balthasar, 1938: 218-220; Blackwelder, 1944: 203; Vaz-de-Mello & Génier, 2005: 45-46

Pedaridium hirsutum; Pessôa & Lane, 1941: 437

Pedaridium brasiliensis Ferreira & Galileo, 1993; Koller *et al.*, 1999 : 405, 407; Vaz-de-Mello, 2000: 194; Verdú & Galante, 2001: 599-601

Type series:

Pedaridium bidens Balthasar, 1938. Lectotype (designated by Vaz-de-Mello & Génier, 2005): m#, Paraguay (NMP). Paralectotypes: BRAZIL: Goiás: Jatahy (1 NMP, 1 NHMB)

Pedaridium brasiliensis Ferreira & Galileo, 1993: Holotype: BRAZIL: **Bahia:** Encruzilhada, 980 m, XI-1972, Alvarenga (MZSP)

Paratypes: BRAZIL: **Bahia:** Encruzilhada, 980 m, XI-1972, Alvarenga (8 MZSP); **Mato Grosso do Sul:** Murtinho (luz), I-1930, R Spitz (2 MZSP); Três Lagoas, Faz. Dr. José Mendes, 15-30-V-1964, Exp. Dep. Zool. (1 MZSP); Faz. Retiro das Telhas, 15-30-V-1964, Exp. Dep. Zool. (2 CMNC, 11 MZSP); **Mato Grosso:** Chapada dos Guimarães, XI-1963, Alvarenga (3 MZSP); **Minas Gerais:** Arinos, 06-08-XI-1964, Exp. Dep. Zool. (2 MZSP); **Paraná:** Vila Velha, XI-1944, Hatsbach (1 CMNC, 1 MZSP); **São Paulo:** Castilho, marg. esq. Rio Paraná, X-1964, Exp. Dep. Zool. (1 MZSP); Franca, VIII-1910, Garbe (2 MZSP); Itu, Faz Pau d'Alho, 28-29-X-1965, Martins & Biasi (1 CMNC); Itú, 27-XII-1957, U. Martins (4 MZSP); XI-1958, U. Martins (2 MZSP); Pirassununga, 09-X-1945, Schubart (1 MZSP).

Non-type material examined: BRAZIL: **Bahia:** no data, Bondar (1 MNRJ); Encruzilhada, 980 m, XI-1972, Alvarenga (1 IBSP); XI-1974, Alvarenga (1 CMNC); XII-1980, Alvarenga & Martínez (8 CMNC); Vitória da Conquista, I-1993 (2 MZSP); **Distrito Federal:** Est. Florestal Cabeça do Veado, 1100 m, X-1971, EG, I & EA Munroe (1 CNCI); **Goiás:** Bom Jesus, X-1996, J Carlos (1 FVMC); Niquelândia, X-1993, arm luminosa (1 FVMC); Rio Verde, 17-XI-1984, Bello (1 FVMC); X-1992, J Carlos (2 AMBC); XI-1993 (1 AMBC); XI-1995 (2 AMBC); **Mato Grosso do Sul:** Costa Rica, 17-XII-1993, S Ide (2 MZSP); Murtinho, XII-1929, Malkin (1 MNRJ); Selvíria, UNESP farm, 01-V-1990, CAH Flechtmann, ex Guzerá bovine dropping, Brachiaria decumbens pasture (1 FEIS); 01-VI-1991 (2 FEIS); 06-VII-1991 (1 FEIS); 06-VIII-1991 (1 FEIS); 13-XII-1992 (1 FEIS); 15-VI-1991 (2 FEIS); 16-II-1991 (1 FEIS); 18-III-1999, ex black light (2

FEIS); 18-V-1991, ex Guzerá bovine dropping (1 FEIS); 20-I-1999, ex black light (24 FEIS); 20-VIII-1991, ex Guzerá bovine dropping (1 FEIS); 20-X-1991 (3 FEIS); 22-IV-1992 (2 FEIS); 23-II-1991 (3 FEIS); 23-II-1992 (1 FEIS); 27-IV-1991 (1 FEIS); 31-X-1993 (1 FEIS); Terenos, 01-IV-1994, WW Koller (1 FVMC); **Mato Grosso:** Chapada dos Guimarães, XI-1963, Alvarenga (1 MZSP); **Minas Gerais:** Águas Vermelhas, XII-1997, Bello (3 AMBC); XII-1998, Bello & Vaz-de-Mello (1 FVMC); Cordisburgo, Faz Pontinha, X-1993, FZ Vaz-de-Mello (1 CMNC, 2 BDGC); Ipatinga, XI-1992, E Grossi (1 FVMC); Montes Claros, I-2000, JNC Louzada (1 FVMC); Três Marias, X-1989 (2 FVMC); **Pará:** Belém, IX-1964, E Dente (1 MZSP); Canindé (Rio Gurupi), X-1964, Malkin (1 CMNC); **São Paulo:** Bálsamo, 12-XI-1987, C Bergmann, seringueira (1 IBSP); 12-XII-1987 (1 IBSP); 13-X-1988 (1 IBSP); 19-II-1987 (1 IBSP); 29-X-1987 (1 IBSP); Castilho, marg. esq. Rio Paraná, 15-22-IX-1962, Exp. Dep. Zool. (1 IBSP); Itirapina, 15-IX-1996, JR Verdú (2 FVMC); Itu, Faz Pau d'Alho, I-1959, Martins (1 CMNC); Mirante do Paranapanema, 09-X-1991, J Rodrigues, black light, pasture area (2 FEIS); 13-XI-1991 (2 FEIS); Pradópois, XII-1976, PM Botelho (1 FVMC, 4 ESAP); São Carlos, 02-XII-1993, J Mendes (1 FVMC); 11-XI-1993 (1 FVMC); PARAGUAY**: no data:** (1 HMNH); Anisits (1 HMNH); **Boquerón:** Pto Casado, XI-1950, Martínez (2 CMNC); **Caaguazú:** Caaguazú, Piscicultura, II-1986, A Martínez (1 BDGC, 6 CMNC); **Central:** Asunción, 10-X-1904, Vezényi (1 HMNH); 28-IX-1904 (1 HMNH); **Concepción:** Horquetá, XII-1950, Martínez, a la luz (6 CMNC); **Paraguary:** Sapucay, 05-XI-1991, U Drechsel (9 ABC); **San Pedro:** Cororó, XI-1999, G Arriágada (1 FVMC); Rio Ypane, Cororó, XI-1979, A Martínez (1 BDGC, 19 CMNC).

Diagnosis: 3.8-5.3 mm. Surface dull. Clypeal teeth obtuse and equilaterous, continous (same plane) with clypeal margin, separated by wide V-shaped emargination. Eyes dorsally visible and very small (Fig. 55). Elytral striae lacking punctures. Very similar to *G. margareteae*, but laking punctures in striae, and anterior clypeal carina. Paramera as in Fig. 56.

Distribution: The entire Cerrado province of the Chacoan subregion, with invasion of pasturelands in neighboring provinces (Fig. 104).

Remarks: This is a common pastureland species in Brazil, and may be related to *G. margareteae*.

6.2. *Genieridium bordoni* (Martínez, 1992), **new combination**
Pedaridium bordoni Martínez, 1992: 22-23; Vaz-de-Mello & Canhedo, 1998: 100

Type series: Holotype m# and allotype f#: VENEZUELA: **Barinas:** Santa Bárbara, IV-1981, G&H Martínez (BRBA).
Paratypes: VENEZUELA: **Anzoátegui:** Pariaguán, 09-VIII-1967, J&B Bechyné (1 CMNC); 12-VIII-1967 (1 CMNC); **Barinas:** Santa Bárbara, IV-1981, G&H Martínez (1 BDGC, 9 CMNC); **Guárico:** Calabozo, VI-1963, Bordón & Martínez, (1 CMNC); 15-VII-1962, Estación Biol. leg. (2 CMNC); **Monagas:** Jusepín, IX-

1965, F.Fernandez & CJ Rosales (1 BDGC); 500 m, 08-VIII-1966, CJ Rosales & F Fernández Y (1 CMNC); 17-IX-1965 (1 CMNC); 21-IX-1965 (1 CMNC); 04-X-1965 (1 CMNC); 07-VIII-1966 (2 CMNC).

Non-type material examined: VENEZUELA: **Anzoátegui:** Aramina (Santa Clara), I-195, R Lichy (1 BDGC); **Bolívar:** 15 km E Caicara, 12-VI-1996, B Gill (20 BDGC); 12-13-VI-1996, H&A Howden (38 CMNC, 4 FVMC); 20 km SW Ciudad Bolívar, 19-VI-1987, S&J Peck, woodland on sand UV (1 CMNC); 25 km SW Pto. Ordaz, 21-VI-1987, S&J Peck, sandy woodland UV (1 CMNC); 8 km SW Caicara, 16-VI-1987, S&J Peck, woodland UV (2 CMNC); **Delta Amacuro:** 15 km E Los Castillos, 4.5 km NE Ciudad Guyana, 26-IV-1987, MA Ivie, at light (1 BDGC, 11 CMNC); **Guárico:** Hato Masajuaral (44 km S Calabozo), 3-10-V-1985, Menko & Carpenter (3 BDGC).

Diagnosis: 4.7-5.5 mm. Surface dull. Clypeal teeth lacking, but clypeal emargination clearly rounded, widely V-shaped and with bottom declivitous (Fig. 57). Elytral striae not punctured. Male apical tooth of metatibia flattened. Paramera as in Fig. 58.

Distribution: Maracaibo, Venezuelan Coast and Venezuelan Llanos provinces of the Caribbean subregion (Fig. 107).

Remarks: This species is undoubtedly related to *G. medinae*, based on secondary sexual characters, but shares with *G. paranense* the absence of clypeal teeth.

6.3. *Genieridium cryptops* (Arrow, 1913), **new combination**

Pedaridium cryptops Arrow, 1913: 458; Arrow, 1932: 226; Balthasar, 1938: 220; Blackwelder, 1944: 203; Génier & Vaz-de-Mello, 2002: 186-187; Hamel *et al.*, 2006: 12.
Pedaridium mansosotoi Martínez, 1951: 35-40; Martínez, 1959: 62; Ferreira & Galileo, 1993: 7, 18-20; Forsyth *et al.*, 1998: 371; Koller *et al.*, 1999: 405, 407; Vaz-de-Mello, 2000: 194
Pedaridium bidens (misidentification, not Balthasar, 1938); Ferreira & Galileo, 1993: 7, 15-16; Vaz-de-Mello, 2000: 194

Type series:
Pedaridium cryptops Arrow, 1913: **Lectotype** f# (designated by Génier & Vaz-de-Mello, 2002): BRAZIL: Goiás: Jatahy (BMNH)
Pedaridium mansosotoi Martínez, 1951: Holotype m#: ARGENTINA: **Formosa:** Clorinda, 12-XII-1950, A Martínez (BRBA); allotype f#: PARAGUAY: **?:** km 50 de Río Paraguay entre Asunción y B. Negal, 30-XI-1950, A Martínez (BRBA).

Non-type material examined: BRAZIL: **Bahia:** Barreiras, X-1991 (1 FVMC); XII-1991, luz (3 FVMC); Encruzilhada, 980 m, XI-1972, Alvarenga (11 MZSP, 3 IBSP, 2 FVMC); XI-1974, Alvarenga (1 CMNC);

XII-1980, Martínez & Alvarenga (2 CMNC); **Distrito Federal:** Brasília – Aeroporto, I-1964, Martínez (1 CMNC); Brasília 1100 m, III-2001, N Degallier (1 FVMC); XI-2000 (5 FVMC); XII-2000, luz (2 FVMC); XI-1999 (1 CMNC); Est. Florestal Cabeça do Veado, 1100 m, 27-X-1971, EG, I & EA Munroe (11 CNCI); X-1971, EG, I & EA Munroe (5 CNCI); RECOR-IBGE, 09-XII-1997, I Diniz (2 FVMC); XI-1999, M Milhomem, campo sujo (1 FVMC); **Goiás:** Aruanã, Rio Araguaia, II-1961, Dirings (1 MZSP); Bom Jardim de Goiás, II-1997, FZ Vaz-de-Mello (1 FVMC); Campinas, XII-1925, Borgmeier & Lopes (1 MZSP); Goiatuba, I-1953, J Guérin (1 IBSP); Jataí, Faz. Nova Orlândia, I-1964, Martins, Morgante & Silva (1 MZSP); Rio Verde, XI-1993, J Carlos (1 AMBC); **Mato Grosso do Sul:** Costa Rica, 17-XII-1993, S Ide (10 MZSP); Selvíria, UNESP farm, 02-II-1993, CAH Flechtmann, ex Guzerá bovine dropping, Brachiaria decumbens pasture (1 FEIS); 09-XI-1994 (1 FEIS); Três Lagoas, margem esq. Rio Sucuriú, Faz. Canaã, I-1967, Lane (1 MZSP); **Mato Grosso:** Barra do Tapirapé, XI-1964, B. Malkin (4 MZSP); Chapada dos Guimarães, XI-1963, Alvarenga (1 MZSP); Macaúba, XII-1966, R Schmitz (1 CMNC); Virapuru (*sic*) 160 km S, 8-10-III-1979, CR Owen (2 HMNH); **Minas Gerais:** Águas Vermelhas, XII-1997, Bello (2 AMBC); XII-1998, Bello & Vaz-de-Mello (3 FVMC); Cordisburgo, Faz Pontinha, I-1994, FZ Vaz-de-Mello (5 FVMC); I-1999 (1 FVMC); XII-1993 (6 AMBC, 5 FVMC); Ibitira, XI-1988, luz (1 FVMC); Montes Claros, I-2000, JNC Louzada (30 FVMC); XII-1999 (2 FVMC); Paracatu, II-1997, S Lourenço (3 FVMC); XII-1996, S Lourenço (190 FVMC); Paraopeba, 03-XI-1992, UV (1 FVMC); Serra do Caraça, 27-XI-05-XII-1972, Exp. Mus. Zool. (1 MZSP); Três Marias, III-1990 (1 FVMC); X-1989 (3 FVMC); XII-1993 (1 FVMC); Unaí, Faz. Bolívia, 22-24-X-1964, Exp. Dep. Zool. (1 MZSP); **Piauí:** São Raimundo Nonato - PN Serra da Capivara, I-1999, CA Matrangolo (2 FVMC); **São Paulo:** Agudos, Duraflora SA, 07-XII-1993, CAH Flechtmann, P car. v. bahamensis log-baited tent trap, P oocarpa stand (1 FEIS); Bálsamo, 10-XII-1987, EC Bergmann, seringueira (1 IBSP); Boa Esperança do Sul, Faz. Itaquerê, 27-I-1964, K. Lenko (3 MZSP); Botucatu, 17-XI-1963, Mantovani (2 IBSP); Itu, Faz. Pau d' Alho, 1-5-I-1961, Martins (1 MZSP); Itu, II-1959, Martins (1 MZSP); Osasco, Fca Fósforos, XII-1962 (2 CMNC); Pirassununga, 03-XI-1996, MA Ruiz Díaz (2 ESAP); Teodoro Sampaio, Morro do Diabo State Reservation, 03-III-1993, CAH Flechtmann, ex bovine dropping baited pitfall trap (1 FEIS); 16-II-1993 (1 FEIS); 29-IX-1993 (1 FEIS); **Tocantins:** Pium, XI-1971, J da Silva (2 CMNC); PARAGUAY: **Amambay:** Srra. Amambay, I-1960, Schultz (2 CMNC); **Caaguazú:** Caaguazú, XII-1977, Martínez (1 CMNC); **Concepción:** Horquetá, XI-1950, Martínez (2 CMNC); **San Pedro:** Cororó, Rio Ypane, II-1979, A Martínez (2 BDGC, 12 CMNC); II-1974 (1 CMNC); III-1979 (4 CMNC); XI-1979 (1 CMNC); XI-1979 (11 CMNC); Cororó, XI-1999, G Arriágada (1 FVMC).

Diagnosis: Surface shining. Clypeal teeth long and acute, located bellow the surface of clypeal margin and separated of clypeal disc by strong and sharp carina (the clypeal central margin itself, that is centrally widely curved inward) (Fig. 60). Elytral striae with weak punctures. Elytral discal interstriae with either one or two rows of setose punctures. Paramera as in Fig. 61.

Distribution: Cerrado, Caatinga and Chaco provinces of the Chacoan subregion (Fig. 105).

Remarks: This species unusual by having either one or two rows of punctures in the discal interstriae; it is the most variable in size within the genus. It appears to be related to *G. zanunciorum,* with which it shares elongated clypeal teeth and shining dorsal surface. The internal sac is unique by having a helicoid pseudoflagellum. Like *G. bidens*, this species is a common pastureland species, easily attracted to lights.

6.4. *Genieridium margareteae* (Génier & Vaz-de-Mello, 2002), **new combination**
Pedaridium cryptops; Ferreira & Galileo, 1993: 7, 20-21; Vaz-de-Mello, 2000: 194
Pedaridium margareteae Génier & Vaz-de-Mello, 2002: 192-193

Holotype m# and allotype female: BRASIL: Piauí: São Raimundo Nonato, Parque Nacional da Serra da Capivara, I-1999, CA Matrangolo (MZSP).

Paratypes: **BRAZIL**: **Bahia**: Caetité, C. Uran. Lagoa Real - INB, 8-16.I.2000 (4 FVMC); Encruzilhada, XII.1980/ A. Martínez e M. Alvarenga (3 CMNC); same as before except XII-1997, Vaz-de-Mello & Bello (4 FVMC); Jequié, II.1995, C. Sperber (1 FVMC); S. Antonio da Barra, XI-XII.1888, Gounelle (1 ZMHB); Vila Nova, 1908 (1 MZSP); same as before except: X.1938, Dr. Nick, Coll. Martínez (2 CMNC). **Mato Grosso**: Chapada do Guimarães, XI.1963, Alvarenga (9 MZSP). **Minas Gerais**: Águas Vermelhas, XII.1997, A. Bello (4 AMBC). **Pernambuco**: Pery-Pery, V-VI.1892, Gounelle (1 ZMHB, 1 FVMC); same as before except: XI-XII.1892 (1 ZMHB). **Piauí**: São Raimundo Nonato, PN Serra da Capivara, I.1999, C.A. Matrangolo (5 FVMC). **Rio Grande do Norte**: Natal (5 NHMB); same as before except: W. M. Mann, Stanford Exped., 1913-56 (1 BMNH); same as before except: III. 1952, Alvarenga (4 MZSP); III.1954, Alvarenga leg, Coll. Martínez (1 CMNC).

Diagnosis: This species is almost identical to *G. bidens*, but differs by having the elytral discal striae strongly punctured and the clypeal teeth feebly transversely carinated basally (Fig. 62). Paramera as in Fig. 63.

Distribution: Caatinga province of the Chacoan subregion, with one record from northeastern Pantanal province of the Amazonian subregion (Fig. 106).

Remarks: This species is probably the sister to *G. bidens*, but apparently occupies a more restricted habitat.

6.5. *Genieridium medinae* (Gill & Vaz-de-Mello, 2003), **new combination**
Pedaridium medinae Gill & Vaz-de-Mello, 2003: 47.

Type Material: Holotype m#: COLOMBIA: Risaralda: PNR Ucumari, La Pastora, 2400 m Aliso, 07-V-1995, C. Medina (IAHC); allotype female: COLOMBIA: Risaralda: PNR Ucumari 1800m, La Suiza, 29-III-1995, C. Medina (IAHC).

Paratypes: COLOMBIA: Cundinamarca: Tecadama (*sic*) [Tequendama?] Falls, 30 km SW Bogotá, 27-II-6-III-1972, S&J Peck, forest dung trap (1 CMNC); Quindio, 5 km E Salento, 1800 m, 9-XII-1995, BD Gill, dung trap (9 BDGC; 1 CMNC; 4 FVMC); R Herencia Verde, 1800 m, 12-XII-1995, Medina & Gill, excr hum. (1 CAMC); Risaralda: Pereira, SFF Otún Quimbaya, Est. La Suiza, 1850 m, 25-IV-04-V-1997, A Vitolo (1 FVMC); Pque. Nat. Reg. Ucumari, La Suiza 1800 m, CA Medina (1 CMNC); Pque. Nat. Reg. Ucumari, La Suiza 1800 m, 29-III-1995, F Escobar, excr hum. (2 CAMC).

Diagnosis: Clypeal teeth triangular, obtuse, equilaterous and continuous with clypeal margin. Eyes not visible dorsally. Elytral striae composed of contiguous large umbilicate punctures, elytral disk weakly tectiform in the posterior half. Male hind tibia strongly modified (Fig. 66-67). Paramera as in Fig. 65.

Distribution: Central Colombia (Fig. 107).

Remarks: This is the only species of Scatimina whose eyes are not exposed dorsally.

6.6. *Genieridium paranense* (Arrow, 1932), **new combination**

Pedaridium paranense Arrow, 1932: 224-226; Balthasar, 1938: 219; Blackwelder, 1944: 203; Génier & Vaz-de-Mello, 2002: 191-192
Pedaridium paranensis; Ferreira & Galileo, 1993: 9; Vaz-de-Mello & Canhedo, 1998: 100; Vaz-de-Mello, 2000: 194

Type series: Lectotype m# (designated by Génier & Vaz-de-Mello, 2002): BRAZIL: Paraná: Castro, 1926 (BMNH)
Paralectotypes: Same data as lectotype (3 BMNH).

Non-type material examined: BRAZIL: **Minas Gerais:** Belo Horizonte, XI-1950, A Machado (1 MZSP); **Paraná:** Curityba, XI-1941, Claretiano (1 CMNC); Ponta Grossa, VIII-1942, F Justus (5 CMNC); Castro (5 MZSP, 1 FVMC); 1907, E Garbe (4 MZSP); Londrina, XII-1935, B Pohl (1 FVMC); **Rio de Janeiro:** Estr Rio-São Paulo km 47, XI-1944, Wygod (1 MNRJ); **São Paulo:** Cerqueira César, 12-X-1992, J Carlos (1 AMBC).

Diagnosis. Clypeal teeth absent (Fig. 68), as in *G. bordoni*. First elytral stria effaced on anterior half, stria 2 well defined for entire length, striae 3-5 effaced posteriorly, stria 6 effaced on entire length. Paramera as in Fig. 69.

Distribution: Southeastern Brazil, Paraná Forest and *Araucaria angustifolia* Forest provinces of the Parana subregion (Fig. 104).

Remarks: This rare species appears to be the sister taxon to *G. bidens-margareteae*; the clypeal structure shared with *G. bordoni* is probably homoplasic.

6.7. *Genieridium zanunciorum* (Vaz-de-Mello & Canhedo, 1998), **new combination**
Pedaridium zanunciorum Vaz-de-Mello & Canhedo, 1998: 98-100; Vaz-de-Mello, 2000: 194

Type series: Holotype m#: BRAZIL: **Minas Gerais:** Santa Bárbara, 17-XI-1994, armadilha UV, Zanúncio (MZSP).
Paratype: BRAZIL: **Minas Gerais:** Santa Bárbara, 22-X-1993, JC Zanúncio (FVMC).

Non-type material examined: BRAZIL: **Goiás:** Goiatuba, 1941, J Guérin (1 IBSP); **Minas Gerais:** Araguari, II-1970, H Martínez (1 CMNC); **São Paulo:** Ypiranga, F. Ohaus (1 MNHU); Ipiranga, II-1927, Spitz (1 CMNC).

Diagnosis: Length 5.3-6.3 mm. Dorsum black, shining. Clypeal teeth very acute, same plane as lateral margins and separated of them by feeble emarginations (Fig. 70). In other aspects similar to *G. cryptops*, except that interstriae always have a double row of setose punctures. Paramera as in Fig. 71.

Distribution: Scattered localities in Central and Southeastern Brazil (Fig. 106).

Remarks: This species appears to be associated with some special habitat; the few known specimens were collected at light.

7. *Leotrichillum* **new genus**

Diagnosis: Small (2.2-2.8 mm) oval-elongated body (Fig. 23), color tan to brown, clypeus with two teeth and evenly rounded laterally (Fig. 72). Pronotum separated of hypomeron by sharp carina, hypomeron with sharp lateral longitudinal carina posteriorly. Elytral interstriae with single row of setose punctures; pseodepipleuron glabrous and gradually narrowed posteriorly. Middle and hind legs with oval femora; apical width of tibia much more than 1/3 of tibial width. Hind tarsi with basal tarsomere slightly longer than second. Paramera with an apico-lateral invagination (Fig. 73).

Description: Length 2.2-2.8 mm, body oval-elongated, convex (Fig. 23), tan to brown, shining, lacking metallic sheen, dorsal setae slightly claviform. Clypeus with two short triangular teeth, separated by wide

V-shaped emargination, evenly curved laterally, continuous with genal margin. Clypeo-frontal and clypeo-genal sutures indistinct. Eyes dorsally rounded, each about as wide as 0.7 of its length, separated by five to six eye widths (Fig. 72). Pronotum without anterior or posterior bead, lateral pronotal callosity indicated by indistinct dark spot. Pronotal disk covered by simple setose punctures, separated from hypomeron by very weak carina. Hypomeron with strong longitudinal lateral carina; mesoepimeron with weak anterior transverse carina, stronger mesally; metasternal disk covered by simple punctures. Elytral interstriae with one row of setose punctures, flat all along. Elytrans striae not distinctly widened or deeper on declivity. Pseudoepipleuron glabrous, gradually narrowed to apex, with a longitudinal fold near metacoxa making the anterior part of the pseudoepipleuron to be almost vertical in position, and the posterior part almost horizontal. Front tibia with three strong teeth occupying apical three fifths of lateral margin, that is denticulate from base to basal tooth, with ventral scale-like setae on teeth. Middle and metafemora oval, meso- and metatibia apically wider than one third of tibial length. Pygidium nearly vertical. Paramera shorter than one-half of length of phallobase, flattened and apically rounded, laterally incised (Fig. 73). Pseudoflagellum helicoidal and thick, with flat elongated auxiliary lamella. Coxites large, oval and symmetrical. Spermatheca simply C-shaped, gradually narrowed apically, bulbous at base, with the duct inserted in the ventral part of the base of the spermathecal body.

Secondary sexual characters: Males with front claws bent in the middle, front apical tarsomere modified to receive claws; meso- and metatarsi with claws bigger and stronger than in females. All tibiae with apico-mesal tooth in males, middle and hind tibial teeth smaller than front tibial one. Metasternum slightly concave in males, flat in females; pygidium slightly longer in males than females.

Type species: *Pedaridium louzadaorum* Vaz-de-Mello & Canhedo, 1998 (monotypy) = *Leotrichillum louzadaorum* (Vaz-de-Mello & Canhedo, 1998), **new combination**.

Etymology: After my son, Léo Falqueto Vaz de Mello. Gender neutral.

Distribution: Northern Argentina and southern Paraguay, central and northeastern Brazil, occupying the Chaco, Caatinga and Cerrado provinces of the Chacoan subregion.

Remarks: The pygidial sulcus of *L. louzadaorum* is, in fact, not divided as described by Vaz-de-Mello & Canhedo (1998); it is entire. The relationship of *Leotrichillum* to other genera is uncertain, as it has several chacaters relating it both to *Genieridium* (e.g. oval-elongated body, presence of meso- and metatibian meso-apical teeth in males, slightly modified meso- and metatibial male claws, weak pronoto-hypomeral carina) and to *Degallieridium* (e.g. very small size, color tan to brown with darkened pronotal callosities, claviform dorsal setae, longitudinally bent epipleuron, large eyes). Unambiguous synapomorphies for *Leotrichillum* are the laterally incised paramera and the ventral position of spermathecal duct insertion, apart of others that depend on the resolution of its phylogenetic position.

Composition: Besides the type species, the genus contains at least one undescribed species.

Material examined:

7.1. *Leotrichillum louzadaorum* (Vaz-de-Mello & Canhedo, 1998)
Pedaridium louzadaorum Vaz-de-Mello & Canhedo, 1998: 96-97, 100; Vaz-de-Mello, 2000: 194

Type series: Holotype m#: BRAZIL: **Minas Gerais:** Três Marias, XII-1993, Zanúncio (MZSP)
Paratypes: BRAZIL: **Minas Gerais:** Três Marias, X-1989 (1 BDGC); XII-1990, Zanúncio (1 CMNC); XII-1990, Zanúncio (3 FVMC); XII-1993 (1 FVMC); IX-1994 (1 FVMC).

Non-type material examined: BRAZIL: **Minas Gerais:** Três Marias, X-1989 (1 FVMC); X-1994 (1 AMBC); XII-1990, Zanúncio (2 FVMC); XI-1993 (2 FVMC); Águas Vermelhas, XII-1997, Bello (1 AMBC), Montes Claros, XII-1992, Zanúncio (1 FVMC); I-2000, JNC Louzada (2 FVMC); XII-1990 (1 FVMC); **Piauí:** São Raimundo Nonato - PN Serra da Capivara, I-1999, CA Matrangolo (1 FVMC).

8. *Martinezidium* **new genus**

Diagnosis: Clypeus with two, four or six teeth (Fig. 74, 76). Males without modified front claws or apico-mesal protibial tooth. Elytral interstriae either with one or two rows of setose punctures; pseudoepipleuron gradually narrowed to apex and with row of setae. Middle and hind tibiae longer than four times tibial width at apex. Paramera conical (Fig. 75).

Description: Length 2.8-5.0 mm. Body oval-elongated (Fig. 24-25), dorsally brown or black, sometimes with metallic sheen. Clypeus rounded, with two to six triangular teeth separated by wide U- or V-shaped emargination. Clypeofrontal suture indistinct, clypeo-genal suture very weak. Each eye dorsally as wide as 0.4-0.7 eye length, interocular space about six to eight eye widths (Fig. 74, 76). Pronotum separated from hypomeron by strong lateral carina, hypomeron with strong posterior carina parallel to lateral border. Both anterior and posterior pronotal angles obtuse, anterior margin not beaded. Mesoepimeron with anterior transverse carina. Front tibia with three strong lateral teeth, middle one broader, all acute; teeth occupying apical three fifths of tibia. Tibia laterally denticulate from base to basal tooth; with ventral scale-like setae on teeth. Front claws small, evenly curved in both sexes. Length of hind basitarsus equal or less than that of second tarsomere. Interstriae flat to feebly convex on disc, with one to two rows of setigerous punctures. Pseudoepipleuron gradually narrowed posteriorly, with setigerous punctures all along the mesal margin (in worn specimens lacking in the anterior third). Striae much deeper and with larger punctures apically. Aedeagus with each parameron conical (Fig. 75). Coxites small and symmetrical. Spermatheca C-shaped, with very long and swollen unsclerotized duct.

Sexual dimorphism: Females differ from males by having broader front tibia, lateral teeth slender and less conspicuous than in males, front tibial spur shorter and basally broader than in males; abdominal sternite VI longer medially than in males, pygidium wider than in males.

Type species: *Pedaridium galileoae* Génier & Vaz-de-Mello, 2002 (present designation) = *Martinezidium galileoae* (Génier & Vaz-de-Mello, 2002), **new combination**.

Etymology: After Antonio Martínez, from whose collection a great part of the examined material came, and who contributed much to the study of *Trichillum* and *Pedaridium* from the 1950's to just before his death in 1993. Gender neutral.

Distribution: The genus has a very widely disjunct distribuition, with one nucleus in Southern Paraguay and Argentina, from Jujuy to Chubut, occupying the Chaco and Pampa provinces of the Chacoan subregion in the Neotropical region, and the Monte province in the South American transition zone; and the other in Mexico (Jalisco, San Luis Potosí, Veracruz, Yucatán, Quintana-Roo, Chiapas, Campeche) and Guatemala (Petén), equivalent to Mexican Gulf and Yucatán Peninsula provinces of the Caribbean subregion of the Neotropical region, and the western part of Transmexican Volcanic Belt province of the Mexican Transition Zone.

Remarks: The relationships of this genus are unclear. Its disjunct distribution is correlated to morphological differences indicating that the geographic nuclei likely correspond to species-group clades. Northern species are black, without traces of metallic sheen, and clearly flatter than southern species, and with slightly convex discal elytral striae (Fig. 25). Southern species are brown, with slight to very strong cupreous to green metallic sheen, and have unique modifications in paramera mesally, making them asymmetrical (Fig. 75). Synapomorphies for this genus are the conical paramera and the lack of sexual differences in tarsi and mesally in front tibia.

Composition: Besides the type species, the genus contains also *M. martinsi* (Ferreira & Galileo, 1993), **new combination**, *M. fulgens* (Arrow, 1913), **new combination***, M. maya* (Vaz-de-Mello, Halffter & Halffter, 2004), **new combination** (all described as *Pedaridium*) and at least five new species currently being described.

Material examined:

8.1. *Martinezidium fulgens* (Arrow, 1913)
Pedaridium fulgens Arrow, 1913: 458; Arrow, 1932: 226; Blackwelder, 1944: 203; Génier & Vaz-de-Mello, 2002: 187-188

Pedaridium martinezi Ferreira & Galileo, 1993: 30

Type series:
Pedaridium fulgens Arrow, 1932: Lectotype and paralectotype f#f# (designated by Génier & Vaz-de-Mello, 2002): ARGENTINA: Gran Chaco: Río Salado, E. Wagner (BMNH).
Pedaridium martinezi Ferreira & Galileo, 1993: Holotype not seen (not located).
Paratypes: ARGENTINA: **Córdoba:** Do. Santa Maria, Diquecito, XII-1965, Martínez (1 CMNC); **La Rioja:** Olta, II-1934, González (1 CMNC).

Non-type material examined: PARAGUAY: **Boquerón:** km 145 a Puerto Casado, XI-1950, Martínez (1 CMNC).

8.2. *Martinezidium galileoae* (Génier & Vaz-de-Mello, 2002)
Pedaridium fulgens (misidentification, not Arrow, 1913); Balthasar, 1938: 458; Martínez 1959: 62; Ferreira & Galileo 1993: 37; Monteresino et al., 1996: 107
Pedaridium galileoae Génier & Vaz-de-Mello, 2002: 195-196

Type series:
Holotype m#: ARGENTINA: Corrientes, Ituzaingó, Arenal de la Costa, Set. 975, Coll. Martínez; allotype f#, same data (CMNC).
Paratypes: **ARGENTINA**: **Córdoba**: Ciudad, I.1945, Coll. Martínez (1 CMNC); Do. Cruz del Eje, Guanaco Muerto, I.1977, Coll. Martínez (1 CMNC). **Corrientes**: Alto Paraná, Ituzaingó, XI.1975, Coll. Martínez (1 FVMC); Ituzaingó, Arenal de la Costa, IX. 1975, Coll. Martínez (1 BDGC, 6 CMNC); Dº Ituzaingo, Villa Olivari, Coll. Martínez (8 CMNC); same as before except: XII.1982 (1 BDGC). **La Rioja**: no locality, XI.1959, M.J. Viana (1 CMNC); Olta, II.1934, M. Gómez leg., Coll. Martínez (1 CMNC). **Mendoza**: no locality, Bruch (1 CMNC). **San Luis**: 18 km S. Arizona, 18-23.I.1982, 250m, H.& A. Howden (1 CMNC); Desaguadero, II.2000, G. Arriágada (1 FVMC); San Geronimo, II.1974, M. Viana (2 CMNC).

Non-type material examined: **ARGENTINA**: **San Luis**: Desaguadero, 20-II.2000, G. Arriágada (1 FVMC).

8.3. *Martinezidium martinsi* (Ferreira & Galileo, 1993)
Pedaridium martinsi Ferreira & Galileo, 1993: 7, 23-24

Type series: not seen.

Non-type material examined: ARGENTINA: **Neuquén:** Ag. Florencio, Ruta 40, XII-1967, A Martínez (2 BDGC, 5 CMNC); Bajada Marucho, XII-1966, Gentili (1 CMNC); XII-1966, Martínez (4 CMNC); C Cura - Buitres - 650 m, X-1968, Gentili (1 CMNC); Covunco, II-1976, Martínez (3 CMNC); La Pintada, XI-1957, Schajovskoy (2 CMNC, 1 FVMC); Lotena-Granito, 800 m, X-1971, Gentili (1 CMNC); P del Águila, X-1961, Grai (1 CMNC); Pampa del Saldo, III-1964, Gentili (1 CMNC).

8.4. *Martinezidium maya* (Vaz-de-Mello, Halffter & Halffter, 2004), **new combination**
Pedaridium maya Vaz-de-Mello, Halffter & Halffter, 2004: 247; Deloya & Peraza, 2006: 341; Morón, 2006: 122

Type series. Holotype m#: **MEXICO**: **Quintana-Roo**, 5 km N Carrillo Puerto, IX-1984, A. Martínez (IEX), Allotype f#: México: **Quintana-Roo**, Reserva de Sian Ka'an, VIII-1984, NTP4A, M. A. Morón (IEX). Paratypes: **GUATEMALA**: **Petén**, San Andrés, San Miguel La Palotada, 06-VI-1999, M. Tolon, EX1-L4-KK3 (1 UVG); Tikal, 23-26-VIII-1972, S. & J. Peck (1 Halffter, 1 Vaz-de-Mello, 1 CMN); **MEXICO**: **Campeche**, Chicana, 10 km W Xpujil, 300 m, 12-14-VII-1983, S. & J. Peck (1 CMN); **Chiapas**, Pque. Nal. Sumidero, Coyote Mirador, 1700 m, 19-VI-1989, H. Howden (1 CMN); Pque. Nal. Sumidero, 26-V-1-VI-1990, B. Gill, dung (2 BDGC); Pque. Nal. Sumidero, 21-VI-1989, E. Zuccaro & P. K. Lago (2 BDGC); **Quintana-Roo**, 100' 20 mi S Felipe C Puerto, 13-VIII-1971, A. Newton (1 GVHC, 1 FVMC); 5 km N Carrillo Puerto, IX-1984, Martínez (1 GVHC); Reserva de Sian Ka'an 1 km al NNE del Rancho "E124", 23-VIII-1985, J. F. Camal, Trampa NTP 80 (1 GVHC); Reserva de Sian Ka'an 2 km al W del Rancho "El Ramonal", 23-VIII-1985, O. Canul, Trampa NTP 80 (1 Halffter); Reserva de Sian Ka'an 5 km del Crucero del camino nuevo a Vigía Chico, 23-VIII-1985, O. Canul, Trampa NTP 80 (1 GVHC); Reserva de Sian Ka'an Bosque Tropical Subcaducifolio, 10 m, 19-VI-1984, O. Canul & S. F. Camal, Trampa NTP 80 (2 GVHC, 1 FVMC, 1 MAMC); Reserva de Sian Ka'an km 12 Carretera nueva al Rancho "El Ramonal", 19-VI-1984, J. F. Camal, Trampa NTP 80 (1 GVHC); 5 km N Puerto, IX-1984, Martínez (2 CMN); Reserva de Sian Ka'an 300 m S de la unión de caminos nuevo y antiguo al Rancho Yuras, 10 m, 19-VI-1984, O Canul & SF Camal, selva tropical subcaducifolia, NTP80 (1 LDC).

Non-type material examined: **MEXICO**: **Quintana-Roo**, Carrillo Puerto, IX-1984, A. Martínez (2 FVMC); **Veracruz:** Apazapan, 280 m, IX-1999, E. Montes de Oca & Q. Santiago (1 EMOC); Jalcomulco, 450 m, IX-2000, E. Montes de Oca & Q. Santiago (1 EMOC).

9. *Nunoidium*, **new genus**

Diagnosis: Body dark, elongated (Fig. 26). Head with two short triangular teeth separated by wide V-shaped emargination. Eyes as wide as 0.4 of their length, separated by seven to eight eye widths (Fig. 77). Pronotum and hypomeron separated by strong carina, pronotum with basal bead. Middle and hind femora oval, middle and hind tibiae strongly widened apically. Male claws and tarsi unmodified.

Description: Length 3.2-5.0 mm, body elongated, parallel sided (Fig. 26), color dark brown to black, shiny, without metallic sheen. Clypeus with two triangular upturned teeth, separated by wide V-shaped emargination, laterally rounded, margin continuous with that of gena. Clypeo-frontal and clypeo-genal sutures indistinct. Each eye dorsally as wide as 0.4 of its length, separated by seven to eight widths (Fig. 77). Pronotum not beaded anteriorly, with continuous posterior bead; separated from hypomeron by smooth carina; lateral callosity ill-defined, elongated. Pronotal disk covered by setose punctures. Hypomeron with strong lateral longitudinal carina; mesoepimeron with anterior transverse carina, metasternum covered by simple setose punctures on disk. Elytral discal interstriae (except sutural interstria) with double row of setose punctures, intertriae flat on disk, the mesal ones slightly convex on declivity; striae deeper and wider on declivity than on disc. Pseudoepipleuron gradually narrowed posteriorly, with a continuous row of punctures. Front tibia with three strong teeth, occupying apical three fifths of length, denticulate at base, with ventral scale-like setae on teeth. Middle femur elongated-oval, as long as three times its medial width; hind femur short oval, as long as twice its medial width; middle and hind tibiae strongly widened apically; middle tibia at apex as wide as one third of its length, hind tibia as long as two times its apical width. Pygidium vertical, transverse. Paramera flattened (Fig. 78), shorter than one-half of length of phallobase, right-angled in relation to phallobase. Internal sac with helicoid pseudoflagellum and three flattened elongated acessory lamellae. Coxites symmetrical, rectangular, mesally toothed. Spermatheca very elongated, C-shaped, apically slightly spiraled.

Secondary sexual characters: Males with apico-mesal tooth in all tibiae; metasternum slightly concave (flat in females), abdominal disc flat (slightly concave in females) and pygidium less transverse.

Type species: *Pedaridium argentinum* Arrow, 1913 (= *Nunoidium argentinum* (Arrow, 1913), **new combination**).

Etymology: After my son, Nuno Falqueto Vaz de Mello. Gender neutral.

Distribution: Central, northern and northwestern Argentina, occupying about the Southern Chaco province of the Chacoan subgregion (Fig. 108).

Remarks: *Nunoidium* appears to be closely related to *Genieridium*, however, the completeness of the carina separating pronotal disk from hypomeron, the vertical pygidial position, and the presence of basal pronotal bead, among other characters, will readily separate it. Synapomorphies of this genus are the presence of pronotal basal bead, the absence of modification in male claws, the elongation of spermatheca, and the psammophilous modifications of hind legs.

Composition: Only the type-species is known.

Material examined:

9.1. *Nunoidium argentinum* (Arrow, 1913)
Pedaridium rugiceps; (*lapsus*) Arrow, 1913: 458
Pedaridium argentinum Arrow, 1913: 459; Arrow, 1932: 226; Balthasar, 1938: 220; Blackwelder, 1944: 203; Martínez, 1959: 62; Martínez, 1959: 63; Martínez, 1987: 60; Ferreira & Galileo, 1993: 8, 24-26; Monteresino et al., 1996: 107*;* Génier & Vaz-de-Mello, 2002: 188; Vaz-de-Mello & Génier, 2005: 46
Trichillum elongatum Balthasar, 1939: 24
Pedaridium elongatum; Martínez, 1969: 119

Type series:
Pedaridium argentinum: **Lectotype** m# (designated by Génier & Vaz-de-Mello, 2002)**:** ARGENTINA: **Chacho:** Río Salado (BMNH), paralectotypes 4 m# 3 f#f#, same data as lectotype (3 m#m# BMNH), same data except: Icano (1 m#, 2 f#f# BMNH, 1 f# MNHN).
Trichillum elongatum: Lectotype m# (designated by Vaz-de-Mello & Génier, 2005), paralectotypes 2 f#f#: ARGENTINA: **Cordoba** (NMP).

Non-type material examined: ARGENTINA: **Chaco:** Gancedo, XII-1939, Biraben-Bezzi (1 CMNC); **Córdoba:** San Vincente, J. Franzel S. (3 MNHU); 4 km NE Cruz del Eje, 20-II-1982, H&A Howden (7 CMNC); Cruz del Eje, I-1977, Martínez (4 CMNC); Do. Santa Maria, Diquecito, XII-1965, Martínez (2 CMNC); La Falda, I-1945, Martínez (2 CMNC); **Formosa:** Ing. Juarez, XII-1953, Martínez (1 CMNC); **Mendoza** (1 MZSP); **Salta:** Do. San Martín, Hickmann, II-1949, Martínez (1 CMNC); **San Luis:** Do. Capital, San Gerónimo, II-1980, A Martínez (1 BDGC, 1 CMNC, 1 FVMC); Do. Ayacucho, El Milagro, XI-1966, Martínez (1 CMNC); San Geronimo, XII-1972, GJ Williner (4 CMNC); Bruch (1 CMNC); 18 km S Arizona, 250 m, 18-23-I-1982, H&A Howden (1 FVMC); **Santa Fé?:** Carcarana (1 UNSM); **Santiago del Estero:** Ojo de Agua, II-1974, A Martínez (1 BDGC, 4 CMNC); no data (9 MNHU, 5 FVMC); Ciudad, XI-1947, A Amigo (1 CMNC); Frías, I-1949, Martínez (1 CMNC); Ojo de Agua, XI-1944, Maldonado (1 CMNC); Río Salado, Wagner (2 CMNC); Santiago del Estero, Wagner (3 CMNC); 11-XII-1939, Biraben-Bezzi (1 CMNC); Chaco de Santiago, Wagner (1 MZSP); no locality, 1936, Wagner (2 NHMB); **Tucumán:** Do. Capital, Rio Sali, XI-1950, Martínez (1 CMNC); **Province?:** Between Santa Fe and Reconquista, 23-XII-1965, Hungarian Soil-Zool. Exp (1 HMNH).

10. *Onoreidium* **new genus**

Diagnosis: Body oval (Fig. 27-28). Head with clypeal teeth upturned and widely separated, area between teeth shallow, very widely U-shaped; clypeal margin with sides rounded (separately from gena) or straight, giving clypeus a trapezoidal shape. Head disk strongly convex with clypeo-frontal suture at least feebly elevated and indicated at sides, frequently strongly carinated. Clypeal teeth separated by a distance at least as wide as a half of interocular width, generally much more (Fig. 79, 82-83). Middle tibiae, in ventral view, with a strong single tooth near middle of lateral border, with very strong short seta inserted apically;

tibial ventral apical transverse margin interrupted by similar structures and without longer setae (Fig. 81). Pseudoepipleuron gradually narrowed posteriorly (Fig. 6), elytral discal interstriae with two rows of setose punctures.

Description: Length 3.5-5.5 mm. Body oval (Fig. 27-28). Color grey to black, sometimes with strong metallic sheen. Clypeus with two very widely separated triangular, upturned teeth, emargination shallow. Clypeus rounded laterally (separately from gena) or straight, general clypeal form trapezoidal. Head disc strongly convex, clypeo-frontal suture well indicated, carinate at least laterally. Clypeo-genal suture indicated at least in front of each eye. Eyes dorsally elongated to oval, width ½ to 1/5 of eye length, eyes separated by 7 to 14 eye widths (Fig. 79, 82-83). Pronotum covered by elongated setose punctures; lacking posterior and anterior beads; separated from hypomeron by very strong longitudinal carina. Hypomeron with strong lateral longitudinal carina, mesoepimeron with strong anterior transverse carina; metasternal disk with setose punctures around middle. Elytra with flat interstriae, discal interestriae with two rows of punctures. Striae deeper and wider apically. Pseudoepipleuron with one row of setose punctures and extra scattered setose punctures in the basal half. Front tibia with three teeth occupying about the apical half or slightly less, without ventral scale-like setae. Front tarsi with last tarsomere modified to receive claws. All claws evenly curved but with a very sharp basal tooth. Middle (and in a lesser degree hind) tibiae, in ventral view, with a strong single tooth about in the middle of lateral border, with a very strong short seta inserted apically, this tooth being similar to others interrupting ventral transverse apical carina of same tibia (Fig. 81). Middle and hind tibiae very strongly expanded laterally very near apex, about 3.5 to four times as long as wide at apex. Paramera flattened apically (Fig. 80), length shorter than one-half of phallobase length. Internal sac with a very thick helicoidal pseudoflagellum. Coxites symmetrical, laminar, strongly toothed mesally. Spermatheca thin, C-shaped, gradually narrowed apically, rounded basally, with a very long partially sclerotized duct.

Secondary sexual characters: Males possess an apically directed small apico-mesal tooth in front tibiae; a concave metasternal disk (flat in females), flat shorter abdominal last sternite (longer and convex in females) and longer pygidium.

Type species: *Trichillum cristatum* Arrow, 1931 (present designation) = *Onoreidium cristatum* (Arrow, 1931), **new combination**.

Etymology: After Giovanni Onore (PUCE, Ecuador), who kindly sent me specimens for study and is a great activist on the study of Latin American Scarabaeoids. Gender neutral.

Distribution: Ecuador, northern Peru, and Panama, comprising the Arid Ecuador and Tumbes-Piura in the Northwerstern South American dominion, and Eastern Central America, in the Mesoamerican dominion, both in the Caribbean subregion. Cited from coastal Venezuela by Ferreira & Galileo (1993).

Remarks: *Onoreidium* presents several synapomorphies, such as the unusual clypeal form, the uniquely developed lateral meso- and metatibial tooth, the thick pseudoflagellum, and the convex head. It appears to be the sister group of *Pereiraidium*, sharing with that genus the modified anterior tarsi in both males and females, the strong tooth in claws, and same general head shape. This clade appears to be related to the *Trichillidium-Bradypodidium* clade (absence of ventral protibial scale-like setae, widely emarginated clypeus, strong lateral pronotal carina, and relative apical position of front tibial tooth); however, it is not clear if that is a sistergroup relationship, or if they form different grades of a paraphyletic group basal to the remaining genera of Scatimina with fused abdominal sternites.

Composition: Besides the type species, the new genus contains *O. ohausi* (Arrow, 1931), **new combination** (described as *Trichillum*), *Onoreidium howdeni* (Ferreira & Galileo, 1993), **new combination**, *Onoreidium bottimeri* (Howden & Young, 1981), **new combination** (described as *Pedaridium*)**;** and at least two new species are under study.

Material examined:

10.1. *Onoreidium bottimeri* (Howden & Young, 1981), **new combination**
Pedaridium bottimeri Howden & Young, 1981: 45; Ferreira & Galileo, 1993: 6, 11-12; Ratcliffe, 2004: 14; Harvey *et al.*, 2006: 578.

Type series: Holotype m#: PANAMA: **Canal Zone:** Barro Colorado Island, 13-VI-1963, LJ Bottimer (CNCI).

Non-type material examined: PANAMA: **Panamá:** Aeropuerto de Panamá, VII-1975, Martínez (unknown f#? CMNC, doubtful); **Canal Zone:** Base of Cerro Galera, 06-VI-1985, E.G. & M.A. Riley (1 TAMU).

10.2. *Onoreidium cristatum* (Arrow, 1931)
Trichillum cristatum Arrow, 1931: 610; Paulian, 1936: 206; Balthasar, 1939: 22; Blackwelder, 1944: 204; Martínez 1969: 119; Génier & Vaz-de-Mello, 2002: 191
Pedaridium equatoriensis Ferreira & Galileo 1993: 14

Type series:
Trichillum cristatum: Lectotype f# (Designated by Génier & Vaz-de-Mello, 2002): ECUADOR: **Loja**: Piscobamba, M. Witt (BMNH); Paralectotype: ECUADOR: Loja, Ohaus S. 2200m (1 BMNH).
Pedaridium equatoriensis Holotype f#: ECUADOR: **Loja:** Maracá/Catacocha, 1100 m, 14-VIII-1977, L Peña (CMNC).

Non-type material examined: ECUADOR: **Loja:** Maracá/Catacocha, 1100 m, 14-VIII-1977, L Peña (1 BDGC, 4 CMNC); Río Catamayo, 29-VIII-1997, C Carpio (1 FVMC, 1 PUCE); PERU: **Lambayeque**: 28 mi. E Olmos, 2000 m, 19-I-1955 (1 WDEC, 1 FVMC).

10.3. *Onoreidium howdeni* (Ferreira & Galileo, 1993)
Pedaridium howdeni Ferreira & Galileo, 1993: 8, 26-27

Type series: Holotype f#: ECUADOR: **Guayas:** 40 km SW Guayaquil, 50 m, 21-22-II-1981, HF Howden (CMNC).
Paratypes: ECUADOR: **Guayas:** 40 km SW Guayaquil, 50 m, 21-22-II-1981, HF Howden (1 MZSP); 45 km W Guayaque, 22-II-1981, HF Howden (3 CMNC).

Non-type material examined: ECUADOR: **Guayas:** 40 km SW Guayaquil, 50 m, 21-22-II-1981, B Gill (8 BDGC); HF Howden (3 CMNC); 22-II-1981(42 CMNC, 1 FVMC, 4 EMRL); Guayaquil, 50 m, 21-22-II-1981, HF Howden (9 CMNC, 2 FVMC).

10.4. *Onoreidium ohausi* (Arrow, 1931)
Trichillum ohausi Arrow, 1931: 610; Paulian, 1936: 206; Balthasar, 1939: 22; Blackwelder, 1944: 204
Pedaridium ohausi; Martínez, 1969: 119; Ferreira & Galileo, 1993: 12; Génier & Vaz-de-Mello, 2002: 190-191

Type series: **Lectotype** m# (designated by Génier & Vaz-de-Mello, 2002): Ecuador: Loja: Punzara (BMNH); Paralectotypes: Same data as lectotype except: Loja Calvario, 4.8.05 (1 BMNH), Loja (1 BMNH), Ecuador, no locality (2 BMNH).

Non-type material examined: ECUADOR: **Loja:** Loja, Ohaus (2 NHMB, 1 FVMC); III-1965, L Peña (1 BDGC, 6 CMNC, 1 NHMB); XII-1984, P. Ponce (1 FVMC); Abé Gaujon (1 NHMB, 1 FVMC).

11. *Pedaridium* Harold, 1868

Diagnosis: Body very large (5.2-8.6 mm) and elongated (Fig. 29). Pronotum clearly flat to concave posteriorly (Fig. 87). Elytra tentiform (suture elevated in relation to disk, each elytron separately flattened), disk forming a feeble fold at apex; interstriae with a double row of setose punctures (Fig. 29). Males with front claws strongly bent (Fig. 86). Scattered longer setae present in sides and anterior part of pronotum and elytral apex (Fig. 29).

Description: Length 5.2-8.6 mm, body very elongated and parallel-sided (Fig. 29), color brown to dark grey, completely opaque and lacking metallic sheen, with yellow to orange setae. Clypeus with two teeth, separated by wide shallow emargination rounded at bottom; clypeus laterally unequally rounded, mesally strongly so and laterally straight, continuous to genal margin. Head flat, feebly depressed near eyes. Clypeo-frontal and clypeo-genal sutures indistinct. Each eye dorsally as wide as one-half its length, eyes separated by 10 to 15 eye widths (Fig. 84). Pronotum lacking anterior and posterior beads, separated from hypomeron by distinct longitudinal carina. Pronotal disk covered by setose puntures, setae much longer anteriorly and laterally; disk surface with posterior shallow to deep concavity, prolonged anteriorly along midline; and slightly explanate (shallowly concave) on anterior angles. Pronotal lateral outline sinuate, wider at anterior angles than at middle (Fig. 87). Hypomeron with distinct longitudinal carina; mesoepimeron with distinct transverse anterior carina. Elytral discal interstriae with two rows of setigerous punctures, flat. Elytra tentiform for entire length, with sutural interstria clearly elevated and each elytron flat on disk; apically with an lateral fold between declivity and pseudoepipleuron. Striae clearly deeper and wider at apex. Pseudoepipleuron gradually narrowed to apex (Fig. 8), with a row of large setae-bearing punctures along entire length and smaller irregular setae in the anterior half. Front tibiae with three teeth concentrated in the apical half of lateral margin, basally denticulate and with small scale-like setae on the ventral face of teeth only. Middle and hind femora elongate, middle and hind tibiae four times as long as wide at apex. Pygidium transverse, vertical, last abdominal sternite long. Phallobase very thin, parameres as long as one-third of phallobase length, apically flattened (Fig. 85). Internal sac with a very thin canaliculate straight pseudoflagellum, with a basal curved auxiliar elongated lamella. Spermatheca C-shaped in the apical half, gradually narrowed apically, basally strongly narrowed, pointed (Fig. 12), duct not sclertotized. Coxites minute, symmetrical and multidentate apically.

Secondary sexual characters: Males have front claws strongly bent (Fig. 86), a very strong meso-apical protibial tooth; small meso- and metatibial meso-apical teeth (Fig. 1-2); metasternal disk strongly concave (flat in females), abdominal disk flat (convex in females), and less transverse pygidium than in females.

Type species: *Pedaria hirsuta* Harold, 1859 (monotypy) = *Pedaridium hirsutum* (Harold, 1859).

Distribution: Brazil (Minas Gerais, São Paulo, Rio de Janeiro and Paraná). Present only in the Eastern Parana subregion, in the Parana Forest and *Araucaria angustifolia* Forest provinces.

Remarks: These are the only representatives of the group that really have a body shape similar to that of the African genus *Pedaria*. Synapomorphies shared by species of this genus are the unique form of the pronotum and elytra; the dual-length dorsal pilosity, reduction of number of internal sac sclerites; reduction of coxite size; and elongation of phallobase (see also under *Genieridium*).

The designation of a lectotype for *P. hirsutum* is necessary because of the sympatry and great resemblance of that species to another one, yet undescribed, that is under study. Although examined specimens that could be confirmed to belong to the type series (two) belong to the same species, Harold (1859) does not mention the number of specimens seen by him for the description, and the original description fits both species. So, given the possibility of existence of other syntypes of *P. hirsutum*, I decide to fix here the name-bearing type in order to warrant the application of the species name in its current sense.

Composition: In the present restricted sense, *Pedaridium* contains at least one new species currently under study, in addition to the type-species.

Material examined:

11.1. *Pedaridium hirsutum* (Harold, 1859)
Pedaria hirsuta; Harold, 1859: 194-195
Pedaridium hirsutum; Harold, 1869: 1001; Gillet, 1911: 48; Arrow, 1913: 458; Arrow, 1932: 224, 226; Balthasar, 1938: 219; Blackwelder, 1944: 203; Ferreira & Galileo, 1993: 7, 16-18, 48-51; Vaz-de-Mello & Canhedo, 1998: 100; Vaz-de-Mello, 2000: 194

Type series: Lectotype is here designated in order to maintain nomenclatoral stability (see remarks). LECTOTYPE **here designated**: m#, pinned, in MNHU. Labels: [1.] 26438 / [2.] *São João del Rey, Sellow* / [3. green label] *hirsutum Harold* / [4.] Zool. Mus. Berlin / [5. red label] LECTOTYPE / [6.] *Pedaria hirsuta Har. LECTOTYPE,* Vaz-de-Mello det. 200*1*
PARALECTOTYPE: m#, pinned, in MNHU. Labels: [1. green label] *St Joao d R, Sello*, *Nr 26438* / [2.] Zool. Mus. Berlin / [3. yellow label] PARALECTOTYPE / [4.] *Pedaria hirsuta Har. PARALECTOTYPE,* Vaz-de-Mello det. 200*1*.

Non-type material examined: BRAZIL: **Minas Gerais:** Vila Monte Verde, 20-IV-1966, J. Halik (4 MZSP); **Paraná:** Campo Largo da Roseira, VII-1942, Hatsbach (1 CMNC); Curitiba, V-1942, Hatsbach (1 CMNC); no date (1 MNRJ); IV-1942 (1 IBSP, 3 MZSP); Deodoro, 1943, Hatsbach (2 CMNC); VI-1942 (1 CMNC, 3 MZSP); Florestal (Deodoro), X-1943, Hatsbach (1 CMNC); Florestal (Piraquara), XII-1942, B. Pohl (2 MZSP); Guaraúna, VI-1937, Pinheiro Machado (1 MZSP); VI-1947 (1 MNRJ); Penha, VI-1940, Hatsbach (1 MZSP); Purunã, V-1942, Hatsbach (1 MZSP); Rincão, IV-1942, Hatsbach (1 CMNC); Xaxim, V-1942 (1 IBSP, 1 MZSP); **Rio de Janeiro:** Itatiaia, 19-IV-1992, CL Godinho Jr (2 FVMC); I-1992 (1 FVMC); IV-1995 (2 FVMC); Nova Friburgo, Três Picos, Salinas, X-2000, P Grossi (4 FVMC); Nova Friburgo, VI-2000, P Grossi (1 FVMC); **Santa Catarina:** São Bento, II-1989, Pereira (1 CMNC); **São Paulo:** São Bernardo, VIII-1934, Guérin (2 IBSP); **No data:** (2 IRSN, 1 NMHB); Candèze (2 IRSN).

12. *Pereiraidium* **new genus**

Diagnosis: Large species, sides of head sinuate, clypeo-genal margin not incised (Fig. 88, 90). Male with two long frontal horns (Fig. 30, 88), females with two poorly defined tubercles (Fig. 31, 90). Anterior pronotal bead present and distinct. Claws strongly toothed at base, last tarsomere of front tarsi modified in both sexes.

Description: Length 5.5-6.1 mm, body oval-elongated (Fig. 30-31), color dark brown, opaque, lacking metallic sheen. Clypeus with two large, weakly defined teeth, separated by wide V-shaped emargination. Clypeus laterally sinuated, continuous with genal margin. Clypeo-frontal and clypeo-genal sutures indistinct; front medially with a longitudinal concavity separating frontal structures (each side with either a long horn or a convexity, mesal to eyes), and transverse concavities anterior to eyes. Eyes dorsally wider than one half of their length, separated by about six eye widths (Fig 88, 90). Anterior pronotal bead present and distinct; lateral pronotal callosity indistinct, disk with setose punctures. Pronotum separated from hypomeron by distinct longitudinal carina. Hypomeron laterally with distinct longitudinal carina, mesoepimeron with distinct transverse carina. Elytral interstriae convex, each with two widely separated rows of setigerous punctures. Striae much deeper and wider on apical declivity. Pseudoepipleuron gradually narrowed posteriorly, with one row of setigerous punctures along length and sparse setigerous punctures ventrally in the anterior half. Front tibiae with three strong teeth, located in the apical half, ventrally lacking scale-like setae. Middle and hind tibiae longer than three times their apical width. Pygidium vertical. Paramera apically flattened (Fig. 89), as long as one third of phallobase length. Internal sac with a strong sinuated and bent pseudoflagellum and two auxiliary lamellae. Coxites small, symmetrical and triangular; spermatheca very elongated, slightly spiralled apically, gradually narrowed at both ends.

Secondary sexual characters: Males with strong frontal, upturned horns (Fig. 30, 88) that can be as long as, or slightly longer than prothorax; horns with hairs similar to those on remainder of head at least on basal half (Fig. 88); females with only two distinct convexities in place of horns (Fig. 90). Pronotum of large males with flat anterior declivity (Fig 30), declivity absent or very slightly indicated in females (Fig. 31). Metasternum concave in males and flat in females; and pygidium slightly longer in males.

Type species: *Pedaridium almeidai* Pereira, 1946 = *Pereiraidium almeidai* (Pereira, 1946), **new combination**.

Etymology: The name is after Padre Francisco Silvério Pereira, CMF (1912-1992), Brazilian scarabeidologist who described the single species here included in this genus. Gender neutral.

Distribution: South and southeastern Brazil (Rio Grande do Sul, Paraná and São Paulo). Endemic to the southernmost part of the Brazilian Atlantic Forest province (Fig. 108).

Remarks: The main apomorphies of this genus are the presence of horns in males and two frontal concavities in females, the presence of an anterior pronotal bead, and the convex discal interstriae. It is supported also by the absence of the synapomorphies supporting *Onoreidium*, its sister genus. See more remarks under *Onoreidium.*

Composition: Only the type species is known.

Material examined:

12.1. *Pereiraidium almeidai* (Pereira, 1946), **new combination**
Pedaridium almeidai Pereira, 1946: 289; Ferreira & Galileo, 1993: 6, 10-11; Vaz-de-Mello, 2000: 194; Verdú & Galante, 2001: 597-599

Type series: Holotype m# and allotype f#: BRAZIL: **Paraná:** Deodoro, V-1942, Hatsbach (MZSP).
Paratypes: BRAZIL: **Paraná:** Guaraúna, V-1937, J. Pinheiro Machado (1 CMNC); XII-1937 (1 CMNC); Deodoro, V-1942, Hatsbach (2 MZSP); **Rio Grande do Sul:** Glória, 1927, P. Buck (1 IRSN).

Non-type material examined: BRAZIL: **Rio Grande do Sul:** Glória, 06-VI-1927, P. Buck (2 CMNC); 20-IX-1927 (1 CMNC); X-1927 (1 NMHB); 26-VII-1928, P Buck (1 FVMC); **São Paulo:** Est Biol. Boracéia, 24-VIII-1996, JR Verdú (2 FVMC).

13. *Scatimus* Erichson, 1847

Diagnosis: Head with a transverse carina or conical tubercle (Fig. 32). Dorsum lacking setigerous punctures. Abdomen with intersternal sutures clearly visible. Trochanterofemoral pit of anterior leg rounded. Middle and hind tibiae each with two transverse lateral carinae.

Type-species: *Scatimus cucullatus* Erichson, 1847 (monotypy).

Distribution: From Sonora province in the Continental Nearctic dominion of the North American Pacific subregion of the Nearctic region to Napo, Guyana and Roraima provinces of the Amazonian subregion of the Neotropical region.

Remarks: This genus contains twelve species and has been recently revised by Génier and Kohlmann (2003). Valid species and their synonyms are:

13.1. *Scatimus cribrosus* Génier & Kohlmann, 2003
13.2. *Scatimus cucullatus* Erichson, 1847
13.3. *Scatimus erynnios* Kohlmann & Solís, 1996
13.4. *Scatimus fernandezi* Martínez, 1988

13.5. *Scatimus furcatus* Balthasar, 1939
13.6. *Scatimus monstrosus* Balthasar, 1939
13.7. *Scatimus onorei* Génier & Kohlmann, 2003
13.8. *Scatimus ovatus* Harold, 1862
=*Scatimus patruelis* Preudhomme de Borre, 1886
=*Scatimus quadridentatus* Balthasar, 1939
13.9. *Scatimus pacificus* Génier & Kohlmann, 2003
13.10. *Scatimus quadricuspis* Génier & Kohlmann, 2003
13.11. *Scatimus simulator* Martínez, 1988
13.12. *Scatimus strandi* Balthasar, 1939

14. *Scatrichus* Génier and Kohlmann, 2003

Diagnosis: Head with two parallel transverse carinae (Fig. 33). Pronotum with sparse setigerous punctutes laterally; elytra with setigerous punctures on apex and pseudoepipleuron. Abdomen with sternites clearly differentiated on disk. Trochanterofemoral pit of anterior leg oval. Middle and hind tibiae each with two transverse lateral carinae ventrally.

Type-species: *Scatimus bicarinatus* Harold, 1869 (original designation).

Distribution: Cerrado province of the Chacoan subregion, and Brazilian Atlantic Forest and Parana Forest provinces of Parana subregion.

Remarks: This genus contains three species and has been recently revised by Génier and Kohlmann (2003) and this work is here refered to. Recognized species are:

14.1. *Scatrichus bicarinatus* (Harold, 1869)
= *Scatimus bicarinatus* Harold, 1869
14.2. *Scatrichus goiasensis* Génier & Kohlmann, 2003
14.3. *Scatrichus sulcifer* Génier & Kohlmann, 2003

15. *Silvinha* **new genus**

Diagnosis: Dark brown to black, shining, with sparse setae only on sides and apex of elytra (Fig. 34); clypeal teeth acute, emerging from below clypeal margin, that is sinuate in the middle (Fig. 91). Pseudoepipleuron strongly narrowed posteriorly, forming a sharp angle near metacoxal apex (Fig. 9). Aedeagus with latero-apical region of paramera expanded and curved inwards (Fig 92).

Description: Length 3.5-3.8 mm, body form elongate oval (Fig. 34), dark brown to black, shining, without traces of metallic sheen. Clypeus with two very acute teeth, separated from clypeus by transverse carina delimiting clypeal margin; clypeal margin between teeth simply sinuate in the middle, with a rounded to truncate lobe over each clypeal tooth; sides straight to lateral genal angle. Clypeo-frontal suture indicated laterally only, clypeo-genal suture not indicated. Dorsal width of eye equal to half of its length, not narrowed posteriorly, separated by about eight eye widths (Fig. 91). Pronotum lacking anterior and posterior beads, with lateral callus very feebly indicated. Pronotum separated from hypomeron by strong longitudinal carina. Hypomeron with strong lateral longitudinal carina, mesoepimeron lacking anterior transverse carina; metasternal disk smooth. Elytral interstria on disk lacking rows of punctures and setae, flat; very few setose punctures present at apex only, organized in one row with at most three setose punctures. Mesal striae with enlarged punctures at apex only. Pseudoepipleuron with separation to disk lacking anteriorly, glabrous, sinuated near metasternal lateral lobe, strongly narrowed near metacoxa, forming an strong angle (Fig. 9). Front tibia with three lateral teeth, concentrated in the apical half, not denticulate basally, with ventral scale-like setae. Middle and hind tibiae gradually widened to apex, apex as wide as ¼ of their length. Hind tarsi with basal tarsomere as long as 1.3 times the second one. Abdomen with pygidium vertical, transverse. Paramera smaller than one half of phallobase length, laminate, divergent medially and apically strongly convergent (Fig. 92). Internal sac with a three-folded pseudoflagellum and two acessory lamellae. Coxites small, symmetrical and triangular. Spermatheca C-shaped, bulbous at base and gradually narrowed apically, apex inwardly curved.

Secondary sexual characters: Males have front tibia with a triangular apically and ventrally directed apico-mesal tooth; the last tarsomere modified to receive claws, and front tarsi with ventral scale-like setae; front tibia slender and gently curved inwards (almost straight and wider in females), metasternum concave (nearly flat in females), last abdominal sternite shorter than in females and pygidium less transverse.

Type species: *Silvinha unica* **new species** (monotypy).

Composition: Monobasic.

Etymology: After my wife, Silvia (Silvinha) Altoé Falqueto. The name is feminine in gender.

Distribution: Southeastern Brazil (São Paulo, Minas Gerais and Rio de Janeiro). Endemic to the southeastern part of the Parana Forest province in the Parana subregion (Fig. 108).

Remarks: This genus is related to *Trichillum, Besourenga, Eutrichillum, Degallieridium* and Feeridium, although its exact position in that group is not resolved yet. Its main autapomorphies are the absence of organized punctation in elitral discal interstriae, uniquelly shaped pseudoepipleuron and clypeal teeth. See more remarks under *Besourenga.*

15.1. *Silvinha unica* **new species**

Type series:
Holotype m#: BRAZIL: **Rio de Janeiro:** Nova Friburgo, VII-1994, P Grossi (IBSP ex-FVMC).
Paratypes: BRAZIL: **Minas Gerais:** Viçosa, X-1998, FZ Vaz-de-Mello (2 FVMC); II-1995, FZ Vaz-de-Mello (1 FVMC); **Rio de Janeiro:** Nova Friburgo, VII-1994, P Grossi (1 FVMC); 1000 m, XII-1996, P&E Grossi (2 FVMC); **São Paulo:** Serra do Japi, 1050 m, floresta, 1998, MIM Hernández, armadilha pitfall com fezes (5 FVMC).

Description: Holotype m#. 3.6 mm. Body color very dark brown. Head covered by simple punctures separated by one to three diameters, clypeus and gena with few intermixed larger setose punctures, clypeus anteriorly with also minute punctures intermixed (Fig. 91). Pronotum covered by simple round punctures, at disk punctures separated by three to five diameters and minute in size, laterally punctures much larger and denser. Hypomeron covered posteriorly by large round punctures separated by four to six diameters. Elytral interstriae covered by minute unorganized punctures; discal striae with large round punctures, about as wide as twice the stria, and separated by about four diameters on disk. Mesoternum covered by large transverse ocellated punctures separated by less than on diameter, slightly larger than similar punctures present on metasternal lateral lobes. Front tibia with an anteriorly and ventrally directed triangular apico-mesal tooth. Abdominal disk with ocellate punctures separated by one to three diameters. Pygidium with mixed very scattered setose and minute punctures intermixed. Paramera as in Fig. 92.

Variation: Paratypes vary only in color (brown to nearly black), size (3.4-3.8 mm) and sexual features (see above).

Etymology: *unica*: unique, only one, referring to only one species known in the genus.

16. *Trichillidium* **new genus**

Diagnosis: Clypeus with four variably shaped teeth, central pair separated by U-shaped emargination. Beyond outer teeth clypeal margin concave, continuous with that of gena (Fig. 93, 95, 97). Elytral striae very strongly impressed apically. Pseudoepipleuron gradually narrowed apically, with one row of setose punctures and irregular ventral punctures in the anterior half. Front tibia with two to three apical teeth; if three then basal one very small; teeth concentrated in the apical one-half or less of tibial margin. Middle and hind tibiae with dense setae apically and ventrally.

Description: Length 2.7-4.1 mm. Body short oval, with maximum width in the middle of elytra (Fig. 35-36); color grey to black, sometimes with slight metallic sheen. Clypeus with four teeth, inner two separated by wide U-shaped emargination. Beyond lateral teeth, clypeal margin continuous with genal margin, concave; genal lateral angle protruded. Head uniformly convex, with shallow concavities anterior to eyes only. Clypeo-frontal suture distinctly indicated only laterally, clypeo-genal sutures indistict. Eyes dorsally as wide as 1/3 to ½ of their length, separated by 8 to 12 eye widths (Fig. 93, 95, 97). Pronotum lacking anterior or posterior beads, laterally with callosity only very feebly indicated; hypomeron separated from pronotum by strong longitudinal carina. Hypomeron with strong lateral longitudinal carina; mesoepimeron anteriorly with transverse carina indistinct; metasternal disk covered by small setose punctures. Elytral interstriae flat, with two rows of setose punctures. Striae moniliform, with large coalescent punctures, strongly widened and deeper at apex. Pseudoepipleuron gradually narrowed apically, with one row of setose punctures all along. Front tibia with two to three teeth (if three then basal one very small), occupying less than one-half of length of tibia; scale-like setae lacking ventrally. Middle and hind tibiae slender (apical width less than 1/3 of tibial length) with very dense setae apically and ventrally, surface difficult to see. Front tarsomeres and claws simple. Pygidium elongated, inclined, not exactly vertical. Internal sac with large, thick pseudoflagellum. Coxites large, laminate, triangular and symmetrical; spermatheca C-shaped, base bulbous, gradually narrowed to acute apex.

Secondary sexual characters: Males with small apico-mesal tooth in front tibia, scale-like setae ventrally in front tarsi, metasternal disk convex (concave in females) and abdominal disk shorter than in females.

Type species: *Pedaridium quadridens* Arrow, 1913 = *Trichillidium quadridens* (Arrow, 1913), **new combination**.

Etymology: Combination of *Trichillum* and *Pedaridium*, due to the fact that species included have been originally described in different genera. Gender neutral.

Distribution: Southern Nicaragua to Central Argentina, absent in Western Amazonia, Central and Northeastern Brazil. Exhibits disjunct distribution comprising southern Mesoamerican dominion (Eastern Central America and Western Panamanian Isthmus provinces) and Choco and Western Ecuador provinces in Northwestern South American dominion, in the Caribbean subregion; Amapa and southern Pantanal provinces in the Amazonian subregion; Chaco and Pampa provinces in Chacoan subregion, and Parana Forest in Parana subregion.

Remarks: This genus is undoubtedly related to *Bradypodidium* (q.v.), and is defined by the following synapomorphies: protrusion of lateral part of gena; convexity of head disk, and shallow concavities anterior to the eyes. This genus has very variable parameral shapes (e.g. Fig. 94, 96).

Composition: Apart of the type-species, this genus includes *T. brevisetosum* (Howden & Young, 1981), **new combination** (described as *Pedaridium*), *T. caingua* (Martínez, 1974), **new combination** (described as *Pedaridium* with a question mark), *T. pilosum* (Robinson, 1948), **new combination** (described as *Trichillum*), and at least one or two species yet undescribed.

Material examined:

16.1. *Trichillidium brevisetosum* (Howden & Young, 1981), **new combination**
Pedaridium brevisetosum Howden & Young, 1981: 44; Ferreira & Galileo, 1993: 8, 32; Ratcliffe, 2004: 14

Type series: Holotype m#: PANAMA: **Canal Zone:** Barro Colorado Island, 16-VI-1977, HA Hespenheide (CMNC).
Non-type material examined: PANAMA: **Panamá:** Nusagandi, 18-20-V-1993, E. Riley, UV light (1 TAMU).

16.2. *Trichillidium caingua* (Martínez, 1974)
Pedaridium (?) *caingua* Martínez, 1974: 65
Pedaridium caingua; Ferreira & Galileo, 1993: 8, 31-32

Type series: Holotype f#: ARGENTINA: **Misiones:** P.N. Iguazú, Pto. Iguazú, XII-1958, Martínez (BRBA).
Paratype: ARGENTINA: **Misiones:** Do. Frontera, San Antonio, IX-1957, Martínez (1 CMNC).
Non-type material examined: BRAZIL: **Rio de Janeiro:** Miguel Pereira, XI-1997, J Carlos (1 AMBC); **Santa Catarina:** Nova Teutônia, XI-1975, F Plaumann (1 CMNC); XI-1976 (1 CMNC); XII-1970 (1 IBSP).

16.3. *Trichillidium pilosum* (Robinson, 1948), **new combination**
Trichillum pilosum Robinson, 1948: 149
Pedaridium pilosum; Howden & Young, 1981: 43; Barbero, 2001: 17; Medina *et al.*, 2001: 139; Ratcliffe, 2004: 14; Harvey *et al.*, 2006: 568-569; 578.

Type series: Holotype not seen (USNM).
Non-type material examined: COLOMBIA: **Chocó:** PNN Ensenada de Utría, 18-VI-1997, Llanos-Jurado, pitfall exr. humanos selva, día (1 FVMC); COSTA RICA: **Alanjuela:** Penas Blancas River Valley, 500-1000 m, 15-IV-1985, B Lyon (1 CMNC); San Ramón, Río San Lorencito, 800 m, 28-II-1987, A Solís (1 CMNC); **Cartago:** Turrialba, 650 m, II-1980, H&A Howden (22 CMNC); **Guanacaste:** above Tilaran, 18-VII-1966, S Peck, in litter wet forest (1 CMNC; 1 CNCI); Monteverde 1400 m, II-1980, RS Anderson, MegaDung Trap (3 CMNC); Monteverde Reserve 1400 m, 24-V-1979 H&A Howden (2 CMNC); 1500 m, 23-V-1979, H&A Howden (1 CMNC); 27-V-1979, H&A Howden, (2 CMNC); Parque Nac Monteverde, 13-VIII-1999, Moreno & Mestre, trampa excr. humano (1 FVMC); **Heredia:** 10 km W Puerto Viejo, 170 m, 2-5-III-1991, H&A Howden, dung traps (5 CMNC); flight intercept traps (2 CMNC, 1 FVMC); **Limón:** 4 km E

Puerto Viejo, 10-30 m, 28-30-XI-1996, Génier & Barret (3 CMNC); Valle de la Estrella, Pandora, 17-20-II-1984, H&A Howden (3 CMNC); **Península de Osa:** Est. Fund. Neot. Aguas Buenas, 7 km W Rincón de Osa, 80 m, VI-1997, S&J Peck (1 CMNC); **Puntarenas:** PN Manuel Antonio, 8-14-XII-1987, Génier & Bertrand (9 CMNC); San Vito, Las Cruces, 1200 m, 22-II-3-III-1983, B Gill (7 CMNC); Coto Brus, Est. Biol. Las Cruces, 31-III-01-IV-2002, A Cline & A Tishechkin, FIT (1 FVMC); San Vito, Las Cruces, 1200 m, 22-II-3-III-1983, BD Gill (1 FVMC); **San José:** 2 km S Colón, 1100 m, 1-16-II-1984, H&A Howden (4 CMNC); ECUADOR: **Esmeraldas:** La Chiquita, 5 m, 11 km SE San Lorenzo, VI-1975, S Peck (8 CMNC); **Guayas:** 27 km S Pto. Lopez, 76 km N Santa Elena, VII-1976, S Peck (1 CMNC); **Los Ríos:** Quevedo, Pichilingue, VIII-1972, Martínez (25 CMNC); IX-1972 (8 CMNC); VI-1976 (1 FVMC); Quevedo, V-1976, Martínez (50 FMLT); **Manabí:** 73 km NE Chone, 90 km W Sto Domingo, 300 m, VI-1976, S Peck (3 CMNC); **Pichincha:** 113 km NW Quito, en Puerto Quito Rd, 2600 m, VIII-1976, J Cohen (1 CMNC); 16 km E Sto Domingo, Tinalandia, 680 m, 4-V-25-VII-1985, S Peck, dung trap (11 CMNC); 47 km S Sto Domingo, II-1976, Howden & Nealis (3 CMNC); Rio Palenque Station, 18-30-V-1975, L Ling (3 CMNC); 230 m, 19-25-V-1975, S Peck, dung trap (10 CMNC); 28-31-VII-1976, S Peck, dung trap (6 CMNC); Pachijal Rd 104 km NW Quito, VIII-1976, J Cohen (1 CMNC); Río Palenque, 28-29-VII-1976, S Peck (1 CMNC); 16 km SE Santo Domingo, Tinalandia, 680 m, 22-28-VI-1975, S & J Peck (3 CNCI); no date (1 CNCI); 16-28-VI-1975, S Peck, for. dung traps (1 FVMC); PANAMA: **Canal Zone:** Gamboa, VI-1983, B Gill (1 BDGC); Barro Colorado Island, 13-I-1959 (4 CMNC); same but H.S. Dybas leg. (88 FMNH); same but 28-I-1959 (16 FMNH); Madden Forest, 10-VI-1977, H&A Howden (2 CMNC); Barro Colorado Island, Gatun L., V-1981, BD Gill (1 FVMC); **Chiriqui:** 4 km N Santa Clara, Hartmann's Finca, 1500 m, 27-VI-3-VII-1981, B Gill (3 BDGC); Cerro Hornito, 15 km NE Gualaca, 1200 m, VI-1982, B Gill (7 BDGC, 2 FVMC); 15 km NW H Volcán, 1200 m, Hartmann Finca, 3-V-1977, S Peck (1 CMNC); 20-31-V-1977, S Peck (2 CMNC); **Colón:** 10 mi SE Colón, Santa Rita Ridge, 270 m, 10-12-VI-1977, S Peck (2 CMNC); **Darién:** Est. Ambiental Cana, 500 m, 04-VI-1996, RS Anderson, human dung trap (1 CMNC).

16.4. *Trichillidium quadridens* (Arrow, 1932), **new combination**

Pedaridium quadridens Arrow, 1932: 225; Balthasar, 1938: 220; Blackwelder, 1944: 203; Martínez, 1959: 62; Martínez, 1987: 60; Ferreira & Galileo, 1993: 33; Monteresino et al., 1996: 107; Génier & Vaz-de-Mello, 2002: 192; Hamel *et al.*, 2006: 12.

Type series: **Holotype** f#: ARGENTINA: Entre Ríos: Santa Elena, Entre Rios, G. E. Bryant, 30.I.1912 (BMNH)

Non-type material examined: ARGENTINA: **Buenos Aires:** Tigre, V-1945, MJ Viana (2 CMNC); **Córdoba:** Cruz del Eje, Guanaco Muerto, II-1980, Martínez (2 CMNC); Do. Santa Rosa, Diquecito, XII-1965 (1 CMNC); Río Primero, 12-X-1905, F. Schulz (1 FMLT); **Corrientes:** Ituzaingó, Apipé Grande, XI-1945, Martínez (1 CMNC); **Formosa:** 50 km NW Clorinda, PN Río Pilcomayo, 17-XII-1990, S&J Peck, UV (1 CMNC); **Jujuy:** 1 km N Pampa Blanca, 700 m, 7-II-1982, H&A Howden (3 CMNC); 12 km S Ledesma, 500 m, Río Ledesma, 27-XII-1987, S Peck, substr. seas. forest (1 CMNC); **Salta:** Do. Anta, Las Lajitas, XII-1984, Martínez (2 CMNC); XII-1982 (2 CMNC); Viñaco, 15 km S El Carril, 12-II-1982, H&A Howden (1 CMNC); La Viña, 2000-2200 m, 24-XI-1983, L. Peña (1 EMRL); **San Luis:** Do. Belgrano, Las Quijadas, II-1969, Hernández (1 CMNC); **Santiago del Estero:** no locality, Wagner (1 CMNC); Río Salado, Icaño, Bosq (1 CMNC); Wagner (1 CMNC); Villa Unión, X-1943, Prosen (1 CMNC); **Tucumán:** Ciudad, Pte. Río Salí (2 CMNC); Ciudad, Río Sali – Puente, XI-1950, Martínez (1 MZSP); Do. Burruyacu, B Ataoz, III-1946, Martínez (1 CMNC); Do. La Cocha, Dique los Pizarros, 10-13-XII-1982, R. Golbach (1 FMLT); BOLIVIA: **Santa Cruz:** Pampa Grande 1360 m, 26-29-I-1999, F Génier, dry cactus scrub, dung (2 CMNC); 28-29-III-1998, H&A Howden (1 CMNC); El Refugio Res., X-1994, A Forsyth (1 BDGC); BRAZIL: **Mato Grosso do Sul:** Corumbá, Passo do Lontra, II-1996, Louzada & Vaz-de-Mello (5 AMBC, 12 FVMC); VIII-1998, J Raiser (1 AMBC); **Mato Grosso:** Poconé, Pousada Araras, 3-XII-1998, Moreno & Mestre (1 FVMC); PARAGUAY: **Boquerón:** Guarn. Oruro, XI-1950, Martínez (1 CMNC); Loma Plata, XII-1993 (1 BDGC); **Caaguazú:** Ybicui, 15-19-XII-1990, G Arriágada (3 CMNC); **Caazapá:** Caazapá, II-1993, G Arriágada (3 CMNC).

17. *Trichillum* Harold, 1868

Diagnosis: Body form oval (Fig. 37-38); color grey to black, shining or not, always lacking metallic sheen. Clypeal teeth variable, but always two (or indicated by anterior sinuosity) and always in continuation with clypeal border (Fig. 98, 100, 102). Pseudoepipleuron with strong sinuation in anterior half and strong angle near metacoxa; in the basal half with a longitudinal carina parallel to pseudoepipleural-epipleural division (Fig. 5). Aedeagus with short subrectangular paramera (Fig. 99, 101)and phallobase very short (about twice as long as wide); spermatheca particularly spiral-shaped, spermathecal duct sclerotized and feebly differentiated from spermatheca itself (Fig. 13).

Description: Size 2.2-5.0 mm, body oval (Fig. 37-38), color grey or brown to black, always lacking metallic sheen. Clypeus with two strong teeth separated by U- or V-shaped emargination. Clypeo-genal and fronto-clypeal sutures indistinct. Clypeal margin lateral to clypeal teeth strongly curved or angled, becoming straight nearing clypeo-genal border, which is straight or slightly sinuate. Gena straight or slightly mesally to lateral angle (Fig. 98, 100, 102). Anterior and posterior pronotal beads absent (Fig. 102). Pronotal disc with indistinct lateral callosity. Hypomeron posteriorly with longitudinal lateral carina. Mesoepimeron with a transverse anterior carina. Metasternal disk glabrous. Elytral nterstriae with single row of setose punctures, mesal striae slightly widened and deepened at apical declivity. Pseudoepipleuron with angle near metacoxa, resulting from very strong narrowing angle to apex, and a sinuosity in its anterior half; glabrous, with a longitudinal carina in anterior half, ending in shallow medial concavity (Fig. 5). Front tibiae with three strong lateral teeth, distributed along apical four fifths of tibial length; with scale-like setae ventrally to teeth basis. Length of parameres smaller than one-half of the length of phallobase; parameres rectangular, apically flattened (Fig. 99, 101); phallobase only twice as long as its width. Coxites large, laminar, asymmetrical or centrally fused. Spermatheca spiral-shaped, spermathecal duct sclertotized and difficult to differentiate from spermatheca itself (Fig. 13).

Secondary sexual characters: Males with a downward directed apico-mesal tooth in front tibia and concave metasternal disk (convex in females).

Type species: *Trichillum heydeni* Harold, 1868 (monotypy)

Distribution: Brazil, French Guyana, Argentina, Bolivia, Paraguay and Uruguay, always eastern of the Andes. Comprises the Humid Guyana, Amapa, Para, Pantanal, Tapajos-Xingu and Roraima provinces of the Amazonian subregion, and the entire Chacoan and Parana subregions.

Remarks: *Trichillum* in its present sense is undoubtedly sister taxon to *Besourenga* (see remarks under that genus), and is supported by the following synapomorphies: presence of a pseudoepipleural carina, parallel to the pseudoepipleuron-epipleuron delimitation in the anterior half; middle and hind tibiae strongly widened apically, with apical width less than 1/3 of tibial length; coxites large and asymmetrical, or if symmetrical, centrally fused as single piece; spermathecal duct uniformly sclerotized, not differentiated from the spermatheca itself. The strong sinuosity of pseudoepipleuron in its anterior half is shared with *Silvinha*, however it is probably a symplesiomorphy. *Trichillum* in the present sense is almost equivalent to the subgenus *Trichillum* as defined by Martínez, except for the inclusion of *T. pauliani*, which Martínez placed (1969) in *Eutrichillum. Trichillum adjunctum* and *T. pauliani* form a somewhat isolated group within the genus, distinguished by the dull grey color and the uniquely centrally fused coxites; that form a large vaginal plaque continuously sclerotized with the spermathecal duct and spermatheca.

Composition: Besides the type species, this genus contains *T. externepunctatum* Preudhomme de Borre, 1880; *T. arrowi* Saylor, 1935; *T. pauliani* Balthasar, 1939; *T. depilatum* Balthasar, 1942; *T. adjunctum* Martínez, 1969; *T. halffteri* Martínez, 1969; *T. morellii* Verdú & Galante, 1998; *T. tischechkini* Vaz-de-Mello & Génier, 2005; *T. pseudoarrowi* Vaz-de-Mello & Génier, 2005; *T. cordobense* Vaz-de-Mello & Génier, 2005; and at least 30 new species currently under description.

Material examined:

17.1. *Trichillum adjunctum* (Martínez, 1969)
Trichillum (Trichillum) adjunctum Martínez, 1969: 123, 129-133; Vaz-de-Mello, 2000: 195
Trichillum adjunctum; Vaz-de-Mello *et al.*, 2001: 3-4

Type series: Holotype m# not seen (BRBA?), allotype f#: BRAZIL: **São Paulo:** São Paulo, Aclimação, XII-1958, A Martínez (BRBA).

Paratypes: **Paraná:** Curitiba, II-1942, Hatsbach (1 CMNC); **São Paulo:** Capital, XI-1929, J Lane (1 CMNC); Ipiranga, XII-1956 (1 CMNC); M. Parnaíba, Três Pedras, XII-1958, Martínez (1 CMNC).

Non-type material examined: BRAZIL: **Distrito Federal:** Est. Florestal Cabeça do Veado, 1100 m, 27-X-1971, EG, I & EA Munroe (1 CNCI); **Goiás:** Mineiros, X-1989, CL Godinho Jr (1 FVMC); **Mato Grosso do Sul:** Selvíria, UNESP farm, 05-VI-1990, CAH Flechtmann, ex Guzerá bovine dropping, Brachiaria decumbens pasture (5 FEIS); Campo Grande, 1990-1992, I Bianchin (1 FVMC); Costa Rica, 17-XII-1993, S Ide (7 MZSP); **Minas Gerais:** Cordisburgo, Faz Pontinha, I-1994, FZ Vaz-de-Mello (1 CMNC, 1 FVMC); XII-2000 (1 FVMC); Lavras, 18-I-1999, JNC Louzada (1 FVMC); 29-I-1999 1 FVMC); Paracatu, II-1997, S Lourenço (33 FVMC); XII-1996, S Lourenço (350 FVMC); Serra do Caraça, 24-II-03-III-1972, Exp. MZUSP (1 MZSP); Vespasiano, XI-1952, A Machado (1 FVMC); **São Paulo:** Bragança Paulista, D Vaglio (1 CMNC); Ipiranga, I-1963, Martínez (1 CMNC); XII-1956 (1 CMNC); São José dos Campos, XII-1934, HS Lopes (2 MNRJ); São Paulo, Ypiranga, I-1963, A Martínez (1 BDGC); **Tocantins:** Pium, XI-1971, J da Silva (1 CMNC).

17.2. *Trichillum arrowi* Saylor, 1935

Trichillum arrowi Saylor, 1935: 208; Balthasar, 1939: 19, 22; Blackwelder, 1944: 204

Type series: Holotype m#: PARAGUAY: **Concepción:** Horquetá (USNM).

Non-type material examined:

BRAZIL: **Distrito Federal:** Est. Florestal Cabeça do Veado, 1100 m, 17-X-1971, EG, I & EA Munroe (1 CNCI); 23-27-X-1971 (1 FVMC).

17.3. *Trichillum cordobense* Vaz-de-Mello & Génier, 2005

Trichillum (Trichillum) depilatum (misidentification, not Balthasar, 1942); (*pars*) Martínez, 1969: 123, 128-129; (*pars*) Verdú & Galante, 1997: 96

Trichillum cordobense Vaz-de-Mello & Génier, 2005: 50-51

Type series: Holotype m#: ARGENTINA: **Córdoba:** El Sauce, Diquecito, XII-1964, Martínez (CMNC).

Paratypes: ARGENTINA: **Buenos Aires:** S. de la Ventana, XI-1981, Bolle (5 CMNC); **Córdoba:** Do. Santa Maria, Diquecito, XII-1965, A Martínez (1 BDGC, 1 CMNC); Alta Gracia, XI-1920, Bruch (2 CMNC); Cabana, I-1944, Prosen (1 CMNC); 28-XII-1925 (1 CMNC); El Sauce, Diquecito, XII-1964, Martínez (1 CMNC).

17.4. *Trichillum depilatum* Balthasar, 1942

Trichillum depilatum Balthasar, 1942: 40-41; Martínez, 1947: 110

Trichillum (Trichillum) depilatum; (*pars*) Martínez, 1969: 123, 128-129; (*pars*) Verdú & Galante, 1997: 96; Vaz-de-Mello, 2000: 195; Vaz-de-Mello & Génier, 2005:

Type series: Holotype f#: BRAZIL: **São Paulo:** no locality, Mráz (NMP).

Non-type material examined:

BRAZIL: **Mato Grosso:** Diamantino, XI-1967, A Maller (1 CMNC); **Santa Catarina:** Rio Natal, X-1945 (1 CMNC); **São Paulo:** Barueri, XII-1955, K Lenko (2 CMNC); I-1956 (1 CMNC).

17.5. *Trichillum externepuctatum* Preudhomme de Borre, 1880

Trichillum externepunctatum Preudhomme de Borre, 1880: xxvii-xxviii; Gillet, 1911: 52; Arrow, 1931: 609; Paulian, 1936: 206-207; Balthasar, 1939: 17, 21; Pessôa & Lane, 1941: 447; Blackwelder, 1944: 204; Louzada *et al.*, 1996: 164, 166; Koller *et al.*, 1999 : 405-408; Aidar *et al.*, 2000 : 817, 819; Marchiori *et al.*, 2000: 167-170; Louzada *et al.*, 2001 : 6; Vaz-de-Mello *et al.*, 2001: 3-4; Verdú & Galante, 2001: 603; Vaz-de-Mello *et al.*, 2002: 675; Marchiori, 2003 : 378-379; Marchiori *et al.*, 2003 : 174-175; Schiffler *et al.*, 2003: 208-209; Scheffler, 2005 : 19; Hamel *et al.*, 2006: 12; Lopes *et al.*, 2006: 263

Uroxys hirta Guérin *in litt.*; Preudhomme de Borre, 1880: xxvii

Trichillum (Trichillum) externepunctatum; Martínez, 1959: 63; Martínez, 1969: 123-126; Martínez, 1987: 60; Monteresino et al., 1996: 107; Verdú & Galante, 1997: 96; Vaz-de-Mello, 2000: 195

Trichillum externopunctatum Preudhomme, 1889 (*sic*); Medina *et al.*, 2001: 139

Type series: Holotype f#: COLOMBIA: **No locality** (IRSN).

Non-type material examined: More than 5000 specimens seen, only localities listed.

NO DATA (ESAP, IBSP); ARGENTINA: **Province?:** Between Rosario and Santa Fe (HMNH); S. Ignacio (IRSN); **Chaco:** 100 km NW Resistencia (CMNC); Colonia JJ Castelli (CMNC); Resistencia (CMNC); Río Tapenagá (IRSN); **Córdoba:** Cabana (CMNC); Capilla del Monte (FVMC); Ciudad (CMNC); Cruz del Eje (CMNC, FVMC); Diquecito (MZSP); Do. Santa Maria, Diquecito (CMNC); La Peca (FVMC); San Vincente (FVMC); **Corrientes:** Alto Paraná (CMNC); Ituzaingó, Villa Olivari (CMNC); **Entre Ríos:** Do. Concórdia, Concórdia (CMNC); Liebig (FVMC); **Formosa:** 50 km NW Clorinda (CMNC); Ciudad (MZSP); **Jujuy:** Dique La Ciénaga (MZSP); Do. Santa Barbara, Termas del Palmar (CMNC); Pampa Blanca (CMNC); **Misiones:** Do. Concepción, Santa Maria (CMNC); Iguazú (CMNC); Loreto (CMNC); **Salta:** Aguaray (MZSP); Carapari (CMNC); Diquecito (CMNC); Do. Anta, Las Lajitas (CMNC, BDGC); Lumbreras (CMNC); Do. San Martín, Hickmann (CMNC); Guemes (CMNC); Pocitos (MZSP); Rosario de la Frontera, El Naranjo (CMNC); S. Victoria (CMNC); Tartagal (CMNC, MZSP); Urundel (CMNC); Viñaco, 15 km S El Carril (BDGC, CNCI, CMNC); **San Luis:** Do. Belgrano, Las Quijadas (CMNC); **Santa Fé:** no locality (IRSN); Tostado (CMNC); **Santiago del Estero:** no locality (CNCI); Do. Copo (CMNC); Río Dulce (IRSN); Río Salado (IRSN); Termas del Río Honda (CMNC); **Tucumán:** Ciudad (MZSP, FMLT); Do. Cruz Alta, Las Cejas (FMLT); BOLIVIA: **Chuquisaca?:** Villa Monte am Pilcomayo (MNHU); **Cochabamba:** Chapare, Agrigento (CMNC); Yungas del Palmar (MZSP); **Ichilo:** Buenavista (MZSP, CMNC, FMNH); **Nor Yungas:** Caranavi (CMNC); **Santa Cruz:** Sara, Gutiérrez, Portachuelo (MZSP); Cordillera, Parapetí (CMNC, MZSP); Cordillera, Quebr. de Caracara (CMNC); Cordillera, Río Seco (MZSP); Cordillera, Tunalito (CMNC); El Cidral (FMLT); Pampa Grande 1360 m (CMNC); Pampa Grande, Ciudad (CMNC); Sara

(FVMC); Sara, Santa Rosa (CMNC, FVMC); **Tarija:** Gran Chaco, Villamontes (CMNC); Ing. Bermejo (FMLT); BRAZIL: **State?:** no data (IRSN); **Acre:** Rio Branco, PZ-UFAC (FVMC); **Bahia:** Bonfim (CMNC, MZSP); Encruzilhada (CMNC); Ilhéus (Pontal) (MZSP); Maracás (MZSP); Mucuri (1 FVMC); **Distrito Federal:** Brasília 1100 m (FVMC, CMNC); **Espírito Santo:** Córrego Itá (MNRJ); Linhares, Faz Lagoa do Macuco, 10 m (CMNC); Linhares (CMNC, MZSP); Vitória - Pque do Tabuazeiro (FVMC); **Goiás:** Aruanã, Rio Araguaya (MZSP); Bom Jardim de Goiás (FVMC); Bom Jesus (FVMC); Corumbá de Goiás (IBSP); Goiatuba (MZSP, MNRJ); Jataí, Faz. Cachoeirinha (MZSP); Jataí, Faz. Nova Orlândia (MZSP); Jataí (MZSP); Leopoldo Bulhões (MNRJ); Luziânia (FVMC); Rio Verde (CMNC, MZSP, AMBC, FVMC); **Mato Grosso do Sul:** Brasilândia, Faz. Barma (MZSP); Campo Gande (MZSP, FVMC); Corumbá, Passo do Lontra (FVMC); Corumbá (CMNC, IRSN, HMNH, CNCI); Costa Rica (MZSP); Coxim, Olímpia e Terra ForteFarm (FEIS); Murtinho (CMNC, MZSP, MNRJ); Rio Caraguatá (MZSP); Rio Paraná - Riacho do Herval (MZSP); Santa Luzia (ex Juí), Mun. Caarapó (MZSP); Selvíria, UNESP farm (ESAP, FEIS); Três Lagoas, Faz. Beija Flor (MZSP); Três Lagoas, Faz. Retiro de Telha (MZSP); Três Lagoas, marg. esq. Rio Sucuriu, Faz. Canaã (MZSP); **Mato Grosso:** Barra do Bugres (FVMC); Barra do Tapirapé (MZSP); Cáceres (MNRJ, MZSP, NHMB); Chapada dos Guimarães (MZSP); Diamantino, Alto Rio Arinos (AMBC, FVMC); Poconé (MZSP); Rio Tapirapé (MZSP); Rosário d'Oeste (MZSP); Tapirapé Indian Village at confluence of R. Tapirapé and R. Araguaia (FMNH); **Minas Gerais:** no locality (IRSN); Açucena (FVMC); Águas Vermelhas (AMBC, FVMC); Buritis (Rib. Confins) (MZSP); Carmo do Rio Claro (MNRJ); Centralina (MZSP); Cordisburgo, Faz Pontinha (FVMC, AMBC); Ipatinga (FVMC, AMBC); Lavras - Poço Bonito (FVMC); Lavras (FVMC); Montes Claros (FVMC); Nova Era (FVMC); Paracatu (FVMC); Pedra Azul 700 m (MZSP); Sete Lagoas (MZSP); Viçosa (FVMC); **Pará:** Belém, Utinga (CMNC); Belém (MZSP); **Paraíba:** Coremas (MZSP); Mamanguape (MZSP); **Paraná:** Londrina (MZSP, FVMC); Rio Caraguatá (CNCI); **Pernambuco:** no locality (MNHU, IRSN); Bonito (CMNC); Pery-Pery (MNHU); Serra de Communaty (MNHU); **Piauí:** São Raimundo Nonato, Pq Nac. Serra da Capivara (FVMC); Teresina (MZSP); **Rio de Janeiro:** km 47, Itaguaí (MZSP, MNRJ); Santa Cruz (FVMC); **Rio Grande do Norte:** Canguaretama (MZSP); Natal (NHMB); Parnamirim (CMNC, MZSP, MNRJ); **Rio Grande do Sul:** Eldorado do Sul (FZRS, FVMC); General Câmara (FZRS); Gravataí (MZSP); Guaíba (FZRS); Livramento (FZRS); Pelotas, Passo da Michaela (FZRS); Porto Alegre (CMNC); Santa Maria (FZRS); São Jerônimo (FVMC, FZRS); São Leopoldo (CMNC, MZSP, CNCI); Viamão (FZRS); **Rondônia:** Vilhena (FVMC); **Santa Catarina:** Nova Teutônia (IBSP); **São Paulo:** Assis (MZSP); Bálsamo (IBSP); Batatais (MZSP); Campinas – Souza (CMNC); Campinas (MZSP); Castilho, marg esq. Rio Paraná (MZSP); Fátima Paulista (FEIS); Flora Rica (FEIS); Ibiré (Termas) (CMNC, MZSP); Ilha Solteira (FEIS); Indiana (MZSP); Itu, Faz. Pau d' Alho (MZSP); Itu (MZSP); Mirante do Paranapanema (FEIS); Piracicaba (CMNC); Pirassununga (ESAP); Rib. Preto (Fac. Medicina) (MZSP); Rio Claro (MZSP); São Carlos (FVMC); São Paulo, Villa Marianna (MZSP); Teodoro Sampaio, Morro do Diabo State Reservation (FEIS); **Tocantins:** Dianópolis (IBSP); Palmas (FZRS); Santa Isabel, R. Araguaia, Ilha do Bananal (FMNH); PARAGUAY: **Do.?:** no locality (HMNH); Mbovevo bei Villarrica (MNHU); **Alto Paraná:** Limoy (FVMC); Puerto Stroessner (HMNH); RB Itabo (FVMC); **Amambay:** Pedro Juan Caballero (ESAP, FVMC, FMLT); **Boquerón:** Col. Ferheim

(CMNC); Cruce Loma Plata (FVMC); Gran Chaco, km 145 de Pto. Casado (BDGC); **Caaguazú:** Ybicui (CMNC); Mandijhé (FMLT); **Caazapá:** Est. Cristal (FVMC); **Central:** Asunción, Est. Mburicao (FVMC); Asunción (CMNC, FMLT); Mburicá (CMNC); Trinidad (CMNC); Univ. Nal. Agric. San Lorenzo (BDGC); **Concepción:** Horquetá (CMNC); **Guayrá:** Villarrica (CMNC, IRSN, MNHU); **Itapua:** Est. Los Belgas (FVMC); **Misiones:** Ayolas (CMNC); Iguazú (CMNC); Pto. Iguazú (CMNC); **Paraguary:** Sapucay (ABC); **Presidente Hayes?:** Río Tebicuarí (CMNC); **San Pedro:** Altos (MZSP); Cororó (FVMC, CMNC); San Lorenzo (MZSP), Carumbé (FMLT); **San Pedro?:** Capiata, Río Paraguay (IRSN); Peribebuy (CMNC); San Estanislao (CMNC); URUGUAY: **Montevideo:** Montevideo (IRSN).

17.6. *Trichillum halffteri* Martínez, 1969

Trichillum (Trichillum) halffteri Martínez, 1969: 124, 137-141; Verdú & Galante, 1997: 96; Vaz-de-Mello, 2000: 195

Type series: Holotype m# and allotype f#: ARGENTINA: **Misiones:** Alba Posse, Puerto, X-1966, A Martínez (BRBA).

Paratypes: BRAZIL: **Rio Grande do Sul:** Estrela, XII-1964, Partridge (2 CMNC); **Santa Catarina:** Barros-Casal, IX-1960, F Plaumann (2 CMNC); Nova Teutonia, X-1969, F Plaumann (1 CMNC).

Non-type material examined: BRAZIL: **Rio de Janeiro:** Nova Friburgo, Macaé de Cima, XII-1998, Grossi, Moreno & Vaz-de-Mello (1 FVMC); **Santa Catarina:** Barros-Casal, 700 m, IX-1960, F Plaumann (2 CNCI); no date (2 CNCI); Nova Teutonia, X-1967, F Plaumann (1 FVMC); XII-1976 (1 CMNC); **São Paulo:** Campos do Jordão, Pq Estadual, 15-19-X-1992, Exp. MZSP (1 MZSP).

17.7. *Trichillum heydeni* Harold, 1868

Trichillum heydeni Harold, 1868: 53-54; Harold, 1869: 1003; Preudhomme de Borre, 1880: xxvii; Gillet, 1911: 52; Arrow, 1931: 609-610; Paulian, 1936: 206, 207; Pessôa & Lane, 1941: 446-447; Blackwelder, 1944: 204; Vaz-de-Mello & Génier, 2005: 42-44

Trichillum (Trichillum) pereirai Martínez, 1969: 123, 133-137; Verdú & Galante, 1997: 96; Vaz-de-Mello, 2000: 195

Type series:

Trichillum heydeni: Lectotype m# (designated by Vaz-de-Mello & Génier, 2005): no data (MNHN); paralectotypes: BRASIL (2 MNHU).

Trichillum pereirai Martínez, 1969: Holotype m#: BRASIL: São Paulo: São Paulo, Aclimação, XII-1962, Martínez (BRBA); allotype f#: BRASIL: Minas Gerais: Viçosa, 1931 (BRBA); paratypes: BRASIL: **São Paulo:** Campos do Jordão, Eug. Lefevre, 1800 m, 13-20-XI-1952, d'Almeida & Pereira (1 CMNC); São Paulo - Aclimação, XII-1962, Martínez (1 CMNC).

Non-type material examined: BRAZIL**: Bahia:** Barreiras, XII-1991, arm luminosa (1 FVMC); Encruzilhada, 980 m, XI-1972, M Alvarenga (74 MZSP); XI-1974 (6 CMNC); XII-1980, Alvarenga & Martínez (6 CMNC); Vitória da Conquista, I-1993 (1 MZSP); **Distrito Federal:** Est. Florestal Cabeça do Veado, 1100 m, X-1971, EG, I & EA Munroe (16 CNCI); **Espírito Santo:** Linhares, Pq Nac Sooretama, XI-1962, Martínez (2 CMNC); **Goiás:** Goiânia, Faz. Dione, 1-V-1993, J. Sár, at light (2 HMNH); Goiatuba, X-1931 (1 MZSP); Niquelândia, X-1993, arm luminosa (5 FVMC); Pirineus, 02-II-1962, Bechyné (1 IBSP); **Mato Grosso:** Barra do Tapirapé, 2-16-I-1966, B Malkin (1 MZSP); Chapada dos Guimarães, XI-1963, Alvarenga (1 CMNC); **Minas Gerais:** Águas Vermelhas, XII-1997, Bello (3 AMBC); Araguari, 17-II-1970, H Martínez (2 CMNC); Barbacena, Van Volxem (3 IRSN); Buritis (Rib. Vermelho), 29-31-X-1964, Exp. Dep. Zool. (1 MZSP); Cordisburgo, Faz Pontinha, X-1993, FZ Vaz-de-Mello (1 CMNC); XII-1993 (3 AMBC); Guanhães, 07-XII-1993 (1 FVMC); Lavras, UFLA, 04-X-1997 (3 FVMC); 15-XI-1997 (3 FVMC); Martinho Campos, X-1991 (1 FVMC); Monte Alegre, Faz. Sta. Maria 1100 m, 24-30-XI-1942, :Zoppe & D'Amico (1 MZSP); Montes Claros, I-2000, JNC Louzada (53 FVMC); XII-1999 (1 FVMC); Paracatu, II-1997, S Lourenço (8 FVMC); XII-1996 (900 FVMC); Pedra Azul, 700 m, XI-1972, Seabra & Oliveira (1 MZSP); Santa Bárbara, 17-XI-1994 (2 FVMC); 25-XI-1993, JC Zanúncio (1 FVMC); Serra do Caraça, 27-XI - 05-XII-1972, Exp. Mus. Zool. (2 MZSP); Unaí, Faz Bolivia, 22-24-X-1964, Exp Dep Zool. (1 CMNC); Vespasiano, XII-1952, A Machado (2 FVMC); **São Paulo:** Assis, XI-1942, B. Pohl (1 MZSP); Atibaia, 18-XI-1969, J. Halik (1 MZSP); Barueri, 18-XI-1963, K. Lenko (1 MZSP); XII-1965, Martínez (1 CMNC); Itu, Faz Pau d'Alho, 28-29-X-1965, Martins & Biasi (1 CMNC, 7 MZSP); XII-1963, Martins (1 MZSP); 06-XI-1960 (1 MZSP); 29-X-1965, U. Martins (4 MZSP); X-1965 (3 MZSP); Osasco, Fca Fósforos, XII-1962, Martínez (2 CMNC); Parnaíba, Três Pedras, XII-1962, Martínez (1 CMNC); Pradópolis, VIII-1976, PSM Botelho (2 ESAP); Salesópolis, Est. Biol. Boracéia, XI-1966, E.X.Rabello (5 MZSP); São Paulo - Aclimação, XII-1962, Martínez (1 CMNC); X-1929, Spitz (1 MZSP); XI-1937, F. Lane (1 MZSP); São Paulo, Ipiranga (1 MZSP); **Tocantins:** Palmas, XI-1992, MHM Galileo (1 FZRS).

17.8. *Trichillum morellii* Verdú & Galante, 1997
Trichillum (Trichillum) morellii Verdú & Galante, 1997: 94-96
Type series: holotype in MEUA, not seen.
Paratype: URUGUAY: **Rocha:** Cerro de Lechiguana, Castillos, 24-IX-1995, JR Verdú (1 MEUA).

17.9. *Trichillum pauliani* (Balthasar, 1939).
Trichillum arrowi Paulian, 1936 (not Saylor, 1935): 205-206; Martínez,1947: 113
Trichillum pauliani Balthasar, 1939 (replacement name): 21, 25
Trichillum homonymum Blackwelder, 1944 (replacement name): 204
Trichillum (Eutrichillum) pauliani; Martínez, 1969: 120-121; Ratcliffe, 1980: 341; Vaz-de-Mello, 2000: 195

Type series: holotype m#: BRAZIL: Pará: Bragance (*sic*), M. de Mathan (MNHN).

Non-type material examined: BRAZIL: **Amapá:** Serra do Navio, Cava Urucum-Amapari, IX-2000, R Ribon (5 FVMC); **Pará:** Tucuruí, VI-1985 (3 CMNC); IV-1988 (2 CMNC); **Roraima:** Cantá - Serra Negra, IX-1996, Ribeiro & Vaz-de-Mello, primary forest (166 FVMC); FRENCH GUYANA: **Cayenne:** Nourages, 21-XI-1998, F Feer (3 FVMC); **Saint Laurent du Maroni:** L'Acarouany, 6-XI-1975, P Arnaud (4 BDGC).

17.10. *Trichillum pseudoarrowi* Vaz-de-Mello & Génier, 2005

Trichillum arrowi (misidentification, not Saylor, 1935); Pereira & Martínez, 1959: 453-458; Forsyth *et al.*, 1998: 371; Spector & Ayzama, 2003: 399

Trichillum (Trichillum) arrowi; Martínez, 1969: 123, 127; Verdú & Galante, 1997: 96

Trichillum pseudoarrowi Vaz-de-Mello & Génier, 2005: 49-50; Hamel *et al.*, 2006: 12.

Type series: Holotype m#: PARAGUAY: **Boquerón:** Gran Chaco, km 145 de Pto. Casado, 25-XI-1950, A. Martínez (CMNC).

Paratypes: BOLIVIA: **Tarija?:** Boyoiú, IV-1949, Daguerre (1 CMNC); PARAGUAY: **Boquerón:** Gran Chaco, km 145 de Pto. Casado, XI-1950, A Martínez (1 BDGC); 25-XI-1950 (8 CMNC); 25-XI-1950 (1 FVMC); **Concepción:** Horquetá, IV-1934, Schultze (2 CMNC).

17.11. *Trichillum tishechkini* Vaz-de-Mello & Génier, 2005

Trichillum (Trichillum) heydeni (misidentification, not Harold, 1868); Martínez, 1959: 64; Martínez, 1969: 122-124; Monteresino et al., 1996: 107; Verdú & Galante, 1997: 96

Trichillum tishechkini Vaz-de-Mello & Génier, 2005: 47-49

Type series: Holotype m#: BRASIL: **Rio Grande do Sul:** Glória, 7-IX-1925, P. Buck, #109a (IBSP ex-FVMC).

Paratypes: ARGENTINA: **Chaco:** Río Bermejo, Pcia. Roca, II-1945, Martínez (1 CMNC); **Córdoba:** Do. Calamuchita, El Sauce, XII-1938, MJ Viana (2 CMNC); Do. Cruz del Eje, Los Leones, II-1967, Chichero (1 CMNC); Do. Santa Maria, Diquecito, XII-1965, Martínez (6 CMNC, 1 CNCI); La Falda, I-1945, Martínez (1 CMNC); San Javier, I-1943, Martínez (1 CMNC); **Formosa:** Ciudad, Puerto, II-1949, Martínez (1 CMNC); **Misiones:** Loreto, Est. Experim., X-1966, Martínez (2 CMNC); **Santa Fé:** Rosario, Ciudad, I-1941, Martínez (1 CMNC); BRAZIL: **Rio Grande do Sul:** locality unreadable, 20-IX-1926, P. Buck, Ex.: Acromyrmex sp. nest. #168 (1 FVMC, 6 NMM); Glória, 7-IX-1925, P. Buck, #109a (4 FVMC, 1 BDGC); 26-VIII-1925:P. Buck, #98 (1 FVMC, 2 NMM); 3-IV-1925, #50 (1 NMM); Teresópolis, 6-IX-1925, P. Buck, coletado Ex.: Acromyrmex sp. nest. #103 (1 FVMC); Floresta, 20-IX-1925, P. Buck, Ex.: Acromyrmex sp. nest. #115 (1 NMM). All the specimens from Rio Grande do Sul from E.Wasmann's Coll'n Alcohol, mounted by A. Tishechkin, 2000.

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FIGURE CAPTIONS

Figures 1-4. *Pedaridium hirsutum*, apex of right anterior tibia and tarsus, respectively dorsal and ventral views: 1-2. m#; 3-4. f#.

Figures 5-11. Left epipleuron and pseudoepipleuron, ventral view. 5. *Trichillum externepunctatum*; 6. *Onoreidium cristatum*; 7. *Scatrichus bicarinatus*; 8. *Pedaridium hirsutum*; 9. *Silvinha unica*; 10. *Besourenga minutus*; 11. *Degallieridium lilliputanum*. Scale = 1.0 mm.

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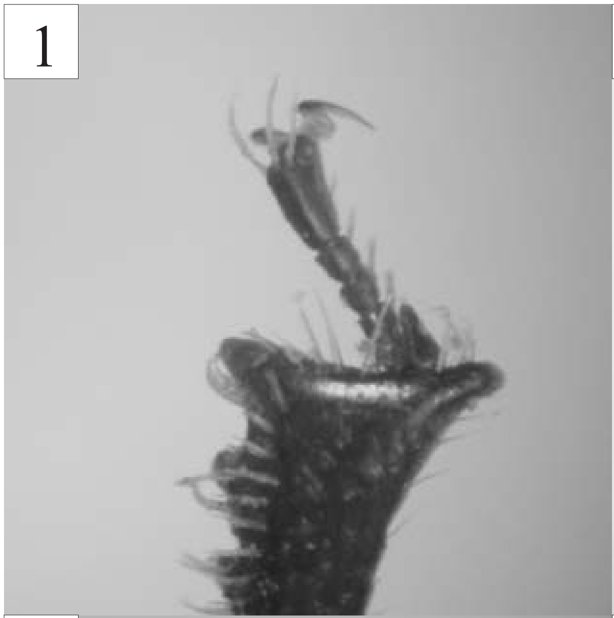
Table 1. Tribal and subtribal position of genera formerly or here included in the Ateuchini and some close relatives, as proposed here. An * indicates genera not examined.

Ateuchini		
Ateuchina	Scatimina	Incertae sedis
Aphengium Harold, 1868	*Besourenga*, **new genus**	*Bdelyropsis* Pereira, Vulcano & Martínez, 1960
Ateuchus Weber, 1801	*Bradypodidium*, **new genus**	*Bdelyrus* Harold, 1869
Deltorhinum Harold, 1867	*Degallieridium*, **new genus**	*Coptorhina* Hope, 1830
Sinapisoma Boucomont, 1928	*Eutrichillum* Martínez, 1969, **new status**	*Delopleurus* Erichson, 1847
	Feeridium, **new genus**	*Demarziella* Balthasar, 1961
	Genieridium, **new genus**	*Onychothecus* Boucomont, 1912
	Leotrichillum, **new genus**	*Paraphytus* Harold, 1877
	Martinezidium, **new genus**	*Pedaria* Laporte, 1832
	Nunoidium, **new genus**	**Pleronyx* Lansberge, 1874
	Onoreidium, **new genus**	**Pseuduroxys* Balthasar, 1938
	Pedaridium Harold, 1868	*Sarophorus* Erichson, 1847
	Pereiraidium, **new genus**	*Uroxys* Westwood, 1842
	Scatimus Erichson, 1847	
	Scatrichus Génier & Kohlmann, 2003	
Transferred to Canthonini	*Silvinha*, **new genus**	Transferred to Coprini
Anomiopus Westwood, 1842	*Trichillidium*, **new genus**	*Canthidium* Erichson, 1847
Hypocanthidium Balthasar, 1938	*Trichillum* Harold, 1868	*Holocanthon* Martínez & Pereira, 1956
Scatonomus Erichson, 1835		*Parachorius* Harold, 1875



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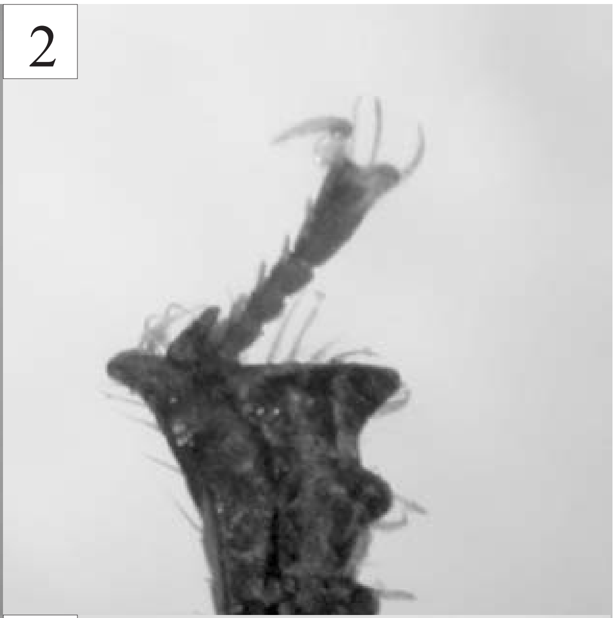

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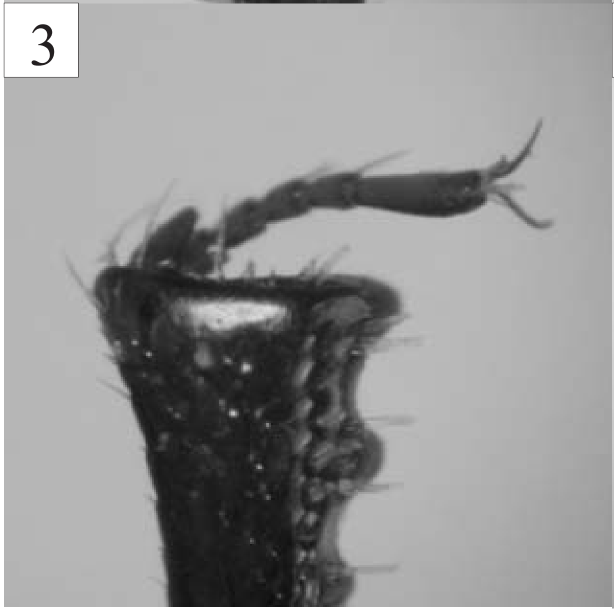

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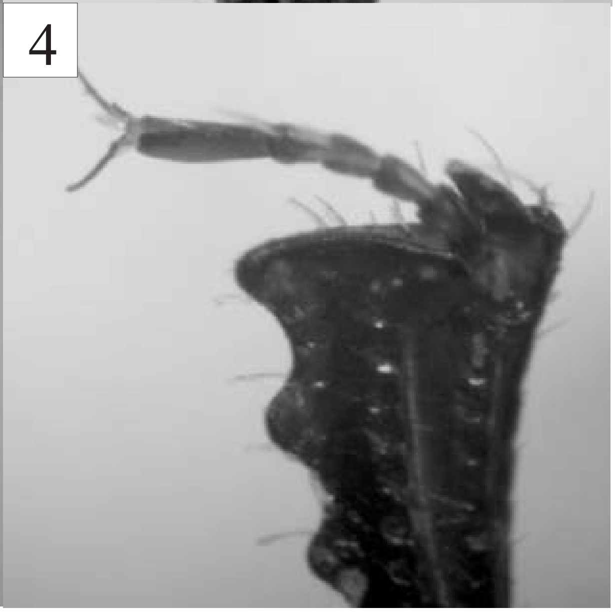

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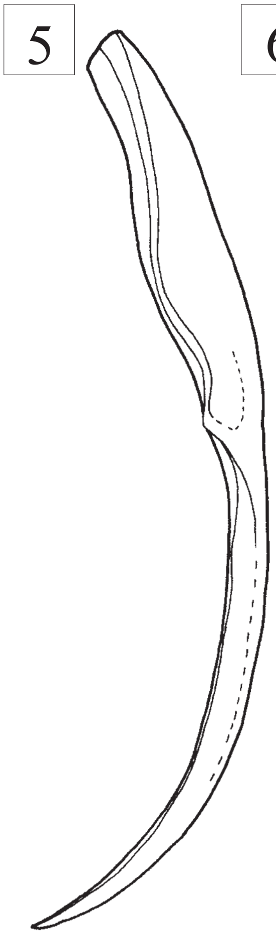

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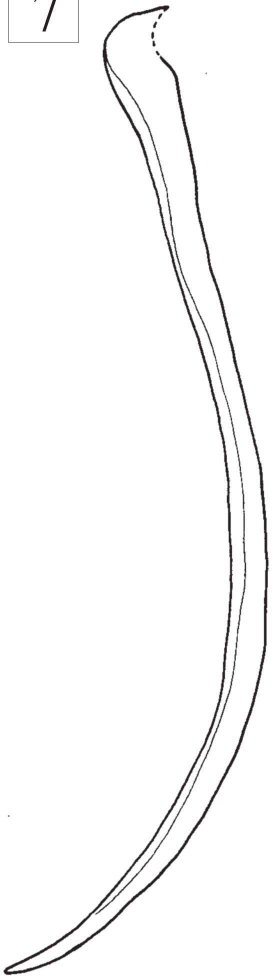

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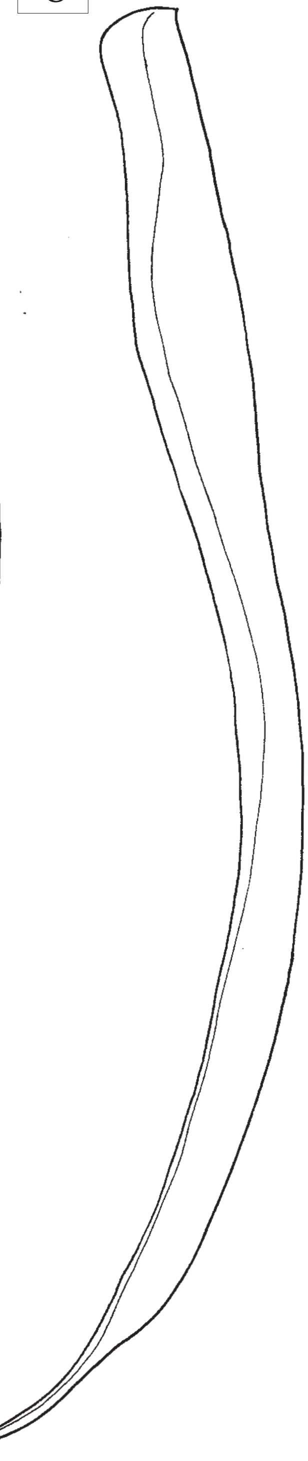

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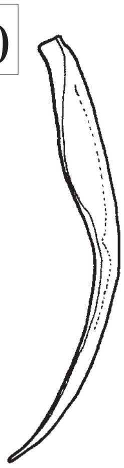

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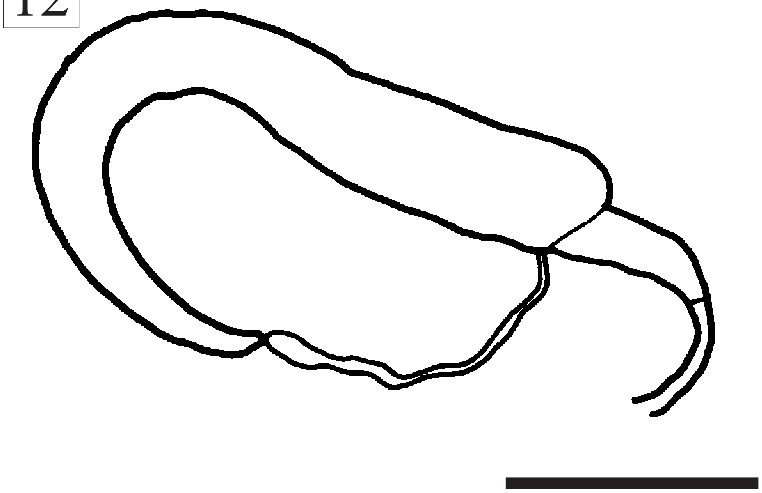

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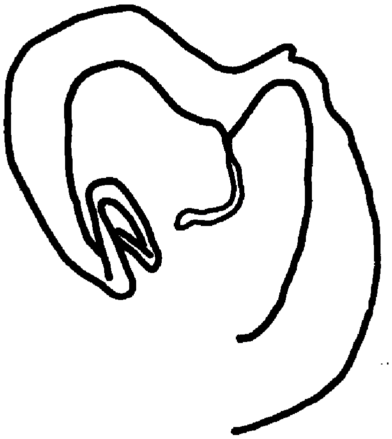

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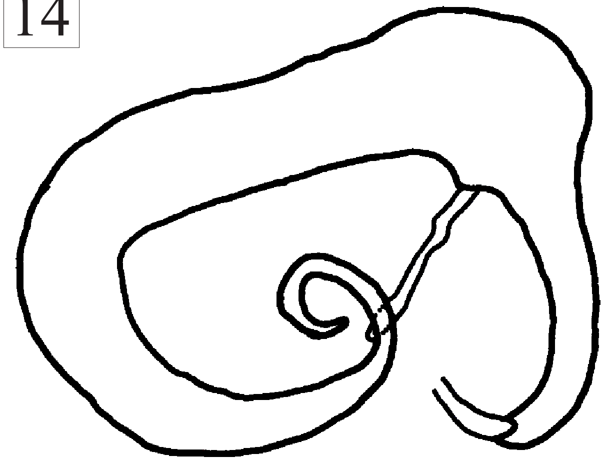

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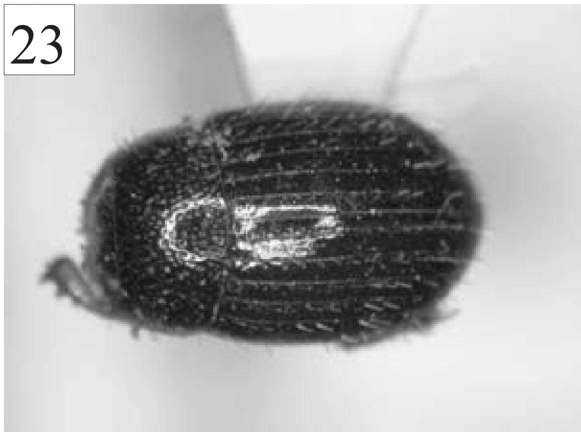

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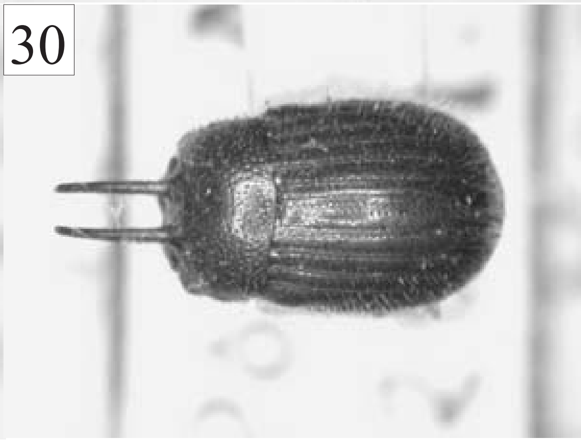


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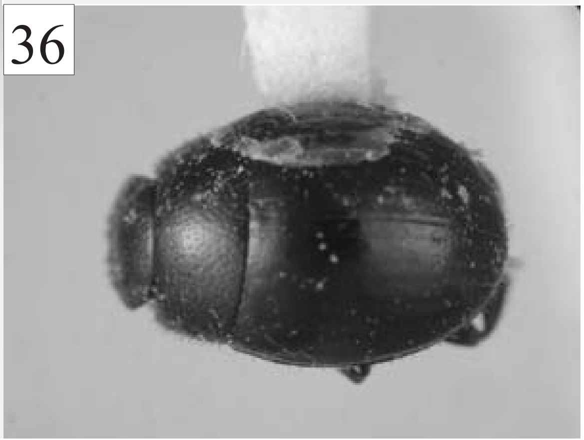
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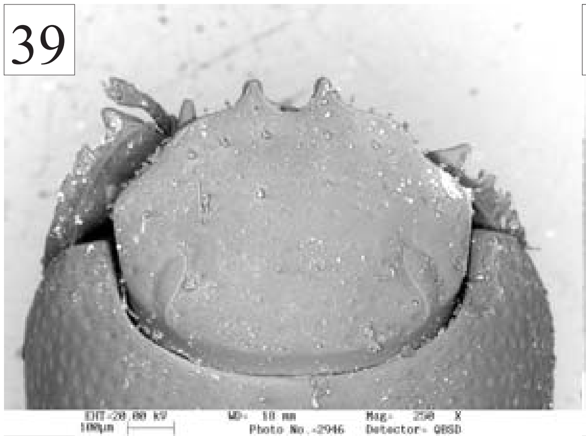

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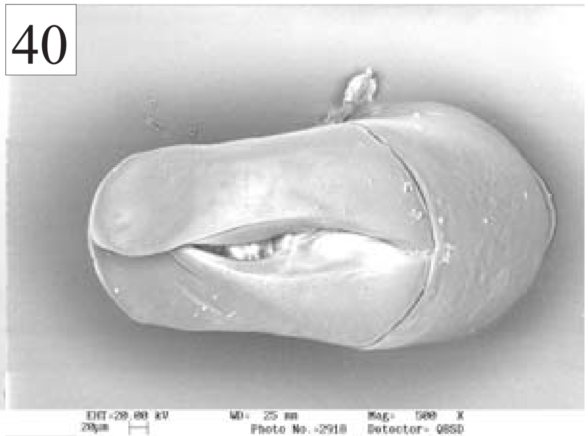

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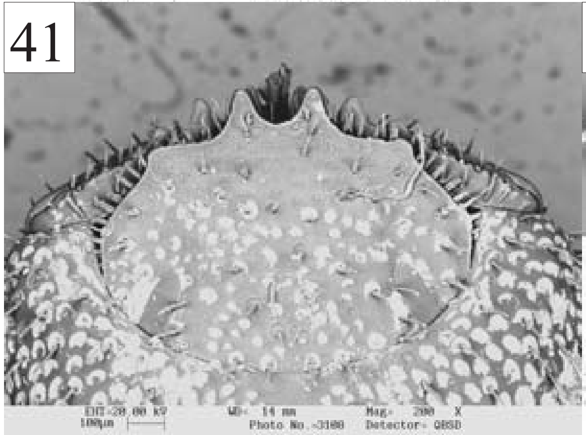

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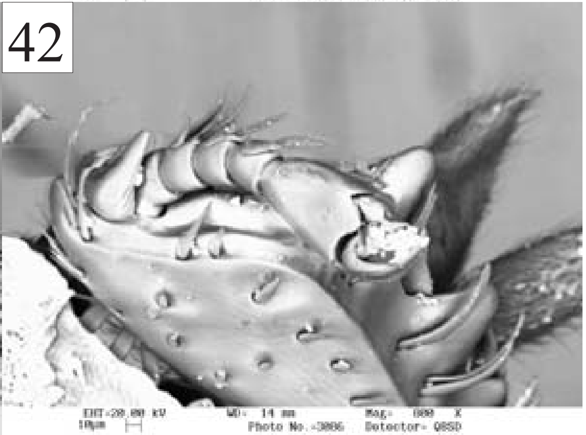

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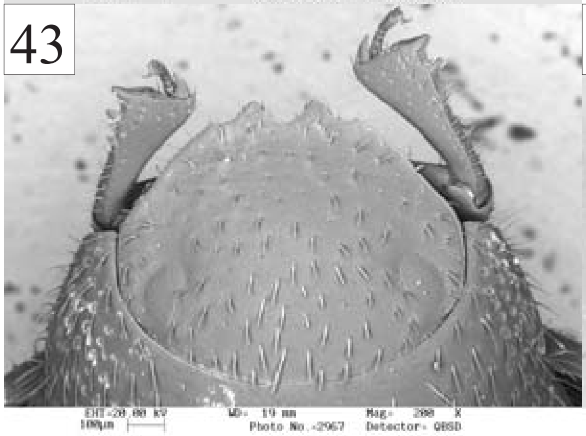

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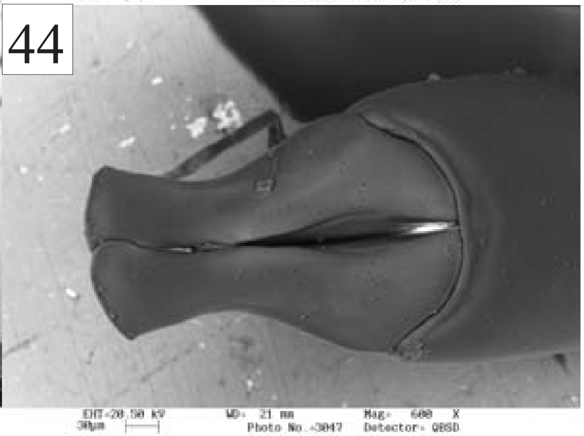

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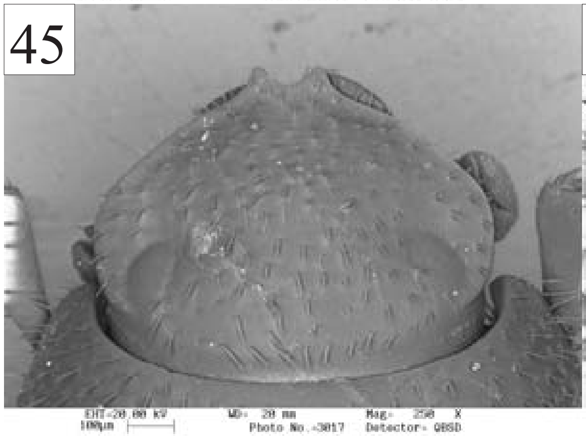

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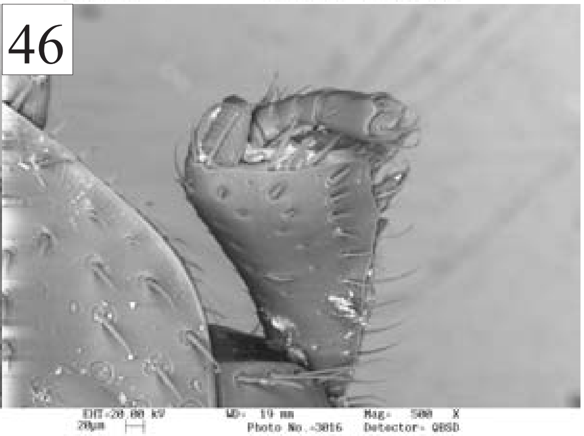

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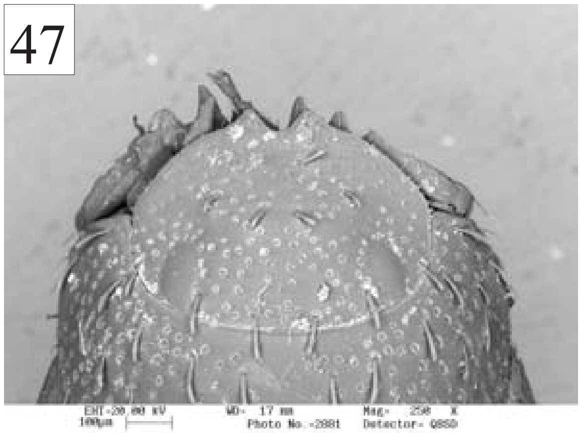

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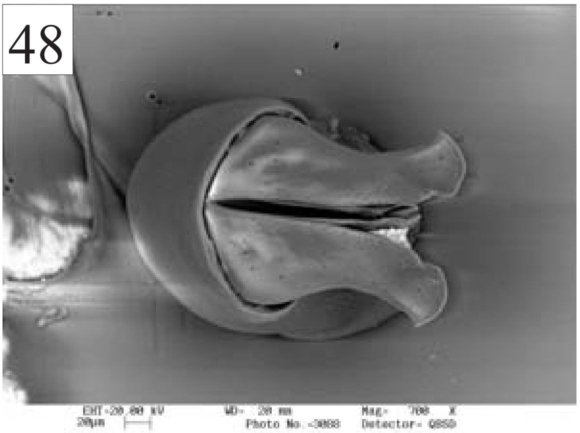

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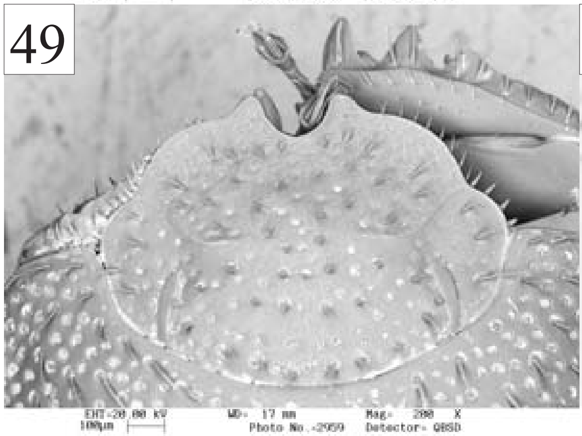

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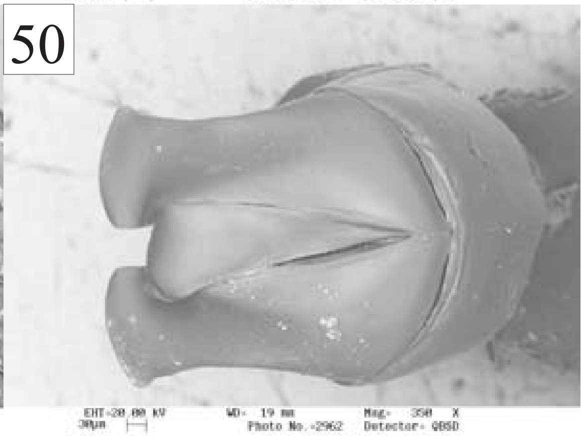

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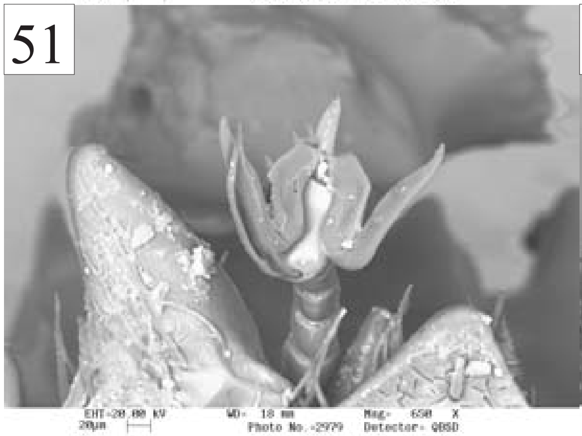

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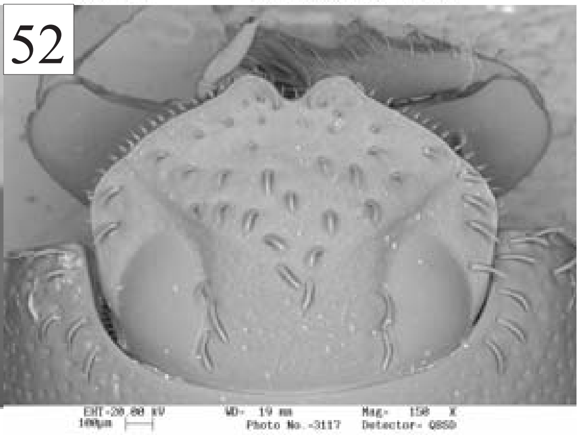

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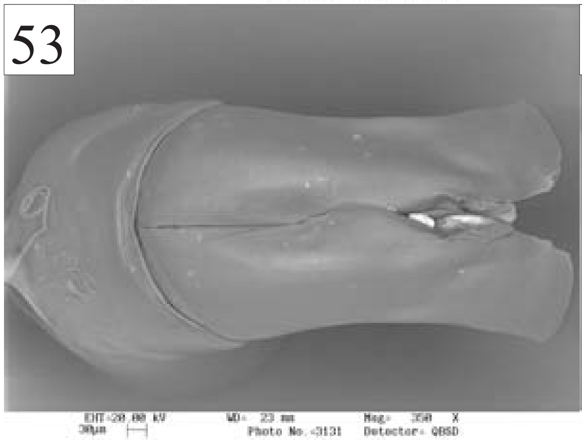

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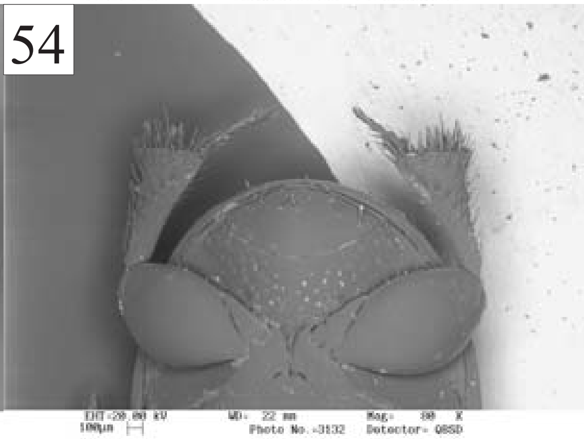

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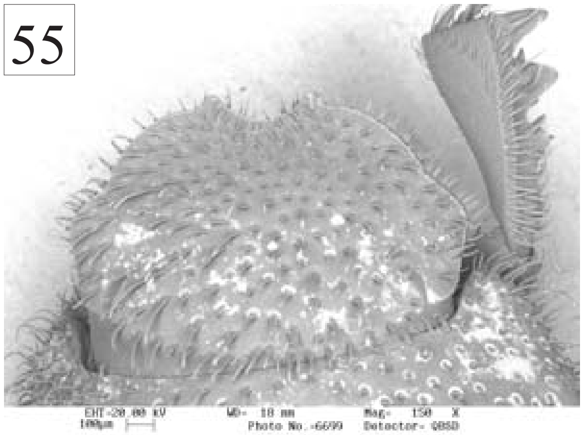

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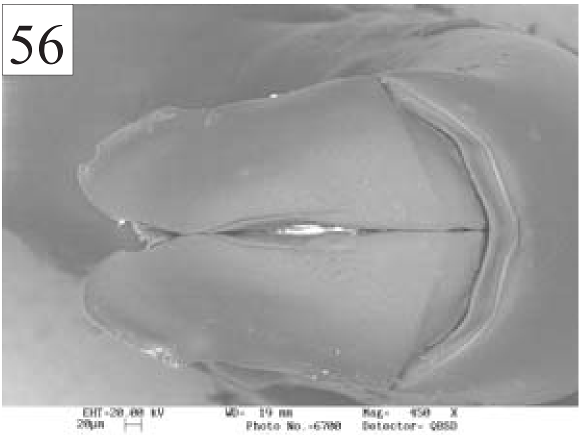

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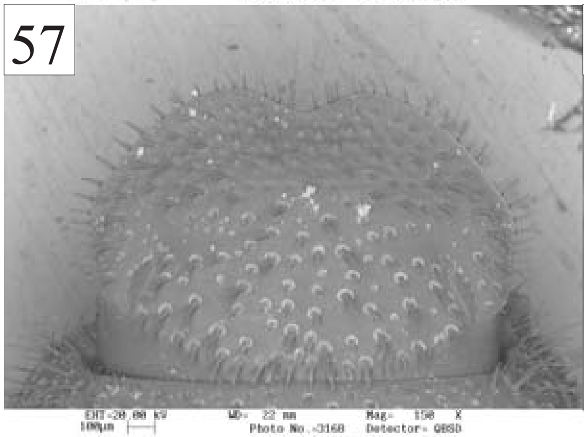

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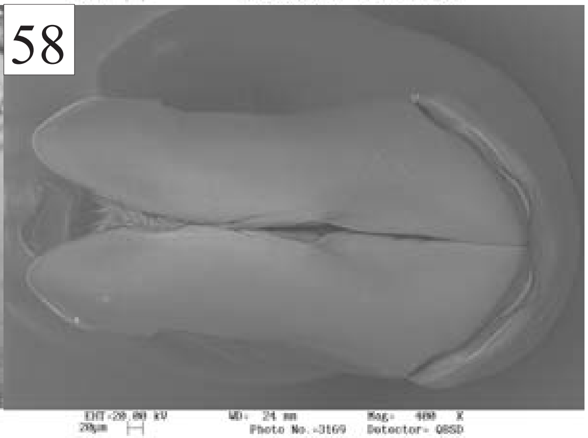

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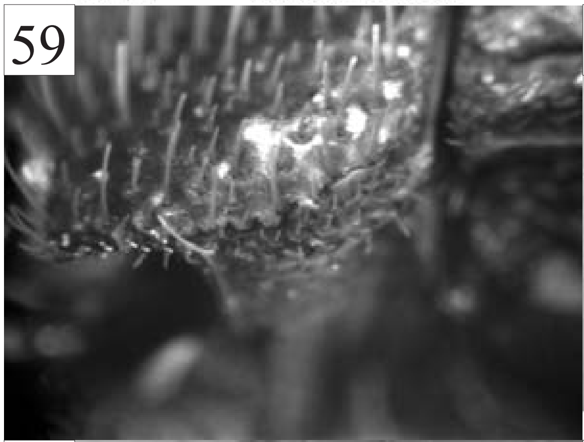

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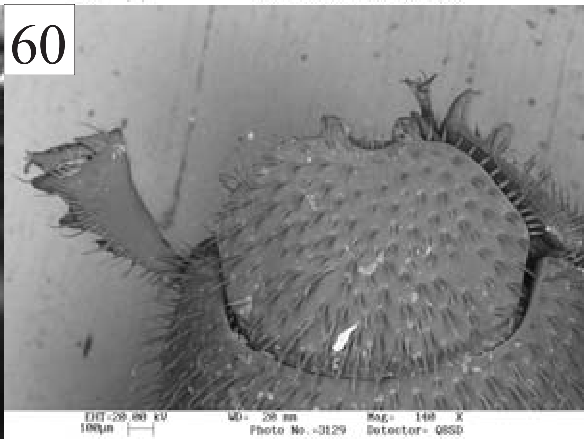

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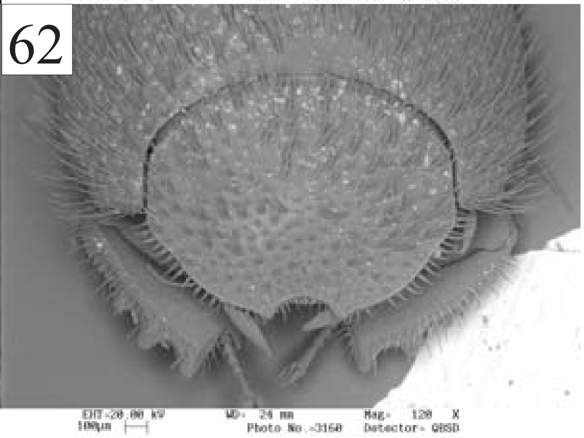

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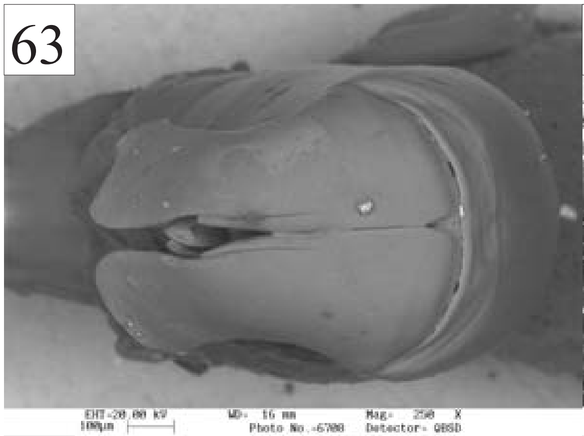

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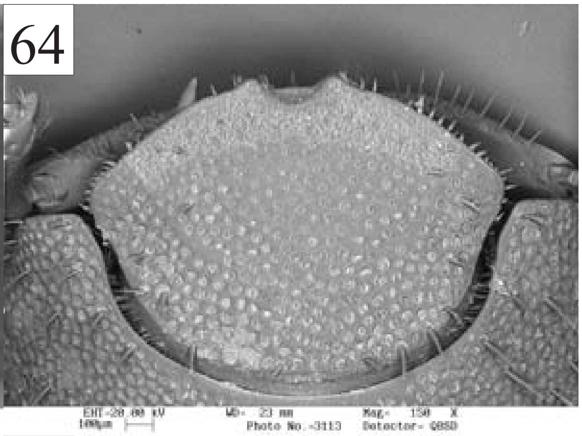

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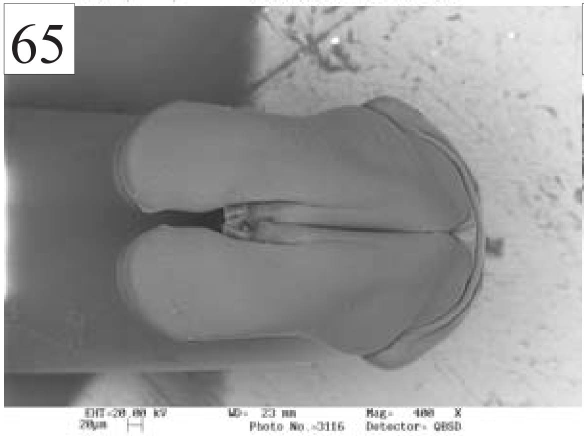

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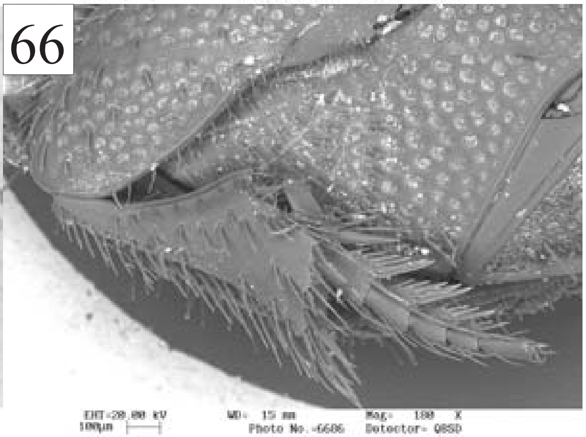

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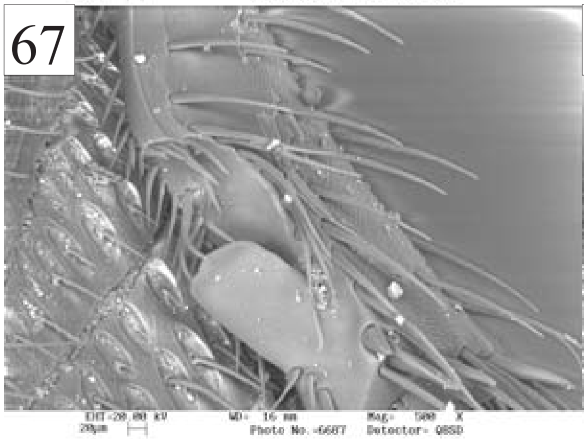

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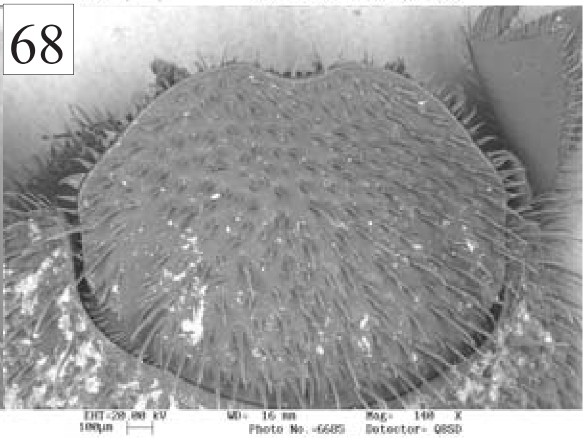

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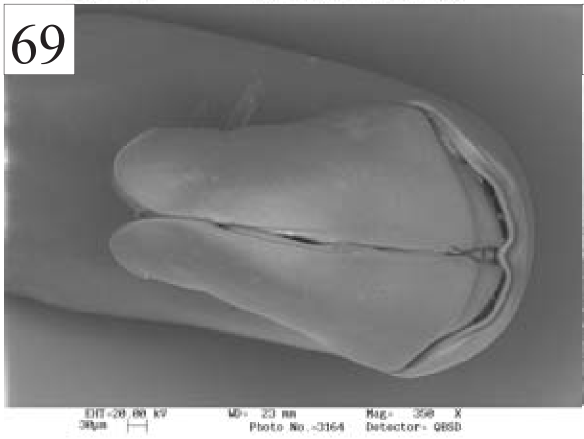

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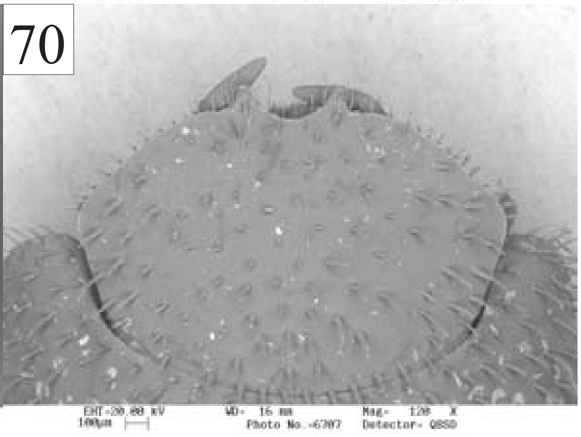

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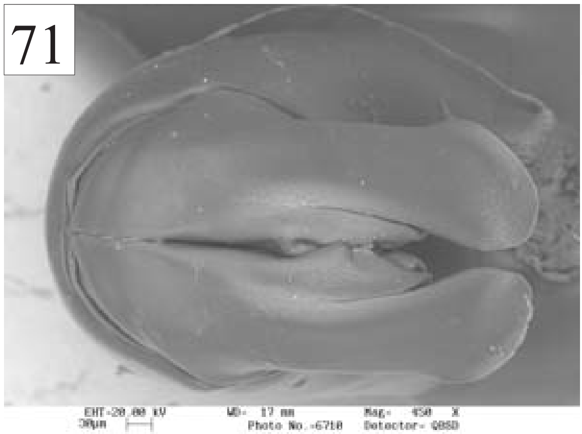

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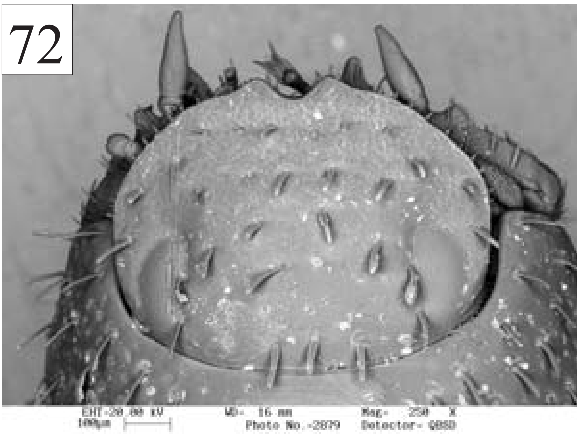

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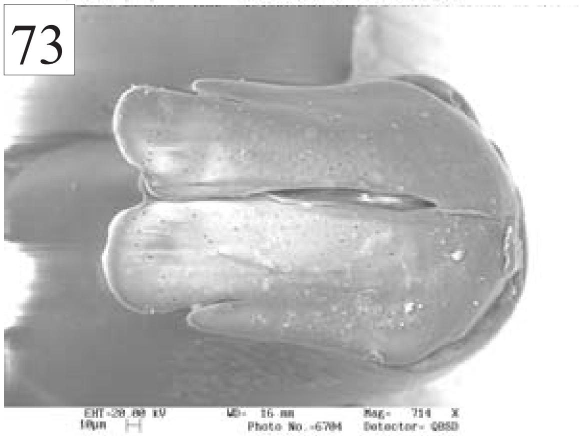

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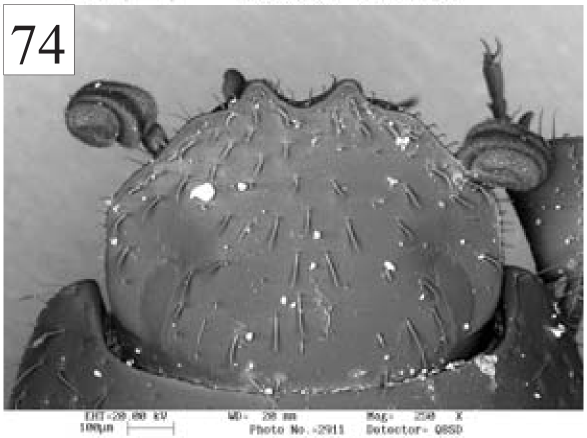

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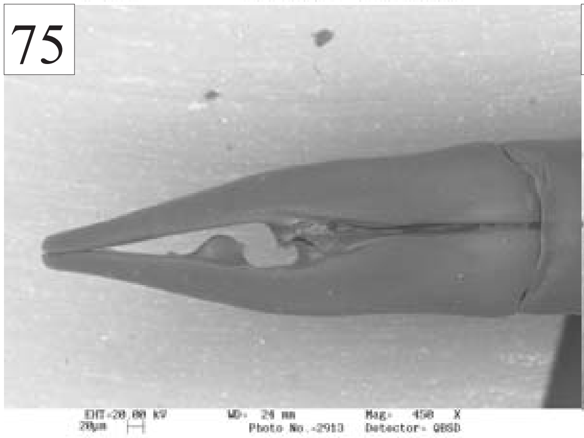

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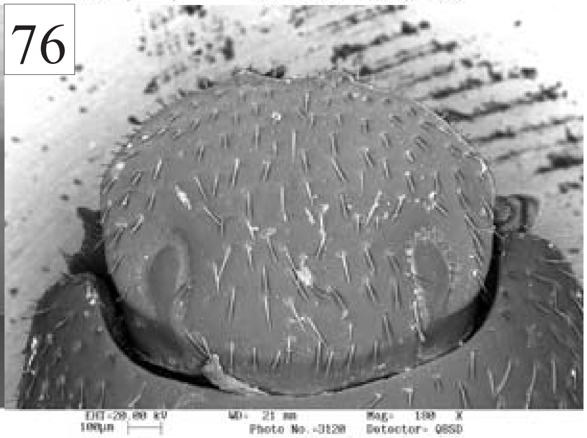

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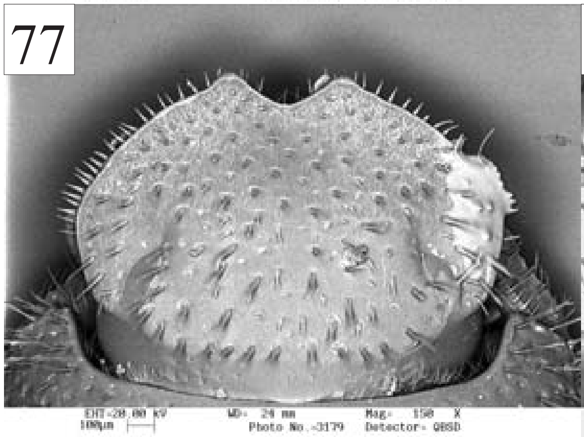

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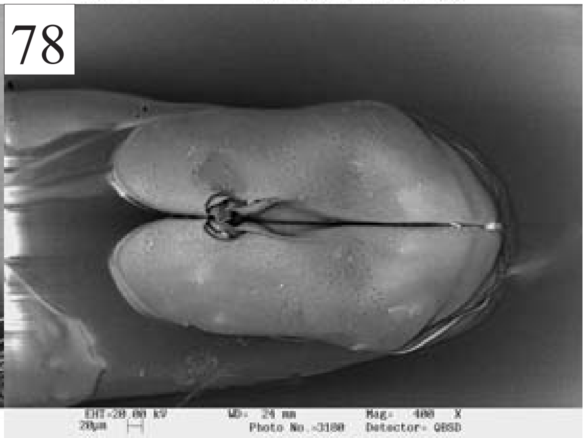

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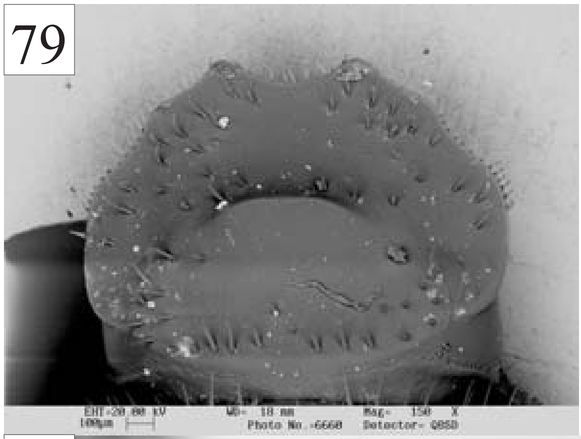

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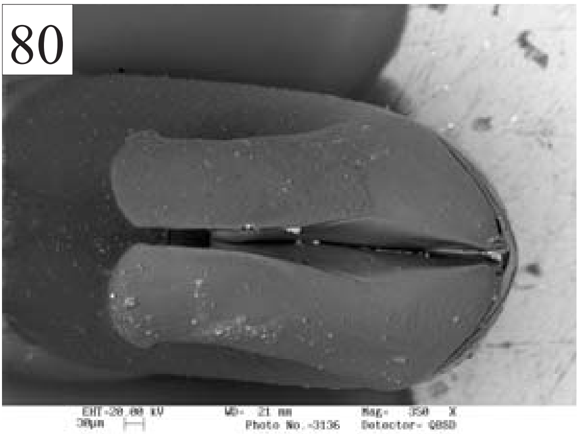

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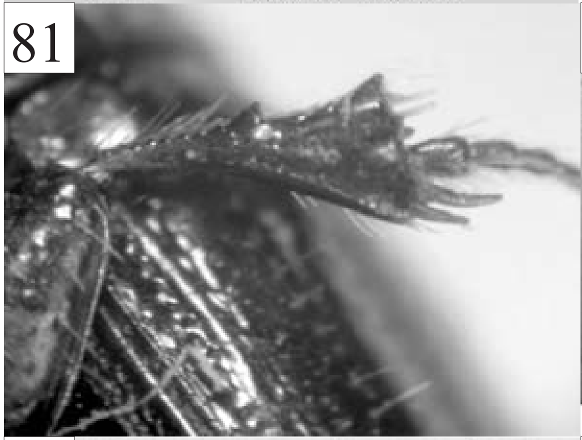

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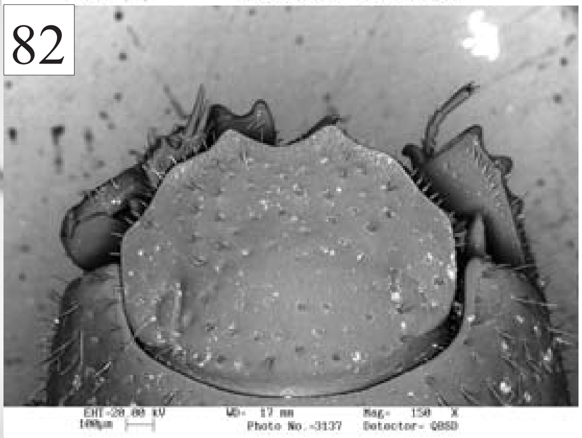

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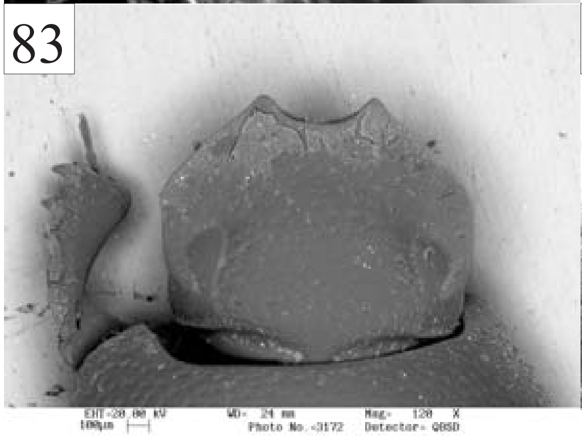

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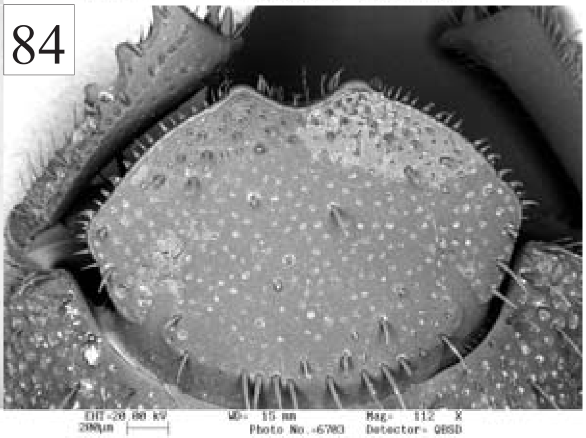

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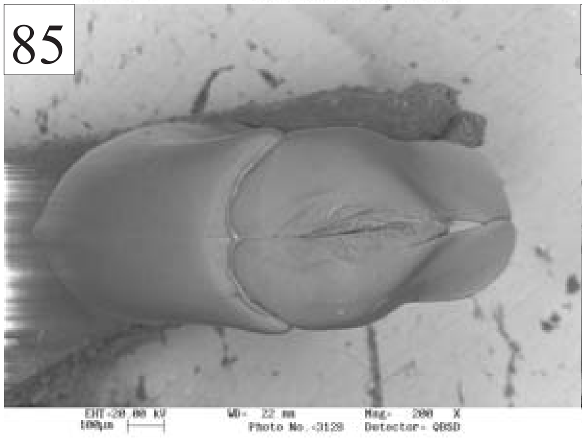

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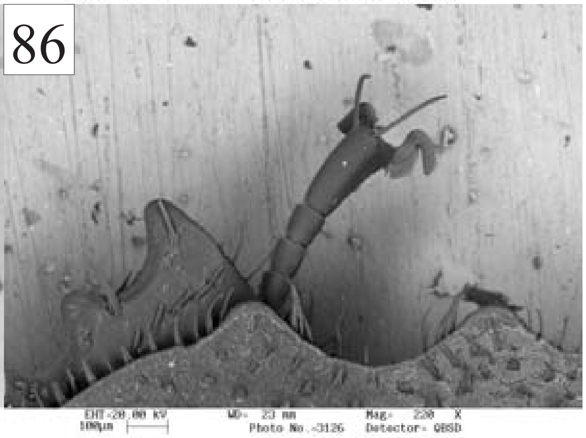

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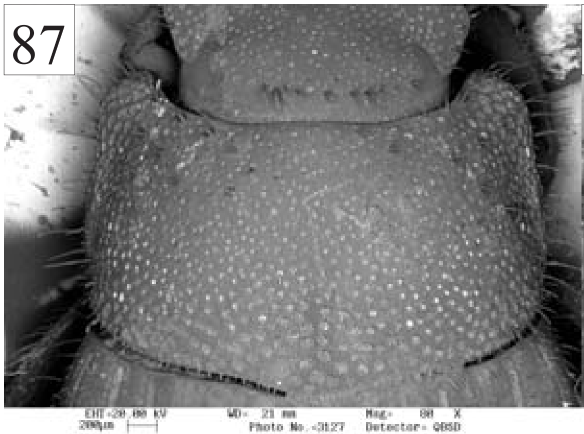

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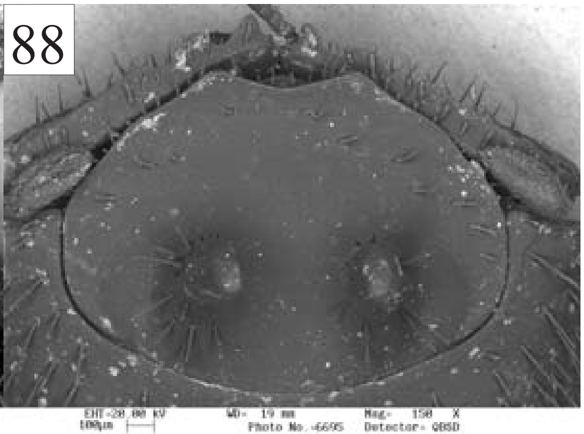

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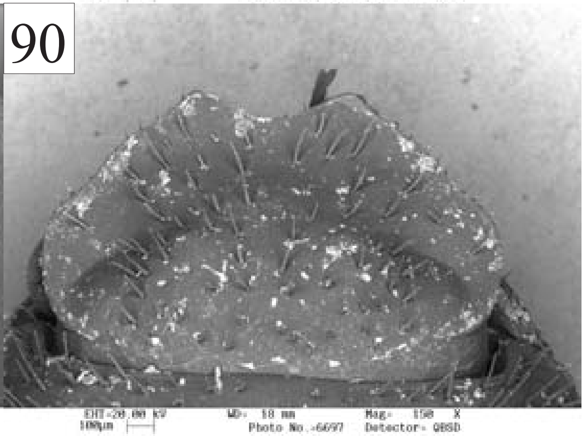

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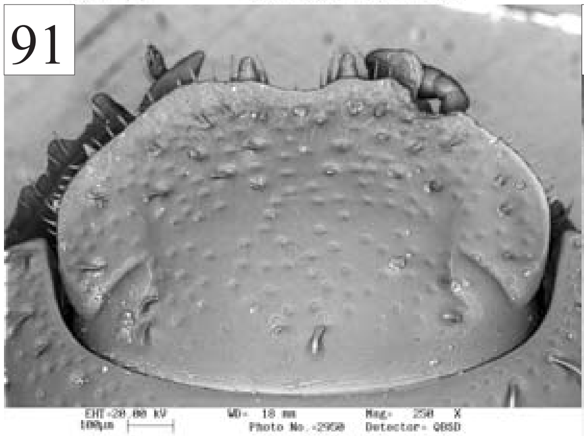

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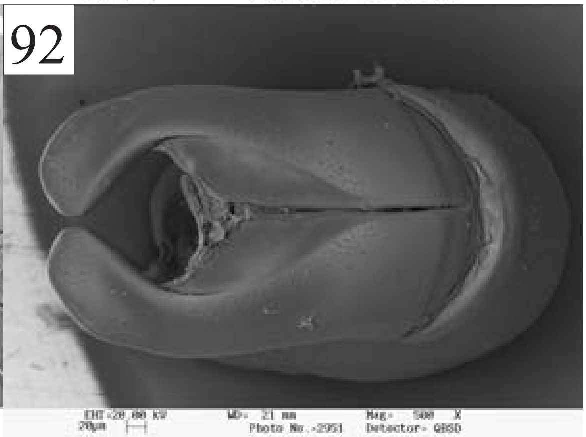

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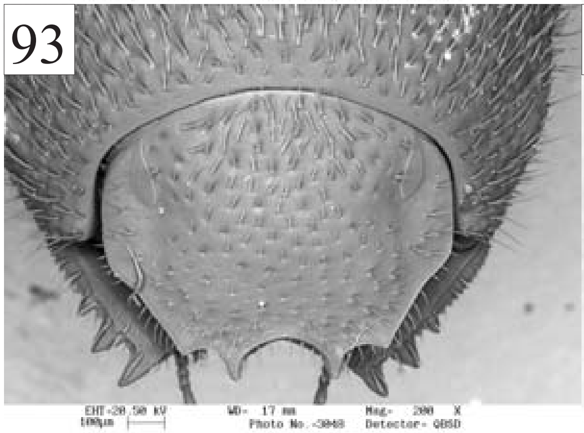

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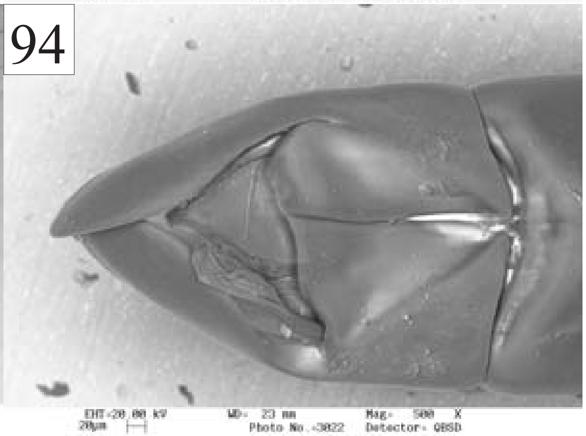

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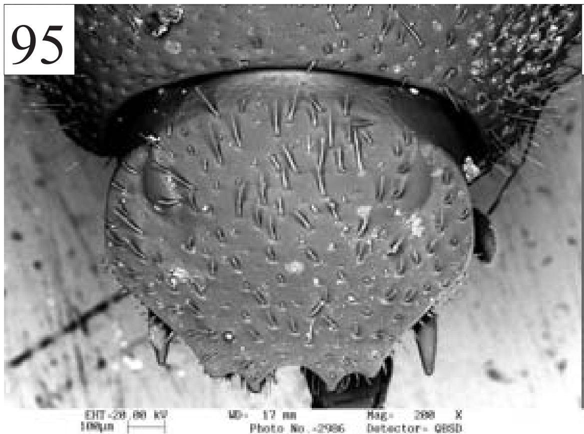

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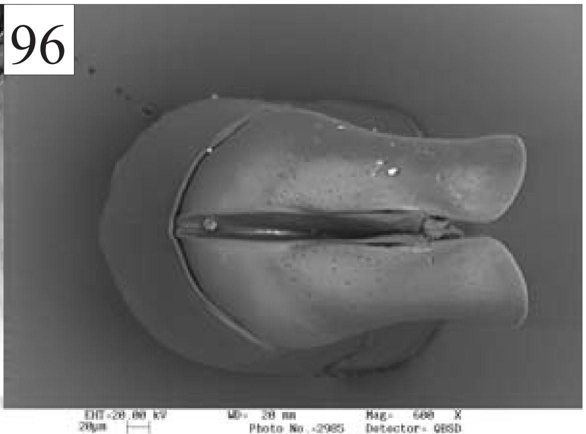

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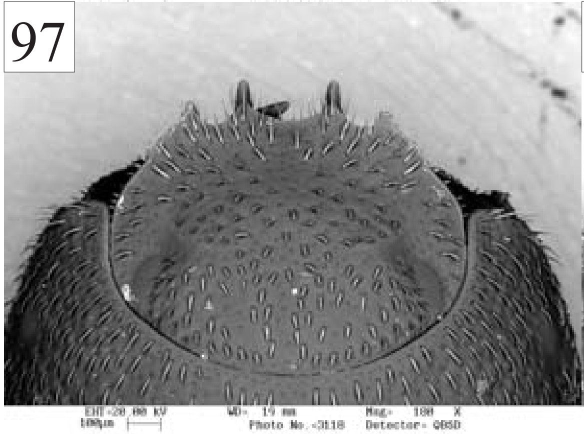

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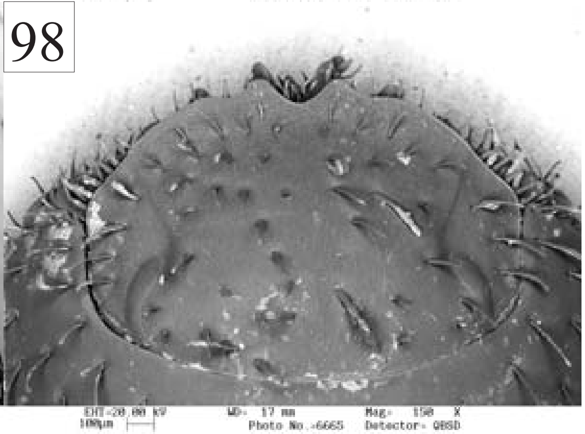

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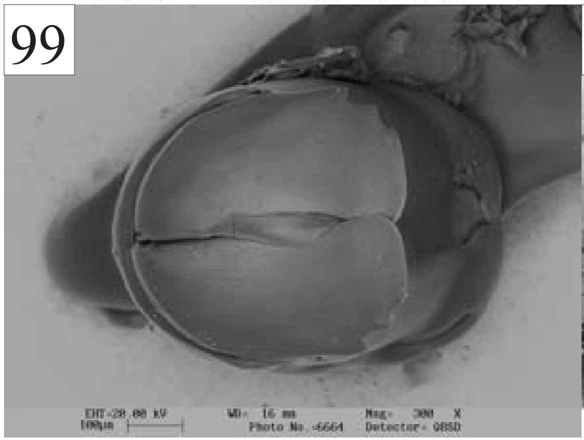

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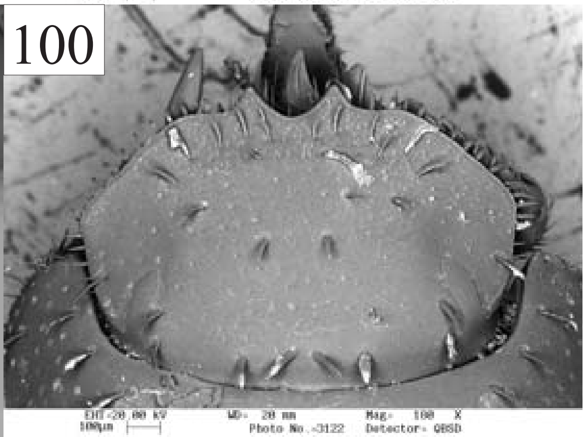

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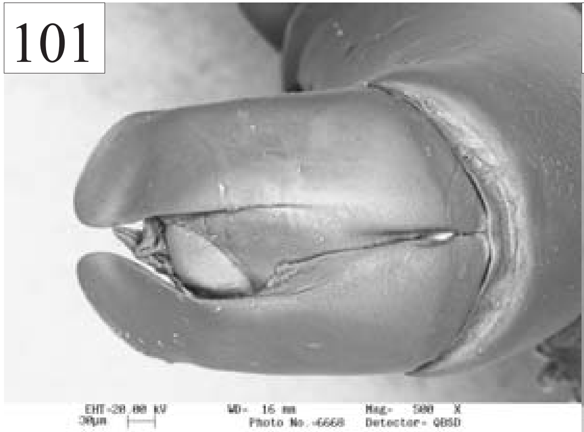

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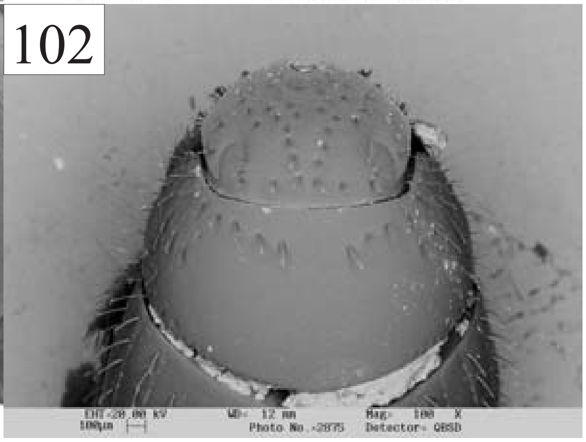

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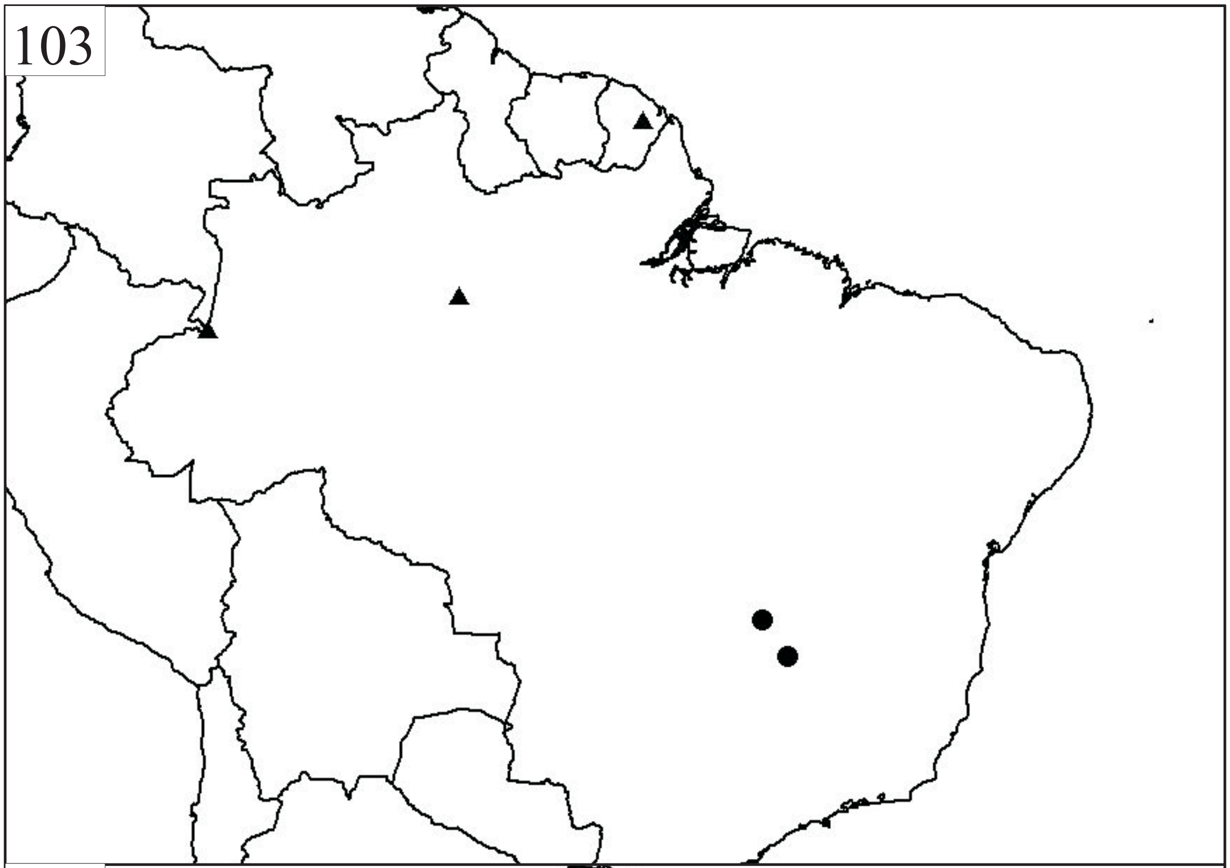

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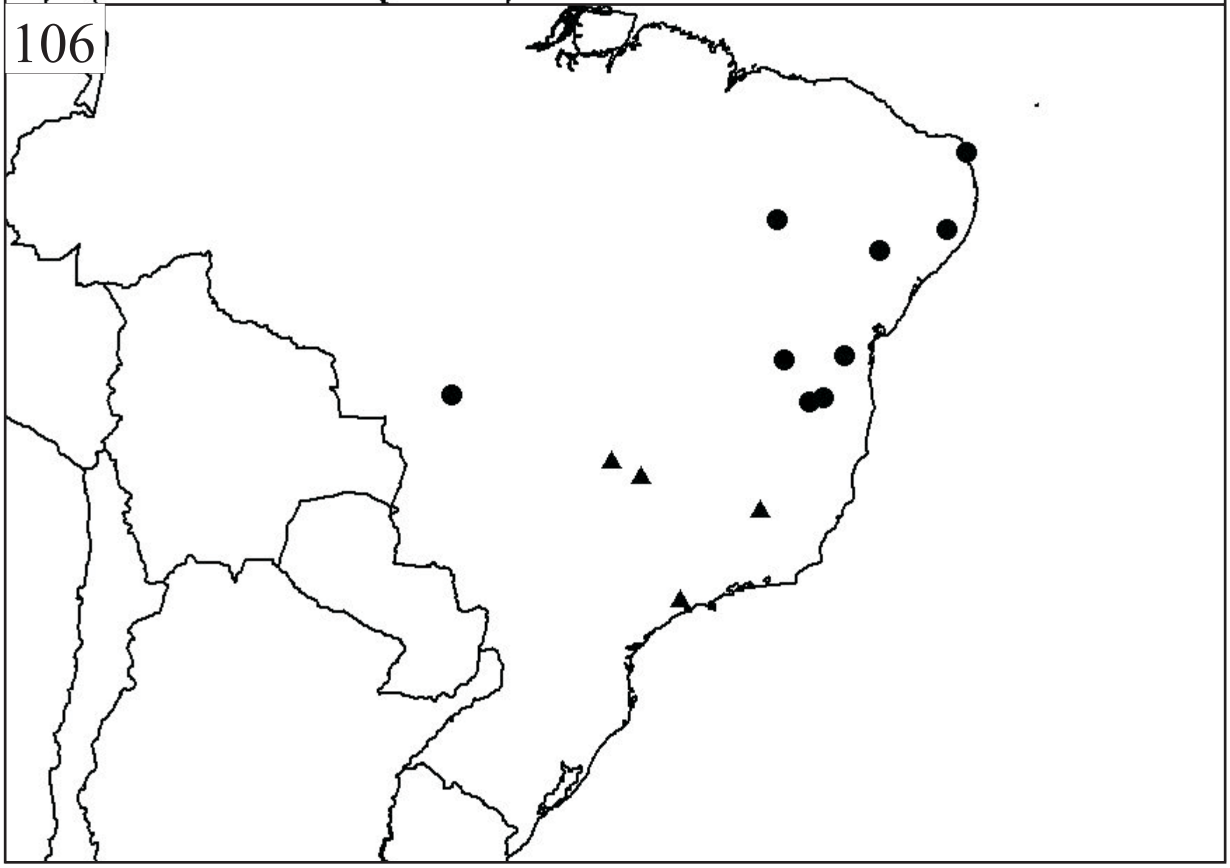

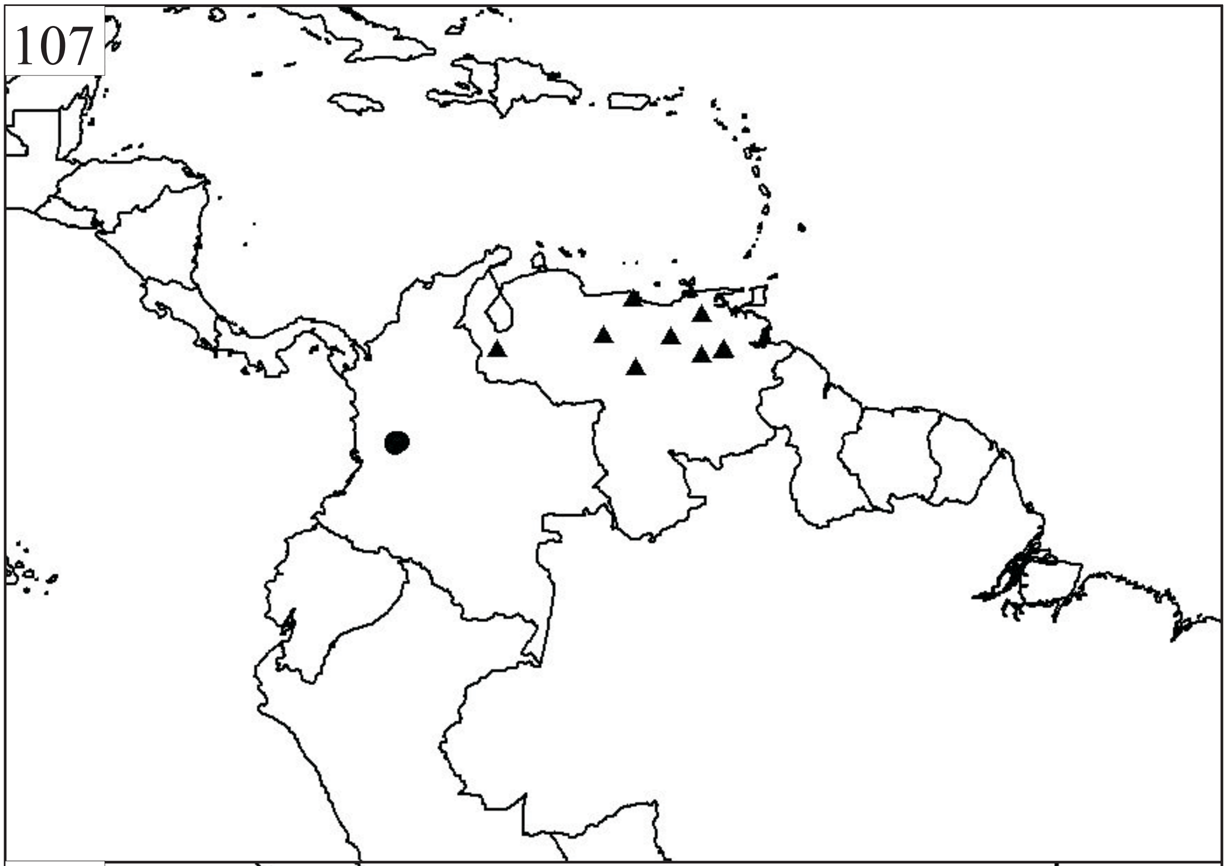
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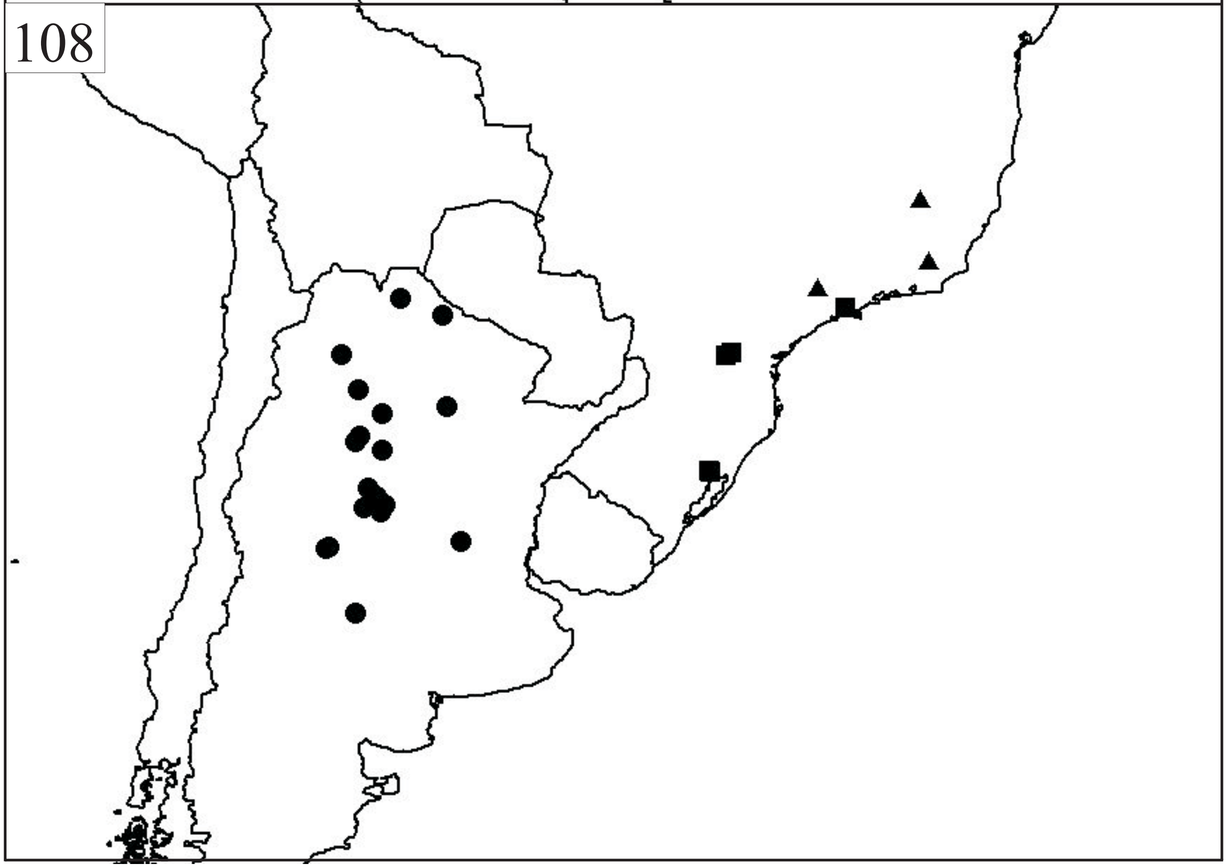
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Capítulo III

The genera formerly placed in the tribe Ateuchini (Coleoptera: Scarabaeidae: Scarabaeinae) and their phylogenetic position

Fernando Z. Vaz-de-Mello

"A gente nunca deve de declarar só, que aceita, inteiro, o alheio - essa é a regra do rei!"
(Guimarães Rosa: Grande Sertão: Veredas, 1956)

The genera formerly placed in the tribe Ateuchini (Coleoptera: Scarabaeidae: Scarabaeinae) and their phylogenetic position

Introduction

In a previous work (Vaz-de-Mello, submited), I begun the study of the tribe Ateuchini, defining two subtribes and reviewing in genus-level one of them. I left several genera as *incertae sedis* and transferred others to other already established tribes. The intent of the present work is to accommodate the remaining genera of the tribe, and to finish up the still opened internal classification of the tribe Ateuchini, defining it as a monophyletic group.

History of the tribe Ateuchini

The genus *Ateuchus* was described by Weber (1801) to accommodate a single new species of Scarabaeinae from North America, *A. histeroides*. However, Fabricius (1801), in a subsequent work, without citing Weber's species, used the same name to accommodate all Scarabaeinae dung beetles with inemarginated mentum, in contrast to *Copris* Geoffroy, 1762, which he considered to include those with emarginated mentum. In 1828, the new genus *Choeridium* was described by Lepeletier & Serville to accommodate a new species from French Guyana, *C. simplex*, and seven species previously described in other genera (*Scarabaeus* Linnaeus and *Onthophagus* Latreille). In 1840, Castelnau, considered his first tribe of the family Lamellicornes, the Coprophages, divided in four groups: the Onitides, Aphodites, Coprites and Ateuchites. The Onitides and Aphodites, comprised those taxa with scutellum exposed or "indicated"; while Coprites and Ateuchites, those with unexposed and "not indicated" scutellum. The Coprites included those with apically expanded middle- and hind tibiae; and the Ateuchites, those with non-expanded middle and hind tibiae. It is clear from the original work and included groups that Castelnau considered the genus *Ateuchus* in its Fabrician sense – he did not list Weber's species among listed species of *Ateuchus* and did include the (present) synonym *Choeridium* among the Coprites, listing under that genus one species that is currently a synonym of the type species of *Ateuchus*. Burmeister (1846) considered four groups: Ateuchidae, Coprididae, Onitididae and Onthophagididae. Erichson (1847) maintained the basic division of Castelnau, Ateuchini vs. Coprini, and considered Coprini to be divided in several unnamed groups, two corresponding to Onitididadae and Onthophagididae of Burmeister, and the others mostly corresponding to tribes considered later, with some important exceptions: the genus *Canthidium* Erichson was considered in the same group as *Pinotus* Erichson and *Ontherus* Erichson, and placed near *Heliocopris* Hope, *Catharsius* Hope*, Copris*, and *Macroderes* Westwood and the genera *Choeridium*, *Scatonomus* Erichson, *Onthocharis* Westwood, *Uroxys* Westwood and *Pedaria* Castelnau were considered in the same group, placed near the group comprised by *Coptorhina* Hope, *Delopleurus* Erichson and *Sarophorus* Erichson.

Lacordaire (1856) considered practically the same classification, only naming Scatonomides the group formed by the two last mentioned Erichson's groups. Harold (1867), based on an extensive comparison of several genera, established the division of the Scatonomides of Lacordaire in Scatonomidae and Choeridiidae, including in the first only *Scatonomus* and *Onthocharis*, and in the latter all other previously included genera as well as *Canthidium*. In 1905, Kolbe named Phanaeinae a group composed of *Phanaeus* and closely related genera (already separated by Erichson but not named); and Pinotinae, a group including all the genera then included in Lacordaire's Scatonomides, Harold's Choeridiidae, and all genera considered to be closely related to *Pinotus* and *Ontherus*, considering as Coprinae only *Copris, Heliocopris*, *Coptodactyla* Hope and *Catharsius*. Lüderwaldt (1929) followed Kolbe (1905), but later (Lüderwaldt, 1931) he transferred *Scatimus* Erichson from the Pinotides to the Coprides. Paulian (1933) described the new subtribe Coptodactylides for the genus *Coptodactyla* and its synonym *Arrowianella* Paulian. Chapin (1946) rediscovered the original sense of *Ateuchus* Weber and considered *Choeridium* to be a synonym of the latter. Janssens (1946) considered the tribe Coprini to include the subtribes Pinotides, Coprides and Phanaeides, and three years latter (Janssens, 1949) he included Coptodactilina as another subtribe of Coprini.

Martínez (1951) synonymized the genera *Pinotus* and *Dichotomius* Hope, and renamed the tribe Pinotini as Ateuchini, because *Ateuchus* was the oldest genus. Pereira (1954) referred to the ancient tribe Pinotini as Dichotomiini, based on the synonym of the type genus. Most subsequent workers (Halffter & Matthews, 1966; Halffter & Edmonds, 1982, Hanski & Cambefort, 1991) followed the later, the sole modifications being that Edmonds & Halffter (1978) transferred *Scatimus* and *Heliocopris* to Dichotomiini, based mainly on larval morphology; and Branco (1991) that transferred some African genera to the Onthophagini. It seems important to point out that both Balthasar (1963) and Ferreira (1972) considered the name of the group to be Pinotini.

Montreuil (1998) presented a phylogenetic analysis of the then-called Dichotomiini and Coprini, and found those to comprise two monophyletic groups. One of those groups, Coprini, included both *Copris* and *Dichotomius*, making it impossible to call Dichotomiini or Pinotini the other (then called Ateuchini). In another work (Vaz-de-Mello, submited), I deal with a group within the tribe Ateuchini, as considered by Montreuil (1998), dividing it in two subtribes, and considering several genera as *incertae sedis*.

The purpose of the present work is to define the tribe Ateuchini in a new sense, to provide tools for identifying its included genera (apart of those of the subtribe Scatimina Vaz-de-Mello) and subtribes, and to define the tribal position of other genera formerly included in the Ateuchini but not belonging to it in its new sense. In addition, it presents definitions of new tribes and resurrection of previous synonyms occasioned by the change in the new identity of Ateuchini.

Methods

A phylogenetic analysis was performed to define the tribe Ateuchini and its subtribes as monophyletic groups, and to identify the phylogenetic position of genera previously considered as *incertae sedis*.

The ingroup included genera previously and currently included in the tribe Ateuchini, and genera currently included in the tribe Canthonini that have been hypothesized to be related to some Ateuchini genera (Cook, 1998; 2002; Howden & Cook, 2002; Vaz-de-

Mello & Halffter, 2006; Vaz-de-Mello, 2007). Those are listed in Table 2. Outgroups where chosen among representatives of all described (including many currently synonymized) Scarabaeinae tribes, genera thought to be related to some Ateuchini genera, and three genera representing three other Scarabaeidae subfamilies for rooting. They are listed in Table 1. The entire matrix included 87 terminal taxa (tables 1. and 2.) and 297 morphological characters (Appendix 1.), and is showed in text form in Appendix 2.

Specimens have been softened in hot water, cleaned and examined under a stereomicroscope. For examining mouthparts and genitalia, those were extracted and placed in KOH solution (concentration, temperature and time variable according to specimen size and sclerotization, evaluated individually under a stereomicroscope).

Phylogenetic analysis was performed using Nona (Goloboff, 1993) and for some functions and graphics, Winclada (Nixon, 2002). All characters were considered as unordered (Fitch parsimony) and of equal weigth. Trees were searched with parsimony ratchet (Nixon, 1999) as implemented in Nona by Winclada, with limits fixed in one tree per iteration, ten replications, two hundred iterations in each replication, character sampling of 10%, random constraint of 10, and polytomies allowed. The resulting trees have been read by NoNa and new or better trees were searched using TBR and SPR of trees found by the ratchet. A holistic search of 4000 repetitions of TBR, followed by SPR, was performed to check the ratchet efficacy.

Clade support was inferred by decay index (Bremer,1994), normal bootstrap, and modified bootstrap (Vaz-de-Mello, 2007) using Nona (and Winclada for bootstrap analyses). Bremer index was searched doing a SPR search of up to 30 extra steps on the trees found to be the most parsimonious, with results plotted in strict consensus of those last; 1000 extra trees up to 30 steps longer were allowed. Both normal and modified bootstrap indexes were found allowing a maximum of 1000 trees found under a search of 100 replications of 10 TBR searches.

Results and Discussion

Analyses found eight trees of maximum parsimony, each of 3141 steps (CI=13, RI=51). The strict consensus was 3153 steps long (CI=12, RI=50) and is presented (along with supporting statistics) in Figures 1. and 2. Bootstrap searches resulted in 109 trees for normal bootstrap, and 106 trees for modified bootstrap (1000 trees were allowed for each). Figures 1. and 2. also include numbered clades that are those referred below. Ateuchini as currently considered is clearly polyphyletic (Figs. 1.-2.) and those clades including taxa included in the ingroup are discussed below. It is important to point out that given the enormous proportion of homoplasies and for practical purposes, diagnoses referred below are morphological differential diagnoses, not necessarily lists of synapomorphies.

Clade 1. (Figure 1.): Tribe Coptorhinini, **new tribe.**

This clade is composed of three lineages from the Ateuchini and one from the Canthonini. It does have an important combination of characters, and is the sister taxon to all remaining Scarabaeinae except Oniticellini+Eurysternini, so it deserves tribal status.

1. Tribe Coptorhinini, **new tribe**.

Type-genus: *Coptorhina* Hope, 1830.

Diagnosis: Clypeus with two teeth, separated by wide U- or V-shaped emargination. Lateral genal angle conspicuous, obtuse or acute. Mandibles at least more sclerotized than in remaining groups, lacking lateral membranous area. Labial palpus with three cylindrical palpomeres, mentum trapezoidal, at most apically widely incised. Transversal hypomeral carina present, hypomeron excavated or concave anteriorly to transverse carina. Fore tibia apically truncated in straight angle, with two or three lateral teeth. Mesosternum not shortened medially. Elytra with eleven striae (counting epipleural stria).

Composition: The four new subtribes described below.

Distribution: Afrotropical and Oriental regions, excluding Madagascar, with one species in southern Japan in the Palaearctic Region.

Remarks: Relationships between subtribes are complicated especially by presumably derived characters that *Paraphytus* shares either with the *Coptorhina* group, or with *Onychothecus*.

1.1. Subtribe Coptorhinina, **new subtribe** (clade 1a in Figure 1.).
Type-genus: *Coptorhina* Hope, 1830.
Diagnosis: Gula medially divided by longitudinal sulcus; elytra laterally notched, with metepisternon wider apically, with medial posterior angle coincident with elytral notch. Other important characters are: fore tibiae apically truncated in right angle; fore tarsal insertion in the ventral part of tibia, or in a chamber positioned completely between dorsal and ventral parts; epypharynx apically not emarginated; prothorax in posterior view rounded; and hypomeron anteriorly deeply excavated; elytra lacking pseudoepipleuron.
Composition: *Coptorhina*, *Delopleurus* Erichson, 1847, *Sarophorus* Erichson, 1847, *Frankenbergerius* Balthasar, 1938.
Distribution: Indoafrican.
Remarks: The general epipharyngeal shape and the gular longitudinal sulcus appear to relate this subtribe to Paraphytina, although the latter shares shares other unique characters with Onychothecina. The uniqueness of this group has been already mentioned by Frolov & Scholtz (2003, 2005).

1.2. Subtribe Onychothecina, **new subtribe** (terminal 1b in Figure 1.).
Type genus: *Onychothecus* Boucomont, 1912
Diagnosis: Characters defining this subtribe are the same as for the genus *Onychothecus*: fore tarsal insertion on the upper surface of tibia, that presents a distinct oblique sulcus that can be occupied by tarsi; last tarsomere of all legs with lateral and mesal regions apically expanded, forming walls around the claws. Other important characters are the presence of a strongly developed ventral clypeal tubercle, arising from a ventral clypeal longitudinal carina; hypomeron anteriorly feebly excavated; elytron forming a pseudoepipleuron lateral to the eigth stria; and unusual sexual dimorphism, in

which males are unarmed, wherea females have a very distinctive clypeal horn and a pronotal anterior double knob.

Composition: *Onychothecus*.

Distribution: Chinese transition zone (southeastern China and northern Indochina).

Remarks: This tribe shares many characters with *Paraphytus*, such as the dorsal insertion of anterior tarsi and the clypeal ventral longitudinal carina.

1.3. Subtribe Paraphytina, **new subtribe** (clade 1c in Figure 1.).

Type genus: *Paraphytus* Harold, 1877 (= *Xynophron* Harold, 1880; = *Maraxes* Lewis, 1895; = *Freyus* Balthasar, 1958)

Diagnosis: As for the genus *Paraphytus*: Clypeus with two or three teeth at each side; with longitudinal ventral carina; mandibles with strong lateral tooth; hypomeron anteriorly feebly excavated; fore tarsi inserted in the dorsal side of front tibia; front tibia with rounded ventral apical fovea.

Composition: *Paraphytus*.

Distribution: Subsaharan Africa, tropical Asia and southern Japan.

Remarks: This group has been considered by Montreuil (1998) as sister to *Onychothecus*. However, the genera conforming the subtribe Byrrhidiina have not been included in that analysis.

1.4. Subtribe Byrhidiina, **new subtribe** (clade 1d in Figure 1.).

Type genus: *Byrrhidium* Harold, 1869

Diagnosis: Clypeus with paired teeth widely separated; labrum sclerotized and multidented, visible in frontal view; mandibles almost completely sclerotized, with only an internal narrow unsclerotized band on apex of the incisive lobes, lacking ventral stridulatory molar bands; elytron with pseudoepipleuron lateral to eighth stria; elytra fused, hind wings reduced.

Composition: *Byrrhidium*, *Namakwanus* Scholtz & Howden, 1987 (not included in the analysis nor examined, but undoubtedly very closely related to *Byrrhidium*) and *Dicranocara* Frolov & Scholtz, 2003.

Distribution: Southwestern Africa.

Remarks: Until very recently (Frolov & Scholtz, 2003), it was unknown that some Scarabaeinae genera had sclerotized mouthparts. That is the main unique feature of this subtribe (another feature of minor importance are elytral characters associated to brachyptery and brachyptery itself), that comprises three small genera localized in southwestern Africa and apparently associated with desert habitats.

Clade 2. (Figure 1.) (part of tribe Canthonini Lansberge)

This clade, nested in the group that includes the type-genus of Canthonini, comprises the genera *Scatonomus*, *Anomiopus* and *Hypocanthidium*, all previously included in Ateuchini, and transferred to Canthonini by me (Vaz-de-Mello, submited). Its sister-group relationship with *Canthon virens* (or, more correctly, with the *Canthon virens* group as defined by Halffter & Martínez [1977]) is something to be worked in a phylogenetic analysis of the group, where the monophyly of the genus *Canthon* should be also tested. Medina *et al.* (2003) already questioned the monophyly of that genus, however, a larger taxonomic sample is necessary to establish well supported groups. The inclusion of the genus *Scatonomus* in the Canthonini automatically places the name Scatonomini Lacordaire, up to now considered as a synonym of Ateuchini, as a senior synonym of Canthonini instead. Article 23.9.1.1. of the ICZN (1999) rules that a senior synonym not used as valid after 1899 is to have its priority reversed in favor of the currently used junior synonym. As the last use of Scatonomini as valid appears to be that of Harold (1867), Canthonini is maintained as the valid name for that tribe (*nomen protectum*).

Grade 3. (Figure 1.) (part of tribe Coprini Leach)

That grade is composed of two lineages previously placed in Ateuchini. One of them (*Canthidium* + *Parachorius*) (clade 3a.) has been transferred to Coprini (Vaz-de-Mello, submited). The other, comprising several species of *Ateuchus* and herein represented by *A. mutillatus* Harold (terminal 3b.), is described below as a new genus that might also be included in the Coprini. The genus *Pleronyx* Lansberge probably (by description) also belongs to that tribe.

New Genus 1.

Type species: *Choeridium mutillatum* Harold

Diagnosis: Body form rectangular. Clypeus with two triangular teeth separated by wide V-shaped emargination, clypeal ventral transverse carina present. Fore tibiae strongly elongated and modified in males, where it is much narrower than in females, apically curved inwards, and bearing mesal teeth. Pronotum with well defined dorsal longitudinal sulcus; hypomeron lacking transverse carina or anterior excavation. Elytra with nine striae, and a pseudoepipleuron lateral to eighth stria.

Composition: Various species previously placed in *Ateuchus* and originally *Choeridium*, at least *A. mutillatus*, *A. hypocrita*, *A. tenebrosus* and *A. robustus*.

Distribution. Southeastern and southern Brazil, northeastern Argentina, and Uruguay.

Clade 4. (Figure 2.). Tribe Coptodactylini Paulian.

This clade comprises three genera previously placed in the Coprini (*Coptodactyla*, *Thyregis* and *Microcopris*) and the ateuchine genus *Uroxys* (the group comprising its type-species, *U. cuprescens*). A tribe name is already avaliable for that clade:

2. Tribe Coptodactylini Paulian, 1933

Type-genus: *Coptodactyla* Burmeister, 1846

Diagnosis: Hypomeron anteriorly deeply excavated, excavation with posterior vertical wall; fore trochanto-femoral pit present, sometimes inserted inside the communicated anterior sulci of profemur and trochanter. Fore tibia truncated in right angle apically, with three lateral teeth. Middle and hind tibiae strongly expanded apically, with transverse external carinae at least in hind tibia. Elytra with ten to eleven striae, and pseudoepipleuron out of penultimate stria.

Composition. *Coptodactyla*, *Microcopris* Balthasar, 1958, *Uroxys* Westwood, 1842, and *Thyregis* Blackburn, 1904.

Distribution. Subsaharan Africa, southeast Asia, Australia, Papua New Guinea, northern Andes in South America.

Remarks. The species of the genus *Pseudocopris* Ferreira, 1960 included in the analysis also belongs to that group. However, it is not the type-species of *Pseudocopris*. According to drawings and descriptions of the type-species of *Pseudocopris* presented by Ferreira (1972) and Marchisio (1983), that genus clearly belongs to the Coprini and the species used in the phylogenetic analysis is to be transferred alone to the Coptodactylini, probably included in *Microcopris*.

Clade 5. (Figure 2.). Tribe Demarziellini Balthasar.

This clade includes several genera previously included in the Canthonini, and three considered as part of the Ateuchini: *Pedaria*, *Bdelyrus* and *Demarziella* (not included in the analysis, but very similar to *Pedaria* in most aspects). A name is already available for this tribe, which is the sister-group of the Ateuchini *sensu novo*.

3. Tribe Demarziellini Balthasar, 1961

Type-genus: *Demarziella* Balthasar, 1961.

Diagnosis: Clypeus with two to six paired teeth. Hypomeron deeply excavated anteriorly, excavation delimited by a vertical wall. Fore trochantofemoral pit generally present. Fore tibia apically truncated in right angle, except for apico-mesal tooth in males. Elytra with ten striae, and pseudoepipleuron external to seventh or eighth stria.

Composition: *Demarziella*, *Pedaria*, *Bdelyrus*, *Tesserodoniella*, *Zonocopris*, and several other genera previously placed in the Canthonini, at least *Saphobium, Saphobiamorpha*, *Tesserodon*, *Peckolus*, *Cryptocanthon*, *Paracryptocanthon* and *Onthobium*.

Distribution. Southern Mexico to southeastern Brazil in the Neotropical region, Central Chile, Australia, New Zealand, New Caledonia, and southern Africa.

Remarks: The tribe Demarziellini was erected by Balthasar (1961) when describing *Demarziella*, that was though by him to be an Aphodiinae. A deep study of this group is necessary, at least for assigning other genera presently placed in the Canthonini.

Clade 6 (Figure 2.). Tribe Ateuchini Martínez.

This clade comprises the tribe Ateuchini as herein considered, including the two subtribes already diagnosed (Vaz-de-Mello, submited) and a third one that is the sister taxon to those two.

4. Tribe Ateuchini Martínez, 1951
= Choeridiidae Harold, 1867
Type-genus: *Ateuchus* Weber, 1801
Diagnosis: Clypeus with central emargination, and ventral transverse carina. Hypomeron with transverse carina and deep anterior excavation, with vertical posterior wall. Fore tibia apically truncated in straight angle, except for male apico-mesal tooth. Elytra with nine striae, with pseudoepipleuron lateral to eighth stria.
Composition: Three subtribes: Ateuchina Martínez, Scatimina Vaz-de-Mello, and Agamopina, **new subtribe**.
Distribution: Neotropical and Nearctic regions.
Remarks: Until very recently, Ateuchini in its present sense (that is, including *Ateuchus* Weber) was credited to Martínez. Smith (2006) considered its author to be Castelnau. However, as Castelnau clearly erected his group based on a junior homonym of *Ateuchus* Weber (*Ateuchus* Fabricius), Ateuchini Castelnau may not be available (art. 39, ICZN, 1999). The following most ancient available name would be Choeridiini Harold, 1867, however, it has not been used as valid after 1899 (art. 23.9.1.1, ICZN, 1999), and Ateuchini Martínez, 1951, should in my opinion be considered the valid name, because of its character of substitutive name over Choeridiini caused by the synonym of *Choeridium* with *Ateuchus* (Martínez, 1951). Anyway, as Ateuchini Martínez is a junior homonym of Ateuchini Castelnau, I will refer the case to the International Commission on Zoological Nomenclature (following art. 39, ICZN, 1999), asking the Commission to rule Castelnau’s name unavailable.

Key to the subtribes of Ateuchini:

1. Fore trochanto-femoral pit absent … 4.1. Ateuchina

1’ Fore trochanto-femoral pit present … 2

2. Pronotum laterally lacking longitudinal sulcus or round pit. Mesepimeron concave externally or bearing a transverse carina. Propygidial longitudinal groove with subparallel sides … 4.3. Scatimina

2’ Pronotum laterally with either round pit or longitudinal sulcus. Mesepimeron externally flat and always lacking oblique carina. Propygidial longitudinal groove V-shaped … 4.2. Agamopina, **new subtribe**.

4.1. Subtribe Ateuchina Martínez, 1951 (Clade 6a. in Figure 2.).

Type-genus: *Ateuchus* Weber, 1801

Diagnosis: Same as in Vaz-de-Mello (submited)

Composition: *Ateuchus* (=*Choeridium* Lepeletier & Serville, 1828); *Deltorhinum* Harold, *Aphengium* Harold; *Sinapisoma* Boucomont; *New Genus 2.*

Distribution. Neotropical and Nearctic regions.

Remarks: Although *Sinapisoma* was not included in the phylogenetic analysis, it shares all synapomorphies with *New Genus 2* and appears to be its sister group.

Key to the genera of Ateuchina

1. Hind tibia apically obliquely truncated, mesal angle clearly more apical in position than lateral angle; hind basitarsus almost as long as or slightly longer than the length of 2nd and 3rd tarsomeres combined … 2

1’ Hind tibia aproximately transversaly truncated apically; hind basitarsus clearly shorter than the length of 2nd and 3rd tarsomeres combined … 3

2. Smaller than 4 mm in size, body bicolorous; middle tibia greately expanded in the mesal side apically … 4.1.4. *Sinapisoma*

2’ Larger than 6 mm in size, body unicolorous; middle tibia not greately expanded in the mesal side, or at least not much more than in the lateral side … 4.1.5. *New Genus 2.*

3. Abdominal ventrites fused, intersegmental sulci effaced, body covered by hairs … 4.1.3. *Aphengium*

3’ Abdominal ventrites separated by distinct sutures, body dorsally glabrous … 4

4. Clypeus clearly incised medially, semicircular in form … 4.1.1. *Ateuchus*

4’ Clypeus not incised medially, triangular in form … 4.1.2. *Deltorhinum*

4.1.1. *Ateuchus* Weber, 1801

=*Choeridium* Lepeletier & Serville, 1828

Type species: of *Ateuchus*: *A. histeroides* Weber, 1801; of *Choeridium*: *C. simplex* Lepeletier & Serville

Composition: This genus comprises more than 60 species presently described, and is in great need of revision.

Distribution: Neotropical and Nearctic regions.

Remarks: The genus *Ateuchus* is still a very heterogeneous one, and a careful study of its species is greatly necessary for establishing good generic limits.

4.1.2. *Deltorhinum* Harold, 1868

Type species: *D. batesi* Harold, 1868.

Composition: Besides the type species, this genus includes at least four other species presently under study.

Distribution: Amazonia.

Remarks: This genus is probably phylogenetically nested within *Ateuchus*. The reduced tarsi and lack of capture with baits indicates that species in this genus are very probably associated with some special habitat, such as ant nests.

4.1.3. *Aphengium* Harold, 1868

Type species: *A. sordidum* Harold, 1868.

Composition: Besides the type-species, this genus includes *A. cupreum* Shipp (probable synonym of the type species) and one new species currently under study.

Distribution: Eastern Atlantic rainforest lowlands of Brazil.

Remarks: This genus is probably phylogenetically nested within *Ateuchus*.

4.1.4. *Sinapisoma* Boucomont, 1928

Type species: *S. minuta* Boucomont, 1928 (=*Canthon minutus* Castelnau, 1840?)
Composition: Besides the type-species, this genus includes at least one other described species, currently in *Canthonella*, and two or three new species closely related to the type species.
Distribution: Amazonia.

4.1.5. *New Genus 2*.

Type species: *Agamopus convexus* Balthasar, 1967
Diagnosis: Body oval, short. Clypeus with two rounded teeth, separated by V-shaped emargination. Head without tubercles or carinae. Eyes large, at least as wide as one half of their length. Middle tibia obliquely truncated apically, with lateral margin straight, and mesal margin clearly expanded apically. Hind tibia as middle tibia, except that the mesal angle of the tibial apex is much more expanded in males.
Composition: The new genus includes, besides the type-species, at least the following (under their original genera): *Ateuchus confusus* Martínez & Martínez, 1987; *Choeridium cernyi* Balthasar, 1938; and *Canthidium ovale* Boucomont, 1928. Maybe *Choeridium contractum* Balthasar, 1938 and *Choeridium vigilans* Lansberge, 1874, would be also part of that genus.
Distribution. Non-amazonian parts of Brazil, Argentina, Paraguay and Bolivia.

4.2. Subtribe Agamopina, **new subtribe** (Clade 6b. in Figure 2.).

Type-genus: *Agamopus* Bates, 1887
Diagnosis: Ateuchini with trochantofemoral pit present; pronotum laterally with distinct round fovea or longitudinal sulcus; mesepimeron externally flat and always lacking oblique carina; propygidial longitudinal groove V-shaped.
Composition: besides the type-genus, the subtribe comprises *Canthochilum* (transferred from Canthonini); *Bdelyropsis*; and two new genera herein described.
Distribution. Almost the entire Neotropical region.
Remarks. *Pseuduroxys* Balthasar, 1938 is very probably also a member of this tribe; however, no specimens could be examined. The genus *Pseuduroxys* includes one

single species from Ecuador, but it appears that two species described by Martínez & Martínez (1990) as *Ateuchus* should also be part of that genus.

Key to the genera of Agamopina.

1. Pygidium with a transverse sulcus in the middle of disc … 4.2.1. *Agamopus*
1’ Pygidium lacking transverse sulcus in the middle of disc … 2
2. Pronotum laterally with strong longitudinal sulcus … 3
2’ Pronotum lacking lateral longitudinal sulcus … 4
3. Elytron with strong longitudinal carina lateral to 7th stria, forming a double pseudoepipleuron; body strongly convex and short, shorter that 1.3 times its maximum width … 4.2.5. *New Genus 4.*
3’ Elytron lacking double pseudoepipleura or carina external to 7th stria; body squared or elongated, at least as long as 1.4 times its maximum width … 4.3.4. *New Genus 3.*
4. Middle and hind tibiae with lateral margin inwardly curved, forming an apical expansion. Paramera not reduced … 4.2.3. *Bdelyropsis*
4’ Middle and hind tibiae with lateral margin slightly curved outwardly, if tibia expanded apically, then only internally. Paramera reduced, length equal to or smaller than width of phallobase … 4.2.2. *Canthochilum*

4.2.1. *Agamopus* Bates, 1887
Type species: *Agamopus lampros* Bates, 1887
Distribution. Western Mexico (Nayarit) to southern Brazil.

4.2.2. *Canthochilum* Chapin, 1934
= *Antillacanthon* Vulcano & Pereira, 1966
= *Chapincanthon* Vulcano & Pereira, 1966
Type species: *Canthochilum oakleyi* Chapin, 1934
Distribution. Cuba, Puerto Rico and Hispaniola.

4.2.3. *Bdelyropsis* Pereira, Vulcano & Martínez, 1960

Type species: *Bdelyrus bowditchi* Paulian, 1938

Distribution. Southern Mexico, Guatemala, and northern Venezuela.

4.2.4. *New Genus 3*.

Type species: *Uroxys aterrima* Harold, 1867

Diagnosis: Clypeus with two or four teeth. Pronotum laterally with a strong longitudinal sulcus. Elytron lacking double pseudoepipleura or carina external to 7th stria; body squared or elongated, at least as long as 1.4 times its maximum width. Males generally with fore tibia and femur, lateral part of pronotum, and elytral apices expanded/modified.

Composition: This genus comprises most species up to now assigned to *Uroxys*, including all species known to occur outside South America and most South American lowland species.

Distribution. The entire Neotropical region.

4.2.5. *New Genus 4*.

Type species: *Choeridium epipleurale* Boucomont, 1928.

Diagnosis. Clypeus with four strong acute teeth. Elytra lacking humeral calli. Elytron with strong longitudinal carina external to 7th stria, forming a double pseudoepipleura; body strongly convex and short, shorter that 1.3 times its maximum width. Males solely externally differentiated of females by the presence of an apico-mesal tooth in protibia.

Composition: Besides the type species, this genus also includes *Uroxys dureti* (considered a synonym of the type species, however, this status must be confirmed) and *Uroxys thoracalis* Balthasar, 1939.

Distribution. Central Brazil, eastern Bolivia, Paraguay, and northern Argentina.

4.3. Subtribe Scatimina Vaz-de-Mello (Clade 6c. in Figure 2.)

Type-genus: *Scatimus* Erichson, 1847

Diagnosis: Same as in Vaz-de-Mello (submited)

Composition: *.*

Distribution. Neotropical and (southern) Nearctic regions.

Remarks: For identification of genera, refer to Vaz-de-Mello (submitted).

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Table 1. Species composing the outgroup used for phylogenetic analysis. Tribes in *italics* in right column are presently considered as synonyms of those in central column.

Species studied	Current Subfamily or tribe placement	Previous tribal placement
Chiron sp.	CHIRONINAE	
Aegialia arenaria	AEGIALIINAE	
Aphodius fimetarius	APHODIINAE	
Arachnodes splendens	Canthonini	*Epilissini*
Byrrhidium ovale	Canthonini	
Canthon pilularius	Canthonini	
Canthon virens	Canthonini	
Canthonella silphoides	Canthonini	
Cephalodesmius armiger	Canthonini	*Menthophilini*
Circellium bacchus	Canthonini	
Dicranocara deschodti	Canthonini	
Epilissus prasinus	Canthonini	*Epilissini*
Mentophilus hollandiae	Canthonini	*Menthophilini*
Panelus parvulus	Canthonini	*Panelini*
Sylvicanthon foveiventris	Canthonini	
Temnoplectron bornemisszai	Canthonini	
Catharsius molossus	Coprini	
Copris lunaris	Coprini	
Coptodactyla glabricollis	Coprini	*Coptodactylini*
Metacatharsius opacus	Coprini	
Microcopris hidakai	Coprini	
Paracopris punctulatus	Coprini	
Pseudocopris tubericollis	Coprini	
Pseudopedaria grossa	Coprini	
Synapsis davidi	Coprini	
Thyregys kershawi	Coprini	
Ennearabdus lobocephalus	Eucraniini	*Ennearabdini*
Eurysternus parallelus	Eurysternini	Sisyphini
Gymnopleurus sp.	Gymnopleurini	
Oniticellus cinctus	Oniticellini	
Sinodrepanus thailandicus	Oniticellini	
Onitis belial	Onitini	
Onthophagus taurus	Onthophagini	
Phanaeus triangularis	Phanaeini	
Bolbites onitoides	Phanaeini	*Gromphini*
Scarabaeus semipunctatus	Scarabaeini	
Sisyphus schaefferi	Sisyphini	

Table 2. Species composing the ingroup used for phylogenetic analysis. Tribes in *italics* in right column are presently considered as synonyms of those in central column. Central column: tribes marked with an asterisk indicate that such genera had been considered *a priori* as more closely related to some genus of Ateuchini than to the tribes they were included in. Right column: tribes marked with an asterisk indicate that such genera were included in Ateuchini in a sense different than that used by Montreuil (1998), and equivalent to Dichotomiini.

Species Studied	Current subfamily or tribe placement	Previous tribal placement
Agamopus convexus	Canthonini	Ateuchini
Agamopus viridis	Canthonini	Ateuchini
Anomiopus aff. virescens	Canthonini	Ateuchini
Aphengium sordidum	Ateuchini – Ateuchina	
Ateuchus histeroides	Ateuchini – Ateuchina	
Ateuchus mutillatus	Ateuchini	
Bdelyropsis bowditchi	Ateuchini	
Bdelyrus howdeni	Ateuchini	
Canthidium cupreum	Coprini	Ateuchini
Canthidium lentum	Coprini	Ateuchini
Canthochilum oakleyi	Canthonini*	
Chalcocopris hespera	Coprini	Ateuchini*
Coptorhina sp.	Ateuchini	
Cryptocanthon otonga	Canthonini*	
Delopleurus gilleti	Ateuchini	
Deltorhinum sp.	Ateuchini – Ateuchina	
Dichotomius achamas	Coprini	Ateuchini*
Dichotomius bos	Coprini	Ateuchini*
Dichotomius nisus	Coprini	Ateuchini*
Dichotomius smaragdinus	Coprini	Ateuchini*
Dichotomius torulosus	Coprini	Ateuchini*
Eutrichillum hirsutum	Ateuchini – Scatimina	
Frankenbergerius gomesi	Ateuchini	
Genieridium bidens	Ateuchini – Scatimina	
Heliocopris dominus	Coprini	Ateuchini*
Hypocanthidium sp.	Canthonini	Ateuchini
Isocopris inhiata	Coprini	Ateuchini*
Ontherus obliquus	Coprini	Ateuchini*
Ontherus sulcator	Coprini	Ateuchini*
Onthobium tilliersi	Canthonini*	
Onychothecus ateuchoides	Ateuchini	
Parachorius thomsoni	Coprini	Ateuchini
Paracryptocanthon borgmeieri	Canthonini*	
Paraphytus africanus	Ateuchini	
Paraphytus doriae	Ateuchini	
Pedaria criberrima	Ateuchini	
Pedaridium hirsutum	Ateuchini – Scatimina	
Saphobiamorpha maoriana	Canthonini*	
Saphobium sp.	Canthonini*	
Sarophorus tuberculatus	Ateuchini	
Scatimus ovatus	Ateuchini – Scatimina	
Scatonomus thalassinus	Canthonini	Ateuchini
Scatrichus bicarinatus	Ateuchini – Scatimina	
Tesserodon novaehollandiae	Canthonini*	
Tesserodoniella elguetai	Canthonini*	
Trichillum heydeni	Ateuchini – Scatimina	
Uroxys aterrima	Ateuchini	
Uroxys epipleuralis	Ateuchini	
Uroxys magnus	Ateuchini	
Zonocopris gibbicollis	Canthonini*	Ateuchini

Figure Captions

Figure 1. Strict consensus tree, superior half. Clades/grade referred in text are numbered on the right. Numbers above each branch are bootstrap values / bremer index: number below each branch is modified bootstrap value. Taxa in **bold** are those previously considered to be included in the Ateuchini.

Figure 2. Strict consensus tree, inferior half. Clades/grade referred in text are numbered on the right. Numbers above each branch are bootstrap values / bremer index: number below each branch is modified bootstrap value. Taxa in **bold** are those previously considered to be included in the Ateuchini.

Appendix 1. Characters used for phylogenetic analysis (numbered from 0).

Head capsule:

0. clypeal central emargination: 0. completely absent; 1. very wide U-shaped 2. U-shaped with parallel sides; 3. V-shaped.
1. clypeal paired teeth: 0. absent; 1. only central teeth present; 2. both central and lateral teeth present; 3. central, lateral and external teeth present.
2. clypeal ventral transverse carina: 0. absent; 1. present.
3. clypeal ventral proccess when present: 0. posterior to clypeal dorsal border; 1. visible just below or anteriorly to clypeal border.
4. clypeus ventrally externally to clypeal ventral process: 1. with setose bands; 2. glabrous.
5. clypeus anteriorly to ventral clypeal process: 1. mainly horizontal; 2. vertical posteriorly and horizontal anteriorly; 3. completely vertical.
6. clypeal ventral tubercle : 0. absent; 1. present.
7. clypeal ventral longitudinal carina: 0. absent; 1. present.
8. subclypeal medial tufts of setae: 0. absent; 1. present.
9. paired clypeal ventral longitudinal oblique carinae: 0. absent; 1. present.
10. paired clypeal ventral longitudinal parallel carinae: 0. absent; 1. present.
11. superepipharyngeal ridge: 0. present; 1. absent.
12. superepipharyngeal ridge medially: 0. straight or arqued; 1. angled or pointed.
13. clypeal anterior dorsal marginal bead: 0. absent; 1. present.
14. clypeo-genal suture: 0. clearly indicated; 1. feebly indicated; 2. not indicated.
15. genal border anteriorly: 0. straight or arqued; 1. forming an angle.
16. internal dorsal eye borders: 0. not carinated; 1. carinated.
17. external dorsal eye borders (on canthus): 0. not carinated; 1. carinated.
18. eye dorsal insertion: 0. absent; 1. present but not trespassing occipital border; 2. present and trespassing occipital border (forming a canthus).
19. eye dorsally ahead occipital border: 0. triangular; 1. linear; 2. ovoid .
20. eyes laterally: 0. entire; 1. divided.
21. external genal angle: 0. absent or obtuse; 1. straight or acute.
22. lateral genal expansion (external to eye): 0. absent; 1. present; 2. feebly present.
23. clypeo-frontal suture: 0. unvisible (except for the existence of tubercle or tubercles); 1. visible (marked or with a carinna).
24. head frontal pilosity: 0. absent; 1. present.
25. lateral occipital carina: 0. absent in the middle; 1. continued in the middle.
26. occiput posterior medial lobe: 0. rounded; 1. pointed.
27. occipital vertical delimitation: 0. absent; 1. present.

28. separation between submentum and gula: 0. acutely V-shaped; 1. simply arqued to obtusely V-shaped.
29. separation between submentum and gula: 0. not carinated; 1. carinated.
30. lateral gulal sculptured area: 0. much narrower than gulal disc; 1. quite as wide as gulal disc.
31. gula laterally: 0. glabrous; 1. with lateral bands of setae.
32. gula proximally: 0. truncate to slightly emarginate; 1. pointed; 2. distinctly emarginate.
33. disc of gula: 0. without longitudinal groove; 1. with a longtudinal groove.

Antenna

34. scape “elbow” near base: 0. present; 1. absent.
35. third antennomere: 0. subequal to second in length; 1. much longer.
36. first segment of antennal club: 0. relatively elongated and parallel sided; 1. relatively curved and cup-shaped or rounded.
37. first segment of antennal club: 0. completely tomentose; 1. lacking tomentosity on proximal surface.
38. first and second segments of antennal club: 0. small cavity on anterior surface; 1. cavity absent.
39. apical antennomere: 0. about as long as scape or slightly longer (excluding the basal insertion point or ball); 0. distinctly shorter.

Labrum-epipharynx

40. labrum: 0. sclerotized; 1. indistinct or reduced.
41. epipharynx apically: 0. straight or curved outwardly; 1. emarginate.
42. epipharynx apex centrally: 0. without central prolongation; 1. with central prolongation.
43. median brush region: 0. protruded and sclerotized; 1. not sclerotized; 2. exagerately protruded.
44. shape of cavity on dorsal side of proximal portion of epipharynx: 0. transverse; 1. ovoid.
45. cavity on dorsal side of proximal portion of epipharynx: 0. reaching clypeal-labral suture; 1.not reaching suture; 2. cavity absent.
46. sclerorized triangle on dorsum of epypharynx: 0. not differentiated; 1. differentiated.
47. medial dorsal epipharyngeal lateral oblique proccesses: 0. absent; 1. present.
48. medial dorsal epipharyngeal oblique processes when present: 0. joined together apically; 1. not joined together apically.
49. medial epipharyngeal proccess at base, ventrally: 0. absent; 1. present.
50. medial epipharyngeal proccess: 0. normally shaped; 1. very wide, triangular.
51. antero-median process of labral suspensorium, dorsally: 0. without a triangular pit; 1. with a triangular pit.
52. cavity in dorsal side of epipharynx: 0. present; 1. absent.

53. central epipharyngeal main parteate combs: 0. absent; 1. complete; 2. present only apically; 3. present only basally.
54. mesal epipharyngeal paired combs: 0. absent; 1. present.
55. lateral epipharyngeal paired combs: 0. absent; 1. present.
56. epipharyngeal central setal band (excluding median brush): 0. only tiny setae; 1. both tiny and large setae; 2. only large setae.
57. lateral epipharyngeal setal band: 0. present; 1. absent.

Mandible

58. mandibular sclerotization: 0. only molar and external lobes; 1. complete; 2. complete except for mesal and apical incisive lobe.
59. mandible apico- laterally border: 0. curved outwards; 1. straight.
60. mandibular external tooth: 0. absent; 1. present.
61. mandibular ventral stridulatory bands: 0. absent; 1. present.
62. membranaceous lateral part of mandible: 0. absent; 1. linear; 2. triangular; 3. not limited medially.
63. mandibles ventrally: 0. only one longitudinal carina; 2. two longitudinal carinae; 3. three longitudinal carinae.

Maxilla

64. galeal shape: 0. approximately transverse; 1. relatively ovoid.
65. galea: 0. apically membranaceous and expanded; 1. completely sclerotized except for a short membranaceous tip.
66. galeal articular sclerite: 0. short and indistinct; 1. large and distinct.
67. lacinia: 0. membranaceous; 1. sclerotized.

Labium

68. apical mentum emargination; 0. absent; 1. not trespassing apical half; 2. trespassing apical half.
69. mentum: 0. distinctly transverse; 1. lenght about equal to width.
70. medial dorsal prolongation of apical mentum: 0. bifurcated; 1. pointed; 2. rounded; 3. absent.
71. mentum ventral apical longitudinal carina: 0. absent; 1. present.
72. X-shaped carina on mentum: 0. absent; 1. present.
73. mentum discal paired tubercles: 0. absent; 1. present.
74. parallel longitudinal carinae on disk of mentum: 0. absent; 1. present.
75. anterior transversal carina of mentum: 0. absent; 1. present.
76. mentum medial longitudinal groove: 0. absent; 1. present.

77. ligulae: 0. sclerotized; 1. membranaceous.
78. basipalpomere: 0. longer than second segment; 1. shorter than second segment; 2. subequal in lenght to second segment.
79. basipalpomere: 0. cylindrical; 1. dorso-ventrally flattened and medially expanded; 2. flattened but not expanded.
80. number of palpomeres: 0. two; 1. three; 2. three but third minute.
81. third palpomere compared to second: 0. smaller, less than 1/3 the max. width of the 2nd palpomere; 1. smaller, ~1/2 to 3/4 the width; 2. about the same size.
82. third palpomere form: 0. absent; 1. minute; 2. spheroid; 3. elongated or fusiform.

Prothorax

83. pronotum at head insertion: 0. without thick fridge of setae or membrane; 1. with a thick fridge of setae; 1. with a thick membrane.
84. pronotal posterior margin: 0. beaded; 1. not or very feebly beaded.
85. pronotal surface: 0. smooth, unsculptured, smootly convex; 1. protuberance or one or more cavities present.
86. pronotal lateral carina (above noto-hypomeral carina): 0. absent; 1. present ; 2. present only basally.
87. lateral noto-hypomeral carina: 0. absent; 1. present only posteriorly; 2. complete; 3. present anteriorly and posteriorly effaced.
88. noto-hypomeral carina posteriorly: 0. simple; 1. strongly sinuate (posterior part elevated).
89. meso-posterior pronotal foveae: 0. absent; 1. present.
90. posterior hypomeral longitudinal carina: 0. absent; 1. present.
91. hypomeral anteriorly: 0. not distinctive from posteriorly; 1. deeply excavated, excavation limited by vertical posterior wall; 2. feebly excavated and differently sculptured to remaining hypomeral regions.
92. transversal hypomeral carina: 0. absent; 1. present.
93. hypomeron anterior oblique carina (extends from procoxal cavity to anterior angle of prothorax): 0. absent; 1. present.
94. hypomeron anteriorly to oblique carina: 0. vertical; 1. concave.
95. posterior hypomeral transversal concavity: 0. absent; 1. present.
96. hypomeral anterior longitudinal carina (extends from procoxal cavity to anterior border mesally to anterior angle): 0. absent; 1. present.
97. posterior hypomeral transversal carina parallel to posterior border: 0. absent; 1. present.
98. basisternal-hypomeral sutures anteriorly: 0. position completely horizontal; 1. position at least anteriorly vertical.
99. transversal posterior hypomeral carina: 0. complete laterally; 1. interrupted laterally.
100. prothorax in posterior view (lateral to prothoracal posterior foramen): 0. simple; 1. with a pit.
101. lateral angle of prothorax in posterior view: 0. present; 1. absent.

102. ventral side of prosternellum: 0. not carinated; 1. carinated.
103. dorsal side of prosternellum: 0. not carinated; 1. carinated.

Mesothorax

104. scutellum: 0. not visible between bases of elytra; 1. with a small visible portion; 2. completely visible.
105. scutellum posteriorly: 0. vertical; 1. horizontal.
106. mesepimeron anterior transverse carina (not anterior border): 0. absent; 1. present.
107. mesepimeron anterior border carina: 0. absent; 1. present only externally; 2. present througout.
108. mesepimeron internally (longitudinal axis): 0. flat; 1. convex.
109. mesepimeron externally (transverse axis): 0. flat; 1. convex; 2. concave.
110. mesepimeron anterior transversal sulcus (anterior face): 1. absent; 2. present.
111. mesepimeron discal oblique carina: 0. absent; 1. present.
112. mesepimeron discal transverse carina: 0. absent; 1. present.
113. transverse pubescent sulcus anteriorly: 0. absent; 1. present and deep; 2. sulcus indicated, not deep.
114. mesosternum anterior transverse carinna: 0. absent; 1. present.
115. mesosternum meso-posterior pilose or sculptured area: 0. entire; 1. divided longitudinally.
116. anterior mesosternal setose band: 0. absent; 1. present.
117. mesosternon in the middle: 0. much narrower than laterally; 1. not much narrower than laterally.
118. mesosternum anterior transverse sulcus: 0. divided; 1. entire.
119. mesosternon posterior to transverse anterior carina in the middle: 0. not or slightly reduced; 1. completely reduced.
120. posterior border of transverse setose mesosternal band: 0. absent; 1. present.
121. anterior border of transverse setose mesosternal band: 0. absent; 1. present.
122. mesosternum setose band centrally if present: 0. without carina or sulcus; 1. with a longitudinal carina; 2. witha longitudinal sulcus.
123. mesosternum anterior transverse carina or border posterior to setose band: 0. not interrupted medially; 1. interrupted medially.

Metathorax

124. Meso-metasternal suture: 0. straight or slightly curved; 1. strongly curved (more than 90 degrees of arc) or angled; 2. sinuate.
125. metasternal anterior marginal sulcus: 0. absent; 1. present.
126. metasternal lobe lateral sulci: 0. absent; 1. present.
127. mesocoxal external pseudosclerite: 0. absent; 1. present.
128. external mesocoxal pseudosclerite when present: 0. linear; 1. triangular.
129. metaepisternon: 0. subtriangular; 1. subrectangular; 2. linear.

130. metaepisternon: 0. anterior border wider than posterior border; 1. anterior border subequal to much less wider than posterior border.
131. metaepisternon posterior dorsal tooth: 0. absent; 1. present.

Fore legs

132. fore trochanto-femoral pit: 0. absent; 1. present.
133. fore trochanter anterior sulcus: 0. absent; 1. present.
134. fore femoral dorsal setal brush at base: 0. with only long setae; 1. with long and short setae in juxtaposed patches.
135. profemoral anterior dorsal carinna: 0. absent; 1. present only basally; 2. present only apically; 3. present troughout.
136. profemoral anterior ventral carinna: 0. absent; 1. present only basally; 2. present only apically; 3. present troughout.
137. profemoral anterior medial carinnae: 0. absent; 1. only one; 2. two parallel and very close; 3. two well separated.
138. profemoral anterior longitudinal ventral sulcus: 0. absent; 1. present.
139. profemoral discal ventral longitudinal carina: 0. absent; 1. present.
140. protibial apex internally: 0. truncated in straight angle, except for internal apical tooth in males; 1. obliquely truncated.
141. protibial apex externally: 0. anterior border of apical tooh not forming angle to anterior border of protibia; 1. anterior border of apical tooh forming angle to anterior border of protibia.
142. number of protibial external teeth in females: 0. three; 1. four; 2. less than three; 3. more than four.
143. internal anterior protibial angle in males: 0. straight, no tooth; 1. with a tooth.
144. protibia ventrally laterally: 0. without oblique carinulae; 1. with several oblique carinulae.
145. protibia ventral main longitudinal carina: 0. interrupted apically at tarsal insertion; 1. prolonged externally to tarsal insertion; 2. prolonged externally to apical external tooth; 3. interrupted well before tarsal insertion; 4. absent.
146. protibia ventral main longitudinal carina: 0. without setigerous pit at apical end; 1. with setigerous pit at apical end.
147. protibia ventrally, mesally to main longitudinal carina: 0. with only one carina; 1. with two parallel longitudinal carinae.
148. protibia ventrally, laterally to main longitudinal carina: 0. with no carina; 1. with one longitudinal carina.
149. protibia ventrally, laterally to main longitudinal carina: 0. without oblique carinnae related to external teeth; 1. with three strong oblique carinnae related to external teeth.
150. protibia dorsally: 0. without longitudinal main (internal) carina; 1. with longitudinal main carina.

151. protibia dorsally: 0. without longitudinal carina parallel to external teeth; 1. with longitudinal carina parallel to external teeth.
152. protibia apically: 0. without ventral internal pit; 1. with ventral internal pit.
153. fore tibia longitudinal main inner carina: 0. present; 1. absent.
154. protibia dorsal accessory medial longitudinal carinna: 0. absent; 1. present.
155. protibial apico-mesal tooth in females: 0. absent; 1. present.
156. fore tibial mesal apical dilatation: 0. absent; 1. present at least in males.
157. fore tibial mesal basal dilatation: 0. absent; 1. present.
158. external basal ventral protibial sulcus: 0. absent; 1. present.
159. supplementary apico-ventral-external tooth in protibia: 0. absent; 1. present.
160. fore tibial apical dorsal transverse carina: 0. absent; 1. present.
161. fore tibial apical dorsal transversal sulcus: 0. absent; 1. present.
162. insertion of fore spur: 0. near or at inner apical angle; 1. near middle of distal edge.
163. protarsi insertion: 0. in the ventral surface of protibiae; 1. in the dorsal surface of protibia; 2. in an intermediate chamber.
164. Fore tarsi: 0. present; 1. absent.
165. protarsi insertion: 0. near midline of tibia; 1. near inner border.
166. protarsi insertion: 0. near apex of tibia; 1. near middle of tibia.

Middle and hind legs

167. orientation of midcoxae: 0. strongly oblique(~45dg); 1. slightly oblique(~10-25dg); 2. nearly parallel; 3. nearly parallel and then strongly oblique anteriorly.
168. mesofemoral discal ventral longitudinal carina: 0. absent; 1. present.
169. metafemoral discal ventral longitudinal carina: 0. absent; 1. present.
170. mesotibiae externally: 0. without transversal carina or tubercle; 1. with transversal or oblique carinae; 2. with transversal tubercles.
171. mesotibial apex: 0. transversely truncate; 1. obliquely truncate; 2. transversely trncated with oblique external projection.
172. mesotibial apex mesally: 0. without spines; 1. with one spine ventral to tarsal insertion; 2. with two spines ventral to tarsal insertion.
173. mesotibial apex laterally: 0. without spines; 1. with one spine; 2. with two spines.
174. mesotibial discal lateral longitudinal carina: 0. absent; 1. present; 2. indicated by row of punctures.
175. mesotibial discal mesal longitudinal carina: 0. absent; 1. present; 2. indicated by row of punctures.
176. mesotibial mesal dilatation in basal half: 0. absent; 1. present.
177. mesotibial mesal dilatation in apical half: 0. absent; 1. present.
178. mesotibial lateral apical dilatation: 0. absent; 1. present.
179. mesotibial lateral dilatation in basal half: 0. absent; 1. present.

180. mesotibial tibia lateral dorsal longitudinal carina: 0. absent; 1. present; 2. indicated by setal row.
181. mesotibial lateral dorsal longitudinal carina: 0. absent; 1. present; 2. indicated by setal row.
182. mesotibial mesal ventral longitudinal carina: 0. absent; 1. present; 2. indicated by setal row.
183. ventral mesal carina of mesotibia: 0. in the ventral mesal border; 1. in the ventral discal border.
184. male mesotibial apico-mesal digitiform tooth: 0. absent; 1. present.
185. mesotibial ventral mesal longitudinal carina if present: 0. simple; 1. expanded apically.
186. lateral mesotibial angle: 0. angled; 1. rounded.
187. mesotibial spurs: 0. inserted contiguously; 1. inserted at each side.
188. tarsal claws: 0. absent; 1. present.
189. tarsal claws when present: 0. simple; 1. angulate at base only; 2. dentate.
190. meso and metatarsi supraunguicular spine: 0. absent; 1. present.
191. meso- and metatarsal segments: 0. cylindrical or coniform; 1. flattened.
192. tarsal claws: 0. without axilary lamella; 1. with axilary lamella.
193. mesotarsus protarsomere disco-lateral carina: 0. absent; 1. present.
194. interunguicular ventral sclerite (onychium?): 0. lamellate and feeby elongate only; 1. very elongated.
195. mesotarsi insertion: 0. in the middle; 1. in the internal angle; 2. in the external angle.
196. metacoxal cavities: 0. separated of epipleuron by ventrite I; 1. contiguous to epipleuron.
197. metafemoral posterior dorsal carina: 0. absent; 1. present only basally; 2. present only apically; 3. present troughout.
198. metafemoral posterior ventral carina: 0. absent; 1. present only basally; 2. present only apically; 3. present troughout.
199. metafemoral posterior medial carina: 0. absent; 1. only one; 2. two parallel and very close; 3. two well separated.
200. metatibiae laterally: 0. without transversal carina; 1. with transversal carina.
201. metatibial apical ventral border: 0. not crenulated; 1. crenulated.
202. metatibial expansion towards apex: 0. absent or slight (sometimes expanded just at apex); 1. moderately expanded (approximately parallel on basal half); 2. greatly expanded throughout; 3. broad throughout.
203. ventro-external longitudinal metatibial setose ridge: 0. absent; 1. present; 2. only setae, without ridge.
204. metatibial apex ventrally: 0. simple; 1. emarginated.
205. metatibail ventro-lateral disc: 0. posteriorly glabrous; 1.covered with setae.
206. metatibial apex mesally: 0. without spines; 1. with one spine ventral to tarsal insertion; 2. with two spines ventral to tarsal insertion.
207. metatibial apex laterally: 0. without spines; 1. with one spine; 2. with two spines.
208. metatibial discal lateral longitudinal carina: 1. absent; 2. present; 3. indicated by row of punctures.
209. metatibial discal mesal longitudinal carina: 0. absent; 1. present; 2. indicated by row of punctures.
210. hind tibia lateral dorsal longitudinal carina: 0. absent; 1. present; 2. indicated by setal row.
211. hind tibia lateral ventral longitudinal carina: 0. absent; 1. present; 2. indicated by setal row.

212. apical metatibial ventral fimbriae: 0. uniform; 1. alternate in size and thickness.
213. hind tibia mesal dorsal longitudinal carina: 0. absent; 1. present; 2. indicated by setal row.
214. hind tibia mesal ventral longitudinal carina: 0. absent; 1. present; 2. indicated by setal row.
215. ventral mesal carina of metatibia: 0. in the ventral mesal border; 1. in the ventral distal border.
216. metatibial apical transverse ventral carina: 0. same level as taral insertion or more apical; 1. more basal.
217. metatibial spurs: 0. two; 1. one; 2. absent.
218. number of non-discal longitudinal carinae in metatibial protarsus: 0. none; 1. one; 2. two; 3. four; 4. three.
219. metatarsi: 0. first tarsomere distinctly longer than fifth; 1. first distinctly shorter than fifth; 2. first about equal to fifth.
220. metatarsi: 0. first metatarsomere distinctly shorter than second; 1. slightly longer than second (1.1-1.5X); 2. greatly longer than second (~2X or more); 3. about equal to second.

Elytra

221. elytral disc pilosity: 0. absent; 1. present.
222. elytra at base: 0. not beaded; 1. beaded at least partially.
223. number of intervals dorsally, including pseudoepipleura: 0. ten; 1. nine; 2. eight; 3. seven; 4. six; 5. eleven.
224. basal portion of fifth interval: 0. equivalent to fourth and sixth; 1. much wider than fourth or sixth; 2. slightly wider than fourth and sixth.
225. 5th elytral interval anteriorly: 0. not widened; 1. widened.
226. 8th and 9th elytral striae: 0. not conjointened; 1. conjointened and discernable only at apex.
227. 9th and 10th elytral striae: 0. not conjointened; 1. conjointened and discernable only at apex or base.
228. elytral external emargination showing abdominal tergites: 0. absent; 1.present.
229. elytral external emargination uncovering lateral metathorax sclerites: 0. absent; 1. present.
230. carina outside seventh stria: 0. absent; 1. present.
231. carina outside eight stria: 0. absent; 1. present.
232. pseudoepipleura: 0. absent; 1. out of seventh stria; 2. out of eighth stria; 3. out of 10th stria; 4. out of 9th stria.
233. pseudoepipleural notch near mesoepimeron: 0. absent; 1. present.
234. pseudoepipleural notch near mesocoxa: 0. absent; 1. present.
235. epipleura near posterior tip of metepisternon: 0. notch present; 1. notch absent.

Abdomen

236. first ventrite: 0. distinctly visible troughout entire lenght; 2. reduced to a thin line posteriorly to metacoxal cavity.
237. supplementary basal ventrite laterally: 0. indicated as a simple anterior bead; 1. indicated as a wide band.
238. ventrites 2-5: 0. normally visible; 1. atrophiated in the middle.
239. third ventrite at middle compared to lateral edge: 0. reduced slightly, down to ~1/2 the length of lateral edge; 1. reduced greatly, only 2/5 or less the length at lateral edge; 3. unreduced.
240. 4th and 5th ventrites laterally: 0. suture discernable; 1. suture not discernable.
241. fifth and sixth ventrites: 0. suture entirely visible; 1. suture completely hidden; 2. suture visible only laterally.
242. abdominal suture between 5th and 6th ventrites: 0. simple; 1. sulciform.
243. fragma in last abdominal ventral suture: 0. absent; 1. present.
244. Last abdominal sternite: 0. not much longer than others; 1. occupying more than a half of abdominal disc.
245. sixth ventrite in ventral view, horizontal orientation: 0. distinctly visible; 1. partially hidden.
246. propygidium anterio-medial groove: 0. distinct with complete lateral edges troughout; 1. indistinct or faintly visible; completely absent.
247. propygidium anterio-medial groove: 0. V-shaped; 1. nearly parallel sided; 2. distinctly parallel sided.
248. propygidium anterio-medial groove: 0. extending ~1/2-3/4 the length propigydium; 1. extending up to transverse ridge (ridge still visible); 2. extending through ridge.
249. propygidium transverse ridge: 0. strong and distinct; 1. slightly pronounced; 0. absent.
250. pygidial basal sulcus: 0. absent; 1. present.
251. pygidial lateral sulci: 0. absent; 1. present.
252. pygidial lateral bead: 0. absent; 1. present.
253. pygidial disc: 0. simple; 1. with longitudinal carina on basal half.
254. discal pygidial transverse sulcus: 0. absent; 1. present.
255. pygidium position (measured at base of disk): 0. vertical; 1. horizontal.
256. pygidial lateral fragma: 0. absent; 1. present.

Male genitalia

257. genital capsule (spiculum gastrale) dorsal mesal sclerite: 0. present; 1. absent.
258. genital capsule (spiculum gastrale) lateral ventral sclerites position: 0. transverse; 1. longitudinal.
259. genital capsule (spiculum gastrale) lateral ventral sclerites form: 0. absent; 1. rounded or squared; 2. elongated.
260. genital capsule (spiculum gastrale) central paired sclerites: 0. absent; 1. transverse; 3. rounded; 4. elongated.
261. genital capsule (spiculum gastrale) dorsal paired lateral sclerites: 0. absent; 1. present.

262. phallobase basal "expansion": 0. absent; 1. present.
263. paramera overall form: 0. apically conical or vertical; 1. flattened apically.
264. paramera relative size: 0. almost symmetrical; 1. left much larger than right; 2. right much larger than left.
265. parameres in lateral view: 0. parameres distinctly tapered to a point; 1. somewhat blunt or truncate.
266. paramere position relative to basal piece: 0. perpendicular; 1. obliquely angled; 2. acutely angled; 3. parallel.
267. size of paramera in relation to phallobase: 0. smaller than 1/2; 1. larger than 1/2; 2. larger than phallobase.
268. paramera: 0. normally separated; 1. fusionated together.
269. lupe-shaped lamella: 0. absent; 1. present.
270. double apical flagellum: 0. absent; 1. present.
271. lamella copulatrix: 0. absent; 1. present.
272. medium unique lamela (reduced lamella copulatrix?): 0. absent; 1. present.
273. large submedial lamella (=modified lupe-shaped): 0. absent; 1. present.
274. triangular apical lamella: 0. absent; 1. present.
275. parietal accesory lamella not lupe shaped nor modified lupe shaped: 0. absent; 1. present.
276. number of accessory apical lamellae not flagellum nor triangular: 0. none; 1. one; 2. two; 3. three.
277. basal paired lamellae: 0. absent; 1. present.
278. accessory medial flagellum: 0. absent; 2. present.
279. internal sac: 0. normally develloped; 1. reduced.

Female genitalia

280. central (pygidial) plate: 0. absent; 1. present.
281. coxites (distinguishable from hemisternites): 0. absent; 1. present.
282. coxites/hemisternites when present: 0. glabrous; 1. with apical seta(e).
283. central vaginal plate: 0. absent; 1. present.
284. hemisternites/vaginal plate: 0. separated; 1. fused.
285. ventral vaginal paired sclerites: 0. absent; 1. present.
286. dorsal vaginal paired sclerites: 0. absent; 1. present.
287. external vaginal paired sclerites (hemisternites): 0. absent; 1. present.
288. bursa copulatrix: 0. well separated from vagina; 1. indistinguishable from vagina; 2. a simple vaginal pleague.
289. infundibulum: 0. absent; 1. present.
290. sclerotization of vagina/bursa: 0. absent; 1. present.
291. spermatheca: 0. C-shaped; 1. helicoidal; 2. spiral-shaped.
292. spermathecal basal ampulla: 0. absent; 1. present.

293. spermathecal basis: 0. simple; 1. bilobed.

294. spermatheca apically: 0. gradually pointed; 1. abruptly pointed; 2. rounded.

295. spermathecal basis: 0. globular; 1. gradually pointed; 2. abruptly pointed.

296. spermatheca apically: 0. simple; 1. bilobed.

Appendix 2. Matrix used for phylogenetic analysis (each taxon followed by its character states: -: inapplicable; ?: unknown).

Aegialia arenaria 000-0-000001-110000-000002-01000001000110--0-210-0-01000-
01001001011011000000120123210020000000-00001011021000100000001-000--0000-
0000002200010000110010001000000000000000001100000011000-0-
0010001000133010200000000000-0000200500000000300110020001002--
0100000111231000031000000000000000100111100??????
Agamopus convexus 011000001000010000220011012010000000001011010100-
100011020000022100011200010100012321002000110-000100100000202010111100011100110-
001010003000001000000000110010000000102000100120100110101101000100003300012100011111
111014020012010000121001001000100001010000011011000003101110010000010000001000000100
Agamopus viridis 111001000000000100022001100101000100000111111111100-
0020010000122000001100001100011320002001110-000100101000210000110110011000110-
000110331100001000000010110010011000101002100121000111000101100100003301011110011121
11001223001000-000121000001000100001010001011123011003101100011000000-0-000110000000
Anomiopus aff. virescens 110-01001002-000102201110111100000000001010010100-
02000?0100001221000112000011001122010020000111001100100001211000100110010000010-
0000000311011000210000101101100000000110002100211011110-0-
00100100000330003000001111010-
0122200511100000310100000101000010001000110221100132011000112000000000001010001100
Aphengium sordidum 111102011100110011220011010010001000001111101111-
101011010000122000011200001000012321002000111000010010000021200011011101010011110010
1032100000100100000001100100000001020001000111001111110010001000033000120000211211110
1221101000-0011210010110001101010111000110111110011001000101000100000001000000000
Aphodius fimetarius 000-1-000001-120--1-0001010010001010001010110110-
110010010000122100001200001000012220002000000-00001001021000200000001-000-0-000-
000010000000100000100000001000100000000001001010000011112-0-
00100000000330101000100010012-0010200510010000301100020000002--
200000011123100003100000000200000100111000310000
Arachnodes splendens 1110000100001101002200210000100010000001111010100-
010020110200100100011100001100011320002000110-
0001000010002101001001100101000010000000231100000011000000011110001010010000000022010
11120001012000000013300000100022120120010100002010000120011101001110000000010001112301
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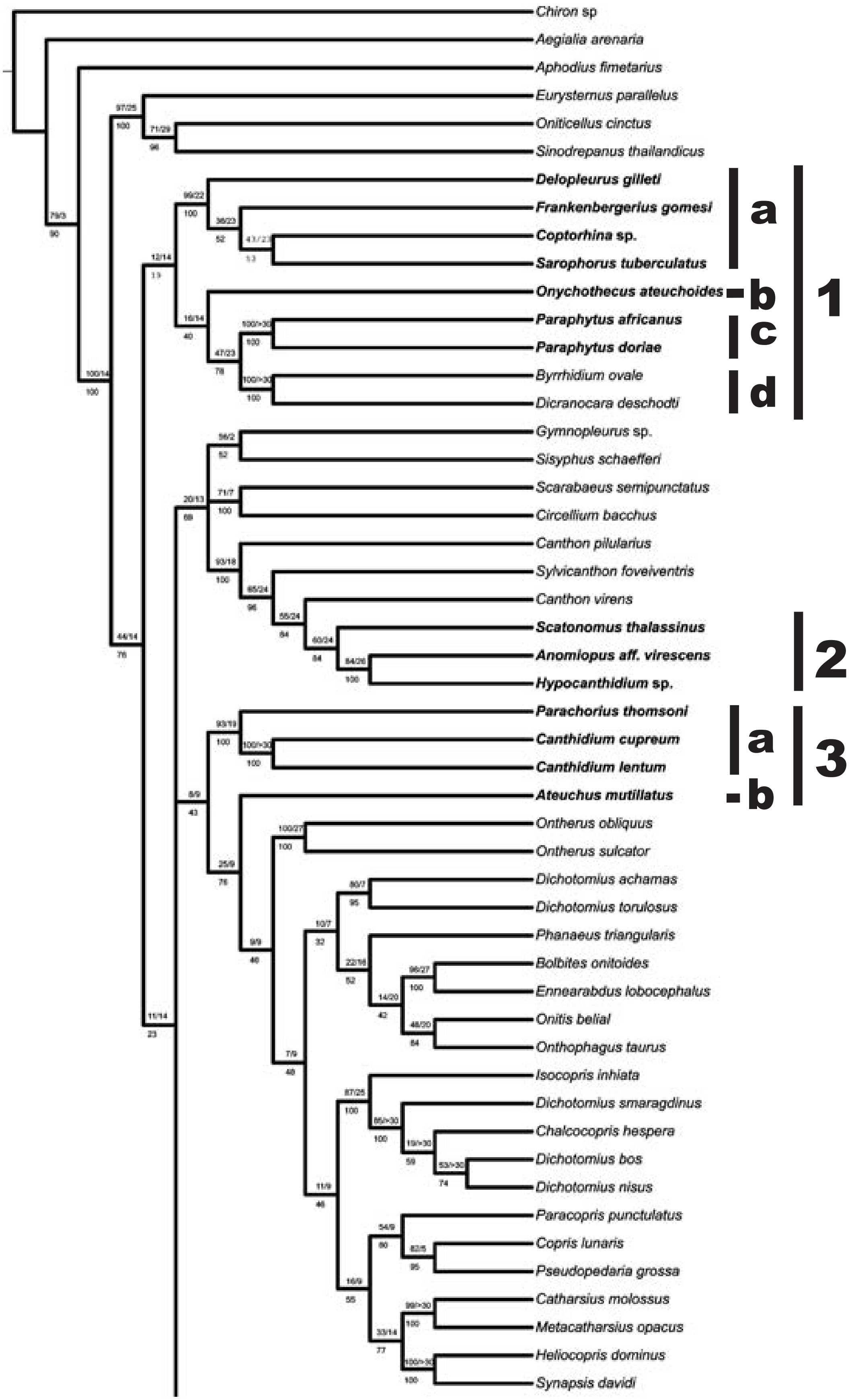
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Onychothecus ateuchoides
Paraphytus africanus
Paraphytus doriae
Byrrhidium ovale
Dicranocara deschodti
Gymnopleurus sp.
Sisyphus schaefferi
Scarabaeus semipunctatus
Circellium bacchus
Canthon pilularius
Sylvicanthon foveiventris
Canthon virens
Scatonomus thalassinus
Anomiopus aff. virescens
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Parachorius thomsoni
Canthidium cupreum
Canthidium lentum
Ateuchus mutillatus
Ontherus obliquus
Ontherus sulcator
Dichotomius achamas
Dichotomius torulosus
Phanaeus triangularis
Bolbites onitoides
Ennearabdus lobocephalus
Onitis belial
Onthophagus taurus
Isocopris inhiata
Dichotomius smaragdinus
Chalcocopris hespera
Dichotomius bos
Dichotomius nisus
Paracopris punctulatus
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Pseudopedaria grossa
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Metacatharsius opacus
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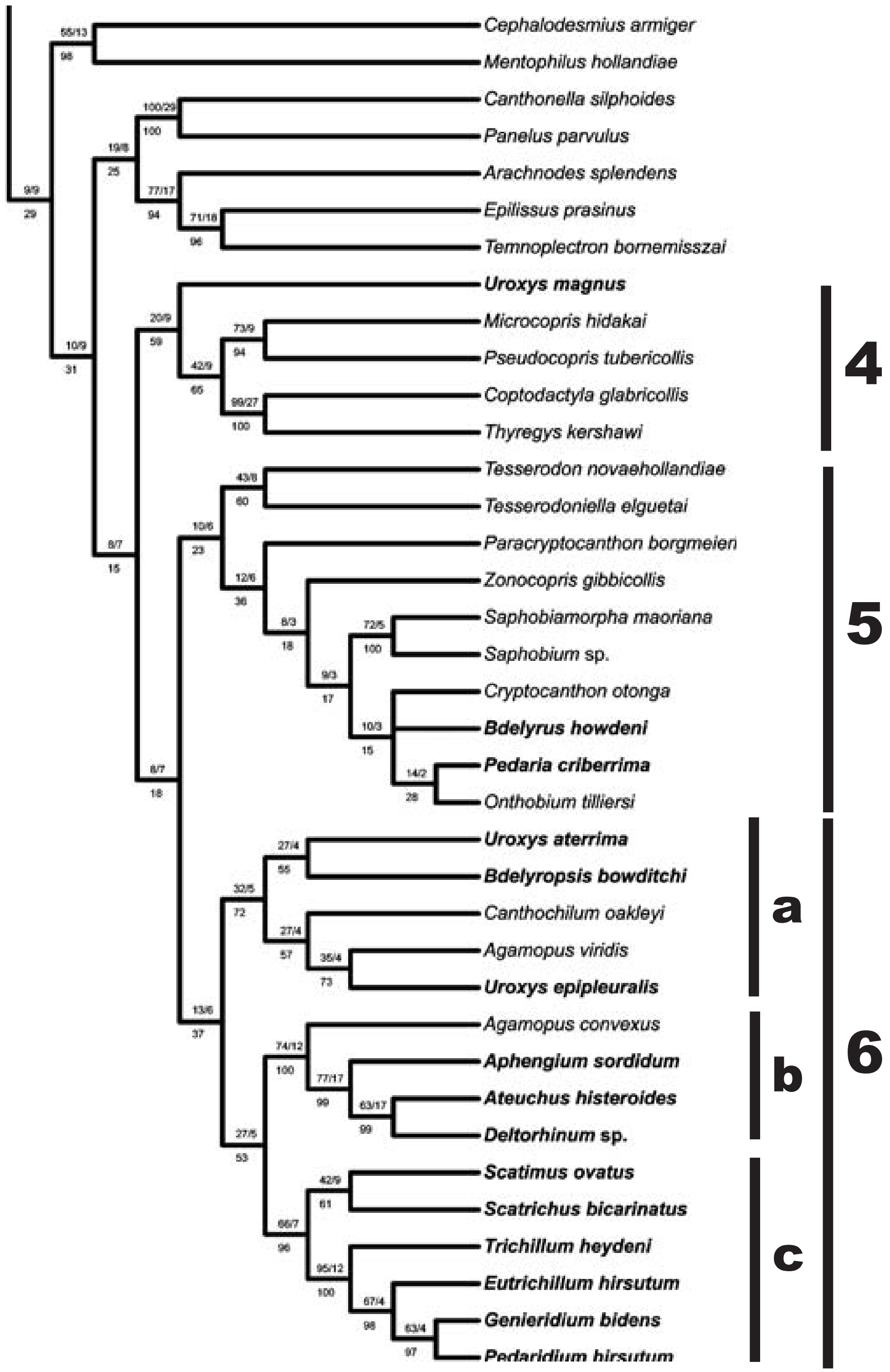

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Panelus parvulus
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77/17
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Arachnodes splendens
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Epilissus prasinus
Temnoplectron bornemisszai
Uroxys magnus
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Microcopris hidakai
Pseudocopris tubericollis
42/9
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Coptodactyla glabricollis
Thyregys kershawi
4
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60
Tesserodon novaehollandiae
Tesserodoniella elguetai
10/6
23
8/7
15
Paracryptocanthon borgmeieri
12/6
36
Zonocopris gibbicollis
8/3
18
72/5
100
Saphobiamorpha maoriana
Saphobium sp.
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17
Cryptocanthon otonga
10/3
15
Bdelyrus howdeni
14/2
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Pedaria criberrima
Onthobium tilliersi
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18
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Uroxys aterrima
Bdelyropsis bowditchi
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Canthochilum oakleyi
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Agamopus viridis
Uroxys epipleuralis
a
13/6
37
Agamopus convexus
74/12
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Aphengium sordidum
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Ateuchus histeroides
63/17
99
Deltorhinum sp.
b
6
27/5
53
42/9
61
Scatimus ovatus
Scatrichus bicarinatus
66/7
96
Trichillum heydeni
95/12
100
Eutrichillum hirsutum
67/4
98
Genieridium bidens
63/4
97
Pedaridium hirsutum
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Capítulo IV

A new dung beetle genus with two new species from Chile (Coleoptera: Scarabaeidae: Scarabaeinae).

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A new dung beetle genus with two new species from Chile (Coleoptera: Scarabaeidae: Scarabaeinae)

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Abstract

A new scarabaeine genus (*Tesserodoniella* n. gen.) with two new species (*T. elguetai* **n. sp.** and *T. meridionalis* **n. sp.**) from Chile are described, and provisionally included in the tribe Canthonini. Species in the new genus are most similar to species from two Australian genera and appear not to be closely related to other New World canthonines.

Key words: dung beetle, new genus, new species, Gondwanaland, Scarabaeinae, Chile, *Tesserodon*, *Aptenocanthon*

Resumen

Se describe el género *Tesserodoniella* n. gen., con dos especies nuevas (*T. elguetai* **n. sp.** y *T. meridionalis* **n. sp.**) de Chile, ubicado provisionalmente en la tribu Canthonini. El nuevo género presenta gran similitud con dos géneros australianos, no presentando aparentemente relaciones con el resto de la fauna americana de la tribu.

Introduction

Until now, only three species of scarabaeine dung beetles were reported in Chile, none of which are endemic to that country. In the tribe Canthonini, only *Megathopa villosa* Eschscholtz and *Scybalophagus rugosus* (Blanchard) were known from Chile. *Megathopa villosa* occurs in Chile from Coquimbo (Region IV) to Malleco Province (Region IX), which corresponds to the "precordilleran floor" of the Andes, and extends into similar habitats in Argentina in Río Negro and Chubut provinces (Halffter & Martínez 1966; Ovalle & Solervicens 1980; M. Elgueta, *in litt.*). *Scybalophagus rugosus* is restricted in

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Chile to the Northern *puna* in Arica Province, Region I, ranging from 3,000 to 4,400 m. The greater distribution of *S. rugosus* extends along the Andes from Cuzco, Peru to Catamarca and Tucumán, Argentina (Halffter & Martínez 1968). Undoubtedly, the presence of these species in Chile represents relatively recent arrivals due to range extensions by Neotropical taxa.

Thanks to Mr. Mario Elgueta, as well as other colleagues (see acknowledgements), we were able to study two new species of Chilean Scarabaeinae belonging to a new genus with Australian affinities. Here we tentatively place this genus within the tribe Canthonini, a largely heterogeneous group, and present observations on its affinities to other genera and discuss biogeographical implications of its distribution.

Specimens studied

The specimens studied belong to the following collections (acronyms and contact personnel in parenthesis):

Canadian Museum of Nature, Ottawa, Canada (CMNC — François Génier)
Fernando Vaz-de-Mello private collection, Lavras, Brasil (FVMC)
Gonzalo and Violeta Halffter private collection, Coatepec, Mexico (GVHC)
José Mondaca private collection, Santiago, Chile (JMEC)
Museo Nacional de Historia Natural, Santiago, Chile (MNNC — Mario Elgueta)
Pedro Vidal private collection, Santiago, Chile (PVC)
University of Nebraska State Museum, Lincoln, Nebraska, U.S.A. (UNSM — Federico Ocampo)

***Tesserodoniella* gen. nov.**

(Figs. 1–10)

Type species

Tesserodoniella elguetai **sp. nov.**

Etymology

Tesserodon, a similar genus, and *–iella*, small, refers to the proximity of this genus to the Australian genus *Tesserodon* Hope and to its small size relative to other Chilean Scarabaeinae. The name of this genus is feminine in gender.

Diagnosis

The new genus is distinguished from all other New World Scarabaeinae by the following combination of characters: Eyes small, feebly visible dorsally when head is retracted (Figs. 1, 6); anterior trochantofemoral pit (as defined by Génier & Kohlmann

2003) present; elytra with wide pseudepipleuron externally to seventh discal stria; mesosternal disc with a transverse depression; abdomen with ventrites articulated, sixth abdominal ventrite as long as ventrites 3–5 together; pygidium with a basal transverse sulcus.

Description

Body: oval and short, size small (5.1–6.1 mm). Dorsal surface microgranulate; head and pronotum covered by irregular, dense, conspicuous punctures. *Head*: as long as wide, without visible dorsal carinae or sutures. Clypeus with two teeth separated by short U-shaped emargination, and external lobe beside each tooth. Dorsal eye surface reduced, triangular, or elongated. Head without occipital bead. Clypeal ventral process cariniform, bordering clypeal emargination. Mentum anteriorly concave. Labial palpus with first segment subcylindrical, widened medially; second segment almost spherical, slightly longer than first; third segment short, cylindrical, narrower than others. *Prothorax*: subrectangular or rhomboidal. Anterior angles acute. Laterally with ventrally directed carina in posterior two-thirds; carina externally directed in anterior third, originating at strong angle in lateral border, subparallel in posterior two-thirds, convergent in anterior third. Posterior margin straight. Hypomeron with acute transverse carina, extending from external side of procoxal cavity to anterior third of lateral pronotal carina. Hypomeral surface concave anterior to transverse carina, flat to feebly convex posterior to transverse carina, with longitudinal keel parallel to external margin. *Elytra*: Disc convex, with seven double striae; striae with small umbilicate punctures separated by five or more diameters. Humerus without conspicuous calli. Pseudoepipleuron with two inconspicuous striae; one dividing pseudoepipleuron in almost equivalent halves, conspicuous only medially; second stria juxtaposed to epipleural carina, conspicuously impressed from basal fifth to pseudoepipleural apex. Epipleuron wide, gradually narrowed to apex, except for strongly widened basal region. Microgranulations on elytral disk and pseudoepipleuron more conspicuous than on remaining body parts. Hind wings reduced. *Mesosternum*: long, narrowed medially. Surface covered by large, dense, ocellate punctures. Disc with evident, transverse concavity; convex at each side of depression. Mesoepimeron trapezoidal with strong carina parallel to anterior margin. Meso-metasternal suture straight, inconspicuous, effaced, in obtuse angle. *Metasternum*: covered by large, dense ocellate punctures; punctures larger laterally, denser, deeper, smaller on disc. Anterior lobe narrower at base than apically, apically 4/3 as wide as basal width; with small lateral round depression at base, depressions linked to each other by concave, inconspicuous U-shaped sulcus; sulcus with vertex posteriorly directed. *Legs*: apico-anterior femoral pit present, rounded. Protibia conspicuously curved internally, externally less curved due to apical expansion; externally with three conspicuous teeth in apical half, median tooth closer to apical tooth. Ventral median longitudinal carina with strong tubercle at tarsal insertion. Spur conical, narrow, as long as tarsal segments 1–3 combined. Protarsus feebly longer than apical tibial width;

segments 1–4 subequal, subcylindrical, as long as wide; tarsomere 5 as long as tarsomeres 2–4 together, laterally flattened, distally widened. Claws small, simple, falciform. Mesofemur elongated. Mesotibia triangular with straight sides, evenly widened to apex, as long as mesofemur. Larger mesotibial spur subconical, just shorter than mesotarsomeres 1–2 combined. Mesotarsomeres 1–4 decreasing in size towards claw; tarsomere 5 with claw as long as tarsomeres 3–4 combined. Metafemur evenly and strongly widened at middle, with strong posterior ventral carina; posterior margin prolonged into conspicuous lobe in apical fourth. Metatibia long, narrow, weakly widened apically; externally serrate in apical two thirds; apex strongly widened externally, obliquely truncate. Metatibial spur subconical, as long as tarsomeres 1–2 combined. Metatarsi similar to that of middle legs. *Abdomen* with ventrites 2–4 of equal length, ventrite 5 one third the length of ventrite 4; ventrite 6 as long as 3–5 combined, not narrowed medially. Pygidium almost twice as wide as long; disc strongly convex with ocellate punctures medially; bordered complete, with strong basal sulcus. *Male genitalia* with asymmetric parameres, left paramere (in dorsal view) longer and wider at apex.

Sexual dimorphism

Male protibia with strong internal apical tooth directed foreward and downward, external teeth narrower than in females; male metatibiae with larger external serrations; and male abdominal ventrite 5 narrowed medially (width even in females).

Remarks

The new genus is readily distinguishable from other New World canthonine genera. The genus is quite similar to two Australian genera: *Tesserodon* Hope and *Aptenocanthon* Matthews. These three genera are all characterized by the presence of the anterior trochantofemoral pit and the position and form of the pseudoepipleuron. Based on our study of dung beetle genera, we predict that these characters are phylogenetically informative and that the three genera form a clade. The three genera may be related, although more distantly, to the South American genera *Zonocopris* Arrow, *Cryptocanthon* Balthasar, *Paracryptocanthon* Howden & Cook, as well as the New Zealand genus *Saphobius* Broun, because they all share the trochantofemoral pit structure. However, *Zonocopris*, *Cryptocanthon*, *Paracryptocanthon*, and *Saphobius* all have a somewhat distinct pseudoepipleuron. *Tesserodoniella* differs from both Australian genera in the form of the prothorax, elytral striae, and in having the first metatarsomere slightly larger than the second.

Key to the species of *Tesserodoniella*

1 Clypeo-genal margin with sharp denticle (Fig. 6); interstriae 3–5 and 7 with apical tubercles (Fig. 7) .... *T. meridionalis* **sp. nov.**

- Clypeo-genal margin rounded (Fig. 1); interstriae 3–5 and 7 without apical tubercles (Fig. 2)..*T. elguetai* **sp. nov.**

***Tesserodoniella elguetai* sp. nov.**

(Figs. 1–5, 10)

Holotype

♂. CHILE: Región Metropolitana de Santiago: Maipo, Rangue, 5–11 June 2004, M. E lgueta & M. Guerrero leg., "trampa barber, bosque higrófilo + esclerófilo" (MNNC).

Paratypes

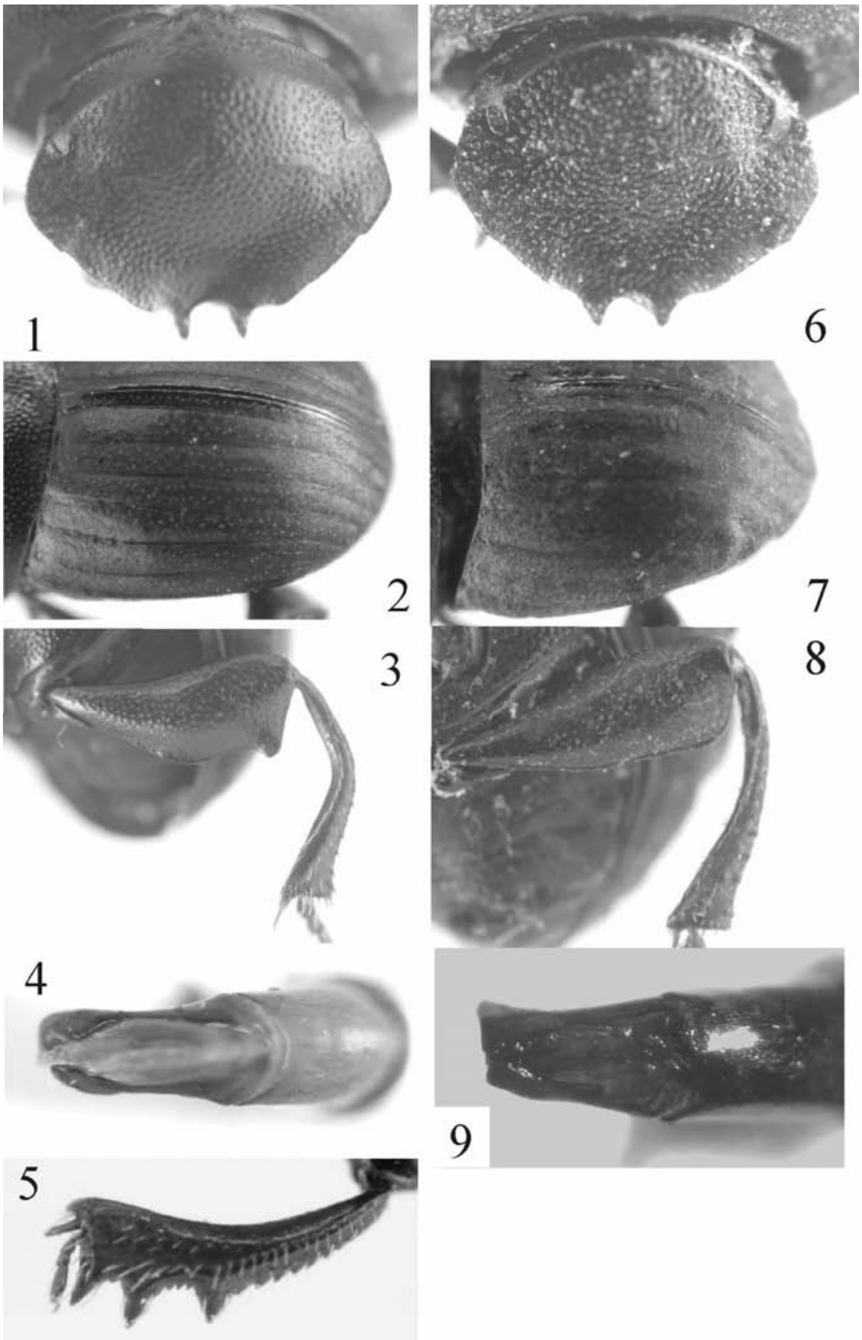
4♂, 4♀. CHILE: Región Metropolitana de Santiago: same as holotype except "bajo excrementos de caballo, suelo arcillo arenoso" (1♀ FVMC**,** ♀ MNNC, 1♀ UNSM); Maipo, Rangue, 2–8 August 2000, A. Fierro leg., barber trap. (1♂ GVHC); SW Santiago, Alto Cantillana, Alhué, 3 September 2000, Vidal leg. (1♂, 1♀ PVC); Cachapoal, R. N. Roblerías de Loncha, 20-XI-2004, J. Mondaca, "en trampa barber" (1♂ JMEC, 1♂ CMNC).

Etymology

A patronym honoring Mario Elgueta, MNNC, Santiago, Chile, who kindly offered specimens of both species of this genus for study.

Description

Holotype male. *Head* (Fig. 1) clypeus with two narrow, parallel-sided, elongated teeth; teeth separated by short, wide U-shaped emargination, each tooth with external angulate lobe. Dorsal eye surface reduced, triangular, visible only when head protracted; interocular dorsal region wider than 20 times one eye width. *Prothorax* subrectangular, almost twice as wide as long medially. Medium longitudinal line feebly indicated in posterior half by impunctate region. Posterior angles obtusely rounded. *Elytra* (Fig. 2) with discal striae conspicuous. Interstriae without discal tubercles, with two irregular rows of inconspicuous punctures; some punctures with short, erect setae; punctures and setae denser apically. Lateral carina sharp, juxtaposed and external to seventh stria, extended from elytral base to just before apex of sixth stria. *Legs* with protibia (Fig. 5) internally curved; external border with 3 well-defined teeth, narrower apically; internally with strong apical tooth, tooth anteroventrally directed. Metafemur (Fig. 3) with posterior, ventral carina forming rounded lobe in median third; with acute subapical lobe. Metatibia with external row of five conspicuous serrations. *Venter* with mesosternum twice as long as wide. *Pygidium* basal sulcus with obtusely rounded, median angle. *Parameres* (Fig. 4) as long as two-thirds of phallobase.



FIGURES 1–9. 1–5. *Tesserodoniella elguetai* **n. sp.**: 1. head; 2. elytron; 3. hind leg; 4. parameres; 5. protibia; 6–9. *Tesserodoniella meridionalis* **n. sp**.: 6. head; 7. elytron; 8. hind leg; 9. parameres.

Variation

Paratypes vary in size (5.1–6.0 mm) and width (widest at prothorax) 3.0–3.3 mm. Females differ from males in the following respects: protibial teeth wider and stronger, apical internal tooth almost lacking; hind femur with posterior apical lobe rounded; metatibia straighter, widened apically, with less conspicuous external serrations; abdominal ventrite 5 feebly narrowed medially.

Remarks

All specimens are from the Cordillera de la Costa mountain system close to the Central Chilean Coast, parallel to the Andes (Fig. 10). Apart from anthropogenic habitats, the area has dry savannas and sclerophyllous, hygrophyllous, and *Nothofagus* forests. This area is within the Santiago Biogeographical Province as defined by Morrone (2001, 2006).

Tesserodoniella meridionalis **sp. nov.**

(Figs. 6–10)

Holotype

♂. CHILE: VII Región del Maule**:** Constitución, Pantanillos, 17 December 2003, “Tramp barber bosque de *Nothophagus* (sic) *glauca*”, leg. W. Navarrete leg. (MNNC).

Paratypes

4♂, 2♀. CHILE: VII Región del Maule**:** same as holotype (2 ♂ JMEC, 1 ♀ MNNC, 1♂ UNSM); Constitución, Pantanillo, Empedrado, September 2002, Wilson Navarrete leg., barber trap. (1♂ FVMC). CHILE: VIII Región del Biobío: Ñuble: Cerro Cayumanqui, 5 December 2004, 36º42’08’’ S, 72º30’36’’ W, “barber”, J. Mondaca E. leg. (1 ♀ CMNC).

Description

Holotype male. *Head* (Fig. 6) clypeus with two elongated triangular teeth separated by U-shaped emargination; each tooth with small, obtuse, external lobe. Clypeo-genal border sharply angulate. Dorsal eye surface ovoid, twice as long as wide; interocular region more than 15 eye widths wide. *Prothorax* rhomboidal, almost one and a half times wider than long. Median longitudinal line absent. Posterior angles completely rounded. *Elytra* (Fig. 7) with discal striae weak but conspicuous. Interstriae with small rounded shiny spots on microgranulated surface. Seventh interstria with conspicuous discal tubercle, tubercle located where seventh interstria meets sixth. Fifth interstria with tubercle in apical third, third and fourth interstriae each with one conspicuous apical tubercle. Lateral carina absent, but pseudoepipleuron conspicuously delimited. *Legs.* Protibia internally curved with external border bearing three conspicuous and apically narrowed teeth, internal border with apical tooth directed forward and downward. Metaemur (Fig. 8) with posterior ventral carina subapically forming rounded lobe. Internal border of metatibiae without tubercles. *Venter* with mesosternum approximately twice as long as wide. *Pygidium* with basal sulcus obtusely angulate medially. *Parameres* (Fig. 9) half the length of phallobase.

Variation

Paratypes vary in size (5.1–6.1 mm) and width (widest at prothorax: 3.2–4.1 mm). Females differ from males in the following respects: protibial teeth wider and stronger, apical internal tooth almost lacking; hind femur with posterior apical lobe rounded; metatibia straighter and more widened apically, external serrations less conspicuous; abdominal ventrite 5 feebly narrowed medially.

FIGURE 10. Map of central Chile showing distribution of *Tesserodoniella elguetai* **n. sp.** (circles) and *T. meridionalis* **n. sp.** (triangles).

Remarks

Specimens were caught in a region originally covered by *Nothofagus* forests, and both sclerophyllous (in arid areas) and hygrophyllous riparian vegetation. This distribution is within the Maule Biogeographical Province (as defined by Morrone 2001, 2006). The northernmost distributions of austral biotic elements are found in this region (Fig. 10).

Biogeography of *Tesserodoniella*

The discovery of *Tesserodoniella* in South America and its hypothesized close relationship with the Australian genera *Tesserodon* and *Aptenocanthon* leads to a series of interesting biogeographical considerations:

1. As pointed out before, the other two canthonine species occurring in Chile belong to predominantly Neotropical genera. *Scybalophagus* has four species distributed in the Patagonian biogeographical subregion (as defined by Morrone 2001, 2006). A fifth species, occurring in Chile, occurs in what Morrone (2006) called the South American Transition Zone. *Megathopa* (with two species) is occurs from Regions IV to IX in Chile, from Córdoba to Chubut in Argentina, and in Uruguay. Neither *Scybalophagus* or *Megathopa* are closely related to or sympatric with *Tesserodoniella*.

2. The presence of *Tesserodoniella* in the Santiago and Maule biogeographic provinces supports Morrone's (2001, 2006) proposals on the composition and biogeographic affinities of those areas. Morrone (2001, 2006) divided South America into two regions (Neotropical and Andean) with a transition zone that roughly corresponds with the Andes. The Andean Region is included in the Austral kingdom, originating from Western Gondwana, which also includes the Antarctic, Cape (or Afrotemperate), Neoguinean, Temperate Australian, and Neozealandic regions. The Andean Region was divided by Morrone into subregions and provinces. Santiago Province is included in the Central Chilean subregion, and Maule Province in the Subantarctic subregion. However, both provinces are strongly related, as Maule is the southern limit of many distributional areas. Interestingly, the Santiago Province contains the highest number of endemic species in the southern part of South America (Morrone *et al.* 1997).

3. Of the closely related Australian genera, *Tesserodon* is widely distributed in northern and western Australia, with two species in New Guinea; while *Aptenocanthon* is distributed in eastern and northern Australia (Matthews 1974, Storey 1984, Paulian 1985, Storey 1991, Storey & Monteith 2000). The biogeographical affinities between southern South America, Australia, and New Zealand, known as the southern Gondwana distributional pattern (Sanmartín & Ronquist 2004), have been illustrated by many plant and insect examples (Crisci *et al*. 1991, Sequeira & Farrell 2001, Sanmartín & Ronquist 2004).

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Capítulo V

Revision and phylogeny of the dung beetle genus *Zonocopris* Arrow, 1932 (Coleoptera: Scarabaeidae: Scarabaeinae), a phoretic of land snails.

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Revision and phylogeny of the dung beetle genus *Zonocopris* Arrow 1932 (Coleoptera: Scarabaeidae: Scarabaeinae), a phoretic of land snails

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Abstract. A revision of the Neotropical genus *Zonocopris* is presented. This genus consists of two species, *Z. gibbicollis* (Harold 1868), distributed in Bolivia, Argentina, Paraguay and Brazil and *Z. machadoi* **n. sp.**, from Paraguay and Brazil. Based on morphological data, a phylogenetic analysis of the relationships of the genus *Zonocopris* found it to be closely related to *Cryptocanthon, Paracryptocanthon* and *Bdelyrus*. Brief comments are made on the behaviour of *Zonocopris* and its association with giant land snails.

Résumé. Révision et phylogénie des scarabées du genre *Zonocopris* Arrow 1932 (Coleoptera : Scarabaeidae : Scarabaeinae), phorétiques sur des escargots terrestres. L'auteur présente une révision du genre néotropical *Zonocopris*, qui comprend deux espèces, *Z. gibbicollis* (Harold 1868), distribuée en Bolivie, en Argentine, au Paraguay et au Brésil, et *Z. machadoi* **n. sp.**, du Paraguay et du Brésil. Une analyse phylogénétique des affinités du genre *Zonocopris,* fondée sur des caractères morphologiques, a montré qu'il était étroitement apparenté aux genres *Cryptocanthon, Paracryptocanthon* et *Bdelyrus.* L'association des deux espèces de *Zonocopris* avec des gastéropodes terrestres géants, ainsi que leur comportement, sont brièvement discutés.

Keywords: Dung beetle, Gastropoda, Neotropical region, new species, phoresy.

The genus *Zonocopris* Arrow 1932 has been placed throughout its history among different Scarabaeinae tribes and subtribes. This genus is known for its poorly understood relationships with giant South American land snails (figs 1, 2).

In a short note, Stein (1867) commented about a collection made in Brazil by Dr. Hensel, that included an interesting scarab, probably belonging to the genus *Onthocharis*, collected on the mantle of a living giant snail of the genus *Bulimus* Scopoli. Harold (1868) described that same scarab as *Canthon gibbicollis*, based on the same specimens, and citing Stein's note. Burmeister (1873) and Kolbe (1905) also made reference to the relationship between these scarabs and the giant land snails.

Arrow (1932) described a new scarab genus and species from Porto Alegre, Rio Grande do Sul state, Brazil, collected by P. Buck on snails then identified as *Bulimus (Strophocheilus) oblongus* Müller. He mentions that P. Buck had found up to twelve specimens on the same snail. He also listed examined specimens from Paraguay in the same paper, and called the new species *Zonocopris bucki*, characterizing it by the conspicuous mesosternal foveae, similar to those found in some species of the genus *Synapsis* Bates, and by its overall similarity with an Indian species, *Panelus setosus* Arrow.

Gillet (1933) transferred *Canthon gibbicollis* to his new monotypic genus *Plesiocanthon*. Paulian (1938, 1939) did not include *Plesiocanthon* or *Zonocopris* in his key to the American Canthonina, mentioning (1939, p. 23) that "*Le genre* Canthon *a été récemment morcelé par divers auteurs, ici je lui conserve son ancienne extension…*" [The genus *Canthon* has been recently fragmented by various authors. Herein, I consider it in its former extension...]. He did mention *Plesiocanthon gibbicollis* in the introduction on Canthonina biology. However, the original descriptions of *Zonocopris* or *Plesiocanthon* are not cited in his bibliography, nor is *Plesiocanthon* cited among the synonyms of *Canthon*.

In his key, Balthasar (1939), considered *Plesiocanthon* as a synonym of *Canthon* Hoffmannsegg, but commented (p. 189) "*Ich habe diese Art noch vorläufig im Rahmen der Gattung belassen, da ich eher geneigt bin, in ihr eine Untergattung zu erblicken*" [I left this species provisionally in this genus, as I am rather inclined to consider it as a subgenus)]. Later, in his description of the genus *Cryptocanthon* Balthasar 1942, he related it to *Zonocopris*.

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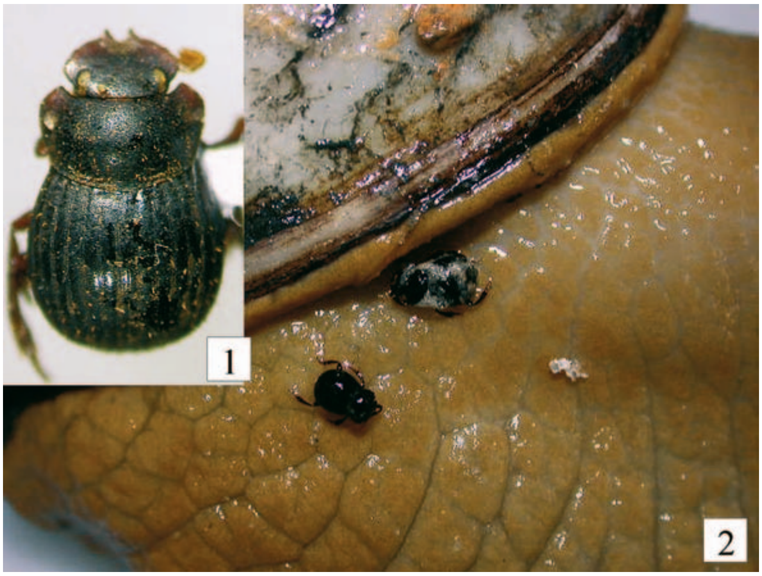


Figures 1–2
Zonocopris gibbicollis. **1**, habitus; **2**, two specimens on *Megalobulimus* sp. mantle.

Blackwelder (1944) included in his catalogue *Zonocopris bucki* and *Canthon gibbicollis* (as *gibbicolle*), without mentioning *Plesiocanthon*.

Pereira (1946) synonymized Harold's and Arrow's specific names, and, consequently, *Plesiocanthon* and *Zonocopris* (the latter being valid), adding as a synonym *Diciphycus* Burmeister *in litt.* The capture of individuals of *Zonocopris gibbicollis* (Harold) on live snails was once again cited in that paper, and he added to its distribution the provinces of Salta and Misiones in Argentina and the states of Mato Grosso do Sul (then part of the Mato Grosso) and Goiás in Brazil. Martínez (1947) published an *addenda* and *corrigenda* to Blackwelder's (1944) catalogue, including the synonymies proposed by Pereira (1946).

Pereira & Martínez (1956) also commented on the relationship between *Zonocopris* and snails, but did not include the genus in their key to the genera of American Canthonini, nor did they make comments about its tribal or subtribal placement. Martínez (1959) included this genus among the Ateuchini (=Dichotomiina), citing *Zonocopris gibbicollis* from Misiones, Salta, Jujuy (Argentina), Bolivia, Paraguay and Brazil. There are no comments about the reasons for including the genus among the Ateuchini, and once again its presumed "symbiosis" with snails of the genera *Helix* Linnaeus and *Strophocheilus* Spix is mentioned, adding that the scarab apparently feeds on feces and not mucus as mentioned in earlier literature.

Balthasar (1963) cited *Zonocopris* in his listing of Canthonina genera, and its phoresy on *Bulimus haematostoma* Scopoli and *Strophocheilus* sp. Vulcano & Pereira (1964) did not include it in their catalogue of the Canthonina of the Western Hemisphere. Halffter & Matthews (1966) included it among the Dichotomiina, probably following Martínez (1959), but without comments on its placement.

Halffter & Martínez (1977) finally included *Zonocopris* among the Canthonina, associating it with the "Menthophilina" that Matthews (1974) considered for the Australian fauna.

Bacchus (1978) reported eight syntypes of *Zonocopris bucki*, two in the British Museum collection, collected by Pio Buck in 1931, and six at the Museu de Zoologia da Universidade de São Paulo, all from Porto Alegre, Rio Grande do Sul, Brazil. He mentions that the exact syntype number was unknown, but that in the original description, Arrow noted that "...*there were many examples and 12 specimens were found inside one snail shell*" (sic). He did not mention any syntype specimens from Paraguay.

Halffter & Edmonds (1982), Martínez (1987) and Hanski & Cambefort (1991) included this genus among the Canthonina, and Cambefort (1991a, b) and Gill (1991) commented again on its relationship with snails.

The aim of this study is three-fold: to review the species in the genus *Zonocopris*, to explore its phylogenetic relationships with other scarab genera, and to present some new data on its behaviour.

Material and methods

The specimens examined belong to the following collections (curators in parenthesis):

CMNC, Canadian Museum of Nature, Ottawa, Canada (François Génier);
IBSP, Adolph Hempel Entomological Collection, Instituto Biológico, São Paulo, Brazil (Sergio Ide);
GVHC, Gonzalo and Violeta Halffter private collection, Coatepec, Mexico;
FMNH, Field Museum of Natural History, Chicago, USA (Alfred Newton);
FVMC, Fernando Z. Vaz-de-Mello private collection, Lavras, Brazil;
MNKC, Museo Noel Kempf, Santa Cruz de la Sierra, Bolivia (Julieta Ledezma);
MZSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (Sonia Casari and Carlos Campaner);
USNM, United States National Museum, Washington, USA (Nancy Adams).

I examined and dissected the specimens under a stereomicroscope and photographed them using a digital Nikkon Coolpix 4500. I conducted the phylogenetic analyses using NoNa (Goloboff, 1993), with Fitch parsimony and equally weighted characters. None of the morphological characters contained codification difficulties. I also included genera that present a general similarity to *Zonocopris*, genera representative of the tribes to which *Zonocopris* has been historically assigned to, and two unrelated scarab genera as outgroups. I inferred clade support by the Bremer index (decay index), with up to ten extra steps (about 50% of the coded characters), and applying a Bootstrap of the original matrix resampling it to a ten-fold matrix.

I conducted behavioural observations from October 2002 to February 2004, using three *Zonocopris gibbicollis* males and four females, collected in Diamantino municipality (Mato Grosso state, Brazil), as well as two giant unidentified snails from the same site. I maintained the specimens in a terrarium at the Zoology Laboratory, Biology Department, Universidade Federal de Lavras, Minas Gerais state, Brazil.

Results and Discussion

The genus *Zonocopris* Arrow 1932

Synonymy

Dicyphicus Burmeister *i. litt.*, Pereira 1946: 294 (considered as a synonym of *Zonocopris*).

Zonocopris Arrow 1932: 223; Blackwelder 1944: 203; Pereira 1946: 293; Martínez 1947: 113; Martínez 1959: 61; Balthasar 1963: 57, 257; Halffter & Matthews 1966: 257; Halffter & Martínez 1977: 34, 44, 51, 59; Halffter & Edmonds 1982: 139; Martínez 1987: 59; Hanski & Cambefort 1991: 473; Vaz-de-Mello 2000: 186, 195.

Plesiocanthon Gillet 1933, Paulian 1938: 227, Balthasar 1939: 189 (considered as synonym of *Canthon*), Pereira 1946: 293 (considered as synonym of *Zonocopris*).

Diagnosis. This genus is readily distinguishable from all other Scarabaeinae genera by the combination of two characters: the presence of a conspicuous round fovea at each side of the mesosternum, and the presence of a supraunguicular spine in the last tarsomere of all legs.

Description. Body: small-sized species (2.5–5.0 mm), color black, except for reddish-brown mouthparts, tibiae and tarsi, and grey antennal clubs. General body form ovoid, but pronotum and elytra each separately rounded and convex, separated by a conspicuous humeral constriction (fig 1). Head: clypeus anteriorly with two large acute teeth, separated by a U-shaped emargination that exposes posteriorly the spiniform ventral clypeal process, which is visible from above. Head dorsally flat, without any traces of tubercles or carinnae. Eyes big (width of the dorsal interocular area seven to nine times greater than one eye dorsal width), ovoid, and narrowed posteriorly. Prothorax strongly convex, disc almost transverse, separated from the posterior margin by a wide transverse depression extending to the lateral borders and anterior angles. Anterior pronotal angles flat and expanded laterally, lateral foveae inconspicuous and incorporated to the anterior-lateral flat region. Posterior margin bordered by a transverse row of umbilicated setigerous puntures bearing scale-like setae. Elytra with wide and deep striae, composed by anastomosed punctures. Striae wider and deeper on apex, where interstriae bear short erect setae that are also present on the sides. Humeri narrowed, calli absent. Pseudoepipleuron wide, bearing a carina, extending from the elytral base to the apex of the second elytral stria. Disc separated from pseudoepipleuron by a conspicuous lateral carina exterior to the seventh elytral stria, that extents from the base almost to the apex of the sixth elytral stria. Hind wings normally developed. Legs: trochanters with an acute anterior angle. Fore femurs ovoid, with a distinct, rounded basal anterior trochantofemoral pit. Protibiae subtriangular, flat, with three external teeth, the apical one much more prominent than the others, apical internal angle straight. Protibial spur short, a bit longer than the first two tarsomeres together. Length of protarsi equal to two thirds of the apical tibial width; last tarsomere with a large, straight and conical supraunguicular spine and short falciform claws. Mesotibiae strongly widened at base, subconical. Metatibiae subconical, with a strong ventro-apical longitudinal carina, bearing a conspicuous row of red to yellow setae. Meso- and metatibial spurs short, conical. Length of first tarsomere subequal to the second one in the middle legs, and slightly shorter than the second one on the hind legs. Last tarsomeres similar in all legs. Venter: mesosternum as long as one third of its width, with a conspicous round pit on each side of the disc. Each mesosternal pit covered by long thick setae. Metasternum barely convex, without discrimen, laterally covered by large, rough punctures and short setae. Abdomen short, ventrites covered by umbilicated punctures. Pygidium transverse and strongly convex, with a deep basal sulcus, and apical border effaced. Parameres shorter than two thirds of the fallobase in length, apically narrowed, flattened and with apex truncated.

Sexual dimorphism. Males have protibiae more strongly widened apically, and with the internal edge more curved than in females; in females protibiae are subtriangular; an internal apical tooth is present in males; male protibial spurs are also shorter than in females, and spatuliform and conical respectively. Differences of metatibiae vary according to species. Apparently there are no sexual differences in metasternal disc shape, and very few differences in the shape of the last urosternite, which is centrally narrower in males.

Distribution. Brazil, northern and northeastern Argentina, southern Bolivia and Paraguay (fig. 9).

Remarks. All specimens with capture data were collected on giant land snails of the genera *Strophocheilus* and *Megalobulimus*, in malaise-flight intercept traps, and in one case in a pitfall baited with human feces. In this last case, however, a giant land snail was also inside the trap (G. Schiffler, *pers. comm.*).

Key for the species of *Zonocopris* Arrow

1. Clypeus rounded externally to median teeth; elytral insterstriae without punctures; protibiae denticulated between teeth; male metatibiae curved internally; parameres very short, with strong hook-like external prolongations in the apico-lateral angles .... *Z. gibbicollis* (Harold 1868)
- Clypeus bisinuated externally to median teeth; elytral insterstriae with two irregular rows of umbilicated punctures; protibiae not denticulated between teeth; male metatibia strongly medially internally widened; parameres longer, barely arqued externally in the apices .... *Z. machadoi* **sp. nov.**

Zonocopris gibbicollis (Harold 1868)

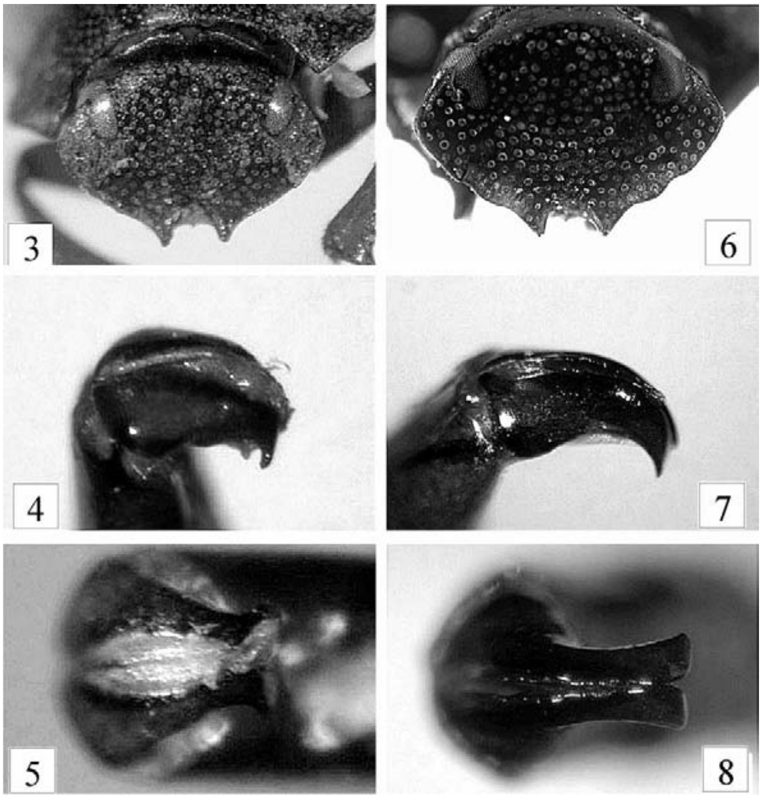
Canthon gibbicollis Harold 1868: 138; Gemminger & Harold 1869: 991; Kolbe 1905: 494; Gillet 1911: 29; Balthasar 1939: 189.
Coprobius gibbicollis (Harold 1868); Burmeister 1873: 417.
Zonocopris bucki Arrow 1932: 223; Blackwelder 1944: 203, Bacchus 1978: 100 (synonymized by Pereira 1946: 293).
Canthon gibbicolle Harold 1868; Blackwelder 1944: 199.
Dicyphicus gibbicollis (Harold 1868): Burmeister *in litt.* (Pereira 1946: 294)
Plesiocanthon gibbicollis (Harold 1868): Gillet 1933: 323, Paulian 1938: 227.
Zonocopris gibbicollis (Harold 1868): Pereira 1946: 293; Martínez 1947: 113; Martínez 1959: 61; Balthasar 1963: 57; Halffter & Matthews 1966: 22; Halffter & Martínez 1977: 59; Martínez 1987: 59; Cambefort 1991a: 32; Cambefort 1991b: 57; Gill 1991: 215; Vaz-de-Mello 2000: 195.

Type material. *Canthon gibbicollis* Harold 1868: Number of syntypes not specified, originally at the Berlin Museum (Harold 1868), but not found at the Museum für Naturkunde der Humboldt-Universität (J. Frisch *in litt.*). Possibly some syntypes have been later deposited in the Oberthür collection. However those have not been found at the Muséum National d'Histoire Naturelle (O. Montreuil *in litt.*).
Zonocopris bucki Arrow 1832: The Natural History Museum, London, specimens not examined; five specimens examined in São Paulo that appear to correspond to the original series (of six cited by Bacchus 1978), but are not labelled as types.

Description. Body size 2.5–3.5 mm. Head (fig. 3) with clypeus rounded at each side of median teeth. Head surface covered by dense umbilicated punctures, separated by half to one puncture diameter. Dorsal interocular region as wide as seven times one eye width. Pronotum covered by umbilicated puntures, that are denser in the anterior discal declivity (where punctures are separated by about ¾ of one puncture diameter), and of greater size on the anterior angles. Posterior border with punctures less dense. Elytra with discal interstriae without punctures, each interstria with one row of small irregular and inconspicuous tubercles, visible only under good light conditions. Legs: protibiae with the internal border slightly curved in males, straight in females. Basal and medial teeth poorly developed in males, acute and conspicuous in females. Metatibiae internally curved in males, straight in females. Genitalia: Parameres short, length equal to half that of the fallobase, ventrally strongly curved, with a conspicous externally-directed apico-lateral hook (figs 4, 5).

Distribution. Northern and northeastern Argentina, southern and western Brazil (one specimen is labeled from northern Brazil), southeastern Bolivia and eastern Paraguay (fig. 9.).

Remarks. Although labelled type specimens have not been examined, little doubt remains about the synonymy proposed by Pereira (1946) for *Zonocopris bucki*, because, according to Papavero (1973), the collector of the type-series of *Canthon gibbicollis*, Hensel, lived from 1863 to 1866 in Porto Alegre, Rio Grande do Sul State, Brazil, and collected mostly there. This is exactly the type locality for Arrow's *Z. bucki.*



Figures 3–8
Zonocopris spp. **3-5,** *Z. gibbicollis*; **6-8,** *Z. machadoi*; 3, 6, head. dorsal view; 4, 7, paramera, lateral view; 5, 8, paramera, dorsal view.

Examined specimens. ARGENTINA: **Jujuy:** 6 km W Yuto, INTA, 13-14.II.1982, H.& A.Howden (5 CMNC); Calilegua Nat. Park, Aguas Negras, 500 m, 18-28.XII.1987, S.&J. Peck, forest ravine litter (6 CMNC); Calilegua Nat. Park, Estación el Cerro, 900 m, 18-28.XII.1987, S.&J. Peck, forest malaise FIT (3 CMNC); Calilegua Nat. Park, Mirador, 600 m, 18-28.XII.1987, S.&J. Peck, forest malaise FIT (15 CMNC); **Misiones:** no data, Richter (1 MZSP); Est. Exp. Loreto, A.A. Ogoblin (2 CMNC); Loreto, 16.III.1949, Rosas-Costa (6 CMNC); **Salta:** Sin localidad, I.1948, A. Martínez (3 USNM); Metán, II.1956, Pereira & Martínez (6 MZSP) ; Do. Oran *(sic)*, Tablillas, 1000 m, II.1944, A. Martínez, sobre *Helix* sp. (2 GHC, 4 MZSP); Do. Oran, El Oculto, XII.1984, H. Martínez (1 CMNC); Do. San Martín, Tablillas, II.1944, A. Martínez (3 CMNC); Do. San Martín, Tartagal, XI.1971, A. Martínez (1 CMNC); Do. San Martín, Pocitos, I.1950, A. Martínez (1 USNM); Do. San Martín, Pocitos, XI.1959, A. Martínez (1 MZSP), General Ballivian, 1931, G. L. Harrington (6 USNM); Tablillas/Tartagal, II.1944, Duret & Martínez (1 CMNC); BOLIVIA: **Santa Cruz:** Pampa Grande, 18º05'S, 64º06'W, 10.I.1996, A. Langer (2 CMNC); Florida, Pampagrande, 03.XI.1996, Fray A. Langer (1 MNKC); Andres Ibáñez, Santa Cruz de la Sierra, 18.IV.1989, Israel Vargas, encontrado entre pié y concha de un gasterópodo (4 MNKC); Roboré, 28.II-1.III.1964, C. Gans & F. Pereira (2 GHC, 11 MZSP); BRAZIL: **No Data:** (2 FMNH); USDA Intercept at Houston, TX #10687, with snails from Brazil, PHH#502, Plane N788, 29.IX.1966, O.E. Hunt (3 USNM); **Mato Grosso:** Diamantino, Alto Rio Arinos, I.2001, E. Furtado, sobre caracóis gigantes (12 FVMC); Poconé, IX.1948 (10 MZSP); **Mato Grosso do Sul:** Salôbra, 10.I.1941, F. Lane (6 MZSP); **Pará:** Canindé (Rio Gurupi), XII.1964, B. Malkin col. (1 IBSP); **Rio Grande do Sul:** (shipped from) Porto Alegre, 15.IX.1966, symbiont on *Strophocheilus oblongus musculus* from L.S. Dillon (16 FMNH); Porto Alegre, IV.1931, Pio Buck (1 MZSP, probably syntype, but not labelled); Porto Alegre, X.1931, Pio Buck (3 MZSP, probably syntypes, but not labelled); Porto Alegre, II.1933 (10 GVHC, 3 CMNC); Porto Alegre, II.1933, Pohl (2 MZSP); Porto Alegre, II.1933, Pio Buck (1 IBSP); Porto Alegre, II.1934, Pio Buck (4 MZSP); Porto Alegre, 25.IX.1966, C.P. Jaeger (22 USNM); Porto Alegre, Jardim Botânico, 30.I.2001, L. Moura & I. Heydrich, *Megalobulimus* sp. (1 FVMC); no data (1 MZSP); PARAGUAY: **Central:** A. Mburicao, 4.XI.1990, G. Arriagada (4 CMNC); A. Mburicao, 4.I.1991, G. Arriagada (3 CMNC); Asunción, 24.I.1957, C.J.D.Brown, on big land snail (2 CMNC); Asunción, 26.IX.1980, D.C. Lowrie, on snail (10 USNM); Asunción, Villa Morra (1 CMNC); San Lorenzo, Lavrelty, 3.II.1997, C Aguilar, ex. *Megalobulimus* sp. (4 CMNC); **Cordillera:** Dist. Caacupé, Cabañas, 13.VII.1981 (2 CMNC); **San Pedro:** San Bernardino, 10.VIII.1903, K. Fiebrig, am Schnecken-Schleimspur (1 FVMC).

Zonocopris machadoi sp. nov.

Zonocopris gibbicollis (Harold 1868) (*pars*): Pereira 1946: 294 (specimens cited from Goiás).

Type material. Holotype male: BRAZIL: **Minas Gerais:** Ribeirão Vermelho, mata do Leleco (21°11'13"S, 45°04'10"W), XII.2001, G. Schiffler, pitfall fezes humanas (MZSP, ex FZVM). Paratypes: BRAZIL: **No Data** (1 CMNC); **Goiás:** Campinas (14°18'36"S, 49°09'04"W), I.1934, R. Spitz (2 MZSP, 1 IBSP); **Mato Grosso:** Chavantina *(sic)* (14°40'24"S, 52°21'11"W), 26.XII.1946, Sick (1 CMNC, 1 MZSP); **Minas Gerais:** Arcos, Mineração CSN, área Bocaina (20°16'55"S, 45°32'22"W), 28.I.2006, R.L. Ferreira (4 FVMC); Itaúna (20°04'43"S, 44°34'35"W), 15.II.2002, M. Souza-Silva, mata seca, sobre *Megalobulimus* (2 FVMC)**;** Lagoa Santa (19°37'38"S, 43°52'23"W), 28.I.1963, Papavero & Leme (1 CMNC); Ribeirão Vermelho, mata do Leleco (21°11'13"S, 45°04'10"W), XII.2001, G. Schiffler, pitfall fezes humanas (4 FVMC); Sete Lagoas (19°27'57"S, 44°14'48"W), Reinhardt, paa em *Bulimus (sic)* (1 CMNC); Vespasiano (19°41'31"S, 43°55'24"W), I.1951, A. Machado, sobre *Strophocheilus* sp. (1 FVMC); **Santa Catarina:** Nova Teutônia (27°09'49"S, 52°25'12"W), XI.1936, B. Pohl (1 MZSP); PARAGUAY: **Caazapá:** Estero Cristal (26°06'00"S 55°45'36"W), 20.IX.1999, J. Jensen (2 FVMC).

Etymology. A patronym honouring Dr. Ângelo Machado, eminent Brazilian odonatologist, conservationist and writer, who provided me with invaluable help since I became interested in scarabs. The first specimen that I examined of this new species, was collected by him in 1951, and was part of a general reference collection identified by Pereira that Ângelo presented to me as a gift when I was 12 years old.

Diagnosis. Clypeus laterally bisinuated. Elytral interstriae with two rows of umbilicated punctures.

Description. **Holotype** male. Head (fig. 6) with clypeus bisinuated each side of median teeth, forming a conspicuous rounded external lobe. Head surface covered by very dense umbilicated punctures, separated by less than half of the diameter of one puncture. Dorsal intercular area as wide as nine times one eye width. Pronotum covered by umbilicated punctures, denser in the discal anterior declivity (separated there by about one half punctures diameter) and twice as large on anterior angles. Pronotal posterior border almost without punctures in the middle, with sparse lateral punctures. Elytra: discal interstriae with two rows of umbilicated punctures, separated by less than one diameter between rows and less than a half diameter within, each row without tubercles. Legs: protibiae with internal borders conspicuously curved, and basal and medial teeth inconspicuous. Metatibiae strongly dilated at the apical half of internal borders.

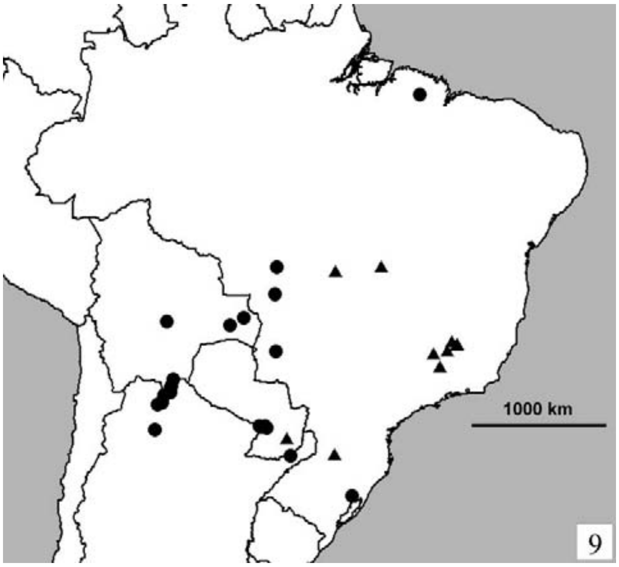
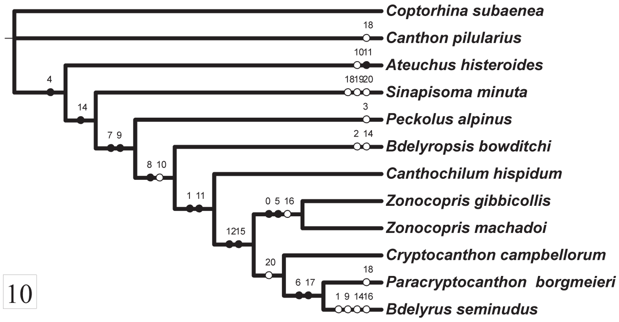


Figure 9
Zonocopris spp., distribution in South America. circles: *Z. gibbicollis*; triangles: *Z. machadoi*.



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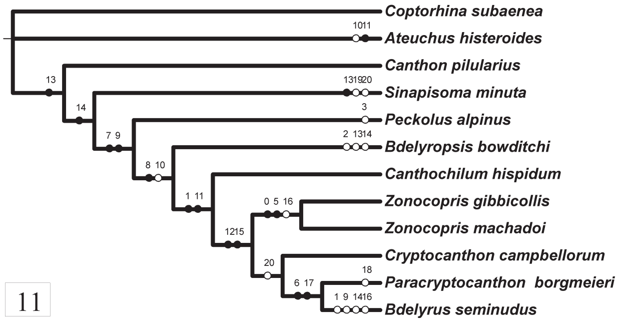

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Figures 10–11

Trees 1 and 2 of five most-parsimonious trees, length = 40 , consistency index = 0.57 and retention index = 0.68.

Genitalia: Parameres (figs 7, 8) as long as 3/5 of phallobase, ventraly curved. Apico-lateral angles slightly externally directed.

Variation. Paratypes vary in size (4.0–5.0 mm) and in sexual characters. Females have anterior tibiae less curved internally, with basal and medial teeth acute and conspicuous; metatibiae almost straight.

Distribution. Brazil (Santa Catarina, Minas Gerais, Goiás and Mato Grosso) and Paraguay (Caazapá) (fig. 9).

Remarks. Specimens collected in pitfall traps were probably asociated with a giant land snail found in the same trap (see above). The locality for Mato Grosso, *Chavantina* (sic) is dubious. Although it is labeled as Mato Grosso, the right name for this locality should be *Xavantina*, and there is another locality with the same name in Santa Catarina state.

Cladistic Analysis

The genera selected for sister-group prospection were *Cryptocanthon*, *Paracryptocanthon*, *Bdelyropsis*, *Bdelyrus*, *Canthochilum* and *Peckolus*, and outgroups used for rooting were *Canthon*, *Canthonella*, *Sinapisoma, Ateuchus*, and *Coptorhina*. I chose the first ones for their general resemblance with *Zonocopris* and previous conjectures of sister-group relationships (Howden 1973; Cook 1998; Cook 2002; Howden & Cook 2002; pers. obs.). On the other hand, the outgroups represent tribes in which the genus *Zonocopris* has at some time been placed or related to in literature. I included *Coptorhina* in order to give a strong root to the tree.

Twenty-one informative morphological characters were used (see tab. 1 and appendix). I conducted an exhaustive search with NoNa, using command "mswap+". It resulted in five equally parsimonious trees of length = 40 , consistency index = 0.57 and retention index = 0.68 (figs 10–15). I calculated the support of clades using the decay index (Bremmer support) (fig. 17). This index was the result of searching up to 31487 trees, from 40 to 50 steps long, that is, up to ten steps longer than the optimal ones, using the command "find" in NoNa. Bootstrap values were calculated with bootstrap matrices of 210 characters (insted of the original 21) in order to eliminate the effect of small character number decreasing bootstrap values, maintaining bootstrap as an indicator solely of character conflict. I conducted one hundred bootstrap replications, and found 119 trees, of the 1000 allowed

Table 1. Matrix used for phylogenetic analysis.

character	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**2**
species	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**
Coptorhina subaenea	0	0	1	0	1	0	-	0	0	0	0	0	0	1	0	0	0	0	1	1	1
Ateuchus histeroides	0	0	1	0	0	0	0	0	0	0	1	2	0	1	0	0	0	0	1	1	1
Canthon pilularius	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Bdelyropsis bowditchi	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	1	1	1
Bdelyrus seminudus	0	0	1	1	0	0	1	1	1	0	1	1	1	0	0	1	1	1	1	1	0
Canthochilum hispidum	0	1	1	0	0	0	0	1	1	1	1	1	0	0	1	0	0	0	1	0	1
Cryptocanthon campbellorum	0	1	0	1	0	0	0	1	1	1	1	1	1	0	1	1	0	0	1	1	0
Paracryptocanthon borgmeieri	0	1	0	0	0	0	1	1	1	1	?	1	1	0	1	1	0	1	0	?	?
Peckolus alpinus	0	0	-	1	0	0	0	1	0	1	0	0	0	0	1	0	0	0	1	1	1
Sinapisoma minuta	0	0	1	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0
Zonocopris gibbicollis	1	1	1	0	0	1	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1
Zonocopris machadoi	1	1	1	0	0	1	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1

as maximum (fig. 16).

The monophyly of *Zonocopris* is supported by three characters, two of them which are non-homoplasic (presence of mesoesternal foveae and shape of the clypeal ventral process, dentiform and foreward directed), and the other (supraunguicular spine) that is also present in *Bdelyrus*. Wether this is a case of convergence, or a simplesiomorphy, would be the subject of a larger analysis involving more species of both *Bdelyrus* and *Cryptocanthon*. Decay index for this node is 3 and bootstrap is 100%.

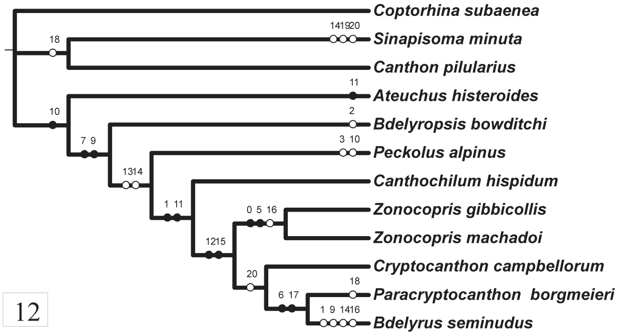
Our results show a sister group relationship between *Zonocopris* and the clade formed by *Cryptocanthon*, *Paracryptocanthon* and *Bdelyrus*. This node is supported by two characters in the metatibiae: they are uniquely ventrally apically emarginated, and with discal apical pilosity. This clade (*Zonocopris* + (*Cryptocanthon* + (*Bdelyrus* + *Paracryptocanthon*))) has a decay index of one, and a bootstrap of 94%. All these genera represent Neotropical endemics, and except for *Bdelyrus* and *Cryptocanthon* that present a few Central American species, they are all distributed in South America.

The sisterhood of *Canthochilum* to (*Zonocopris* + (*Cryptocanthon* + (*Bdelyrus* + *Paracryptocanthon*))) is supported by two non-homoplasic characters: the clypeal process located beneath the clypeal emargination and the presence of a ventro-external longitudinal metatibial setose ridge. The bootstrap value is 99%, and decay index is two. *Canthochilum* is a Greater Antillean endemic restricted to Cuba, Hispaniola and Puerto Rico.

Finally, the group of the above mentioned genera, together with *Peckolus* and *Bdelyropsis*, is well supported by two characters, the presence of elytral setae, which is non-homoplasic in relation to other species used in this analysis, but scattered over at least some species in many Scarabaeinae genera, and the unique anterior trochantofemoral pit (first described by Génier and Kohlmann, 2003), that is also present in a number of other poorly studied groups of tropical Scarabaeinae. These may represent an important clade within the Scarabaeinae, that could also include other small-sized genera, such as *Agamopus*, *Uroxys* and *Odontoloma*, as well as the group formed by *Tesserodoniella*, *Tessedoron* and *Aptenocanthon* (see Vaz-de-Mello and Halffter 2006) and many others presently ascribed to both the Ateuchini and the Canthonini.

Behavioural data for *Zonocopris gibbicollis*

During the hotter and wetter season (October to March) the observed specimens were active on the snails, rarely moving from one snail to another. The beetles were almost always walking over the mantle, and seemed to feed exclusively on mucus. They were never observed on snail feces, that were abundant in the terrarium. Many copulations were observed, and the soil in the terrarium was periodically checked for nests or larvae. However, no nests, larvae, or any new adult were ever found.



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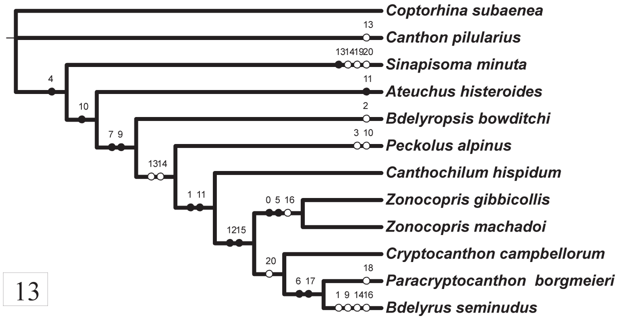

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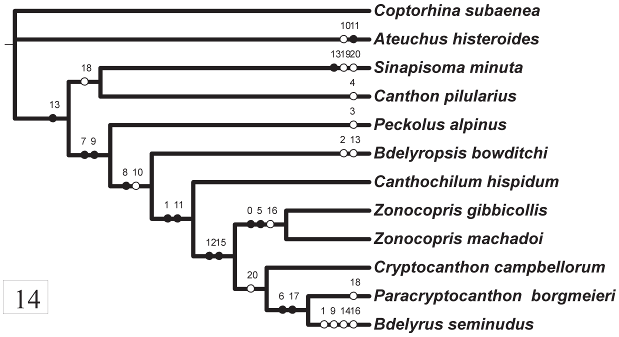
Figures 12–13
Trees 3 and 4 of five most-parsimonious trees, length = 40 , consistency index = 0.57 and retention index = 0.68.

In the dryer and colder season (April to August), the snails buried themselves in the soil, withdrew inside their shells, without forming an operculum, but producing small amounts of mucus. During that time, the beetles remained over the exposed part of the mantle, apparently less active. There was no sign of nesting or oviposition, although large quantities of both faeces and mucus were available from each estivating snail.

The possibility that *Zonocopris gibbicollis* larvae feed on dead snails, was not examined. However, in that case, an extremely long adult stage could be expected because of the snails longevity and the apparently unharmfullness of the relationship with the beetles for the snail.

Acknowledgements. This work is part of the author's Ph.D. thesis in Systematics, at the Instituto de Ecología A. C., Xalapa, Mexico, thanks to a Capes grant (BEX 1208020). I thank Gonzalo Halffter, Juan José Morrone, Mario Zunino, Alejandro Espinosa de los Monteros and Esther Quintero for reading the manuscript and making valuable comments. François Génier was partly responsible for an enthousiastic discussion on the subject. Gustavo Schiffler, Ângelo Machado, Rodrigo Lopes Ferreira, Eurides Furtado and the curators cited in the Methods section provided me with important specimens. Júlio Louzada, Renato Gregorin and Léa Schurter helped me maintain the *Zonocopris* terrarium in Lavras and provided me a place for



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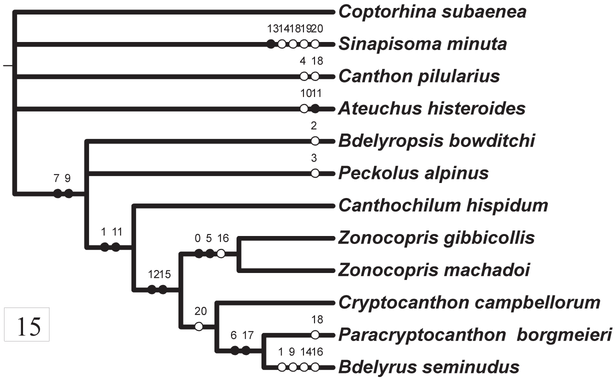

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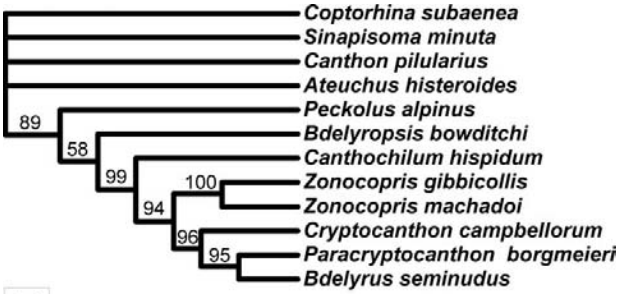
Figures 14–15
14, tree 5 of five most-parsimonious trees, length = 40 , consistency index = 0.57 and retention index = 0.68; **15**, strict consensus of five most parsimoniuos trees.



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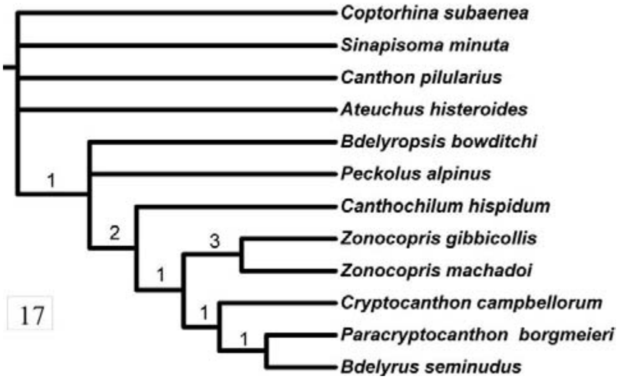

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Figures 16-17.
16, majority consensus resulted from 119 trees found by modified Bootstrap (see text), bootstrap values shown for each clade; **17**, Bremer support (decay index) values found for clades of strict consensus tree.

it. Joe Kirkbride, Denis Keith and Johannes Frisch indicated and provided important literature. Efraín de Luna provoked an interesting discussion of a first analysis of phylogenetic data presented here, and Esther Quintero (again) and Daniel Curoe revised the English manuscript.

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Appendix

Character list

0. Ventral clypeal process: 0. rounded or directed downward; 1. dentiform and foreward directed.

1. Ventral clypeal process: 0. located posteriorly; 1. located beneath clypeal emargination.

2. Dorsal ocular area: 0. not narrowed posteriorly; 1. narrowed posteriorly.

3. Labial basipalpomere: 0. cylindrical; 1. flattened.

4. Hypomeron anteriorly: 0. distinctly excavated; 1. not excavated.

5. Mesosternal lateral foveae: 0. absent; 1. present.

6. Pseudoepipleura: 0. without longitudinal carinae; 1. with longitudinal carina(e).

7. Seta on elytra: 0. absent; 1. present.

8. Elytral lateral carina just external to 7th stria: 0. absent; 1. present.

9. Anterior trochantofemoral pit: 0. absent; 1. present.

10. Apical internal pretibial angle in males: 0. simple; 1. toothed.

11. Ventro-external longitudinal metatibial setose ridge: 0. absent; 1. present; 2. setose only, without ridge.

12. Metatibial apex ventrally: 0. simple; 1. emarginated.

13. Metatibial basitarsomere: 0. shorter or subequal to next tarsomere; 1. longer than next tarsomere but less than twice; 2. more than twice the length of the next tarsomere.

14. Medium and hind tibia: 0. apically expanded (both internal and external borders divergent); 1. not expanded apically.

15. Metatibial ventro-external disc: 0. posteriorly glabrous; 1. covered with setae.

16. Supraunguicular spine: 0. absent; 1. present.

17. Pygidium position: 0. vertical; 1. horizontal.

18. Basal pygidial sulcus: 0. absent; 1. present.

19. Size of paramera in relation to phallobase: 0. smaller than 1/2; 1. larger than 1/2.

20. Parameral axis in relation to phallobase: 0. distinctly angled; 1. not angled.

Capítulo VI

Discusión General

"Heráclito dijo (lo he repetido demasiadas veces) que nadie baja dos veces al mismo río. Nadie baja dos veces al mismo río porque las aguas cambian, pero lo más terrible es que nosotros somos no menos fluidos que el río. Cada vez que leemos un libro, el libro ha cambiado, la connotación de las palabras es otra. Además, los libros están cargados de pasado."

(El Libro, Borges: Borges Oral, 1979)

Análisis autocrítico de los cuatro capítulos centrales

La necesidad de mostrar los resultados de este trabajo en un orden lógico hizo que los artículos que lo componen no estén presentados cronológicamente, lo que lleva a algunas inconsistencias aparentes que necesitan ser explicadas. El orden cronológico de concepción de dichos artículos convertidos en capítulos, es IV-V-II-III, lo que tiene una explicación.

Los capítulos IV (sobre el género *Tesserodoniella*) y V (sobre el género *Zonocopris*) fueron concebidos como estudios previos de casos particulares de grupos considerados por mí como muy emparentados con algunos géneros entonces incluidos en Ateuchini, pero que pertenecían, por los criterios ampliamente empleados, a Canthonini. Así, que se trata de artículos sobre dos géneros de “Canthoninos” aberrantes, uno de los cuales es nuevo, y el otro con un historial previo de ubicación en Ateuchini. La ubicación de éstos géneros en el análisis presentado en el capítulo III (sobre la ubicación de los géneros entonces en Ateuchini), en la tribu Demarziellini, justifica la inclusión de dichos capítulos en la tesis, así mismo corrobora mis sospechas iniciales sobre la mezcla entre géneros ubicados en las dos tribus citadas.

Por otro lado, la importancia de estos estudios particulares para la ejecución de los primeros capítulos, sobre todo el capítulo III, fue inestimable, ya que dichos estudios fueron los que permitieron encontrar los caracteres diagnosticos de la tribu Demarziellini, generando la hipótesis de su existencia como grupo monofilético, y que permitieron demostrar la estrecha relación entre grupos entonces pertenecientes a Canthonini y a Ateuchini (ver capítulo V).

El capítulo II (un primer acercamiendo a los Ateuchini, con la nueva subtribu Scatimina) fue desarrollado a partir de ideas presentadas en mi tesis de maestría, pero de ninguna manera se superpone con ésta. Mi tesis de maestría (Vaz-de-Mello, 2003) fue un estudio acerca del grupo formado por las especies entonces incluidas en los géneros *Trichillum* y *Pedaridium*, con una primera propuesta, en verdad muy preliminar, de sus relaciones filogenéticas y sobre su estatus genérico. Como queda claro en el capítulo II, este trabajo tiene un foco mucho más amplio, ya que trata de un grupo mayor en el cual se anida el grupo estudiado en mi maestría, cuyas conclusiones tanto filogenéticas como taxonómicas se presentan de manera reevaluada. Este capítulo está bastane más profundizado que el siguiente, en cuanto a composición y delimitación de los géneros, principalmente.

Finalmente, el capítulo III está presentado todavía en forma preliminar. Es un trabajo mucho más amplio, definiendo muchos grupos más, y que en su versión final incorporará otros autores. Muchas ideas discutidas más adelante como posibilidades, están ahora en proceso de evaluación para incorporación a dicho trabajo. En la forma presentada aquí, el capítulo III trata solamente de los grupos previamente ubicados en Ateuchini, y aún así los resultados sobre los géneros que quedan en Ateuchini estarían mejor soportados que aquellos para géneros movidos a otros grupos. La idea es que en su formato final sean también ubicados los Canthonini “aberrantes”, correspondientes a Menthophilini, Epilissini y Panelini. Así mismo serán incorporados al análisis filogenético datos sobre algunos géneros faltantes para un buen entendimiento de las relaciones filogenéticas de los Scarabaeinae, como por ejemplo *Deltochilum, Eudinopus,* *Megathopa, Anachalcos* y el “grupo” *Haroldius* (Krikken & Huijbregts, 2006). Estos grupos no fueron incluidos en el análisis presentado por no tener evidencia histórica ni potencial (en mi opinión) de relacionarse estrechamente con ningún género previamente incluido en Ateuchini, pero su inclusión es esencial para la correcta comprensión de las relaciones entre grandes grupos de Scarabaeinae.

Presento en la figura 1. una simplificación del árbol por mí presentado en el capítulo III, en que sustituyo los grupos terminales por las tribus a que pertenecen según la clasificación que propongo, incluyendo ahí a tres grupos sacados de Canthonini que discuto más adelante.

La taxonomía supragenérica de los Scarabaeinae: problemas para trabajos ecológicos

Como queda claro en el confuso historial de las divisiones supragenéricas de Scarabaeinae presentado en el capítulo I, la taxonomía supragenérica del grupo no es sencilla y mucho menos obvia. Queda clara, por ejemplo, la poca atención puesta por mucho tiempo a los géneros de las Américas, de Madagascar y de Australia. Las divisiones clásicas en tribus y subtribus muestran un conjunto de tribus relativamente bien resuelto con amplia ocurrencia paleártica y afrotropical, y un conjunto de géneros gondwánicos (generalmente escasos o francamente raros de África) consistentemente mal ubicados, ya sea porque se ubican en grupos definidos por no presentar las características de los demás (o sea, en grupos “basurero”, como lo son claramente Ateuchini-Dichotomiini y Canthonini), o por tener un historial de “saltar” entre grupos distintos.

Por otro lado, hubo un esfuerzo por mantener una consistencia lógica entre taxonomía y caracteres etológicos, como el rodaje, que también es en parte responsable de esta confusión. La división de los Scarabaeinae entre rodadores y no-rodadores fue práctica, pero está claro en todos los análisis filogenéticos hasta ahora disponibles (incluso en el presentado en el capítulo III) que éstos no corresponden a grupos recíprocamente monofiléticos. Una mala extrapolación de una clasificación en tribus rodadoras y no-rodadoras, llevó a considerarse históricamente como rodadores a especies que no lo son, y viceversa. Por ejemplo, los Eurysternini, por su anterior ubicación en Sisyphini y después en Scarabaeini (como Eurysternina) fueron considerados como rodadores en muchos análisis de grupos funcionales. Hanski & Cambefort (1991) presentan una división muy simple de los “Scarabaeidae” en dos subfamilias (Scarabaeinae para incluir a las tribus rodadoras y Coprinae para las no-rodadoras), que no está sustentada por ninguna discusión y ni por análisis anteriores o posteriores, pero que ha sido ampliamente usada como fuente de datos sobre comportamiento de géneros cuyo comportamiento jamás ha sido observado. Ahí están, por ejemplo, *Agamopus*, *Zonocopris*, y todos los géneros entonces incluidos en Canthonini, como rodadores, cuando no lo son. De igual manera, los géneros *Trichillum* y *Pedaridium* aparecen ahí como paracópridos (por su ubicación en Dichotomiini), cuando en ese entonces ya había una publicación con datos referentes a su comportamiento, dejando claro que eran endocópridos (Ohaus, 1909; también citado por Halffter & Matthews, 1966). Para añadir otro ejemplo, en Hanski & Cambefort (1991) figuran *Cryptocanthon* y *Paracanthon* como rodadores. Sin embargo, no existen datos publicados que sustenten tal conclusión.

Esta crítica me parece muy importante, porque los datos de comportamiento listados en trabajos que se guiaban exclusivamente por la ubicación tribal de los géneros han sido sistemáticamente usados en varios análisis de importancia relativa de grupos funcionales en comunidades de Scarabaeinae, en trabajos ecológicos, que tienen por lo tanto conclusiones sin sustento empírico. Esto, porque las proporciones de rodadores/cavadores presentadas en dichos trabajos, y ahí discutidas, muchas veces incluyen a géneros de hábitos desconocidos, incluídos entre los que presentan uno de éstos comportamientos.

La lección que se saca de ahí, es que los géneros que no poseen datos sobre comportamiento publicados deben ser considerados como de comportamiento desconocido, lo que lejos de ser un problema, es un estímulo para su estudio.

Caracteres, árboles, e iluminación recíproca

Todos los análisis filogenéticos de amplio muestreo taxonómico ya publicados para Scarabaeinae, sean de datos morfológicos o moleculares (véase capítulo I), tienen en común una alta cantidad de homoplasia y el bajo soporte para los clados que tratan relaciones intertribales (esto por supuesto también es válido para el análisis presentado en el capítulo III). Las razones de este fenómeno necesitan ser bien investigadas. El alto número de homoplasias no necesariamente tiene relación con los bajos soportes, sino, en el caso de caracteres morfológicos, con la interpretación de estados.

Quizá se esté interpretando de manera demasiado simple algunos caracteres, usando solamente presencia y ausencia, pero hay que resaltar que además hay indicaciones fuertes de alta convergencia morfológica entre grupos (por ejemplo Eucraniini-Scarabaeini). Por otro lado, la resolución de la filogenia de un grupo complejo como son

Scarabaeinae parece exigir un ejercicio de iluminación recíproca: los resultados de un árbol filogenético deben guiar la recodificación de algunos caracteres y la búsqueda de otros, con el objetivo de crear árboles sucesivamente más cercanos a la filogenia real del grupo. Por supuesto existe el riesgo de que dichos árboles sean sucesivamente más cercanos a la idea que uno se ha creado sobre la filogenia del grupo que a la realidad, pero esto se podrá probar a través de la optimización de nuevos caracteres añadidos a posteriori e incluidos en nuevos análisis futuros.

Adicionalmente, para el capítulo III incluí representantes de grupos aberrantes y taxones que no habían sido examinados en estudios previos. Con ello, la originalidad e impacto del presente trabajo se ve reforzada.

Los árboles basados en datos moleculares (e.g. Ocampo y Hawks, 2006) presentan un ejercicio interesante, ya que permiten buscar nuevos caracteres morfológicos con más especificidad (por ejemplo, caracteres morfológicos que soportarían un clado nuevo encontrado en un análisis molecular), en un ejercicio de iluminación recíproca que es la única posibilidad mientras no se pueda tener un muestreo de taxones para un análisis molecular amplio como el que se puede obtener para un análisis morfológico. No estoy afirmando que un análisis molecular basado en un buen muestreo sería mejor que uno morfológico, solamente que puede llenar datos faltantes a éste en un futuro análisis amplio combinado. Los clados “moleculares” (aquéllos rescatados solamente en análisis moleculares) no permiten mejorar el conocimiento taxonómico del grupo directamente, ya que un taxón para ser reconocido necesita ser monotético, y me parece demasiado absurdo que consideremos a una diagnosis puramente molecular como válida, ya que sería una restricción muy seria a las posibilidades de estudio de este mismo taxón. Pero los clados “moleculares” sí pueden generar nuevas hipótesis de homologías táxicas o transformacionales morfológicas, que pueden entrar como hipótesis de homología primaria en el mecanismo sucesivo descrito más arriba.

Tribus y subtribus de Scarabaeinae: ¿que grupos siguen con problemas?

El análisis presentado en el capítulo III trae implicaciones que van más allá de los Ateuchini, y presenta alguna inconsistencia con análisis anteriores (siempre en grupos externos) que necesita ser investigada:

La cercanía entre los Eurysternini y Oniticellini ya había sido sugerida desde Castelnau (1840), y se presenta en el análisis de Philips *et al.* (2004), aunque no en el de Ocampo & Hawks (2006). Hay mucha similitud morfológica y comportamental entre ambos grupos, que justificarían un análisis específico para investigar sus relaciones. Por otro lado, tradicionalmente a Oniticellini se les ha relacionado a Onthophagini y a Onitini, lo que también es corroborado por Villalba *et al.* (2002), Philips *et al.* (2004) y Ocampo & Hawks (2006), pero no por el presente estudio. Este último hecho, lo considero más como una debilidad del análisis presentado por mi que de los demás. Hay que considerar que se trata de relaciones entre grupos que en mi análisis se consideran como externos y que entraron más que todo para enraizar los cladogramas, por lo que no hubo búsqueda de caracteres compartidos por ellos. En mi análisis, Onthophagini-Onitini se presenta como un grupo anidado en los Coprini, hermano de Phanaeini-Eucraniini, mientras que Eurysternini-Oniticellini se presenta como grupo externo a los demás Scarabaeinae. Considero que una futura investigación dirigida podría ubicar a estos grupos (Eurysternini-Onthophagini-Oniticellini-Onitini) como monofiléticos, y muy probablemente anidados en lo que hoy consideramos Coprini.

En el análisis que presento, el clado hermano de la tribu Coptorhinini tiene una tritomía, en que se separan: 1. los Scarabaeini clásicos, incluyendo a Scarabaeina, Sisyphina, Gymnopleurina y al núcleo central de Canthonina – me referiré a éstos como “Scarabaeini”; 2. los Coprini, incluyendo a las tribus anidadas Phanaeini, Eucraniini, Onitini y Onthophagini – me referiré a éstos como “Coprini”; y 3. los demás formando un solo clado, a que me referiré como “los demás”.

Sobre los “Scarabaeini”, el clado parece consistente tanto del punto de vista morfológico como etológico, y podría incluir a otros grupos como *Deltochilum*, *Eudinopus-Megathopa*, *Epirinus*, y quizás *Anachalcos-Gyronotus*.

Sobre los “Coprini”, la anidación de Phanaeini-Eucraniini ya había sido propuesta, y su cercanía, en el análisis, con el género *Homocopris* (compuesto por las especies ahí tratadas como *Dichotomius achamas* y *D. torulosus*) es una hipótesis muy interesante que necesita ser mejor investigada.

Sobre “los demás”, están ahí los grupos *Menthophilus-Cephalodesmius*, *Panelus-Canthonella-Epilissus-Arachnodes*, y los tratados en el capítulo III que no serán discutidos aquí: Coptodactylini, Demarziellini y Ateuchini. Los dos primeros clados forman parte de los hoy considerados Canthonini, y serán tratados en un artículo en preparación.

El clado *Menthophilus-Cephalodesmius*, que conformaría la tribu Menthophilini Lacordaire, debe incluir también, por lo menos, a los géneros *Canthonosoma*, *Aulacopris*, *Labroma* y *Coproecus* (australianos) y muy probablemente *Streblopus* (neotropical).

El clado *Panelus-Canthonella-Epilissus-Arachnodes* parece dividirse bien en lo que serían las tribus (o subtribus) Panelini Arrow y Epilissini Lansberge. Un estudio profundo propondrá si se deben considerar como una sola tribu o dos. A este grupo parecen pertenecer también diversos otros géneros en su mayoría paleotropicales y australianos, pero algunos también neotropicales: *Monoplistes*, *Diorygopyx*, *Lepanus*, *Macropanelus*, *Bohepilissus*, *Tanzanolus*, *Pseudocanthon*, *Sauvagesinella*, *Nesovinsonia* y por lo menos la mayor parte de los géneros de Canthonini malgaches.

La evolución del comportamiento: ¿qué hay de nuevo?

Un análisis superficial (optimización “a ojo” del árbol presentado en el capítulo III) permite cuestionar la hipótesis del surgimiento múltiple del comportamiento de rodaje: el comportamiento de rodaje surgiría en el ancestro del clado formado por “Scarabaeini”-“Coprini”-“los demás” (véase arriba) (hipótesis 1.) o, si “Scarabaeini” es hermano de “los demás”, en el ancestro de éstos (hipótesis 2.).

La hipótesis 1 supone la pérdida del comportamiento de rodaje en el ancestro de los “Coprini“. La hipótesis 2 supone el estado no-rodador de los “Coprini” como ancestral. En cualquiera de los dos casos, hay varias pérdidas dentro de lo que llamé “los demás”:

En Menthophilini, por lo menos algunos géneros perdieron la capacidad de hacer bolas, pero no de arrastrar piezas de alimento. Por lo menos en un caso, no hay arrastre pero sí confección de bolas, o sea, hay evidencia de pérdidas de distintas partes de la pauta de comportamiento, probablemente de manera independiente, en distintos géneros del grupo (Matthews, 1974; Halffter & Halffter, 1988).

En Panelini-Epilissini, al parecer no hubo pérdida total del comportamiento, pero hay géneros pequeños que son considerados como “malos rodadores”, o sea, hacen bolas menos uniformes (Halffter & Edmonds, 1982).

En el clado formado por Coptodactylini-Demarziellini-Ateuchini, la situación es bastante más compleja: en los Coptodactylini, hay pérdida total del hábito de rodaje, y como al parecer no hay nidos descritos, no se puede establecer si hubo o no pérdida de la capacidad de hacer bolas; en los Ateuchini, al parecer solamente *Canthochilum* es en algunas ocasiones un mal rodador (Halffter & Edmonds, 1982), lo que puede, dada la filogenia del grupo, ser considerado como una re-ganancia parcial de la capacidad de rodaje, aunque los hábitos cleptocópridos de *Agamopus* y desconocidos de *Bdelyropsis* no permitan afirmar nada. Entre los Demarziellini, hay por lo menos un género que ha conservado el hábito rodador, *Paracanthon* (observación personal), pero no es posible saber más por el desconocimiento de los hábitos del resto de los géneros (sin embargo, es necesario aclarar que *Pedaria* y *Bdelyrus*, no son rodadores, aunque al parecer tampoco son paracópridos).

Para facilitar este análisis, y haciendo una simplificación quizás excesiva, presento el comportamiento de relocalización como compuesto por cuatro distintos “caracteres” etológicos:

- El moldeo de una pelota *in situ* en la masa de recurso;
- La relocalización horizontal del recurso encontrado o separado a partir de una fuente más grande;
- La relocalización vertical o enterramiento del recurso;
- La confección de una bola-nido.

La simplificación es excesiva porque hay comportamientos bien diferentes bajo cada uno de los citados. Así, el moldeo de la pelota *in situ* se puede hacer con material bruto o con material procesado, tomado de regiones distintas de la boñiga, pero el problema es la falta de datos sobre esto para practicamente todos los géneros reconocidamente rodadores (Doube, 1990); la relocalización horizontal se puede hacer con pelotas o materia no formada (Halffter & Halffter, 1988); el enterramiento se puede dar a distintas velocidades, con o sin una cámara de estocaje entre enterrar y manejar el recurso para la cámara-nido, cuando sea el caso (Doube, 1990); y finalmente la bola-nido puede tener distintas formas y distribuciones de diferentes materiales (Halffter & Edmonds, 1982).

Presento en las figuras 2. a 5. el resultado de optimización de estos caracteres sobre el cladograma simplificado.

En la figura 2. se puede observar la ganancia única del comportamiento de moldeo, con várias pérdidas posteriores, en el ancestro de los “Scarabaeini”+”Coprini”+”los demás”. En la figura 3., el comportamiento de relocalización horizontal es ancestral para el clado formado por todos excepto Oniticellini-Eurysternini, también con algunas pérdidas posteriores. En la figura 4., la relocalización vertical es ancestral a todos los Scarabaeinae, y parece que el caso conocido en Aphodiinae sea un desarrollo paralelo. Finalmente, en al figura 5., la confección de bola-nido es también ancestral para los Scarabaeinae, con pérdidas en algunos grupos.

Es importante señalar que el conocimiento muy incompleto del comportamiento de los Coptodactylini, Menthophilini, Epilissini, Panelini y Demarziellini es el principal responsable por las indefiniciones encontradas en algunas optimizaciones, y su incremento es esencial para hacer un análisis más allá del preliminar.

Ateuchini, Demarziellini, y qué falta hacer

En este trabajo, dejo más o menos resuelta la sistemática de los Ateuchini, que ya están definidos morfológica y filogenéticamente, así como sus tres subtribus. El principal problema que queda es el género *Ateuchus*, que aunque dividido en dos en el presente trabajo – uno en Coprini y otro en Ateuchini – es todavía muy heterogéneo, y muy probablemente no sea monofilético: al parecer, los géneros *Deltorhinum* y *Aphengium* se anidarían en *Ateuchus*.

Estoy conduciendo en este momento estudios taxonómicos sobre los géneros *Deltorhinum* y *Aphengium*, y supongo que estos estudios permitirán ubicar a estos dos géneros junto a las especies de *Ateuchus* más cercanas, posibilitando así la toma de decisiones sobre el status taxonómico de los tres géneros.

Los Demarziellini, aquí delimitados, merecen ser estudiados con mayor detalle e incluir muchos más géneros que los usados en este análisis. Puedo citar por lo menos los siguientes géneros pertenecientes a la tribu y no incluidos en el análisis: *Demarziella, Pedaria, Amphistomus, Tesserodon, Aptenocanthon, Tesserodoniella, Cassolus, Onthobium, Ignambia, Pseudignambia, Caeconthobium, Anontobium, Paronthobium, Falsignambia, Baloghonthobium, Boletoscapter, Saphobiamorpha, Saphobium, Zonocopris, Cryptocanthon, Bdelyrus, Paracryptocanthon, Ochicanthon, Paracanthon, Pycnopanelus, Janssensantus, Peckolus, Endroediolus* y *Outenikwanus*. El análisis filogenético de todo el grupo, aunado a nuevos datos de comportamiento, podrá responder a las preguntas ya planteadas sobre pérdidas y ganancias del hábito de rodaje y sus distintas pautas de comportamiento, quizá elucidando mejor las relaciones entre morfología y hábitat, y distintos patrones etológicos.

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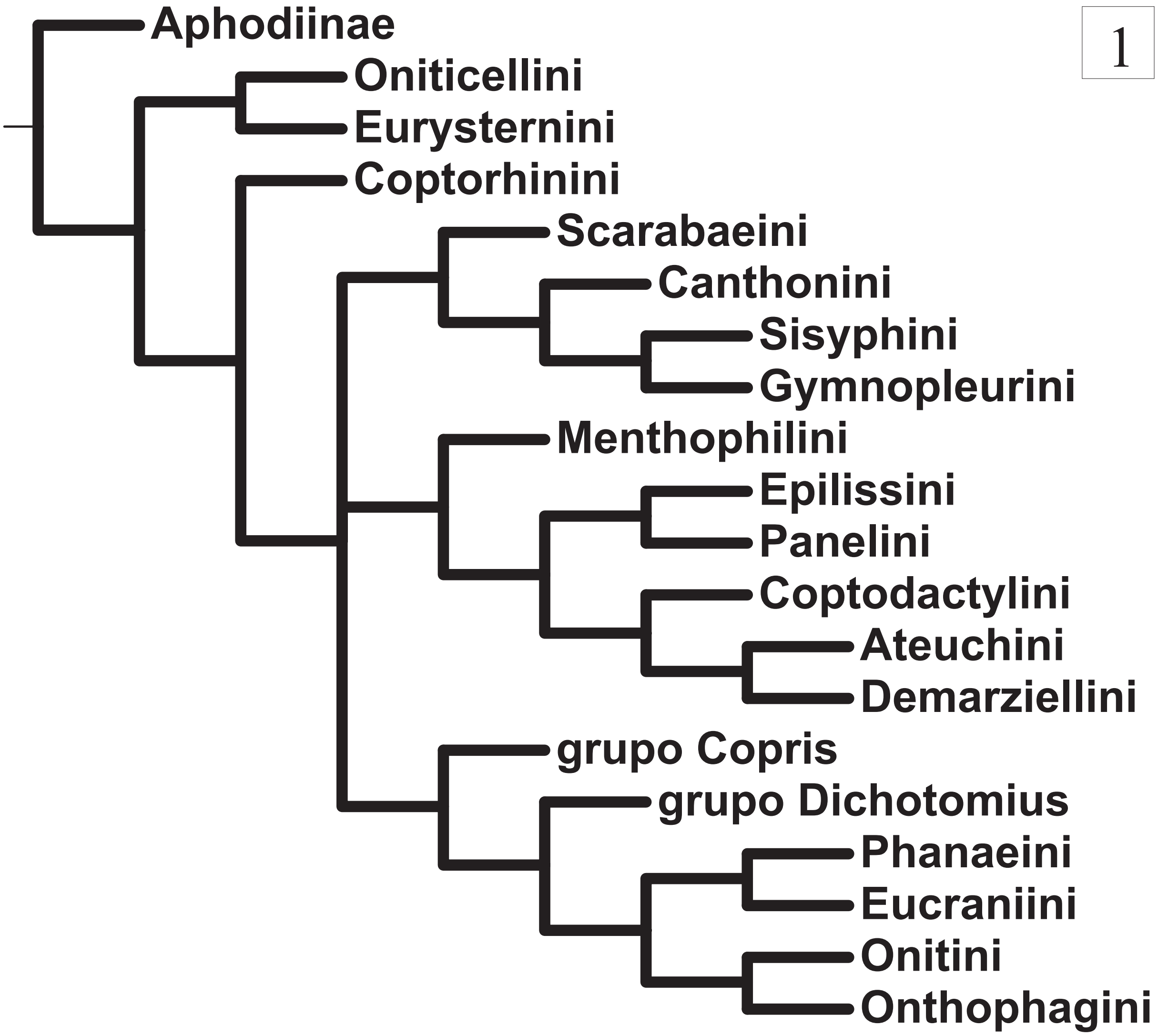
Legendas de las figuras:

Figura 1. Simplificación del cladograma presentado en el capítulo III, sustituyendo los terminales por las tribus a éllos asignadas o propuestas como probables en la presente discusión.

Figuras 2-3. Optimizaciones sobre el cladograma de la figura 1. Bolas negras son ganancias del comportamiento, bolas blancas pérdidas, y bolas de dos colores ganancias o pérdidas parciales (en algunos taxa del grupo). 2. Moldeo de pelota *in situ*; 3. relocalización horizontal de recurso.

Figuras 4-5. Optimizaciones sobre el cladograma de la figura 1. Bolas negras son ganancias del comportamiento, bolas blancas pérdidas, y bolas de dos colores ganancias o pérdidas parciales (en algunos taxa del grupo). 4. relocalización vertical del recurso (enterramiento); 5. confección de bola-nido.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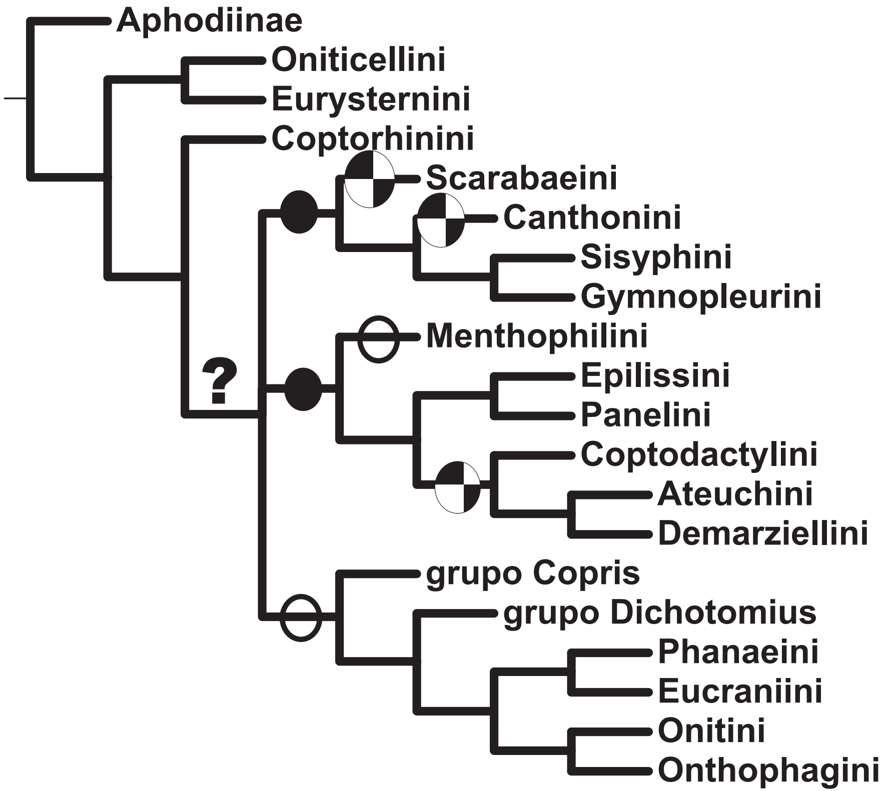
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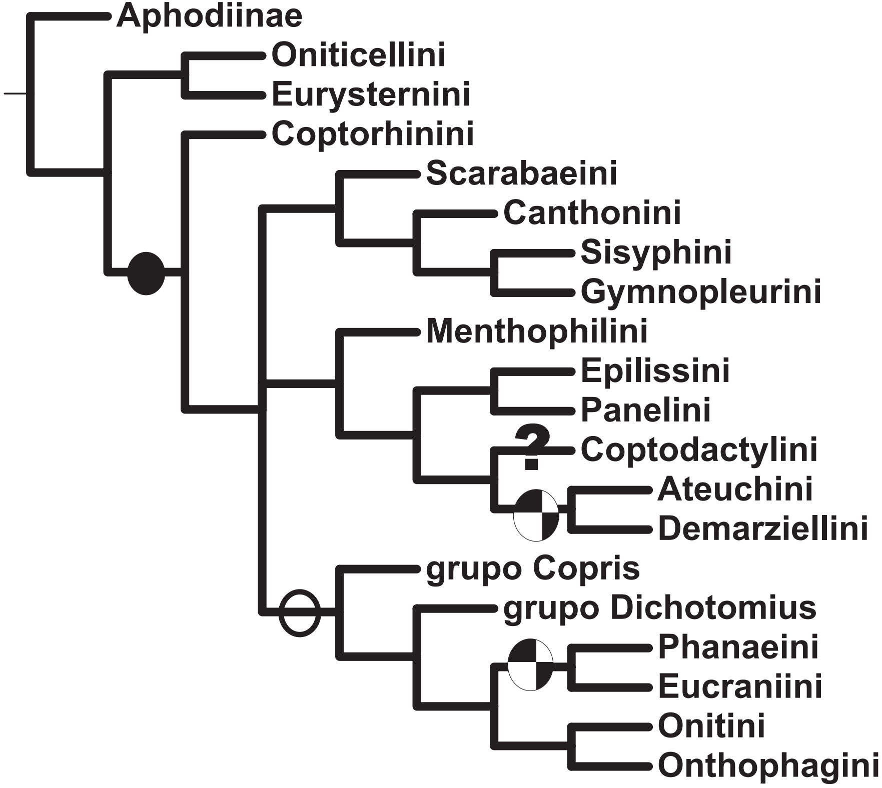
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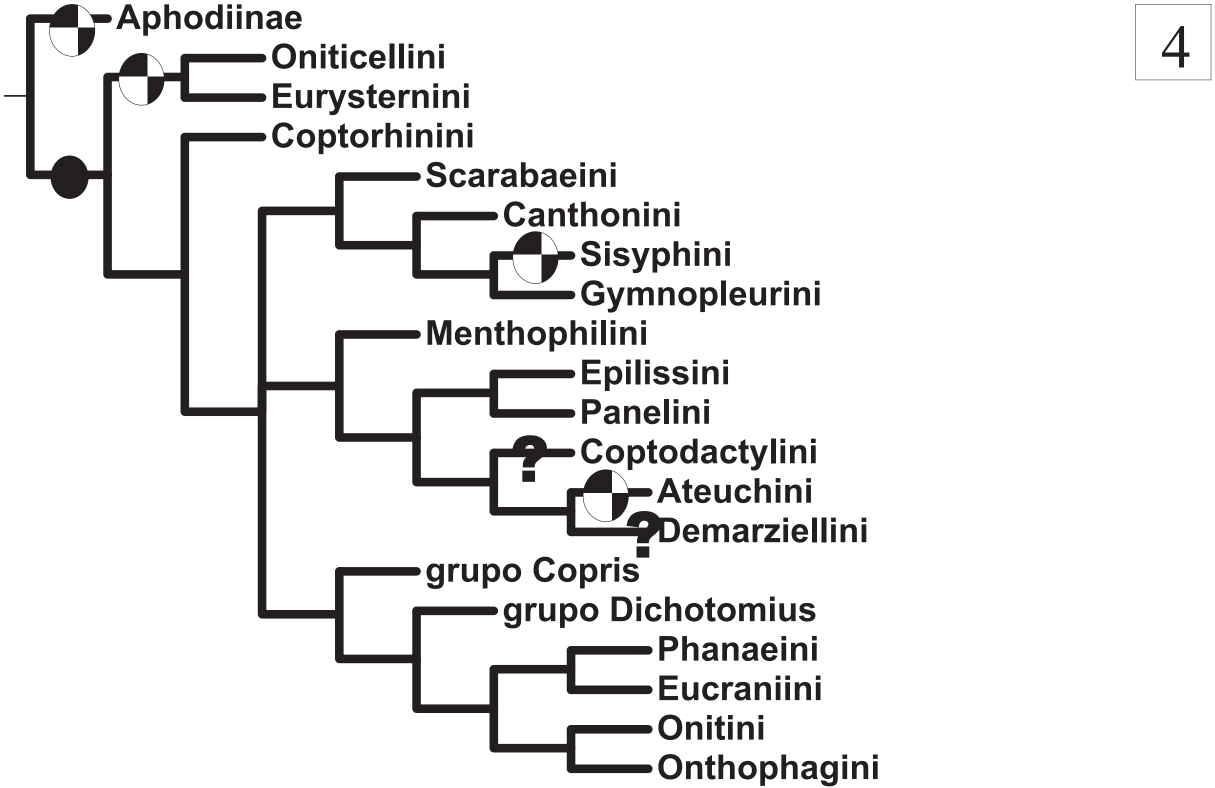
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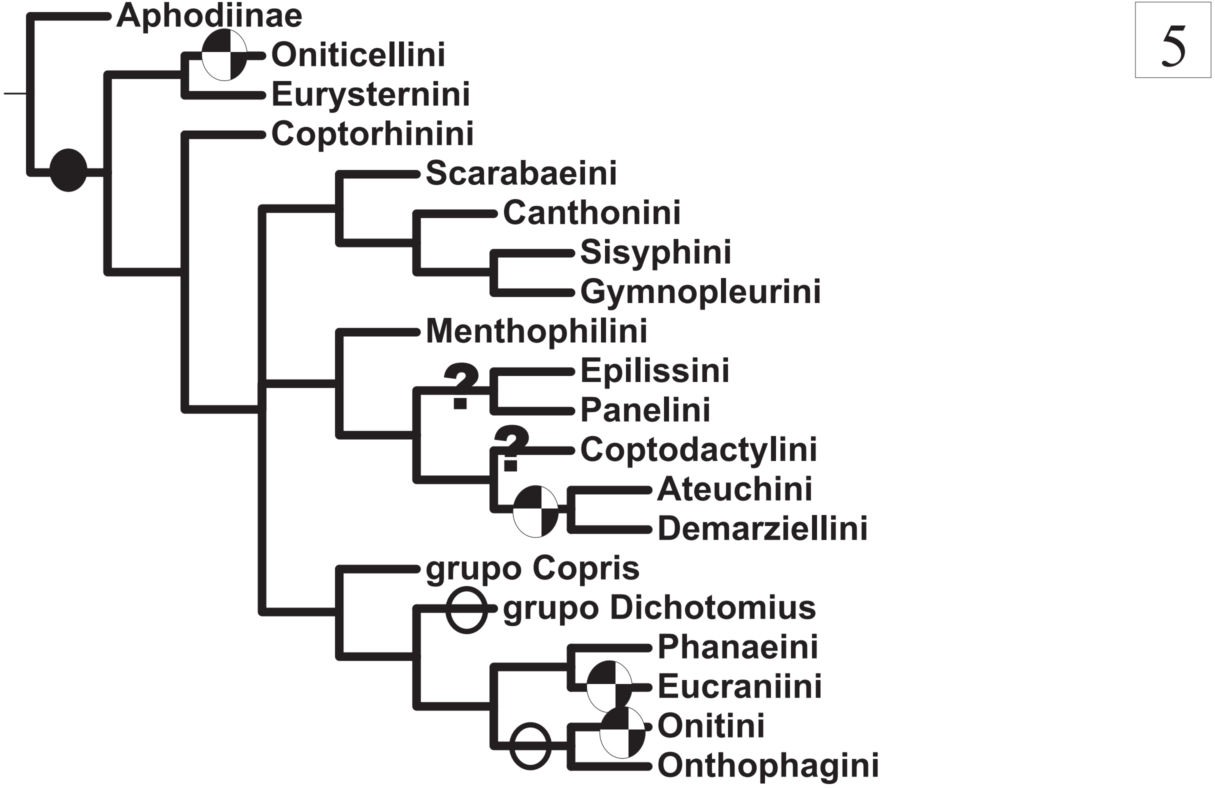
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