

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

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Abstract

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

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

Resumen

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

Introduction

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

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

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

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

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

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

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

Methods and material

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

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

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

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

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

The following institutions provided material to the study:

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

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

Results and discussion

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

Morphology of male genitalia in Scarabaeinae

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

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

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

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

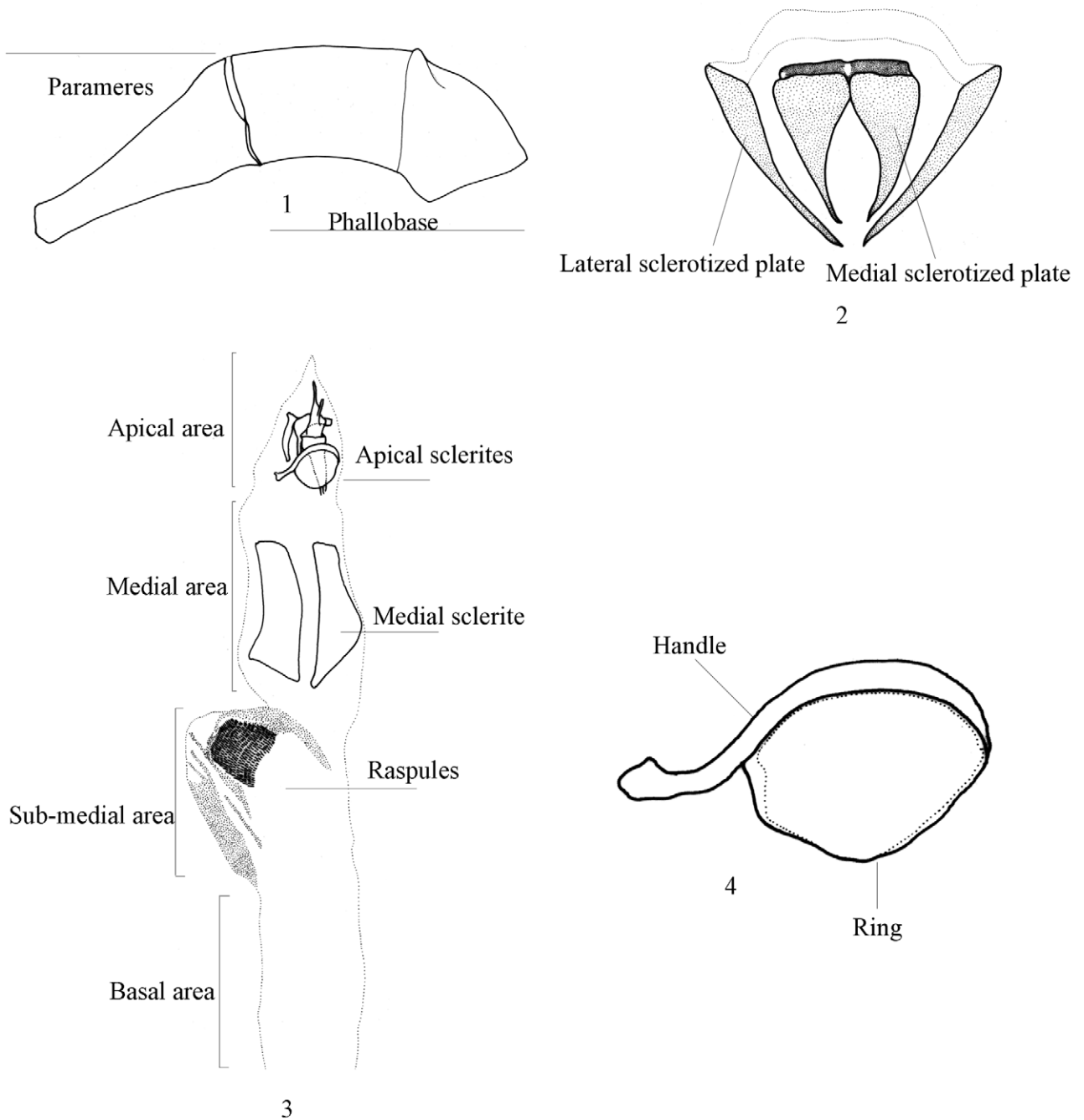


PLATE 1. Figures 1–4. 1. Aedeagus. 2. Genital segment. 3. Internal sac of the aedeagus. 4. Basal sclerite.

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

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

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

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

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

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

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

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

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

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

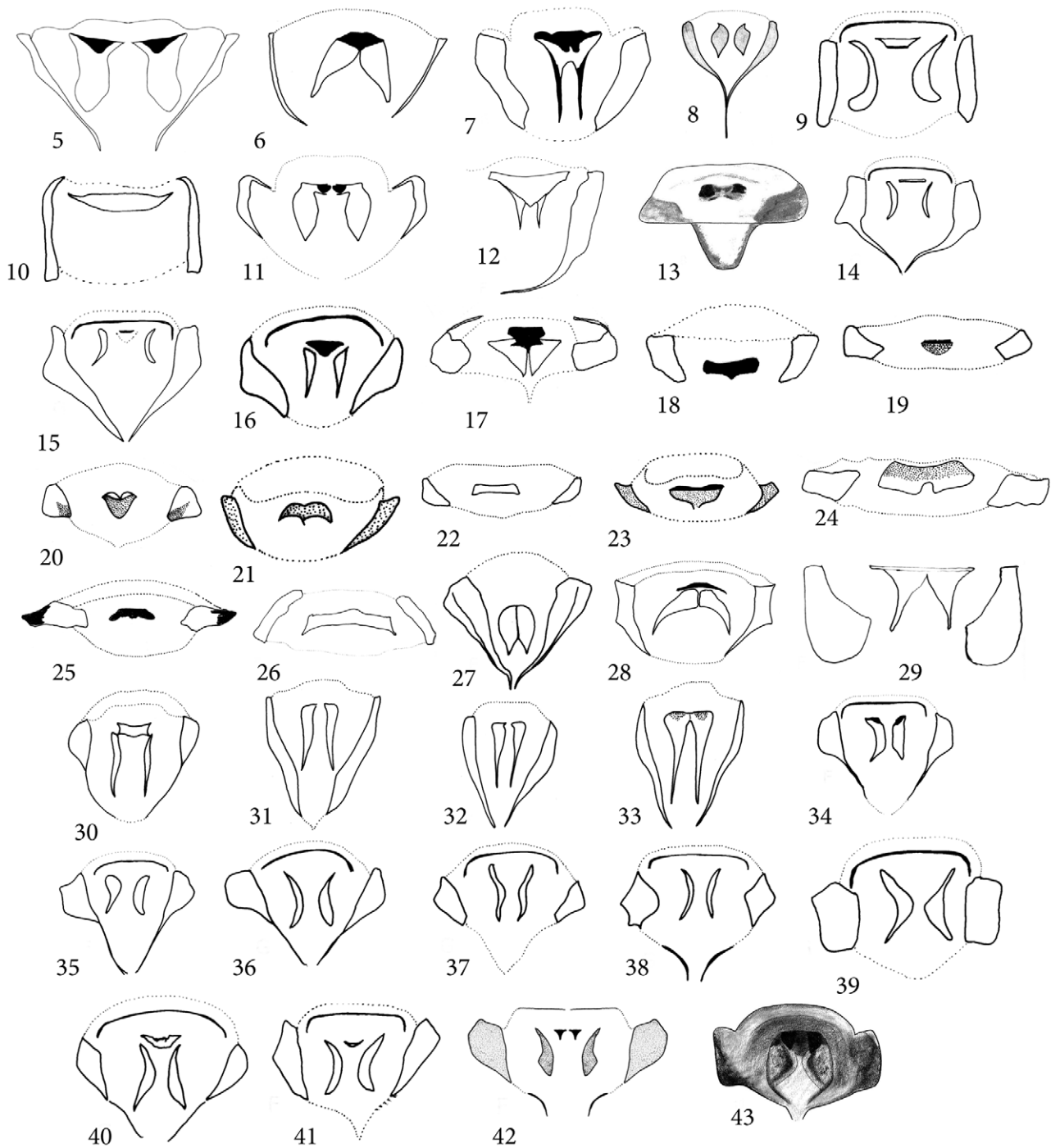


PLATE 2. Figures 5–43. Genital segment. 5. *Arachnodes splendidus* (Fairmaire, 1889). 6. *Onitis* sp. 1. 7. *Gyronotus fimetarius* Kolbe, 1894. 8. *Coptorhina excavata* Frollov, Akhmetova, & Scholtz, 2008. 9. *Canthon cyanellus* LeConte, 1859. 10. *Amphistomus inermis* Matthews, 1974. 11. *Canthon quinque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

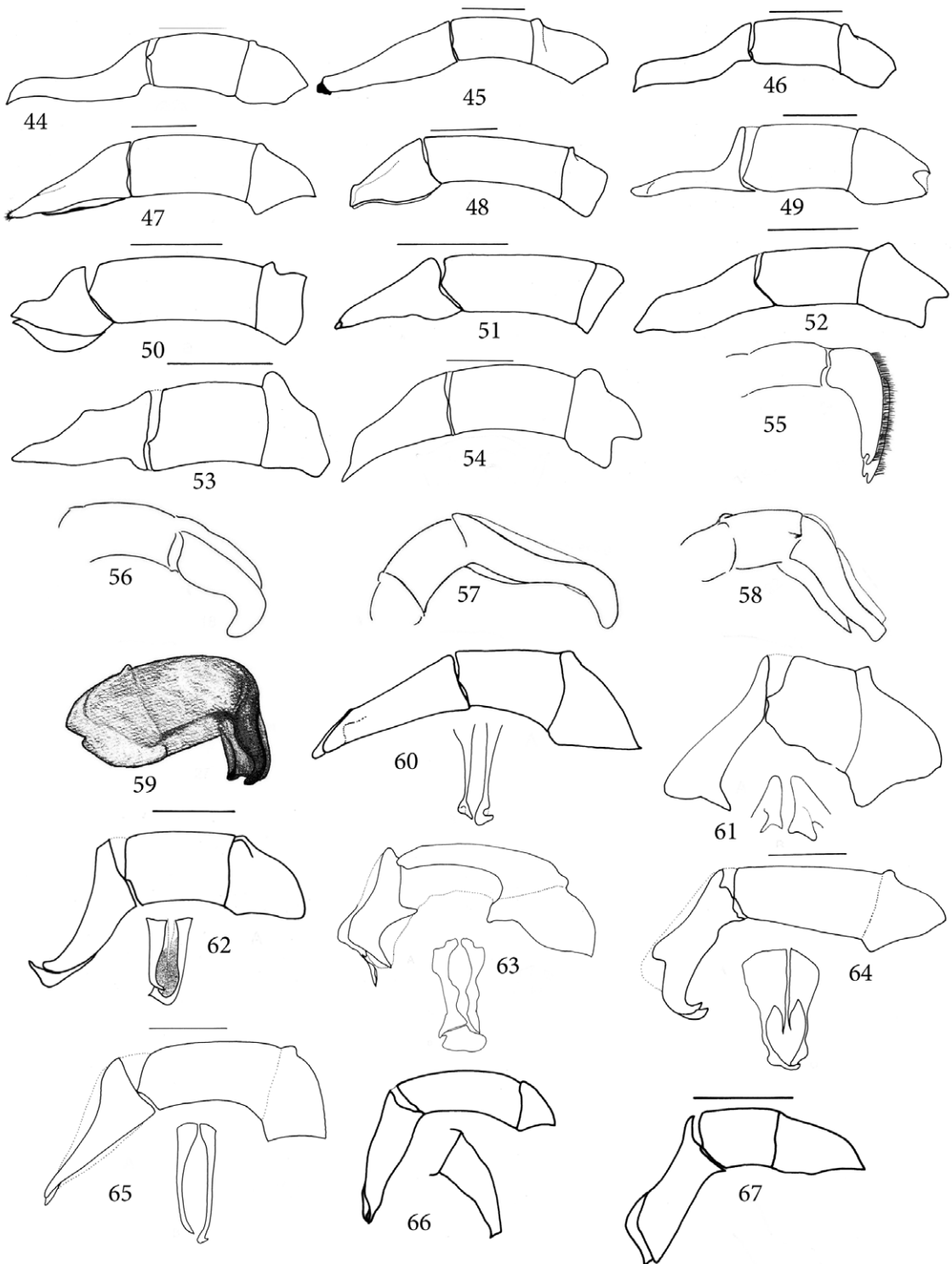


PLATE 3. Figures 44–67. Aedeagus. 44. *Copris dracunculus* Ferreira, 1959. 45. *Copris incertus* Say, 1835. 46. *Copris mesacanthus* Harold, 1878. 47. *Dichotomius bos* (Blanchard, 1846). 48. *Onterhus sanctaemartae* Génier, 1996. 49. *Oxysternon palaemon* Laporte, 1840. 50. *Garreta unicolor* Fahraeus,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

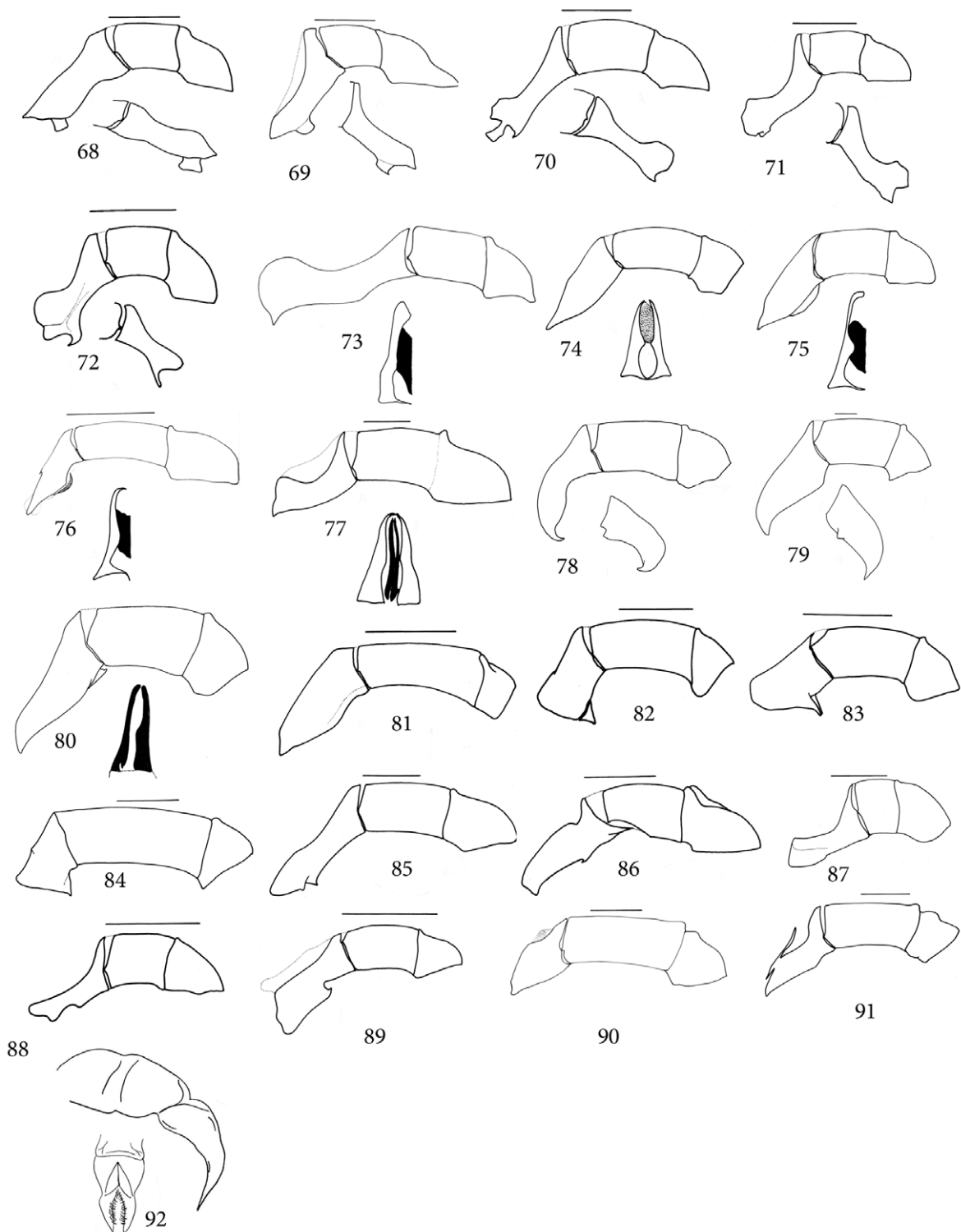


PLATE 4. Figures 68–92. Aedeagus. 68. *Canthon cyanellus* LeConte, 1859. 69. *Canthon quinquemaculatus* Laporte, 1840. 70. *Canthon aberrans* (Harold, 1868). 71. *Canthon angularis* Harold, 1868. 72. *Canthon* sp. 73. *Eudinopus dytiscoides* (Schreibers, 1802). 74. *Malagoniella astyanax columbica* Harold,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

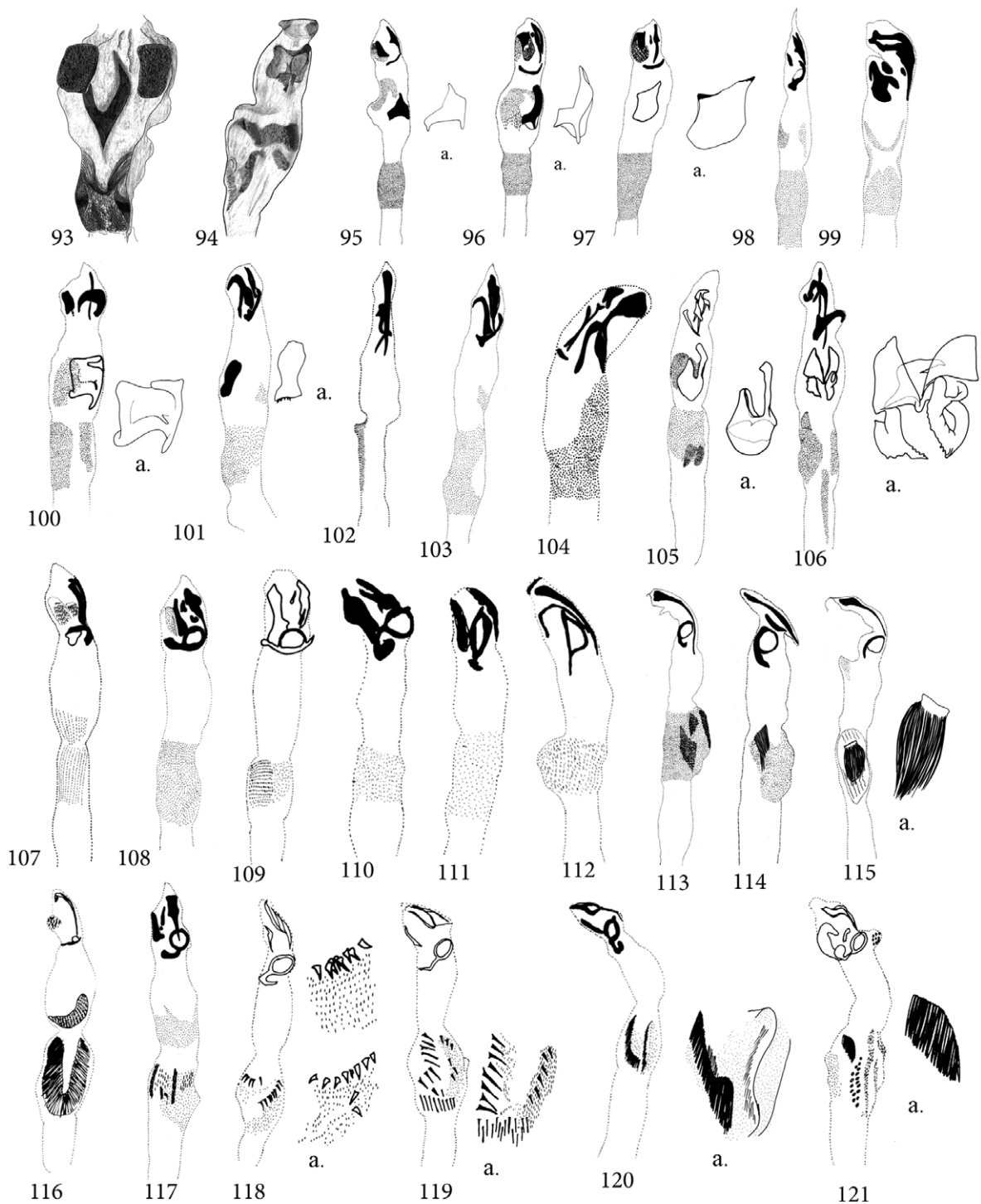


PLATE 5. Figures 93–121. Internal sac. 93. *Ataenius* sp. 94. *Byrrhidium convexum* Scholtz & Howden, 1987. 95. *Anomiopsoides heteroclyta* (Blanchard, 1845). 96. *Ennearabds lobocephalus* Harold, 1868. 97. *Eucranium* sp. 98. *Bdelyrus* sp. 99. *Coptorhina excavata* Frolov, Akhmetova, & Scholtz, 2008.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

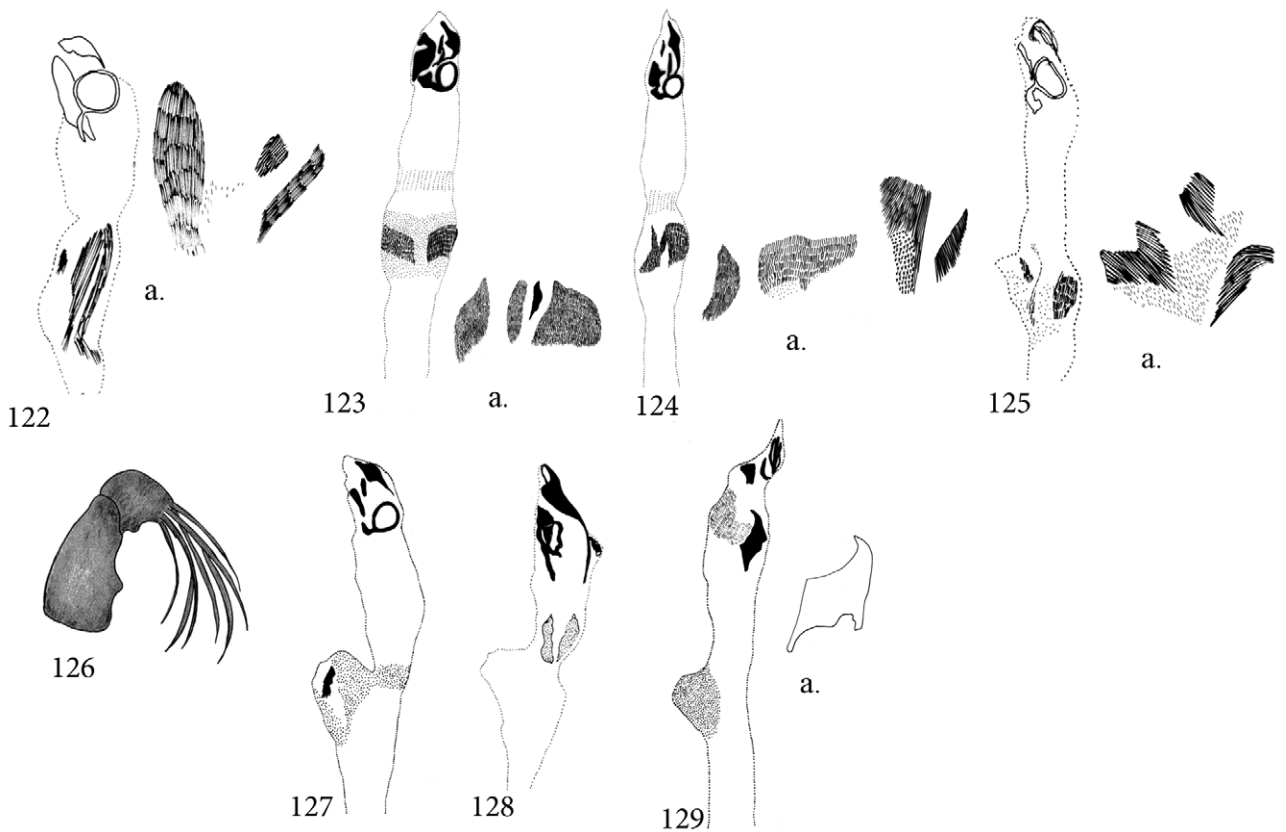


PLATE 6. Figures 122–129. Internal sac. 122. *Canthon cyanellus* LeConte, 1859. 122a. Raspule. 123. *Canthon quinquemaculatus* Laporte, 1840. 123a. Raspule. 124. *Canthon septemmaculatus* (Latreille, 1812). 124a. Raspule. 125. *Canthon triangularis* (Drury, 1773). 125a. Raspule. 126. *Scarabaeus canaliculatus*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

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

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

In other small genera, where more than one species of the genus were dissected, differences in the aedeagus were also observed. In the genus *Namakwanus* Scholtz & Howden, 1987 two extremely different aedeagus were observed (Figs. 55, 56). Species of the African genus *Gyronotus* van Lansberge, 1874 presented two different

recognizable types of aedeagus, as was also observed in the genus *Anachalcos*. Larger species of *Anachalcos* presented a truncate border different to those in smaller species. On the contrary, genera such as *Odontoloma* Boheman, 1857 and *Epirinus* have a constant pattern in the shape of the parameres of the aedeagus. For the genus *Epirinus*, where all the species were observed (Medina & Scholtz 2005), small variation among the species could be detected, but the general pattern in the shape of the aedeagus is constant. *Epirinus* is a monophyletic genus and taxonomically well defined, and that may be the reason for the small variation in the shape of the parameres (Figs. 57, 58).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

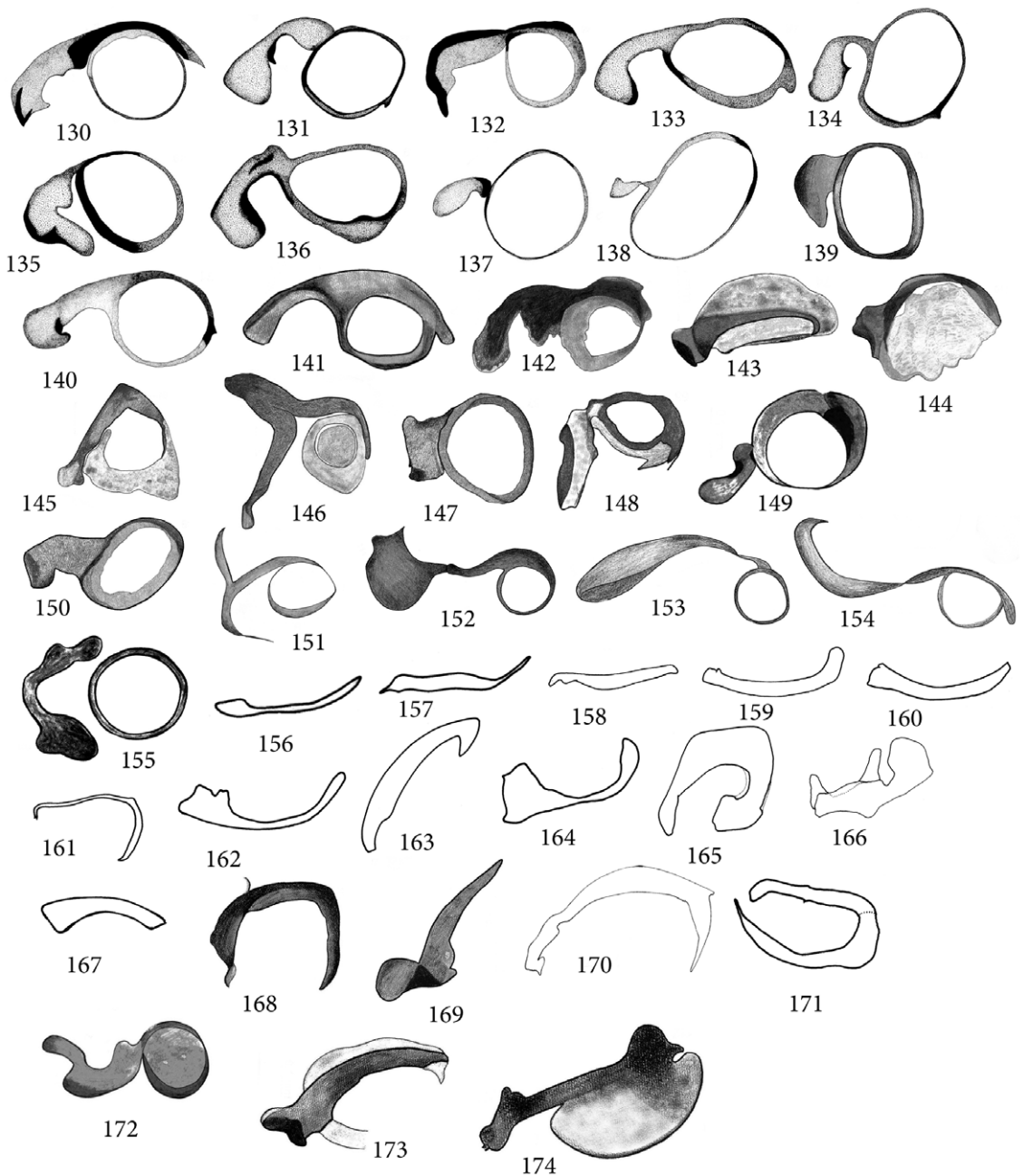


PLATE 7. Figures 130–174. Basal sclerite. 130. *Canthon tetraodon* Blanchard, 1846. 131. *Sylvicanthon bridarollii* (Martínez, 1949). 132. *Melanocanthon bispinatus* (Robinson, 1941). 133. *Canthon humectus* (Say, 1832). 134. *Canthon triangularis* (Drury, 1773). 135. *Canthon quinquemaculatus* Laporte,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

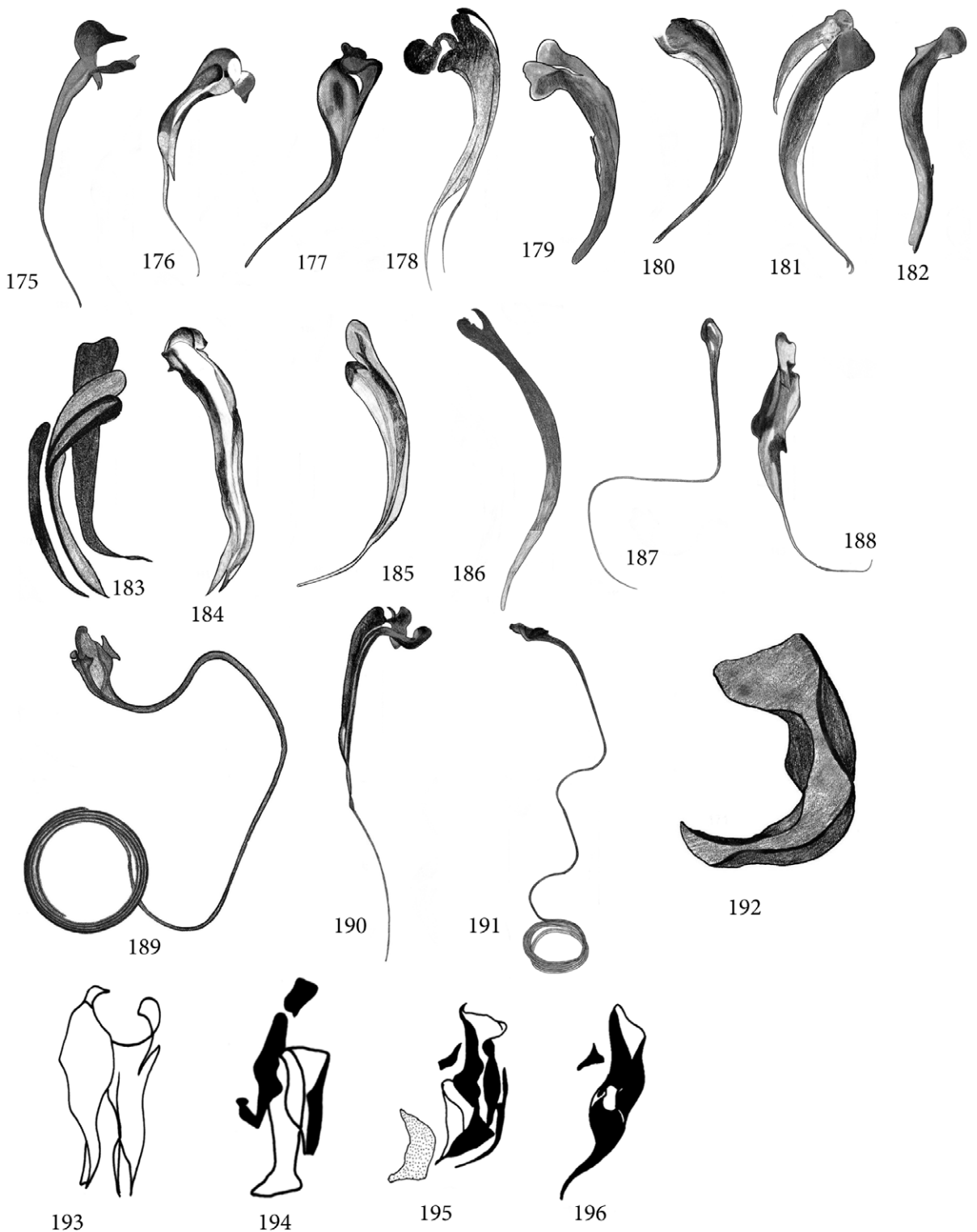


PLATE 8. Figures 175–196. Elongate sclerite. 175. *Gyronotus carinatus* Felsche, 1911. 176. *Demarziella interrupta* (Carter, 1936). 177. *Mentophilus hollandiae* Laporte, 1840. 178. *Epirinus mucrodentatus* Scholtz & Howden 1987. 179. *Aulacopris maximus* Matthews, 1974. 180. *Circellium bacchus* (Fabricius,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

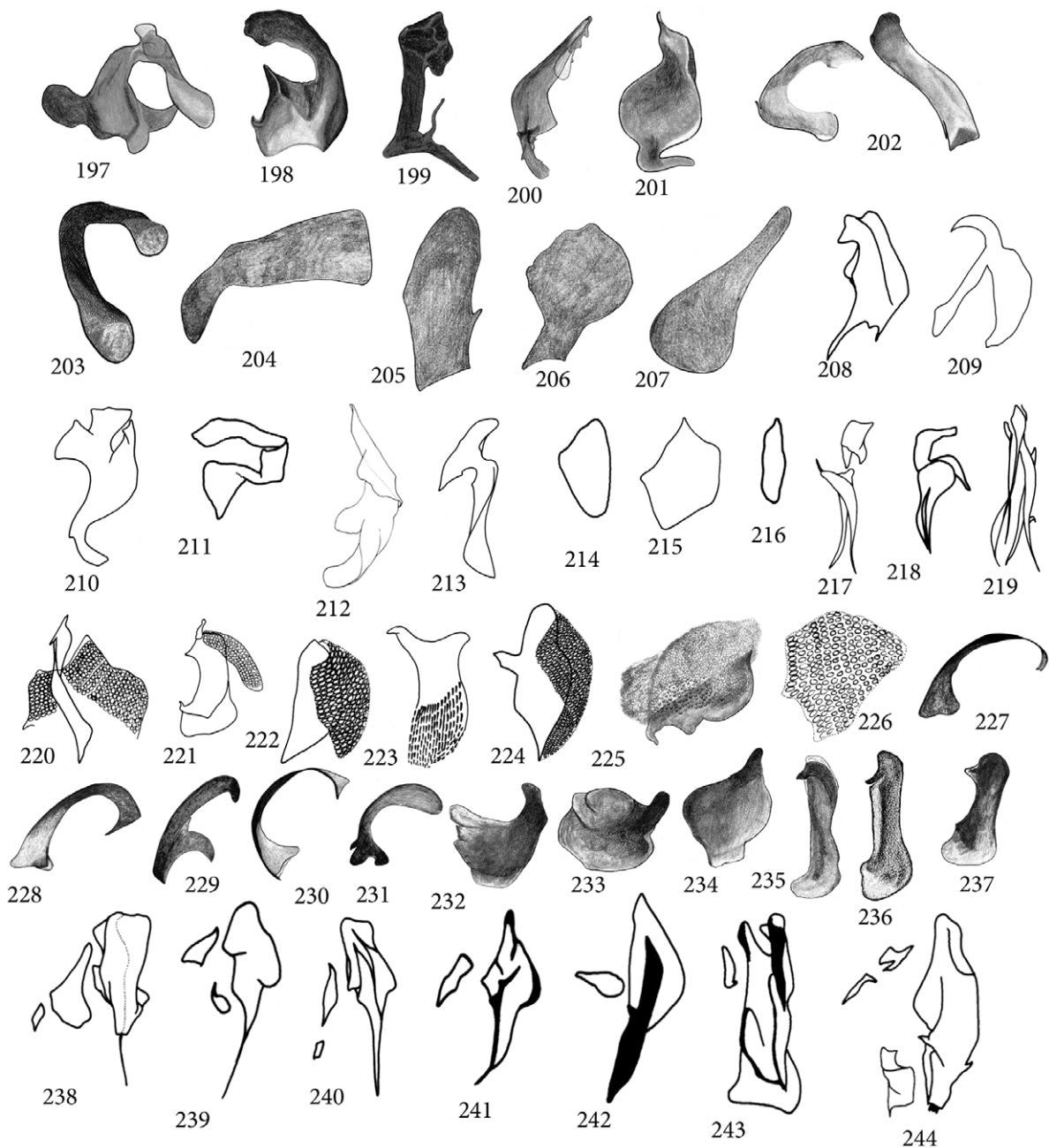


PLATE 9. Figures 197–244. Plate sclerite. 197. *Diorigopyx tibialis* (MacLeay, 1871). 198. *Gyronotus carinatus* Felsche, 1911. 199. *Arachnodes nitidus* (Laporte, 1840). 200. *Epilissus splendidus* (Fairmaire, 1889). 201. *Eudinopus dytiscoides* Schreibers, 1802. 202. *Pedaria* sp. 203. *Hansreia affinis*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

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

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

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

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

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

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

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

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

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

The variation in this sclerite is enormous, with differences in general shape, grade of sclerotization, and presence or absence of filaments (Figs. 175–191). In some genera, the sclerite may end in long filaments of different grade of thickness and length. As with the basal sclerite, the elongate sclerite can be constant or highly variable within determined groups. For species of *Canthon*, Medina *et al.* (2003) found a high variation and not a

constant pattern in the elongate sclerites. On the contrary, the same type of elongate sclerite was observed in all the species of the genus *Epirinus* (Fig. 192). Generally the sclerite has short filaments; nonetheless, in some cases the filaments can be well developed as in *Paracanthon*, *Nanos* (Fig. 189, 191), and *Cryptocanthon*. The filaments can also be absent as in *Malagoniella* (Fig. 193), *Saphobiamorpha*, and *Tesserodon*, and in different species of *Canthon* (Figs. 194–196).

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

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

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

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

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

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

Conclusions

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

Historically, some classical names have been used for the sclerotized structures in the internal sac; a summary of used names for each structure is presented in Table 2. A common name for the sclerotized structures is lamellae, and the structure located in the medial area of the sac has been called lamella copulatrice. The term sclerite is defined as a hardened body part, and for arthropods has been used to design sclerotized structures of segmental origin; it has also been used to name sclerotized pieces of the body. In recent literature regarding internal male

genitalia, the word sclerite has been widely used to name the sclerotized structures of the internal sac instead of lamellae. After a careful revision of the names used for male genitalia structures, we have synthesized the names as proposed in Table 2. We hope that this revision of names will help unify the nomenclature for future comparisons of genitalia structure in studies of functional anatomy, taxonomy, and systematics.

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

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