Diagnostic and phylogenetic character variation in the genus *Canthon* Hoffmannsegg and related genera (Coleoptera: Scarabaeidae: Scarabaeinae).

by

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Diagnostic and phylogenetic c [illegible] genus *Canthon* Hoffmannsegg and related genera (Coleoptera: Scarabaeidae: Scarabaeinae).

by

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ABSTRACT

Morphological variation was examined in 58 species of *Canthon* and 18 species of other genera of the subtribe Canthonina (*Anisocanthon*, *Canthonella*, *Cryptocanthon*, *Deltochilum*, *Hansreia*, *Holocanthon*, *Malagoniella*, *Melanocanthon*, *Scybalocanthon*, and *Sylvicanthon*). A total of 667 specimens was used for examination of morphological characters. Variation in head structures such as clypeus, eyes, labium, gula, and epipharynx is described. Thoracic structures examined include the pronotum, prosternum, and posterior and medial tibiae. Other structures examined were the elytra, pygidium, and male genitalia, including the sclerites and brushes of the internal sac of the aedeagus. Secondary sexual features (shape of anterior tibial spur and shape of last abdominal segment) were also examined. The characteristics examined include diagnostic characters for the genus *Canthon*.

This analysis revealed that *Canthon* is a very heterogeneous and artificial group, the limits of which are based on a combination of characters that is not exclusive to genus. Many characters that have been used in the diagnosis of *Canthon* are general characters that show wide variation within *Canthon* as well as in other genera of Canthonina. Only a few derived characters were exclusively shared by species of

Canthon. However, several genera of Canthonina shared with *Canthon* some characters, mainly in structures such as the epipharynx and the internal sac of the aedeagus, (epipharynx with two well-defined lateral combs, internal sac with a complete ring-shaped sclerite, reduction in the postero-dorsal aperture of the eye, and reduction in the setae of the anterior margin of the mentum). Due to the fact that the external morphology shows great variation, it is important to consider the study of the other possible sources of characters to resolve the phylogenetic relationships among groups.

KEYWORDS FOR THESIS RETRIEVAL: Coleoptera, Scarabaeidae, Scarabaeinae, Canthonina, *Anisocanthon*, *Canthon*, *Canthonella*, *Cryptocanthon*, *Deltochilum*, *Hansreia*, *Holocanthon*, *Malagoniella*, *Melanocanthon*, *Scybalocanthon, Sylvicanthon*, character variation, diagnostic characters, internal sac of aedeagus, morphology, phylogenetic characters, sclerites, systematics.

INTRODUCTION

Canthon is a group of coprophagous beetles (Scarabaeidae: Scarabaeinae) widely distributed in America, with about 100 species from tropical forests and savannas (Halffter & Martínez 1966). It is one of the largest and most complex genera of the subtribe Canthonina, which is in turn part of the tribe Scarabaeini (Halffter & Matthews 1966), characterised by having thin and long medial and posterior legs, and a head free of horns or tubercles (Halffter & Martínez 1966). The subtribe Canthonina is a group of coprophagous beetles, known for their particular behavior of making and rolling dung balls for feeding and nesting (Halffter & Edmonds 1982). *Canthon* is the genus with the greatest number of species in the subtribe and along with the genus *Deltochilum* represents 67% of the American species in the subtribe.

Coprophagous beetles have recently received much attention in studies of basic ecology, behavior, and conservation biology (e.g., Hanski & Cambefort 1991). In the latter field, dung beetles have been proposed as useful tools for biodiversity monitoring and for designating areas for conservation priority (Favila & Halffter 1997). Many species of Canthonina, including those of *Canthon,* are stenotopic: they are restricted to specific habitats such as inner forest, ecotones, and savannas (Díaz 1997). Additionally, many species of *Canthon* are associated with dung of particular mammals, such as that of different species of monkeys (Gill 1991, Medina 1997, Castellanos et al. 1999). These characteristics make the Canthonines an important group for biodiversity assessment and other studies in modern biology. However, despite much research devoted to studying different aspects of *Canthon* biology, and many isolated works with information on species of this genus, the basics of the systematics of this group have yet to be studied. Thus, it is unknown whether *Canthon* is a natural (i.e., monophyletic) group of species.

Although the genus has suffered successive divisions and regroupings, it is currently composed of a heterogeneous group of species with no clear limits and with a diagnosis based mainly on character combinations. For this reason it is necessary to study *Canthon* from a modern taxonomic and systematic perspective. This includes a study of morphological variation within the group, including internal morphology, so as to be able study of the phylogenetic relationships within the group.

This work presents a preliminary analysis of morphological variation in a group of

Canthon species compared with other genera of Canthonina. An analysis of characters traditionally used for delimiting genera and subgenera is included. Other characters not previously used, but potentially useful for improving the taxonomic definition of *Canthon*, are described. Species of all the *Canthon* subgenera defined by Halffter & Martínez (1977) were examined, as well as species in related genera such as *Anisocanthon*, *Canthonella*, *Cryptocanthon*, *Deltochilum*, *Hansreia*, *Holocanthon*, *Malagoniella*, *Melanocanthon*, *Scybalocanthon* and *Sylvicanthon*.

The variation in structures of the head, thorax, legs, and male genitalia was examined in detail. In the head, I studied the variation mainly in the anterior edge of the clypeus, the eyes, the labium, the gula, and the epipharynx. In the thorax, I examined the variation in the lateral edge of the pronotum, the prosternum, the mesosternum, and the legs (mainly the shape and position of the teeth of the anterior leg, and the spines on the dorsal side of the medial leg). I also examined the variation in the sculpture of the elytra, and the elytral grooves and tubercles. The pygidium, and the male genitalia, including the shape of the parameres the internal sac of the aedeagus, as well as the sclerites of the internal sac were also studied.

Historical aspects

The genus *Canthon* was created by Hoffmannsegg in 1817 based on *Ateuchus septemmaculatus* Latreille. Although there were some contributions after the description of the genus (e.g., LeConte 1859), the most important study of *Canthon* was Harold's (1868) monograph. In this work he listed 120 species of *Canthon*, described 47 new species, and presented a key for 97 species. Since that time the genus *Canthon* has been divided into various subgenera and grouping with some species removed to other genera. In 1887 Bates proposed the genus *Pseudocanthon*, which was considered by many authors as a synonym of *Canthon*, until Martínez (1947) revalidated it as a genus (see Halffter 1961).

Between 1948 and 1966, what Harold (1868) considered to be *Canthon*, was fragmented into several genera, mainly by Antonio Martínez and Francisco Pereira. Martínez (1948) created the genera *Scybalocanthon* and *Glaphyrocanthon,* and in 1950 placed several species of *Canthon* in the subgenus *Coprocanthon*. In 1952 the same author proposed the genus *Xenocanthon*. Subsequently, Pereira (1953) created the genus *Peltecanthon* on the basis of the presence of a visible scutellum. Pereira & Martínez (1956) proposed the genera *Geocanthon*, *Goniocanthon*, and *Nesocanthon* and validated the genus *Tetraechma*, which Harold (1868) had synonymized with *Canthon*. Halffter (1958) described the genera *Boreocanthon* and *Melanocanthon* for a group of North American species. The same year Pereira & Martínez (1958) proposed the genus *Canthomoechus* (later synonymized with *Canthon*), and the genera *Francmonrosia* and *Trichocanthon*, which are currently considered to be subgenera of *Canthon* (Halffter & Martínez 1968, 1977). Halffter (1961) reviewed the taxonomic history of *Canthon* and did a morphological study of some *Canthon* species, but this work included only North American species, and neither showed the variation in the morphological structures studied.

In his work on the scarabs of the Antilles, Matthews (1966), broadened the diagnosis of *Canthon* by including as a diagnostic character the presence of a marginal carina on the posterior edge of the head and discarded the margination of the posterior femur, thus allowing the inclusion of species previously excluded from *Canthon*. This author did not recognise as valid the genus *Nesocanthon*, created by Pereira & Martínez (1956), and considered the Antillean species under the genus *Canthon*.

In 1966, Halffter and Martínez began what they called a “monographic revision of the American Canthonines”. In this work, which was subsequently published in four parts, the authors proposed to standardise the criteria for delimitation of the genera and subgenera of the subtribe Canthonina and provide a definitive delimitation of the genus *Canthon*. The second part of the monograph the authors dealt with several canthonine genera other than *Canthon* (*Eudinopus*, *Megathopa*, *Malagoniella*, *Megathopomima*, *Streblopus*, *Canthonella*, *Agamopus*, *Sinapisoma*, *Canthotrypes* and *Scybalophagus*). In the second part (1967), the authors dealt in detail with the genus *Peltecanthon*, which in 1977 was considered as a subgenus of *Canthon* by the same authors. In the third part of the monograph (Halffter & Martínez 1968), in addition to the study of other genera, the authors began the study of the genus *Canthon* and presented a key for the three subgenera of *Canthon* so far defined: *Pseudepilissus*, *Francmonrosia* and *Canthon*. In this work the authors lowered the status of the genus *Pseudepilissus*, created by Martínez (1954), and the genus *Francmonrosia*, created by Pereira & Martínez (1958), to subgenera of *Canthon*. At the end of this third contribution they also provided the diagnosis of the subgenus *Pseudepilissus* and presented a key and descriptions of species in this subgenus.

In the fourth and final part of the monograph on Canthonina, Halffter & Martínez (1977) presented a new definition of the genus *Canthon* and changed the status of the genera *Boreocanthon*, *Glaphyrocanthon*, *Goniocanthon*, *Nesocanthon* and *Trichocanthon* from genus to subgenus, including them in *Canthon* once again. Halffter & Martínez (1977) also created the genus *Sylvicanthon*, the monospecific genus *Hansreia*, and listed the synonyms of some genera. In this paper, the authors presented a key for all the genera of American Canthonina and subgenera of *Canthon*, as well as diagnoses and lists of species for some genera, including *Canthon* and its nine subgenera.

In this monograph (Halffter & Martínez 1977), the species of *Canthon* were distributed in the following subgenera: *Boreocanthon*, *Canthon*, *Glaphyrocanthon,* Gonicanthon, *Francmonrosia*, *Nesocanthon*, *Peltecanthon*, *Trichocanthon*, and *Pseudepilissus*. Seven species could be placed in any subgenus, and 20 species were grouped in the lines *septemmaculatus* (group *septemmaculatus* and group *maldonadoi*), *quinquemaculatus*, and *quadratus* for a total of 174 species. Since the publication of the last part of the monograph, the genus *Canthon* has not been studied from a taxonomic perspective, and its taxonomy is currently based on this publication.

METHODOLOGY

Specimen preparation

Dry specimens were softened by immersion in hot water for 30 – 60 min, depending on specimen size. Each specimen was washed with water and soap, and when necessary a small brush was used to clean the beetle's body. The mouthparts and external genitalia of the males were removed under the stereoscope, using fine dissection forceps. The aedeagus is found by gently opening the pygidium and pulling the most external membranes. Once the aedeagus was cleaned, its internal sac was drawn out by gently pulling one end of the sac from the inside of the sclerotized capsule. The mouthparts were removed from the head, using a dissecting needle.

Both the internal sac of the aedeagus and the mouth parts were immersed in KOH dissolved in water in a sorting tray for 30 – 60 min or more depending on the size of the structure. The KOH was used for cleaning and clearing the structures. These were then rinsed with water and immersed in 70% ethyl alcohol for 5 min.

The structures were mounted in Canada balsam on a microscope slide or a small piece of vinyl. Structures were briefly immersed in xylol (a solvent of Canada balsam) and placed on slides with Canada balsam. Preparations were allowed to dry in a dust free environment inside or else were covered to prevent the deposition of dust. The dissected specimen was again remounted on a pin with the head while the mouthparts and the aedeagus were mounted on cardboard. Once dry, preparations on vinyl were mounted under each specimen, and collection and identification labels were added. Preparations on microscope slides were labelled with the corresponding species name and a number corresponding to the dry specimen on a pin.

Character examination

An initial list of characters used in the delimitation of different groups of *Canthon* and Canthonina was made based on the literature (Halffter 1958, 1961, Halffter & Martínez 1966, 1967, 1968, 1977, Martínez 1948, 1949, 1950,1952, Martínez & Pereira 1956, 1959,1967, Martinez & Halffter 1972, Matthews 1966, Pereira 1953, Pereira & Martínez 1963). However, as structures were being examined, new characters were found, added to the list, and their variation described.

A stereoscope with 60-x magnification was used for the examination of structures. To compare sizes and proportions of the structures studied, a piece of clear acetate printed with a grid of 0.05 mm was placed over the structure when it was necessary.

Specimens from the insect collections of the Instituto Alexander Von Humboldt (Villa de Leyva, Colombia), Canadian Museum of Nature (Aylmer, Canada), Canadian National Collection of Insects of Agriculture Canada (Ottawa, Canada) and from the personal collections of Alejandro Lopera (Santafé de Bogota, Colombia), Bruce Gill, and François Génier (Ottawa, Canada) were examined.

A total of 667 specimens of 84 species was examined. Of these, 58 were species of *Canthon* (Table 1), and 26 species belonged to other genera, which included 11 genera of Canthonina (Table 2), and five genera of other tribes of Scarabaeinae: Phanaeini (*Oxysternon conspicillatum* and *Phanaeus pyrois*), Dichotomini (*Dichotomius satanas*), Eurysternini (*Eurysternus caribaeus*) and Onthophagini (*Onthophagus curvicornis*). These last five genera were used mainly to compare the epipharynx and the sclerites of the internal sac of the aedeagus.

Dissections of approximately 70 species were prepared and the external morphology of the remaining species was examined in the museums and collections visited. In general, one or two specimens of each sex of each species were dissected. Depending on the availability of material, I dissected more than one specimen in some species. To examine intraspecific variation, mainly in structures not previously studied such as the epipharynx and the internal sac of the aedeagus, I dissected series of specimens of *C. angustatus*, *C. cyanellus*, *C. luteicollis* and *C. politus*.

Table 1. List of species of *Canthon* examined. The assignment of species to subgenera and phyletic lines was taken from Halffter & Martinez (1977) and Rivera-Cervantes & Halffter (1999).

Subgenus or line	Species	Sex
Boreocanthon	*C. ebenus* (Say)	M F
	C. lecontei Harold	
	C. nyctelius Harold	
	C. praticola LeConte	M F
	C. simplex LeConte	M F
Canthon *aberrans* Line	*C. aberrans* (Harold)	M F
Chiriguano Line	*C. chiriguano* Martínez &Halffter	M F
Humectus Line	*C. humectus humectus* (Say)	M F
Pilularius Line	*C. chalcites* (Haldemann)	M F
	C. imitator Brown	M F
	C. pilularius (Linnaeus)	M F
Indigaceus Line	*C. indigaceus* indigaceus Harold	M F
Deyrollei Line	*C. deyrollei* Harold	M F
Lituratus Line	*C. lituratus* (Germar)	M F
Cinctellus Group	*C. mutabilis* Harold	M F
	C. podagricus Harold	
	C. curvodilatatus Schmidt	
Cyanellus Group	*C. cyanellus cyanellus* Leconte	M F
	C. cyanellus sallaei Harold	M F
Aequinoctialis Line	*C. aequinoctialis* Harold	M F
Juvencus Line	*C. morsei* Howden	M F
	C. juvencus Harold	M F
Francmonrosia	*C. tetraodon* Blanchard	M F
	C. dives Harold	
Glaphyrocanthon	*C. acutoides* Schmidt	
	C. acutus Harold	M F
	C. angustatus Harold	M F
	C. brunneus Schmidt	
	C. columbianus Schmidt	M F
	C. femoralis femoralis (Chevrolat)	M F
	C. femoralis bimaculatus Schmidt	M F
	C. lamprimus Bates	F
	C. luteicollis Erichson	M F
	C. pallidus Schmidt	M F
	C. politus Harold	M F
	C. quadriguttatus (Olivier)	M F

Table 1 continue

Subgenus or line	Species	Sex
	C. semiopacus Harold	M F
	C. subhyalinus Harold	M F
viridis Group	*C. viridis* (P. de Beauvois)	M F
	C. championi Bates	M F
	C. meridionalis (Martínez, Halffter & Halffter)	M F
Goniocanthon	*C. fulgidus* Redtenbacher	M F
Nesocanthon	*C. callosus* Harold	
	C. violaceus (Olivier)	M F
Peltecanthon	*C. staigi* (Pereira)	M F
Pseudepilissus	*C. lunatus tibialis* Schmidt	M F
Trichocanthon	*C. sordidus* Harold	M F
Septemmaculatus Line	*C. monilifer* Blanchard	M
	C. septemmaculatus septemmaculatus (Latreille)	M F
	C. septemmaculatus histrio (Serville)	M F
Maldonadoi Line	*C. maldonadoi* Martínez	M F
	C. cf. sericatus Schmidt	
Quinquemaculatus Line	*C. quinquemaculatus* Laporte	M F
Canthon incertae sedis	*C. bicolor* Laporte	M
	C. balteatus Redtenbacher	
	C. perseverans Matthews	M F
	C. triangularis (Drury)	M F
	C. hartmanni Howden & Gill	

Table 2. Species list of genera of Canthonina other than *Canthon* examined.

Genus	Species	Sex
Anisocanthon	*A. villosus* (Harold)	M F
Deltochilum	*D. aequinoctiale* (Buquet)	M*
	D. gibbosum (Fabricius)	M F
	D. mexicanum (Burmeister)	M
	D. hypponum (Buquet)	M
	D. parile Bates	M*
	D. orbignyi (Blanchard)	M*
Holocanthon	*H. mateui* Martínez & Pereira	M
Malagoniella	*M. astyanax columbica* (Harold)	M F
Melanocanthon	*M. bispinatus* (Robinson)	M F
Scybalocanthon	*S. trimaculatus* (Schmidt)	
	S. maculatus (Schmidt)	
	S. moniliatus (Bates)	M F
	S. pygidialis (Harold)	M F
	S. sexpilotus (Guérin)	
Sylvicanthon	*S. bridarollii* (Martínez)	M F
Cryptocanthon	*C. parvus* Howden	M
	Cryptocanthon sp.	M F
Canthonella	*C. gomezi* (Halffter & Martínez)	M F
Hansreia	*H. affinis* (Fabricius)	M F
Megathopa	*M. punctatostriata* (Blanchard)	M*

* Species in which only the male genitalia was studied.

Although I included species from all subgenera of *Canthon*, a limitation of this work is that the morphological study does not include all the species in the genus; the morphology of only 34% of the described species of *Canthon* was studied. The descriptions in this study only refer to those species listed in Tables 1 and 2. Occasionally, references are made to other species that were studied in the collections visited or cited from descriptions in the literature.

RESULTS

In general, the dorsal appearance of *Canthon* is smooth, and most species have flat head and reduced èyes. The lack of horns, tubercles or other structures on the dorsal surface of *Canthon* results in a simple external morphology (Figure 1). However, much variation was observed in structures such as the epipharynx, aedeagus (including the internal sac), proepisternum, proepimeron, and spines of the medial leg. These structures have not been comparatively studied in previous works.

General description

Canthon is composed of a group of beetles of variable colour and size including very small species (3 mm), medium sized, and large species up to 22 mm in length. Many species are dark-coloured (opaque or glossy) whereas some species are green, bronze, or black with a bronze glare. Other species show bright colours on their surface, generally combined with a dark colour. Many species of *Canthon* have a light-coloured pronotum, generally yellow or brown with dark dots or spots (Figure 2), and can alternate this same light colour on the femur or tibiae and pygidium

The thorax is very convex and smooth and the elytra are generally smooth, although some species have tubercles in the humeral area and small tubercles at the base of the elytral grooves. The pygidium is generally large and is not covered by the elytra. Species of *Canthon* show sexual dimorphism in the shape of the anterior tibial spur, and the shape of the last abdominal sternite.

In contrast with other dung beetles, Canthonines do not show sexual dimorphism in the form of horns and tubercles on the male's head and thorax. As in other rolling

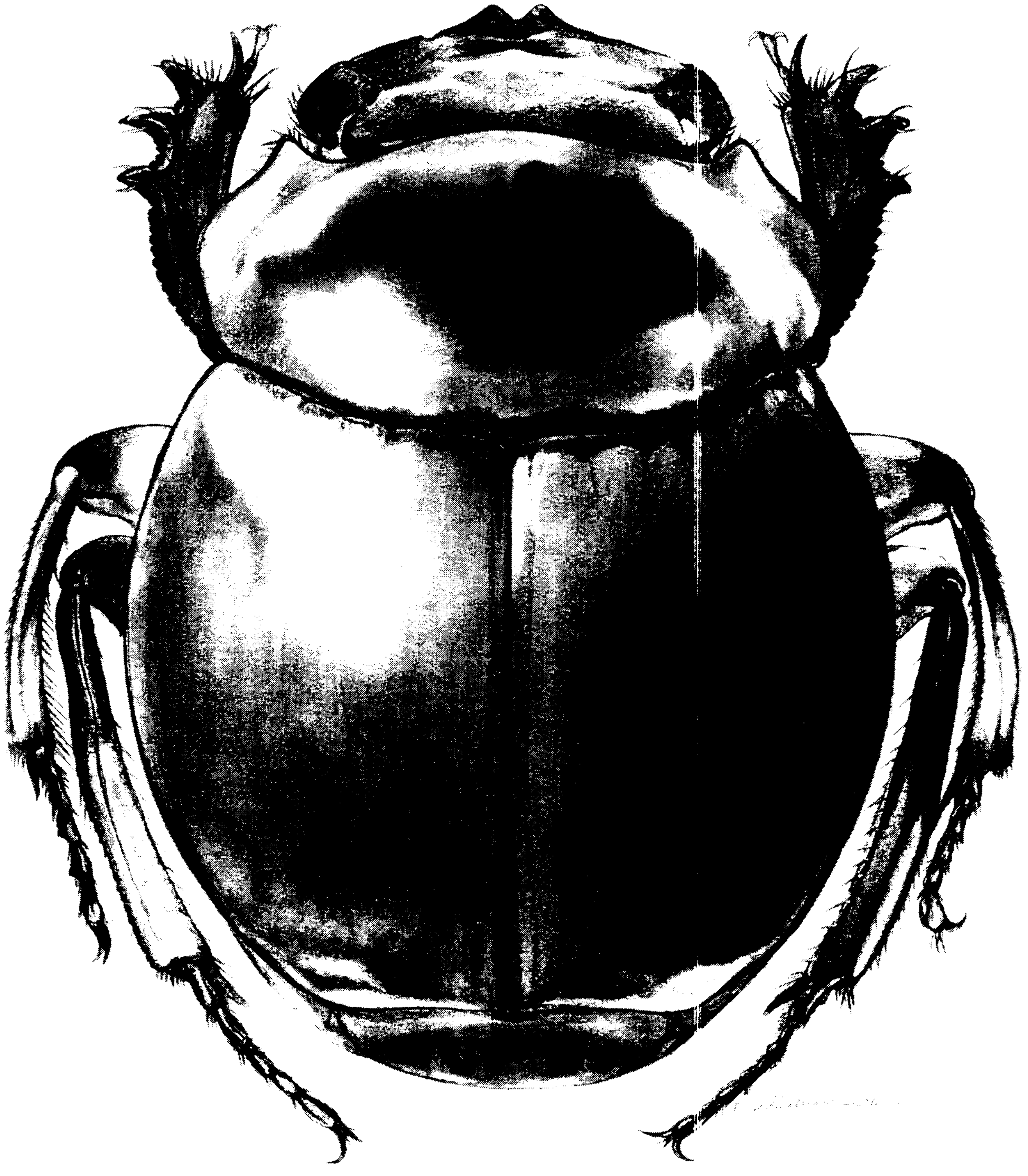


Figure 1. Habitus: *Canthon luteicollis* Erichson.

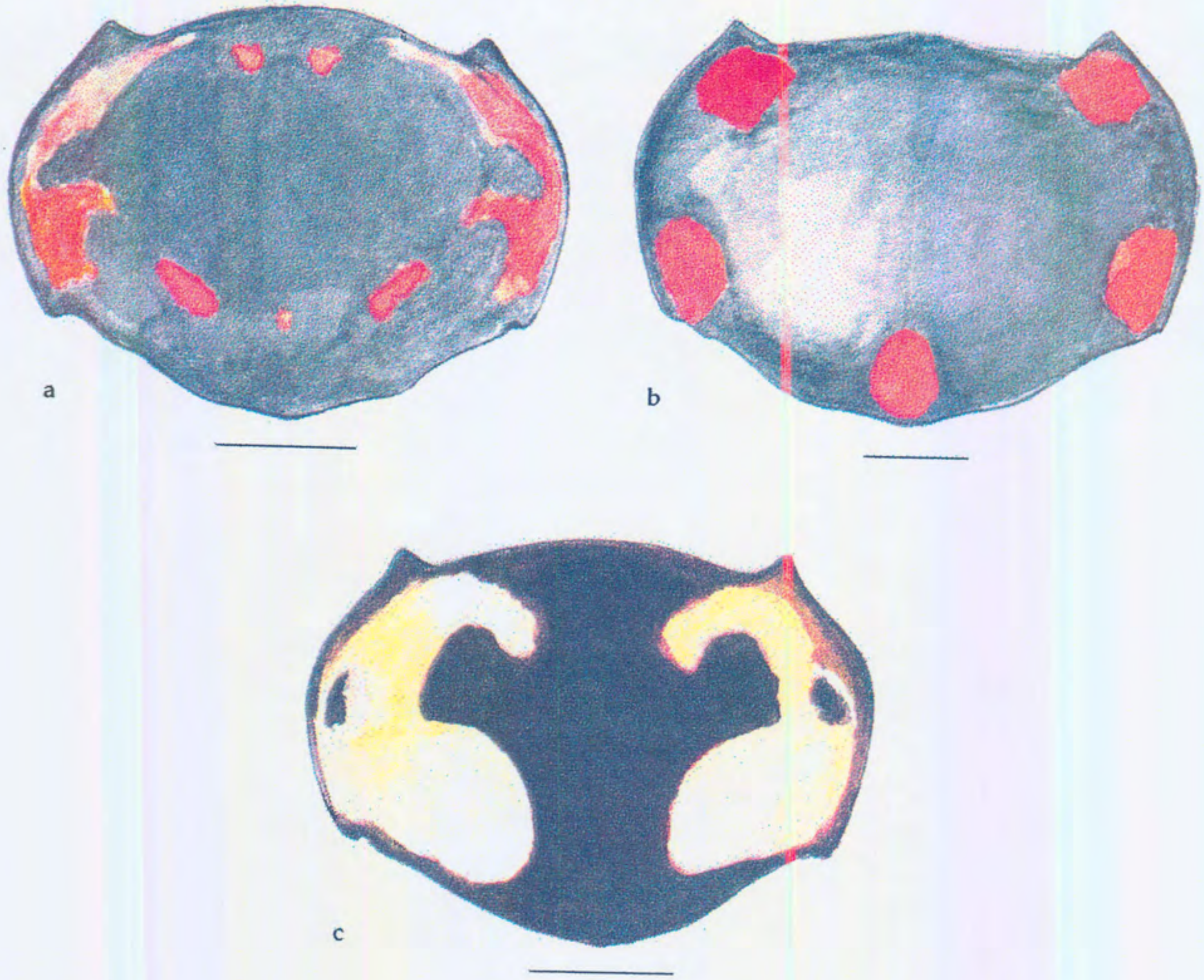


Figure 2. Pronotum. **a**. *C. septemmaculatus septemmaculatus* Latreille **b**. *C. septemmaculatus* histrio Serville. **c**. *C. cyanellus sallaei* Harold. Scale bar = 2 mm.

beetles, species of *Canthon* have long and thin medial and posterior legs, a characteristic that differentiates them from the burrowing beetles, which have clearly shorter and thicker tibiae.

Head

The head of *Canthon* is typically prognathous, with the main axis oriented on a horizontal plane. The mouthparts are positioned ventrally and directed anteriorly. The head capsule is fully sclerotized and darkly coloured in most species. Its dorsal surface is generally flat and smooth, without tubercles, horns, or raised carinae. The head is bordered anteriorly by the clypeus, which is often medially emarginated, forming clypeal teeth. The exposed dorsal surface of the eye is normally much reduced in size compared to the ventral portion, and is bordered laterally by an ocular canthus (Figure 3a). The gula, mentum, and labium are exposed in ventral view (Figure 3b), and cover the maxillae, mandibles and epipharynx. A pair of nine-segmented antennae is inserted ventrally in the head capsule near the lower portion of the eye. The antennal club is composed of the last three antennomeres (Figure 3b).

Clypeus

In species of *Canthon* the clypeus is generally divided, with two or four well marked teeth. However, species of the subgenus *Canthon* in the *pilularius* line (*C. chalcites*, *C. imitator*, and *C. pilularius*), have an entire or slightly sinuated clypeus (Figure 4a). *C. lunatus tibialis* presents the clypeus more sinuated than species in the *pilularius* group, but without marked teeth (Figure 4b). Among species with well developed teeth on the clypeus, there is great variation, and although this variation is not exclusive of the genus *Canthon* or the tribe Canthonina, within *Canthon* the number and form of the teeth could be important for delimiting subgenera or groups within the genus.

Many species of *Canthon* have two well-marked teeth on the clypeus. Depending of their shape and size, these teeth may form a depression in the middle of the clypeus that can end sharply forming a V, or can be broadly rounded in the form of a U. The most common pattern is the presence of two triangular, blunt teeth as

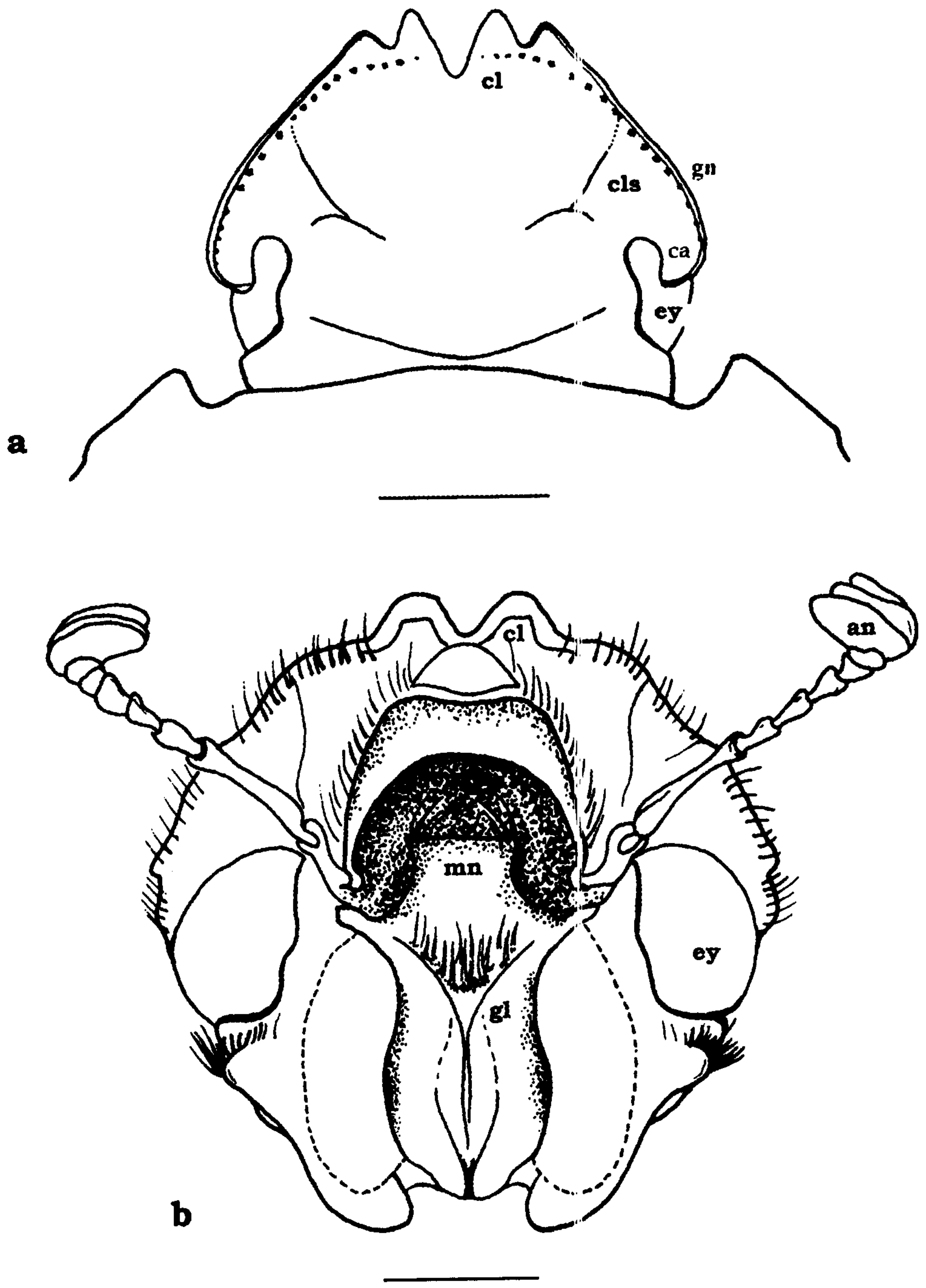


Figure 3. **a**. Dorsal view of the head of *Canthon angustatus* Harold. **b**. Ventral view of the head of *C. fulgidus* Redtenbacher. **ca** = canthus, **cl** = clypeus, **cls** = clypeal suture, **ey** = eye, **an** = antennae, **mn** = mentun, **gl** = gula, **gn** = gena. Scale bar = 1 mm.

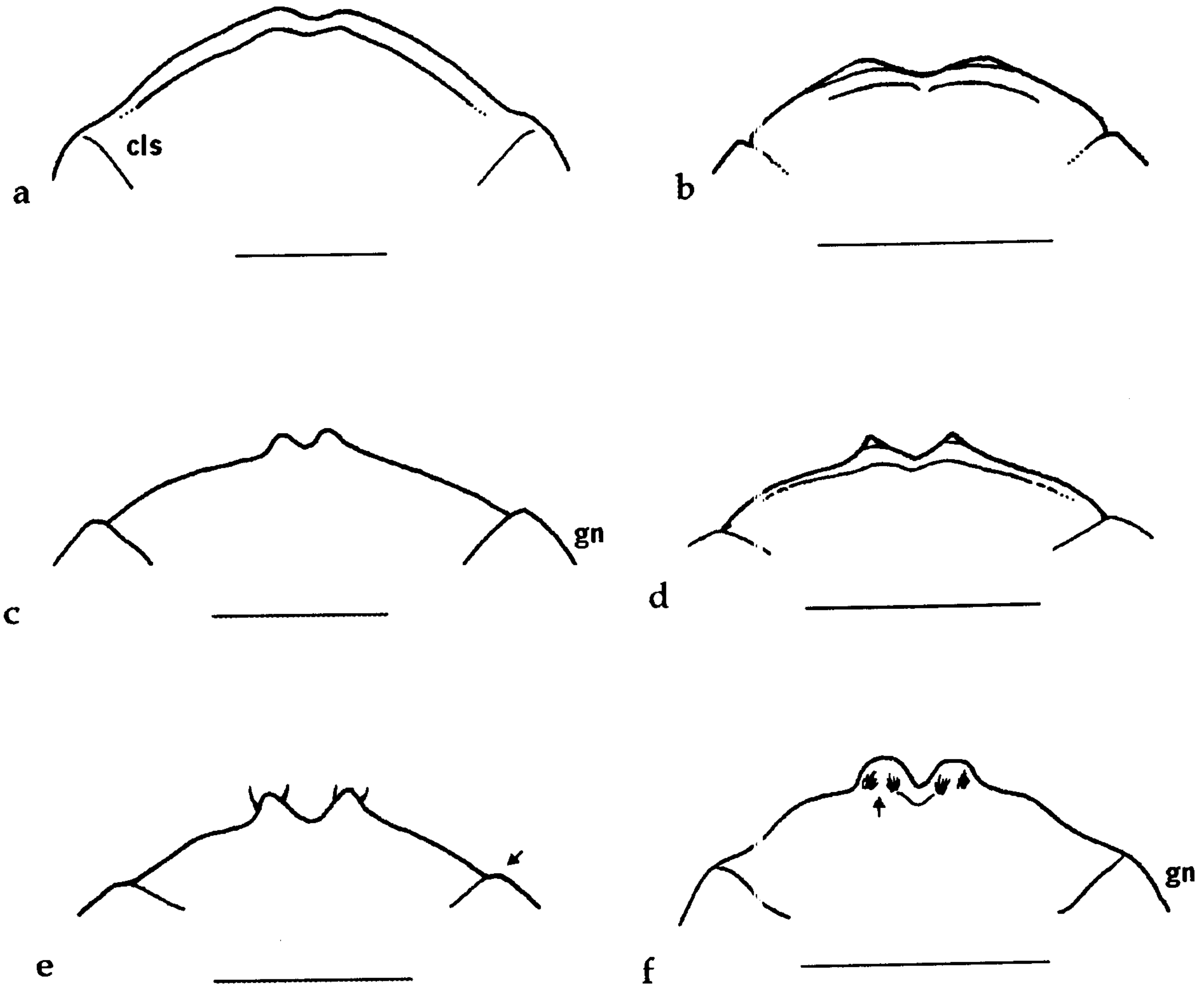


Figure 4. Anterior clypeal margins, dorsal view. **a**. *Canthon chalcites* Haldemann. **b**. *C. lunatus tibialis* Schmidt. **c**. *C. aequinoctialis* Harold. **d**. *C. monilifer* Blanchard. **e**. *C. bicolor* Laporte. **f**. *C. fulgidus* Redtenbacher. **cls** = clypeal suture, **gn** = gena. Figures a. c, d and e scale bar = 2 mm. figures b and f scale bar = 1 mm.

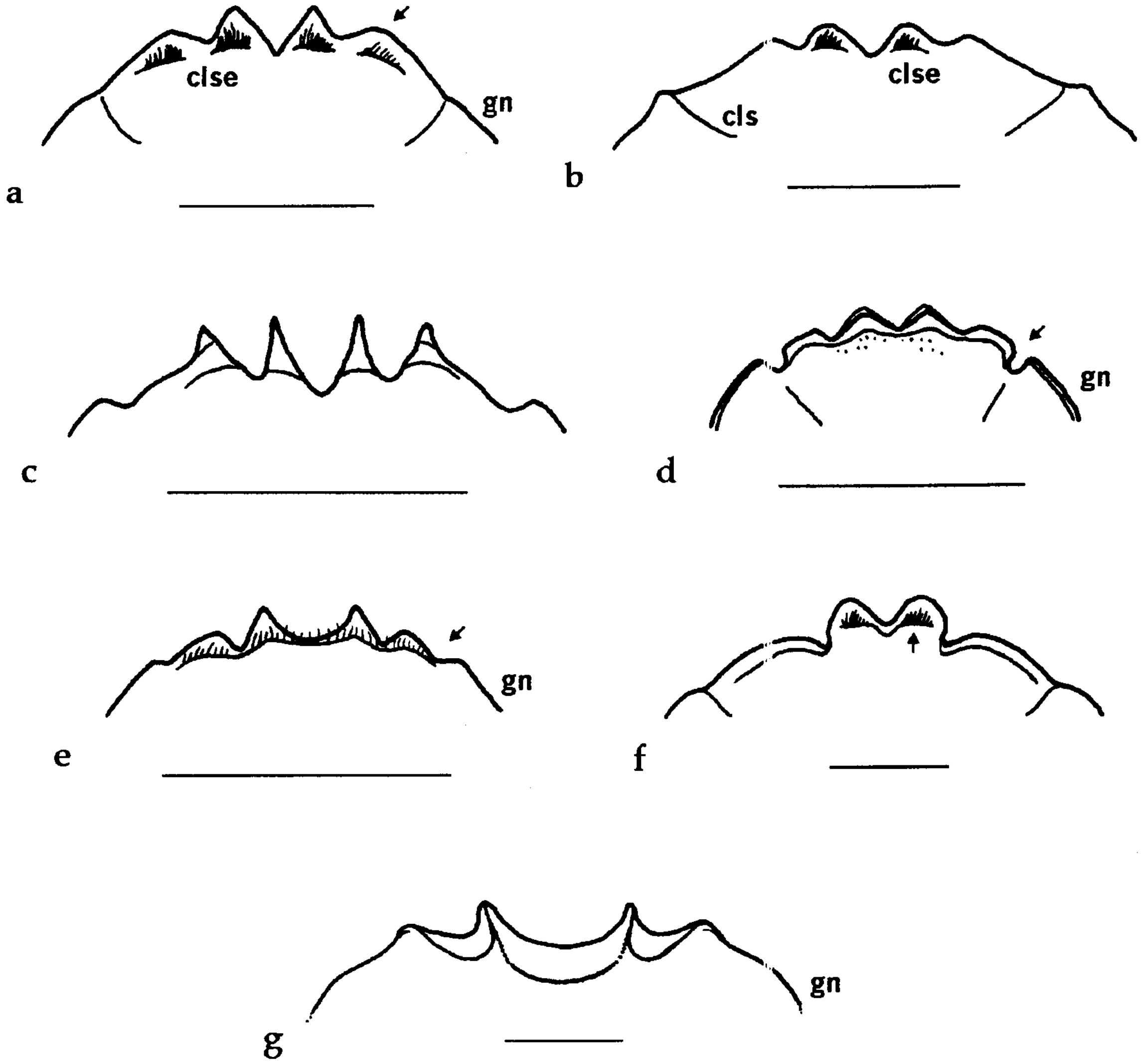


Figure 5. Anterior clypeal margins, dorsal view. **a**. *Canthon femoralis* Chevrolat. **b**. *C. luteicollis* Erichson. **c**. *C. quinquemaculatus* Laporte. **d**. *C. ebenus* Say. **e**. *Melanocanthon bispinatus* Robinson. **f**. *Malagoniella astyanax* Blanchard. **g**. *Deltochilum gibbosum* Fabricius. **cls** = clypeal suture, **clse** = clypeal setae, **gn** = gena. Figure a scale bar = 1 mm, figures b-g scale bar = 2 mm.

in *C. aequinoctialis*, *C. bicolor*, *C. luteicollis*, *C. indigaceus* and *C. perseverans* (Figures 4c and 4e). These teeth are sharp and form a wide V in *C. monilifer* (Figure 4d), and are blunt in *C. tetraodon*, *C. fulgidus*, C. *deyrollei*, and C. *subhyalinus* (Figure 4f). In some species of the subgenus *Glaphyrocanthon* (*C. angustatus*, *C. femoralis femoralis*, and *C. femoralis bimaculatus*), the teeth of the clypeus form a deep V and laterally there is a wide notch, which makes the clypeus appear as if it had another pair of teeth (Figure 5a). In other species of the same subgenus such as *C. lamprimus*, *C. luteicollis*, and in the viridis group (C. *viridis viridis*, and *C. meridionalis*), the clypeus is of the same type described above but the teeth do not form a deep V (Figure 5b). Species of other subgenera like *C. tetraodon* and *C. deyrollei* show a similar notch, but the teeth are blunt rather than sharp.

In the species that have four teeth, different patterns were observed. Some species have very long and sharp central teeth such as *C. cyanellus* and *C. quinquemaculatus* (Figure 5c). *C. acutus* also has four teeth, but the two central teeth form an arched depression and not a deep V. The gena, can be whole or divided by the clypeogenal suture. In species of the subgenus *Boreocanthon* and the genus *Melanocanthon*, the clypeogenal suture divides the gena, which makes them appear as if they had another pair of teeth on the sides of the clypeus (Figures 5d and 5e). The gena can have a notch at the level of the clypeogenal suture. This notch can be wide like in *C. quinquemaculatus*, *C. cyanellus*, *C. deyrollei*, *C. indigaceus* and *C. bicolor*, or narrow as in *C. luteicollis*, *C. septemmaculatus*, *C staigi*, *C. sordidus*, and *C. triangularis* (Figures 4e and 5b). A complete gena (without a notch) is present in *C. fulgidus* and in some species of the subgenus *Glaphyrocanthon* (*C. femoralis*, *C. angustatus*) and in species of the *pilularius*, *indigaceus* and *humectus* lines (Figures 4a, 4f and 5a). The gena is also complete in species of the genera *Scybalocanthon, Silvicanthon*, *Canthonella*, *Cryptocanthon* and *Deltochilum* (Figure 5g). The portion between the clypeogenal suture and the anterior margin of the clypeus can be rounded, as in most species of *Canthon*, or straight as in *C. luteicollis*, *C. angustatus*, *C. cyanellus*, *C. tetraodon*, *C. deyrollei*, *C. maldonadoi*, *C. indigaceus* and *C. humectus* (Figure 3a).

The anterior margin of the clypeus can have setae or be completely glabrous. The setae are generally arranged in a row at the base of the clypeal teeth. In species of the subgenus *Boreocanthon* and the genus *Melanocanthon* this row extends towards the sides of the genae, whereas in other species this row is in the centre of the clypeus, mainly at the base of the teeth (Figures 5a, 5b and 5e). In *C. maldonadoi*, these setae are as long as the teeth. In *C. fulgidus*, *C. quinquemaculatus*, *C. bicolor*, and *C. staigi*, the setae do not form a row but are clumped in a pair of hair bundles at the base of the teeth (Figure 4e, 4f and 28g). In *Malagoniella astyanax*, these setae are conspicuous at the base of the teeth (Figure 5f).

Ventrally, the clypeus shows great variation within *Canthon*. On the ventral side of the clypeal teeth there is a U-shaped structure, delineated by conspicuous punctures and long and thick setae (Figure 6d). This structure is present in most of the *Canthon* subgenera with the exception of the subgenus *Boreocanthon*, and is present in other genera such as *Malagoniella*, *Anisocanthon*, *Hansreia*, *Scybalocanthon,* and *Sylvicanthon* (Figures 6e, 6f and 6g). It is also present in other dung beetles species such as the Phanaeines (Edmonds 1972). Behind the teeth, between the base of the teeth and the anterior margin of the epipharyngeal cavity, there is an area that is generally smooth in most *Canthon* species. However, in *C. femoralis*, *C. luteicollis* and *C. tetraodon* a longitudinal central carina and a few small lateral protuberances were observed (Figure 6b). This longitudinal carina is also present in *Hansreia affinis*, *Malagoniella astyanax* and *Sylvicanthon bridarollii* (Figures 6c and 6d). This area is generally covered by setae, but *C. fulgidus*, *C. chalcites*, *C. bicolor*, *C. praticola*, *C. simplex* and *C. staigi* have the area behind the base of the clypeal teeth completely glabrous. In other species of Canthonina this area is mostly glabrous, except in *A. villosus*, *S. pygidialis*, and *S. bridarollii* (Figure 6g). In species of the subgenus *Boreocanthon* there is a sharp margin at the base of the clypeal teeth and the area posterior to the teeth is generally reduced in relation to other species of *Canthon* (Figure 6e). In the genus *Melanocanthon*, a longitudinal keel and a well-developed tooth is present at the base of the clypeus (Figure 6f).

The anterior margin of the epipharyngeal cavity is slightly raised, forming a small transverse carina. This carina is present in all the species of the subgenera

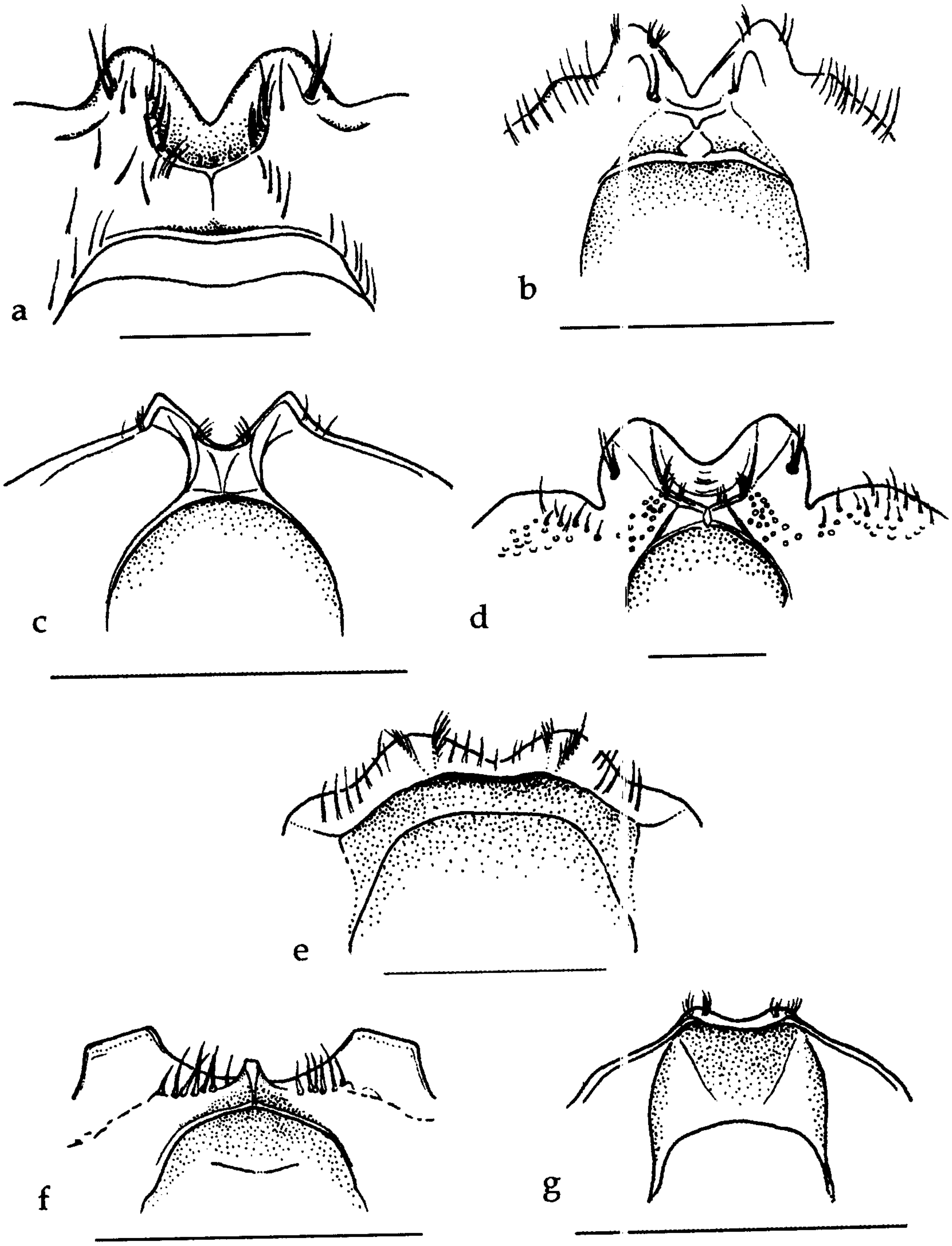


Figure 6. Ventral view of the clypeus **a**. *Canthon fulgidus* Redtenbacher. **b**. *C. femoralis* Chevrolat. **c**. *Hansreia affinis* Fabricius. **d**. *Malagoniella astyanax* Blanchard. **e**. *C. praticola* LeConte. **f**. *Melanocanthon bispinatus* Robinson. **g**. *Anisocanthon villosus* Harold. Scale bar = 1 mm.

Boreocanthon and *Canthon* examined, with the exception of *C. cyanellus*. It is also present in some species of the subgenus *Glaphyrocanthon*: *C. femoralis*, *C. luteicollis*, *C. angustatus*, *C. fulgidus*, *C. staigi*, and *C. lunatus tibialis*. Other genera of Canthonina such as *Hansreia*, *Melanocanthon* and *Deltochilum* also possess this same transversal plate (Figure 6).

Eyes

In dorsal view, the eyes of most species of *Canthon* are narrow (Figure 7b). A projection of the integument of the head rests over the eye surface (forming the canthus) and gives the eye a long and narrow appearance. However, some species of *Canthon* (e.g., *C. aequinoctialis*, *C. perseverans*, and *C. bicolor*) have dorsally wide eyes, as do species of the genera *Sylvicanthon* and *Canthonella* (Figures 7a and 7g). Other genera of Canthonina, such as *Melanocanthon*, *Scybalocanthon, Anisocanthon* and *Hansreia* have dorsally narrow eyes as in most species of *Canthon* (Figure 7c).

In many species of *Canthon* the posterior part of the eye is narrower than the medial part of the eye (Figure 7d). This kind of eye is present in species of the subgenera *Glaphyrocanthon* and *Canthon*, in contrast to *C. pilularius*, *C. bicolor*, *C. staigi*, *C. perseverans*, and species of the subgenus *Boreocanthon*, which have a wide posterior opening of the eye. In other genera, such as *Canthonella*, *Deltochilum*, *Malagoniella*, *Sylvicanthon*, and *Melanocanthon*, the posterior part of the eye is wide, whereas *Scybalocanthon, Anisocanthon*, and *Hansreia* have posteriorly narrow eyes as do most *Canthon*.

In species of *Canthon* the eyes are fringed by a flattened band. In some groups of species this band can be broad and raised. Species of the subgenera *Boreocanthon* and *Canthon*, mainly the *aberrans*, *chiriguano*, *humectus*, *indigaceus* and *deyrollei* lines, as well as *C. tetraodon* and *C. lunatus tibialis*, have this band fringing the eye. In *C. deyrollei* and *C. indigaceus*, the band is conspicuously broad (Figures 7d, 7e and 7f).

Ventrally, the eyes are well developed, rounded, and vary in size depending on the species. In species with very well developed eyes, the area posterior to the genae, between the eye and the mouth cavity, is narrow as in species of *Sylvicanthon*, and some species of *Canthon* such as *C. bicolor*.

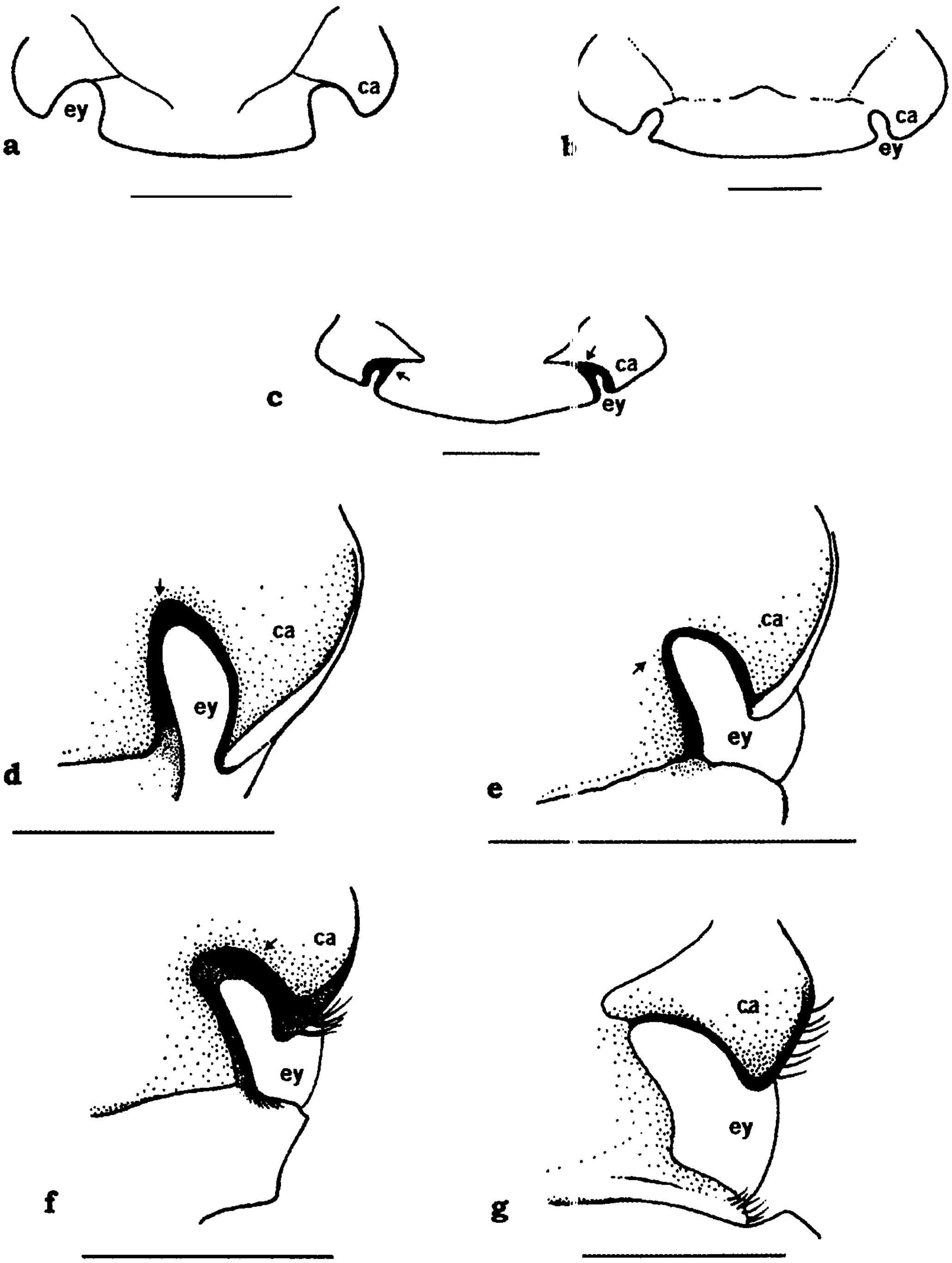


Figure 7. a-c. Dorsal view of the eyes **a**. *Canthon bicolor* Laporte. **b**. *C. politus* Harold. **c**. *Hansreia affinis* Fabricius. d-g. Dorso-lateral view of the eye. **d**. *C. deyrollei* Harold. **e**. *C. lecontei* Harold. **f**. *C. indigaceus* Harold. **g**. *Sylvicanthon bridarollii* Martínez. **ca** = canthus, **ey** = eye. Arrows showing the flattened band around the eye. Figures a-c scale bar = 2 mm, figures d-g scale bar =1 mm.

Epipharynx

The epipharynx is oriented horizontally, and located above the ventral side of the clypeus, under the mandibles and maxillae. It is a hollow structure formed by a double membrane thickened in its central portion. In the upper membrane, a transverse suture joins the epipharynx to the clypeus. This suture crosses the epipharynx at the medial part, and is known as the labro-clypeal suture (Nel & Scholtz 1990), or the labro-clypeal sulcus (Edmonds 1972). The ventral membrane is covered by numerous thick and thin setae. The thickest setae are located in the central region and clumped in the medial process of the epipharynx (Figures 8 and 9c).

The medial process of the epipharynx is a slightly sclerotized, anterior enlarged structure that crosses the epipharynx longitudinally. This structure is known as the antero-medial process, which is formed by the median brush (Edmonds 1972), or "vástago claviforme" (Halffter 1961). Anteriorly, the medial process is club-shaped and is covered by abundant setae. Toward the medial and posterior portions, the medial process is thin, free of setae and ends in an inverted cone shaped structure, with a row of hook-shaped hairs, usually curved forward and downward (Figure 12). In species of *Canthon*, the medial process varies in shape, and in the number and arrangement of the setae. The central region of the epipharynx (lateral to the medial process) has thick setae, each with a small fovea at its base (Figure 9d). These setae are usually thin, erect, curved downward at their apex, and show variation in their number and arrangement in the central region. Among the thick setae there are other kinds of setae, mostly smaller ones or very small and silky ones that cover the central area. To the sides of the central region, are the lateral combs, formed by longitudinal bands of setae (Figure 8). In species of *Canthon*, two well-defined lateral combs are observed. The first lateral comb (nearest to the medial process) is formed by a longitudinal row of thick setae with their ends pointing toward the central region. The setae gradually decrease in size from the anterior part of the epipharynx to the posterior end of the comb, approximately on the posterior portion of the medial process (Figure 10c). In general, the last setae of the first comb differ in size and thickness from the setae of the second comb, which are thinner and shorter. The second comb is not formed by a single row of setae, but is a wide band of short and thin setae interwoven without forming well defined rows (Figures 10a,10b and 10c).

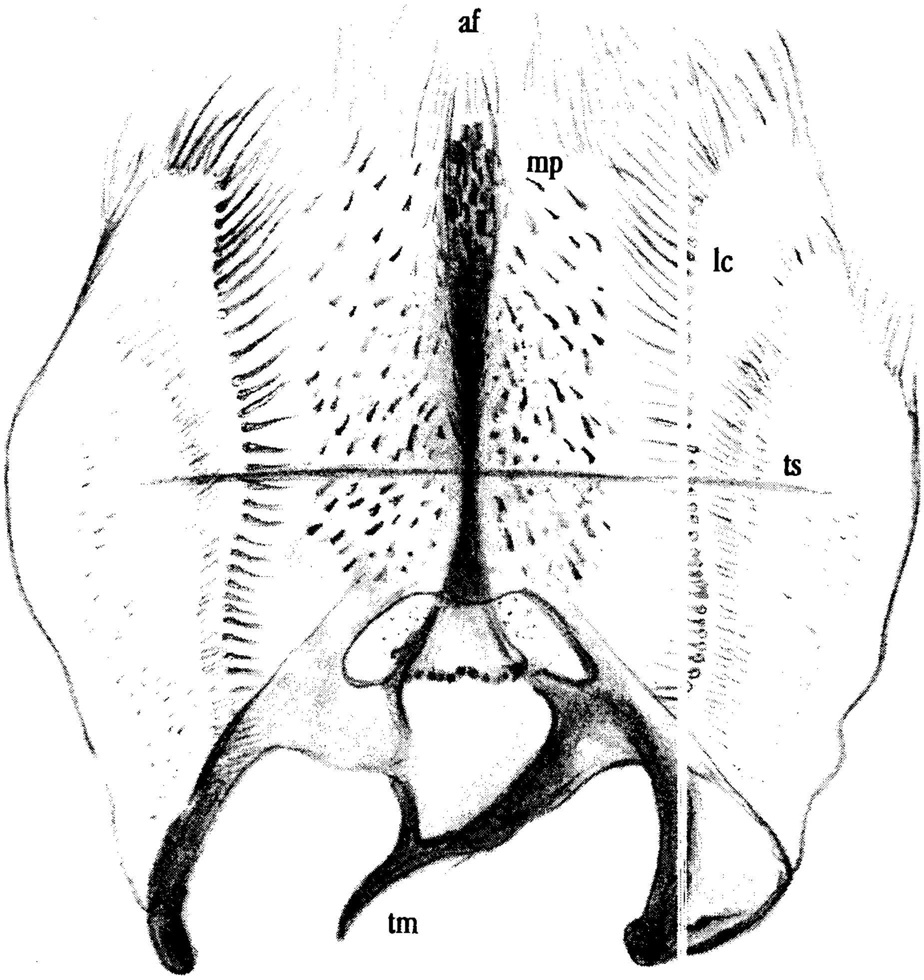


Figure 8. Generalized epipharynx of *Canthon*. **mp** = medial process, **af**= apical fringe, **lc** = lateral combs, **ts** = transverse suture, **tm** = tormal process.

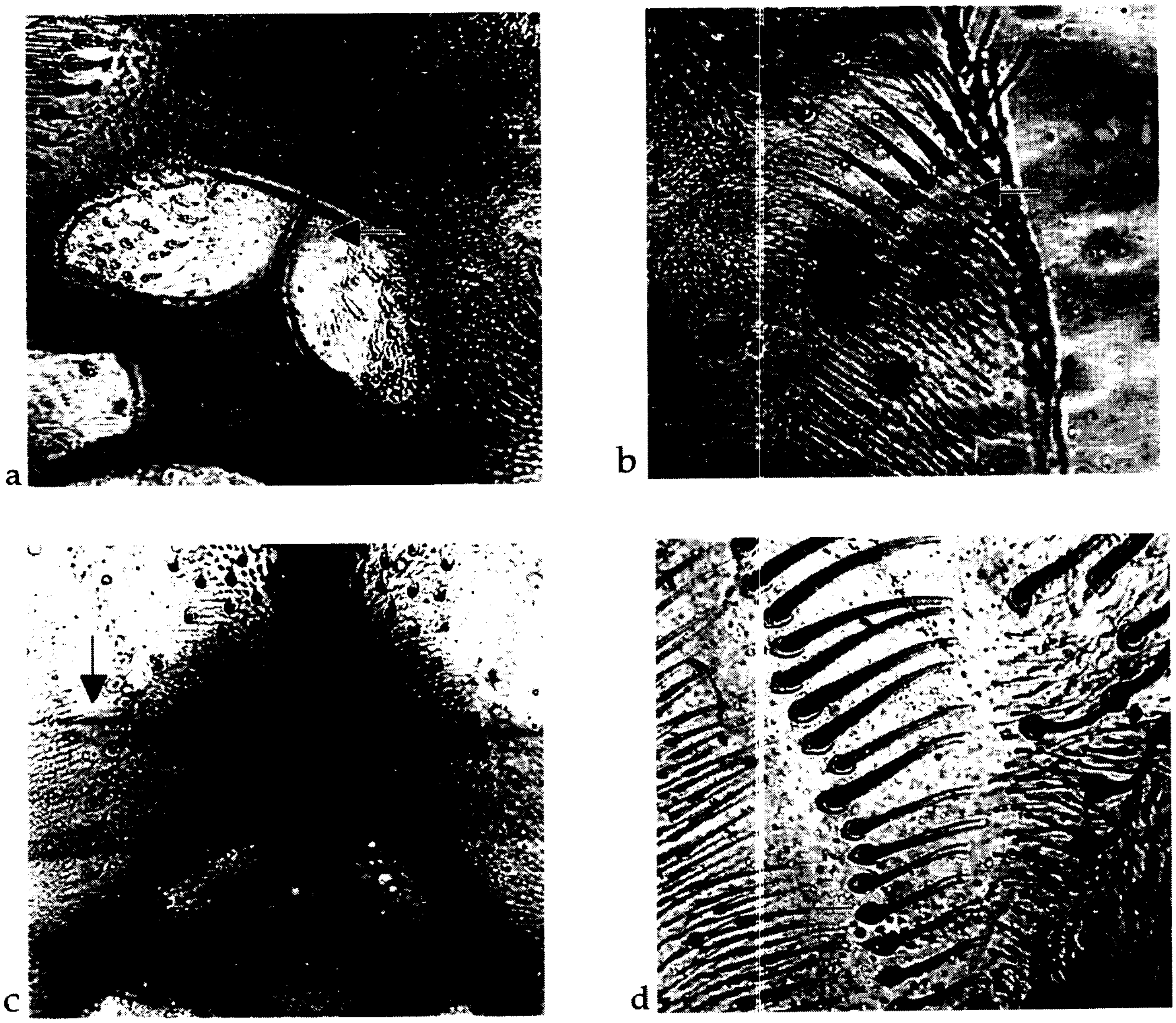


Figure 9. **a**. Detail of posterior area of medial process of epipharynx, *Canthon politus* Harold. **b**. Lateral comb of *Canthonella gomezi* Halffter & Martínez. **c**. Ventral view of the epipharynx of *C. acutus* Harold; arrow indicates the transverse suture. **d**. Detail of different kinds of setae covering the epipharynx of *C. chalcites* Haldemann. Setae on the extreme right of the image correspond to the central area of the epipharynx, those in the middle correspond to setae of the first lateral comb, and those on the extreme left correspond to the second lateral comb of the epipharynx. Magnification = 40x.

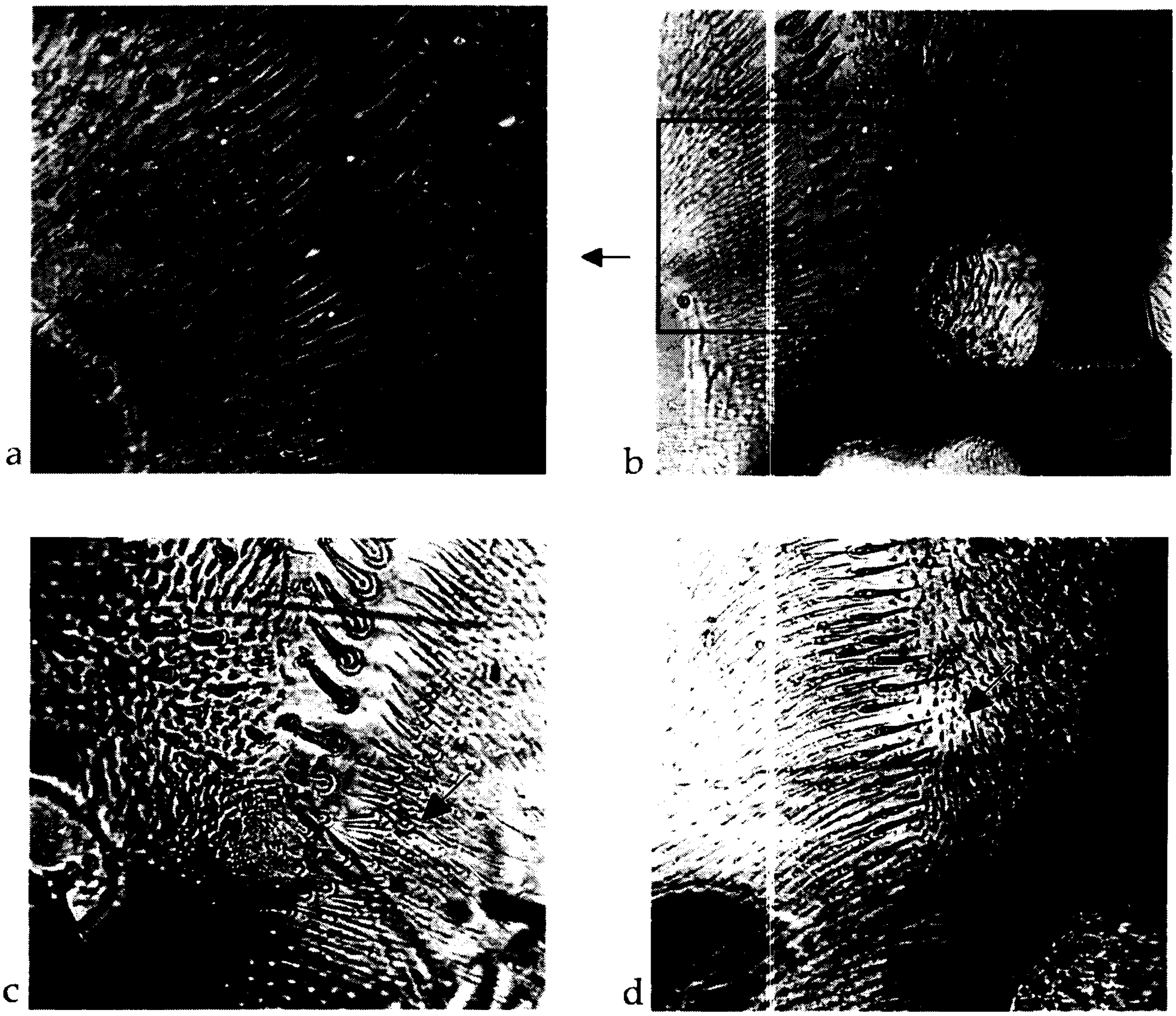


Figure 10. Detail of the lateral combs of the epipharynx. **a and b**. *Canthon ebenus* Say. **c.** *C. lunatus tibialis* Schmidt. **d**. *C. bicolor* Laporte. Figures b, c, and d magnification = 20x, figure a magnification = 10x.

The base of the epipharynx or proximal epipharynx (Nel & Scholtz 1990), is a slightly more sclerotized area that forms a plate with two more or less circular hollows in the medial area, and one central and two lateral chitinous projections (Figure 8). The lateral projections, called tormae (Snodgrass 1935), or tormal process of labral suspensorium (Edmonds 1972, Nel & Scholtz 1990), are connected with the sclerites, in which the muscles that move the epipharynx are inserted.

The epipharynx has not been well studied in the genus *Canthon.* Halffter (1961) described the epipharynx of some species of *Canthon* of North America, and Pereira & Martínez (1956) presented drawings of the epipharynx of several species of *Canthon*, but without any description of the structure. The epipharynx of most species of *Canthon* is quadrangular, with the medial process well developed and covered by abundant setae. It differs from other genera of Scarabaeinae, by having two well defined lateral combs. In other groups of Scarabaeinae such as species in the tribes Phanaeini (*Oxysternon conspicillatum* and *Phanaeus pyrois*) and Dichotomini (*Dichotomius satanas*), only one defined comb is observed.

The general pattern observed in *Canthon* is the presence of a narrow strip free of setae between the two lateral combs. This strip is evident on the anterior half of the epipharynx and becomes somewhat narrower on the posterior half. In a few species of *Canthon* the fringe is lost due to the posterior fusion of the combs, usually behind the transverse suture. However, in the few species of *Canthon* in which the combs are fused, it was possible to identify the first comb because its setae were larger than those in the second comb. *C. bicolor* and *C. staigi* were the only two species in which the combs fuse before the transverse suture (Figure 10d); in *C. cyanellus* and *C. fulgidus* the combs fuse at the level of the transverse suture. In the other genera of Canthonina studied, the setae of the first comb are not as thick and long as those in the first comb of *Canthon*, and gradually become smaller until they cannot be differentiated in size and thickness from the setae in the second comb. In species of *Deltochilum* and in *Malagoniella astyanax*, the second lateral comb fuses with the first comb from the posterior half of the epipharynx, more or less at the level of the transverse suture, forming a broad fringe of hairs, in which the combs are no longer recognisable. In genera such as *Cryptocanthon* and *Canthonella* the first comb is not complete; it only runs over the anterior third of the epipharynx (Figure 9b). In *Scybalocanthon, Sylvicanthon* and *Hansreia*, the first comb is well differentiated on the anterior part, but it fuses with the second comb just after of the transverse suture. In *Anisocanthon* and *Melanocanthon*, the lateral combs of the epipharynx are well defined and are not different from the lateral combs of *Canthon*.

Within *Canthon*, the medial process shows great variation in the shape of the anterior end, which can be enlarged and rounded anteriorly, or end in a point (Figure 11). In species of the *pilularius* group of the subgenus *Canthon*, the subgenus *Boreocanthon*, and in some species of the subgenus *Glaphyrocanthon*, the medial process is pointed (Figure 11b). In the rest of the species examined, the medial process does not end in a point and in most of the species it is rounded (Figures 11a, 11c and 11d).

There is also variation within *Canthon* in the general shape of the medial process, but I did not observe a clear pattern within subgenera or species groups. In most of the species studied, the medial process ends over the anterior margin of the epipharynx. In *C. staigi* of the subgenus *Peltecanthon* there is a space between the medial process and the anterior margin of the epipharynx (Figure 11a). In *C. bicolor* the medial process ends before the anterior margin but this space is smaller than that observed in *C. staigi.*

The posterior end of the medial process also shows great variation. In general, the medial process ends in a conical structure that shows varies widely in size and shape, and is usually fringed by a single row of hairs, which in some species are curved forward and downward, and in other species are less curved (Figure 12b). In some species there is not a well-defined row of hairs but rather a clump of hairs such as in *C. bicolor*, or a double row of hairs such as in *C. acutus* or *C. lunatus tibialis* (Figures 12a, 12c and 12d). Due to the difficulty in distinguishing these hairs, their variation was not studied in detail in all the species.

The anterior margin of the epipharynx is covered by a row of setae, referred to by Edmonds (1972) as the apical fringe, which is present in most families of Scarabaeoidea (Nel & Scholtz 1990). Within *Canthon*, the hairs of the apical fringe are long and thin, in

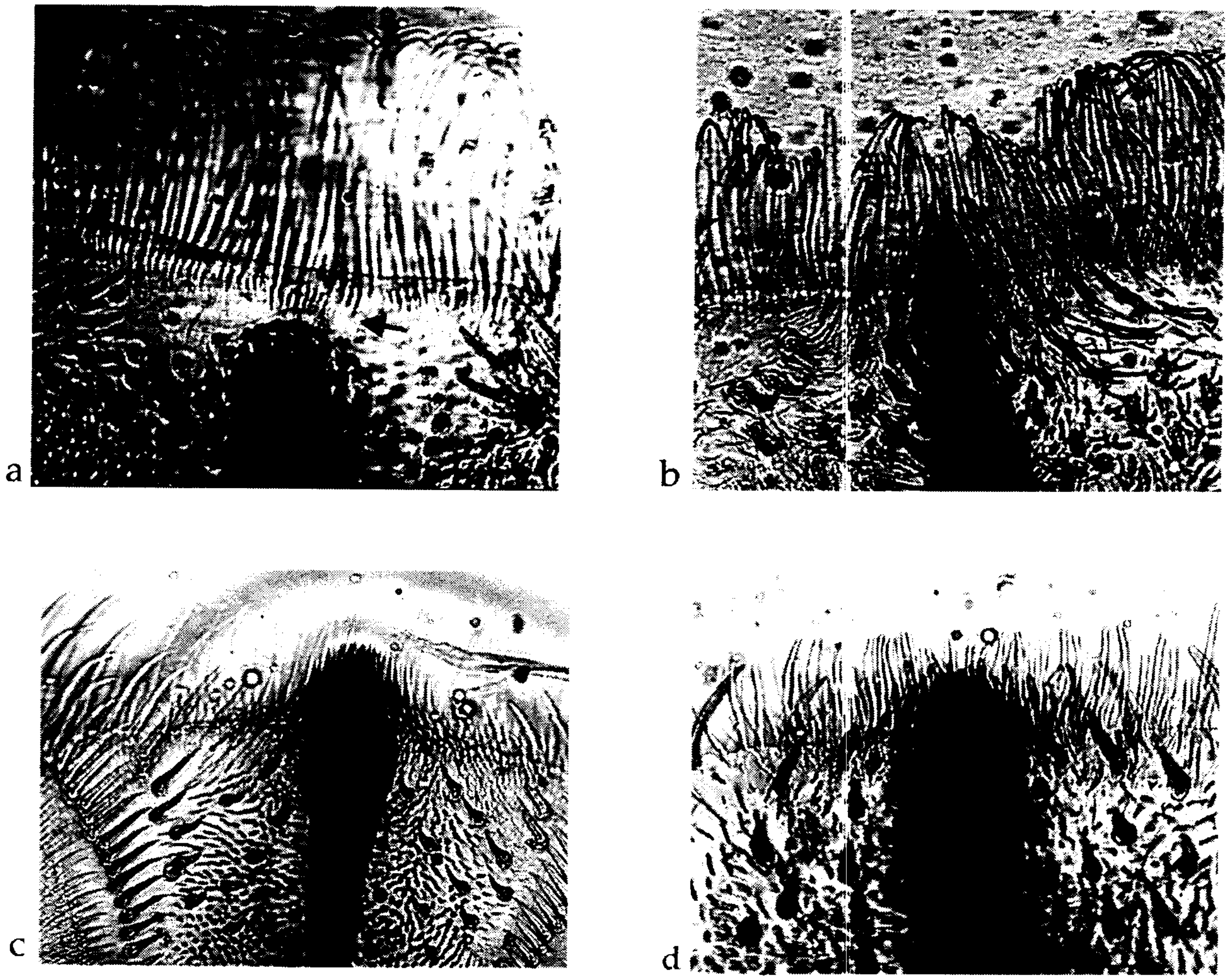


Figure 11. Detail of the anterior area of the medial process of the epipharynx. **a**. *Canthon staigi* Pereira; arrow indicates the space between the medial process and the anterior border of the epipharynx. **b**. *C. tetraodon* Blanchard. **c**. *C. lunatus tibialis* Schmidt. **d**. *C. ebenus* Say. Magnification 40x.

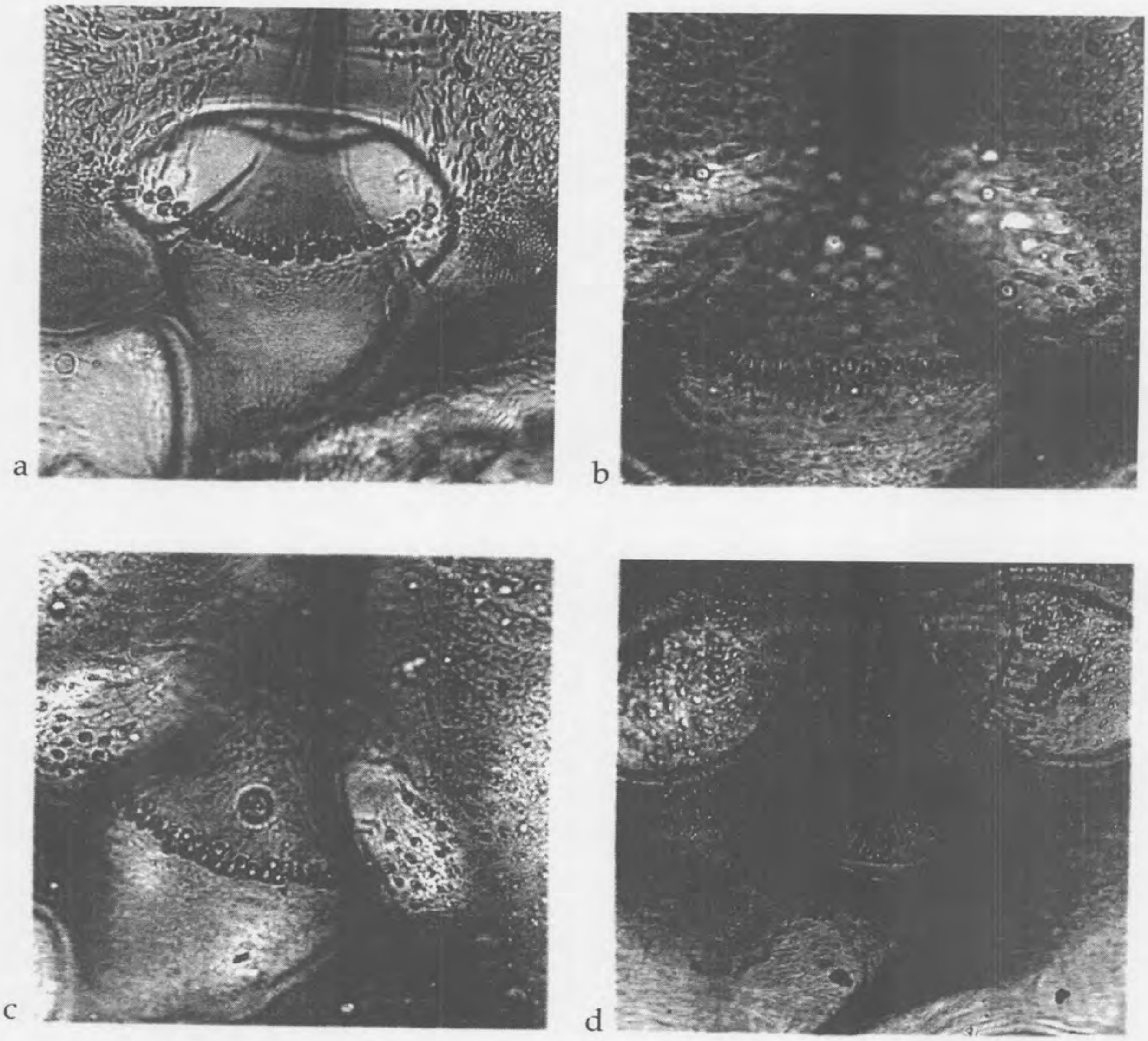


Figure 12. Detail of the posterior region of the medial process of the epipharynx **a**. *Canthon lunatus tibialis* Schmidt. **b**. *C. acutus* Harold. **c**. *C. cyanellus sallaei* Harold. **d**. *C. bicolor* Laporte. Figures a, c and d magnification 20X, figure b magnification 40X.

contrast with species of the other genera of Canthonina, which have short and thick hairs such as in *Canthonella*, *Cryptocanthon*, and *Deltochilum*. In most of the species of *Canthon* these long hairs are present, except in species of the subgenera *Boreocanthon* and *Pseudepilissus* (Figures 11c and 11d). The lateral ends of the anterior margin of the epipharynx are covered by long and thick hairs, which are slightly curved towards the center. The abundance of these hairs varies among species, but I did not observe a clear pattern.

Labium and gula

The labium is a ventral lobe, anterior to the gula, fused with the mentum and submentum. The most evident variation is present on the anterior border of the mentum, which can be complete, sinuated or completely divided. Species of *Canthon* usually has a sinuated mentum; slightly so in some species such as *C. angustatus*, *C. politus*, *C. fulgidus*, *C. pallidus*, and species of the *viridis* group (Figure 13b), and deeply sinuated in species of the subgenera *Boreocanthon*, *Francmonrosia*, species of the *pilularius* group, and others of the subgenus *Canthon* (Figures 13c and 13d). In *Canthonella*, *Cryptocanthon* and *Hansreia*, the anterior border of the mentum is complete (Figure 13a), whereas in *Scybalocanthon, Sylvicanthon*, *Malagoniella*, and *Deltochilum* it is sinuated as in *Canthon*. A completely divided mentum is present in the genus *Holocanthon*.

In general, beetles have a well-developed gula, a characteristic associated with the general prognathous condition. The gula is a bulging, enlarged, smooth, and usually glossy sclerite. It is delimited by the ventral extensions of the post-occipital suture, which are referred to as gular sutures (Snodgrass 1935, Edmonds 1972). Anteriorly, the gula is separated from the submentum by a well-marked transverse suture. In most Scarabaeidae this separation is not evident; instead a row of setae is present that could be homologous to the suture that separates the gula from the submentum, as in the Melolonthinae genus *Phyllophaga* (Edmonds 1972). In *Canthon* and other Scarabaeinae this row of setae has modifications and is not a true separation between these two areas. In species of *Canthon* this section of the gula is recognised by having a different sculpture, not smooth (as the rest of the surface of the gula) and being covered by

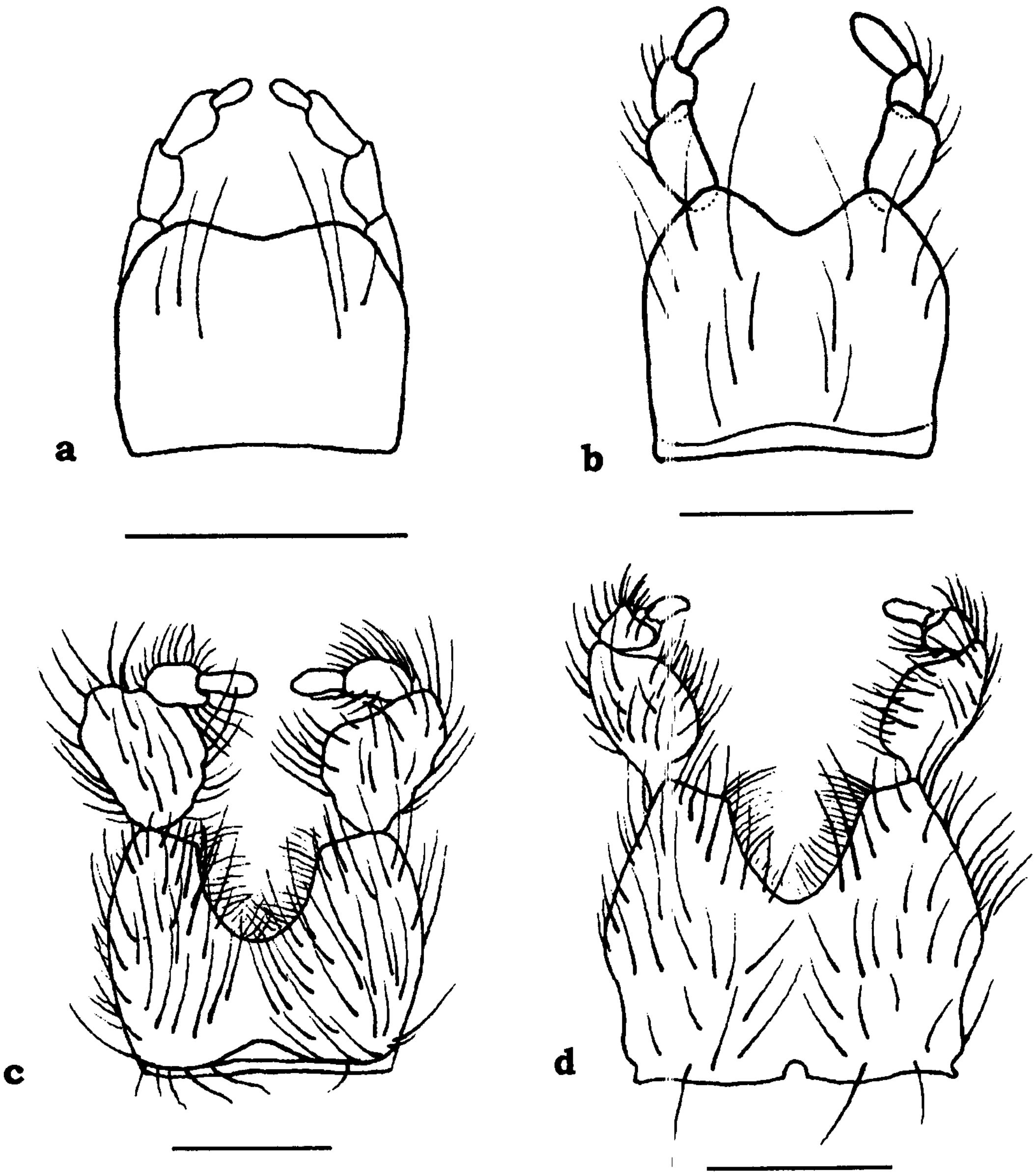


Figure 13. Dorsal view of labium. **a**. *Canthonella gomezi* Halffter & Martínez. **b**. *Canthon pallidus* Schmidt. **c**.*C. ebenus* Say. **d**. *C. tetraodon* Blanchard. Scale bar = 0.5 mm.

setae. Within *Canthon* there is much variation in the shape of this area and in the abundance and length of the setae, but this variation is not exclusive to the genus. Most of the variation is in the shape of this area and in the abundance of the setae that cover it. Some species have a groove with a row of setae that runs transversally over the gula, as in some species of the subgenus *Glaphyrocanthon* (*C. angustatus*, *C. lamprimus*, *C. pallidus*, *C. femoralis femoralis*, *C. femoralis bimaculatus*, and species of the *viridis* group) and in *C. perseverans*. Outside of *Canthon* this row of setae is present in *Canthonella gomezi* and in the species of *Cryptocanthon* examined (Figures 14a and 14b). The row of setae becomes thicker, with more setae, and in some species it is curved as in the subgenus *Pseudepilissus* (*C. lunatus tibialis*), species of the subgenera *Canthon* (*C. aberrans*, *C. cyanellus*, *C. deyrollei*, *C. indigaceus*, *C. humectus*), *Glaphyrocanthon* (*C. politus*, *C. semiopacus*, *C. luteicollis*), *Francmonrosia* (*C. tetraodon*), and in *C. quinquemaculatus* and *C. septemmaculatus* (Figure 14c). Other species, have a triangular area with a different sculpture, marked with punctures and thick setae. Species of the subgenus *Boreocanthon*, the *pilularius* group, and other species of *Canthon*, as well as the genera *Anisocanthon*, *Hansreia*, *Scybalocanthon*, *Sylvicanthon*, *Deltochilum*, *Malagoniella*, and *Melanocanthon* have this triangular area (Figures 14d, 14e and 14f). In *C. fulgidus*, *C. staigi*, *C. bicolor*, and *C. violaceus*, and also in species of *Deltochilum* the setae of this area are noticeable long (Figure 14g).

Thorax

The pronotum in the Scarabaeidae is well developed, transversally expanded, and usually wider than long. In species of *Canthon* the pronotum is usually smooth, glossy and very convex, without tubercles or protuberances (Figures 2 and 15a). Although in other groups of Scarabaeinae, including some genera of Canthonina, the scutellum is visible at the base of the elytra, in *Canthon* this segment is reduced, and only in species of the subgenus *Peltecanthon* is the apex visible between the bases of the elytra (Halffter & Martínez 1977).

In descriptions of the species of *Canthon* it is common to use the shape of the lateral margin of the pronotum, as well as the shape of the anterior and posterior angles. The anterior angles of the pronotum are usually well marked in *Canthon*, and in some

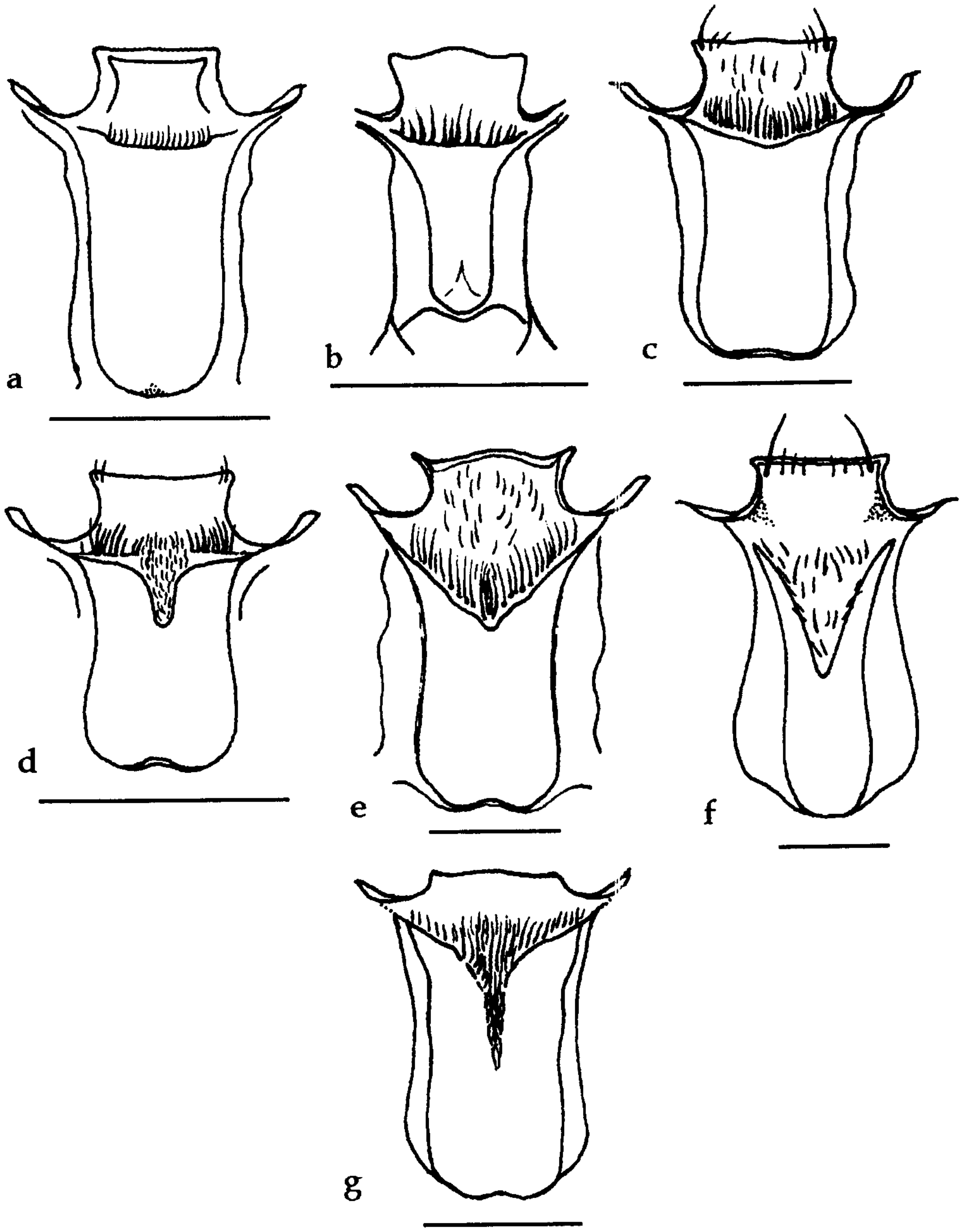


Figure 14. Dorsal view of the gula and mentum. **a**. *Canthon angustatus* Harold. **b**. *Canthonella gomezi* Halffter & Martínez. **c**. *C. humectus* Say. **d**. *C. praticola* LeConte. **e**. *C. chalcites* Haldemann. **f**. *Hansreia affinis* Fabricius. **g**. *C. violaceus* Olivier. Figure a, scale bar = 0.5 mm, figures b-g scale bar = 1 mm.

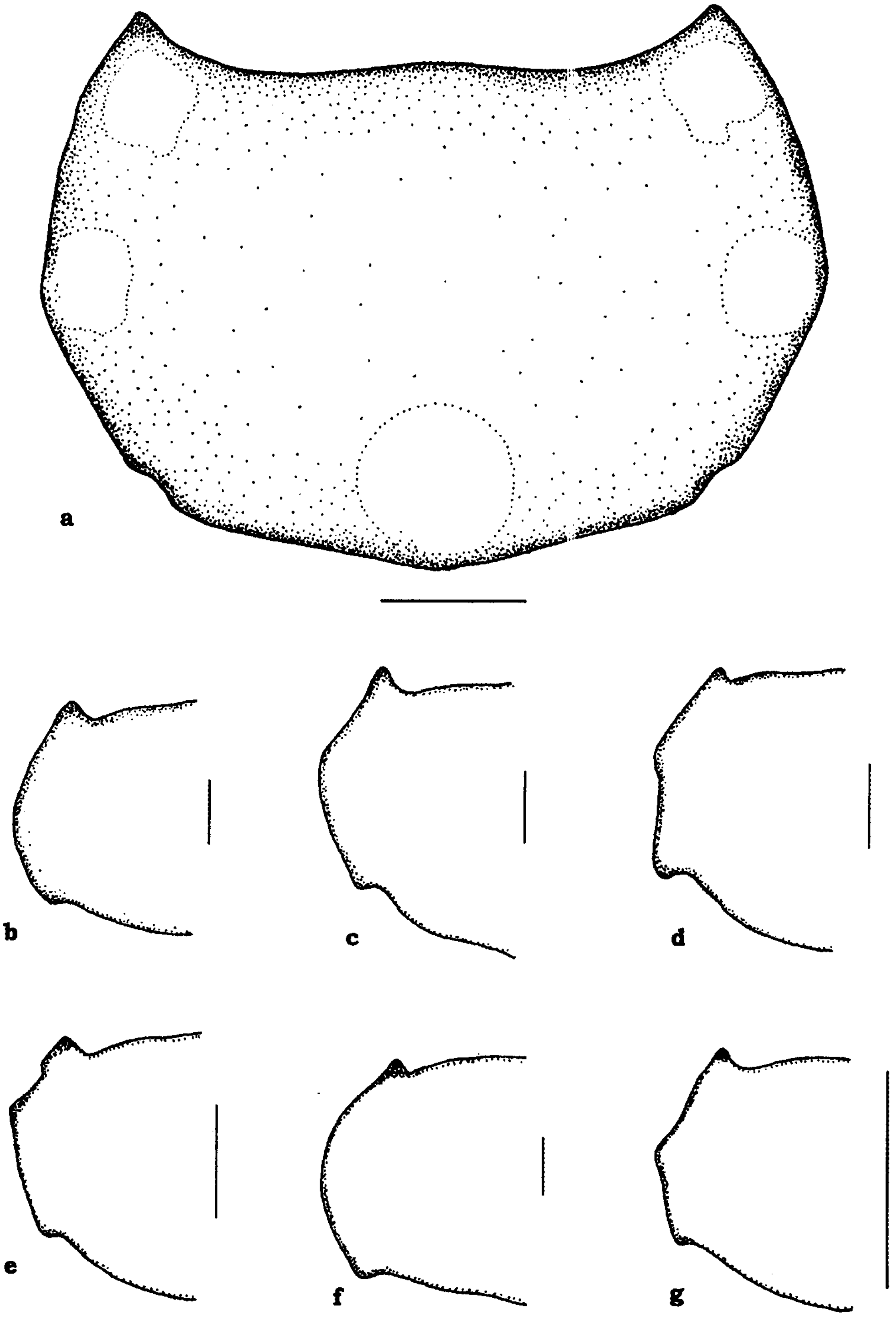


Figure 15. **a**. Dorsal view of pronotum of *Canthon septemmaculatus septemmaculatus* Latreille. Figures b-g: Lateral margin of pronotum. **b**. *C. bicolor* Laporte. **c**. C. *aequinoctialis* Harold. **d**. *C. femoralis* Chevrolat. **e**. *C. angustatus* Harold. **f**. *C. deyrollei* Harold. **g**. *C. juvencus* Harold. Scale bar = 1 mm.

species they are very acute. The posterior angles of the pronotum are rounded and inconspicuous in most of the species examined, although in some species a well-marked angle is present, as in the case of *C. imitator*.

The lateral border of the pronotum shows variation in the contour and shape of the anterior angles. The border can be rounded with the anterior angles slightly marked such as in *C. septemmaculatus*, *C. indigaceus*, *C. monilifer*, *C. chiriguano*, *C. mutabilis*, *C. bicolor*, *C. pilularius*, *C. violaceus*, *C. perseverans*, *C. lunatus tibialis*, *C. praticola*, *C. triangularis*, and *C. quinquemaculatus* (Figure 15b). A rounded and slightly sinuated lateral border with an angle in the antero-medial part is present in species of different subgenera such as *C. viridis*, *C. lamprimus*, *C. aequinoctialis*, *C. chalcites*, *C. sordidus* and *C. cyanellus* (Figure 15c). In *C. angustatus*, *C. politus*, *C. staigi*, and *C. femoralis*, the border is straight with an angularity in the medial part (Figures 15d and 15e). The lateral border without angles and slightly sinuated is a feature shared by *C. deyrollei*, *C. humectus*, *C. imitator*, *C. ebenus*, *C. tetraodon*, *C. luteicollis* and *C. fulgidus* (Figure15f and 15g). In *C. juvencus* the anterior angle is acute, and the border has a small notch anteriorly.

Proepisternum and proepimeron

The ventral side of the thorax in the Scarabaeinae is occupied mainly by the pleural region. The pleura have expanded ventro-mesally and cover the bases of the coxae; their transverse orientation has also caused a reduction of the prosternum (the first ventral segment of the thorax) (Edmonds 1972). Thus the prosternum in the Scarabaeinae is formed by a thin central fringe, laterally limited by the coxal cavity. In the prosternum it is possible to observe the basisternum (area posterior to the frontal coxae) and the sternellum (area posterior to the coxal cavity). In *Canthon*, most of the variation observed in this part of the body is in the proepisternum and proepimeron (Figure 16).

The proepisternum is the anterior most region of the ventral thorax and is where the anterior legs are lodged when they are retracted. In *Canthon* and other genera of Canthonina, the proepisternum can be deeply excavated and limited posteriorly by the proepisternal keel, also called the propleural carina (Edmonds 1972), transversal keel

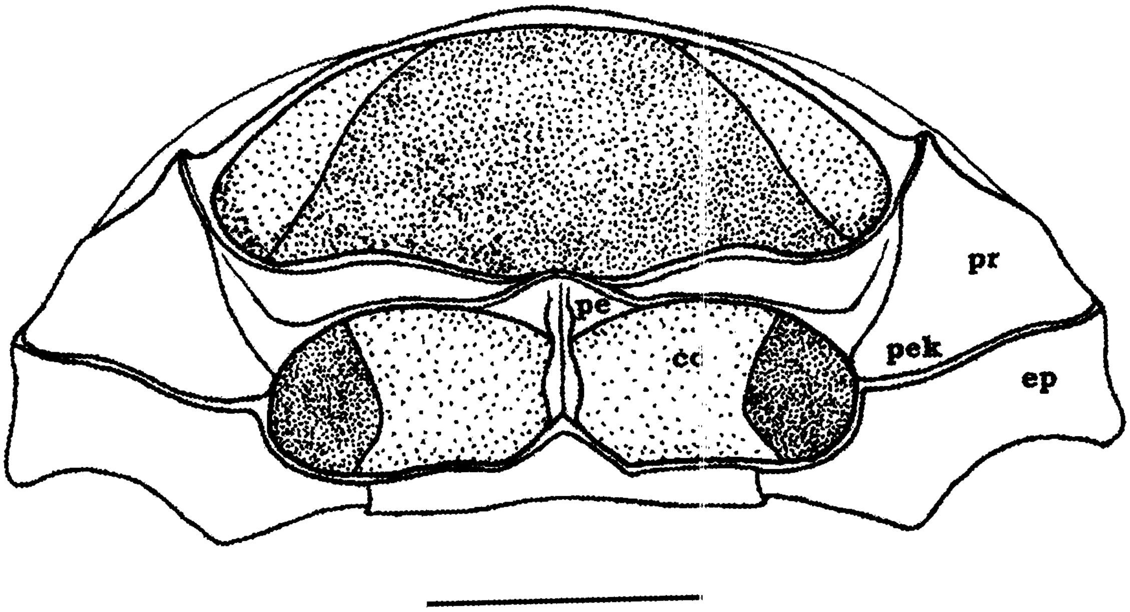


Figure 16. Generalized ventral view of first segment of the thorax of *Canthon*. **pr** = proepisternum, **ep** = proepimeron, **pek** = proepisternal keel, **cc**= coxal cavity, **pe** = prosternum. Scale bar = 1 mm.

(Halffter 1961) or proepimeral keel (Howden & Gill 1987). The proepisternal keel is homologous to the pleural suture that separates the episternum from the epimeron in a general plan of the pleura of an insect (Snodgrass 1935). In *Canthon* and other genera of Canthonini this suture is not a true separation of the latter two pleural segments, but it is more like a keel of the integument, which in some cases can be well-marked or slightly insinuated.

Among the species of *Canthon* examined there is great variation and perhaps even a gradient in the extension of the proepisternal keel. In some species the keel is complete and runs over the thorax from the base of the coxa to the lateral border of the pronotum, where it usually ends in a fold of the lateral border. Many authors refer to this fold as a "tooth of the lateral border of the pronotum", which can be well marked in some species, such as *Hansreia affinis* (Halffter & Martínez 1977).

In general, species that have a deeply excavated proepisternum also have a complete proepisternal keel. These two features were used by Martínez (1948) in the description of the genus *Glaphyrocanthon*. However, neither an excavated proepisternum nor a complete proepisternal keel is exclusive to the subgenus *Glaphyrocanthon*. Species of other subgenera of *Canthon* (i.e., *C. aberrans*, *C. deyrollei*, and *C. humectus*) and other genera of Canthonina such as *Anisocanthon*, *Canthonella* and *Cryptocanthon* have an excavated proepisternum and a complete proepisternal keel. These features were also used by Martínez & Pereira (1967) to separate the species of the genus *Sylvicanthon* (Figures 17a–17d). Although the complete proepisternal keel is common in several species of *Glaphyrocanthon* (*C. acutus*, *C. femoralis*, C. *lamprimus*, *C. luteicollis*, *C. politus*, C. *semiopacus*, including species of the *viridis* group), other species in this same subgenus (*C. angustatus*, *C. brunneus*, *C. columbianus*, C. *pallidus* and C. *subhyalinus*) show an incomplete proepisternal keel, overlapping at least half of the proepisternal area. Species of the subgenus *Canthon* also show an incomplete proepisternal keel as in *C. chiriguano* and, according to Martínez & Halffter (1972), in a closely related species (*C matthewsi*). In *C. delpontei*, *C maldonadoi* and *C. luctuosus*, and the genus *Hansreia*, the proepisternal keel is also incomplete.

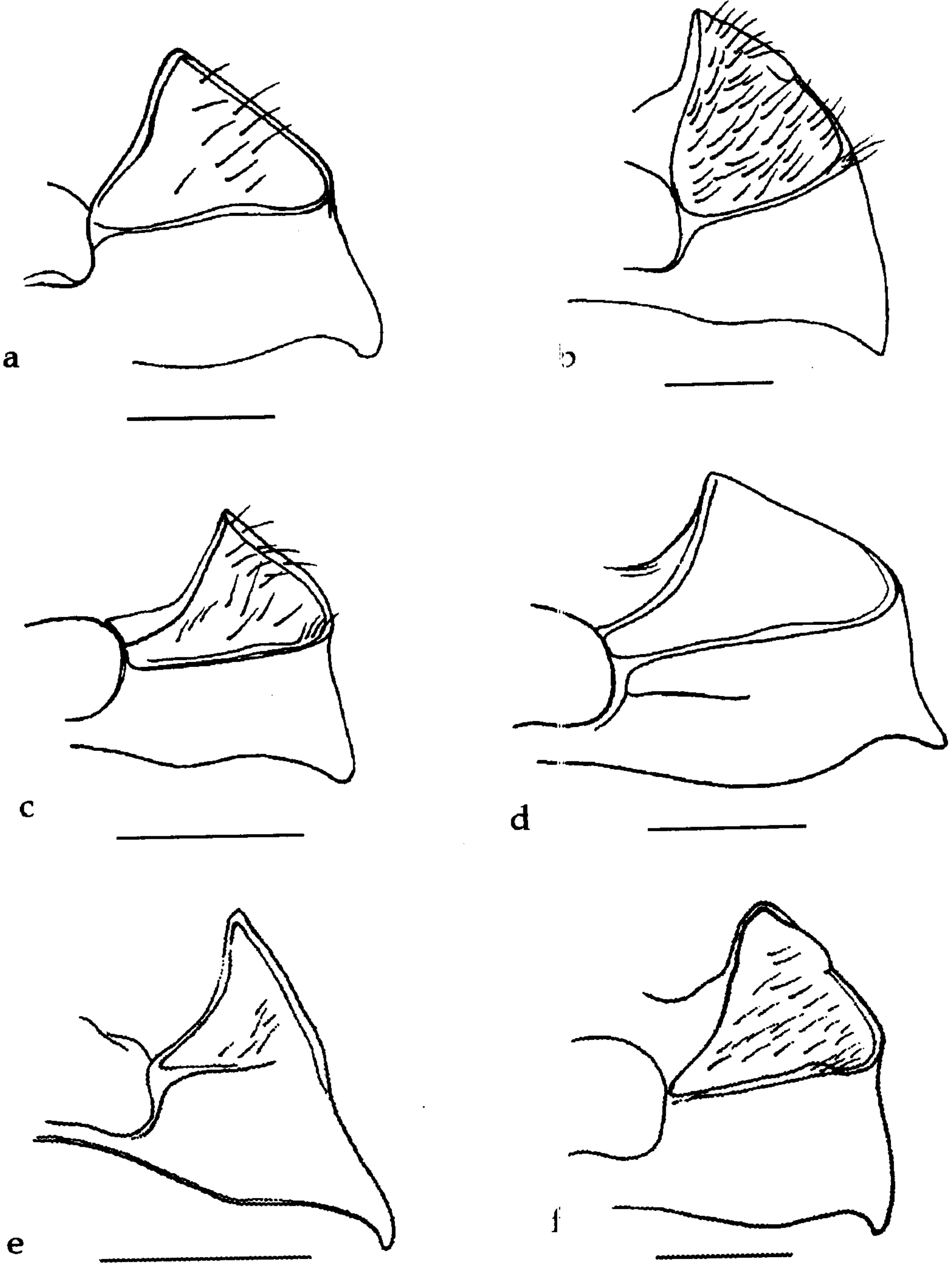


Figure 17. Proepisternum and proepimeron. **a**. *Canthon politus* Harold. **b**. *C. humectus* Say. **c**. *C. morsei* Howden. **d**. *Sylvicanthon bridarollii* Martínez. **e**. *C. pallidus* Schmidt. **f**. *C. angustatus* Harold. Scale bar = 1 mm.

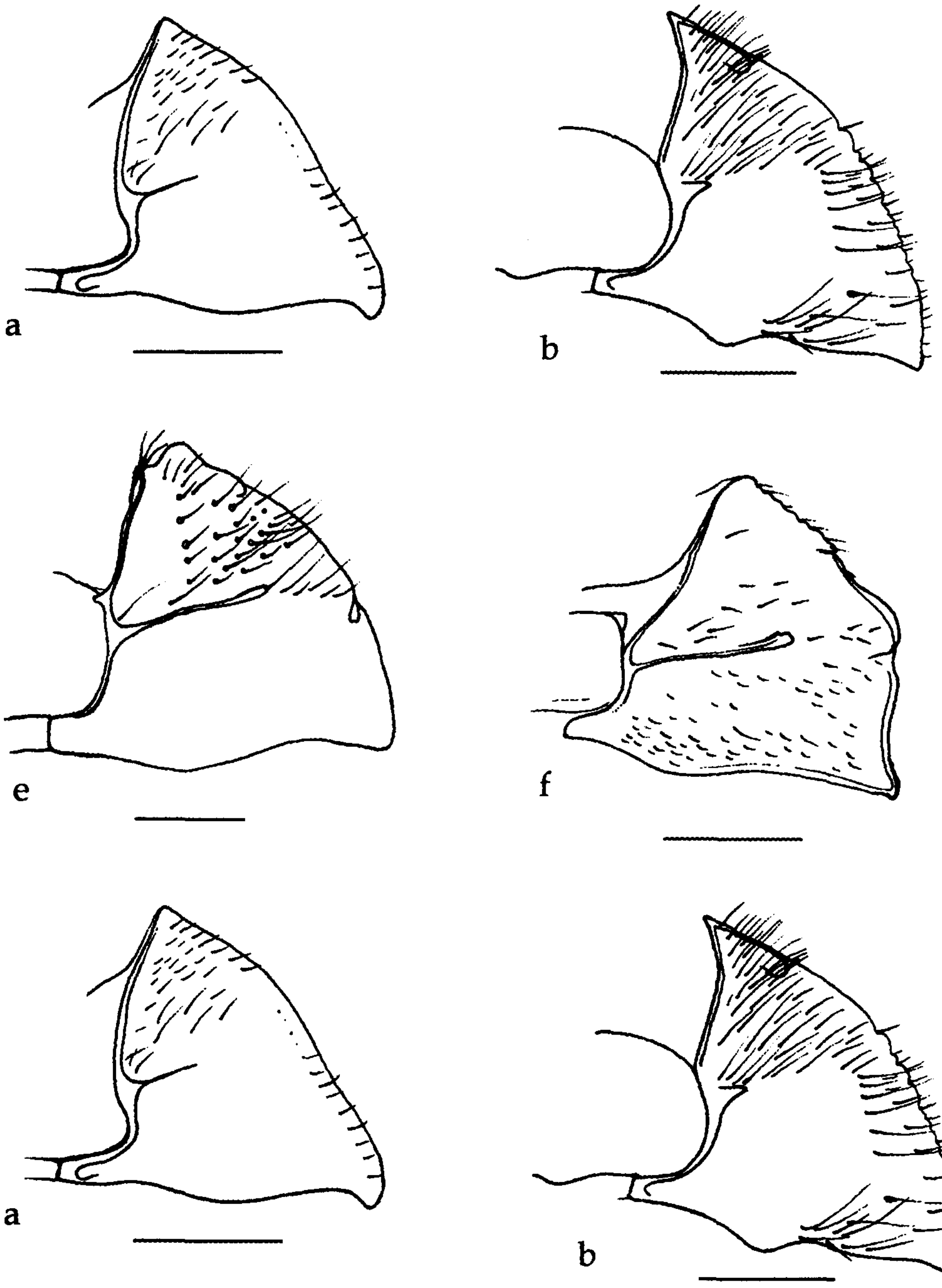


Figure 18. Proepisternum and proepimeron. **a**. *Canthon brunneus* Schmidt. **b**. *C. deyrollei* Harold. **c**. *C. staigi* Pereira. **d**. *Hansreia affinis* Fabricius. **e**. *C. cyanellus sallaei* Harold. **f**. *C. ebenus* Say. Scale bar = 1 mm.

The proepisternal keel is insinuated at the base of the coxae in *C. lunatus tibialis*, *C. cyanellus*, *C. bicolor*, *C. tetraodon*, *C. quinquemaculatus*, the subgenus *Boreocanthon* (Figures 18e, 18f and 19a), and the genus *Holocanthon*. In *C. sordidus* the keel is insinuated, but it runs near the anterior border of the proepisternum, almost parallel to it, and is not directed towards the lateral border (Figure 19b).

The pleural area can also lack a proepisternal keel; in this case there is no division between the proepisternum and proepimeron, the proepisternum is not excavated and the general appearance of this area is flat. Additionally, the proepisternum can be convex in some areas such as in some species of the subgenus *Canthon* like *C. indigaceus*, species of the *pilularius* line, and *C. violaceus*, *C. perseverans*, *C. septemmaculatus*, *C. triangularis* and also in the genus *Deltochilum* (Figures 19e).

In *Canthon* the proepisternum has long setae. This feature was observed in all the species of *Canthon* examined, except *C. humectus*. The other genera of Canthonina, except for *Canthonella*, *Cryptocanthon*, *Scybalocanthon*, and *Sylvicanthon*, also showed setae on the proepisternum. There is variation in the abundance and size of the proepisternal setae. Most of the species of *Canthon* have long and abundant setae (more than 12); only *C. cyanellus*, *C. triangularis*, and *C. bicolor* have a few, short setae.

The proepimeron, (posterior part of the proepisternum), is either setose or glabrous. Species of *Boreocanthon* have setae, although their abundance and size vary among species. Abundant and long setae are present in *C. simplex* and *C. ebenus*, whereas in *C. praticola* few and short setae are present. In species of several subgenera of *Canthon* the presence/absence, abundance and size of the setae on the proepimeron vary without a clear pattern. However, in species examined of the subgenus *Glaphyrocanthon*, the proepimeron was glabrous.

One of the characters traditionally used to separate the genus *Megathopa* from *Malagoniella* is the presence of a fine keel on the epipleura and proepimeron (Martínez 1961). This keel is parallel to the lateral border of the pronotum and is usually accompanied by setae and punctures (Halffter & Martínez 1977). In species of the genus *Malagoniella* the keel is not present, but several setae overlap the proepisternum

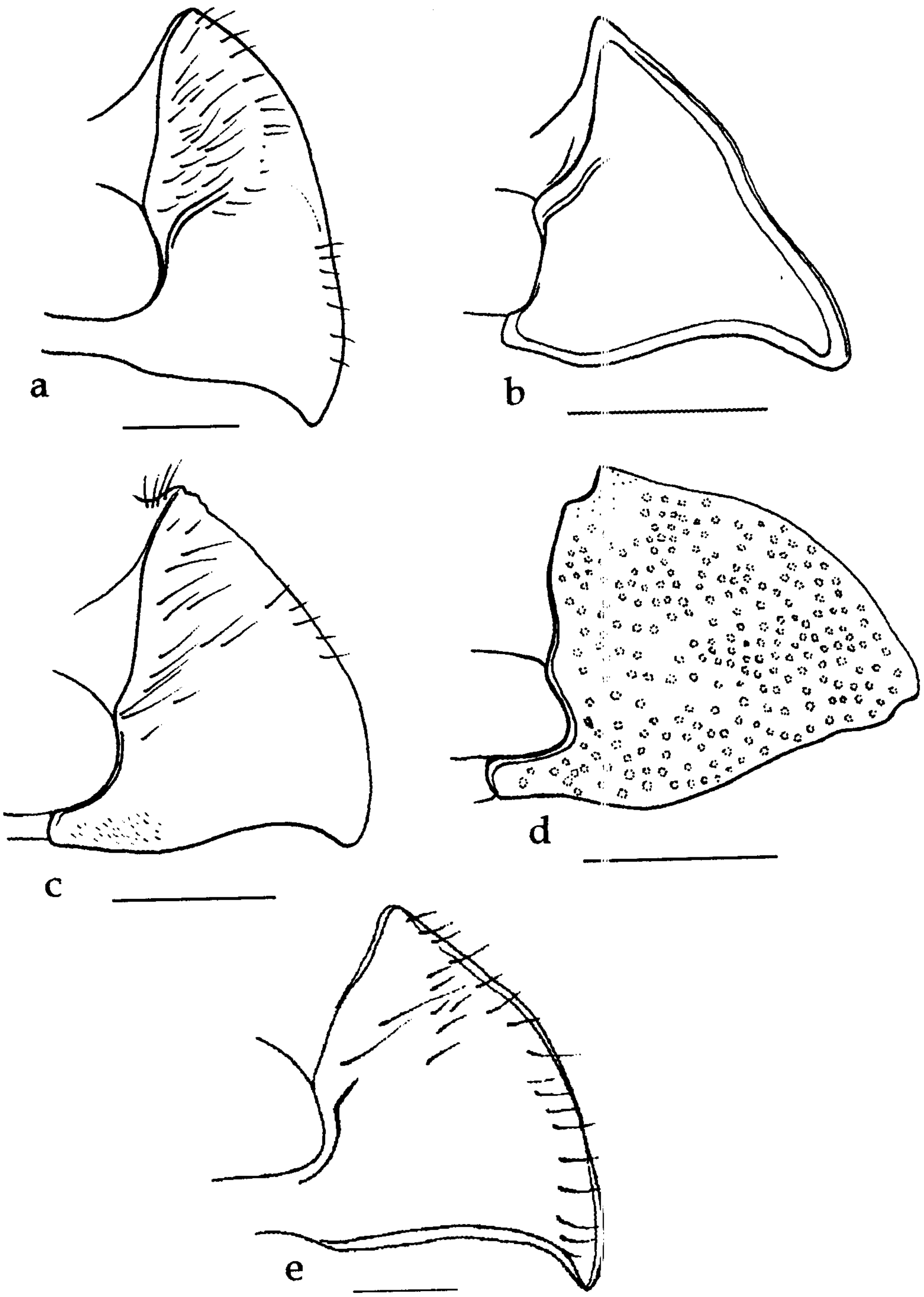


Figure 19. Proepisternum and proepimeron. **a**. *Canthon lunatus tibialis* Schmidt. **b**. *C. sordidus* Harold. **c**. C. *septemmaculatus* Latreille. **d**. *Deltochilum gibbosum* Fabricius. **e**. *C. violaceus* Olivier. Figures b, c, e, scale bar = 1 mm, Figure a scale bar = 0.5 mm, figure d scale bar = 3 mm.

and the proepimeron, without reaching the posterior border of the pronotum (Martínez 1950). In the species of *Canthon* and other Canthonina examined, I observed great variation in this row of setae and punctures. In the species examined, a well-defined keel was not observed. In some species only a row of setae was observed and, in others, a row of setae and punctures was observed. The row of setae can run over both the proepisternum and the proepimeron, as in several species of *Canthon* (e.g., *C. cyanellus*, *C. maldonadoi* and *C. violaceus*; Figure 19a). This row can also overlap the proepisternum only as in *C. septemmaculatus*, *C. perseverans*, *M. astyanax* and *H. affinis* (Figures 18e and 19e), or overlap the proepimeron only, as in *C. deyrollei* and *M. bispinatus* (Figure 18b).

Mesosternum

The mesosternum is located ventrally and posterior to the prosternum, over the medial coxae (Figure 20). It is a very narrow and reduced transverse sclerite present in some species of *Canthon*. Although the width of the mesosternum has taxonomic value, and has been used in the descriptions of species of *Canthon*, it is difficult to discern a pattern among the subgenera. Although it is usually reduced in species of *Canthon*, in some species the mesosternum can be wider, as in *C. obliquus* (Halffter 1961). The genera *Sylvicanthon*, *Hansreia*, and *Scybalocanthon* have the mesosternum reduced as in *Canthon*, in contrast to other genera of Canthonina such as *Pseudocanthon*, *Canthonella*, and *Cryptocanthon*, which have a broad mesosternum (Figures 20a - 20d).

Legs

Fore legs

The forelegs are short and flattened. The femur is usually rounded and thick basally and narrowed distally. Species of the subgenera *Francmonrosia* and *Goniocanthon* have the ventral side of the femur excavated, and teeth on the anterior margin. The ventral side of the femur has a well-marked anterior margin, and in *C. fulgidus* (subgenus *Goniocanthon*) the margin forms a keel. In none of the specimens of this species examined did I observe a well-marked tooth as mentioned by Pereira &

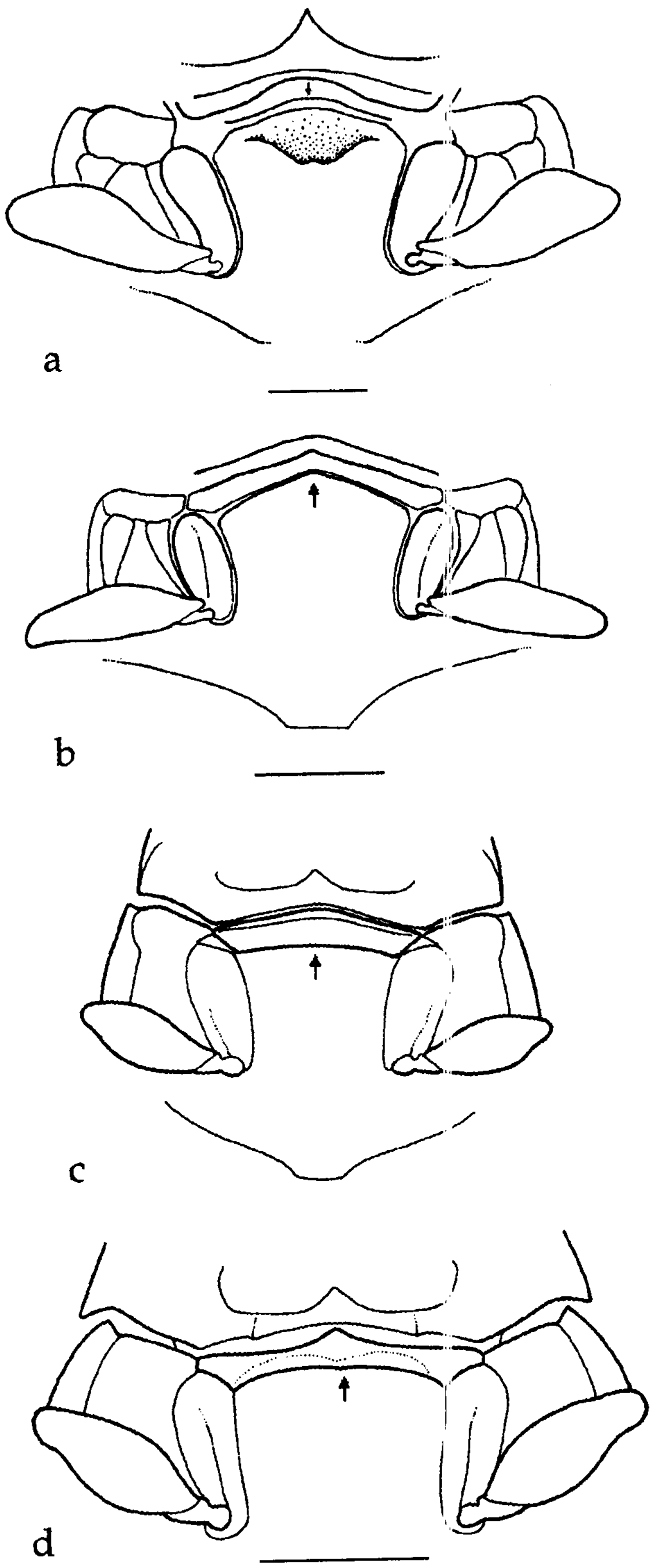


Figure 20. Mesosternum. **a**. *Canthon fulgidus* Redtenbacher. **b**. *C. luteicollis* Erichson. **c**. *Pseudocanthon* sp. **d**. *Sylvicanthon bridarollii* Martínez. Scale bar = 2 mm.

Martínez (1956) and Halffter (1961). The variation of the femur in species of *Canthon* is mainly in the form and in the sculpture, but no discernible pattern was observed.

The tibia is dorsally flattened, distally broad, and is overlapped over by two longitudinal keels dorsally as well as ventrally. These keels are generally parallel to the lateral margin of the tibia, but the pattern they follow varies among species. The dorsal keels are covered by long and thick setae, whereas the ventral keels are covered by short spines. The outer lateral margin of the tibia is serrated with small teeth, and in the medial and distal part there are three well-developed triangular teeth. In some species the third tooth is very reduced, and in the males of *C. angustatus* it is absent. These teeth vary in position and orientation. In many species of *Canthon* the teeth occupy the distal half of the tibia, as in the subgenera *Boreocanthon* and *Canthon*, including the species of the *pilularius* group. In the subgenus *Glaphyrocanthon* (except *C. angustatus*), *C. tetraodon*, *C. staigi*, and *C. perseverans*, the teeth also occupy most of the distal half of the tibia (Figures 21a, 21b and 22a). Outside of *Canthon* this pattern is present in the genus *Malagoniella* and in species of the genus *Melanocanthon*. In other species the teeth are located on the distal one-third of the tibia, as in *C. aequinoctialis*, *C. bicolor*, *C. cyanellus*, *C. fulgidus*, *C. quinquemaculatus*, *C. triangularis*, and *C. septemmaculatus* (Figures 21c and 21d). The other genera of Canthonina examined also have the teeth distally located, except *Malagoniella* and *Melanocanthon* (Figures 22c, 22d and 23a).

The size and orientation of the teeth on the tibia vary among species. The anterior tooth is usually larger than the second, and this is in turn larger than the third. In *C. lunatus tibialis* and *C. maldonadoi* the anterior tooth is larger than the second, much more so than what is usually observed in other species of *Canthon* (Figure 23b). In general, species with teeth on the anterior half of the tibia have them laterally oriented, whereas species with apical teeth have them directed obliquely.

One feature that has been traditionally used in the separation of subgenera is the shape of the anterior margin of the tibia, which can be transversal or oblique. The most common pattern in species of *Canthon* is the tibia with the anterior margin obliquely truncated as was clearly observed in *C. bicolor* (Figure 22b). However, much variation was observed in this feature. In general, the species of the subgenus *Boreocanthon* and

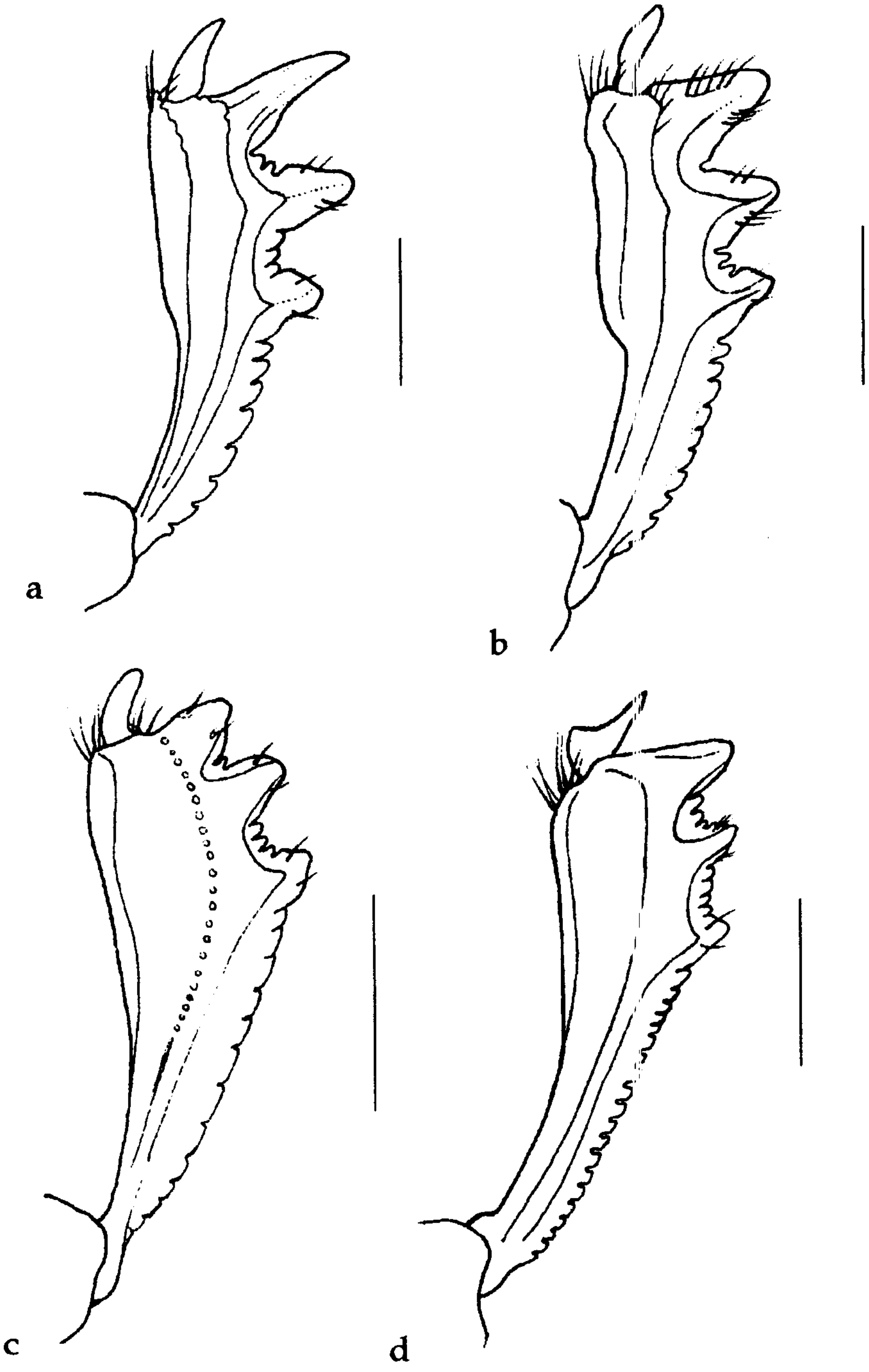


Figure 21. Fore leg. **a**. *Canthon ebenus* Say. **b**. *C. deyrollei* Harold. **c**. *C. triangularis* Drury. **d**. *C. aequinoctialis* Harold. Scale bar = 1 mm.

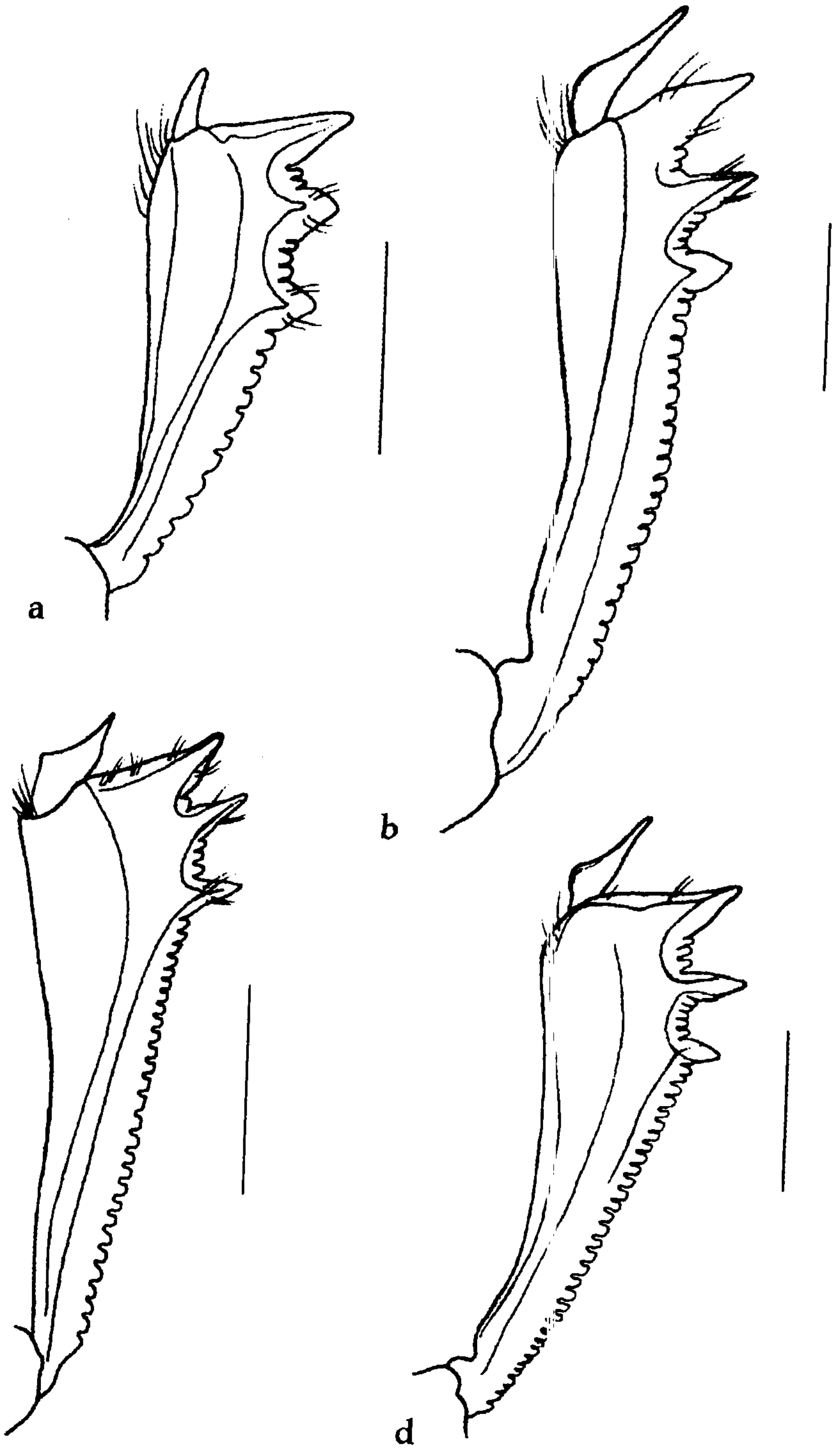


Figure 22. Fore leg. **a**. *Canthon femoralis* Chevrolat. **b**. *C. bicolor* Laporte. **c**. *Hansreia affinis* Fabricius. **d**. *Sylvicanthon bridarollii* Martínez. Scale bar = 1 mm.

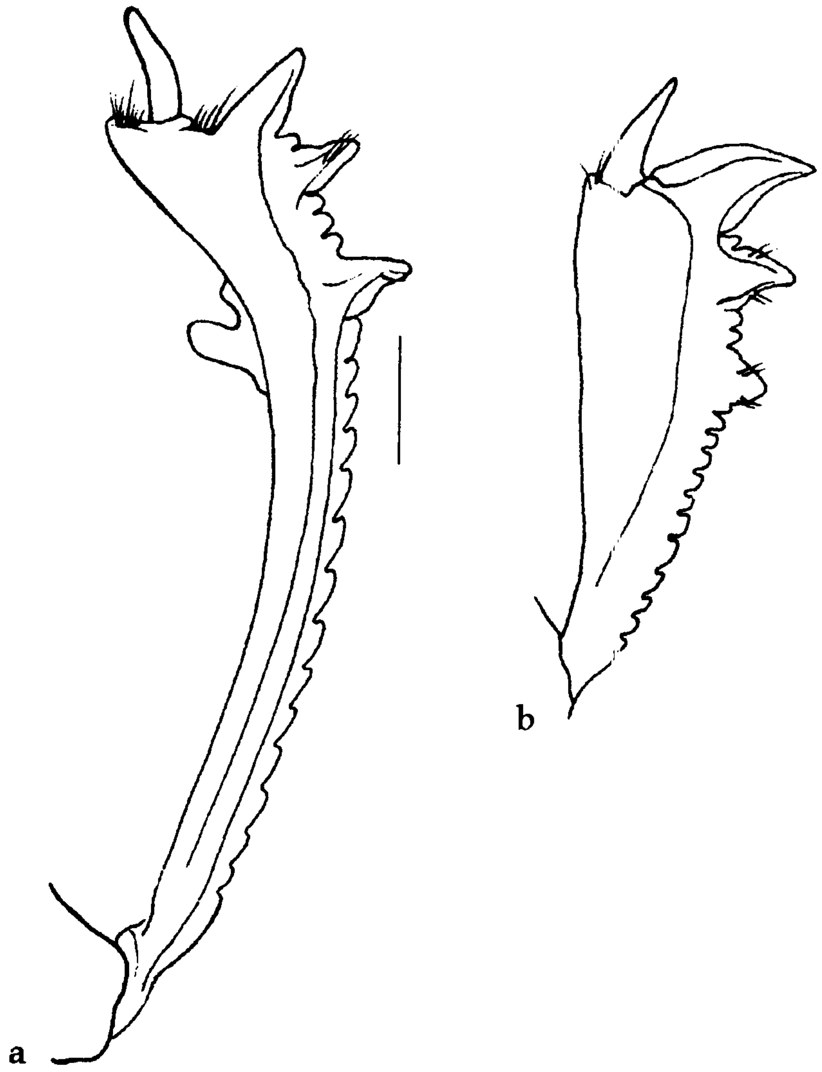


Figure 23. Fore leg. **a**. *Deltochilum gibbosum* Fabricius. **b** *Canthon lunatus tibialis*. Scale bar = 1 mm.

the species of the *deyrollei* and *pilularius* lines have a transverse margin on the tibia (Figure 21b).

Medial and posterior legs

The medial and posterior tibiae are elongated and rectangular. The middle femur is thick and can have a fringe on its anterior margin, a feature that has been used in the definition of some subgenera of *Canthon*. The ventral surface of the medial femur is usually smooth and without long setae. However, in *C. violaceus*, *C. bicolor*, *C. tetraodon*, and *Malagoniella astyanax* there is a small series of setae longitudinally arranged on the posterior end of the femur (Figures 24a-24d).

The dorsal side of the medial tibia has two parallel rows of spines over the lateral margins of the tibia. With the exception of *C. lunatus tibialis* and the species of the subgenus *Boreocanthon*, all the species of *Canthon* studied shared this pattern (Figures 25a-25f). In the other genera of Canthonina examined, the rows of spines running over the lateral margins of the dorsal surface were also observed, except in *Canthonella*. In *Malagoniella* I did not observe continuous parallel rows of spines as in *Canthon*. In most of the species the spines of the internal row are thin and close together forming a comb-like structure. In species of the subgenus *Boreocanthon* a continuous row of spines was not observed; there are fewer spines on the inner row (less than ten) and they are widely separated (Figure 25b). In *C. violaceus* the outer row is interrupted before reaching the posterior end of the tibia (Figure 25c), and in *C. staigi* the outer row of spines begins approximately at the posterior half of the tibia (Figure 25d). In species of the subgenus *Boreocanthon* the outer row has more than one spine arising from the same point, in contrast with the other species, which have a single spine at each point (Figure 25b). In *M. astyanax* the outer row has setae spread on the anterior half of the tibia and then small clumps of setae.

In several species of *Canthon* the posterior half of the dorsal face of the middle tibia has small tubercles with setae. In *C. tetraodon* the integument is raised forming a small transversal carina (Figure 25e). This carina crosses the dorsal face of the tibia transversally and has spines over its surface. In other species of *Canthon*, mainly in the subgenera *Boreocanthon* and *Canthon* (including the *pilularius* group and *C. aberrans*),

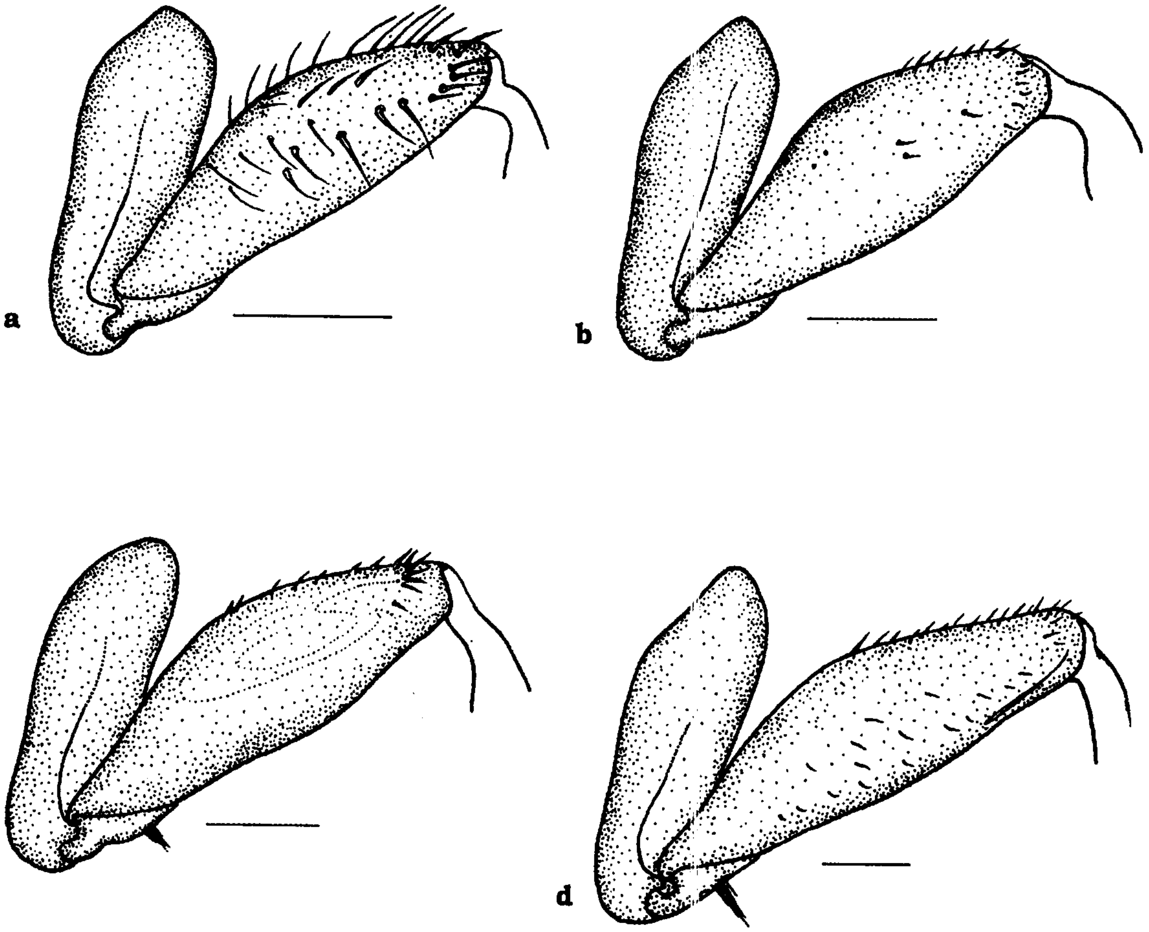


Figure 24. Ventral face of the femur of the middle leg. **a**. *Canthon violaceus* Olivier. **b**. *C. tetraodon* Blanchard **c**. *C. bicolor* Laporte. **d**. *Malagoniella astyanax* Blanchard. Scale bar = 1 mm.

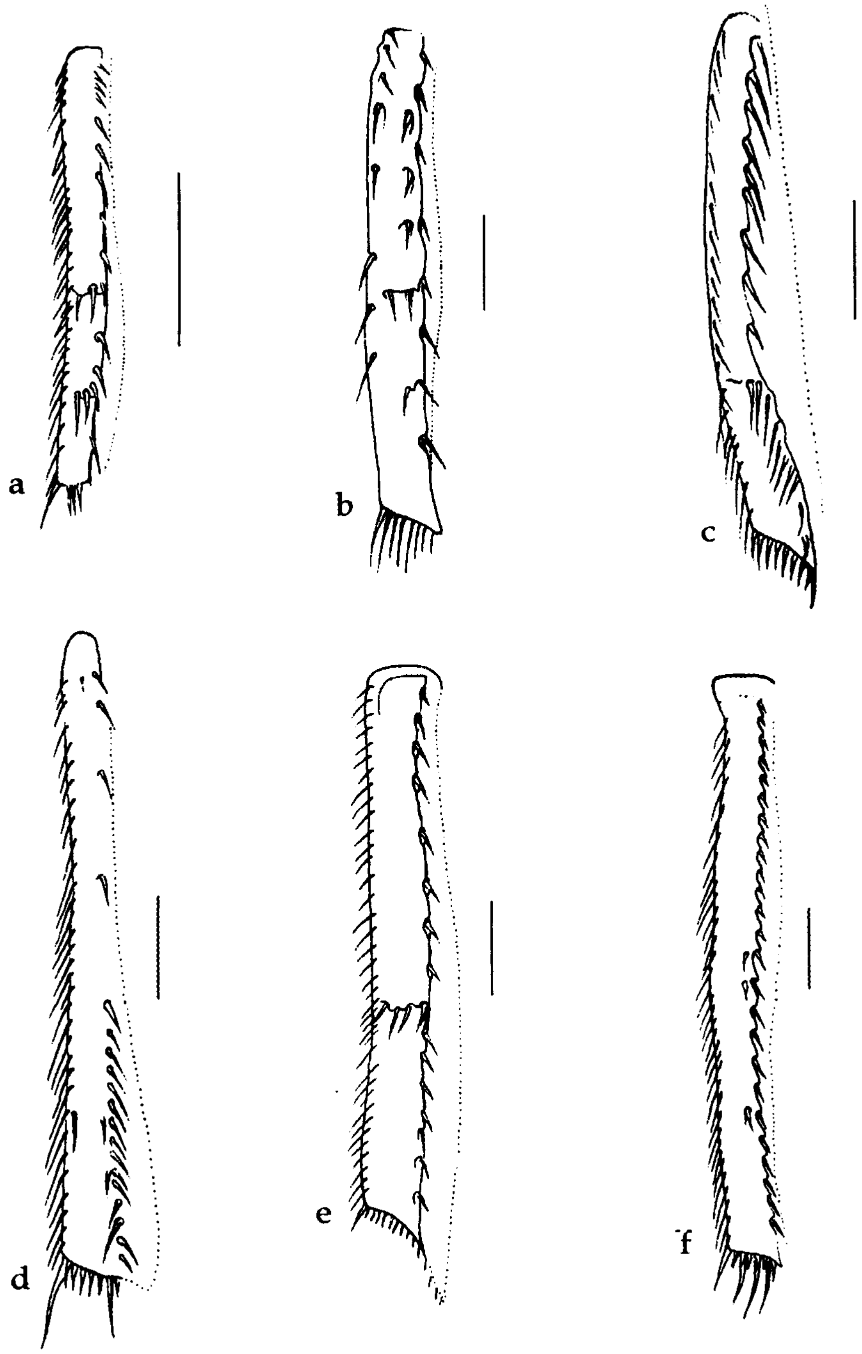


Figure 25. Dorsal face of the middle tibia. **a**. *Canthon lunatus tibialis* Schmidt. **b**. *C. ebenus* Say **c**. *C. violaceus* Olivier. **d**. *C. staigi* Pereira. **e**. *C. tetraodon* Blanchard. **f**. *C. chalcites* Haldemann. Scale bar = 0.5 mm.

small protuberances with spines on top were observed, next to the main outer row of spines (Figures 25b and 25f). In some species of the subgenera *Glapyrocanthon* (*C. angustatus*, *C. femoralis*, *C. politus*, *C. semiopacus*), *Trichocanthon* (*C. sordidus*), *Peltecanthon* (*C. staigi*), and also in *C. quinquemaculatus*, *C. perseverans*, *C. septemmaculatus* and *C. triangularis*, there are one or more extra spines on the posterior half of the tibia, next to the outer row of spines (Figures 26a-26d). Only in specimens of *C. pallidus* were no extra spines or setae observed near the outer row of spines (Figure 26e).

On the apex of the dorsal face of the middle tibia there is usually a continuous row of spines. There is variation in this row; usually in *Canthon* this row is continuous, but it also can be interrupted such as in species of the subgenus *Glaphyrocanthon* (Figure 26e).

At the distal end of the middle tibia there are two spurs, one larger than the other. In the posterior tibia only one spur is present, a character common to all Scarabaeinae, except in species of *Melanocanthon*, which have two well-developed spurs.

The tarsi of the middle and hind legs are similar. They are usually trapezoidal, although in some species they are triangular. The size of the first tarsal segment of the hind leg relative to the second one has had taxonomic value. In the species of *Canthon* examined, however, differences in the size of the tarsi not were found; most species have the first tarsus as large as the second; only in *C. tetraodon* and *C. lunatus tibialis* is the first tarsus shorter than the second. In the genera *Scybalocanthon* and *Sylvicanthon* the basal tarsus is smaller than the second, and this character is useful for differentiating these genera from *Canthon*. Species of the genus *Deltochilum* also have the first tarsus smaller than the second. The tarsi of *Scybalocanthon* also show differences with respect to those of *Canthon*; in *Scybalocanthon* they are rectangular, usually thin and without separations between tarsi, which gives them the appearance of a complete block. Nonetheless, in some species of *Scybalocanthon* the tarsi are like those of *Canthon*.

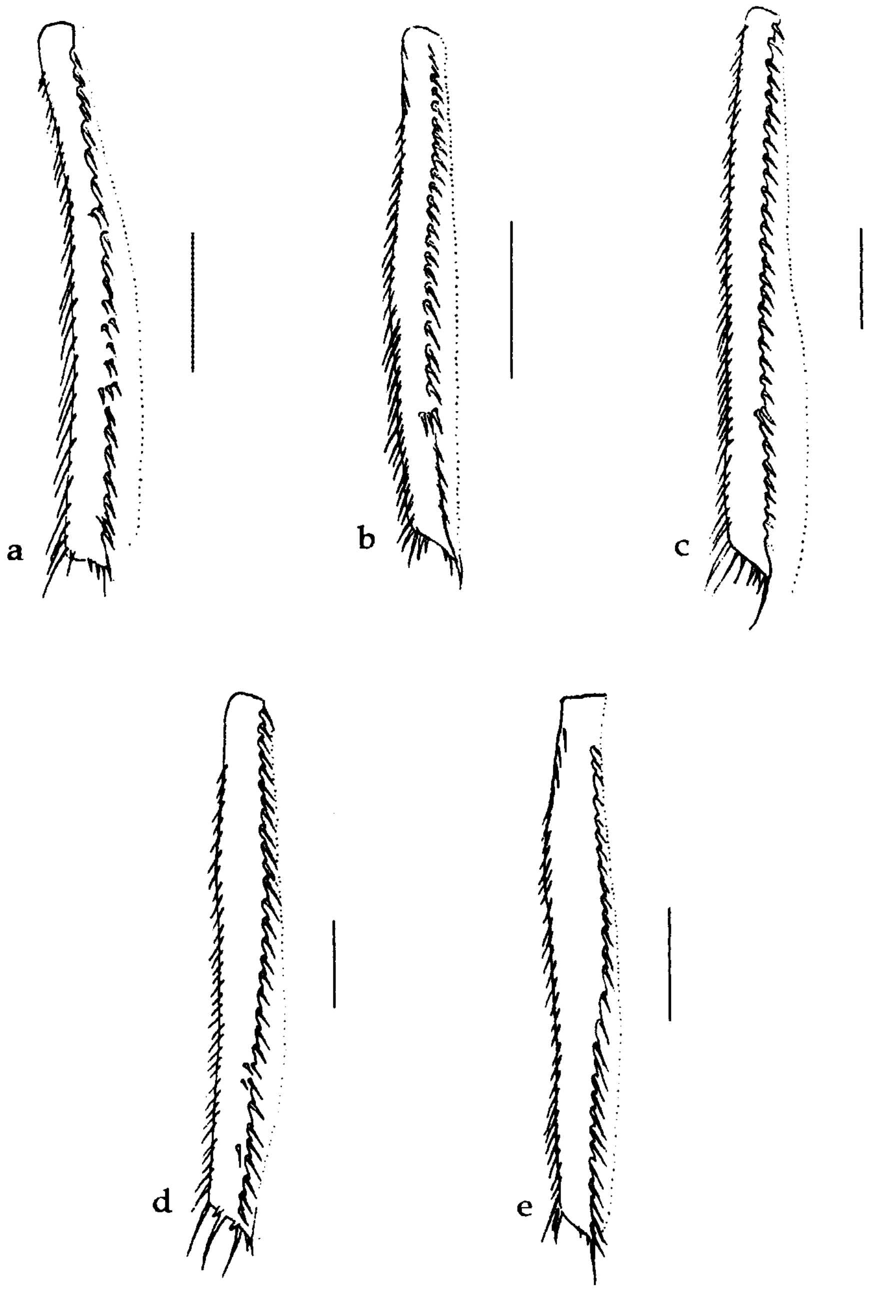


Figure 26. Dorsal face of the middle tibia. **a**. *Canthon simplex* LeConte. **b**. *C. sordidus* Harold. **c**. *C. quinquemaculatus* Laporte. **d**. *C. femoralis* Chevrolat. **e**. C. *pallidus* Schmidt. Scale bar = 0.5 mm.

Elytra

In the Scarabaeinae, the elytra completely cover the abdomen except for the pygidial area. In *Canthon* the elytra are rectangular and slightly convex, with the margins curved inward. In species of *Canthon*, the anterior and humeral regions of the elytra have gibbosities and protuberances. These protuberances are well-developed in species of the subgenus *Nesocanthon* (*C. callosus* and *C. violaceus*).

In species of the subgenus *Boreocanthon* such as *C. ebenus*, *C. nyctelius* and *C. praticola*, these protuberances are in the medial part of the elytron. In other species they are restricted to the humeral region, and are smaller (e.g., *C. chalcites*, *C. sordidus*, C. *lunatus tibialis*, *C. maldonadoi* and *C. tetraodon*).

Canthon species have nine elytral striae, except *C. sordidus* of the subgenus *Trichocanthon* which only has eight. The ninth stria is generally difficult to observe, and in some species it is visible only on the posterior part of the elytron. The striae can be well marked or slightly marked on the elytra; usually the well-marked striae are present in species with coarsely sculptured elytra, whereas the slightly impressed striae are present on very smooth and glossy elytra. The humeral striae can have a thin keel that runs over the anterior half of the elytron. This keel is well marked in *C. bicolor*, *C. staigi* and *C. triangularis*, whereas in other species such as *C. praticola*, *C. cyanellus*, *C. deyrollei* and *C. fulgidus*, it is less pronounced. The humeral keel can show intra-specific variation. Robinson (1948) reported variation in the presence of this keel in individuals of *C. probus*. In other Canthonina, the humeral keel is also present in M. *astyanax* and in species of the genus *Deltochilum*, in which this keel is well developed and an important character in the taxonomy of this group.

In many species of *Canthon*, there are small tubercles among the elytral striae at the base of the elytra. These tubercles vary in their location between the different striae, and can vary in number and size (Figures 27a and 27b). They are also present in *Deltochilum gibbosum*, *Malagoniella astyanax*, and in the genera *Melanocanthon*, *Anisocanthon* and *Scybalocanthon*. Tubercles were not present at the base of the elytra in *C. fulgidus*, C. *septemmaculatus*, *C. tetraodon*, *C. staigi*, *C. sordidus* and *C. triangularis*, or in *Canthonella* and *Cryptocanthon*.

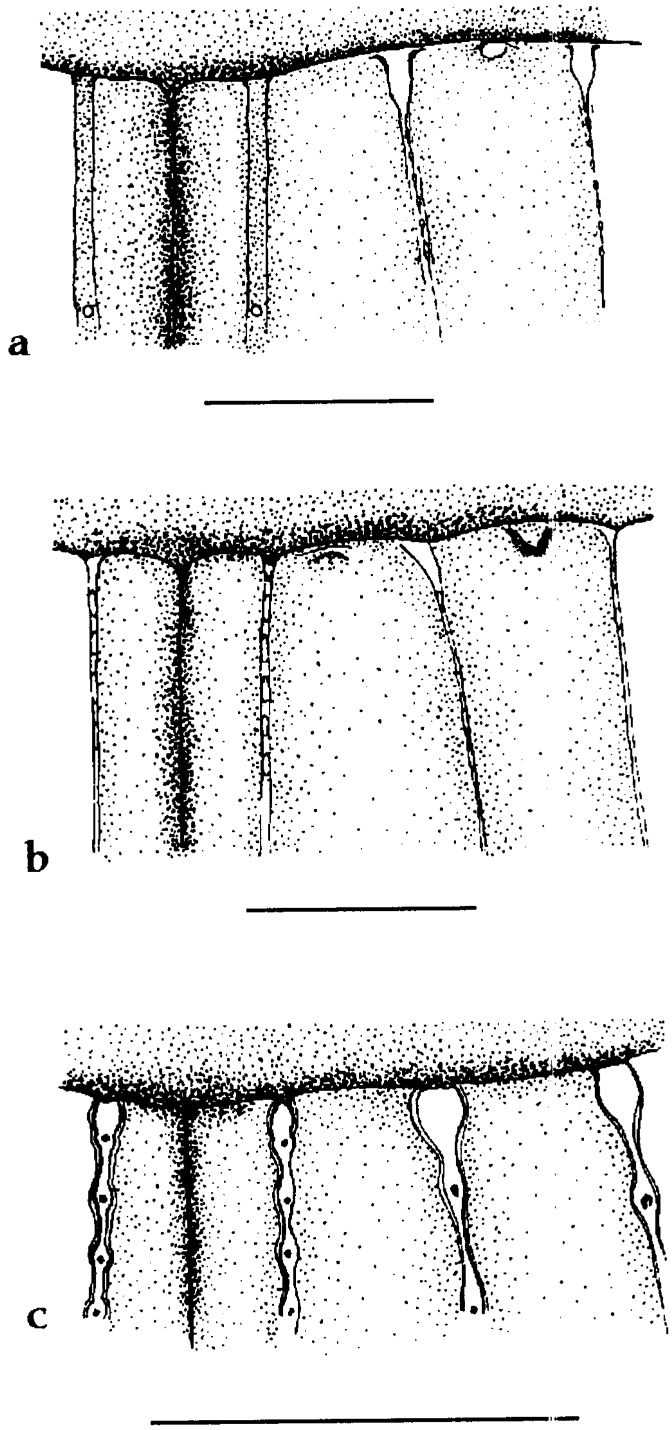


Figure 27. Detail of the base of the elytra, showing tubercles and striae. **a**. *Canthon politus* Harold. **b**. *C. humectus* Say. **c**. *Hansreia affinis* Fabricius. Scale bar = 1 mm.

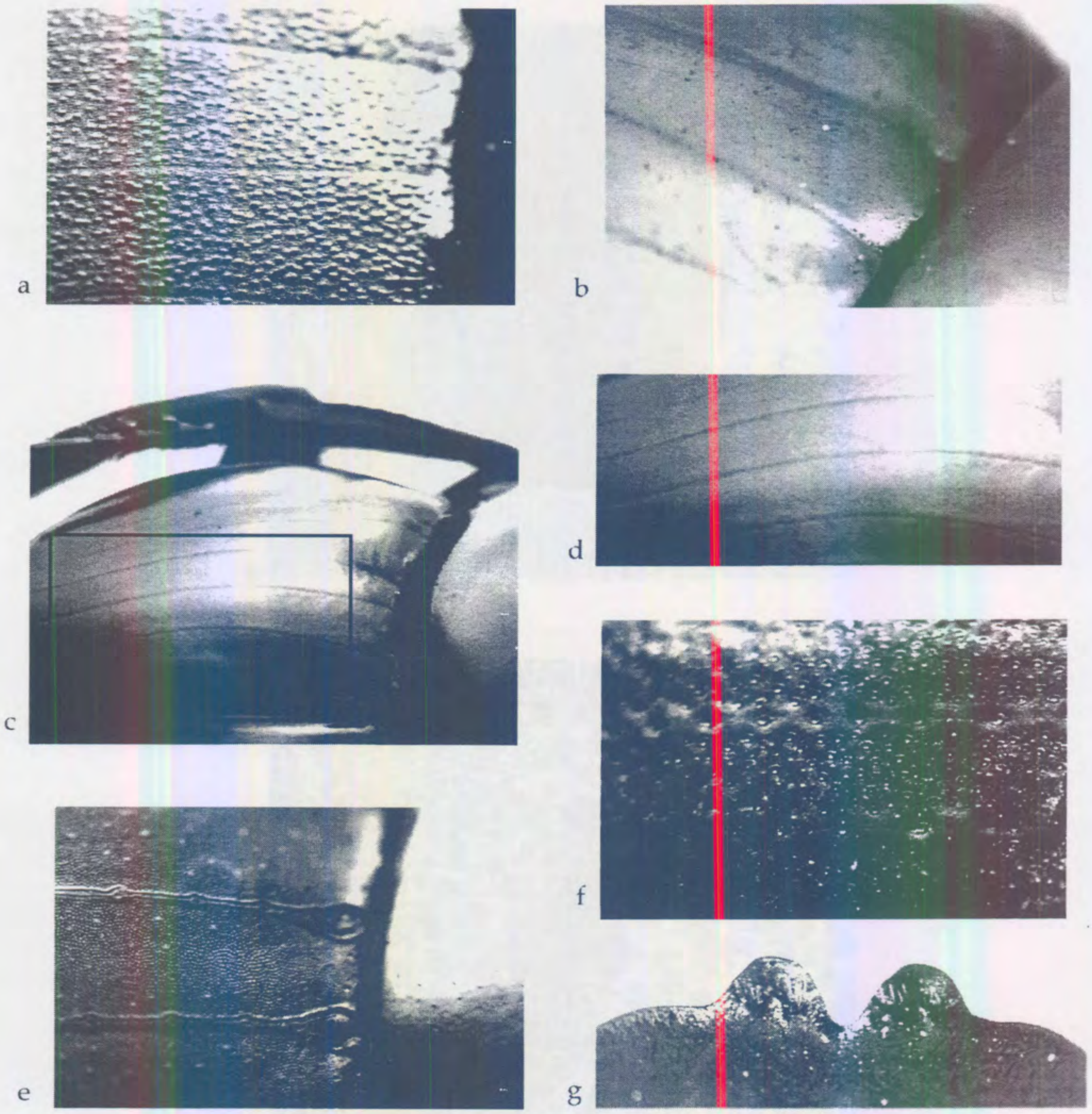


Figure 28. a-f Sculpturing of the base of the elytron. **a**. *Canthon chalcites* Haldemann. **b**. *C. fulgidus* Redtenbacher. **c**. *C. indigaceus* Harold. **d**. Detail enlargement of inset in Figure c, showing the striae of the elytron. **e**. *Hansreia affinis* Fabricius. **f**. *Deltochilum gibbosum* Fabricius. **g**. Detail of the clypeus of *C. fulgidus* Redtenbacher. Figure a magnification = 20x, figures b, d, and f magnification = 40x, figure c magnification = 15x, figure e and g magnification = 30x.

In several groups of *Canthon* the striae of the elytra are weakly impressed and barely noticeable. However, in species of the *pilularius* group, the striae are deep furrow-like in shape, or form continuous grooves along the elytron (Figure 28a). In the species of the subgenus *Boreocanthon* the striae are also formed by furrows; in some species the furrow can be wide and well-marked as in *C. nyctelius*. In *Canthon*, the striae are usually formed by thin lines interrupted by smooth areas. The striae are formed by continuous lines only in the species of the *pilularius* group, in *C. lunatus tibialis*, *C. ebenus* and *C. praticola*. In other genera of Canthonina the striae are more developed than in *Canthon*, and can be formed by a wide fringe and with punctures in the middle as was observed in species of *Deltochilum* and *Hansreia* (Figures 27c, 28e and 28f). In some species of *Canthon* the striae are wide at the base of the elytron where the sculpture is more marked, but they become slender and weak on the smoother and polished areas of the elytron (e.g., *C. politus*, Figure 27a).

The elytra of *Canthon* are generally glabrous, although some species have thick setae. These setae can be arranged in rows among of striae of the elytron, as in *C. sordidus* and *A. villosus*, or be randomly distributed over the surface as in *C. juvencus*

Sculpture

The sculpturing is responsible for the general appearance of the body, which can be smooth and glossy, coarse and opaque, or smooth and translucent. It includes granules, different kinds of punctures and microsculpture (fine sculpturing among granules and punctures). In *Canthon* it can vary on the surface of the head, thorax and elytra. I studied the variation of the sculpturing (including the microsculpturing) mainly on the elytra.

The dorsal appearance of most species of *Canthon* is smooth, without marked sculpturing. However, in some species, particularly those of the subgenus *Boreocanthon*, the texture is coarse. Species in this subgenus have the surface of the body with granules and marked punctures (Figures 28a). Four main sculpturing patterns were found on the elytra of the species of *Canthon* examined. The first is a sculpturing of large and small granules that was observed in *C. praticola*, *C. ebenus*, and *C. chalcites* (Figure 28a). The second pattern consists of small granules uniformly distributed on the surface of the head and elytra, as in *C. monilifer*, *C. sordidus*, *C. humectus*, and C.

lunatus tibialis. Another pattern consists of widely spaced minute punctures, which can be observed only at 60x magnification with a light diffuser. This pattern is common in species of *Canthon* and it was observed in *C. quinquemaculatus*, *C. femoralis*, *C. cyanellus*, *C. politus*, and *C. quadriguttatus*, among others. The last pattern is present in species with very smooth and shiny elytra such as *C. violaceus*, *C. fulgidus*, *C. bicolor*, species of the *viridis* group, and some species that have translucent elytra like *C. angustatus*. The texture of the elytra in these species is without granules and punctures (Figures 28b, 28c and 28d).

Pygidium

The pygidium is triangular, wider than long and usually convex. Some species have the pygidium more convex and in some species it is a conical projection, as in *C. speculifer* and species of the subgenus *Goniocanthon*. The pygidium is separated from the prepygidium by a carina, which is generally well-marked in species of *Canthon*. The prepygidium is a short sclerite that varies in width, as well as in the presence and shape of the longitudinal sulcus that crosses the prepygidium in its medial part (Figure 29). The presence of a carina on the anterior margin of the pygidium has been useful in the differentiation of genera of Canthonina. According to the literature, genera such as *Anisocanthon* and *Scybalocanthon* differ from species of the genus *Canthon* because they lack both a carina and keel on the anterior region of the pygidium (Martínez & Pereira 1956, Halffter & Martínez 1977). However, species of *Canthon* such as *C. septemmaculatus*, *C. monilifer* and *C. triangularis* do not have a carina on the anterior margin of the pygidium either (Figure 29c). According to Howden & Gill (1987), *C. hartmanni* also lacks of a fringe on the anterior margin of the pygidium either.

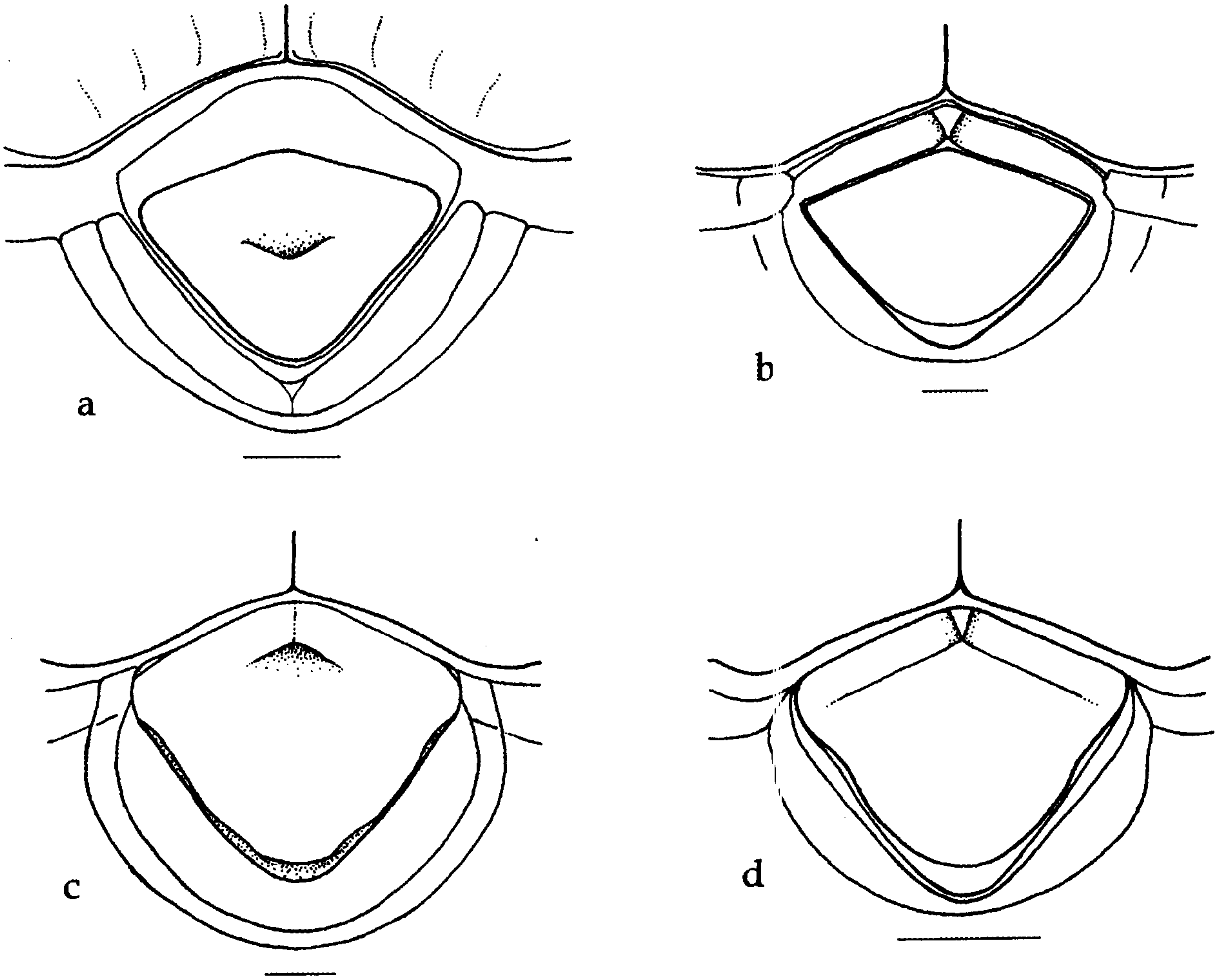


Figure 29. Pygidium. **a**. *Canthon politus* Harold. **b**. *C. indigaceus* Harold. **c**. *C. triangularis* Drury. **d**. *Scybalocanthon moniliatus* Bates. Scale bar = 1 mm.

Male genitalia

Aedeagus

In the literature on Scarabaeinae the term aedeagus is commonly used to refer to the copulatory organ of the male. It is a sclerotized capsule externally formed by a tube known as the tegmen. The latter is formed by a basal piece, the medial lobe, and the parameres, which are distally located (Sharp & Müir 1912). Different authors use different nomenclature to refer to the external genitalia of the male. Halffter (1961) called the basal part "tambor" (drum) and Snodgrass (1935) used aedeagus to refer to the distal part of the phallus. I use the term aedeagus to refer to the entire copulatory capsule, formed by the tegmen and the parameres, as used in d`Hotman & Scholtz (1990).

The aedeagus has had taxonomic value in *Canthon* (Halffter 1961) and related groups (Halffter & Martínez 1976). The form of the parameres is of taxonomic importance and marks the difference among different types of aedeagus. The parameres can be asymmetrical as in *C. aberrans*, or symmetrical as in most species of *Canthon*. In *Canthon* the parameres are usually rectangular, although in some species they narrow toward the apex. There are four main types of aedeagus in *Canthon*. The most simple has triangular parameres, such as in *C. violaceus*, *C. perseverans*, *C. bicolor*, *C. aequinoctialis* and *C. luteicollis* (Figure 30a). Another type has more or less rectangular parameres, with the apex completely truncated transversally as in some species of the subgenus *Canthon* (*C. humectus*, *C. chiriguano*), the subgenus *Glaphyrocanthon* (*C. angustatus*, *C. femoralis*, C. *semiopacus* and species of the *viridis* group), and in *C. triangularis*, *C. septemmaculatus*, C. *lunatus tibialis*, C. *fulgidus*, and *C. staigi* (Figure 30b). A third type is shared by species of the subgenus *Boreocanthon*, as well as the subgenus *Canthon* (*pilularius* and *quinquemaculatus* lines). These species have boot-shaped parameres, with an inwardly curved tooth in ventral position (Figure 31d). The tooth can vary from sharp to truncate but was always present in the species of this group.

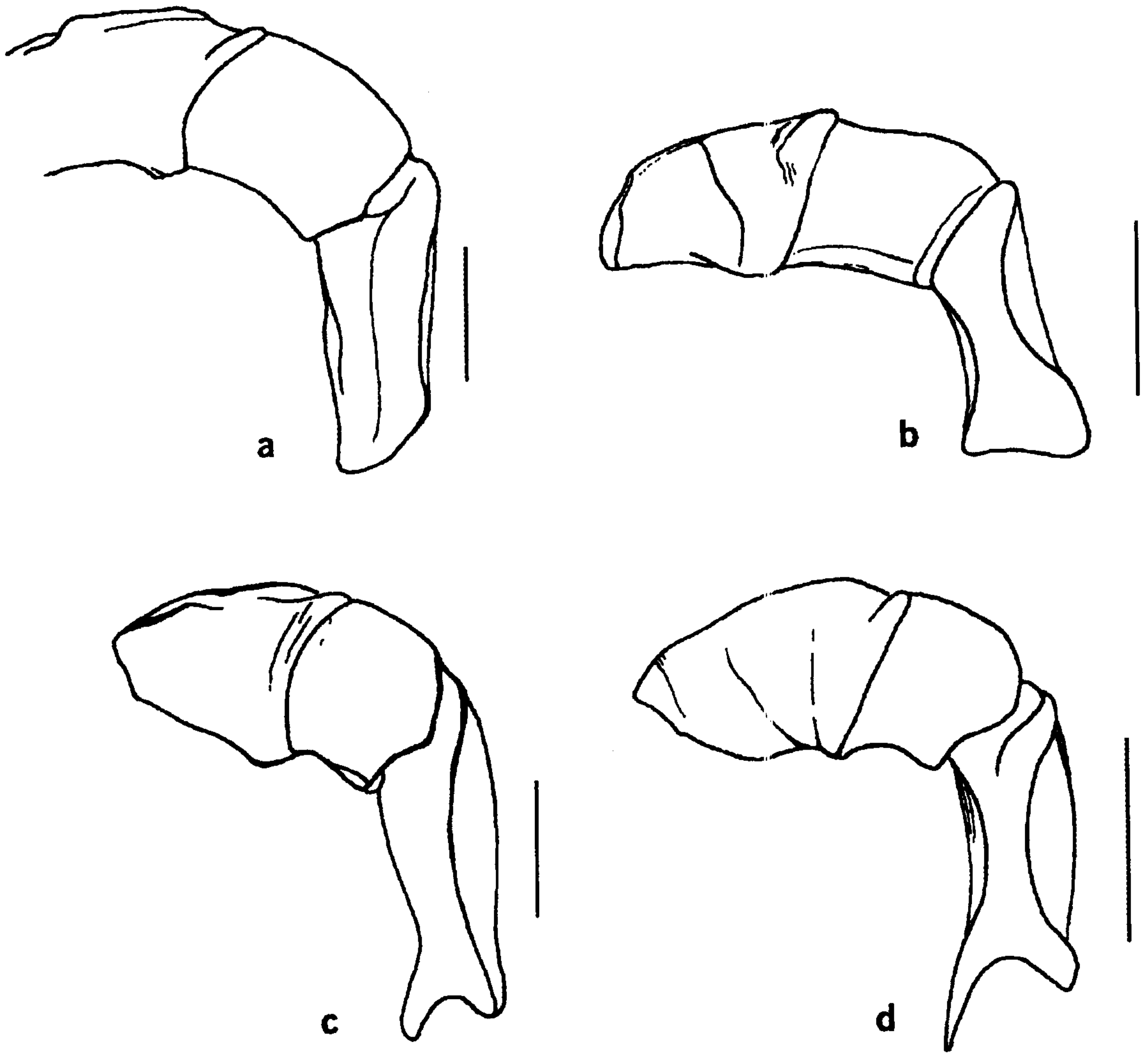


Figure 30. Lateral view of the aedeagus. **a**. *Canthon aequinoctialis* Harold. **b**. *C. staigi* Pereira. **c**. *C. monilifer* Blanchard. **d**. *C. deyrollei* Harold. Scale bar = 1 mm.

Figure 31. Scheme of the internal sac of the aedeagus of *Canthon bicolor*. **sc** = sclerites **br** = brushes of internal sac. **te** = temones. Scale bar = 2 mm.

A fourth type of aedeagus was observed in other species such as *C. politus* and *C. cyanellus*. The parameres in these species narrow toward the apex and in ventral side is sinuate. This type was also observed in *C. maldonadoi* and *C. monilifer* but the ventral side is deeply sinuated forming an outward projection (Figure 30c). In the other genera of Canthonina the parameres were generally triangular, with the exception of *Hansreia*, which has rectangular and distally truncated parameres as in species of *Canthon*. In *Canthonella* the aedeagus is completely distinct from the rest of *Canthon* or Canthonina examined; the medial lobe is more developed and the parameres are reduced.

Internal sac of the aedeagus

The internal sac of aedeagus is an elongated membranous bag, in which different structures can be distinguished (Figure 31). The internal sac is encased within itself and takes the shape of the chitinous capsule of the aedeagus. Once the sac is extracted different sclerites surrounded by a thick membrane are found. Zunino (1978) called these sclerites accessory lamellae. This same author described for *Onthophagus* a sclerotized structure: the lamella copulatrice, located posteriorly to the accessory lamellae. In *Canthon* the area posterior to the sclerites is generally widening and corrugated (Figure 32a), but is not a defined structure such as in *Onthophagus*, or the chitinous structures found in species of *Deltochilum*.

The medial part of the internal sac has an area where the membrane is internally covered by small spines that give a corrugated appearance to the internal sac. In this area there are some sclerotized structures formed by groups of spines of variable shape and size, which I will refer to as brushes of the internal sac Zunino (1978) referred to this structure as the raspula.

In the posterior end of the internal sac there are two slightly sclerotized plates, called temones (d´Hotman & Scholtz 1990). Before unfolding the internal sac, the temones are folded on both sides of the sac. When the sac is stretched they look like flat plates that have variable shape.

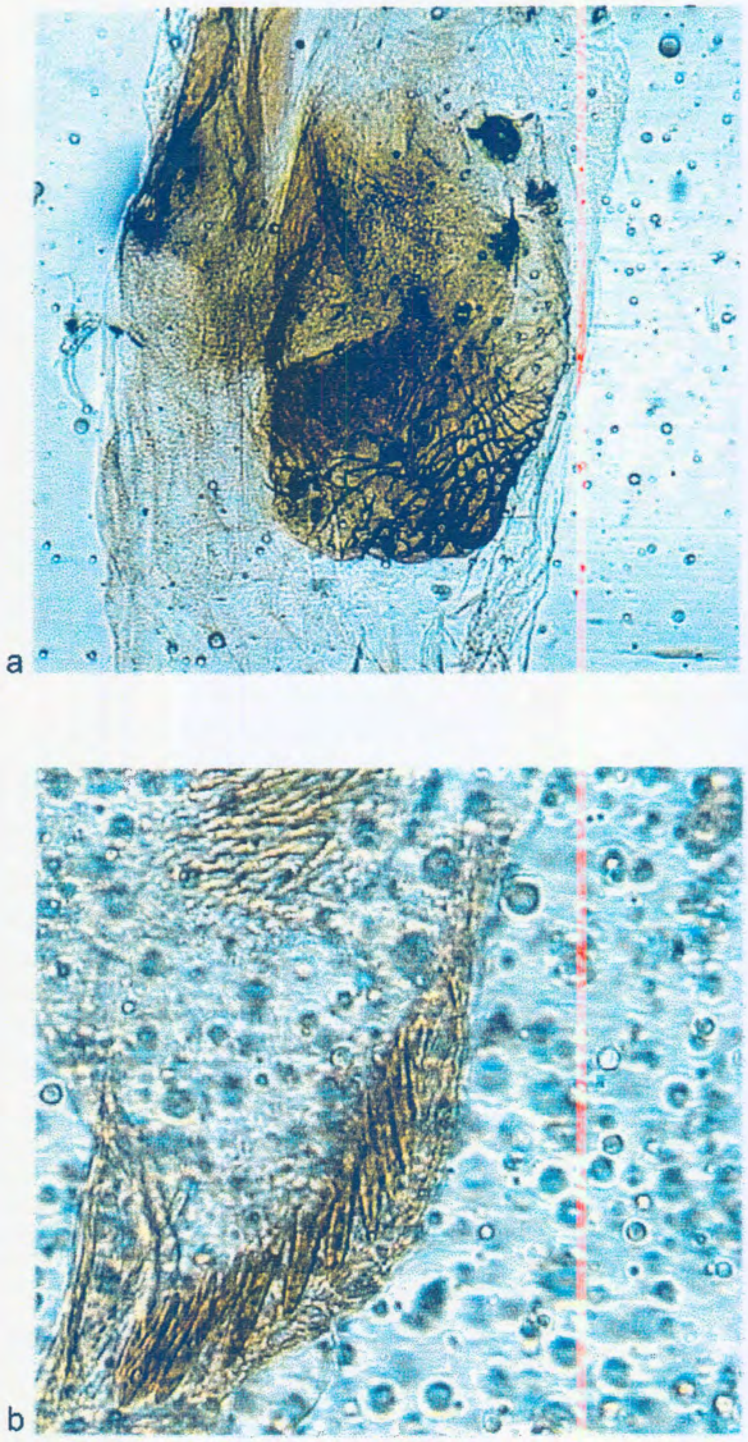


Figure 32. **a.** Detail of posterior area of sclerites in the internal sac of the aedeagus of *Canthon bicolor* Laporte. **b.** Brush of the internal sac of *C. lunatus tibialis* Schmidt. Figure a magnification = 10x, figure b magnification = 40x.

Sclerites of the internal sac

Different types of sclerites are found in the internal sac of *Canthon* and Canthonina. A circular and elongated sclerite is found in all species examined, except in *M. astyanax* and *C. gomezi.* The elongated sclerite is much more variable in its shape and size; it is usually enlarged at one end, and has a projection that narrows toward the other end. These sclerites have some areas strongly sclerotized areas while others are poorly sclerotized (Figure 33). In most species of *Canthon* the elongated sclerite varies in size from 0.3 - 2.0mm; *C. staigi* was the only species of *Canthon* with a 3.0mm elongated sclerite, as large as those found in species of *Deltochilum.*

Other shapes of sclerites were found in *Canthon* (Table 3). These forms include a sclerite with an irregular and generally flattened shape that was found in most species of *Canthon* (Figure 34b and 35a). In species of *Glaphyrocanthon* this sclerite has the appearance of a convex plate (Figure 34a). *C. fulgidus*, *C. violaceus*, *C. staigi* and *C. bicolor* have a horse shoe-shaped sclerite; different from that found in other species (Figure 36). Species of the genus *Deltochilum* also have this type of sclerite. Some species of *Canthon* have one or more small and irregularly shaped sclerites (0.3 - 0.4mm; Figure 35b, 35c and 35d).

Circular sclerite

The circular sclerite is formed by a ring and a chitinous like handle shaped extension. The ring can be rounded or oval, and has a regular or irregular (with deformations) external border. Relative to the ring the handle has a proximal end generally fused or nearest to the ring, and a distal end, which is free, wider and can have a protuberance that I call the handle process (Figure 37a and 37b).

Six different types of circular sclerite were found (Table 4). The type I circular sclerite is a circular plate in which the ring and handle are not completely differentiated, giving the appearance of a coiled structure beginning to unwind. The inner area of the ring is reduced (Figure 38a, 38b). The circular sclerite type II has a differentiated ring fused with the handle. The handle's end distal to the ring is wide and the handle process is not well developed (Figure 38c). This type of sclerite was observed only in species of *Deltochilum.* The type III sclerite has the ring completely separated from the handle,

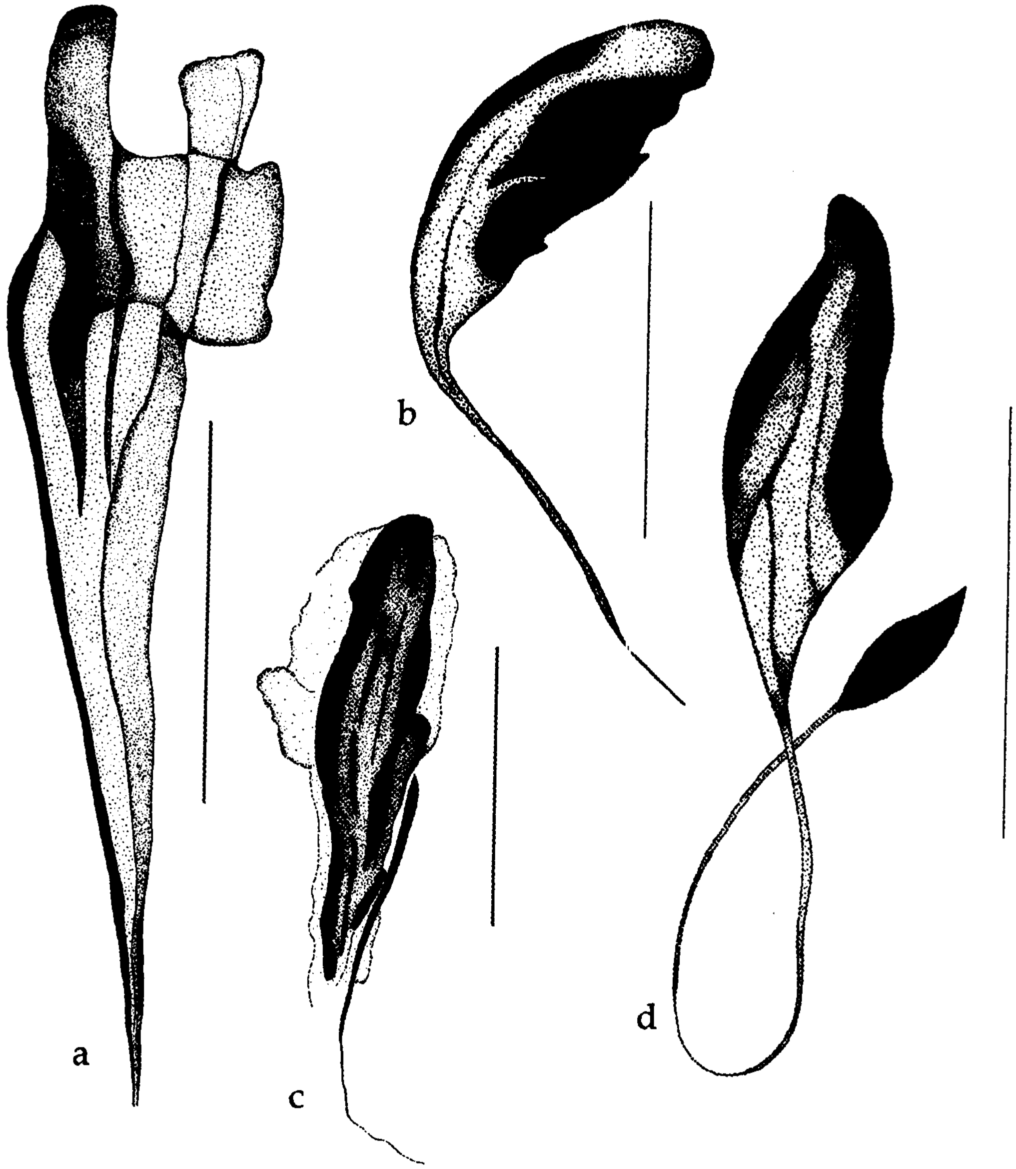


Figure 33. Elongated sclerites of the internal sac of the aedeagus **a.** *Deltochilum hyponnum* Buquet. **b.** *Canthon quinquemaculatus* Laporte. **c.** *C. monilifer* Blanchard. **d.** *C. septemmaculatus* Latreille. Scale bar = 1 mm

Table 3. Sclerites of the internal sac of the aedeagus found in *Canthon* and other genera of Canthonina.

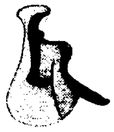
Species					
Canthon ebenus	X	X			
C. praticola	X	X			
C. simplex	X	X			
C aberrans	X	X			
C. chiriguano	X	X			
C. humectus	X	X			X
C. chalcites	X	X			X
C. imitator	X	X			X
C. pilularius	X	X			X
C. indigaceus	X	X			X
C. deyrollei	X	X			X
C. lituratus	X	X			X
C. mutabilis	X	X			X
C. cyanellus cyanellus	X	X			X
C. cyanellus sallaei	X	X			X
C. aequinoctialis	X	X			X
C. morsei	X	X			X
C. juvencus	X	X			X
C. tetraodon	X	X			
C. acutus	X	X			X
C. angustatus	X	X	X		
C. brunneus	X	X	X		
C. columbianus	X	X	X		
C. femoralis femoralis	X	X	X		
C. femoralis bimaculatus	X	X	X		
C. luteicollis	X	X	X		
C. pallidus	X	X	X		
C. politus	X	X			
C. semiopacus	X	X			
C. subhyalinus	X	X	X		
C. viridis viridis	X	X			X
C. meridionalis	X	X			X
C. fulgidus	X			X	
C. violaceus	X			X	
C. staigi	X			X	
C. lunatus tibialis	X	?			X
C. monilifer	X	X			

Table 3 continued

Species					
C. septemmaculatus	x	x			
C. maldonadoi	x	x			
C. quinquemaculatus	x	x			x
C. bicolor	x			x	
C. perseverans	x	x			
C. triangularis	x	x			x
Anisocanthon villosus	x	x			x
Deltochilum aequinoctiale	x			?	
D. gibbosum	x			?	
D. hypponum	x			x	
D. mexicanum	x			x	
D. orbignyi				?	
D. parile	x			?	
Cryptocanthon parvus	x	?			
Hansreia affinis	x	?			
Holocanthon mateui	x	?			
Malagoniella astyanax					?
Melanocanthon bispinatus	x	x			
Megathopa punctatostriata	x				
Scybalocanthon pygidialis	x				
S. trimaculatus	x				
Sylvicanthon bridarollii	x	x			

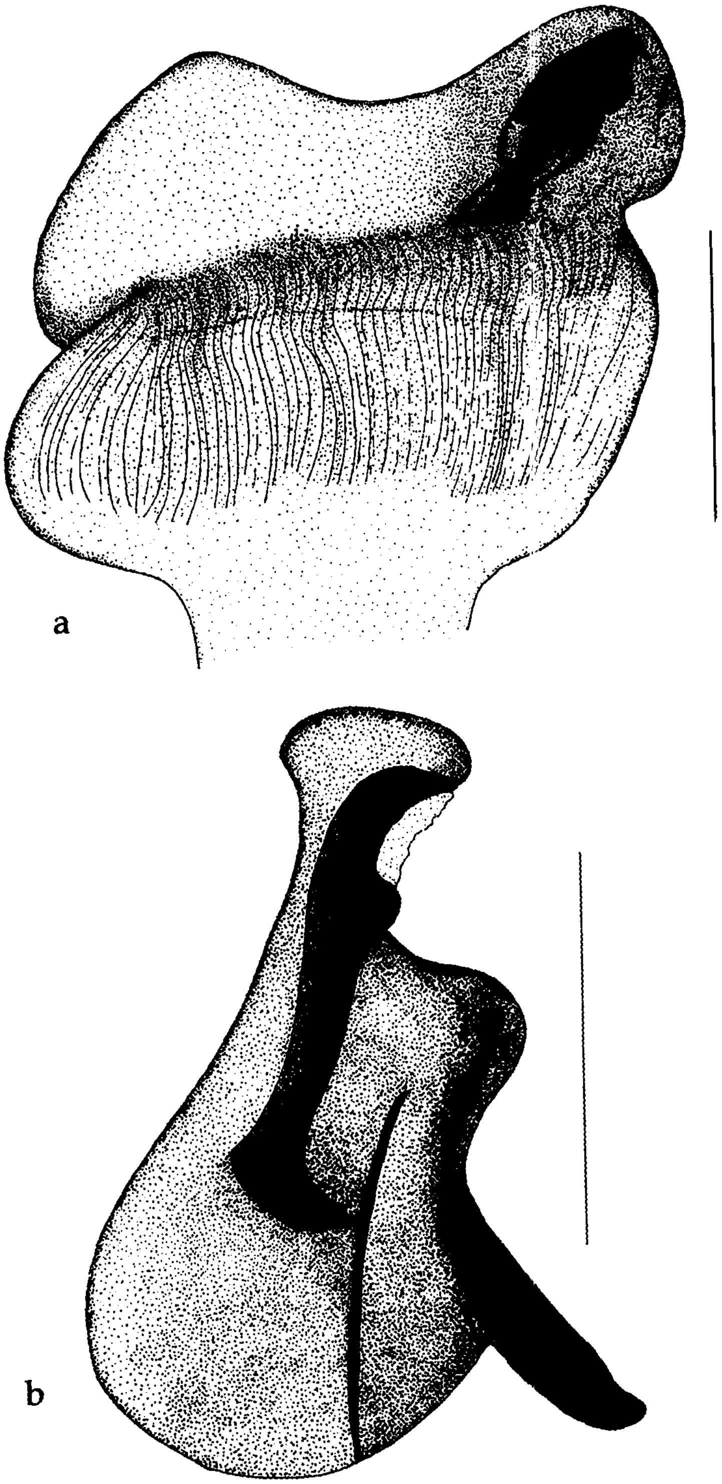


Figure 34. Sclerites of the internal sac of the aedeagus. **a.** *Canthon angustatus* Harold. **b.** *C. politus* Harold. Scale bar = 0.5 mm.

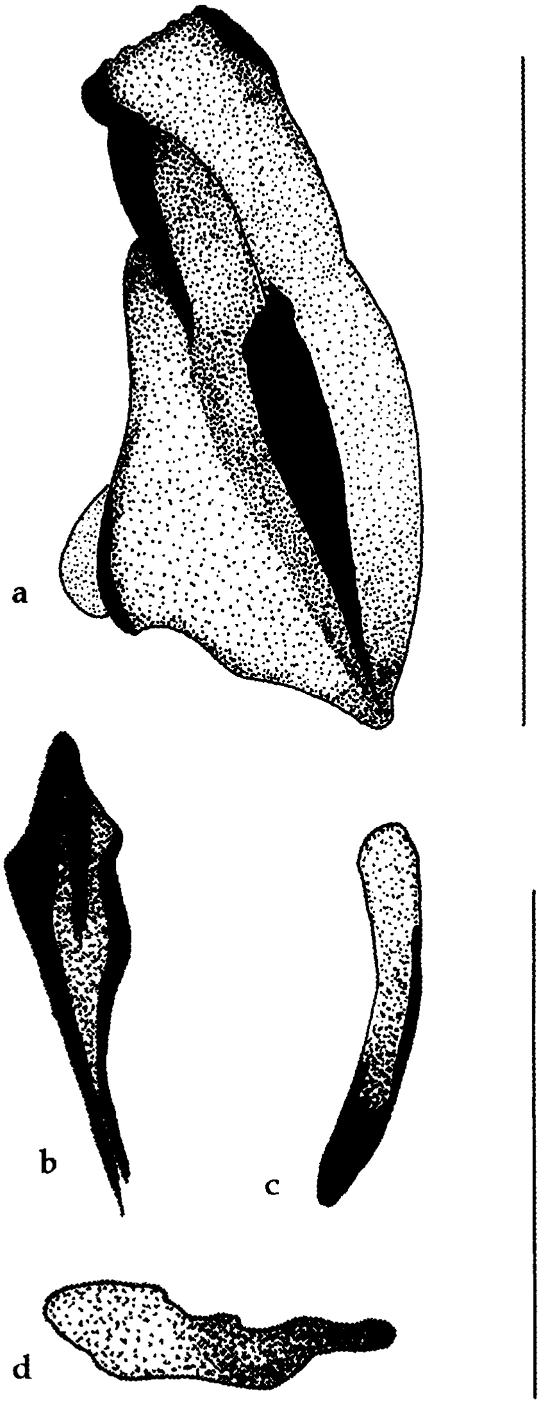


Figure 35. Sclerites of the internal sac of the aedeagus. **a.** *Melanocanthon bispinatus* Robinson. **b and d.** *Canthon indigaceus* Harold. **c.** *C. triangularis* Drury. Scale bar = 0.5 mm.

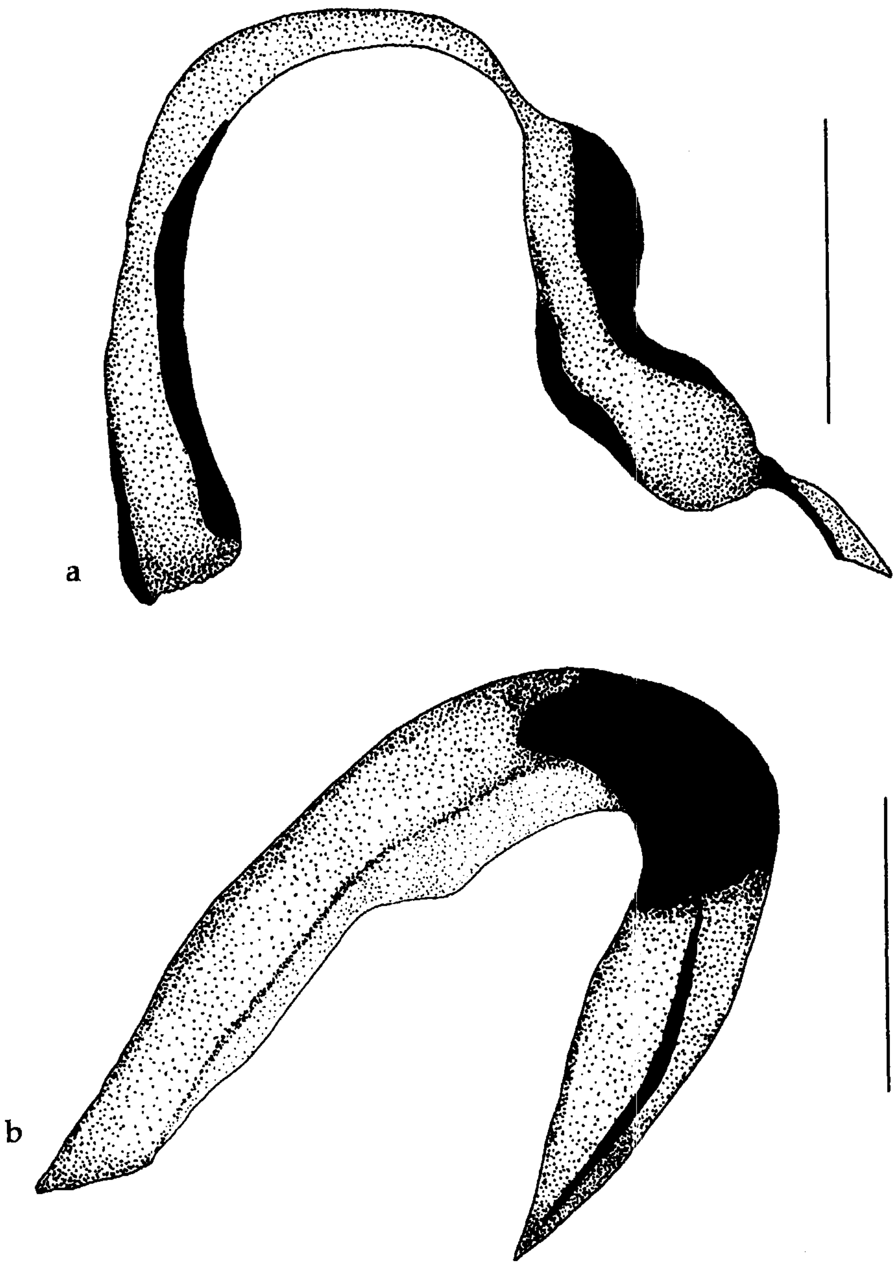


Figure 36. Sclerites of the internal sac of the aedeagus. **a.** *Canthon fulgidus* Redtenbacher. **b.** *C. violaceus* Olivier. Scale bar = 0.25 mm.

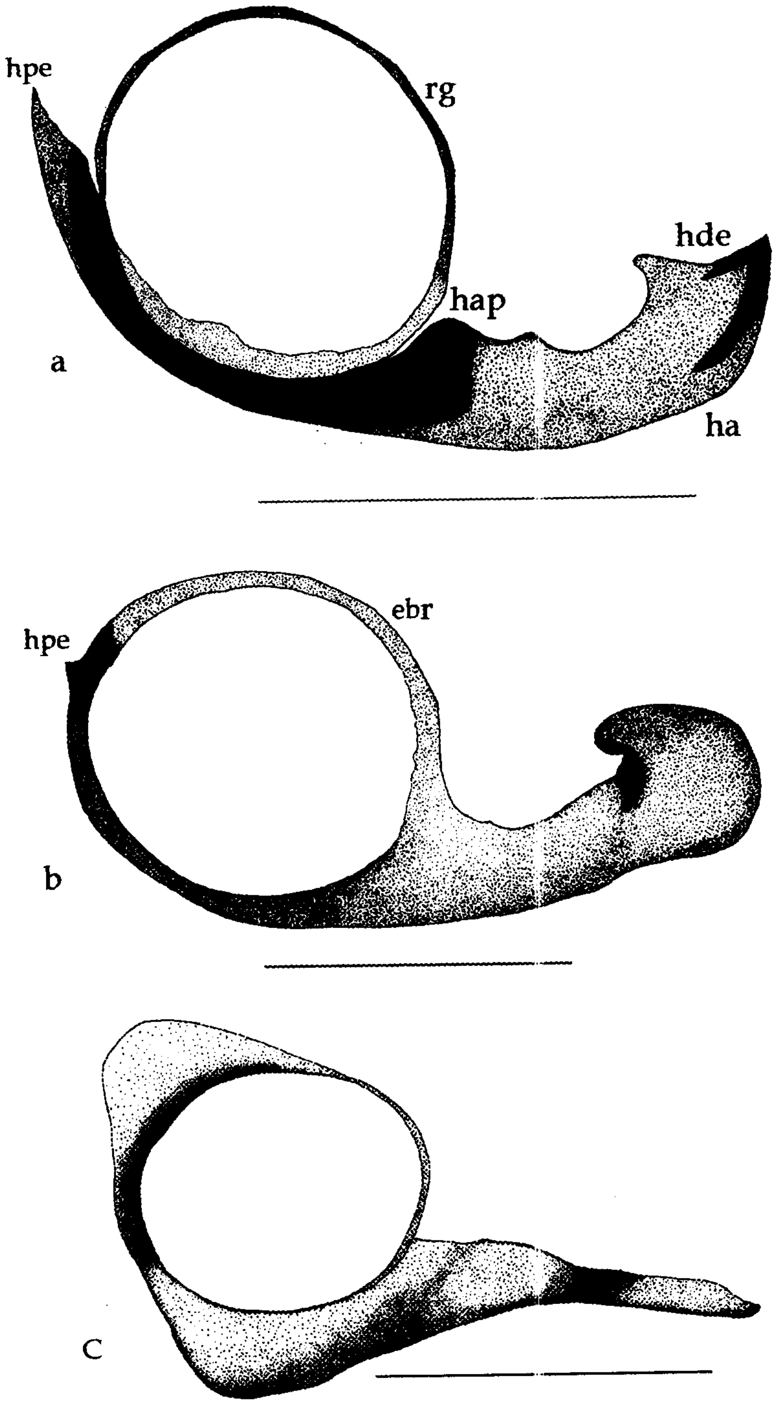


Figure 37. Sclerites of the internal sac of the aedeagus. **a.** *Canthon tetraodon* Blanchard. **b.** *C. politus* Harold. **c.** *C. fulgidus* Redtenbacher. **ebr** = external border of ring, **ha** = handle, **hap** = handle process, **hed** = distal end of handle, **hpe** = proximal end of handle, **rg** = ring. Scale bar = 0.5 mm.

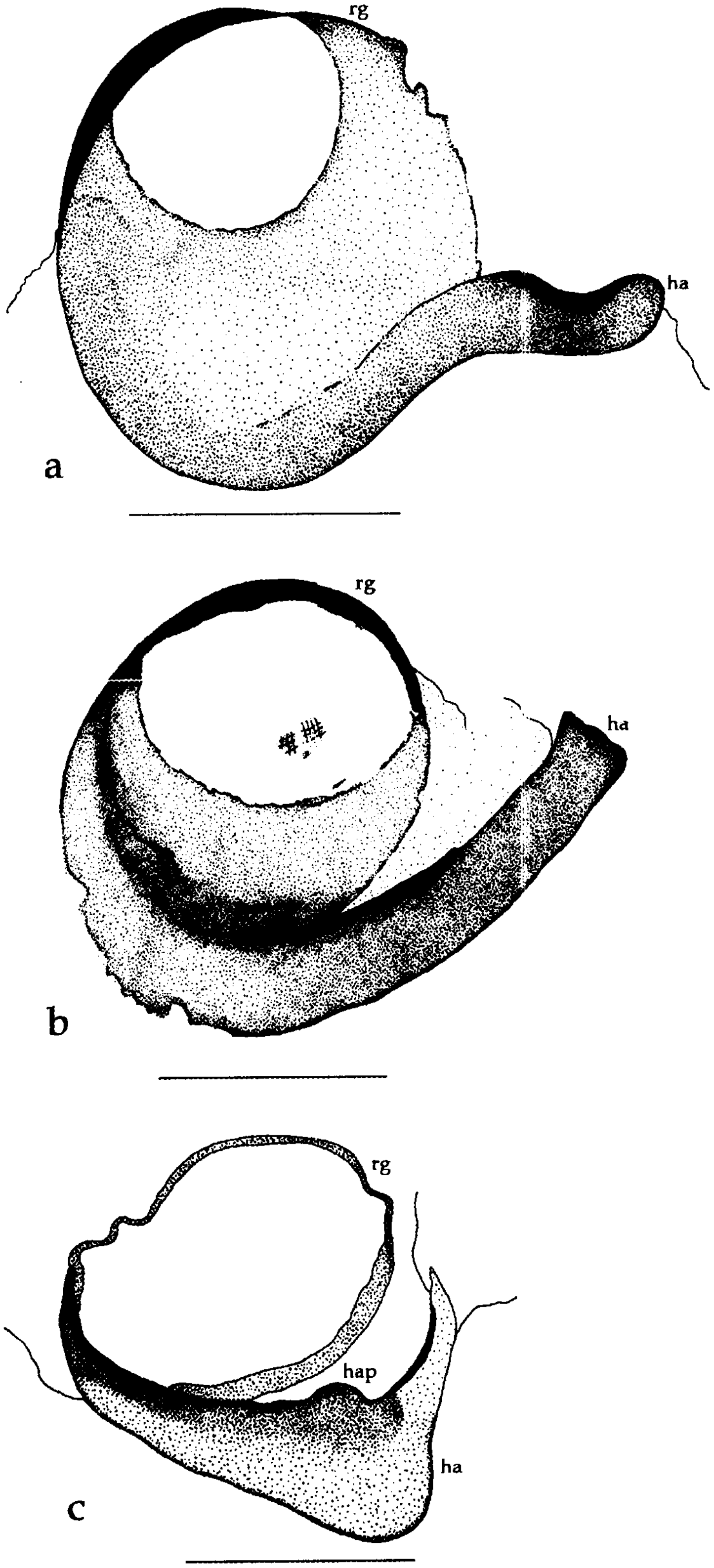


Figure 38. Different types of circular sclerites in species of *Deltochilum*. Figure a and b. Type I. **a.** *D. mexicanum* Burmeister. **b.** *D. hyponumm* Buquet. **c.** Type II *D. orbignyi* Blanchard. **ha** = handle, **hap** = handle process, **rg** = ring. Scale bar = 0.5 mm

Table 4. Different types of circular sclerites in the aedeagus internal sac in species of Canthonina examined.

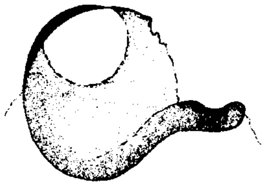
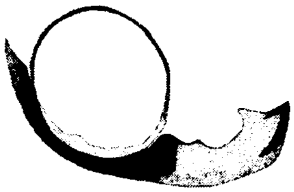
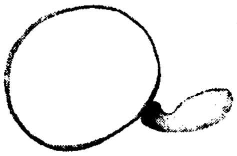
Type of sclerite		Description	Species
I		- Ring not completely differentiated - Inner area of ring reduced - External border of ring rounded or regular - Handle partially fused with ring - Narrow handle - Distal end of handle without process	*Cryptocanthon parvus* *Deltochilum mexicanum* *D. hypponum* *Canthon fulgidus* (?)
II		- Ring not completely differentiated - Inner area of ring wide - External border of ring irregular - Proximal end of handle with protuberance - Handle partially fused with ring - Distal extreme of handle with a process - Handle wide	*Deltochilum orbignyi* *D. gibbosum* *D. aequinoctiale*
III		- Ring completely differentiated - Inner area of ring wide - External border of ring irregular - Proximal end of handle with protuberance - Handle and ring completely separated - Distal end of handle with a process - Handle wide - Handle enlarged	*Megathopa punctatostriata*
IV		- Ring differentiated - Inner area of ring wide - Proximal end of handle with protuberance - External border of ring irregular - Handle and ring partially fused - Ring thick or thin - Distal end of handle with a process - Handle wide - Handle enlarged	*C. aberrans* *C. praticola* *C. simplex* *C. tetraodon* *Holocanthon mateui*

Tabla 4 continued

	Description	Especie
V 	- Ring differentiated - Inner area of ring wide - Proximal end of handle with or - without protuberance - External border of ring regular or irregular - Handle and ring fused completely - Ring thick - Distal end of handle with a process - Handle wide - Handle enlarged	*C. chiriguano* *C. humectus* *C. chalcites* *C. imitator* *C. pilularius* *C. indigaceus* *C. deyrollei* *C. lituratus* *C. mutabilis* *C. cyanellus cyanellus* *C. aequinoctialis* *C. morsei* *C. juvencus* *C. acutus* *C. angustatus* *C. brunneus* *C. columbianus* *C. femoralis femoralis* *C. luteicollis* *C. pallidus* *C. politus* *C. semiopacus* *C. subhyalinus* *C. viridis viridis* *C. meridionalis* *C. lunatus tibialis* *C. sordidus* *C. maldonadoi* *C. septemmaculatus* *C. monilifer* *C. perseverans* *C. quinquemaculatus* *Anisocanthon villosus* *Melanocanthon bispinatus* *Scybalocanthon pigidialis* *Sylvicanthon bridarollii*
VI 	- Ring differentiated - Inner area of ring wide - (Different in *H. affinis*) - Proximal end of handle without protuberance - External border of ring regular - Handle and ring fused completely - Ring thin - Distal end of handle without a process - Handle Narrow - Handle Short	*C. bicolor* *C. staigi* *C. violaceus* *Hansreia affinis* (?)

the distal end of the handle is wide and well developed, and has a well-developed process. This type of sclerite was only found in *M. punctatostriata* (Figure 39c). In the type IV sclerite the ring is not completely fused with the handle, and the proximal end is separated, or barely joined to the ring, the distal end is wider and with a well developed process. This type of sclerite is present in a few species of *Canthon* and in *H. mateui* (Figure 37a). The type V sclerite has the ring and handle well defined. Though the ring is completely fused to the handle, in many species the side of the ring where the handle joins is thicker, and has a protuberance formed by the proximal end of the handle (Figure 40a-40d). Most of species of *Canthon*, as well as *A. villosus*, *S. bridarollii*, *M. bispinatus* and *Scybalocanthon* have this type of sclerite (Figure 39a and 39b). The type VI sclerite is present only in few species of *Canthon*. In these species the ring is rounded, thin and without a protuberance. The Handle is short, narrow and does not have a process (Figure 40 e and 40 f). *H. affinis* has an circular sclerite with the same features of a type VI sclerite, but the inner area of the ring is partially reduced as in the type I sclerite. However more specimens need to be examined for confirming this observation. *C. fulgidus* has an different circular sclerite sharing features with type I and II sclerites (Figure 37C).

Brushes of the internal sac

The shape, number, and size of brushes of the internal sac vary among species of *Canthon*. Some species have brushes with fine bristles close together and clustered forming a defined structure. *C. lunatus tibialis* has only one brush formed by thick and separated bristles (Figure 32b), while species of the *pilularius* line have a half-moon shaped brush, formed by closely packed bristles (Figure 41f). In *C. indigaceus*, *C. deyrollei*, and *C. sordidus* the bristles are thicker, shorter and grouped without forming a defined structure. In other species there are some brushes with variable shapes; generally there are two brushes as in *C. quinquemaculatus*, *C. columbianus* and *C. cyanellus*, and more than three as in *C. triangularis*, *C. monilifer* and *C. septemmaculatus* (Figure 41). The brushes of *S. bridarollii*, are formed by broad and short spines, which look unlike those in the remaining species (Figure 41e). *C. aequinoctialis* and *H. affinis* have a compact

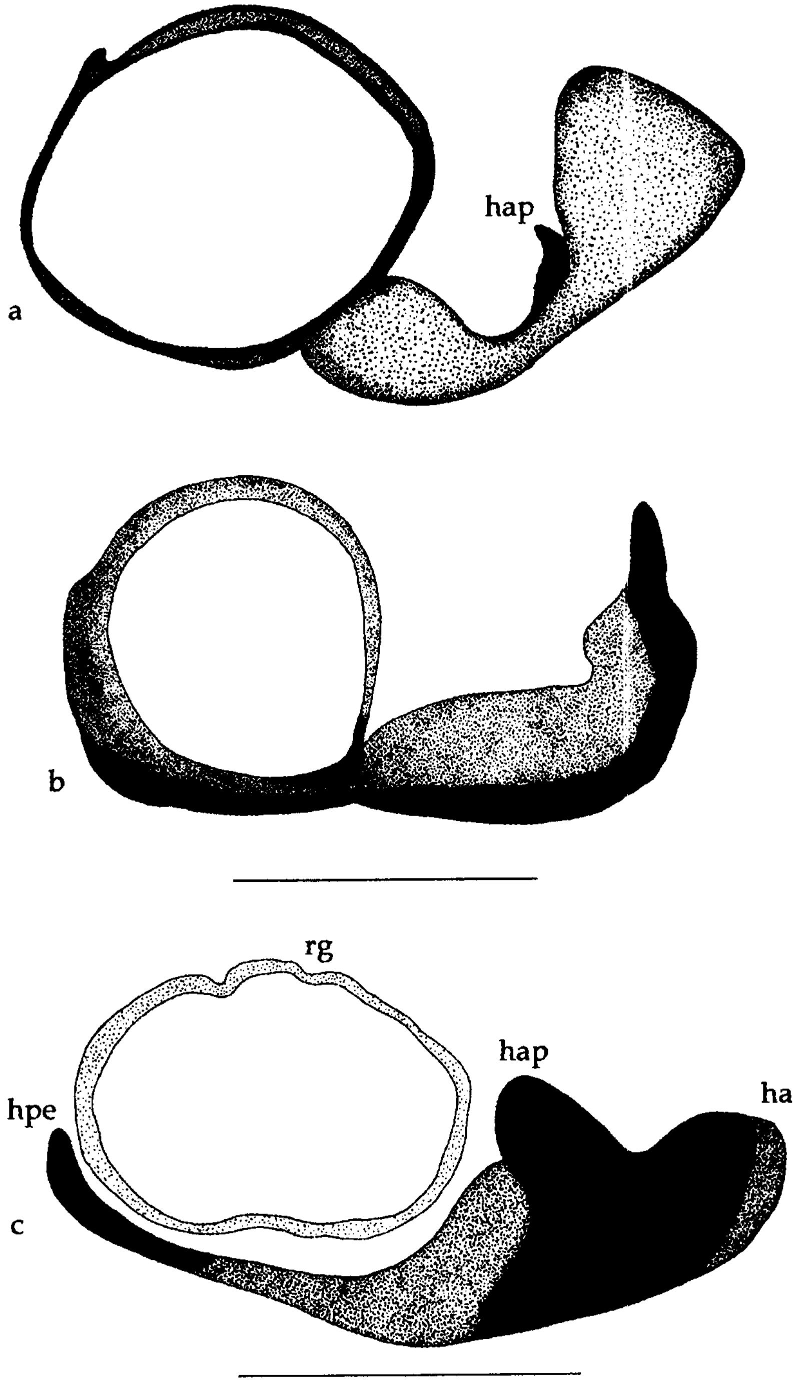


Figure 39. Different types of circular sclerites of Canthonina. **a.** *Sylvicanthon bridarollii* Martínez. **b.** *Melanocanthon bispinatus* Robinson. **c.** *Megathopa punctatostriata* Blanchard. **ha** = handle, **hap** = handle process, **hed** = distal end of handle, **hpe** = proximal end of handle, **rg** = ring. Figures a and b scale bar = 0.5 mm. Figure c scale bar = 0.25 mm.

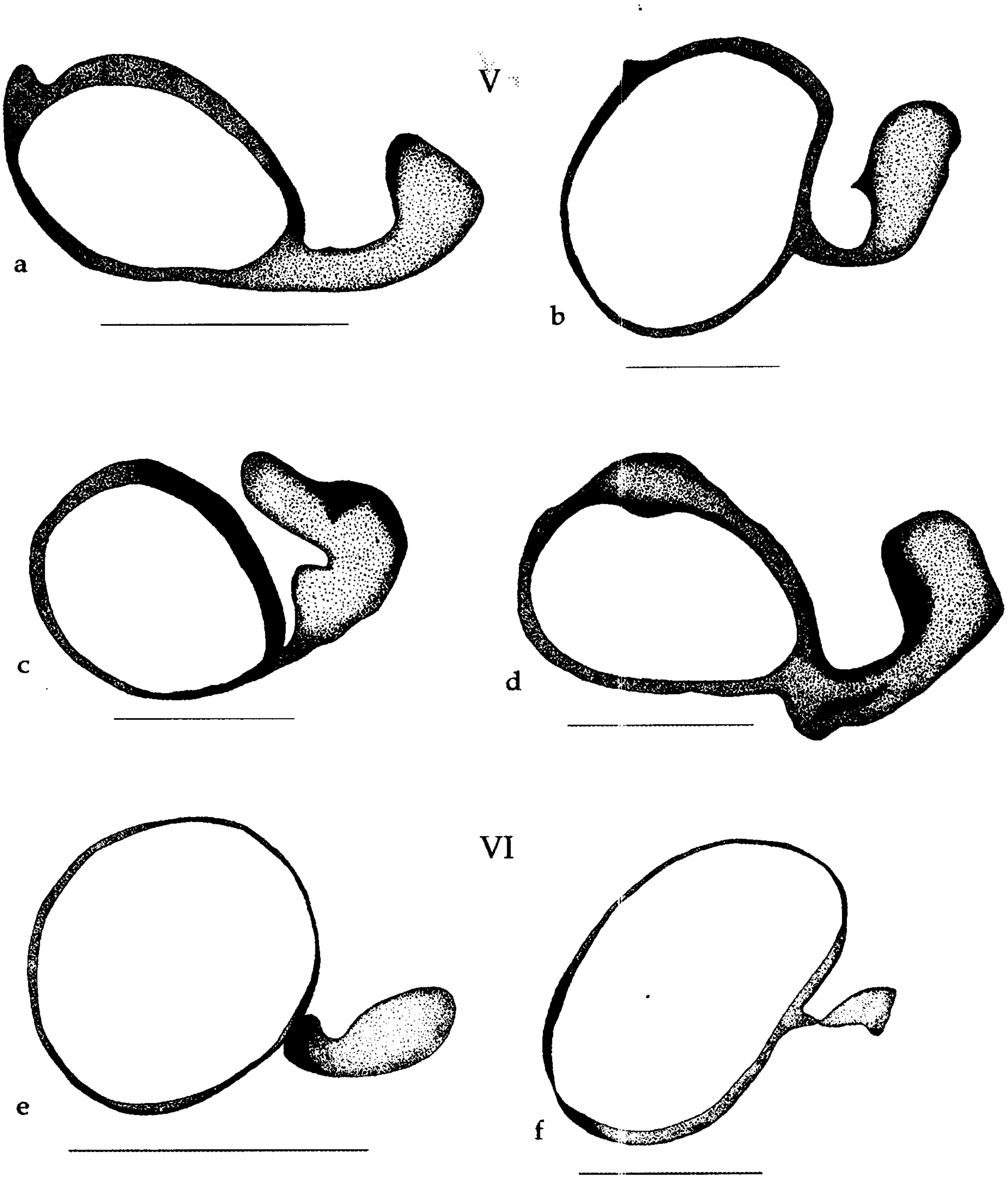


Figure 40. Circular sclerite of *Canthon* (type V and VI). **a.** *C. humectus* Say. **b.** *C. triangularis* Drury. **c.** *C. quinquemaculatus* Laporte. **d.** *C. pilularius* Linnaeus. **e.** *C. violaceus* Olivier. **f.** *C. bicolor* Laporte. Figures b, d, e and f scale bar = 0.5 mm. figures a and c scale bar = 1 mm.

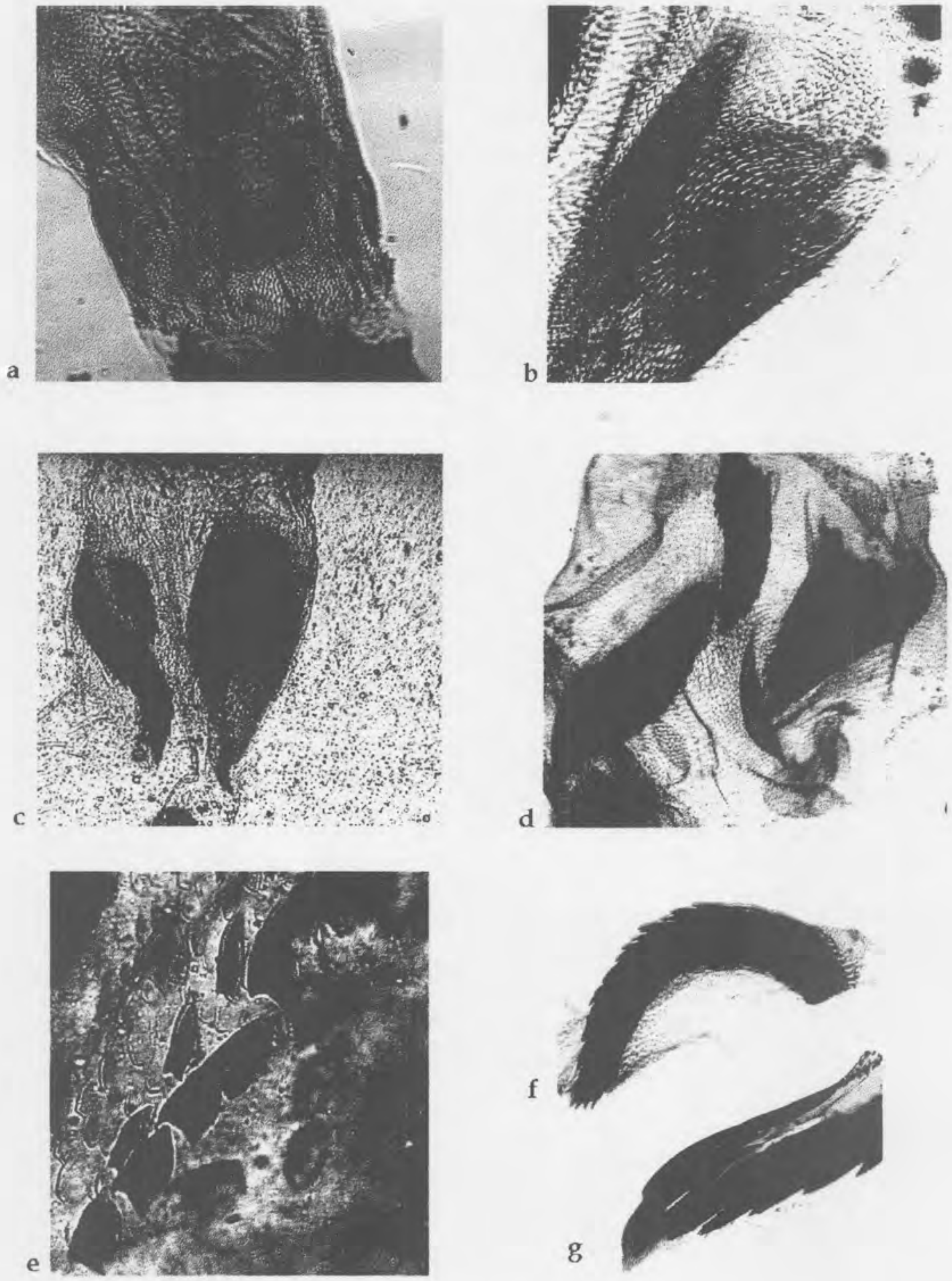


Figure 41. Detail of brushes of the internal sac of the aedeagus. **a**. *Canthon luteicollis* Erichson. **b**. *C. indigaceus* Harold. **c**. *C. quinquemaculatus* Laporte. **d**. *C. triangularis* Drury. **e**. *Sylvicanthon bridarollii* Martínez. **f**. *C. pilularius* Linnaeus. **g**. *C. humectus* Say. Figures a and c magnification = 10x, figure b and d magnification = 20x, figures e-g magnification = 40x.

and well sclerotized structure, surrounded by small spines. This structure is completely different to those brushes observed in other species.

In some species of *Canthon* (*C. aberrans*, *C. bicolor*, *C. luteicollis*, *C. violaceus*, *C. tetraodon*, *C. perseverans*, *C. staigi*, *C. praticola*, *C. ebenus* and *C. simplex*), the middle part of the internal sac does not have well defined brushes and this area has a strip in which the membrane is internally covered by even spines (Figure 41a and 41b).

Sexual dimorphism

The genus *Canthon*, in contrast to other groups of Scarabaeidae, does not exhibit marked morphological differences between the sexes. The spur of the foreleg and width of the last abdominal sternite are the main features used for separation of sexes. In males the spur is usually wider and bifurcated, whereas in females it is longer and sharp (Figures 42a and 42b). Despite that most species of *Canthon* have sexual dimorphism in the spur of the fore tibia, in some species of *Glaphyrocanthon* the female also possesses a bifurcated spur just like the male. Species of the subgenera *Pseudepilissus* and *Trichocanthon* have morphological differences between the sexes in the fore and middle tibia. In species of *Pseudepilissus* the males have the middle tibia elongated and curved, whereas the females have a shorter and less curved middle tibia (Figure 42c). This kind of dimorphism is also present in species of *Deltochilum*, in which males have longer and more curved middle and hind tibia than females. In *C. sordidus* (subgenus *Trichocanthon*), the apical tooth of the anterior tibia of the male is curved and larger than that of the female; it is also larger than the apical tooth of males of other species.

Another morphological difference between males and females of *Canthon* is observed in the shape of the last abdominal sternite. Males have a longer pygidium, and a shorter last abdominal segment with a small inlet, whereas in the females the last abdominal segment is longer (Figure 43).

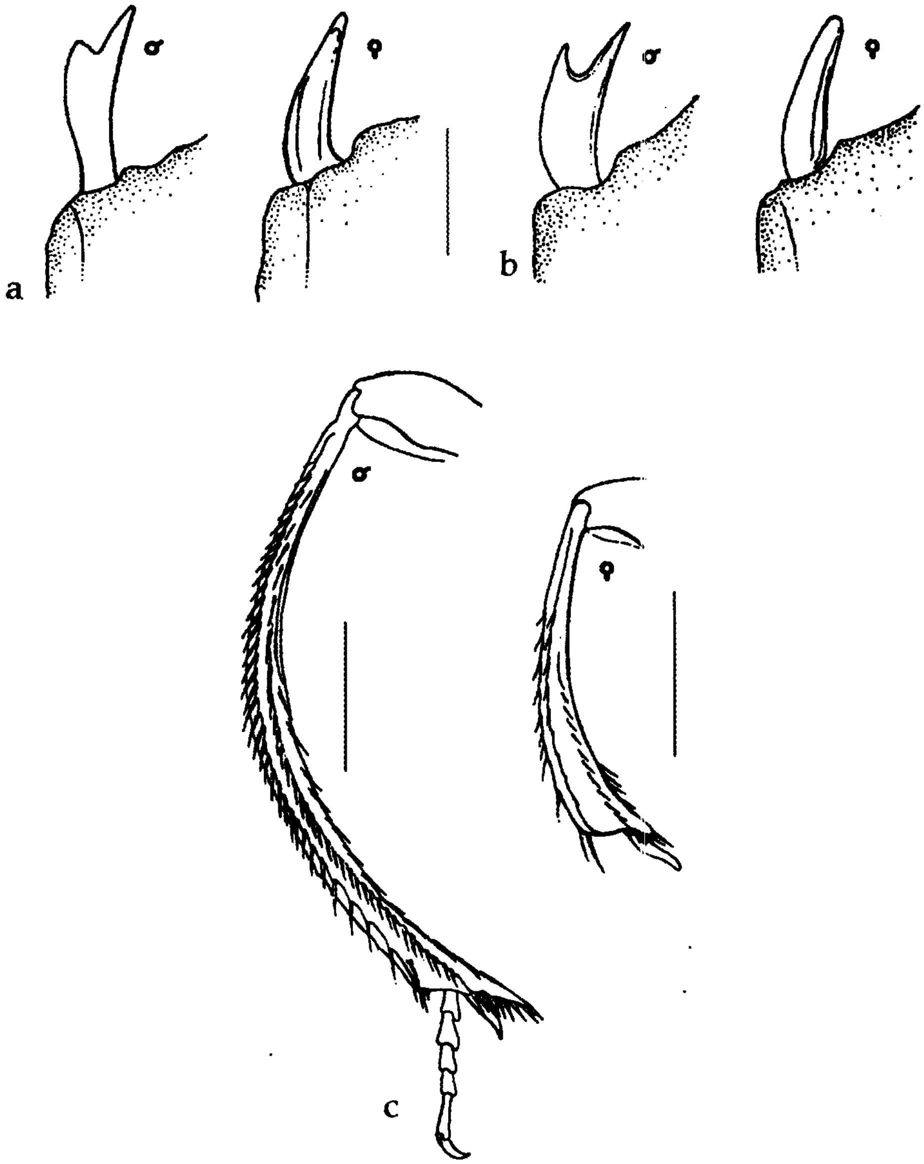


Figure 42. a-b: Spur of the fore tibia. **a**. *Canthon septemmaculatus* Latreille. **b**. *C. cyanellus sallaei* Harold. **c**. Middle tibia of *C. lunatus tibialis* Schmidt. Figures a and b, scale bar = 0.5 mm, figure c, scale bar = 1 mm.

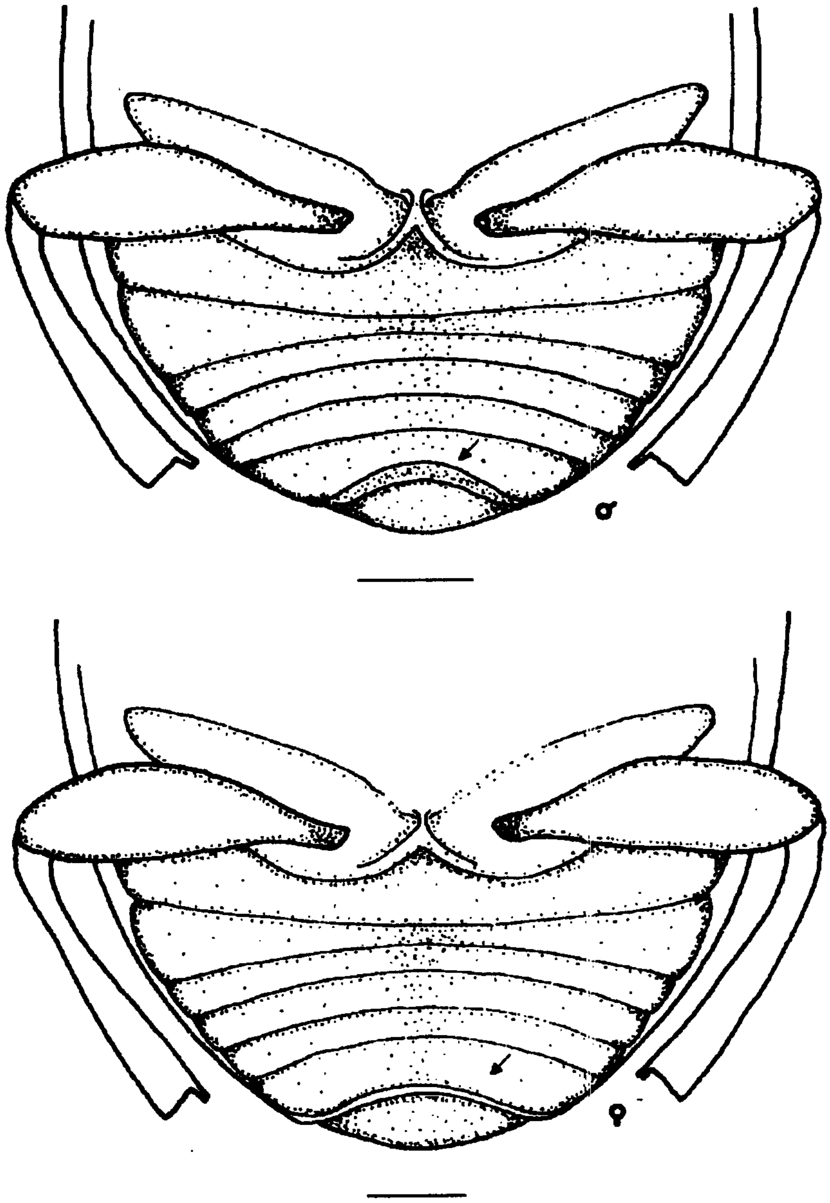


Figure 43. Abdominal sternites of the female and male of *Canthon pilularius* Linnaeus. Scale bar = 1 mm.

DISCUSSION

The delimitation of the genus *Canthon* has differed among authors who have worked on the group since it was proposed. It seems, however, that the successive divisions and groupings of species of *Canthon* in different genera and subgenera, has been a consequence of deficient diagnoses. This study shows that the characters used in the delimitation of *Canthon* are not shared throughout the group. Most of the characters used in the diagnosis of *Canthon* given by Halffter & Martínez (1977) are general characters that show wide variation among the species studied and are also present in other genera of Canthonina. Some characters are not clearly defined and their interpretation can be ambiguous. The following is a discussion of the more problematic characters, which I believe have contributed to a deficient definition of the genus *Canthon*.

According to the diagnosis of *Canthon*, the ventral structure of the clypeus is characterised by having a short keel (Halffter & Martínez 1977). In the species examined, this area showed great variation, not only in species of *Canthon*, but also in other genera. A short clypeal keel does not group the species of *Canthon* because some species lack a keel and others have protuberances different from a single keel. The division between the submentum and the gula, defined for *Canthon* to be arcuate or V-shaped, similarly showed great variation among species within *Canthon*. Additionally, in other genera this division is either arcuate (e.g., *Canthonella*) or V-shaped (e.g., *Deltochilum*, *Hansreia*, *Malagoniella*). Therefore, this character cannot be considered useful for delimiting the genus *Canthon*.

The variation in the ventral region of the prothorax, including the different degrees of excavation of the proepisternum, as well as the separation or not between the proepisternum and proepimeron by the presence of a keel, needs more careful evaluation. The presence or absence of the proepisternal keel is not a diagnostic character for *Canthon* due to the great variation in the shape and length of this keel within *Canthon* and without.

A short mesosternum is another character listed in the diagnosis of *Canthon* (Halffter, 1961). that does not help in to delimit the genus. The mesosternum is usually reduced in species of *Canthon*, but it is similarly reduced in other genera such as

Sylvicanthon and *Scybalocanthon.* Other species of *Canthon* have a long mesosternum, a state which has been used as a defining feature of the genus *Pseudocanthon* and has been a source of controversy regarding the separation of this genus

The shape of the anterior margin of the fore tibia has been defined as obliquely truncated in the genus *Canthon* (Halffter, 1961), but in several species, such as the *pilularius* group, the tibia is transversally truncated; this character is also present in the genus *Melanocanthon*.

According to Halffter & Martínez (1977), the shape of the parameres is rectangular and usually straightly truncated in *Canthon*. There was, however, much variation in the shape of the parameres among species of *Canthon*. Although many species have rectangular parameres, others have triangular parameres and show much variation in the shape of the end of the aedeagus.

At the subgeneric level there was much variation in the morphological structures studied. Although some characters are shared by small groups of species, the results show that the characters used in the separation of subgenera are not decisive for an unequivocal delimitation. Species of the subgenus *Boreocanthon* had the greatest consistency (i.e., the most characters shared by species in the group). These species, however, share many morphological features with species of the *pilularius* line (subgenus *Canthon*) and the genus *Melanocanthon*. These groups, besides sharing many morphological features, also share the same geographic distribution and some behavioural features (Gordon & Cartwright 1974).

The revision of diagnostic characters of *Canthon* and other genera of Canthonina show that *Canthon* and perhaps *Anisocanthon*, *Melanocanthon*, *Scybalocanthon,* and *Sylvicanthon* are artificial groups of species. Although traditional biological classifications have not necessarily recognised natural groups, at present it is considered imperative that classification reflect the evolutionary history of groups, supported by shared derived characters (sinapomorphies; Hennig 1966, Wiley 1988, Forey et al. 1992). Within the subtribe Canthonina, some genera have true sinapomorphies (e.g. *Deltochilum*, *Canthonella*, *Holocanthon*, and *Cryptocanthon*), which facilitate their taxonomic separation, while the previously mentioned genera (*Anisocanthon*, *Canthon*, *Melanocanthon*, *Scybalocanthon*, and *Sylvicanthon*) are defined based on combinations of characters.

In a general analysis of all the characters examined, it is easy to recognise that while there are few derived characters exclusively shared by species of *Canthon* (with the exception of some characters shared by groups of two or three species), other characters are shared between *Canthon* and other genera such as *Anisocanthon*, *Melanocanthon*, *Sylvicanthon* and *Scybalocanthon*. Characters present in structures such as the eyes, mentum, epipharynx, and male genitalia are shared by a group of species that include *Canthon* and species of the aforementioned genera (see Table 5).

The tendency in the taxonomic study of *Canthon* (sensu Harold 1868), has been to divide the genus into small subgroups, defined by plesiomorphic characters (characters with an ancestral condition) or homoplastic characters, which has resulted in the formation of artificial groups. The results from the present work show that despite having examined different structures, most morphological characters until now examined are not sufficiently informative to improve the knowledge of the phylogenetic relationships among these groups of Canthonina. However, some structures of the internal morphology such as the epipharynx and the internal sac of the aedeagus appear to be important sources of informative characters.

The sclerites of the anterior end of the internal sac of the aedeagus have characters that are shared by groups of species of Canthonina (Table 3). The changes observed in the different types of circular sclerites provide an idea of which morphological states are ancestral and which are derived. The circular sclerite with a well-differentiated ring completely fused with the handle (type V and VI) could be a derived condition of sclerites with an incomplete ring partially fused with the handle (type I and II). It is notable that groups that share type V and VI sclerites also share a few other morphological characters, including some characters in the epipharynx. Species that have the type V sclerite have two defined lateral combs on the epipharynx, and the medial process of the epipharynx reaches the anterior border, while species that have the type VI sclerite (*C. staigi* and *C. bicolor*) have the lateral combs of the epipharynx fused, and the medial process does not reach the anterior border. Species of *Canthon* that have the sclerite type VI also have in common a horse-shoe-shaped sclerite.

Table 5. Main characters shared by species of *Canthon* and other genera of Canthonina.

Characters	*Canthon*	*Anisocathon*	*Melanocanthon*	*Scybalocanthon*	*Silvicanthon*	*Hansreia*
Eyes wide in dorsal view	X	x	x	x		x
Eye surrounded by a wide band	X	x	x	x		
Posterior opening of eye narrow	X	x	x	x		x
Medial process of epipharynx reaching anterior border	X[1]	x	x	x	x	x
First lateral comb of epipharynx complete	X	x	x	x	x	x
Epipharynx with two defined lateral combs	X	x	x	x	x	
Anterior border of labium complete	X	x	x	x	x	x
Setae of regular adornment short	X	x	x	x	x	x
Anterior border of proepisternum with a notch	X	x	x			x
Mesosternum narrow	X	x	x	x	x	x
Apex of ventral face of femur without setae	X	x	x		x	x
External row of setae on dorsal face of middle tibiae complete	X	x	x	x	x	x
First and second segment of hind tarsi same size	X	x	x			x
Lateral border of elytra without keel	X	x	x	x	x	
Internal sac with circular defined sclerite	X	x	x	x	x	x
Circular sclerite with a defined ring	X[2]	x	x	x	x	x
Internal area of ring of circular sclerite wide	X	x	x	x	x	
Ring of the circular sclerite with a protuberance	X[1]	x	x	x	x	
Circular sclerite with a differentiated handle	X	x	x	x	x	x
Distal end of handle of circular sclerite elongated	X[1,3,4]	x	x	x	x	
Sclerite elongated	X	x	x	x	x	x

[1] Except in *C. staigi*

[2] Except in *C. fulgidus*

[3] Except in *C. violaceus*

[4] Except in *C. bicolor*

Different studies on Scarabaeidae have recognised the importance of the genitalia as a source of diagnostic characters as well as an important source of evidence for testing hypothesis about phylogenetic relationships (d`Hotman & Scholtz 1990, Martín-Piera 1992, Coca-Abia et al. 1993, Zunino & Halffter 1997). At the level of Canthonina, the morphology of the genitalia has not been studied in detail; a more detailed analysis of these structures (external and internal) should provide better information to elucidate the phylogenetic relationships within the tribe.

Recently, phylogenetic analysis Scarabaeoidea families have shown how different sets of characters can provide information at different taxonomic levels (Browne & Scholtz 1995, 1999). For example, characters from the hindwing articulation have supported the relationship at the family level with a high level of confidence, while other characters have been less reliable (Browne & Scholtz 1999). These same authors have argued that characters from mouthparts and male genitalia are highly homoplastic at intermediate and higher taxonomic levels, but can be useful at lower taxonomic levels.

Few morphological and phylogenetic studies have considered the American genera of Canthonina. Despite the descriptive nature of this work, I have illustrated taxonomic problems of *Canthon* and related genera, and have demonstrated the need for a better systematic knowledge of these groups. It is important to widen the search for characters suitable for cladistic analysis. This search must include structures not considered in the present work (mouthparts, antennae, membranous wings, abdominal sternites, spiracles, and hind legs, among others). Finally, other sources of characters such as the morphology of immature states, chemical substances, morphology of the glands that produce them, and behavioural features must be explored.

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APPENDIX 1. List of abbreviations used in the figures.

an	antennae
af	apical fringe
br	brushes of internal sac
ca	canthus
cc	coxal cavity
cl	clypeus
cls	clypeal suture
clse	clypeal setae
ebr	external border of ring
ep	proepimeron
ey	eye
gn	gena
gl	gula
ha	handle
hap	handle process
hed	distal end of handle
hpe	proximal end of handle
lc	lateral combs
mn	mentum
mp	medial process
pe	prosternum
pek	proepisternal keel
pr	proepisternum
rg	ring
sc	sclerite
te	temones
tm	tormae
ts	transverse suture