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COMPARATIVE MORPHOLOGY OF THE FEMALE GENITALIA AND SOME ABDOMINAL STRUCTURES OF NEOTROPICAL CRYPTOCEPHALINI (COLEOPTERA: CHRYSOMELIDAE: CRYPTOCEPHALINAE)

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**COMPARATIVE MORPHOLOGY OF THE FEMALE GENITALIA AND SOME
ABDOMINAL STRUCTURES OF NEOTROPICAL CRYPTOCEPHALINI
(COLEOPTERA: CHRYSOMELIDAE: CRYPTOCEPHALINAE)**

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Abstract

The female genitalia of New World Cryptocephalini was studied and illustrated based on representatives of 11 of the 13 genera of the tribe. It was found that female genitalia contain pleurites IX, a rare and apparently primitive feature among leaf beetles. In other features cryptocephaline female genitalia are simpler than genitalia of other leaf beetles in having a poorly sclerotized sternite VIII and lacking the tignum. It is also hypothesized that the vagina is formed by sternites IX (dorsally) and VIII (ventrally), and that sclerotized plate of sternite IX can be homologized with vaginal palpi of flea beetles. A set of characters of diagnostic and of possible phylogenetic value was found. In general, Cryptocephalina and Monachulina bear the greatest affinity in overall morphology of the female genitalia, with Pachybrachina possessing a different set of unique morphological states. Of particular diagnostic and phylogenetic value at the subtribal level, as revealed by this study, are the shape and degree of sclerotization of tergite VIII, tergite IX, and sternite VIII.

Knowledge of the female genitalia of most main groups of leaf beetles is greatly lacking compared to current knowledge of the male genitalia. The earliest documented observation of the male genitalia of leaf beetles are ones by Foudras (1859). Since then characters provided by male genitalia were used for species differentiation and became an essential part of a species description. Suzuki (1978) listed major papers which provide information on both reproductive organs and genitalia, citing Stein (1847) as the first comparative anatomical study of female reproductive system in most leaf beetle group except Cryptocephalinae (cited from Suzuki 1978). The first attempt known to us of a description of the female genitalia in leaf beetles was by Spett and Levitt (1925). They placed greater emphasis on the description of the spermatheca and leaf beetle subfamilies were largely separated based on the differences in this structure. In most

leaf beetle groups the spermatheca provides reliable species level characters. It is also useful for separating flea beetle genera. Other parts of the female genitalia in leaf beetles have also been used successfully in segregating species: vaginal palpi in the genus *Altica* Geoffroy (Lyubishchev 1959; Kevan 1962; Konstantinov 1987) and the tignum in the genus *Aphthona* Chevrolat (Konstantinov 1998a).

The female reproductive system, including the ovaries, oviducts, spermathecal and accessory glands of the ovipositor, as well as the spermatheca of leaf beetles are reviewed in detail by Suzuki (1988). Comparative studies, or more or less, complete descriptions of female genitalia in leaf beetles are not that common. Askevold (1988) described and illustrated the female genitalia of some donaciines. Mann and Crowson (1991) discussed the female genitalia of the Sagrinae. Konstantinov and Rusakov (1993) studied the female genitalia of 17 Palearctic genera of Chrysomelinae. Konstantinov (1998b, 2002) described, in relative detail, the structure, potential functions, and possible homology of the female genitalia of flea beetles (Alticini). A stimulating study by Kasap and Crowson (1985) compared the female genitalia of the main leaf beetle subfamilies, reviewed existing, and proposed their own terminology. The latter paper is one of a few that mentions or illustrates the female genitalia of Cryptocephalinae. Erber (1968) studied in detail the anatomy of the female abdomen of Cryptocephalini and Clytrini, including the structures of the genitalia. Taxonomic treatments of various cryptocephalines (for example Reid 1999) contain bits of information on the female genitalia, but they do not describe or illustrate the complete genitalia nor do they comment on the potential function of its parts.

This paper describes and compares the female genitalia of the Neotropical genera of Cryptocephalini, as well as contrasting with Clytrini (*Clytra* sp.) and Chlamisini (*Chlamisus* sp.) female genitalia. The tribe Cryptocephalini is one of the most diverse groups of Neotropical leaf beetles with approximately 1,000 described species (Blackwelder 1957; Riley *et al.* 2002; Wilcox 1975), of which *Cryptocephalus* Geoffroy, *Pachybrachis* Chevrolat, *Griburius* Haldeman, *Lexiphanes* Gistel, and *Metallactus* Suffrian make up about 95% of the total species diversity.

Reproductive Biology and Oviposition

Little has been recorded on the reproductive and oviposition behavior of the Cryptocephalini. Most of what is known comes from Erber (1988). His observations of various species in the subfamily Cryptocephalinae have revealed a characteristic oviposition behavior. Before each egg is released, Cryptocephaline females individually envelop each egg with several small, tightly packed plates (tiles) of excrement (Erber 1988). The fecal shell surrounding each egg is known as the scatoshell. Erber (1988) also documented in detail the oviposition behavior of some species of lamprosomatines.

Materials and Methods

This study follows the same general format and the same set of taxa as the one on cryptocephaline prothorax (Chamorro-Lacayo and Konstantinov 2004). The beetles examined for this study were obtained from the chrysomelid collection at the National Museum of Natural History (USNM), Smithsonian Institution. We selected one or two species as representatives of each genus from different areas of the New World except for *Mastacanthus* Suffrian and *Sternoglossus* Suffrian (*Pachybrachina*) due to their rarity in collections (see Table 1 for the list of examined species). We looked at more than one specimen of each species and found no significant intraspecific variability of structures and characters under consideration.

Beetles were initially relaxed in distilled water and subsequently cleared using 10%

Table 1. Variability in female genitalia of New World Cryptocephalini.

Subtribe	Species author	VIII tergite		Attachment of duct to spermatheca		Spermatheca		IX tergite		IX sternite		Ventrines			
		Anterior margin	Medially	Sclerotization	Shape	Shape	Shape	Apex of both halves	Anterior margin	Connection to IX pleurite	Shape in rear view	Vagina	Medial projection of ventrite I	Ventricle IV	Location
<i>Basareus</i>	<i>brunipes</i> (Oliver)	Entire	Apically sclerotized	Pair of lateral C-shaped unconnected sclerotizations	Rigid Base	Straight near vagina, densely coiled near spermatheca	C-shaped, flattened at both ends	Directed medially	Digitate, apex acute	Sclerotized Basal	With small appendage	Small, wrinkled, compressed	Broad, anterior margin truncate	Light posterior margin	Medially
		Entire	Apically sclerotized	Pair of lateral C-shaped unconnected sclerotizations	Rigid Base	Straight near vagina, densely coiled near spermatheca	C-shaped, flattened at one end	Directed medially	Digitate, apex acute	Sclerotized Basal	With small appendage	Small, wrinkled, compressed	Broad, anterior margin truncate	Light posterior margin	Medially
<i>Cryptocephalus</i>	<i>arizonicus</i> Schaeffer	Entire	Apically sclerotized	Pair of lateral C-shaped unconnected sclerotizations	Rigid Base	Straight near vagina, densely coiled near spermatheca	C-shaped	Directed medially	Digitate, apex acute	Sclerotized Basal	With small appendage	Broad, smooth	Broad, anterior margin slightly rounded	Light posterior margin	Partially under ventrite IV
		Entire	Apically sclerotized	Pair of lateral C-shaped unconnected sclerotizations	Rigid Base	Straight near vagina, densely coiled near spermatheca	C-shaped	Directed medially	Digitate, apex acute	Sclerotized Basal	With small appendage	Broad, smooth	Broad, anterior margin slightly rounded	Light posterior margin	Partially under ventrite IV
<i>Cryptocephalina</i>	<i>Cryptocephalus</i> <i>andicus</i> Halderman	Entire	Apically sclerotized	Pair of lateral C-shaped unconnected sclerotizations	Rigid Base	Straight near vagina, densely coiled near spermatheca	C-shaped	Directed medially	Digitate, apex acute	Sclerotized Basal	With small appendage	Broad, smooth	Broad, anterior margin slightly rounded	Light posterior margin	Partially under ventrite IV
		Entire	Apically sclerotized	Pair of lateral C-shaped unconnected sclerotizations	Rigid Base	Straight and wide near vagina, densely coiled near spermatheca	U-shaped/ Both ends bulbous connected by a narrow passage	Directed medially	Digitate, apex acute	Sclerotized Along lateral margin	With small appendage	Broad, smooth	Broad, anterior margin slightly rounded	Light posterior margin	Medially, towards posterior margin
<i>Diachus</i>	<i>aratus</i> (F.) Suffran	Entire	Apically sclerotized	Pair of light lateral C-shaped connected sclerotizations	Rigid Base	Straight and wide near vagina, densely coiled near spermatheca	Both ends bulbous connected by a narrow passage	Directed medially	Digitate, apex acute	Sclerotized Along lateral margin	With small appendage	Small, wrinkled, compressed	Broad, anterior margin slightly rounded	Light posterior margin	Medially, towards posterior margin
		Entire	Apically sclerotized	Pair of light lateral C-shaped connected sclerotizations	Rigid Base	Straight and wide near vagina, densely coiled near spermatheca	Both ends bulbous connected by a narrow passage	Directed medially	Digitate, apex acute	Sclerotized Along lateral margin	With small appendage	Small, wrinkled, compressed	Broad, anterior margin slightly rounded	Light posterior margin	Medially, towards posterior margin

Table 1. Continued.

Subtribe	Species author	Spermatheca										IX tergite		IX sternite		Ventriles			
		VIII sternite		Attachment of duct to spermatheca		Spermathecal duct		Shape		Apex of both halves		Connection to IX pleurite		Shape in rear view		Medial projection of ventrite I		Depression	
		Anterior margin	Medially sclerotized	Shape	Rigid	Base	Extremely long, curved spiral	Somewhat L-shaped	As big as rest of genitalia	Directed medially	Digitate, apex acute	Sclerotized along lateral margin	With small appendage	Small, ?smooth	Not as broad anterior margin slightly produced	Very light posterior margin	Ventrite I	Ventrite IV	Location
	<i>Triachus vacuus</i> LeComte	Entire	Apically sclerotized	Absent	Rigid	Base	Extremely long, curved spiral	Somewhat L-shaped	As big as rest of genitalia	Directed medially	Digitate, apex acute	Sclerotized along lateral margin	With small appendage	Small, ?smooth	Not as broad anterior margin slightly produced	Very light posterior margin	Ventrite I <td>Ventrite IV</td> <td>Partially under ventrite IV</td>	Ventrite IV	Partially under ventrite IV
	<i>Triachus certinus</i> LeComte	Entire	Apically sclerotized	Absent	Rigid	Base/Side	Spiral, long	C-shaped	As big as rest of genitalia	Directed medially	Digitate, apex acute	Sclerotized along lateral margin	With small appendage	Broad, smooth	Very broad, anterior margin slightly produced	Very light posterior margin	Very light posterior margin	Very light posterior margin	Partially under ventrite IV
	<i>Heparthrius longimanus</i> Suffrian	Medially depressed	Apically sclerotized	Moderately throughout, basal margin produced mesally	Rigid	Side	Spiral	C-shaped	Smaller than rest of genitalia	Directed medially	Digitate, apex rounded	Sclerotized basal	With an appendage facing mesally	Broad, smooth	Broad, anterior margin truncate	Distinct	Distinct	Medially	
Monachulina	<i>Leptophanes coenobita</i> Suffrian	Medially depressed	Apically sclerotized	Strongly present throughout	Rigid	Side	Very wide, short? (broken)	Broadly V-shaped	Smaller than rest of genitalia	Directed medially	Digitate, apex acute (slightly rounded)	Sclerotized basal	With an appendage facing mesally	Broad, smooth	Broad, anterior margin truncate	Distinct	Distinct	Medially	
	<i>Leptophanes saponatus</i> (F.) Baly	Medially depressed	Apically sclerotized	Strongly present throughout	Rigid	Side	Very short, wide	C-shaped, wide	Smaller than rest of genitalia	Directed medially	Digitate, apex acute (slightly rounded)	Sclerotized basal	With an appendage facing mesally	Broad, smooth	Broad, anterior margin truncate	Distinct	Distinct	Medially	
	<i>Steganocephala discoidalis</i> Baly	Medially depressed	Apically sclerotized	Lightly present	Rigid	/	/	/	/	Directed medially	Broadly digitate, apex rounded	Sclerotized along lateral margin	With an appendage facing mesally	Broad, smooth	Broad, anterior margin truncate	Distinct	Distinct	Medially	
	<i>Steganocephala costata</i> (Suffrian)	Medially depressed	Apically sclerotized	Lightly present	Rigid	Side	Densely coiled near spermatheca	C-shaped	Smaller than rest of genitalia	Directed medially	Broadly digitate, apex rounded	Sclerotized along lateral margin	With an appendage facing mesally	Broad, smooth	Broad, anterior margin truncate	Distinct	Distinct	Medially	

Table 1. Continued.

Subtribe	Species author	VIII tergite		VIII sternite		Attachment of duct to spermathecal duct		Spermatheca		IX tergite		IX sternite		Ventriles						
		Anterior margin	Medially depressed	Apically depressed	Sclerotization	Shape	Attachment of duct to spermatheca	Spermathecal duct	Shape	Size	Apex of both halves	Shape	Anterior margin	Connection to IX pleurite	Shape in rear view	Vagina	Medial projection of ventrite I	Distinct	Medially	Location
<i>Ambrotodes chilensis</i> Blanchard		Medially depressed	Apically depressed	Absent	Not rigid, bearing setae medially	Base	Coiled, highly sclerotized	C-shaped, narrow	Smaller than rest of genitalia	Directed laterally	Triangular	Lightly sclerotized	Along lateral margin	Without appendage	Broad, smooth	Narrow, anterior margin rounded	Distinct	Medially	towards posterior margin	
		Medially depressed	Apically depressed	Absent	Not rigid, bearing few setae medially	Side	Not densely coiled, highly sclerotized	Broadly V-shaped, bulbous	Smaller than rest of genitalia	Directed laterally	Triangular	Lightly sclerotized	Along lateral margin	Without appendage	Broad, wrinkled	Narrow, anterior margin rounded	Distinct	Medially	towards posterior margin	
<i>Pachynechina Griburinus</i> sp.		Medially depressed	Apically depressed	Absent	Not rigid	Side	Not densely coiled, highly sclerotized	C-shaped, bulbous	Smaller than rest of genitalia	Directed laterally	Triangular	Lightly sclerotized	Along lateral margin	Without appendage	Broad, wrinkled	Broad, anterior margin truncate	Distinct	Partially under ventrite IV		
		Medially depressed	Apically depressed	Absent	Not rigid	Side	Not densely coiled, highly sclerotized	Broadly V-shaped, bulbous	Smaller than rest of genitalia	Directed laterally	Triangular	Lightly sclerotized	Along lateral margin	Without appendage	Broad, wrinkled	Narrow, anterior margin truncate	Distinct	Partially under ventrite IV		
<i>Griburinus equicaris</i> (Oliver)		Medially depressed	Apically depressed	Absent	Not rigid	Side/Base	Not densely coiled, highly sclerotized	S-shaped, narrow	Smaller than rest of genitalia	Directed laterally	Triangular	Lightly sclerotized	Along lateral margin	With small appendage, close to apex	Broad, smooth	Broad, anterior margin slightly truncate	Distinct	Medially, towards posterior margin		
		Medially depressed	Apically depressed	Absent	Not rigid	Side	Not densely coiled, highly sclerotized	Broadly V-shaped, bulbous	Smaller than rest of genitalia	Directed laterally	Triangular	Sclerotized	Along lateral margin	Without appendage	Small, wrinkled, compressed	Not as broad, anterior margin slightly truncate	Distinct	Medially	towards posterior margin	
<i>Pachybrachis govi</i> Blanchard		Medially depressed	Apically depressed	Absent	Not rigid	Side (two knobs)	Not densely coiled	Broadly V-shaped	Smaller than rest of genitalia	Directed laterally	Triangular	Sclerotized	Along lateral margin	Without appendage	Small, wrinkled, compressed	Not as broad, anterior margin slightly produced	Distinct	Medially	towards posterior margin	
		Medially depressed	Apically depressed	Absent	Not rigid	Side	Not densely coiled	C-shaped, base bulbous	Smaller than rest of genitalia	Directed laterally	Triangular	Sclerotized	Along lateral margin	Without appendage	Broad, wrinkled	Not as broad, anterior margin slightly produced	Distinct	Medially	towards posterior margin	
<i>Pachybrachis hepaticus</i> Melzheimer		Medially depressed	Apically depressed	Absent	Not rigid	Side	Not densely coiled	C-shaped, base bulbous	Smaller than rest of genitalia	Directed laterally	Triangular	Sclerotized	Along lateral margin	Without appendage	Broad, wrinkled	Not as broad, anterior margin slightly produced	Distinct	Medially	towards posterior margin	
		Medially depressed	Apically depressed	Absent	Not rigid	Side	Not densely coiled	C-shaped, base bulbous	Smaller than rest of genitalia	Directed laterally	Triangular	Sclerotized	Along lateral margin	Without appendage	Broad, wrinkled	Not as broad, anterior margin slightly produced	Distinct	Medially	towards posterior margin	

NaOH, either by leaving it overnight or by using a heat source to speed up the process. The abdomen was separated from the rest of the body in a dissecting dish filled with distilled water. The rest of the body was stored in glycerin with a small amount of 70% ethanol.

Abdominal tergites 1–6 were separated from the rest of the abdomen by making two incisions, with a pair of microscissors, along the lateral margin of the tergum followed by a transverse cut between segments VI and VII. A first incision along the mesal line of the tergum up to segment VII was helpful. The intersegmental membrane between tergites VII and VIII was carefully torn apart by gently pulling on the genitalia and tearing the membrane using fine tipped forceps or microscissors. The same was also done for the intersegmental membrane between sternites VII and VIII. The hindgut was cut off and tergite VIII was carefully removed. The genitalia were stained using Chlorazol Black.

The genitalia were observed using a Zeiss Stemi SV 11 Apo stereomicroscope. Images were taken with a JVC model KY-F70 digital camera mounted on a Wild Photomakroshop M400 stereomicroscope using the software AutoMontage.

Terminology

Here we follow a widely accepted definition of what constitutes the female genitalia as the “ectodermal structures . . . involved in copulation, fertilization, and oviposition” (Torre-Bueno *et al.* 1989). This separates the sclerotized parts of the female genitalia formed mostly by genital segments VIII and IX of the abdomen from the internal “soft parts,” which include ovaries, oviducts, spermathecal and accessory glands of the ovipositor that were reviewed by Suzuki (1988). Some authors (Kasap and Crowson 1985) used the term ovipositor instead or as a synonym for female genitalia. We prefer to separate these terms, and follow the commonly accepted view that the ovipositor is a narrower term defining an “organ by which eggs are deposited, formed by a prolongation or modification of the posterior abdominal segments . . .” (Torre-Bueno *et al.* 1989).

Terminology for various parts of the female genitalia is much more confused. Kasap and Crowson (1985) provided an overview of the various terms applied to the female genitalia and proposed to consider the dorsal sclerite situated below tergite VIII, tergite IX, or the proctiger; the lateral sclerites to be pleurites of the segment IX, the paraprocts and the sclerites situated ventrad to the gut as sternite IX or valvifer. An elongated sclerite situated below the vagina is considered a modified sternite VIII and called the spiculum gastrale (spiculum ventrale = tignum in Konstantinov 1998*a*). However, sternum VIII is not modified into an anteromedian rod (spiculum gastrale) in Cryptocephalinae and higher Chrysomelines (Kasap and Crowson 1985). Kasap and Crowson (1985) did not illustrate the relative position of the gut and the vagina, but a limited number of illustrated sclerotized parts leave no other choice than the previous interpretation of their proposed terminology, which we generally accept. However, we noticed a discrepancy in figure 9 (Kasap and Crowson 1985:144): the ventral paired sclerite, what should be called sternite IX or valvifer, has instead been called vaginal palpi. Erber (1968) used a slightly different terminology for the female genitalia, thus calling the pleurites of segment IX (paraprocts) hemisternites IX, sternite IX (valvifers) as styli, and tergite IX (proctiger) as hemitergites. In a subsequent publication discussing the biology of the Camptosomata he does not use this terminology (Erber 1988:527), and simply refers to the sclerites of the IX in the text as “the six sclerites surrounding the anus” (Erber 1988:523).

Connection of Segments

The female genitalia is situated at the apex of the abdomen between the sclerites of segment VII. Cryptocephalines, like other beetles, have a telescoping ovipositor, which

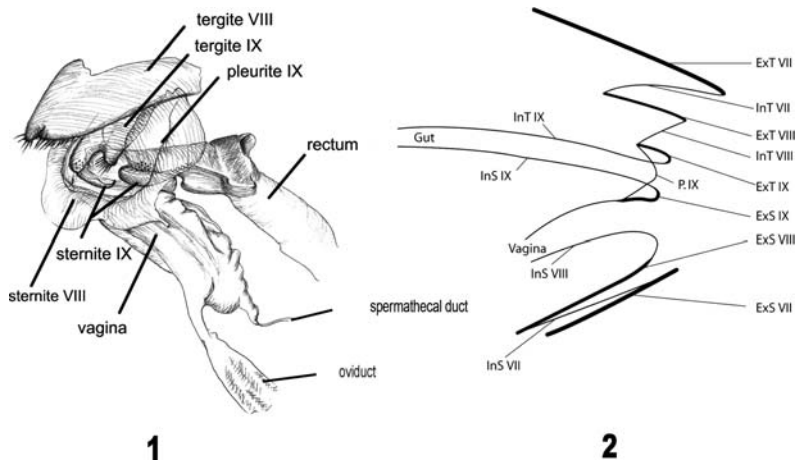
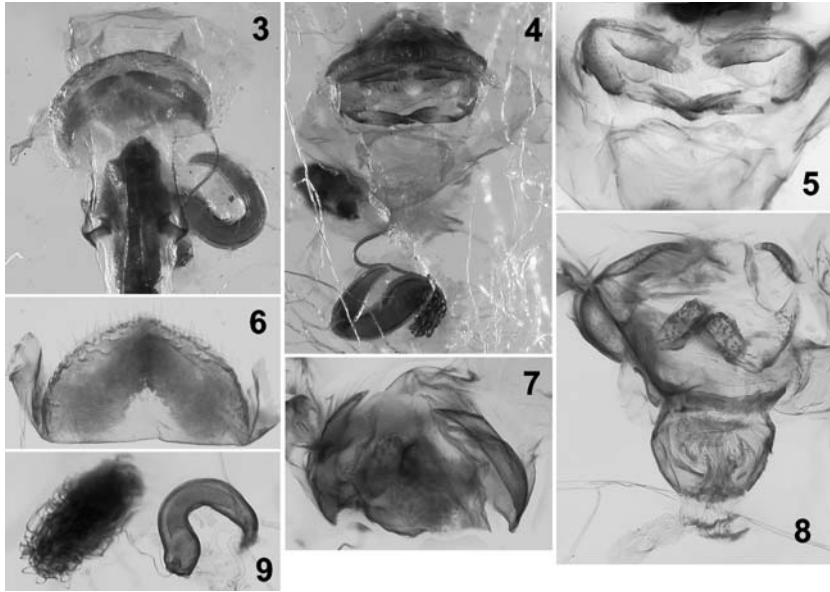


Fig. 1. Schematic representation of the female genitalia of *Griburius equestris*, laterocaudal view. **Fig. 2.** Schematic representation of the female genitalia of *Cryptocephalinae*. Abbreviations: ExT (S) – external layers of tergites (sternites), InT (S) – internal layers of tergites (sternites).

is shorter than in most other chrysomelids (Kasap and Crowson 1985). At rest, segment IX is concealed under segment VIII and these are concealed by segment VII. Tergite VII extends beyond the elytra and is more sclerotized than the preceding tergites. Tergite VII is also known as the pygidium and is not visible dorsally being positioned vertically. At rest the ventral margin of the pygidium tightly comes together with sternite VII. In caudal view, the sclerotized pygidium is the predominantly visible structure.

The telescoping ability of the female genitalia is facilitated by the presence of the internal membrane of each sclerite (intersegmental membrane) (Konstantinov 2002). For instance, the internal membranes are connected distally to the dorsal tergites and proximally to the ventral tergites (Figs. 1, 2).

The external sclerotized layer of the pygidium (tergite VII) connects to the external sclerotized layer of tergite VIII by the internal membranous layer of tergite VII. The external sclerotized layer of tergite VIII, which retracts under tergite VII at rest, connects to the external sclerotized layer of tergite IX by the internal membranous layer of tergite VIII. The external sclerotized layer of tergite IX is hidden (at rest) below tergite VIII. The anus is surrounded by the tergites, sternites, and pleurites of the segment IX. The internal membranous layers of segment IX form the walls of the rectum. Pleurites IX are fused dorsolaterally to tergite IX and ventrolaterally to sternite IX. The degree to which tergites IX appear to be fused along the lateral margin with pleurites IX seems to be dependent on the shape of tergite IX. Those with tergite IX being more triangular and less digitate, as in *Pachybrachina* (Figs. 50, 55, 58, 63, 65, 73), *Diachus* (Figs. 18, 21, 23), *Triachus* (Fig. 28), and *Stegnocephala* (Figs. 41, 42, 43, 46) the connection seems to be along the entire lateral margin. Whereas in *Heptarthrius* (Fig. 32), *Lexiphanes* (Figs. 34, 36, 38), *Cryptocephalus* (Fig. 5), and *Bassareus* (Figs. 12, 15), for which the shape of tergite IX is digitate or broadly digitate, the fusion to pleurite IX appears to be restricted largely to the base with the lateral (posterior) margin almost entirely free. Sternite IX and pleurite IX are fused along the basal margin.

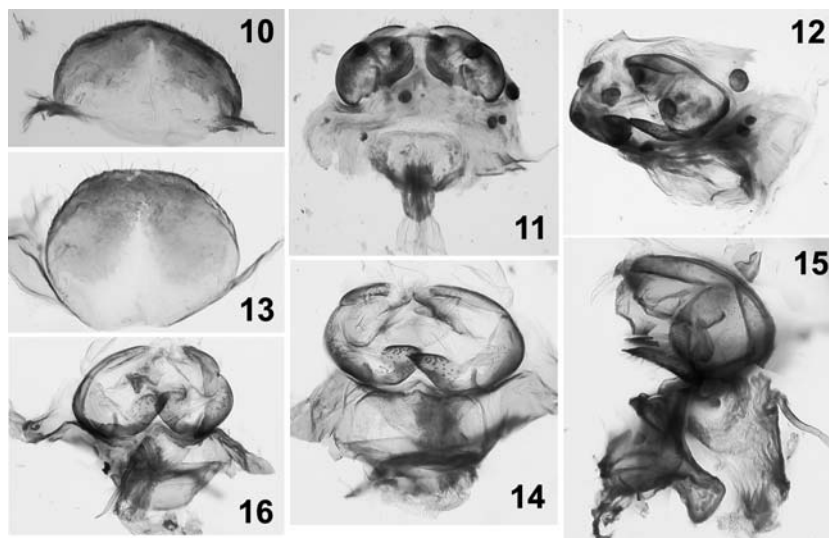


Figs. 3–5. *Cryptocephalus aulicus*. **3)** dorsal view of genitalia, tergite VIII not removed, spermatheca in the background; **4)** caudal view, tergite VIII not removed; **5)** caudal view, tergite VIII removed. **Figs. 6–9.** *Cryptocephalus arizonicus*. **6)** tergite VIII, dorsal view; **7)** dorsal view of genitalia, tergite VIII removed; **8)** caudal view, tergite VIII removed; **9)** spermatheca and spermathecal duct (coiled onto itself).

The internal membranous layer of sternum IX forms the ventral wall of the rectum, which distally connects to the external sclerotized layer of sternum IX. The external sclerotized layer of sternum IX proximally is membranous and forms the dorsal wall of the vagina. The sclerotized parts of tergite and sternite IX project posteriorly beyond the internal membranous parts of tergite and sternite VIII and IX. Less so in *Pachybrachina* and is especially true for tergites IX. Medially tergite and sternite IX are membranous throughout (Fig. 12). The internal membranous layer of sternum VIII forms the ventral wall of the vagina (Fig. 2). The external sclerotized layer of sternite VIII is connected to the external sclerotized layer of sternum VII by the internal membranous layer of sternum VII. The vulva is located between sternites VIII and IX. The spermathecal duct originates along the dorsal wall of the vagina (Fig. 1) and connects to the variably shaped and sclerotized spermatheca. The spermathecal duct is attached to the spermatheca, basally (Figs. 9, 17, 29) or sub-basally (Figs. 35, 44, 48, 64). However, whether the attachment is basal or on the side may be subject to personal interpretation, as in the case of *Metallactus decumanus* (Fig. 59). The oviduct is located along the ventral wall of the vagina (Fig. 1).

Abdominal Depression and Sternite VII (Ventricle V)

Cryptocephalines, like other leaf beetles, have seven visible tergites, and only five ventrites are readily visible. The first true sternite is reduced and unapparent, thus the first visible sternite (ventrite I) is fused sternites II and III. In *Cryptocephalinae* females, abdominal sternite VI (ventrite IV) is reduced, at times half or a quarter the size of the



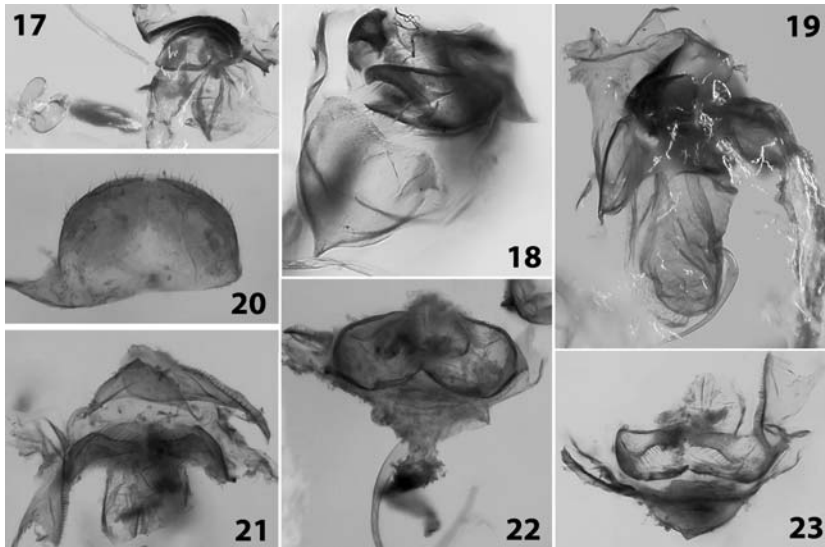
Figs. 10–12. *Bassareus brunnipes*. **10**) tergite VIII, dorsal view; **11**) ventral view of genitalia, tergite VIII removed; **12**) laterocaudal view of genitalia, tergite VIII removed. **Figs. 13–16.** *Bassareus* sp. **13**) tergite VIII, dorsal view; **14**) caudal view of genitalia, tergite VIII removed; **15**) lateral view of genitalia, tergite VIII removed; **16**) rear view of genitalia, tergite VIII removed.

previous sternite (in *Triachus* ventrite IV is barely distinguishable from ventrite V) and sternite VII (ventrite V) is modified. Ventrite V bears a median, concave, circular depression surrounded by setae. This dimple, or depression, called eimörser (roughly translated as “egg bowl”) by Erber (1968), serves to hold each egg in place while the scatoshell is being applied (see above under reproductive biology and oviposition). The shape, depth, and relative location of the eimörser may vary among genera. In *Cryptocephalus* the eimörser is located next to the margin of ventrite IV whereas in *Diachus* it is located more posteriad and farther away from the margin of ventrite IV. However, the relative location of the eimörser with respect to ventrite IV and the edge of ventrite V remains constant within genera (based on the taxa examined in this study). Nonetheless, the eimörser varies within genera in depth. For example, the eimörser of *Griburius equestris* (Olivier) is shallower than that of *Griburius* sp. Both species of *Triachus* examined have very shallow eimörser.

Apart from the above mentioned characters, the shape of the anterior margin of ventrite I, specifically the shape of the medial projection, and the shape and degree of sclerotization of ventrite IV are also consistent characters within a genus. The shape of the medial projection can range from narrowly rounded, as in *Ambrotodes*, to broadly rounded in *Cryptocephalus* and *Diachus*, to truncate in Monachulina. Ventrite IV proved to also be a valuable diagnostic character. For example, ventrite IV is barely discernable in *Triachus* while in *Pachybrachina* it is just as prominent as the other ventrites.

Tergite VIII

The sclerotized tergite VIII is dorsoventrally flattened, plate-like, being broad basally and broadly tapers apically. The apical margin may be entire, as in *Cryptocephalina* (Figs. 6, 10, 13, 20, 25), or mesally depressed as in *Monachulina* (Figs. 33, 39, 40, 45)



Figs. 17–19. *Diachus auratus*. **17)** near ventral view of genitalia with tergite VIII, spermatheca and spermathecal duct to the left; **18)** laterocaudal view, tergite VIII removed; **19)** lateral view of genitalia, tergite VIII removed. **Figs. 20–23.** *Diachus catarius*. **20)** tergite VIII, dorsal view; **21)** dorsal view, tergite VIII removed; **22)** rear view; **23)** caudal view.

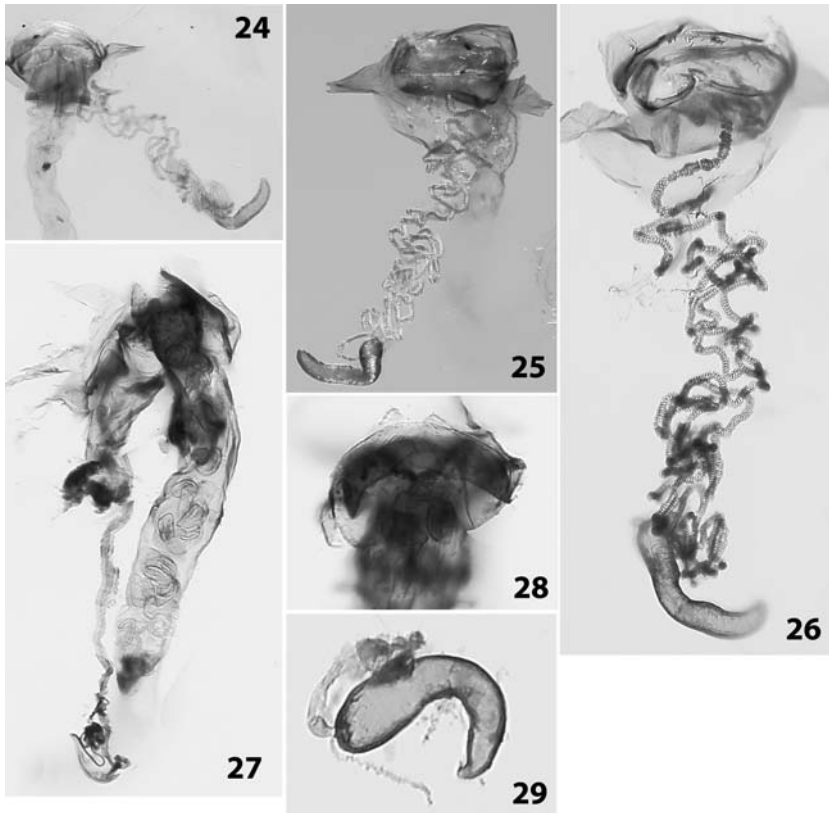
and Pachybrachina (Figs. 51, 56, 60, 66, 71). The apical margin is setose and may be sclerotized, as in *Cryptocephalina* and *Monachulina*, or medially membranous as in *Pachybrachina*. At rest tergite VIII is concealed beneath the pygidium.

Sternite VIII

Sternite VIII is largely membranous yet mesally it retains a rigid structure that conforms to a broadly, inverted triangle with an acuminate apex in *Cryptocephalina* (Figs. 3, 11, 18). The base of this rigid structure forms the lip of the vulva and at times may be lightly sclerotized (*Bassareus* Fig. 11). The rigid and at times sclerotized, concave area fits directly over (anterad) the abdominal depression on segment VII. The degree of sclerotization of the external layer of sternum VIII may differ in several ways: In *Pachybrachina* sternum VIII is largely membranous and not sclerotized, however in some genera sparse setae are present (Figs. 50, 62, 70). In *Monachulina*, *Lexiphanes* (Figs. 34, 36, 38) has a highly sclerotized mesal plate-like region, less sclerotized in *Heptarthrus* (Fig. 32), and even less so in *Stegnocephala* (Fig. 43). In *Cryptocephalina* sternum VIII is characterized by retaining a rigid, broadly triangular structure laterally bearing a pair of C-shaped sclerites (Figs. 3, 4, 11, 12), which meet apically in *Diachus* (Figs. 18, 19) and are absent in *Triachus* (Fig. 25).

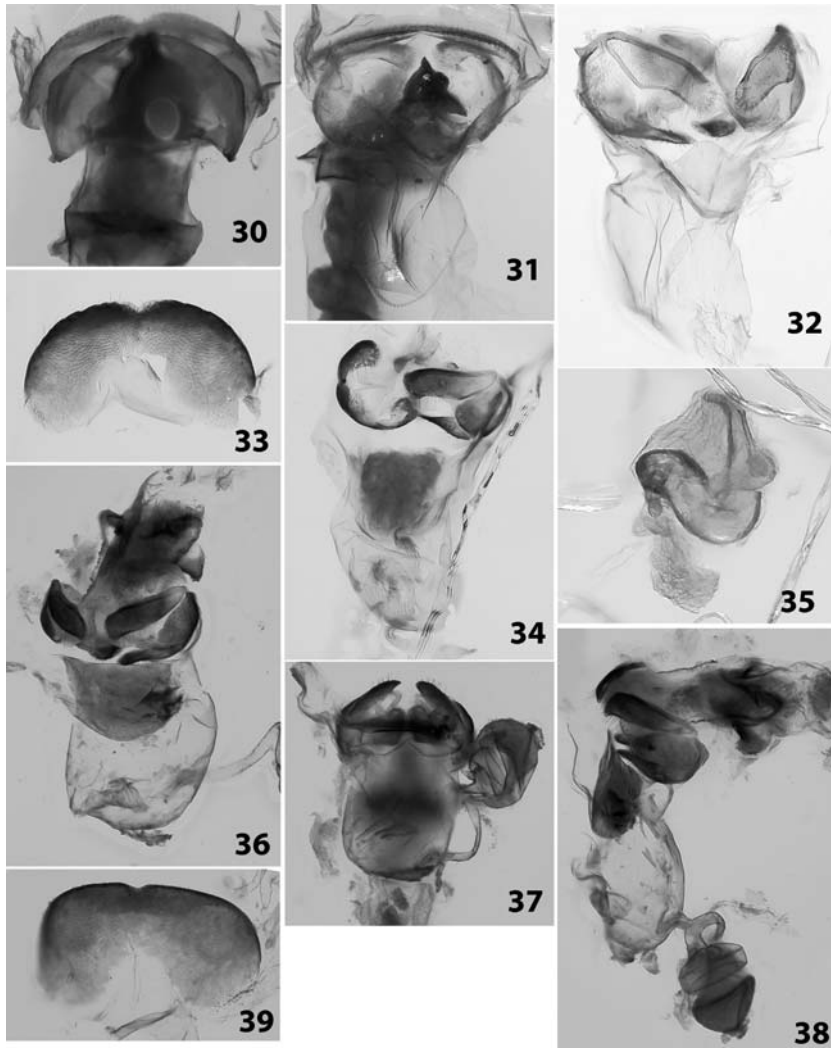
Sclerites of Segment IX

The sclerotized, setose paired tergite IX are variably shaped, with either an acute or broad apex and somewhat dorsoventrally flattened. In *Cryptocephalina* (Figs. 5, 7, 12, 23, 28) and *Monachulina* (Figs. 32, 36) they are digitate, more broadly so in *Stegnocephala* (Figs. 41, 46) with the apices directed medially. In *Pachybrachina* they



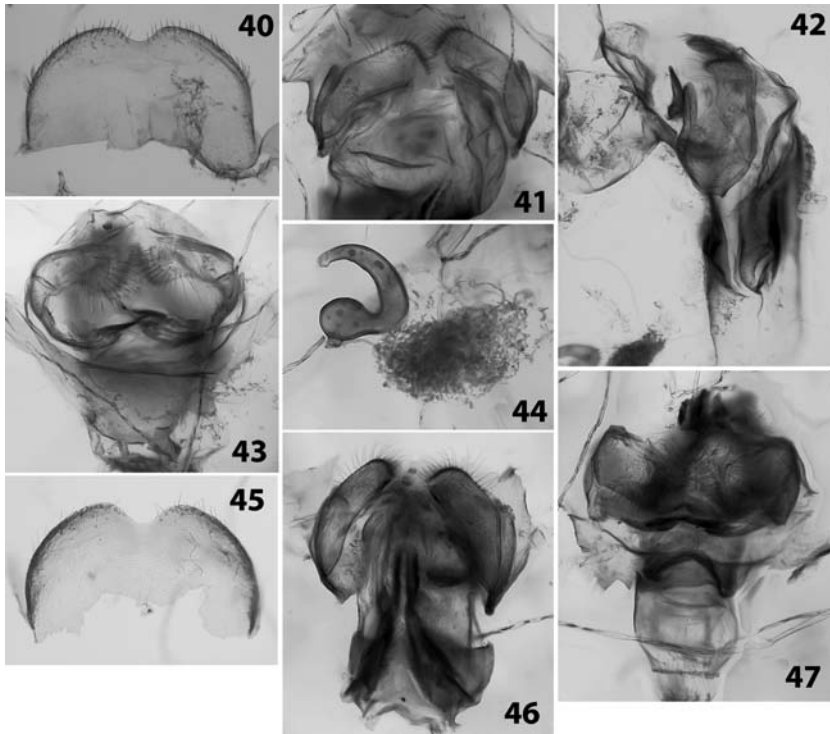
Figs. 24–26. *Triachus vacuus*. **24)** dorsal view of genitalia with tergite VIII, long spermathecal duct and spermatheca to the right; **25)** caudal view; **26)** rear view. **Figs. 27–29.** *Triachus cerinus*. **27)** lateral view; **28)** dorsal view; **29)** spermatheca, lateral view.

are triangular and apices directed laterally (Figs. 50, 55, 58, 63, 73). The anterior margin of tergites IX is sclerotized as in *Cryptocephalina* and *Monachulina* or membranous as in *Pachybrachina*. Basolaterally tergites IX are fused dorsolaterally with pleurites IX (as discussed above). The pleurites IX are slightly convex and triangular, broad basally and tapering into acute or rounded, setose apices (Figs. 1, 8, 15, 32, 36, 41, 42, 52, 57). Pleurites IX ventrally articulate with sternites IX. Sternites IX are also sclerotized, digitate, setose, and dorsoventrally flattened with apices variably shaped. They are concave (spoon-shaped) and directed dorsally, at times exposing caudally most of the ventral surface. The internal cavity of the apices is not completely enclosed and can be penetrated from dorsal side, so the whole structure looks like invagination of the dorsal side of the vagina. This allows to consider these structures to be homologous to the vaginal palpi of flea beetles. In rear view a pair of small projections or small appendages (apodems) are discernable at the edge of the lateral margin of sternite IX in *Cryptocephalina* and *Monachulina* that most possibly serves as a site for muscle attachment (Figs. 14, 16, 22, 26). These are not present in *Pachybrachina* (Figs. 54, 67, 72). The sclerites of segment IX work in conjunction with



Figs. 30–32. *Heparthrius longimanus*. **30)** ventral view, note shape of tergite VIII; **31)** near caudal view with tergite VIII; **32)** near caudal view, tergite VIII and rectum removed. **Figs. 33–35.** *Lexiphanes coenobita*. **33)** tergite VIII, dorsal view; **34)** laterocaudal view of genitalia, tergite VIII removed; **35)** spermatheca. **Figs. 36–39.** *Lexiphanes saponatus*. **36)** laterocaudal view of genitalia, tergite VIII removed; **37)** ventral view; **38)** lateral view showing vagina, spermathecal duct, and spermatheca; **39)** tergite VIII, dorsal view.

the pygidium to apply individual fecal plates to the egg and, with the help of the rectal sclerites, to give each “tile” its peculiar specific shape (Erber 1988). The sclerites of segment IX possibly move independently of each other with limited movement by sternites IX in a dorsal and ventral direction and possibly of pleurites IX in a laterad and mesad direction.



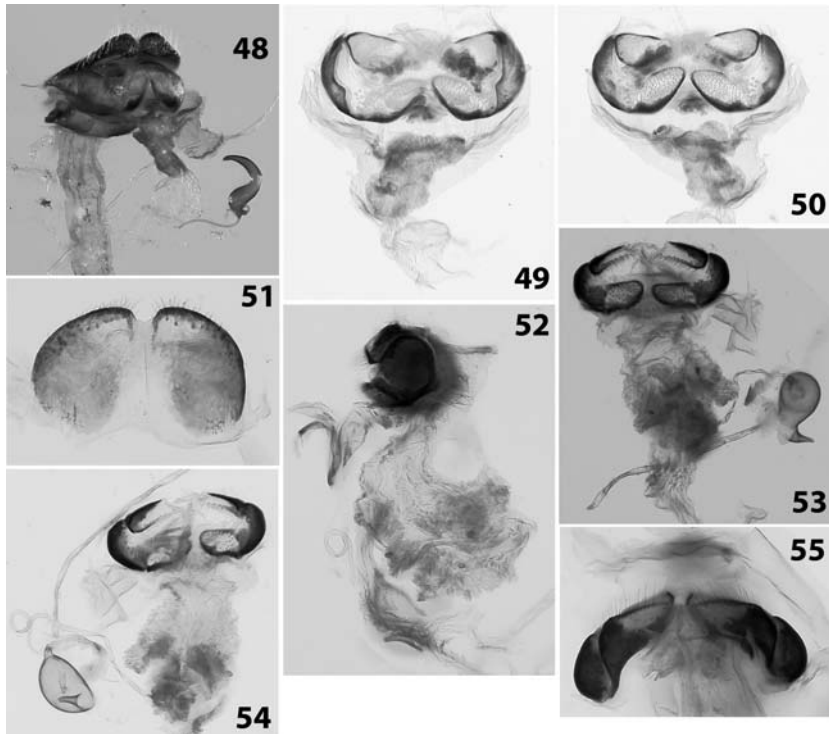
Figs. 40–44. *Stegnocephala costulatus*. **40)** tergite VIII, dorsal view; **41)** dorsal view of genitalia, tergite VIII removed; **42)** lateral view; **43)** caudal view; **44)** spermatheca and spermathecal duct. **Figs. 45–47.** *Stegnocephala discoidalis*. **45)** tergite VIII, dorsal view; **46)** dorsal view of genitalia, tergite VIII removed; **47)** near caudal view.

Vagina

The vulva is horizontally elongate and narrow and lies between sternum IX and sternum VIII. The forces exerted on the membranes that comprise the entrance to the vagina ensure that the vulva remains closed. In addition, the posterior edge of the external part of sternum VIII is rigid, at times being lightly sclerotized, as in *Bassareus brunripes*, and remaining pressed against the vulva. The dorsal wall of the vagina is made up of the membranous continuation of the external layer of sternite IX and the ventral wall is made up of the internal membranous layer of sternite VIII. The shape and size of the vagina ranges from being small, compressed and wrinkled as in *Bassareus*, to medium sized as in *Triachus* and *Diachus*, or to larger and sac-like as in *Cryptocephalus*. The shape and size of the vagina is not a consistent character within genera.

Spermatheca

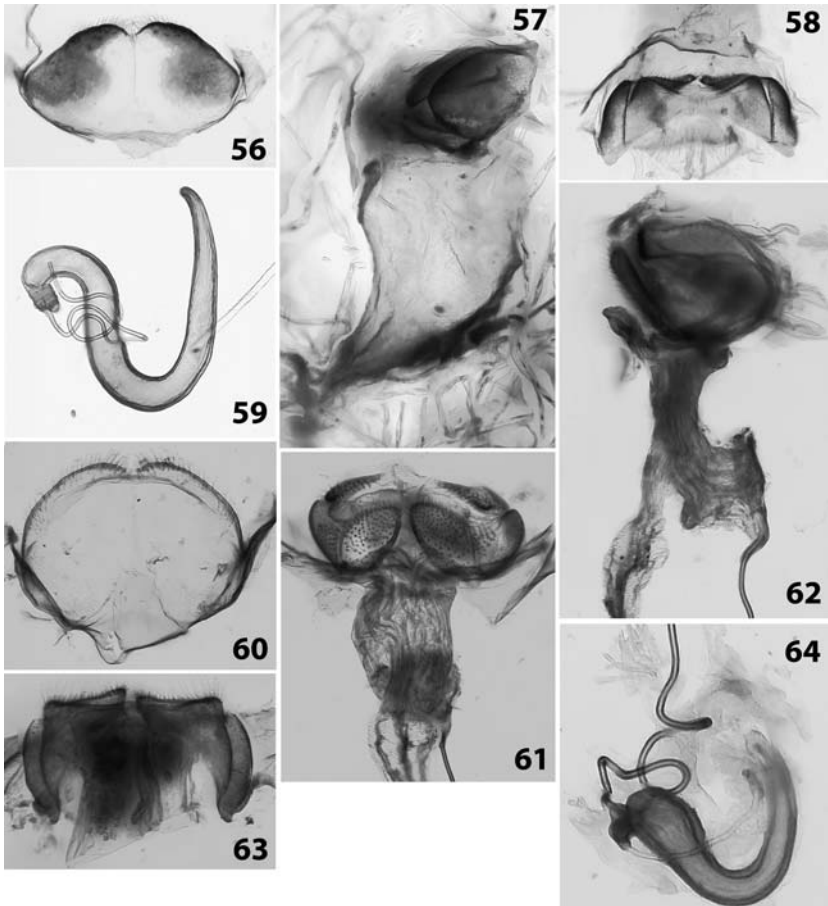
The spermathecal duct is a lightly or highly sclerotized narrow cylinder. The length and shape differs among genera. Near the base the spermathecal duct may be initially straight and as it reaches the spermatheca the duct becomes densely coiled and wrapped onto itself many times, as in *Cryptocephalus*, *Bassareus*, *Diachus*, *Stegnocephala*



Figs. 48–50. *Pachybrachis gayi*. **48)** laterocaudal view of genitalia with tergite VIII and spermatheca; **49)** rear view, tergite VIII removed; **50)** caudal view, tergite VIII removed. **Figs. 51–55.** *Pachybrachis hepaticus*. **51)** tergite VIII, dorsal view; **52)** lateral view of genitalia, tergite VIII and rectum removed; **53)** caudal view, tergite VIII removed, spermatheca to the right; **54)** rear view and spermatheca; **55)** dorsal view, tergite VIII removed.

(Figs. 4, 9, 17, 44); or it may be long, curved and tightly spiraled as in *Triachus vacuus* LeConte (Fig. 24), or without the tight spiral, as in *Triachus cerinus* LeConte (Fig. 27), or narrow, straight and tightly spiraled as in *Heptarthius longimanus* Suffrian (Fig. 31). The spermathecal duct may also be very short and wide as in *Lexiphanes* (Figs. 37, 38). In *Pachybrachina* the spermathecal duct is highly sclerotized but does not spiral or coil unto itself as much as *Cryptocephalina* and *Monachulina* (Figs. 48, 54, 62, 64), except for *Ambrotodes chilensis* Blanchard (Fig. 69).

The spermatheca is sclerotized, usually cylindrical with the base usually being broader than the apex. The apex of the spermatheca is either rounded or narrow. The shape of the spermatheca is species specific; however several characteristics remain consistent within the different genera. The place of attachment of the spermathecal duct to the base of the spermatheca may be directly at the end of the base, as in *Cryptocephalina* [except *Triachus cerinus* (Fig. 29)], *Ambrotodes chilensis*, and possibly *Metallactus* (Fig. 59), or it may be on the side of the base, as in *Monachulina*, *Pachybrachis*, and *Griburius*. Additionally, both species of *Bassareus* observed had either one (*B. sp.*) or two [*B. brunnipis* (Olivier)] flattened ends on the venter of the spermatheca. Also, both species of *Diachus* (Fig. 17) had bulbous ends connected by a narrower channel. In *Diachus* and *Triachus* the large

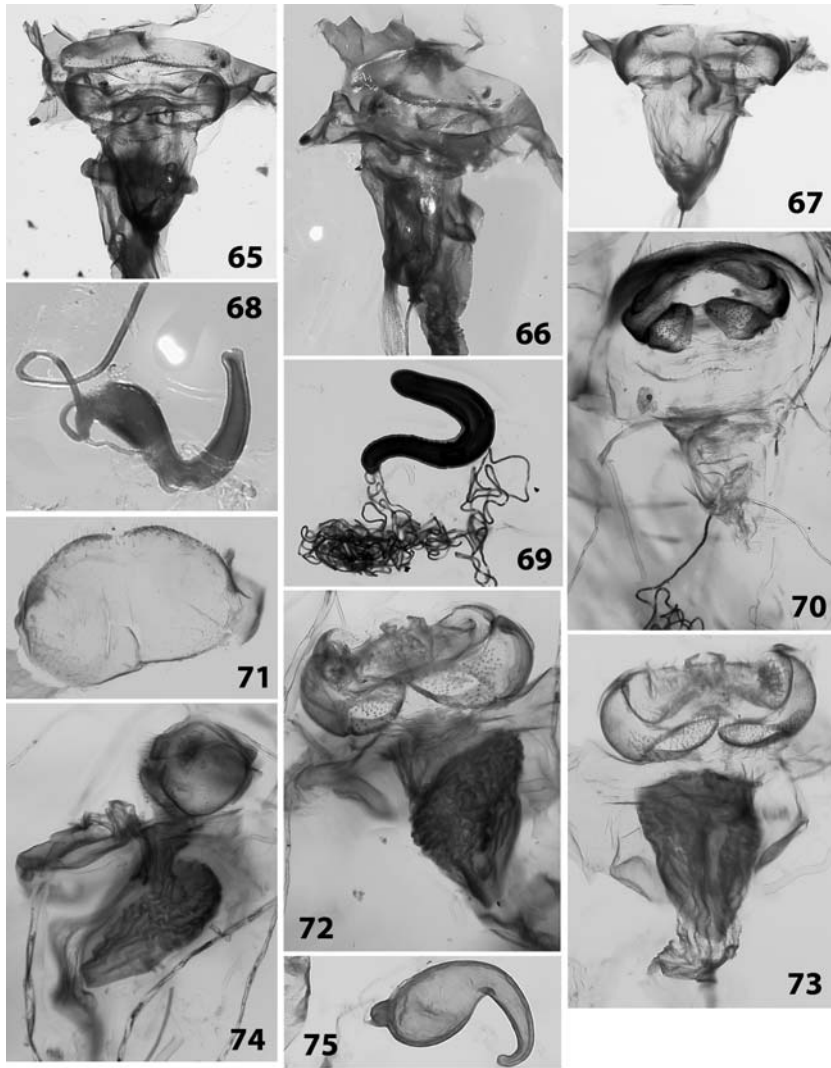


Figs. 56–59. *Metallactus decumanus*. **56)** tergite VIII, dorsal view; **57)** lateral view, tergite VIII removed; **58)** dorsal view, tergite VIII removed; **59)** spermatheca. **Figs. 60–64.** *Griburinus* sp. **60)** tergite VIII, dorsal view; **61)** caudal view, tergite VIII removed; **62)** lateral view, tergite VIII removed; **63)** dorsal view, tergite VIII removed; **64)** spermatheca.

size of the spermatheca was immediately apparent as it was almost the same size as all genitalic segments combined, whereas in other genera the spermatheca is much smaller in relation to the genitalia as a whole.

Rectum

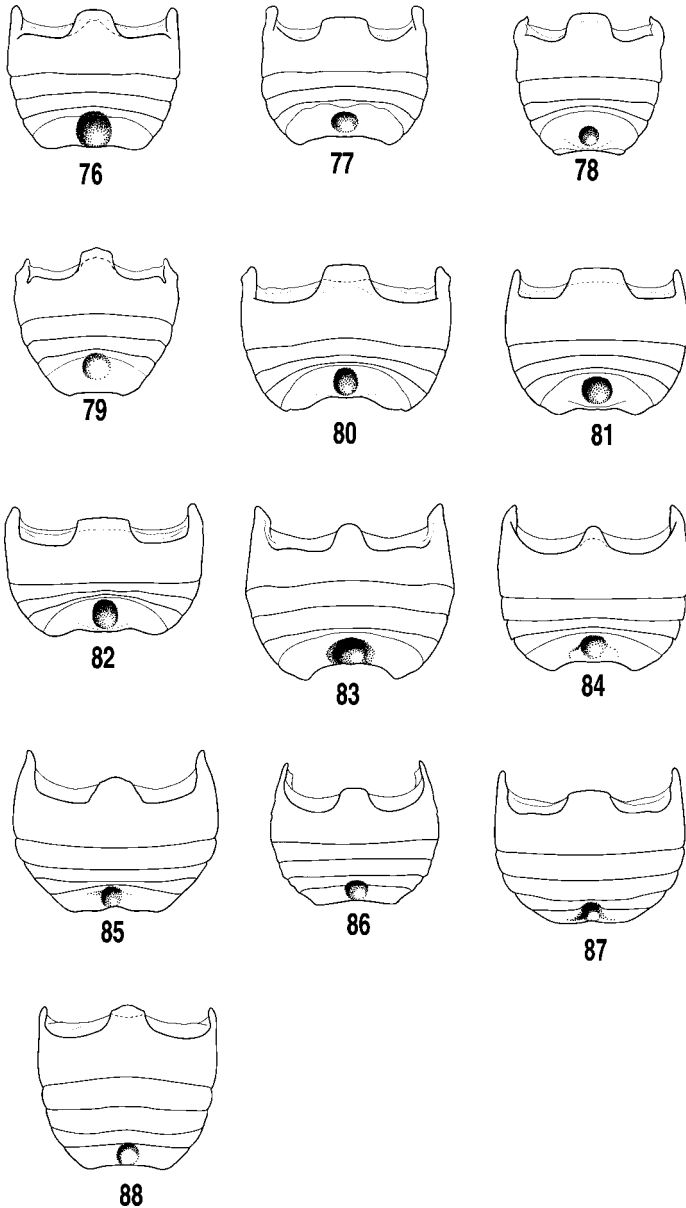
The anus is located between sclerites of the segment IX. The dorsal wall of the rectum is made up of the internal membranous layer of tergite IX and the ventral wall is made up of the internal membranous layer of sternum IX. The rectum is a highly specialized structure in Cryptocephalinae and was not examined for this study. Erber (1968) studied the rectum in considerable detail for Cryptocephalini and Clytrini.



Figs. 65–68. *Griburius equestris*. **65)** near caudal view, tergite VIII attached; **66)** laterocaudal view, tergite VIII attached; **67)** rear view, tergite VIII removed; **68)** spermatheca. **Figs. 69–70.** *Ambrotodes chilensis*. **69)** spermatheca; **70)** caudal view, tergite VIII attached. **Figs. 71–75.** *Ambrotodes signatipennis*. **71)** tergite VIII, dorsal view; **72)** rear view, tergite VIII removed; **73)** caudal view, tergite VIII removed; **74)** lateral view, tergite VIII removed; **75)** spermatheca.

Variability in Female Genitalic Structures of New World Cryptocephalini

Our study of New World Cryptocephalini revealed a set of characters of obvious diagnostic and possible phylogenetic value. The more informative of which were the shape of tergite VIII, the shape of tergites IX and the direction of the apices, the



Figs. 76–88. Abdominal ventrites. **76)** *Cryptocephalus arizonicus*; **77)** *Bassaricus* sp.; **78)** *Diachus auratus*; **79)** *Triachus cerinus*; **80)** *Heptarthrus longimanus*; **81)** *Lexiphanes saponatus*; **82)** *Stegnocephala costulatus*; **83)** *Ambrotodes chilensis*; **84)** *Ambrotodes signatipennis*; **85)** *Metallactus decumanus*; **86)** *Griburius equestris*; **87)** *Griburius* sp.; **88)** *Pachybrachis hepaticus*.

presence of projections on sternite IX, the degree of sclerotization and shape of sternum VIII, the shape of the medial projection of ventrite I and ventrite IV, and the location, shape and depth of the eimörser. Distribution of these characters is described below.

CRYPTOCEPHALINA:

Tergite VIII has an entire anterior margin and is apically sclerotized. Tergites IX are digitate and the acute apices are directed medially; the anterior margins are well defined and sclerotized. Sternites IX in rear view have a small appendage or projection. Sternite VIII bears a triangular rigid area with a pair of lateral C-shaped sclerotizations. Medial projection of ventrite I broad with anterior margin truncate, except *Diachus* has a less broad projection and the anterior margin is slightly produced. Ventrite IV less prominent than other ventrites.

Cryptocephalus: Connection between tergite IX to pleurite IX appears basal. Sclerotizations on sternite VIII not meeting. Spermathecal duct attaches to the base of the spermatheca and is relatively straight near the vagina and densely coiled near the spermatheca. Vagina broad and smooth. Abdominal depression or eimörser located medially on ventrite V.

Bassareus: Connection between tergite IX to pleurite IX appears basal. Sclerotizations on sternite VIII not meeting. Spermatheca with one or two C-shaped flattened ends. Spermathecal duct attaches to the base of the spermatheca and is relatively straight near the vagina and densely coiled near the spermatheca. Vagina small and wrinkled. Eimörser located partially under ventrite IV.

Diachus: Connection between tergite IX to pleurite IX appears to be along the lateral margin. Sclerotizations on sternite VIII meeting. Spermatheca as big as the rest of the genitalia. Spermathecal duct attaches to the base of the spermatheca and is relatively straight near the vagina and densely coiled near the spermatheca. Vagina broad and smooth or small and wrinkled. Eimörser located medially on ventrite V and posteriad towards margin.

Triachus: Connection between tergite IX to pleurite IX appears to be along the lateral margin. No sclerotizations on sternite VIII. Spermatheca as big as the rest of the genitalia. Spermathecal duct may appear as attached to the side or the base of the spermatheca and is curved and spiral. Vagina broad and smooth. Eimörser located partially under ventrite IV.

MONACHULINA:

Tergite VIII has a medially depressed anterior margin and is apically sclerotized. Tergites IX are digitate and the rounded apices are directed medially; the anterior margins are well defined and sclerotized. Sternites IX in rear view have a small appendage or projection. Spermathecal duct attaches to the side of the base of the spermatheca. Vagina broad and smooth. Eimörser located medially on ventrite V. Medial projection of ventrite I broad with truncate anterior margin. Ventrite IV as prominent as other ventrites.

Heptarthrius: Connection between tergite IX to pleurite IX appears basal. Sternite VIII moderately sclerotized, rigid, and the basal margin is produced mesally. Spermathecal duct spiral and thin.

Lexiphanes: Connection between tergite IX to pleurite IX appears basal. Sternite VIII strongly sclerotized and rigid. Spermathecal duct short and wide.

Stegnocephala: Connection between tergite IX to pleurite IX appears to be along the lateral margin. Sternite VIII lightly sclerotized and rigid. Spermathecal duct densely coiled near spermatheca.

PACHYBRACHINA:

Tergite VIII has a medially depressed anterior margin and is apically membranous. Tergites IX are triangular and the apices are directed laterally; the anterior margins are lightly sclerotized and not well defined; connection to pleurite IX along the lateral margin. Sternite IX in rear view do not have any projection (except *Metallactus*). Sternite VIII membranous. Vagina is broad, may be smooth, wrinkled and or compressed (see Table 1). Ventrite IV as prominent as other ventrites.

Ambrotodes: Sternite VIII membranous bearing setae medially. Spermathecal duct attaches to the base or side of the base of the spermatheca and duct is highly sclerotized coiled or not coiled. Medial projection of ventrite I narrow with anterior margin rounded. Eimörser located medially towards posterior margin.

Griburius: Spermathecal duct attaches to the side of the base of the spermatheca and is densely coiled and highly sclerotized. Medial projection of ventrite I broad (*G. sp.*) or narrow (*G. equestris*) with anterior margin truncate. Eimörser located partially under ventrite IV.

Metallactus: Sternites IX in rear view with a small appendage near the apex. Spermathecal duct attaches to the base or side of the base of the spermatheca and is not densely coiled. Medial projection of ventrite I broad with anterior margin slightly truncate. Eimörser located medially towards posterior margin.

Pachybrachis: Spermathecal duct attaches to the side of the base of the spermatheca and is not densely coiled (*P. gayi* has two knobs on the side of the base of the spermatheca). Medial projection of ventrite I slightly broad and anterior margin slightly produced. Eimörser located medially.

Conclusions

Kasap and Crowson (1985) consider the presence of pleurites in female genitalia of leaf beetles as a primitive feature. Following this idea, cryptocephalines have both primitive and advanced features. They have well developed pleurites as in Orsodacnines and some Chrysomelines (*Timarcha* Latreille) and a sclerotized plate that can be viewed as slightly modified sternite IX. Both features are completely absent in alticines and galerucines. However, in other respects cryptocephaline female genitalia is simpler than that of alticines and galerucines in having no or extremely poorly sclerotized sternite VIII, and no tignum. It seems reasonable to consider vaginal palpi of alticines and sternite IX of cryptocephalines to be homologous [as Kasap and Crowson (1985) suggest in their figure 9 (but not in the text)]. Indeed both are situated on the dorsal side of the vagina, both are hollow inside and look like invaginations of the dorsal side of the vagina, and both have setae on the top. The difference is that vaginal palpi of flea beetles are situated deep inside the vagina, where's in cryptocephalines, they are close to vulva.

The female genitalia of Cryptocephalini are very similar to the female genitalia of Clytrini and Chlamisini. They have the same, similarly placed sclerites, which differ only in small details: an extremely short vagina and spermatheca without a distinct border between the receptacle and the pump. The tignum is absent in all three groups. In *Clytra quadripunctata* (L.) (the only clytrine in this study) tergite VIII is strongly sclerotized with the proximal margin thick and vertical (upright). Sternite IX is situated vertically, proximally covering the entrance to the gut. The entrance to the vagina is armed with a well sclerotized, oval-shaped plate mesally divided into two parts and covered with setae. *Bassareus* sp. has a membranous hump on the same place. The main differences in female genitalia between the only studied chlamisine, *Chlamisus luteola* (Germar) and the other Cryptocephalines in this study, is the presence of an additional paired, sclerotized plate just above sternite IX. The plate is thin, membranous

mesally and attached posteriorly to sternite IX. This, however, does not change the position of the vagina. The dorsal wall of the vagina is still a continuation of sternite IX, sclerotized part of which lies inside the vagina.

All together the female genitalia in Cryptocephalinae are much more uniform than in Galerucinae and Chrysomelinae where variations range from maintaining a complete set of structures, including vaginal palpi, tignum, and spermatheca in *Timarcha* sp. to genitalia lacking sternite VIII, vaginal palpi, and spermatheca in *Gonioctena viminalis* (L.) (Konstantinov and Rusakov 1993).

In general, Cryptocephalina and Monachulina bear the greatest affinity in overall morphology of the female genitalia, with Pachybrachina possessing a different set of unique morphological states. This confirms the results of the study of cryptocephaline (Chamorro-Lacayo and Konstantinov 2004). According to this study, Cryptocephalina and Monachulina share a number of important prothorax characters with each other. While prothorax of Pachybrachina is quite unique (Chamorro-Lacayo and Konstantinov 2004). Among characters of female genitalia of particular diagnostic and phylogenetic value at the subtribal level, are the shape and degree of sclerotization of tergite VIII, tergite IX, and sternite VIII.

Relative position of the openings of the gut and vagina deserves special attention. Major works on general morphology of female genitalia in beetles (Tanner 1927; Lindroth 1957) do not address this question. Snodgrass (1935) briefly mentioned that the vulva is situated on either genital segment VIII or IX. Lawrence and Britton (1994) placed the rectum and vagina of *Atomaria* sp. (Cryptophagidae) in between tergite and sternite IX. Their drawing illustrates the ventral wall of the gut continuing posteriorly as a dorsal wall of the vagina. Our dissections of cryptocephaline genitalia show that the rectum is surrounded by segment IX, with tergite IX placed dorsally and pleurite and sternite IX laterally and ventrally, respectively. The dorsal wall of the gut is formed by the internal membranous (Konstantinov 2002) layer of tergite IX and the ventral wall is formed by the continuation of the internal, membranous layer of sternite IX. The sclerotized external layer of sternite IX in *Griburius* is situated right above the entrance into the vagina. Therefore an entrance to the vagina lies between sternite IX (forming a dorsal wall of the vagina) and sternite VIII (forming a ventral wall). The latter is much less sclerotized compared to the female genitalia of other known leaf beetles. The same conclusion was made in the study of the female genitalia in flea beetles (Konstantinov 2002), however in flea beetles tergite IX is located laterad rather than dorsad to the anus and sternite IX is modified into vaginal palpi.

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