Kipling W. Will

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James K. LIEBHERR and Kipling W. WILL*

Inferring phylogenetic relationships within Carabidae (Insecta, Coleoptera) from characters of the female reproductive tract

ABSTRACT

Characters of the female reproductive tract, ovipositor, and abdomen are analyzed using cladistic parsimony for a comprehensive representation of carabid beetle tribes. The resulting cladogram is rooted at the family Trachypachidae. No characters of the female reproductive tract define the Carabidae as monophyletic. The Carabidae exhibit a fundamental dichotomy, with the isochaete tribes Metriini and Paussini forming the adelphotaxon to the Anisochaeta, which includes Gehringiini and Rhysodini, along with the other groups considered member taxa in Jeannel's classification. Monophyly of Isochaeta is supported by the groundplan presence of a securiform helminthoid sclerite at the spermathecal base, and a rod-like, elongate laterotergite IX leading to the explosion chamber of the pygidial defense glands. Monophyly of the Anisochaeta is supported by the derived division of gonocoxa IX into a basal and apical portion. Within Anisochaeta, the evolution of a secondary spermatheca-2, and loss of the primary spermatheca-1 has occurred in one lineage including the Gehringiini, Notiokasiini, Elaphrini, Nebriini, Opisthiini, Notiophilini, and Omophronini. This evolutionary replacement is demonstrated by the possession of both spermatheca-like structures in *Gehringia olympica* Darlington and *Omophron variegatum* (Olivier). The adelphotaxon to this spermatheca-2 clade comprises a basal rhysodine grade consisting of Clivinini, Promecognathini, Amarotypini, Apotomini, Melaenini, Cymbionotini, and Rhysodini. The Rhysodini and Clivinini both exhibit a highly modified laterotergite IX; long and thin, with or without a clavate lateral region. This may represent a synapomorphous derivation, or convergence based on a tubular abdomen and burrowing habit. The basal grade gives rise to a grade of taxa sharing the presence of a ramus--a sclerotized portion of the vaginal wall situated medially to each gonocoxal base--along with the plesiomorphic spermatheca-1. The previous interpretation of the gonocoxal rami as a groundplan feature of Carabidae representing portions of abdominal segment VIII is rejected based on its derived occurrence relative to the origin of the family. The gonocoxal ramus or cicindine grade includes 1) Cicindini, 2) a monophyletic "carabine" clade including Siagonini, Cychrini, Pamborini, Carabini, and Cicindelini, 3) and the Scaritini and Hiletini which are paraphyletically related to a monophyletic group exhibiting the harpalidian abdominal configuration, including Broscini and all remaining tribes of Carabidae. Broscini retain the separate accessory gland and spermathecal arrangment of Scaritini and Hiletini, and comprise the adelphotaxon to the other remaining tribes. Patrobini repre-

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*Department of Entomology, Comstock Hall, Cornell University, Ithaca, New York 14853-0901, U.S.A.

sent the next divergent group, exhibiting an appended spermathecal gland but retaining the ramus at the base of gonocoxite 1. The remaining tribes, including member tribes of Jeannel's Stylifera (in part) and Conchifera, are ambiguously related based on female characters at a highly polytomous node. Within this polytomous clade, Pseudomorphini share a derived basal spermathecal sclerite with Geobaenini, Lachnophorini, and Odacanthini. Cnemalobini are placed as the adelphotaxon to Morionini. Other tribal relationships remain ambiguous due to basic homogeneity of the female reproductive tract observed throughout these tribes. The problematic Brachinini appear best placed among these tribes, although a less preferred but equally parsimonious placement is as adelphotaxon to Clivinini. Psydrini and Zolini appear polyphyletic based on female characters, with constituent subtribes placed at various positions between the gonocoxal ramus grade and the highest polytomous clade. The basal position of Clivinini and Apotomini supported by female characters is contrasted with Jeannel's placement in Scrobifera and Stylifera, respectively, based on thoracic structure.

Key words: phylogeny, cladistics, ovipositor, spermatheca, abdomen

INTRODUCTION

"Grâce aux organes génitaux femelles, ces oppositions, un peu stériles, de petits caractéres - caractéres que nous sommes loin de sous-estimer - dans bien des cas, ne sont plus à retenir lorsqu'il s'agit de définir des lignées supérieures et des attributions contestées (Leon Schuler, 1963a)."

"As one knows, no two builders are apt to develop their structures in exactly the same way though both may use very similar materials (George E. Ball, 1979)."

The history of classification of carabid beetles has involved the progressive integration of various character systems, including general habitus, antennal structure, mouthparts, tibial configuration, elytral shape, thoracic morphology, chaetotaxy, larval stages, and male genitalia (Ball, 1979). Presentation of successive classifications, each attempting to define natural groups that either expressed concepts of pre-evolutionary similarity or phylogenetic affinity, required assessment of prior character systems. By this incremental increase in knowledge, analogy has been discerned from homology, with the ultimate goal a classification that best represents the phylogenetic history of the family.

In the earliest monographic treatment of the female reproductive tract known to us, Stein (1847) described extensive variation in the spermathecal and bursal configurations of representatives of 12 genera of Carabidae. Given this context, it is surprising that until Schuler's series of papers (1960, 1962, 1963a, 1963b, 1965, 1974) on the use of female genitalic and reproductive tract characters for classification of the taxa proposed in Jeannel's (1941, 1942) "Faune de France", anatomical variation in this character system was not comprehensively studied. Schuler's studies concentrated on the particular types of spermathecal configurations present within various carabid tribes; his intent was the circumscription of natural genera (e.g., Schuler, 1963a).

In the intervening years, two major studies have addressed the utility of female tract characters for the higher classification of Carabidae; Bils (1976) and Deuve (1993). Bils based his phylogenetic conclusions on examination of taxa representing 38 presently recognized carabid tribes, and determination of putative homology among 39 synapomorphous characters. These

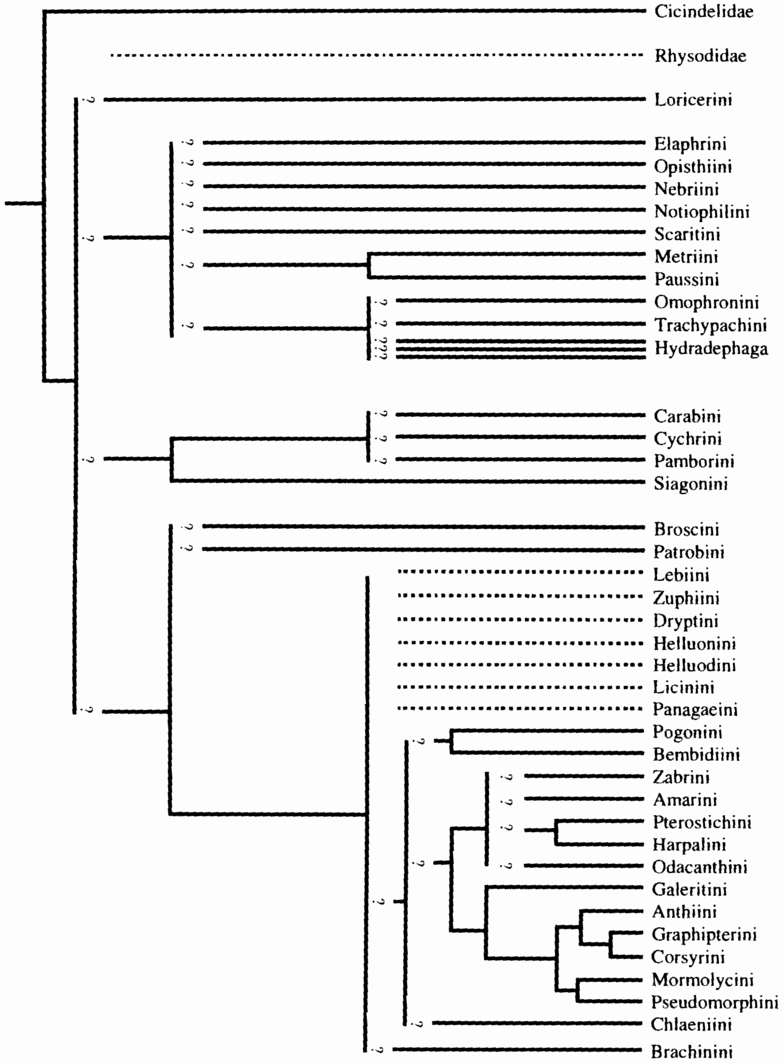


Fig. 1 - Cladogram of adephagan taxa based on muscular and cuticular characters of the female abdomen (Bils 1976).

characters included both variation of cuticular sclerites and the development, presence or absence of various muscles. Following on both Bell's (1966) conclusion that Trachypachidae are closely related to the adephagan water beetles, and the previous recognition of tiger beetles (Cicindelini herein) as a distinct lineage (Cicindelinae of Horn [1926] equivalent to Carabinae and Harpalinae [Csiki, 1927a et seq.]), Bils considered Cicindelidae to be the most basal clade of Adephaga (fig. 1). This rooting resulted in Trachypachini (considered Trachypachidae herein) being placed very close to the Hydradephaga within the Carabidae. Subsequent analysis of the antenna cleaner (Hlavac, 1971, Regenfuss, 1975), prothoracic structures (Baehr, 1979), wings (Ward, 1979), pterothoracic structures (Beutel, 1992a), and larvae (Arndt, 1993, Beutel, 1993), support the close relationship of the trachypachines with adephagan water beetles excluding Gyrinidae, but with that clade adelphotaxon to the remaining Geadephaga, i.e., the Carabidae including tiger beetles (Beutel, 1995a). This hypothesis remains somewhat unstable based on our present knowledge of characters, illustrated by Trachypachidae being considered the adelphotaxon of Carabidae, with those taxa adelphotaxon to Hydradephaga excluding Gyrinidae in a subsequent computer parsimony analysis by Beutel & Haas (1996).

For purposes of carabid classification, either hypothesized sister group of Carabidae can be interpreted in light of Bils' (1976) analysis by rerooting his cladogram to his Trachypachini (fig. 2). Monophyly of Carabidae sensu stricto is determined by a single character, the reduction of intertergal muscle M24 between tergites IX and X. In a cladistic classification, Omophronini would be recognized as a distinct lineage equivalent in rank to the trachypachines and the remaining Carabidae. Within Carabidae, tribes are arrayed as a primitive grade-scaritines, nebriines, elaphrines, opisthiines, notiophilines plus the isochaete tribes of Jeannel (1941); a mid-level grade including tribes associated with Carabini plus rhysodids; a somewhat higher grouping of several tribes of Jeannel's (1941) Limbata Sylifera-the tribes Broscini and Patrobini; and most apically, a majority of tribes comprising Jeannel's (1941) Limbata Conchifera, but also including bombardier beetles of the tribe Brachinini.

Deuve's (1993) treatment of carabid classification based on female abdominal and reproductive tract characters represents the integration of information on a broad variety of taxa, and is a prime example of how intensive taxon sampling can lead to robust phylogenetic conclusions. Deuve (1986, 1988) first reported the significance of the configuration of abdominal tergum VIII, including the presence of anterolateral apophyses as a defining character of his family Harpalidae (Carabidae Limbata Conchifera plus Pseudomorphini of Jeannel [1941]). Correlated with this state is the proximity of the pygidial gland opening to the posterior margin of tergum VIII, not the plesiomorphic condition near the anterior margin of tergum IX (Deuve, 1988).

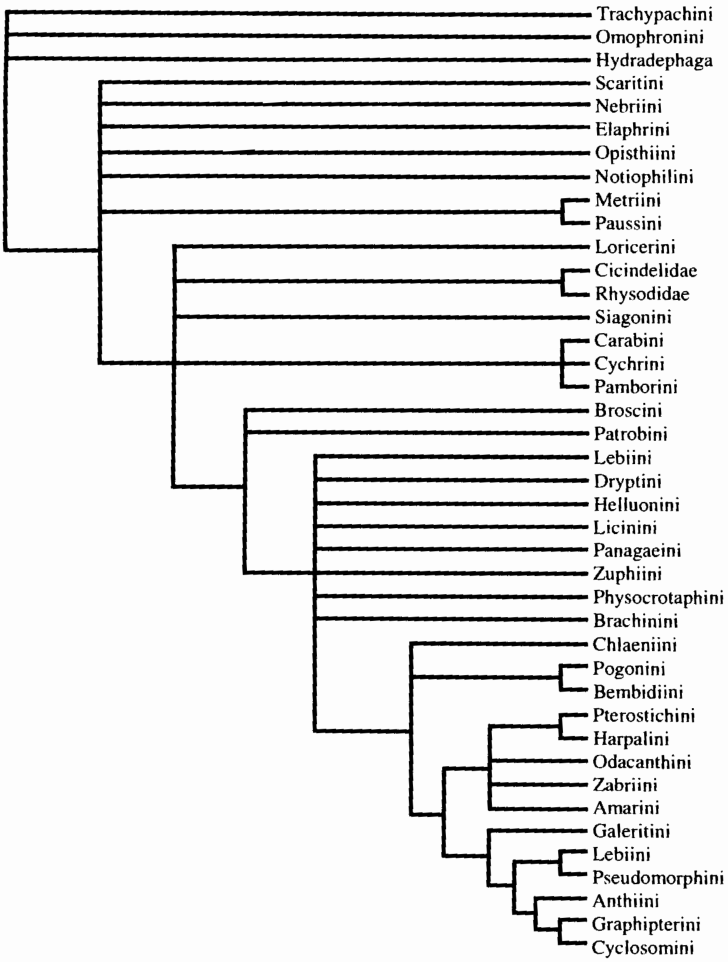


Fig. 2 - Cladogram of Bils (1976) rerooted in reference to comprehensive analysis of Adephaga (Beutel 1995a). Taxon names changed to reflect current tribal synonymies without changing taxonomic ranks of Bils.

Deuve (1988, 1993) recognized five basic configurations of the female abdomen, herein called nebridian, carabidian, harpalidian, cicindelidian, and brachinidian. In the nebridian condition, the last apparent abdominal tergum is VIII, which closes off the dorsal abdominal extremity. Tergum VII is undifferentiated, being about as long as tergum VI. This condition is observed in Hydradephaga, Trachypachidae, Omophronini, Nebriini, Loricerini, Elaphrini, Migadopini, Hiletini, Scaritini, Promecognathini as well as a number of other related tribes. In the carabidian configuration, the terminal apparent abdominal tergum is IX. Tergum VIII is partially invaginated with a simple anterior margin, and tergum VII is telescoped into tergum VI. Tribes exhibiting this configuration include those associated with Carabini (i.e., Cychrini and Pamborini) and Siagonini (including Enceladini). Males of carabidian taxa have tergum X present. The third major configuration is found in most tribes, including most of the species of Carabidae. This harpalidian abdomen is characterized by tergum VIII being partially or totally invaginated, with large forwardly directed apophyses arising on each side of the anterior margin. In extreme cases, tergum VIII is divided into hemitergites by a medial membranous area. Specialized configurations are observed in the cicindeline and brachinine lineages. In the cicindelines, the last apparent female tergite is VII, with the eighth segment invaginated to comprise part of the long telescoping abdomen used in oviposition. In male tiger beetles, as in the carabidian taxa, tergum X is present. In the brachinine bombardier beetles, the last visible tergum is VIII, which is largely telescoped into segment VII.

Deuve used these configurations to support the monophyly of his Harpalidae including the Pseudomorphini, previously placed by Jeannel (1941) in the unfortunate taxon Balteifera (Ball, 1979). Beyond that, however, he came to no definitive conclusions concerning whether these conditions defined monophyletic groups. By his positioning Cicindelini adjacent to Carabini (Deuve, 1993, pp. 103-107), and commenting on the general similarity of cicindeline and carabine female characters and male abdominal terga, he highlighted the similarity of these taxa, but did not conclude that the similarity represented synapomorphy.

Deuve's conclusions about the position of Brachinini are tentative, but he felt that an orthotopic condition of the female reproductive tract observed in several cave-adapted Paussini and in the brachinine genus *Crepidogaster* was evidence supporting the affinity of brachinines and the Isochaeta (tribes Metriini and Paussini). The orthotopic condition of the female tract is characterized by the gonopore opening in the membrane between segments VII and VIII, with sternal areas VIII and IX present posteroventrally from the gonopore. By Deuve's scenario, this condition transforms to the derived epitopic condition, observed in most Coleoptera-indeed most pterygote insects-through invagination of sternal areas VIII and IX forming the definitive vagina, with the functional gonopore thereby situated between the gonocoxae of segment IX (fig. 3). The orthotopic condition of *Crepidogaster* occurs because the laterotergites and gonocoxae of segment IX are apomorphically absent, and laterotergites VIII overlap medially. Therefore the gonopore opens at the base of segment VIII. In the orthotopic Paussini-the cave dwelling *Ozaenophaenops leclerci* Deuve and *Eustra lebretoni* Deuve-large genital plaques interpreted as coxosternum VIII are located between laterotergites VIII, and the gonopore opens into the membrane just anterad. In these paussines, gonocoxa IX is fully formed, and of the unsegmented configuration typical for Paussini and Metriini. Deuve argues that although this configuration must be considered a specialization secondarily acquired, it is evidence of an underlying primitive condition. Presence of orthotopy in *Crepidogaster*, then, serves not as a synapomorphy of Brachinini and Paussini, but as an underlying non-homologous indicator of affinity. The shared use of quinones in the pygidial defensive secretions of Brachinini, Metriini and Paussini (Schildknecht, 1957, Moore & Wallbank, 1968, Eisner et al., 1977) released in an explosive manner (Aneshansley et al., 1983) is congruent with this hypothesis.

In this paper, we build upon the previous two papers, sampling a comprehensive set of taxa representing nearly all carabid tribes, and analyzing the characters found using numerical cladistic analysis (Farris 1970). In order to get the broadest representation of taxa, we have restricted our study to the analysis of cuticular structures of cleared specimens. Deuve (1993) serves both as our foundation for taxon sampling, as well as our assignment of homologies for structures of the bursa copulatrix, oviduct, and spermathecal assemblies. We specifically address the placement of problematic taxa-Rhysodidae or Rhysodini, Omophronidae or Omophronini, Cicindelidae or Cicindelini, Brachininae or Brachinini, and Pseudomorphinae or Pseudomorphini-in light of comprehensive taxon sampling and analysis using female tract characters. We present and interpret our results in the context of what has been proposed based on previously used character systems, showing that female tract characters contribute greatly to understanding the phylogenetic structure of the family Carabidae, and should be considered part of the building materials used as the basis for any natural classification.

MATERIALS AND METHODS

Dissections

Specimens were prepared for examination by gently boiling them in distilled water containing a small amount of dish washing detergent for 0.5 hr. The entire abdomen was removed and placed in cold 10% KOH, covered, and allowed to sit for 24 hr. The cleared abdomen was then dissected by removing the tergites from the exposed sternites. In general the invaginated tergites and sternites could be easily removed with the exposed tergites. This dissected piece was then placed in 4% acetic acid for 5 min. During that time the exposed tergites were removed from the apical invaginated tergites. The abdominal apex, including female reproductive tract and hindgut, were then placed in a saturated solution of chlorazol black® in methyl cellosolve.

For specimens still exhibiting large amounts of fat surrounding the cuticular structures, gently tapping the preparation allowed the cellosolve to dissolve the fat, assisting in clearing the dissection. Segment VIII and associated defensive glands were generally removed from segment IX bearing the genitalia and reproductive tract, and hindgut. Female tracts were inspected in porcelain spot trays filled with glycerine when determination of the 3-dimensional relations of the various structures was necessary. For illustration, dissections were mounted in glycerine on glass microscope slides with cover slips, with spacer glass chips inserted under the cover slip for thicker dissections. All drawings were made using an ocular grid, first using a stereo dissecting microscope at 16-100x. Fine structures were examined and drawn under a phase contrast compound microscope at from 40-400x.

Taxonomic Material

We attempted to obtain the broadest taxonomic representation of taxa for this analysis to minimize problems in cladistic analysis due to the absence of any extant annectant taxa. By this, we proposed to test hypotheses of character-state transformations for female tract characters using the greatest possible number of combinations for those states in various taxa. By this manner, our data set could be used as the basis for study of other character systems, with the ultimate goal a comprehensive, robust classification of the family. We used three classifications to guide our choice of study taxa. Of the 78 tribes of Carabidae including Trachypachidae recognized by Kryzhanovsky (1976), we were able to include 77 (Cuneipectini lacking). Erwin (1979) recognized 72 tribes of Carabidae, of which we included representatives of 70 (Bascanini and Protopaussini lacking). Bousquet & Larochelle (1993) presented the most recent comprehensive classification of Carabidae at the tribal level. They include 76 carabid tribes in their conspectus, recognizing all tribes previously proposed and not definitively synonymized in later publications. Of these 76, we included representatatives of 68 (Microcheilini, Chaetodactylini, Cuneipectini, Bascanini, Idiomorphini, Glyptini, Sugimotoini, and Omphreini are not included). We used the tribal definitions of Bousquet & Larochelle (1993) as the basis for defining the terminals for our cladistic analysis, with the following three exceptions: 1), rhysodid beetles were considered part of the monophylum Trachypachidae+Carabidae; 2), Pentagonicini was combined with Odacanthini (Liebherr, 1988, 1990, unpubl. data); and 3), Metriini is considered a tribe distinct from Paussini in recognition of the inverted, or catopic, configuration of the oviduct and bursa copulatrix (Deuve, 1993). Beutel (1992c) also considers Metriini the adelphotaxon of the monophylum Ozaenini +Paussini. We did not recognize Carenini (Moore & Lawrence, 1994) or Pelophilini (Kavanaugh, 1996), although these may prove to be distinct tribal-level lineages when more comprehensive analyses of their relationships are published. Based on this most recent classification, all other tribes we have not included would be considered member taxa of the Harpalinae of Csiki (1928a) or Limbata Conchifera of Jeannel (1941). Our tribal-level cladogram was rooted at Trachypachidae, for which we examined one species each for the two genera constituting the family (*Trachypachus* and *Systolosoma*) (Beutel 1994, 1995b).

Our taxonomic sampling was based on personal examination of taxa representing 64 carabid and trachypachid tribes, 236 genera, and 709 species (Appendix 1). In addition, we relied on Kavanaugh & Nègre (1983), Kavanaugh & Erwin (1991), Deuve (1993, 1994), and Moret & Bousquet (1995) for scoring characters of Notiokasiini, Cicindini, Amarotypini, Cymbionotini, Nototylini, and Dercylini. Inclusion of observations reported by Deuve (1993) permitted us to evaluate the character-state distributions for tribal-level terminals-which formed the focus of our study-on the basis of taxa in 266 carabid genera. We refer to figures illustrating personally observed taxa as "fig." or "figs."; illustrations in other publications are cited as "Fig." or "Figs."

Characters

Because we wished to comprehensively sample taxa throughout the family, we focused on the variation in cuticular characters of the female reproductive tract and abdomen, an approach identical to that of Deuve (1993). In this way we could compare our results to Deuve's, and extend his work in a cladistic framework. Bils (1976) used cuticular characters as well as muscular, but because he worked with uncleared material, his character-state coding differs from ours for several important characters. Perhaps the most important involves the median articulation of the gonocoxae, whereby the plesiomorphic single gonocoxa becomes separated into a subgonocoxite and apical gonocoxite (gc1 and gc2, fig. 3). Bils considered the derived state to not occur in Omophronini and tribes of the grade Elaphrini to Scaritini (fig. 2), a coding used by Beutel & Haas (1996). As we will show, this interpretation is incorrect. Our character examinations agree with Deuve (1993) on this and most other characters (although our homology assessments and cladistic deductions differ).

Based on our studies, we recognize 20 informative-i.e., potentially synapomorphous-characters of the female reproductive tract, ovipositors, and abdominal apex. We have presented these as the plesiomorphic state (0) versus various derived states (1-4) based on rooting the cladogram at Trachypachidae. Several of the characters were considered unordered multistate characters, i.e., states of the character were not constrained, and transformations could occur from one state to any other state. When tribal members varied in the possession of a particular character state, we coded that tribe as ambiguous for the character (state P, Appendix 2). In some multistate characters, members of a tribe might exhibit more than one but less than all states. These were coded as subset-polymorphisms (Nixon 1995); i.e., the

6.) Spermathecal diverticulum absent (0); a diverticulum, apparently nonglandular, arising from reservoir of spermatheca (1) (fig. 25).

7.) Epispermathecal sclerite absent (0); epispermathecal sclerite present, extended along spermathecal duct from bursa copulatrix onto apical spermathecal reservoir (1) (fig. 25).

8.) Helminthoid sclerite present as a thin, filamentous sclerite extended from base of spermathecal duct ventrally onto wall of bursa copulatrix toward gonopore (0) (figs. 4, 12-15); helminthoid sclerite present, securiform (1) (figs. 5-8, 10); helminthoid sclerite absent (2) (figs. 11, 16-55).

The presence or absence, and configuration of the helminthoid sclerite was coded as a 3-state, unordered character. Deuve (1993) considered the securiform condition for this structure to represent a structure he called the vaginal apophysis (Deuve, 1993, Fig. 36), but we wish to make a stronger statement about homology of the securiform and primitively filiform conditions. Broscini exhibit either a filiform or securiform helminthoid sclerite.

9.) Villous canal absent (0); a tortuously contorted villous canal extended along surface of common oviduct starting from near oviduct-bursal junction, or spermathecal duct-bursa junction (1) (figs. 46-50).

10.) Spermathecal duct not exhibiting sclerotized extension onto common oviduct (0); base of spermathecal duct extended onto common oviduct as a spermathecal basal sclerite (1) (figs. 52-55).

11.) Spermatheca with a single reservoir (0) (e.g., figs. 52, 53); spermatheca bipartite, with a basal bulb and an apical bulb assembly (1) (figs. 54, 55).

12.) Area where common oviduct joins bursa copulatrix not sclerotized ventrally (0) (e.g., figs. 10, 16, 21, 23); a sclerotized ligular apophysis present on ventral surface of common oviduct near junction with bursa copulatrix (1) (e.g., figs. 11, 19, 20, 22).

This sclerotized ligular apophysis differs from the helminthoid sclerite in that it is a sclerotized evagination, securiform or not, of the oviduct wall. It is best developed in the securiform condition in the Carabini (fig. 22), though the condition in *Elaphrus* (fig. 11) approaches that of the Carabini. The ligular apophysis of Promecognathini (figs. 19, 20) is a hemispherical ring extended transversely across the oviduct base, a configuration fundamentally different from that seen in Carabini. Nonetheless, both occurrences indicate a sclerotized region of oviduct suitable for muscle insertion. Iuga & Roşca (1966) determined that muscles attaching to this apophysis are connected to hemisternites VIII. Therefore, it would appear this sclerite functions as a means of attachment for muscles that would be involved with evagination of the vagina, perhaps during oviposition. Schuler (1976) called this structure the vaginal plaque.

13.) Spermathecal gland duct lacking diverticula (0) (e.g., fig. 40); spermathecal gland duct with a non-glandular diverticulum (1), either a single filiform tube (fig. 42), a tube with apical reservoir (fig. 41), or ramifying diverticula (fig. 43).

cies function without a recognizable spermatheca; a possibility, but considered a less desirable conclusion given the double structures in *O. variegatum*. Stein (1847, Plate 1, Fig. 1) illustrated a ventral spermatheca-1 accompanied by a dorsal glandular structure entering the apex of an expanded excretory duct in the European *Omophron limbatum* (F.). This configuration suggests there may be variation among the European *Omophron* species in the configuration of the dorsal glandular structure and its basally associated receptacle.

Interpretation of the dorsal structure in *Omophron* as a spermatheca plus appended spermathecal gland assembly (fig. 15) also maximizes homologies between the female tracts of *Omophron* and those of *Notiophilus* (fig. 13), two tribes that have historically been considered closely related (Nichols 1985) .

Deuve (1993) did not observe the dorsal spermatheca-2 in his dissection of *Gehringia*. We found it difficult to discern, as the large helminthoid sclerite ventral to it causes the bursa to distort when placed under a microscope cover slip. Nonetheless, the structure was observed by JKL in 1983 when dissections were made for the John L. LeConte Workshop on Coleoptera (Ivie and Stribling, 1984), and seen again in dissections made by both authors in 1996.

Assigning the state for the spermatheca was assisted by position of the various spermathecae relative to the helminthoid sclerite, a plesiomorphically present structure that extends from the basal part of the spermatheca or spermathecal duct onto the bursa copulatrix. Notiokasiini, Opisthiini, Nebriini, Notiophilini, and some Omophronini possess the helminthoid sclerite but not the associated spermatheca-1. Elaphrini lack a helminthoid sclerite, thereby making an assessment of the position relative to this structure impossible. For this taxon, the markedly dorsal position of the spermatheca formed the basis of assigning this tribe spermatheca-2 status. Two other tribes include-member taxa that exhibit dorsal spermathecal insertions. The first, Hiletini (see Erwin & Stork, 1985, Fig. 8; Deuve, 1993; *Eucamaragnathus bocandei* [Alluaud] of this study, fig. 26) exhibits a female tract very similar to that of Scaritini of Bousquet & Larochelle (1993; figs 27, 28), thereby leading us to code hiletines as possessing spermatheca-1. These similarities include possession of separate spermatheca and accessory gland, and absence of a helminthoid sclerite. The Psydrini represent the second tribe with member taxa exhibiting a dorsal spermatheca, including *Mecyclothorax montivagus* (Blackburn) (fig. 30). Heterogeneity of the position of spermathecal insertion across the tribe (e.g., fig. 29; Deuve, 1993, Figs. 224-234), including many taxa with ventral spermathecae adjoining the common oviduct, suggests that unless Psydrini is massively polyphyletic, it should be coded as uniformly possessing spermatheca-1. The various consequences of our coding of spermathecal configuration are discussed in the context of the results of our cladistic analysis below.

tribal taxon was regarded as only possessing the two or more states exhibited by the various member species examined. Character-state information was entered using DADA (Nixon, 1995), which permitted easy submission to tree finding and visualization programs mentioned below.

Descriptions of the states for the 20 characters forming the basis of the analysis follow, along with a glossary defining various terms (Table 1), and taxon x character data matrix (Appendix 2).

1.) Accessory gland absent (0) (e.g., fig. 4); accessory gland present that enters the bursa copulatrix separately from the spermatheca (1) (figs. 5, 7, 8, 26, 27, 28, 29, 31).

2.) Appended spermathecal gland absent from spermatheca-1 (0) (e.g., fig. 4-15); appended spermathecal gland present, entering onto spermathecal duct of spermatheca-1 (1) (figs. 16, 17, 30, 32, 35-55). See also characters 4, 5. Melaenini and Cymbionotini were coded ambiguous (?) for this character as we wished to test the homology of the appended spermathecal gland with the spermathecal diverticulum (character 6).

3.) Appended spermathecal gland absent from spermatheca-2 (0); appended spermathecal gland present, entering onto spermathecal duct of spermatheca-2 (1) (figs. 10, 13-15). See also characters 4, 5.

4.) Spermatheca-1 present, situated near junction of common oviduct and bursa copulatrix, plesiomorphically in association with a helminthoid sclerite (character 8) (0) (figs. 4-10, 14, 16-55); spermatheca-1 absent, replaced by a dorsal spermatheca-2 (1) (figs. 11-13, 15).

5.) Spermatheca-2 absent (0); spermatheca-2 present on the dorsal surface of the bursa copulatrix, entering the bursa without any association with the oviduct or a helminthoid sclerite (1) (figs. 10-15).

The spermathecal configurations defined by characters 4 and 5 are equivalent to finding angels living amongst us, the angels' existence proving that human arms and bird wings are not homologous because their joint presence in angels results in failure to pass the conjunction test (Patterson 1982, de Pinna 1991). Were it not the for the female tract configurations observed in *Gehringia olympica* Darlington (fig. 10) and *Omophron variegatum* (Olivier) (fig. 14), one might hypothesize that all Carabidae possess a single homologous spermatheca that attaches to the bursa copulatrix in various positions. However, *G. olympica* and *O. variegatum* both possess a long spermatheca-like structure associated with a helminthoid sclerite that we call spermatheca-1, and a second dorsally entering structure we call spermatheca-2. Deuve (1993) observed the dorsal structure of *O. variegatum* and interpreted it as an accessory gland. However, the clearly glandular portion of the structure (sg2, fig. 14) does not enter the globular, more basal reservoir at its apex, but on its lateral surface, as would an appended spermathecal gland. Moreover, if this structure is not serving as a spermatheca in *Omophron*, the absence of a structure near the base of the helminthoid sclerite in *O. dentatum* LeConte (fig. 15) and other American *Omophron* would mean these spe-

14.) Spermathecal duct digitiform process absent (0) (e.g., figs. 38, 39, 41); spermathecal duct with a short digitiform process near junction with common oviduct (1) (figs. 37, 40, 42, 43).

When multiple branching structures comprise the spermathecal assembly, the spermatheca can be discerned from either the spermathecal gland duct diverticulum or the spermatheca duct digitiform process by its annulated or microreticulate surface, as the diverticula and digitiform processes are smooth, or with characteristically different surface structure (fig. 42). Because we studied only KOH-cleared specimens, we were only able to examine the remaining cuticular intima. More intensive studies using stained preparations would greatly increase the information available concerning the cell types associated with these various structures.

15.) Gonocoxae without sclerotization mesally between bases of gonocoxa 1 (0) (figs. 4-11, 16-20, 30, 33-55); gonocoxae with a sclerotized region-the ramus- just mesad the base of gonocoxa 1 (1) (figs. 12-15, 21-29, 31, 32).

Bils (1976) and Deuve (1993) considered this sclerotized, often lunular patch, to represent plesiomorphic presence of portions of sternite VIII. Bils named each structure the ramus of the gonocoxa, and Deuve called them the gonopods of segment VIII (gonopod VIII). We reject Deuve's homology assessment based on absence of the structure in the outgroup, Trachypachidae, and other groups placed basally in our cladistic analysis (see below). We retain the use of Bils' segment-neutral term, ramus, to describe it. The sclerotized area appears to lie just mesally and/or dorsally from the sclerotized base of the gonocoxa 1. It is associated with the gonocoxa of segment IX, and we interpret it as a secondary sclerotization of membrane associated with the gonocoxal bases. Cicindelini would appear to plesiomorphically possess this sclerite, as *Amblycheila* (fig. 23) and *Omus* exhibit it, whereas in *Cicindela* (fig. 24) it is doubtfully present in much reduced form, and in *Megacephala* and other cicindelines (Deuve 1993) it is absent.

16.) Laterotergite IX triangular, articulating with the lateral base of the gonocoxae at the inner apex of its sclerotized anterior margin (0) (fig. 4); laterotergite IX consisting of a highly sclerotized, rod-like anterior margin, connected posterolaterad the explosion chamber of the pygidial glands (1) (figs. 5-7); sclerotized anterior margin of laterotergite IX thin, but with clavate lateral reaches, broadly connecting to mediotergite IX (2) (figs. 8, 9); anterior margin of laterotergite IX thin, connecting posterolaterally to thin, strap like mediotergite IX (3) (figs. 17, 18).

This character was coded as unordered multi-state. States 2 and 3 are autapomorphic for Rhysodini and Clivinini respectively, and express our wish to test the possible synapomorphous nature of the laterotergites in these two groups. Grouping of these taxa based on other characters would support consideration of states 2 and 3 as homologous.

17.) Gonocoxae IX single segmented, unarticulated medially (0) (figs. 4-7, 12, 18, 19, 34); gonocoxae IX with a medial articulation, separated into distinct segments called gonocoxite 1 and gonocoxite 2 (1) (figs. 8-11, 13-17, 20-33, 35-55).

As mentioned above, our assessment of the distribution of this character differs significantly from that of Bils (1976), but is identical to that of Deuve (1993). Because Deuve (1993) is equivocal about possible gonocoxal segmentation in Cicindini, whereas Kavanaugh & Erwin (1991) considered cicindine gonocoxae to be unsegmented-though their drawings suggest remnant segmentation-we coded Cicindini as ambiguous (?, Appendix 2) for this character.

18.) Laterotergite IX triangular, without an anteriorly extending apophysis (0) (figs. 20, 22, 23); laterotergite with an elongate apophysis extending anteriorly (1) (fig. 21).

19.) Spermatheca without an appended spermathecal gland, or with a single appended gland (0) (figs. 36, 37); spermatheca with a second appended spermathecal gland-like structure, distal to the spermathecal gland which in observed taxa possesses the more apparently glandular surface (1) (figs. 38, 39).

20.) Abdomen of the nebridian type (Deuve, 1993), the last apparent tergum is the unmodified VIII (0); abdomen of the carabidian type, with tergum IX the last apparent tergum (1); abdomen of the harpalidian type, in which the last apparent tergum is VIII, modified by the presence of anterolateral apodemes (2); abdomen of the cicindelidian type, with the last apparent tergum VII in the female, with an invaginated tergum VIII (3); abdomen of the brachinidian type, in which the last visible tergum VIII is largely telescoped into segment VII (4).

These five states were treated as unordered, with any state equidistant from all other states. By this coding, we could test the most parsimonious pattern of transformation in this character using information from the other characters.

Cladistic Analysis

The data matrix (Appendix 2) was analyzed cladistically using Goloboff's (1996) NONA program. Because so many of the terminals had identical character scores, we combined 17 tribes into an "idem taxon", thereby easing computational requirements of the analysis. We chose to represent two tribes with multiple terminals because female tract characters varied among their constituent subtribes. Psydrini is represented by four subtribes, including Psydrina, Amblytelina, Mecyclothoracina, and Melisoderina. Zolini is represented by the subtribes Merizodina and Oopterina. By this means we were able to eliminate many polymorphic characters that would have to be included were we to restrict our analysis to the tribal level alone, thereby enhancing resolution of the computer parsimony analysis.

The data matrix was analyzed using 200 multiple runs, holding 1,000 possible trees in memory, and starting with 50 trees for each multiple run. Trees and character-state distributions were examined using CLADOS (Nixon, 1993). Within the set of multiple equally parsimonious trees, those trees that resulted in the fewest steps for selected characters were preferred. This tree selection method is justified based on two criteria; 1) preferred trees are among the set of most parsimonious cladograms, 2) selected female characters are those judged less likely to have undergone homoplastic transformation. These characters make assumptions about character evolution that are supported by only some of the multiple equally parsimonious cladograms. We defend each specific use of the second criterion below in the presentation of results.

In order to facilitate viewing all most parsimonious trees consistent with minimal steps for our preferred characters, dummy characters possessing distributions supporting our preferred characters were added to the original matrix. We could then examine those most parsimonious trees consistent with certain assumptions in a reasonable amount of time. We discuss those assumptions and the coding of the dummy characters below. As the goal of our analysis was to demonstrate the contribution female tract characters can make to carabid classification, not to classify 70 odd tribes based on only 20 characters, we feel such limitations are reasonable.

Once we determined a preferred cladogram, we used the swap option of NONA to investigate alternate positions of taxa on the cladogram given the preferred cladogram topology. The swap command moves the taxon of interest to all possible positions on the cladogram, calculating the number of steps added to the cladogram assuming all other taxa remain in their same relative positions. Taxa that can be placed at alternate positions without adding any steps to the cladogram are discussed below under Alternate Placements.

Table 1. Abbreviations used in anatomical drawings.

ag --- accessory gland; enters directly onto bursa copulatrix.
ap --- forward extending apophysis of laterotergite IX.
bc --- bursa copulatrix; generally expanded area near junction of spermathecal duct and common oviduct.
bd --- bursal diverticula; various unhomologized diverticula entering bursa copulatrix.
bsc --- bursal sclerite; circular sclerotized region of bursa copulatrix observed in Patrobini.
co --- common oviduct.
dg --- defensive gland reservoir.
dl --- dorsal lobe of bursa copulatrix.
dls --- sclerite on dorsal lobe of bursa copulatrix.
ed --- efferent duct of defensive gland.
ess --- epispermathecal sclerite; a sclerotized canal on spermathecal duct extending from bursa copulatrix to spermathecal reservoir.
gc --- single segmented, unarticulated gonocoxa of abdominal segment IX.
gc1 --- gonocoxite 1, basal segment of a two-segmented, articulated gonocoxa.
gc2 --- gonocoxite 2, apical segment of a two-segmented, articulated gonocoxa.
gc1+2 --- secondarily fused gonocoxites 1 + 2.
hs --- helminthoid sclerite; a sclerite, either filiform or securiform, situated at base of spermathecal duct, and extending on ventral wall of bursa copulatrix.
la --- ligular apophysis; a sclerite, transverse or longitudinal, filiform to securiform, situated near base of common oviduct where it enters bursa copulatrix.
lt --- laterotergite of abdominal segment IX.
mt --- mediotergite of abdominal segment IX.
r --- gonocoxal ramus; a sclerite associated with mesobasal margin of gonocoxite 1.
sab --- spermathecal apical bulb; one of two reservoirs in a bipartite spermatheca, usually larger, more apical, and less associated with entry of spermathcal gland duct.
sbb --- spermathecal basal bulb; one of two reservoirs in a bipartite spermatheca, usually smaller, more basal, and more closely associated with entry of spermathecal gland duct.
sbs --- spermathecal basal sclerite; a sclerotized spermathecal duct extending onto common oviduct towards ovaries.
scl --- any of various unhomologized sclerites.
sd --- spermathecal diverticulum; a diverticulum entering spermathecal reservoir.
sdd --- spermathecal duct digital diverticulum; a diverticulum of spermathecal duct near duct-common oviduct junction.
sg --- appended spermathecal gland of plesiomorphic spermatheca-l.
sg2 --- appended spermathecal gland of apomorphic spermatheca-2.
sgd --- spermathecal gland duct diverticulum; a diverticulum of spermathecal gland duct, sometimes bifurcating.
sp --- spermatheca.
sp1 --- spermatheca-1; plesiomorphic spermatheca, situated near junction of common oviduct and bursa copulatrix.
sp2 --- spermatheca-2; apomorphic spermatheca, situated on dorsal surface of bursa copulatrix, often diametrically opposed to junction of oviduct and bursa copulatrix.
ssg --- secondary spermathecal gland; a diverticulum with apical reservoir entering apicad on spermathecal duct to spermathecal gland. Reservoir may appear smooth in contrast to spermathecal gland, which exhibits a clearly glandular reservoir surface.
v --- vagina; unexpanded portion of female reproductive tract lying between gonopore and expanded bursa copulatrix.
vc --- villous canal; a tortuously contorted sclerotized canal extending along common oviduct, often originating in or near base of spermathecal duct.

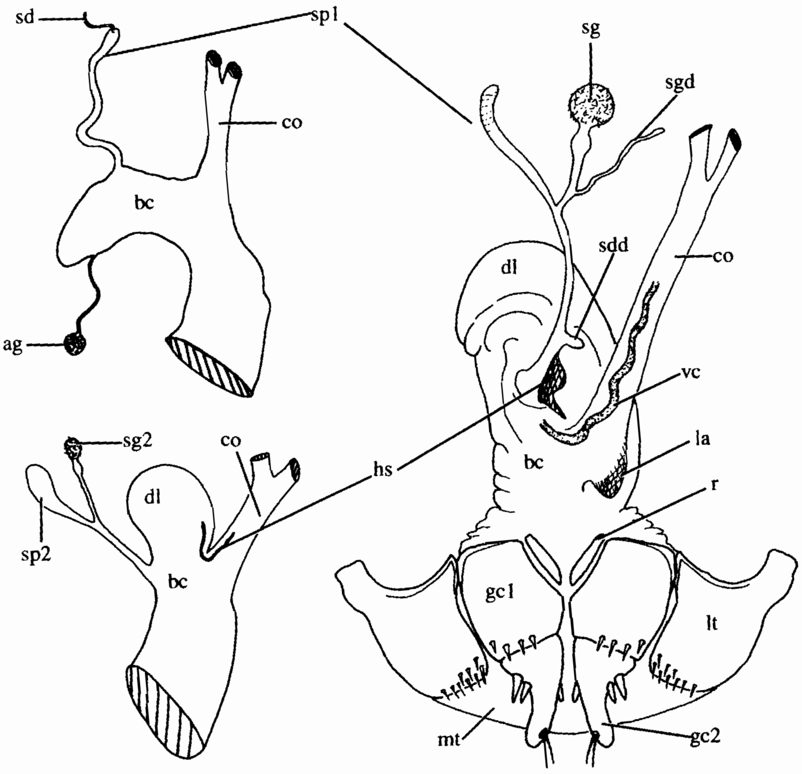
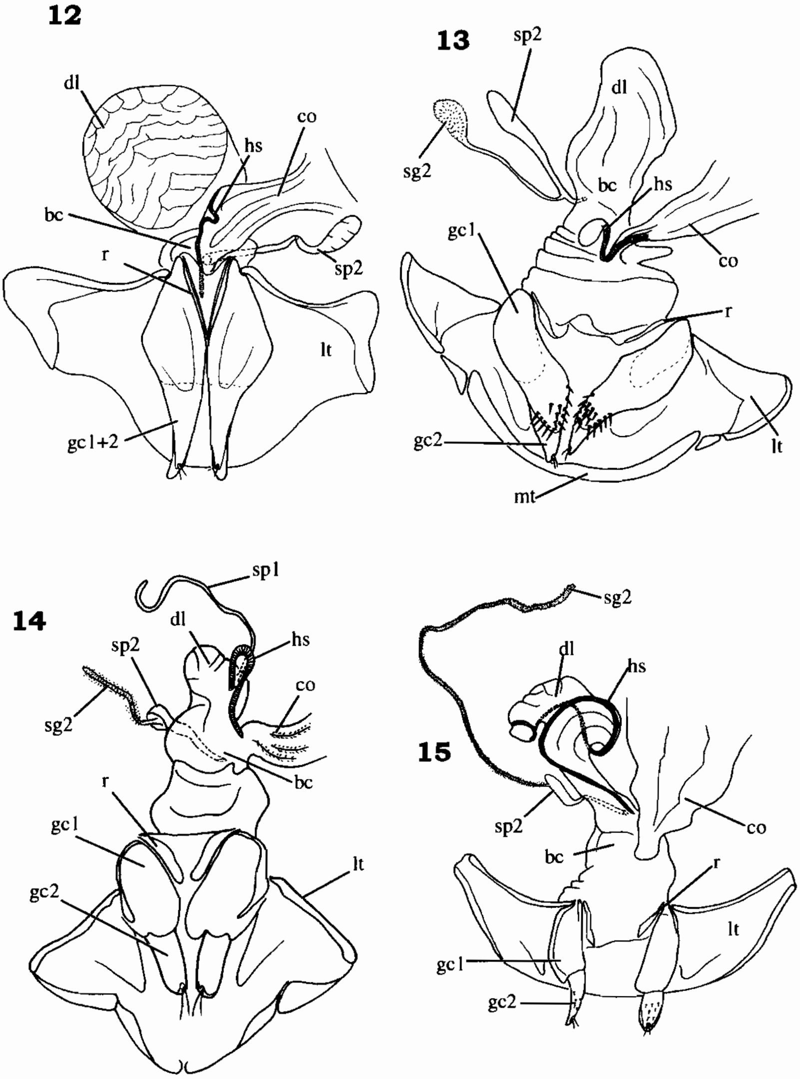
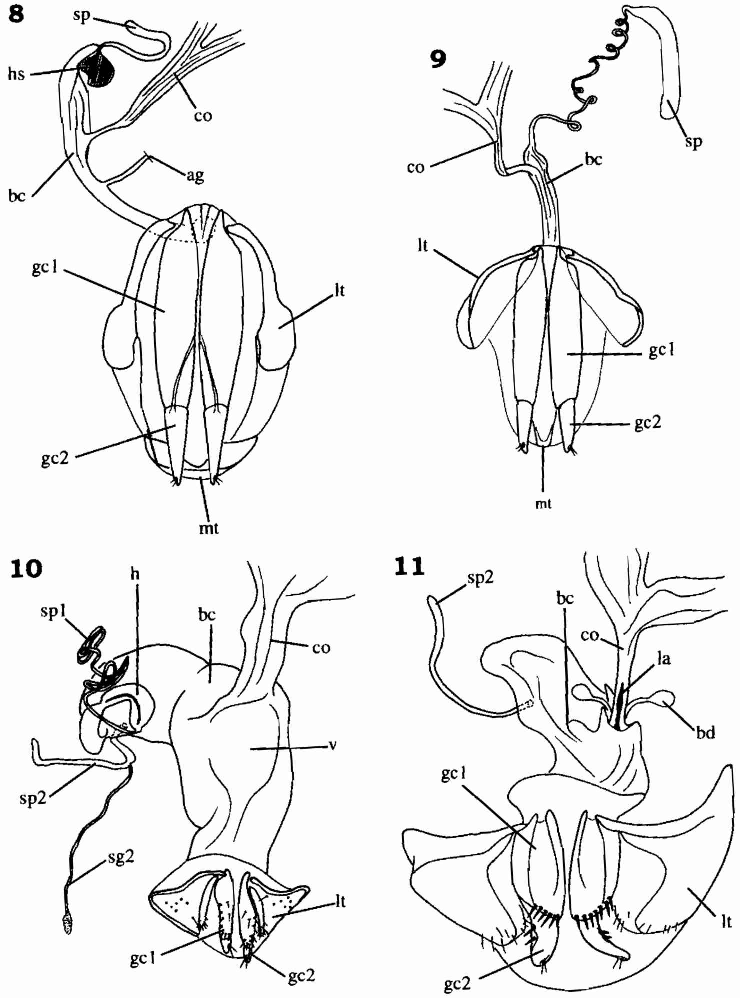


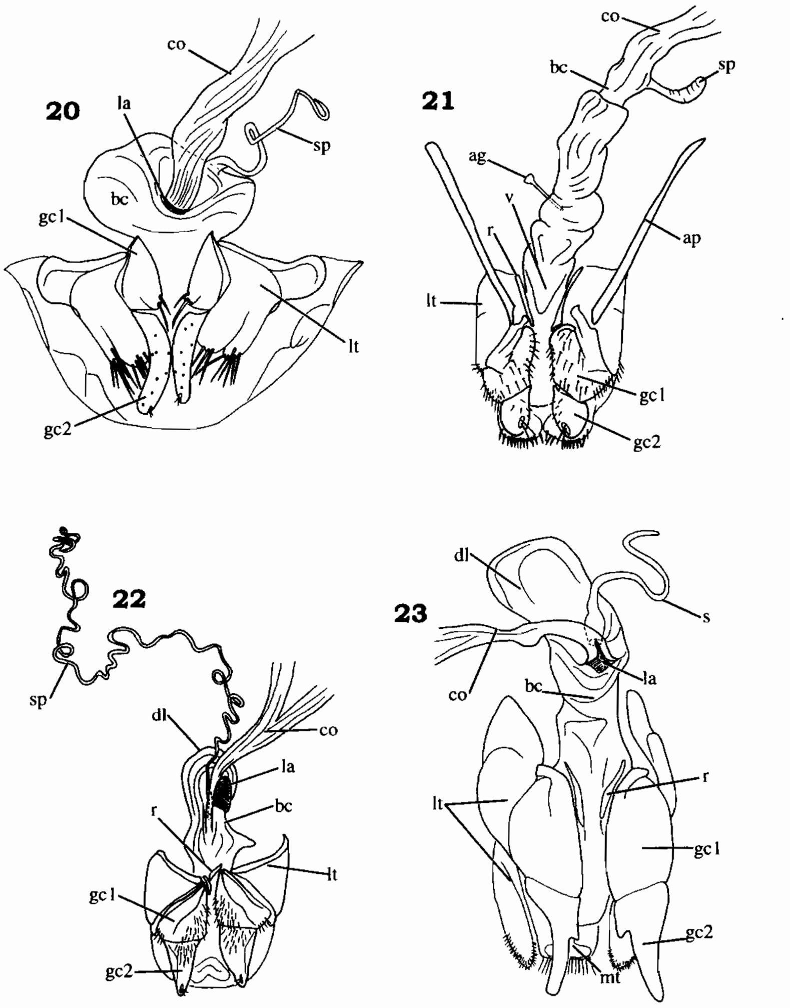
Fig. 3 - Hypothetical composite of carabid beetle female reproductive tract and ovipositors, illustrating characters used in cladistic analysis. Abbreviations for anatomical structures provided in Table 1.



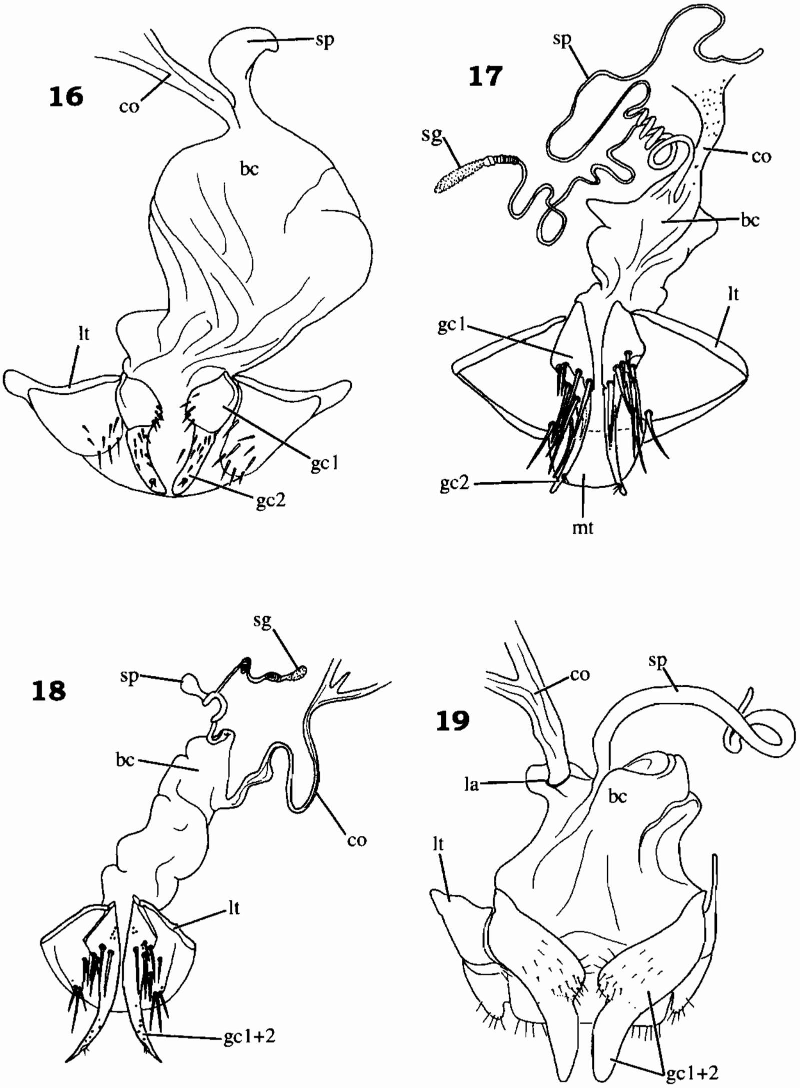
Figs. 12-15 - Female ovipositors and reproductive tracts, ventral view, *Opisthius richardsoni* Kirby (12), *Notiophilus novemstriatus* LeConte (13), *Omophron variegatum* (Olivier) (14), *Omophron dentatum* LeConte (15).



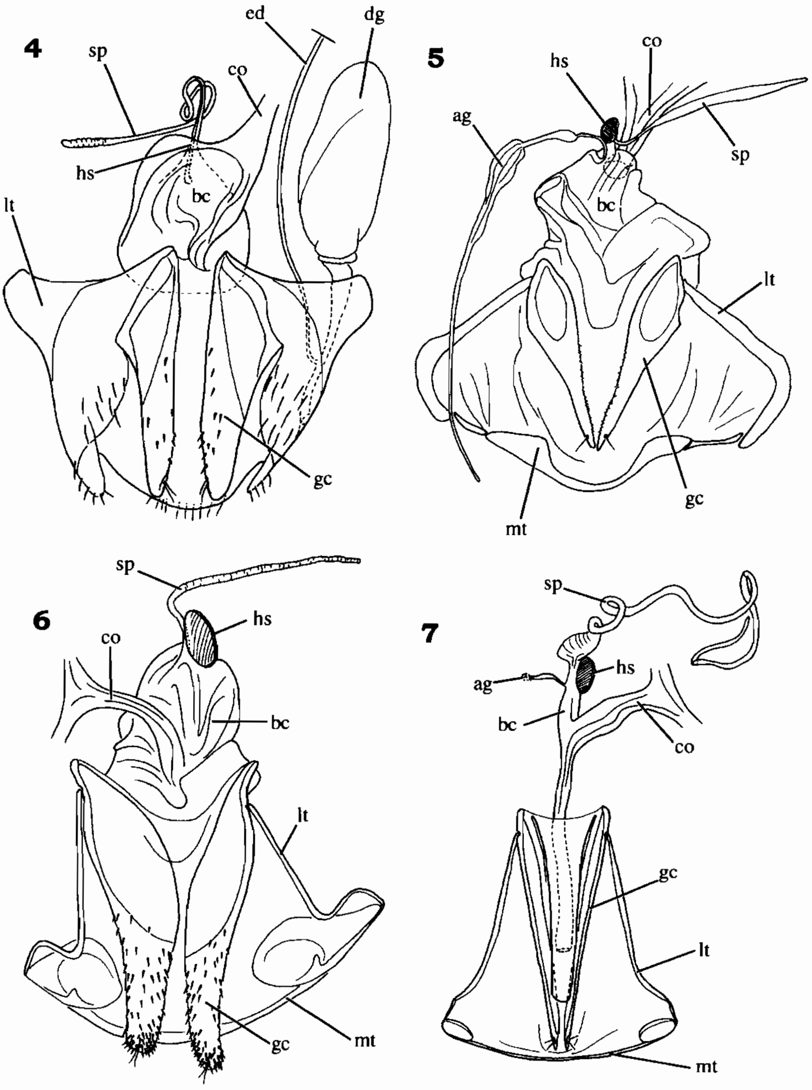
Figs. 8-11 - Female ovipositors and reproductive tracts, ventral view, *Omoglymmius hamatus* (LeConte) (8), *Clinidium calcaratum* LeConte (9), *Gehringia olympica* Darlington (10), *Elaphrus lecontei* Crotch (11).



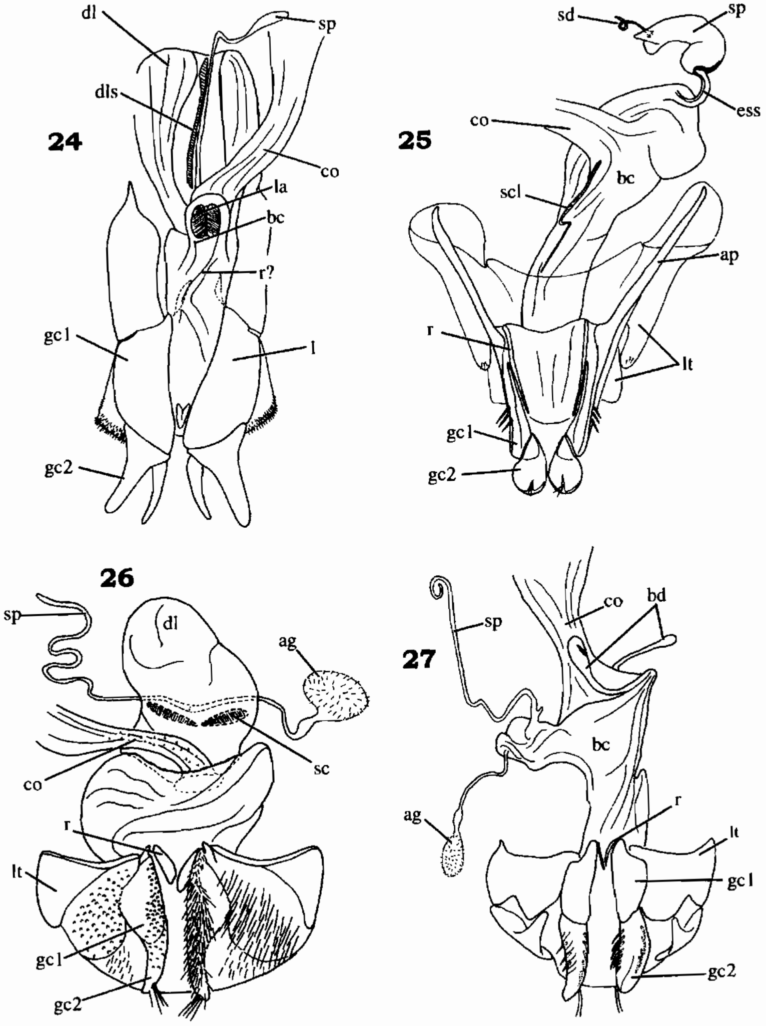
Figs. 20-23 - Female ovipositors and reproductive tracts, ventral view, *Paraxinidium andreaei* Basilewsky (20), *Siagona* sp. (21), *Carabus nemoralis* Müller (22), *Amblycheila picolominii* Reiche (23).



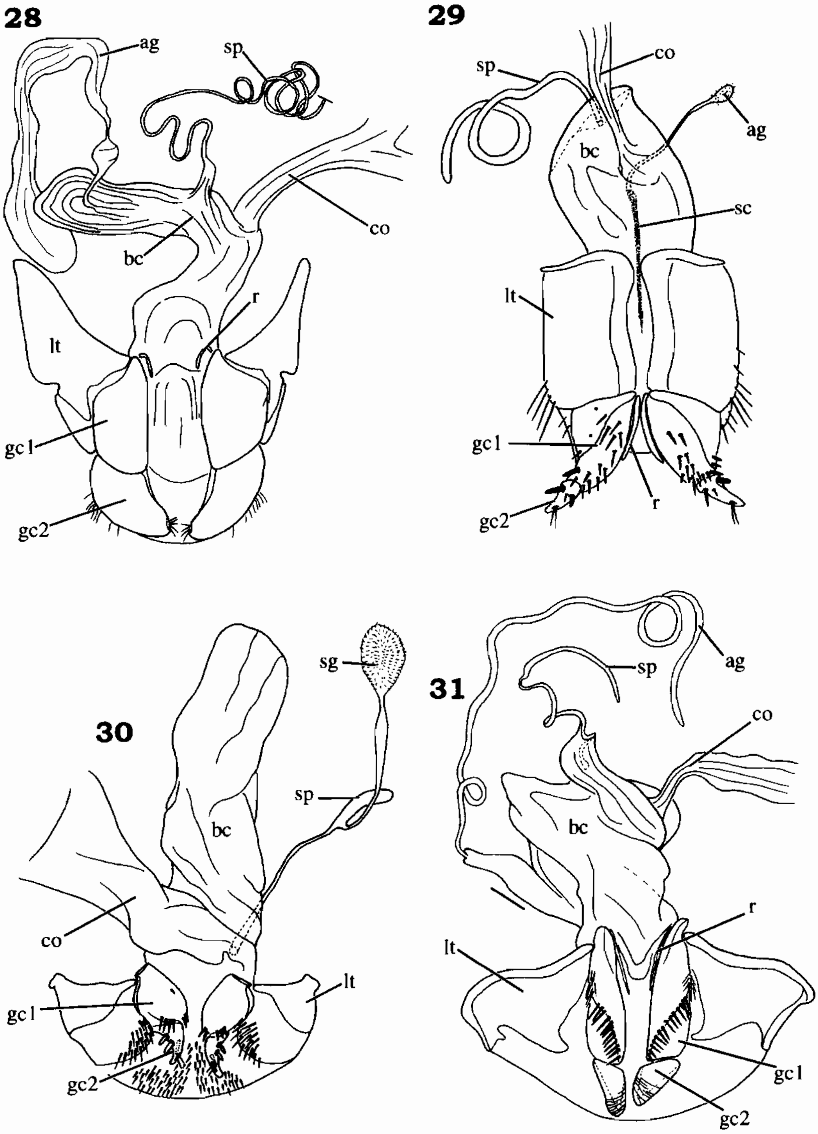
Figs. 16-19 - Female ovipositors and reproductive tracts, ventral view, *Migadops latus* (Guérin) (16), *Clivina americana* Dejean (17), *Salcedia perrieri* Fairmaire (18), *Promecognathus laevissimus* (Dejean) (19).



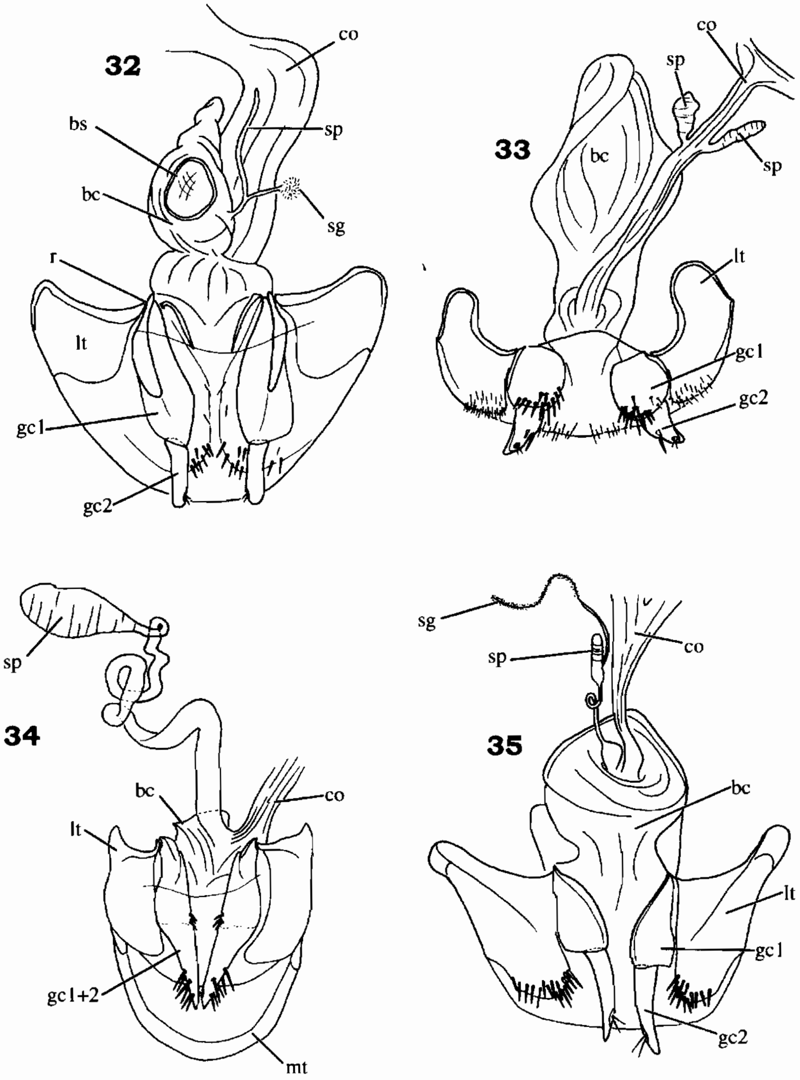
Figs. 4-7 - Female ovipositors and reproductive tracts, ventral view (abbreviations provided in Table 1), *Trachypachus holmbergi* Mannerheim (4), *Metrius contractus* Eschscholtz (5), *Pachyteles* (*Goniotropis*) sp. (6), *Physea tomentosa* Chaudoir (7).



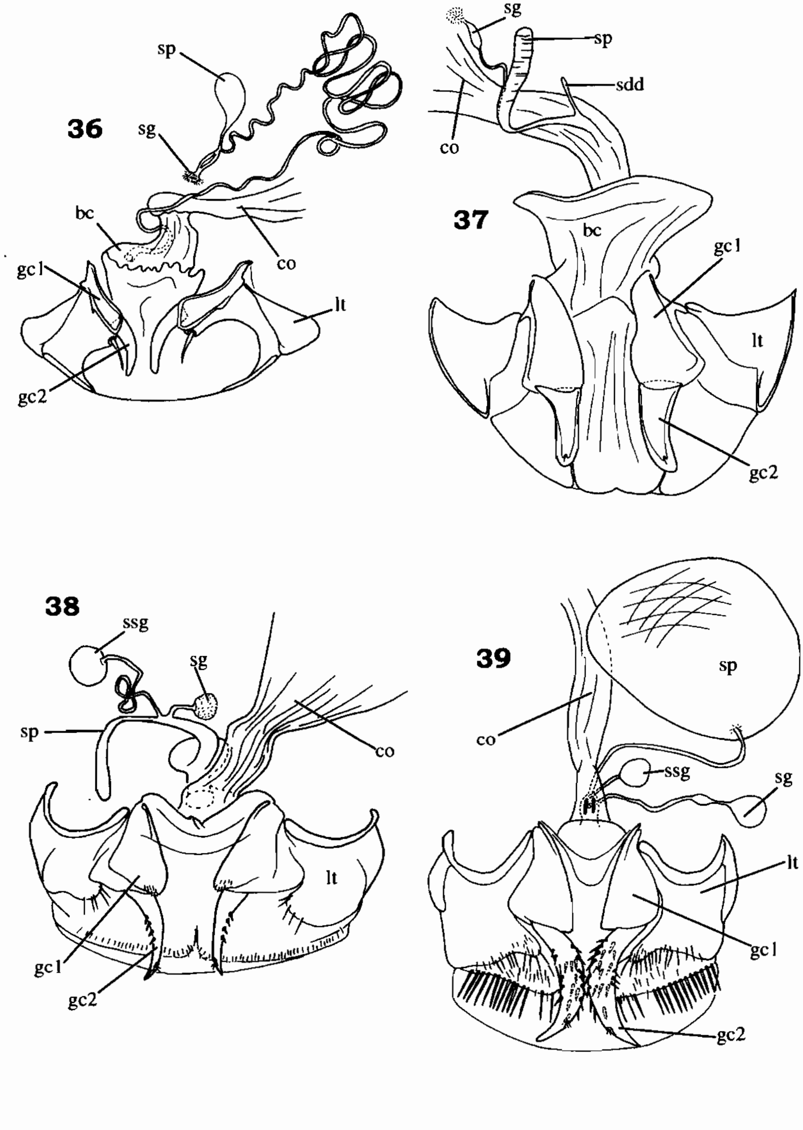
Figs. 24-27 - Female ovipositors and reproductive tracts, ventral view, *Cicindela longilabris* Say (24), *Melaenus piger* (F.) (25), *Eucamaragnathus bocandei* (Alluaud) (26), *Carenum* sp. (27).



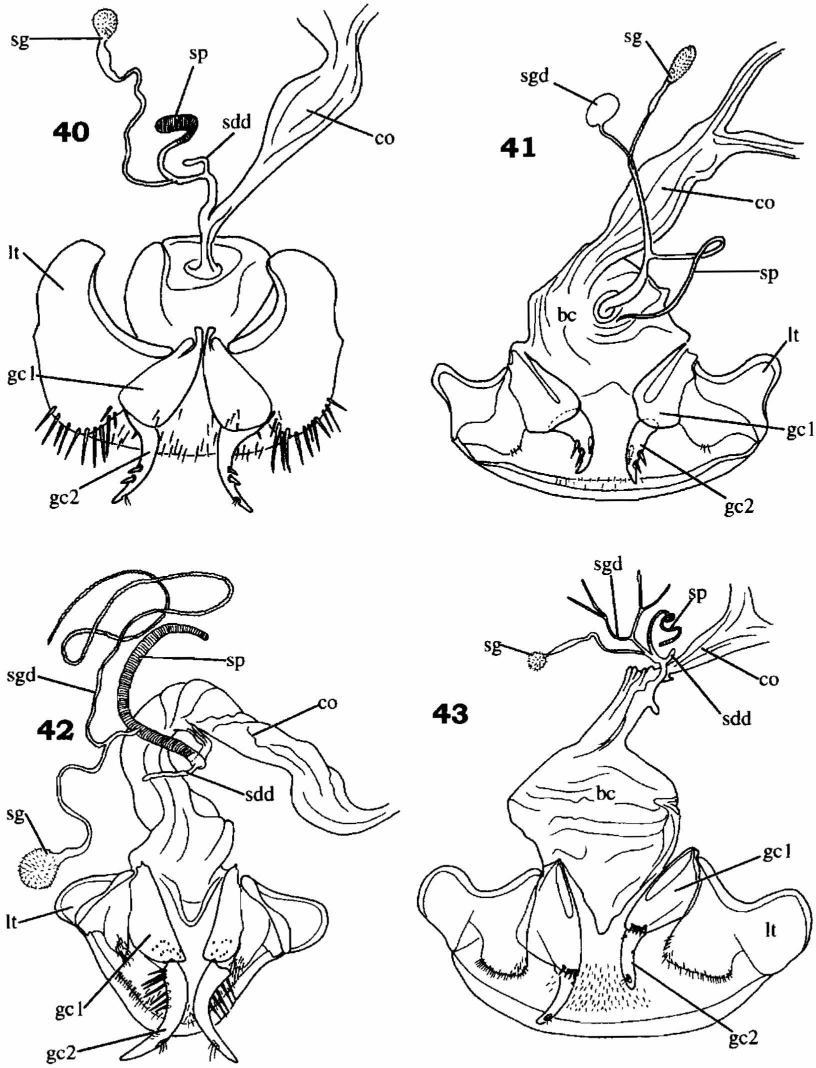
Figs. 28-31 - Female ovipositors and reproductive tracts, ventral view, *Pasimachus californicus* Chaudoir (28), *Psydrus piceus* LeConte (29), *Mecyclothorax montivagus* (Blackburn) (30), *Broscus cephalotes* (L.) (31).



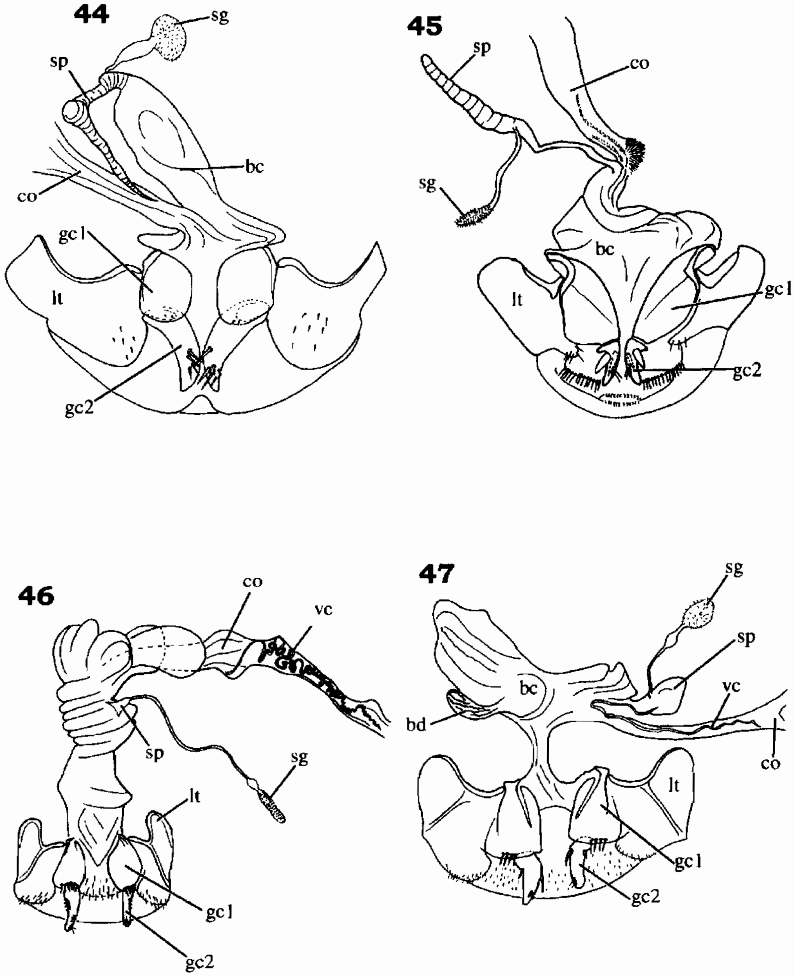
Figs. 32-35 - Female ovipositors and reproductive tracts, ventral view, *Diplous californicus* Motschulsky (32), *Trechus chalybaeus* Dejean (33), *Catapiesis attenuata* Chaudoir (34), *Bembidion planatum* LeConte (35).



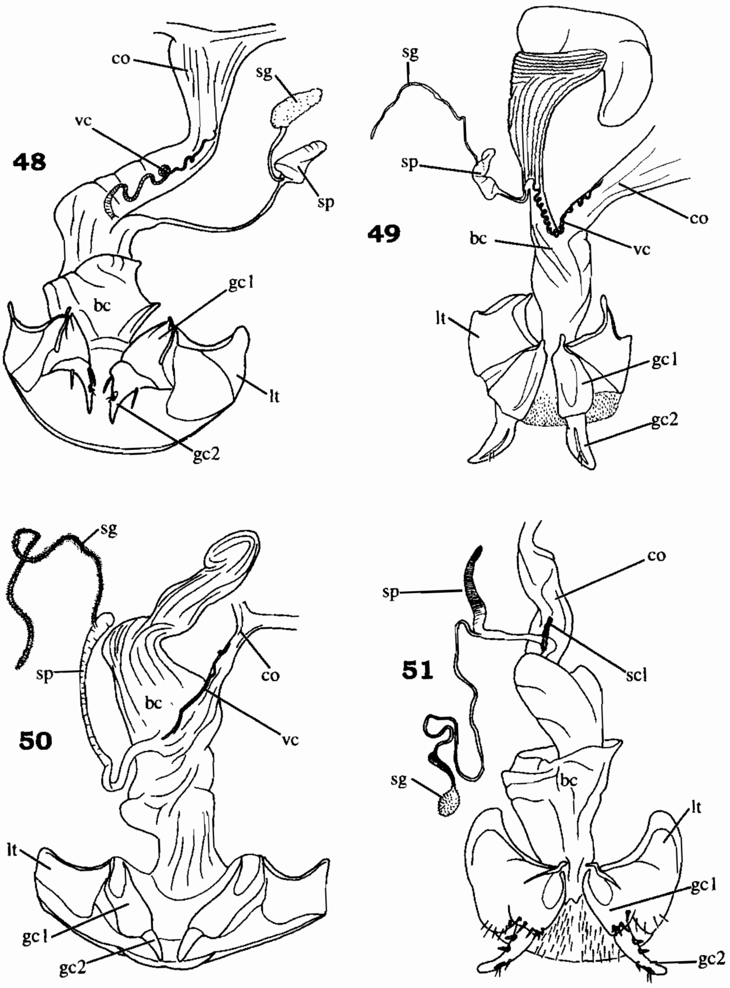
Figs. 36-39 - Female ovipositors and reproductive tracts, ventral view, *Mastax histrio* (F.) (36), *Brachinus favicollis* Erwin (37), *Helluomorphoides texanus* (LeConte) (38), *Galerita bicolor* (Drury) (39).



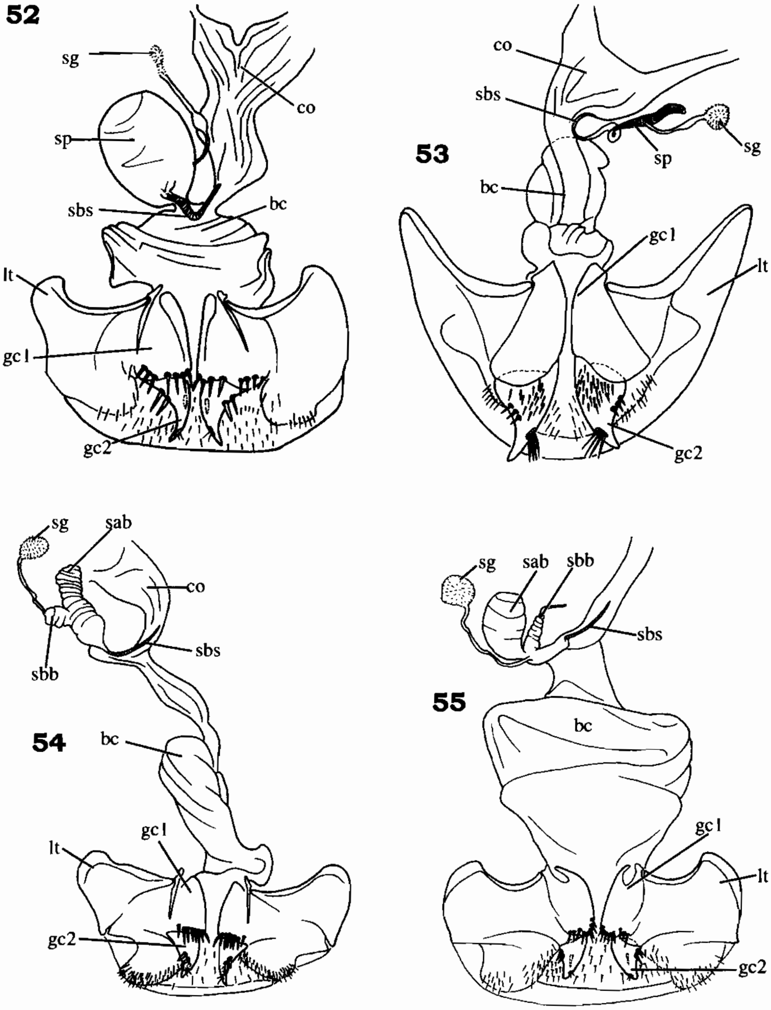
Figs. 40-43 - Female ovipositors and reproductive tracts, ventral view, *Pogonoglossus tagalus* Heller (40), *Morion monilicornis* (Latreille) (41), *Cnemalobus obscurus* Brullé (42), *Paranurus macleayi* Sloane (43).



Figs. 44-47 - Female ovipositors and reproductive tracts, ventral view, *Camptotoma freyi* Nègre (44), *Eripus oaxacanus* Straneo & Ball (45), *Loxandrus celeris* (Dejean) (46), *Melanchiton kenyensis* Straneo (47).



Figs. 48-51 - Female ovipositors and reproductive tracts, ventral view, *Panagaeus fasciatus* Say (48), *Orthogonius alternans* MacLeay (49), *Graphipterus atrimedius* Chaudoir (50), *Rhadine longicollis* Benedict (51).



Figs. 52-55 - Female ovipositors and reproductive tracts, ventral view, *Geobaenus lateralis* Dejean (52), *Sphallomorpha dubia* (Castelnau) (53), *Odacantha melanura* L. (54), *Anchonoderus darlingtoni* Liebherr (55).

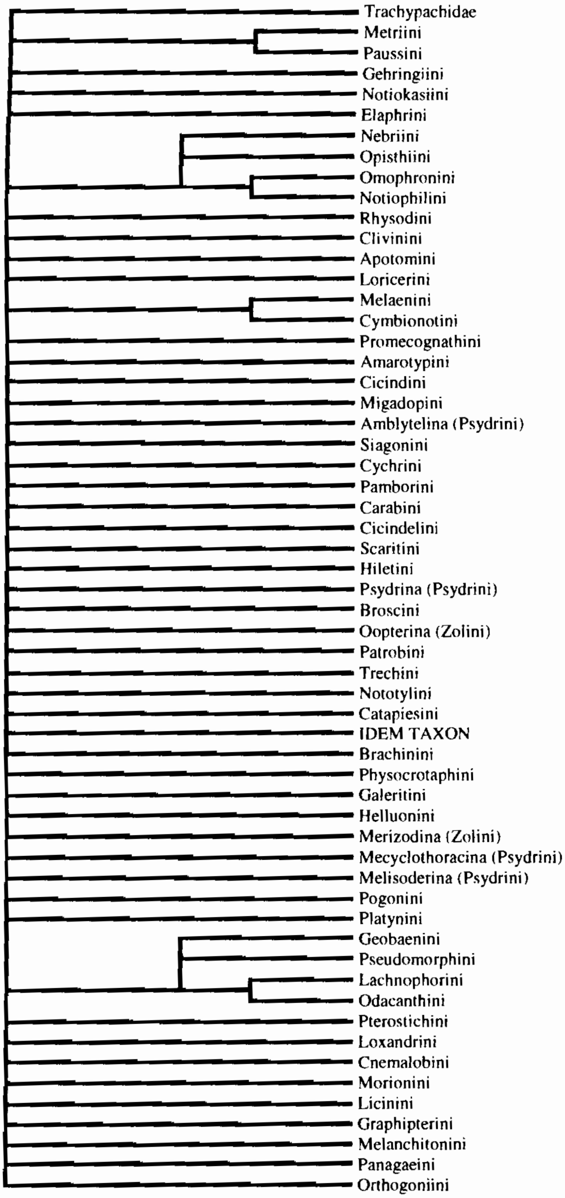


Fig. 56 - Strict consensus cladogram of 4850 equally parsimonious cladograms.

RESULTS AND DISCUSSION

Cladistic Analysis

More than 45,000 equally parsimonious cladograms of 44 steps exist for this data set of 58 taxa and 20 characters. The strict consensus (fig. 56) of 4850 trees is extremely uninformative, and based on examination of restricted synapomorphies using CLADOS, not further collapsible. Four clades are preserved in the strict consensus; 1) the isochaete tribes Metriini and Paussini, 2) four of the tribes possessing spermatheca-2 and gonocoxal rami (Nebriini, Opisthiini, Notiophilini, and Omophronini), 3) the sister tribes Melaenini and Cymbionotini, possessing both an apparently non-glandular spermathecal diverticulum and an epispermathecal canal, and 4) the Pseudomorphini, Geobaenini, Lachnophorini, and Odacanthini, all possessing a basal spermathecal sclerite.

Because the lack of resolution in this strict consensus is largely based on several troublesome taxa which can alternate between apical and basal positions on the cladogram, thereby collapsing nodes between those positions, we believed a more informative result could be obtained by considering certain characters more likely to be indicative of phylogenetic history. Seven assumptions were made, resulting in certain preferred groupings that were preserved in the search among the forest of more than 45,000 equally parsimonious trees.

1.) We postulate that the primitively unsegmented gonocoxa was restricted to the Trachypachidae and the isochaetous tribes Metriini and Paussini, and other instances of unsegmented gonocoxae represented secondary fusion. These instances include the Opisthiini (fig. 12), clivinines such as *Salcedia* (fig. 18) and *Schizogenius*, *Promecognathus laevissimus* (Dejean) (fig. 19), and *Catapiesis* (fig. 34). Secondary fusion in Opisthiini is supported by Kavanaugh's (1996) analysis of basal grade Carabidae. In the Clivinini, *Clivina americana* Dejean (fig. 17) exhibits segmented gonocoxae, indicating character transformation within the tribe. In the Promecognathini, *Paraxinidium andreaei* Basilewsky (fig. 20) has segmented gonocoxae, and the gonocoxae of *Promecognathus* (fig. 19) retain a setiferous inner margin basal to a glabrous apical lobe, indicative of fusion of a basal and apical gonocoxite. Likewise, *Catapiesis attenuata* Chaudoir exhibits a setal patch localized in the position of the inner apical margin of a basal gonocoxite. Use of this assumption precludes alternate placement of Catapiesini at the base of the cladogram due to its single-segmented gonocoxae and lack of a spermathecal gland. The character-state distribution of this taxon alone can cause drastically alternative placements, leading to the lack of resolution observed in the strict consensus. This restricting postulate was implemented by a dummy character with the derived state scored for all taxa except Trachypachidae, Metriini, and Paussini.

2, 3.) We postulate that overall abdominal configuration was less likely to undergo homoplastic change than any single character of the female tract housed within the abdomen. Therefore, we considered the harpalidian and carabidian abdominal configuration to define monophyletic groups, with the nebridian type, shared with Trachypachidae, to represent the plesiomorphic condition. As trees found in the initial runs did not have the harpalidian type being derived from the carabidian type, separate conditions of monophyly for these two abdominal types are appropriate. These assumptions were implemented by scoring taxa with state 1 of character 20 with the derived state of a second dummy character, and taxa with state 2 of character 20 as the derived state for a third dummy character. Cicindelini and Brachinini were coded ambiguous for Carabidian and Harpalidian abdominal-type dummy characters respectively, as two goals of the analysis were placing these taxa based on as few assumptions as possible.

4.) The remarkably similar female tracts of Cnemalobini and Morionini (figs. 41, 42), which both possess a spermathecal gland duct diverticulum, suggested that these taxa are very closely related, a sentiment shared by Roig-Juñent (1993). The alternate placement of Cnemalobini that was precluded by using a fourth dummy character uniting Cnemalobini and Morionini, was as adelphotaxon to the Physocrotaphini-due to Physocrotaphini and Cnemalobini sharing the digitiform process of the spermathecal duct (figs. 40, 42). The vastly different habitus of these latter two tribes, and the otherwise similarity of the physocrotaphine tract to other truncatipennine groups such as *Brachinus* (fig. 37) served as our justification.

5.) The substitution of a spermatheca-2 for the plesiomorphic spermatheca-1 was judged to be a unique event. Therefore we used a fifth dummy character uniting Gehringiini, Notiokasiini, Elaphrini, and the four taxa of the resolved nebriiform clade (fig. 56). Of these taxa, Elaphrini finds alternate placement on the cladogram in some of the most parsimonious trees, causing collapse of the base of this clade of seven tribes. Elaphrine placement is considered in more depth below in Alternate Placements.

6.) The absence of the gonocoxal rami from the Conchifera of Jeannel (1941; fig. 58), plus Trechini, Bembidiini, Pogonini, some Psydrini, some Zolini, and Pseudomorphini is judged an apomorphic loss. Use of a dummy character uniting these taxa (those ultimately placed at the apical unresolved polytomy in the preferred cladogram [fig. 57]), precludes the placement of Trechini+Catapiesini at the base of the cladogram due to extensive reduction in the female tract of these tribes (fig. 33). As in criterion 2, Brachinini was considered ambiguous for this criterion.

7.) We also assumed the minimal number of times the appended spermathecal gland could have arisen given the above assumptions; i.e., three times, once in the ancestral Clivinini, a second time in the psydrine subtribe Amblytelina, and a third time in the ancestor of the Patrobini and all more apically placed tribes (see character 2, fig. 57). This dummy character united

Patrobini with taxa of the apical polytomy. Again, Brachinini were considered ambiguous for this criterion.

We must emphasize that these seven criteria, implemented by adding seven restrictive dummy characters to the original data matrix, were simply a means for us to sift through the many thousands of equally parsimonious cladograms in search of the ones that possessed topologies most congruent with the body of previous information on carabid phylogeny (Ball 1979). These dummy characters were not used for any tree statistic calculations, nor did they result in any suboptimal topologies not possible given our 20 informative characters. Their use allowed us to more efficiently use CLADOS to view trees, by restricting our survey to classes of trees expressing relationships laid out by the above criteria. Finding those topologies allowed us to interpret female tract characters in light of data from other character systems, and to pinpoint remaining areas of incongruence.

Preferred Cladogram

The preferred of the most parsimonious cladograms (fig. 57) shows a basal dichotomy within the Carabidae, i.e., the sister-group relationship of the Isochaeta, including the Metriini and Paussini, versus the Anisochaeta, including Gehringiini and Rhysodini. Relative to Trachypachidae, Carabidae share no autapomorphic characters of the female tract. Monophyly of the Isochaeta is supported by the groundplan derivations of a securiform helminthoid sclerite (character 8) and the thin, rod-like laterotergite IX associated with the explosion chamber (character 16). Anisochaete monophyly is defined by the possession of articulated gonocoxae (character 17), a derivation reversed to a secondarily fused state in some member taxa. This is the first unambiguous synapomorphy discovered for this particular circumscription of the Anisochaeta (see Beutel, 1992c, 1995a).

Within the Anisochaeta, a basal clade of tribes possessing spermatheca-2 (character 5) serves as the adelphotaxon for a more diverse assemblage comprising most of the Carabidae. The spermatheca-2 clade includes tribes traditionally considered related, e.g., the Nebriini, Notiophilini, and Opisthiini of Jeannel's (1941) Nebriidae. The inclusion of Omophronini in this clade runs counter to recent classifications (e.g., Kavanaugh & Nègre, 1983; Bousquet & Smetana, 1991, 1995; Kavanaugh, 1996), but a close relationship between Omophronini and Notiophilini has been a very common component of many prior classifications (Nichols, 1985). Character congruence and incongruence relative to this placement are discussed below.

We have been conservative in scoring taxa for the presence of spermatheca-2. Because of the presence of two spermatheca-like structures in *Gehringia* and *Omophron variegatum*, we must necessarily consider the two structures non-homologous. Notiokasiini, Nebriini, Opisthiini, and

Notiophilini were scored for the presence of spermatheca-2 based on dorsal spermathecal position definable relative to the position of the helminthoid sclerite. The Elaphrini were the only taxon scored for spermatheca-2 without reference to a helminthoid sclerite (see Alternate Placements below). Other taxa exhibiting an anatomically dorsal spermathecal position but lacking a helminthoid sclerite, such as Hiletini (fig. 26) or Mecyclothoracina of the Psydrini (fig. 30), were considered to possess spermatheca-1 because they possessed derived conditions for other characters that precluded their placement with Gehringiini and Omophronini (fig. 57).

The adelphotaxon to the spermatheca-2 clade is arrayed in three major polytomous assemblages, two being paraphyletic grades and the third a highly polytomous clade. The basal grade taxa-Loricerini, Apotomini, Rhysodini, Clivinini, Melaenini+Cymbionotini, and Promecognathini+Amarotypini are characterized by the loss of a helminthoid sclerite (character 8) (polymorphic in Rhysodini), and the absence of gonocoxal rami (character 15). The mid-level grade includes those taxa possessing rami, but lacking the harpalidian abdominal type (character 20). Within the mid-level grade are those taxa evolving the carabidian, and then the cicindelidian abdominal types, i.e., the Carabinae sensu stricto including Cicindelini. The Cicindini are placed at this grade because of their possession of gonocoxal rami, and lack of accessory or spermathecal glands. Moreover, their tract configuration, with the spermatheca entering the bursa between a dorsal lobe and the common oviduct (Kavanaugh & Erwin 1991, Fig. 32), is similar to those of Cicindelini or Carabini. The Hiletini and Scaritini (excluding Clivinini) possess a separate accessory gland emptying into the bursa copulatrix (character 1; figs. 26, 27) while retaining the nebridian abdominal type. The Broscini are derived from the grade comprising these tribes, plesiomorphically retaining the accessory gland spermathecal configuration (fig. 31), but exhibiting the apomorphic harpalidian abdominal configuration (character 20).

Following upward, the Zolini (Oopterina) have lost the accessory gland, and the Patrobini have the spermathecal gland appended to the spermathecal duct, not separately entering the bursa (fig. 32). All of these taxa retain the gonocoxal rami. The highest polytomous clade includes most carabid species, and representatives of 41 tribes included in our analysis. The Zolini and Psydrini are not monophyletic based on this set of characters. The psydrines exhibit abundant variation in the presence or absence of an accessory gland/appended spermathecal gland, in presence or absence of the gonocoxal rami, and in possessing either the nebridian or harpalidian abdominal configuration. Similarly, the Zolini are paraphyletic, with the Oopterina exhibiting rami but no accessory or spermathecal gland, and the Merizodina lacking rami and possessing an appended spermathecal gland.

Resolution within the large apical clade is minimal, this ambiguity based on the fundamental similarity of female reproductive tracts throughout the clade. Extensive evolution of ovipositors and spermathecal assemblies has

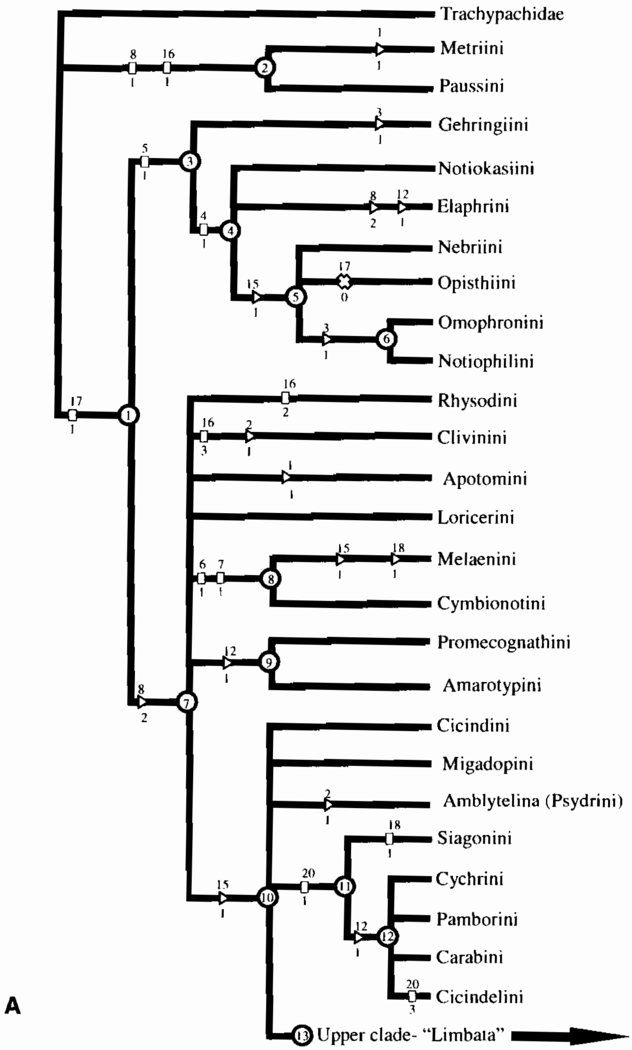
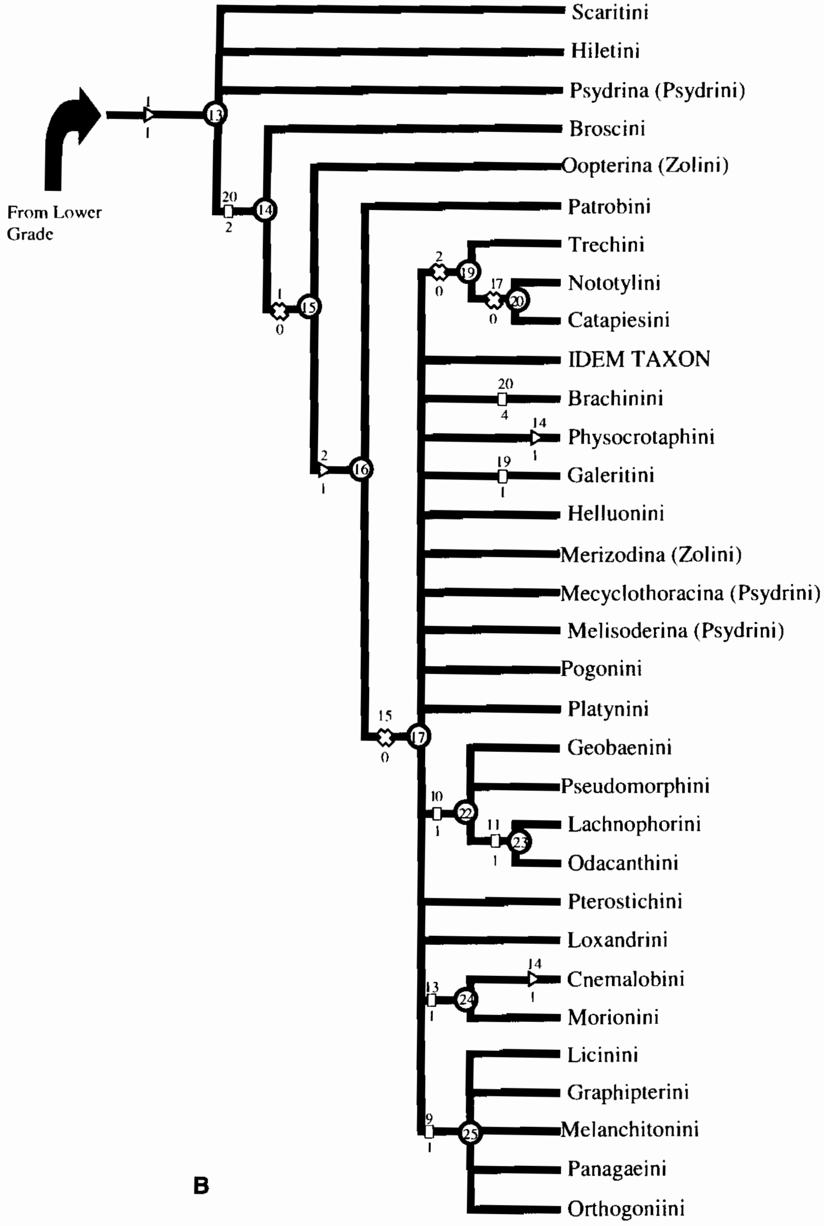


Fig. 57 - Preferred 44-step cladogram based on 20 characters of female ovipositors and reproductive tract; CI = 0.59, RI = 0.84. Character numbers indicated above lines; character states below lines; homoplastic forward character transformations indicated by triangles; homoplastic reversals indicated by X's; uniquely occurring synapomorphies indicated by rectangles; node numbers in circles indicate components of the cladogram. Trachypachidae and cladistically basal tribes of Carabidae, including those of the Isochaeta, spermatheca-2 clade, rhysodine grade, and cicindine, or intergonocoxite grade (A). Scaritini, Hiletini, Psydrina, and more derived tribes of Carabidae (B).


From Lower Grade
13
14
15
16
17
19
20
22
23
24
25
Scaritini
Hiletini
Psydrina (Psydrini)
Broscini
Oopterina (Zolini)
Patrobini
Trechini
Nototylini
Catapiesini
IDEM TAXON
Brachinini
Physocrotaphini
Galeritini
Helluonini
Merizodina (Zolini)
Mecyclothoracina (Psydrini)
Melisoderina (Psydrini)
Pogonini
Platynini
Geobaenini
Pseudomorphini
Lachnophorini
Odacanthini
Pterostichini
Loxandrini
Cnemalobini
Morionini
Licinini
Graphipterini
Melanchitonini
Panagaeini
Orthogoniini
B

occurred (e.g., figs. 36-39), but many of these derivations are polymorphic within currently circumscribed tribes, and their meaningful investigation must await denser taxonomic sampling.

Several characters stand out as both restricted and uncontested synapomorphies. Members of the Orthogoniini, Panagaeini, Melanchitonini, Graphipterini, Licinini, and Loxandrini possess a villous canal extended forward on the common oviduct (figs. 46-50). Apparent plesiomorphic presence of this structure in the first five tribes suggests that they at least are united by this synapomorphy. The function of the villous canal is unknown. It is a highly sclerotized, hemicircular, rolled evagination of the oviduct wall that is tortuously contorted along its length. Microscopic examination suggests parallel cuticular ridges running perpendicular to the long axis of the canal. It is present in New World *Loxandrus*, including species such as *L. omiltemi* Allen & Ball (1980) that possess a fully developed, tubular spermatheca, and the species such as *L. celeris* (Dejean) that have an extremely reduced spermatheca that is no more than an atrium for the spermathecal gland duct (fig. 46). *Loxandrus variabilis* Straneo from South America lacks a villous canal, as does *Zeodera atra* Castelnau of the Australian *Loxandrus* series (Moore 1965). We also considered Pterostichini to be polymorphic for this character based on similar canal-like structures in *Metius* spp., *Abropus carnifex* (F.), *Poecilus* spp., and *Pterostichus* species of the subgenera *Morphosoma*, *Argutor*, and *Oreophilus*. Whether the villous canal serves as a synapomorphy of a tribal level Loxandrini (Bousquet & Larochelle 1993) relative to Pterostichini or any of the other currently recognized tribes characterized by such a canal must await comprehensive cladistic analysis of these groups.

A second uncontested synapomorphy unites the Geobaenini, Pseudomorphini, Lachnophorini, and the Odacanthini (including Pentagonicini). The spermathecal duct in these taxa is joined to the common oviduct by an elongate sclerite (figs. 52-55). This differs from an helminthoid sclerite in that it appears hollow, whereas helminthoid sclerites appear to be cuticular thickenings without a lumen. The independent origins of the structure based on our cladistic hypothesis (fig. 57) confirms this assessment (de Pinna, 1991). Within the Pseudomorphini, *Sphallomorpha* comprises the basal adelphogenus to the rest of the tribe (Baehr 1994); their basal position is supported by possession of the most plesiomorphic female tract, including broad, relatively unspecialized gonocoxae. *Pseudomorpha hubbardi* Notman-a member of the second most basal generic taxon in the tribe-possesses a much smaller spermatheca, but it is also attached to the common oviduct by a basal sclerite. Joint possession of a basal sclerite in these two genera supports its role in the definition of the groundplan for the tribe. The basal sclerite is present throughout Lachnophorini and Odacanthini (Liebherr, 1988), suggesting that a close relationship among these three tribes bears further investigation.

The Geobaenini is a monobasic tribe represented by four species of *Geobaenus* Dejean, three in South Africa (Basilewsky, 1963) and one in Australia (Lawrence et al., 1987). The palps possess an attenuate tip, much like those seen in species of the lachnophorine genera *Eucaerus* and *Lachnophorus*, and the right paramere of the aedeagus is much reduced, as observed in both lachnophorines and odacanthines. The more generalized aedeagus of pseudomorphines, with more subequal parameres, sometimes with setose apices (Erwin, 1981, Baehr, 1992), would place Pseudomorphini as the basally divergent tribe in this clade. Placement of pseudomorphines in a derived position within Harpalinae is consistent with use of formic acid in their defensive secretions (Moore & Wallbank, 1968).

Based on the possession of a secondary spermathecal gland (figs. 38, 39), it would appear that the Helluonini and Galeritini might be sister groups. However, within Helluonini, the *Gigadema* sp. studied did not exhibit the secondary gland, and therefore this character cannot serve as a synapomorphy uniting all members of both tribes unless it is judged to be secondarily lost in *Gigadema*. *Trichognathus marginipennis* Latreille also possesses this gland. Study of species of *Planetes* is required to determine whether this character is part of the galeritine groundplan (Ball, 1985). If so, paraphyly of Helluonini relative to Galeritini would be supported.

The apical polytomy of our preferred cladogram includes one clade that is supported strictly by reduction or secondary absence characters. The enigmatic tribes Nototylini and Catapiesini are drawn together by their lack of: 1) a spermathecal gland (character 2), and 2) loss of gonocoxal segmentation (character 17). This analysis disregards the fact that lack of gonocoxal segmentation in these two tribes has occurred by fundamentally different trajectories. In *Catapiesis*, the gonocoxae are stiletto-like, with the apical sensory furrow present, and a medial patch of setae suggesting the previous apical margin of a basal gonocoxite (fig. 34). In *Nototylus fryi* (Schaum), conversely, the gonocoxae are unsegmented due to the extensive reduction of the apical gonocoxite 2, leaving a basal stump (Deuve 1994, Fig. 17); i.e., the apical sensory furrow is absent. Gonocoxal reduction in *Nototylus* is therefore accomplished much like that observed in *Molops* (Giachino & Sciaky 1991), which exhibit a basal, broadly rounded gonocoxite 1 without apical sensory nematiform nor ensiform setae characteristic of gonocoxite 2. Given all else, such reductions must be considered independently derived. The spermatheca of *Catapiesis* is thickly sclerotized and exhibits a very broad duct. This configuration may be functionally connected to the bizarre coiled flagellum of the male aedeagus (Reichardt, 1973). The Trechini are also implicated with these two tribal taxa due to reduction of the spermathecal gland. Spermathecal configuration in Trechini involves variable levels of reduction of the bursa copulatrix and spermatheca (Schwieger 1952). Relationships of this group should be based on information from other characters.

Alternate Placements

In this section we discuss other equally parsimonious placements of taxa given the basic topology of the preferred cladogram (fig. 57). In the subsequent section on Incongruent Placements, we discuss how taxonomic placements defined by female tract characters result in relationships that are fundamentally different from those defined by other characters, principally thoracic structure and male aedeagal characters.

Elaphrini

Based on our analysis, the Elaphrini are placed in the spermatheca-2 clade, as the adelphotaxon to Opisthiini+Nebriini+Notiophilini+Omophronini. This placement is due to our interpretation that the dorsally entering spermatheca of elaphrines (fig. 11) is homologous with spermatheca-2 of Omophronini (fig. 14) and Gehringiini (fig. 10). Lack of a helminthoid sclerite in Elaphrini makes assessment of spermathecal position more difficult. Absence of gonocoxal rami is plesiomorphic, excluding Elaphrini from membership in its adelphotaxon. One alternate position for Elaphrini is possible given our cladogram; they may equally parsimoniously be placed with Promecognathini and Amarotypini in an unresolved trichotomy at node 9 (fig. 57). This placement is supported by the shared absence of rami (symplesiomorphy), shared absence of an accessory gland (symplesiomorphy), and shared presence of a ligular apophysis (synapomorphy). Elaphrines have previously been considered related to Migadopini based on similar setation and configuration of the male aedeagal parameres (Jeannel, 1941). Erwin (1985) proposed Amarotypini for the species *Amarotypus edwardsi* Bates of New Zealand. Deuve (1993) included *Amarotypus* in Migadopini, but the female tract is fundamentally different (Deuve, 1993, Fig. 192), justifying Erwin's proposal. Migadopine female tracts are exceedingly heterogeneous. *Migadops latus* (Guérin) lacks rami and possesses a short broad spermatheca (fig. 16). *Monolobus testaceus* Solier and *Aquilex diabolicola* Moret also lack rami, but in these taxa there is no visible spermatheca (Moret, 1989, Deuve, 1993, Fig. 194). *Lissopterus quadrinotatus* Waterhouse, *Rhytidognathus ovalis* (Dejean), and *Loxomerus nebrioides* (Guérin) all possess rami, while lacking a definable spermatheca. Monophyly of this assemblage is definitely not supported by observed variation in the female tract. Therefore, if elaphrines are related to this group, the relationship is restricted to *Amarotypus* and the Promecognathini.

If we recode Elaphrini to possess spermatheca-1, we remove one step from the analysis, and obtain trees of 43 steps that place Elaphrini at the alternate position of an unresolved relationship with Amarotypini and Promecognathini. We refrain from this reciprocal illumination for the following reasons.

1.) Procoxal muscle M17 is absent from Nebriini, Opisthiini, Notiophilini, Omophronini, and Elaphrini, and present and thick in *Promecognathus* (Baehr, 1979). Trachypachidae and *Metrius* have M17, establishing its presence as a groundplan condition of Carabidae, and its absence as a loss and thus synapomorphous; *Gehringia* and *Loricera* also lack M17.

2.) The metepimeron is plesiomorphically narrow and exposed in Gehringiini, Omophronini, and Elaphrini, among others (Beutel, 1992a), but not visible externally in Promecognathini.

3.) The elaphrine ventral nerve cord shares the plesiomorphic condition of I, II, III, 1, 2, 3, 4, 5+ with some Nebriini, Opisthiini, and Notiophilini, versus the reduced nerve cord configuration observed in *Amarotypus* (I, II, III, 1, 2, 3, 4+) (Heath & Evans, 1990).

4.) Elaphrine larvae share the derived state of a protuberant median nasale with Omophronini, Nebriini, and Notiophilini (Luff, 1976, 1978; Landry & Bousquet, 1984), whereas the larva of *Promecognathus laevissimus* has a medially flat nasale (Bousquet & Smetana, 1986).

5.) Elaphrine larvae share the derived presence of a mandibular penicillus with Opisthiini (Bousquet & Smetana 1991) and *Pelophila* (Arndt, 1993), but *Promecognathus* lacks a penicillus (Bousquet & Smetana, 1986).

The other principal position previously suggested for Elaphrini is affiliation with the Broscini (Goulet, 1983). This suggestion is based on the presence of aedeagal internal sac sclerites judged homologous with those observed in Broscini (Ball, 1956). A similar derived position for Elaphrini is supported by larval head characters (Beutel, 1993). However, thoracic structures, such as the disjunct mesocoxae and narrowly exposed metepimera, do not support such a derived position (Beutel, 1992a). Generally, female tract characters do not support placement of Elaphrini near styliferous groups such as Broscini.

Migadopini

As alluded to above, Migadopini exhibit infratribal variation in the presence of the gonocoxal rami. As presently circumscribed, migadopines also exhibit either segmented, articulated gonocoxae, or secondarily fused gonocoxae. Variable presence of the first character permits two equally parsimonious placements on the cladogram; either as shown (fig. 57) on the grade with Cicindini (node 10), or one grade lower with Rhysodini (node 7). The preferred position presumes the evolution of gonocoxal rami in the common ancestor indicated by node 10, with their subsequent reduction. The alternate, lower position would posit one more origin of gonocoxal rami. More importantly in our opinion than their position in this analysis, is the possibility that Migadopini as currently circumscribed is not monophyletic.

Clivinini

The female reproductive tract configuration of Clivinini (figs. 17, 18) is quite different from that observed in Scaritini of Bousquet & Larochelle (1993) (figs. 27, 28). Their distinctly different placements in our preferred cladogram support their recognition as separate entities. The Clivinini are excluded from any close relationship to Scaritini by their lack of gonocoxal rami, and possession of an appended spermathecal gland instead of an accessory gland. Erwin (1985) recognized these two groups as distinct based on the setose unguitractor plate of the Clivinini. Defensive secretions differ dramatically among the two groups; Clivinini use quinones or ketones, whereas Scaritini use aliphatic acids (Moore & Wallbank, 1968, Schildknecht et al., 1968, Kanehisa & Murase, 1977, Moore, 1979).

In our study, Clivinini can be placed as the adelphotaxon of Amblytelina without requiring any additional steps on the cladogram, because Amblytelina possess an appended spermathecal gland along with a nebridian abdominal type. Amblytelines also possess rami, so an association between Amblytelina and Clivinini saves a step for gland origin, while necessitating an extra step for loss of gonocoxal rami in Clivinini. Placement near Amblytelina on the same grade as Scaritini is not preferred because such a move greatly separates Clivinini and Rhysodini, which share several potential synapomorphies. Among these is the lobe formed by the longitudinal juncture of the metepisternum and metepimeron that extends between the lateral reaches of the metacoxae and the elytral episternum (Beutel, 1990). We have observed this configuration in *Omoglymmius, Clinidium, Aspidoglossa, Schizogenius, Clivina, Salcedia, Apotomus, Scarites, Melaenus*, and the new broscine genus from Guerrero, Mexico to be named after John Rawlins (R. L. Davidson & Ball, pers. comm.). This lobe is not present in the scaritines *Pasimachus* or *Mouhotia*, though this may be due to shortening of the metasternum associated with wing reduction. Is this configuration found in all taxa with tubular bodies? It is not seen in Promecognathini. It cannot serve as a synapomorphy of all above listed taxa, as rhysodines cannot be moved anywhere on the cladogram without a resultant increase in total character state changes. Are the Clivinini associated with basal Scaritini or with Rhysodini? Answers to the above questions must await parsimony analysis using a comprehensive set of characters.

A second possible synapomorphy of Clivinini and Rhysodini, and the reason we prefer the association of Rhysodini and Clivinini, involves the rod-like configuration of the laterotergite IX (figs. 8, 9, 17, 18). We did not consider these configurations homologous before the analysis, however, if such a determination were made in light of information from the other characters, the sister-group relationship of Rhysodini and Clivinini would be affirmed.

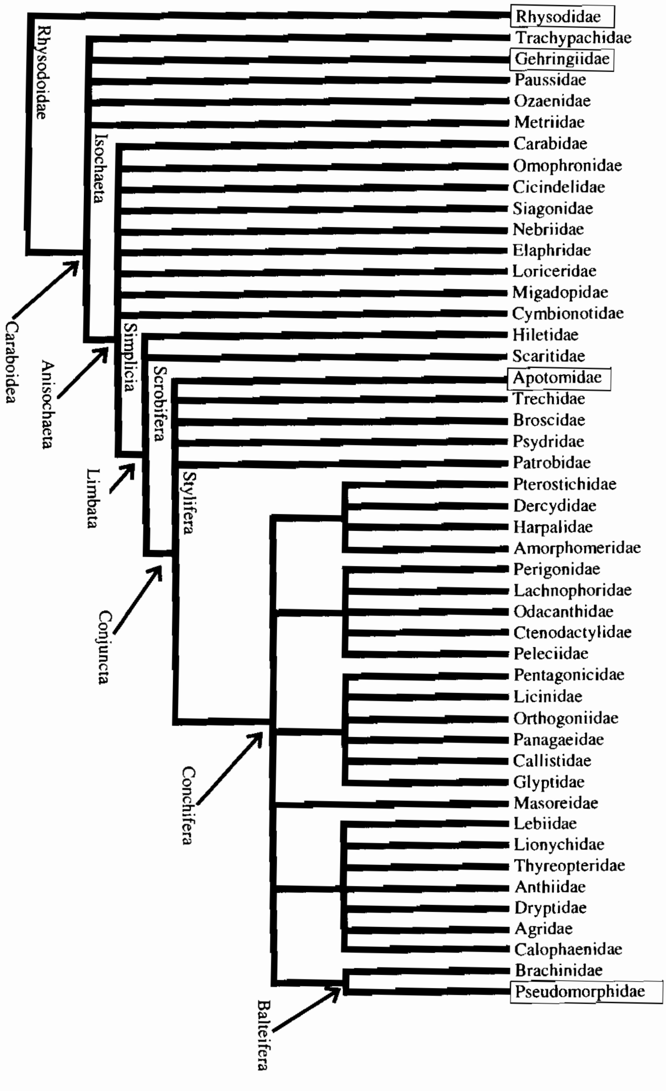


Fig. 58 - The classification of Rhysodoidea and Caraboidea of Jeannel (1941, 1942, 1946, 1948, 1949). Clades defined by synapomorphy are paired with grades characterized by plesiomorphic alternate character states. Groupings within Conchifera-Harpalomorphi, Odacanthomorphi, Callistomorphi, Masoreomorphi, and Lebiomorphi-portrayed as monophyletic, though not implicitly defined as such by Jeannel (1946, 1948, 1949). Boxed tribal names represent taxonomic placements by Jeannel that differ greatly from those found in present study (see text).

Apotomini

We have placed the Apotomini on the basal grade with Clivinini and Rhysodini, but it could also be placed in an unresolved relationship with Scaritini and Hiletini (node 13). The Apotomini lack gonocoxal rami, and possess a laterotergite IX that shares a thickly sclerotized anterior margin with those of Rhysodini and Clivinini. However, the laterotergites of Apotomini are markedly convex laterally, with their lateral margins connected to a very narrow, trident-shaped mediotergite IX. This configuration belies the very round tubular abdomen of *Apotomus* beetles, with the laterotergites comprising more than half of the diameter of segment nine. As with Clivinini, we retain Apotomini at the rhysodine grade due to similarities related to a tubular habitus, and by the absence of rami. This necessitates another origin of the accessory gland; a gland that had independently developed in Metriini, Siagonini, the ancestor of the Hiletini, Scaritini, and Broscini, and possibly another time in the subtribe Psydrina.

Jeannel (1946) placed Apotomini as the first group in his Stylifera (fig. 58); i.e., carabids with conjunct mesocoxal cavities, lobate metepimera, setose mandibular scrobes, and setose male parameres. His assessment of the mesocoxal cavities was incorrect, as the mesepisternum clearly abuts the mesocoxae, though it is depressed longitudinally, and if careful attention is not paid to the position of its marginal sutures, one might mistakenly consider the cavities conjunct. Apotomines' lobed metepimeron is of the same type as Clivinini and Rhysodini, discussed above. The setose mandibular scrobe is also found in *Melaenus piger* (F.), a taxon placed at the rhysodine grade with Apotmini in our analysis. Setose male parameres are plesiomorphic. Therefore, Jeannel's placement appears to be based on incorrect, weak, or plesiomorphic evidence, and must be rejected.

Melaenini and Cymbionotini

The close relationship of these tribes suggested by female characters is congruent with Erwin and Sims' (1984) placement of them together in a supertribe Melaenitae. The female tract data can place this pair of tribes either at our preferred placement in the rhysodine grade (fig. 57), or in the cicindine grade. The alternate position assumes that the presence of gonocoxal rami in Melaenini (character 15) is a groundplan feature of the clade, and that this structure has been secondarily lost in Cymbionotini. We prefer the position as shown because we suspect the spermathecal diverticulum (character 6) may be homologous with the appended spermathecal gland of Clivinini. Also, melaenines share the lobate metepisternum+metepimeron of Clivinini and Rhysodini, mentioned above. The Amblytelina of the cicindine grade also possess an appended spermathecal gland, but based on the sum of evidence we feel a relationship between Clivinini and Melaenini+Cymbionotini is more defensible. Placement on the cicindine grade would place Melaenini+Cymbionotini in close proximity with Siagonini, a placement satisfying based on general habitus. Siagonini and Melaenini also both possess a long apophysis extending anterad from laterotergite IX. However, siagonines (including Enceladini) lack an appended spermathecal gland, and are polymorphic for presence of an accessory gland, a female tract arrangement fundamentally different from melaenines and cymbionotines.

Melaenini differ from other taxa placed nearby in our preferred cladogram by having the mesocoxae broadly closed by the mesosternum (conjunct). That, plus their setose mandibular scrobe mentioned above, would place them in the Stylifera of Jeannel (fig. 58). Contrarily, our preferred placement of Melaenini+Cymbionotini in the rhysodine grade is congruent with Jeannel's placement of Cymbionotini in Caraboidea Simplicia (fig. 58). Therefore, the alternate placements of these two tribes runs counter to hypotheses supporting their close relationship, underscoring the incongruence of character support. Erwin and Sims (1984) place them close to Broscini and Apotomini in association with other styliferous tribes. As mentioned above, female characters would place Apotomini, as well as Melaenini+Cymbionotini and Clivinini as basal groups of the rhysodine grade.

Cicindelini

We believe tiger beetles are highly autapomorphic derivatives of a carabine lineage. Female tract characters permit one other placement, as a third member of the Promecognathini+Amarotypini clade (node 9). This is supported by shared presence of a ligular apophysis in Cicindelini plus the node-9 taxa, and the polymorphism within Cicindelini for presence of gonocoxal rami. We do not consider the ligular apophysis of the node-9 taxa (figs. 19, 20) to be homologous with that of cicindelines (figs. 23, 24). The promecognathine apophysis is a hemispherical ring, and the amarotypine ligular apophysis is a broad sclerite between the bases of the gonocoxae (Deuve 1993, Fig. 192). Cicindelines have a variably shaped sclerite at the ventral base of the common oviduct far basal to the gonocoxae that contains a longitudinal ligular attachment. This longitudinal attachment is similar but less developed than the strongly securiform apophysis observed in *Carabus* (fig. 22; Schuler 1976). Within cicindelines, the rami are distinct in the megacephalines *Amblycheila picolominii* Reiche (fig. 23), *Omus californicus* Eschscholtz, *Platychila pallida* (F.), and *Pycnochila fallaciosa* (Chevrolat); reduced and difficult to trace in *Cicindela longilabris* Say (fig. 24); and absent from *Mantichora, Megacephala, Dromica, Tricondyla*, and *Pogonostoma* (Deuve 1993). Postulating that gonocoxal rami represent part of the cicindeline groundplan is congruent with considering carabine and cicindeline ligular apophyses homologous, a combination we prefer.

Other characters support placement of cicindelines near Carabini, including the derived condition of the ventral nerve cord, with seven distinct abdominal ganglia (Heath & Evans, 1990), the use of benzaldehyde as the defensive secretion versus salicylaldehyde in *Calosoma* (Moore & Wallbank, 1968, Schildknecht et al., 1968), and the abdomen with both pygidial defense glands and accessory glands (Forsyth, 1970, 1972). Based on thoracic and larval head capsule characters, Beutel (1993) places them in a grade just basal to Stylifera, not closely related to Carabini. Our placement supports the derivation of the cicindelidian abdominal configuration from the carabidian type. This relationship confirms the homology of tergite-X presence in the males of Carabini and Cicindelini. The modifications of the female cicindeline abdomen would seem most likely related to the necessity of extending the abdominal apex during oviposition into sandy substrates. Such behavior is associated with numerous autapomorphies, including loss of the apical gonocoxal nematiform setae, large gonocoxal ensiform setae, as well as several muscular autapomorphies (Bils, 1976).

Scaritini+Hiletini

Just as Apotomini can be placed higher on the cladogram with Scaritini and Hiletini, the latter two tribes can be placed on the rhysodine grade either as the adelphotaxon to Apotomini, or in a clade with Apotomini and Rhysodini. This placement requires an independent origin of the gonocoxal rami in the Scaritini+ Hiletini, but saves a step in the origin of accessory glands. We reject this position because it would place the Hiletini, with the derived state of large, lobate metepimera, into the tribes with narrow metepimera. Moreover, even though the tract of *Apotomus* has an accessory gland, the overall configuration with an extremely long accessory gland with a glandular tip (Deuve, 1993, Fig. 218), is very different from the tracts of Scaritini, Hiletini, and Broscini (figs. 26-28, 31). Therefore, the position of Scaritini and Hiletini as basal outgroups to the conjunct Carabidae, as in Jeannel (1941; fig. 58) is also judged the preferred position based on female tract characters.

Brachinini

Placement of the Brachinini remains one of the major challenges of carabid beetle classification. Our preferred cladogram places them within tribes including Harpalinae (Erwin and Sims, 1984, Deuve, 1988)-i.e., the Conchifera of Jeannel (1941; fig. 58)-plus the styliferous tribes Bembidiini, Trechini, Pogonini, Zolini (part), and Psydrini (part) (fig. 57). The brachinine female reproductive tract is characterized by an appended spermathecal gland, segmented gonocoxae, absence of gonocoxal rami, and in some taxa, by the presence of a digitiform diverticulum (figs. 36, 37) of the spermathecal duct.

Crepidogaster is considered the most basally divergent lineage of the Brachinini (Jeannel, 1949, Erwin, 1970), but possesses a markedly reduced, autapomorphic female tract (Deuve, 1993). Therefore, establishing the groundplan for the brachinine female tract is made more difficult. Nonetheless, characters of the larval head (Beutel 1993), thorax (Beutel, 1992a), and male aedeagus (Jeannel, 1942, 1949) firmly argue for placement within higher harpaline tribes, and support our preferred placement.

The alternate brachinine position as adelphotaxon to the isochaete tribes Metriini and Paussini is supported by the shared use of quinone defensive secretions that are ejected with a hot reaction (Schildknecht and Koob, 1969, Aneshansley et al., 1983, Moore, 1979, Erwin, 1985). Quinones are not uniquely restricted to these groups, however, with Clivinini, Callistini, and Panagaeini also employing these chemicals for defense. That the catalytic oxidation of hydroquinones in the presence of hydrogen peroxide might be derived independently is suggested by the other character systems mentioned above.

Given this context, it may be of interest that the alternate possible position of Brachinini in our cladistic hypothesis is as the adelphotaxon of Clivinini. This placement is possible due to the sharing of an appended spermathecal gland, absence of gonocoxal rami, and the fact that we did not restrict derivation of the brachinidian abdominal configuration from any particular ancestral state. Association of Clivinini and Brachinini suggests that the brachinidian abdomen was derived through modification of a nebridian configuration. We reject this transformation because we can observe one of the principal facets of the brachinidian abdominal type-the invagination of tergum VIII underneath tergum VII- in harpalidian taxa, e.g., *Peliocypas insularis* Fairmaire of the Lebiini (Deuve, 1993). Couple this with the other character systems mentioned above-larvae, thorax, and male terminalia-and the taxonomic placement of Brachinini in any place other than higher harpalines would require many acts of "mental gymnastics (Beutel, 1993). "

Incongruent Placements

In this section we present aspects of our cladistic hypothesis that contradict previous classifications. We use Jeannel (1941, 1942, 1946, 1948, 1949) as the standard classification, given that much of the more recent work is based on his general system (Ball, 1979). We interpret Jeannel's classification in a cladistic sense, resulting in a hierarchical set of clade versus grade relationships (fig. 58). Assignment of character polarities for this classification is based on knowledge of carabid relationships summarized in Beutel (1995a) and Beutel & Haas (1996).

The relationships of several tribes not conforming to Jeannel's system have already been discussed. Placement of Pseudomorphini by Jeannel (1941, 1949) in Balteifera along with Brachinini must have been based on a misunderstanding of pseudomorphine characters, including male terminalia (Erwin, 1981). Our placement of this tribe is congruent with placements in recent studies (Erwin, 1981, Beutel, 1992a). The tribes Zolini and Psydrini are composed of subunits that are arrayed polyphyletically on our preferred cladogram (fig. 57). Therefore, assignment of them to any particular grade or clade is impossible. Clearly, the relationships of these groups should be examined within a broad context of possible relatives. The Apotomini were placed by Jeannel in Stylifera. Our two possible positions discussed above are as allies to Scaritini+Hiletini or Rhysodini.

Rhysodini

The rhysodid beetles have been classified as a distinct superfamilial lineage equal in rank to Caraboidea (fig. 58) including Trachypachidae (Jeannel, 1941), or as a family equal in rank to Carabidae excluding Trachypachidae (Beutel, 1992b), or as a tribe of anisochaetous Carabidae (Bell, 1967), allied with Scaritini (Baehr, 1979; Beutel, 1990, 1992a), and possibly related to the clivinine subtribe Salcediina (R. T. Bell, pers. comm.). These varied placements are due to the conflicting information in different character systems. Adding information from the female reproductive tract helps choose among these options. The segmented gonocoxae of Rhysodini (figs. 8, 9) place them within the anisochaetous Carabidae. The helminthoid sclerite varies in the group from a large securiform structure reminiscent of Isochaeta (fig. 8) to absent (fig. 9). Our cladogram optimizes the base of Rhysodini as the *Clinidium* configuration, i.e., lacking a helminthoid sclerite (fig. 9). This is in agreement with Beutel's (1990) representation of *Clinidium* as plesiotypic taxon within the group. Rhysodine placement in our analysis is on the same basal grade of anisochaetes as the Apotomini and Clivinini. The three tribes lack rami, and Rhysodini and Clivinini share similar narrowly arcuate laterotergites, with the laterally convex apotomine laterotergites dissimilar in shape, but sharing the thickly sclerotized anterior margin and membranous center. They also share the lobate metathorax composed of a longitudinally fused anepisternum and epimeron (Beutel, 1990). Given the biomechanical constraints brought to bear in insects with thick cuticle and tubular bodies, relationships of these groups might best be examined using characters that are likely to be more independent of morphology; i.e., molecular genetic data.

Gehringiini

We consider *Gehringia* to be an anisochaetous carabid, based on its possession of segmented gonocoxae. Jeannel's (1946) placement in Isochaeta (fig. 58) has been equivocally challenged and affirmed by analyses of thoracic structure (Bell, 1967, Beutel, 1992a). Bell grouped Carabini, Cychrini, Nebriini, Notiophilini, Opisthiini, and Gehringiini together based on confluent, open, internally unbridged procoxae. The first two conditions are plesiomorphic, the latter apomorphic relative to *Trachypachus*. Gehringiini have the metacoxal cavities broadly separated as in Rhysodini. Laterally, the gehringiine metacoxae do not reach the body margin as they do in Trachypachidae, and the metepimeron is narrowly visible as in *Mystropomus, Omophron, Elaphrus, Loricera, Clivina*, and *Omus* (Beutel, 1992a). Beutel & Haas (1996) place *Gehringia* as an isochaete based on the antenna cleaner being extended proximally but with isochaete apical setae, and by the presence of a sparsely setose prehypopharynx. Whereas the latter character is an intermediate state between a non-setose prehypopharynx and fully setose preoral filter apparatus, Beutel & Haas treated the three states as unordered. If our data were combined with those of Beutel & Haas, and the hypopharyngeal filter apparatus coded as a three-step ordered character, *Gehringia* would be placed in Anisochaeta while possessing an "isochaete " antenna cleaner. This interpretation downplays the importance of antenna cleaner configuration as a phylogenetic indicator, but that has already been done by the shared isochaetous configurations of Trachypachidae, Opisthiini, Cicindelini, and Carabini (Hlavac, 1971, Regenfuss, 1975, Beutel, & Haas 1996).

Omophronini

The Omophronini have recently been placed as most closely related to Trachypachidae and water beetles (Bils, 1976, Nichols, 1985), as the outgroup to the rest of the anisochaete Carabidae (Beutel, 1991, 1993, 1995a), and in a clade also containing Hiletini and Nebriini (Beutel & Haas, 1996). Their placement as outgroup to the rest of the Anisochaeta has been justified due to their plesiomorphic lack of a larval mandibular penicillus (Beutel, 1991), however the penicillus is also absent from Nebriini, Notiophilini, and Cicindelini (Arndt 1993), as well as scattered taxa of higher Carabidae. Their placement with Hiletini and Nebriini in a preferred cladogram of Beutel & Haas (1996) is based on three characters: 1) independent derivation of an anisochaetous antenna cleaner in a basal clade isolated from the rest of the higher anisochaetous tribes due to the isochaetous configuration in Cicindelini, Opisthiini, and Carabini (their character 54); 2) internalized metepimeron (their character 65) (also observed in Opisthiini, Carabini, Cychrini, Nebriini, and Notiophilini, but not Hiletini [Beutel, 1992a], and 3) larval mandibular penicillus absent (their character 18). Of these, character 65 appears to be incorrectly scored, character 18 is inapplicable to Hiletini as larvae are unknown, and character 54 is extensively homoplastic. Thus their placement is based on incorrect coding and/or an incomplete survey of possibly annectant taxa or ontogenetic stages.

Placement of Omophronini in a nebriiform clade as we propose it (fig. 57) is supported by the following potentially synapomorphic characters.

1.) There are less than 10 gMX setae on the larval maxillary stipes; shared with *Leistus, Notiophilus,* and *Loricera* (Arndt, 1993).

2.) Larval nasale protuberant; shared with *Leistus, Notiophilus, Elaphrus, Blethisa, Loricera,* among others (Arndt, 1993) less closely placed on our cladogram.

3.) Posterior tentorial grooves of larva fissure-shaped and shifted posteriorly; shared with *Opisthiini* (Beutel, 1991).

4.) Penicillus of larval mandible absent, a secondary loss shared with *Notiophilus, Nebria, Eurynebria,* and *Leistus* (Beutel, 1991, Arndt, 1993).

5.) Hypopleurites not apparent in the first instar larva; shared with Opisthiini (Landry & Bousquet, 1984).

6.) Adult procoxal muscle M17 absent; shared with *Blethisa, Diacheila, Elaphrus, Opisthius, Eurynebria, Leistus, Nebria, Pelophila, Notiophilus* (Baehr 1979), a loss also observed in Paussini.

7.) Internally unbridged procoxae; shared with Gehringiini, Opisthiini, Nebriini, and Notiophilini, but also Carabini and Cychrini (Bell, 1967). The procoxae of Omophronini differ in another respect from those tribes, however, being closed posteriorly.

Cnemalobini

Erwin & Stork (1985) proposed uniting Hiletini with Cnemalobini, Elaphrini, Migadopini, Promecognathini, Pseudomorphini, Scaritini, and Siagonini based on structure of the unguitractor plate and lateral guard setae of the terminal tarsomere. Our position for Cnemalobini does not recognize such a grouping, placing the cnemalobines in the highest polytomous clade as adelphotaxon of Morionini. This position is in agreement with more recent suggestions for the group. Roig-Juñent (1993) considered them to be closest to either the Zabrini or the Morionini. His placement in Harpalinae (Harpalidae sensu Deuve, 1988) is based on presence of anteriorly directed apodemes on tergite VIII, placement of the pygidial gland opening adjacent to tergite VIII, asetose mandibular scrobe, and conchoid left paramere. Arndt (1993) argues that Cnemalobini should be considered part of the above Harpalinae based on reduction of larval ligular setae LA_7. Our placement based on female tract characters is therefore in accordance with recent analyses based on numerous characters.

Peleciini

Straneo & Ball (1989) consider Peleciini to be members of the higher Carabidae, possibly allied with basal pterostichite lineages. Bousquet & Larochelle (1993) placed Peleciini adjacent to Promecognathini based principally on derivations likely associated with feeding on millipedes. Characters of the female tract unequivocally place Peleciini (fig. 45). They possess an appended spermathecal gland with an elongate spermathecal reservoir typical for Pterostichini (e.g., Giachino & Casale, 1983, Bousquet, 1984a, 1984b, Giachino & Sciaky, 1991). The ensiform setae of the apical gonocoxite 2 are broad, also observed in other Pterostichini, e.g., species of *Blennidus* (Moret, 1995). The common oviduct near the base of the spermathecal duct exhibits a hirsute appearance in *Eripus* (fig. 45), the function of which is unknown. Similar "hirsute " patches are observed in the caelostomine pterostichines such as *Mallopelmus linearis* Alluaud, *Barylaus estriatus* (Darlington), and *Cyrtolaus ricardo* Whitehead & Ball (Liebherr, 1986). Therefore, placement of Peleciini as a basal group of pterostichine stock is firmly supported.

Spermathecal Evolution

Our cladistic hypothesis is based on characters with distributions typically observed in all morphologically based analyses, i.e., structures whose homology or homoplasy can only be determined in light of a cladistic hypothesis (de Pinna, 1991). Multiple origins of identically appearing structures must have occurred if we are to accept the hierarchical diversification of taxa exhibiting incongruent patterns of character evolution. The origin of what we call spermatheca-2, however, appears within only one clade of basal Carabidae. We hypothesize the substitution of spermathecal function among two structures, with two taxa so far observed-*G. olympica* (fig. 10) and *O. variegatum* (fig. 14)-retaining both a structure similar in appearance to the plesiomorphic spermatheca-1 observed in most Carabidae, as well as a second novel structure that has assumed the spermathecal function. Though what follows is strictly speculation, we feel compelled to explain how such a transformation might have taken place.

We suspect that the dorsal spermatheca-2 was plesiomorphically an accessory gland, comprised of a glandular membranous reservoir and a basal, more sclerotized ampulla (e.g., fig. 5). In order to become the functional spermatheca, the base of the gland assumed the function of a spermathecal reservoir, with the apical membranous and glandular area becoming segregated by a thin duct (as in figs. 10, 13). In *Omophron*, this segregation did not develop as strongly, for the glandular area extends along the length of the gland (figs. 14, 15). In several taxa-Elaphrini, Opisthiini, and Nebriini-the gland portion was lost leaving the accessory gland transformed to a glandless spermatheca. These transformations suggest fundamental differences in the function of these structures.

In ants, where sperm may be stored for a number of years, the spermatheca is composed of an outer epithelial layer and an inner cuticular layer, whereas the associated glands exhibit infolded basal membranes, many mitochondria, and apical microvilli, all structures associated with transport epithelia (Wheller & Krutzsch, 1994). This suggests that the spermathecal glands serve to provide a hospitable environment for the sperm through their secretory function. Absence of such glands in certain carabid taxa may suggest that sperm are not held long, and therefore sperm nutrition is not necessary, or that males pass nutritive substances with the sperm. Comparing the contents of spermathecae and spermathecal glands of females with glands to spermathecae of females without glands may prove enlightening.

Repeated switching of the sperm storage structure has occurred during the evolutionary divergence of the genus *Drosophila* Fallén (Pitnick, pers. comm.). Sperm storage has switched from plesiomorphic storage in the seminal receptacles to storage in a secondarily functional spermatheca no less than 11 times. In some species, sperm are stored in none of these structures, being held loosely within the uterus.

The functions of the various components of the female reproductive tracts described above remain totally unknown. For example, the villous canal observed in taxa such as *Loxandrus, Melanchiton, Panagaeus, Orthogonius*, and *Graphipterus* (figs. 46-50) is positionally analogous to the sclerotized regions of the common oviduct at the base of spermathecal ducts in taxa such as *Rhadine*, and the Pseudomorphini and Odacanthini (figs. 51-55). Heming-Van Battum and Heming (1986) showed that similarly positioned intimal oviduct linings in velvet water bugs (Heteroptera: Hebridae) serve as fecundation canals for sperm passing from the female spermatheca to the egg micropyle while eggs are held in the common oviduct. The position of the helminthoid sclerite in more basal carabid taxa suggests a similar function for that structure. What of fertilization in the many taxa apparently lacking these types of structures? Going a step further, where are sperm stored in taxa such as *Loxandrus celeris* (Fig. 46) that possess a very reduced spermatheca? Investigating the functional implications for these structural configurations, in the context of phylogenetic history, could provide information on the conditions associated with their origin.

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We would like to dedicate this paper to the memory of Professor George C. Eickwort, who instilled in students of all ages the importance of morphological study for the understanding of biology. We shall not forget.

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RIASSUNTO

Vengono analizzati i caratteri dell'apparato riproduttore femminile e dell'addome, mediante analisi cladistica basata sulla parsimonia, al fine di evidenziare una filogenesi complessiva delle tribù di Carabidae. Il cladogramma risultante è radicato alla famiglia Trachypachidae. Nessun carattere dell'apparato riproduttore femminile è in grado di definire i Carabidae come unità monofiletica. I Carabidae evidenziano una dicotomia fondamentale, con le tribù " isochete " Metriini e Paussini che formano l'adelphotaxon degli Anisochaeta, che includono a loro volta Gehringiini e Rhysodini, insieme agli altri gruppi considerati membri di Anisochaeta nella classificazione di Jeannel. La monofilia di Isochaeta è avvalorata dalla presenza generalizzata di uno sclerite elmintoide securiforme alla base della spermateca, e di un laterotergite IX allungato, astiforme, connesso con la camera di esplosione delle ghiandole difensive pigidiali. La monofilia di Anisochaeta è avvalorata dalla divisione, apomorfa, della gonocoxa IX in una porzione basale e in una porzione apicale. All'interno di Anisochaeta, l'evoluzione di una spermateca-2 secondaria, e la perdita della spermateca-1 primaria, si è verificata in una linea filetica che comprende Gehringiini, Notiokasiini, Elaphrini, Nebriini, Opisthiini, Notiophilini e Omophronini. Questa sostituzione, nel corso dell'evoluzione, è dimostrata dal fatto che *Gehringia olympica* Darlington e *Omophron variegatum* (Olivier) posseggono entrambe tali strutture, simili a spermateche. L'adelphotaxon di questo clade " spermateca-2 " comprende un grado basale, di tipo risodino, consistente in Clivinini, Promecognathini, Amarotypini, Apotomini, Melaenini, Cymbionotini e Rhysodini. I Rhysodini e i Clivinini evidenziano entrambi un laterotergite IX molto modificato, lungo e sottile, con o senza area laterale clavata. Questo carattere può rappresentare una sinapomorfia, o una convergenza basata su un addome tubolare e su un comportamento fossorio in entrambi. Il grado basale dà poi origine a un grado composto da taxa caratterizzati dalla presenza di un "ramus" - porzione sclerificata della parete vaginale situata al centro di ogni base gonocoxale - insieme con la plesiomorfica spermateca-1. L'interpretazione che era stata data di tali "rami" gonocoxali, come caratteristica di base dei Carabidae, corrispondenti a porzioni del segmento addominale VIII, è qui rifiutata in base al fatto che tale struttura risulta derivata rispetto ai caratteri originari della famiglia. Il ramus gonocoxale, o " grado cicindino ", comprende: 1) Cicindini; 2) un clade monofiletico " carabino " comprendente Siagonini, Cychrini, Pamborini, Carabini e Cicindelini; 3) Scaritini e Hiletini, che sono correlati parafileticamente a un gruppo monofiletico che possiede una configurazione addominale arpaloide, e che include i Broscini e tutte le rimanenti tribù di Carabidae. I Broscini mantengono ancora la ghiandola accessoria separata e la struttura spermatecale propria di Scaritini e Hiletini, e rappresentano l'adelphotaxon delle rimanenti tribù. I Patrobini rappresentano il gruppo divergente successivo, evidenziando una ghiandola spermatecale appesa, ma ancora mantenendo il ramus alla base del gonocoxite 1. Le altre tribù, comprese parte delle tribù di Stylifera di Jeannel, e i Conchifera, risultano correlate in maniera ambigua, in base ai caratteri genitali femminili, in un nodo fortemente politomico. All'interno di questo clade politomico, gli Pseudomorphini condividono, con Geobaenini, Lachnophorini e Odacanthini, uno sclerite spermatecale basale, derivato. I Cnemalobini si collocano come adelphotaxon di Morionini. Altre relazioni fra tribù permangono ambigue, a causa della fondamentale omogeneità dell'apparato riproduttore femminile osservato in queste tribù. I problematici Brachinini sembrano collocarsi meglio fra queste tribù, per quanto sussista una possibile collocazione, egualmente parsimoniosa ma meno preferibile, come adelphotaxon dei Clivinini. Le tribù Psydrini e Zolini appaiono polifiletiche in base ai caratteri genitali femminili, e costituite da sottotribù che si collocano in varie posizioni fra il grado "ramus gonocoxale" e il più elevato clade politomico. La posizione basale di Clivinini e Apotomini, sostenuta dai caratteri genitali femminili, è in contrasto con la posizione attribuita ad essi da Jeannel, rispettivamente in Scrobifera e Stylifera, in base alla struttura del torace.

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Note added in proof. Dissection of a female *Amblytelus curtus* (F.) indicates that this taxon exhibits the harpalidian abdominal configuration, not the nebridian state as reported by Deuve (1993: 152). Possession of the derived states of appended spermathecal gland present (character 2), gonocoxal rami present (character 15), and harpalidian abdomen (character 20, state 2) indicates that *Amblytelus* is most parsimoniously placed at a trichotomy with Patrobini (Fig. 57). This result condenses the extent of paraphyly of Psydrini, while reiterating the need for a comprehensive analysis of that tribe and related groups.

APPENDIX 1

Taxa examined by authors: 64 tribes, 241 genera, 733 species (citations given for 6 tribes and 2 subtribes known only from literature).

TRACHYPACHIDAE
Trachypachus holmbergi Mannerheim
Systolosoma breve Solier
CARABIDAE
ABACETINI
Abacetus (3 spp.)
AMAROTYPINI
Amarotypus edwardsi Bates [from description and illustration in Deuve 1993]
AMORPHOMERINI
Amorphomerus raffrayi Chaudoir
ANTHIINI
Anthia sexguttata (F.)
Cypholoba tetrastigma (Chaudoir)
APOTOMINI
Apotomus sp.
BEMBIDIINI
Asaphidion flavipes (L.)
Bembidion planatum Le Conte
Micratopus aenescens (Le Conte)
BRACHININI
Brachinus favicollis Erwin
Crepidigaster bioculata Chaudoir
Mastax histrio (F.)
BROSCINI
Broscus cephalotes (L.)
Zacotus matthewsi Le Conte
Gen. nov. sp. nov., from Mexico, Davidson & Ball unpublished
CARABINI
Calosoma luxatum Say
Carabus nemoralis Müller
CATAPIESINI
Catapiesis (3 spp.)
CHAETOGENYINI
Camptotoma freyi Nègre
CHLAENIINI
Chlaenius brevilabris Le Conte
CICINDELINI
Amblycheila picolominii Reiche
Megacephala carolina (L.)
Cicindela longilabris Say
Manticora sp.
Omus californicus Eschscholtz
Platychila pallida (F.)
Pycnochila fallaciosa (Chevrolat)
CICINDINI
Cicindis horni Bruch [from description and illustration in Kavanaugh & Erwin 1991]
CLIVININI
Aspidiglossa subangulata Chaudoir
Clivina (2 spp.)
Dyschirius marinus (LeConte)
Salcedia perrieri Fairmaire
Schizogenius (2 spp.)
CNEMALOBINI
Cnemalobus obscurus Brullé
CTENODACTYLINI
Ctenodactyla drapiezi Gory
Hexagonia sp.
Leptotrachelus dorsalis (F.)
Omphreoides bucculentus Alluaud
CYCHRINI
Scaphinotus cristatus (Harris)
Sphaeroderus stenostomus lecontei Dejean
CYCLOSOMINI
Tetragonoderus (2 spp.)
CYMBIONOTINI
Cymbionotum basale Dejean [from description and illustration in Deuve 1993]
DERCYLINI
Dercylus spp. [from description and illustration in Moret and Bousquet 1995]
DRYPTINI
Drypta dentata Rossi
ELAPHRINI
Blethisa multipunctata L.
Elaphrus lecontei Crotch
GALERITINI
Galerita (2 spp.)
Trichognathus marginipennis Latreille
GEHRINGIINI
Gehringia olympica Darlington
GEOBAENINI
Geobaenus lateralis Dejean
GRAPHIPTERINI
Graphipterus atrimedius Chaudoir
HARPALINI
Amphasia interstitialis (Say)
Anisodactylus discoideus Dejean
Bradycellus lugubris (LeConte)
Geopinus incrassatus (Dejean)
Harpalus (3 spp.)
Hartonymus alternans (LeConte)
Parabaris gourlayi Britton
Selenophorus sp. Arizona
Stenolophus lineola (F.)
HELLUONINI
Gigadema sp.
Helluomorphoides texanus (LeConte)
HILETINI
Eucamaragnathus bocandei (Alluaud)
LACHNOPHORINI
Anchonoderus (4 spp.)
Calybe laetula (LeConte)
Eucaerus (3 spp.)
Euphorticus pubescens (Dejean)
Lachnophorus (3 spp.)

LEBIINI
Agra sp.
Cymindis limbatus Dejean
Dromius piceus Dejean
Lebia grandis Hentz
Tecnophilus croceicollis Ménétries
LICININI
Dicaelus (2 spp.)
Diplocheila (8 spp.)
LORICERINI
Loricera foveata LeConte
LOXANDRINI
Adrimus (2 spp.)
Cosmodiscus picturatus Andrewes
Loxandrus (22 spp.)
Oxycrepis leucocera Reiche
Zeodera atra Castelnau
MELAENINI
Melaenus piger (F.)
MELANCHITONINI
Melanchiton kenyensis Straneo
Dicaelindus sp.
METRIINI
Metrius contractus Eschscholtz
MIGADOPINI
Migadops latus (Guérin)
Stichonotus limbatus Sloane
MORIONINI
Morion (3 spp.)
NEBRIINI
Leistus ferrugineus (L.)
Nebria (5 spp.)
NOTIOKASIINI
Notiokasis chaudoiri Kavanaugh & Nègre [from description and illustration in Kavanaugh & Nègre 1983]
NOTIOPHILINI
Notiophilus novemstriatus LeConte
NOTOTYLINI
Nototylus freyi (Schaum) [from description and illustration in Deuve 1993]
ODACANTHINI
Aeolodermus emarginatus (Chaudoir)
Calophaena bicincta Dejean & Boisduval
Colliuris (3 spp.)
Cyphocoleus (2 spp.)
Dicraspida brunnea Chaudoir
Eudalia latipennis MacLeay
Homethus guttifer Germar
Lachnothorax sp.
Odacantha melanura (L.)
Pentagonica picticornis (Bates)
Scopodes aeneus MacLeay
OMOPHRONINI
Omophron (3 spp.)
OODINI
Oodes amaroides Dejean
OPISTHIINI
Opisthius richardsoni Kirby
ORTHOGONIINI
Orthogonius (2 spp.)
PAMBORINI
Pamborus pradieri Chaudoir
PANAGAEINI
Brachygnathus sp.
Panagaeus fasciatus Say
Tefflus zebulianus Raffray
PATROBINI
Diplous californicus (Motschulsky)
Patrobus (2 spp.)
PAUSSINI
Pachyteles (*Goniotropis*) sp.
Physea tomentosa Chaudoir
PELECIINI
Eripus oaxacanus Straneo & Ball
Agonica sp.
PERIGONINI
Perigona nigriceps (Dejean)
PHYSOCROTAPHINI
Pogonoglossus tagalus Heller
PLATYNINI
Agonum (49+ spp.)
Anchomenus (9 spp.)
Arhytinus minimus Jedlička
Atranus pubescens (Dejean)
Blackburnia (128 spp.)
Calathus (3 spp.)
Colpodes (20 spp.)
Elliptoleus (10 spp.)
Euleptus intermedius Péringuey
Glyptolenus (3 spp.)
Incagonum (21 spp.)
Notagonum (3 spp.)
Olisthopus parmatus (Say)
Onypterygia (2 spp.)
Oxypselaphus puncticeps (Casey)
Paranchus albipes (F.)
Paranchodemus (2 spp.)
Platynus (96+ spp.)
Rhadine (6 spp.)
Sericoda (7 spp.)
Synuchus (2 spp.)
Tanystoma (5 spp.)
Tetraleucus picticornis (Newman)
POGONINI
Thalassotrechus barbarae (Horn)
Diplochaetus lecontei (Horn)
PROMECOGNATHINI
Paraxinidium andreaei Basilewsky
Promecognathus laevissimus (Dejean)
PSEUDOMORPHINI
Pseudomorpha hubbardi Notman
Sphallomorpha dubia (Castelnau)

PSYDRINI
-Amblytelina-
Amblytelus curtus (F.) [from description and illustration in Deuve 1993]
-Melisoderina-
Celanida montana Castelnau
-Psydrina-
Nomius pygmaeus (Dejean)
Psydrus piceus LeConte
-Mecyclothoracina-
Mecyclothorax (2 spp.)
PTEROSTICHINI
Abaris (4 spp.)
Abax parallelepipedus (Piller & Mitterpacher)
Abropus carnifex (F.)
Amolopsa multiseta Britton
Barylaus estriatus (Darlington)
Blennidus (2spp.)
Bothynoproctus (2 spp.)
Brachidius crassicornis Chaudoir
Caelostomus (2 spp.)
Camptoscelis hottentotus Olivier
Castelnaudia marginifera Chaudoir
Catadromus tenebroides (Olivier)
Cophosomorpha alticola Péringuey
Cratoferonia phyllarcus (Sloane)
Cratogaster sp.
Cyclotrachelus (2 spp.)
Cyrtolaus ricardo Whitehead & Ball
Darodilia sp.
Delinius essingtoni Westwood
Dyschromus nitidipennis Putzeys
Eucamptognathus dostojewski Tschitscherine
Feroniola sp.
Feroniomorpha nebrioides Curtis
Fouquetius ferrugineus Schmidt-Göbel
Gastrellarius (2 spp.)
Gourlayi regia Britton
Hemitelestus howa Alluaud
Holcaspis deurigera Broun
Lesticus (2 spp.)
Lophoglossus (2 spp.)
Loxodactylus carinulatus Chaudoir
Mallopelmus linearis Alluaud
Marsyas sp.
Mecynognathus damelii MacLeay
Megadromus antarcticus Chaudoir
Metius (3spp.)
Molops piceus Panzer
Myas (2 spp.)
Nebrioferonia strigitarsis Straneo
Neoferonia procerula Broun
Nirmala indica Hope
Notobax monteithi Moore
Notolestus sulcipennis MacLeay
Notonomus (2 spp.)
Nurus medius Darlington
Ogmopleura (3 spp.)
Ophryogaster flohri Bates
Orthomus (2 spp.)
Paranurus macleayi Sloane
Parhypates (2 spp.)
Pediomorphus (2 spp.)
Percus (2 spp.)
Piesmus submarginata Say
Poecilus (7 spp.)
Prosopogmus (2 spp.)
Pseudabarys (2 spp.)
Pseudoceneus iridescens (Castelnau)
Pterostichus (34 spp.)
Rhabdotus reflexus Chaudoir
Rhathymus carbonarius Dejean
Rhytisternus sp.
Sarticus (2 spp.)
Secatophus australis (Hope)
Setalis niger Castelnau
Simodontus (2 spp.)
Stereocerus haematopus Dejean
Stomis pumicatus Panzer
Teratotarsa schoberti Tschitscherine
Teropha sturtii (White)
Tiferonia parva Darlington
Trichosternus (2 spp.)
Trirammatus unistriata Dejean
Wahlbergia inordinata Péringuey
Zeopoecilus putus Broun
RHYSODINI
Clinidium calcaratum LeConte
Omoglymmius hamatus (LeConte)
SCARITINI
Carenum sp.
Mouhotia sp.
Pasimachus californicus Chaudoir
Scarites subterraneus F.
SIAGONINI
Siagona sp.
Enceladus gigas Bonelli
TRECHINI
Blemus discus (F.)
Trechus chalybeus Dejean
ZABRINI
Amara (2 spp.)
Pseudamara arenaria (LeConte)
ZOLINI
-Merizodina-
Idacarabus troglodites Lea
Merizodus angusticollis Solier
-Oopterina-
Oopterus soledadinus (Guérin) [from description and illustration in Deuve 1993]
ZUPHIINI
Pseudaptinus pygmaeus Dejean
Zuphium longicolle LeConte

APPENDIX 2

Character state × taxon data matrix. Polymorphic characters (P) and ambiguously assigned character states (?) treated identically by NONA (Goloboff 1996); subset polymorphisms (Nixon 1995) shown by bracketed states present in various member taxa of tribe.

	Characters																			
Taxon	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20
Tracbypachidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhysodini	P	0	0	0	0	0	0	[12]	0	0	0	0	0	0	0	2	1	0	0	0
Gehringiini	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Metriini	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Paussini	P	0	0	0	0	0	0	1	0	0	0	0	0	0	P	1	0	0	0	0
Omophronini	0	0	1	P	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Opisthiini	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Nebriini	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	P	0	0	0
Notiophilini	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Notiokasiini	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Elaphrini	0	0	0	1	1	0	0	2	0	0	0	1	0	0	0	0	1	0	0	0
Loricerini	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0
Migadopini	0	0	0	0	0	0	0	2	0	0	0	0	0	0	P	0	P	0	0	0
Cicindini	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	?	0	0	0
Promecognathini	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	P	0	0	0
Clivinini	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	3	P	0	0	0
Amarotypini	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	1	0	0	0
Nototylini	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2
Hiletini	1	0	0	0	0	0	0	2	0	0	0	0	P	0	1	0	1	0	0	0
Cnemalobini	0	1	0	0	0	0	0	2	0	0	0	0	1	1	0	0	1	0	0	2
Scaritini	1	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	1	0	0	0
Siagonini	P	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	1	1	0	1
Cychrini	0	0	0	0	0	0	0	2	0	0	0	1	0	0	1	0	1	0	0	1
Carabini	0	0	0	0	0	0	0	2	0	0	0	1	0	0	1	0	1	0	0	1
Cicindelini	0	0	0	0	0	0	0	2	0	0	0	1	0	0	P	0	1	0	0	3
Pamborini	0	0	0	0	0	0	0	2	0	0	0	1	0	0	1	0	1	0	0	1
Broscini	1	0	0	0	0	0	0	[01]	0	0	0	0	0	0	P	0	1	0	0	2
Apotomini	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0
Melaenini	0	?	0	0	0	1	1	2	0	0	0	P	0	0	1	0	1	1	0	0
Cymbionotini	0	?	0	0	0	1	1	2	0	0	0	0	0	0	0	0	1	0	0	0
Trechini	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	2
Zolini (Merizodina)	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	2
Zolini (Oopterina)	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	1	0	0	2
Pogonini	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	2
Psydrini (Amblytelina)	0	1	0	0	0	0	0	2	0	0	0	0	0	0	1	0	1	0	0	0
Psydrini (Melisoderina)	0	1	0	0	0	P	0	2	0	0	0	0	0	0	0	0	1	0	0	2
Psydrini(Psydrina)	P	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	1	0	0	0
Psyd. (Mecyclothoracina)	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	2

APPENDIX 2 (cont.)

	Characters																			
Taxon	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20
Patrobini	0	1	0	0	0	0	0	2	0	0	0	0	0	0	1	0	1	0	0	2
Brachinini	0	1	0	0	0	0	0	2	0	0	0	0	0	P	0	0	1	0	0	4
Morionini	0	1	0	0	0	0	0	2	0	0	0	0	1	0	0	0	1	0	0	2
Catapiesini	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2
Pterostichini	0	1	0	0	0	0	0	2	P	0	0	0	P	P	0	0	P	0	0	2
Geobaenini	0	1	0	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	2
Melanchitonini	0	1	0	0	0	0	0	2	1	0	0	0	0	0	0	0	1	0	0	2
Panagaeini	0	1	0	0	0	0	0	2	1	0	0	0	0	0	0	0	1	0	0	2
Orthogoniini	0	1	0	0	0	0	0	2	1	0	0	0	0	0	0	0	1	0	0	2
Loxandrini	0	1	0	0	0	0	0	2	P	0	0	0	0	0	0	0	1	0	0	2
Licinini	0	1	0	0	0	0	0	2	1	0	0	0	0	0	0	0	1	0	0	2
Platynini	0	1	0	0	0	0	0	2	0	0	P	0	0	0	0	0	1	0	0	2
Lachnophorini	0	1	0	0	0	0	0	2	0	1	1	0	0	0	0	0	1	0	0	2
Odacanthini	0	1	0	0	0	0	0	2	0	1	1	0	0	0	0	0	1	0	0	2
Graphipterini	0	1	0	0	0	0	0	2	1	0	0	0	0	0	0	0	1	0	0	2
Galeritini	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	1	2
Physocrotaphini	0	1	0	0	0	0	0	2	0	0	0	0	0	1	0	0	1	0	0	2
Helluonini	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	P	2
Pseudomorphini	0	1	0	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	2
IDEM TAXON*	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	2

* IDEM TAXON includes tribes of the identical character state distribution: Bembidiini, Peleciini, Abacetini, Zabrini, Chaetogenyini, Dercylini, Oodini, Chlaeniini, Amorphomerini, Harpalini, Perigonini, Ctenodactylini, Cyclosomini, Lebiini, Dryptini, Zuphiini, Anthiini.