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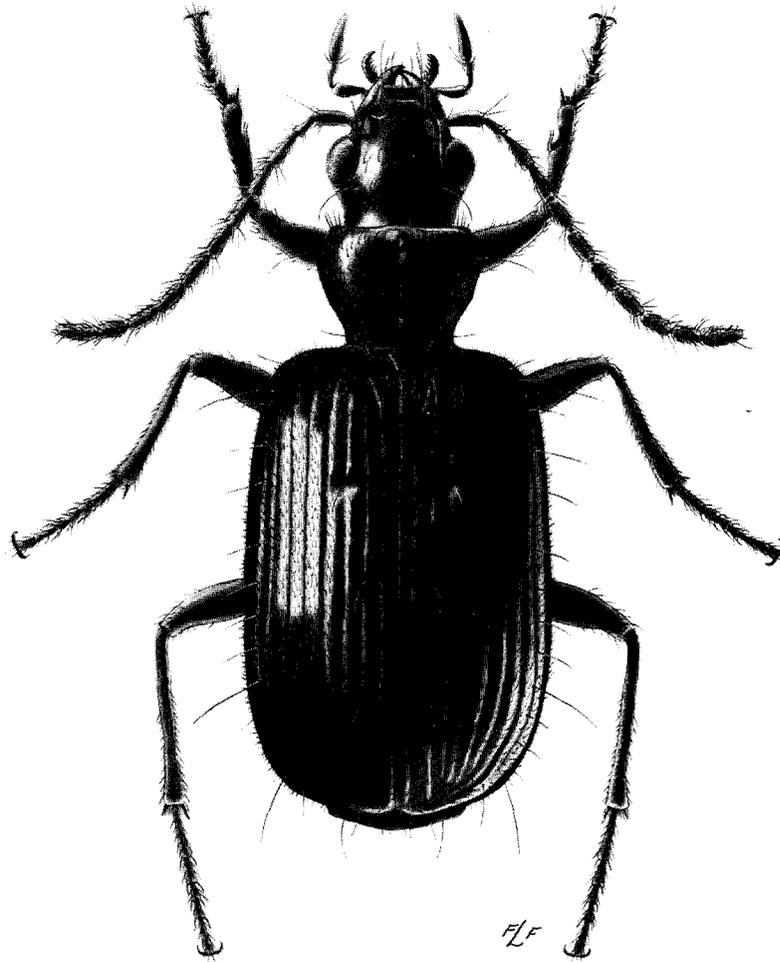


Figure 1. Male paratype of *Anchonoderus darlingtoni*, new species, type locality.

**REDEFINITION OF THE SUPERTRIBE ODACANTHITAE, AND  
REVISION OF THE WEST INDIAN LACHNOPHORINI  
(COLEOPTERA: CARABIDAE)**

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**ABSTRACT**

*Based on cladistic analysis of exemplar generic taxa using 57 morphological characters of the adult stage, the carabid supertribe Odacanthitae is redefined to include the tribes Odacanthini and Lachnophorini. Based on shared-derived states of the female reproductive tract, these sister taxa are hypothesized to be derivatives of platynine stock. Genera previously considered to comprise the tribe Pentagonicipini possess synapomorphies of Odacanthini, and the more restricted synapomorphies previously used to distinguish Pentagonicipini are shown to be insufficient to justify recognition of the tribe in a cladistically based classification. Pentagonicipini is thus combined with Odacanthini.*

*The genera of Lachnophorini are defined using characters of the cladistic analysis. The tribe comprises the genera Calophaena Klug, Asklepiä Liebke, Phaedrusium Liebke, Eucærus LeConte, Anchonoderus Reiche, Euphorticus Horn, Calybe Laporte, and Lachnophorus Dejean, and is restricted to the warmer areas of the Neotropical and Nearctic regions. A key to genera is provided.*

*The West Indian lachnophorine fauna is revised, with keys to species, diagnoses, illustrations, and distributional data provided. Anchonoderus darlingtoni, n.sp., is described from Hispaniola and Jamaica, and A. jamaicensis, n.sp., is described from Jamaica. Lectotypes are designated for Anchonoderus humeralis (Bates), n. comb., A. subtilis Bates, and Lachnophorus leucopterus Chevrolat.*

**RÉSUMÉ**

*La supertribue des carabides Odacanthitae est redefinie, basée sur une analyse cladistique de genres sélectionnés, utilisant 57 caractères morphologiques du stade adulte afin d'y inclure les tribues Odacanthini et Lachnophorini. Basée sur des caractères dérivés-communs du système reproductif femelle, nous émettons l'hypothèse que ces taxons-soeurs sont dérivés d'un groupe platynine souche. Des genres précédemment considérés comme faisant partie de la tribue Pentagonicipini possèdent des synapomorphies de la tribue Odacanthini, et les synapomorphies les plus restrictives précédemment utilisées pour distinguer Pentagonicipini sont démontrées insuffisantes pour justifier la reconnaissance de cette tribue dans une classification basées sur la cladistique. Pentagonicipini est donc combinée avec Odacanthini.*

*Les genres Lachnophorini sont définis utilisant les caractères de l'analyse cladistique. La tribue comprend les genres Calophaena Klug, Asklepia Liebke, Phaedrarium Liebke, Eucerus LeConte, Anchonoderus Reiche, Euphorticus Horn, Calybe Laporte, et Lachnophorus Dejean, et est restreinte aux zones plus chaudes des régions néotropicales et néarctiques. Une clef d'identification aux genres est présentée.*

*La faune lachnophorine de l'Inde de l'Ouest est révisée, et des clefs d'identification à l'espèces, de même que des descriptions diagnostiques, des illustrations et des informations sur la distributions sont présentées. Anchonoderus darlingtoni, n.esp., est décrite pour l'Hispaniola et la Jamaïque, et A. jamaicensis, n.esp., est décrite pour la Jamaïque. Des lectotypes sont désignés pour Anchonoderus humeralis (Bates), n. comb., A. subtilis Bates, et Lachnophorus leucopterus Chevrolat.*

## INTRODUCTION

Both the composition and placement of the tribe Lachnophorini have proved enigmatic to carabid systematists. I believe there are two major reasons for the uncertainty regarding this group. First, the Lachnophorini are principally distributed in the New World tropical and subtropical regions. The carabid fauna of these areas has been extensively described (*e.g.*, Bates, 1881-1884), but only recently has attention turned to detailed investigation of the natural affinities of taxa within this fauna. Secondly, some Lachnophorini exhibit a derived ant-like habitus. Past classificatory attempts have focused on this suite of unique derivations, at the expense of searching for shared-derived characters held with other taxa.

The initial purpose for this study was to revise the West Indian species of Lachnophorini as part of a group effort to monograph the West Indian carabid fauna (Erwin and Sims, 1984). So little was known of the affinities of Lachnophorini, however, that I determined to provide a better definition of the tribe, and elucidate its phylogenetic affinities. To this end, a cladistic analysis was performed, which was based on characters of the adult stage of Lachnophorini. Representatives of 14 other carabid genera previously implicated as relatives to lachnophorines were also studied. Based on this investigation, the Odacanthini and Lachnophorini proved to possess synapomorphies in the female reproductive tract, leading me to propose the Odacanthini and Lachnophorini as sister groups. Analysis of taxa within Lachnophorini provided characters useful for diagnosing the genera of the tribe. The resulting generic diagnoses are provisional, and it will require an extensive revision of mainland species to confirm what is presented here. Nonetheless, based on the characters examined, and their analysis using cladistic principles (*i.e.*, grouping of taxa by shared-derived similarity), the Lachnophorini is judged to be a natural assemblage.

### Taxonomic History

LeConte (1853) proposed Lachnophori to comprise the genera *Lachnophorus* Dejean and *Ega* Laporte (= *Calybe* Laporte). The following year Lacordaire (1854) proposed Anchonoderides for *Anchonoderus* Reiche, *Lachnophorus*, *Calybe*, *Ega*, and three other genera currently placed elsewhere: *Callistus* Bonelli, *Lasiocera*

Dejean, and *Camptotoma* Reiche. Horn (1881), impressed by the many peculiar characters of the genus *Ega*, proposed the monogeneric tribe Egini. The first concept of Lachnophorini largely reflecting current ideas was that of Bates (1883), who proposed Lachnophorinae for *Anchonoderus*, *Lachnophorus*, *Euphorticus* Horn, *Calybe*, and *Ega*.

The Lachnophorini was later dismembered by Liebke (1936, 1938), who placed *Calybe* in the Colliurini (=Odacanthini), separated from *Lachnophorus*. He also included in Colliurini genera previously placed in Ctenodactylini and Platynini.

More recently, Lachnophorini has been recognized as a tribe distinct from Odacanthini and Platynini (Reichardt, 1977, Liebherr, 1983) and as a component of an expanded Pterostichini (Erwin *et al.*, 1977).

*Eucaerus* LeConte was considered "an osculant form which is equally out of place in any tribe here defined" (LeConte, 1861). Ball and Hilchie (1983), through an investigation of taxa previously considered members of the subtribe Cymindina of Lebiini, placed *Eucaerus* in Lachnophorini. They considered it part of a eucaerine complex also comprising *Asklepia* Liebke and *Phaedrusium* Liebke. Reichardt (1974) had previously noted the similarity in palpal structure between *Asklepia* and *Calybe*.

Laporte (1835) first proposed the Odacanthidae. LeConte (1861) included the Casnoniae (genera *Casnonia* [= *Colliuris* Dejean] and *Leptotrachelus* Latreille), Lachnophori (genera *Ega* and *Lachnophorus*) and Eucaeri (genus *Eucaerus*) in his interpretation of Odacanthini. Jeannel (1948) proposed Odacanthomorphi at superfamilial rank, comprising his families Perigonidae, Peleciidae, Lachnophoridae, Odacanthidae, and Ctenodactylidae. Kryzhanovskiy (1976) united the tribes Odacanthini and Ctenodactylini in the supertribe Odacanthitae, whereas Lachnophorini was joined with Perigonini and Omphreini in the Perigonitae.

#### MATERIALS AND METHODS

##### Taxonomic Material

Specimens used in this study were obtained from the following institutions through the assistance of their respective curators:

AMNH	American Museum of Natural History, New York, L.H. Herman;
BMNH	British Museum (Natural History), London, N.E. Stork, M.J.D. Brendell;
CNC	Canadian National Collections, Ottawa, A. Smetana;
CUIC	Cornell University Insect Collection;
HDEO	Hope Dept. of Entomology, Oxford, G.C. McGavin, D.S. Smith;
IOJK	Institute of Jamaica, Kingston, T.H. Farr;
IREC	Institut de Recherches Entomologique de la Caraïbe, F.

- Chalumeau;
- IZPW Institut Zoologique, Académie Polonaise des Sciences,  
Warsaw, S.A. Slipinski;
- MCZ Museum of Comparative Zoology, Harvard University,  
Cambridge, MA, J.M. Carpenter, A.F. Newton, S.R. Shaw;
- MNHP Museum National d'Histoire Naturelle, Paris, H. Perrin;
- NMNH National Museum of Natural History, Smithsonian Institution,  
Washington, D.C., T.L. Erwin;
- TAMU Texas A. & M. University, College Station, H.R. Burke;
- UASM University of Alberta Strickland Museum, Edmonton, G.E. Ball  
and D. Shpeley;
- UMMZ University of Michigan Museum of Zoology, Ann Arbor, B.M.  
O'Connor;
- RLDC Robert L. Davidson Collection, c/o Carnegie Museum of  
Natural History, Pittsburgh, PA.

#### **Taxonomic Methods**

Microscopic techniques follow Liebherr (1986b). Where possible, types of West Indian Lachnophorini have been examined. Lectotype designations are included where appropriate. Complete listings are included for West Indian localities, with extra-limital circum-Caribbean records summarized from museum findings and publications.

Body length was measured as the distance from mandibular apex to elytral apex. This total was the sum of head length from mandibular apex to cervical collar, median pronotal length, plus elytral length from base of scutellum to elytral apex.

Scanning electron micrographs are used to illustrate certain aspects of these beetles' structure. Specimens were sonicated for 30 seconds in 95% ethanol, mounted on double-sided scotch tape, and sputter coated for four minutes with gold/palladium mixture. The micrographs were taken on an AMR 1000A microscope at 5kV.

*Methods of Cladistic Analysis.*— An initial set of taxa that included all West Indian Lachnophorini, plus representatives of 14 other genera, was examined to determine taxa to be included in the cladistic analysis (Fig. 2). This study set included representatives of five genera hitherto included in Lachnophorini. Fifty-seven unit characters of the adult stage were examined (Appendix 1). Inspection of these data and published information on larvae determined the taxa to be included in the cladistic analysis.

A number of the unit characters represent further derivation of a more generalized derived state. Such pairs of more general and more derived synapomorphies are characters 1 and 2, 3 and 4, 5 and 6, 11 and 12, 13 and 14, 19 and 20, 24 and 25, 26 and 27, 31 and 32, 34 and 35, 36 and 37, 45 and 46. The final cladograms were scanned to determine that the changes to the most derived states

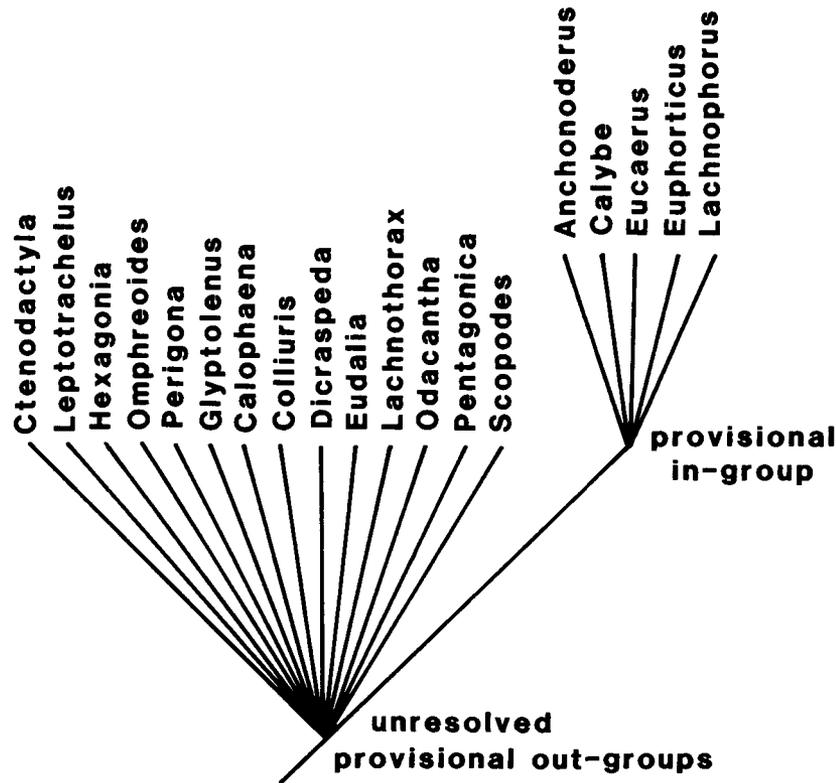


Figure 2. Five lachnophorine genera included in cladistic analysis, and 14 other genera provisionally allied with Lachnophorini in earlier classifications.

occurred above changes to the intermediate states.

Character state polarity was determined using out-group comparison (Watrous and Wheeler, 1981). The ancestral character state for the study set was determined based on three preliminary taxonomic groupings (Fig. 3), and the polarity algorithm derived from Farris (1970) by Maddison *et al.* (1984). Using this method, the character states at the secondary out-group node (Fig. 3) were determined, these states serving as the basal states for cladogram construction. For those instances in which this method could not unambiguously assign ancestral character states, additional species of *Glyptolenus* Bates and *Platynus* Bonelli were used as unresolved secondary out-groups.

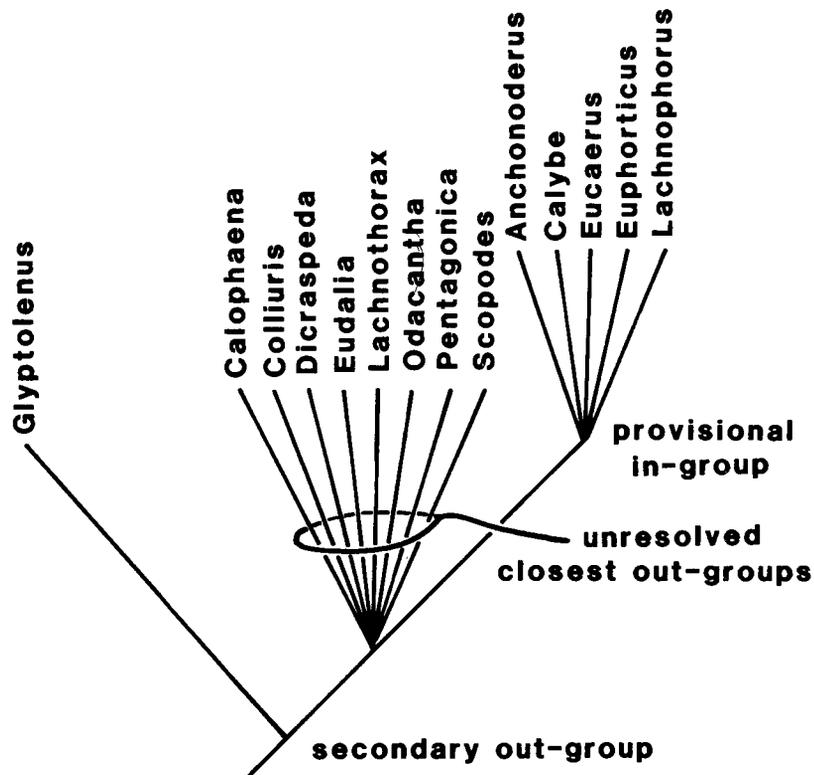


Figure 3. Provisional lachnophorine in-group, genera considered close neighbors based on preliminary investigations, and platynine genus *Glyptolenus* used as the out-group for the cladistic analysis. All taxa possess synapomorphy of bipartite spermatheca.

Cladistic network building was accomplished using the Phylogeny Inference Package (PHYLIP) Mix algorithm, version 2.0 of Felsenstein,<sup>1</sup> and the Phylogenetic Analysis Using Parsimony program (PAUP) of Swofford (1984). Based on character state polarities determined as above, the Mix Algorithm was run using: 1) Wagner Parsimony (Farris, 1970) for all characters, 2) Camin-Sokal (1965) coding for all characters, and 3) a variety of Wagner and Camin-Sokal coding for various characters. PAUP was run with *Glyptolenus chalybaeus* Dejean specified as the outgroup, hold trees = 5, swap = local, and the mulpars option employed. The PAUP cladograms did not depend on prior character polarity assessment, and are simply

<sup>1</sup>J. Felsenstein, Dept. of Genetics, Univ. of Washington, Seattle, WA 98195

the shortest network rooted at the outgroup.

The assumption of irreversibility of character evolution implicit in Camin-Sokal coding is not considered to represent the general case for character evolution. The probabilities of gains or losses for the characters in this study are largely unknown, and use of Wagner parsimony is preferred in most cases. Three characters, however, were judged to be largely irreversible, leading to use of mixed coding in the PHYLIP Mix algorithm. Characters 37-39, respectively, involve complete loss of the oblongum cell, loss of the wedge cell, and loss of the 1st anal vein on the flight wings. Simplification of wing venation is a trend generally observed during the evolution of brachyptery (Darlington, 1936). In the taxa observed herein, vein and cell loss appears correlated with smaller body size. It is assumed for this study that loss of wing veins and cells is irreversible. This assumption is based on the many examples of vein and wing loss observed throughout the Carabidae. Rederivation of lost veins and cells is deemed possible, but because of the prevalence of brachyptery and venational simplification, it is considered much less likely than repeated losses.

The shortest cladogram may be preferred based on adherence to the principle of parsimony but other factors must also be considered. First, it is recognized that characters of greater complexity most likely have more complex genetic and developmental bases. While parsimony is an objective criterion useful for comparing cladograms (Wheeler, 1986), a less parsimonious cladogram may express a more likely sum of character transformations. This might occur if reduction in changes of a conservative character is offset by additional changes in several labile characters. I judge the utility of a character in indicating phylogenetic affinity by the number of times the character changes state on the cladogram: *i.e.*, the fewer state changes the better the character (Sober, 1986). In this analysis, I present several more parsimonious cladograms, each based on specific assumptions of character transformation probabilities, plus a less parsimonious but preferable cladogram that requires fewer state changes in what are considered better characters.

The choice of a cladogram to use as a basis for classification is extremely important if we believe our classification should represent cladistic affinity. If a single cladogram is clearly more parsimonious than all others, it should be adopted as the basis for classification, with associated nomenclatural changes. But, if a marginally more parsimonious solution portends substantial nomenclatural changes, such as proposing new genera or dismemberment of currently recognized genera, the consequences of adhering strictly to parsimony as an arbiter of taxonomy must be carefully weighed. A major aim of this study is the presentation of synapomorphies deemed likely to define monophyletic groups in the Lachnophorini. Thus, I have chosen the preferred cladogram based on three criteria: 1) it is among the more parsimonious solutions, if not the most parsimonious; 2) it does not entail wholesale nomenclatural changes; 3) it includes synapomorphies for currently recognized genera of Lachnophorini (*i.e.*, lachnophorine genera are considered monophyletic). This cladogram and attendant classification are proffered as

preliminary hypotheses to be tested when mainland taxa are analyzed.

#### CLADISTIC ANALYSIS OF ODACANTHITAE

##### Taxa Included in the Analysis

Of the initial survey of 14 genera with potential affinities to the Lachnophorini (Fig. 2), five were excluded based on lack of synapomorphies.

The genus *Perigona* Laporte was considered closely related to Lachnophorini by Jeannel (1948). The spermatheca of *Perigona* (Fig. 4a) is unipartite, unlike the bipartite spermatheca of Lachnophorini (Liebherr, 1983). The larva of *Perigona termitis* Grassé and Jeannel (1941) lacks the segmented urogomphi observed in the odacanthines *Eudalia macleayi* Bates and *Scopodes simplex* Blackburn (Moore, 1965), and the lachnophorine *Calybe sallei* Chevrolat (Liebherr, 1983). For these reasons, *Perigona* is excluded from the analysis.

The ctenodactyline-hexagoniine taxa *Hexagonia* Kirby, *Leptotrachelus* Latreille, *Ctenodactyla* Dejean, and *Omphreoides* Fairmaire, were also found to lack synapomorphies uniting the rest of the taxa examined. The ctenodactyline female reproductive tract is characterized by a tubular or sac-like spermatheca attaching broadly near the junction of the common oviduct and bursa copulatrix (Figs. 4b,c). The spermathecal gland duct is long and enters near the base of the spermatheca. The male aedeagus is in the inverse position, on its left side in repose, unlike the aedeagus of most Platynini, and all Odacanthini and Lachnophorini examined. Thus, the ctenodactyline-hexagoniine taxa are not considered closely related to Lachnophorini. The tubular spermatheca and multiple nematiform setae on the apical gonocoxite (Figs. 4b, c) are states observed in Lebiini (e.g., *Tecnophilus* Chaudoir, *Dromius* Bonelli) (unpubl. data).

The cladistic analysis includes 22 taxa (Table 1); nine species of West Indian Lachnophorini, two non-West Indian lachnophorine species, eight species hitherto considered Odacanthini, two species hitherto considered Pentagonicini, and *Glyptolenus chalybaeus* of the Platynini.

All species included in the analysis possess female spermathecae that can be derived from a ground-plan represented by the bipartite spermatheca of *Glyptolenus chalybaeus* (Fig. 4d). Other *Glyptolenus* spp. possess unipartite tubular spermathecae typical for Platynini (Liebherr, 1986a). The use of *G. chalybaeus* as the outgroup for Odacanthitae is based on the assumption that the Odacanthitae is derived from a platynine-like ancestor. Other as yet unexamined platynines may prove more closely related than *G. chalybaeus*, but this species is the only platynine known to me with a bipartite spermatheca. The two non-West Indian lachnophorine taxa are included for different reasons. *Calybe laetula* LeConte is included as an exemplar of that genus. *Lachnophorus pilosus* Dejean is the type species of that genus, and its inclusion is used to represent prior subgeneric concepts of *Lachnophorus* (e.g., subgenera *Lachnophorus* and *Aretaonus* of Liebke [1936]).

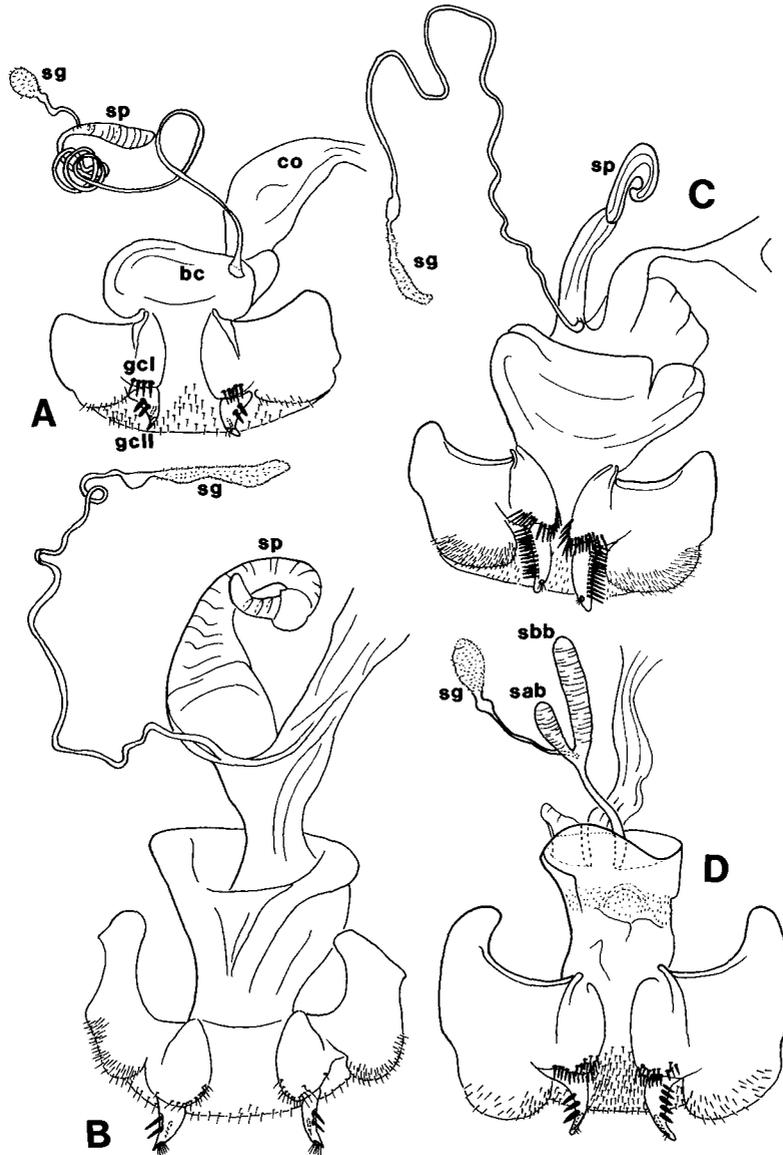


Figure 4. Female reproductive tracts, ventral view; A, *Perigona nigriceps* Dejean; B, *Leptotrachelus dorsalis* F.; C, *Ctenodactyla drapiezi* Gory; D, *Glyptolenus chalybaeus* Dejean. bc-bursa copulatrix, co-common oviduct; gcl-basal gonocoxite; gclI-apical gonocoxite; sp-spermatheca; sg-spermathecal gland; sab-spermathecal apical bulb; sbb-spermathecal basal bulb.

For the Odacanthini, single generic exemplars are included, with the exception of *Colliuris* Dejean, where three species are included. Placement of these three congeners in a monophyletic group is one means to judge resultant cladograms.

Two genera assignable to the Lachnophorini are not included; *Asklepia* Liebke and *Phaedrusium* Liebke (Reichardt, 1974; Ball and Hilchie, 1983). Affinities of these taxa are discussed below based on published information.

#### Character Polarity – Results

The character-state transformation series determined via out-group comparison are presented in Appendix 1, with taxon X character-state data in Table 1. Using the method of Maddison *et al.* (1984) with the 3-group statement of Fig. 3, 53 characters can have primitive and derived states unambiguously assigned. Primitive states of characters 47, 53, 54, and 57 are ambiguous because the unresolved closest out-groups all possess one state, and *Glyptolenus* possesses the other (Table 1). The primitive state for these characters was assigned based on character states found generally in other *Glyptolenus* and *Platynus*. Character 50 was coded the reverse of that determined by out-group comparison within this data set. Throughout Platynini, two lateral ensiform setae on the apical gonocoxite is the more generalized state. Other *Glyptolenus* spp. possess only two such setae whereas *G. chalybaeus* possesses three, making the necessity to reverse the polarity of this character an artifact of picking a single species as the secondary out-group.

The character-state transformation series were used with the Mix algorithm to determine several cladograms. The preferred cladogram placed one of the closest out-group taxa, *Calophaena* Klug, as the basal member of the in-group, Lachnophorini. This change did not affect any of the prior character-state polarities. On the contrary, inclusion of *Calophaena* in the in-group made polarity assessment of characters 1, 3, and 5 more clear-cut, as it resulted in all closest out-groups and the secondary out-group possessing the same character-state: 0 (Fig. 7, Table 1).

#### Cladistic Analysis – Results

If the character polarities of above are used to designate an hypothetical ancestor, the Mix algorithm of PHYLIP determines the shortest cladogram to be one of 147 steps (Fig. 5). This cladogram results using Wagner parsimony coding for all characters, and Camin-Sokal coding for all characters. If character polarities are not used, and the cladogram is rooted at the outgroup *Glyptolenus*, the PAUP algorithm finds 12 cladograms of 146 steps, all with the same topology (Fig. 6) but differing in the placement of character state changes. This most parsimonious cladogram has several undesirable attributes: 1) Odacanthini is not recognized as a monophyletic group, and the overall structure is of sequential addition of one or two out-group genera to the in-group; 2) the various representatives of *Colliuris* are separated; 3) this scheme necessitates evolution of the lachnophorine female reproductive tract (Figs. 9c, d) by reversal from the highly derived female tract of Odacanthini (Figs.

Table 1. Character state x taxon data matrix for cladistic analysis of Odacanthitae; 0=primitive state, 1=advanced state, ?=character state inapplicable or sex unknown.

Species	Character																					
	1	11111	11112	22222	22223	33333	33334	44444	44445	55555	55	12345	67890	12345	67890	12345	67890	12345	67890	12345	67	
<i>Glyptolenus chalybaeus</i> Dejean	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00
<i>Calophaena bicincta</i> Dej. & Bois.	10101	01011	10000	00110	00100	00001	00110	00000	00000	01001	01011	01011	01011	01011	01011	01011	01011	01011	01011	01011	01011	01
<i>Eucaerus insularis</i> Darlington	11111	11101	11000	10000	00000	00000	00100	10111	01000	01011	01011	01011	01011	01011	01011	01011	01011	01011	01011	01011	01011	??
<i>Eucaerus haitianus</i> Darlington	11111	11101	11000	10000	00000	00000	00100	11111	01000	01010	01010	01010	01010	01010	01010	01010	01010	01010	01010	01010	01010	01
<i>Anchonoderus jamaicensis</i> , n. sp.	10001	01000	11001	00000	00011	00000	11110	10100	01100	01011	01011	01011	01011	01011	01011	01011	01011	01011	01011	01011	01011	??
<i>Anchonoderus humeralis</i> Bates	00000	01000	10001	00000	00010	00010	00111	00110	11100	01000	01000	01000	01000	01000	01000	01000	01000	01000	01000	01000	01000	11
<i>Anchonoderus darlingtoni</i> , n. sp.	00000	01000	11001	00000	00010	00000	11110	00110	01100	01010	01010	01010	01010	01010	01010	01010	01010	01010	01010	01010	01010	11
<i>Anchonoderus subtilis</i> Bates	00000	01000	11001	00000	00000	00100	10010	00100	11100	01000	01000	01000	01000	01000	01000	01000	01000	01000	01000	01000	01000	11
<i>Anchonoderus subaeneus</i> Reiche	00000	01000	11001	00000	00000	00100	00011	00100	01000	01000	01000	01000	01000	01000	01000	01000	01000	01000	01000	01000	01000	11
<i>Euphorticus pubescens</i> Dejean	10101	01000	11001	01100	01000	00000	00111	11110	01100	01011	01100	01100	01100	01100	01100	01100	01100	01100	01100	01100	01100	11
<i>Calybe laetula</i> LeConte	11111	11010	11001	00100	01000	11010	00100	11110	01100	01010	01010	01010	01010	01010	01010	01010	01010	01010	01010	01010	01010	10
<i>Lachnophorus leucopterus</i> Chevrolat	11111	11000	10001	01000	01011	00010	00110	10110	01101	01010	01010	01010	01010	01010	01010	01010	01010	01010	01010	01010	01010	11
<i>Lachnophorus pilosus</i> Dejean	10111	11000	11001	01100	01011	00010	00111	11110	01101	01010	01010	01010	01010	01010	01010	01010	01010	01010	01010	01010	01010	10
<i>Eudalia latipennis</i> Macleay	00000	00010	00001	01000	00100	00000	00010	00000	01001	01011	01011	01011	01011	01011	01011	01011	01011	01011	01011	01011	01011	01
<i>Pentagonica picticornis</i> Bates	00000	00011	00100	11000	10000	00000	00100	00000	01011	01101	01101	01101	01101	01101	01101	01101	01101	01101	01101	01101	01101	01
<i>Scopodes aeneus</i> Macleay	00000	00001	00110	00000	10010	00000	00110	11110	01011	01110	01110	01110	01110	01110	01110	01110	01110	01110	01110	01110	01110	01
<i>Lachnothorax</i> sp.	00000	01010	11001	00010	00100	00000	00110	00000	01011	01110	01110	01110	01110	01110	01110	01110	01110	01110	01110	01110	01110	01
<i>Dicraspeda brunnea</i> Chaudoir	00000	00010	00000	01010	00000	00000	00110	00000	01011	01110	01110	01110	01110	01110	01110	01110	01110	01110	01110	01110	01110	01
<i>Odacantha melanura</i> L.	00000	00010	00000	00110	00000	00001	00100	00000	01001	01110	01110	01110	01110	01110	01110	01110	01110	01110	01110	01110	01110	01
<i>Colliuris pennsylvanicus</i> L.	00000	00010	00000	01111	00000	00001	00111	00000	01011	01110	01110	01110	01110	01110	01110	01110	01110	01110	01110	01110	01110	01
<i>Colliuris</i> sp.	00000	01010	11001	01111	01000	11010	00110	00000	01011	01110	01110	01110	01110	01110	01110	01110	01110	01110	01110	01110	01110	01
<i>Colliuris hubenthalii</i> Liebke	00000	00010	00001	01011	01000	10010	00100	00000	01011	01110	01110	01110	01110	01110	01110	01110	01110	01110	01110	01110	01110	01

8, 9a). Objections 1 and 2 reflect taxonomic considerations, and the desire to conserve the current nomenclature in the light of an insignificant (1 step or 0.68%) gain in parsimony. The third objection is based on rejection of what is considered an unlikely character transformation. Thus, the most parsimonious cladogram usefully portraying taxonomic categories and phylogenetic affinity is considered to be the 147 step cladogram found by PHYLIP (Fig. 5).

When Camin-Sokal coding is used for the three wing cell and vein characters (37, 38, 39), and Wagner coding is used for the balance, the result is a cladogram of 149 steps with the same topology as the 147 step cladogram (Fig. 5). The two extra steps are necessitated by the required repeated derivations of cell and vein loss (characters 37 and 39).

The preferred cladogram (Fig. 7) differs from the 147 and 149 step cladograms by placing *Eucaerus* close to the base of the lachnophorine clade. With characters 37-39 coded as Camin-Sokal characters, the cladogram is 150 steps long, or one step longer than the most parsimonious cladogram using such coding (Fig. 5). The more basal placement of *Eucaerus* results in a single-step transformation series for character 43: spermatheca with a gradually narrowing basal bulb (Figs. 9b, 12c, d) evolving once to a basal bulb with apical filament (Figs. 9c, d, 13a, 14b, e, 15d). The 147 and 149 step cladograms (Fig. 5) require an additional reversal to the

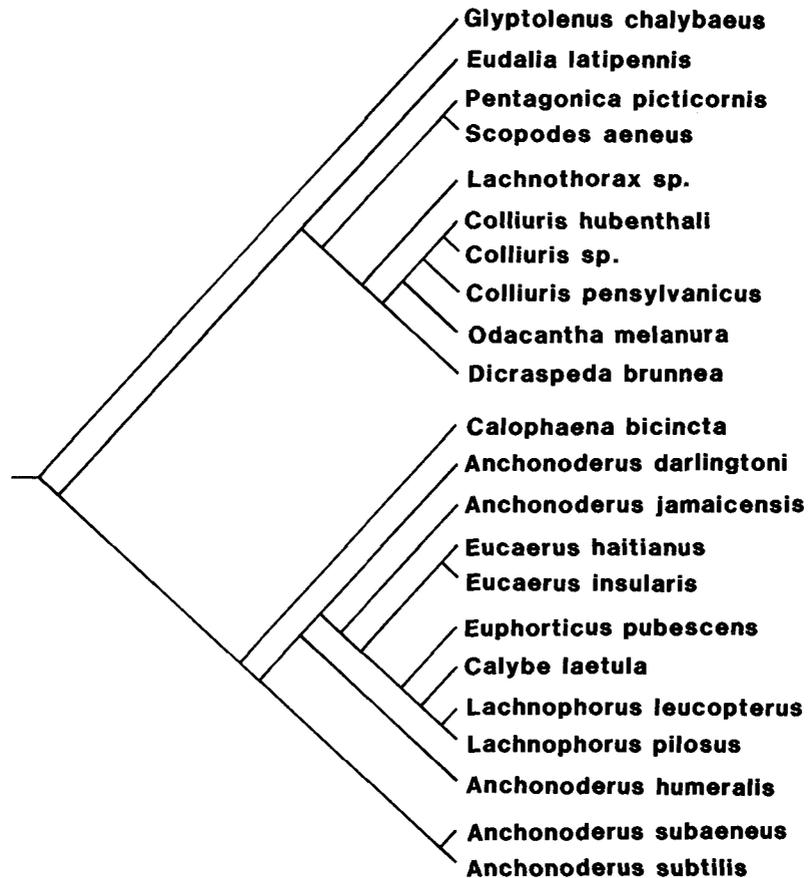


Figure 5. Cladogram of both 147 steps determined using PHYLIP Wagner algorithm, and 149 steps determined using PHYLIP Mix algorithm in which characters 37, 38, and 39 are coded using Camin-Sokal Coding; *i.e.*, irreversible.

primitive state for this character in the genus *Eucaerus*. Placement of *Eucaerus* basal to *Anthonoderus* also results in one fewer step in characters 15, 29, 50, and 56. The presence (Figs. 13b, 16a, c) or absence (Fig. 12e) of a V-shaped sclerite on the dorsum of the aedeagus (character 56) changes state only once on the preferred cladogram, raising its value as an indicator of affinity under this hypothesis.

The preferred cladogram requires an extra step in characters 17 and 36, and two extra steps in characters 49 and 54. Character 17, presence or absence of a pronotal basal seta, changes five times on the most parsimonious cladogram (Fig. 6), and thus

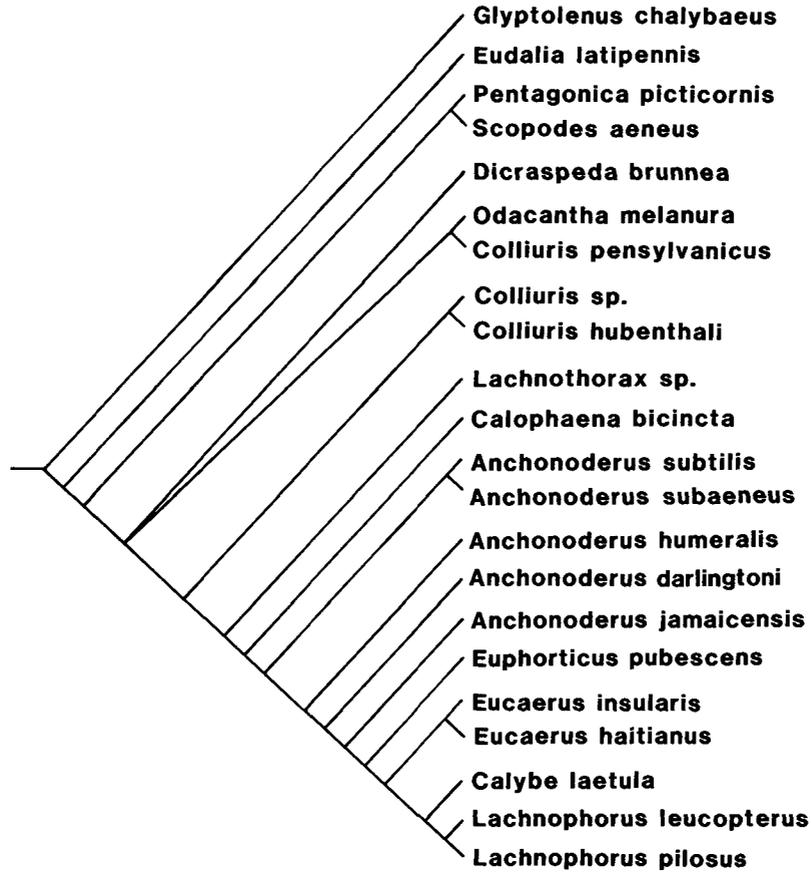


Figure 6. 146 step, most parsimonious cladogram determined using the PAUP algorithm, with *Glyptolenus* the designated outgroup.

would appear a poor indicator of affinity. Character 36 is the reduction of the oblongum cell from complete (Fig. 13c) to incomplete (Fig. 16e). This character too is not expected to be a good indicator of phylogeny due to repeated reduction of flight wings. The other two characters (49 and 54) change three and two times respectively on the most parsimonious cladogram, but are considered poorer indicators of affinity than spermathecal configuration.

The placement of *Eucaerus* adjacent to *Calophaena* results in recognition of *Anchnoderus* as the monophyletic sister group to *Euphorticus* - *Calybe* - *Lachnophorus*. If *Eucaerus* is moved basal to *Anchnoderus* with the other lachnophorine relationships of Figure 5 retained, the resultant cladogram is 154

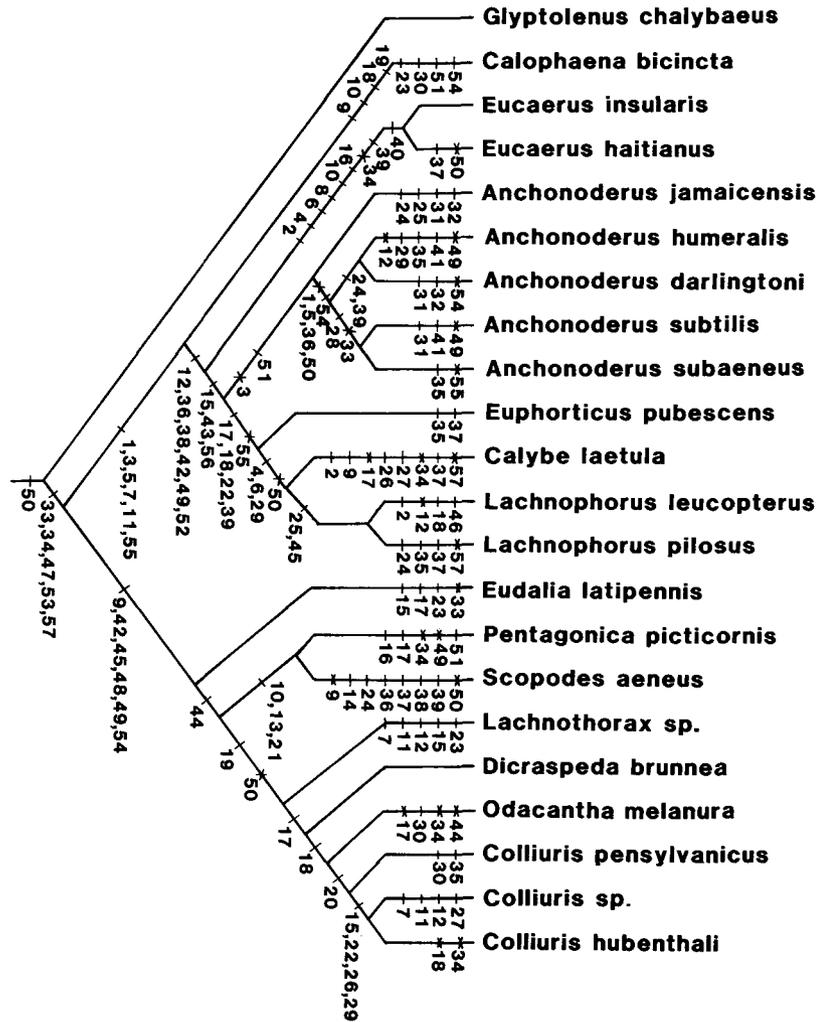


Figure 7. Preferred cladogram 150 steps in which *Eucera* is placed basal to *Anthonoderus*; character state advances are shown by slashes, reversals to more primitive stage by X's, character numbers correspond to Appendix 1.

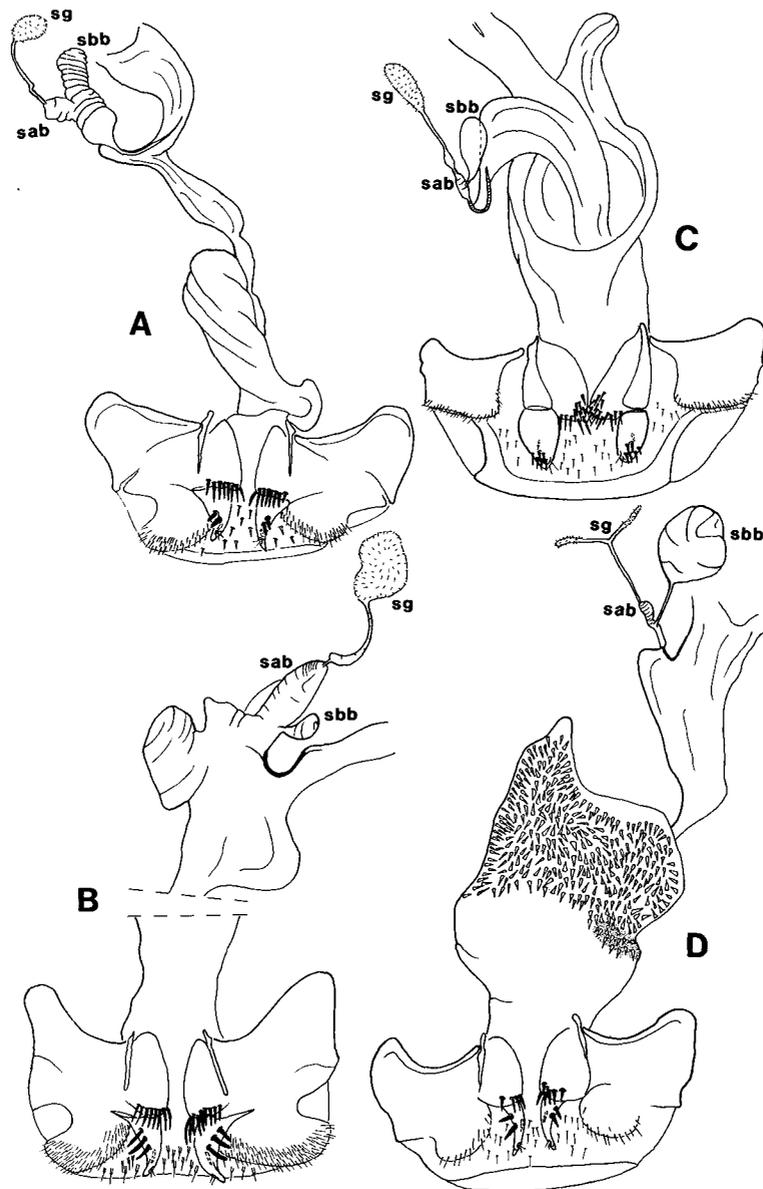


Figure 8. Female reproductive tracts, ventral view; A, *Odacantha melanura* L.; B, *Eudalia latipennis* MacLeay; C, *Pentagonica picticornis* Bates; D, *Scopodes aeneus* MacLeay. sab-spermathecal apical bulb; sbb-spermathecal basal bulb; sg-spermathecal gland.

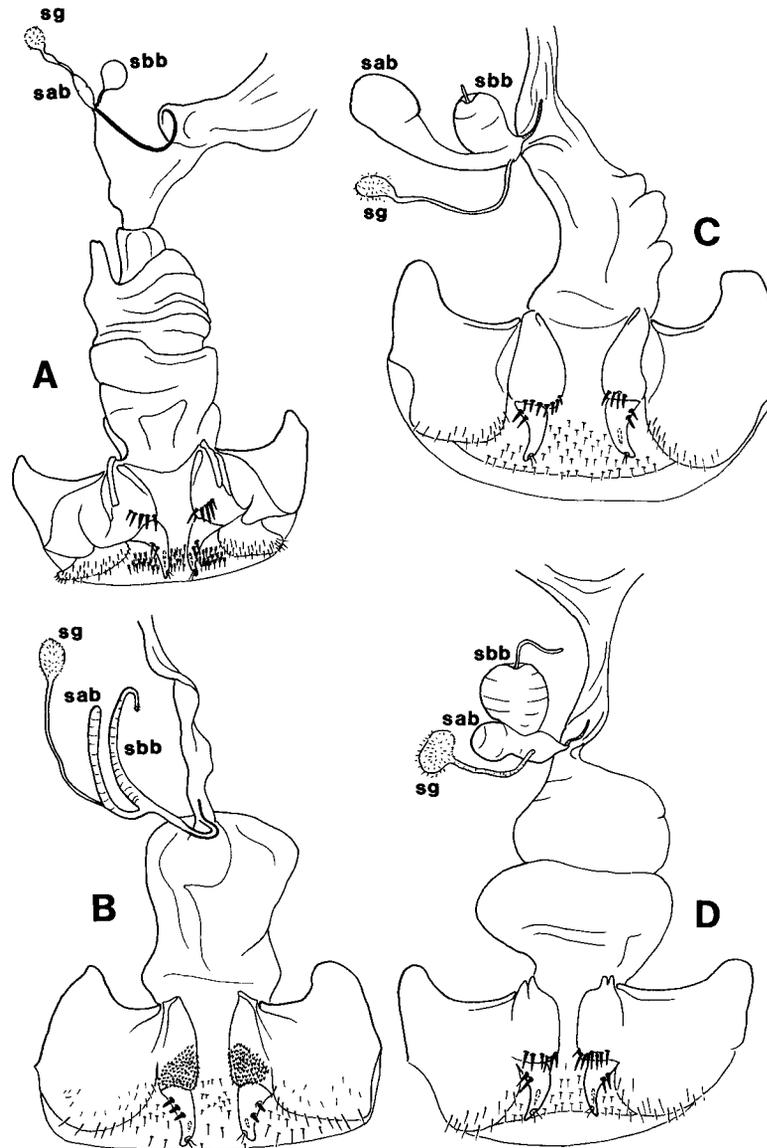


Figure 9. Female reproductive tracts, ventral view; A, *Colliuris hubenthalii* Liebke; B, *Calophaena bicincta* Dejean and Boisduval; C, *Calybe laetula* LeConte; D, *Lachnophorus pilosus* Dejean, sab-spermathecal apical bulb; sbb-spermathecal basal bulb; sg-spermathecal gland.

steps long. By the preferred 150 step cladogram (Fig. 7), the rounded gonocoxal apices (character 51) of *Anchonoderus* have been derived once and have not subsequently reversed to the ancestral state. Also, the setose body condition (character 15) is hypothesized to have arisen once within Lachnophorini based on this cladogram.

The taxa with setose body and setose maxillary palps (*Euphorticus* - *Calybe* - *Lachnophorus*) constitute a third lineage of the Lachnophorini. *Euphorticus* possesses moderately inflated apical maxillary palpomeres with sparse long setae (Fig. 11c), whereas *Calybe* and *Lachnophorus* possess more inflated, densely setose apical palpomeres (Fig. 11d). Development of inflated, densely setose palpomeres has occurred in two lineages; once in *Eucaerus* (Fig. 11b) and again in *Calybe* and *Lachnophorus*. The infrageneric variation in palpal shape exhibited between *L. pilosus* and *L. leucopterus* suggests that this characteristic has evolved three or more times. *Anchonoderus* spp. generally have fusiform palps (Fig. 11a), but those of *A. jamaicensis*, are slightly inflated (Fig. 14f), suggesting that the apparently generalized fusiform palpomere shape of most *Anchonoderus* spp. has evolved via reversal from a moderately inflated palpomere (Fig. 7, character 3).

This analysis places *Calophaena* as the basal taxon in the lachnophorine clade. *Calophaena* shares derived states of the palpi (characters 1,3,5,), antennal setation (character 7), subgenal setation (character 11), and aedeagal sac spination (character 55) with other lachnophorines. It has previously been grouped with Odacanthini (Bates, 1883, Liebke, 1938), and shares the general habitus of the genera *Colliuris* and *Odacantha* F. But, *Calophaena bicincta* Dejean and Boisduval lacks the distinctive U-shaped sclerite joining the spermatheca to the oviduct observed in other Odacanthini (Figs. 8, 9a, b). The elongate prothorax observed in *Calophaena* cannot characterize Odacanthini, as *Eudalia latipennis* MacLeay possesses a quadrate prothorax. Thus, based on cladistic affinity, *Calophaena* is more closely related to Lachnophorini than Odacanthini.

If one wished to classify *Calophaena* in Odacanthini, placing it at the base of the odacanthine clade in a modification of Figure 7, the cladogram would be four steps longer than the preferred cladogram. Additional derivations of characters 1, 3, 5, 7, 11, and 55 would be offset by saving one step each in characters 9 and 54. The six characters requiring extra steps change two, two, two, three, three, and three times, respectively, on the shorter preferred cladogram (Fig. 7). Characters 9 and 54 both require three state changes on the modification of Figure 7, showing that the saving in steps for these characters still leaves them as homoplasious as characters 7, 11, and 55 on the preferred cladogram. Thus, there is no justification based on parsimony, or character weighting to retain *Calophaena* in Odacanthini.

*Pentagonica* Schmidt-Goebel and *Scopodes* Erichson have previously been recognized along with *Actenonyx* White as the tribe Pentagonicini. Bell (1985) revised the West Indian species of *Pentagonica*. Based on cladistic analysis of adult characters, the Pentagonicini must be combined with Odacanthini. Thus, even

though *Pentagonica* and *Scopodes* possess a characteristic pronotal shape (character 21), and fused gula and mentum (characters 13, 14), these synapomorphies occur in a matrix of odacanthine synapomorphies that include spermathecal configuration (characters 44, 45, 48; Figs. 8, 9a), and a derived aedeagal apex (character 54; Figs. 10a-d). Moore (1965) noted the similarities of larvae of *Scopodes simplex* Blackburn and *Eudalia macleayi* Bates. Moreover, the “pentagonicine” prothoracic shape is approached in *Eucaerus* (Fig. 12a). Based on cladistic principles, there is no justification for recognition of Pentagonicini.

#### Taxonomic Conclusions of Cladistic Analysis

Based on the preferred cladogram (Fig. 7), the supertribe Odacanthitae is comprised of two tribes, the Odacanthini and Lachnophorini. The Odacanthini includes those genera previously considered in the tribe (Jeannel, 1948; Darlington, 1968; Reichardt, 1977), plus those previously considered Pentagonicini (*Pentagonica*, *Scopodes*, *Actenonyx*). The genus *Calophaena* is removed from the Odacanthini and placed in Lachnophorini.

Lachnophorini is considered the sister group to Odacanthini. The major synapomorphy grouping these two tribes is a bipartite spermatheca in the female. Supporting synapomorphies of more erratic occurrence throughout the Platynini and Lebiomorphi include segmented urogomphi and absence of a maxillary inner lobe in the larval stages.

The Lachnophorini as presently constituted comprises eight genera: *Calophaena*, *Eucaerus*, *Anchonoderus*, *Euphorticus*, *Calybe*, *Lachnophorus*, and the two genera included by Ball and Hilchie (1983) in the eucaerine complex, *Asklepia* and *Phaedrusium*. The tribe is distributed in the warmer regions of the Neotropical and Nearctic regions.

### TAXONOMIC TREATMENT

#### Tribe Lachnophorini LeConte.

- Lachnophori LeConte, 1853: 370.
- Anchonoderides Lacordaire, 1854: 373.
- Eucaeri LeConte, 1861: 22.
- Egini G. Horn, 1881: 152.

*Tribal Diagnosis*.— A group of disparate external appearance, as evidenced by the numerous classificatory proposals above, but possessing the following characteristics: (1) a patch of setae on the subgena ventrad eye (Fig. 11); (2) antennomeres 2 and 3 setose over length (except in *Phaedrusium*); (3) body size small, generally less than 8 mm in length; (4) elytra usually moderately truncate apically; (5) apical palpomeres inflated and setose (Figs. 11b-d), or if fusiform, covered by very short setae (Fig. 11a); (6) spermatheca bipartite (Figs. 9b, c) or derivable from a bipartite ground-plan (Fig. 16d).

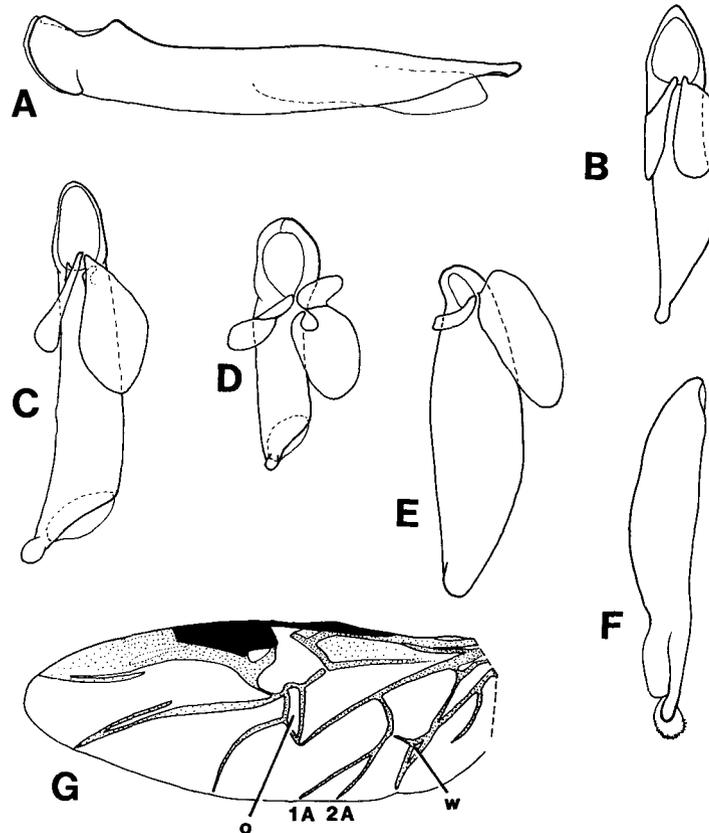


Figure 10. A-F, Male aedeagus; A, *Odacantha melanura* L., median lobe dextro-ventral view; B, *Colliuris pensylvanicus* L., median lobe and parameres, ventro-laevo view; C, *Dicraspeda brunnea* Chaudoir, median lobe and parameres, ventro-laevo view; D, *Scopodes aeneus* MacLeay, median lobe and parameres, ventro-laevo view; E, *Calophaena bicincta* Dejean and Boisduval, median lobe and parameres, ventro-laevo view; F, *Calophaena bicincta*, median lobe, dextro-ventral view, inner sac partially everted. G, *Colliuris* sp., flight wing. 1A, 2A -- 1st and 2nd anal veins; O - oblongum cell; w - wedge cell.

*Way of Life.*— Lachnophorines are riparian and can be found along stream banks and on the shores of temporary and permanent ponds. Adults may be observed if water is splashed on sandy shorelines. Some species, such as *Euphorticus pubescens*, *Lachnophorus leucopterus*, and *Calybe sallei* are diurnal in activity. *Anchonderus* spp. are less often observed during daytime, except by splashing and are most commonly taken at light at night.

Liebherr (1983) described the larval stages of *Calybe (Ega) sallei*. The larvae and adults are active on the clay-sand surface during May in the southern United

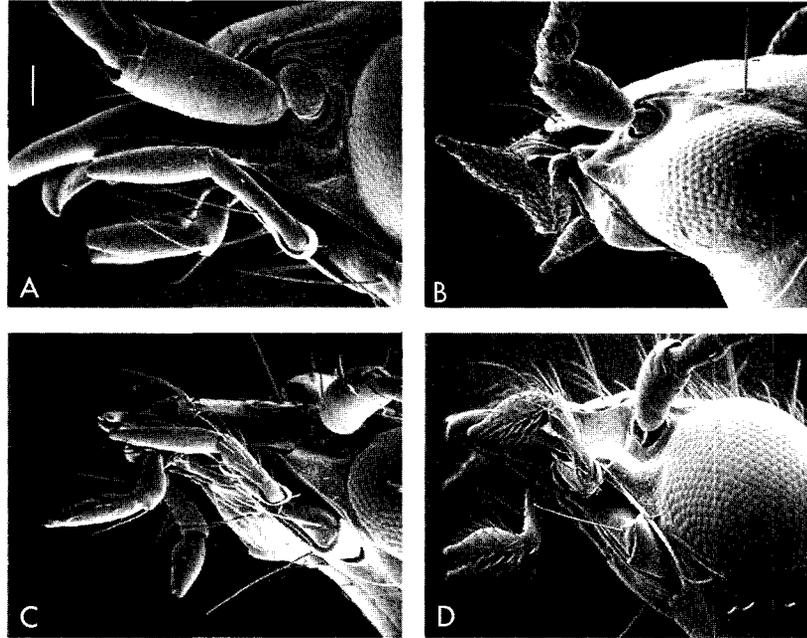


Figure 11. SEM micrographs of lachnophorine mouthparts, lateral view: A, *Anchonoderus subtilis* Bates; B, *Eucaerus* sp., Trinidad, Simla Biol. Sta. N Arima; C, *Euphorticus pubescens* Dejean; D, *Lachnophorus leucopterus* Chevrolat. Scale bar = 0.1 mm.

States. The larvae possess long urogomphi with whitish tips which they move in apparent imitation of antennae. Their movements are quick and erratic, much the same as the adults.

**Provisional Key to Genera of Lachnophorini**

Based on the characters recorded in the West Indian taxa, in other mainland taxa used in the cladistic analysis, and in publications, the following provisional key is presented. The generic concepts are based on characters of the type species, and to the degree that the herein recognized genera are natural, this key will be useful. I have derived key characters for *Asklepia* and *Phaedrusium* from Reichardt (1974) and Ball and Hilchie (1983).

- 1 Dorsal integument glabrous, except for macrosetae in standard positions ..... 2
- 1' Pronotum, elytra, and head with a pelage of shorter secondary setae in addition to standard macrosetae ..... 5
- 2 (1) Pronotum elongate; neck constricted; tarsomeres 1-4 of all legs broadly expanded laterally.....*Calophaena* Klug

- 2' Pronotum broad, wider than long; neck not strongly constricted; tarsomeres of mid- and hindlegs not expanded ..... 3
- 3 (2') Pronotum with base truncate, lacking median lobe; elytra with striae effaced; body bicolored; microsculpture not evident at lower magnifications (to 50X)..... *Asklepia* Liebke
- 3' Pronotum with basal median lobe (Figs. 12a, b); elytral striae effaced or evident; body bicolored or concolorous; microsculpture of elytra not evident, or strong transverse mesh, or parallel lines ..... 4
- 4 (3') Antennomeres 2-3 without vestiture of short setae, bearing long preapical setae; male protarsomeres lacking ventral adhesive setae ..... *Phaedrusium* Liebke
- 4' Antennomeres 2-3 with vestiture of short setae as well as longer preapical setae; male protarsomeres 2-3, or 2-4 with ventral adhesive setae ..... *Eucaerus* LeConte, p. 21
- 5 (1') Maxillary apical palpomeres fusiform or at most slightly inflated, covered with very short setae and thus appearing glabrous (50X); pronotum with well-developed lateral margin (Figs. 1, 14a, d, 15a, c) ..... *Anchonoderus* Reiche, p. 24
- 5' Maxillary apical palpomeres moderately to strongly inflated with at least a sparse covering of long setae (Figs. 11c, d); pronotum cylindrical with poorly developed lateral margin ..... 6
- 6 (5') Maxillary apical palpomeres moderately inflated (Fig. 11c) with sparse coating of longer setae ..... *Euphorticus* Horn, p. 28
- 6' Maxillary apical palpomeres more strongly inflated (Fig. 11d) densely covered by setae at least in basal 0.50 ..... 7
- 7 (6') Elytra with secondary setation composed of stout black setae over twice as long as fine yellow setae and with well-developed transverse impression at basal 0.33 ..... *Calybe* Laporte
- 7' Elytra with secondary setation more concolorous, longer setae rufous, shorter setae yellow; elytra with three impressions in third interval that may be foveate, but transverse impression absent ..... *Lachnophorus* Dejean, p. 34

## TAXONOMIC REVISION OF WEST INDIAN LACHNOPHORINI

*Eucaerus* LeConte*Eucaerus* LeConte, 1853: 386.*Lachnaces* Bates, 1872: 201.

*Type species*.— Of *Eucaerus*, *E. varicornis* LeConte (monotypy); of *Lachnaces*, *L. sericeus* Bates (Ball and Hilchie, 1983).

*Generic Diagnosis.*— Body glabrous dorsally except for standard macrosetae; apical palpomeres inflated and densely setose (Fig. 11b); pronotum broad with well-developed basal median lobe (Figs. 12a, b); antennae with apical four or five segments pale, basal segments rufo-brunneous; female spermatheca bipartite, the basal and apical lobes subequal, not bearing an apical filament (Figs. 12c, d).

#### Key to West Indian Species

- 1 Pronotum maximum width 1.5–1.6X median length; pronotal basal bead angled between hind angles and basal median lobe (Fig. 12a).....*E. haitianus* Darlington  
 1' Pronotum maximum width 1.35–1.45X median length; pronotal basal bead nearly straight between hind angles and basal median lobe (Fig. 12b).....*E. insularis* Darlington

#### *Eucaerus haitianus* Darlington

*Eucaerus haitianus* Darlington 1935: 210.

*Diagnostic Combination.*— Pronotum broader than in *E. insularis*, hind angles more strongly produced, median lobe more strongly developed (Fig. 12a); flight wings either fully developed (Fig. 12f) or with reduced apex (Fig. 12g); length 3.3–4.1 mm.

*Male Genitalia.*— Aedeagal median lobe straight apically, apex blunt, basal bulb open (Fig. 12e); aedeagal internal sac with apico-ventral patch of stout spines.

*Female Reproductive Tract.*— Gonocoxae with apical fringe of 6–8 setae on penultimate segment, 2–3 lateral and one dorsal ensiform setae on apical segment (Fig. 12c); spermatheca with basal bulb gradually tapering to an acuminate tip, apical bulb broadly rounded with small apical nipple.

*Type.*— Holotype ♀ (MCZ No. 22035), Haiti, l'Ouest, Etang Lachaux, SW Peninsula, under 1000 ft., 26-27-X-1934, P.J. Darlington, Jr.

*Distributional Records.*— A Hispaniolan endemic with the following non-type records: DOMINICAN REPUBLIC: Samana: Sanchez, VII-1938 (88, MCZ). HAITI: l'Ouest: Etang Lachaux, SW Peninsula, <1000' el., 26-27-IX-1934 (12, MCZ).

#### *Eucaerus insularis* Darlington

*Eucaerus insularis* Darlington 1934: 120.

*Diagnostic Combination.*— Pronotum quadrate with base constricted, hind angles poorly developed, base evenly rounded posteriorly (Fig. 12b); flight wings either developed (Fig. 12h) or a vestigial flap not reaching beyond metathorax; length 3.7–3.9 mm.

*Female Reproductive Tract.*— Gonocoxae with apical fringe of 8–10 setae on penultimate segment, 3–4 lateral and one dorsal ensiform setae on apical segment

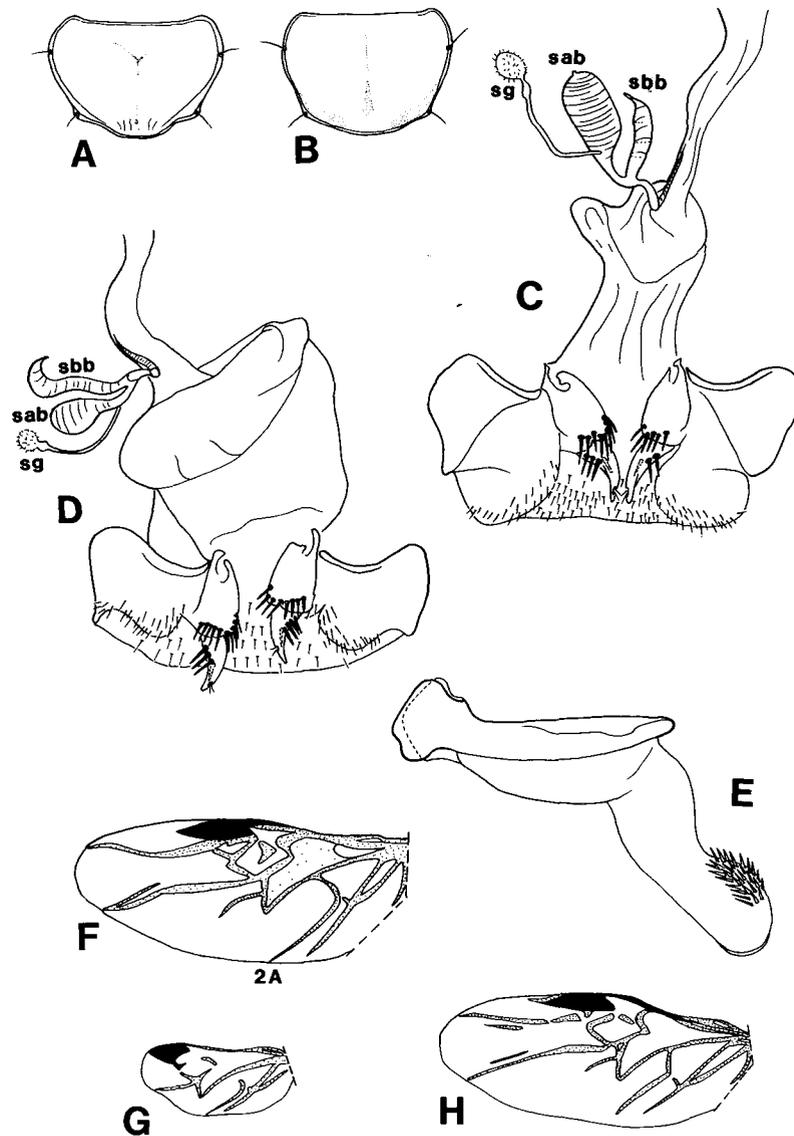


Figure 12. A, *Eucærus haitianus* Darlington, pronotum; B, *E. insularis* Darlington, pronotum; C, *E. haitianus*, female reproductive tract, ventral view; D, *E. insularis*, female reproductive tract, ventral view; E, *E. haitianus*, aedeagal median lobe with everted inner sac, dextro-ventral view; F, *E. haitianus*, flight wing; G, *E. haitianus*, micropterous flight wing; H, *E. insularis*, flight wing. sab-spermathecal apical bulb; sbb-spermathecal basal bulb; sg-spermathecal gland; 2A -- 2nd anal vein.

(Fig. 12d); spermatheca with basal bulb apically hooked, apical bulb globose.

*Type*.— Holotype ♀ (MCZ no. 19536), Cuba, Las Villas, Soledad, June 1929, P.J. Darlington, Jr.

*Distributional Records*.— A Cuban endemic with the following non-type record: Cuba: Las Villas: Soledad, 2-12-VIII-1934 (17, MCZ).

#### *Anchonoderus* Reiche

*Anchonoderus* Reiche, 1843:38.

*Lachnophorus* (*Axylosius*) Liebke, 1936:461 (NEW COMBINATION, NEW SYNONYMY).

*Type species*.— Of *Anchonoderus*, *A. eximius* Audouin by original designation; of *Axylosius*, *A. humeralis* (Bates) by original designation.

*Generic Diagnosis*.— Body with dense pelage of secondary setae; apical palpomeres fusiform, appearing glabrous but covered with very short setae (Fig. 11a), penultimate maxillary palpomere appearing glabrous or bearing sparse, long setae (Fig. 14f); pronotum cordate, hind angles evident, setose, one lateral seta; female spermatheca bipartite, basal lobe expanded basally and bearing an apical filament, apical lobe globose and subequal or larger than basal lobe (Figs. 13a, 14b, e, 15d); apical gonocoxites rounded at tips.

#### Key to West Indian Species

- |        |   |                                      |
|--------|---|--------------------------------------|
| 1      | Testaceous maculae on 5th or 6th, to 8th or 9th elytral interval behind humeri .....  | <i>A. humeralis</i> (Bates), p. 25   |
| 1'     | Elytra concolorous piceous, at most with sutural interval slightly paler .....  | 2                                    |
| 2 (1') | Apical maxillary palpomere moderately inflated, penultimate palpomere with long setae (Fig. 14f); length 4.3–4.4 mm.....                            | <i>A. jamaicensis</i> , n.sp., p. 26 |
| 2'     | Apical maxillary palpomere fusiform, penultimate palpomere with very short setae except for those in apical ring (Fig. 11a); length 4.6–7.6mm ..... | 3                                    |
| 3 (2') | Dorsal elytral impressions of third interval evident, the anterior impression foveate (Fig. 1); length 4.6–5.8 mm.....                              | <i>A. darlingtoni</i> , n.sp., p. 25 |
| 3'     | Dorsal elytral impressions inconspicuous, difficult to discern amidst secondary elytral punctation; length 6.3–7.6 mm .....                         | 4                                    |
| 4 (3') | Pronotum quadrate, hind angles well developed, protruding (Fig. 15c).....   | <i>A. subtilis</i> Bates, p. 27      |
| 4'     | Pronotum cordate, hind angles more weakly developed, not protruding (Fig. 15a).....   | <i>A. subaeneus</i> Reiche, p. 27    |

*Anchonoderus darlingtoni*, n.sp.

*Lachnophorus humeralis* Darlington, 1953: 4.

**Diagnosis.**— Vertex of head shiny black, pronotum and elytra concolorous piceous, elytra lacking maculae; pronotum with sides parallel before obtuse hind angle (Fig. 1); dorsal elytral impressions evident, the anterior and posterior impressions slightly foveate; size moderate among West Indian species, length 4.6–5.8 mm.

**Description.**— *Head.* Moderately elongate, eyes convex; mandibles, labrum, and clypeal edges rufous; maxillae and labrum testaceous; mentum tooth broad, about 0.50X length lateral lobes of mentum; antennae with moderately robust segments, scape testaceous, segments 2–11 slightly darker. *Prothorax.* Pronotum with base constricted; hind angles obtuse-angulate; basal seta situated before hind angle; lateral margin parallel for at least short distance anterad hind seta; lateral pronotal seta nearly 0.75 distance toward front angle; front angle narrowly rounded, moderately projecting; median longitudinal depression well developed, especially in basal 0.25, transverse wrinkles intersecting depression in basal 0.50; base of pronotum with continuous marginal bead; very small triangular depression inside hind angles. *Elytra.* Sides subparallel, humeri broad, apex subtruncate with subapical sinuation nearly obsolete; scutellum and basal 0.50 of sutural edge rufous, rest of elytra piceous; striae complete and smooth apically, more incomplete and broken into series of fine punctures medio-basally; intervals moderately convex; 13–16 umbilicate setae in or adjacent to eighth stria from humerus to subapical sinuation. *Pterothorax and Abdomen.* Metepisternum 1.67X as long as wide; flight wings (Fig. 13c) with oblongum cell complete, wedge cell and first anal vein absent (compare to Fig. 10g); first visible abdominal segment with longitudinal wrinkles adjacent to metacoxae, segments 3–6 densely setose. *Legs.* Femora testaceous with rufous apices, coxae and trochanters rufous, tibiae with rufous longitudinal seta-bearing ridges and testaceous canaliculi, tarsomeres rufo-testaceous; male protarsomeres moderately expanded laterally, segments 1–3 bearing four longitudinal rows of adhesive setae. *Microsculpture.* Vertex of head with strong isodiametric microsculpture; pronotum with transversely stretched isodiametric mesh; elytra with regular isodiametric mesh. *Male Genitalia.* Median lobe of aedeagus nearly straight with pointed apex (Fig. 13b); internal sac bearing two patches of spines apically; V-shaped sclerite present at base of internal sac. *Female Reproductive Tract.* Apical gonocoxites bearing two lateral and one dorsal ensiform setae, their apices rounded (Fig. 13a); basal gonocoxites with apical fringe of nine setae; spermatheca with basal bulb narrow, apical bulb much wider than basal bulb.

*Holotype:* ♂, HAITI: Artibonite: Ennery, nr. 1000' el., 6-11-IX-1934, P.J. Darlington, Jr. (MCZ).

*Allotype:* ♀, same data (MCZ).

*Paratypes:* DOMINICAN REPUBLIC: Puerto Plata: 25 km S by rd. of Puerto Plata, VI-1938 (1♂, MCZ). HAITI: Artibonite: Ennery, nr. 1000' el., 6-11-IX-1934 (44♂♂, 64♀♀, MCZ; 1♂, 3♀♀, BMNH). Nord: Cape Haiten (1♂, MCZ). l' Ouest: Carrefour, V-1908 (1♀, BMNH); Port au Prince, R. Froide, 3-X-1934 (1♂, MCZ). Sud: Camp Perrin, nr. 1000' el. (3♂♂, 3♀♀, MCZ); Massif de la Hotte, Desbarrier, 12-14-X-1934 (3♂♂, MCZ), NE Foothills, 2-4000' el., 10-24-X-1934 (10♂♂, 15♀♀, MCZ). JAMAICA: St. Thomas: Corn Puss Gap, 2060' el., 14-XI-1946, ex fallen tree (1♂, IOJK)

**Etymology.**— The very large type series exemplifies the efforts Philip Darlington made in procuring specimens from the field. The species is respectfully dedicated to his memory.

*Anchonoderus humeralis* (Bates), n.comb.

*Lachnophorus humeralis* Bates, 1883: 153; Csiki, 1931: 890.

*Lachnophorus (Axylosius) humeralis*, Liebke, 1936: 461.

**Diagnostic Combination.**— Placed in *Anchonoderus* based on fusiform and glabrous apical palpomeres, setose pronotal hind angles (Fig. 14a); head and

pronotum shiny piceous with slight aeneous cast; elytra with testaceous maculae at humeri, extending from 5th to 9th interval; dorsal elytral impressions evident, foveate; legs testaceous with smoky femoral apices, tibial apices and tarsi dark; length 4.6–5.1 mm.

*Male Genitalia*.— Median lobe of aedeagus bluntly rounded apically, internal sac bearing apical fringe of spines (Fig. 14c), sclerotized straps at base of internal sac on dorsum of aedeagus (retracted position).

*Female Reproductive Tract*.— Apical gonocoxites with two lateral and one dorsal ensiform setae, basal gonocoxite with apical fringe of 11–12 setae (Fig. 14b); spermatheca with basal bulb columnar basally, more constricted at apical filament, apical bulb large and globose.

*Type*.— LECTOTYPE ♂ hereby designated: [Panama] Caldera, 1200 ft., Champion; *Lachnophorus humeralis* Bates; B.C.A. Col. I. 1, *Lachnophorus humeralis* Bates; Lectotype ♂, *Lachnophorus humeralis* Bates, By Erwin '76 (BMNH).

*Extralimital distribution*.— Recorded from Guatemala and Panama (Bates, 1883). NICARAGUA: Chontales (1, BMNH). West Indian Records. GRENADA: Chantilly Est. (windward side)(12, BMNH). ST. LUCIA: 29-III-1936 (2, NMNH); Marisule, 11-IV-1978 (2, IREC).

*Anchonoderus jamaicensis*, n.sp.

*Diagnosis*.— Apical maxillary palpomere fusiform with acute tip (Fig. 14f), appearing glabrous but with very short setae covering surface (125X); penultimate maxillary palpomere setose; pronotum constricted with nearly obsolete, setose hind angles (Fig. 14d); dorsal elytral impressions strongly foveate; upper body surface shiny aeneo-piceous; length 4.7 mm.

*Description*.— *Head*. Vertex convex dorsally, eyes moderately convex; mandibles, labrum, clypeus and apical palpomeres rufous; maxillae, labium, and basal palpomeres testaceous; median tooth of mentum slender, acute, 0.6X length lateral lobes of mentum; antennae with basal four segments rufo-brunneous, segments 5–11 darker; outer segments robust, width of segment 10 0.6X length. *Prothorax*. Pronotum with narrow lateral margins, constricted base, and nearly obsolete hind angles (Fig. 14d); basal seta situated just before obtuse-angulate hind angle; lateral margin slightly concave before hind angle; lateral pronotal seta set 0.7X distance from pronotal base to front angles; front angle angulate, not projecting forward; median longitudinal depression fine; basal bead broad, evenly developed across pronotal base; latero-basal depression nearly obsolete, only slight depression inside hind angle. *Elytra*. Humeri well developed, lateral margin of elytra slightly constricted at about basal 0.33 of length; apex subtruncate, wider elytral margin evident before nearly obsolete subapical sinuation; three strongly foveate dorsal depressions in third interval, each fovea with an associated macroseta; elytral intervals convex, with surfaces roughened by secondary setation; striae complete, though punctate and nearly evanescent near base; 14 umbilicate setae in or adjacent to eighth stria from humerus to subapical sinuation. *Pterothorax and Abdomen*. Metepisternum elongate; flight wings with oblongum cell complete, wedge cell and first anal vein absent (as in Fig. 13c); first two visible abdominal segments nearly smooth, shiny, segments 3–6 setose. *Legs*. Femora, tibiae, and tarsi piceous, coxal apices and trochanters rufo-testaceous on front two pairs, coxae concolorous with femora on hind legs. *Microsculpture*. Vertex without visible microsculpture, very shiny; pronotum with very faint transverse mesh obscured by punctations of secondary setation; elytra with weak isodiametric mesh, the surface shiny. *Female Reproductive Tract*. Apical gonocoxite with two or three lateral and one dorsal

ensiform setae, basal gonocoxite with apical fringe of seven to eight setae (Fig. 14e); spermatheca with basal bulb wide basally, strongly constricted at apical filament, outer bulb longer than basal bulb plus filament.

*Holotype*: ♀, JAMAICA: St. Andrew: Kingston, 20-II-1936, Sta. 184, Chapin and Blackwelder (MCZ). The type also bears the label: 25527, MCZ Paratype, jamaicensis.

*Nomenclatural Note*.— . This specimen was labelled a paratype and entered into the MCZ type book as “25527, *Lachnophorus jamaicensis* Darl., 1 para-Carabidae.” There is no evidence of a manuscript description of this species, nor is there any evidence of a specimen labelled as holotype either in the MCZ or NMNH (T.L. Erwin, pers. comm.). As such, I retain Darlington’s specific epithet, validly describe the species, and place the taxon in *Anchonoderus* based on the generic diagnosis.

#### *Anchonoderus subaeneus* Reiche

*Anchonoderus subaeneus* Reiche, 1843: 40; Bates, 1883: 153; Csiki, 1931: 888.

*Diagnostic Combination*.— Head elongate, eyes strongly convex; pronotum narrow (Fig. 15a), basal width 0.4X width at humeral angles; dorsal elytral impressions obsolete, difficult to discern from punctations of secondary setation; elytral striae with strong punctures in basal 0.50; 17–18 umbilicate punctures in or adjacent to eighth stria anterad obsolete subapical situation; elytral apex rounded; length 6.8–7.6 mm.

*Male Genitalia*.— Aedeagal median lobe straight, narrow, with a rounded knob apically (Fig. 15b); internal sac globose, with fine spicules apically; V-shaped sclerite on base of membranous dorsum of median lobe.

*Type*.— Type not found in MNHP. Bates’ determined material was examined in BMNH, and this serves as basis for species interpretation.

*Extralimital Distribution*.— Recorded from Guatemala and Colombia (Bates, 1883). ECUADOR (5, BMNH). FRENCH GUIANA: Cayenne (1, BMNH). GUATEMALA: Guatemala City (1, BMNH). PANAMA: San Feliz (1, BMNH). West Indian Records. GUADELOUPE: Deux Mamelles, 24-II-1973 (4, IREC); Duclos (Htrs.), 22-V-1978 (1, IREC).

#### *Anchonoderus subtilis* Bates

*Anchonoderus subtilis* Bates, 1871: 33; Bates, 1883: 153; Csiki, 1931: 889; Darlington, 1934: 98; Darlington, 1941: 13.

*Diagnostic Combination*.— Head moderately elongate, eyes strongly convex; pronotum broad (Fig. 15c), basal width >0.50X width at humeral angle; dorsal elytral impressions obsolete, difficult to discern amidst secondary setation; elytral striae smooth, weakly punctate in basal 0.50; 17–18 umbilicate punctures in or adjacent to eighth stria anterad obsolete subapical situation; elytral apex angulate, margin laterad apex straight; length 6.6–7.7 mm.

*Male Genitalia*.— Median lobe of aedeagus straight, broadly rounded at apex (Fig. 15e); internal sac with expansion just apicad apex of median lobe, two rows of large spines on ventral surface about 0.50 distance to apex, and broad field of fine

spicules; V-shaped sclerite at base of membranous dorsum of median lobe.

*Female Reproductive Tract.*— Apical gonocoxite with two lateral and one dorsal ensiform setae (Fig. 15d); basal gonocoxite with apical fringe of 11–12 setae; spermatheca with small basal bulb bearing long apical filament, apical bulb larger than basal.

*Type.*— LECTOTYPE ♀ hereby designated: Guatemala; *Anchonod. subtilis* Bates; H.W. Bates, Biol. Cent. Amer.; LECTOTYPE (purple border); LECTOTYPE, *Anchonoderus subtilis* Bates, det. George E. Ball, 1972 (MNHP).

*Extralimital Distribution.*— Cordova and Paro del Macho, Veracruz, Mexico, and Guatemala (Bates, 1883), north to Nuevo Leon, vicinity of Linares (unpubl. data).

West Indian Records. CUBA: Las Villas: Soledad, Cienfuegos, VI-1929 (1, MCZ), 2-12-VIII-1934 (29, MCZ), IV-1936 (39, MCZ), V-1936 (2 MCZ); Trinidad Mtns., San Blas and vic., 9-V-1936 (3, MCZ). Oriente: Aguadores, 6-VI-1936 (1, MCZ); Maisi, 17-VII-1936 (2, MCZ); coast below Pico Turquino, 26-30-VI-1936 (3, MCZ); Sierra Maestra, VI-1965 (1, MCZ); Upper Ovando R., 1-2000' el., 17-20-VII-1936 (7, MCZ). Pinar del Rio: Rangel Mtns., ~1500' el., 24-VIII-1936 (4, MCZ). JAMAICA: Portland: Comfort Castle, Rio Grande R., 170 m el., riparian gravel, 7-9-V-1985 (2, UASM), 16-V-1985 (1, UASM). St. Catherine: Rio Cobre 5 mi. above Spanishtown, 29-VIII-1934 (39, MCZ). St. Thomas: Bath Fountain, 18-VII-1961 (1, IOJK).

### *Euphorticus* G. Horn

*Euphorticus* Horn, 1881: 144.

*Type species.*— *Lachnophorus pubescens* Dejean by original designation.

*Generic Diagnosis.*— Apical maxillary palpomere fusiform, with sparse long setae (Fig. 11c), penultimate palpomere setose; body with pelage of erect golden secondary setae; pronotum lacking basal seta, one large lateral seta, and four to five smaller lateral setae set in lateral margin, all setae stouter than secondary setation; elytra lacking dorsal impressions associated with third interval; elytral striae strongly punctate and discontinuous basally, smooth and complete apically.

### *Euphorticus pubescens* (Dejean)

*Lachnophorus pubescens* Dejean, 1831: 30.

*Euphorticus pubescens*, Horn, 1881: 144; Bates, 1883: 156; Blatchley, 1910: 137; Csiki, 1931: 891; Darlington, 1941: 13.

*Lachnophorus niger* Gory, 1833: 245.

*Lachnophorus laevicollis* Reiche 1843: 180.

*Lachnophorus pubescens* var. *aeneolus* Bates, 1883: 156.

*Diagnostic Combination.*— A shiny black ant-like lachnophorine, length 4.1–4.9 mm; antennomeres 2–4 rufo-testaceous, scape and apical segments darker with a smoky cast; microsculpture of dorsum greatly reduced, surface shiny; leg bases rufo-testaceous, femora piceous.

*Male Genitalia.*— Median lobe of aedeagus with short rounded apex, shaft convex ventrally (Fig. 16a); internal sac globose, constricted basally, lacking spines

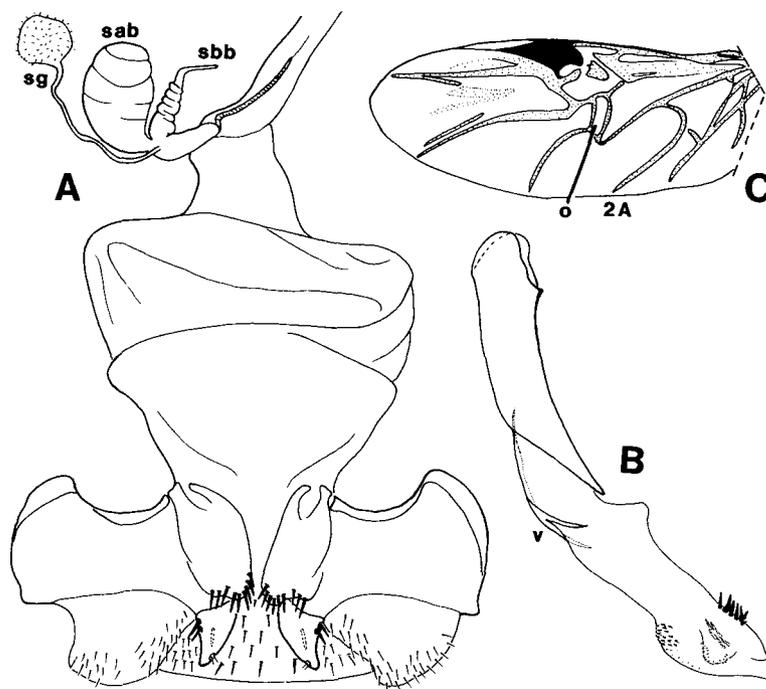


Figure 13. *Anchonoderus darlingtoni*, new species: A; female reproductive tract, ventral view; B, male aedeagal median lobe with everted inner sac, dextro-ventral view; C, flight wing. sab-spermathecal apical bulb; sbb-spermathecal basal bulb; sg-spermathecal gland; 2A -- 2nd anal vein; O - oblongum cell; v-vee-shaped sclerite of median lobe dorsal membrane.

or spicules, with two strap-like dorsal sclerites.

*Female Reproductive Tract.*— Apical gonocoxites pointed apically, bearing two lateral and one dorsal ensiform setae (Fig. 16b); basal gonocoxite with apical fringe of six setae; spermatheca with smaller basal bulb bearing apical filament, and longer gradually widening outer bulb, which is bluntly rounded at apex.

*Type.*— I could not find Dejean specimens of this species in the Chaudoir collection (MNHP). My interpretation of this widespread species is based on specimens in North American collections, including those below.

*Habits.*— *E. pubescens* occurs on peaty shores of waterways in the southeastern United States. At a pond 4.1 miles west of Bonifay, Washington Co., Florida, it was taken with *Calybe sallei* and the fire ant, *Solenopsis geminata* (F.) (ant determination by W.L. Brown, Jr.).

*Extralimital Distribution.*— Specimens examined from the southeastern United States, eastern Mexico, Honduras, Colombia, and Trinidad (CUIC and MCZ

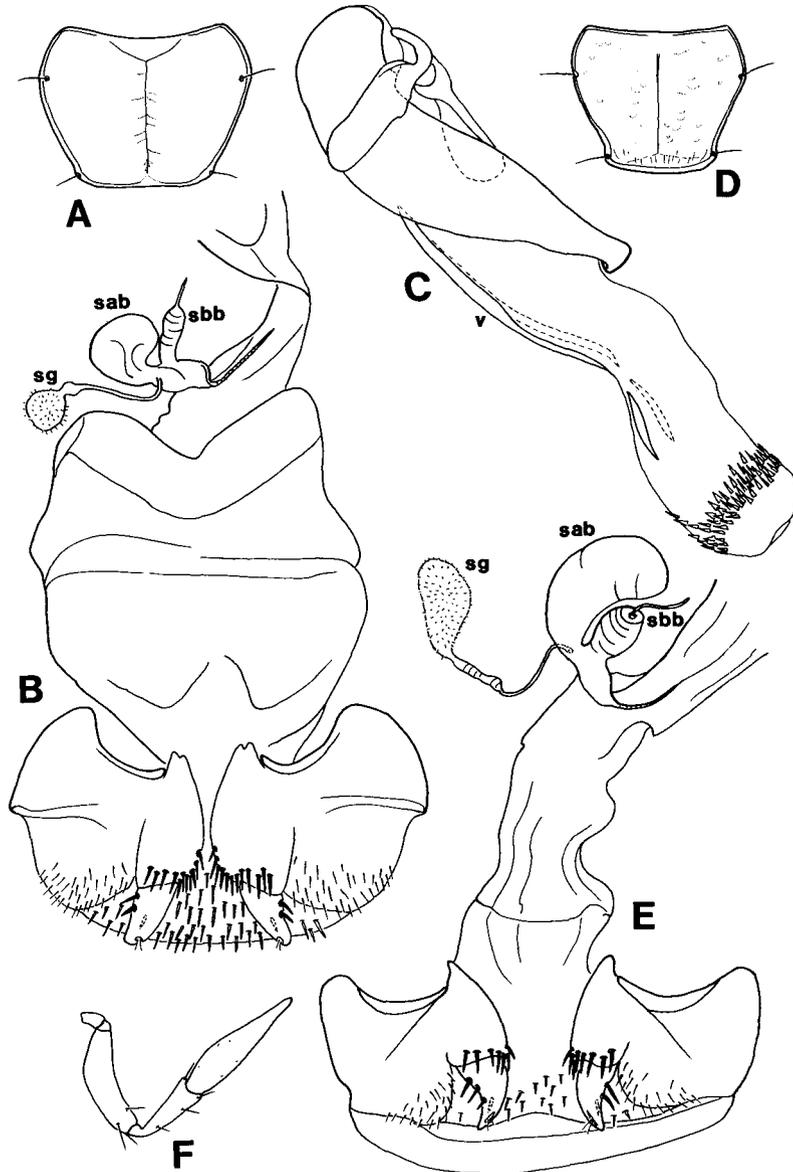


Figure 14. A, *Anchonoderus humeralis* Bates, pronotum; B, *A. humeralis*, female reproductive tract, ventral view; C, *A. humeralis*, male aedeagal median lobe and parameres with everted inner sac, dextro-ventral view; D, *Anchonoderus jamaicensis*, new species, pronotum; E, *A. jamaicensis*, female reproductive tract, ventral view; F, *A. jamaicensis*, maxillary palp, ventral view. sab-spermathecal apical bulb; sbb-spermathecal basal bulb; sg-spermathecal gland; v-vee-shaped sclerite of aedeagal median lobe dorsal membrane.

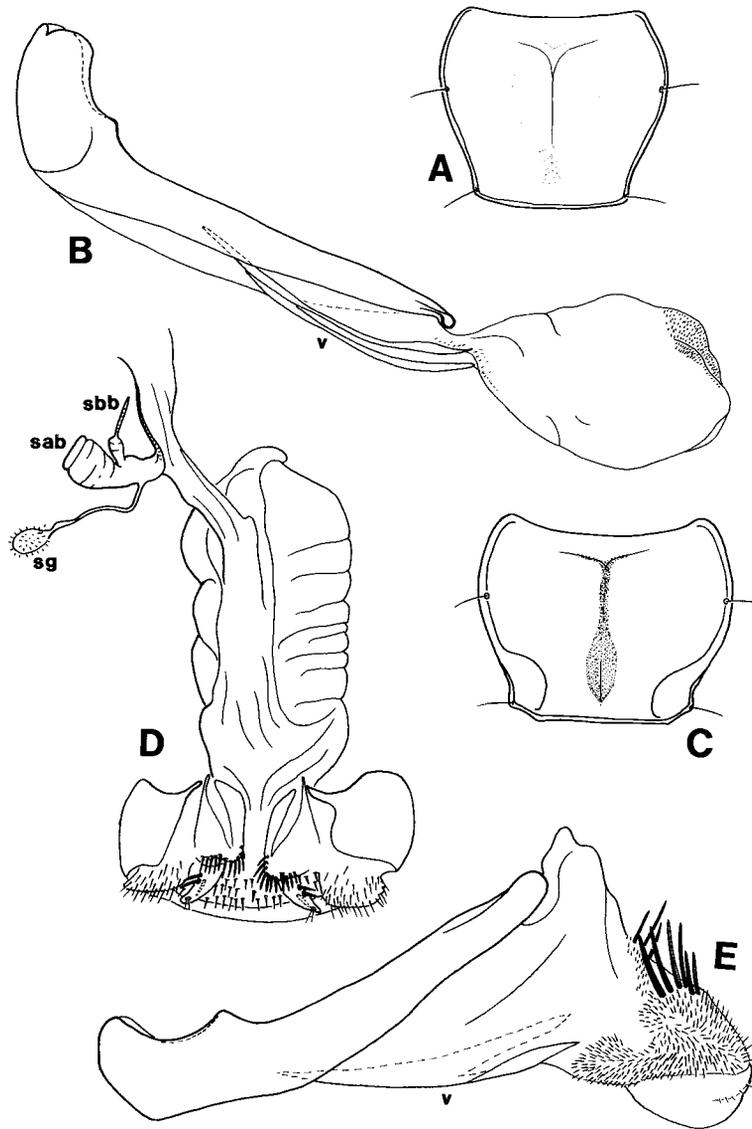


Figure 15. A, *Anchonoderus subaeneus* Reiche, pronotum; B, *A. subaeneus*, male aedeagal median lobe with everted inner sac, dextro-ventral view; C, *A. subtilis* Bates, pronotum; D, *A. subtilis*, female reproductive tract, ventral view; E, *A. subtilis*, male aedeagal median lobe with everted inner sac, dextro-ventral view. sab-spermathecal apical bulb; sbb-spermathecal basal bulb; sg-spermathecal gland; v-vee-shaped sclerite of aedeagal median lobe dorsal membrane.

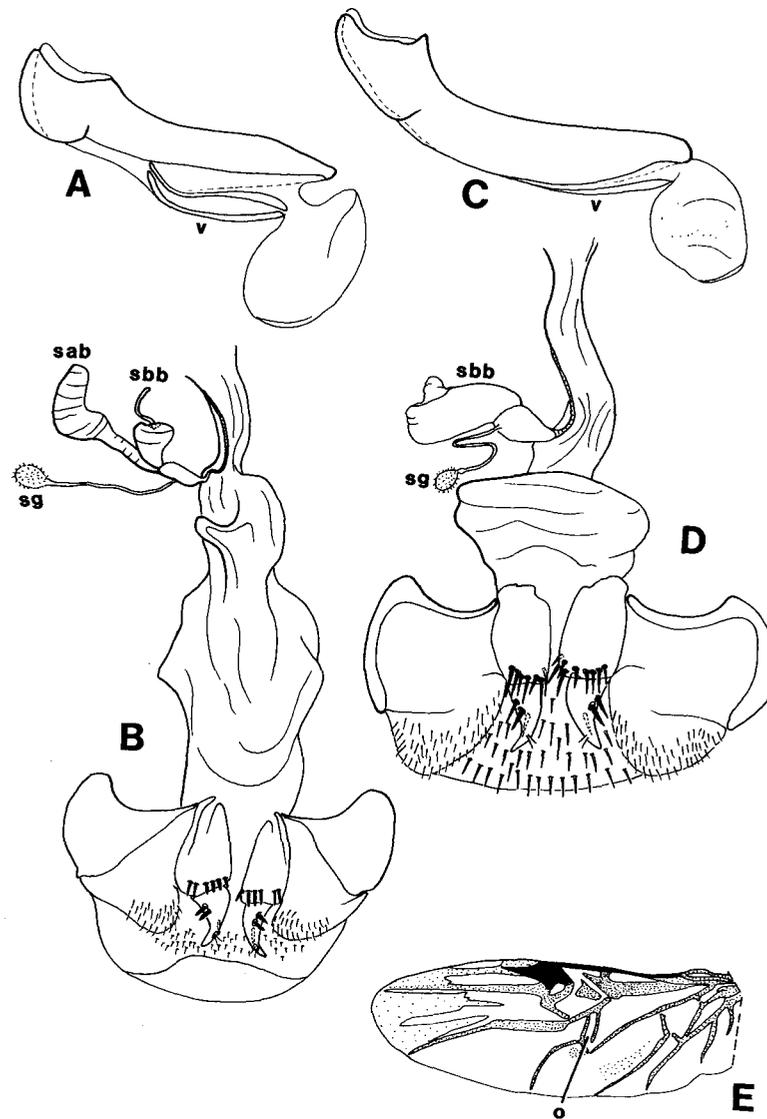


Figure 16. A, *Euphorticus pubescens* Dejean, male aedeagal median lobe with everted inner sac, dextro-ventral view; B, *E. pubescens*, female reproductive tract, ventral view; C, *Lachnophorus leucopterus* Chevrolat, male aedeagal median lobe with everted inner sac, dextro-ventral view; D, *L. leucopterus*, female reproductive tract, ventral view; E, *L. leucopterus*, flight wing. o - oblongum cell; sab-spermathecal apical bulb; sbb-spermathecal basal bulb; sab-spermathecal gland; v-vee-shaped sclerite of aedeagal median lobe dorsal membrane.

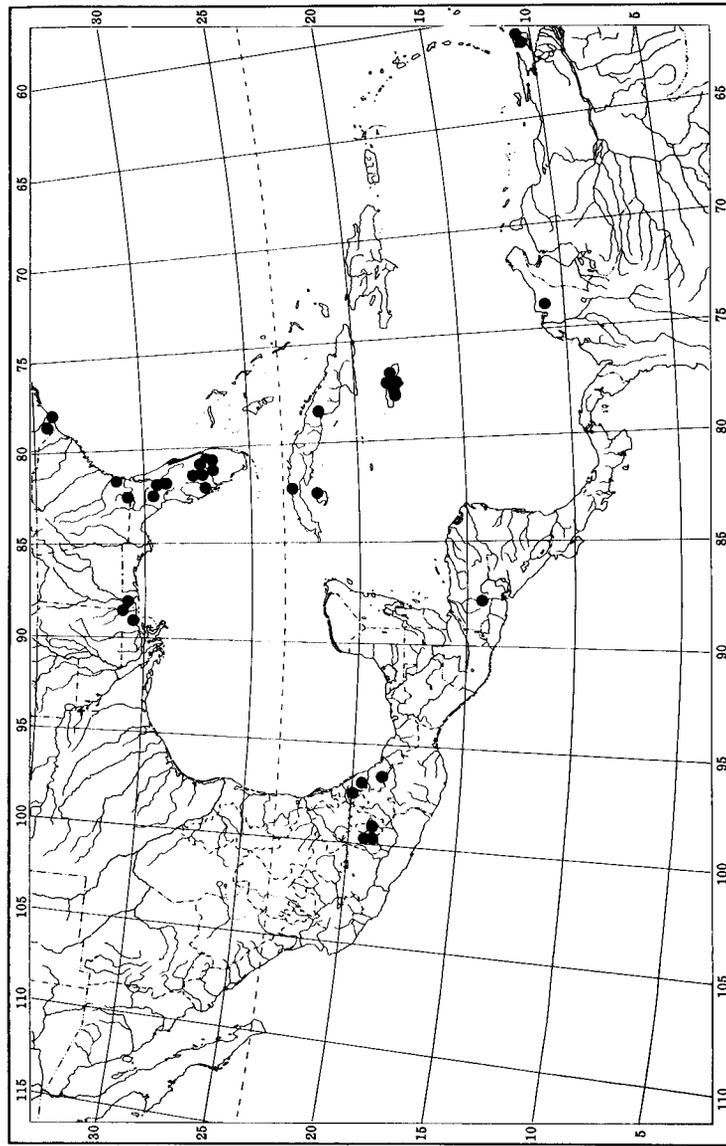


Figure 17. Distribution records of *Euphoriticus pubescens* Dejean for which specimens have been examined.

records, Fig. 17). Reported from Guatemala, and the Amazon south to Santa Catarina, Brazil (Bates, 1883), and Colombia and French Guiana (Csiki, 1931).

*West Indian Records.* CUBA: Camagüey: Baragua, 10-XI-1926 (2, MCZ), 16-X-1927 (1, MCZ). Habana: Santiago de las Vegas, 2-VII-1930 (1, MCZ). Isla de Pinos: Nueva Gerona, 18-I-1967 (1, IZPW). JAMAICA: Clarendon: nr. Kellits, Mason R. Field Sta., 700 m el., treading *Typha* marsh, 30-V-1985 (3, UASM); Mason R., 16-II-1984 (3, IOJK). Portland: Hope Bay W Port Antonio, 3 m el., treading *Typha* marsh, 18-V-1985 (1, UASM). St. Ann: Ocho Rios, 20-24-VIII-1934 (18, MCZ). St. Elizabeth: Frenchman at Black R., 0 m el., *Typha* marsh, 2-VI-1985 (9, UASM); Maggoty, 7-III-1976 (1, IOJK).

#### *Lachnophorus* Dejean

*Lachnophorus* Dejean, 1831: 28.

*Lachnophorus* (*Aretaonus*) Liebke, 1936: 461.

*Type Species.*— Of *Lachnophorus*, *L. pilosus* Dejean by Chenu (1851); of *L. (Aretaonus)*, *L. elegantulus* Mannerheim by original designation.

*Nomenclatural Note.*— Csiki (1931) places *Stigmaphorus* Motschulsky as a junior synonym of *Lachnophorus*. The description of *Stigmaphorus tessellatus* Motschulsky (1864) directly follows a key to *Lachnophorus* species, but based on Motschulsky's (1862) diagnosis of *Stigmaphorus*, this genus should not be considered the same as *Lachnophorus*.

*Generic Diagnosis.*— Apical maxillary palpomere fusiform to strongly inflated, subulate, densely setose basally to entirely setose (Fig. 11d), penultimate palpomere setose; body with secondary setation of two setal types – abundant anteriorly recurved setae, and intermittent erect setae; pronotum lacking basal seta, bearing one lateral seta; elytral dorsal impressions of third interval foveate, associated setae indiscernible from secondary setation; elytral striae continuous, punctate basally, smooth apically.

#### *Lachnophorus leucopterus* Chevrolat

*Lachnophorus leucopterus* Chevrolat, 1863: 198; Csiki, 1931: 890; Darlington, 1934: 98; Darlington, 1941: 13.

*Lachnophorus* (*Aretaonus*) *leucopterus*, Liebke, 1936: 463.

*Diagnostic Combination.*— Vertex of head with longitudinal wrinkles, area between wrinkles with strong isodiametric microsculpture; scape testaceous ventrally, smoky metallic green dorsally, antennomeres 2–4 rufo-testaceous, outer segments piceous; head and pronotum metallic cupreous-green; elytra pale creamy white with white humeral macula, white discal macula at basal 0.33 on 6th interval, and two oblique sequences of white maculae extending from 0.66 length at margin, to 0.90 length at suture, dorsal elytral impressions at lateral umbilicate punctures darker; length 4.1–4.9 mm.

*Male Genitalia.*— Median lobe of aedeagus bluntly rounded apically (Fig. 16c), internal sac globose, not spinose; two strap-like sclerites at base of dorsal membranous area.

*Female Reproductive Tract.*— Apical gonocoxite pointed apically, bearing two lateral and one dorsal ensiform setae (Fig. 16d); basal gonocoxite with apical fringe of seven to nine setae; spermatheca with a sclerotized base bearing the gland duct, and a single bulb that possesses a short broad apical filament.

*Type.*— Lectotype ♀ hereby designated: [Cuba] Sto. Dgo., Sallé; Lachnophorus, leucopterus, Chev. 1817; Chevrolat, Carabidae, Fr. V.d. Poll, Pres. 1909, E., B.P. Boulton; Type Col: 150 1/2, Lachnophorus, leucopterus Chevr., Hope Dept. Oxford; Lectotype, Lachnophorus, leucopterus, Chevrolat, J.K. Lieberr 1987.

*Habits.*— *L. leucopterus* is found along the gravel shores of creeks. At Rio Cain near San Germán, Puerto Rico, it occurred on bare gravel banks after recent flooding, where it was the only carabid species observed. On the Rio Guanajibo near Sabana Grande, Puerto Rico, it was taken along with beetles of the genus *Bembidion*. It is active in bright sunlight.

*Distributional Records.*— Endemic to the West Indies, with the following records.

CUBA: Las Villas: Soledad, Cienfuegos, Arimao R., 19-X-1926 (12, MCZ), 31-X-1926 (3, MCZ), 3-XII-1926 (4, MCZ), 13-XII-1926 (2, MCZ), VI-1929 (1, MCZ), 2-12-VIII-1934 (10, MCZ), IV-1936 (3, MCZ); Trinidad Mtns., 600–2000' el., VI-1929 (2, MCZ), Hanabanillo Falls, 30-IV-1936 (1, MCZ). Oriente: Aguadores, 6-VI-1936 (2, MCZ); Baracoa, 12-VII-1936 (4, MCZ); Cauto el Cristo (Cauto R.), 12-VIII-1936 (4, MCZ); Daiquiri, 30-V-1936 (3, MCZ); Hongolosongo, 7-VII-1936 (1, MCZ); Imias, 24-VII-1936 (5, MCZ); Maisi, 17-VII-1936 (1, MCZ); Marcata, Rio Bayamo, 1913 (5, MCZ); Upper Ovando R., 1–2000' el., 17-20-VII-1936 (1, MCZ). Pinar del Rio: San Diego, 18-V-1931 (3, MCZ); Sierra de Rangel, XII-1933 (4, MCZ).

DOMINICAN REPUBLIC: Distrito Nacional: San Cristobal, 18-IX-1938 (1, MCZ), 5-IX-1966 (15, TAMU); Villa Altigracia, VII-1938 (1, MCZ). La Vega: Constanza to Jarabacoa, 2–4000' el., VIII-1938 (4, MCZ). Puerto Plata: 25 km by road S Puerto Plata, VI-1938 (7, MCZ). Santiago: San José de las Matas, 1000–2000' el., VI-1938 (3, MCZ); S of Santiago, fthills Cord. Cent., VI-1938 (2, MCZ).

HAITI: Artibonite: Ennery, nr. 1000' el., 6-11-IX-1934 (23, MCZ). Ile de la Gonave: La Source, 15-II-1983 (7, RLDC). l'Ouest: Port au Prince, R. Froide, 3-X-1934 (2, MCZ). Sud: Camp Perrin, 1-III-1983 (14, RLDC), nr. 1000' el., 8-27-X-1934 (2, MCZ), Grand R. du Sud, 20-II-1983 (51, RLDC); Massif de la Hotte NE, fthills 2–4000' el., 10-24-X-1934 (9, MCZ).

JAMAICA: Wag Water, 6-III-1958 (3, BMNH). Clarendon: Rock R. 2 mi. NE Chapelton, 23-XII-1946 (2, IOJK). Portland: Blue Mtns., nr. 4500' el., 13-20-VIII-1934 (27, MCZ); Comfort Castle, Rio Grande, 170 m el., riparian gravel, 7-9-V-1985 (1, UASM), 16-V-1985 (2, UASM); nr. Windsor, Rio Grande, 40 m el., 18-V-1985 (7, UASM). St. Andrew: Castleton Bot. Gard. (2, MCZ); Hope R., 26-V-1908 (28, BMNH), nr. Gordontown, 213 m el., 7-XII-1985 (9, UASM); Kingston, 14-II-1928 (4, MCZ), 26-IV-1937 (1, UMMZ); St. Peter's Yallah's R., 850 m el., gravel, 21-V-1985 (21, UASM). St. Catherine: Rio Cobre 5 mi. above Spanishtown, 29-VIII-1934 (3, MCZ); Spanishtown, 3-II (2, MCZ); nr. Zion Hill along Rio Pedro, 21-III-1954 (1, CNC).

PUERTO RICO: Caguas, 28-29-V-1915 (7, AMNH); Coamo Spgs., 11-II (9, AMNH), 17-19-VII-1914 (13, AMNH); Carite St. For. nr. Guavate, 650 m el., 1-V-1985 (7, CUIC); Las Vegas, 1-VI-1938 (2, MCZ); Maricao, 30-V-1938 (3, MCZ); Mayagüez, 21-23-VI-1915 (2, AMNH), 28-II-1931 (3, MCZ), 19-I-1936 (20, MCZ), 27-III-1936 (7, MCZ); Rio Cain at Hwys. 2 and 360, 3-V-1985 (12, CUIC); Rio Guanajibo at Sabana Grande, 100 m el., 4-V-1985 (33, CUIC); San Germán, XII-1933 (1, MCZ); Viñoles, Rio S. Vicente, 15-III-1937 (1, MCZ).

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## APPENDIX 1

The primitive (0) and derived (1) states of the 57 characters used in the cladistic analysis of Odacanthitae are described below.

**Maxillary Palps**

1. 0– apical maxillary palpomere fusiform (Fig. 11a).  
1– apical maxillary palpomere inflated (Figs. 11b-d).
2. 0– apical maxillary palpomere moderately inflated (Fig. 11c).  
1– apical maxillary palpomere strongly inflated (Figs. 11b, d).
3. 0– apical maxillary palpomere glabrous or with very short setae (Fig. 11a).  
1– apical maxillary palpomere with at least some long setae (Figs. 11b-d).
4. 0– apical maxillary palpomere with sparse long setae (Fig. 11c).  
1– apical maxillary palpomere with dense covering of longer setae (Figs. 11b, d).
5. 0– penultimate maxillary palpomere glabrous except for apical ring of setae (Fig. 11a).  
1– penultimate maxillary palpomere setose over length (Figs. 11b-d).
6. 0– setae sparse over length of penultimate maxillary palpomere (Fig. 11c).  
1– setae dense over length of penultimate maxillary palpomere (Figs. 11b, d).

**Head**

7. 0– antennomeres 2–3 glabrous except for ring of apical setae  
1– antennomeres 2–3 setose over entire length.
8. 0– apical 4–antennomeres concolorous with basal segments.  
1– apical 4–5 antennomeres pale, basal segments contrasting, darker.
9. 0– neck not constricted.  
1– neck with distinct constriction, head pedunculate.
10. 0– mentum medial tooth present.  
1– mentum medial tooth absent.
11. 0– subgenal setae absent.  
1– subgenal setae present (Fig. 11).
12. 0– five or fewer subgenal setae each side of head.  
1– six or more subgenal setae each side of head.
13. 0– suture between mentum and gula fully formed and evident.  
1– suture between mentum and gula reduced to indistinct depression.
14. 0– suture between mentum and gula reduced but traceable.  
1– suture between mentum and gula absent.

**Body Surface**

15. 0– integument glabrous except for standard macrosetae.  
 1– integument with pelage of short setae in addition to standard macrosetae (Fig. 1).

**Pronotum**

16. 0– pronotal base straight (Figs. 1, 14a, d)  
 1– pronotal base recurved with a median lobe (Figs. 12a, b).  
 17. 0– laterobasal seta present.  
 1– laterobasal seta absent.  
 18. 0– a single lateral pronotal seta.  
 1– more than one seta along medio-lateral margin of pronotum.  
 19. 0– pronotal shape quadrate, median length less than or equal to width.  
 1– pronotal median length greater than maximum width.  
 20. 0– pronotum longer than wide.  
 1– pronotum two or more times as long as wide.  
 21. 0– pronotal shape cylindrical or quadrate.  
 1– pronotum with angulate side, outline hexagonal.

**Elytra**

22. 0– three setae in or adjacent to third elytral interval (Fig. 1).  
 1– dorsal elytral setae absent.  
 23. 0– three setae in or adjacent to third elytral interval.  
 1– more than three dorsal elytral setae.  
 24. 0– dorsal elytral impressions small, indistinct.  
 1– dorsal elytral impressions foveate (Fig. 1).  
 25. 0– dorsal elytral impressions moderately foveate (Fig. 1).  
 1– dorsal elytral impressions strongly foveate, very evident.  
 26. 0– elytra without transverse depression at basal 0.33.  
 1– elytra with transverse depression at basal 0.33.  
 27. 0– basal transverse elytral depression weak.  
 1– basal transverse elytral depression strongly developed, broad and deep.  
 28. 0– elytra with 11–16 macrosetae in 8th interval from base to subapical situation (Fig. 1).  
 1– elytra with 17–18 macrosetae in 8th interval from base to subapical situation.  
 29. 0– elytra concolorous, or with only subtle differences in color across surface.  
 1– elytra with distinct testaceous maculae on a darker ground color.  
 30. 0– elytra concolorous or nearly so.

- 1– elytra mostly testaceous with piceous maculae.
- 31. 0– sutural interval concolorous.
  - 1– sutural interval more testaceous than others.
- 32. 0– sutural interval lighter only at apex.
  - 1– sutural interval lighter over length.
- 33. 0– elytral apex broadly rounded.
  - 1– elytral apex truncate, angulate at subapical sinuation.
- 34. 0– elytral striae smooth.
  - 1– elytral striae punctate.
- 35. 0– elytral striae weakly to moderately punctate.
  - 1– elytral striae strongly punctate.

#### Flight Wings

- 36. 0– oblongum cell of flight wing present and complete (Figs. 10g, 13c).
  - 1– oblongum cell with incomplete venation, or absent (Fig. 16e).
- 37. 0– oblongum cell with incomplete venation (Fig. 16e).
  - 1– oblongum cell absent (Figs. 12f-h).
- 38. 0– wedge cell of flight wing present (Fig. 10g).
  - 1– wedge cell absent (Figs. 12f-h, 13c, 16e).
- 39. 0– first anal vein of flight wing present (Fig. 10g).
  - 1– first A vein absent (Figs. 12f-h, 13c, 16e).
- 40. 0– flight wings constantly macropterous.
  - 1– wings of some individuals brachypterous.

#### Male Protarsomeres

- 41. 0– tarsomeres 1–3 moderately broad.
  - 1– tarsomeres 1–3 broader, more robust, mediodorsal surface broadly flattened.

#### Pygidial Glands

- 42. 0– dorsal lobe of defense gland present.
  - 1– dorsal lobe absent.

#### Female Reproductive Tract

- 43. 0– basal bulb of spermatheca gradually narrowing to apex (Figs. 9b, 12c, d).
  - 1– basal bulb of spermatheca with apical filament narrower than base of bulb (Figs. 9c, d, 13a, 14b, e, 15d, 16b).
- 44. 0– basal bulb of spermatheca wide basally (*e.g.*, Figs. 8a, 13a).

- 1– basal bulb of spermatheca with narrow basal duct and apical reservoir (*e.g.*, Figs. 8c-d, 9a).
- 45. 0– apical bulb of spermatheca large (*e.g.*, Figs. 4d, 9c, 13a).
  - 1– apical bulb of spermatheca reduced (*e.g.*, Figs. 8, 9a, d, 16d).
- 46. 0– apical bulb of spermatheca reduced but evident (Fig. 9d).
  - 1– apical bulb of spermatheca absent (Fig. 16d).
- 47. 0– junction of spermathecal duct and common oviduct lacking distinct sclerite (Fig. 4d).
  - 1– junction of spermathecal duct and common oviduct with elongate sclerite (*e.g.*, Figs. 8, 9, 12c, d, 13a).
- 48. 0– sclerite at spermathecal duct base present (*e.g.*, Figs. 12c, d, 13a).
  - 1– sclerite at spermathecal duct base well-developed, U-shaped (*e.g.*, Figs. 8, 9a).
- 49. 0– more than 10 setae on penultimate gonocoxite (*e.g.*, Figs. 14b, 15d).
  - 1– from 5–9 setae on penultimate gonocoxite (*e.g.*, Figs. 13a, 14e).
- 50. 0– apical gonocoxite with two lateral ensiform setae (*e.g.*, Figs. 13a, 16b).
  - 1– apical gonocoxite with at least three lateral ensiform setae unilaterally or three or four on both sides (*e.g.*, Figs. 4d, 9b, 14e).
- 51. 0– apical gonocoxite pointed at tip (*e.g.*, Figs. 9c, d).
  - 1– apical gonocoxite rounded at tip (*e.g.*, Figs. 13a, 14b, e).

#### Male Genitalia

- 52. 0– aedeagal basal bulb complete, base closed (*e.g.*, Figs. 10a-f).
  - 1– basal bulb of aedeagus incomplete, base open (*e.g.*, Figs. 12e, 13b, 16a, c).
- 53. 0– aedeagal median lobe with curved shaft.
  - 1– aedeagal median lobe with straight shaft.
- 54. 0– aedeagal median lobe apex simple, acutely rounded (*e.g.*, Figs. 12e, 13b).
  - 1– aedeagal median lobe apex modified as a knob-like or hook-like projection (Figs. 10a-f, 15b).
- 55. 0– aedeagal inner sac without spines or tubercles (*e.g.*, Figs. 10a, 16a, c).
  - 1– aedeagal sac with sclerotized spines (*e.g.*, Figs. 10f, 15e).
- 56. 0– aedeagal median lobe shaft cylindrical (*e.g.*, Figs. 10a-f).
  - 1– aedeagal median lobe shaft membranous dorsally with V-shaped sclerite (*e.g.*, Figs. 13b, 15b, 16a).
- 57. 0– parameres subequal.
  - 1– ventral paramere reduced (*e.g.*, Figs. 10b-e).