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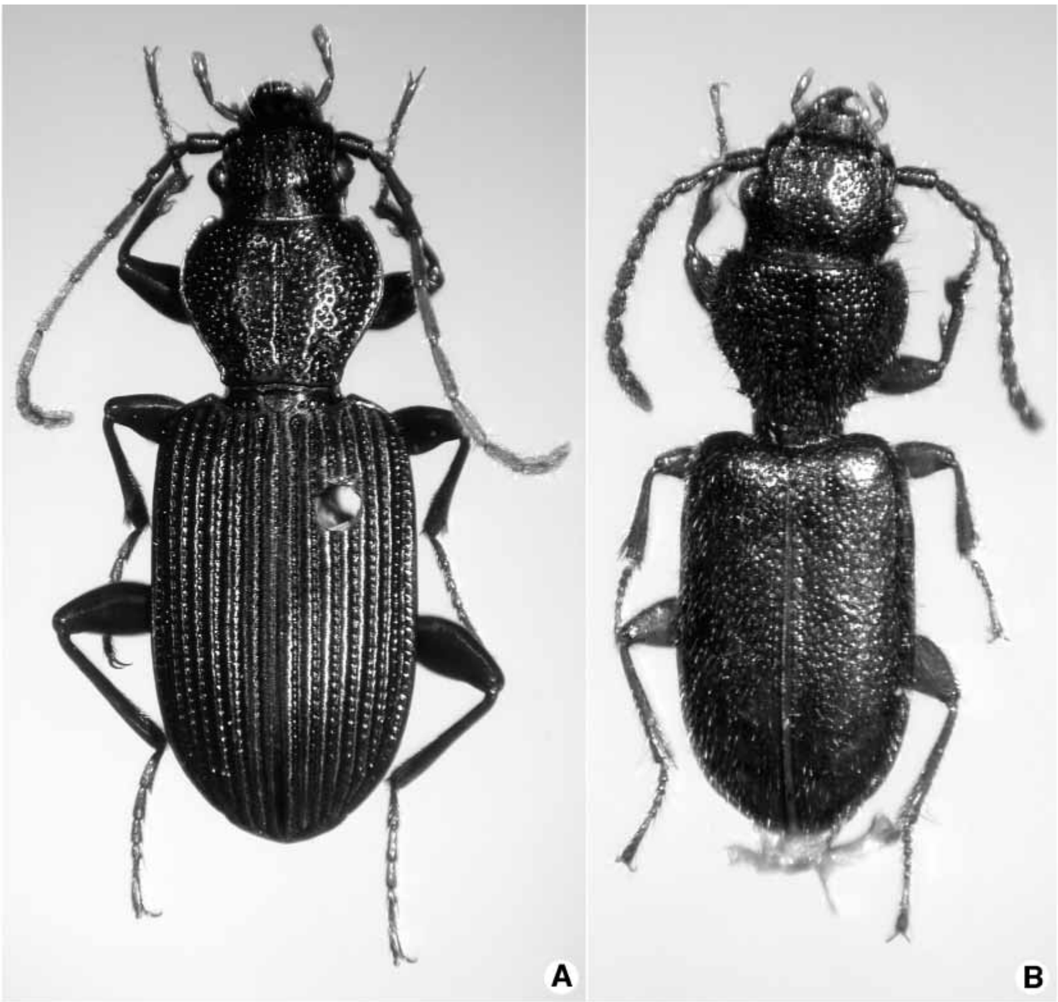

FIGURE 1. Photographs illustrating dorsal habitus: A, *Melaenus piger* Fabricius (SBL 7.33 mm); B, *Cymbionotum fernandezi*, new species (SBL 3.96 mm).

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Abstract

A taxonomic review of the tribe Melaenini *(sensu novo)*, this paper includes a classification, keys at all taxonomic levels, descriptions (tribe to species), re-rankings, and new synonymy. In total, two genera and 22 species (three of which are new) are treated.

Arrangement of taxa is in the following sequence, with junior synonyms and type localities of new species in parentheses, following name of the taxon. The Eastern Hemisphere genus *Melaenus* Dejean, 1831 includes *M. piger* (Fabricius, 1801), and *M. elegans* Dejean, 1831 (with *M. elongatus* Chaudoir, 1843, as a new junior synonym), which exhibits marked dimorphism in East Africa. The genus *Cymbionotum* Baudi di Selve, 1864 includes 20 species, arranged in two subgenera, as follows. The Western Hemisphere *Procoscinia*, **n. subg.** (type species, *C. fernandezi*, **n. sp.** [Zambrano, Bolivar, Colombia]), includes the type species and *C. negrei* Perrault, 1994. The Eastern Hemisphere subgenus *Cymbionotum (sensu stricto*) includes 18 species in three species groups, and three superspecies. The *basale* species group includes two species: *C. semirubricum* (Reitter, 1914) (new junior synonyms *Graniger aethiopicus* Alluaud, 1923, *C. minax* Andrewes, 1935, and *C. a. airense* Basilewsky, 1950), and *C. basale* (Dejean, 1831). The *semelederi* species group includes three species: *C. semelederi* (Chaudoir, 1851) (new junior synonyms, *Coscinia funerula* Fairmaire, 1885, *Cymbionotum luniferum* Andrewes 1935, and *Graniger houskai* Jedlička, 1951), *C. striatum* Reitter, 1894, and *C. mandli* Jedlička, 1963.

The *schueppelii* species group includes 13 species arrayed in three superspecies *schueppelii* superspecies, with three species: *C. schueppelii* (Dejean, 1825) (new junior synonym: *C. capicola rufofasciatum* Basilewsky, 1948), *C. rufotestaceum* (Fairmaire, 1893), and *C. capicola* (Péringuey, 1908); *fasciatum* superspecies, with five species: *C. helferi* (Chaudoir, 1850), *C. fasciger* (Chaudoir, 1852), *C. fluviale* Andrewes, 1935; *C. pictulum* (Bates, 1874), and *C. fasciatum* (Dejean, 1831) (new junior synonym: *Graniger volkonskyi* Colas, 1943); and *microphthalmum* superspecies, with five species: *C. namwala,* **n. sp.** (Namwala, Zambia), *C. candidum* Andrewes, 1935, *C. subcaecum,* **n. sp.** (Quetta, Pakistan), *C. transcaspicum* (Semenov, 1891) (new junior synonyms: *Graniger rufotestaceus* Pic, 1904 and *G. mesopotamicus* Csiki, 1929), and *C. microphthalmum* (Chaudoir, 1876). The taxonomic status of *Graniger martin*i Bedel, 1908 remains doubtful, though it seems highly probable that it is conspecific with *C. capicola* (Péringuey), and is treated as such.

The elongate diverticulum of the spermathecal gland establishesmonophyly of the Melaenini. Major postulates regarding structural evolution is that, of the two genera, most of the character states of *Melaenus* are ancestral relative to the character states of *Cymbionotum*. However, for *Melaenus*, loss of a pair of supraorbital setae and the posteriolateral pronotal setae, and gain of a transverse microsculpture mesh pattern, fimbriate sculpticells, and markedly convex elytral intervals are apotypic features. Many diagnostic character states of *Cymbionotum* are reductions or losses: body size, antennal length, elytral striae, metathoracic wing veins, parameral setae, endophallic sclerite x and rami of the ovipositor. Gains are: general body setation, and microtrichiate paraglossae.Within *Cymbionotum*, prominent changes are: color reduction (loss of melanin from the cuticle); reduction of eyes; reduction of antennomere 2; reduction and increase in setal density and gain and subsequent loss of the clypeal tooth; extension of the pronotum posteriad; and developent and subsequent loss of a beaded posterior margin of the pronotum.

Ecologically, change was probably from rain forest tropical vegetation zone to dry forest, to grassland, marginally to desert/semi-desert, and at least one reversion to the rain forest vegetation zone. Altitudinal change was from lowland to highland. Chorologically, the most striking feature within the extant melaenines is evidence for pre-Cretaceous (or early Cretaceous) origin of both genera, and then evidence of Plio-Pleistocene differentiation from the many allopatric ranges of closely related species. But the distribution patterns provide no evidence about differentiation between the Cretaceous Period and Miocene Epoch. Each of the Neotropical, Afrotropical, Palaearctic, and Oriental Regions has two or more precinctive species, indicating that each region has provided one or more refugia, and hence the isolation required to make allopatric speciation possible.

Key words: Coleoptera, Carabidae, Melaenini, classification, dimorphism, Western Gondwana, Neotropical Region, Afrotropical Region, Palaearctic western Asia, Oriental Region, dispersal, vicariance, superspecies

Introduction

Continental carabid faunas are comprised primarily of precinctive species that are included in indigenous genera. In turn, these taxa of lower rank are members of tribes, most of which are distributed through at least several continents, more or less conterminous at their borders. Thus, most tribes inhabiting South America are residents also of the adjacent North American continent. But five South American carabid tribes (Hiletini, Siagonini, Apotomini, Peleciini and Dryptini) are exceptional, being represented elsewhere on continents widely separated by ocean basins from South America, but not present in the temperate parts of the more proximal North American continent. One such group of tribes was designated by Jeannel (1942: 161) as "Inabresian" (an adjective derived from the first letters of India, Africa and Brazil). Reichardt (1979) discussed the Inabresian tribes known to him. Then Perrault (1994) added to Reichardt's list the Cymbionotini, with a description of the Venezuelan *Cymbionotum negrei* Perrault.

The rather perfunctory description of that species was based on three specimens, found by Perrault in the extensive carabid holdings of the late Jacques Nègre, collected in 1933 from two Venezuelan localities. Because all of the other species of *Cymbionotum* were known only from areas on the eastern side of the Atlantic basin, the collector of the few Venezuelan specimens was not well known, and the author of *C. negrei* did not make adequate comparisons of the new species with previously described species (Perrault was mortally ill at the time, and the paper describing this species was one of the last that he wrote), the record was regarded as suspect. That is, the specimens putatively from and precinctive in Venezuela, might very well have been mislabeled specimens of a previously described Eastern Hemisphere species, or of a previously unknown species from a locality in the Eastern Hemisphere and accidentally introduced into the Western Hemisphere.

Several years ago, we received for identification from our Colombian colleagues, Fernando Fernandez and Claudia Martinez, several specimens of *Cymbionotum* that had been collected at light in the Rio Magdalena valley of northern Colombia. This discovery established that *Cymbionotum* was indeed in South America and such confirmation seemed worthy of recording in a published note.

But the question of whether or not the species was introduced from the Old World remained unanswered. The fact that the Colombian specimens were collected in a plantation of a tree species (white teak, *Gmelina arborea* Roxb.), imported from the Oriental Region and grown in Colombia for commercial exploitation, seemed only to increase the probability of a recent and accidental introduction. So, rather than offering a simple report of this new Colombian record we decided to attempt to determine whether the South American occurrence of *Cymbionotum* was the result of a natural, presumably much older, event (Perrault's explicit assertion), or if it represented an accidental man-mediated introduction.

For many taxa, making such a determination would not be unduly complicated, involving principally consultation of a recent revision, or of some regional faunal work. But for *Cymbionotum*, the previous general treatment was published more than a century ago (Chaudoir 1876) and more than half of the known species had been described after that date. Most of those descriptions (references given in the species treatments below) were single species treatments in more general papers treating regional carabid assemblages. Andrewes (1935) treated the known Oriental species, but because of taxonomic difficulties with recognition of *Cymbionotum* species, his work proved difficult to interpret in the absence of adequate comparative material.

A preliminary investigation of the literature treating *Cymbionotum* indicated difficulties that extended to higher taxonomic levels, involving composition of the tribe to which this genus belonged. Reluctantly, we found ourselves drawn into a taxonomic vortex from which we have emerged with the offering of clarifications on the relationships of *Cymbionotum* Baudi di Selve to *Melaenus* Dejean and treatments for all of the species of the two genera known to us. Further, the evidence presented supports Perrault's assertion that *Cymbionotum* is an old native resident of South America and that *C. negrei* is a valid species. We are pleased to make this acknowledgement and dedicate this taxonomic treatment to the memory of Georges Perrault.

Material, Methods and Terms

Material

This study is based on examination of approximately 1400 specimens of Melaenini, representing all known species, including holotypes or lectotypes (valid names and junior synonyms) of all but *Melaenus piger* Fabricius, and *Graniger martini* Bedel. Few specimens were available in our collection, i.e., the Strickland Museum, Department of Biological Sciences, University of Alberta (UASM). Most of the material was borrowed from, or deposited in, the following institutions, noted in the text by the associated codens. Names of curators are included in parentheses.

ACCT	Achille Casale Collection, Museo Regionale di Scienze Naturali, Via Giolitti, 36-I-10123 Torino, Italy
BMNH	Department of Entomology, British Museum (Natural History), Cromwell Road, London, England SW7 5BD (M. J. D. Brendell, S. J. Hine)
CASC	Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California, U.S.A. 94118 (D. H. Kavanaugh, R. Brett).
CMNH	Section of Entomology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania, U.S.A. 15213 (R. L. Davidson)
CNIF	Corporación Nacional de Investigación y Fomento Forestal, Bogotá D. C., Colombia (Helena Moreno)
HNHM	Zoological Department, Hungarian Natural History Museum, Zirc, Rakoczi Ter 1, H-8420, Hungary (O. Merkl).
IAVH	Instituto Alexander von Humboldt, Villa de Leyva, Colombia (F. Fernandez, C. Martinez).
MNHP	Museum National d'Histoire Naturelle, Departement de Systématique USM n°601, Entomologie Case Postale n° 50F-75231 Paris cedex 05, France (T. Deuve).

MRAC	Section d'Entomologie, Musee Royal de l'Afrique Centrale, Leuvensesleenweg 13, B-3040 Tervuren, Belgium (M. DeMeyer)
MRSN	Museo Regionali di Scienze Naturali, Via Giolitti 96, Torino, 10123, Italy (M. Daccordi, M. Giachino).
NHMW	Naturhistoriches Museum Wien, Postfach 417, Burgring 2, 1040 Wien, Austria (H. Schönmann).
NMPC	Department of Entomology, National Museum (Natural History), 148 00 Praha 4, Kunratice 1, Czech Republic (J. Jelínek).
OXUM	Hope Entomological Collections, University Museum, Parks Road, Oxford OXI 3PW, United Kingdom.
PMGC	Pier Mauro Giachino Collection, Museo Regionale di Scienze Naturali, Via Giolitti, 36-I-10123 Torino, Italy
RFFC	R. F. F. L. Felix Collection, Hazelaariaan 51, 5056 XP, Beakel Enschot, Netherlands.
SAMC	Entomology Department, South African Museum, P.O. Box 61, Queen Victoria Street, Cape Town 8000, Republic of South Africa (M. Cochrane).
UNCB	Insect Collection, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá D.C., Colombia
USNM	Department of Entomology, United States National Museum of Natural History, Smithsonian Institution, Washington, D. C., U.S.A. 20560 (T. L. Erwin, W. Steiner).
ZMAS	Zoological Museum, Academy of Science, Universitetskaya, Naberzhnayal, B-164, St. Petersburg, Russia (B. Kataev).
ZSMC	Zoologische Staatssamlung. Münchhausenstrasse 21, D-8000 München 60 Germany (M. Baehr).

Methods

We used an exemplar approach in characterizing the tribe and genera; that is, for study of features requiring detailed dissection and use of SEM illustrations, we relied on a few specimens that we regarded as typical. For the structural features of *Melaenus* illustrated by SEM figures, we used a few specimens of *M. piger*. For the internal female genitalia we dissected specimens of *Melaenus piger*, *M. elegans* Dejean, *Cymbionotum fernandezi*, **n. sp.**, *C. basale* Dejean and *C. microphthalmum* Chaudoir. In general the dissections matched the figures of *M. elegans* and *C. basale* prepared by Deuve (1993: 148, Figs. 222, 223). Only the female internal genitalia of *C. fernandezi* were drawn, primarily to provide a more detailed representation of the long convoluted spermathecal diverticulum, which *contra* Deuve (loc. cit.) was present also in the specimens of *Melaenus*. Measurements and ratios were reported without statistical analysis because sufficient population samples of adequate size did not support more detailed consideration.

Measurements. Measurements of external body parts were made with an ocular micrometer in a Wild M5 stereoscopic microscope at 25X and 50X. Measurements and abbreviations used for them in the text are:

Length of head (**HL**)—linear distance from anterior margin of clypeus to posterior transverse sulcus;

Width of head (**HW**)—maximum distance across head, including eyes;

Width of vertex (**VW)**—maximum distance across head between inner margins of eyes;

Length of eye (**OL**) linear maximum distance between anterior and posterior margins, measured in lateral aspect;

Length of antennomeres 2 (pedicel—**A2L**) and 3 (first article of flagellum—**A3L**)**-** linear distance from basalmost constriction to apex, in dorsal aspect;

Length of pronotum (**PL**)—linear distance from anterior to posterior margin, measured along the midline;

Width at anterior margin ("apex") of pronotum (**PWA**)—linear transverse distance between both anteriolateral angles;

Maximum width of pronotum (**PWM**)—greatest linear transverse distance;

Width at posterior margin ("base") of pronotum (**PWB**)—linear transverse distance between both posteriolateral angles;

Length of elytra (**EL**)—linear distance from basal ridge to apex of longer elytron (if the pair of elytra is asymmetrical), measured along the suture;

Width of elytra (**EW**)—greatest linear transverse distance across both elytra;

Standardized Body Length (**SBL**), used as an index of overall size, is the sum of HL, PL, and EL (Table 3). Width of elytra (**EW**) represents maximum body width (Table 4);

Values for various ratios (more or less diagnostic for species groups or species) were computed, using the measurements above (Tables 5–11).

HW/PWM—an approximate measure of relative pronotal width, with higher values indicating a relatively narrower pronotum (Table 5);

PL/EL an approximate measure of relative elytral length, with higher values indicating longer elytra (Table 6);

PL/PWM—an approximate measure of relative pronotal width, with higher values indicating a relatively narrower pronotum (Table 7);

VW/HW—an expression of eye size or form, with higher values indicating smaller eyes (Table 8);

PWB/PWA—a within-tagma measure of relative basal width, with higher values indicating a relatively wider posterior margin (Table 9);

A2L/A3L—a between-article measure of relative length of the two antennomeres, with higher values indicating a longer antennomere 2 (Table 11).

Because of the general paucity of material, data presented for size measurements and body ratios are variously composite with most values being derived from more than one population sample and the samples being from localities throughout a given species' range. For antennae, samples of 8–10 individuals were measured for one species from each subgenus and species group. We regard the numerical data as illustrative rather than definitive.

Quantitative aspects of integumental punctation and vestiture, characteristic of *Cymbionotum* adults, were expressed as density and setal length, and were measured for exemplar taxa from stereoscan micrographs (Table 1 and Figs. 2, 3).

TABLE 1. Classification of the Tribe Melaenini.

- Genus *Melaenus* Dejean
  - *M. piger* Fabricius
  - *M. elegans* Dejean
- Genus *Cymbionotum* Baudi di Delve
  - Subgenus *Procoscinia*, **new subgenus**
    - *C. fernandezi*, **new species**
    - *C. negrei* Perrault
  - Subgenus *Cymbionotum (sensu stricto)*
    - Species group *basale*
      - *C. semirubricum* Reitter
      - *C. basale* Dejean
    - Species group *semelederi*
      - *C. semelederi* Chaudoir
      - *C. striatum* Reitter
      - *C. mandli* Jedlièka
    - Species group *schueppelii*
      - Superspecies *schueppelii*
        - *C. schueppelii* Dejean
        - *C. rufotestaceum* Fairmaire
        - *C. capicola* Péringuey
      - Superspecies *fasciatum*
        - *C. helferi* Chaudoir
        - *C. fasciger* Chaudoir
        - *C. fluviale* Andrewes
        - *C. pictulum* Bates
        - *C. fasciatum* Dejean
      - Superspecies *microphthalmum*
        - *C. namwala*, **new species**
        - *C. candidum* Andrewes
        - *C. subcaecum*, **new species**
        - *C. transcaspicum* Semenov
        - *C. microphthalmum* Chaudoir

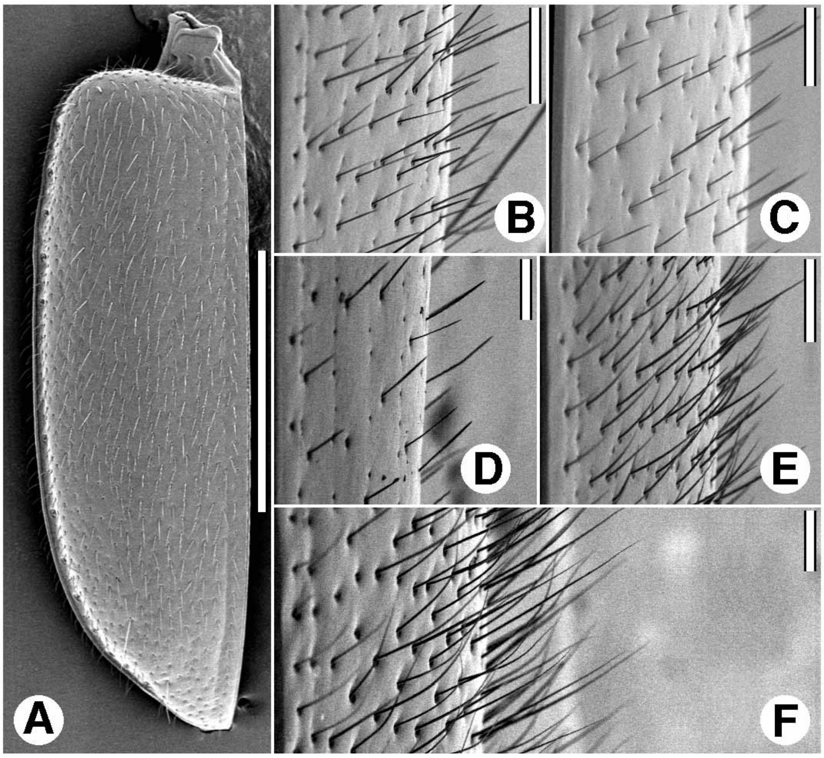

FIGURE 2. Elytra of *Cymbionotum* species. SEM photographs illustrating setal length. A, left elytron, dorsal aspect, of *C. fernandezi*, new species. B–F, portions of left elytra, dorsolateral aspect, of: B, *C. pictulum* Bates; C, *C. semelederi* Chaudoir; D, *C. striatum* Reitter, E, *C. fernandezi*, new species; and F, *C. semirubricum* Reitter. Scale bars: A = 1.0 mm; B–F = 100 µm.

Density was estimated, based on a square of surface area, each side of which was one half the width of and in the basal third of an elytron. Four grades of density were recognized: very dense (50 or more setae per unit)—*C. fernandezi*); dense (30 to 40 setae per unit) - *C. semirubricum, C. schueppelii,* and *C. pictulum*; intermediately dense (20 to 30 setae per unit) - *C. semelederi*; sparse (less than 20 setae per unit) - *C. striatum*; and very sparse (elytral punctures confined to striae) - *C. namwala,* new species, not illustrated.

Setal length was determined by measurement from micrographs of lateral aspects of elytra (Figs. 2B–F and Table 1). The setae for measurement were chosen at random by a naive observer. Three grades were chosen by inspection of the data: short, average length less than 70 µm (*C. pictulum, C. semelederi)*; moderately long, average length more than 80 µm (*C. striatum, C. fernandezi)*; and very long, average length more than 150 µm (*C. semirubricum*). Note the marked overlap between "short" and "moderately long." These grades for other taxa were assigned by visual comparison with members of the exemplar taxa.

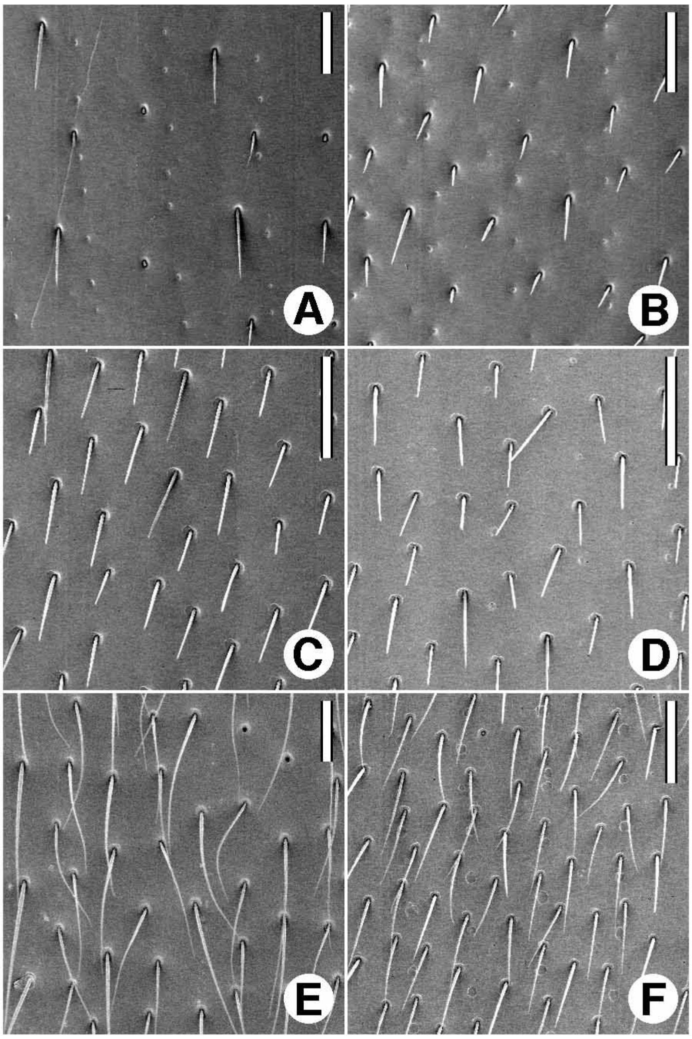

FIGURE 3. Elytra of *Cymbionotum* species. SEM photographs of sections of elytral discs in anterior one third, illustrating density of elytral punctation: A, *C. striatum* Reitter; B, *C. semelederi* Chaudoir; C, *C. schueppelii* Dejean; D, *C. pictulum* Bates; E, *C. semirubricum* Reitter; and F, *C. fernandezi,* new species. Scale bars = 100 µm.

Preparation of material. Dissections were made by using standard techniques. Genitalia and other small structures were preserved in glycerine in microvials and pinned beneath the specimens from which they were removed. Larger structures and those that were gold-coated for study with the SEM were glued to cards pinned beneath the specimens from which they were removed. Photographs of isolated structures were taken with a JEOL JSM 6301 FXV field emission SEM. Line drawings of selected body parts were prepared by using a camera lucida on a Wild W5 stereoscopic microscope. Plates were prepared by using Adobe Photoshop 4.0.1.

Types. Because of the absence of any recent synthetic treatments of the melaenines, we thought it of particular importance to provide details relating to location and recognition of type specimens. Most authors publishing in the latter half of the 20th Century indicated type material by precise labeling, including distinction between holotypes and paratypes, and specified place of deposition. Earlier authors were less precise about such matters: some did not distinguish among different components of the type series; others did not designate types, as such. In the course of our work, based on study of publications and specimens, we have indicated by labels and in the following text, the status of nomenclaturally important specimens, that is, as holotype, lectotype, paratype, and paralectotype.

Labeling of the type material of specimens described by the Baron Maximilien de Chaudoir, and housed in the Oberthür/ Chaudoir Collection (MNHP) poses a special problem. Most specimens are labeled only with a museum label ("Ex Musaeo Chaudoir"). To determine the identity of specimens, one has to refer to hand-printed labels located behind them, and pinned to the bottom of the box. In our text herein, these are referred to as "box labels." The problem of type identification was compounded by prior (probably before 1988) removal of almost all specimens of *Cymbionotum* from the box containing the identification labels to a separate container. The specimens were in continuous rows. Each species was identified by a small hand-printed label providing only the specific epithet pinned to the first (or only) specimen of a species. In a move of this sort accidents are possible. We are satisfied, however, that mistakes were not made and that the relocated specimens were identified correctly.

For type material, the information on each label is reproduced as exactly as possible using ordinary type. Information on each label is enclosed in quotation marks; as well, a semicolon marks the end of a label. A slash mark (/) indicates the end of each line of text, for each label. Enclosed in square brackets is information about color of label paper (other than white) or printing (handwriting; color of ink, other than black), and form of the label (other than rectangular). Enclosed in parentheses is the appropriate coden for the collections in which the repective type is housed.

Typification. If it was clear from the original description that a new species name was based on a single specimen, it was recognized as a holotype and was labeled accordingly. For species descriptions based on multiple specimens, these specimens were recognized as syntypes with one of them chosen as lectotype, the remaining becoming thereby paralectotypes. Selection of a lectotype was made to ensure that the species name henceforth would be associated with a single specimen, thus providing "the objective standard of reference for the application of the name" (International Code of Zoological Nomenclature, 2000: 63, Article 61.1).

Descriptions. To reduce repetition, character states of most low-ranking taxa recorded in the descriptions of higher-ranking taxa are not repeated in the descriptions of the included low-ranking taxa. Thus, the complete description of a species must be assembled from its taxonomic placement. Such a description is obtained by reading the descriptions and recognition features of the sequence of higher-ranking taxa in which the lower-ranking taxon is placed. However, the descriptions of new species are more complete, in spite of the repetition of many of the character states.

Habitat, habits, and seasonal occurrence. For each species, a section thus entitled summarizes the label data available, with "habitat" indicating primarily vegetation zone, altitude, and any special features about a species way of life. But most labels do not provide information about habitat and altitude. The statements about altitude are inferences based on examination of suitable maps. Figure 24, derived from Newton (2003: 124, Fig. 5.2) and Map B (Hall and Moreau, 1970: xiii) provides the basis for statements about vegetation zones "Seasonal occurrence" summarizes months of the year during which the specimens were collected and is taken as an indication of activity of adults.

Material examined. For material other than types, we report in full the locality data, date of collection and collectors. Label data about altitude and dates of collection are reported in summary fashion under "Habitat." Codens were taken from Arnett et al. (1993), for which there is an online version: http:bishopmuseum.org/codens/codens-inst.html.

Specific ranking. Species are clusters of morphologically similar adults, distinguished from other clusters by discontinuity in one or more structural features, in particular differences in the male genitalia. We expect that the discontinuity between morphologically similar clusters will be reflected more or less clearly in features of other life stages. Further, we expect that the clusters we recognize as distinct are reproductively isolated from each other. Expressed in the fashion of Hennig (1966: 19–20), the tokogenetic relations that previously connected these clusters have been interrupted. Thus, we accept the (now) classical "biological" species definition, as formulated and defended over the years by Mayr (1942). See also Darlington (1980: 125–126).

Supraspecific ranking. We accept as appropriate the traditional ranking as genera of the two major clusters of Melaenini. Clusters of species of *Cymbionotum* are evident, based on features postulated to be synapotypic. We were able to recognize three levels, designating these putative monophyletic clusters, from less inclusive to more inclusive, as superspecies (Mayr, 1942: 169, and Mayr, 1963: 499–501), species group, and subgenus. Because most of the putatively closely related species are allopatric in relation to one another, use of the superspecies category is appropriate (Hall and Moreau, 1970: x and xi).

Sequence of taxa. The taxonomic treatment begins with the putatively more primitive genus, *Melaenus*, and its species, followed by *Cymbionotum*. The subgenera and species groups of *Cymbionotum* are arranged from generalized to derived. Within these species groups and the Neotropical subgenus *Procoscinia*, the included species are arranged from generalized to derived, if such a postulate seems warranted. Otherwise, they are arranged from east (southeastern Asia) to west (Africa), and within India and Africa, from north to south.

Terms for morphological features

Most of the terms used to designate details of structures are found in textbooks of general entomology, or are used by coleopterists, generally. Other words, used to designate particular structures or parts thereof, are not in general use, though they have been used by us in previous publications. We provide information about these words here, as well as names that have been changed for certain structural features.

Microsculpture. A "sculpticell" is the space on the surface of the cuticle enclosed by adjacent microlines of the integumental system of microsculpture (Allen and Ball 1980:485–486). Microsculpture of the elytra varies from mesh pattern isodiametric, to transverse with sculpticells flat or with surface more or less convex. Adults of *Melaenus* exhibit a typical markedly transverse mesh pattern (Figs. 5F–G), but the microlines, rather than appearing as shallow linear impressions in the cuticle, are rows of closely spaced microtrichia, named here microtrichial ridges (Fig. 5B, **mtr**).

Setae. Most setae on melaenine cuticle are hair like, or trichoid (cf. Figs. 2A–F, 3A–F), but on the elytron of adult *Melaenus*, a very small branched seta, here named the quadrifurcate seta (Fig. 5G, **qfs**) is associated with the anterior margin of many of the strial punctures

Chaetotaxy. This term refers to the fixed setae, which are the long, evidently tactile, commonly encountered setae on carabids: dorsal labral (6); clypeal (1 pair); supraorbital (1 or 2 pairs); stipital (1 to several on each stipes); submental; mental; glossal; palpigeral; pronotal; elytral parascutellar, discal, and umbilicate (or lateral); coxal, trochanteral, femoral, and tarsomeral; abdominal sternal ambulatory (sterna IV, V, VI); and abdominal sternal terminal (sternum VII, near posterior margin). Chaetotaxy is reported only for dorsal surface, mouthparts, and abdominal sternum VII.

Body parts. The term "segment" is restricted for use to those body parts that reflect embryonic somites; thus, somite-like portions of the abdomen are referred to as segments. Abdominal segments are designated by Roman numerals corresponding to their respective somites. The first complete sternum is III, and the last one normally exposed is VII. For numbering the genital somites, we follow Bils (1976).

Portions of appendages are designated by the suffix "-mere", the prefix depending on the appendage in question: antenno-, palpo-, tarso-, etc.

Mandibles. Shpeley and Ball (2001: 9–21) characterized the mandibles of the lebiine subtribe Pericalina, and illustrated the major features with SEM figures. We use here the same system (Figs. 6A–I, 12A–H).

Labium. The melaenine labium is standard for Carabidae. For the combined glossae and paraglossae, we use the standard term ligula. The central sclerotized, apically setigerous structure is the glossal sclerite (Figs. 7C–D, 13A, 13C).

Elytra. Shallow longitudinal grooves on the dorsal surface are designated as striae, rather than as interneurs (Erwin 1974:3–5). Although we appreciate Erwin's arguments (and accepted them in previous publications [Shpeley and Ball, 2001: 21]), we bow here to the weight of general usage.

Male genitalia. In our previous publications (for example, Shpeley and Ball, 2001) we have used "median lobe" for the predominantly sclerotized basal part of the intromittent organ, and "internal sac" for the membranous apical part that, during copulation, enters the bursa copulatrix. These terms, although generally understood by carabid specialists, are, beyond their contextual sense, without meaning, because they are insufficiently specific. Here, we adopt the terms phallus (Nichols, 1989: 543) and endophallus (Nichols, 1989: 239) for median lobe and internal sac, respectively.

The surface of the phallus treated by convention as dorsal may be the ventral surface, and vice versa (Deuve 1993:88). We have chosen to remain with the conventional usage.

The phallus (Figs. 8B, 15B 15F, 17D–E, 17I–K, 19C–D, 19G–H, 19K, 19O, 22D–I), illustrated in left lateral aspect, with dorsal surface toward the top of the page, exhibits interspecific differences in form. These differences are seen readily as overall patterns ('Gestalt') but are not so easily described, except with notation of differences in size and shape of the distal area.

To provide the basis for verbal description for melaenine phalli, two principal regions are distinguished (Fig. 17D), the shaft (**s)** and basal lobe (**bl**). The latter is the more or less extensive left lateral flange subtending the basal opening (**bo**), set at an angle to the ventrally curved shaft. Two areas of the shaft are recognized: a more distal preapical portion (**pa**), and a more proximal middle area (**ma**) between basal lobe and preapical portion. The preapical area, in males of most taxa, is short in relation to the medial area, and is more constricted.

Female genitalia. For naming the sclerites and membranous parts of the adephagan ovipositor, we accept the system used by Liebherr and Will (1998: 103, Fig. 3), and thus abandoning the older system used by, for example, Shpeley and Ball (2001: 21). Comparing the systems, laterotergite = valvifer; gonocoxite 1 = stylomere 1; and gonocoxite 2 = stylomere 2. For the gonocoxites, the surfaces that are ventral in the infolded position are lateral when the ovipositor is extended; thus such surfaces are designated as lateral, and the other surfaces are designated accordingly. Gonocoxite 2 is much simplified, evidently by loss of the basal lobe and ensiform setae. For the internal genitalia, we follow Deuve (1993: 148, Figs. 222–223).

Biogeographical terms

For the boundaries of the biogeographical regions in the Eastern Hemisphere (Oriental, Palaearctic, and Afrotropical), we follow Löbl and Smetana (2003: 8–10), except that southwestern Arabia is included in the Afrotropical Region (Darlington, 1957: 428); for the Western Hemisphere, records of melaenines are in the Neotropical Region by any current definition.

Following Frank and McCoy (1990), we use "indigenous" (synonyms autochthonous, native) for a taxon that is inferred to have its place of origin in the area where it is living. If an indigenous taxon occurs nowhere else, it is referred to as "precinctive" (from Latin, meaning to gird, or encircle). A taxon whose place of origin is elsewhere than in a given area where it occurs now, is "adventive" in the latter area. An adventive taxon is either "introduced" if moved to a given area by man; or it is "immigrant" if it was not introduced.

Phylogenetic terms

In place of sister group or sister taxon, we use "adelphotaxon" (Ax 1987:36), for reasons given by that author. In place of "plesiomorphic" and "apomorphic", we use "plesiotypic" and "apotypic", on the basis that the latter pair have a more general connotation than the former pair (Tuomikoski 1967).

Taxonomic Treatment

Historical notes about classification and relationships of melaenine Carabidae

Dejean (1831) described both melaenine genera (Figs. 1A, 1B): *Coscinia*, p. 478 (the name later shown to be a junior homonym of *Coscinia* Hübner 1822, and replaced by *Cymbionotum* Baudi di Selve 1864); and *Melaenus*, p. 481, placing them in his suprageneric Scaritides on the basis of pedunculate body form. The Scaritides included 17 genera (*l. c.*, p. 471), grouped in two units: those with mentum articulated (i.e., the gular-submental suture evident) and those with the mentum "inarticulate" (gula and submentum fused). In the latter group, Dejean included *Enceladus* Bonelli and *Siagona* Latreille (now Siagonini), and *Coscinia* and *Melaenus* (now Melaenini). The siagonine genera were distinguished as having a broad mentum, covering almost the entire anterior part of the under surface of the head capsule, whereas the mentum of the melaenine genera was described as being less extensive, leaving uncovered a large portion of mouthparts. From these details, one may infer that Dejean regarded the "inarticulate scaritides" as a distinctive unit of two groups, each group comprised of two genera.

Subsequent authors classified variously the scaritide genera and ranked the groups variously. Lacordaire (1854: 166) included the melaenine genera in the Ditomides, along with *Apotomus* (now Apotomini) and seven other genera, now recognized as ditomine Harpalini. From this group, he excluded the siagonine genera (Siagonides), though his linear sequence of taxa (the melaenine genera following immediately the Siagonides and preceding the remaining ditomines) indicates the structural affinities perceived by Dejean.

Chaudoir (1876: 113–118) affected melaenine classification profoundly in two ways. First, he established the monogeneric Coscinides, distinguishing it from the Siagonides by middle coxal cavities (conjunct in the former group and disjunct in the latter) and from the Ditomides by the metepimera (present in Ditomides, absent from the Coscinides). As well, Chaudoir provided a detailed characterization of the Coscinides. Second, he synonymized with the name *Coscinia* the generic names *Graniger* Motschulsky 1864, and *Cymbionotum* Baudi di Selve 1864. Interestingly, Chaudoir made no reference to *Melaenus*, although that genus exhibited the combination of thoracic features held to be diagnostic of the Coscinides by him.

Horn (1881: 130–131), mindful of the thoracic features of the melaenines, placed *Coscinia* and *Melaenus* in the Nomiini (subfamily Harpalinae), stating that "All of the genera of this tribe as thus defined have a well marked elytral plica internally, a character sufficiently restricted in its distribution to indicate more or less approximately the relationships of the genera possessing it."

Bates (1892: 286) and Bedel (1895: 15 and 1897: 109) following Chaudoir, and using the name Cosciniinae or Cosciniini recognized at least *Coscinia* as tribally distinct, placing this genus near the siagonines. Like Chaudoir, neither of these authors referred to *Melaenus.*

As observed in the synonymical notes below, the tribal name changed from Cosciniini to Granigerini (Bedel 1900: 24), and then to Cymbionotini (Andrewes 1933: 3).

Sloane (1923: 244, 247) included in the Granigerini both *Cymbionotum* (as *Graniger*) and *Melaenus*. Referring to the difference in scrobal setation (*Cymbionotum* with several short setae; *Melaenus* with a single long one), Sloane stated that probably one of the short setae of *Cymbionotum* would be the homologue of the single seta in *Melaenus.* This perceptive inference permitted the two genera to be included in the same supratribal group.

Other authors took a different position. Péringuey (1926: 607), in a treatment of South African Carabidae, placed *Melaenus,* along with *Bascanus* Péringuey and *Bascanidius* Péringuey in the tribe Ditomini, noting specifically that he was thereby separating *Coscinia* from the ditomines. Csiki (1933: 1650) proposed the tribe Melaenini for *Melaenus*, *Bascanus,* and *Bascanidius,* thus isolating this group from the Ditomini (Harpalini, subtribe Ditomina). Previously, Csiki (1929: 477) had treated *Cymbionotum*, for which he used the generic name *Graniger,* and the tribal name Granigerini. Although Csiki did not characterize either tribe, the Roman numerals assigned to each indicated their relative positions in a linear sequence. The Granigerini, numbered XVI, followed XV Amarini, and preceded XVII, Pterostichini. This would seem to indicate the author's belief that the Granigerini belonged in the upper part of the subfamily Harpalinae. Similarly, Melaenini (treated in the corrigenda part of the Catalogus) was numbered VIa, and thus located between VI Pogonopsini (= Pogonini), and VII Merizodini, that is, in the lower part of the Harpalinae, among the styliferous genera.

Andrewes (1935) evidently reached a conclusion similar to Csiki's, in that he included *Cymbionotum* and *Melaenus* in separate tribes, but treated the Melaenini as monogeneric (either he was unaware of the previous work of Péringuey and Csiki, or he did not believe that *Melaenus, Bascanus* and *Bascanidius* formed a natural group). For *Cymbionotum* and *Melaenus* (and thus tribes Cymbionotini and Melaenini) Andrewes provided a diagnosis of 12 character states, in eight of which the two groups differed from each other. Although he regarded these genera as sufficiently different from one another to require separation at the tribal level, Andrewes placed both of them sequentially toward the beginning of the subfamily Harpalinae, following the Hexagoniini, and preceding the Apotomini and Broscini.

Van Emden (1936: 46) recognized the distinctness of the Cymbionotini and Melaenini. He concluded that the two tribes were unrelated (a conclusion matching that of Csiki), including Melaenini in the supratribal group Harpalinae piliferae, from which he excluded the Cymbionotini, without further comment.

Jeannel (1941: 291–292) placed *Melaenus* (tribe Melaenini) in his styliferous family Psydridae, subfamily Psydritae, along with the tribes Psydrini (including *Nomius* Castelnau de la Porte) and the Southern Hemisphere Melisoderini and Meonidini. He did not refer to *Cymbionotum* in the 1941 publication (Carabiques, Faune de France), but in his great Madagascan faunal study (1946: 97) Jeannel treated the Cymbionotidae, which implicitly he placed following the Siagonidae, as the last group of the Simplicia. This last-named taxon, the equivalent of Horn's subfamily Carabinae, which included the more primitive carabid tribes, was characterized partly by disjunct middle coxal cavities. However, the middle coxal cavities of *Cymbionotum* are conjunct. So, in overlooking this feature, Jeannel must have been impressed by the siagonine body form of adult *Cymbionotum*, and perhaps also by the middle tibial oblique setal combs shared by both siagonines and cymbionotines. Because *Cymbionotum* was not known from Madagascar, Jeannel did not elaborate on how he classified the Cymbionotidae.

Antoine (1955: 64) followed Jeannel's ranking system, placing *Cymbionotum* in its own family, and in his linear arrangement, following the Siagonidae. He alluded to the similarity in body form and mid-tibial setal combs, but stated that the two groups differed profoundly from one another. He elaborated on their distinction with a list of 11 diagnostic character states.

Kryzhanovskij (1976; cited by Ball 1979: 95) included Cymbionotini in his supertribe Siagonitae, but did not list the Melaenini. Erwin (1979: 592) included *Cymbionotum* in the Siagonini, well apart from the Melaenini. Later, however (Erwin and Sims, 1984: 355; and Erwin 1985: 467), he placed the Cymbionotini with the Melaenini in the supertribe Melaenitae, one of the three supertribes (the other two, monotribal, Broscitae and Apotomitae) of the subfamily Broscinae, which, in turn was the only subfamily in the Division Melaeniformes. In the Erwin system, the Melaeniformes + Psydriformes comprised the more derived tribes of Carabidaethe Harpalinae of authors, and Caraboidea Limbata of Jeannel.

Erwin (1985: 469), to justify his decision, wrote: "I now believe the Cymbionotini are related to the Melaenini by virtue of the following synapotypic features: conjunct mesocoxae, mesotibial cleaning brush, enlarged upper spur on front tibia, scrobe setiferous, sulcus above eye. I here rank these groups accordingly."

Bousquet and Larochelle (1993: 29) maintained the tribal status of Melaenini and Cymbionotini, but placed them in the text sequentially. They did not offer an opinion about relationships of the two groups.

Deuve (1993: 146), in his study of the female abdomen of the Adephaga, included *Cymbionotum* and *Melaenus* in the family Melaenidae, but expressed doubt about monophyly of the group. Deuve did not offer a formal classification, but placed the Melaenidae between the Siagonidae and Psydritae, that is, either at the end of the "lower" Carabidae (Carabinae, Caraboidea Simplicia), or at the beginning of the "higher" group (Harpalinae, Caraboidea Limbata) of suprageneric taxa.

Lawrence and Newton (1995: 812), in their simplified, sensible synoptic classification of Carabidae, included both *Cymbionotum* and *Melaenus* in their subfamily Trechinae, which they declared to correspond to the Stylifera of Jeannel. They did not offer a tribal classification, simply listing as trechines additional exemplar genera included by other authors in Apotomini, Broscini, Bembidiini, Psydrini, Pogonini, and Trechini.

Roig-Juñent (1998: 352, and 2000: 12–13) did not comment about relationships between *Cymbionotum* and *Melaenus*, but he included as outgroups the latter genus as well as *Apotomus* Illiger (Apotomini) in his cladistic analysis of the broscine genera. In effect, he accepted the subfamily Broscinae as established previously by Erwin. Further, Roig-Juñent (2000: 4) stated explicitly that the Broscinae comprised a monophyletic group.

Based on cladistic analysis of structural details of the female genitalia, Liebherr and Will (1998: 137) concluded that the Cymbionotini + Melaenini comprised a monophyletic assemblage of basal grade carabids, slightly apart from the Apotomini, moderately apart from the Siagonini, and widely separated from the Broscini, which group they included in the upper clade, or "Caraboidea Limbata." Maddison et al (1999: 126–127) in a cladistic analysis of exemplar carabids, based on 18S ribosomal DNA, showed various affinities of *Cymbionotum* (they did not have material for *Melaenus* nor for *Apotomus*), but not a close association with their broscine exemplar.

By way of summary regarding relationships of *Cymbionotum* and *Melaenus* to one another, Dejean, Lacordaire, Horn, and Sloane included these genera in the same tribe. Andrewes, Erwin, Liebherr and Will, Roig-Juñent (1998), and Lorenz (1998b) placed the genera in separate tribes, but indicated their close relationship by including them in a unique higher taxon (subfamily, or supertribe). Bousquet and Larochelle included these genera in separate tribes but placed them sequentially in their discussion of carabid groups. Péringuey, Csiki, Jeannel, van Emden, and Kryzhanovskij separated the groups rather widely. Other authors, such as Chaudoir and Bates, studied either one or the other of the two genera, but not both, so their views on relationships were not expressed explicitly. We believe that *Cymbionotum* and *Melaenus*, though their adults are readily distinguished from one another, share enough presumably derived features to be not only monophyletic, but members of one tribe, the Melaenini *(sensu lato).*

Regarding relationships of this tribe to other carabid tribes, early authors (Dejean, Lacordaire, Chaudoir, and Bates) placed its genera (or at least *Cymbionotum*) in more or less close association with the siagonines, as did some more recent authors (Jeannel, Antoine, and Kryzhanovskij). Horn seems to have been the first author to sever the siagonine-melaenine association, placing the siagonines in the less evolved Carabinae, and the melaenine genera in the more evolved Harpalinae (*sensu lato*- tribe Nomiini). Lorenz, and Lawrence and Newton indicated essential agreement with Horn. Erwin and Roig-Juñent placed the Melaenini (*sensu lato*) in subfamily association with the Broscini and Apotomini, that is, at the lower end of the more highly evolved Carabidae. The exemplar data, presented by Liebherr and Will and Maddison et al., seem to indicate a position for the melaenines nearer to the siagonines than to the broscines.

In conclusion, the data available seem to support adequately the proposition that *Cymbionotum* and *Melaenus* are each other's closest relative, and thus together they form a monophyletic group (ranked here as a tribe), but the data are equivocal about the relationships of this more inclusive Melaenini: external features, especially of the pterothorax and rami of the ovipositor, point to closer association with the less evolved groups of the higher Carabidae; whereas features of the internal female genitalia and those derived from molecular analysis point to membership among the lower Carabidae. We favor the former, accepting a close relationship with the generally less evolved styliferous genera, as indicated by Lawrence and Newton.

Tribe Melaenini

Scaritides (in part) Dejean 1831: 471, 478–483.
Ditomides (in part) Lacordaire 1854: 166–167.
Coscinides Chaudoir 1876: 115–118.
Nomiini (in part) Horn 1881: 130–131.
Cosciniinae Bates 1892: 296.—Bedel, 1895: 15.—1897: 109.
Granigerini Bedel 1900: 24.—Sloane 1923: 244–247.—Andrewes 1930: XI.—Burgeon 1935: 192.
Granigerina Iakobson 1905 200.
Siagonini (in part) Peringuey 1908: 276.—Erwin 1979: 592.—1984: 381.
Ditomini (in part) Peringuey 1926: 607.
Cymbionotini Andrewes 1933: 3.—1935: 18.—van Emden 1936: 46.—Burgeon 1937: 402.—Kryzhanovskij 1976 (cited by Ball 1979: 93).—Erwin and Sims 1984: 355.—Erwin 1985: 468, 469.—Madge 1989: 462.—Erwin 1991: 30.—Bousquet and Larochelle 1993: 29.—Kryzhanovskij et al. 1995: 61.—Liebherr and Will 1998: 137, 150.—Lorenz 1998b: 149.
Melaenini Csiki 1933: 1650.—Andrewes 1935: 26.—van Emden 1936: 46.—Erwin 1979: 590.1985: 468–469.—Erwin and Sims 1984: 355.—Erwin 1991: 50.—Bousquet and Larochelle 1993: 29.—Liebherr and Will 1998: 150.—Roig-Juñent 1998: 352, Fig. 10.—2000: 2, 13, Figs. 14 and 15, respectively.
Melaeninae Alluaud 1934: 30.—Basilewsky 1953: 14.—Madge 1989: 465.—Lorenz 1998b: 149.
Melaenitae (subfamily) Jeannel 1941: 291–292.
Cymbionotidae Jeannel 1946: 97.—Antoine 1955: 64.
Cymbionotinae Basilewsky 1953: 13.
Melaenitae (supertribe) Erwin 1984: 374.1985: 468, 469.—Erwin and Sims 1984: 355.—Erwin 1991: 30.—Liebherr and Will 1998: 137.
Melaenidae Deuve 1993: 146.
Trechinae (in part) Lawrence and Newton 1995: 812.

Notes about synonymy. The suprageneric names Scaritides (Dejean 1831) and Ditomides (Lacordaire 1854), with which the melaenines were associated in the first part of the 19th Century, referred to groups now recognized as paraphyletic or polyphyletic. These taxa were systematically disassembled until each comprised only the genera presently included in the Scaritini and Ditomina, respectively.

The names Coscinides and Granigerini (and derivatives depending upon formally accepted rank-designating suffixes) were invalid as applied to melaenines: Coscinides, because *Coscinia* Dejean 1831 was a junior homonym of *Coscinia* Hübner 1822; and the type species of *Graniger* Motschulsky 1864 (*G. algirinus* Motschulsky 1864) proved to be a ditomine (tribe Harpalini) (see International Code of Zoological Nomenclature, 1999, page 46, article 39). Two names were proposed independently, in the same year, for the melaenines: Cymbionotini (Andrewes 1933), with type genus *Cymbionotum* Baudi di Selve the valid generic name; and Melaenini (Csiki 1933), with type genus the name *Melaenus* Dejean, 1831. Both Andrewes (1935) and Csiki (1933) concluded that *Cymbionotum* and *Melaenus* were tribally distinct from one another, an opinion accepted by most subsequent authors, although Erwin (1979 and 1984), with the erroneous oral advice and encouragement of G. E. Ball, treated Cymbionotini as a junior synonym of Siagonini.

Names of the suprageneric taxa are not problematic, so long as each genus is included in its own tribe. But what is the tribal name to be, with both *Cymbionotum* and *Melaenus* in the same tribe? Both tribal names were proposed in the same year (1933), but in different months: Melaenini in May and Cymbionotini in June. Therefore Melaenini has priority.

Recognition. Melaenine adults are recognized by the following combination of character states: overall size small to moderate (length ca. 4–10 mm); fronto-vertex of head with deep paraocular longitudinal groove (cf. Figs. 11A–C) each side; mandibular scrobes each with one to several setae; submentum and gula fused (i.e., without submental-gular suture- Figs. 7C, 13A); prothoracic coxal cavities closed by insertion of apex of proepimeron into lateral socket of prosternum; mesothoracic coxal cavities conjunct; metepisternum and metepimeron fused (i.e., metapleuron without pleural suture); elytron with distinct plica posteriolaterally; front tibia anisochaete; and middle tibia with distal lateral setal comb. Perhaps the most distinctive feature, but one that is seen only by dissection of females, is the very long spermathecal diverticulum (Fig. 15E). This alone would seem sufficient to establish monophly of the Melaenini. Larvae are unknown (Grebennikov 2001: 50).

Description. Adult beetles (Figs. 1A, 1B) exhibiting the recognition features of Melaenini, and following. Color of body black to testaceous, elytra concolorous or bicolored. Body form terete to depressed. Antennae and mouthparts rufotestaceous, concolorous, to bicolored, proximal antennomeres black, distal antennomeres rufous, to all antennomeres black. Legs testaceous to black.

Microsculpture. Dorsal surface generally with isodiametric mesh pattern, microlines shallow, or microlines and sculpticells confined to postocular transverse impression, or scutellum; or microlines absent, surface without evident mesh pattern; or mesh pattern transverse (Figs. 5F–G), microlines shallow; some appendages with fimbriate sculpticells (see generic descriptions, for details).

Luster. Body surface dull, shiny, or iridescent.

Macrosculpture. Surface generally moderately densely punctate, or smooth with only elytral striae punctate.

Vestiture. Body surface glabrous (except fixed setae), or with dense to very sparse covering of testaceous setae (Figs. 2, 3).

Fixed setae (body sclerites, mouthparts, elytra). Head capsule with one or two pairs of supraorbital setae; with or without row of long setae posteriad eyes, and curved forward over eye surface. Mouthparts: labrum dorsally (Figs. 6J, 12I**)** with row of six apical setae (**as**), near distal margin; mandible with single seta or with several setae in scrobe (Figs. 6A–D, **ss,** and Figs. 12A–D, **pss, sss**); maxillary stipes with two setae (Figs. 7A–B, 12K–L, **dls, vls**), palpifer with single seta (Figs. 7A–B, 12K–L, **pfs**); labial submentum with four or more setae (Figs. 7C, 13A, **sms, psms, ssms**); mentum with pair of paramedial setae (Figs. 7C, 13A, **ms**); glossal sclerite distally quadrisetose or bisetose (Figs. 7C, 13A, **gs**); labial palpomere 2 bisetose (i.e., with two long setae on anterior margin, near apex). Pronotum with single pair or two pairs of lateral setae. Elytron dorsally with or without parascutellar seta, without discal setae, laterally about 20 setae in continuous umbilicate series. Abdominal sterna IV–VI each with pair of ambulatory setae or asetose; sternum VII with (*Cymbionotum,* both sexes, and *Melaenus* females) or without pair of setae (*Melaenus* males) near posterior margin.

Head. Moderately to distinctly wide, dorsal surface moderately to slightly convex, with or without distinct transverse impression posteriad eyes; frontoclypeal suture not evident, frontal impressions hardly indicated, or broad and shallow; frontovertex each side laterad eye with distinct longitudinal sulcus extended posteriorly, to transverse groove (if present); also sharp supraorbital ridge each side extended sinuously anteriorly to mandibular fossa, and here joined to apex of fronto-vertical ridge; posteriolaterally, genae rather broad, broader than antennomere 1.

Eyes (Fig. 1A–B, 11A–C). Rather small, convex.

Antennae. Filiform (Fig. 1A), rather long, extended posteriorly beyond basal third of elytra, or nearly moniliform (Fig. 1B), shorter, extended to about basal third of elytra. Antennomeres variously proportioned, antennomeres 5–10 symmetric, slightly asymmetric, or markedly asymmetric (for details, see descriptions of genera).

Mouthparts. (Figs. 6A–K**,** 7A–D**,** 12A–L, 13A–C) Labrum (Figs. 6J–K**,** 12I–J) transverse, distal margin very shallowly to moderately concave, or distinctly notched medially. Ventrally, epipharynx as in Figs. 6K and 12J: pedium (**ped**) triangular, either approximately equilateral or isosceles, with broad base along distal margin; parapedial projection (**pp**) acute or obtuse; lateral parapedial setae (**lps**) four to seven; extra parapedial setae (**eps**) either mediad or laterad parapedial ridge (**pr**); coeloconic sensilla (**cs**) relatively few to many.

Mandibles (Figs. 6A–I, 12A–H). Trigonal, narrowed distally and in dorsal aspect curved mediad, in lateral aspect curved ventrad; terebra (**t**) with or without series of short, diagonal sulci (**dts, vts**) and ventral condylar sulci (**vcs**); dorsolateral surface with dorsal groove (**dgs**) extended from scrobe (**s**); basal brush (**bb**) evident at base of occlusal margin; ventral surface with moderately long ventral groove (**vg**), bearing dense row of short microtrichia (**mtr**); also, secondary ventral groove (**svg**) and medial ventral depression (**vd**). Left mandible, dorsal surface (Figs. 6B**,** 12B) with sharply inflexed incisor tooth (**it**), terebral tooth (**tt**) moderately prominent, retinaculum with anterior and posterior tooth (**art, prt**), anterior tooth evident or not, from dorsal surface, premolar (**pmt**) and molar (**mt**) tooth evident; posterior occlusal groove (**pog**) distinct; ventral surface (Figs. 6F**,** 12F) of occlusal margin with molar ridge (**mr**) and its basal and occlusal extensions (**bemr, omr**). Right mandible (Figs. 6C, 6G, 12C, 12G) similar to left mandible in most respects, but more curved and shorter.

Maxillae (Figs. 7A–B, 12K–L). Standard for Carabidae, with basal trianguloid cardo, rectanguloid stipes with dorsal and ventral lobes (**dls, vls**), dimerous galea (**g1, g2**), and lacinia (**lc**) with prominent distal tooth (**lct**), and occlusal margin thickly setose; palpus of four articles, (**mp1- 4**), palpomere 1 shortest and palpomere 2 longest.

Labium (Figs. 7C–D, 13A–C). Submentum (**sm**) continuous with gula (not shown); mental-submental suture (**m-sms**) distinct; mentum (**m**) transverse, with pair of prominent, broad lateral lobes (**ll**); epilobes (**e**) broad, mental tooth (**mt**) small, broad, anterior margin distinctly notched. Prementum: ligula, ventral aspect (Figs. 7C, 13A), with broad glossal sclerite (**gsc**) and broad longitudinal keel medially, distal margin broadly rounded, pair of paraglossae (**pg**), each paraglossa slender, narrow lobe, attached to glossal sclerite at base, only, surface with or without extensive covering of seta-like microtrichia (Fig. 13B, **mtr**); in dorsal aspect (Figs. 7D, 13C), glossal sclerite tripartite, basal portion (**gsbp**) narrow, medial (**gsmp**) and distal (**gsap**) portions variously extended; palpiger (**pge**) moderately large; palpus with three articles (**lp1-3**), palpomere 1 short, palpomeres 2 and 3 longer, subequal, palpomere 3 broader, fusiform, apex narrowed, surface more or less setose.

Prothorax. Pronotum (Figs. 1A, 1B) subcordate, markedly to slightly wider than long, broader at anterior than at posterior margin; anterior margin slightly concave, posterior margin almost straight, very shallowly sinuate; lateral margins anteriorly rounded, posteriorly sinuate; anteriolateral angles subacute, projected slightly anteriorly; posteriolateral angles acute, prominently projected or not; anterior margin not beaded, flat, posterior margin beaded or not, lateral margins narrowly beaded or not; transverse discal impressions not evident, medial longitudinal impression, distinct, evident medially, not extended to either anterior or posterior margins; lateral grooves broad to narrow; disc slightly convex, lateral declivity each side gradual or rather steep. Prosternum with intercoxal process short, broad posteriorly, ventral surface with shallow longitudinal groove.

Scutellum. Trianguloid, apex pointed.

Elytra (Figs. 1A, 1B). Extended length of abdomen. Each elytron oblong, humerus broadly or narrowly rounded, preapically narrowed to narrowly rounded sutural apex, lateral margin straight, not sinuate; dorsal surface plane for most of length, apical declivity gradually to moderately steeply sloped; basal ridge narrow, not extended to edge of scutellum, anteriorly angulate (Fig. 1A), or not (Fig. 1B); striae not evident, or very slightly impressed, intervals flat, or striae distinct throughout length, nine in number, intervals moderately convex; parascutellar stria and diagonal portion of stria 1 absent, parascutellar setigerous puncture at base of stria 1. Plica posteriolaterally distinct.

Hind wings (Figs. 8A, 15A). Macropterous. Oblongum cell (**o**) large; wedge cell (**w**) large or absent. Veins **RP 3 + 4** and **AA 3 + 4** present or absent. Vein **MP 4** more than, or less than, half-length of **MP 3**.

Legs. Articles of about average proportions for ground-inhabiting carabid adults. Front tibia with antenna cleaner type B (Hlavac 1971: 57); upper spur unusually large. Middle tibia distally with sculpticells (Figs. 7F, 13D, **ifs, ofs**) fimbriate or not. Hind coxae narrowly in contact with one another in midline. Tarsomere 5 distoventrally (Figs. 7G**,** 13E) with prominent lobe, rounded at apex (**avl**); unguitractor plate (**up**) narrow or broad; claws (**tc**) with ventral margins smooth, not serrate or pectinate. Front tarsi of males without adhesive vestiture.

Abdominal sclerites. Tergum VIII partially invaginated; with anterior projections (Roig Juñent 1998: 345, Table 2, and 357). Sterna III and IV evidently fused, with intersegmental suture fine and incomplete, not extended width of abdomen. Sterna IV–VI narrowly transversely sulcate, posteriorly. Sternum VII with posterior margin rounded, and beaded.

Male genitalia (Figs. 8B–D**,** 15B–D, 15F, 17D–E, 17I–K, 19C–D, 19G–H, 19K, 19O, 22D–I). Phallus with base open dorsally (Roig Juñent 1998: 345, Table 2, and 357), right basal lobe absent, most of dorsal surface membranous. Endophallus with sclerite **X** contained wholly within phallus, large, more than half length of phallus, or much shorter than phallus; or small, basad and partially outside phallus; or absent; parameres slender, elongate, with dense row of long setae distally (Figs. 8C–D), or glabrous (Figs. 15C–D; cf. also van Emden 1936: 45, Fig. 11).

Ovipositor (Figs. 7H–K, 13F–J). Laterotergite IX (Fig. 15E, **lt**) with or without anteriorly directed apophysis. Rami present, in *Melaenus* about 0.80 length of gonocoxite 1, in *Cymbionotum* (Fig. 15E, **r**) 0.50–0.80 length of gonocoxite 1. Gonocoxa dimerous, gonocoxites 1 and 2 subequal (Fig. 13F, **gc1, 2**), or gonocoxite 2 much shorter than gonocoxite 1 (Fig. 7H, **gc1, 2**). Gonocoxite 1 with trichoid setae (**ts**) and row of ensiform setae (**es**). Gonocoxite 2 with subapical sensory furrow (**ssf**) and pair of nematiform setae (**ns**); without furrow pegs distad setal insertions.

Female internal genitalia (Fig. 15E). Bursa copulatrix (**bc**) elongate, voluminous; spermathecal duct (**spd**) with origin near junction of bursa and common oviduct (**co**); spermathecal duct with epispermathecal sclerite extended from bursa copulatrix to spermathecal reservoir (Liebherr and Will 1998: 118, and 169, Appendix 2); spermathecal duct shorter or much longer than spermathecal reservoir (**sp**), latter reniform, or sausage shaped; spermathecal reservoir with diverticulum (**di**) long and convoluted. Following features absent (Liebherr and Will 1998: 169, Appendix 2): accessory gland; spermatheca 2 and its appended gland; helminthoid sclerite; villous canal; sclerotized extension of spermathecal duct; diverticula of spermathecal gland; and spermathecal digitiform process.

Way of life. Little is known about this topic. Evidently, most taxa occupy drier open habitats, but the group is represented also in the tropical rain forest vegetation zone (Table 17 and Fig. 24). Bedel (1897: 109) wrote that specimens of *Cymbionotum semelederi* occur on sandy clay soil on desert plains, and that they come to light on warm evenings. In contrast, specimens of *C. negrei* Perrault were found under bark of fallen trees.

Included taxa. This tribe includes only two genera: *Melaenus* Dejean (with two species), and *Cymbionotum* Baudi di Selve (with 20 species). The classification is outlined in Table 1.

TABLE 2. Length of elytral setae, in microns, of exemplar taxa of *Cymbionotum* Baudi di Selve.

	Range	Mean
C. pictulum Bates	38–90	61
C. semelederi Chaudoir	40–88	58
C. striatum Reitter	59–128	92
C. fernandezi, **n. sp.**	60–124	94
C. semirubricum Reitter	131–322	194

Geographical distribution (Fig. 4). The range of the Melaenini includes the Oriental, southern Palaearctic (principally south of 40º N. Lat.), and Afrotropical (principally north of the Equator) Regions of the Eastern Hemisphere; and northernmost South America, in the Neotropical Region of the Western Hemisphere.

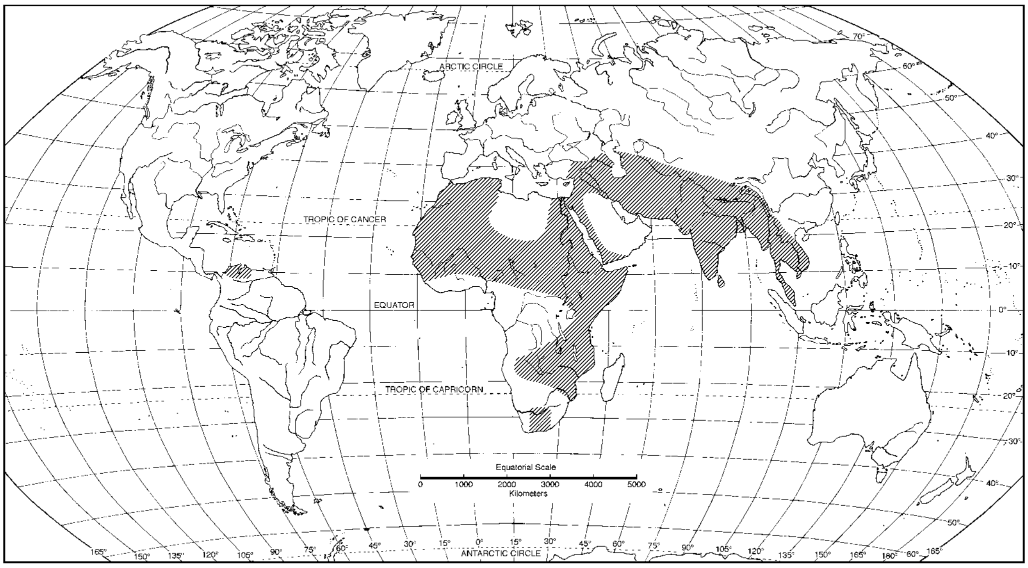

FIGURE 4. Generalized distribution of members of the Tribe Melaenini illustrated with cross-hatching on a Winkel's 'Tripel' Projection map of the world.

Key to Tribes of Carabidae in the Western Hemisphere

To make possible ready identification of the Melaenini in the Western Hemisphere, we offer portions of, and modifications to, a key to carabid tribes of the Neotropical Region (Reichardt, 1977: 361), beginning with couplet 17, as follows.

17 (13') Middle coxal cavities disjunct (not entirely enclosed laterally by mesosternum and metasternum) .... 18†

17' Middle coxal cavities conjunct (entirely enclosed laterally by mesosternum and metasternum) 21

****

21 (17') Scrobe of mandible with one or more setigerous punctures, each with large tactile seta.. 22

21' Scrobe of mandible without setigerous punctures (with or without vestiture of short setae).. 29†

22 (21) Head with single pair of supraorbital setae .... 23†

22' Head with two or more pairs of supraorbital setae... 24

****

24 (22') Head with three or more pairs of supraorbital setae. Size larger, length of body more than 10 mm .... BROSCINI (in part)

24' Head with two pairs of supraorbital setae. Size various 24A

24A (24') Metapleuron without pleural suture, metepisternum and metepimeron fused. Head with submentum laterally fused to head capsule. Body depressed, integument generally setose (Fig. 1B), color uniformly rufous .... MELAENINI, *Cymbionotum* Baudi di Selve

24A' Metapleuron with pleural suture, metepisternum and metepimeron separated. Submentum laterally separated from head capsule by lateral extension of gular suture. Body form, integument, and color various .... 25†

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† for continuation, see Reichardt (1977)

Key to the genera, subgenera and species of Melaenini

1. Head dorsally with single supraorbital seta over each eye. Dorsal surface of body with fixed setae only, without general setose vestiture. Antennomeres 1–4 with setae near distal margin of each article. Elytron with striae distinctly impressed, intervals convex .... *Melaenus* Dejean 2

– Head dorsally with two supraorbital setae over each eye. Dorsal surface of body with general setose vestiture. Antennomeres 1–4 with setae over surface of each article. Elytron with striae shallow (stria 1), or indistinct; intervals flat.. *Cymbionotum* Baudi di Selve ... 3

2 (1). Pronotum each side with two posteriolateral projections. Specimen from locality in Africa (Fig. 10).. *M. elegans* Dejean, **p. 39**

– Pronotum each side with one posteriolateral projection. Specimen from locality in India (Fig. 10) .... *M. piger* Fabricius, **p. 38**

3 (1) Antennomere 2 (Fig. 11E, **A2**) globose, spherical in outline, not pyriform; antennomeres 5–10 (Fig. 11G, **A6, A7**) markedly asymmetric .... *semelederi* species group ... 4

– Antennomere 2 (Fig. 11D, **A2**) pyriform, margins markedly constricted proximad base; antennomeres 5–10 (Fig. 11F, **A6, A7**) moderately asymmetric........ 6

4 (3). Elytral vestiture denser (Figs. 2C, 3B) .... *C. semelederi* Chaudoir, **p. 68**

– Elytral vestiture sparser (Fig. 2D, 3A) 5

5 (4). Phallus in left lateral aspect markedly curved preapically and endophallus with two microtrichial fields (Fig. 17J). Specimen from locality in or near Afghanistan (Fig. 18) .... *C. striatum* Reitter, **p. 73**

– Phallus in left lateral aspect gradually curved preapically and endophallus with single microtrichial field (Fig. 17K). Specimen from locality in or near Iran (Fig. 18) .... *C. mandli* Jedlička, **p. 74**

6 (3). Dorsal surface uniformly dark rufous. Pronotum (Fig. 14A) with posteriolateral angles distinctly anteriad posterior margin, proepipleuron not visible. Specimen from locality in Western Hemisphere (northern South America—Fig. 16)...........

.... *Procoscinia,* new subgenus 7

– Dorsal surface various in color: uniformly dark concolorous to uniformly pale concolorous, to bicolored (Figs. 17A–C, 17F-H, 19A-B, 19E-F, 19I-J, 19L-N, 22A-C). Pronotum (Fig. 14B) with posteriolateral angles near posterior margin, proepipleuron visible. Specimen from locality in Eastern Hemisphere (Afrotropical, southern Palaearctic, Oriental Regions- Figs. 16, 20, 21, 23) .... Subgenus *Cymbionotum* (*sensu stricto*) 8

7 (6). Dorsal surface with shallow microlines, mesh pattern isodiametric. Specimen from locality in northern Colombia........................... *C. fernandezi,* **n. sp., p. 56**

– Dorsal surface without microlines, smooth. Specimen from locality in northern Venezuela .... *C. negrei* Perrault, **p. 58**

8 (6). Body size large (SBL more than 5.0 mm, EW more than 1.5 mm). Elytron bicolored (Figs. 17A–C), pale anteriorly, dark posteriorly. Femora and tibiae piceous to rufous ....*basale* species group 9

– Body size smaller (SBL less than 4.5 mm, EW less than 1.5 mm). Elytron concolorous or bicolored. Femora and tibiae rufous to testaceous 10

9 (8). Dorsal vestiture (Fig. 2D) of elytron relatively long setae. Specimen from locality in Palaearctic southwestern Asia or in the Afrotropical Region west to Niger (Fig. 16) .... *C. semirubricum* Reitter, **p. 61**

– Dorsal vestiture of elytron relatively shorter setae. Specimen from locality in northwestern Afrotropical Region (Mali and Sénégal, Fig. 16)........................... .... *C. basale* Dejean, **p. 65**

10 (8). Elytron with punctation in straight lines, stria-like. Dorsal integument uniformly rufotestaceous. Clypeus (cf. Fig. 11B) without dentiform projection .... *C. namwala,* **n. sp., p. 99**

– Elytron with punctation scattered over surface (if lines of punctation apparent, punctures also in between). Dorsal integument various in color. Clypeus with (Fig. 11C) or without (Fig. 11B) dentiform projection 11

11 (10). Eyes somewhat flattened, only slightly projected laterad dorsolateral carina of head (Fig. 11B). Values for VW/HW 0.87 or more. Dorsal integument concolorous, uniformly pale 12

– Eyes rounded, moderately projected laterad dorsolateral carina of head (Fig. 11C). Values for VW/HW 0.87 or less. Dorsal integument various: distinctly or indistinctly bicolored, or uniformly pale 15

12 (11). Clypeus anteriomedially with dentiform projection (Fig. 11C, **ct**) 13

– Clypeus anteriomedially without dentiform projection (Fig. 11B) 14

13 (12). Scutellum with microsculpture mesh pattern isodiametric, sculpticells convex .. .. *C. candidum* Andrewes, **p. 100**

– Scutellum smooth, without microlines .... *C. subcaecum,* **n. sp., p. 101**

14 (12). Scutellum with slightly transverse mesh pattern over much of surface, smooth

apically. Specimen from locality in southwestern Asia, west to eastern Palaearctic Africa (Fig. 23) .... *C. transcaspicum* Semenov **p. 102**

– Scutellum with slightly transverse mesh pattern near anterior margin, smooth apically. Specimen from locality in Afrotropical Region, east to Anatolian peninsula in Palaearctic Region (Fig. 23) ...... *C. microphthalmum* Chaudoir, **p. 104**

15 (11). Specimen from locality in South Africa or Botswana (Fig. 20). Male genitalia as in Fig. 19D.. *C. capicola* Péringuey, **p. 83**

– Specimen from locality farther north in Africa, and eastward in Palaearctic southwestern Asia, to Vietnam, in the Oriental Region. Male genitalia otherwise (Figs. 19C, 19G–H, 19K, 19O and 22D)... 16

16 (15). Head with postocular transverse impression with microsculpture mesh pattern (Figs. 11B–C) isodiametric to slightly transverse 17

– Head with postocular transverse impression smooth, without microlines, or microlines not joined in form of a network... 20

17 (16). Specimen from locality in Palaearctic southwestern Asia, or in eastern Afrotropical Region, north of South Africa (Fig. 21); elytron bicolored (Figs. 19L–N; cf. Fig. 19F)... *C. pictulum* Bates, **p. 93**

– Specimen from locality in Oriental Region (Fig. 21) 18

18 (17). Elytron concolorous, rufous, or bicolored, with piceous or black mark small, confined to disc (Figs. 19E–F). Specimen from locality in Burma, or farther east (Fig. 21) .... *C. helferi* Chaudoir, **p. 88**

– Elytron bicolored, dark marks more extensive, extended to lateral margin. Specimen from locality in India, Sri Lanka, or Nepal 19

19 (18). Phallus in left lateral aspect gradually curved preapically (Fig. 19K). Specimen from locality in southern India (Calcutta area southward) or Sri Lanka ....
....*C. fluviale* Andrewes, **p. 92**

– Phallus in left lateral aspect markedly curved preapically (Fig. 19H). Specimen from locality in northern India or Nepal .... *C. fasciger* Chaudoir, **p. 91**

20 (16). Elytron concolorous, pale 21

– Elytron bicolored (Figs. 19A–B, 22A–C) 24

21 (20). Scutellum entirely smooth or surface wrinkled basally, without microlines ....
.... *C. rufotestaceum* Fairmaire, **p. 81**

– Scutellum basally with microlines in form of mesh pattern 22

22 (21). Dissected specimen female (one of two species) ....
.... *C. schueppelii* Dejean (in part), **p**. **78**, *C. fasciatum* (in part), **p. 95**

– Dissected specimen male 23

23 (22). Male genitalia (Fig. 19C) with microtrichial field (**mf**) of endophallus extensive; phallus with preapical portion shorter, curved ventrad rather sharply ....
....*C. schueppelii* Dejean (in part), **p. 78**

– Male genitalia (Fig. 22D) with microtrichial field (**mf**) of endophallus very small; phallus with preapical portion longer, curved ventrad more gradually .... *C. fasciatum* Dejean (in part), **p. 98**

24 (20). Elytron bicolored, with dark marking (Figs. 19A–B) extended to entire posterior margin ....*C. schueppelii* Dejean, **p. 78**

– Elytron bicolored, fasciate (Figs. 22A–C), fascia narrow or broad, but complete posterior margin not dark, at most bicolored..............*C. fasciatum* Dejean, **p. 95**

Melaenus Dejean 1831

Melaenus Dejean 1831: 481. TYPE SPECIES: *Melaenus elegans* Dejean 1831 (by original designation).—Brullé 1835: 85.—Lacordaire 1854: 166.—Andrewes 1921: 184.—Péringuey 1926: 607.—Andrewes 1930: 212.Csiki 1933: 1651.Andrewes 1935: 26

Recognition. In general form, adults of *Melaenus* (Fig. 1A) resemble small platynines. However, they exhibit the features of the tribe Melaenini (see above) and are recognized by the following combination of character states: overall size moderate (length ca. 8–10 mm); body form terete, subpedunculate; color black; dorsal surface subiridescent; mandibular scrobes each with one seta; head with single pair of supraorbital setae, pronotum with single pair of lateral setae; and elytra deeply, regularly striate, humerus projected anteriorly, subdentiform.

Description. Adult, with character states of tribe Melaenini, and recognition features of *Melaenus*, restricted and/or amplified as follows. Measurements of body. SBL more than 6.5 mm, and maximum width (EL) 2.5 mm or more (Tables 3 and 4). Head relatively narrow, values for HW/PWM (Table 5) less than 0.80. Elytra relatively long, values for PL/EL (Table 6) 0.41 or less. Pronotum relatively narrow, values for PL/PWM (Table 7) 0.84 or less, with base relatively broad (values for PWB/PWA (Table 9) 0.78 or more.

Color of body black, elytra concolorous. Appendages: antennae piceous; labrum rufopiceous; mandibles, femora and tibiae black; palpomeres and galeomeres rufous; tarsi rufopiceous to rufous.

Microsculpture. Dorsal surface (head capsule, pronotum, scutellum, and elytra) generally with mesh pattern transverse, sculpticells very narrow, microlines microtrichiate (Figs. 5B, 5F–G); mandibular scrobes (Fig. 6I, **f**) and distal portion of middle tibia (Fig. 7F, **ifs**) with fimbriate sculpticells.

Luster. Body surface shiny, iridescent.

Macrosculpture. Head capsule with surface of frons and vertex generally moderately densely punctate, except clypeus smooth; ventral surface with anterior half laterally punctate like fronto-vertex, but median portion and all of posterior half of head capsule impunctate; or smooth with only elytral intervals punctate. Pronotum, proepisterna, proepimera and prosternum punctate like head, but proepipleura smooth. Abdominal sterna laterally punctate, like pronotum, but narrow medial area impunctate.

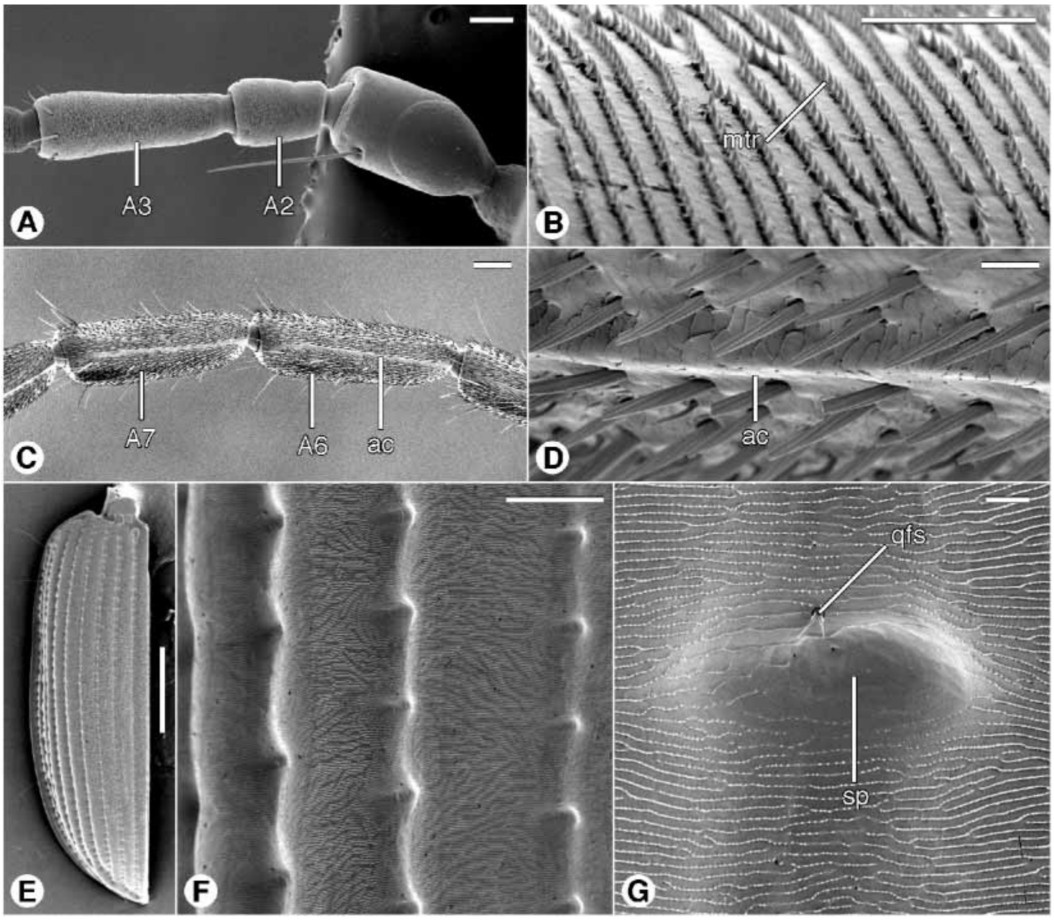


FIGURE 5. Antenna and elytron of *Melaenus piger* Fabricius illustrated with SEM photographs. A, antennomeres 1–3, anterior aspect. B, antennomere 3, illustrating ridged microsculpture. C, antennomeres 6 and 7, posterior aspect, illustrating form and setation. D, antennomere 6, illustrating setae and medial longitudinal carina. E, left elytron, dorsal aspect, illustrating form and striation. F and G, left elytron, dorsal aspect, illustrating microsculpture mesh pattern, punctation and setation. Legend: **A2, A3**, **A6** and **A7**, antennomeres 2, 3, 6 and 7; **ac**, antennal carina; **mtr**, microtrichial ridge; **qfs**, quadrifurcate seta; **sp**, strial puncture. Scale bars: A, C and F = 100 µm; B, D and G = 10 µm; and E = 1mm.

Vestiture. Body surface glabrous (except fixed sensory setae).

Fixed setae (body sclerites, mouthparts, elytra). Head capsule with one pair of clypeal setae and one pair of supraorbital setae; without row of long setae posteriad eyes. Mouthparts: mandible with single seta in scrobe (Figs. 6A–D, **ss**); glossal sclerite (Fig. 7C, **gsc**) with single pair of setae distoventrally. Elytron with parascutellar seta and lateral series. Abdominal sterna IV–VI without pair of ambulatory setae; sternum VII of males asetose; females with one pair setae near posterior margin, medially, inserted close together.

Head. Head capsule with dorsal surface posteriorly even, without pronounced transverse impression but with more or less distinct indentation posteriad eyes. Clypeus without dentiform projection medially on anterior margin.

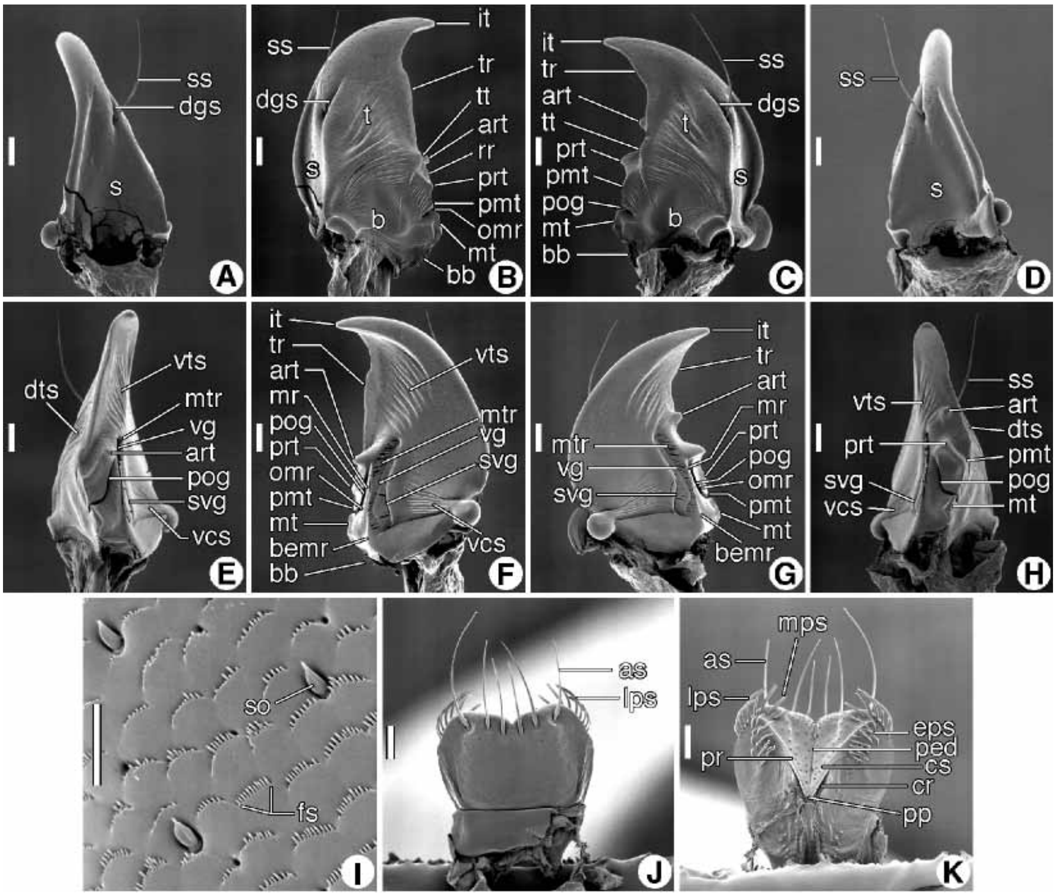


FIGURE 6. Structural features of *Melaenus piger* Fabricius illustrated with SEM photographs. A–I, mandibles: A, D, lateral aspect, left and right mandible, respectively; B, C, dorsal aspect, left and right mandible, respectively; E, H, occlusal aspect, left and right mandible, respectively; and F, G, ventral aspect, left and right mandible, respectively; I, scrobe of left mandible, microsculpture. J, K, labrum, dorsal and ventral aspect, respectively. Legend: **art**, anterior retinacular tooth; **as,** apical seta; **b;** basal portion of mandible; **bb**; basal brush; **bemr,** basal extension of molar ridge; **cr,** crepis; **cs**, coeloconic sensillum; **dgs**, dorsal groove of scrobe; **dts**, dorsal terebral sulcus; **eps,** extra parapedial seta; **fs,** fimbriate sculpticell; **it,** incisor tooth; **lps,** lateral parapedial seta; **mps,** medial parapedial seta; **mr,** molar ridge; **mt,** molar tooth; **mtr,** microtrichia; **omr,** occlusal part of molar ridge; **ped,** pedium; **pog,** posterior occlusal groove; **pp,** parapedial projection; **pr,** parapedial ridge; **prt**, posterior retinacular tooth; **rr**, retinacular ridge; **s,** scrobe; **so**, sense organ; **ss,** scrobal seta; **svg**, secondary ventral groove; **t**, terebra; **tr**, terebral ridge; **tt,** terebral tooth; **vcs**, ventral condylar sulcus; **vg**, ventral groove; **vts**, ventral terebral sulcus. Scale bars: A–H and J–K = 100 µm; I = 10 µm.

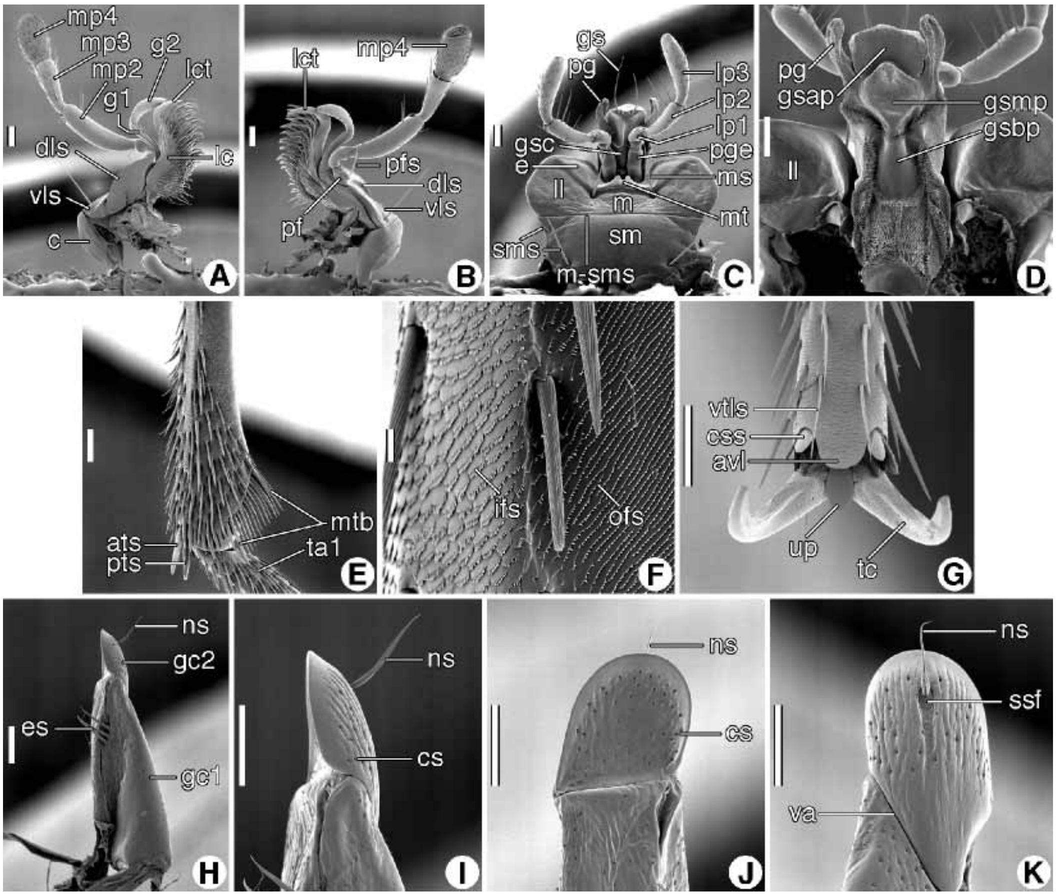


FIGURE 7. Structural features of *Melaenus piger* Fabricius illustrated with SEM photographs. A, B, left maxilla, dorsal and ventral aspect, respectively; C, D, labium, ventral and dorsal aspect, respectively; E, F, left middle tibia, apical portion, and basal portion of tarsomere 1, anterior aspect, E—low magnification, F—high magnification, showing microsculpture; G, middle tarsomere 5, apical portion, and claws, ventral aspect; H–K, ovipositor, left gonocoxa—H, gonocoxa 1 and 2; I–K , gonocoxite 1, apical portion and gonocoxite 2, lateral, dorsal and ventral aspects, respectively. Legend: **c**, cardo; **cs,** coeloconic sensillum; **ats**, anterior tibial spur; **avl**, apical ventral lobe of t-5; **css**, clamshell sensillum; **dls**, dorsal lobe of stipes; **e,** epilobe of mentum; **es**, ensiform seta; **g1,** galeomere 1; **g2,** galeomere 2; **gc1,** gonocoxite 1; **gc2,** gonocoxite 2; **gs**, glossal apical seta; **gsap**, glossal sclerite, apical portion; **gsbp,** glossal sclerite, basal portion; **gsc**, glossal sclerite; **gsmp,** glossal sclerite, medial portion; **ifs,** inner face sculpticell; **lc,** lacinia; **lct**, lacinial tooth; **ll**, lateral lobe of mentum; **lp1**, labial palpomere 1; **lp2**, labial palpomere 2; **lp3**, labial palpomere 3; **m**, mentum; **mp2,** maxillary palpomere 2; **mp3,** maxillary palpomere 3; **mp4,** maxillary palpomere 4; **ms**, paramedial seta of mentum; **m-sms**, mental-submental suture; **mt**, mental tooth; **mtb**, middle tibial brush; **ns**, nematiform seta; **ofs**, outer fimbriate sculpture; **pf**, palpifer; **pfs,** palpiferal seta; **pg**, paraglossa; **pge,** palpiger; **pts,** posterior tibial spur; **sm,** submentum; **sms**, submental seta; **ssf**, subapical sensory furrow; **ta1**, tarsomere 1; **tc**, tarsal claw; **up**, unguitractor plate; **va**, ventral articulation; **vls**, ventral lobe of stipes; **vtls,** ventrolateral seta. Scale bars: A–E and G–K = 100 µm; F = 10 µm.

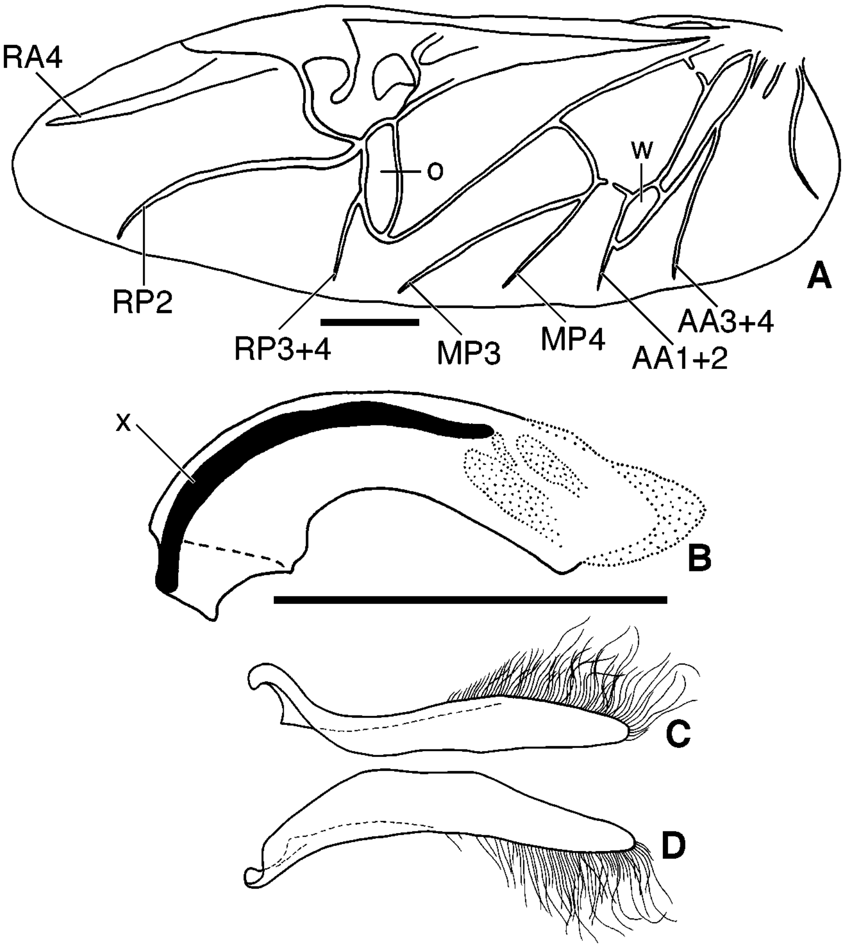
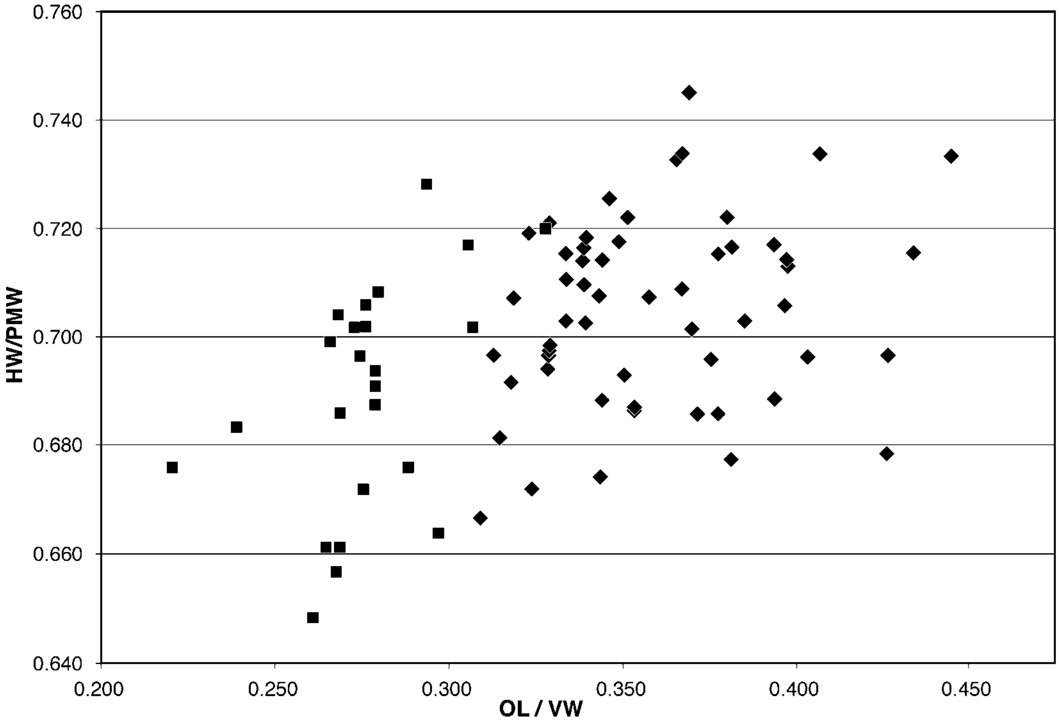


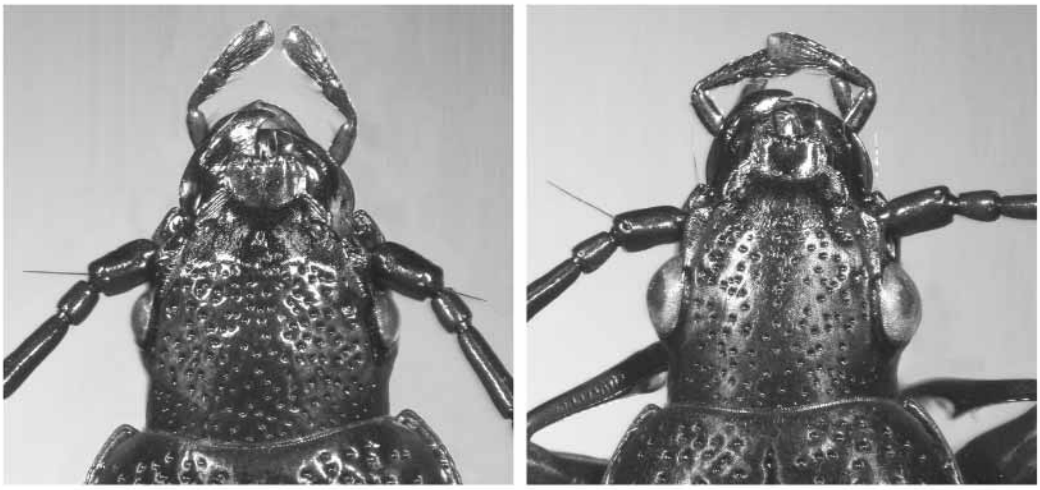
FIGURE 8. Structural features of *Melaenus piger* Fabricius illustrated with line drawings. A, left hind wing with venation, dorsal aspect. B–D, phallus and endophallus, in part. Legend: wing veins and cells—**AA1+2** and **AA3+4,** anal veins 1+2 and 3+4, respectively; **MP3** and **MP4,** posterior median veins 3 and 4, respectively; **o**, oblongum cell; **RA4**, anterior radial vein 4; **RP2** and **RP3+4**, posterior radial veins 2 and 3+4, respectively; **w**, wedge cell. Male genitalia: **x,** sclerite x of endophallus. Scale bars = 1.0 mm.

Eyes (Fig. 9). Various: relatively large, values for OL/VW 0.31–0.44, or relatively small, values for OL/VW 0.22–0.33 (Table 10).

Antennae (Fig. 1A). Filiform, relatively long, extended distinctly posteriad pronotum**.** Antennomeres 1–4 (cf. Fig. 5A) with few setae, inserted near distal margin of respective articles; antennomeres 5–11 (cf. Fig. 5C, **ac,** and 5D) densely, uniformly setose, except for narrow, shiny carina extended longitudinally on anterior and posterior surfaces; antennomeres evenly constricted proximally, not pyriform; antennomere 3 distinctly longer than antennomere 2, Ant 2 L/Ant 3 L 0.50 or less (Table 11); antennomeres 5–10 about 2.5X longer than wide, slightly asymmetrical in form (Fig. 5C); antennomere 11 similar in form to 5–10, but tapered distally to narrow apex.



A. Relationship between variation in the ratios 0L/VW and HW/PMW for microphthalmous ■ (B) and euphthalmous ◆ (C) specimens.



B. microphthalmous **C.** euphthalmous

FIGURE 9. Dimorphism in *Melaenus elegans* Dejean. A, Relationship between variation in the ratios 0L/VW and HW/PMW for B, microphthalmous, and C, euphthalmous, specimens.

Mouthparts. Labrum: apical margin slightly, evenly, to rather deeply subangularly concave. Epipharynx (Fig. 6K) with pedium (**ped**) long, in form of equilateral triangle; extra parapedial setae (**eps**) laterad parapedial ridge (**pr**).

Mandibles. Left mandible in dorsal aspect (Fig. 6B) with anterior retinacular tooth (**art**) evident. Right mandible (Fig. 6C) in dorsal aspect with both retinacular teeth evident, but retinacular ridge concealed beneath terebral ridge.

Labium (Figs. 7C–D). Paraglossae (**pg**) slender, narrow lobe, attached to glossal sclerite at base, only, surface without extensive covering of seta-like microtrichia.

Prothorax. Pronotum (Fig. 1A) with lateral margins beaded; lateral grooves broad; posterior margin not beaded, flat; proepipleuron not evident in dorsal aspect; disc slightly convex, lateral declivity each side steep; posteriolateral angles acute, slightly projected.

Elytra (Fig. 5E). Dorsal surface flat for most of length, apical declivity moderately steeply sloped; basal ridge narrow, extended to base of stria 5, not to edge of scutellum, anteriorly angulate; striae deep, distinct throughout length, punctate; intervals moderately convex.

Hind wings (Fig. 8A). Macropterous. Wedge cell (**w**) large. Veins **RP 3 + 4** and **AA 3 + 4** present. Vein **MP 4** more than half-length of **MP 3.**

Legs. Unguitractor plate (Fig. 7G, **up**) broad.

Abdominal sclerites. Sterna IV–VII narrowly transversely sulcate, posteriorly.

Male genitalia (Figs. 8B–D). Endophallus with sclerite x (Fig. 8B, **x**) large, more than half length of median lobe; parameres slender, elongate, with dense row of long setae distally (Figs. 8C–D).

Ovipositor (Figs. 7H–K). Laterotergite IX with anteriorly directed apophysis. Ramus about 0.80 length of gonocoxite 1. Gonocoxite 2 much shorter than gonocoxite 1 (Fig. 7H, **gc1, 2**), in lateral aspect (Fig. 7I) with dorsal margins straight, not curved; broad in outline, distal margin broadly rounded (Figs. 7J–K), ventral surface longitudinally rugulose (Figs. 7I–K).

Female internal genitalia (Deuve 1993: 148, Fig. 222). Spermathecal duct shorter than spermathecal reservoir (**sp**), latter sausage shaped.

Included taxa. This genus includes two species, *M. piger* Fabricius and *M. elegans* Dejean.

Habitat. The members of *Melaenus* occupy primarily the tropical deciduous forest/savannah vegetation zone, but also desert/semi desert and tropical rain forest zones (Table 17 and Fig. 24).

Geographical distribution. The range of *Melaenus* (Fig. 10), confined to the Eastern Hemisphere, is discontinuous, including only the Oriental Region, eastern Palaearctic Africa, and the central to northern parts of the Afrotropical Region, excluding the Congo Basin.

Relationships and chorological affinities. This genus is the more generalized putative adelphotaxon of *Cymbionotum* Baudi di Selve. The geographical ranges of these genera overlap broadly in the Oriental Region, and in Africa (cf. Table 17).

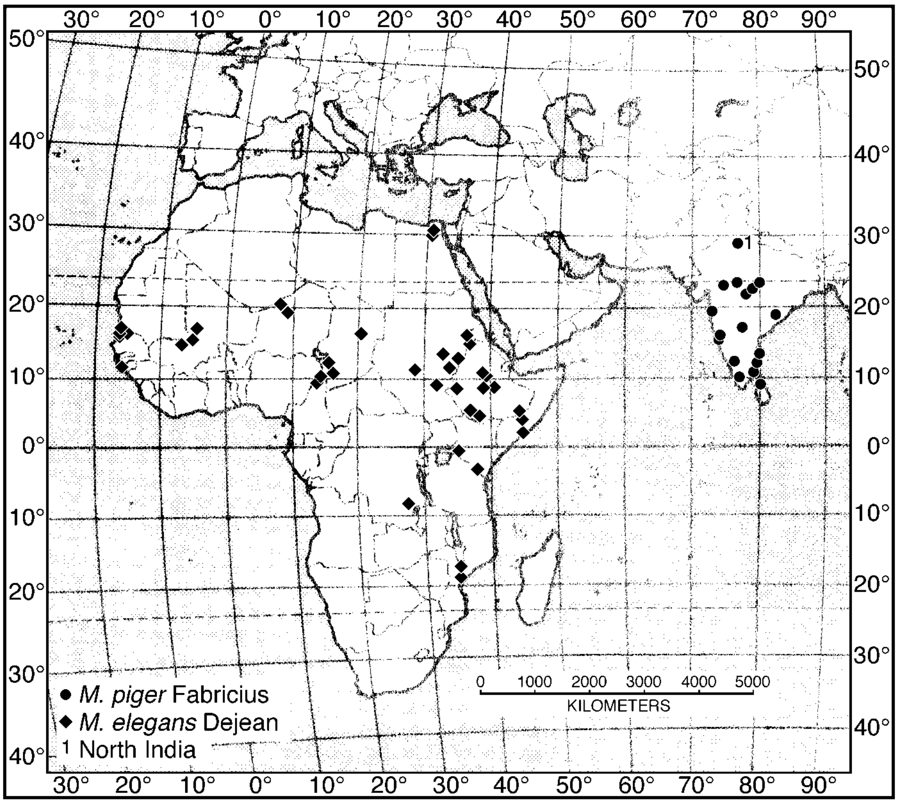


FIGURE 10. Geographical range of the species of *Melaenus* Dejean illustrated on an outline map of southwestern Asia, southern Europe, and Africa.

Melaenus piger (Fabricius 1801)

(Figs. 1A, 5A–G, 7A–K, 8A–D, 10)

Brachinus piger Fabricius 1801: 219. TYPE MATERIAL: not seen (the type is in the Zoological Museum, University of Copenhagen Copenhagen, Denmark (Andrewes 1921: 164)).

Melaenus piger Schaum 1847: 49.—Erichson 1847: 142.—Motschulsky 1855: 42.—Andrewes 1921: 164, 185.—1930: 212.—1935: 28.

Type locality. Eastern India, as recorded in the original description (Fabricius 1801: 219).

Recognition. See Fig. 1A and key to melaenine taxa.

Description. With character states of genus *Melaenus*, restricted as follows. Habitus as in Fig. 1A. Measurements: see *Melaenus* in Tables 3–11, and "Comparisons" below, under *M. elegans* Dejean. Male genitalia: phallus, endophallus and parameres as in Figs. 8B–D.

Habitat, habits and seasonal occurrence. This species lives primarily in the tropical deciduous forest/savannah vegetation zone, but also the rain forest zone (Table 17), at altitudes between sea level and 1000 m. Andrewes (1935: 27) recorded specimens to be common in refuse bordering rice fields, and wrote that the beetles fly at night. Erwin (1984: 379) wrote that specimens "are found in disturbed areas, in decaying vegetation." From these statements we infer that members of *C. piger* may occupy open areas, rest under cover by day, and are active at night. Based on label data, we infer that the period of maximum adult activity is in June, extending overall from March to December.

Geographical distribution (Fig. 10). This species is known only from Sri Lanka and India, in the western part of the Oriental Region.

Relationships and chorological affinities. This species is the putative adelphotaxon of *M. elegans* Dejean, the only other known species of *Melaenus.* Their marked structural similarities to one another suggest a very close relationship. They form a vicariant pair with *M. piger* restricted to the Indian sub-continent and *M. elegans* occurring only on the African continent.

Material examined. We have seen 86 specimens from the following localities, all of which are in the Oriental Region. Included also are records published by Andrewes (1930).

INDIA. Andhra Pradesh State: Kurnool (Andrewes, 1930) **Bombay State:** Bandra; Belgausa; "Bombay State"; Igatpuri Nagpur (Andrewes, 1930). **Madhya State:** Balaghat; Hoshangabad (Andrewes, 1930); Jabalpur, VI.1906, F. Benton, 1 (USNM); Mhow (Andrewes, 1930). **Madras State.** Bonamalea, VI.1962, P.S. Nathan, 1 (USNM); Karikal, 1 (MRAC); Karikal, VIII.1964, 2 (USNM); Karikal, T.R.S. Nathan (CMNH): VIII.1982, 5; VII.1984, 2; VIII.1986, 3; VII.1987, 1; VII.1988, 2; Kurumbagaram, IX.1951, P.S. Nathan, 33 (UASM); same, VI.1952, 11 (UASM); same, IV.1962, 1 (UASM); Madras; Ootacamund (Andrewes, 1930); Pondicherry, 2 (USNM); same, VII.1963, 2 (USNM); Tinnevelly (Andrewes, 1930); Uppaluru, VI.1962, Biff, 4 (UASM). **Mysore State:** Belgaum, 1927, C.F. Baker, 1 (USNM); same, 2 (OXUM). **New Goa State:** Panjim, XII.1924, J.C. Bridwell, 1 (USNM). **Orissa State:** Chatrapur (Andrewes, 1930). **State not determined.** "Bengal"; Kunavaram (Andrewes, 1930); "India", 1 (OXUM); "North India", Capt. Boys, 1 (OXUM); "South India", 2 (MRAC); Tabalpun, 1600', X.1957, P.S. Nathan, 3 (USNM); W. W. Jar[*sic*],Worth, 1 (OXUM). **SRI LANKA. Anu District:** Belaya Wowai, 8ºS, 80º30'E, nr. Padaviya, 150', 4–5.XI.1970, O.S. Flint, Jr., 1 (USNM); Padaviya, 180', 2–8.XI.1970, O.S. Flint, Jr., 1 (USNM); Padaviya, 180', 27.II–9.III.1970, Davis & Rowe, 1 (USNM). **North Central District:** Horouwpotana (Andrewes, 1930).

Melaenus elegans **Dejean 1831**

(Figs. 9, 10)

Melaenus elegans Dejean 1831: 482. TYPE MATERIAL: in Oberthür/ Chaudoir Collection (MNHP). LECTOTYPE, here designated, (sex undetermined), labeled: "elegans"; "Sénégal"; "Dumolin" [this and the preceding, handwritten on blue paper]; "Ex Musaeo/Chaudoir" [red print].—Lacordaire 1854: 167.—Péringuey 1926: 608.—Burgeon 1935: 175.

Melaenus elongatus Chaudoir 1843: 721. TYPE MATERIAL: in Oberthür/ Chaudoir Collection (MNHP), associated with the following box label: "elongatus/ Chaud./ Kordofan/ Parrey s." LECTOTYPE, here designated, female, labeled: "type/ Parreyss"; "atramentarius/ Nobis Bohem" [both labels handwritten]; "Ex Musaeo/ Chaudoir" [red print]. **NEW SYNONYMY.**

Notes about type material. Dejean (1831: 482) gave two measurements for *M. elegans*, indicating he had at least two specimens. Chaudoir (1843:721) gave only one measurement for *M. elongatus*, but it is possible that he had more than one specimen. Although each of these nominal species was represented by a single specimen in the Oberthür/ Chaudoir collection, each is designated as LECTOTYPE for its respective species.

Notes about synonymy. The principal difference between the types of the two putative taxa is size (for *M. elegans*, the SBL is 6.56 mm; for *M. elongatus*, 9.38 mm). The latter is indeed large for an African *Melaenus*, and is euphthalmous (large-eyed, see “Geographical Variation”, below). However, that is the only difference of the few specimens noted by Chaudoir (1843: 721) and that were examined quantitatively. This difference is bridged by other specimens. So, larger size is not a basis for species recognition.

Type area. Sénégal.

Recognition. See key to melaenine taxa. This is the only African species of *Melaenus*.

Comparisons. A description is not required here because of the marked similarity between adults of this species and those of *M. piger.* The two groups overlap broadly in size and proportions, with *M. elegans* averaging larger in size, as indicated by values for SBL:

M. piger (N = 20) 6.19–8.19 mm, Mean 7.61 mm;

M. elegans (N = 19) 6.80–9.89 mm, Mean 7.70 mm.

Geographical variation. Eye size and surface punctation exhibit an interesting pattern. In western Africa (Mali to Sénégal) eye size and density of head and pronotal punctation is monomorphic: eyes relatively large, and punctation moderately dense (Fig. 9C). In eastern Africa, these features are markedly dimorphic: most individuals that we have seen from the Sudan, Ethiopia, and Somalia are like their western counterparts, comprising a euphthalmous form (Fig. 9C). But some individuals, sympatric with the euphthalmous form, exhibit smaller eyes and denser punctation, and are grouped as the microphthalmous form (Fig. 9B). The differences are expressed as two ratios: relative eye length (OL/VW), and eye convexity (HW/PMW). Values for these ratios are presented in Table 10.

For the ratio OL/VW, values are non-overlapping for males (microphthalmous, 0.22–0.31; euphthalmous, 033–044). For females, overlap in values overall is slight (microphthalmous, 0.24–0.33; euphthalmous 0.31–0.43), but within regions, values do not overlap.

For the ratio HW/PMW, values overall overlap broadly: for males (microphthalmous, 0.66–0.73; euphthalmous, 0.69–0.75) and for females (microphthalmous, 0.65–0.72; euphthalmous, 0.69–0.75). But on a regional basis, males of the two eye morphs of the Sudanese and Somalian samples exhibit non-overlapping values, whereas for females, only the Somalian samples exhibit non-overlapping values. For both males and females, overlap is most extensive for the Ethiopian/Eritrean samples, least for the Somalian sample, with the Sudanese sample being intermediate.

The overall pattern of variation is one of continuity, as shown by a combination of the two ratios (Fig. 9A). Size range, as indicated by values for SBL (Table 10), overlaps broadly for the two morphs, but larger individuals seem to be more frequent for the euphthalmous morph.

Regarding surface punctation, overall the microphthalmous individuals exhibited more punctures on the dorsal surface of the head (Fig. 9B), and ventral surface of the metasternum, and medial areas of abdominal sterna III–IV. In euphthalmous individuals, the ventral surface of the metasternum was either impunctate or punctate; the medial area of abdominal sterna III–IV was either impunctate, punctate in apical half only, or punctate throughout. A few of the euphthalmous individuals exhibited more punctures on the dorsal surface of the head than some microphthalmous individuals.

In summary, morphometric dimorphism is especially marked in Somalia. In Ethiopia/ Eritrea, one finds typical euphthalmous and microphthalmous individuals, but also some whose features bridge the gap between the extremes. Further, extent of surface punctation is partially correlated with eye size, but not completely. These differences may indicate specific distinction, but in view of the virtual continuity of variation among the small samples, the marked overlap in geographical range, and the absence of other features to distinguish the two morphs, we infer that they are conspecific, One might make a case for recognition of a western monomorphic subspecies, and an eastern one that is dimorphic for eye size, but such taxonomic recognition is not recommended at this time.

Habitat, habits and seasonal occurrence. This species occupies primarily the tropical deciduous forest/savannah vegetation zone (dry woodland and grassland; see Hall and Moreau 1970: xiii, Map B), but also marginally, the desert/semi desert zone (Figs. 10, 24 and Table 17), at altitudes between sea level and 2000 m. The "desert" record concerns a specimen from Cairo, which might have reached that locality by way of the Nile River, a more mesic route across the Sahara desert. Based on label data, we infer that the period of adult activity extends throughout the year, with records for every month. However most specimens were collected in October.

Geographical distribution (Fig. 10). This species is confined to the African continent, and is probably indigenous in the Afrotropical Region.

Relationships and chorological affinities. This species is the putative adelphotaxon of *M. piger*, the only other known species of *Melaenus*. See comments under "Geographical distribution" for *M. piger*, above.

Material examined. Excluding types, we have seen 134 specimens from the following localities, most of which are in the Afrotropical Region. The locality records are grouped by morph (euphthalmous; and microphthalmous).

EUPHTHALMOUS MORPH

CAMEROON: Garova, 2.X.1966, and 27.IX.1974, P. Bruneau de Miré, 2 (MNHP); Koze, Guétalé, IX.1970 P. Bruneau de Miré, 1 (MNHP); Mayo Kebi, route de Béré, 2.XI.1977, Bruneau de Miré, 1 (MNHP); Yagova, VIII.1971, Bruneau de Miré, 9 (MNHP); **CHAD.** Bas Chari, Fort Lamy, 1904, D.J. Decorse, 2 (MRAC); Ouadi Ouargalla=Ouadi Goumer, 18.IX.1935, 2 (MRAC). **DEMOCRATIC REPUBLIC OF THE CONGO. Tanganika Dist.:** Moero Ankoro, 21.VI.1930, D.R. Gerard, 1 (MRAC). **ERITREA.** Setit Humera, 14.X.1973, T.J. Crowe, 6, 17 (MRAC). **ETHIOPIA. Ilubador**: Gambela, XI.1972, R.O.S. Clarke, 7 (MRAC). **Sidamo:** 18 km NE Yavello, 1550 m, 7–10.V.1975, R.O.S. Clarke, 6 (MRAC). **District not determined:** Omo Valley, I.1942, H.T.E. Jackson, 1 (MRAC); same, 2 (USNM). **GUINEA-BISSAU.** Susana**,** 12º18'23", 16º28'28", VII.1953, Andreoletti, 2 (MRAC). **KENYA.** Da Dime, al bas Narok, VIII–IX.1896, Bottego, 1 (Nègre Coll., MNHP); 750 m., III.1912, Alluaud & Jeannel, 2 (MRAC). **MALI.** Dogo, 5.VIII.1950, G. Remaudiere, 1(MRAC); Goundam, XII.1954, R. Mauny, 2 (MRAC); Kogoni, X.1966, G. Schmitz, 11 (MRAC); Kouya Lac-Fati, R. Mauny, 2 (MRAC). **MAURITANIA.** Bafrechie, IFAN, 15.IX–10.X.1953, A. Villiers, 1 (MRAC); Boghe, X.1968, R. Frieser, 1 (MRAC); Rosso, J.L. Amiet, 4 (MRAC). **MOZAMBIQUE.** Nova Chupanga, near Chemba,1928, P. Lesne, 1 (MRAC); Nova Chupanga, XII.1928–I.1929, J. Surcouf, 1 (MRAC); Sone, 1929, J. Surcouf, 1 (MRAC). **NIGER:** Aïr, Agadez, 23.X.1953, P. Bruneau de Miré, 1 (MNHP); Temesna Irhazer, 22.I.1951, P. Bruneau de Miré, 1 (MNHP). **SÉNÉGAL.** Richard Toll, IX.1948, A. Villiers, 1 (MRAC); same, XI.1967, A. Descarpentries, T. Leye, & A. Villiers, 2 (MRAC); same, at light, 8.X.1969, G. Schmitz, 1 (MRAC); St. Louis, environs, VII.1952, L. Laurent, 1 (MRAC); "Sénégal". 3 (OXUM). **SOMALIA.** Afgoi, 1.VIII.1977, Olmi, 1 (MRAC); Belet Amin (Giuba), P. Basilewsky, 1 (MRAC); Giohar, 18–20.IV.1968, 1 (MRAC); Pnd. di Fungalongha, III–IV.1923, Patrizi, 1 (Nègre Coll., MNHP). **SUDAN. Blue Nile Province:** Abu Hashim-Galegu, 23–24.II.1962, Linnavuori, 1 (MRAC);; same, 14.3ºN, 5–20.X.1901, W.L.S. Loat, 1 (OXUM); Wad Medani, at light, 9–29.X.1979, F. Hieke, 4 (MRAC). **Kassala Province**: Kassala-Haiya, 1–3.XII.1962, Linnavuori, 3 (MRAC). **Kordofan Province:** 1 [holotype, *M. elongatus* Chd.] (MNHP); 1 (MNHP); Kadugli, VII.1952, C. Sweeney, 1 (CASC). **Upper Nile Province:** Malakal, 4.VI.1927, L. Burgeon, 1 (MRAC); same, 1963, Linnavuori, 1 (MRAC); same, 5–20.I.1963, Linnavuori, 4 (MRAC). **TANZANIA. Mesal District:** Longido, 1500m, 17–20.IV.1957, P. Basilewsky & N. Leleup, 3 (MRAC).

PALAEARCTIC REGION. EGYPT: "Egypt", 1 (OXUM); Kafr Hakim, 23.X.1932, A. Alfieri, 1 (USNM); Sakkara, 9.10.1932, W. Wittmer, 2 (Antoine Coll., MNHP); Talbich, 9.X.1932, A. Alfieri, 1 (USNM).

NO LOCALITY DATA: 1 (USNM); 4 (OXUM).

MICROPHTHALMOUS MORPH

ERITREA. Guridet, Clermont, 1 (MRAC). **ETHIOPIA. Gemu-Gofa**: Arba-Minch, 1250m, 21.IX.1974, G. de Rougemont, 1 (MRAC). **Gojjam:** 5 km E Bahar Dar, 19.X.1973, G. de Rougemont, 3 (MRAC); Tissigat Falls, 19.X.1973, R.O.S. Clarke, 4 (MRAC). **Harer:** Gode-Ogaden, 7.XI.1974, T.J. Crowe, 2 (MRAC). **Shoa:** Awash National Park, 1000 m, 14–15.VIII.1971, R.O.S. Clarke, 2 (MRAC); Gibbie Gorge, VII.1971, G. de Rougemont, 1 (MRAC). **SOMALIA**. Belet Amin (Giuba), P. Basilewsky, 1 (MRAC). Mogadishu, 28.IV.1988, P. Kuchar, 1 (UASM); same, at light, 28–29.IV.1988, P. Kuchar, 1 (UASM). **SOMALIA. Blue Nile Province:** bank of Rosaires, 12ºN, X.1901, W.L.S. Loat, 1 (OXUM); **Kassala Province**: Kassala-Haiya, 1–3.XII.1962, Linnavuori, 1 (MRAC).

TABLE 3. Data about variation in Standardized Body Length (SBL, mm) for supraspecific taxa of Melaenini.

	N	Range	Mean
Melaenus Dejean	39[1]	6.91–9.89	7.65
Cymbionotum Baudi di Selve			
Procoscinia, **n. subg.**	40[2]	3.66–4.51	4.15
Cymbionotum (sensu stricto)			
basale species group	21[3]	5.17–6.22	5.87
semelederi species group	56[4]	4.46–5.79	5.02
schueppelii species group			
schueppelii superspecies	54[5]	3.23–4.08	3.59
fasciatum superspecies	109[6]	3.01–4.29	3.73
microphthalmum superspecies	37[7]	2.74–3.80	3.37

[1] 2 species, 9 samples

[2] 2 species, 3 samples

[3] 2 species, 5 samples

[4] 3 species, 10 samples

[5] 2 species, 7 samples

[6] 5 species, 17 samples

[7] 5 species, 9 samples

TABLE 4. Data about variation in maximum width of elytra (EW, mm) for supraspecific taxa of Melaenini.

	N[1]	Range	Mean
Melaenus Dejean	39	2.56–3.68	2.97
Cymbionotum Baudi di Selve			
Procoscinia, **n. subg.**	40	1.26–1.55	1.44
Cymbionotum (sensu stricto)			
basale species group	21	1.68–2.13	1.92
semelederi species group	56	1.44–2.03	1.67
schueppelii species group			
schueppelii superspecies	54	0.99–1.33	1.16
fasciatum superspecies	109	0.98–1.44	1.20
microphthalmum superspecies	37	0.85–1.88	1.04

[1] See Table 3 for details about composition of samples.

TABLE 5. Data about variation in values for the ratio HW/PWM for supraspecific taxa of Melaenini.

	N[1]	Range	Mean
Melaenus Dejean	39	0.68–0.75	0.72
Cymbionotum Baudi di Selve			
Procoscinia, **n. subg.**	40	0.84–0.96	0.88
Cymbionotum (sensu stricto)			
basale species group	21	0.83–0.95	0.90
semelederi species group	56	0.87–0.96	0.90
schueppelii species group			
schueppelii superspecies	54	0.87–0.97	0.91
fasciatum superspecies	109	0.83–1.03	0.89
microphthalmum superspecies	37	0.85–0.98	0.90

[1] See Table 3 for details about composition of samples.

TABLE 6. Data about variation in values for the ratio PL/EL for supraspecific taxa of Melaenini.

	N[1]	Range	Mean
Melaenus Dejean	39	0.35–0.41	0.37
Cymbionotum Baudi di Selve			
Procoscinia, **n. subg.**	40	0.40–0.45	0.42
Cymbionotum (sensu stricto)			
basale species group	21	0.40–0.48	0.45
semelederi species group	56	0.40–0.48	0.42
schueppelii species group			
schueppelii superspecies	54	0.41–0.47	0.44
fasciatum superspecies	109	0.40–0.49	0.44
microphthalmum superspecies	37	0.40–0.47	0.45

[1] See Table 3 for details about composition of samples.

TABLE 7. Data about variation in values for the ratio PL/PWM for supraspecific taxa of Melaenini.

	N[1]	Range	Mean
Melaenus Dejean	39	0.715–0.84	0.74
Cymbionotum Baudi di Selve			
Procoscinia, **n. subg.**	40	0.79–0.86	0.83
Cymbionotum (sensu stricto)			
basale species group	21	0.87–1.04	0.95
semelederi species group	56	0.78–0.95	0.86
schueppelii species group			
schueppelii superspecies	54	0.82–0.97	0.92
fasciatum superspecies	109	0.75–1.03	0.90
microphthalmum superspecies	37	0.84–0.96	0.92

[1] See Table 3 for details about composition of samples.

TABLE 8. Data about variation in values for the ratio VW/HW for supraspecific taxa of Melaenini.

	N[1]	Range	Mean
Melaenus Dejean	39	0.71–0.84	0.77
Cymbionotum Baudi di Selve			
Procoscinia, **n. subg.**	40	0.76–0.86	0.80
Cymbionotum (sensu stricto)			
basale species group	21	0.75–0.81	0.78
semelederi species group	56	0.82–0.92	0.86
schueppelii species group			
schueppelii superspecies	54	0.77–0.87	0.82
fasciatum superspecies	109	0.67–0.88	0.80
microphthalmum superspecies	37	0.80–0.96	0.91

[1] See Table 3 for details about composition of samples.

TABLE 9. Data about variation in values for the ratio PWB/PWA for supraspecific taxa of Melaenini.

	N[1]	Range	Mean
Melaenus Dejean	39	0.78–1.03	0.84
Cymbionotum Baudi di Selve			
Procoscinia, **n. subg.**	40	0.68–0.90	0.81
Cymbionotum (sensu stricto)			
basale species group	21	0.64–0.76	0.71
semelederi species group	56	0.59–0.73	0.64
schueppelii species group			
schueppelii superspecies	54	0.60–0.76	0.69
fasciatum superspecies	109	0.61–0.82	0.68
microphthalmum superspecies	37	0.58–0.74	0.67

[1] See Table 3 for details about composition of samples.

TABLE 10. Data about variation in values for SBL and ratios OL/VW and HW/PMW among euphthalmous and microphthalmous samples of *Melaenus elegans* Dejean.

Area	N	SBL		OL/VW		HW/PMW	
		Range	Mean	Range	Mean	Range	Mean
				Euphthalmous Males			
Mali	5	6.88–7.62	7.21	0.38–0.40	0.39	0.71–0.72	0.71
Sudan	7	6.88–8.44	7.57	0.35–0.44	0.37	0.71–0.75	0.73
Eth./Erit.	10	7.30–9.72	8.29	0.33–0.39	0.35	0.69–0.72	0.70
Somalia	2	8.68–9.12	8.90	0.43		0.70–0.72	0.71
				Euphthalmous Females			
Mali	5	7.23–8.10	7.82	0.36–0.40	0.38	0.68–0.72	0.70
Sudan	4	7.36–8.80	8.11	0.34–0.41	0.36	0.70–0.73	0.72
Eth./Erit.	21	6.08–9.22	7.34	0.31–0.38	0.34	0.67–0.72	0.70
Somalia	2	8.24–9.89	9.06	0.40–0.43	0.41	0.68–0.70	0.69
				Microphthalmous Males			
Sudan	2	7.72–7.84	7.78	0.22–0.31	0.26	0.68–0.70	0.69
Eth./Erit.	6	6.80–8.20	7.35	0.27–0.31	0.28	0.69–0.73	0.71
Somalia	1	8.44		0.27		0.66	
				Microphthalmous Females			
Sudan	5	6.80–8.60	7.82	0.28–0.33	0.30	0.66–0.72	0.69
Eth./Erit.	9	6.92–9.16	8.00	0.24–0.28	0.27	0.66–0.70	0.69
Somalia	2	8.60–8.76	8.68	0.26–0.27	0.27	0.65–0.66	0.66

TABLE 11. Data about variation in proportion of antennomeres 2 and 3 (A2L/A3L) for selected species samples of Melaenini

	N	Range	Mean
Melaenus Dejean			
M. piger Fabricius	20	0.42–0.50	0.47
Cymbionotum Baudi di Selve			
Procoscinia, **n. subg.**			
C. fernandezi, **n. sp.**	37	0.64–0.80	0.66
Cymbionotum (sensu stricto)			
basale species group			
C. semirubricum Reitter	7	0.61–0.75	0.70
semelederi species group			
C. semelederi Chaudoir	10	0.47–0.57	0.54
schueppelii species group			
C. schueppelii Dejean	10	0.67–0.78	0.71
C. fasciatum Dejean	10	0.64–0.70	0.68
C. microphthalmum Chd.	25	0.67–0.78	0.74

Cymbionotum Baudi di Selve 1864

Synonymy. See following treatment of subgenus *Cymbionotum*.

Recognition. In general form, adults of *Cymbionotum* (Fig. 1B) resemble small adults of *Siagona* Latreille. However, they exhibit the features of the tribe Melaenini (see above), and are recognized by the following combination of character states: overall size small (length ca. 3–7 mm); body form depressed, broad, pedunculate; integument generally setose; color pale (though elytra of some species bicolored); vertex of head with distinct postocular transverse sulcus; head with two pairs of supraorbital setae, mandibular scrobes each with several setae; pronotum with two pairs of lateral setae; elytral surface virtually smooth, striae absent or very shallowly impressed.

Description. Adult, with character states of tribe Melaenini, and recognition features of *Cymbionotum*, restricted and/or amplified as follows. Color of body black to rufotestaceous, elytra concolorous or bicolored. Body form depressed. Antennae and mouthparts rufotestaceous to testaceous, concolorous. Legs rufotestaceous.

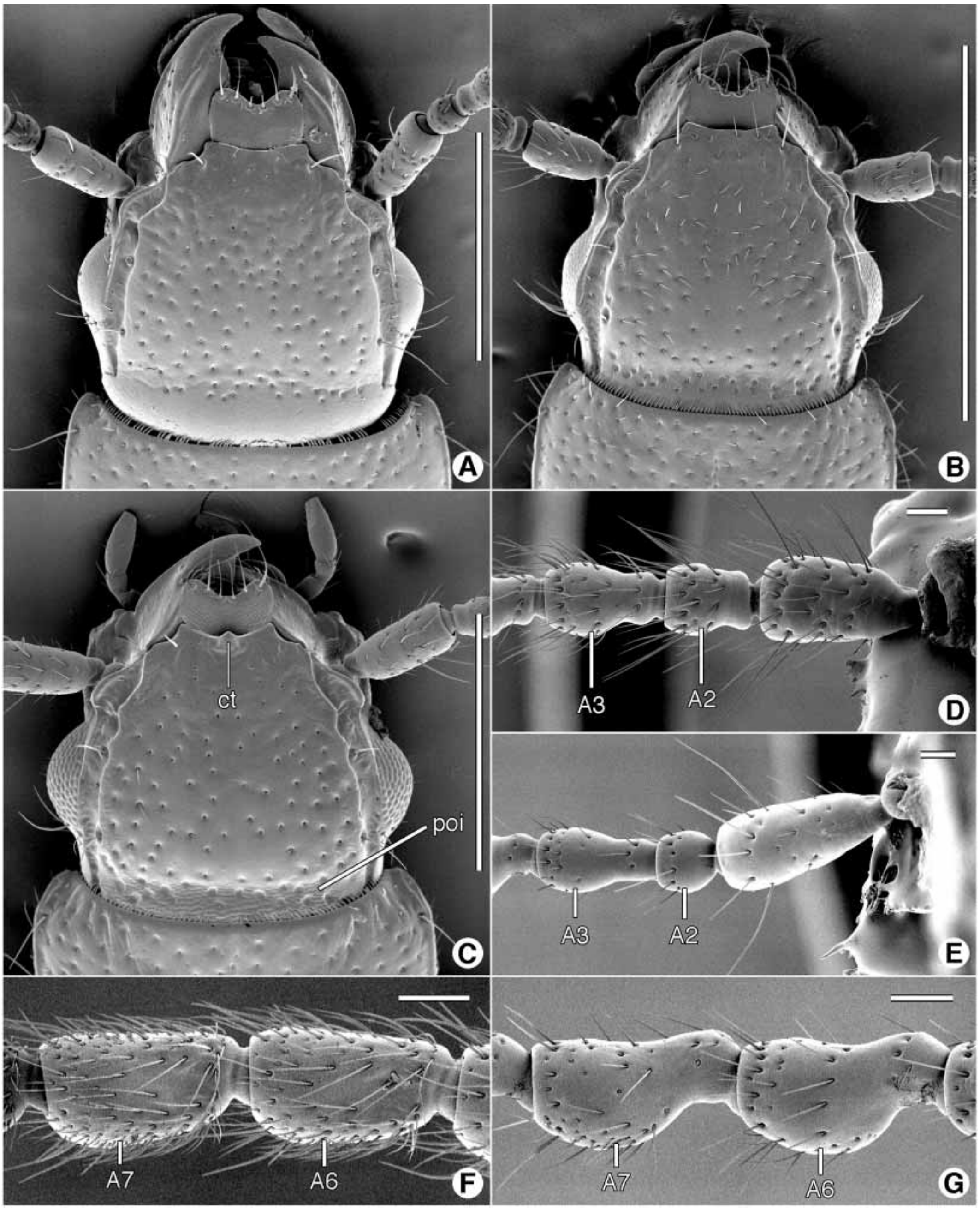


FIGURE 11. Heads and antennae of *Cymbionotum* species illustrated with SEM photographs: A–C, head, dorsal aspect of: A, *C. semelederi*, Fabricius; B, *C. microphthalmum* Chaudoir; C, *C. helferi* Chaudoir. D–G, left antenna of: D, *C. semirubricum* Reitter (antennomeres 1–3, anterior aspect); E, *C. striatum* Reitter (antennomeres 1–3 and base of 4); F and G, *C. semirubricum* and *C. striatum*, respectively (antennomeres 6 and 7, posterior aspect). Legend: **A2, A3**, **A6** and **A7**, antennomeres 2, 3, 6 and 7; **ct**, clypeal tooth; **poi**, postocular impression. Scale bars: A–C = 1.0 mm; D–G = 100µm.

Microsculpture. Dorsal surface generally with isodiametric mesh pattern, microlines shallow; or microlines absent, except in postocular transverse impression of dorsal surface of head (Fig. 11C, **poi**) with isodiametric to slightly transverse mesh pattern, or smooth, without microlines; or microlines absent, surface without evident mesh pattern. Scutellum with mesh pattern isodiametric to slightly transverse, microlines confined to anterior area, or generally distributed; or completely smooth, without microlines. Middle tibia (Fig. 13D, **ifs**) with mesh pattern on inner surface elongate, sculpticells flat, microlines not fimbriate. Luster. Body surface dull or shiny.

Punctation and vestiture (cf. Figs. 2A–F, 3A–F, 11A–C). Body surface generally punctate and setose, elytral punctures relatively small (Figs. 2B–E) to large (Fig. 2F), and sparse (Fig. 3A), intermediate (Fig. 3B), dense (Figs. 3C–E), and very dense (Fig. 2A, 3F); elytral setae short (Figs. 2B–C), intermediate (Figs. 2D–E), or long (Fig. 2F). Head posteriad eyes each side with row of anteriorly directed setae (Fig. 11B). Proepipleuron with row of up-turned setae (Figs. 11A–C). All antennomeres setose; all setae relatively long and not especially dense (Figs. 11D–G).

Fixed setae (body sclerites, mouthparts, elytra). Head capsule with two pairs of supraorbital setae. Mouthparts: mandible with several setae in scrobe (Figs. 12A–D, **pss, sss**); glossal sclerite distally quadrisetose (Fig. 13A, **gs**). Pronotum with two pairs of lateral setae. Elytra dorsally without parascutellar or discal setae. Abdominal sterna IV–VII each with pair of setae near posterior margin.

Head (Figs. 11A–C). Wide, dorsal surface slightly convex, with distinct transverse impression posteriad eyes (Fig. 11C, **poi**); clypeus with anterior margin evenly curved, almost straight (Figs. 11A–B), or more markedly concave, with dentiform projection (Fig. 11C, **ct**) in both sexes, or only in males; frontoclypeal suture not evident, frontal impressions hardly indicated, or broad and shallow; frontovertex each side laterad eye with slightly elevated longitudinal ridge extended posteriorly to postocular transverse impression; supraorbital ridge sharp, each side sinuously extended anteriorly to mandibular fossa, here joined to apex of fronto-vertical ridge, and posteriolaterally extended to postocular transverse impression.

Antennae. Nearly moniliform (Fig. 1B), shorter, extended to about basal third of elytra. Antennomere 2 pyriform (Fig. 11D) or globose (Fig. 11E); antennomeres variously proportioned: 2–4 and 11 slightly longer than wide, antennomeres 5–10 slightly longer than wide, slightly (Fig. 11F) or markedly (Fig. 11G) asymmetric.

Mouthparts (Figs. 12A–L, 13A–C). Labrum dorsally (Fig. 12I) with anterior margin broadly and shallowly concave, or more deeply and angularly so (Figs. 11A–C). Epipharynx (Fig. 12J): pedium (**ped**) triangular, approximately isosceles, with broad base along distal margin; parapedial projection (**pp**) obtuse; extra parapedial setae (**eps**) mediad parapedial ridge (**pr**); coeloconic sensilla (**cs**) relatively few.

Left mandible, dorsal surface (Fig. 12B) with anterior retinacular tooth not evident, from dorsal aspect. Maxilla as in Figs. 12K–L. Labium (Figs. 13A–C): paraglossae (**pg**), surface with extensive covering of seta-like microtrichia (Fig. 13B, **mtr**); in dorsal aspect (Fig. 13C), distal portion of glossal sclerite (**gsap**) small, relative to medial portion (**gsmp**).

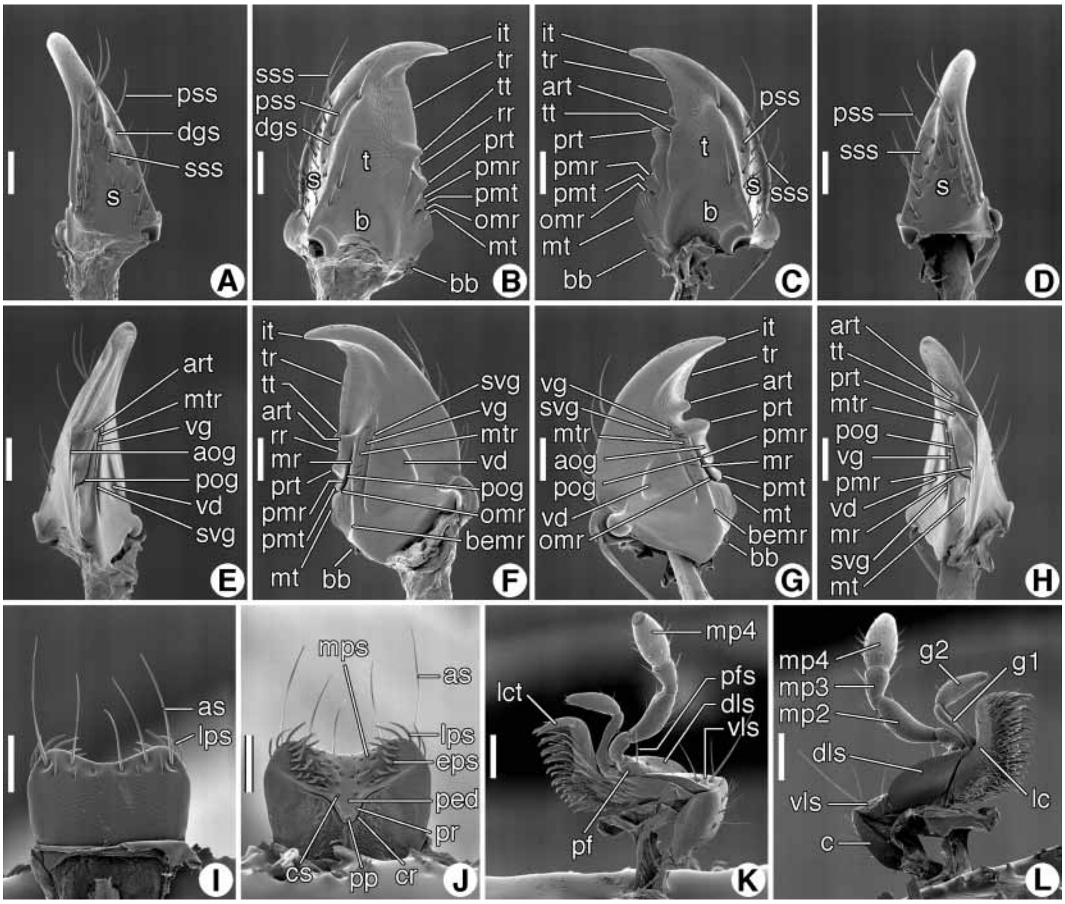


FIGURE 12. Structural features of *Cymbionotum fernandezi*, new species, illustrated with SEM photographs. A–H, mandibles: A, D, lateral aspect, left and right mandible, respectively; B, C, dorsal aspect, left and right mandible, respectively; E, H, occlusal aspect, left and right mandible, respectively; and F, G, ventral aspect, left and right mandible, respectively. I, J, labrum, dorsal and ventral aspect, respectively. K,L, left maxilla, ventral and dorsal aspects, respectively. Legend: **aog**, anterior occlusal groove; **art**, anterior retinacular tooth; **as,** apical seta; **b;** basal portion of mandible; **bb**; basal brush; **bemr,** basal extension of molar ridge; **c**, cardo; **cr,** crepis; **cs**, coeloconic sensillum; **dgs**, dorsal groove of scrobe; **dls**, dorsal lobe of stipes; **eps,** extra parapedial seta; **g1,** galeomere 1; **g2,** galeomere 2; **it,** incisor tooth; **lc**, lacinia; **lct**, lacinial tooth; **lps,** lateral parapedial seta; **mp2,** maxillary palpomere 2; **mp3,** maxillary palpomere 3; **mp4,** maxillary palpomere 4; **mps,** medial parapedial seta; **mr,** molar ridge; **mt,** molar tooth; **mtr,** microtrichia; **omr,** occlusal part of molar ridge; **ped,** pedium; **pf**, palpifer; **pfs,** palpiferal seta; **pmr**, premolar ridge; **pmt**, premolar tooth; **pog,** posterior occlusal groove; **pp,** parapedial projection; **pr,** parapedial ridge; **prt**, posterior retinacular tooth; **pss,** primary scrobal seta; **rr**, retinacular ridge; **s,** scrobe; **sss,** secondary scrobal seta; **svg**, secondary ventral groove; **t**, terebra; **tr**, terebral ridge; **tt,** terebral tooth; **vd,** ventral depression; **vg**, ventral groove; **vls**, ventral lobe of stipes. Scale bars = 100 µm.

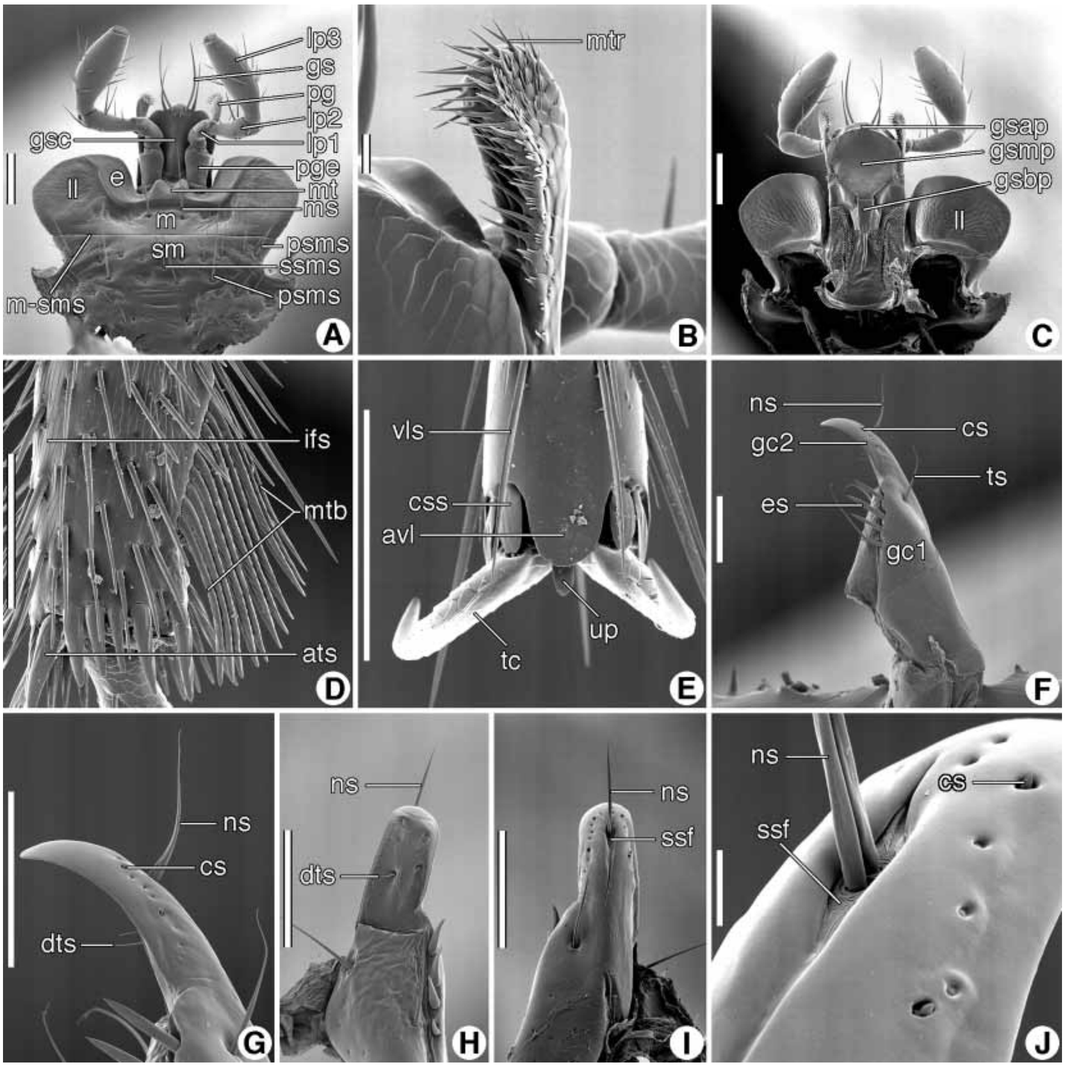


FIGURE 13. Structural features of *Cymbionotum fernandezi*, new species, illustrated with SEM photographs. A, labium, ventral aspect; B. paraglossa, dorsal aspect; C, labium, dorsal aspect; D, middle tibia, apical portion, anterior aspect; E, middle tarsomere 5, apical portion, and claws, ventral aspect; F–J, ovipositor, left gonocoxa—F, gonocoxa 1 and 2, lateral aspect; G–I, gonocoxite 1, apical portion and gonocoxite 2, lateral, dorsal and ventral aspects, respectively; J, gonocoxite 2, apical portion, oblique aspect. Legend: **cs,** coeloconic sensillum; **ats**, anterior tibial spur; **avl**, apical ventral lobe of t-5; **css**, clamshell sensillum; **dts**, dorsal trichoid seta; **e,** epilobe of mentum; **es**, ensiform seta; **gc1,** gonocoxite 1; **gc2,** gonocoxite 2; **gs**, glossal apical seta; **gsap**, glossal sclerite, apical portion; **gsbp,** glossal sclerite, basal portion; **gsc**, glossal sclerite; **gsmp,** glossal sclerite, medial portion; **ifs,** inner face sculpticell; **ll**, lateral lobe of mentum; **lp1**, labial palpomere 1; **lp2**, labial palpomere 2; **lp3**, labial palpomere 3; **m**, mentum; **ms**, paramedial seta of mentum; **m-sms**, mental-submental suture; **mt**, mental tooth; **mtb**, middle tibial brush; **mtr**, microtrichia; **ns**, nematiform seta; **pg**, paraglossa; **pge,** palpiger; **psms**, primary submental seta; **sm,** submentum; **ssf**, subapical sensory furrow; **ssms**, secondary submental seta; **tc**, tarsal claw; **ts**, trichoid seta; **up**, unguitractor plate; **vls;** ventrolateral seta. Scale bars: A, C– F, and I = 100 µm; B and J = 10 µm.

Prothorax. Pronotum (Figs. 1B, 14) cup-like in outline from dorsal perspective, lateral margins not beaded, more or less sinuate posteriorly; posteriolateral angles rectangular to acute, prominently projected; lateral grooves narrow; posterior margin beaded or not; proepipleuron evident (at least posteriorly) in dorsal aspect; disc almost flat, lateral declivity each side slightly sloped.

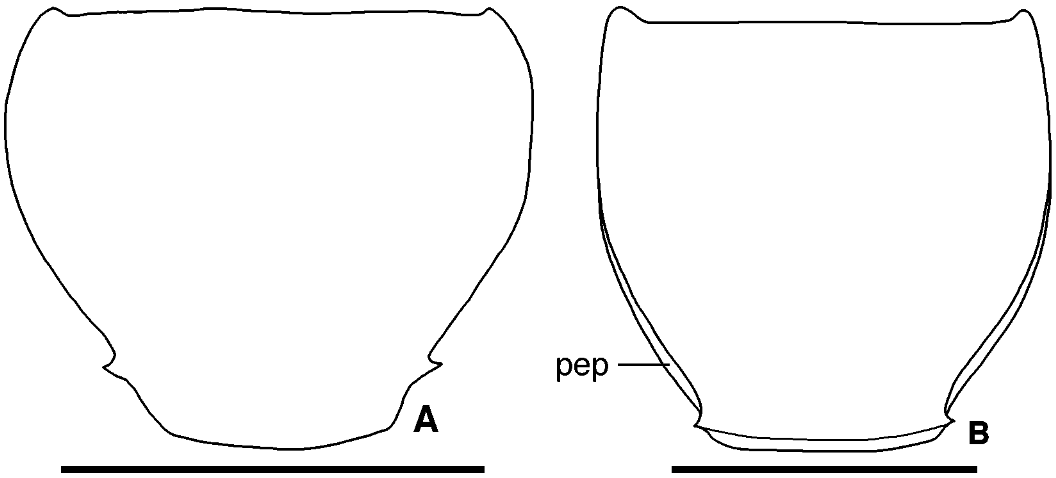


FIGURE 14. Pronotum, dorsal aspect, of *Cymbionotum* species, illustrating subgeneric differences with outline drawings. A, *C. (Procoscinia) fernandezi*, new species. B, *C. (Cymbionotum) semelederi* Chaudoir. Legend: **pep**, proepipleuron. Scale bars = 1.0 mm.

Elytra (Figs. 1B, 2A). Dorsal surface plane for most of length, apical declivity gradually sloped; basal ridge narrow, not extended to edge of scutellum, anteriorly smooth, not angulate; stria 1 shallow, striae 2–8 not or hardly evident; intervals flat.

Hind wings (Fig. 15A). Macropterous. Wedge cell absent. Veins **RP 3 + 4** and **AA 3 + 4** absent. Vein **MP 4** less than half length of **MP 3.**

Legs. Middle tibia with distinct distal brush of setae (Fig. 13D, **mtb**). Unguitractor plate (Fig. 13E, **up**) narrow.

Male genitalia (Figs. 15B–D, 15F, 17D–E, 17I–K, 19C–D, 19G–H, 19K, 19O, 22D). Endophallus with sclerite x much shorter than median lobe, or absent; microtrichial field various, from very small to large; parameres (Figs. 15C–D) distally glabrous.

Ovipositor (Figs. 13F–J). Ramus about 0.5–0.8 length of gonocoxite 1. Laterotergite IX (Fig. 15E, **lt**) without anteriorly directed apophysis. Gonocoxa dimerous, gonocoxites 1 and 2 subequal (Fig. 13F, **gc1, 2**), gonocoxite 2 dorsally with pair of trichoid setae in lateral aspect (Fig. 13G, **dts)**, dorsal margins curved; narrow in outline, distal margin narrowly rounded (Figs. 13H–I), ventral surface smooth, each side with row of coeloconic sensilla (Fig. 13G, **cs**).

Female internal genitalia (Fig. 15E). Spermathecal duct much longer than spermathecal reservoir (**sp**), latter reniform.

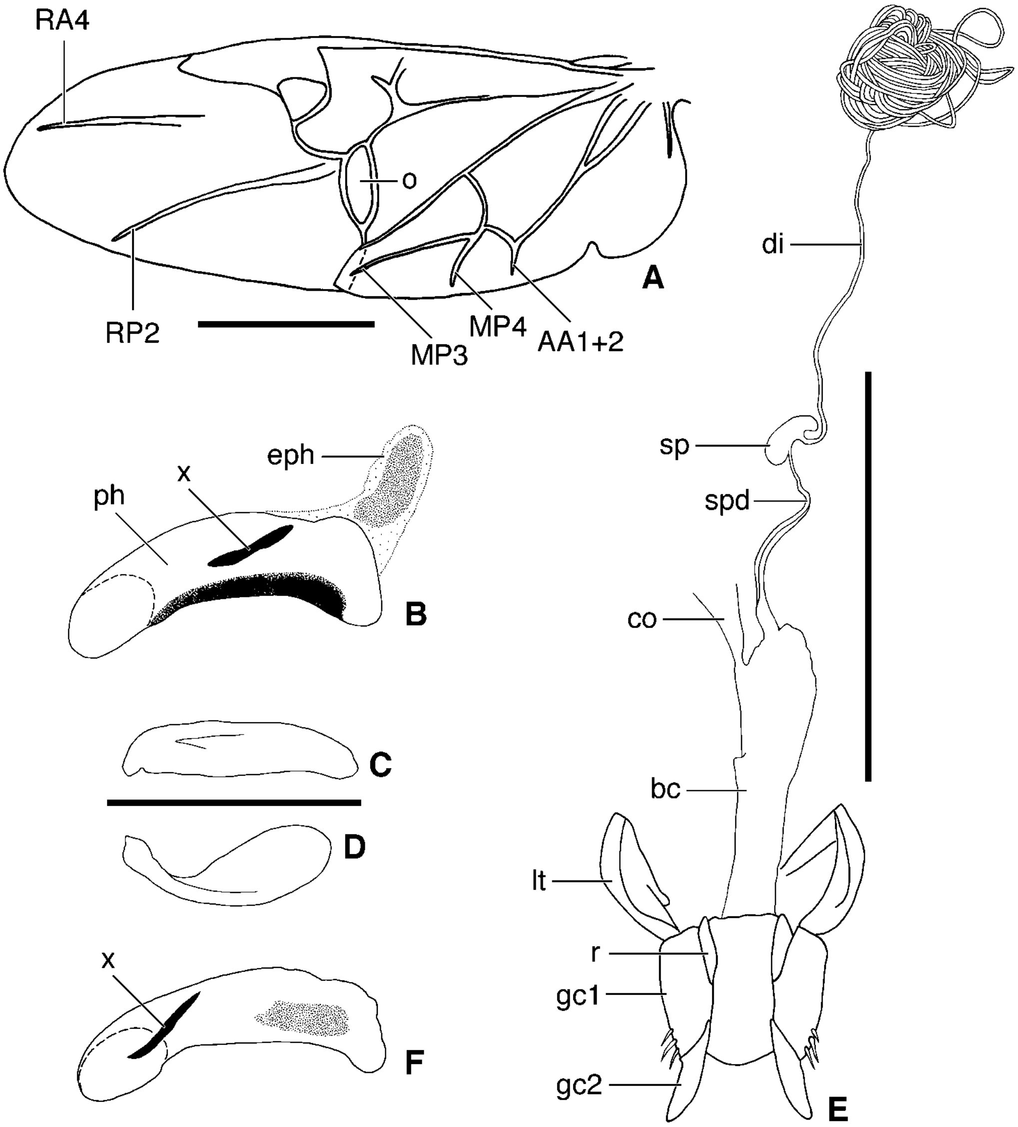


FIGURE 15. Structural features of *Cymbionotum fernandezi,* new species (A–E) and *C. negrei* Perrault (F) illustrated with line drawings. A, left hind wing, dorsal aspect. B, male genitalia: phallus, left lateral aspect, with endophallus partially everted; C–D left and right paramere; respectively, ventral aspect. E, female genitalia, ventral aspect. F, male genitalia, left lateral aspect. Legend: wing veins and cells-- **AA1+ 2,** anal vein 1 + 2; **MP3** and **MP4,** posterior median veins 3 and 4, respectively; **o**, oblongum cell; **RA4**, anterior radial vein 4; **RP2**, posterior radial vein. Male genitalia: **eph**, endophallus; **ph**, phallus; **x,** sclerite x of endophallus. Female genitalia: **bc**, bursa copulatrix; **co**, common oviduct; **di**, spermathecal diverticulum; **gc 1** and **2,** gonocoxite 1 and 2, respectively; **lt**, laterotergite of abdominal segment IX; **sp,** spermatheca; **spd**, spermathecal duct. Scale bars: A and E = 1.0 mm; and B–D and F, = 0.5 mm.

Included taxa. This genus includes two subgenera: *Procoscinia*, **n. subg.**, and *Cymbionotum* (*sensu stricto*).

Habitat. The members of *Cymbionotum* occupy the five vegetation zones occupied by the tribe Melaenini, with concentration in temperate grassland and tropical deciduous forest and savannah vegetation zones (Table 17)

Geographical distribution (Figs. 16, 18, 20, 21, 23). The range of this genus, including both Western and Eastern Hemispheres, is co-extensive with the range of tribe Melaenini.

Procoscinia, new subgenus

Type species. *Cymbionotum fernandezi*, **n. sp.**, (here designated).

Subgeneric name. Based on two Latin terms: the prefix *pro*, meaning before, implying primitiveness; and *Coscinia*, the original (but homonymous) name of the genus now recognized as *Cymbionotum*. Thus, the subgeneric name implies a generalized member of the genus within which it is included.

Recognition. Precinctive in the Neotropical Region of the Western Hemisphere, adults of *Procoscinia* have the posteriolateral dentiform projections distinctly anteriad the posterior margin of the pronotum. The posterior margin of the pronotum is not beaded, and the proepipleuron (**pep**) is not visible from a dorsal perspective (Fig. 14A; cf. Fig. 14B). Males have sclerite x of the endophallus about one third length of phallus, and in infolded position near base of phallus (Fig. 15F, **scx**).

Descriptive notes. With character states of genus *Cymbionotum*, restricted as follows. Size and ratios of body parts (Tables 3–9). Average size (SBL and EW, Tables 3 and 4) for genus intermediate, but broad overlap with *schueppelii* group, and distinctly smaller than members of *basale* and *semelederi* species groups. Pronotum relatively broad, values for PL/PWM (Table 7) more than 0.90; base broad, values for ratio PWB/PWA (Table 9) more than 0.65.

Color. Dorsal surface uniformly rufous, or head and pronotum slightly darker than elytra. Appendages: antennae, labrum and mandibles rufous; palpi testaceous; femora, tibiae and tarsi rufotestaceous.

Microsculpture. Dorsal surface with mesh pattern isodiametric, though microlines very fine and in places effaced, or microlines absent; scutellum with mesh pattern evident throughout, more or less isodiametric, sculpticells convex, surface beaded.

Vestiture. Dorsal surface with setation very dense (Figs. 2A, 3F), setae of moderate length (Table 1 and Fig. 2E)

Head. Clypeus: anterior margin medially without a dentiform projection, or distinct swelling.

Antennae. Antennomere 2 pyriform (cf. Fig. 11D), and relatively longer (about two thirds length of antennomere 3, Table 11); antennomeres 5–10 moderately asymmetrical

(cf. Fig. 11F)

Labrum. Anterior margin distinctly, but broadly concave.

Included taxa. This subgenus includes two species: *C. fernandezi*, new species, and *C. negrei* Perrault.

Habitat. The members of *Procoscinia* occupy the tropical rain forest vegetation zone (Table 17), but may be confined to riparian situations.

Geographical distribution. The range of *Procoscinia* (Fig. 16) is confined to northern South America.

Relationships and chorological affinities. This subgenus is the putative, primitive adelphotaxon of subgenus *Cymbionotum*, from which it is widely isolated (by the South Atlantic Ocean) geographically (Figs. 16, 18, 20, 21, 23).

Cymbionotum (Procoscinia) fernandezi, Ball and Shpeley, n. sp.

(Figs. 1B, 2A, 2E, 3F, 12A–I, 13 A–J, 14A, 15A–E, 16)

Type material. Thirty eight specimens (20 males and 17 females). HOLOTYPE male, card-mounted, labeled: "COLOMBIA Bolivar/ Zambrano bosque seco/ Lote Papayo cultivo/ Gmelina arborea. Luz/ 10–15. V. 1999/Col. H.M.-M.A.-M.G./ No. 967597". A microvial, pinned beneath the whole specimen, contains its genitalia (UNCB). PARATYPES, 4 labeled same as holotype: male, point-mounted, head and prothorax missing (broken and parts lost, following for habitus picture, Fig. 1B); female, point-mounted, reproductive tract removed, in microvial pinned beneath whole specimen; female, card-mounted, with left elytron removed, and attached to card; and female, card-mounted, disassembled for SEM photographs of mouthparts and ovipositor sclerites). Eighteen males, 15 females, labeled: "COLOMBIA Bolivar Zam-/brano. Hda. Monterrey For-/estal BsT 9¼42'N, 74¼53'W/ 20m. May 1999"; "Lote Papayo Interior de/ cultivo *Gmelina arborea*/ trampa de luz,/ H. Moreno y M. çvila/ No. 967543" With the agreement of H. Moreno, the paratypes were distributed as follows: BMNH, 2; CASC, 2; CNIF, 7; IAVH, 7; MNHP, 2; MRAC, 2; UASM, 2; UNCB, 11; and UASM, 2.

Specific epithet. This Latinized eponym, genitive case, is based on the surname of Prof. Fernando Fernandez, who loaned the type specimens to us, and with whom we have cooperated in extending knowledge of Colombian Carabidae.

Type locality. Colombia: Bolivar: Zambrano.

Recognition. Compared to *C. negrei*, adults of *C. fernandezi* are on average, larger, both in length and width, with wider vertex, wider head in relation to pronotum, and wider pronotal base (Table 12). The phalli (Figs. 15D, F) of these two species are similar in form, but that of *C. fernandezi* (Fig. 15B) is broader, with the preapical portion of the shaft bent more gradually ventrad, and ventral surface generally dark (cf. Fig. 15F).

Description. With recognition features as noted above, and other details specified in the subgeneric description, and illustrations, as follows: habitus, Fig. 1B; integumentary setal length, Fig. 2E; density of elytral punctation, Fig. 3F; labrum and epipharynx, Figs. 12I and J, respectively; mandibles, Figs. 12A–H; maxillae, Figs. 12K–L; labium, Figs. 13A–C; pronotum, dorsal aspect, Fig. 14A; hind wings, Fig. 15A; middle tibia and tarsomere 5, Figs. 13D and E, respectively; phallus and endophallic armature, Fig. 15B; gonocoxa of ovipositor, Figs. 13F–J; internal genitalia of female, Fig. 15E.

Habitat, habits, and seasonal occurrence. All specimens were collected in May, at an ultraviolet light, within a plantation of an exotic tree *(Gmelina arborea* Roxb., white teak, family Verbenaceae), a species indigenous in the Oriental Region and southern China. We infer that *C. fernandezi* is mesophilic, occupying disturbed areas in the tropical rain forest zone (Table 17, Fig 24), at less than 200 m altitude with adults active in mid-year.

Geographical distribution (Fig. 16). This species is known only from the Rio Magdalena valley, Colombia.

Relationships and chorological affinities. Based on shared morphological features, geographical distribution and allopatric ranges, *C. fernandezi* and *C. negrei* are postulated to be adelphotaxa.

Material examined. We have seen the type series, only. For details, see "Type material", above.

TABLE 12. Data about diagnostically useful measurements and ratios for the species of *Procoscinia* (*C. fernandezi*, **n. sp.** [N = 37] and *C. negrei* Perrault [N = 3]).

SBL (mm)	Range	Mean	**EW (mm)**	Range	Mean
C. fernandezi	3.95–4.51	4.16		1.38–1.55	1.45
C. negrei	3.66–4.26	3.98		1.26–1.36	1.29
VW/HW	Range	Mean	**HW/PWM**	Range	Mean
C. fernandezi	0.76–0.84	0.80		0.84–0.91	0.88
C. negrei	0.81–0.86	0.84		0.91–0.96	0.93
PWB/PWA	Range	Mean			
C. fernandezi	0.77–0.90	0.82			
C. negrei	0.68–0.76	0.71			

Cymbionotum (Procoscinia) negrei **Perrault 1994**

(Fig. 15F, 16)

Cymbionotum negrei Perrault 1994: 208. TYPE MATERIAL: three specimens, card-mounted (MNHP). HOLOTYPE male, labeled: "MUSEUM PARIS/ VENEZUELA/ BAS SARARE/ F. GEAY 33-96"; "Sous les écorce/ darbres" [handwritten]; "HOLOTYPE" [red paper]. PARATYPES, male and female. Male, labeled: "MUSEUM PARIS/ VENEZUELA/ HAUT APURE/ F. GEAY 33-96"; "PARATYPE" [red paper]; Cymbionotum/ negrei m. [handwritten]/ PARATYPE/ G. G. Perrault det. [printed] 1992" [handwritten]. Female, "Venezuela, S. Fern. do Apure, L. Laglaize 1896"; "MUSEUM PARIS/ ex. Coll./ R. Oberthur" [pale green paper]; "PARATYPE" [red paper]; "PARATYPE/ Cymbionotum /negrei m. [handwritten]/ G. G. Perrault det. [printed] 1992" [handwritten].

Type area. Venezuela: Bas Sarare.

Recognition. Adults of this species are markedly similar to those of *C. fernandezi*, differing in absence of microlines from most of the dorsal surface, and by average smaller size, narrower vertex, narrower head in relation to pronotum, and narrower pronotal base (lower values for PWB/PWA, Table 12). The phalli of these two species are similar in form, but that of *C. negrei* (Fig. 15F) is narrower, with the preapical portion of the shaft bent more distinctly ventrad, and ventral surface generally pale (cf. Fig. 15B).

Description. With recognition features as specified above, and in the subgeneric treatment; similar generally to *C. fernandezi*. Male genitalia with phallus as in Fig. 15F.

Habitat. The holotype was collected from under bark of a (presumably fallen) tree. From the locality data, we infer that *C. negrei* is mesophilous, living in the rain forest vegetation zone (Table 17), at an altitude of less than 200 m. We do not believe that the species is subcortical, but that is a possibility.

Geographical distribution (Fig. 16). This species is known only from two localities in the Apure River Basin of Venezuela.

Relationships and chorological affinities. Based on shared morphological features, geographical proximity, and allopatric ranges, *C. negrei* is inferred to be the adelphotaxon of *C. fernandezi,* new species.

Material examined. We have seen the type series, only. For details, see the synonymical section, above.

Cymbionotum **(sensu stricto)**

Coscinia Dejean 1831: 478 (not Hübner 1822). TYPE SPECIES: *Siagona schueppelii* Dejean 1831(designated by Bedel 1897). —Chaudoir 1876: 118.

Cymbionotum Baudi di Selve 1864: 212. TYPE SPECIES: *Cymbionotum collare* Baudi di Selve 1864 = *Coscinia semelederi* Chaudoir 1851 (designated by original monotypy).—Marschall 1873: 187.—Andrewes, 1933: 3.—1935: 18.

Graniger Chaudoir 1871: 282 (not Motschulsky 1864). TYPE SPECIES: *G. algirinus* Motschulsky 1864.—Semenov, 1903: 169.—Csiki, 1929: 477.

Cymbionostrum (misspelling) Burgeon 1937: 395.

Notes about synonymy. The generic name *Coscinia* Dejean was a junior homonym of *Coscinia* Hübner, and was thus not available for use by Dejean (Chaudoir 1871). Claiming incorrectly that *G. algirinus,* the type species of *Graniger,* was conspecific with *Coscinia semelederi,* Chaudoir proposed *Graniger* as a substitute name for *Coscinia*. This proposal was generally accepted by subsequent authors. Andrewes (1933), based on study of the types involved, recognized that *G. algirinus* was a ditomine harpaline, and thus the generic name *Graniger* was unavailable for use as proposed by Chaudoir. That left *Cymbionotum* as the name available to replace *Coscinia* Dejean.

Recognition. Precinctive in the Eastern Hemisphere, adults of this subgenus have the posteriolateral dentiform projections close to the posterior margin of the pronotum (Fig. 14B). The posterior margin of the pronotum is beaded or not (*C. striatum*, only), and the proepipleuron (**pep**) is visible from a dorsal perspective (Fig. 14B; cf. Fig. 14A). Males have sclerite x of the endophallus about one eighth length of phallus, and in infolded position near the basal lobe (Figs. 17D–E, 17I, **x**), or sclerite x is absent.

Descriptive notes. Size and ratios of body parts (Tables 3–9). Size range (SBL and EW, Tables 3 and 4) extends over the range of the genus. Pronotum relatively narrow, values for PL/PWM (Table 7) 0.75 or more; base relatively narrow, values for ratio PWB/PWA (Table 9) 0.82 or less.

Color. Dorsal surface and appendages with range same as for genus, but with paler colors predominant.

Microsculpture. Most of dorsal surface without microlines, smooth; postocular transverse impression of head smooth or with mesh pattern isodiametric to slightly transverse; scutellum with mesh pattern evident throughout, more or less isodiametric, or microlines in anterior part only, posterior part smooth, or surface entirely smooth.

Vestiture. Dorsal surface with setae short to long (Table 1 and Figs. 2B–D, 2F), setation very sparse to moderately dense (Figs. 3A–E).

Head. Clypeus: anterior margin medially with (Fig. 11C) or without (Figs. 11A–B) a dentiform projection, or distinct swelling.

Antennae. Antennomere 2 globose (Fig. 11E), relatively short (about half length of antennomere 3), or pyriform (Fig. 11D), and relatively longer (about two thirds length of antennomere 3, Table 11); antennomeres 5–10 moderately (Fig. 11F) to markedly (Fig. 11G) asymmetrical.

Labrum. Anterior margin rather deeply, subangularly concave (Figs. 11A–C).

Included taxa. This subgenus includes 18 species arranged in three species groups and three superspecies.

Habitat. Like *Cymbionotum (sensu lato),* the members of *Cymbionotum* (*sensu stricto*) occupy the five vegetation zones occupied by the tribe Melaenini, with a concentration in temperate grassland and tropical deciduous forest and savannah vegetation zones (Table 17 and Fig. 24), and marginal to the desert/semi-desert zone.

Geographical distribution. The range of *Cymbionotum (sensu stricto)* (Figs. 16, 18, 20, 21, 23) is confined to the warmer parts of the Eastern Hemisphere, principally north of the Tropic of Capricorn.

Relationships and chorological affinities This subgenus is the more derived putative adelphotaxon of subgenus *Procoscinia*, from which it is isolated geographically.

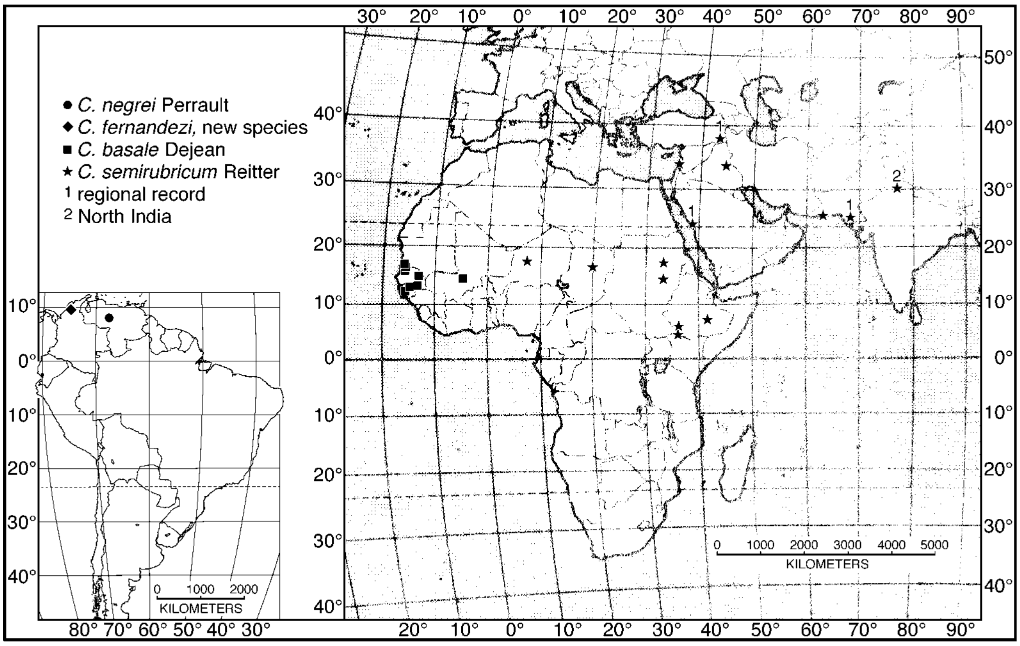


FIGURE 16. Geographical range of the species of *Cymbionotum (Procoscinia),* and of *Cymbionotum (s. str.) basale* species group illustrated on an outline map of South America and of southwestern Asia, southern Europe and Africa.

basale species group

Descriptive notes. Size and ratios of body parts (Tables 3–9). Size large, SBL (Table 3) more than 5.0 mm, and EW (Table 4) more than 1.6 mm. Pronotum relatively narrow, values for PL/PWM (Table 7) 0.87 or more; base relatively narrow, values for ratio PWB/PWA (Table 9) 0.76 or less.

Color. Head and pronotum black; elytra (Figs. 17A–C) bicolored, anteriorly principally bright rufous, but humeral area black to rufous, posteriorly (including posterior margin) black; antennae and mandibles black; palpi and tarsi rufotestaceous; femora and tibiae piceous to rufous.

Microsculpture. Dorsal surface without microlines, smooth, except scutellum with slightly transverse beaded convex sculpticells.

Punctation and vestiture. Dorsal surface with setae moderately long (cf. Fig 2E) to long (Fig. 2F; Table 1), punctation moderately dense (Fig. 3E).