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Classification, natural history, phylogeny, and subfamily composition of the Cleridae and generic content of the subfamilies (Coleoptera: Cleroidea)

by Weston Opitz

Abstract. The higher classification of the Cleridae is revised to include 12 subfamilies as follows: Anthicoclerinae subfam.nov.; Clerinae Latreille, 1802; Enopliinae Gistel, 1856; Epiphloeinae Kuwert, 1893; Hydnocerinae Spinola, 1844; Isoclerinae Kolibáč, 1992; Korynetinae Laporte, 1836; Neorthopleurinae Opitz, 2009; Peloniinae subfam.nov.; Tarsosteninae Jacquelin du Val, 1862; Thaneroclerinae Chapin, 1924; and Tillinae Leach, 1815. The concept of the genus is discussed, a partial list of taxa on which the study is based is provided, as is a list of character states that suggest taxa placement in the various higher categories. A key to the subfamilies, their description, and generic composition is provided. Thirty-eight adult and larval character states are used to generate a computer based phylogeny of the subfamilies. In addition to the conventional external characteristics, those of the alimentary canal and mesodermal reproductive organs of both sexes are also used. This treatise includes 227 illustrations of which 90 are SEM's, 71 line drawings of adult morphology and 22 of larvae, 12 maps, 16 color figures and 1 of the proposed phylogeny of the subfamilies.

Keywords. Coleoptera – Cleridae – classification – natural history – subfamilies

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Introduction

Cleridologists vary in views about rooting genera to higher categories (LAPORTE 1836; SPINOLA 1844A; LACORDAIRE 1857; JACQUELINE DU VAL 1861; SCHENKLING 1910; CHAPIN 1924; CORPORAAL 1950; BARR 1962; CROWSON 1964; WINKLER 1982; KOLIBÁČ 1997; and SOLERVICENS 2005). These researchers, along with many others, have contributed significantly to Cleridae taxonomy.

In his 10th edition of *Systema Naturae*, LINNEAUS (1758), notes five species of Cleridae. He placed three species in *Attelabus* Linnaeus, and one each in the genera *Dermestes* Linnaeus and *Chrysomela* Linnaeus. LATREILLE (1804), then combined these genera, and others, under Cleridae, which became the fifth known family of the Coleoptera. Spinola 1844, was the first to consolidate all of the available knowledge of this group. In his classical monograph of the Cleridae, which contained 47 color illustrations and numerous new genera and species; he established four subfamilies: Cleroidés, Hydnoceroidés, Platinopteroidés, and Corynetoidés. LECONTE (1849), published the first synopsis of the North American Cleridae and in 1861 subdivided the clerids into two tribes, the Clerini and the Enopliinae, essentially following the classification of LACORDAIRE (1857). SCHENKLING (1903), classified Cleridae taxa into six groups that he assigned subfamily rank: Tillini, Clerini, Phyllobaeini, Hydnocerini, Enopliinae, and Corynetini.

The next comprehensive contribution to higher Cleridae comes from BÖVING & CHAMPLAIN (1920), in the form of a valuable summation about Cleridae larvae, with a categorization of higher taxa into alphabetical groupings. This work was followed by CHAPIN who in 1924 followed, in essence the higher organization of SCHENKLING (1903), and, in addition, established the subfamily Thaneroclerinae. Then, CORPORAAL (1950), brought forth his immensely valuable catalog of the Cleridae in which he lists the known species under subfamilies Tillinae, Phyllobaeninae, Thaneroclerinae, Clerinae, Epiphloeinae, Enopliinae, and Korynetinae. BARR (1962) altered Corporaal's classification scheme by dividing the North American Cleridae into two subfamilies, Clerinae and Korynetinae, and grouping genera into tribes Tillini Phyllobaeini, Thaneroclerini, and Clerini, under Clerinae, and tribes Epiphloeini, Enopliini, and Korynetini, under Korynetinae. CROWSON (1964), follows the higher classification of CORPORAAL (1950A) but, in addition, recognizes DUVAL's (1862), Tasosteninae.

In more recent years we have the work of Winkler who established the subfamilies Dieropsinae (WINKLER 1964) and Cleropiestinae (WINKLER 1978); the latter questioned by MENIER (1981) and the both synonymized by KOLIBÁČ (1989A,B). Then, most recently, there are the works of KOLIBÁČ who in 1992 elevated Thaneroclerinae to family status and in 1997 established a higher classification whereby Cleridae is grouped into subfamilies Tillinae, Clerinae, Hydnocerinae, and Korynetinae. In 2005, Solervicens made a significant find to define his concept of subfamily Korynetinae.

The most daunting task in this subfamilial work has been to fulfill the initial goal of this study, which was to examine the majority of species among diverse world Cleridae genera. I partially succeeded in doing this over a period of about 40 years of investigation that involved 24 field expeditions to 15 nations, 64 museum excursions, visits to 12 university collections, and numerous loans from museums and private

collections. The particulars about these on-sight research experiences are enumerated in the section entitled Material and Methods.

Investigation of most, and sometimes the entire, venue of species of a genus develops a strongly supported generic and suprageneric concept. I have made this a lifetime goal that is to some extent being brought to fruition with this contribution. To date aforementioned the entire goal remains unfulfilled as many more species need to be examined. However, in my judgment the extent of my coverage of World checkered beetles has now attained a level of comprehensiveness that a contribution to Cleridae higher classification is warranted. As always, today's classification is tomorrow's history, and I expect, and indeed I hope, that my present and future colleagues of Cleridology will challenge my results with as much fervor as they were generated. This, along with vital collegial manuscript reviews, particularly among Cleridae specialists, will eventually produce a classification of the Cleridae that is congruent with evolutionary theory and one that will serve the greater community of biologists.

Perhaps the most perplexing problems in Cleridae taxonomy have been the general morphological imbalance in the delimitation of genera and the lack of a credible suprageneric classification, particularly for those genera of Cleridae whose members have a reduced fourth tarsomere, the Korynetinae of BARR (1962: 121) and KOLIBÁČ (1997: 307). The difficulty and frustration of correcting these problems is inherent in the work of KOLIBÁČ (1997: 338) who writes, "*There is no synapomorphy in such Korynetinae. On the contrary, Enopliinae are simply "advanced Korynetinae"; therefore, Enopliinae must be synonymized*".

Kolibáč is perhaps correct if we accept the generic and suprageneric characterizations prevalent during CORPORAL'S (1950A) time. However, Cleridae genera were historically framed with a very wide brush. Taxonomic decisions about species and higher categories were usually based on readily observable characters, and species assignments to genera had many elements of convenience. But then, such was the general character of taxonomy in the 20th century, a Renaissance period for the discovery of new species creating a thrust towards specimen fortification of the great museum and private collections. Today, it behooves us to advance our knowledge about these great taxa assemblages with equally great vigor in a comprehensive and balanced research approach that implements the best of the past ideas and methodologies with those that are most promising for the future. I vehemently encourage my present and future colleagues in cleridology to become thoroughly familiar with intellectual writings concerning the systematic theory and methodologies of our times [as found in such journals as Systematic Zoology, Cladistics, and in the comprehensive works of DOBZHANSKY (1937); MAYR (1969); CROWSON (1970); HENNIG (1966); WILEY (1981); and SCHUH (2000)]. And, of course, a working understanding of the International Code of Zoological Nomenclature (ICZN 1999) is of utmost importance for international coherence in our taxonomic endeavors. Foremost, it is imperative that our higher classification work is comprehensive in taxa coverage and that such work complements the proven canons of evolutionary thoughts brought forth by the great scientific minds of the past and the present. To do less would be equivalent to regressing to the times when taxonomic efforts were based on convenience, numerics, and other unsound and discredited working principles.

I have investigated Cleridae higher classification from morphologic and non-morphologic views and have delayed publication of results to avoid premature nomenclatural changes. My research began with a project designed to overview the extent to which checkered beetle mesodermal internal organs provide significant characteristics for elucidation of Cleridae higher phylogenetics (EKIS & GUPTA 1971; CROWSON 1972). This project was continued in conjunction with a variety of generic revisions (EKIS 1977A, 1977B; OPITZ, 1997, 1998, 2004, 2005, 2006, 2007, 2008A, 2008B, 2008C, 2009A, 2009B, 2009C, 2009D). My objective still is to understand better the forces of evolution that yielded the morphologically diverse taxa of world Cleridae. Through my research it has become obvious that selection towards predatory and mimetic life styles have been major adaptive trends in the Cleridae (GAHAN 1910: 68. EKIS 1977A: 4; MAWDSLEY 1994: 115; MENIER 1985: 1071; RIFKIND 1996: 72, and OPITZ 2005: 13).

The concept of the genus in the Cleridae

CORPORAAL'S catalog (1950a) will always serve as an essential component of Cleridae research; however in that work, the definition of genera and their classification into subfamilies was minimally scrutinized via modern concepts of evolution. Considerable species-level research remains to be done to align species into credible phylogenetic generic units. This will be possible, if we prioritize our taxonomic research to focus on establishment of heuristic classifications, which are, in so far as possible, based on monophyly.

LINNAEUS (1737) proclaimed, "It is the genus that pronounces the characters, and not the characters that pronounces the genus" (Mayr 1969: 93). Otherwise stated, rank conferred on supraspecific character state discontinuities is an arbitrary endeavor, irrespective of whether we deal with the genus, tribe, or subfamily categories.

Of considerable relevancy to this issue are the factors that cause such observed character discontinuities: extinction of intermediate taxa, intermediate taxa remain undiscovered, or intermediate taxa are unavailable while nested among our vast collections. Given the uncertainties about the causes of taxa discontinuities, and fully recognizing the value of nomenclatural stability in our supraspecific classifications, I suggest that the majority of the known species of a higher taxon be considered in attempts to establish supraspecific classifications. The same may be said for an understanding towards supraspecific evolution. I offer my revisionary sequence with the Epiphloeinae as a *modus* in comprehensiveness towards potentially stable higher classifications. At the very least such an approach produces classifications that are readily tested via new discoveries of taxa and/or nuances in methodology that do not violate the credible methods of the past.

A fringe benefit to such a comprehensive approach to higher classification is that it can lead to some degree of objectivity in our task of assignment of rank to gaps among character states. For example, in the Cleridae some morphological organs do not vary appreciably within historically stable genera. Moreover, their stability is retained within genera across subfamilial lines. I refer to the intrageneric consistency among such adult

organs as the structure of the metendosternite, number of tibial spurs, number of tarsal pulvilli, and level of sclerotization and shape of the spermathecal capsule. Among mature larvae we may list consistencies in epistomal suture, abdominal spiracles, and particulars about the urogomphi. It seems that variations of these characters, and a variety of others characters of checkered beetles, which have been extensively studied since the time of LINNAEUS (1737), do provide clues to frame a definition of a genus. Ideally, of course, a genus is a group of species linked by synapotypy [*sensu* HENNIG (1966) and TUOMIKOSKY (1967)]. Further, from the biologic perspective, a genus should tell a story of natural history, ala *Culex* Linnaeus or *Canis* Linnaeus. Sometimes, in the quagmire of entomologic species diversity, such a story must be indirectly gleaned from morphological attributes.

My research objective has, to a considerable extent, involved the search for information to solidify the often overly “loose”, convenience based, concept of the genus in the Cleridae. It is my hope that comprehensiveness of species taxa coverage, especially when framing the species composition of genera and higher categories, and more detailed gestalt analyses, will contribute information that will enable us to get a reasonable handle on which morphological organ systems are likely to provide clues of apotypies worthy of generic, tribal, and subfamilial ranking; fully understanding that in theory evolutionary rates are not constant among groups of taxa and that there is always a degree of subjectivity when we assign species to higher taxa.

Some progress has been made in the abovementioned arena by simply addressing the entire known species inventory of higher taxa; an approach to higher classification research that has – to date – led to some promising results. For example, as previously mentioned, the tibial spur formula and the tarsal pulvillar formula (OPITZ 2004: 21) are very consistent among taxonomically stable genera. In fact, species-level incongruity in these characteristics suggests species misplacement that is subsequently corroborated by discovery of other incongruous characteristics.

Material and Methods

This study is based on hundreds of adult disarticulations involving familial representation of superfamilies Cleroidea, Lymexyloidea, and Cucujoidea. My focus with non-cleroid specimens was to determine the morphological characteristics of their maxillary lacinia and characteristics of the gula. This was done to strengthen the discovery that only in the Cleridae is the lacinia divided into two lobes, the mediolacinia and the laterolacinia (Fig. 46) and only among checkered beetles do we find a postgular plate (Fig. 12) and/or derivative postgular process (Fig. 15). Specimens of a variety of cleroid species were investigated to view character states of the maxilla, gula, metendosternite, and tibial spurs. Moreover, one or more specimens of checkered beetle species were disarticulated to investigate what aspects of the morphology of these beetles might provide consistent information for the separation of genera, tribes, and subfamilies of the Cleridae. Gulas and metendosternites of every available Cleridae (hundreds of species that involve all major lineages within the family) were studied to establish character-state polarity of the variations of these organs in Cleridae. The list of

species noted under Table II, that involve families of Cucujoidea, Lymexyloidea, and non-Cleridae Cleroidea, represent the outgroups for the phylogenetic analysis of character states used herein.

Dissection techniques were as follows: Specimens were first boiled in soapy water (3 drops of 409 liquid detergent into 15 ml of warm water), then subjected to 10% hot KOH for one minute to soften the intersegmental membranes. A surgical eye knife, microscissors, and fine-tipped forceps were used to, disconnect the antennae and mouthparts from the cranium, disarticulate the three body parts, remove half of the number of legs and wings from the thorax, and dislodge the metendosternite from the metathorax. Line drawings were prepared with a camera lucida mounted on an M5 Wild stereoscopic microscope. The SEM photographs were produced on a Scanning Electron Microscope-S-3500N. Measurements involving body length and body width were done with a plastic ruler at 12 X. Body length measurements involved the lateral aspects of the body and extended from the frons to the elytral apex. Body width involved the greatest observable width across the widest portion of the elytra in dorsal view.

Information about characters of internal mesodermal organs was obtained from specimens killed and preserved in Pampel's fixative (glacial acetic acid, 4 parts; 40 % formaldehyde, 6 parts; 95 % alcohol, 15 parts; water 30 parts). These specimens were dissected in tap water. To extract the alimentary canal and dorsal nerve cord, the beetle was cut with microscissors at each side of the head, which permitted extraction of the foregut. A most critical step in this procedure was dislodging the ventricular portion of the alimentary canal from the narrow lumen framed by the mesoscutellum and the mesepisternum. The prothorax was then severed along one side to separate the alimentary canal from an abundance of locomotor muscles. The dissection was continued with a lateral cut along the abdomen, approximately at the level of the spiracles. Lastly, the proctodaeum was separated from the mesodermal internal reproductive organs and the considerable webbing of trachea. Next, I severed a side of the stomodaeal valve and flattened the stomodaeum, submerged in glycerin, on a glass slide to investigate the attributes of the stomodaeal valve lobes, which was observed with a M3300-D SWIFT compound microscope. Figures of the alimentary canal (Fig. 134) show only half of the cryptonephridial Malpighian tubules, and figures of the mesodermal internal reproductive organs show only one of two ovaries (Fig. 154), one of two testes, and one of two pairs of male accessory glands (Fig. 155).

Preparation of the metathoracic wings was as follows. One metathoracic wing was severed at its base of the thorax and submerged into a drop of tap water set on a microscopic slide. The folded membranous wing was then spread out on the slide by manipulation of the longitudinal veins, which facilitated movements of the membranous portions. Then, I used a piece of paper towel to blot excess water from the slide. This left the wing moist and sufficiently flattened. After a few minutes under a desk lamp, the dried wing was lifted from the slide, glued onto a support card, drawn, and pinned beneath the appropriate specimen.

Verification of the presence and number of tibial spurs (Fig. 90) was a particularly difficult task in many instances because of their often-small size and cryptic position.

This portion of the dissection work involved tonicity and a knowledge of the principles of liquid chemistry. First, one set of tibiae was severed from the femora, then submerged in 15 ml of hot tap water laced with 3 KOH pellets (85 %, A. C. S. reagent). The solution and legs were simmered for about one minute to establish a hypertonic condition in the tibial lumen. Next, the tibiae were submerged in tap water. Under these conditions, simple diffusion will cause water molecules to rush into the tibial lumen, which inflates the tibia, especially the membranous portions between the tibia and tarsus and between the tarsomeres. With a gentle squeeze at the distal portion of the tibia, with microforceps, the spur is clearly exposed due to the established hydrostatic pressures in the tibial interior. Even the smallest of tibial spurs become visible when the tibia is treated in the aforementioned manner.

This research generated a considerable collection of disarticulated specimens. Each disarticulation involves representatives of a species (usually male and female) and is maintained separately in white caps with glycerin. A pin with an identification label is affixed to the cap, which is stored in wooden store boxes. The morphological orismology stems from EKIS & GUPTA (1971); EKIS (1977A); MAJER (1987); NICHOLS (1989); and KOLIBÁČ (1989A). The terminology used to identify the “laterolacinia” (EKIS 1977A: 11), a synapotypic character state of the maxilla that in part defines the monophyly of Cleridae, needs clarification. KOLIBÁČ (1989A: 21) implemented the term “lacinial lamina” for the aforementioned maxillary structure following the terminology of STEINMANN & ZOMBORI (1985: 26). However, I retain the use of laterolacinia as this clerid lacinial development is not present in any other Cleroidea, Lymexyloidea, or Cucujoidea. Also, it is unlikely that the clerid laterolacinia is homologous with the generalized lamina as listed by STEINMANN & ZOMBORI (*l.c.*).

Variations of 39 morphological characters were polarized evolutionarily by outgroup methods discussed by WATROUS & WHEELER (1975), STRAUCH (1984), NEFF (1986), WHEELER (1986), FUNK & WHEELER (1986), and NIXON & CARPENTER (1993). The character matrix (Table 1) was analyzed with NONA (GOLOBOFF 1993) in conjunction with Winclada version 1.00.08 (NIXON 2002). A heuristic analysis [maximum trees (hold)] = 100, number of replications 9 (mult) = 100, multiple TBR+TBR (mult max was used). This project could not have been possible without the cooperation of numerous persons and institutions during fieldwork, visits to collections, and institutional and private loans. The fieldwork involved expeditions to Australia, Brazil, Canada, Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, India, Japan, México, Nicaragua, Panamá, Sri Lanka, United States of America, and Venezuela.

Museum collection oriented research was performed and loans secured in/from American Museum of Natural History, Australian National Insect Collection, Bernice P. Bishop Museum, British Museum of Natural History, California Academy of Natural Science, California Department of Food and Agriculture, Canadian Museum of Nature, Canadian National Collection of Insects, Arachnids and Nematodes, Carnegie Museum of Natural History, C. P. Gillette Arthropod Biodiversity Museum, Dehra Dun Forest Research Insect Collection, Deutsches Entomologisches Institute, Essig Museum of Entomology, Field Museum of Natural History, Florida State Collection of Arthropods,

Harvard Museum of Comparative Zoology, Humbolt-Universität museum für naturkunde, Insect collection of the Universidad del Valle de Guatemala, Instituto Nacional de Bioversidad, Instituto de Zoología Agrícola de Venezuela, Leiden Nationaal Natuurhistorische Museum, Leon Museum Entomologico, Milwaukee City Public Museum, Musee Royal de l'Afrique Centrale, Museo de Insectos de la Universidad de Costa Rica, Museo de Invertebrados Graham B. Fairchild, Museo del Instituto de Zoología Agrícola Maracay, Museo Regionale di Scienze Naturali, Museu de Zoologia Universidade de São Paulo, Natural History Museum of Los Angeles County, Oxford University Museum, Paris Museum d'Histoire Naturelle, Philadelphia Academy of Sciences, Quito Catholic Zoological Museum, Smithsonian National Museum of Natural History, Smithsonian Tropical Research Institute, Spinola Collection in Tassarollo Castle, Sri Lanka National Museum, The Bohart Museum of Entomology, The Natural History Museum of the University of Kansas, University of Colorado Museum, Wilbur R. Enns Entomology Museum, Zoological Survey of India, and the Zoölogisch Museum der Universiteite van Amsterdam.

Research with university collections was conducted at Kansas State University, Louisiana State University, Michigan State University, Northern Arizona University, Ohio State University, Oklahoma State University, North Carolina State University, Rutgers State University, Texas A & M University, University of Georgia, University of Mississippi, and Utah State University. Other university involvements are listed in the above paragraph. Specimen loans were secured during these visits.

It is difficult to enumerate the number of loans that this research has involved. Suffice to say, I have an immense gratitude to the following institutions whom I have not visited, but whose curators generously loaned material: Auckland Museum Entomology Collections, Australian Museums and Galleries of the Northern Territory, Evolutionsmuseet zoology Uppsala, Fundação Zoobotânica do Rio Grande do Sul, Fundacion Miguel Lillo, Hungarian Natural History Museum, Illinois Natural History Survey, Institute de Recherches Entomologiques de la Carad'be, Institute royal des Sciences naturelles de Belgique, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Instituto Biológico São Paulo, Iziko South African Museum, Lund University Museum of Zoology, Museo Civico di Storia Naturale "Giacomo Doria", Museo Nacional de Ciencias Naturales Madrid, Museu Paraense Emílio Goeldi, Natural History Museum Basel, New Zealand Arthropod Collection, Norwegian Institute for Nature, Otago Museum, Peabody Museum of Natural History, Purdue University, Queensland Department of Primary Industries, Royal Ontario Museum, South African Museum, South Australian Museum, Staatliches Museum für Tierkunde, Sweedish Museum of Natural History, Swedish University of Agricultural Science, Universidade Federal do Paraná, Universida Nacional de la Plata, University of California Riverside, University of Idaho, University of Kentucky, University of Minnesota, University of Nebraska, University of Wisconsin, Whangarei Museum, Wilbur R. Enns Entomology Museum, William F. Barr Museum, and the Zoological Museum University of Copenhagen.

Then there are the naturalists and other professionals who assemble, and make available, specimens collected for the love of the trade. I am very much indebted to

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Partial list of taxa involved in this study

To list all of the species studied would result in an exhaustive list, therefore I list below only one of usually many representatives examined of each genus. In aggregate, specimens listed below were studied to various degrees. Observations involved intact-pinned specimens, which yielded information about the easily accessible external organs. Some pinned specimens were partially disarticulated to view the maxilla, gula, and ectodermal genitalia. Most specimens were completely disarticulated to observe the more cryptic structures. Some specimens were originally preserved in Pampel's fixative, which permitted dissections of the viscera to clearly observe and delimit mesodermal characteristics. When specimens of published taxa were not available, I relied on the details in descriptions to glean critical information. *Of particular importance, for a realistic understanding about the characterization of genera, is that among the Cleridae genera listed below I examined a considerable, if not all, of the inventory of the known species.* However, to provide some frame of reference, but avoid exhaustive listing, I record the species that most nearly defines the morphological parameters of the genus, which sometimes does not involve the genus-type species. Usually, more than one specimens of each species or gender were examined simply because I wanted to verify the correctness of character state observations. For example, observation of the tibial spur formula may be distorted due to physical loss if only one specimen is examined. Larval observations involved only external structure. The level of observation of each species is listed in the following table. For detailed information about Cleridae adult external morphology see TREMBLAY (1958), adult alimentary canal see EKIS & GUPTA (1971), larval external morphology see BÖVING (1920), and about larval alimentary canal see KOLIBÁČ (1999).

Partial list of species examined

CUCUJOIDEA

Biphyllidae

Diplocoelus rudis LeConte

Bothrideridae

Bothrideres geminatus (Say)

Brachypteridae

Brachypterus pulicarius (Linnaeus)

Byturidae

Byturus unicolor Say

Cerylonidae

Cerylon castaneum Say

Coccinellidae

Coleomegilla fuscilabris Mulsant

Corylophidae

Molamba ornata Casey

Cryptophagidae

Tisactia subglabra Casey

Cucujidae

Cucujus clavipes Fabricius

Endomychidae

Aphorista vittata (Fabricius)

Erotylidae

Tripla thoracica Say

Passandridae

Catogenus rufus (Fabricius)

Phalacridae

Acylopus ergoty

Laemophloeidae

Laemophloeus biguttatus Say

Languriidae

Languria mozardi Latreille

Lathridiidae

Corticarina cavicollis (Mannerheim)

Monotomidae

Bactridium striolatum (Reitter)

Nitidulidae

Lobiopa falli Parsons

Smicripidae

Smicrips palmicola LeConte

Sylvanidae

Nausibius major Zimmerman

Sphindidae

Odontosphindus clavicornis Casey

LYMEYLOIDEA

Lymeylidae

Elateroides lugubris (Say)

CLEROIDEA

Chaetosomatidae

Malgassochaetus descarpentriesi Ekis & Menier

Metaxina ornata Broun (new familial placement)

Somatochaetus quadraticollis Menier & Ekis

Chaetosoma scaritides Westwood

Chaetosomodes halli Broun

Melyridae

Aplocnemus nigricornis (Fabricius)

Astylus atromaculatus (Blanchard)

Attalus serraticornis Fall

Dasytes niger Linnaeus

Ellanony sculptilis (Leconte)

Hapalorhinus auritus (Leconte)

Mectemycor linearis (Fall)

Melachius horni (Pic)

Melyris viridis Fabricius

Prionocerus caeruleipennis Perty

Semijulistus flavipes (Leconte)

Phycosecidae

Phycosecis limbata Fabricius

Phloiophilidae

Phloiophilus edwardsi Stephans

Trogossitidae

Acalanthus quadrisignata Erichson

Airora cylindrica (Serville)

Anacypta punctata (Fabricius)

Acyrona diversa Pic

Afrocyrona ciskeiensis Kolibáč

Calanthosoma flavomaculatum Reitter

Calithys scabra Thunberg

Decamerus haemorrhoidalis Solier

Diontolobus punctipennis Solier

Eronya angusta (Casey)

Grynocharina peltiformis Reitter

Grynocharis quadrilineata (Melsheimer)

Grynoma diluta Sharp

Gymnochila varia Fabricius

Laperina cirrossa Pascoe

Leipaspis lauricola Wollaston

Larinotus umblicatus Carter et Zeck

Lophocateres pusillus Klug

Indopeltis nilgiriensis Crowson

Necrobiopsis tasmanicus Crowson

Nemozoma elongatum (Linnaeus)

Ostoma columbiana Casey

Peltis grossa (Linnaeus)

Protopeltis viridescens Brown

Promanus depressus Sharp

Seidlitzella procera Kraatz

Temnoscheila acuta Leconte

Tenebroides crassicornis (Horn)

Thymalus marginicollis Chevrolat

Cleridae**Anthicoclerinae subfam.nov.**

- Allonyx quadrimaculatus* (Schaller)
Anthicoclerus anthicoides (Westwood)

Clerinae Latreille

- Aphelocerus coactus* Opitz
Aphelochroa sanguinea (Thomson)
Apopemopsis ater Pic
Apteroclerus brevis Schenkling
Astigmus pygidialis (Pic)
Aulicus edwardsii (Horn)
Aina bifasciata (Chevrolat)
Balcus niger Sharp
Blaima rubripennis (Chevrolat)
Calendyma multiguttata Pic
Cardiostichus gabonicus (Thomson)
Chilioclerus mimus Solervicens
Cleromorpha novemguttata (Westwood)
Cleropiestus oberthuri Fairmaire
Clerus mutillarius Fabricius
Colyphus irazu Ekis
Coptoclerus iodinus (Gorham)
Dacyrocclerus tergocinctus (Gorham)
Dieropsis quadriplagiata Gahan
Dologenitus cyanipennis (Klug)
Eburneoclerus nigroapicalis Pic
Eleale aulicodes (Gorham)
Enoclerus leehermani Ekis
Epiclones basalis Blanchard
Eurymetomorphon bigguttatus Solervicens
Graptoclerus quadripunctatus (Gorham)
Gyponyx apicalis (Chevrolat)
Hemitrachys bizonatus (Gorham)
Homalopilus tristis (Klug)
Inhumeroclerus thomsoni Pic
Languropilus fortipes Pic
Lisaulicus bicoloripes Pic
Metademius penicillatus Schenkling
Myrmecomaera raffrayi Fairmaire
Natalis laplacii Laporte
Neoscrobiger patricius (Klug)
Notocymatodera dimidiata (Germain)
Olesterus australis Spinola
Omadius mediofasciatus Westwood
Opilo mollis (Linnaeus)
Orthrius lateralis Schenkling
Phaeocyclotomus alboplagiatus (Klug)
Phonius sanguinipennis Chevrolat
Perilypus limbatus Gorham
Phloiocopus consobrinus Boheman
Phlogistus imperialis (Gorham)
Phlogistomorpha croesus Blackburn
Placopterus thoracicus (Olivier)
Platyclerus planatus (Laporte)
Plathanocerus albopunctata Hintz
Priocera variegata Kirby
Pseudogyponyx fasciatus Pic
Pseudolesterus novacaledoniensis Miyatake
Rhytidoclerus basipennis (Chevrolat)

- Sallea necrobioides* Chevrolat
Scrobiger splendidus Newman
Stigmatium bimaculatum Blackburn
Systemoderes amoenus Spinola
Thanasimus formicarius (Linnaeus)
Tillicera sorror Schenkling
Trichodes ornatus (Say)
Trogodendron fasciculatum (Schreiber)
Xenorthrius umbratus Schenkling
Zeniticola funestus Chevrolat

Enopliinae Gistel

- Abrosius bipartitus* Pic
Boschella fasciata (Barr)
Crobenia eyrensis Blackburn
Enopliomorpha somalica Pic
Enoplium serraticorne Olivier
Falsocorynetes diversipes (Pic)
Falsolissaulicus rufonitidus Pic
Leptoclerus amoenus Kraatz
Parapelonides nigrescens (Schaeffer)
Pelonides quadripunctatus (Say)
Pyticara duponti (Spinola)
Salarium mirum Fairmaire
Solervencia ovatus (Spinola)
Teneropsis metallicus (Pic)

Epiphloeinae Kuwert

- Acanthocollum melanurum* (Klug)
Amboakis nova (Opitz)
Decaphloeus vitticollis (Schenkling)
Decorosa iviei Opitz
Diapromeces aclydis Opitz
Ellipotoma tenuiformis Spinola
Epiphloeus duodecimmaculatus (Klug)
Hapsidopteris diastenus Opitz
Ichnea lycoides Laporte
Iontoclerus humeralis (Klug)
Katamyurus paxillus Opitz
Madoniella dislocata (Say)
Megaphloeus setulosus (Chevrolat)
Megatrachys paniculus Opitz
Opitzia chiapas (Opitz)
Opitzius thoracicus Barr
Parvochaetus sandaracus Opitz
Pennasolis merkei (Horn)
Pericales albogilvus Opitz
Plocamocera sericella Spinola
Pteroferus zolnerowichi Opitz
Pyticeroidea laticornis (Say)
Silverasia hispidus (Opitz)
Stegnoclava fumigata (Gorham)
Turbophloeus simplex (Schenkling)

Hydnocerinae Spinola

- Alleidea quadrinotata* Lea
Blaesiophthalmus accinctus (Newman)
Callimerus mirandus (Gorham)
Eurymetopum maculatum (Blanchard)
Evenoclerus perrieri (Fairmaire)
Isohydnocera curtispennis (Newman)
Isolemidia pulchella Gorham

Lasiocallimerus vestitus (Corporaal)
Lemidia nitens (Newman)
Neohydus luzonicus Chapin
Parmius longipes Sharp
Paupris aptera Sharp
Phyllobaenus unifasciatus Say
Silviella pehuen Solervicens
Stenocallimerus maderi Corporaal
Wolcottia pedalis (Leconte)

Isoclerinae Kolibáč

Ababa tantilla (LeConte)
Allothaneroclerus tuberculatus (Schenkling)
Compactoclerus robustus Pic
Isoclerus pictus Lewis
Lycosoma parallelum Lewis
Parathaneroclerus triimpressus Pic

Korynetinae Laporte

Corynetinus fimetarius Wollaston
Dolichopsis haplocnemodes Gorham
Korynetes coeruleus Degeer
Necrobia violacea (Linnaeus)
Notostenus viridis Thunberg
Opetiopalpus scutellaris Panzer
Prosymnus testaceiventris Pic

Neorthopleurinae Opitz

Agaphalera janthina (LeConte)
Allochotes bicolor Westwood
Colobotis uncatis Opitz
Decicornis adnatis Opitz
Dermestoides sanguinicollis (Fabricius)
Funicula tubuloides Opitz
Kataspinula omocerina Opitz
Lebasiella pallipes (Klug)
Loedelia mexicana (Gahan)
Megafodina imitans (Kuwert)
Nelsopelonium heterochroma Opitz
Neorthopleura texana (Bland)
Novemera cohibila Opitz
Orthopleuroides nigerrimus Kuwert
Patuleius globulosus Pic
Rifkindius megamera Opitz
Romanaeclerus rufus (Kratz)
Syriopelta funebris (Fairmaire)
Tenerastes mauritanus Lesne
Tenerus praeustus (Laporte)
Tricladus alluaudi Fairmaire

Peloniinae subfam. nov.

Apolopha fryana (Gorham)
Chariessa ramicornis Perty
Corinthiscus insignicornis (Schenkling)
Cregya meieri (Schenkling)
Enoplioides compressicollis Fairmaire
Exochonotus barri Solervicens
Falsoeurymanthus dispar (Schenkling)
Falsopelonium impressipenne Pic
Goyasanum ruficollis Pic
Lasioderma trifasciata (Laporte)
Mimopallenis albonotatus Pic
Muisca bitaeniata Spinola
Neotenerus tuberculatus Schenkling

Pelonium viridis Pic
Pilosirus brunoii Opitz
Phymatophaea pustulifera (Westwood)
Platynoptera lyciformis Chevrolat
Pseudichnea calceata (Chevrolat)
Pyticeropsis bruchi Schenkling
Stenoplium perrieri Fairmaire

Tarsosteninae Jacquelin de Val

Abiliella fasciata Peracchi
Apopylus unumgariensis Kolibáč
Apteropilo chrysocome (Elston)
Blackburniella intricata (Blackburn)
Curacavi dentatus Solervicens
Parapylus bicinctus (Newman)
Pylus fatuus (Newman)
Neopylus nahuelbutensis Solervicens
Rhopaloclerus coquereli Fairmaire
Tarsostenodes simulator Blackburn
Tarsostenus univittatus (Rossi)
Thriocera pectoralis (Klug)
Thriocerodes bifasciatus (Pic)

Thaneroclerinae Chapin

Compactoclerus davidi Kolibáč
Cyrtinoclerus cyrtinoides Chapin
Neoclerus ornatulus Lewis
Thaneroclerus buquet (Lefebvre)
Zenodosus sanguineus (Say)
Viticlerus formicinus Miyatake

Tillinae Leach

Archalius densegranatus Fairmaire
Araeodontia isabellae (Wolcott)
Bogcia oaxacae Barr
Callotillus elegans (Erichson)
Cladiscus obeliscus Lewis
Cylidroctenus chalybaeum (Westwood)
Cylidrus abdominalis Klug
Cymatodera tricolor Skinner
Cymatoderella collaris (Spinola)
Denops albofasciatus (Charpentier)
Diplocladus louvelii (Spinola)
Eucymatodera parva Schenkling
Falsotillus igarashii (Kôno)
Gastrocentrum dux (Westwood)
Lecontella gnara Wolcott
Liostylus posticalis Fairmaire
Magnotillus nodulosus Pic
Monophylla terminata (Say)
Onychotilus vittatus Chapin
Orthocladiscus bipectinatus Westwood
Pallenis vidua (Klug)
Picoclerus ater (Pic)
Pseudopallenis vadoni Pic
Stenocylidrus ruficeps Fairmaire
Strotocera convexa (Hintz)
Teloclerus compressicornis (Klug)
Tilloclerus testaceipes (Fairmaire)
Tillodenops plagiatus (Fairmaire)
Tilloidea unifasciata (Fabricius)
Tillus elongatus (Linnaeus)

Assessments of higher taxa discontinuities

The existence of the impressive diversity of life on earth is biologically best explained by the canons of evolutionary theory as proposed by DARWIN (1859), DOBZHANSKY (1937), MAYR (1942), HENNIG (1966), and POPPER (1968). The applications of their theories and methodologies remain a focus in my investigations of the Cleridae and Cleroidea. However, I am compelled to point out that complete adherence to the working principles of these gentlemen is not always possible as one attempts to unify evolutionarily the diversity of insect taxa, particularly when one deals with taxa that are evolutionarily young. For example, the discovery of synapotypies (*sensu* TUOMIKOSKY 1967) for the elucidation of monophyly of Cleridae has been particularly troublesome at the species level, which percolates to higher phylogenetics as well. An important issue in this matter is that we are investigating relatively recently evolved beetles whose paleontological history may not have been infused with extensive episodes of extinctions. Extinctions may be considered an evolutionary taxonomist's "best friend". They establish interruptions in the evolutionary progression of character states extremely important and convenient in the phylogenetic methodology of HENNIG (1966). Without such interruptions, the discovery and interpretations towards character state polarity becomes difficult, if not impossible. The recognition, albeit tentative, of major phyletic lines that are not based on monophyly, but based on experienced intuition, may be warranted in evolutionarily young taxa. Fortunately, in this study, apotypic character states were found for a full resolution of the proposed phylogeny of Cleridae subfamilies.

Peripherally examined, the Cleridae may be conveniently classified into several major conglomerates of species historically given either tribal or subfamilial status, but the character states on which such divisions are based may become cloudy when genera and their full complement of species are examined on a world-wide basis. As expected, within the Cleridae we find gradations among altered characters, which may or may not involve transformation series, and exceptions in character state distributions (perhaps a manifestation of character reversals, homoplasy, or misplacement of species). Some characters however provide states that are very constant within monophyletic taxa, especially at supraspecific levels. Examples of such characters in adults involve the gula (Fig. 12), laterolacinia (Fig. 46), tibial spurs (Fig. 90), tarsal pulvilli (Fig. 89), prothoracic dorsolateral carina (Fig. 80), metendosternite (Fig. 107), fourth tarsomere (Fig. 92), lobes of the stomodaeal valve (Fig. 149), Malpighian tubules (Fig. 134), spermathecal gland (Fig. 156), spermathecal capsule, saccular bursa copulatrix, testicular follicles, and male accessory glands (Fig. 155). Among larvae, we find useful character variations in the development of the epicranial suture (Fig. 179), shape of the frons (Fig. 187), presence or absence of the cranial endocarina (Fig. 180), structure of the spiracles (Figs 197, 198), and developments of the urogomphi (Fig. 190). "Character transitioning" towards state variations is, of course, what we expect from morphological structure as it proceeds from ancestral conditions to more derived gestalt conditions. Moreover, the transitory character of characters forms the very essence of our analytical process as we attempt to decipher the evolutionary history of character states (and of species upon which they are based) and bring forth classifications of maximal heuristic value.

Given the time and specimen availability limitations that a person has during a lifetime of research, it becomes more than obvious that our efforts in the assignment of species to higher categories must be considered tentative and subject to alterations when future workers discover new phylogenetically significant evolutionary gaps. Such gaps however will only be significant, or credible, taxonomically if they are discovered after careful judgments of species composition of genera, and if adequate representations of species are part of the work strategy; and after methodologies, relevant to character phylogeny, are carefully explained. The evolutionary relationships proposed in this work are based on synapotypes. I invite and urge present and future colleagues in cleridology to take up the cause of involving a full inventory of species during attempts to discover the phylogenetic roots of higher taxa. Thus, I offer the teachings of HORN (1877: 7), who writes, “*Progress in natural history necessarily starts from a basis of species, and until these are accurately described so that others can arrive at knowledge of them no great advance is possible*”.

In conformity with Horn’s idea, I investigated all of the known genera and species of Epiphloeinae Kuwert, Isoclerinae Kolibáč, Neorthopleurinae Opitz, Anthicoclerinae subfam.nov., and nearly all the genera and species of Enopliinae Gistel, Korynetinae Laporte, Tarsosteninae Jacquelin du Val, and Thaneroclerinae Chapin (new status), and as many genera and species made available to me of Clerinae Latreille, Peloniinae, subfam.nov., Hydnocerinae Spinola, and Tillinae Leach (as listed by CORPORAAL 1950). I examined issues of morphology, natural history, and zoogeography. The majority of the work involved adult disarticulated specimens, but I investigated the larval semaphoront as well. When specimens of a taxon were not available, I gleaned information from published descriptions. And, whenever possible I observed the behavioral attributes of my animals in the field. Correspondence and conversations with Justin S. Bartlett, Roland Gerstmeier, Jiří Kolibáč, John Leavengood, Jacques Rifkind, and Jaime Solervicens A., and their published information, were also instrumental in my thinking. The detailed illustrations and general morphologic endeavors of KOLIBÁČ (1989A, 1989B, 1999) have been particularly helpful.

Characters for inferences at supraspecific taxonomic levels

I have devoted many years to the study of world Cleridae. I am confident that I can now offer useful information relevant to a more general question in checkered beetle systematics: What manner of character discontinuities within Cleridae provides credible inferences of higher taxa status? The information provided is based mostly on adult morphological characters, but characters of larval structure were also examined. The characters and the explanation of their states listed below have been consistently found useful for credible placement of species in a higher taxa framework, with exceptions clearly indicated. A frequent difficulty in suprageneric taxonomy is the inevitable species that “seems” to belong to a particular genus, but one that, in fact, does not “fit” according to the convenient external characteristics. The characters listed below may solve such a problem, or perhaps corroborate that designation of a higher taxon is warranted.

The characterizations involving mesodermal and larval organs must be considered tentative because they are based on a limited number of taxa. The belief that character

reversals and homoplasy may also be looked upon as evolutionary novelties are explained elsewhere (OPITZ, in press-*Madoniella*). Such evolutionary realities probably reflect the fact that within Cleridae many species, across phylogenetic lines, have evolved towards a limited number of lifestyle strategies that revolves around mimicry and predation. Such relatively restricted lifestyles would have perhaps a limited amount of genetic expression. Moreover, characteristics involving selection towards mimicry and predation would be highly susceptible to homoplasious manifestations of structure and behavior.

With the above in mind, information about characters that are less prone to the stringent selection pressures towards mimicry and venues of predatory utensils would be particularly relevant in discussions of Cleridae evolution. CROWSON (1964, 1972) is among the few insect systematists that shared this view by including information about larvae and mesodermal organs in his conclusions about supraspecific checkered beetle relationships.

The list of characters, and their states, that follows is intended to serve as a beginning data set towards attempts to formulate a morphologically balanced higher taxa concept within the Cleridae. The states of some characters have been found to be very consistent within those groups that are supported by monophyly. Moreover, the categorical level defined by these character states, is stated with great confidence because they have been tested by historical and modern scrutiny.

Family level characters and their states

Laterolacinia: Among Cucujoidea, Lymexyloidea, and Cleroidea only in the Cleridae do we find the laterolacinia (Figs 8, 46). In the vast majority of the Cleridae the laterolacinia is a distinct lateral lobe of the lacinia, easily distinguished from the mediolacinia (Figs 46–53). Rarely, is the laterolacinia present as an inflexion or, more rarely, it is completely obliterated secondarily. The latter condition is assessed as secondary in view of the presence of that organ across all mayor phylogenetic lines within the Cleridae.

Postgular plate: When considering the abovementioned superfamilies only in the Cleridae do we find a postgular plate and the evolution of the postgular process. In its most basic form, as seen in the Thaneroclerinae Chapin (Figs 11, 12), the postgular plate is a setose transverse extension clearly separated from the gula by a suture. The gular plate evolved into a variety of states, some of which are significant at the subfamily level.

Subfamilial level characters and their states

Tarsomere formula: There are three states in the tarsomere-formula character: 5-5-5 as found in Thaneroclerinae Chapin (Fig. 83), Tillinae Leach, Clerinae Latreille, Hydnocerinae Spinola, Neorthopleurinae Opitz, Epiphloeinae Kuwert, Peloniinae, subfam.nov., and Tarsosteninae Jacquelin du Val; 5-5-4 present in Anthicoclerinae, sufam.nov. (Fig. 86); and 5-4-4 found in Isoclerinae Kolibáč (Fig. 85).

Fourth tarsomere: The fourth tarsomere is of normal size (Fig. 83) in Thaneroclerinae Chapin, Anthicoclerinae, subfam. nov, Isoclerinae Kolibáč, Tillinae Leach, Clerinae Latreille, Hydnocerinae Spinola. This tarsomere is diminutive (Fig. 92) in Epiphloeinae Kuwert, Enopliinae Gistel, Peloniinae subfam.nov., Tarsosteninae Jacquelin du Val, Korynetinae Laporte, and in Neorthopleurinae Opitz.

Gular sutures: The gular sutures are primitively converging (Fig. 12) as seen in the Thaneroclerinae Chapin, Isoclerinae Kolibáč, Tillinae Leach, Hydnocerinae Spinola, Anthicoclerinae, subfam.nov., Epiphloeinae Kuwert, Enopliinae Gistel, Peloniinae, subfam.nov., and Tarsosteninae Jacquelin du Val. They are straight in (Fig. 15) Korynetinae Laporte and very short and diverging (Fig. 16) in Neorthopleurinae Opitz and in various genera of Clerinae Latreille. The potential taxonomic significance of the gula, in matters of Cleridae classification, is first discussed by GAHAN (1910: 62).

Postgular plate: In its evolutionary development, the gular plate becomes progressively more swollen at the extremities where two swollen gular processes are often expressed (Fig. 14). This condition is found in Tillinae Leach, Clerinae Latreille, Anthicoclerinae subfam.nov., Hydnocerinae Spinola, Epiphloeinae Kuwert, Enopliinae Gistel, Neorthopleurinae Opitz, Peloniinae, subfam.nov., and Tarsosteninae Jacquelin du Val. The setose postgular processes coalesce basally into a bifurcated post gular process in the Korynetinae Laporte and is in its most reduced state as a petiolate bifurcated process in the Neorthopleurinae Opitz.

Gular processes: As the third step in gular plate evolution there is the development of two well-developed setose gular processes (Fig. 13) that sometimes approximate each other. The gular processes are widely separated in the Tillinae Leach, Clerinae Latreille (Fig. 14), Anthicoclerinae, subfam.nov., Hydnocerinae Spinola, Epiphloeinae Kuwert, Enopliinae Gistel, Peloniinae, subfam.nov., and in Tarsosteninae Jacquelin du Val. However, the processes are basally contiguous and bilobed in the Korynetinae Laporte (Fig. 15), and contiguous petiolate in Neorthopleurinae Opitz (Fig. 17).

Pronotal commissure: The posterodorsal region of the pronotal subcarinal Plate (Fig. 81) has three states of morphological development. It extends from one side of the pronotum to the other via a pronotal commissure (Fig. 78), below the posterior component of the pronotal dorsolateral carina. We find this state in the Neorthopleurinae Opitz (Fig. 81), and Korynetinae Laporte (Fig. 80). Another state involves the presence of a partially developed pronotal commissure, in which the subcarinal plate extends posteromedially beyond the posterior angle of the pronotum where it conjoins with the pronotal hem (Fig. 65). The abbreviated condition of the pronotal commissure is found only among genera of Enopliinae. Lastly, in Tillinae Leach, Clerinae Latreille, Anthicoclerinae subfam.nov., Hydnocerinae Spinola, Epiphloeinae Kuwert, Peloniinae subfam. nov, and in Tarsosteninae Jacquelin du Val (as redefined herein) the dorsoposterior limit of the pronotal plate meets the pronotal hem at the pronotal dorsoposterior angles (Fig. 66). The commissure is particularly thin in the genus *Solervicensia* Barr and nearly obliterated in *Opetiopalpus* Spinola. In the Thaneroclerinae Chapin and Isoclerinae Kolibáč, the relationship between the posterodorsal portion of the subcarinal plate and the pronotal hem is obscured by the fragmented condition of the pronotal dorsolateral carina. The developments of the pronotal dorsoposterior characteristics were first described by SOLERVICENS (2005: 49).

Pronotal prebasal carina: Only among genera of the Thaneroclerinae Chapin, do we find a transverse setose carina in front of the prebasal pronotal depression (Fig. 67).

Antennal insertion: The point of insertion of the antennae, in relation to the ocular notch, is relevant at this taxonomic level. The insertion may be near the middle of the ocular notch as found in the enopliine genus *Cregya* Leconte (Fig. 5) or considerably below the ocular notch as in all Epiphloeinae Kuwert, as exemplified by the condition in the genus *Epiphloeus* Kuwert (Fig. 1).

Pronotal trichobothria: All 267 species of subfamily Epiphloeinae Kuwert have two pairs of pronotal trichobothria (Figs 59, 69, 70, 72, 74, 75, 76, 98, 99).

Metendosternite: The configuration of this organ is quite variable among Cleridae. However, the furcal lamina (Fig. 107) is absent in all but one genus of Epiphloeinae Kuwert; the exception involves the monotypic *Turbophloeus* Opitz, in which the furcal lamina is well developed (Fig. 111).

Protarsal venter: The cuticle of the first four protarsomeres venter is expanded, strongly chitinized, and profusely setose (Fig. 24) in the Thaneroclerinae Chapin and Isoclerinae Kolibáč. I consider this the primitive state that led to the evolution of tarsal pulvilli as seen in all other Cleridae (Fig. 25), in which the cuticle of the tarsal venter is membrane-like, also setose, and variously expanded. The fully established pulvilli, as seen in Tillinae and Clerinae (Fig. 25), become reduced secondarily in some genera of these and other subfamilies (Figs 26, 27). In all known species of Epiphloeinae, the metatarsus is characterized by having usually only one pulvillus (Fig. 91), rarely two (Fig. 89).

Pronototergosternal suture: The pronototergosternal suture is incomplete among members of the Neorthopleurinae Opitz (Figs 81, 82). It is complete in all other subfamilies (Figs 79, 80).

Carina in the metacoxal abdominal depression: This characteristic has been observed in many genera of the Tillinae Leach. It is particularly pronounced in those tillines that are known to stridulate (Figs 96, 97); as described by Rifkind (2006: 258).

Tegmen: The phallobasic apodeme, whose length is considerably variable throughout the family, is absent in Thaneroclerinae Chapin (Fig. 118) and Isoclerinae Kolibáč (Fig. 117).

Stomodaeum: The stomodaeum is very long in Thaneroclerinae Chapin (Fig. 136), Isoclerinae Kolibáč, and in some Tillinae Leach. A long stomodaeum represents the primitive state of this character with its derived, more shortened state, variously manifested in other Cleridae (Fig. 137).

Stomodaeal valve lobes: The proventricular valve is comprised of 4 primary and 4 secondary lobes in Thaneroclerinae Chapin and in Tillinae Leach (Fig. 147). In Clerinae Latreille and in Hydnocerinae Spinola the valve is comprised of 4 primary and 2 secondary lobes (Figs 148, 149), and in Epiphloeinae Kuwert, Enopliinae Gistel, Neorthopleurinae Opitz, Peloniinae subfam.nov., and Korynetinae Laporte the valve is reduced to 4 primary lobes with the most dorsal lobe being wider and shallower (Figs 142, 143, 150, 151, 152).

Malpighian tubules: Among those species in which the alimentary canal was observable I found the following Malpighian-tube numbers: Neorthopleurinae Opitz, Enopliinae Spinola, Peloniinae, subfam.nov., and Thaneroclerinae Chapin, all have

4 cryptonephridial Malpighian tubules (Figs 139–141, 144, 145), whereas 6 are present in the Tillinae Leach, Clerinae Latreille, Hydnocerinae Spinola, and Korynetinae Laporte, (Figs 134, 137, 138, 146). There are 4 tubules in *Chaetosoma colossa* Opitz (Fig. 135).

Larval epicranial suture: Only in the Thaneroclerinae Chapin and in *Tenerus* Laporte, of Neorthopleurinae Opitz, is there a coronal component of the larval epicranial suture (Figs 179, 188).

Larval frons: Among all Cleridae larvae described, only in the larvae of *Phyllobaenus* Dejean (Fig. 187), *Isohydnocera* Chapin, *Silviella* Solervicens, and *Callimerus* Gorham, of subfamily Hydnocerinae, do we find the frons truncated posteriorly.

Larval cranial endocarina: Among all Cleridae larvae described, the cranial endocarina is missing only in the larvae of *Phyllobaenus* Dejean, *Isohydnocera* Chapin, and *Callimerus* Gorham. Its absence in the thaneroclerines (Fig. 179) is considered secondary and not evolutionarily equivalent to its absence in the abovementioned hydnocerines.

Generic level characters and their states

Size of ommatidia: Among genera there is a clear distinction between small ommatidia (Fig. 1) (described as fine), as found in *Enoclerus* Gahan species, and large ommatidia (Fig. 5) (described as coarse), as found in the *Cregya* Leconte species. It would be helpful, perhaps, if we consider the coarse-eye condition present if we can see the full convexity of each ommatidium and the fine-eye condition when we cannot (at 250×).

Head form: Generally the checkered beetle cranium is subquadrate as in specimens of *Zenodosus* Wolcott, or nearly round but transverse, as in specimens of *Romanaeclerus* Winkler. However, in some genera the cranium is longitudinally expanded behind the mouthparts and behind the eyes, which gives the head a subrostrate appearance. The expanded cranium is exemplified in members of *Dolichopsis* Gorham.

Shape of the maxillary and labial terminal palpomeres: There are two broad states of these characteristics, with intermediates that are also consistent at genus level. The securiform palpomere (Figs, 44, 45) is broadly triangular, as in species of *Pelonium* Spinola (Fig. 44), and the digitiform palpomere is elongate, broadest near the middle or broadest near its base (essentially finger shaped) (Fig. 43), as in species of *Pyticeroides* Kuwert. Sometimes the triangular shape of the terminal palpomere is narrowed in its basal half, a condition I call subsecuriform (Fig. 42), and exemplified in species of *Epiphloeus* Kuwert, and sometimes the maxillary palpi are digitiform and the labial palpi securiform, as in species of *Tillus* Olivier. Whatever the combination of terminal palpi characteristic of a species, I have found that characterization consistent in historically stable genera. A remarkable exception to intrageneric consistency in the shape of the terminal palpomeres is found in *Nelsonoplum* Barr in which the shape of these organs is sexually dimorphic.

Length of the scape: The scape may be very long as in species of *Plocamocera* Spinola and *Epiphloeus* Spinola (Figs 1, 33), in which case it is much longer than the

combined length of the pedicel and the first two antennomeres of the funicle, or it may be normal in length, as in species of *Necrobia* Olivier (Fig. 28) in which case it is about as long as the combined length of the pedicel and the first funicular antennomere. Also, the scape may be very short and nearly globose, as one finds in species of *Wolcottia* Chapin (Fig. 32).

Type of antennae: There is considerable variation of antennal types in the Cleridae. However, most relevant for this treatise is that within a genus antennal basic morphology does not vary. The clavate condition is found in *Wolcottia* Chapin (Fig. 32). The capitate antenna, perhaps the most widespread antennal type in the Cleridae, is exemplified in *Trichodes* Herbst (Fig. 39) and in a variety of other genera in which the capitular antennomeres are variously lobed (Figs 29, 30). In *Cymatodera* Gray the antenna is filiform (Fig. 40), whereas in *Bogcia* Barr it is serrate (Fig. 41). More exotic type of antennal structure is found in the species of *Callotillus* Wolcott in which it is pectinate (Fig. 36), in males of *Chariessa* Perty, in which it is capitular-lamellate (Fig. 34), and in males of *Tenerastes* Lesne, in which the antennae are flabellate, but with antennomere 5 and 7 drastically minute (Fig. 35). Sex dimorphism in antennal form is common in the Cleridae (Figs 37, 38).

Antennomeres: Intrageneric consistency exists in the number of antennomeres that comprise the antenna. In general, the antenna consists of 11 antennomeres, but it may be variously reduced in antennomeral numbers. There are 8 antennomeres in the monotypic epiphloeine genus *Diapromeces* Opitz.

Antennal capitulum: In genera, in which the antennal is capitate, there is considerable intergeneric variation in the shape of the penultimate two antennomeres. These antennomeres are distinctly rectangular in *Necrobia* Olivier (Fig. 28).

Shape of the distal end of the prointercoxal process: The two principal states of this character involve whether the distal end of the prointercoxal process is expanded at its posterior limit (Fig. 60), as in species of *Pylus* Newman, or if not expanded, then the process is linear, as in species of *Placopterus* Wolcott.

Pronotal dorsolateral ridge: If the pronotal ridge is complete, the ridge forms a ring around the pronotum as in species of *Allochotes* Westwood. If the pronotal ridge is only partly formed, it usually coalesces with the pronotal hem at the pronotal posterior angle (Fig. 66) as in species of *Pelonium* Spinola, or the partially developed ridge may become confluent with the pronotal hem slightly mesad to the pronotal posterior angle (Fig. 65) as in *Crobenia* Blackburn or *Enoplium* Latreille.

Primary (1°) and secondary (2°) degree elytral setae: Among the Cleridae, it is common for the elytral disc to have 1° setae and 2° setae. The 1° setae are those that are usually present at the upper periphery of elytral asetiferous punctations. The 2° setae emerge out of small, often minute, setiferous punctations in the spaces between the asetiferous punctations. The 2° setae are most often randomly distributed throughout the elytral disc, but sometimes they form setal fascia as in *Tillicera* Spinola. They may also form setal patches whose taxonomic significance is high at species level as in species of *Callimerus* Gorham. In other examples, the 2° setae are very decumbent to form discal setal mats as in *Neotenerus* Schenkling. The 2° setae are absent in *Lebasiella* Spinola.

Tibial spur formula: This character involves the number of tibial spurs starting with the prothoracic leg. The tibial spurs are present in the membranes between the end of the

tibia and beginning of the basitarsus (Fig. 90). This is one of the strongest characteristic within genera. Incompatibility involving the tibial spur formula has consistently indicated incongruous placement of species. Commonly the states are 2-2-2 as found in *Loedelia* Lucas, 2-2-1 in *Pylus* Newman, 1-2-2 in *Cregya* LeConte, 1-2-1 in *Blackburniella* Chapin, 0-2-2 in *Lyctosoma* Lewis, 0-1-1 in *Platynoptera* Chevrolat, 0-2-1 in *Falsoerymanthus* Pic, 0-1-0 in *Callimerus* Gorham, 0-0-2 in *Allochotes* Westwood, and rarely 1-1-1 in *Lebasiella* Spinola, and 0-0-0 as in *Romanaeclerus* Winkler.

Tarsal pulvillar formula: The development of the tarsal pulvillus beneath each tarsomere is a factor in the establishment of the tarsal pulvillar formula. The formula begins with the most basal pulvillus of each leg. Moreover, while the prothoracic and mesothoracic tarsomeres are usually very apparent, there is ample intergeneric variation in the expression of the pulvillus of the metabasitarsus and second metathoracic tarsomere. I consider a pulvillus present even if only present in a minute form, which must be checked with high magnification under fluid. So far, I have found the following pulvillar combinations; 4-4-4 as in *Lemidia* Spinola, 4-4-3 in *Thanasimus* Latreille, 4-4-2 in *Tillicera* Spinola and *Apopemsis* Schenkling, 4-0-0 in *Thaneroclerus* Lefebvre, 4-3-2 in *Clerus* Fabricius, 3-3-3 in *Pylus* Newman, 3-3-2, in *Incorynetes*, 3-3-1 in *Decorosa* Opitz, 2-2-1 in *Corynetinus* Reitter, or 2-1-1 in *Opetiopalpus* Spinola. It should be noted that there is a general trend in the reduction of pulvillar development from the prothoracic leg to the metathoracic leg, and that there is a tendency towards reduction of pulvillar development of the metatarsus within the family (Figs 87–89, 91). Also, only in *Omadius* Laporte have I found the pulvillar formula to vary. It may be 4-3-2, 4-3-1, 4-2-1, 4-2-0, and 4-1-1. This suggests that *Omadius* Laporte has a long evolutionary history not likely infused with frequent episodes of extinctions, or there may be several genera intermixed in the genus as it is currently interpreted.

Tarsal unguis: The development of the tarsal unguis falls into three broad categories, all three of which are excellent indicators of proper placement of species in genera. Usually, the unguis consist of an acuminate hook-like structure that has a well-developed denticle at its base, as in *Perilypus* Spinola (Fig. 95). However, the unguis may be devoid of the basal denticle (Fig. 93) as is the case in species of *Pelonium* Spinola. In members of *Araeodontia* Barr the unguis is tridentate (Fig. 94). Also, basal denticle development ranges from a slight swelling as in *Wolcottia* Chapin, to a fully developed tooth-like structure (the dentes) as in *Blaxima* Gorham. In some genera the tarsal unguis is sex dimorphic with an extraordinary development in the male protarsus, as is evident in the clerine members of *Perilypus* Spinola. Another extraordinary development in the basal denticle is found in *Enoplioides* Fairmaire in which the prounguis is devoid of a denticle whereas the mesounguis and metaunguis have a well-developed denticle.

Aedeagus: The form of the tegmen has been observed to be quite consistent within monophyletic genera. The tegmen structure and the particulars of the phallus are perhaps the best indicators of genetic discontinuities among populations of the Cleridae (Figs 115, 116). Because of this, it is imperative to examine the morphology of the aedeagus in any descriptive generic or species-level Cleridology. Among species of *Neorthoppleura*

Barr and *Enoplium* Latreille there is a connecting membrane between the tegmen and phallus, and the membrane exhibits hooks whose shape is species-specific. In *Katamyurus* Opitz, the phallic apex has a curious spring-like projection. In *Enoclerus* Gahan and *Perilypus* Spinola, the aedeagus is quite simple with the phallus unspecialized and the tegmen a simple tube with rounded lobes (not parameres) at the distal extremity. However, even in these simplified states the aedeagus is often reliable for identifications at the species level. The development of the phallobasic rod (Fig. 119) is particularly important for the discernment of *Madoniella* Pic species.

Spicular fork: The extent of development of the lateral plates of the spicular fork is consistent within genera (Figs 176, 177). The lateral plate is very triangular in species of *Dolichopsis* Gorham, or narrowly contiguous with the spicular apodemes as in species of *Metademiis* Schenkling.

Spicular apodeme: The extent of fusion of the spicular apodemes is consistent within taxonomically stable genera (Figs 176, 177). The spicular apodemes may be joined laterally as in species of *Brachycallimerus* Chapin, or completely separated as in species of *Tenerus* Laporte.

Spermathecal capsule: For obvious reasons, the internal organs of many genera of the Cleridae have not been studied. To this point, however, there are indications that the shape of the spermathecal capsule is consistent at the genus level. I have examined the mesodermal female reproductive organs of more than 12 species of *Phyllobaenus* Dejean (Fig. 169) and several of *Isohydnocera* Chapin (Fig. 171) and find the capsule highly sclerotized and very round in those genera, whereas in all three species of *Necrobia* Olivier the capsule is barrel-shaped (Fig. 173). In *Tilloidea* Laporte the capsule is partially divided (Fig. 167), whereas in *Lecontella* Wolcott and Chapin it is minimally sclerotized and vermiform. In *Thaneroclerus* Lefebvre the base of the capsule is swollen and the distal two-thirds sinuous (Fig. 160), and in *Aulicus* Spinola the capsule is fully divided into two capitate chambers.

Spermathecal gland: Where the spermathecal gland attaches to the spermathecal capsule does not vary within credibly established genera. In *Notostenus* Dejean the attachment site is at the apex of the capsule, in species of *Thanasimus* Latreille the attachment is at the middle, whereas in species of *Enoclerus* Gahan, the attachment is at the base of the capsule. See SOLERVICENS (2007: 61) for detailed drawings of the mesodermal female reproductive organs of species of *Epiclides* Chevrolat and *Calendyma* Lacordaire.

Bursa copulatrix: The presence or absence of a saccular bursa copulatrix is consistent within stable genera. Its presence is clearly defined in species of *Epiphloeus* Spinola (Fig. 156), while in those of *Phyllobaenus* Dejean the bursa copulatrix is a mere swollen continuation of the vagina (Fig. 169).

Male accessory glands: The number and configuration of the male accessory glands are useful at genus level. In species of *Phyllobaenus* Dejean there is one pair of highly lobulate glands (Fig. 168), and in those of *Isohydnocera* Chapin the single pair of glands are swollen at the base and are very long and convoluted (Fig. 170). There is considerable intrageneric variation of the male accessory glands relative to division of a gland into two branches, each of which may be expressed in various stages of

development (for example see the various accessory-gland branching possibilities in *Enoclerus* Gahan as described by EKIS (1978: 279). *Chaetosoma colossus* Opitz, of Chaetosomatidae, shows only one pair of accessory glands (Fig. 165).

Testicular follicles: When the testis is comprised of multiple follicles, the follicular composition of the testes may vary within a genus. However, the tendency among tillines is for the testes to comprise of one very long follicle as is seen in species of *Cymatodera* Gray and *Tilloidea* Laporte.

Proventricular intima: The primary lobes in species of *Trichodes* Herbst have a particularly thick intima presumably to crush pollen on which they feed.

Larval spiracles: The construction of the abdominal spiracles varies from annuliform (Fig. 197) to biforous, i.e., circular but with variously developed air tubes (Fig. 198). In larvae of *Thaneroclerus* Lefebvre and *Necrobia* Olivier there is a comparatively long pair of tubes extending from the circular peritreme, whereas in members of *Enoclerus* Gahan, *Callimerus* Gorham, and *Cregya* Leconte the air tubes are very small. Apparently, the air tubes are absent in the members of *Cymatodera* Gray, *Priocera* Kirby, and in *Phyllobaenus* Dejean.

Description of family Cleridae

Diagnosis. Members of Cleroidea belong to Cleridae if they have postgular developments in the form of a postgular plate (Fig. 12) or postgular process (Fig. 15), and if they exhibit a laterolacinia (Fig. 8) that may be reduced to a lacinial inflexion. All Cleridae have the protarsus dilated ventrally either in the form of tarsal pulvilli (Fig. 25) or tarsoventral expansions that are highly setose (Fig. 24). A few species have secondarily reduced the metatarsal pulvilli (Figs 26, 27) or lost the laterolacinia.

Observed in nature or in the laboratory, checkered beetles may be recognized by their “scurry-like” movements. Some members exhibit necrocryptic behavior (behavior that involves concealment in postures that simulates death) and may be confused with small morsels of debris. Commonly, they can be seen propped on wood, broad leaves, branches, or flowers intensely vibrating their elevated antennae. Some species catapult to flight, in the fashion of dipteran flight behavior. Others, walk to the highest point of a substrate, and then take full flight (Bartlett, personal communication).

Structurally, these beetles have a firm corneous exoskeleton and are known for their extensive pubescence and striking coloration. They are often stout short or stout long rectangulate with a somewhat flattened body, but can also be dull-colored and subcylindrical. Body-form is most often correlated with their predaceous habits on wood boring beetles whose galleries they frequent. The vast majority of species have a capitate antenna. Some checkered beetles are inquilines, but as a group, their most outstanding attribute is found in the precision of evolution towards a mimetic and/or predatory life style. Bright body coloration as commonly seen in highly aposematic and mimetic species; particularly in those from the environs of South America, Africa, Madagascar, and Asia.

Description. *Shape:* Elongate stout short, stout long, somewhat depressed or cylindrical, from slightly convex to extremely convex. *Size:* Length 1.8–44.0 mm; width 0.7–12 mm.

Integumental Color: Often multicolored, mixture of aposematic ground color and colorful fascia on elytra, also found entirely or predominantly dark brown, black, or metallic blue, violaceous, or green. *Head:* Hypognathous; cranium transverse, quadrate, subglobose, or elongate; epistomal suture expressed as indentation (Fig. 18), epistomal ridge present but usually abbreviated (Figs 19–22); clypeus usually bipartite, with basal portion pigmented and distal part devoid of pigmentation; frontal preantennal angle usually blunt, rarely acute (Fig. 23); eyes finely (Fig. 1) or coarsely faceted (Fig. 5), ocular notch deep (Fig. 5) or faintly visible (Fig. 6); gula broad (Fig. 12) or constricted (Fig. 17), sutures converge (Fig. 12), diverge (Fig. 17), or straight-up (Fig. 15), postgular plate (Fig. 12) or postgular process (Figs 13, 15) present; antenna inserted at middle of ocular notch (Fig. 2) or at base of ocular notch (Fig. 1), composed of 8 to 11 antennomeres, usually capitate (Fig. 28), often capitulum comprised of expanded antennomeres (Fig. 30), sometimes serrate (Fig. 31), pectinate (Fig. 36), capitates (Fig. 32), flabellate (Fig. 35), or filiform (Fig. 40); mandible well sclerotized, stout, apical dens acute (Fig. 55) or blunt (Fig. 54), basal notch large or small; labrum well developed, deeply incised (Fig. 4) or not incised (Fig. 6), tormal process transverse, contiguous or not, sometimes sinuous, epipharynx variously developed; maxilla almost always with well-developed laterolacinia (Figs 8, 46–53), latter sometimes evident as cuticular inflexion, rarely absent, terminal palpomere securiform (Fig. 44), subsecuriform (Fig. 42), or digitiform (Fig. 43); labium well developed, terminal palpomere securiform (Fig. 45) or digitiform (Fig. 42). *Thorax:* Pronotum transverse (Fig. 56), quadrate (Fig. 57), or elongate (Fig. 58), sometimes suboval, anterior transverse depression present or not, dorsolateral ridge present or not, if present partial (Fig. 79) or complete (Fig. 78), subcarinal plate transversally extended posteriorly into commissure (Fig. 81) or not extended posteriorly (Fig. 66), pronotal hem always well developed (Fig. 66), lateral margins smooth or crenulate (Fig. 61), pronotal projections short (Fig. 65) or long, may extend to prointercoxal process; pronototergosternal suture usually complete (Figs 79, 80), rarely incomplete (Figs 81, 82); prosternum expanded anteriorly or not, prointercoxal process linear or expanded distally (Fig. 60); procryptosternum incomplete (Fig. 60) or complete (Fig. 64); procoxal cavities open (Fig. 60) or closed (Fig. 64); trichobothrium (Fig. 59) present or not, when present domed (Fig. 76) or not (Fig. 75); elytral disc with (Fig. 62) or without (Fig. 63) asetiferous punctations, with or without 1° or 2° setae, epipleural fold usually well developed, usually positioned laterally (Fig. 213), but sometimes obliquely (Fig. 212), or ventrally inflexed (Fig. 211), anterior ridge present or not; legs cursorial, tarsal formula usually 5-5-5, rarely 5-5-4, 5-4-4, tibial spur (Fig. 90) formula and tarsal pulvillus (Figs 87–89, 91) formula variable, unguis with (Fig. 95) or without (Fig. 93) basal denticle, sometimes tripartite (Fig. 94), protarsal unguis sometimes asymmetrical (Fig. 95), fourth tarsomere minute (Fig. 92) or not (Fig. 83), tibia with (Fig. 103) or without carina; methathoracic wing venation variously developed, wedge cell closed or open (Fig. 175); metendosternite usually with well-developed furcal lamina (Figs 107–110, 112–114), rarely without furcal lamina (Fig. 111). *Abdomen:* Comprised of 6 visible sternites, 6th often slid under 5th, 6th most often incised distally in males; metacoxal cavities carinate (Figs 96, 97) or not; spicular fork well developed, intraspicular plate linear (Fig. 177) or transverse (Fig. 176), spicular

plates may be variously broadened; aedeagus usually not inverted, well sclerotised or feebly sclerotized, tegmen usually tubular, lobed distally or not, if lobed lobes fimbriate (Fig. 126) or not (Fig. 115), phallobasic apodeme present (Fig. 115) or not (Fig. 118), phallus comprised of two phallic plates that are sometimes adorned with hooks and dentations (Figs 121, 125); ovipositor well developed, with oblique and ventral bacculi, multilobed ventral and dorsal laminae, and setose styli; spiculum ventrale longer than length of 6th sternite. *Alimentary Canal*: Comprised of well-developed stomodaeum, ventriculus, and proctodaeum (Figs 134–141, 144–146); 4 or 6 cryptonephritic Malpighian tubules; proventricular valve comprised of 8 to 4 lobes (Fig. 142, 143, 147–152); ventriculus with well-developed (Fig. 134), or poorly-developed (Fig. 139) crypts. *Mesodermal Male Reproductive Organs*: Usually comprised of multifollicular testes; seminal vesicle, vas deferens, and ejaculatory duct well developed; usually with multilobate accessory glands (Figs 153, 155, 158, 159, 161, 163, 166, 168, 172, 174), rarely comprised of unilobed accessory gland (Fig. 170). *Female Mesodermal Reproductive Organs*: Comprised of multifollicular ovary, lateral oviduct, medial oviduct, bursa copulatrix, spermathecal capsule, spermathecal gland, and vagina (Figs 154, 156, 157, 160, 162, 164, 167, 169, 171, 173); spermathecal capsule highly sclerotized or minimally sclerotized; bursa usually comprised of sac leading from the vagina; spermatheca gland variously attached to spermathecal capsule. *Larva*: Digitiform to vermiform (Fig. 178), cylindrical or somewhat flattened; exposed forms tend towards bright coloration, whitish forms tend to occupy galleries of lignicolous insects; head usually prognathous, rarely hypognathous, protruding or not, capsule transverse or subconical; epicranial suture represented by frontal suture and coronal suture or only by frontal suture (Fig. 179), frons usually triangular, rarely truncated posteriorly (Fig. 187), endocarina present; from 0 to 5 stemmata; clypeus trapezoidal; labrum movable, well-developed; antenna comprised of 3 antennomeres; mandible well developed, sometimes falcate, highly sclerotized, molar absent, retinaculum and lacinia mandibulae present; thorax variously sclerotized; legs well sclerotized, comprised of 5 segments; abdomen usually fleshy, comprised of 9 segments, 9th tergum with or without sclerotized plate or urogomphi (Figs 190–196), abdominal spiracles annuliform (Fig. 197) or biforous (Fig. 198).

Distribution. Checkered beetles are found throughout the world with particular prominence in the Neotropics and Paleotropics.

Member taxa: As defined herein, the Cleridae is comprised of 3,629 species, classified into 334 genera and 12 subfamilies.

Key to subfamilies

I present two levels of characteristics in the couplets of the following key. The first level involves the more readily visible diagnostic features of specimens, whereas the second level pertains to characteristics that may require some efforts of dissection under magnification. Within the superfamily Cleroidea, specimens belong to the Cleridae if the protarsomeres are ventrally dilated (Figs 24, 25) and the posterior limits of the gula show a post gular plate (Fig. 12) or post gular process (Fig. 15). The vast majority of species

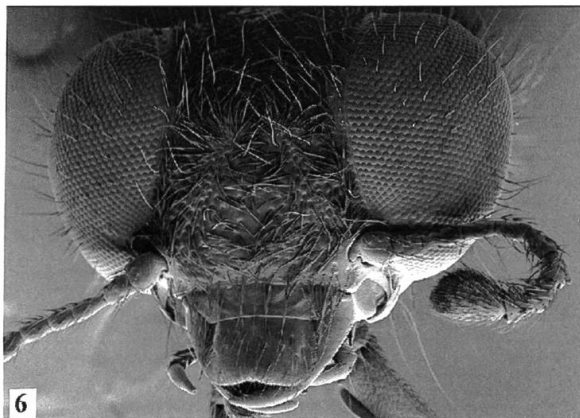
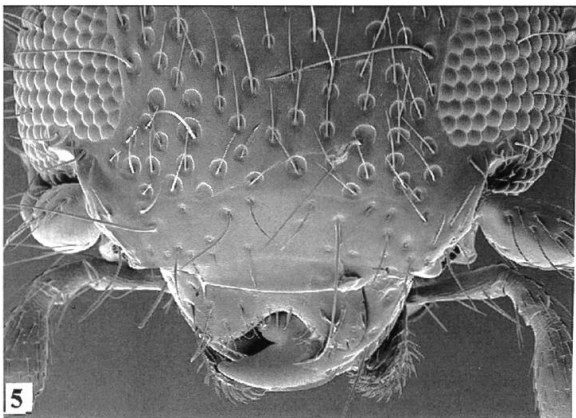
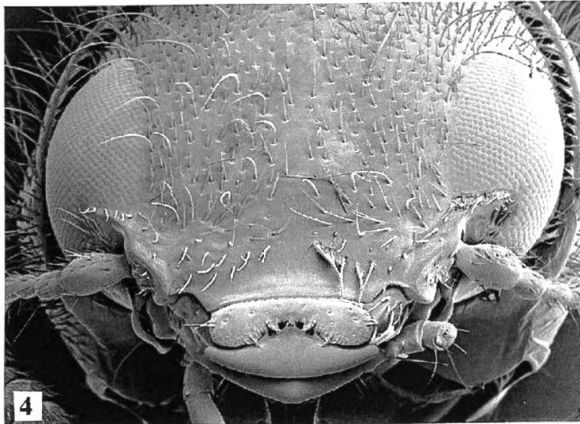
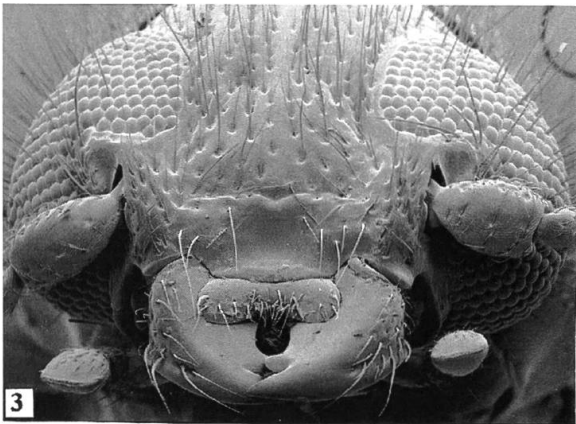
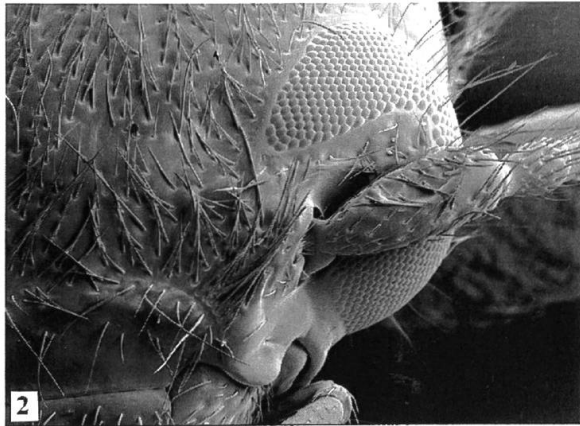
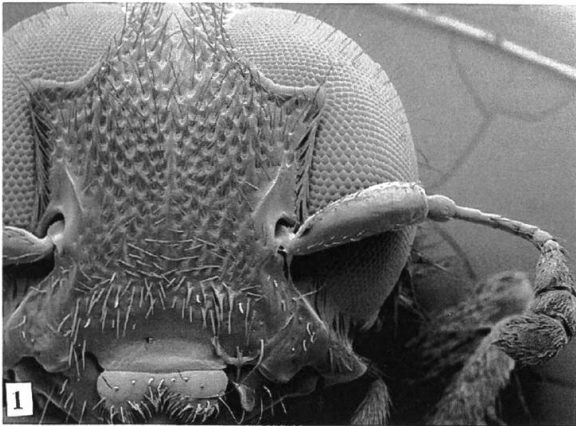
show a laterolacinia (Fig. 46). In the Cleridae, as now defined, there are 3,629 species classified into 334 genera and 12 subfamilies. These numbers were taken from CORPORAAL (1950A) with adjustments made regards subsequent synonymizations and description of new species.

- 1 Protarsomeres consolidated into an oval ventral cluster that is very setose, (Fig. 24). 2.
- 1' Protarsomeres not consolidated into a ventral cluster, each tarsomere with a membraneous pulvillus (Fig. 25). 3.
- 2(1) Tarsal formula 5-5-5 (Fig. 83). **Thaneroclerinae**
- 2' Tarsal formula 5-4-4 (Fig. 85). **Isoclerinae**
- 3(1') Tarsal formula 5-5-4; basimetatarsomere large (Fig. 86); body length about 3–4 mm long. **Anthicoclerinae**
- 3' Tarsal formula 5-5-5; basimetatarsomere not particularly large; usually much longer than 4 mm in body length. 4.
- 4(3') Fourth tarsomere minute (Fig. 92). 5.
- 4' Fourth tarsomere not minute (Fig. 83). 10.
- 5(4) Antenna inserted on lower portion of ocular notch (Fig. 1); pronotum with two pairs of trichobothria (Figs 59, 74); metatarsus with 1 pulvillus or 2 pulvilli. **Epiphloeinae**
- 5' Antenna inserted at middle of antennal notch (Fig. 4); pronotum without trichobothria; metatarsus usually with more than two pulvilli (Figs 87, 88). 6.
- 6(5') Pronotal commissure partially (Fig. 65) or fully (Fig. 78) developed; pronotal dorsolateral carina completely outlines periphery of pronotum (Fig. 77). 7.
- 6' Pronotal commissure absent (Fig. 79); pronotal dorsolateral carina partially developed along lateral aspects of pronotum. 9.
- 7(6) Pronotal subcarinate plate only partly extended posteromedially, thus pronotal dorsolateral carina confluent with pronotal hem beyond and to the middle of the pronotal posterior angle, this results in a partially developed pronotal commissure (Fig. 65). **Enopliinae**
- 7' Pronotal subcarinate plates fully extended across pronotal base, thus pronotal dorsolateral carina not confluent with pronotal hem, this results in a fully developed pronotal commissure (Figs 78, 81). 8.
- 8(7') Gula large (Fig. 15), gular sutures straight-up, not converging or diverging; antennal club length always shorter than length of rest of antenna (Fig. 28), club antennomeres never lobate; pronototergosternal suture complete (Fig. 80). **Korynetinae**

- 8' Gula small, gular sutures oblique-diverging; antenna serrate, subserrate or capitate, if capitate most species with capitulum longer than length of rest of antenna (Fig. 30), club antennomeres usually lobate; pronototergosternal suture almost always incomplete (Figs 81, 82). **Neorthopleurinae**
- 9(6') Antenna always capitate and capitulum always shorter than length of rest of antenna, club antennomeres never lobate (Fig. 29). **Tarsosteninae**
- 9' Antenna capitate, rarely serrate, when capitate capitulum comprised of antennomeres that are highly lobate and the capitulum is usually much longer than the length of rest of the antenna (Fig. 34). **Peloniinae**
- 10(4') Labrum large, most often not incised mediodistally (Figs 6, 10); most species with large bulgy eyes (Fig. 7), and relatively short antenna (Fig. 9). **Hydnocerinae**
- 10' Labrum not particularly large, usually deeply incised (Figs 3, 4); eyes not particularly large or bulgy (Fig. 4); antenna long (Fig. 40). 11.
- 11(10') Cryptosternum complete, therefore procoxal cavity closed internally and externally (Fig. 64); tarsal unguis usually multidentated, with (Fig. 94) or without denticle. **Tillinae**
- 11' Cryptosternum incomplete, therefore prorocoxal cavity never closed internally and almost always open externally (Fig. 60); tarsal unguis usually not multidentated, but often with a well-developed basal denticle (Fig. 95). **Clerinae**

Description and generic composition of Cleridae subfamilies

The 334 genera that comprise the 12 subfamilies described herein are listed at the end of the subfamilial descriptions. To my knowledge, the listing of genera is complete for Anthicoclerinae (2 genera, 6 species) subfam.nov., Epiphloeinae Kuwert (25 genera, 267 species), Isoclerinae Kolibáč (8 genera, 18 species), Korynetinae Laporte (7 genera, 76 species), Neorthopleurinae Opitz (22 genera, 258 species), and Thaneroclerinae Chapin (5 genera, 13 species). However, the generic inventory for Clerinae Latreille (113 genera, 1, 606 species), Enopliinae Gistel (15 genera, 66 species), Hydnocerinae Spinola (25 genera, 473 species), Peloniinae subfam.nov. (31 genera, 234 species), Tarsosteninae Jacquelin du Val (14 genera, 69 species), and Tillinae Leach (67 genera, 543 species), must be considered tentative as we continue to explore questions of generic status, correct subfamilial placement of genera, and general intergeneric relationships. My immediate plan is to clarify such matters in the Enopliinae Gistel, Korynetinae Laporte, Neorthopleurinae Opitz, Peloniinae subfam.nov., and Tarsosteninae, Jacquelin du Val, as I concomitantly bring forth revisionary works of these and other subfamilies. The sequence of works that led to the completion of Epiphloeinae Kuwert (4 manuscripts await publication) will serve as a template to elucidate intrageneric and intergeneric relationships among the abovementioned subfamilies characterized by a reduced 4th tarsomere.



Figs 1–6. Heads. 1 *Epiphloeus duodecimmaculatus*. 2 *Pelonium helopioides*. 3 *Enoclerus coccineus*. 4 *Tarsostenus univittatus*. 5 *Cregya kraatzi*. 6. *Phyllobaenus gorhami*.

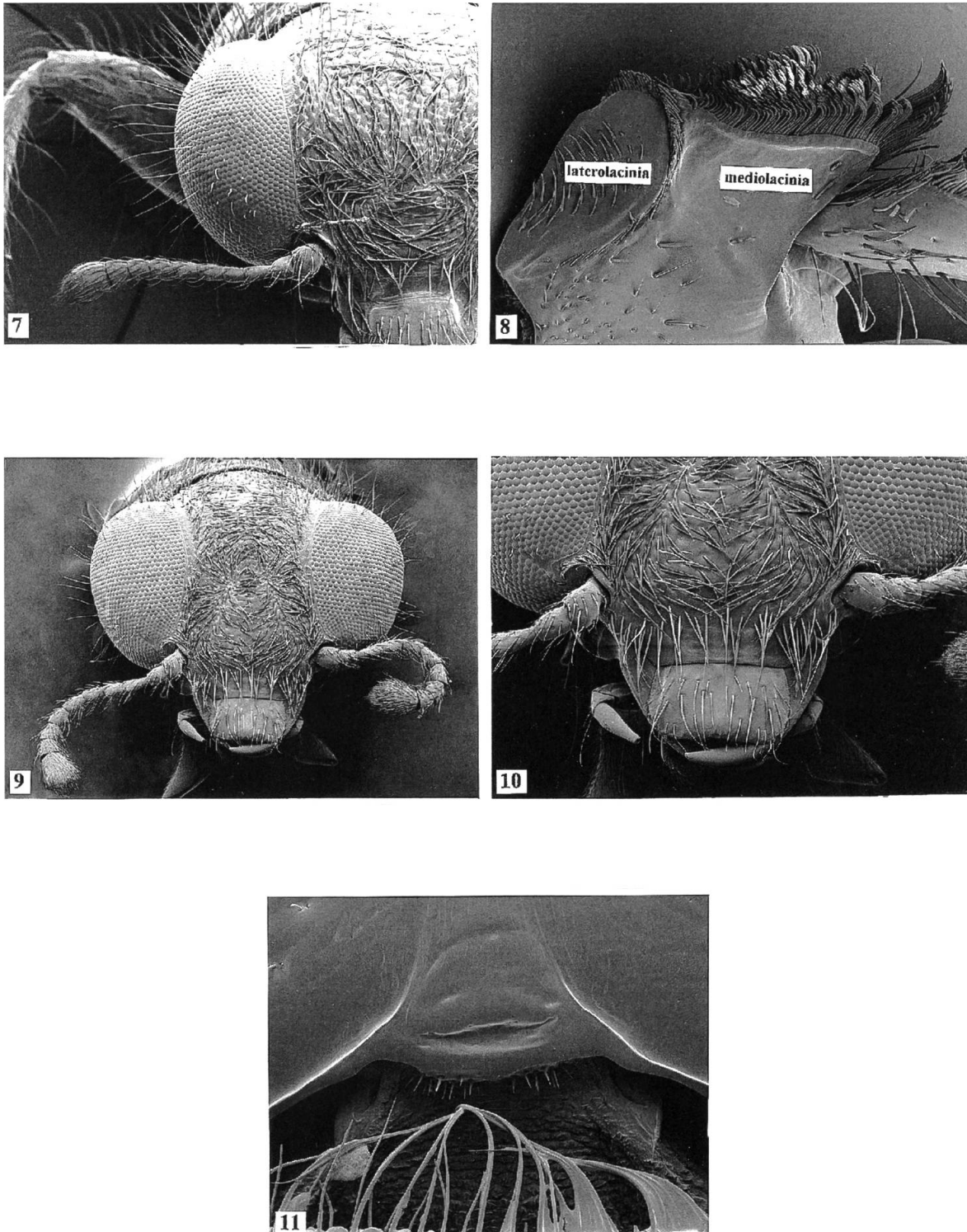
Subfamily Anthicoclerinae subfam.nov.

Figures 86, 102–106, 205.

Type genus: *Anthicoclerus* Schenkling, 1906: 264.

Diagnosis. These very small (about 3.4 mm) checkered beetles are easily distinguished from other members of the family by the extraordinary enlargement of the metathoracic basitarsomere (Fig. 104). Also, only in these beetles do we find a tarsomere formula that is 5-5-4.

Description. *Shape:* Short rectangulate. *Size:* Length 3.5–5.0 mm; width 1.3–1.5 mm. *Integumental Color:* Ranges from dark brown to light brown; pronotum may be reddish; elytra with yellow maculae. *Head:* Hypognathous; epistomal sutures not visible externally; internal epistomal ridge incomplete; clypeus bipartite, comprised of pigmented upper region and nonpigmented lower region; frontal preantennal angle not acute; cranium minutely punctated; eyes small, coarsely faceted, ocular notch very shallow; gular very broad, sutures slightly converging, postgular plate well defined, postgular process present; antenna comprised of 11 antennomeres (Fig. 102), capitate, funicular antennomeres submoniliform; mandible stout, medial dens well developed, posterior dens very broad, penicillus small, basal notch not very large; labrum well developed, anteromedial incision shallow and wide, transverse tormal processes down-curved, contiguous; epipharynx not complex; maxilla with well-developed laterolacinia, terminal palpomere broad-digitiform; labium well developed, terminal palpomere securiform. *Thorax:* Pronotum with well-developed anterior transverse depression that divides pronotum into prominent pronotal arch and pronotal proper, greatly constricted posteriorly, dorsolateral ridge absent, prosternum not particularly expanded anteriorly, prointercoxal process linear, pronotal projection short; pronototergosternal suture complete; procoxal cavities externally open, procryptosternum incomplete; elytral disc with or without 1° and 2° setae, asetiferous punctations present, epipleural fold well developed and positioned laterally, anterior ridge absent; legs, tarsal formula 5-5-4, tarsal pulvilli highly developed and incised distally, two pulvilli, metathoracic leg with one pulvillus on 3rd tarsomere and one on 4th tarsomeres (Figs 105, 106), unguis without basal denticle; femora swollen, tibiae about as long as length of femora, tibiae with carina (Fig. 103), tibial spur formula 1-2-2, tarsal pulvillar formula 4-4-1; metathoracic wing venation well developed, wedge cell open; metendosternite with well-developed furcal lamina. *Abdomen:* Comprised of 6 visible sternites, 6th often slid under 5th; pygidium scutiform, 6th visible sternite incised distally; spicular fork well developed, plates slender but expanded distally, slightly fused basally, intraspicular plate absent; aedeagus not inverted, very sclerotized, tubular, length of phallobasic apodemes variable, phallobase bilobed, lobes not fimbriate; ovipositor shorter than length of abdomen, with multilobed dorsal and ventral lamina; oblique and ventral bacculi well developed; spiculum ventrale slightly longer than length of 6th sternite. *Alimentary Canal:* No information available. *Mesodermal Male Reproductive Organs:* No information available. *Mesodermal Female Reproductive Organs:* No information available. *Larvae:* No information available.



Figs 7–11. Morphological organs. 7, 9, 10 Heads (7 *Phyllobaenus humeralis*, 9, 10 *Phyllobaenus gorhami*), 8 maxilla of *Dieropsis quadriplagiata*, 11 Gula of *Isoclerus pictus*.

Natural History. These checkered beetles are predaceous on scolytids in their larval and adult stages.

Distribution. The combined distribution of these checkered beetles extends from Europe to Southeast Asia (Fig. 205).

Inventory of generic taxa. There are 6 described species classified in 2 genera as follows: *Allonyx* Duval and *Anthicoclerus* Schenkling,

Taxonomic Notes. The taxonomy of these checkered beetles has not progressed beyond the descriptive phase.

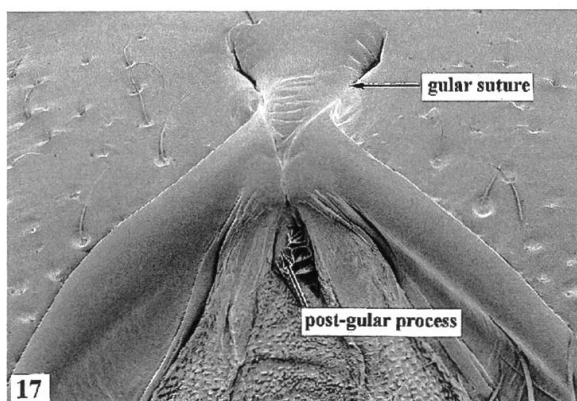
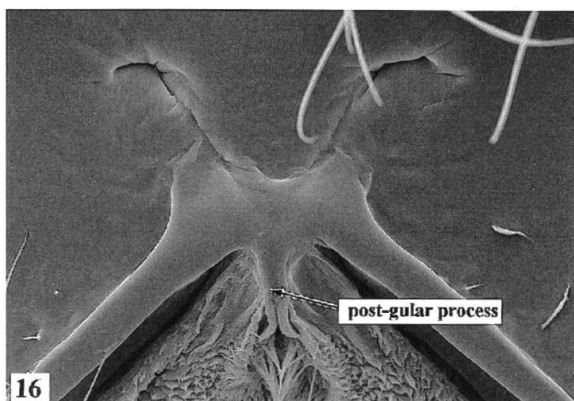
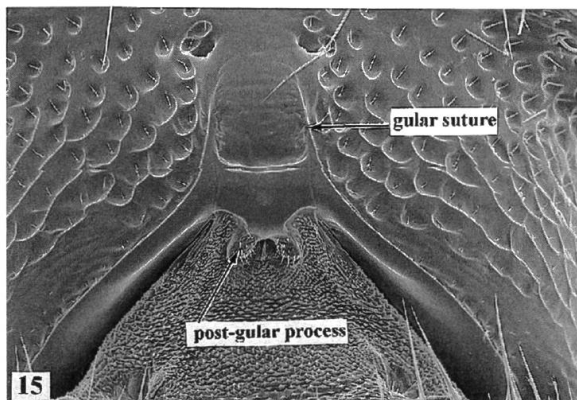
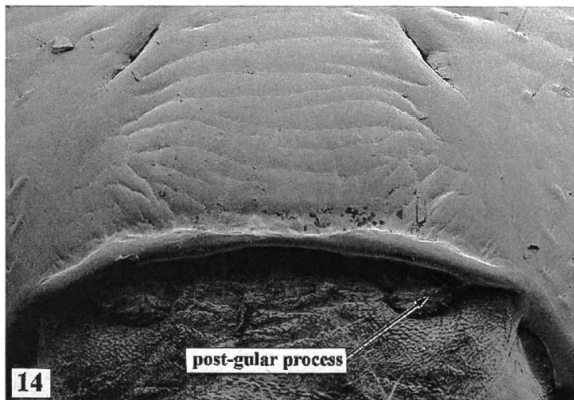
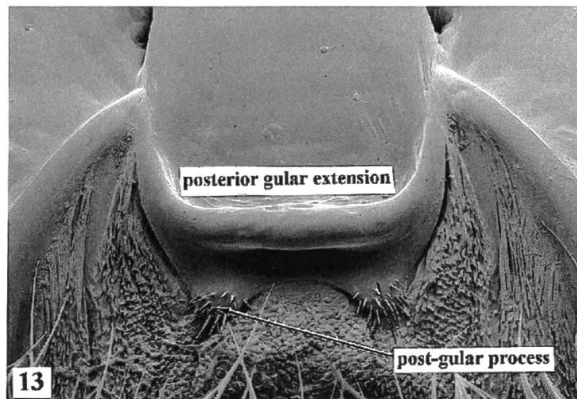
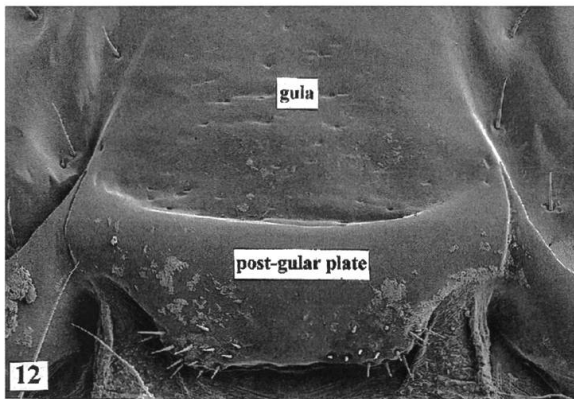
Subfamily Clerinae Latrille, 1802: 110

Figures 3, 13, 14, 21, 25, 26, 27, 39, 43, 48, 60, 63, 87, 95, 100, 112, 115, 116, 148, 153, 154, 175, 176, 178, 185, 190, 198, 206, 213, 214, 215, 216, 217, 219, 220, 221, 223, 225, 226.

Type genus: *Clerus* Geoffroy, 1762: 303.

Diagnosis. Checkered beetles belong to this subfamily if they have a tarsal formula that is clearly 5-5-5, the fourth tarsomere is not greatly reduced, have well-developed protarsal pulvilli that are usually deeply incised distally, an antenna comprised of 11 antennomeres, have procoxal cavities that are almost always open (if closed, the prointercoxal process is not fused to the pronotal projection), and the protarsomeres are not compacted.

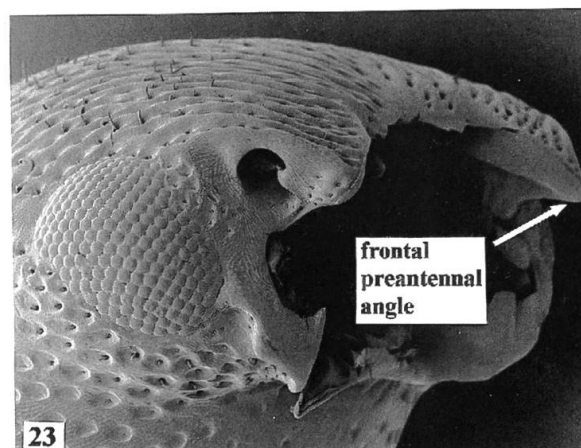
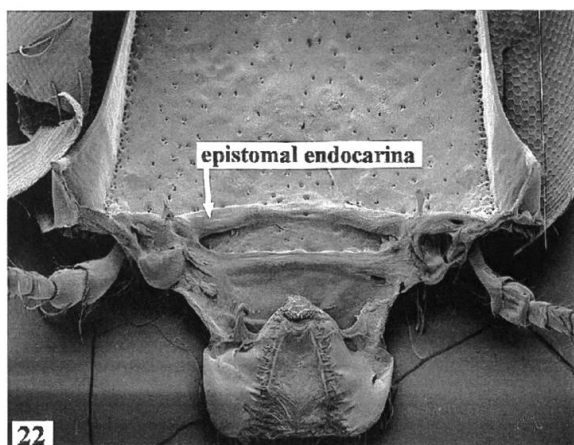
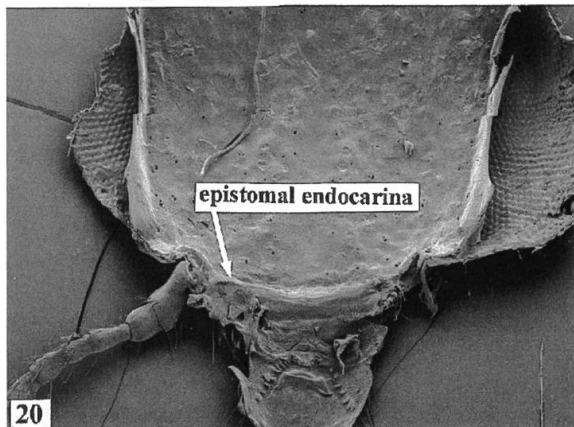
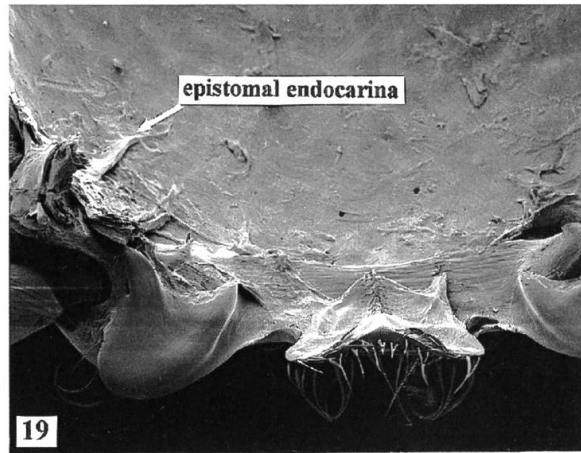
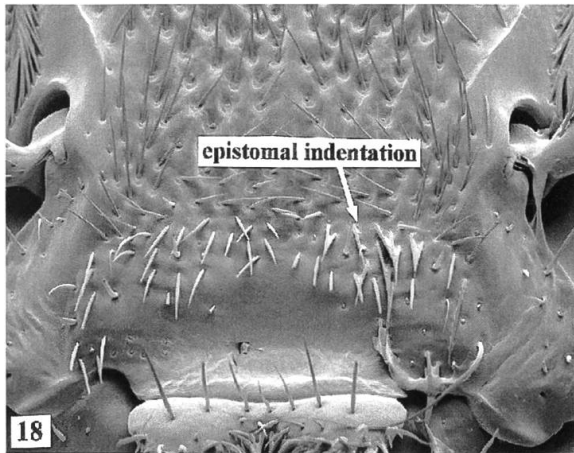
Description. *Shape:* Usually oblong-short or oblong-long rectangulate, sometimes suboval and stout, flat or convex, rarely pronotum petiolate, body extensively flattened, or elytra severely constricted at middle. *Size:* Length 2.8–44.0 mm; width 1.0–12.0 mm. *Integumental Color:* From unicolorous black or brown to bright red, yellow, blue, green, or violaceous, commonly elytra with red or yellow maculae. *Head:* Hypognathous; epistomal sutures faintly indicated, internal epistomal ridge incomplete; clypeus bipartite, comprised of pigmented upper region and nonpigmented lower region; frontal preantennal angle not acute; cranium minutely punctated; eyes usually large, finely or coarsely faceted, ocular notch from large to minute; gular usually broad, sometimes narrow-triangular, sutures usually diverging, sometimes parallel, postgular plate well defined or not, postgular process always present; antenna comprised of 11 antennomeres, usually capitate, sometimes filiform or serrate; mandible stout, dens and penicillus well developed, basal notch not very large; labrum well developed, anteromedial incision deep, transverse tormal processes usually down curved, sometimes sinuous or linear, contiguous or not, sometimes faintly developed and without tormal connecting rod; epipharynx not complex; maxilla with well-developed laterolacinia, terminal palpomere usually boldly securiform, sometimes subsecuriform or digitiform; labium well developed, terminal palpomere usually securiform, sometimes digitiform. *Thorax:* Pronotum with well-developed anterior transverse depression that divides pronotum into distinct pronotal arch and pronotal proper, greatly constricted posteriorly, dorsolateral carina absent; prosternum not particularly expanded



Figs 12–17. Gulas. 12 *Thaneroclerus buqueti*. 13 *Gyponyx apicalis*. 14 *Aulicus edwardsi*. 15 *Korynetes analis*. 16 *Nelsonoplium heterochromum*. 17 *Neorthopleura thoracica*.

anteriorly; prointercoxal process very expanded distally; pronototergosternal suture complete; procoxal cavities open, very rarely closed by extensive pronotal projection, latter may extend to but not fused to prointercoxal process, procryptosternum incomplete; elytral disc profusely vested with 1° and 2° setae, asetiferous punctations present, epipleural fold well developed and positioned laterally, anterior ridge absent; legs, tarsal formula 5-5-5, tarsal pulvilli usually highly developed and incised distally, rarely reduced, unguis with or without basal denticle, femora clubby or not, tibiae about as long as length of femora, protibia and metatibiae with or without carina, tibial spur formula usually 1-2-2, rarely 2-2-2, 1-1-1, or 0-0-0; tarsal pulvillar formula 4-4-4, 4-4-3, 4-4-2, 4-3-2, 4-3-1, 4-2-1, 4-1-1, metathoracic wing venation variable, wedge cell open or not; metendosternite with well-developed furcal lamina. *Abdomen*: Comprised of 6 visible sternites, 6th sternite often slid under 5th and incised distally; pygidium scutiform; spicular fork well developed, plates slender but expanded distally, extent of fusion of spicular apodeme variable, intraspicular plate transverse (Fig. 176) and variously sclerotized; aedeagus not inverted, very sclerotized, tubular, length of phallobasic apodemes variable, phallobase bilobed, lobes not fimbriate; ovipositor shorter than length of abdomen, with multilobed dorsal and ventral lamina; oblique and ventral bacculi well developed; spiculum ventrale slightly longer than length of 6th sternite. *Alimentary Canal*: Stomodaeum short; proventriculus well defined, highly muscular; stomodaeal valve comprised of 4 primary lobes and 2 secondary lobes; ventriculus well developed, crypts conspicuous; 6 cryptonephridial Malpighian tubules; proctodaeum well developed, female colon much longer than male colon. *Mesodermal Male Reproductive Organs*: With two pairs of accessory glands, medial pair and lateral pair, accessory glands uniramous or variously divided; testis multifollicular. *Mesodermal Female Reproductive Organs*: Spermathecal capsule well sclerotized or poorly sclerotized, usually comprised of barrel-shaped organ, rarely elongated and biramous; spermathecal gland variously attached to spermathecal capsule; with well-developed saccular bursa copulatrix or bursa copulatrix comprised of distended portion of vagina; ovary multifollicular. *Larval Morphology*: Cranium comparatively large, subquadrate, somewhat flattened to subglobose; coronal component of epicranial suture absent; endocarina present; gula long or short narrow; 1 to 5 stemmata present, when 5 anterior row of 3 and posterior row of 2; anterior border of labrum with or without very fine hairs; mesonotum and metanotum plates highly to weakly sclerotized; spiracles small, circular peritreme, with basal pair of air tubes; basal plate of 9th abdominal tergum present or not, urogomphi variously developed or absent, when present contiguous basally or not.

Natural History. The members of this subfamily dramatically exhibit a morphological precision towards specific venues of mimicry, aposematic coloration, and predatory activity. Note for example, the ant-like appearance of *Myrmecomaea raffrayi* Fairmaire (Fig. 214), the aradid-like flatness of *Cleropiestus oberthuri* Fairmaire (Figs 215, 216), the mutillid fascies of *Tillicera javana* Spinola (Figs 217, 218), the firefly appearance of *Perilypus ventralis* (Gorham) (Figs 219, 220), the similarity of *Aphelocerus myrmecoides* Opitz to *Myrmex* weevils (OPITZ 2005; Figs 163, 164), the approximation to a tenebrionid of *Colyphus beltoides* Ekis (Figs 223, 224), the precision of similarity

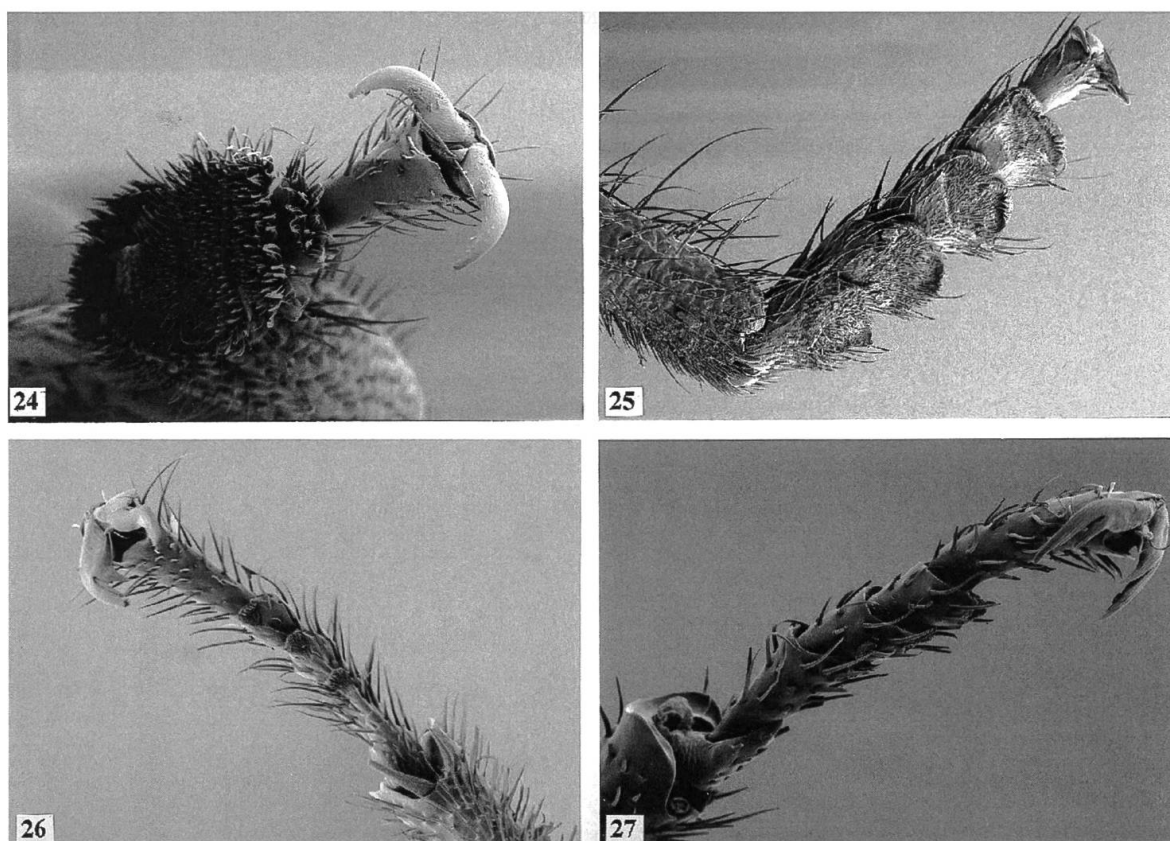


Figs 18–23. Morphological organs. 18 Frons of *Epiphloeus duodecimmaculatus*. 19–22 Interior view of cranium (19 *Thaneroclerus buquet*, 20 *Phyllobaenus humeralis*, 21 *Tillicera javana*, 22 *Brachycallimerus pectoralis*). 23 Cranium of *Thaneroclerus buquet*.

of color and body form between *Perilypus testaceicornis* (Pic) (Fig. 221) and the cantharid niche companion pictured in figure 222, the ground beetle appearance of *Platyclusus* (Laporte) (Fig. 226), and the aposematic coloration of *Aphelochroa sanguinea* (Thomson) (Fig. 225). For additional comments about mimicry in the Cleridae see OPITZ (2005: 13); STAINS (1999: 239), RIFKIND (1997: 299), MAWDSLEY (1994: 115), HESPENHEIDE (1986: 399; 1973: 49), MENIER (1985: 1071), and EKIS (1977B: 200).

There is a plethora of published information about the bionomics of clerine checkered beetles. In general, clerines prey on wood infesting insects and especially on a substantial variety of bark beetles. Most adults of these checkered beetles are diurnal and usually conduct predatory activities on the outside bark while the larvae feed in the tunnel labyrinths of inner bark. Laboratory experiments (EKIS 1977A: 5) suggest that physical manageability of the prey specimen by the predator is an important factor in the feeding choices of these beetles. Among the more unusual predator-prey associations we find that larvae of *Zenithicola crassus* (Newman) feed on the wood-nesting termite *Mastotermes darwiniensis* Frogatt (MOORE 1973: 48), *Trogodendron fasciculatum* (Schreibers) consumes immatures of wood-boring moths (McKEOWN 1952: 368), *Aulicus terrestris* Linsey consume lepidopterous larvae and egg masses of lubber grasshoppers (LINSEY 1936: 258), and *Trichodes* Herbst and *Eleale* Newman species have omnivorous species that feed on pollen and other anthophilic insects (FOSTER 1976: 65; OPITZ 2002: 243). Most recently, BARTLETT (2009: 79) reports that the Australian *Scrobiger splendidus* (Newman) is apivorous as has been recorded for several species of *Trichodes* Herbst (KNOLL 1951: 300; FOSTER 1976: 66) and *Lecontella* Wolcott et Chapin (BITNER 1972: 25).

Most interesting observations regarding clerine feeding behavior has been reported by FOSTER (1971: 128). Females of *Enoclerus opifex* (Gorham) have a trophic relationship with the coreid *Acanthocephala granulose* (Dallas), and a fecundity association with the weevil *Peltophorus polymitus* Boheman. The female of this checkered beetle positions herself near a feeding coreid. When the hemipteran withdraws its proboscis from yucca stalks the beetle consumes the plant secretions that emanate from the plant wound. Moreover, *E. opifex* (Gorham) females also feed at the ovipositional wound made by the aforementioned weevil. After feeding the checkered beetle female places an egg at the edge of the wound into which the weevil deposited her eggs; in this way she secures prey food for the ensuing checkered beetle hatchling. FOSTER (1976: 65) also reports the likely possibility of a phoresial involvement between larvae of *Trichodes bibalteatus* Leconte and of *T. ornatus* Say with bees and wasps. RIFKIND (1993: 75) reviewed the literature, and made some novel field observations, about the feeding habits of *Aulicus bicinctus* Linsley. Lastly, I (OPITZ 2002: 244) noted that members of *Eleale aspera* (Newman) uses inflorescences of *Pyracantha crenulata* (D. Don) M. Roemer, a thorny evergreen, as a meeting place for mating, to imbibe nectar, and to procure polyads for protein. Moreover, I report that the flowers of the plant serve the checkered beetle as an oasis of moisture and food during the drier portions of the south Australian season.



Figs 24–27. Tarsi. 24–25 Protarsi (24 *Thaneroclerus buquet*, 25 *Enoclerus tuberculatus*). 26–27 Metatarsi of *Odontophlogistus rubriventris*.

To my knowledge, the life cycle of clerines involves three (BERRYMAN 1966: 521), four (MIGNOT & ANDERSON 1969: 307), or five (FOSTER 1976: 65) larval instars. Eggs are deposited on flowers, deposited in the cracks of bark, or generally near developing immatures of prey. To prepare for pupation, the mature larva forms a cocoon from fragments of wood, or other debris, or lines preexisting chambers with exudate. The pupation site may involve galleries under bark, abandoned pupal cells, or at the base of trees just below soil level. There are from one to four generations per year. In cold temperate zones, overwintering may take place as mature larvae, pupae, or adults. For a detailed account of the embryology of *Enoclerus lecontei* (Wolcott) see BERRYMAN (1966: 519), and detailed life cycle observations are provided by SOLERVICENS & ORMAZÁBAL (1999: 34–*Epiclynes gayi* Chevrolat), THATCHER & PICKARD [1966: 955–*Thanasimus dubius* (Fabricius)], and LINSLEY & MACSWAIN (1943: 592–*Trichodes ornatus* Say).

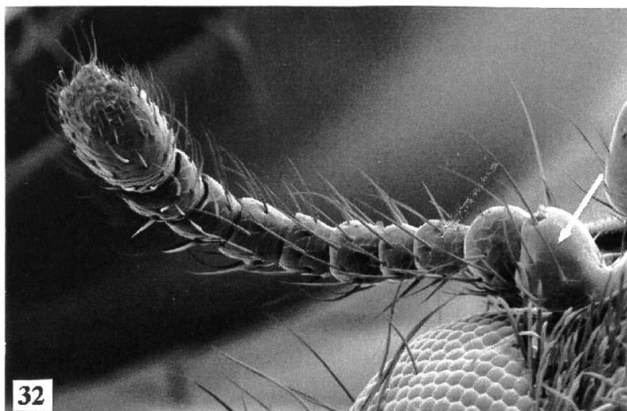
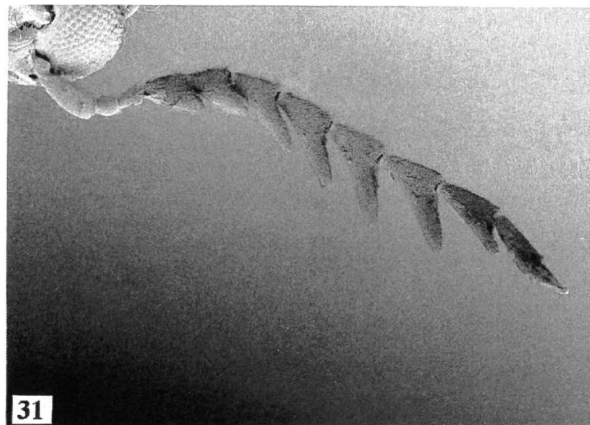
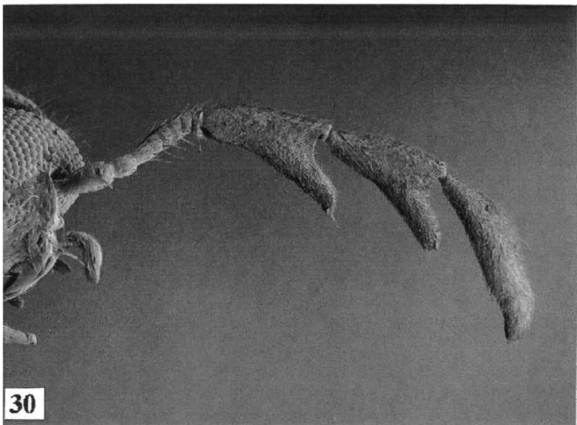
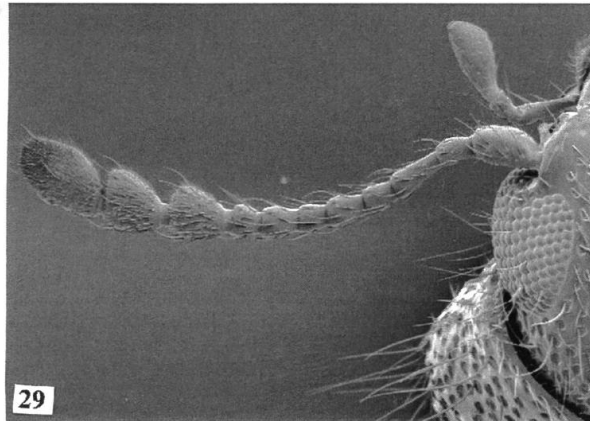
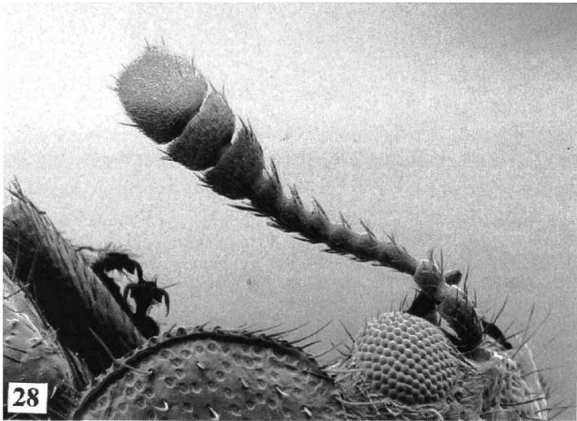
There are many interesting studies that investigate the kairomonal response of clerine species to prey- and to host-tree produced volatiles. Such responses and synergistic effects of pheromones are used by clerines to locate trees infested with bark

beetles. Such chemicals also serve to bring the predator sexes together for mating (VITÉ & WILLIAMSON 1970: 238). A particularly interesting observation relevant to this subject involves the study of BILLINGS & CAMERON (1984: 1546) who wrote that “The ability to respond to pheromones produced by the more ubiquitous *Ips* beetles accommodates survival of *T. dubius* (*Thanasimus*) when its preferred host (*Dendroctonus frontalis* Zimmermann) is unavailable” (mine in parentheses).

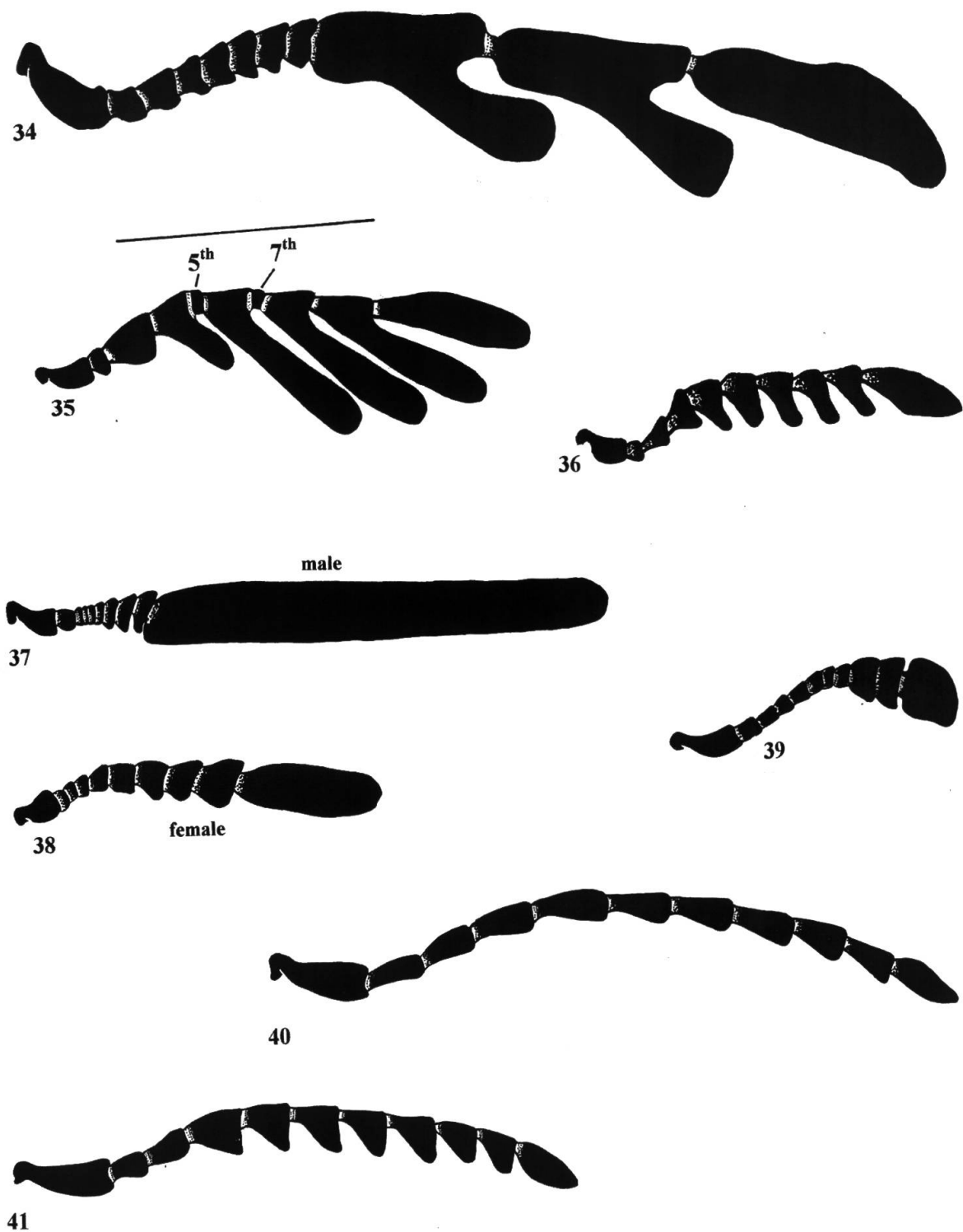
Distribution. Although worldwide in distribution, the members of this subfamily are most abundant in the Old World and New World tropics (Fig. 206).

Inventory of generic taxa. There are 1,606 described species classified in 113 genera as follows: *Aphelocerus* Kirsch, *Aphelochroa* Quedenfeldt, *Apopemopsis* Schenkling, *Apteroclerus* Wollaston, *Aptinoclerus* Kuwert, *Aradamicula* Sedlacek and Winkler, *Arawakis* Opitz, *Astigmus* Kuwert, *Aulicus* Spinola, *Axina* Kirby, *Balcus* Sharp, *Bariella* Opitz, *Basilewskyus* Pic, *Blaxima* Gorham, *Brinckodes* Winkler, *Burgeoneus* Pic, *Caestron* Spinola, *Calendyma* Lacordaire, *Canariclerus* Winkler, *Cardiopus* Schenkling, *Cardiostichus* Quedenfeldt, *Chilioclerus* Solervicens, *Cleromorpha* Gorham, *Cleropiestus* Fairmaire, *Clerus* Geoffroy, *Clytomadius* Corporaal, *Colyphus* Spinola, *Coptoclerus* Chapin, *Cormodes* Pascoe, *Corynommadius* Schenkling, *Ctenaxina* Schenkling, *Ctenoclerus* Solervicens, *Cyclotomocerus* Kuwert, *Dacyceroclerus* Kuwert, *Dasyteneclines* Pic, *Dieropsis* Gahan, *Dozocolletus* Chevrolat, *Eburiphora* Spinola, *Eburneoclerus* Pic, *Ekisius* Winkler, *Eleale* Newman, *Enoclerus* Gahan, *Epiclines* Chevrolat, *Erymanthus* Spinola, *Eunatalis* Schenkling, *Eurymetomorphon* Pic, *Falsoorthrius* Pic, *Graptoclerus* Gorham, *Gyponyx* Gorham, *Hemitrachys* Gorham, *Homalopilo* Schenkling, *Inhumeroclerus* Pic, *Jenjouristia* Fursov, *Languropilus* Pic, *Lissaulicus* Waterhouse, *Metademius* Schenkling, *Microastigmus* Pic, *Microclerus* Wollaston, *Micropteroclerus* Chapin, *Microstigmatium* Kraatz, *Mimoleserus* Gerstmeier, *Mimorthrius* Pic, *Myrmecomaea* Fairmaire, *Natalis* Laporte, *Neogyponyx* Schenkling, *Neoscrobigier* Blackburn, *Notocymatodera* Schenkling, *Odontophlogistus* Elston, *Ohanlonella* Rifkind, *Olesterus* Spinola, *Omadius* Laporte, *Operculiphorus* Kuwert, *Opilo* Latreille, *Orthrius* Gorham, *Oxystigmatium* Kraatz, *Perilypus* Spinola, *Phaeocyclotomus* Kuwert, *Phlogistomorpha* Hintz, *Phlogistus* Gorham, *Phloiocopus* Spinola, *Phonius* Chevrolat, *Pieleus* Pic, *Placocerus* Klug, *Placopterus* Wolcott, *Plathanocera* Schenkling, *Platyclerus* Spinola, *Priocera* Kirby, *Priocleromorphus* Pic, *Prioclerus* Hintz, *Pseudogyponix* Pic, *Pseudolesterus* Miyatake, *Pseudomadius* Chapin, *Pyrrhostigmatium* Kraatz, *Quasibrinckodes* Winkler, *Rhytidoclerus* Kuwert, *Sallea* Chevrolat, *Sedlacekius* Winkler, *Scrobiger* Spinola, *Sikorius* Kuwert, *Stigmatium* Gray, *Systemoderes* Spinola, *Thalerocnemis* Lohde, *Thanasimodes* Murray, *Thanasimus* Latreille, *Tillicera* Spinola, *Tillopilo* Winkler, *Trichodes* Herbst, *Trogodendron* Spinola, *Wilsonoclerus* Mawdsley, *Winklerius* Menier, *Xenorthrius* Gorham, *Xestoclerus* Chapin, and *Zenithicola* Spinola.

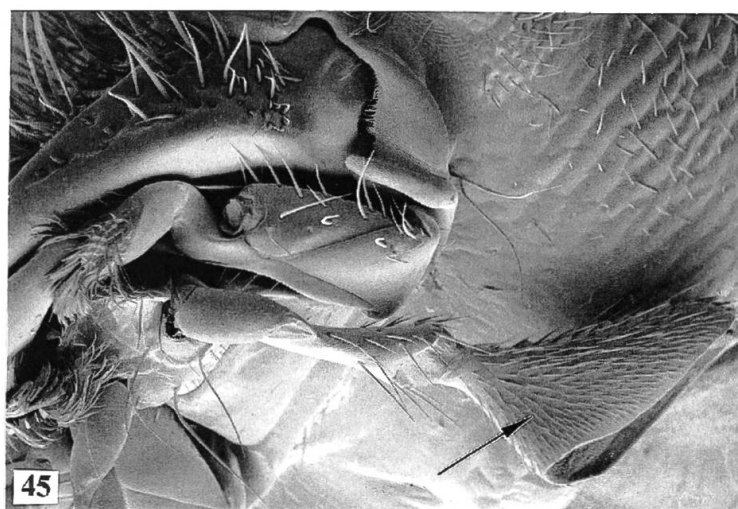
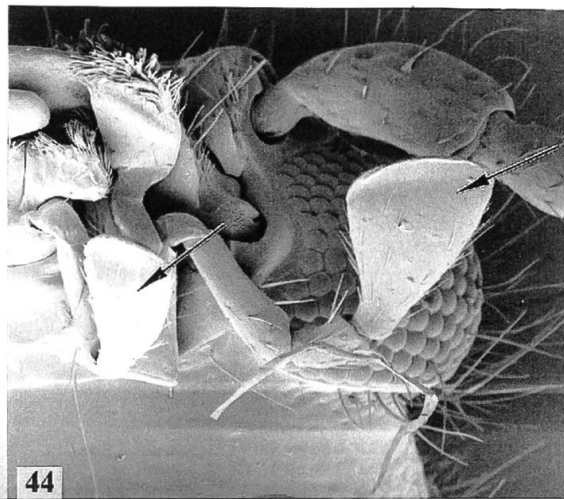
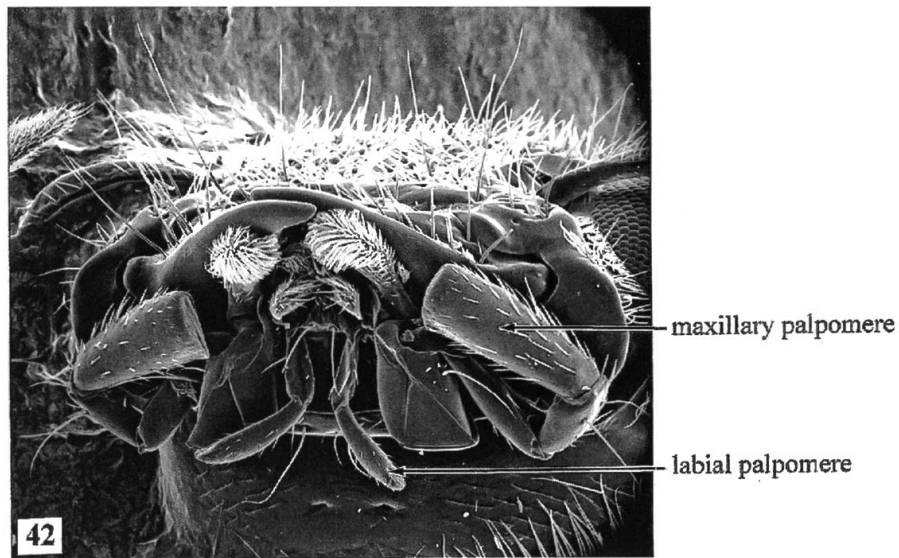
Taxonomic notes. The Clerinae, the largest subfamily in the Cleridae, presents fantastic opportunities for the discovery of new taxa and opportunities of resolution of copious assortments of taxonomic problems. It contains some of the more fascinating beetles in the family. The magnitude of popularity of the group is, perhaps, in proportion to its nomenclatural difficulties. It is a challenging group with an immense opportunity for the



Figs 28–33. Morphological organs. 28–32 Antennae (28 *Necrobis rufipes*, 29 *Tarsostenus univittatus*, 30 *Neorthopleura thoracica*, male. 31 *Tenerus variabilis*, 32 *Wolcottia sobrina*). 33 Head of *Plocamocera coactilis*.



Figs 34–41. Antennae. 34 *Chariessa pilosa*, male. 35 *Tenerastes mauritanus*, male. 36 *Callotillus elegans*, male. 37–38 *Monophylla terminata* (37 male, 38 female). 39 *Trichodes ornatus*. 40 *Cymatodera oblita*. 41 *Bogcia disjuncta*.



Figs 42–45. Mouthparts. 42 *Epiphloeus duodecimmaculatus*. 43 *Enoclerus ichneumoneus*. 44 *Pelonium leucophaeum*. 45 *Enoclerus ichneumoneus*.

discovery of new species, new genera, perhaps new subfamilies, and, unfortunately, a plethora of species-levels synonymies. As an example of the former I offer my work with *Aphelocerus* Kirsch (59 new species; OPITZ 2005), and as an example of the later I offer the work of MAWDSLEY (2006) (118 species-level synonymies).

Although the subfamily has not been comprehensively studied as a whole, there have been some significant attempts to provide detailed generic revisions (MAWDSLEY 1993–*Dieropsis* Gahan and 2006–*Omadius* Laporte; Opitz, 2005–*Aphelocerus* Kirsch; GERSTMEIER 1990–*Olesterus* Spinola, 2002–*Clerus* Geoffroy and allied genera; BARR & FOSTER 1979–*Aulicus* Spinola; EKIS 1977A–*Perilypus* Spinola and 1977B–*Colyphus* Spinola; FOSTER 1976–North American *Trichodes* Herbst; SOLERVICENS 1973A–*Epiclines* Chevrolat, 1973B–*Natalis* Castelnau, 1991–*Eurymetamorphon* Pic, 1996–*Notocymatodera* Schenkling), and Linsley, 1936–*Aulicus* Spinola). Most recently, SOLERVICENS (2007) provided an extensive study of the genera *Calendyma* Lacordaire and *Epiclines* Chevrolat and Opitz revised *Dologenitus* Opitz (OPITZ 2009C).

In addition to the opportunity to discover new taxa, this subfamily is in dire need of a comprehensive review of its generic composition. There are several characters that suggest suprageneric relationships, among which we may list development of the gular process, shape of the metendosternite, form of the tarsal unguis, and reproductive strategies (OPITZ 2003).

Josef Winkler, established subfamilies *Dieropsinae* (1964: 305) and *Cleropiestinae* (1978: 437). Unfortunately, he based his decisions on some misinterpretation of the tarsal formula of *Dieropsis* Gahan and unsound assessments of synapotypic character states involving *Cleropiestus* Fairmaire.

It is clear that the tarsal formula of members of *Dieropsis* Gahan is 5-5-5, not 5-5-4 as indicated by WINKLER (1964: 305). This is noted by KOLIBÁČ (1989A) and MAWDSLEY (1993: 7) who aligned the genus with *Trichodes* Herbst of *Clerinae*. I agree with their assessment. Moreover, there is evidence from mesodermal reproductive organs, sperm transference mechanisms, and aspects of antennal microsensillar, which suggests that *Dieropsis* Gahan and *Trichodes* Herbst are members of a potential monophyletic assemblage of clerine genera along with the North American *Aulicus* Spinola and several genera from Australia (OPITZ 2003: 179).

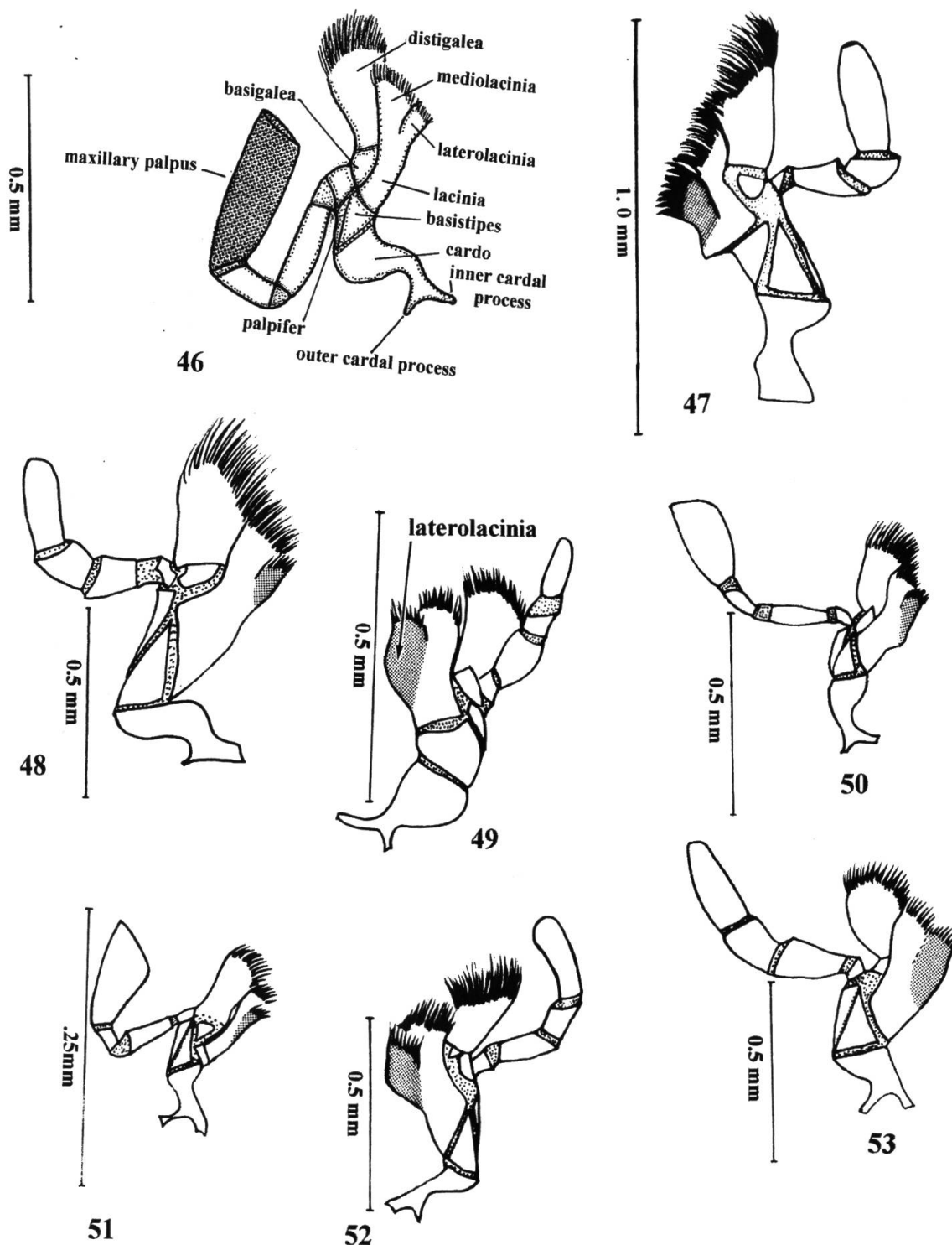
Lastly, I cannot support the recognition of *Cleropiestinae* (WINKLER 1978: 437) because the character states on which that subfamily is based are commonly variable within genera, a view shared by MENIER (1981: 139).

Subfamily Enopliinae Gistel, 1856: 367

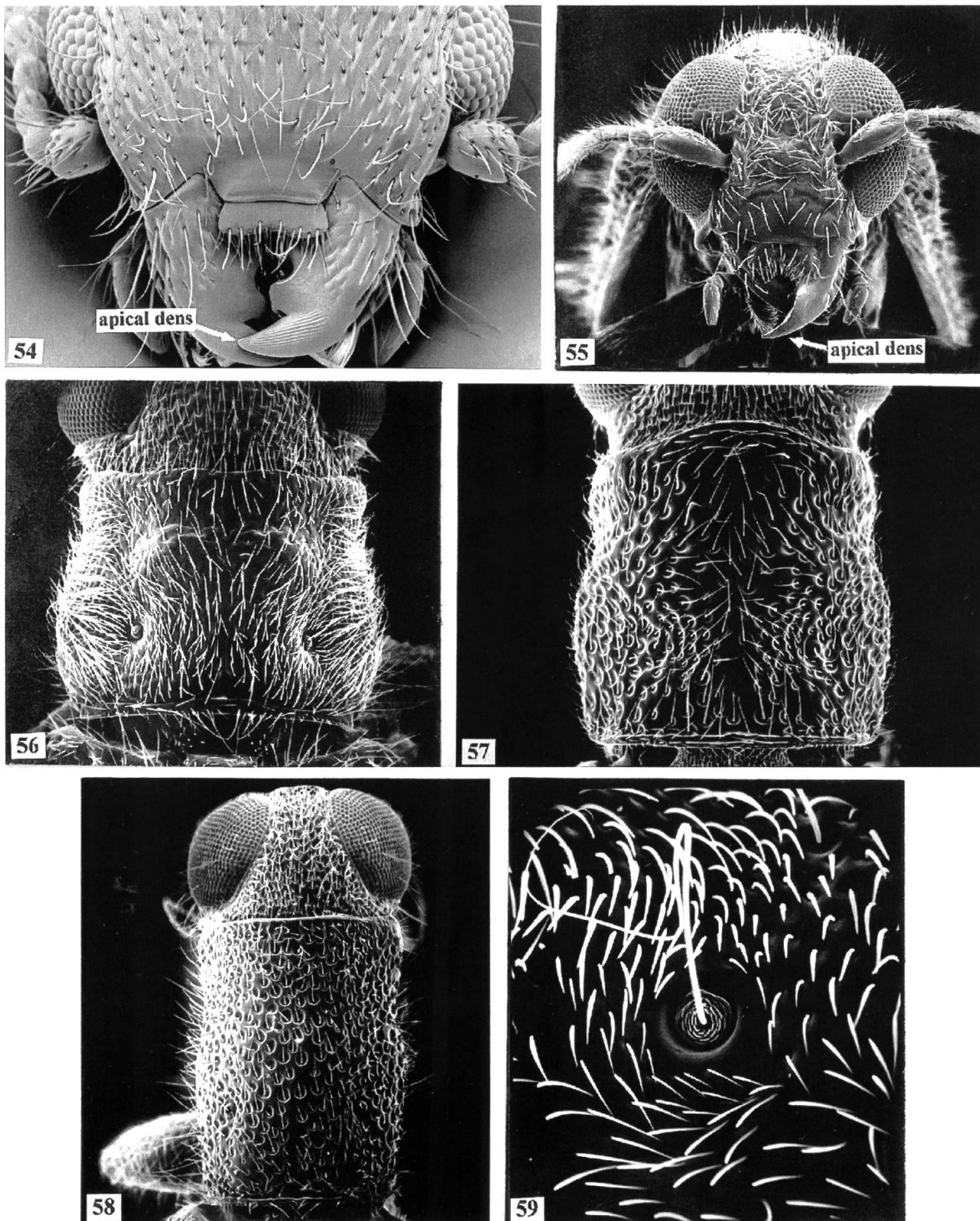
Figures 50, 65, 120, 121, 145, 207.

Type genus: *Enoplium* Latreille, 1802: 11.

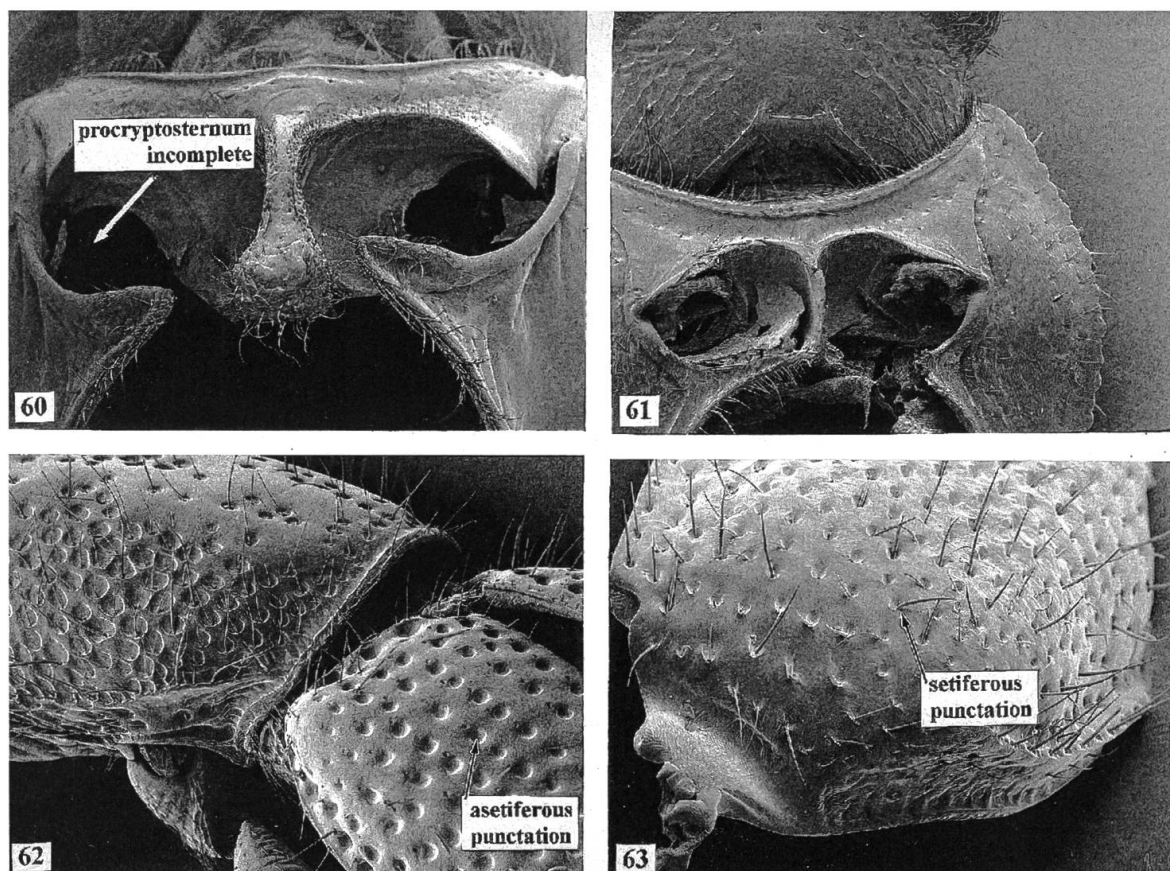
Diagnosis. Specimens with a reduced 4th tarsomere and devoid of pronotal trichobothria, belong to this subfamily if they show a partially developed pronotal commissure. That is, the subcarinal pronotal plate extends mesally beyond the posterior angle of the pronotum before it conjoins with the pronotal hem (Fig. 65).



Figs 46–53. Maxillae. 46 *Epiphloeus duodecimmaculatus*. 47 *Thaneroclerus buquet*. 48 *Clerus mutillarius*. 49 *Phyllobaenus longus*. 50 *Enoplium serraticorne*. 51 *Tarsostennus univittatus*. 52 *Lecontella cancellata*. 53 *Necrobia violacea*.



Figs 54–59. Morphological organs. 54–55 Heads (54 *Thaneroclerus buquet*, 55 *Pyticeroides laticornis*). 56–58 Forebodies (56 *P. laticornis*, 57 *Amboakis nova*, 58 *Katamyurus paniculus*). 59 Trichobothrium of *Iontoclerus humeralis*.



Figs 60–63. Morphological organs. 60–61 Prosterna (60 *Aulicus edwardsi*, 61 *Necrobia rufipes*). 62 Pronotum and elytra of *Tarsostenus univittatus*. 63 Elytra of *Aulicus edwardsi*.

Description. *Shape:* Ranges from rectangulate to suboval, rarely broad subtriangular. *Size:* Length 3.0–15.0 mm; width 1.2–4.0 mm. *Integumental Color:* Usually bicolorous with forebody lighter color than hind body, may be uniformly pastel dark to uniformly metallic dark; elytra frequently exhibit transverse or linear markings. *Head:* Transverse, strongly deflexed, usually narrower than pronotum, surface usually finely punctated; epistomal suture faintly visible externally; internal epistomal ridge complete; clypeus bipartite, comprised of pigmented upper region and nonpigmented lower region; frontal preantennal angle not acute; antenna capitate, comprised of 10 or 11 antennomeres, capitulum short or considerably expanded, funicular antennomeres subfiliform to extensively flared; eyes coarsely to subcoarsely faceted, shallowly or deeply notched anteriorly; labrum shallowly incised, transverse toral processes fused contiguous; epipharynx not complex; last palpomere of maxillary and labial palpus variously securiform, last palpomere of maxillary palpus rarely subdigitiform; mandible with well-developed dens, penicillus minute, basal notch not very large; gula large, gular processes widely separated, gular sutures strongly converging. *Thorax:* Pronotum usually transverse, quadrate, or elongated, side margins usually arcuate, lateral tubercle rarely

present, anterior transverse depression usually present, dorsolateral carina variously developed, confluent posteriorly with pronotal hem mesad to pronotal hind angles, pronotal commissure incomplete, pronotal projections varies in lengths, not confluent with prointercoxal process, procoxal cavity open externally, procryptosternum incomplete, prointercoxal process linear; pronototergosternal suture complete; metendosternite with furcal lamina; elytral form usually elongate rectangular, sometimes suboval or subtriangular, anterior margin usually with carina, disc with or without asetiferous punctations, 1° and 2° usually present, epipleural fold laterally positioned, gradually narrowing to elytral apex; legs cursorial, protibiae rarely spinous along anterior margin, tibial spur formula 2-2-2, 2-2-1, 1-2-2, 1-2-1, 0-2-2; or 0-1-1, tarsal pulvillar formula 3-3-3, unguis with or without basal denticle; wedge cell of metathoracic wing open or closed. *Abdomen*: Robust and compact; pygidium quadrate or scutiform; aedeagus not inverted, well sclerotized, tegmen tubular, very sclerotized or lightly sclerotized, bilobed distally, tegminal lobes usually fimbriate, phallobasic rod variously developed or absent, phallobasic apodeme well developed, phallic plates variously developed; spicular fork well developed, intraspicular plate linear, spicular apodeme variously fused; ovipositor not longer than abdomen, with multilobed dorsal and ventral lamina; oblique and ventral bacculi well developed. *Alimentary Canal*: Stomodaeum short, proventricular valve comprised of 4 primary lobes; ventriculus well developed, ventricular crypts poorly developed; 4 cryptonephridial Malpighian tubules; proctodaeum short in males and long in females. *Mesodermal Male Reproductive Organs*: Two pairs of accessory glands; testes comprised of multiple follicles. *Mesodermal Female Reproductive Organs*: Spermathecal capsule from faintly to highly sclerotized, spermathecal gland attached to subapex of spermathecal capsule; saccular bursal copulatrix, well-developed bursal sclerite present; ovaries comprised of multiple follicles. *Larval Morphology*: No information available.

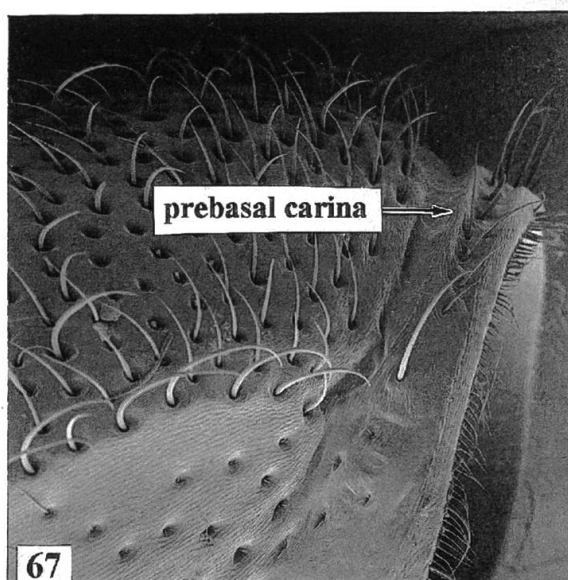
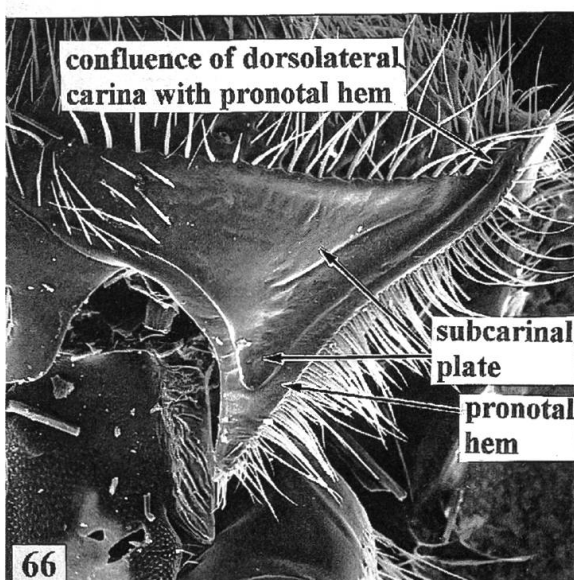
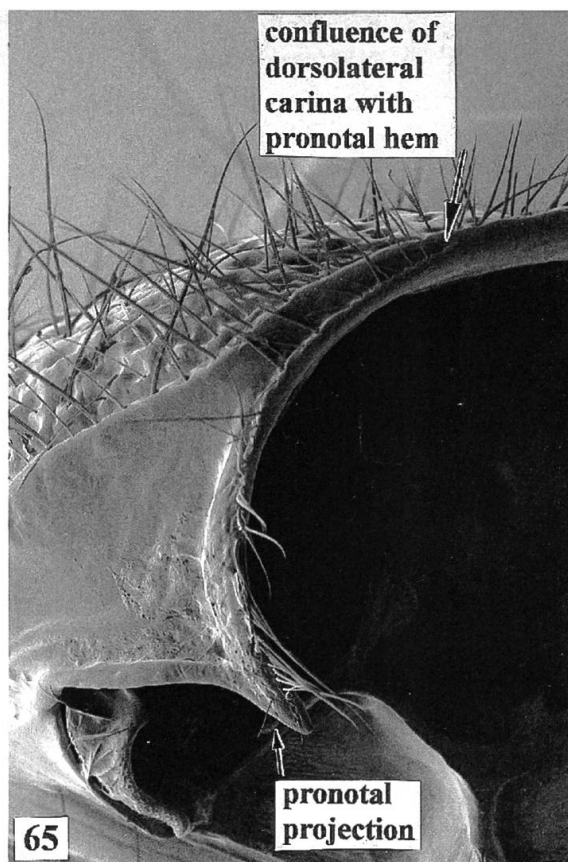
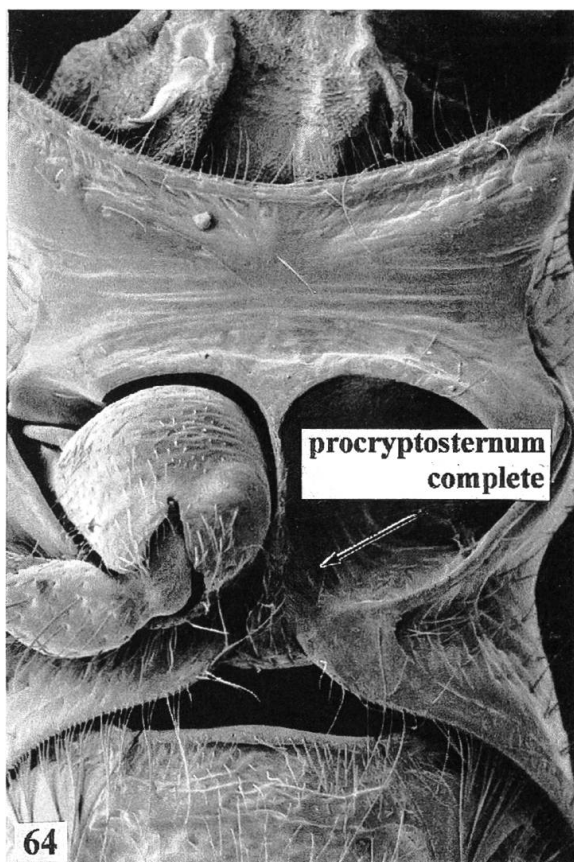
Natural History. The natural history of this group of checkered beetles basically falls in line with what is known about the other members of the Cleridae. SOLERVICENS (2001: 81) reports *Solervicensia ovatus* (Spinola) in diverse vegetation assemblages and suggests the possibility that this beetle is anthophilic and feeds on pollen. Specimens of *Salarium mirum* Fairmaire very closely approximate the lycid body form while members of *Pelonides* Kuwert have a reddish aposematic coloration.

Distribution. This is a Pan World group of checkered beetles with prominence in temperate and subtropical zones (Fig. 207).

Inventory of generic taxa. There are 66 described species classified into 15 genera. The genera are as follows: *Abrosius* Fairmaire, *Bochella* Barr, *Crobenia* Blackburn, *Enopliomorpha* Pic, *Enoplium* Latreille, *Falsocorynetes* Pic, *Falsolissaulicus* Pic, *Leptoclerus* Kraatz, *Parapelonides* Barr, *Pelonides* Kuwert, *Pyticara* Spinola, *Rhopaloclerus* Fairmaire, *Salarium* Fairmaire, *Solervicensia* Barr, and *Teneropsis* Chapin.

Taxonomic notes. The literature about these genera pertains mostly to species descriptions, but SOLERVICENS (2001) revised the bispecific genus *Solervicensia* Barr.

SPINOLA (1844B: 55) proposed the name “Platinoptérod’des” to accommodate *Erymanthus* Spinola, *Platynoptera* Chevrolat, and *Pyticera* Spinola. Spinola’s name was



Figs 64–67. Morphological organs. 64 Prosternum of *Cymatodera californica*. 65 *Enoplium serraticorne*. 66 *Epiphloeus duodecimmaculatus*. 67 *Thaneroclerus buqueti*.

latinized to *Platynopteridae* by DESMAREST (1852: 269). By this action, *Platynopteridae* Spinola (1844B: 55) attained priority over *Enopliinae* Gistel (1856: 367). But, *Platinoptérodes* Spinola has not been used as *Platynopteridae* Spinola since 1857. However, *Enopliinae* Gistel (1856: 367) has been used as valid name since 1857 (LACORDAIRE 1857: 474–*Enopliides*) in more than 25 works and by more than 10 authors in the last 50 years. Therefore, I invoke herein Articles 23.9.1 (and particularly 23.9.1.1) and 23.9.2 of the IZN (1999) and declare *Platynopteridae* Spinola [originally proposed as *Platinoptérodes* Spinola (1844: Tableau Générique des Clérites, page 4), then latinized to *Platynopteridae* by CHENU & DESMAREST (1852: 269)] a *nomen oblitum* and *Enopliidae* Gistel (1856: 367), a *nomen protectum*.

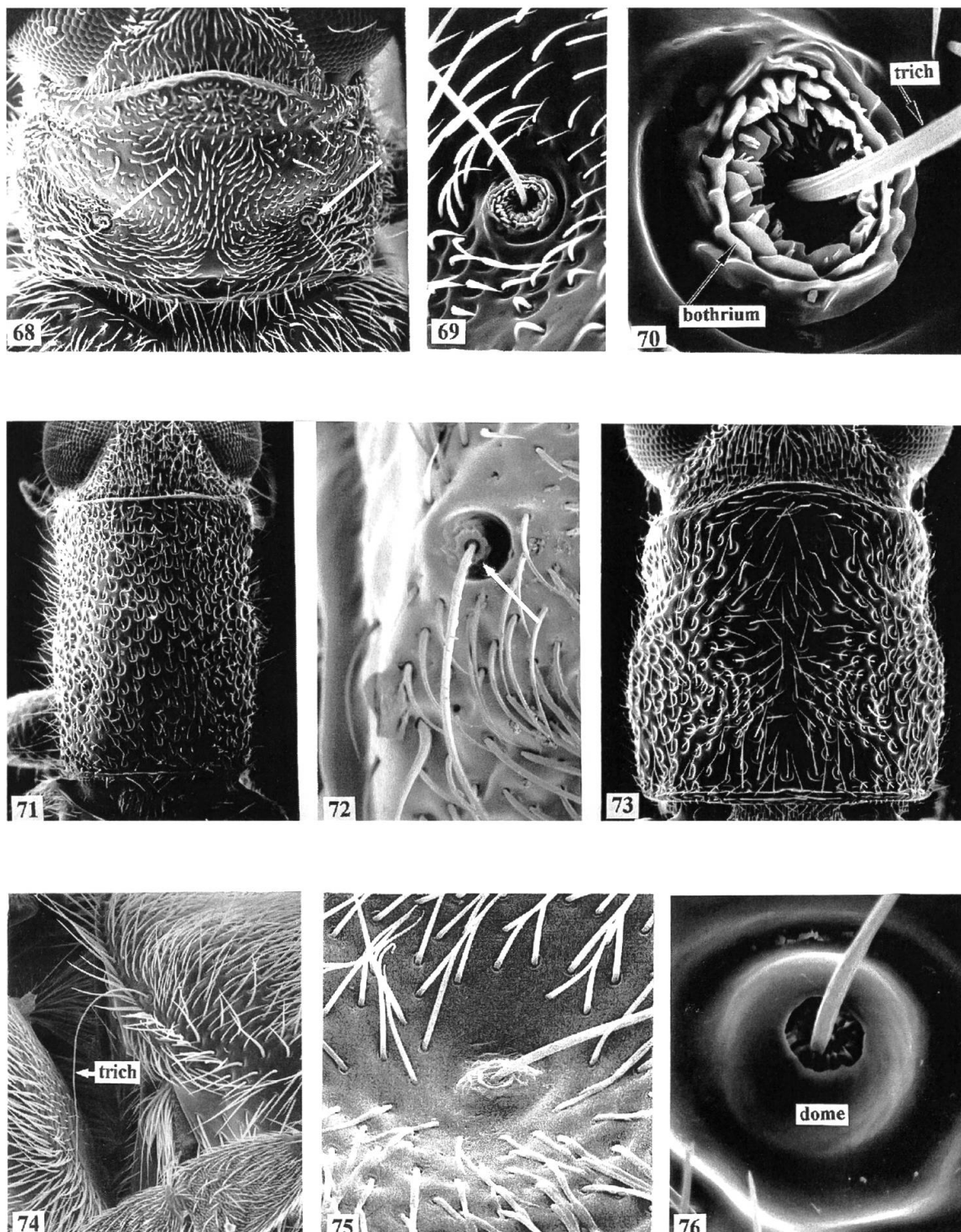
Subfamily Epiphloeinae Kuwert, 1893: 492

Figures 1, 18, 33, 45, 46, 55, 56, 57, 58, 59, 66, 68–70, 71, 72, 73–76, 89–91, 98, 99, 119, 140, 151, 155, 156, 177, 183, 193, 196, 202.

Type genus: *Epiphloeus* Spinola, 1841: 75.

Diagnosis. These beetles are conveniently identified, among checkered beetles with a diminutive 4th tarsomere, by the presence of two pair of trichobothria on the pronotal disc, the antennae are inserted at the lower extremity of the ocular notch, the metatarsus has 1 or 2 pulvilli, and the metendosternite almost always lacks a furcal lamina; the only known exception being *Turbophloeus simplex* (Schenkling) in which the furcal lamina is well developed.

Description. *Shape:* Ranges from rectangulate to suboval, rarely narrow subtriangular. *Size:* Length 2.8–12.0 mm; width 1.0–4.0 mm. *Integumental Color:* Varies from uniformly dark to multicolored; elytra frequently exhibit markings of brown, yellow, and red. *Head:* Triagonal to transverse, strongly deflexed, usually narrower than pronotum, surface usually finely punctated; epistomal suture incomplete, prominent only at sides; clypeus faintly sclerotized; frontal preantennal angle not acute; antenna comprised of 8 to 11 antennomeres, capitate, capitulum short or greatly expanded, funicular antennomeres subfiliform to extensively flared, sometimes highly compacted; eyes finely faceted, deeply notched anteriorly; labrum shallowly incised, transverse tormal processes contiguous, but not fused; last palpomere of maxillary and labial palpus usually digitiform, last palpomere of maxillary palpus rarely subsecuriform; mandible with well-developed dens, penicillus well developed, basal notch not very large; gula large, gular processes widely separated, gular sutures strongly converging, arcuate. *Thorax:* Pronotum usually transverse, rarely quadrate or trapezoidal, anterior transverse depression variously expressed or absent, lateral tubercle present or not; dorsolateral carina present but incomplete, carina confluent posteriorly with pronotal hem; pronotal projection short; pronotal commissure absent, disk with four trichobothria, one pair set dorso-paralaterally, the second set at lower sides, bothrium domed or not; pronotal projections slightly extended to middle, never confluent with prointercoxal process. procoxal cavity always open, procryptosternum incomplete, prointercoxal process linear, never expanded distally; pronototergosternal suture complete; metendosternite almost always without furcal lamina; elytral form usually elongate rectangular, sometimes



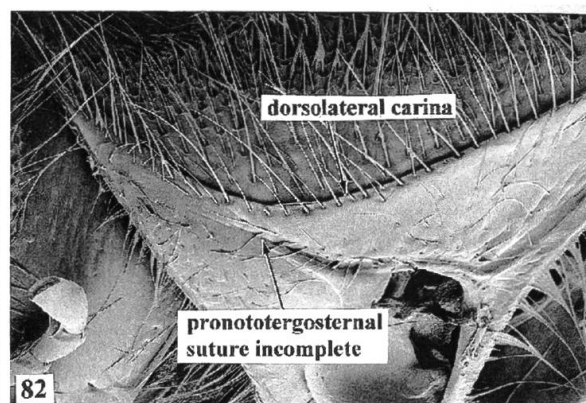
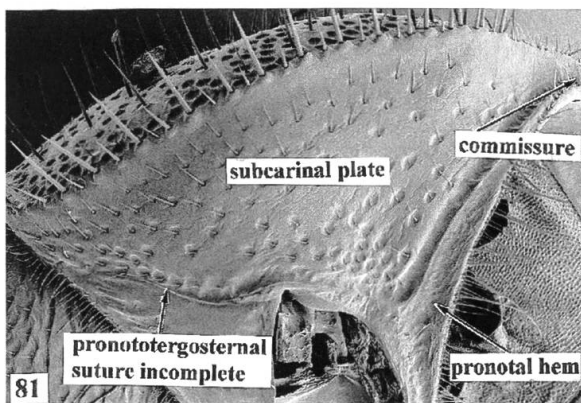
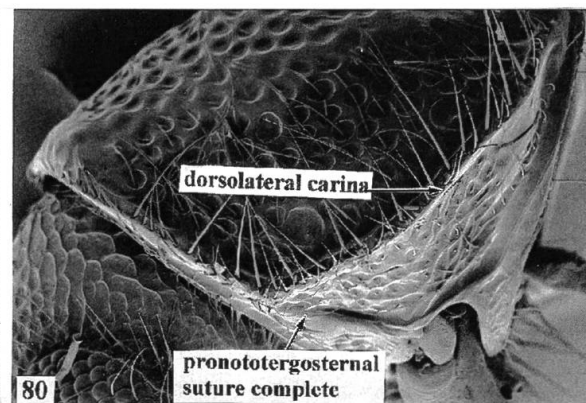
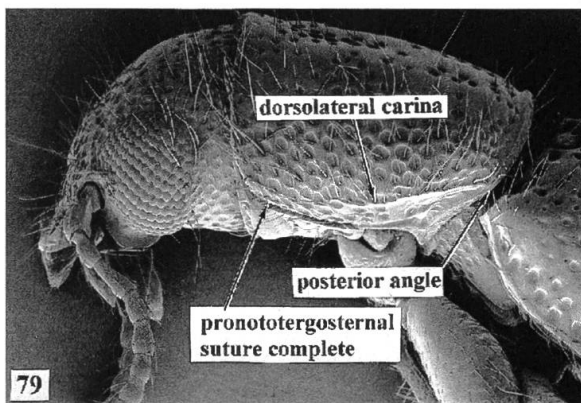
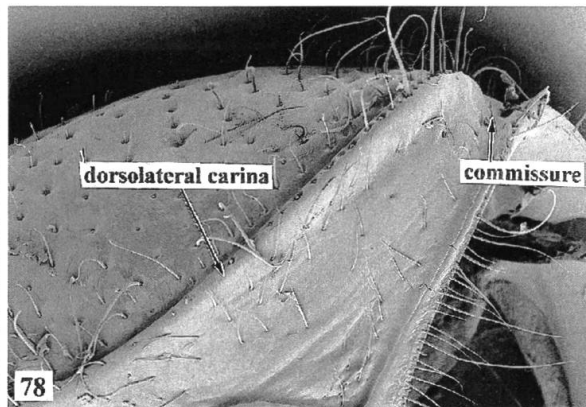
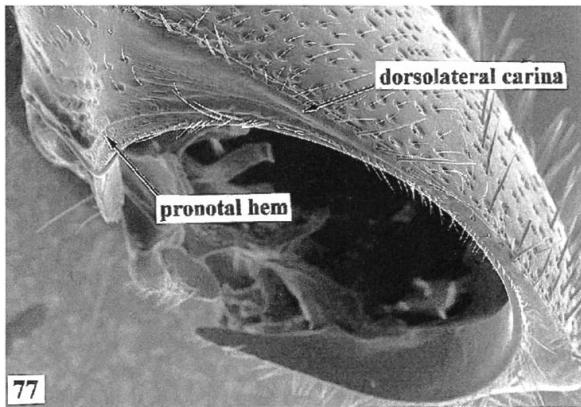
Figs 68–76. Morphological organs. 68–70 *Plocamocera coactilis* (68 forebody, 69 trichobothrium, 70 trichobothrium). 71 *Katamyurus albopaniculus*. 72 *Pyticeroides laticornis*. 73 Forebody of *Amboakis nova*. 74 Pronotum of *Iontoclerus humeralis*. 75 Trichobothrium of *Pyticeroides laticornis*. 76 Trichobothrium of *Katamyurus albopaniculus*.

suboval or subtriangular, anterior margin with carina, disc always set with asetiferous punctations that are usually arranged in rows, 1° and 2° usually present, 2° setae rarely absent, epipleural fold laterally positioned, gradually narrowing to elytral apex; legs, tarsal formula 5-5-5, cursorial, protibiae spinous along anterior margin, tibial spur formula 0-1-1, tarsal pulvillar formula 3-3-2 or 3-3-1, unguis with well-developed basal denticle; wedge cell of metathoracic wing usually closed. *Abdomen*: Robust and compact; pygidium usually scutiform, rarely incised distally; aedeagus not inverted, tegmen tubular and well sclerotized, bilobed distally, tegminal lobes not fimbriate, phallobasic rod variously developed, linearly slender, phallobasic apodeme well developed; phallic plates narrow; spicular fork well developed, intraspicular plate linear, spicular apodeme variously fused; ovipositor not longer than abdomen, with multilobed dorsal and ventral lamina; oblique and ventral bacculi well developed. *Alimentary Canal*: Stomodaeum short, proventricular valve comprised of 4 primary lobes; ventriculus well developed, ventricular crypts poorly developed; 4 cryptonephridial Malpighian tubules; proctodaeum short in males and long in females. *Mesodermal Male Reproductive Organs*: Typically with two pairs of accessory glands, rarely with one pair of accessory glands; testes comprised of multiple follicles. *Mesodermal Female Reproductive Organs*: Spermathecal capsule faintly sclerotized, spermathecal gland attached to subapex of spermathecal capsule; saccular bursal copulatrix well developed, bursal sclerite absent; ovaries comprised of multiple follicles. *Larval Morphology*: Cranium slightly transverse, subglobose; coronal component of epicranial suture absent; endocarina present; gula long and narrow; 5 stemmata present, anterior row of 3 and posterior row of 2; anterior border of labrum with very fine hairs; mesonotum and metanotum plates weakly sclerotized; spiracles small, annuliform; basal plate of 9th abdominal tergum present or not, urogomphi present or absent, when present not contiguous basally.

Natural History. These are lignicolous predators in the larval and adult stage. The body color of many species blends in with the color of bark on which they capture their prey. Other species are brightly colored and are undoubtedly involved in Batesian or Müllerian mimicry complexes. These beetles are most commonly collected during outbreaks of bark beetles, during which time they are abundantly collected from bark with an aspirator. They have also been collected in great numbers in a Malaise trap draped over a pile of freshly cut tree trunks of mahogany or oak. Securing branches and boles of tree infested with bark beetles in rearing tents can also generate many specimens.

Distribution. The Epiphloeinae are exclusively New World in distribution with a combined geographical range that extends from Canada to Argentina (Fig. 202). They are most common in the tropical zones of Middle and South America.

Inventory of generic taxa. There are 267 described species classified into 25 genera. The genera are as follows: *Acanthocollum* Opitz, *Amboakis* Opitz, *Decaphloeus* Opitz, *Decorosa* Opitz, *Diapromeces* Opitz, *Ellipotoma* Spinola, *Epiphloeus* Spinola, *Hapsidopteris* Opitz, *Ichnea* Laporte, *Iontoclerus* Opitz, *Katamyurus* Opitz, *Madoniella* Pic, *Megaphloeus* Opitz, *Megatrachys* Opitz, *Opitzia* Nemésio, *Opitzius* Barr,



Figs 77–82. Pronota. 77 *Necrobia rufipes*. 78 *Tenerus variabilis*. 79 *Tarsostenus univittatus*. 80 *Korynetes analis*. 81 *Neorthopleura thoracica*. 82 *Nelsonoplium heterochromum*.

Parvochaetus Opitz, *Pennasolis* Opitz, *Pericales* Opitz, *Plocamocera* Spinola, *Pyticeroidea* Kuwert, *Pteroferus* Opitz, *Silverasia* Nemésio, *Stegnoclava* Opitz, and *Turbophloeus* Opitz.

Taxonomic notes. Epiphloeinae taxa were studied by KUWERT (1893) and OPITZ (1997, 2004, 2006, 2007, 2008A, 2008B, 2008C, 2010).

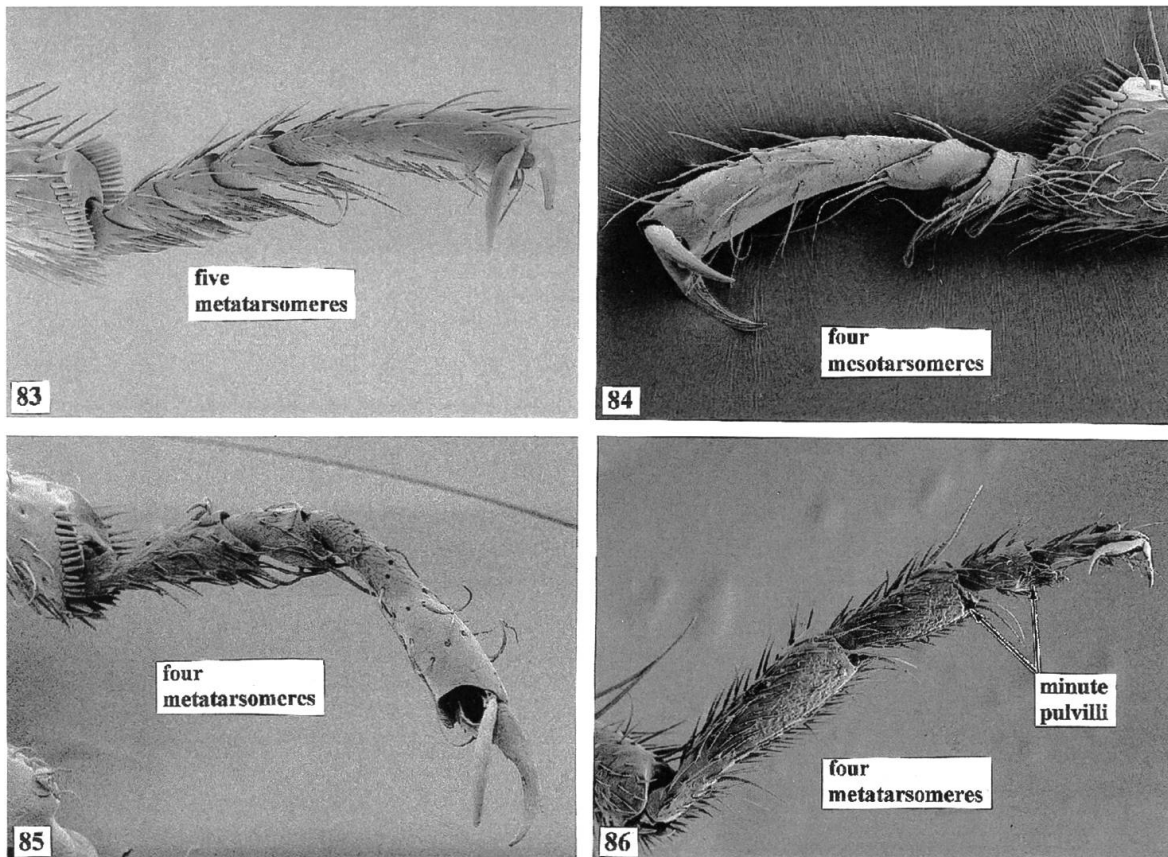
Subfamily Hydnocerinae Spinola, 1844B: 1

Figures 6, 7, 9, 10, 20, 22, 32, 49, 110, 122, 123, 138, 149, 168, 169, 170, 171, 187, 203.

Type genus: *Hydnocera* Newman, 1838: 379.

Diagnosis. The most diagnostic characteristics that distinguish the members of this subfamily are the large hemispherical eyes that are at most often only minutely notched near the antennal insertion (Fig. 6), the narrowness of the pronotum in comparison to the width of the head (Fig. 9), and the protraction and somewhat rotund condition of the labrum that is rarely incised mediodistally (Fig. 6).

Description. *Shape:* Usually oblong-narrow, rarely oblong short; pronotum usually conspicuously narrower than width of head; pronotum constricted behind the front margin and in front of hind margin, pronotum very bulgy between constrictions. *Size:* Length 2.5–12.0 mm; width 0.9–3.0 mm. *Integumental Color:* Predominantly dark, or predominantly yellow, sometimes metallic and with colors of red, green, and yellow, rarely with patterns of white scales. *Head:* Transverse, epistomal sutures not visible externally; clypeus not distinguishable externally, but two ridges present internally that identify clypeus; frontal preantennal angle not acute; eyes large, hemispherical, very minutely notched near antennal insertion, finely or coarsely faceted; gular wide, sutures usually parallel, rarely slightly converging; postgular plate narrow transverse; antenna comprised of 10 or 11 antennomeres, clavate to distinctly capitate, scape often short and about equal in size to pedicel, other preclaval antennomeres from submoniliform to subfiliform; mandible stout, anterior dens subacuminate, penicillus poorly developed, basal notch not large, sometimes with lobulate basal process; labrum protracted and rotund, anterior margin usually very slightly indented, indentation is rarely conspicuous, transverse tormal processes contiguous and sinuous, and well developed; epipharynx highly complex; maxilla with well-developed laterolacinia, terminal palpomere digitiform-acuminate; labium well developed, terminal palpomere securiform. *Thorax:* Pronotal anterior transverse depression deeply impressed, pronotal sides deeply notched in front of, and behind, the pronotal tubercle, dorsolateral ridge absent, pronototergosternal suture complete, prointercoxal process short, linear; procoxal cavities spheroid and open, procryptosternum incomplete, pronotal projection very short; mesosternum not cylindrically projected; elytral disc usually vested with setiferous punctations, elytral 1° and 2° setae present or not, asetiferous punctations present or not, epipleural fold well developed and positioned laterally, anterior ridge absent; legs, tarsal formula 5-5-5, usually extended to elytral apex, rarely much longer



Figs 83–86. Tarsi. 83 *Thaneroclerus buquet*, metatarsus. 84–85, *Isoclerus pictus* (84 mesotarsus, 85 metatarsus). 86 *Anthicoclerus anthicoides*, metatarsus.

than elytral apex, tarsal pulvilli well developed, unguis with or without basal denticle, femora slender, tibiae about as long as length of femora and without carina, tibial spur formula 1-2-2, 0-1-0, or 0-0-0; tarsal pulvillar formula 4-4-4 or 4-4-3, metathoracic wing present or not, when present venation usually reduced; metendosternite usually with well-developed furcal lamina, rarely without furcal lamina. *Abdomen*: Comprised of 6 visible sternites, 6th sternite often slid under 5th, pygidium scutiform, 6th often highly modified; spicular fork well developed, plates slender, apodeme fused at base, intraspicular plate absent; aedeagus not inverted, well sclerotized, phallobasic apodemes well developed, phallobase lobed, lobes not fimbriate, phallobasic apodemes not connected by membrane distally, ovipositor about as long as length of abdomen, with multi-lobed dorsal and ventral lamina; oblique and ventral bacculi well developed, spiculum ventrale not extraordinarily long. *Alimentary Canal*: Stomodaeum short; stomodaeal valve easily distinguishable externally from remainder of stomodaeum; ventriculus papillose, 6 Malpighian tubules; proventriculus with 4 primary and 2 secondary folds. *Mesodermal Male Reproductive Organs*: One or two pairs of accessory glands, when one present gland often multilobed. *Mesodermal Female Reproductive*

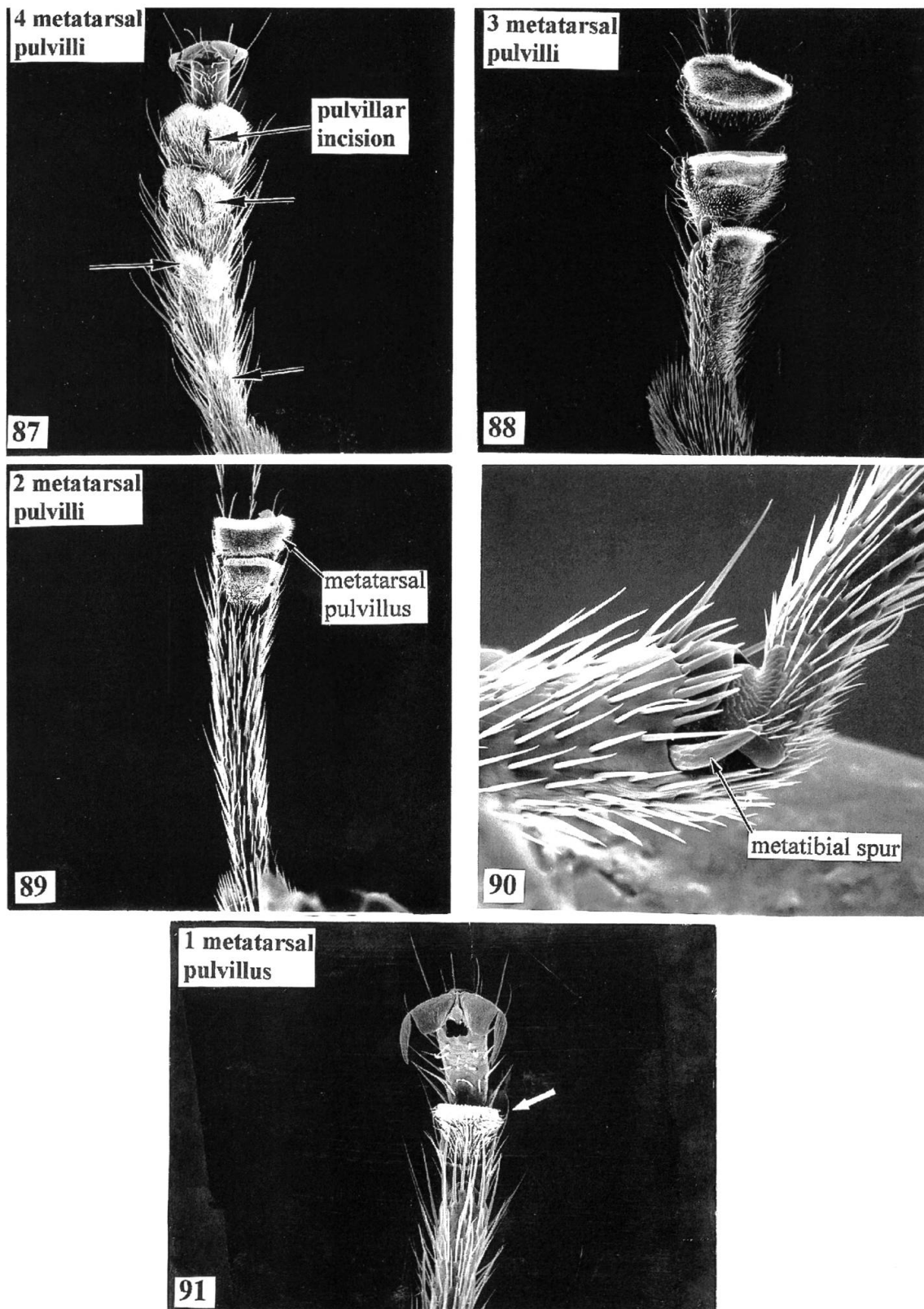
Organs: Spermathecal capsule well sclerotized. **Larval Morphology:** Cranium subquadrate, somewhat tapered to the front giving a trapezoidal appearance, coronal component of epicranial suture absent, frons trapezoidal, ending transversally posteriorly; endocarina absent; gula narrow but slightly expanded near middle, gular sutures subparallel, somewhat sinuous in frontal half; 5 stemmata present, anterior row of 3 and posterior row of 2; protergal plate well developed, mesonotum and metanotum poorly developed; spiracles usually small and biforous; basal plate of 9th abdominal tergum present, urogomphi present or not.

Natural History. These checkered beetles are most often collected by sweeping tall grasses (MORRIL *et al.*, 2001: 181), and they are often captured running on the slender prickly branches of berry bushes. CORPORAAL (1950: 36) reports that species of *Neohydnius* Gorham may be captured by sweeping leaves of bamboo. Hydnocerines may also be reared from the stems of Bayberry (CHITTENDEN 1890: 154), wild grape (CHAMPLAIN 1920: 636), the galls of cynipids and tenthrinids, and from the stems of witch hazel and hickory (SABROSKY 1934: 66). Immature stages of *Phyllobaenus humeralis* (Say) have been found on the sweet fern *Comptonia paregrina* (Linnaeus) Coulter (C. Pulasky, personal communication). A most detailed account of the life history of a hydnocerine is provided by CLAUSEN (1962: 545) who described the life cycle of *Callimerus arcufer* Chapin. Lastly, MAWDSLEY (2002A: 15) reported on the distribution of *Phyllobaenus* Dejean, *Isohydnocera* Chapin, and *Wolcottia* Chapin species in North American prairie environments, and discusses possible hydnocerine mimetic relationships (MAWDSLEY 1994: 115).

A recent trip to the highlands of Cerro Campana, Panamá, provided an unforgettable experience with hydnocerine behavior. While collecting insects from an oak tree laden with moss, via the beating-sheet technique, I proceeded to aspirate my catches among which there were several specimens of Cleridae. Having removed the insects from the sheet I proceeded to remove by hand small twigs and debris from the sheet. With only minute particles of debris remaining I was about to discard the small particles when to my astonishment I noticed that an apparent small morsel of debris transformed its contorted structure into a tiny mobile hydnocerine. This provides a wonderful lesson of the importance of field work to witness one's research organisms alive. Justin Bartlett (personal communication) had a similar experience with specimens of the Australian *Lemidia subaenea* Gorham.

Distribution. This world-wide group of checkered beetles is particularly abundant in North America and in the tropical zones of Middle America, South America, Africa, Asia, and Australia (Fig. 203).

Inventory of generic taxa. Four-hundred and seventy-three species are classified into the following 25 genera: *Abrosius* Fairmaire, *Achlamys* Waterhouse, *Allelidea* Waterhouse, *Blaesiophthalmus* Schenkling, *Brachycallimerus* Chapin, *Brachyptevenus* Pic, *Callimerus* Gorham, *Cephaloclerus* Kuwert, *Cucujocallimerus* Pic, *Emmepus* Motschoulsky, *Eurymetopum* Blanchard, *Evenoclerus* Corporaal, *Isohydnocera* Chapin, *Isolemidia* Gorham, *Laiomorphus* Pic, *Lasiocallimerus* Corporaal, *Lemidia* Spinola, *Neohydnius* Gorham, *Parmius* Sharp, *Paupris* Sharp, *Phyllobaenus* Dejean, *Silviella* Solervicens, *Stenocallimerus* Corporaal and Pic, *Theano* Laporte, and *Wolcottia* Chapin.



Figs 87–91. Morphological organs. 87–89, 91 Metatarsi (87 *Perilypus claudus*, 88 *Pelonium lituratum*. 89–90 *Epiphloeus duodecimmaculatus* (89 metatarsus, 90 distal end of metatibia). 91 *Pyticeroideus laticornis*.

Taxonomic notes. The subfamily was comprehensively studied by KOLIBÁČ (1998A: 127). The available evidence, with particular reference to the composition of the mesodermal male internal reproductive organs and, to a lesser extent, the configuration of the basal denticle of the unguis and general facies of the forebody, does not support the synonymization of *Isohydnocera* Chapin under *Wolcottia* Chapin as advocated by KOLIBÁČ (1998: 144). Solervicens revised *Eurymetopum* Blanchard (1986: 11) and *Silviella* Solervicens (1987: 25). LEA (1907: 301) reported on *Lemidia* Spinola.

A great abundance of new species awaits description among the Middle American Hydnocerinae. The extraordinary modifications of the 6th visible abdominal sternite and the morphological properties of the aedeagus will be very helpful in the discernment of species. The number of male mesodermal accessory glands, shape of the spermathecal capsule, and attachment site of the spermathecal gland on the spermathecal capsule will be very useful for discussions of intergeneric relationships. It is highly recommended that hydnocerine specimens, and other checkered beetles, be collected in Pampel's fixative so that the characteristics of mesodermal reproductive organs can be properly analyzed.

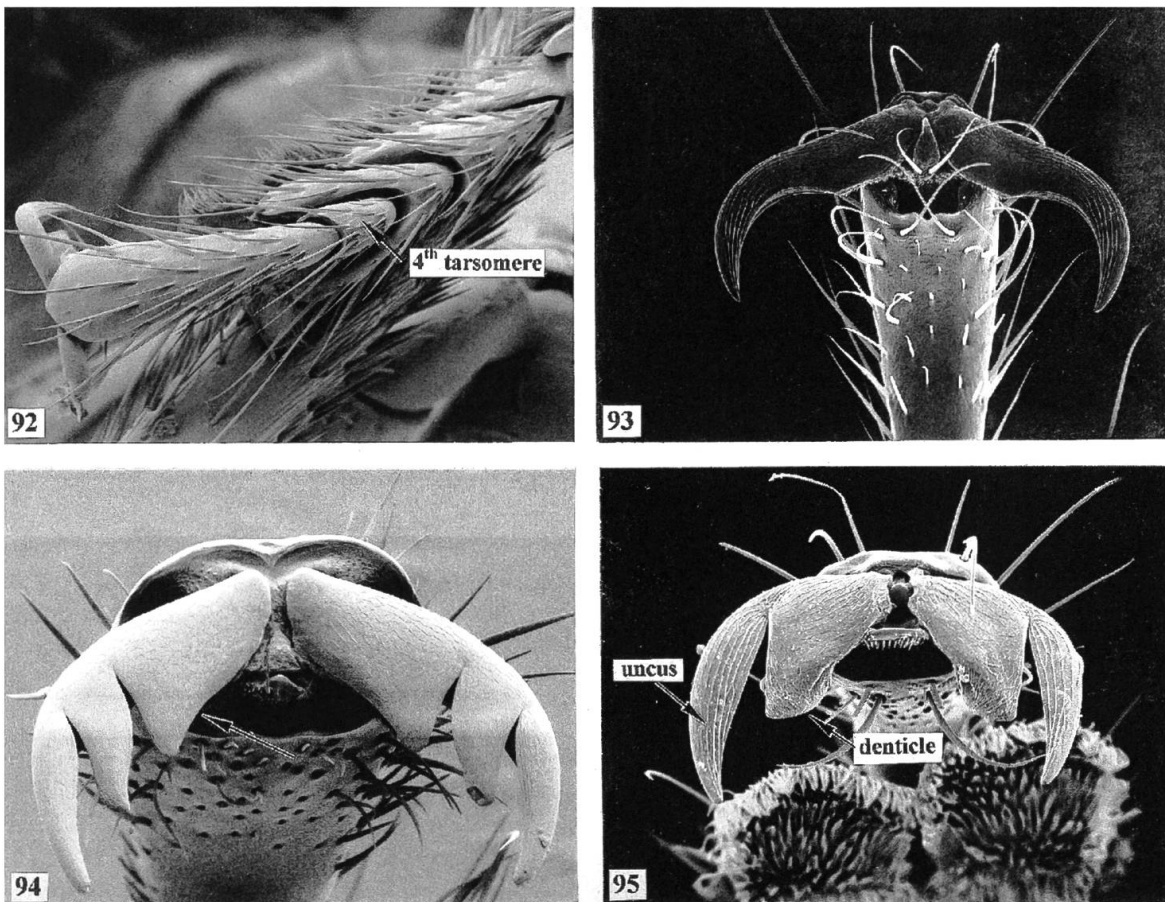
Subfamily Isoclerinae Kolibáč, 1992: 315

Figures 11, 84, 85, 117, 181, 204.

Type genus: *Isoclerus* Lewis, 1892: 191.

Diagnosis. Within Cleridae, only among members of the genera of Isoclerinae, do we find a tarsomeral formula of 5-4-4. Moreover, in these checkered beetles, as in those of Thaneroclerinae Chapin, the protarsomeres do not show pulvilli, but are much widened and densely setose ventrally, and the phallobasic apodeme is absent.

Description. *Shape:* Oblong-short, usually deep bodied, pronotum broad campaniform or narrow campaniform and elytra short-rectangulate; elytral posterior angle subacute; cylindric constriction between forebody and hindbody prominent or not. *Size:* Length 1.8–4.0 mm; width 0.7–1.5 mm. *Integumental Color:* Mostly reddish-brown, some with dark markings, a few predominantly black, some with tufts of silvery setae on elytral disc. *Head:* Rectangulate, postgena extended, epistomal sutures very abbreviated, briefly externally visible only at sides, internal epistomal ridge present only at sides; clypeus not discernible externally; frontal preantennal angle acute; eyes small, coarsely faceted, ocular notch minutely concave; gula narrow, gular sutures very briefly converging, then parallel, postgular plate well defined, narrow transverse, postgular process incipient; antenna comprised of 11 antennomeres, rarely apparently comprised of 10 in which case last two antennomeres conjoined, usually distinctly capitate, rarely clavate, scape short capitate, other preclaval antennomeres from submoniliform to subfiliform; mandible stout, dens and penicillus well developed, basal notch very large; labral anterior incision prominent, transverse tormal processes linear, contiguous, and faintly developed, tormal connecting rod sinuous and well developed; epipharynx not complex; maxilla with well-developed laterolacinia, terminal palpomere narrow digitiform; labium well developed, terminal palpomere from narrow digitiform to broad digitiform. *Thorax:* Pronotum



Figs 92–95. Morphological organs. 92 *Romanaeclerus rufus*, metatarsus. 93–95 Ungues (93 *Pelonium lituratum*, 94 *Araeodontia penninsularis*, 95 *Perilypus limbatus*).

usually narrowly constricted posteriorly, rarely broadly constricted, dorsolateral ridge fragmented, usually rudimentary at pronotal hind angles; pronotal projection long, contiguous with prointercoxal process, rarely just short of prointercoxal process, prointercoxal process usually very expanded distally, rarely not expanded; pronototergosternal suture complete; prosternum usually very expanded anteriorly; coxal cavities spheroid and usually closed externally, rarely slightly open, procryptosternum absent; mesosternum cylindrically projected; elytral disc profusely vested with 2° setae, 1° setae and asetiferous punctations absent, epipleural fold well developed and positioned laterally, anterior ridge absent; legs, tarsal formula 5-4-4, tarsal pulvilli absent, first 4 protarsomeres greatly expanded, protarsomeres venter highly sclerotized and densely setose, 5th tarsomere extraordinarily lengthened, unguis without denticle, mesotarsomeres and metatarsomeres not expanded ventrally, femora clubby, tibiae about as long as length of femora, slightly curved and without carina, tibial spur formula 2-2-2, 0-2-2, or 0-0-0; tarsal pulvilli absent; metathoracic wing venation greatly reduced; metendosternite with well-developed furcal lamina. *Abdomen*: Comprised of 6 visible sternites, 6th sternite often slid under 5th, pygidium scutiform,

6th visible sternite not incised distally; spicular fork well developed, plates slender, apodeme fused entirely, intraspicular plate transverse narrow, slightly setose; aedeagus not inverted, poorly sclerotized, phallobasic apodeme absent, phallobase usually distinctly lobed, rarely minutely lobed, lobes fimbriate, phallobasic dorsum lightly sclerotized, phallobasic venter semimembraneous; ovipositor about as long as length of abdomen, with multilobed dorsal and ventral lamina, oblique and ventral bacculi well developed, spiculum ventrale extraordinarily long. *Alimentary Canal*: Stomodaeum extraordinarily long, about as long as ventriculus; stomodaeal valve not distinguishable externally from remainder of stomodaeum; ventriculus not papillose; proventriculus comprised of 4 primary and 4 secondary lobes. *Mesodermal Male Reproductive Organs*: No information available. *Mesodermal Female Reproductive Organs*: Spermathecal capsule faintly sclerotized; saccular bursa absent. *Larval Morphology*: Cranium oblong-rectangulate (Fig. 181), coronal component of epicranial suture present; endocarina absent; gula with posteriorly expanded gular sutures and without postmedial tubercles; 5 stemmata present, anterior row of 3 and posterior row of 2; mesonotum and metanotum with pair of plates; spiracles small, biforous; basal plate of 9th abdominal tergum and urogomphi absent.

Natural History. Species of *Ababa* Casey and *Allothaneroclerus* Corporaal have been extracted from the fruiting bodies of tree fungi, where they presumably prey on small mycetophagous insects.

Distribution. Although present in the New World, these checkered beetles are most commonly collected in the Palearctic (Fig. 204).

Inventory of generic taxa. Eighteen species are classified into the following 8 genera: *Ababa* Casey, *Allothaneroclerus* Corporaal, *Compactoclerus* Pic, *Cyrtinoclerus* Chapin, *Isoclerus* Lewis, *Lyctosoma* Lewis, *Microababa* Pic, *Parathaneroclerus* Pic.

Taxonomic notes. The genera included in this subfamily were investigated by KOLIBÁČ (1992 and 1998b).

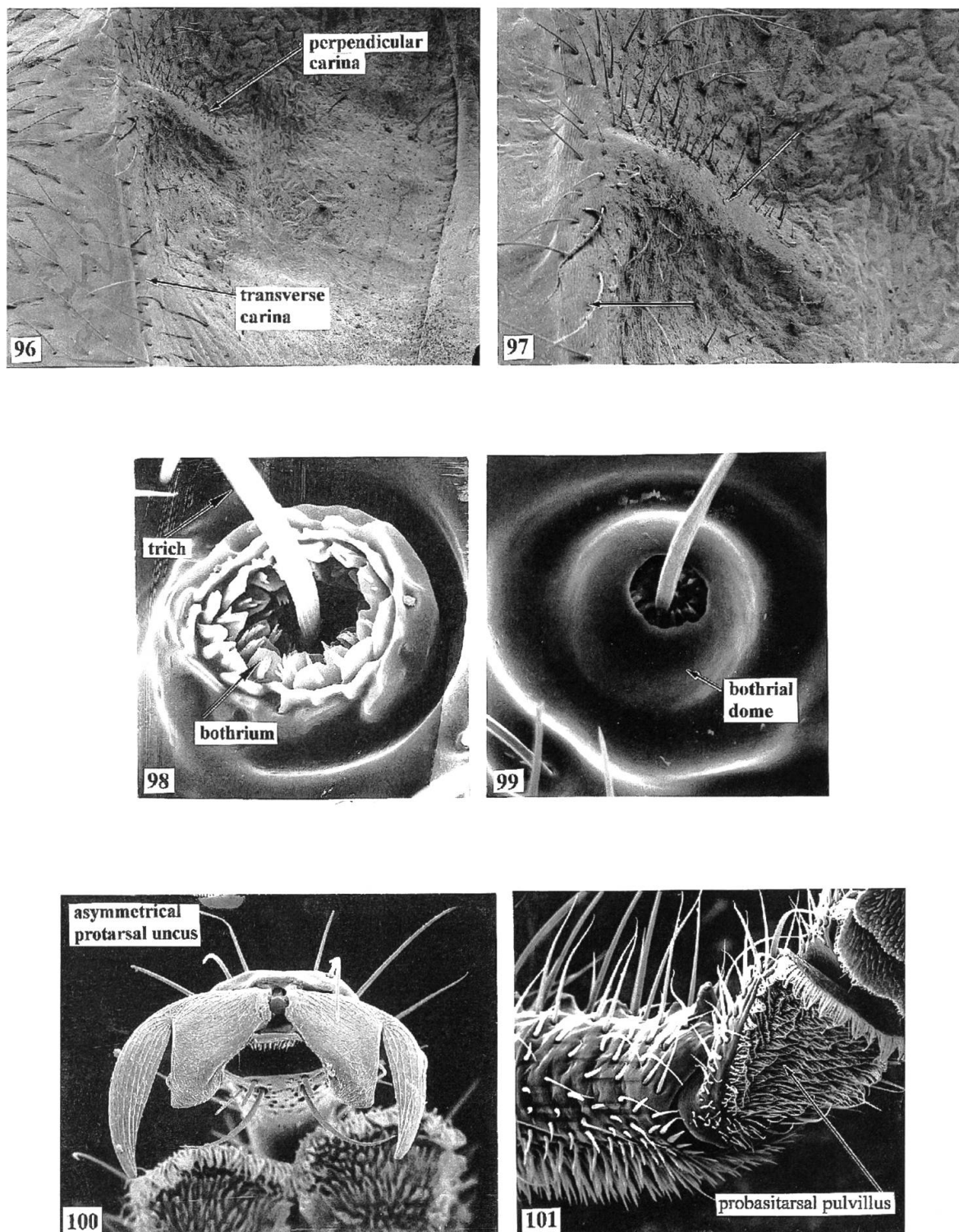
The amalgamation of the first two mesothoracic and metathoracic basal tarsomeres into an elongated basitarsomere is a major evolutionary step towards more efficient cursorial locomotion. The establishment of Isoclerinae, lends morphological balance to the higher classification of these primitive Cleridae. Also, *Ababa* Casey, *Allothaneroclerus* Corporaal, *Lyctosoma* Lewis, and *Parathaneroclerus* Pic are resurrected, herein, to full generic status, as their synonymization under *Isoclerus* Lewis is not warranted according to my observations and my assessment of the information presented by KOLIBÁČ (1992).

Subfamily Korynetinae Laporte, 1836: 34

Figures 15, 28, 53, 61, 77, 80, 113, 131, 132, 146, 152, 172, 173, 189, 208, 212.

Type genus: *Korynetes* Herbst, 1792: 148.

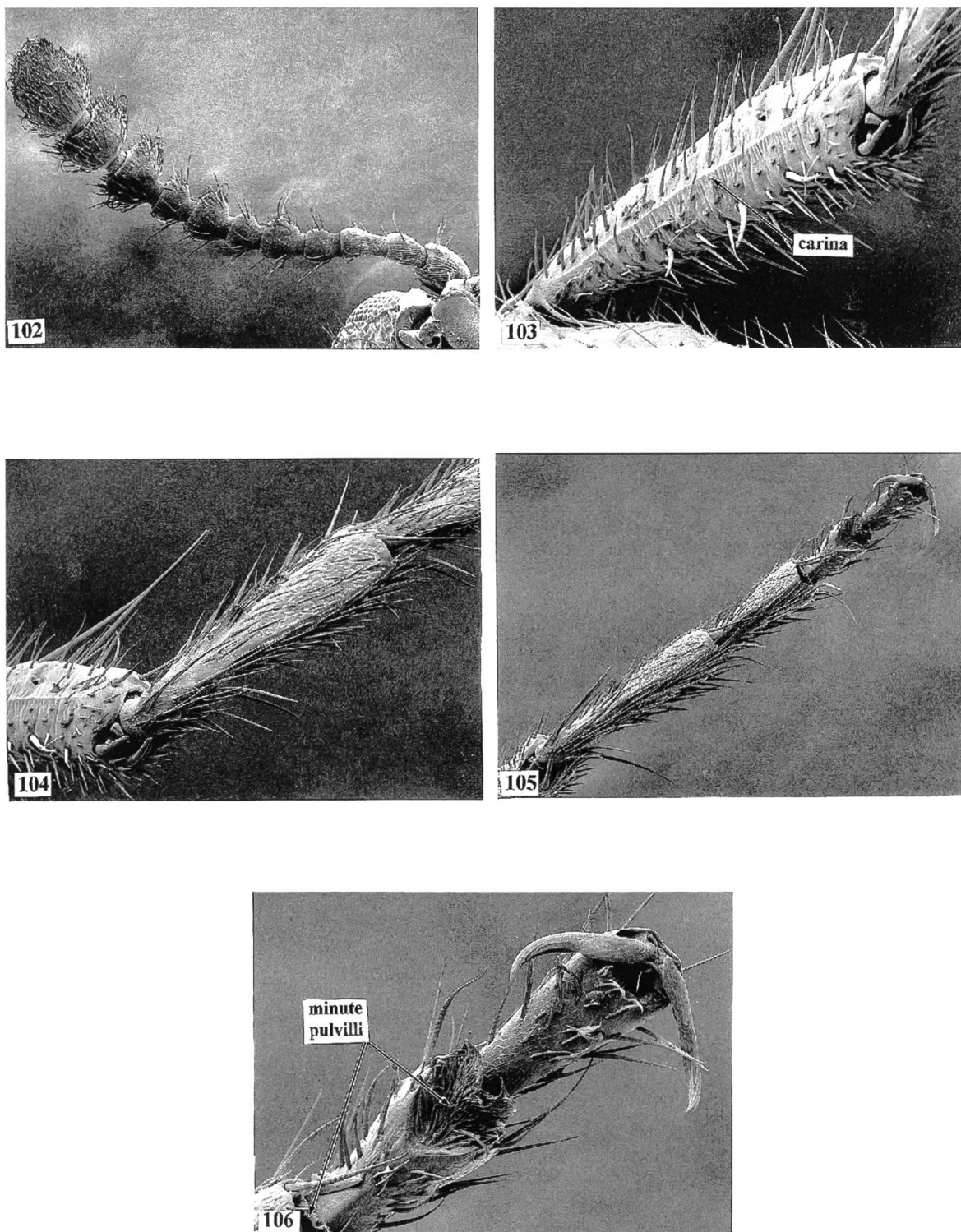
Diagnosis. Checkered beetles belong to this subfamily if they display a reduced 4th tarsomere, have a dorsolateral carina around the periphery of the pronotum, and have a



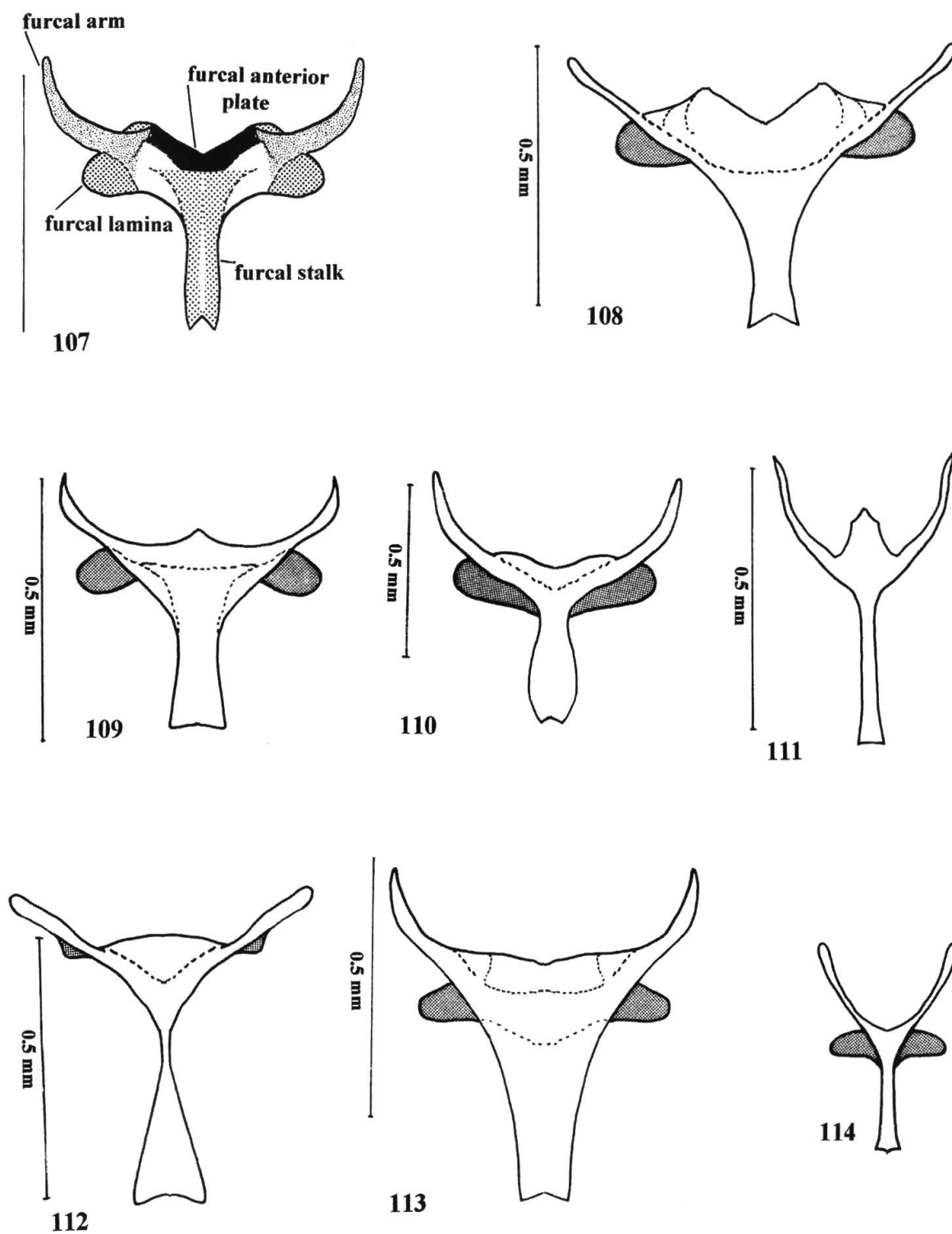
Figs 96–101. Morphological organs. 96–97 Metathoracic cavity of *Cymatodera californica*. 98–99 Trichobothria (98 *Plocamocera coactilis*, 99 *Diapromeces aelydis*). 100 Unguis of *Perilypus limbatus*. 101 Protarsus of *Epiphloeus duodecimmaculatus*.

fully developed pronotal commissure, which may be very narrowly expressed in some species. There is a capitate antennae whose capitulum is usually considerably shorter than the length of the rest of the antenna.

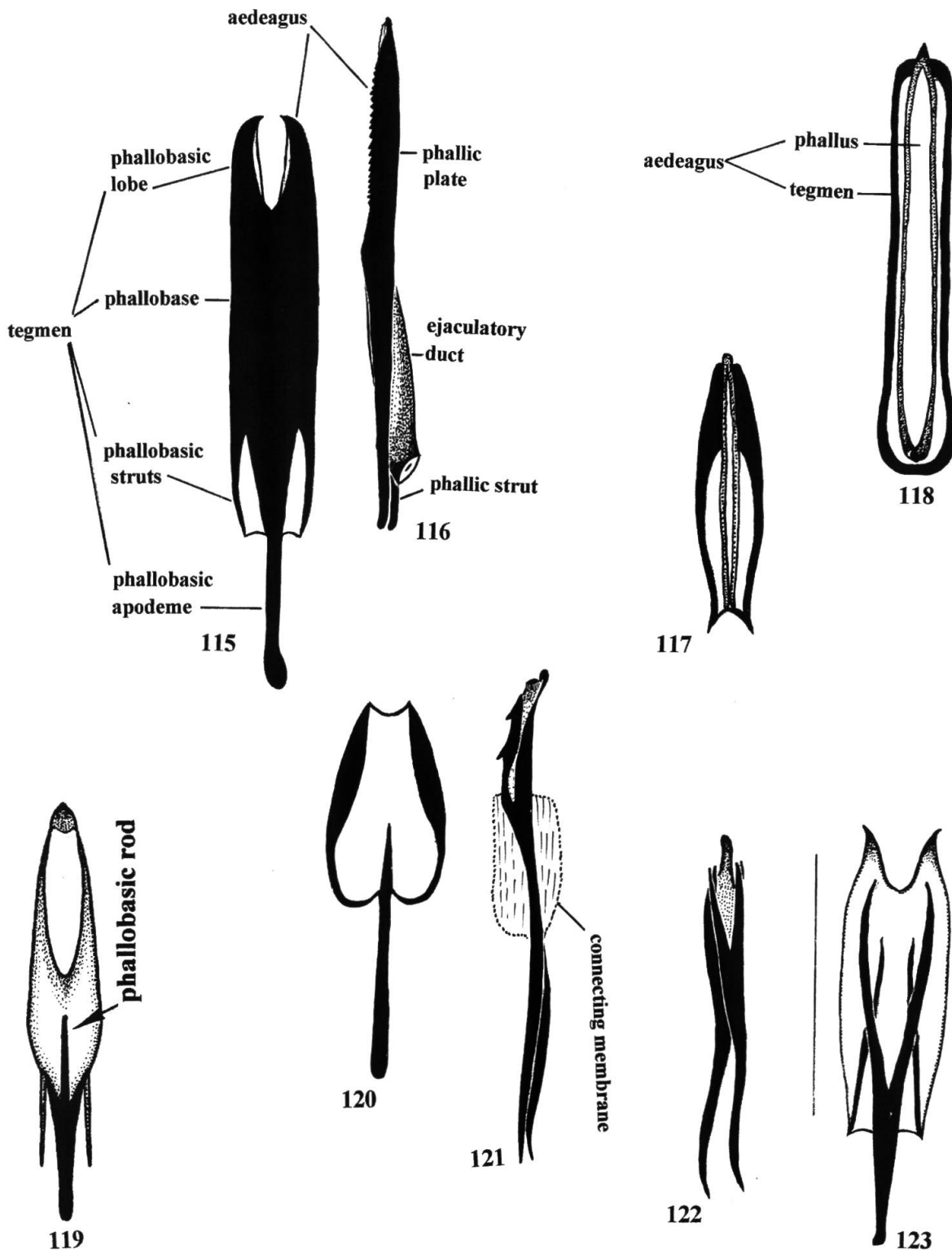
Description. *Shape:* Long rectangulate, short rectangulate, subovoid, rarely very deep bodied. *Size:* Length 2.3–11.5 mm; width 1.0–4.0 mm. *Integumental Color:* Usually concolorous, light to dark brown, blue to green, rarely bicolorous. *Head:* Quadrate to oblong, rarely subrostrate, strongly deflexed or projected, usually narrower than pronotum, surface usually vested with small setiferous punctations, preantennal angle not acute; epistomal suture short, restricted to sides, internal epistomal ridge incomplete; antenna comprised of 11 antennomeres, capitate, capitulum antennomeres usually not compacted, funicular antennomeres subfiliform; eyes coarsely to subfinely faceted, moderately notched anteriorly; labrum shallowly incised, transverse tormal processes fused almost always contiguous, transverse component rarely absent; galea sometimes extraordinarily expanded, epiphary complex or not; laterolacinia almost always present; last palpomere of maxillary and labial palpi from digitiform to securiform; mandible with well-developed dens or with lamina, basal notch not large; gula large, gular sutures linear straight-up, gular process short, broadly contiguous, and usually bilobed, ends of process ciliated. *Thorax:* Pronotum usually transverse, quadrate to suboval, or elongate, lateral tubercle present or not, pronotal sides minutely or coarsely crenulate, sometimes with anterolateral and posterolateral small tubercles, anterior transverse depression absent, dorsolateral carina complete, not posteriorly confluent with pronotal hem, pronotal commissure complete, pronotal projections long or short; procoxal cavity open or closed, prointercoxal process usually expanded distally, rarely linear, procryptosternum incomplete; pronototergosternal suture complete; metendosternite with furcal lamina; elytral form usually elongate rectangular, sometimes suboval, anterior margin with carina, disc with asetiferous punctations, 1° and 2° usually present, epipleural fold usually lateral, rarely oblique, narrowing to elytral apex; legs, tarsal formula 5-5-5, cursorial, tibial spur formula 2-2-2; tarsal pulvillar formula 3-3-3, 3-1-1, 2-2-1, or 2-1-1; unguis with denticle; wedge cell of metathoracic wing usually closed, rarely open. *Abdomen:* Short and compact; pygidium quadrate; 6th sternite incised or not; aedeagus not inverted, very sclerotized or slightly sclerotized or, tegmen tubular, variously bilobed distally, tegmental lobes fimbriate, phallobasic rod acuminate, linear, or capitate, phallobasic apodeme well developed, phallic plates slender, variously shaped; spicular fork well developed, intraspicular plate linear, components of spicular apodeme variously fused; ovipositor not longer than abdomen, with multilobed dorsal and ventral lamina; oblique and ventral bacculi well developed. *Alimentary Canal:* Stomodaeum short, proventricular valve comprised of 4 primary lobes; ventriculus well developed, ventricular crypts well developed; 6 cryptonephridial Malpighian tubules; proctodaeum short in males and long in females. *Mesodermal Male Reproductive Organs:* Two pairs of accessory glands; testes comprised of multiple follicles. *Mesodermal Female Reproductive Organs:* Spermathecal capsule highly sclerotized, spermathecal gland attached to apex of spermathecal capsule; saccular bursal copulatrix well developed, bursal sclerite absent; ovaries comprised of multiple follicles. *Larval Morphology:* Cranium quadrate, coronal component of epicranial suture not present; endocarina



Figs 102–106. *Anthicoclerus anthicoides* (102 antenna, 103 mesotibia, 104–106 metatarsi).



Figs 107–114. Metendosternites. 107 Generalized metendosternite, 108 *Thaneroclerus buquet*. 109 *Tilloidea unifasciata*. 110 *Phyllobaenus longus*. 111 *Iontoclerus humeralis*. 112 *Myrmecomea raffagi*. 113 *Korynetes coeruleus*. 114 *Tarsostenmus univittatus*.



Figs 115–123. Tegmina and phalli. 115–116 *Perilypus revantazon* (115 tegmen, 116 phallus). 117 *Isoclerus pictus*, phallus. 118 *Thaneroclerus buquet*, phallus. 119 *Parvochaetus froeschneri*, phallus. 120–121 *Enoplium serraticorne* (120 Tegmen, 121 phallus). 122–123 *Lemidia nitens* (122 phallus, 123 tegmen).

present; gula long, narrow; 2 stemmata, anterior twice size of posterior; mesonotum and metanotum without plates; spiracles large biforous; basal plate of 9th abdominal tergum well developed; urogomphi very small and widely separated.

Natural History. As a group, these checkered beetles are most commonly involved with the entomofauna associated with the decomposition of vertebrate corpses, particularly fish and mammal. Most of the published information concentrates on species of the cosmopolitan genus *Necrobia* Olivier, which are saprophagous on the proteinaceous remains on bones and skin. They are also known to prey on saprophytic insects including cannibalistic behavior on their immatures. *Necrobia rufipes* Degeer has been associated with the decomposition of Egyptian mummies and human corpses in general, while members of *Corynetinus* Reitter may be found among saprophagous insects in dried cow dung. Finally, the scabrous, rotund body-form of members of *Prosymnus* Laporte aligns these checkered beetles mimetically with those of the trogid genus *Trox* Fabricius, which are commonly found in cow-dung niches.

Distribution. The distribution of the speciose genera, such as *Korynetes* Herbst and *Opetiopalpus* Spinola, and some of the smaller genera such as *Corynetinus*. Reitter, seem to be correlated with the spatial occurrence of the vast assemblages of ungulates on the African savanna. A more cosmopolitan dispersal is found among some *Necrobia* Olivier species, while some of the less speciose groups are widely separated between Australia and South America (Fig. 208). A few endemic species are found in China, Europe, and North America.

Inventory of generic taxa. There are 76 described species classified into 7 genera. The genera are as follows: *Corynetinus* Reitter, *Dolichopsis* Gorham, *Korynetes* Herbst, *Necrobia* Olivier, *Notostenus* Dejean, *Opetiopalpus* Spinola, and *Prosymnus* Laporte.

Taxonomic notes. Taxonomic history exists mostly as descriptive works.

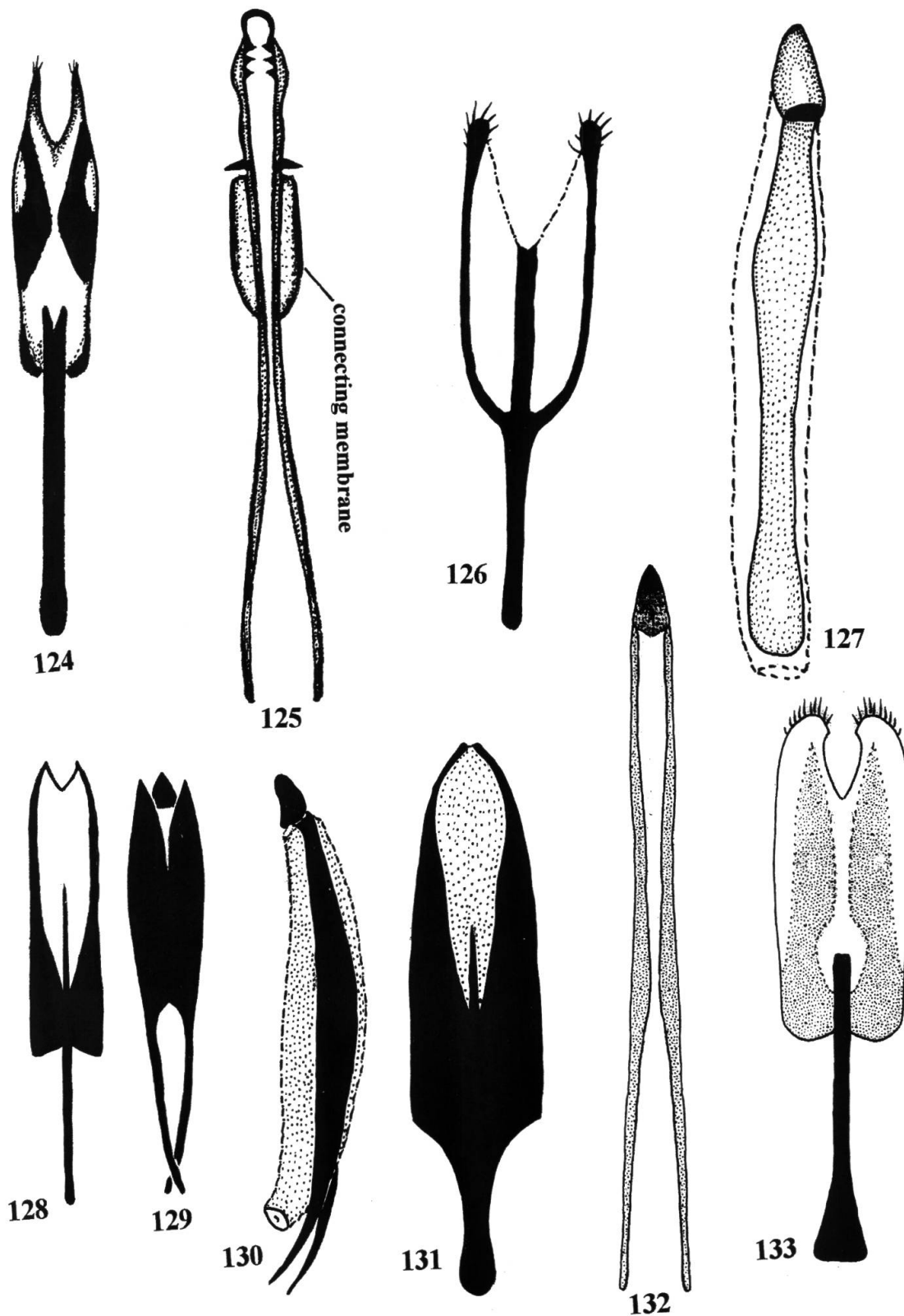
Subfamily Neorthopleurinae Opitz, 2009D: 137

Figures 16, 17, 30, 31, 35, 78, 81, 82, 92, 124, 125, 141, 142,
157, 158, 184, 188, 194, 209, 211.

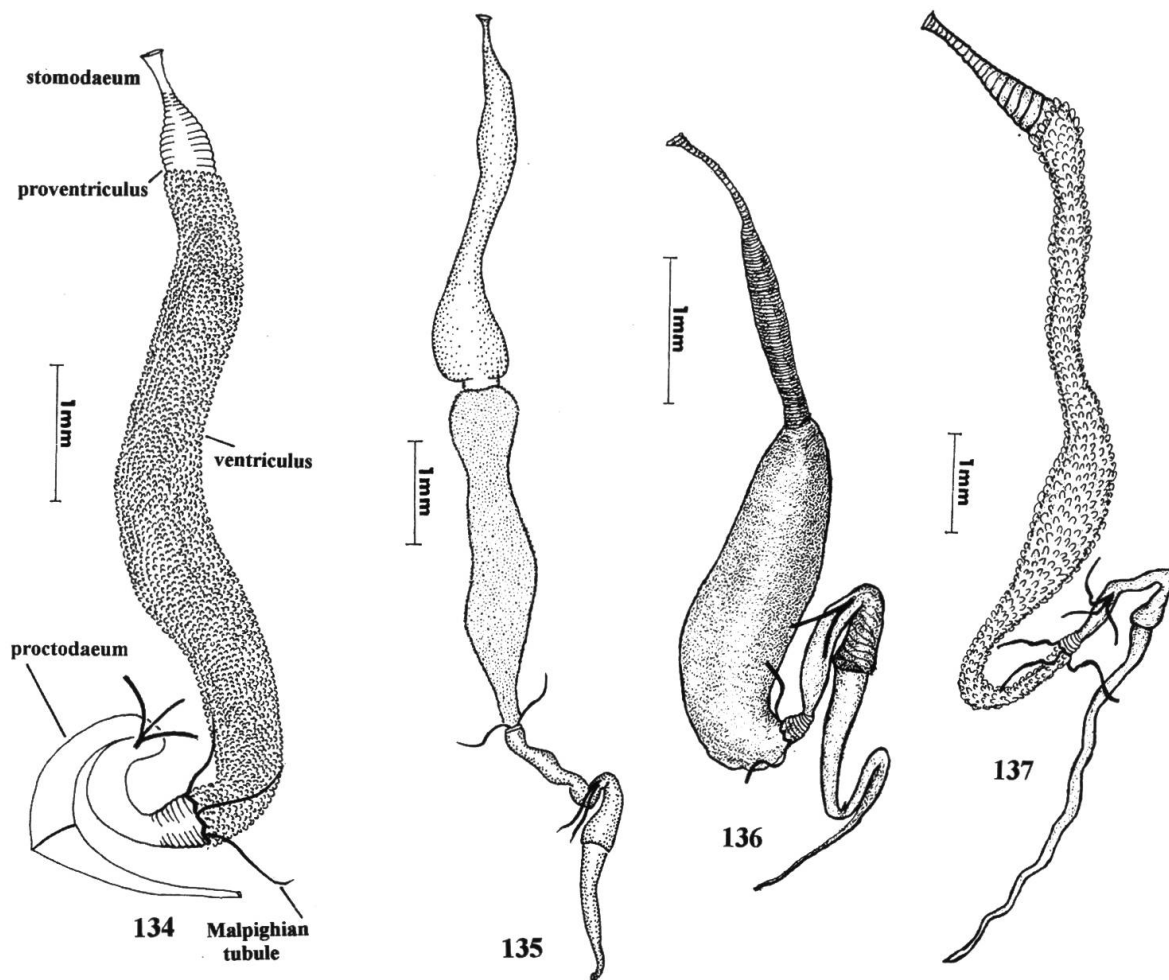
Type genus: *Neorthopleura* Barr 1976: 2.

Diagnosis. The members of this subfamily have the gular processes consolidated to form one bilobed petiolate gular process (Figs 16, 17), the gula are substantially reduced, the gular sutures diverge (Fig. 16), and the pronototegosternal suture is most often incomplete (Figs 81, 82). Also, the dorsolateral ridge of the pronotum is complete and circumvents the pronotum; resulting in a well formed pronotal commissure (Fig. 78). The dorsolateral pronotal carina does not join the pronotal hem. Lastly, the ovipositor is longer than the abdomen.

Description. *Shape:* Long rectangulate, short rectangulate, subovoid, somewhat flattened or deep bodied. *Size:* Length 2.5–12.0 mm; width 0.8–4.2 mm. *Integumental Color:* Combinations of entirely black, predominantly black with the pronotum yellow to yellow-red, predominantly yellow to yellow-red, but with dark markings. *Head:*

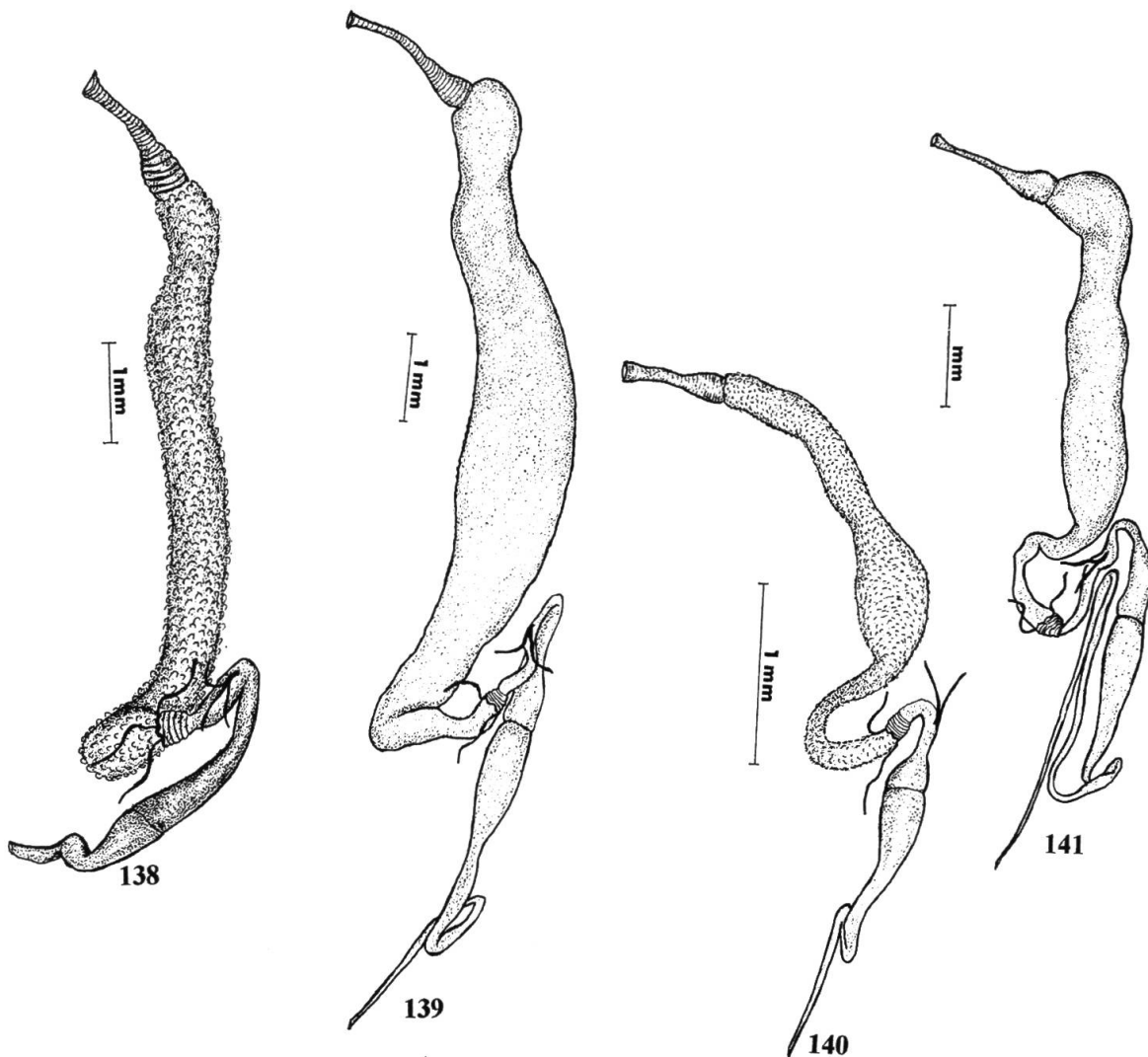


Figs 124–133. Tegmina and phalli. 124–125 *Neorthopleura thoracica* (124 tegmen, 125 phallus). 126–127 *Phymatophaea insula* (126 tegmen, 127 phallus). 128–129 *Strotocera convexa* (128 tegmen, 129 phallus). 130–131 *Neopylus hahuelbutensis* (130 phallus, 131 tegmen). 132–133 *Korynetes coeruleus* (132 phallus, 133 tegmen).



Figs 134–137. Alimentary canals. 134. *Dologenitus cyanipennis*. 135. *Chaetosoma colossa*. 136 *Thaneroclerus buquet*. 137 *Cymatodera bicolor*.

Transverse to subovoid, strongly deflexed, usually narrower than pronotum, surface usually finely punctated; epistomal suture faintly visible externally, inner epistomal ridge incomplete; clypeus bipartite, comprised of pigmented upper region and nonpigmented lower region; frontal preantennal angle not acute; antenna comprised of 10 to 11 antennomeres, capitate, serrate, or partially flabellate, when capitate capitulum short or greatly expanded, funicular antennomeres subfiliform, serrate, or extensively lobate; eyes coarsely to subcoarsely faceted, very deeply notched anteriorly; labrum shallowly incised, medial tormal processes fused contiguous; epipharynx not complex; last palpomere of maxillary and labial palpus digitiform to subsecuriform; mandible with well-developed dens, penicillus well developed, slightly developed, or absent; gula small, gular sutures strongly diverging, gular process petiolate, bifurcated and ciliated at ends. *Thorax*: Pronotum usually transverse, quadrate, suboval, or elongated, lateral



Figs 138–141. Alimentary canals. 138 *Phyllobaenus longus*. 139 *Chariessa pilosa*. 140 *Madoniella dislocata*. 141 *Neorthopleura thoracica*.

tubercle absent; anterior transverse depression absent, dorsolateral carina present, complete, not posteriorly confluent with pronotal hem, pronotal commissure complete, pronotal projections usually short, rarely long, prointercoxal process linear or expanded distally; procoxal cavity open, procryptosternum not complete; pronototergosternal suture incomplete; metendosternite with furcal lamina; elytral form usually elongate rectangular, sometimes suboval, anterior margin with or without carina, disc with or without asetiferous punctations, 1° and 2° usually present, epipleural fold laterally, or obliquely positioned, or internally inflected, abruptly ended at elytral middle or gradually narrowing to elytral apex; legs, tarsal formula 5-5-5, cursorial, tibial spur formula 2-2-2, 1-2-2, 1-1-1, 0-2-2, and 0-0-2, tarsal pulvillar formula 3-3-3; unguis with basal denticle; wedge cell of metathoracic wing usually closed, rarely open. *Abdomen:*

Short compact or elongated and narrowing to pygidium; 5th sternite rarely incised mediodistally; pygidium quadrate, scutiform, pygidial apodemes sometimes very long, 6th sternite incised or not; aedeagus not inverted, very sclerotized or slightly sclerotized or, tegmen tubular, variously bilobed distally, tegminal lobes fimbriate, phallobasic rod variously developed, rarely absent, phallobasic apodeme well developed; phallic plates slender, variously shaped; spicular fork well developed, intraspicular plate linear, spicular apodeme variously fused, or completely separated; ovipositor usually much longer than length of abdomen, with multilobed dorsal and ventral lamina; oblique and ventral bacculi well developed. *Alimentary Canal*: Stomodaeum short, proventricular valve comprised of 4 primary lobes; ventriculus well developed, ventricular crypts poorly developed; 4 cryptonephridial Malpighian tubules; proctodaeum short in males and long in females. *Mesodermal Male Reproductive Organs*: Two pairs of accessory glands; testes comprised of multiple follicles. *Mesodermal Female Reproductive Organs*: Spermathecal capsule faintly sclerotized or highly sclerotized, spermathecal gland attached to subapex or apex of spermathecal capsule; saccular bursal copulatrix well developed, bursal sclerite absent; ovaries comprised of multiple follicles. *Larval Morphology*: Cranium subquadrate, coronal component of epicranial suture present or not; endocarina present; gula short or oblong rectangulate; 1 or 0 stemmata; mesonotum and metanotum with or without pair of plates; spiracles not biforous; basal plate of 9th abdominal tergum absent; urogomphi very small and separated basally.

Natural History. The absence or reduction in the number of stemmata in larvae of *Dermestoides sanguinicollis* (Fabricius), *Neorthopleura thoracica* (Say), *Tenerus signaticollis* Laporte, *T. quadrimaculatus* Corporaal, and *T. femoralis* Corporaal suggest that they inhabit the dark recesses of galleries of lignicolous insects. Adults are known to prey on Buprestidae, Cerambycidae, Curculionidae, and Lymexylonidae. The very coarse ommatidial construction in adults of *Neorthopleura* Barr suggests that they are nocturnal as was reported by Champlain (1920: 639). Coccinellidae-based mimetic associations are very apparent among the species of *Allochotes* Westwood.

Distribution. Members of this subfamily are worldwide in distribution with a distinct prominence in Africa and Asia (Fig. 209).

Inventory of generic taxa. There are 258 described species classified into 22 genera. The genera are as follows: *Agaphalera* Opitz, *Allochotes* Westwood, *Colobotis* Opitz, *Decicornis* Opitz, *Dermestoides* Schaeffer, *Funicula* Opitz, *Kataspinula* Opitz, *Lebasiella* Spinola, *Loedelia* Lucas, *Megafodina* Opitz, *Nelsonoplium* Barr, *Neorthopleura* Barr, *Novemera* Opitz, *Orthopleuroides* Kuwert, *Patuleius* Fairmaire, *Rifkindius* Opitz, *Romanaeclerus* Winkler, *Syriopelta* Winkler, *Tenerastes* Lucas, *Teneromimus* Gahan, *Tenerus* Laporte, and *Tricladus* Fairmaire.

Taxonomic notes. *Neorthopleura* Barr was revised in 1976, and OPITZ (2009B, 2009D) provided a contribution of *Romanaeclerus* Winkler and the first contribution towards a revision of the subfamily, respectively.

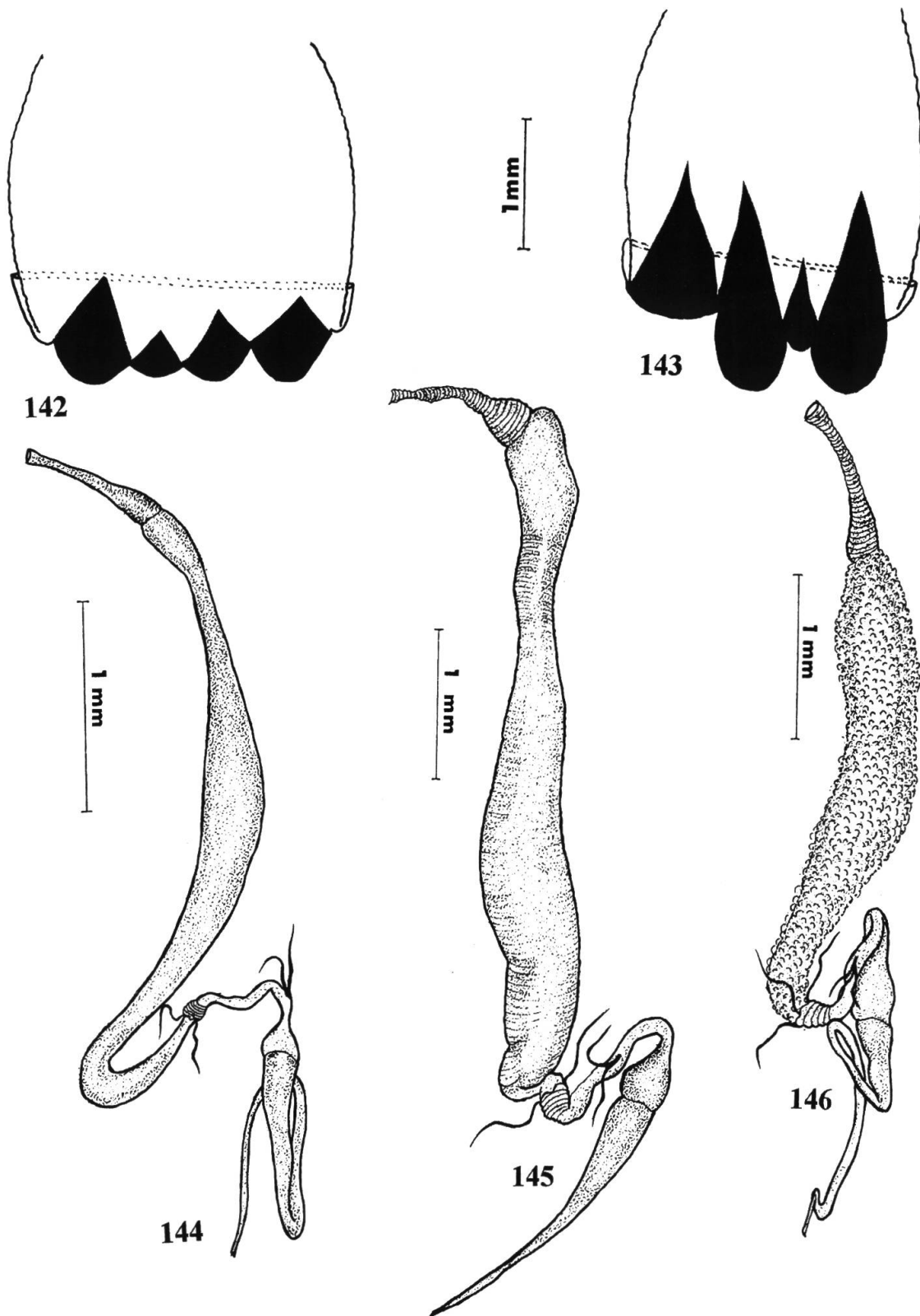
Subfamily Peloniinae Opitz, subfam.nov.

Figures 2, 5, 34, 44, 88, 93, 126, 127, 130, 131, 139, 150, 161, 162, 182, 192, 210.

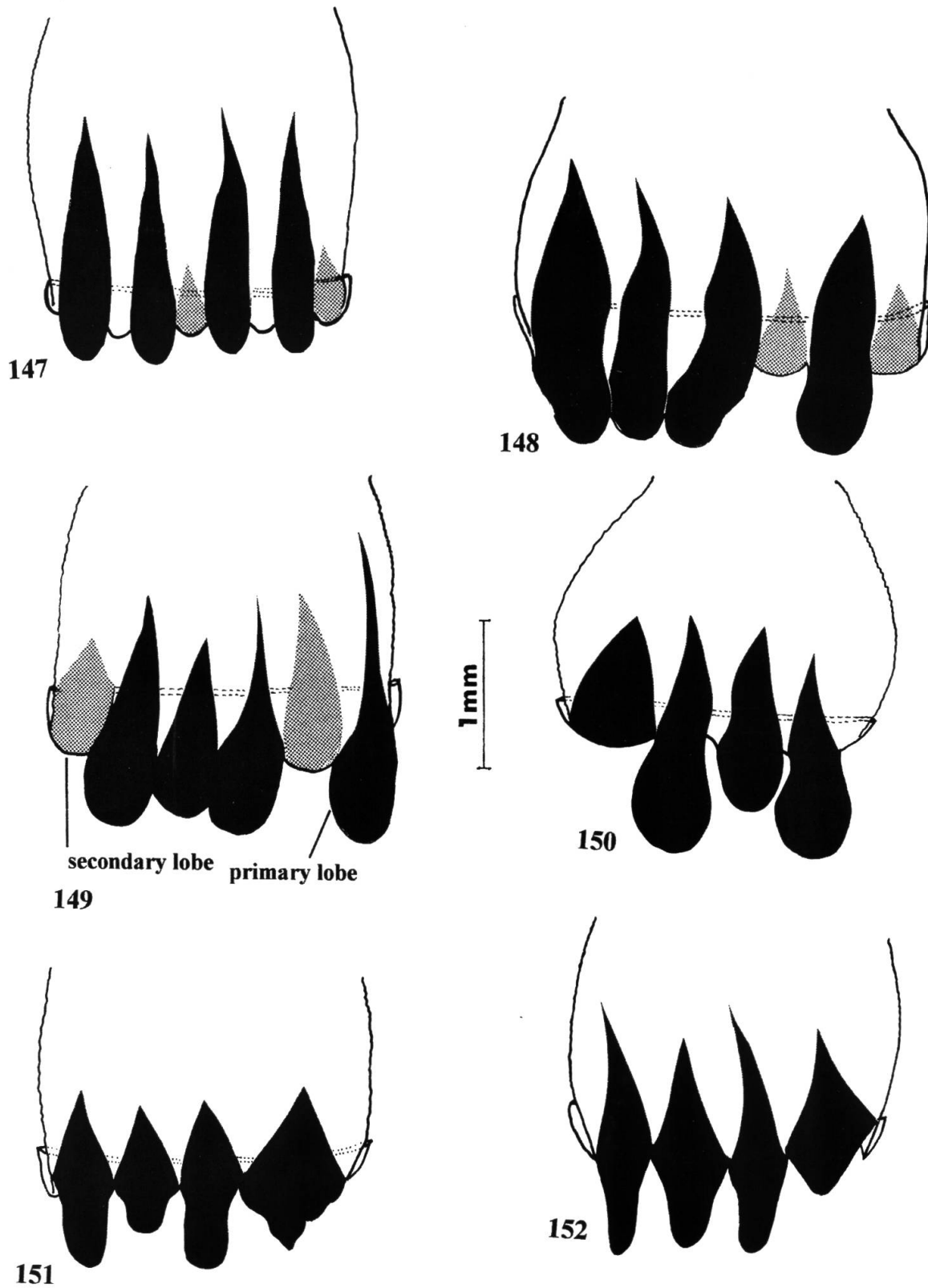
Type genus: *Pelonium* Spinola, 1844A: 347.

Diagnosis. Specimens belong to this subfamily if they show a reduced 4th tarsomere (Fig. 92), lack pronotal trichobothria, have a lengthened, sometimes highly lobate (Fig. 34) antennal capitulum whose combined length is almost always much longer than the combined length of the other antennomeres, and usually have an incomplete pronotal dorsolateral carina. Also, the dorsolateral carina always conjoins the pronotal hem at the posterior angles of the pronotum.

Description. *Shape:* Ranges from short or long rectangulate to suboval. *Size:* Length 2.0–25.0 mm; width 0.6–9.0 mm. *Integumental Color:* Varies from uniformly dark to multicolored; elytra frequently exhibit transverse or linear markings, rarely metallic. *Head:* Transverse, strongly deflexed, usually narrower than pronotum, surface usually finely punctated; epistomal suture incomplete, internal epistomal ridge incomplete; frontal preantennal angle not acute; clypeus bipartite, comprised of pigmented upper region and pigmented lower region; antenna comprised of 10 to 11 antennomeres, capitate, capitulum short or greatly expanded, combined length of funicular antennomeres usually very short, much shorter than combined length of usually highly lobate antennal capitulum, if capitulum short then capitular antennomeres usually triangular, or capitulum often ramous, funicular antennomeres subfiliform to extensively flared; eyes coarsely to subcoarsely faceted, very deeply notched anteriorly; labrum shallowly or deeply incised, transverse tormal processes fused contiguous, sinuous or not; last palpomere of maxillary and labial palpus variously securiform; epipharynx not complex; mandible with well-developed dens, basal notch not very large; gula large, gular processes widely separated, gular sutures strongly converging, then sometimes straight for short distance. *Thorax:* Pronotum transverse, quadrate or elongated, lateral tubercle usually very prominent, rarely absent, anterior transverse depression present or not, dorsolateral carina present but incomplete, carina confluent with pronotal hem at pronotal hind angles, commissure absent; pronotal projections vary in length, pronototergosternal suture complete; prointercoxal process linear or feebly swollen distally; procoxal cavity open externally, procryptosternum incomplete; metendosternite with furcal lamina; elytral form usually elongate rectangular, sometimes suboval, anterior margin with carina, disc with or without asetiferous punctations, elytral 1° and 2° usually present, epipleural fold laterally positioned, gradually narrowing to elytral apex; legs, tarsal formula 5-5-5, cursorial, protibiae rarely scabrous or spinous along anterior margin, tibial spur formula 0-1-1, 0-2-2, 0-2-1, 1-2-2, or 1-2-1, tarsal pulvillar formula 3-3-3; unguis with or without basal denticle; wedge cell of metathoracic wing open or closed. *Abdomen:* Comprised of 6 visible sternites, 6th visible sternite beneath 5th, robust and compact; pygidium quadrate or scutiform; aedeagus not inverted, well sclerotized, tegmen tubular very sclerotized or lightly sclerotized, bilobed distally, tegminal lobes usually fimbriate, phallobasic rod variously developed or absent, phallobasic apodeme well developed, phallic plates variously developed; spicular fork well developed, intraspicular plate linear, spicular apodeme variously fused; ovipositor



Figs 142–146. Morphological organs. 142–143 Internal view of stomadaea (142 *Neorthopleura thoracica*, 143 *Tarsostenus univittatus*). 144–146 Alimentary canals (144 *Tarsostenus univittatus*, 145 *Enoplium serraticorne*, 146 *Necrobia violacea*).



Figs 147–152. Internal view of stomadaea (147 *Cymatodera oblita*, 148 *Trichodes ornatus*, 149 *Phyllobaenus pallipennis*, 150 *Chariessa pilosa*, 151 *Madoniella dislocata*, 152 *Necrobia rufipes*).

not longer than abdomen, with multilobed dorsal and ventral lamina; oblique and ventral bacculi well developed. *Alimentary Canal*: Stomodaeum short, proventricular valve comprised of 4 primary lobes; ventriculus well developed, ventricular crypts poorly developed; 4 cryptonephridial Malpighian tubules; proctodaeum short in males and long in females. *Mesodermal Male Reproductive Organs*: Two pairs of accessory glands; testes multifollicular. *Mesodermal Female Reproductive Organs*: Spermathecal capsule from faintly to highly sclerotized, spermathecal gland attached to subapex of spermathecal capsule; saccular bursal copulatrix well-developed bursal sclerite present; ovaries comprised of multiple follicles. *Larval Morphology*: Cranium comparatively large, subglobose; coronal component of epicranial suture absent; endocarina present; gula long narrow; 5 stemmata present, anterior row of 3 and posterior row of 2; mouthparts poorly sclerotized; mesonotum and metanotum without plates; spiracles small, annuliform; urogomphi recurved.

Natural History. The more stout leg construction of these beetles suggests that they are not particularly rapid hunters of wood infesting beetles. Moreover, the members of various genera have evolved a body shape towards mimetic relationships with aposematic models, have a slow gait, and frequent the surface of broad leaves and vine-like vegetation.

Distribution. This is a pan-world group of checkered beetles with a particular abundance in Middle and South America, Africa, and Asia.

Inventory of generic taxa. There are 234 described species classified into 31 genera. The genera are as follows: *Anthriboclerus* Schenkling, *Anisophyllus* Westwood, *Apolopha* Spinola, *Chariessa* Perty, *Corinthiscus* Fairmaire & Germain, *Cregya* Leconte, *Damiricus* Fairmaire, *Enoplioides* Fairmaire, *Exochonotus* Barr, *Falsoerymanthus* Pic, *Falsoorthopleuroides* Pic, *Falsotricladus* Pic, *Goyasanum* Pic, *Lasioderia* Grey, *Mimenoplioides* Pic, *Mimopallenis* Pic, *Muisca* Spinola, *Neotenerus* Schenkling, *Pallenothriocera* Pic, *Paracregya* Peracchi, *Paratenerus* Chapin, *Pelonium* Spinola, *Phymatophaea* Pascoe, *Pilosirus* Opitz, *Platynoptera* Chevrolat, *Pseudichnea* Schenkling, *Pyticeropsis* Schenkling, *Riotenerus* Pic, *Stenoplium* Fairmaire, *Sulcopatuleius* Pic, and *Theresamora* Pic.

Taxonomic notes. A comprehensive treatment of *Apolopha* Spinola and *Phymatophaea* Pascoe is provided by OPITZ (1998, 2009A), respectively.

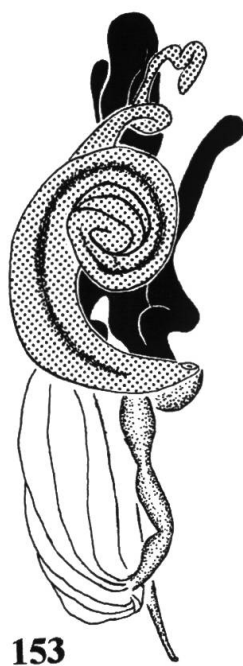
Subfamily Tarsosteninae Jacquelin du Val, 1862: 198

Figures 4, 29, 51, 62, 79, 114, 143, 144, 163, 164, 186, 191, 199.

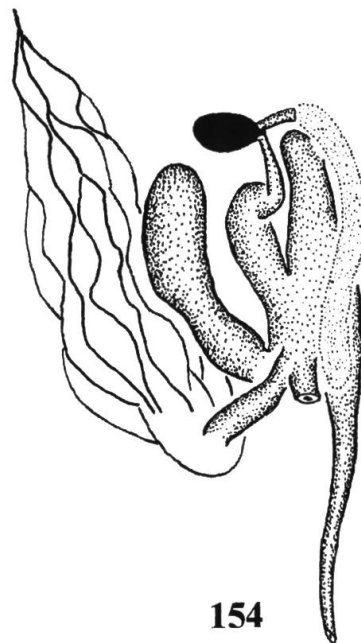
Type genus: *Tarsostenus* Spinola: 1844a: 287.

Diagnosis. Specimens with a reduced 4th tarsomere belong to this subfamily if they do not have a pair of pronotal trichobothria, and have a long capitate antenna in which the funicular antennomeres are filiform and the length of the capitulum is not as long as the combined length of the remainder of the antennomeres (Fig. 29). The incomplete (Fig. 62) dorsolateral pronotal carina is confluent with the pronotal hem at the posterior angles of the pronotum.

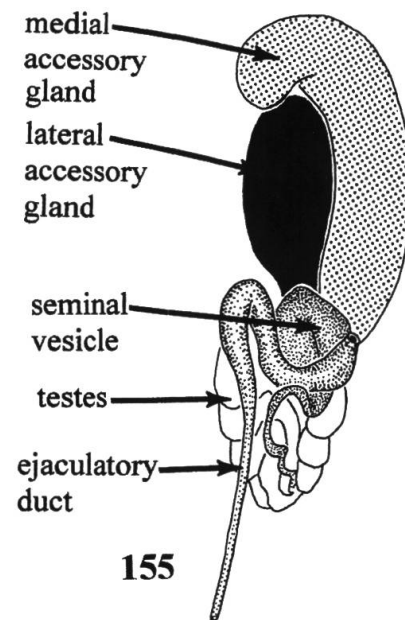
Description. *Shape:* Ranges from narrow rectangulate to short rectangulate. *Size:* Length 2.2–14.0 mm; width 0.6–6.0 mm. *Integumental Color:* Varies from uniformly reddish-brown, to multicolored conditions where the integument is mostly dark brown and the elytral disc shows a paler fascia, in very few cases the integument may be shiny blue or shiny multicolored with red, yellow and brown. *Head:* Transverse, strongly deflexed, usually narrower than pronotum, surface usually finely punctated; epistomal suture faintly indicated; internal epistomal ridge poorly developed; clypeus bipartite, comprised of pigmented upper region and nonpigmented lower region; antenna comprised of 11 antennomeres, capitate, capitulum shorter than length of combined other antennomeres, non-capitular antennomeres filiform; frontal preantennal angle not acute; eyes coarsely to finely faceted, slightly notched anteriorly; labrum shallowly incised, transverse tormal processes fused contiguous; epipharynx not complex; last palpomere of maxillary and labial palpus boldly or slightly securiform; mandible with well-developed dens, basal notch not large; gula large, gular processes widely separated, gular sutures strongly converging. *Thorax:* Pronotum usually transverse-quadrate, or elongated, lateral tubercle absent or strongly developed, anterior transverse depression present or not, dorsolateral carina incomplete or complete, always posteriorly confluent with pronotal hem, pronotal commissure absent; pronotal projections varies in lengths, prointercoxal process linear or expanded distally; pronototergosternal suture complete; procoxal cavity open, procryptosternum incomplete; metendosternite with furcal lamina; elytral form usually elongate rectangulate or short rectangulate, anterior margin with carina, disc with asetiferous punctations, 1° and 2° usually present, epipleural fold laterally positioned, gradually narrowing to elytral apex; legs, tarsal formula 5-5-5, cursorial, tibial spur formula 2-2-2, 2-2-1, 1-2-2, 1-2-1, or 0-2-2, tarsal pulvillar formula 3-3-3; unguis with or without denticle; wedge cell of metathoracic wing present or not, when present closed or open. *Abdomen:* Comprised of 6 visible sternites, 6th visible sternite usually beneath 5th, robust and compact; pygidium quadrate or scutiform; aedeagus sometimes inverted, well sclerotized, tegmen tubular very sclerotized or lightly sclerotized, bilobed distally, tegminal lobes usually fimbriate, phallobasic rod variously developed, phallobasic apodeme well developed, phallic plates variously developed; spicular fork well developed, intraspicular plate linear, spicular apodeme variously fused; ovipositor not longer than abdomen, with multilobed dorsal and ventral lamina; oblique and ventral bacculi well developed. *Alimentary Canal:* Stomodaeum short, proventricular valve comprised of 4 primary lobes; ventriculus well developed, ventricular crypts poorly developed; 4 cryptonephridial Malpighian tubules; proctodaeum short in males and long in females. *Mesodermal Male Reproductive Organs:* Typically with two pairs of accessory glands, rarely with one pair of glands; testes comprised of multiple follicles. *Mesodermal Female Reproductive Organs:* Spermathecal capsule from faintly to highly sclerotized, spermathecal gland attached to apex or subapex of spermathecal capsule; saccular bursal copulatrix well-developed bursal sclerite present or not; ovaries comprised of multiple follicles. *Larval Morphology:* Cranium subtriangular, coronal component of epicranial suture absent; endocarina present; gula narrow and elongate; 4 stemmata present, anterior row of 2 and somewhat obliquely positioned posterior row of 2; mesonotum and metanotum without



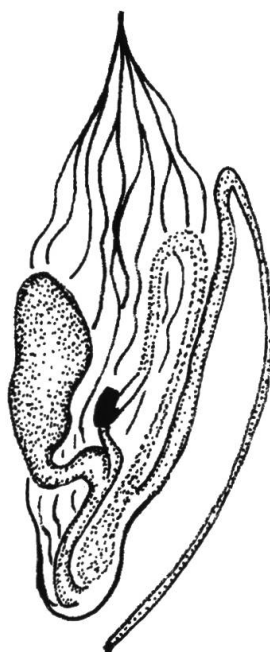
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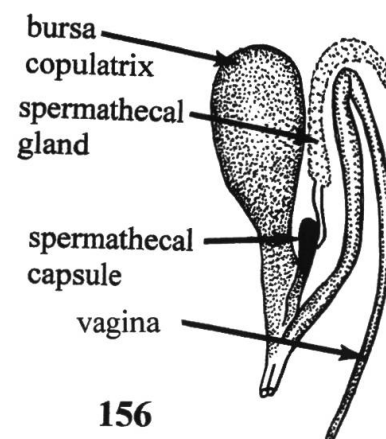
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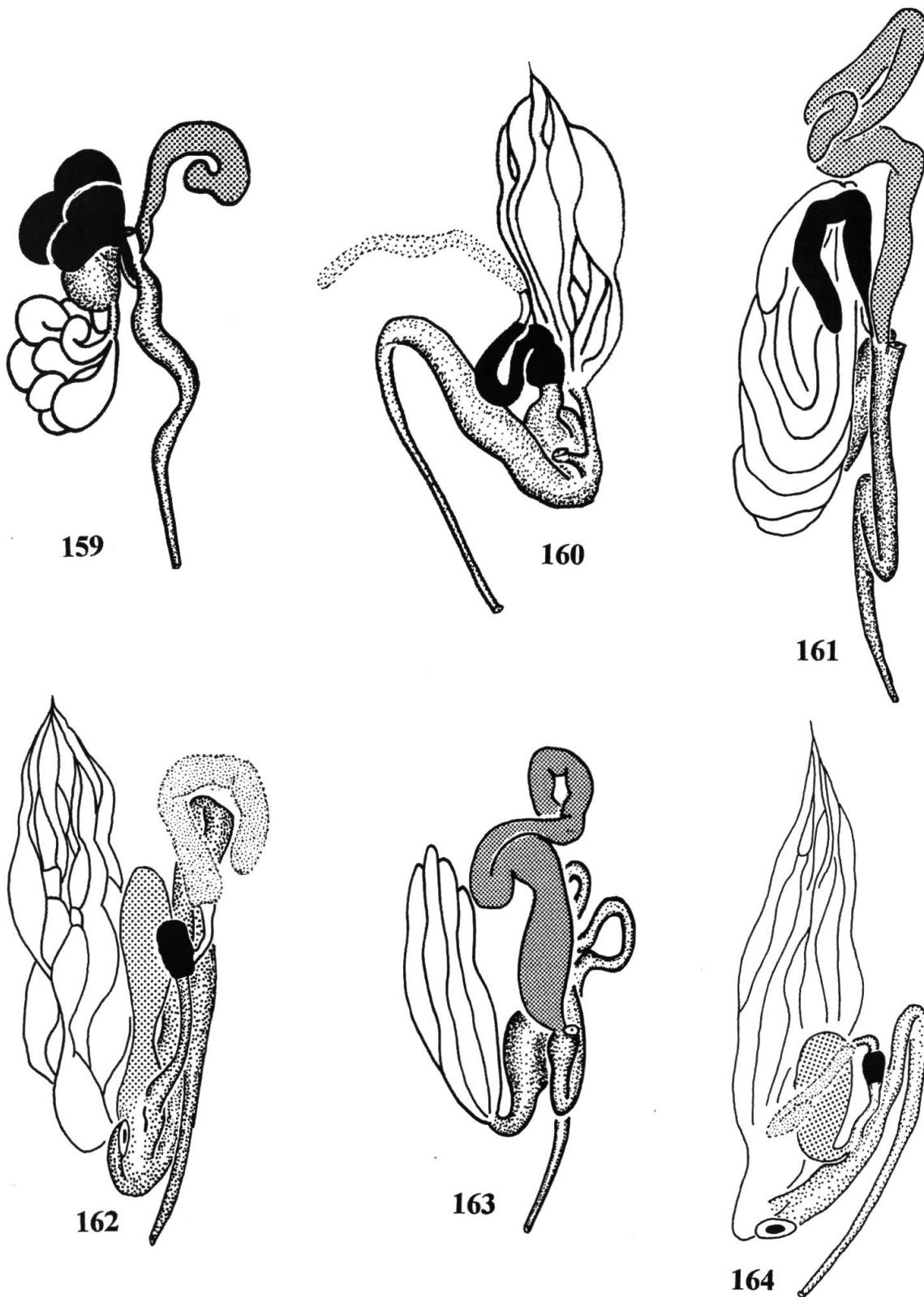


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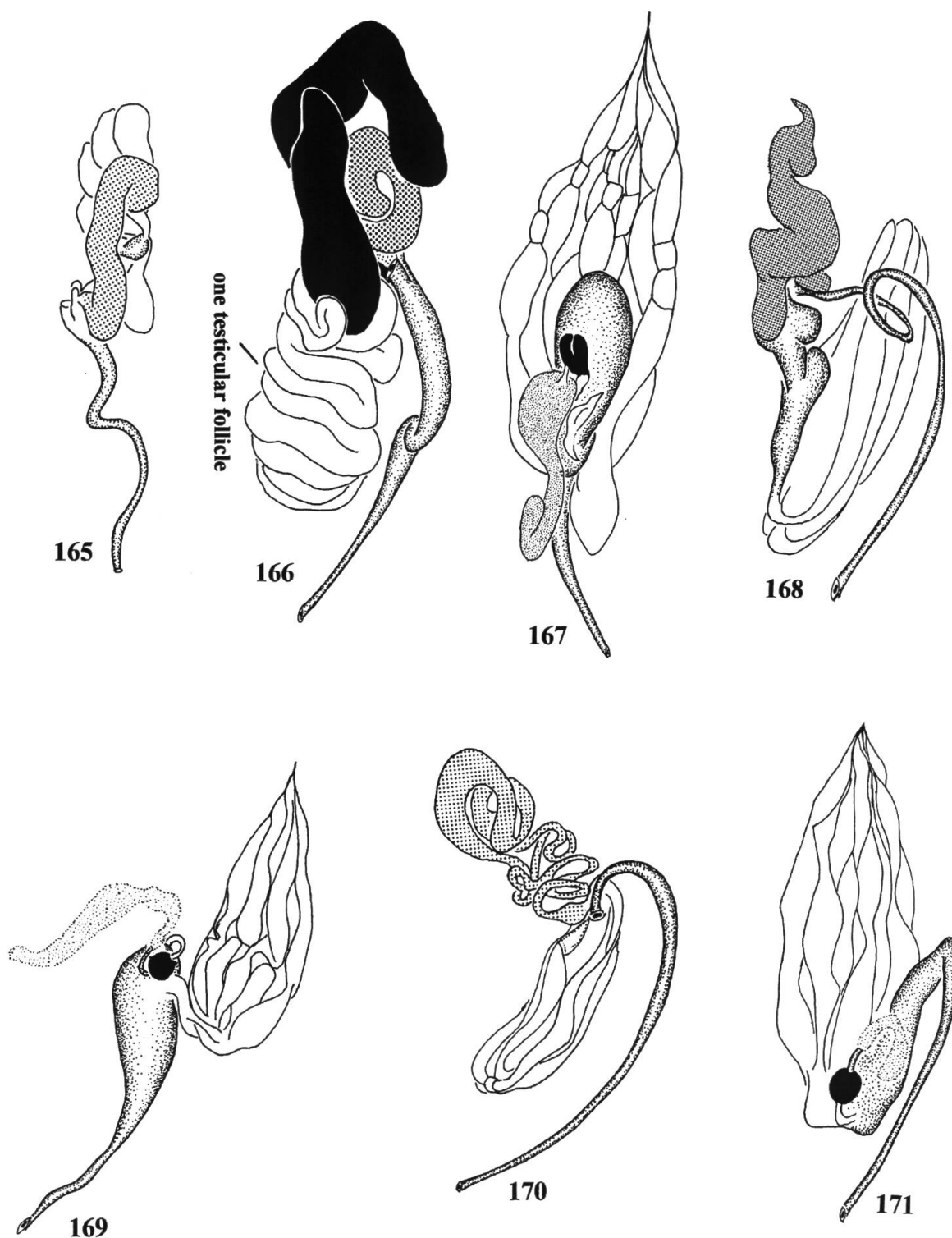


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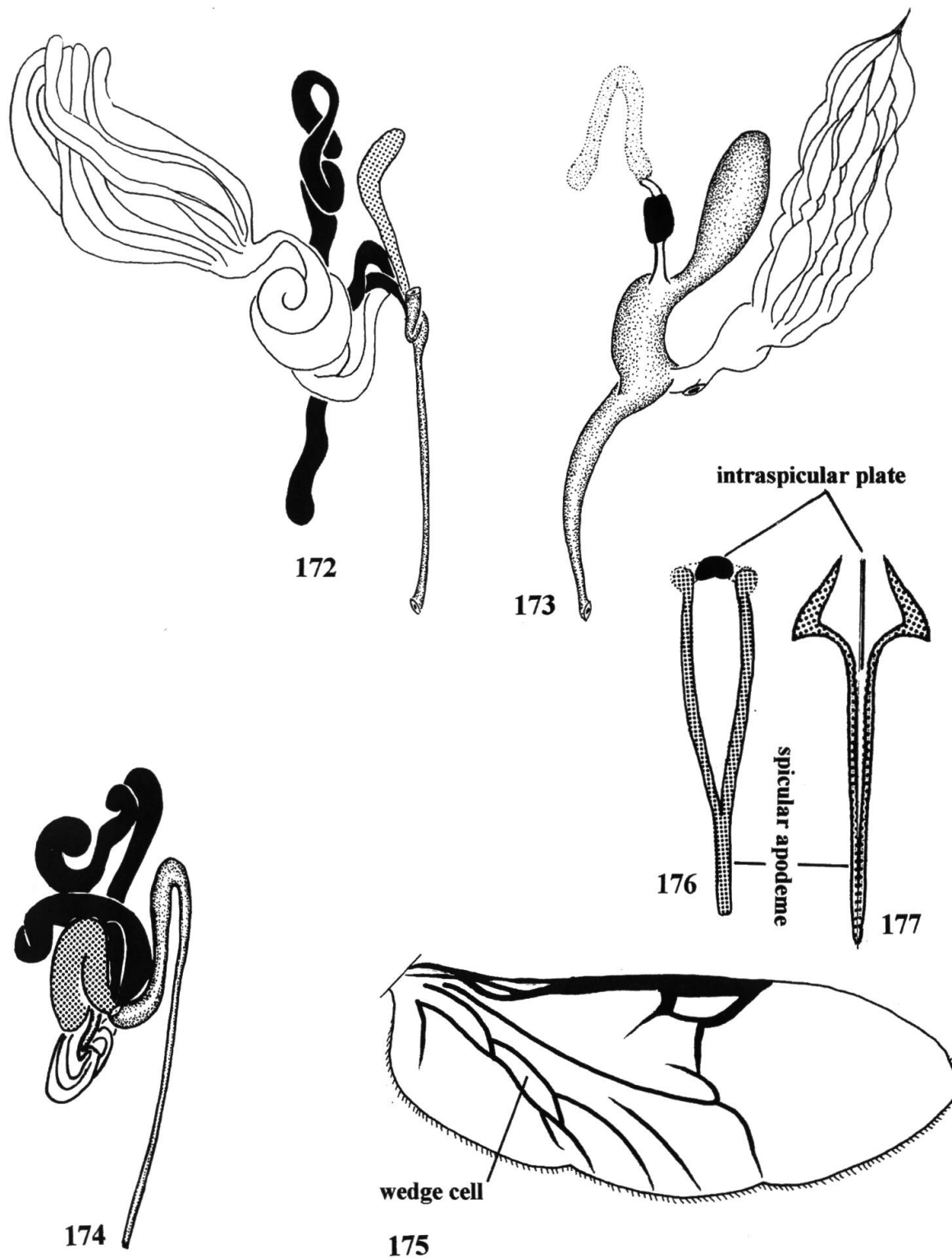
Figs 153–158. Internal mesodermal reproductive organs. 153–154 *Perilypus revantazon* (153 male, 154 female), 155–156 *Epiphloeus duodecimmaculatus* (155 male, 156 female). 157–158 *Neorthoppleura thoracica* (157 female, 158 male).



Figs 159–164. Internal mesodermal reproductive organs. 159–160 *Thaneroclerus buquet* (159 male, 160 female), 161–162 *Pelonium scoparium* (161 male, 162 female). 163–164 *Tarsostenus univittatus* (163 male, 164 female).



Figs 165–171. Internal mesodermal reproductive organs. 165 *Chaetosoma colossus* (male). 166–167 *Tilloidea transversalis* (166 male, 167 female), 168–169 *Phyllobaenus humeralis* (168 male, 169 female). 170–171 *Isohydnocera curtippennis* (170 male, 171 female).



Figs 172–177. Morphological organs. 172–174 Mesodermal reproductive organs. 172–173 *Necrobia rufipes* (172 male, 173 female). 174 *Lebasiella erythrodera*, male. 175 Metathoracic wing of *Perilypus revantazon*. 176–177 Spicular forks (176 *Perilypus revantazon*, 177 *Opitzia chiapas*).

sclerotizations; spiracles small, biforous; basal plate of 9th abdominal tergum well developed, urogomphi well developed and uncinat.

Natural History. The little information that is available about the natural history of this subfamily revolves mostly around what is known about *Tarsostenus univittatus* (Rossi). This little cosmopolitan checkered beetle is most often associated with predatory activity on the bostrichid genera *Lyctus* Fabricius and *Sinoxylon* Duftschmid, with the former causing considerable damage to commercially transported manufactured hardwoods. An excellent account of the life cycle of *T. univittatus* (Rossi) is provided by St. GEORGE (1924: 49).

Distribution. This is a pan-tropical group of checkered beetles, with particular abundance in Africa, Madagascar, and Australia (Fig. 199).

Inventory of generic taxa. There are 69 described species classified into 14 genera. The genera are as follows: *Abiliella* Peracchi, *Apopylus* Kolibáč, *Apteropilo* Lea, *Blackburniella* Chapin, *Curacavi* Solervicens, *Liostylus* Fairmaire, *Neopylus* Solervicens, *Parapylus* Blackburn, *Pylus* Newman, *Rhopaloclerus* Fairmaire, *Tarsostenodes* Blackburn, *Tarsostenus* Spinola, *Thriocera* Gorham, *Thriocerodes* Wolcott et Dybas.

Taxonomic notes. KOLIBÁČ (2003: 52) placed *Parapylus* Blackburn in synonymy with *Pylus* Newman. I cannot agree with this synonymy in view of their significant differences in tibial spur formula; in *Pylus* Newman it is 2-2-1, whereas in *Parapylus* Blackburn it is 2-2-2. BARTLETT (2009) provides a comprehensive treatment of *Apteropilo* Lea.

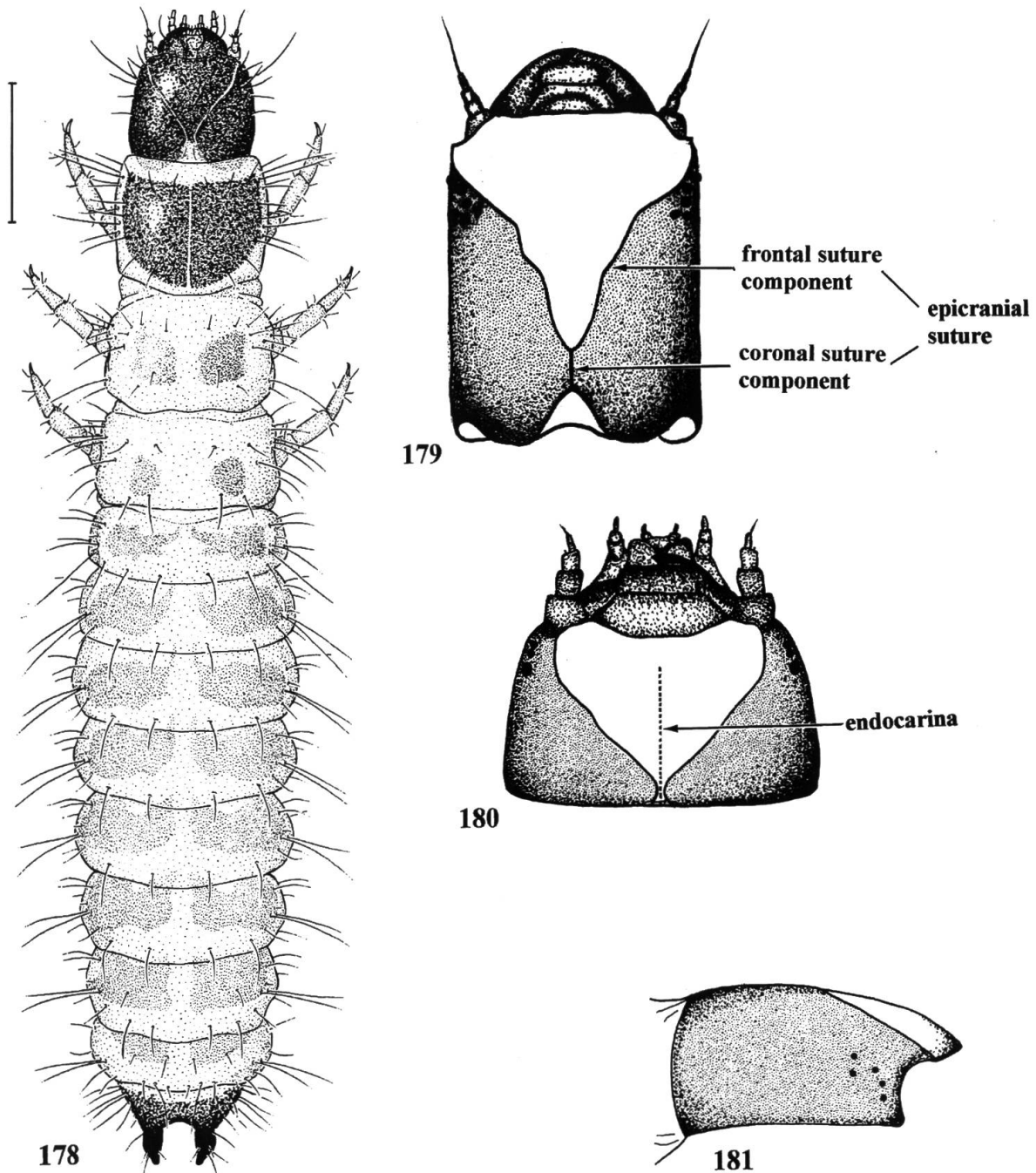
Subfamily Thaneroclerinae Chapin, 1924: 165

Figures 12, 19, 23, 24, 47, 54, 67, 83, 108, 118, 136, 159, 160, 179, 195, 200.

Type genus: *Thaneroclerus* Lefebvre, 1838: 13.

Diagnosis. Checkered beetles belong to this subfamily if they lack pulvilli, have a 5-5-5 tarsomeral formula and have the first four protarsomeres greatly widened and compacted so that when viewed from below one sees a circular or oval setal mat (Fig. 24). Also, there is a setose prebasal carina on the pronotum (Fig. 67).

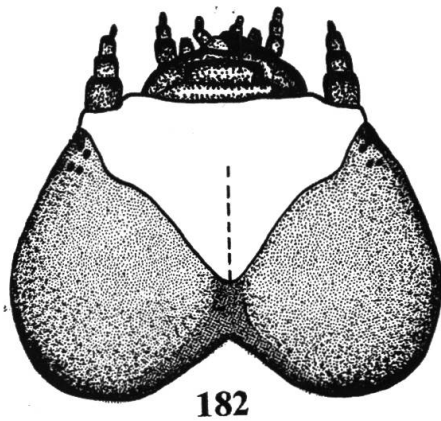
Description. *Shape:* Oblong-short and stout, pronotum campaniform and elytra squarely short-rectangulate; some genera with cylindric constriction between forebody and hindbody. *Size:* Length 3.0–7.0 mm; width 1.1–2.3 mm. *Integumental Color:* Predominantly reddish-brown, some with dark markings, a few predominantly black. *Head:* Elongate-rectangulate, epistomal sutures very abbreviated externally and notable only at sides, internal epistomal ridge limited to short lateral extensions, frontal preantennal angle acute; eyes small, coarsely faceted, ocular notch minute; gular narrow-triangular, sutures converging in basal half then parallel, rarely gula narrow rectangulate with sutures entirely parallel, postgular plate narrow transverse, postgular process incipient; antenna comprised of 11 antennomeres, but sometimes last two antennomeres conjoined giving antenna a superficially 10 component impression, clavate to distinctly



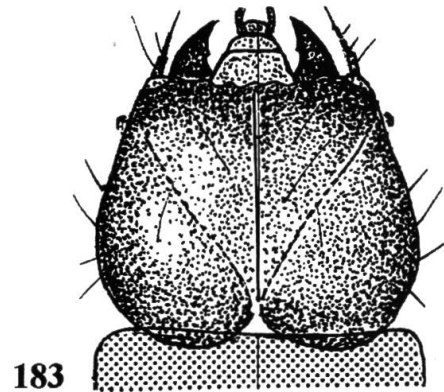
Figs 178–181. Larval habitus and heads. 178 Larvae of *Perilypus limbatus*. 179–181 Larval heads (179 *Thaneroclerus buquet*, 180 *Lecontella brunnea*, 181 *Ababa tantilla*).

capitate, scape short capitate, other precapitular antennomeres from submoniliform to subfiliform, mandible stout, dens and penicillus well developed, basal notch very large, labral incision from distinct to faint, transverse tormal processes linear, contiguous, and faintly developed, tormal connecting rod sinuous and well developed, maxilla with well-developed laterolacinia, terminal palpomere digitiform, labium well developed, terminal palpomere from broadly lobate to distinctly securiform. *Thorax*: Pronotum greatly constricted posteriorly, dorsolateral ridge fragmented, with basal setose carina, prointercoxal process usually very expanded distally, rarely not expanded, pronotal projection long, usually contiguous with prointercoxal process; pronototergosternal suture complete; prosternum usually very expanded anteriorly; procoxal cavities spheroid, cavities usually closed externally, rarely slightly to widely open, procryptosternum incomplete; mesosternum cylindrically projected; elytral disc profusely vested with 2° setae, primary setae and asetiferous punctations absent, epipleural fold well developed and positioned laterally, anterior ridge absent; legs, tarsal formula 5-5-5, first 4 protarsomeres greatly expanded and densely setose ventrally, 5th tarsomere extraordinarily lengthened, unguis without basal denticle, mesotarsomeres and metatarsomeres not expanded, femora swollen, tibiae about as long as length of femora, slightly curved and without carina, tibial spur formula 2-2-2, 0-2-2, or 0-0-0; tarsal pulvilli absent metathoracic wing venation greatly reduced; metendosternite with well-developed furcal lamina. *Abdomen*: Comprised of 6 visible sternites, 6th sternite often slid under 5th, pygidium scutiform, 6th visible sternite not incised distally; spicular fork well developed, plates slender, apodeme fused entirely, intraspicular plate absent; aedeagus poorly sclerotized, phallobasic apodeme absent, phallobase slightly lobed, lobes fimbriate, phallobasic dorsum lightly sclerotized, phallobasic venter semimembraneous; ovipositor about as long as length of abdomen, with multilobed dorsal and ventral lamina, oblique and ventral bacculi well developed, spiculum ventrale extraordinarily long. *Alimentary Canal*: Stomodaeum extraordinarily long, about as long as ventriculus; stomodaeal valve not distinguishable externally from remainder of stomodaeum; ventriculus not papillose, 4 Malpighian tubules; proventriculus with 4 primary and 4 secondary folds. *Mesodermal Male Reproductive Organs*: Two pairs of accessory glands. *Mesodermal female Reproductive Organs*: Spermathecal capsule faintly sclerotized. *Larval Morphology*: Cranium oblong-rectangulate, coronal component of epicranial suture present; endocarina absent; gula with posteriorly expanded gular sutures and postmedial tubercle; 5 stemmata present, anterior row of 3 and posterior row of 2; mesonotum and metanotum with pair of plates; spiracles small, biforous; basal plate of 9th abdominal tergum present or not, urogomphi usually absent, when present very small.

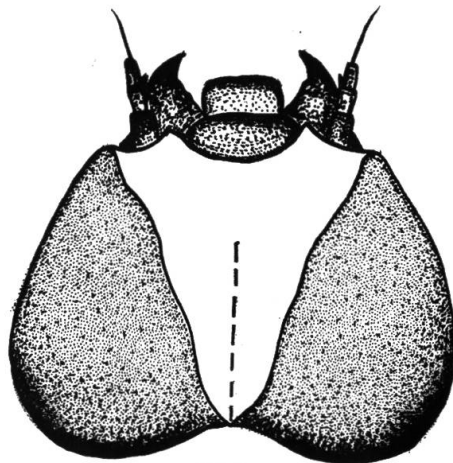
Natural History. The thaneroclerines, as most other checkered beetles, are diurnal voracious predators of other insects. *Thaneroclerus* Lefebvre species, especially *T. buquet* Lefebvre, which is the most widely known species of the subfamily, has been associated with a variety of predatory activities on insects that infest stored products such as spices, grains, teas, tobacco, and medicinal drugs. Most unusual, perhaps, is the association that has been made between thaneroclerines and the presumed ptinine prey



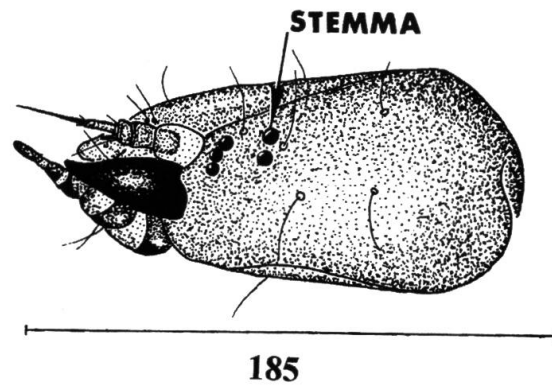
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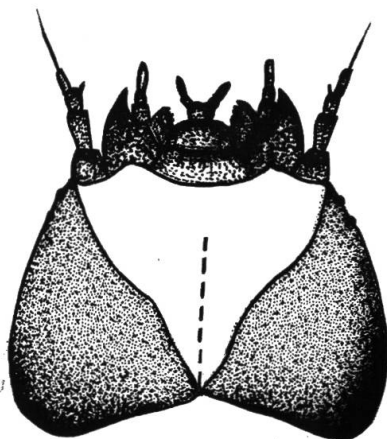
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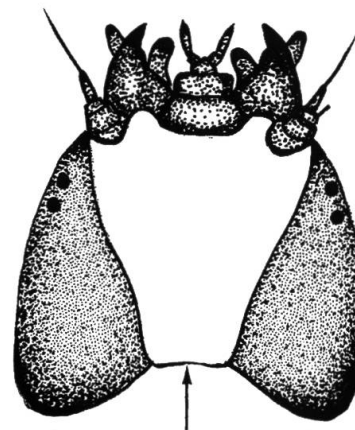
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truncated posterior
limit of frons

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Figs 182–187. Larval heads. 182 *Platynoptera pectoralis*, 183 *Pyticeroides laticornis*. 184 *Neorthopleura thoracica*. 185 *Perilypus limbatus*. 186 *Tarsostennus univittatus*. 187 *Phyllobaenus verticallis*.

in nests of termites. Most other members of the subfamily are more xylophilous. For example, *Zenodosus* Wolcott, which overwinter as adults, is most commonly collected under tree bark of oak and dying spruce infested with bark beetles. Species of *Ababa* Casey, *Allothaneroclerus* Corporaal, and *Neoclerus* Lewis have been extracted from conks of tree fungi, where they presumably prey on small mycetophagous insects. Chapin (1924: 254) comments on the resemblance of *Cyrtinoclerus cyrtinoides* Chapin to a species of Cerambycidae, perhaps a manifestation of mimicry.

Distribution. Although distributed in the New World, thaneroclerines are most commonly known from the paleotropics (Fig. 200).

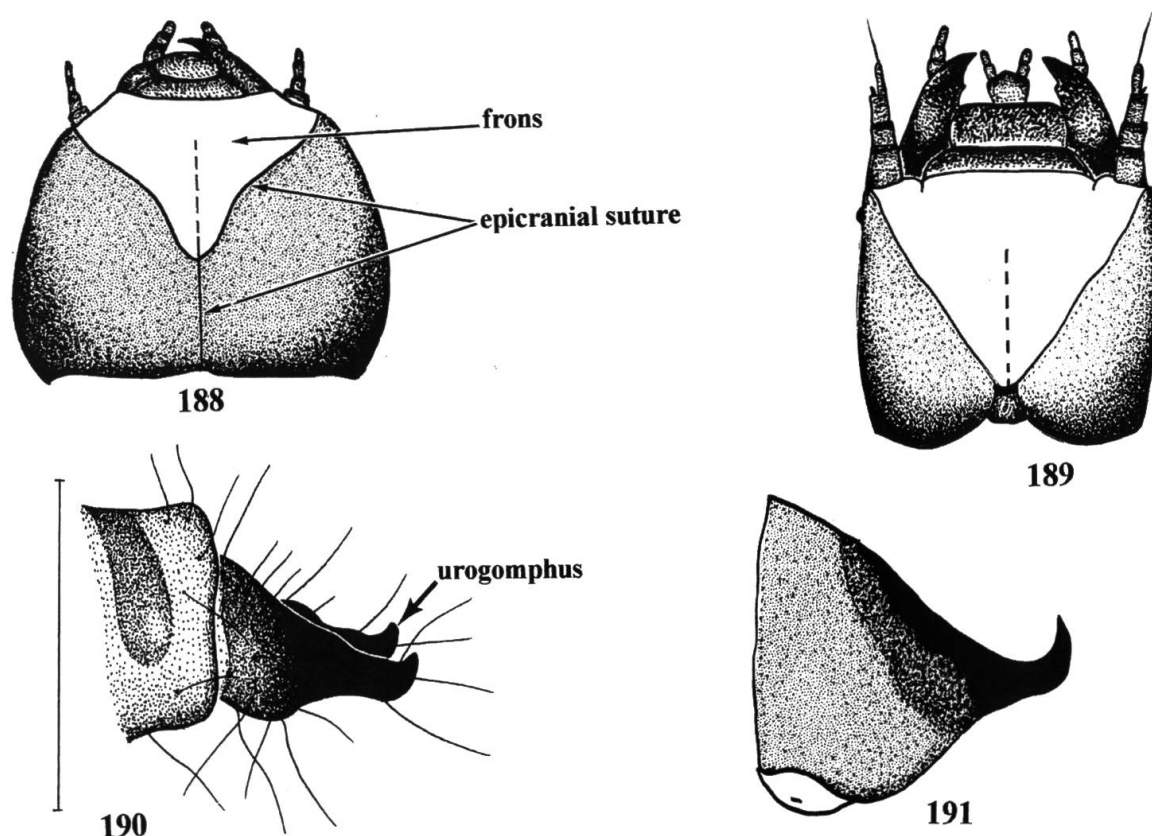
Inventory of generic taxa. Thirteen species are classified into the following 5 genera: *Cleridopsis* Champion, *Neoclerus* Lewis, *Thaneroclerus* Lefebvre, *Viticlerus* Miyatake, and *Zenodosus* Wolcott

Taxonomic notes. The subfamily taxa were studied by CORPORAAL (1939) and KOLIBÁČ (1992).

The presence of a well-developed laterolacinia, postgular plate, and incipient postgular processes in all Thaneroclerinae, new status, and Isoclerinae Kolibáč genera and in the other Cleridae subfamilies, does not support the removal of Thaneroclerinae Chapin (*sensu* CORPORAAL 1950A) from the Cleridae as advocated by KOLIBÁČ (1992: 303). The synapotypic character states laterolacinia and postgular plate with incipient gular processes unite the Cleridae, as envisioned by CORPORAAL (1950A: 92) and CROWSON (1964: 305), into a monophyletic family taxon.

There is no doubt that the Thaneroclerinae Chapin and the Isoclerinae Kolibáč form the most primitive elements of the Cleridae, and that there are very significant morphological differences between the thaneroclerines and isoclerines and other clerid taxa, however, the magnitude of morphological gap expressed by the characteristics used in the decision to separate out the thaneroclerines as a separate family may be easily matched among other taxa within Cleridae. For example, the evolutionary leap from a broadened highly chitinized, protarsal venter, as in all thaneroclerines and isoclerines (Fig. 24), to the equally broadened more membranous pulvillar state, is certainly no more dramatic than the reductionistic morphological leap from a well-formed pulvillus, as found in the majority of Cleridae (Fig. 25), to the slender, filiform tarsomere, minutely pulvillar, condition as found in the Australian genus *Odontophlogistus* Elston (Figs 26, 27).

Indeed, part of the magnificence of the Cleridae is their tremendous morphological diversity, no doubt evolved to refine predation potentialities in the vast variety of nature's niches. The use of larval differences to separate out thaneroclerines from Cleridae is also unjustified. Unfortunately, we are in infancy in our discoveries about the larval semaphoront in the Cleridae and Cleroidea.



Figs 188–191. Larval heads and urogomphi. 188–189 Heads (188 *Tenerus quadrimaculatus*, 189 *Necrobia rufipes*). 190–191 Urogomphi (190 *Perilypus limbatus*, 191 *Tarsostennus univittatus*).

Subfamily Tillinae Leach, 1815: 87

Figures 36, 37, 38, 40, 41, 52, 64, 94, 96, 97, 109, 128, 129,
137, 147, 166, 167, 180, 197, 201.

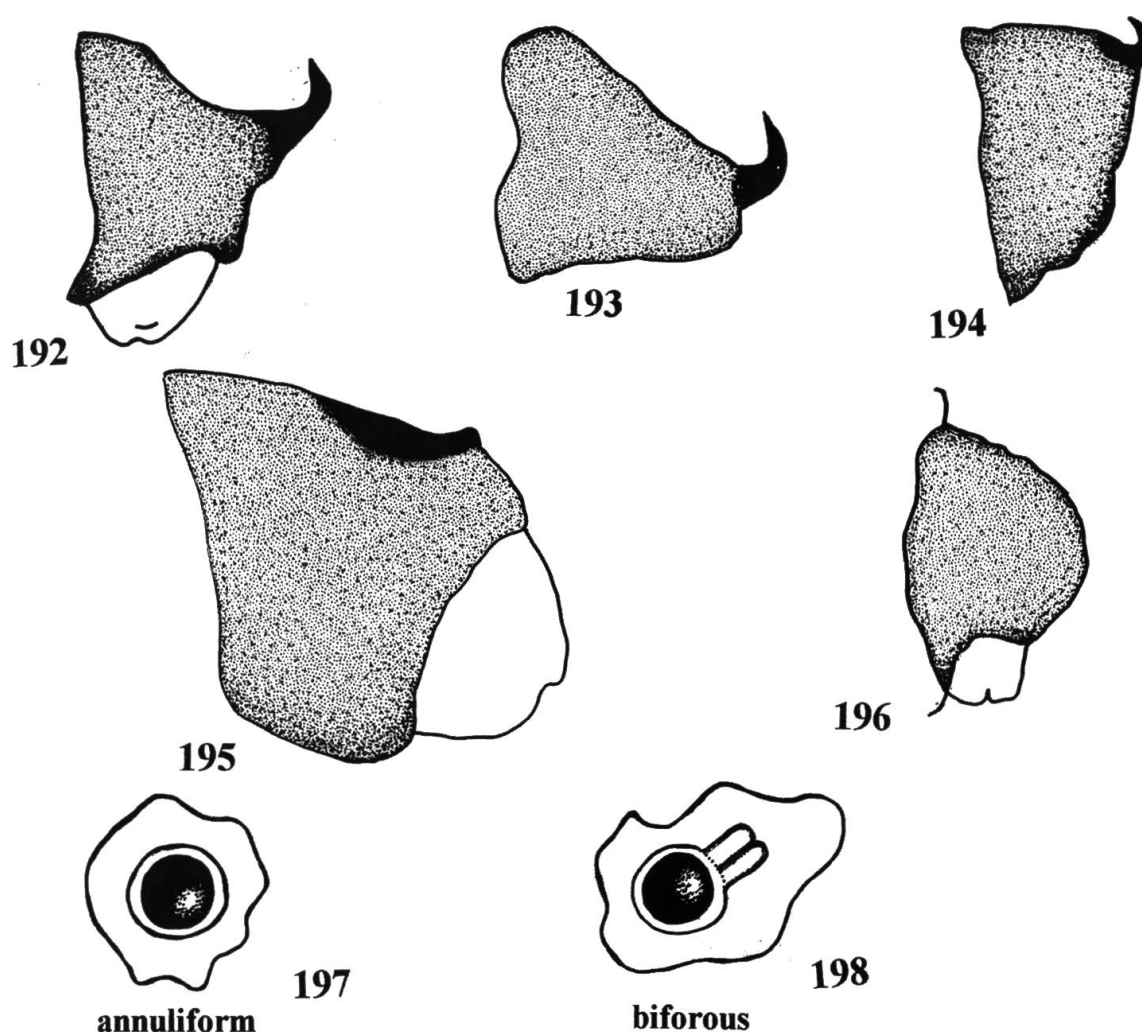
Type genus: *Tillus* Olivier, 1790: Description 22.

Diagnosis. Tilline specimens are most reliably distinguished from those of other Cleridae by the posterior fusion of the procryptosternum with the pronotal extension; that is, the procryptosternum is complete (Fig. 64). This renders the procoxal cavities closed internally and externally, in and around the procoxal cavities. Also, the tarsal unguis is often tripartite or bipartite; when bipartite the basal denticle is elongated and truncate or acuminate. Lastly, in most genera examined there is a carina in the metacoxal abdominal depression (Figs 96, 97).

Description. *Shape:* Oblong-short or long, narrow or robust, pronotum oblong and usually long campaniform, but sometimes constricted behind frontal margin and in front of posterior margin giving side margins a highly sinuous character. *Size:* Length 3.0–25.0 mm; width 1.–9.0 mm. *Integumental Color:* Dorsal fascies predominantly hues of brown, but pronotum and elytra sometimes red and yellow, elytral disc sometimes

with colorful fascia, rarely shiny black or metallic blue. *Head*: Mostly hypognathous, rarely prognathous or long-rectangulate, usually very large; postgenae usually highly expanded; epistomal sutures well defined; clypeus well defined, eyes small, usually coarsely faceted, ocular notch small; gula broad-trapezoidal, almost always extended posteriorly, sutures parallel or slightly converging, postgular processes prominent; antenna comprised of 11 antennomeres, usually filiform or serrate, rarely flabellate of capitate; mandible stout, dens and penicillus well developed, anterior dens often acuminate, basal notch not very large; labral incision distinct or not, transverse tormal processes usually highly sinuous, contiguous or not; maxilla usually with well-developed laterolacinia, very rarely laterolacinia absent, terminal palpomere digitiform; labium well developed, terminal palpomere from broadly securiform. *Thorax*: Pronotum from long campaniform to distinctly biconstricted, dorsolateral ridge absent; tergosternal suture complete, prosternum usually very expanded anteriorly, prointercoxal process very expanded distally, always confluent with procryptosternum; coxal cavities spheroid, closed externally and internally; mesosternum cylindrically projected; elytral disc almost always with asetiferous punctations; 1° setae usually not contiguous with asetiferous punctations, usually profusely vested with 2° setae; epipleural fold well developed and positioned laterally, anterior ridge usually present; legs, tarsal formula 5-5-5, tarsal pulvilli well-developed; unguis usually tripartite or bipartite, or trifid; femora not much wider than tibiae; tibiae about as long as length of femora, without carina, tibial spur formula 2-2-2, 0-2-2, 2-1-1, or 0-0-0; tarsal pulvillar formula 4-4-4, 4-4-3, 4-3-3, or 4-2-1; metathoracic wing venation well developed, wedge cell closed or open; metendosternite with well-developed furcal lamina, with furcal spike, or furcal arm without spike, rarely without spike or furcal lamina. *Abdomen*: Comprised of 6 visible sternites, 6th sternite often slid under 5th, 1st visible abdominal sternite expanded and strongly ridged, ridge often with perpendicular carina (fig. 97); 6th visible sternite incised distally or not; spicular fork well developed, plates slender, apodeme usually widely separated, rarely fused, intraspicular plate expanded anteromedially; aedeagus not inverted, strongly sclerotized, phallobasic apodemes well developed, phallobase subacuminate, usually not lobed, lobes not fimbriate, phallobasic dorsum and venter well sclerotized; ovipositor about as long as length of abdomen, with multilobed dorsal and ventral lamina; oblique and ventral bacculi well developed, spiculum not extraordinarily long, ovipositor rarely biuncinate distally. *Alimentary Canal*: Stomodaeum short or long; proventriculus readily distinguishable externally from remainder of stomodaeum; stomodaeal valve comprised of 4 primary and 4 secondary folds; ventriculus very papillose, 6 Malpighian tubules. *Mesodermal Male Reproductive Organs*: Two pairs of accessory glands. *Mesodermal Female Reproductive Organs*: Spermathecal capsule faintly sclerotized. *Larval Morphology*: Cranium short or elongated, coronal component of epicranial suture absent; endocarina present; gula narrow; 1 or 3 stemmata present, when more than one, one located in front of other two; mesonotum and metanotum with or without pair of plates; spiracles small, biforous or not; urogomphi present, associated or not associated with basal plate.

Natural History. A review of the available information about tilline natural history reveals that they have a genre of predator/prey characteristic attributable to Cleridae in



Figs 192–198. Urogomphi and abdominal spiracles. 192–196 Urogomphi (192 *Platynoptera pectoralis*, 193 *Madoniella dislocata*, 194 *Neorthopleura thoracica*, 195 *Thaneroclerus buquet*, 196 *Pyticeroidea laticornis*-urogomphi absent). 197–198 Abdominal spiracles (197 *Cymatodera morosa*, 198 *Enoclerus ichneumoneus*).

general. As we might expect, across the Tillinae taxon, the predatory activity involves the expected lignicolous prey associated with whatever woody botanical element is available in the distributional range of the prey species. For example, in the Palearctic, *Cylindroctonus chalybaeus* (Westwood) is associated with the Southeast Asian *Dipterocarpus turbinatus* Gaertner infested with the oriental wood borer *Heterobostrychus aequalis* (Waterhouse) (BEESON 1926: 221). In India, *Tillus succintus* Spinola can be reared from the bamboo *Dendrocalamus strictus* (Roxburgh) Nees infested with bostrichids (GARDNER 1937: 34). In North America, *Cymatodera bicolor* Say feeds on the cerambycid *Chryptophorus verrucosus* (Olivier) imbedded in the Floridian dogwood *Cornus florida* Linnaeus.

Unusual checkered beetle prey of North American tillines involve predatory activity of *Cymatodera ovipennis* Leconte on the lepidopterous naval orangeworm *Amyelois transitella* in walnut (*Juglans regia* Linnaeus) (Michelbacher and Davis, 1961) and *C. undulata* (Say) in the gall of the cynipid *Disholcaspis mamma* (Cresson) (Balduf, 1935: 108). An extensive review of the predatory activity and ecology of *Lecontella* Wolcott was done by MAWDSLEY (2002B: 164).

A general morphological observation with possible life habit implications is that several tilline genera (e.g., *Cymatodera* Gray) have coarsely faceted eyes and are reported to be nocturnal. There are many genera in the Cleridae whose species have coarsely faceted eyes; and all are presumed nocturnal predators.

A most interesting article related to the behavior/ecology of a member of Tillinae was recently published by RIFKIND (2006: 258). Rifkind reports that *Cymatodera* Gray stridulates and that their stridulation is a manifestation of selection towards auditory Batesian mimicry with nocturnal mutillids, whose body approximates the cymatoderan fascies and who serve as the behavioral aposematic model. RIFKIND (*loco citato*) indicates that the stridulation sound is correlated with observed femoral vibrations, which he tentatively associates with a transverse carina on the posterior edge of the metacoxal cavity.

RIFKIND'S (*loco citato*) observations may have wide implications relevant to evolutionary relationships among many tilline genera. I have found a short perpendicular carina that extends from the abovementioned transverse metacoxal cavity. This shorter carina is boldly to feebly-developed in the large majority of Tillinae genera (Figs 96, 97) examined. I believe that the perpendicular metacoxal carina strengthens the transverse carina of the metacoxal cavity needed for the cuticle to cuticle rub. In this scenario, the metathoracic cavity ridge would serve as the pars stridens. The transverse metacoxal ridge exhibits a chitinous knob at the exact place where the metacoxal integument is more thickly sclerotized and where an internal ridge is present to strengthen the metacoxal place in question. I surmise that it is this spot on the metacoxae that forms the plectrum in the stridulatory mechanism.

Distribution. Although worldly distributed, concentrations of tillines are now found in the North American temperate zones and in the epiequatorial Neotropics (Fig. 201). However, they are most abundant in all latitudes of the Paleotropics, especially in Africa where historically stable terrain (DARLINGTON 1957: 589) undoubtedly contributed the forbearers of the large number of genera and species of Madagascar.

Inventory of generic taxa. There are 543 described species classified in 67 genera as follows: *Antenius* Fairmaire, *Arachnoclerus* Fairmaire, *Aradamicula* Sedlacek et Winkler, *Araeodontia* Barr, *Archalius* Fairmaire, *Aroterus* Schenkling, *Barrotillus* Rifkind, *Biflabellotillus* Pic, *Bogcia* Barr, *Bostrichoclerus* VanDyke, *Callotillus* Wolcott, *Ceratocopus* Hintz, *Cladiscopallenis* Pic, *Cladiscus* Chevrolat, *Cladomorpha* Pic, *Cteniopachys* Fairmaire, *Cylidroctenus* Kraatz, *Cylidrus* Latreille, *Cymatodera* Gray, *Cymatoderella* Barr, *Dedana* Fairmaire, *Denops* Fischer von Waldheim, *Diplocladus* Fairmaire, *Diplophorus* Heller, *Eburneocladiscus* Pic, *Egenocladiscus* Corporaal and van der Weil, *Elasmocylidrus* Corporaal, *Enoploclerus* Hinz, *Eucymatodera* Schenkling, *Falsopallenis* Pic, *Falsotillus* Gerstmeier and Kuff, *Flabellotilloides* Gerstmeier and

Kuff, *Gastrocentrum* Gorham, *Gracillotillus* Pic, *Impressopallenis* Pic, *Isocymatodera* Hintz, *Lecontella* Wolcott and Chapin, *Macroliostylus* Pic, *Magnotillus* Pic, *Microtillus* Pic, *Monophylla* Spinola, *Nodepus* Gorham, *Onychotillus* Chapin, *Orhocladiscus* Corporaal and van der Weil, *Pallenis* Lapore, *Paracladiscus* Miyatake, *Paradoxocerus* Kraatz, *Paraspinoza* Corporaal, *Philocalus* Klug, *Picoclerus* Corporaal, *Prospinoza* Crowson, *Pseudachlamys* Duvivier, *Pseudopallenis* Kuwert, *Pseudoteloclerus* Pic, *Spinoza* Lewis, *Stenocyldrus* Spinola, *Strotocera* Schenkling, *Synellapus* Fairmaire, *Synellapotillus* Pic, *Teloclerus* Schenkling, *Tillocladiscus* Pic, *Tilloclerus* White, *Tillodenops* Hintz, *Tilloidea* Laporte, *Tillus* Olivier, *Tylostoma* Hintz, and *Wittmeridecus* Winkler.

Taxonomic notes. Most of the taxonomic history of Tillinae involves the description of new species particularly on the part of William F. Barr and Albert B. Wolcott (*Cymatodera* Gray), Léon Fairmaire (*Pallenis* Laporte), and Maurice Pic (*Stenocyldrus* Spinola). Multispecies tilline larval works were provided by BÖVING (1920: 614), GARDNER (1937: 31), and FOSTER (1976: 133). Considerable information about tilline biology was published by CHAMPLAIN (1920: 625), BEESON (1926: 3), and more comprehensive taxonomic contributions were provided by SCHAEFFER (1911:123–*Monophylla* Spinola), WOLCOTT (1910: 339– *Monophylla* Spinola and *Cymatodera* Gray), CHAPIN (1924: 166–*Gastrocentrum* Gorham, *Diplophorus* Heller, *Cladiscus* Chevrolat, *Cylidroctenus* Kraatz, and *Tillus* Olivier), Barr (1950: 488– *Callotillus* Wolcott and *Cymatodera* Gray; 1952: 1– *Araedontia* Barr, 1972: 1– *Cymatodera* Gray), and *Strotocera* Schenkling, 1902: 213. A comprehensive revision of *Diplocladus* Fairmaire and *Strotocera* Schenkling was recently published by GERSTMEIER & WEISS (2009).

The tillines offer an array of possible taxonomic research. There is abundant morphological diversity in the subfamily with particular reference to the unusual cranial structure of genera related to *Cylidrus* Latreille, the apical morphology of the ovipositor of *Cladiscus* Chevrolat and allies, and the monofollicular condition of the testes in *Cymatodera* (Gray). The stridulatory mechanism, involving the metacoxa and the transverse carina of the metacoxal abdominal cavity, widespread across Tillinae, has important suprageneric implications and is considered herein an apotypy for the subfamily.

Phylogenetic analysis

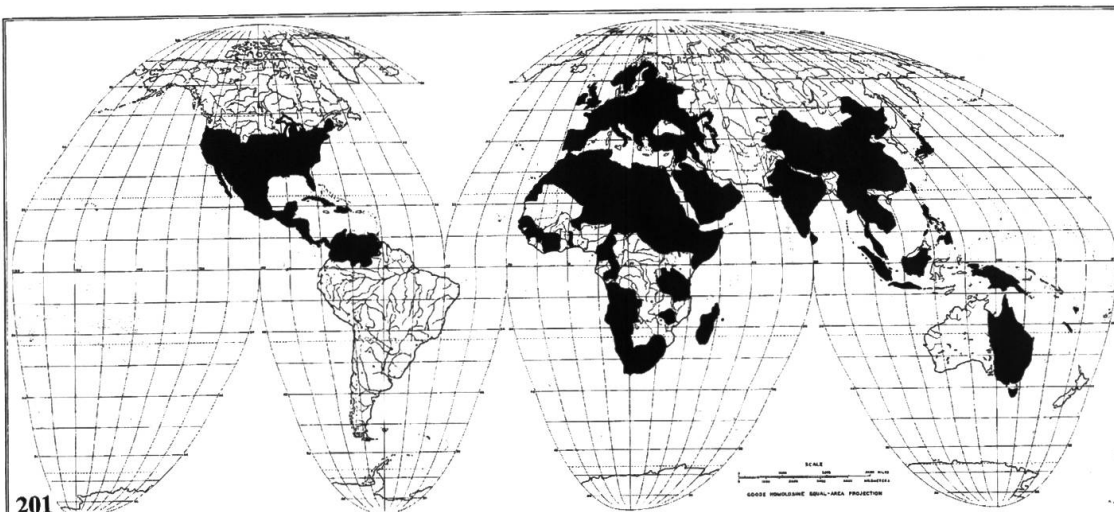
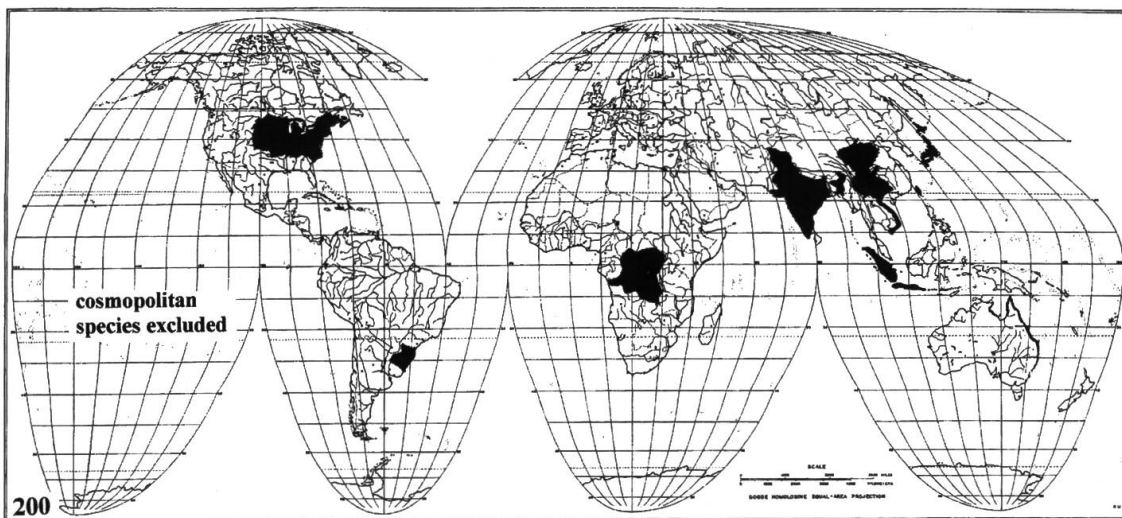
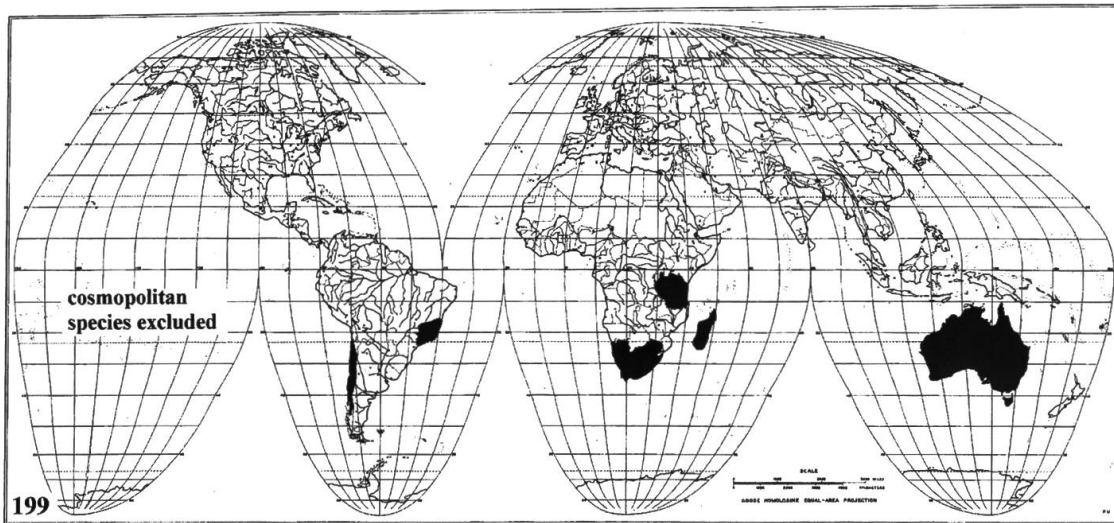
Thirty-eight morphological characters (3 of adult internal structure) of Cleridae and one of Chaetosomatidae were used in the phylogenetic analysis; thirty-eight from adults and 1 from larvae (Tab. 1). To hypothesize the phylogenetic state of character variations I used, as my outgroups, species of Cleroidea families, particularly Chaetosomatidae, and genera of Cucujoidea and Lymexyloidea. Character states designated as “0” are considered plesiotypic whereas those given a value of “1” are judged apotypic. My understanding about the evolutionary history among the Cleridae subfamilies is represented in Tree 1. This phylogeny was prepared by computer via NONA (GOLOBOFF 2003) in concert with Winclada version 1.00.08 (NIXON 2002), and involved 42 steps, an

index of consistency of 92, and an index of retention of 93 (Tree 1). A heuristic analysis [maximum trees (hold)] = 100, number of replications 9 (mult) = 100, multiple TBR+TBR (mult max was used).

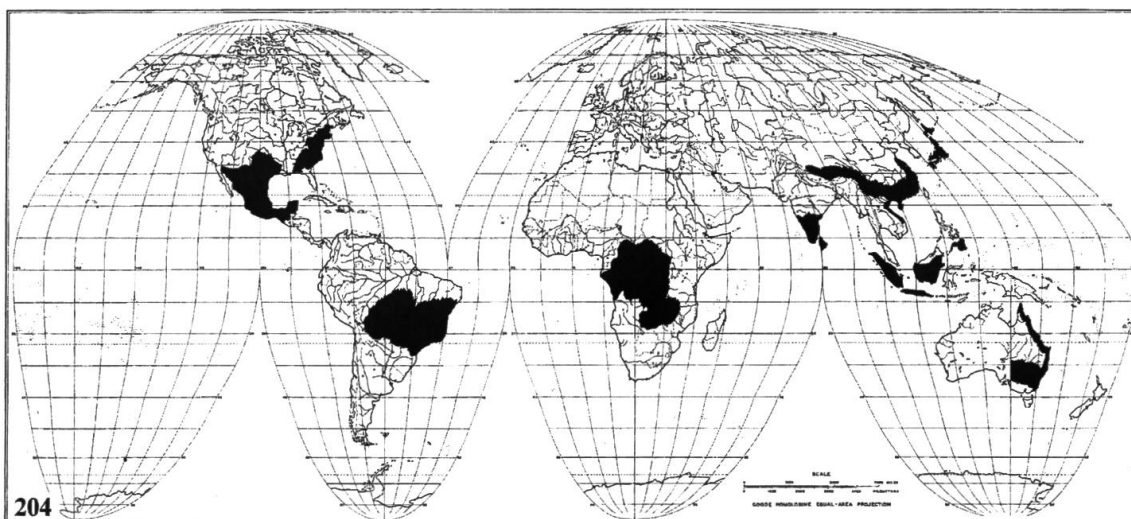
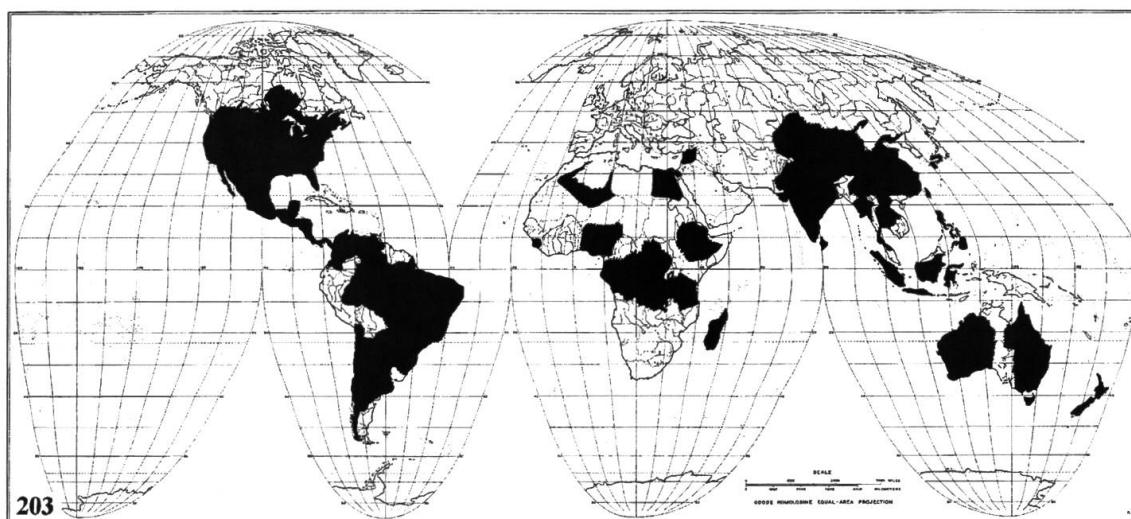
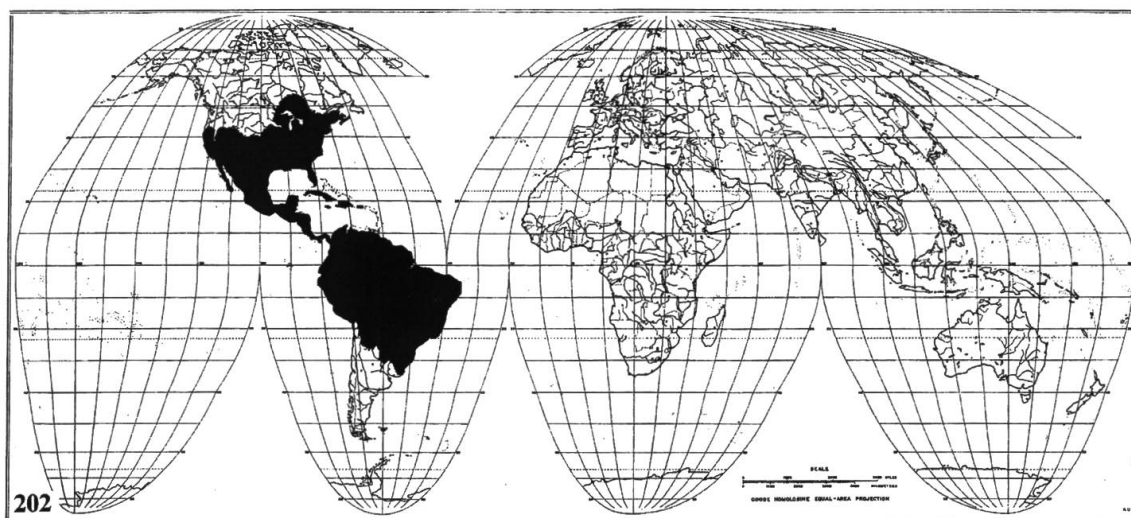
- Character 0. Laterolacinia: (0) absent; (1) present (Fig. 8).
- Character 1. Post-gular plate: (0) absent; (1) present (Fig. 12).
- Character 2. Phallobasic apodeme: (0) present; (1) absent (Fig. 118).
- Character 3. Protarsomere venters: (0) not expanded; (1) expanded (Figs 24, 25).
- Character 4. Pronotal prebasal carina: (0) absent; (1) present (Fig. 67).
- Character 5. Tarsomere formula: (0) 5-5-5; (1) 5-4-4.
- Character 6. Tarsal pulvilli: (0) absent; (1) present (Fig. 25).
- Character 7. Stomodaeal length: (0) not shortened; (1) shortened (Fig. 134).
- Character 8. Pulvilli: (0) not incised; (1) incised (Fig. 87).
- Character 9. Metacoxal cavity: (0) without carina; (1) with carina (Fig. 96).
- Character 10. Number of secondary stomodaeal valve lobes: (0) 4; (1) 2 (Fig. 149).
- Character 11. Shape of intraspicular plate: (0) not transverse; (1) transverse (Fig. 176).
- Character 12. Posterior border of larval epicranium: (0) not truncate; (1) truncate (Fig. 187).
- Character 13. Intraspicular plate: (0) present; (1) absent (Figs 176, 177).
- Character 14. Size of 4th tarsomere: (0) large; (1) small (Fig. 92).
- Character 15. Secondary stomodaeal valves: (0) present; (1) absent (Fig. 151).
- Character 16. Furcal lamina: (0) present; (1) absent (Fig. 111).
- Character 17. Place of antennal insertion: (0) at level of antennal notch; (1) at base of antennal notch (Fig. 1).
- Character 18. Trichobothria: (0) absent; (1) present (Fig. 68).
- Character 19. Tegminal lobes: (0) not fimbriate; (1) fimbriate (Fig. 126).
- Character 20. Depth of eye notch: (0) not very deep; (1) very deep.
- Character 21. Pronotal commissure: (0) absent; (1) present (Fig. 78).
- Character 22. Extent of development of pronotal commissure: (0) not developed; (1) partially developed (Fig. 65).
- Character 23. Extent of development of pronotal commissure: (0) not developed; (1) fully developed (Fig. 78).
- Character 24. Shape of postgular process: (0) not petiolate; (1) petiolate (Figs 16, 17).
- Character 25. Length of ovipositor: (0) shorter than length of abdomen; (1) longer than length of abdomen.
- Character 26. Pronototergosternal suture: (0) complete; (1) incomplete (Figs 81, 82).
- Character 27. Gular process: (0) not conjoined; (1) conjoined (Fig. 15).
- Character 28. Size of adult ommatidia: (0) not very large; (1) very large (Fig. 5).
- Character 29. Eyes size: (0) large; (1) small.
- Character 30. Length of antennal club: (0) not long capitate; (1) long capitate (Fig. 29).
- Character 31. Length of elytral setae: (0) not extraordinarily long; (1) extraordinarily long.
- Character 32. Position of pronotal subcarinal plate: (0) lateral; (1) ventral.
- Character 33. Tarsal formula: (0) not 5-5-4; (1) 5-5-4.
- Character 34. Metabasitarsomere: (0) not very large; (1) very large (Fig. 86).
- Character 35. Epipharynx: (0) not complex; (1) complex.
- Character 36. Intraspicular plate: (0) not linear; (1) linear.
- Character 37. Gula: (0) not expanded posteriorly; (1) expanded posteriorly.
- Character 38. Procryptosternum: (0) incomplete; (1) complete (Fig. 64).

Tab. 1. Character matrix of 39 morphological characters.

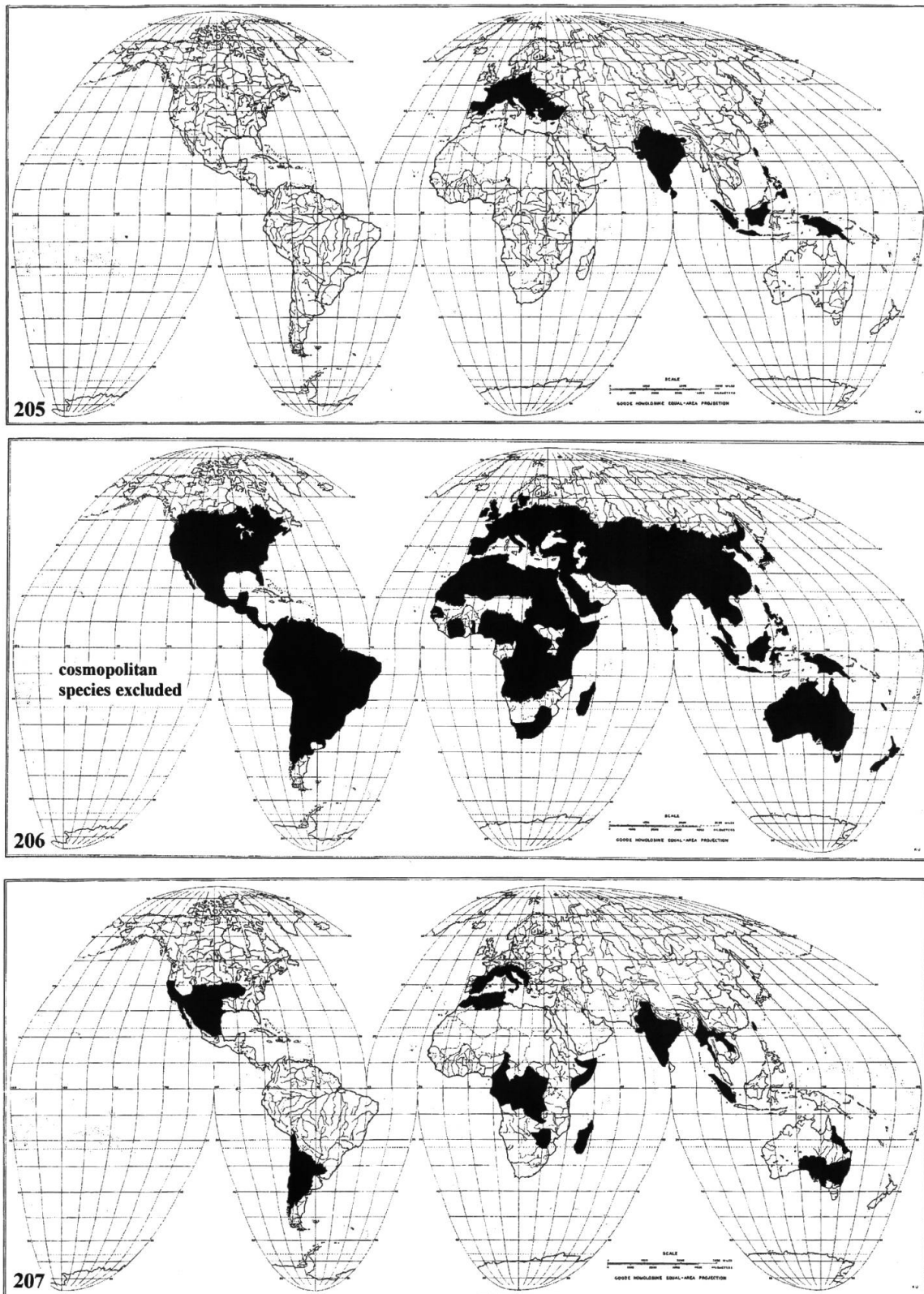
Tree 1. Phylogeny of the subfamilies of the Cleridae.



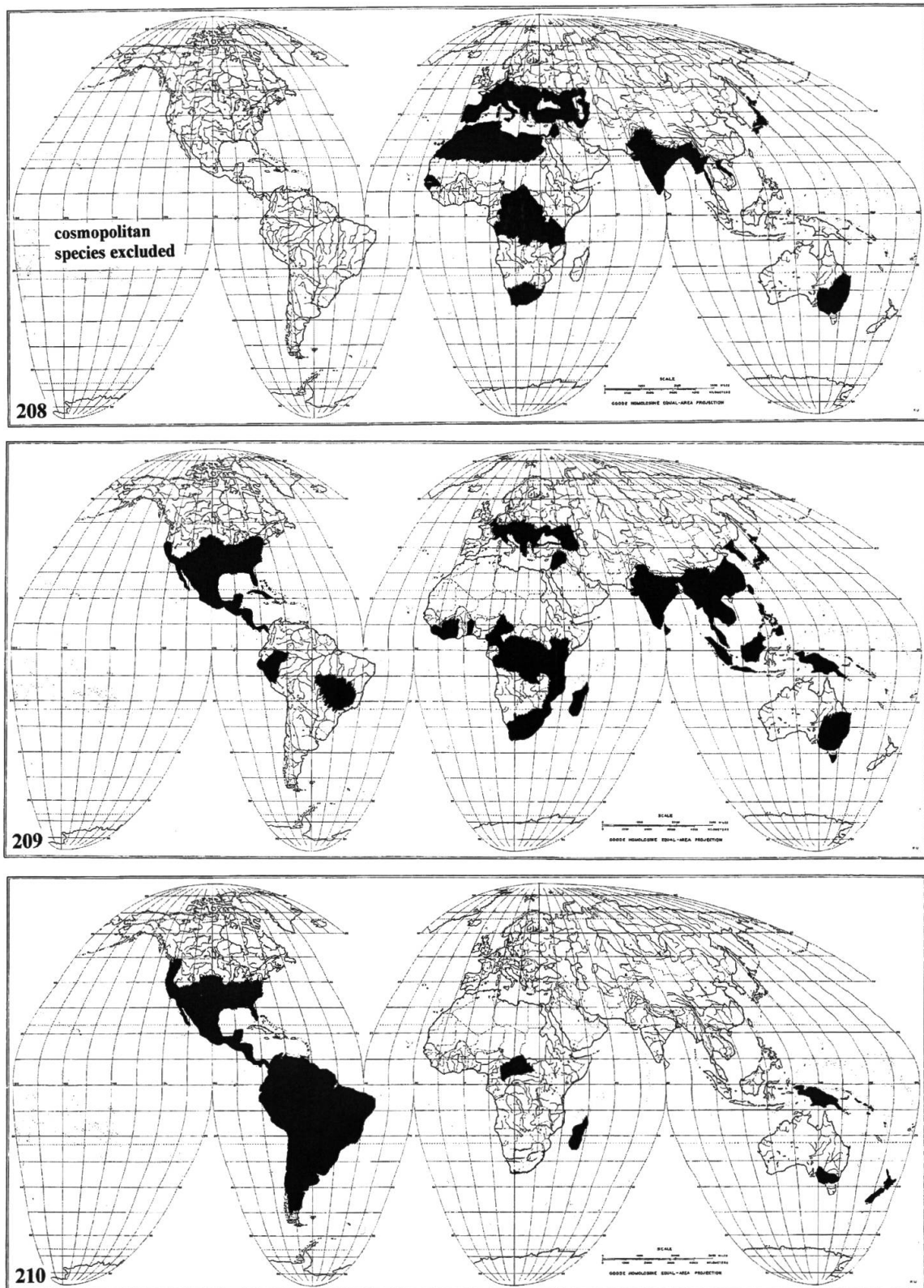
Figs 199–201. Distribution maps of subfamilies. 199 Tarsosteninae. 200 Thaneroclerinae. 201 Tillinae.



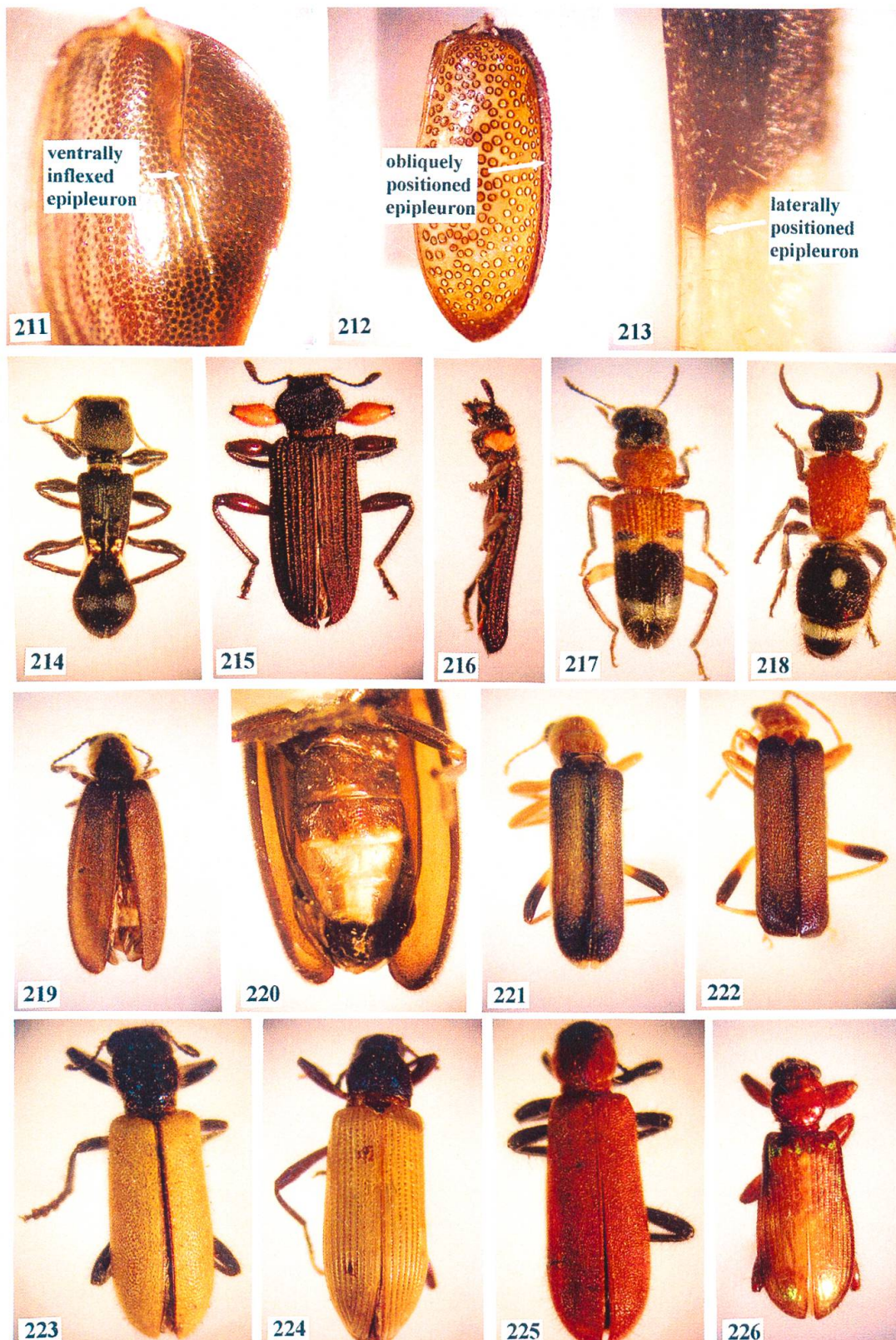
Figs 202–204. Distribution maps of subfamilies. 202. Epiphloeinae. 203 Hydnocerinae. 204 Isoclerinae.



Figs 205–207. Distribution maps of subfamilies. 205 Anthicoclerinae. 206 Clerinae. 207 Enopliinae.



Figs 208–210. Distribution maps of subfamilies. 208 Korynetinae. 209 Neorthopleurinae. 210 Peloniinae.



Figs 211–226. Morphological organs and habiti. 211–213 Elytra (211 *Allochotes bicolor*, ventral view; 212 *Prosymnus cribripennis*, ventral view; 213 *Enoclerus crabronarius*, dorsal view). 214–219 habiti (214 *Myrmecomaea raffrayi*, 215–216 *Cleropiestus oberturii* (215 dorsal view, 216 lateral view). 217 *Tillicera javana*. 218 Mutillid species. 219–220 *Perilypus ventralis* (219 dorsal view, 220 ventral view). 221 *Perilypus testaceicornis*. 222 Cantharid species. 223 *Colyphus beltoides*. 224 Tenebrionid species. 225 *Aphelochroa sanguinea*. 226 *Platycerus metallinus*.

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