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Genus-level revision of the family Phalacridae (Coleoptera: Cucujoidea)

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Abstract

A pre-phylogenetic revision of the family Phalacridae at the genus level is presented. Twenty-eight new generic synonymies are established as follows: *Acylomus* Sharp 1888 (=*Liophalacrus* Sharp 1888, **syn. nov.**; *Ganyrus* Guillebeau 1894, **syn. nov.**; *Podocesus* Guillebeau 1894, **syn. nov.**; *Tinodemus* Guillebeau 1894, **syn. nov.**; *Ledorus* Guillebeau 1895, **syn. nov.**; *Astenulus* Guillebeau 1896, **syn. nov.**; *Afronyrus* Švec 2006, **syn. nov.**), *Apallodes* Reitter 1873 (=*Litolibrus* Sharp 1889, **syn. nov.**; *Sphaeropsis* Guillebeau 1893, **syn. nov.**; *Gyromorphus* Guillebeau 1894, **syn. nov.**), *Augasmus* Motschulsky 1858 (=*Megischius* Guillebeau 1896, **syn. nov.**; *Nematolibrus* Sahlberg 1913, **syn. nov.**), *Entomocnemus* Guillebeau 1894 (=*Stilbomimus* Champion 1924, **syn. nov.**), *Grouvelleus* Guillebeau 1892 (=*Ochrolitoides* Champion 1924, **syn. nov.**; *Litotarsus* Champion 1925, **syn. nov.**), *Litochrus* Erichson 1845 (=*Merobrachys* Guillebeau 1895, **syn. nov.**), *Litostilbus* Guillebeau 1894 (=*Pseudolitochrus* Liubarsky 1993, **syn. nov.**), *Ochrolitus* Sharp 1889 (=*Gorginus* Guillebeau 1894, **syn. nov.**), *Olibroporus* Casey 1890 (=*Parasemus* Guillebeau 1894, **syn. nov.**), *Olibrosoma* Tournier 1889 (=*Lichrotus* Lyubarsky 1993, **syn. nov.**), *Phaenocephalus* Wollaston 1873 (=*Phalacratomus* Scott 1922, **syn. nov.**; *Heterostilbus* Champion 1924, **syn. nov.**), *Phalacrinus* Blackburn 1891 (=*Sphaerostilbus* Champion 1924, **syn. nov.**), *Pseudolibrus* Flach 1889 (=*Biophytus* Guillebeau 1894, **syn. nov.**; *Polyaloxus* Guillebeau 1894, **syn. nov.**), *Pycinus* Guillebeau 1893 (=*Ochrodemus* Guillebeau 1893, **syn. nov.**; *Radinus* Guillebeau 1893, **syn. nov.**; *Euphalacrus* Champion 1925, **syn. nov.**). Ten new genera and seven new species are described: *Antennogasmus*, **gen. nov.** (type species: *A. cordatus*, **sp. nov.**), *Austroporus*, **gen. nov.** (type species: *A. victoriensis* (Blackburn)), *Malagasmus* Gimmel, **gen. nov.** (type species: *M. thalesi*, **sp. nov.**), *Malagophytus*, **gen. nov.** (type species: *M. steineri*, **sp. nov.**), *Neolitochrus*, **gen. nov.** (type species: *N. pulchellus* (LeConte)), *Paracylomus*, **gen. nov.** (type species: *P. asiaticus* (Champion)), *Platyphalacrus*, **gen. nov.** (type species: *P. lawrencei*, **sp. nov.**), *Ranomafanacrinus*, **gen. nov.** (type species: *R. nigrinus*, **sp. nov.**), *Steinerlitrus*, **gen. nov.** (type species: *S. warreni*, **sp. nov.**), *Sveculus*, **gen. nov.** (type species: *S. lewisi*, **sp. nov.**). Generic reassignments resulted in 194 **new combinations**. Nine **new names** have been established for junior primary and secondary homonyms: *Acylomus bicoloratus* **nom. nov.** for *Tinodemus bicolor* Švec 2002; *Acylomus lyubarskyi* **nom. nov.** for *Olibrus capriviensis* Lyubarsky 1998; *Acylomus sveci* **nom. nov.** for *Tinodemus reticulatus* Švec 2002; *Acylomus orientalis* **nom. nov.** for *Stilbus similis* Švec 1992; *Acylomus zdeneki* **nom. nov.** for *Afronyrus snizeki* Švec 2006; *Apallodes championi* **nom. nov.** for *Litolibrus ocellatus* Champion 1925; *Olibrus peringueyi* **nom. nov.** for *Olibrus consanguineus* Péringuey 1892; *Augasmus exquisitus* **nom. nov.** for *Litochrus pulchellus* Blackburn 1895; *Litochrus pronotalis* **nom. nov.** for *Augasmus bimaculatus* Lyubarsky 1996. A type species is designated for *Phalacrinus* Blackburn 1891 (*P. australis* Blackburn 1891). Six new species-group synonymies are established: *Acylomus ergoti* Casey 1890 (=*Tinodemus grouvellei* Guillebeau 1894, **syn. nov.**), *Acylomus curvolineatus* (Champion 1924) (=*Tinodemus meridianus* (Švec 1992), **syn. nov.**; *Olibrus stuporatus* Lyubarsky 1994, **syn. nov.**), *Xanthocomus attenuatus* (Casey, 1890) (=*Xanthocomus concinnus* (Casey, 1916), **syn. nov.**; *Stilbus thoracicus* Casey, 1916, **syn. nov.**; *Stilbus quadrisetosus* Casey, 1916, **syn. nov.**). One name, *Olibrus sternalis* Casey 1916, is resurrected from synonymy. Lectotypes are designated for 23 nominal species. One genus and two species are excluded from Phalacridae: *Sternosternus* Guillebeau 1894 (with its type and only species, *S. grouvellei* Guillebeau 1894) and *Parasemus parvopallidus* Lea 1932, both of which belong in Hydrophilidae. All 34 resulting genera in the family Phalacridae are keyed, described, and illustrated. A phylogenetic hypothesis based on analysis of a matrix of 98 morphological characters was created using parsimony. Results of these analyses were not robust enough at deep levels to create a new subfamilial or tribal classification, but nine genus-groups have been hypothesized.

Introduction

The beetle family Phalacridae, commonly known as shining mold beetles or shining flower beetles, is a moderate-sized family within the superfamily Cucujoidea. Species occur nearly worldwide in terrestrial environments. Prior to this study, the group included approximately 635 described species and 52 described genera (see Lawrence *et al.* 2010 for a generic summary). The family reaches its peak species diversity in tropical regions, and a significant but less diverse fauna occurs in temperate regions. Members are totally absent from polar regions, and appear to be absent from much of the Pacific island region and the most isolated islands of the other oceans. No native species are known from New Zealand or Chile, but at least one introduced species is established in the former (Thompson and Marshall 1980). Based on the few published accounts and personal observations, most members of the family feed on fungi, but a significant number are palynophagous (pollen-feeding) on angiosperm flowers, and at least one species (newly described herein) likely feeds on cycad pollen.

The Phalacridae are a morphologically well-defined group, but among the most poorly known beetles taxonomically. Most species are unidentifiable outside of Europe, and genera have been virtually unidentifiable outside of the Holarctic region using existing literature.

My main objectives in this study were to: (1) define, describe, and provide keys for identification of the world genera of Phalacridae; (2) examine the morphological structures and variation within the family in detail; and (3) use this morphology to test the monophyly and reconstruct the phylogenetic relationships of genera within the family. These objectives are an essential step towards the broader goal of a comprehensive, revised classification based on modern phylogenetic methods.

Phylogenetic position of Phalacridae. Phalacridae are firmly nested within the superfamily Cucujoidea, as evidenced by multiple recent phylogenetic studies using both morphology (Leschen *et al.* 2005; Lawrence *et al.* 2011) and DNA sequence data (Hunt *et al.* 2007; Roberston *et al.* 2008). However, Cucujoidea, as currently defined, appears to be polyphyletic (see Lawrence *et al.* 2011).

Steiner (1984) suggested that the most likely sister group is Nitidulidae, given similarities in larval structures. He also suggested Sphindidae (given the similarity of adult *Tolyphus* Erichson to members of that family) or Mycetophagidae (whose larvae share multiple characters with Phalacridae) as candidates for sister groups. Given the results of more recent studies, these last two families are distantly related to Phalacridae, and any similarity is more likely the result of symplesiomorphy or convergence. As for the "nitidulid group" (Nitidulidae + Kateretidae + Smicripidae), a sister-group relationship with Phalacridae is more plausible, as was suggested by Crowson (1955) who based his hypothesis on aedeagal morphology and larval *Smicrips*. However, more recent studies suggest otherwise.

Thomas (1984) suggested a close relationship of Phalacridae with Laemophloeidae (as Cucujidae: Laemophloeinae) and Propalticidae based on the following characters: unequal anterior tibial spurs, reduced hind wing venation, reduction and fusion of the parameres in the male genitalia, basic plan of the head, and structure of the larval mouthparts and hypostomal sclerotizations. He generalized the condition of the tarsal formulae of males within Phalacridae as never heteromerous, but they are in fact heteromerous in a few genera. As he noted, a few taxa within Laemophloeidae possess the heteromerous tarsal condition. If the sister relationship between these two families is corroborated, then the ancestral state of this character is ambiguous, not necessarily homomerous as he suggests.

Leschen *et al.* (2005), in a study of "basal" Cucujoidea using 37 exemplar taxa and 99 morphological characters of adults and larvae, placed Phalacridae (exemplar taxon: *Acylomus* Sharp) sister to a group containing Nitidulidae, Kateretidae, Smicripidae, Tasmosalpingidae, Cyclaxyridae, Propalticidae, and Laemophloeidae. Hunt *et al.* (2007), in a study of Coleoptera as a whole using 18S rDNA genes (with 16S rRNA and cytochrome oxidase I gene data for half of the species) for 1880 species, placed Phalacridae as sister to the group Laemophloeidae + Propalticidae. Robertson *et al.* (2008) performed a focused molecular phylogeny of the Cucujoidea using 18S and 28S rDNA, but with an emphasis on the Cerylonid Series (to which Phalacridae do not belong). Sampling was sparse outside of the Cerylonid Series, but their results also suggest a sister group relationship with Laemophloeidae (Propalticidae were not sampled).

Lawrence *et al.* (2011), in a phylogenetic anlaysis of the Coleoptera utilizing 359 taxa and 514 larval and adult morphological characters, placed Phalacridae (*Phalacrinus* Blackburn + *Olibrus* Erichson) sister to a clade containing Cerylonidae: Euxestinae (*Hypodacnella* Ślipiński) and Endomychidae: Anamorphinae (*Bystus* Guérin-Méneville). This clade in turn was sister to Myraboliidae (*Myrabolia* Reitter) + Cavognathidae (*Taphropiestes* Reitter). This entire clade was sister to Bothrideridae: Bothriderinae + Phytophaga, and distant from other cucujoid groups. However, with the exception of monophyly of Phalacridae, these hypothesized relationships received low support.

Taxonomic history of Phalacridae. Taxonomic work on Phalacridae began with the publication of Carl Linné (1767) who described the species *Silpha atomaria* [=*Stilbus atomarius* (Linné)]. Most Linnean-era workers classified members of Phalacridae in the catch-all genera *Sphaeridium* or *Anisotoma*, which at the time included a wide variety of small, round, dark-colored beetles. The Phalacridae as presently constituted was first recognized by Gustavi Paykull (1800) who delimited the genus *Phalacrus*, although he did not award it special familial status. Species were slowly added to the genus, mostly from the Palearctic region, with William Elford Leach (1815) being the first to formally elevate the group to family rank (as "Phalacrurida"). Thirty years later, the brilliant coleopterist Wilhelm Ferdinand Erichson (1845) published his seminal work monographing the Coleoptera of Germany. This work marked the first attempt of a detailed study into the structure and internal classification of these beetles. Taking into account the known non-Palearctic species as well, he erected three new genera within the family (*Litochrus*, *Olibrus*, and *Tolyphus*) bringing the total to four. The rate of species description was high during the following period (Fig. 1), primarily because of the rapid increase in scientific expeditions outside of Europe.

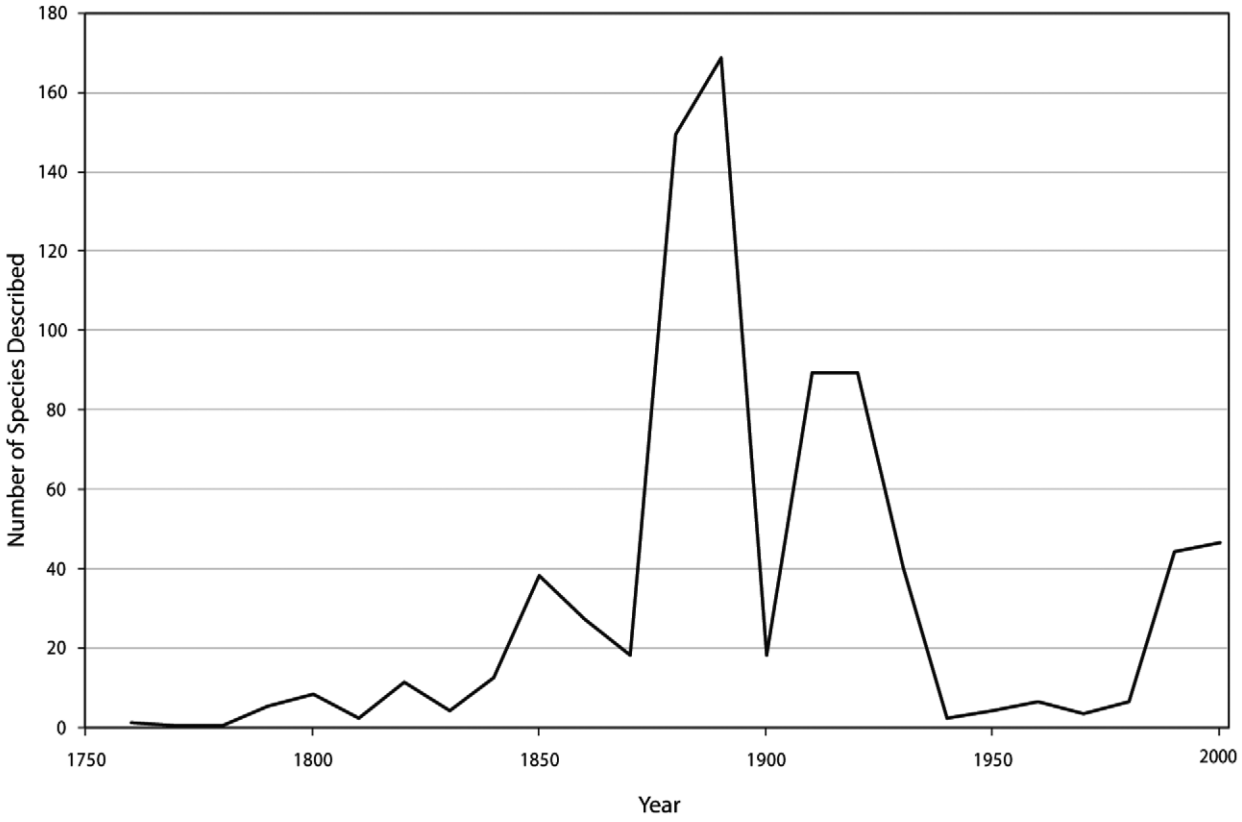

FIGURE 1. Phalacrid species-group taxa described over time, 1767–2006.

Significant numbers of new species and genera were added during this "golden" period, lasting until the 1910s, by Victor Motschulsky (Oriental region), David Sharp (Neotropical region), Henri Tournier (Palearctic region), Thomas Blackburn (Australian region), and Thomas Casey (Nearctic region). However, only one researcher, Francisque Guillebeau, attempted a detailed summary and classification of the world fauna of Phalacridae. He did this in two major works (1892*b* and 1894*a*) and a smattering of others (1892–1897), but these works were highly limited in value since they contained no illustrations. Furthermore, his higher classifications tended to be based on relatively unstable and/or difficult-to-interpret characters, such as the extent of the mesoventral margin anterior to the metaventral process. In the first major work, which focused on Palearctic members of the family, he erected two broad categories based on this latter character, the "Hyposternes" and "Hypersternes", with three tribes in the first group (Phalacrini, Tolyphini, Olibrini) and one tribe in the second group (Eustilbini). This "supratribal" arrangement was abandoned two years later in his second major work, worldwide in scope, in which he recognized 10 tribes in the Phalacridae, including the previous four and six new tribes. Of these new tribes, only three were based on actual genus-group names (Biophytini, Megapalpini, Ochrolitini) while the other three were not ("Olibromorphini", "Heterolibrini", and "Heterosternini"). Probably because of the dubious nature of Guillebeau's classification system, subsequent workers have almost ignored it.

George Champion was the next major worker in Phalacridae, and the first major worker to include illustrations in his several papers (1924–1925) with appropriate detail to be useful in distinguishing members of the group. His wide-ranging work covered Oriental, Afrotropical, and Neotropical species. The terse work of Hetschko (1930) represents the last catalogue of world taxa of Phalacridae, and the posthumous work of Lea (1932) on the Australian fauna was the last major revision until the 1990s.

The period from about 1940–1980 saw virtually no contributions to our understanding of the taxonomy of the group, with even species descriptions experiencing a drought. The works of Zdeněk Švec (1992–2010) and Georgy Lyubarsky (1993–2005) represent a reversal of this trend, with these two workers describing many new species and two new genera and providing genitalia illustrations, which are essential for species delimitation in most genera of phalacrids. However, their works were focused on the Old World fauna, and the New World species remain almost entirely unrevised. Exceptions include the unpublished thesis of Warren Steiner (1977)

treating the North American *Litochrus* (*Neolitochrus* herein) and *Litochropus*; the detailed study of the taxonomy and life history of *Acylomus pugetanus* Casey by Steiner and Singh (1987); and the treatment of North American *Xanthocomus* by Gimmel (2011). Useful modern guides to species occurring in the Palearctic region are Thompson (1958) for the British fauna; Vogt (1967) for the central European fauna; Hisamatsu (1985) and Sasaji (1985, as Phaenocephalidae) for the Japanese fauna; Lafer (1992*a*, *b*) for the Russian Far East; Švec and Angelini (1996) for the Italian fauna; Cmoluch (1997) for the Polish fauna; and Ventura (1997) for the Iberian and Balearic fauna. A useful (albeit terse) catalogue of the Palearctic species may be found in Švec (*in* Löbl and Smetana 2007). Steiner (2002) provided a key to the genera of North America. Gimmel (2009) provided a key to the Seychellois fauna.

The only major contribution regarding the understanding of the limits of the family and its higher classification came from Pakaluk (1991) who synonymized the family Phaenocephalidae (one genus, two species) with the Phalacridae. He speculated that it had affinities with *Phalacrinus*, which led Lawrence and Newton (1995) to hypothesize that the genera *Phaenocephalus*, *Phalacrinus*, and perhaps *Sphaerostilbus* formed a distinct subfamily (Phaenocephalinae) within the Phalacridae.

A genus that had been associated with Phalacridae since Sen Gupta and Crowson (1966), *Cyclaxyra* Broun, was formally removed from Phalacridae and placed into a family of its own by Gimmel *et al.* (2009). This family, with two described species, is endemic to New Zealand, where no phalacrids are known to occur natively.

Immature stages and habits of Phalacridae. The first mention of immature stages of phalacrids was the publication of Johann Ludwig Christian Gravenhorst (1834) in which he describes the observations of Peter Samuel Schilling. The latter observed the larvae of *Olibrus aeneus* (misidentified as *Phalacrus corruscus*) inhabiting the base of the fruit of chamomile, *Matricaria recutita* L.

Larvae have been formally described for members of *Acylomus* (see Steiner and Singh 1987), *Phalacrus* (see Friederichs 1908; Emden 1928; Böving and Craighead 1931; d'Aguilar 1944; Thompson and Marshall 1980), and *Olibrus* (see Urban 1926, 1930; Löben Sels 1934). Particular characters have been illustrated for larvae of *Litochropus*, *Phalacropsis*, and *Stilbus* (Steiner 1984).

Steiner (1984) provided an excellent survey of the biology of Phalacridae, including immature stages. Most Phalacridae whose habits are known are associated with fungi, consuming spores or hyphae as both adults and larvae. Members of the *Stilbus*-group are generally believed to be associated with ascomycete molds growing on the surfaces of dead vegetation, including such habitats as dead hanging leaves and grass tussocks. However, larvae of at least one member of this group, *Acylomus pugetanus* Casey, develop within the sclerotia of *Claviceps* species (ergot). Adult and larval *Litochropus clavicornis* Casey have been taken from the fruiting bodies of *Daldinia*, a genus of Xylariaceae, a family of wood-decaying ascomycetes. Active adult specimens of *Apallodes* have been collected from fruiting bodies of another genus of Xylariaceae in Peru at night (R.A.B. Leschen, pers. comm.).

The *Phalacrus*-group (*Phalacrus* and *Phalacropsis*) represents a departure in habits from other fungus-feeding Phalacridae, being the only genera known to associate with basidiomycete fungi. Members of *Phalacrus* seem to be most commonly associated with smut fungi (Ustilaginales) on grasses (Poaceae) and sedges (Cyperaceae), including the economically important corn smut, *Ustilago maydis* (DC.) Cda., and sugarcane smut, *Sporisorium scitamineum* (Sydow) M. Piepenbr., M. Stoll & Oberw. Other members of *Phalacrus* are associated with rust fungi (Pucciniales), including *Uromycladium* species infesting *Acacia* (Fabaceae) in Australia and (introduced to) New Zealand. Members of *Phalacropsis dispar* (LeConte) are significant consumers of pine stem rust fungi (*Peridermium* species) on pines (*Pinus* species) in western North America (see Nelson 1982).

The *Olibrus*-group (*Olibrus* and *Tolyphus*) are diurnal, flower-visiting pollen feeders as adults, while the larvae (at least of *Olibrus*; *Tolyphus* larvae are unknown) appear to feed on fluid material within flower heads. Members of the plant family Asteraceae are the only known hosts of larval *Olibrus*.

Members of a few other phalacrid genera are known to associate with living (and dead) plants. Peyerimhoff (1907) reported *Olibrosoma testacea* Tournier from flowers of *Orobanche* (Orobanchaceae) in Egypt. Adult members of *Litochrus* have been collected from flowers of a wide variety of plants in Australia, but have also been collected in association with rotting wood. *Austroporus* adults have been taken under bark, and an undetermined species has been taken in large series from flowers of *Xanthorrhoea* (Xanthorrhoeaceae). Members of *Steinerlitrus* (described herein) were collected from the trunk of a living tree (*Macrolobium* species, Fabaceae) at night in Venezuela. The monotypic genus *Platyphalacrus* (described herein) contains the only known phalacrid associate of cycads; adults presumably feed on pollen within the male cones of *Macrozamia* (Zamiaceae).

Phalacridae in the fossil record. One compression fossil attributed to Phalacridae has been described (*Olibrus ornatus* Förster, from the Eocene-Oligocene boundary), but the family identification is poorly supported by the description and illustration given in the original publication (Förster 1891). However, a few phalacrid inclusions are known from Tertiary amber, and these were summarized in Poinar (1992) and catalogued by Spahr (1981*a*, *b*). Poinar (1992: 149) indicated that the genera *Olibrus* and *Phalacrus* have been identified in Baltic amber (ca. 40 mya), and published a photograph of an unidentified phalacrid in Dominican amber (15–45 mya) from his collection; I have seen an additional phalacrid specimen from Dominican amber (FMNH). He also indicated that phalacrids have been found in Mexican (Chiapas) amber (22–26 mya). Kirejtshuk and Nel (2008) mentioned the presence of Phalacridae in lowermost Eocene French amber (specimens in MNHN). Lyubarsky and Perkovsky (2011) described *Stilbus bedovoyi* from Late Eocene Rovno Amber; however, based on the photographs and the drawing included in the publication, the generic and even familial identity of the specimen is questionable.

The Bayesian analysis tree in Hunt *et al.* (2007), with molecular calibration points dated with penalized likelihood, implied a Cretaceous origin for the Phalacridae.

Materials and Methods

Specimens. Approximately 100,000 specimens were examined for purposes of this revision and approximately 27,000 specimens were borrowed from many of the museums in the list below. Loans from institutions housing specimens of Phalacridae were the source of most of the material for this study, although I also examined much material through museum visits and personal collecting.

An attempt was made to locate and examine type specimens for the type species of most genera, with a focus on those for which the identity was dubious. Label data were recorded verbatim from types examined. These are presented within double quotes (“ ”), with labels separated by double forward slashes (//) and lines of text on a given label separated by a backslash (\). For most primary type specimens of genus-bearing taxa examined in this study I provided a red label of the format “[CATEGORY OF TYPE] [♂ or ♀] [complete original combination with authorship] det. [or “des.” in the case of lectotypes] M.L. Gimmel [year of designation]”, especially in cases where the specimen is not adequately marked as a specific primary type (see ICZN 1999, Recommendation 72D). Lectotype designation labels on specimens state the year I selected the specimen for designation. These actions are validated with this publication. Since many of the institutions visited also contained type specimens of species not carrying a genus-group name, these were also examined when time permitted. In the lists of included species appearing in the accounts of individual genera, these instances are indicated by the symbol “type!” appearing on the same line as the species entry. This examination has resulted in a large number of new combinations; however, no special effort was made to establish species-level synonymies. Since all indications are that a large number of species-level synonyms exist in Phalacridae (evidenced by recent published and unpublished revisions and a few personal observations), the current number of described species for certain genera may be artificially inflated. I was not able to examine the types of every phalacrid species whose generic identity is in question because of time constraints. These unexamined species, and those not or poorly illustrated in literature, may be regarded as tentatively placed in their respective genera and must await species-level revisions for their generic and specific identity to be resolved.

Following is the list of institutions, including codens (taken from Evenhuis 2011), used in the remainder of this work, with the primary point-of-contact in parentheses:

AMNH	American Museum of Natural History, New York, New York (Lee Herman)
ANIC	Australian National Insect Collection, CSIRO, Canberra, Australia (Cate Lemann)
BMNH	The Natural History Museum, London, United Kingdom (Roger Booth)
BYU	Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah (Shawn Clark)
CAS	California Academy of Sciences, San Francisco, California (Jere Schweikert)
CSCA	California State Collection of Arthropods, Sacramento, California (Jackie Kishmirian)
EAPZ	Escuela Agricola Panamericana, Tegucigalpa, Honduras (Oliver Schlein)
EGRC	Ed Riley Collection, College Station, Texas
EMEC	Essig Museum of Entomology, University of California Berkeley, Berkeley, California (Cheryl Barr)

FMNH	Field Museum of Natural History, Chicago, Illinois (James Boone)
FSCA	Florida State Collection of Arthropods, Gainesville, Florida (Paul Skelley)
HIC	Hymenoptera Institute, University of Kentucky, Lexington, Kentucky (Michael Sharkey)
LSAM	Louisiana State Arthropod Museum, Louisiana State University, Baton Rouge, Louisiana (Victoria Bayless)
LSUK	Linnean Society, London, United Kingdom
MAIC	Michael A. Ivie Collection, Bozeman, Montana
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (Philip Perkins)
MEM	Mississippi Entomology Museum, Mississippi State University, Starkville, Mississippi (Terry Schiefer)
MLGC	Matthew L. Gimmel Collection, Baton Rouge, Louisiana and Lawrence, Kansas
MNHN	Museum National d'Histoire Naturelle, Paris, France (Azadeh Taghavian)
MSNG	Museo Civico di Storia Naturale "Giacomo Doria," Genova, Italy (Roberto Poggi)
MTD	Museum für Tierkunde, Dresden, Germany (Olaf Jaeger)
MTEC	Montana Entomology Collection, Bozeman, Montana (Michael Ivie)
MZH	Zoological Museum, University of Helsinki, Finland (Hans Silfverberg)
NMPC	National Museum, Prague, Czech Republic (Jiří Hájek)
NZAC	New Zealand Arthropod Collection, Auckland, New Zealand (Richard Leschen)
OSEC	K.C. Emerson Museum, Oklahoma State University, Stillwater, Oklahoma (Don Arnold)
PURC	Purdue University, West Lafayette, Indiana (Arwin Provonsha)
RDCC	Ron D. Cave Collection, Fort Pierce, Florida
SANC	South African National Collection of Insects, Pretoria, Republic of South Africa (Beth Grobbelaar)
SBMN	Santa Barbara Museum of Natural History, Santa Barbara, California (Michael Caterino)
SDMC	San Diego Natural History Museum, San Diego, California (Michael Wall)
SEMC	Snow Entomological Museum, University of Kansas, Lawrence, Kansas (Zack Falin)
TAMU	Texas A&M University Collection, College Station, Texas (Ed Riley)
TMSA	Transvaal Museum, Pretoria, Republic of South Africa (Ruth Müller)
UCDC	Bohart Museum of Entomology, University of California Davis, Davis, California (Steve Heydon)
UDCC	University of Delaware, Newark, Delaware (Charles Bartlett)
UGCA	University of Georgia, Athens, Georgia (Joe McHugh)
USNM	Smithsonian Institution, Washington, DC (Warren Steiner)
WIBF	West Indian Beetle Fauna Project Collection, Montana State University, Bozeman, Montana (Michael Ivie)
ZMUC	Zoological Museum, University of Copenhagen, Denmark (Alexey Solodovnikov)
ZMUM	Zoological Museum, Moscow University, Moscow, Russia (Nikolai Nikitsky)

Routine sorting and identification was accomplished using a Leica™ MZ 7.5 dissecting microscope, the maximum magnification (50×) of which is adequate for almost all genus-level characters in Phalacridae.

For detailed examination and description of both external and internal characters, adult beetles of both sexes from every described genus not obviously a junior synonym of another genus, and all putative new genera (unless represented by fewer than three specimens) were disarticulated. More than one species was dissected from certain widespread or variable genera. Disarticulations were performed by first softening the beetle in hot water (plus immersion in an additional solvent to remove adhesive, if necessary), removing the elytra and hind wings, then placing the rest of the beetle into warm (≈60 C) 10% potassium hydroxide (KOH). After maceration of soft tissues in KOH, the beetle was removed to 95% ethanol where the head, prothorax, and pterothorax were separated and macerated tissues were scraped and palpated from the body cavity using minuten pins. All parts (except hind wings) were then placed in a glycerol slide mount, whereupon they were dissected further as needed. Hind wing mounts were prepared using the dry-mount methodology of Kukalová-Peck and Lawrence (2004). The wings were usually mounted on the same slide as the glycerol mount.

Routine genitalia dissections and dissections of types were performed as follows: 1) the beetle was rehydrated and softened in hot water; 2) the beetle was transferred to 95% ethanol whereupon the abdomen was removed; 3) the beetle (sans abdomen) was remounted on a point using Martha Stewart Crafts™ All-Purpose Gel Adhesive (a

completely transparent acid-free adhesive that is soluble in both water and ethanol) while the entire abdomen was macerated in warm 10% KOH; 4) genital sclerites were removed, separated, and examined (see below); 5) after examination, the sclerites were placed on a small rectangle of cellulose acetate in a drop of dimethylhydantoin formaldehyde resin (DMHF; see Steedman 1958), which was pinned beneath the specimen. The abdomen was remounted on the point containing the beetle, ventral side up, using the aforementioned adhesive.

Preparation for drawing small sclerotized structures (genitalia, metendosternite, mouthparts, etc.) was accomplished as follows (modification of the method described in Werner 1948): the sclerite was taken from 95% ethanol and placed in a small droplet of lactic acid just inside the edge of the circular well on a single-well microscope slide. A circular cover slip was then placed so that it was mostly outside the well, but covered the droplet and sclerite. This allows one to rotate the sclerite into an appropriate position for drawing by simply nudging the cover slip from the dry side. The slide was placed onto an Olympus™ BX50 compound microscope with camera lucida for drawing.

Because of their complexity, the tegmen, median lobe, and spiculum gastrale were always separated prior to drawing and detailed examination. Eversion of the internal sac of the median lobe was unnecessary since all internal sclerites and spicules are clearly visible while contained within the (cleared) structure.

Terminology for morphological characters follows Lawrence *et al.* (2010), and that for iridescence follows Seago *et al.* (2009). Wing veins are identified in Fig. 33e.

Guidelines for generic revision. While I accept monophyly as the ultimate criterion in defining genera, I did not perform a strict test of monophyly for each genus in the family. However, I followed three major guidelines to define genera within the family:

1) A genus must be externally diagnosable. In the definition of each genus I have included at least one external character. Internal characters help to further solidify and corroborate a definition, but for identification purposes disarticulation should not be necessary. I have violated this rule somewhat in one instance with members of the *Stilbus*-group, in which male genitalia should be examined (though generic identities can be gleaned by elimination in most cases). However, generic definitions in that particular group, while much clearer as a result of this study, are still far from settled.

2) A genus must be defined with a straightforward character or set of characters (Occam's Razor). Overly complex definitions, involving multiple conditional statements ("if", "but"), were avoided. While it may be argued that definitions of this nature might be necessary after a full phylogenetic analysis has shown large, complex genera to be monophyletic, these definitions do not belong in a first approximation of generic concepts.

3) Splitting and lumping of previous generic names were minimized. If two diagnosable groups (using guidelines 1 and 2) exist that are ascribable to two different, previously established generic names, these were not synonymized. If one diagnosable, previously established generic concept had more than one recognizable subgroup, but these subgroups taken together were still diagnosable as a single unit, I did not fracture the genus into multiple genera.

A high likelihood exists that forms will be discovered that defy inclusion within any of the genera I have defined herein. This will require revisions of the concepts presented in the current work, potentially including establishment of new genera, dissolution of boundaries between generic concepts, or expansion of established generic concepts.

Systematic treatment

Family PHALACRIDAE Leach, 1815

Phalacrurida Leach 1815: 116. Type genus: *Phalacrus* Paykull.

Diagnosis. Adults. Distinguished from other Coleoptera by the dorsal surface entirely or virtually glabrous (a few genera with extremely sparse, extremely small, completely recumbent setae) and never sculptured, moderately to highly convex (flattened abruptly on middle of dorsal surface in *Platyphalacrus* and an undescribed *Pycinus*); antenna clubbed, club 3-(rarely 4- or 5-) segmented; antenna attached to head via lateral knob on scape; corpotentorium membranous; pronotal hind angles overlapping base of elytra in repose (weakly expressed in

Tolyphus), elytral humeri with corresponding transverse line at posterior extent of pronotal margin; tarsal formula usually 5-5-5, some (mostly males) 5-5-4 or 4-4-4 (*Phaenocephalus*-group), rarely 4-5-4 (*Augasmus*); pretarsal claw with basal tooth or angulation; prosternal process with an internal, vertical foramen; pro- and mesocoxal cavities separated (sometimes quite narrowly so), metacoxae virtually contiguous; mesocoxae closed laterally; with five free abdominal ventrites; aedeagus with tegmen ringlike (cucujiform).

Larvae. Distinguished from other Cucujoidea by the frontal arms lyriform with contiguous bases; protracted ventral mouthparts; reduced cardines; long and diverging hypostomal rods; enlarged and posteriorly oriented spiracles on segment VIII; concealed sternum IX and anal region (Lawrence 1991).

Adult description. Length 0.9–4.8 mm. Body about 1.15–1.95 times as long as wide, usually broadly ovate to circular, with dorsal surfaces moderately to strongly convex (rarely oblong or somewhat flattened) and ventral surfaces flat to somewhat concave. Cuticle subglabrous and shining, often highly spectrally iridescent. Color often black, brown, yellow, or with light and dark pattern.

Head. Slightly to moderately declined, not concealed from above, strongly transverse, somewhat flattened. Without distinct postocular constriction or stridulatory file. Median endocarina absent, or short carina present (in *Phalacrinus*). Vertex without transverse ridge. Eyes moderately large, not protuberant, not or barely emarginate; finely faceted, rarely with interfacetal setae (*Platyphalacrus*; sparse setae in *Austroporus*). Antennal insertions barely exposed or concealed from above; subantennal groove absent. Frontoclypeal suture absent. Labrum slightly to strongly transverse, with broadly rounded to truncate anterior edge and paired rods; tormae long, subparallel or slightly curved. Antennae 11-segmented, scape with knob for attachment to head capsule located mid-laterally, almost always with large, well-defined, elongate and often somewhat asymmetrical, 3-segmented club (4- to 5-segmented club in *Olibrosoma* and an undescribed Brazilian *Pycinus*). Mandible unidentate, bidentate, or tridentate, without dorsal tubercle or cavity, usually with well-developed mola and prostheca (mola somewhat reduced and apex long and slender in *Phalacrinus*). Maxilla with galea distinctly broader than lacinia, which bears an uncus; apical maxillary and labial palpomeres cylindrical to fusiform, the latter nodiform in *Phalacrinus*. Ligula short, broad, truncate or bilobed. Gular sutures usually short, sometimes moderate, but never complete. Tentorium reduced; corpotentorium absent. Cervical sclerites absent.

Thorax. Pronotum 0.25–0.50 times as long as wide; sides moderately to strongly curved, almost always obliquely explanate; lateral carinae complete, simple, with or without narrow bead; anterior angles produced and broadly to narrowly rounded or acute; posterior angles broadly rounded to right or slightly acute; disc simple. Prosternum anterior to coxae shorter than shortest diameter of coxal cavity, not produced anteriorly, flat to slightly convex. Prosternal process complete, parallel-sided or gradually expanded apically (approaching a thin vertical lamina in *Phaenocephalus*-group); dorsally curved or flat and abruptly curved at apex, which is broadly rounded to truncate, overlapping mesoventrite and sometimes abutting edge of metaventrite, often with transverse row of posteriorly directed setae or spines; internally with foramen in vertical plane, so that the prosternal process forms a complete loop postero-ventrally on the prothorax. Notosternal sutures complete. Procoxae not or slightly projecting below prosternum, with or without short concealed lateral extension. Trochantin partly exposed to completely concealed. Procoxal cavities slightly transverse to circular, narrowly separated, externally broadly open, with or without narrow lateral extensions; internally closed. Scutellar shield abruptly elevated at base; posteriorly acute to broadly rounded. Elytra 0.9–1.5 times as long as combined width and 2.6–3.85 times as long as pronotum; usually with nine faint but complete puncture rows or striae and no scutellary striole; sometimes with puncture rows absent or extremely fine or striae reduced to one or a few near suture; apices conjointly rounded; epipleura complete or incomplete, usually broadly, obliquely to vertically explanate. Mesoventrite separated by complete sutures from mesanepisterna, which are distinctly separated from one another; anterior edge usually on different plane than metaventrite, often with paired procoxal rests; posterior portion often steeply sloping and sometimes not or barely visible between prosternal and metaventral processes. Mesocoxal cavities extremely narrowly (*Grouvelleus*) to widely separated, closed laterally by meeting of meso- and metaventrites; mesometaventral junction usually an anteriorly curved line, occasionally concealed by edge of metaventral process. Metaventrite strongly transverse, flattened; discrimen long to quite short; postcoxal lines not separated from coxal cavity or strongly, sometimes acutely, arched; exposed portion of metanepisternum moderately to quite long and narrow. Metacoxae contiguous or quite narrowly separated, not extending laterally to meet elytra; large plates absent. Metendosternite with moderately to quite long lateral arms; laminae well-developed to reduced; anterior process short or absent; anterior tendons moderately close together to widely separated, usually on lateral arms. Hind wing about 2.5–3.5 times as

long as wide; apical field 0.45–0.6 times total wing length, without or with one or two transverse linear sclerites just beyond end of radial bar; radial cell absent; RP with short to moderately long basal section and with short, curved apical extension; medial field with zero to four free veins and no medial fleck; wedge cell absent; anal embayment notch-like. Trochanterofemoral joint slightly to strongly oblique with base of femur separate from coxa; femora usually broad and excavate to receive tibia, which may be widened at or near apex and armed with apical fringe of spines; spurs glabrous, extremely short to long, equal or unequal in length and sometimes reduced to one or none on protibia; tarsi usually 5-5-5 in both sexes or 5-5-4 in males, sometimes 5-5-4 in both sexes; penultimate tarsomere reduced in tarsi with 5 segments, and at least antepenultimate weakly lobed beneath; tarsi 4-4-4 in *Phaenocephalus*-group, 4-5-4 in *Augasmus*; claws toothed or bidentate; empodium more or less concealed or absent.

Abdomen. With five free ventrites. Ventrite 1 not much longer than 2; postcoxal lines usually absent, rarely present as paired oblique straight lines (*Malagophytus*); intercoxal process acute or narrowly rounded. Functional spiracles on segments I–VI or I–VII, located in pleural membrane. Anterior edge of sternite VIII in male without median strut. Sternite IX with spiculum gastrale; tergites IX and X membranous or apparently absent. Aedeagus cucujiform, usually oriented upright in abdomen (resting on side in *Phalacrus* and *Phalacropsis*); anterior edge of tegmen usually with medial dorsal strut, sometimes asymmetrical; parameres fused to one another, sometimes separated from each other by longitudinal cleft, usually separated from basal piece by suture, often hinged, but sometimes completely fused to tegmen; penis usually broad, flattened, often with internal sclerites and spicules, flagellum known to occur in only one species (of *Entomocnemus*); anterior edge without struts. Sternite VIII in female with spiculum ventrale. Ovipositor short and broad to moderately elongate, usually with proctigeral and paraproctal baculi; gonocoxites usually subdivided; apex occasionally heavily sclerotized and complex (*Phalacrus*); gonostyli apical or subapical. Internal tract with slender, curved, sclerotized spermatheca (Lawrence *et al.* 2010).

Larval description. Body elongate and more or less parallel-sided. Dorsal surfaces lightly to more or less heavily pigmented, generally smooth; ventral surfaces lightly pigmented. Vestiture usually consisting of scattered simple setae. Surface-grazing larvae usually with darker dorsal pigmentation and longer legs and antennae, while those living within substrates are generally more robust and unpigmented, with short legs and antennae.

Head. Protracted and usually prognathous or slightly declined. Posterior edge of head capsule not to moderately emarginate. Epicranial stem usually absent or quite short; frontal arms lyriform, their bases contiguous. Median endocarina present or absent; paired endocarinae absent. Stemmata five or six on each side. Frontoclypeal suture present or absent. Labrum usually free (partly or completely fused to head capsule in *Phalacrus* and *Phalacropsis*). Antenna short to moderately long, 3-segmented; sensorium usually on preapical antennomere (on basal antennomere in *Phalacrus* and *Phalacropsis*), shorter than to longer than apical antennomere, conical or palpiform. Mandibles symmetrical, usually broad at base and narrow at apex (rarely more elongate), bidentate or tridentate, occasionally with accessory ventral process; incisor edge simple, with one or two subapical teeth or serrate; mesal surface of mandibular base variable; usually with large, extensive mola or smaller, sub-basal mola, which is finely or coarsely tuberculate, or with two or more hyaline processes and no mola; prostheca absent. Ventral mouthparts strongly protracted; maxillary articulating area present or absent. Cardo not distinct; stipes usually wider than long; mala simple, not cleft, apex rounded or truncate, setose; palp 3-segmented. Labium consisting of prementum and postmentum (rarely more or less fused with maxillae); ligula shorter than labial palp, simple, not bilobed; palp 2-segmented, separated by more than width of first palpomere. Hypopharyngeal sclerome absent or consisting of transverse bar only. Hypostomal rods almost always long, sometimes extending to posterior edge of head, diverging posteriorly (rarely absent). Ventral epicranial ridges absent. Gular sutures separate; gula longer than wide, fused to labium or separated from labium by suture.

Thorax. Prothorax not longer than meso- and metathorax combined. Terga without patches or rows of asperities, sometimes with sclerotised plates. Prosternum without armature. Legs moderately well-developed, 5-segmented; pretarsus claw-like with one seta; seta large and spatulate in *Olibrus*; mesocoxae separated by more than two basal coxal diameters.

Abdomen. More than twice length of thorax (not including appendages). Terga not extending laterally beyond edges of sterna. Terga and sterna sometimes with rows of asperities forming longitudinally oriented, open or closed ovals on either side of midline on one or more segments. Segment IX excluding appendages shorter than segment VIII; tergum extending onto ventral surface and sometimes forming articulated plate, with paired, dorsally or

posterodorsally oriented urogomphi and no pit between them. Sternum IX partly or entirely exposed, simple, not enclosed by sternum VIII. Segment X without paired pygopods; anal region posteriorly or posteroventrally oriented. Spiracles annular-uniforous or annular-biforous, sometimes placed at ends of spiracular tubes on segment I–VIII or on I and VIII only (Lawrence *et al.* 2010).

Pupal description. Body surfaces bearing numerous erect setae, some larger on head, anterior margin of pronotum, and posterolateral corners of abdominal segments. Elytral sheath mostly bare. Urogomphi well-developed, tapered to a fine apex. Surface-grazing forms with dark pigmentation; other genera, which pupate hidden in substrates, are generally unpigmented (Lawrence *et al.* 2010).

Distribution and diversity. A total of 632 species and 34 valid genera are recognized in the family. Members occur worldwide except Antarctica, New Zealand (except two species introduced there), most remote Pacific islands, and Chile.

Using the generic concepts defined in this study, meaningful statements can be made regarding distribution and endemism of the genera in Phalacridae. Table 1 summarizes the distributional information of the genera in the family. The Afrotropical and Oriental regions contain the highest richness of genera, each with 16. The Neotropical region is the third richest area, with 14 genera, followed by the Nearctic and Australian regions (12 each). The regions with the highest average latitude, the Eastern and Western Palearctic regions, are the least rich, each with only seven genera.

TABLE 1. Genera of Phalacridae with distribution by biogeographic region. NE=Nearctic; NT=Neotropical; WP=Western Palearctic; EP=Eastern Palearctic; OR=Oriental; AF=Afrotropical; AU=Australian.

GENUS	NE	NT	WP	EP	OR	AF	AU	GENUS	NE	NT	WP	EP	OR	AF	AU
Acylomus	*	*	*	*	*	*	*	***Olibroporus***	*	*					
Antennogasmus						*		***Olibrosoma***			*			*	
Apallodes	*	*						***Olibrus***	*		*	*	*	*	*
Augasmus			*	*	*	*	*	***Paracylomus***					*		
Austroporus					*		*	***Phaenocephalus***				*	*	*	*
Entomocnemus					*	*		***Phalacrinus***					*		*
Eulitrus		*						***Phalacropsis***	*	*					
Grouvelleus					*	*		***Phalacrus***	*	*	*	*	*	*	*
Litochropus	*	*			*		*	***Platyphalacrus***							*
Litochrus				*	*		*	***Pseudolibrus***						*	
Litostilbus	*	*			*			***Pycinus***		*					
Malagasmus						*		***Ranomafanacrinus***						*	
Malagophytus						*		***Steinerlitrus***		*					
Megistopalpus						*		***Stilbus***	*	*	*	*	*	*	*
Neolitochrus	*	*			*			***Sveculus***					*		*
Nesiotus						*		***Tolyphus***			*				
Ochrolitus	*	*						***Xanthocomus***	*	*					

The Afrotropical region contains by far the largest number of endemic genera of Phalacridae, with seven. This is followed by the Neotropical region (three) and the Australian, Oriental, and Western Palearctic regions (each with one).

The generic diversity of Phalacridae is fairly homogeneous across the biogeographic regions, with a higher concentration in those regions containing extensive tropical belts. Additionally, seven genera occur in both the Eastern and Western Hemispheres.

Revised checklist of genera of Phalacridae. The checklist below includes a summary of the newly proposed genera and genus-level synonymy. Objective synonyms are in parentheses. The sequence of taxonomic accounts in this work follows the arrangement below.

PHAENOCEPHALUS-GROUP

1. ***Phaenocephalus*** Wollaston, 1873
   Phalacratomus Scott 1922, **syn. nov.**
   Heterostilbus Champion 1924, **syn. nov.**
2. ***Phalacrinus*** Blackburn, 1891
   Sphaerostilbus Champion 1924, **syn. nov.**
3. ***Ranomafanacrinus*** Gimmel, **gen. nov.**

STILBUS-GROUP

4. ***Acylomus*** Sharp, 1888
   Liophalacrus Sharp 1888, **syn. nov.**
   Coelocoelius Guillebeau 1893
   Ganyrus Guillebeau 1894, **syn. nov.**
   Podocesus Guillebeau 1894, **syn. nov.**
   Tinodemus Guillebeau 1894, **syn. nov.**
   Ledorus Guillebeau 1895 (=*Dolerus* Guillebeau 1894), **syn. nov.**
   Astenulus Guillebeau 1896, **syn. nov.**
   Afronyrus Švec 2006, **syn. nov.**
5. ***Nesiotus*** Guillebeau, 1896
6. ***Stilbus*** Seidlitz, 1872 (=*Olistherus* Seidlitz 1872; *Eustilbus* Sharp 1888)
   Stilboides Guillebeau 1894
   Microstilbus Guillebeau 1894
7. ***Xanthocomus*** Guillebeau, 1893
   Leptostilbus Casey 1916

PSEUDOLIBRUS-GROUP

8. ***Litostilbus*** Guillebeau, 1894
   Pseudolitochrus Liubarsky 1993, **syn. nov.**
9. ***Megistopalpus*** Guillebeau, 1895 (=*Megapalpus* Guillebeau 1893)
10. ***Pseudolibrus*** Flach, 1889
    Biophytus Guillebeau, 1894, **syn. nov.**
    Polyaloxus Guillebeau 1894, **syn. nov.**

PHALACRUS-GROUP

11. ***Phalacropsis*** Casey, 1890
12. ***Phalacrus*** Paykull, 1800
    Glaurosoma Thomson 1859

OLIBROPORUS-GROUP

13. ***Austroporus*** Gimmel, **gen. nov.**
14. ***Olibroporus*** Casey, 1890
    Parasemus Guillebeau 1894, **syn. nov.**
15. ***Platyphalacrus*** Gimmel, **gen. nov.**
16. ***Pycinus*** Guillebeau, 1893
    Ochrodemus Guillebeau 1893, **syn. nov.**
    Radinus Guillebeau 1893, **syn. nov.**
    Euphalacrus Champion 1925, **syn. nov.**

OCHROLITUS-GROUP

17. ***Ochrolitus*** Sharp, 1889
    Gorginus Guillebeau 1894 (=*Erythrolitus* Casey 1916), **syn. nov.**
18. ***Sveculus*** Gimmel, **gen. nov.**

OLIBRUS-GROUP

19. ***Olibrus*** Erichson, 1845
    Idiobius Gistel 1856
20. ***Tolyphus*** Erichson, 1845
    Pharcisinus Guillebeau 1894

OLIBROSOMA-GROUP

21. ***Antennogasmus*** Gimmel, **gen. nov.**
22. ***Malagasmus*** Gimmel, **gen. nov.**
23. ***Olibrosoma*** Tournier, 1889

Helectrus Guillebeau 1892
Pyracoderus Guillebeau 1892
Litochroides Guillebeau 1892
Lichrotus Lyubarsky 1993, **syn. nov.**

LITOCHROPUS-GROUP

24. ***Litochropus*** Casey, 1890
25. ***Neolitochrus*** Gimmel, **gen. nov.**

INCERTAE SEDIS GENERA

26. ***Apallodes*** Reitter, 1873
Litolibrus Sharp 1889, **syn. nov.**
Sphaeropsis Guillebeau 1893, **syn. nov.**
Gyromorphus Guillebeau 1894, **syn. nov.**
27. ***Augasmus*** Motschulsky, 1858
Liocrus Flach 1889
Heterolitus Guillebeau 1893
Parischius Guillebeau 1896
Megischius Guillebeau 1896, **syn. nov.**
Nematolibrus Sahlberg 1913, **syn. nov.**
28. ***Entomocnemus*** Guillebeau, 1894
Stilbomimus Champion 1924, **syn. nov.**
29. ***Eulitrus*** Sharp, 1889
30. ***Grouvelleus*** Guillebeau, 1892
Ochrolitoides Champion 1924, **syn. nov.**
Litotarsus Champion 1925, **syn. nov.**
31. ***Litochrus*** Erichson, 1845
Merobrachys Guillebeau 1895 (=*Micromerus* Guillebeau 1892), **syn. nov.**
32. ***Malagophytus*** Gimmel, **gen. nov.**
33. ***Paracylomus*** Gimmel, **gen. nov.**
34. ***Steinerlitrus*** Gimmel, **gen. nov.**

Key to world genera of Phalacridae

1 Head capsule width at tempora distinctly narrower than width at eyes (Figs. 2j, k); antennomeres IX and X elongate-cylindrical (Figs. 4b, 5b); mesoventral disc medially on same plane as metaventral process, metaventral process not exceeding middle of mesocoxae (Figs. 4f, 5f); prosternal process usually vertically laminate; tarsi 4-4-4 (penultimate segment fused with terminal segment), all tarsi compressed (Figs. 4d, 5d); warm regions of the Old World (*Phaenocephalus*-group) 2

\- Head capsule width at tempora equal to width at eyes (Fig. 2l); antennomeres IX and X usually wider than long; mesoventral disc either completely divided medially by a mesoventral plate, or sunken anterior to metaventral process, metaventral process usually exceeding middle of mesocoxae; prosternal process usually wide, not laminate; tarsi 5-5-5 (5-5-4 or rarely 4-5-4 in some), penultimate tarsomere embraced by lobed tarsomere III (often difficult to observe in dry-mounted specimens), metatarsi usually distinctly longer than other tarsi, not compressed; worldwide 4

2(1) Prosternal process stout, expanded at tip, mesoventrite with a distinct concavity for its reception just anterior to tip of metaventral process (Fig. 37f); Madagascar . . . . . ***Ranomafanacrinus*, gen. nov.** (p. 26)

\- Prosternal process narrow, vertically laminate, not expanded at tip, mesoventrite flat or gently sloping anterior of metaventral process 3

3(2) Antennal scape flattened, subtriangular (Fig. 5b); clypeus forming a continuous shelf between eyes; mandibular apex simple (Fig. 5a); labial palp with terminal segment flattened, wider than long (Fig. 2h); elytra distinctly explanate laterally; elytra distinctly punctato-striate; anal lobe of hind wing ovate (Fig. 5e); size large, 2.0 mm or more; India to Australia . . . . . ***Phalacrinus*** Blackburn (p. 23)

\- Antennal scape more or less cylindrical (Fig. 4b); clypeus depressed, not forming a continuous shelf between eyes; mandibular apex bidentate (Fig. 4a); labial palp with terminal segment cylindrical, longer than wide (Fig. 2i); elytra not distinctly explanate laterally; elytra not or barely punctate or striate; anal lobe of hind wing straplike (Fig. 4e); size small, 1.8 mm or less; Africa to Japan, northern Australia, and Fiji . . . . . ***Phaenocephalus*** Wollaston (p. 18)

4(1) Mesocoxal cavities nearly contiguous (Fig. 33f); labial palpomere III with one or two long, spinelike setae (Fig. 2g); Old World tropics . . . . . ***Grouvelleus*** Guillebeau (p. 111)

\- Mesocoxal cavities distinctly separated (as in Fig. 27f); labial palpomere III without long setae 5

5(4) With the following combination of characteristics: mesocoxae separated by distinctly less than half width of coxal cavity (Fig. 29f), metatarsomere I much shorter than II (Fig. 29d), AND metaventral postcoxal lines not separated from coxal cavities (Fig.

29f); New World tropics and subtropics . . . . . ***Apallodes*** Reitter (p. 97)

- Either mesocoxae separated by more than half width of coxal cavity, metatarsomere I longer than II, or metaventral postcoxal lines separated from coxal cavities 6

6(5) Protibia with strong ctenidium on outer edge, row parallel to long axis of tibia overall, extending at least one-third length of tibia (Figs. 12c, 32c) 7

- Protibia without ctenidium (Fig. 19c), or with obliquely oriented ctenidium confined to apical one-fourth of tibia (Fig. 34c) 16

7(6) Scutellar shield large, as wide as or wider at base than length of eye at widest point (as in Fig. 2b); elytron rarely with fewer than three striae; prosternum conspicuously setose medially; metaventral process not protruding anteriorly; Afrotropical, southeast Asian, and circum-Caribbean (*Pseudolibrus*-group). 8

- Scutellar shield small, usually narrower at base than greatest length of eye (as in Fig. 2a); elytron rarely with more than two striae; prosternum not setose medially; metaventral process variable; worldwide. 10

8(7) Elytron with one (rarely), two, or three nearly complete striae; elytra with spectral iridescence; southeast Asian and circum-Caribbean . . . . . ***Litostilbus*** Guillebeau (p. 46)

- Elytron with nine nearly complete discal striae; elytra not iridescent; Afrotropical 9

9(8) Maxillary palp greatly enlarged, subequal in length to antenna (Fig. 2f); size large, about 3.2 mm; Yemen. . . . . ***Megistopalpus*** Guillebeau (p. 47)

- Maxillary palp normal; size smaller, 2.7 mm or less; Africa, Madagascar, Seychelles . . . . . ***Pseudolibrus*** Flach (p. 48)

10(7) Metaventral process lobed anteriorly, surpassing mesocoxae, shelflike (Figs. 30f, 32f) 11

- Metaventral process truncate anteriorly, not or barely exceeding mesocoxae, not shelflike (Figs. 20f, 25f). 12

11(10) Metatarsomere I short, much shorter than metatarsomere II (Fig. 32d); apical metatibial ctenidium transverse (Fig. 32d); sutural stria completely absent from elytron; Neotropical . . . . . ***Eulitrus*** Sharp (p. 107)

- Metatarsomere I much longer than metatarsomere II (Fig. 30d); apical metatibial ctenidium oblique (Fig. 30d); sutural stria present (as in Fig. 2b); Old World. . . . . ***Augasmus*** Motschulsky (p. 102)

12(10) Prosternal process projecting, acute apically when viewed laterally, exceeding procoxae when viewed ventrally; mesoventral plate extending posteriorly to metaventrite, dividing mesoventral disc in two (Figs. 20f, 21f) (*Ochrolitus*-group) 13

- Prosternal process rounded or step-like when viewed laterally, not exceeding procoxae when viewed ventrally; mesoventral plate not extending posteriorly to metaventrite, mesoventral disc continuous behind plate (Figs. 24f, 25f, 26f) (*Olibrosoma*-group) 14

13(12) Elytron with 2 or 3 sutural striae (as in Fig. 2a); prosternal process apically with a row of spinelike setae (similar to Fig. 3a); New World . . . . . ***Ochrolitus*** Sharp (p. 71)

- Elytron with 1 sutural stria (as in Fig. 2b); prosternal process with translucent process apically, devoid of setae (Fig. 40g); Indo-Australia and Madagascar . . . . . ***Sveculus*, gen. nov.** (p. 72)

14(12) Metaventral lines separated (sometimes only slightly) from mesocoxal cavities (Fig. 25f); antennomere XI not modified. . . 15

- Metaventral lines not separated from mesocoxal cavity (Fig. 24f); male antennomere XI enlarged, variable, but sometimes nearly as long as remainder of antenna (Fig. 24b); Afrotropical . . . . . ***Antennogasmus*, gen. nov.** (p. 84)

15(14) Antennal club of 4 or 5 articles (Fig. 26b); Middle East and Africa, not including Madagascar. . . ***Olibrosoma*** Tournier (p. 91)

- Antennal club of 3 articles (Fig. 25b); Madagascar only . . . . . ***Malagasmus*, gen. nov.** (p. 87)

16(6) Elytron with 4 distinctly impressed discal striae, striae without obvious punctures, oblique, converging posteriorly towards suture (Fig. 42g); abdominal ventrite I with paired lines (Fig. 3b); scutellar shield large, as wide or wider at base than length of eye at widest point (as in Fig. 2b); metaventrite not protruding anteriorly; Madagascar . . . . . ***Malagophytus*, gen. nov.** (p. 116)

- Discal striae, when present, with row of distinct punctures and/or more or less parallel to suture; scutellar shield usually narrower at base than greatest length of eye (as in Fig. 2a) (large only in *Phalacrus* and *Phalacropsis*, which have a protruding metaventrite); worldwide 17

17(16) Metatarsomere I as long as or longer than metatarsomere II, articulation between them inconspicuous, rigid (Fig. 27d) 18

- Metatarsomere I distinctly shorter than metatarsomere II, or if nearly as long, articulation between segments distinct, flexible (Fig. 15d). 21

18(17) Meso-metaventral margin emarginate at apex for reception of protrusive prosternal process (prosternal process often with horizontally laminate structure) or truncate, not extending anteriorly beyond mesocoxae (Fig. 31e); metaventral lines not separated from coxal cavities; elytra with spectral iridescence (sometimes weak); Old World. . . . . ***Entomocnemus*** Guillebeau (p. 104)

- Meso-metaventral margin truncate or lobed, extending anteriorly beyond mesocoxae (Fig. 34f), prosternal process not protruding; if lobe truncate, metaventral lines separated from coxal cavities and spectral iridescence absent; elytra with or without spectral iridescence; New World and Australasia 19

19(18) Protibia with short ctenidium, with oblique row of 5–10 spines subapically (Fig. 34c); metaventral lines not separated from coxal cavities; Oriental, Australian, and eastern Palearctic regions . . . . . ***Litochrus*** Erichson (p. 112)

- Protibial ctenidium absent, with only 1 or 2 spines at outer apical angle of tibia (Figs. 27c, 28c); metaventral lines separated from coxal cavities (but often difficult to observe); New World and Australian region (*Litochropus*-group) 20

20(19) Mesoventral plate extending posteriorly to metaventral process, borders complete (Fig. 27f) (difficult or impossible to see when beetle is in repose); USUALLY with the following characteristics: elytra without microsculpture (not iridescent), with distinct transverse strigae over virtually entire surface; eye indistinctly emarginate medially; elytra with 1 engraved sutural stria (occasionally with 2); mesotibia with only 1 apical spur (2 in Australasian forms); longest metatibial spur not longer than width of tibial apex; generally more globular species; New World and Australia . . . . . ***Litochropus*** Casey (p. 92)

- Mesoventral plate with lateral borders becoming obsolete posteriorly, not reaching metaventral process (Fig. 28f); USUALLY with the following characteristics: elytra with obvious transverse microsculpture (iridescent), without transverse strigae; eye distinctly emarginate; elytra with 2 engraved sutural striae (rarely with 1); mesotibia with 2 apical spurs; longest metatibial spur distinctly longer than width of tibial apex; generally more flattened species; New World and southeast Asia . . . . . ***Neolitochrus*, gen. nov.** (p. 95)

21(17) Scutellar shield large, width at base exceeding maximum diameter of eye in dorsal view (as in Fig. 2b); frontoclypeus shelflike, concealing antennal insertions (Fig. 2d); metafemora with row of long setae subapically; metaventral process lobed anteriorly, exceeding mesocoxae (Figs. 14f, 15f); metaventral lines not separated from mesocoxal cavities; aedeagus resting on its side in repose (*Phalacrus*-group) 22

- Scutellar shield smaller, width at base subequal to or less than maximum diameter of eye in dorsal view (as in Fig. 2a); frontoclypeus not shelflike, antennal insertions exposed (Figs. 2c, e); metafemora usually without row of long setae; metaventral process and metaventral lines various; aedeagus upright in repose 23

22(21) Sutural stria absent; mandibles short, stout, bidentate (Fig. 14a); ovipositor with gonocoxae not spiniform, gonostyli attached apically (Fig. 3d); color testaceous to brunneous; highlands of the American Cordillera . . . . . ***Phalacropsis*** Casey (p. 51)

- Sutural stria present or (rarely) absent; mandibles usually long, sickle-shaped, with acuminate apex (Fig. 15a); ovipositor with gonocoxae spiniform, gonostyli attached subapically (Fig. 3c); color usually piceous to black, sometimes with subapical elytral maculations, occasionally testaceous or brunneous; worldwide. . . . . ***Phalacrus*** Paykull (p. 53)

23(21) Metaventral lines not separated from mesocoxal cavities (Fig. 22f) 24

- Metaventral lines separated from mesocoxal cavities (Figs. 10f, 35f) 30

24(23) Mesoventral process lobed anteriorly, exceeding mesocoxae (Figs. 22f, 36f) 25

- Mesoventral process not lobed anteriorly, not exceeding mesocoxae (Fig. 17f) (*Olibroporus*-group) 27

25(24) Eye with small acute emargination on posterior border (Fig. 43c); elytron with sutural stria scarcely visible or absent, other striae absent; labrum with lateral apical tufts of stout setae; female ovipositor lightly sclerotized, not modified; male tegmen with parameres fused to basal piece; Neotropical. . . . . ***Steinerlitrus*, gen. nov.** (p. 120)

- Eye without emargination on posterior border; elytron with distinct sutural stria, often with additional striae; labrum without tufts of stout setae; female ovipositor moderately sclerotized and modified into a wedge-like organ (Fig. 3e); male tegmen with parameres articulated with basal piece; all major regions except Neotropical (*Olibrus*-group). 26

26(25) Clypeus broadly emarginate at apex (Fig. 2e); metatibial spurs broad, spatulate (Fig. 23d); protibia abruptly expanded at apex (Fig. 23c); body nearly parallel-sided; pronotal hind angles nearly obliterated, not tightly embracing elytral humeri; elytron with full complement of distinct striae; mandible with apex simple (Fig. 23a); upper portion of eye often with facets abruptly reduced in size; Mediterranean to central Asia . . . . . ***Tolyphus*** Erichson (p. 81)

- Clypeus with apical margin straight or nearly straight (as in Fig. 2c); metatibial spurs narrow, not flattened (Fig. 22d); protibia gradually or not expanded at apex (Fig. 22c); body more ovoid; pronotal hind angles evident, tightly embracing elytral humeri when beetle is in repose; elytron usually with at least lateral striae indistinct; mandible with apex tridentate (Fig. 22a); all eye facets similar in size; all major regions except Neotropical . . . . . ***Olibrus*** Erichson (p. 75)

27(24) Mandibular apex tridentate (rarely apex simple), with dorsal cusp smaller than others but sharply pointed (Figs. 16a, 19a); mesoventral plate with lateral borders not extending posteriorly to mesocoxal cavities (Figs. 16f, 18f); eye with short interfacetal setae; Old World 28

- Mandibular apex bidentate, with a series of two or more small, blunt, dorsal teeth (Figs. 17a, 19a); mesoventral plate with lateral borders extending posteriorly almost to mesocoxal cavities, then curving laterad (Figs. 17f, 19f); eye without interfacetal setae; New World 29

28(27) Highly flattened in lateral view (Fig. 39h); mandible with strong retinaculum and without ventral ridge (Fig. 18a); southwestern Australia . . . . . ***Platyphalacrus*, gen. nov.** (p. 64)

- Rounded in lateral view; mandible without retinaculum and with ventral ridge (Fig. 16a); Australasian region . . . . . ***Austroporus*, gen. nov.** (p. 58)

29(27) Mandible without ventral ridge (Fig. 17a); abdominal ventrite I with calli (normally visible only in slide preparations); elytra without spectral iridescence; globose in lateral view; prosternum not conspicuously setose medially; Nearctic and Neotropical . . . . . ***Olibroporus*** Casey (p. 61)

- Mandible with ventral ridge (Fig. 19a); abdominal ventrite I without calli; elytra with or without spectral iridescence, if without, body flattened in lateral view; prosternum usually densely setose medially; Neotropical only . . . . . ***Pycinus*** Guillebeau (p. 68)

30(23) Elytron with two engraved sutural striae (as in Fig. 2a) and spectral iridescence; prosternal process rounded in lateral view, metaventral process correspondingly anteriorly protruding; Sri Lanka . . . . . ***Paracylomus*, gen. nov.** (p. 119)

- Elytron with only one engraved sutural stria (as in Fig. 2b) and without spectral iridescence, although iridescence is often present as a result of transverse wavy microsculpture; prosternal process angulate in lateral view, metaventral process correspondingly truncate (*Stilbus*-group—NOTE: at present the genera of this group can be reliably separated only by examination of male genitalia) 31

31(30) Tegmen with parameres fused to basal piece, without a complete suture (Figs. 9h, 10h); elytral punctures, when present, round, not crescent-shaped; prosternal process USUALLY with row of stiff setae (*Nesiotus* with pair of setae); elevated portion of mesoventrite USUALLY expressed as more than just a margin anterior to metaventral process; metaventral postcoxal lines smoothly arcuate only in *Nesiotus* (Fig. 9f, endemic to Madagascar), otherwise angulate (Fig. 10f) 32

- Tegmen with parameres articulated and hinged to basal piece (Figs. 6h, 11h); elytral punctures, when present, USUALLY crescent-shaped, especially laterally; prosternal process with or without row of stiff setae, often with pair of setae; elevated portion

of mesoventrite USUALLY expressed as merely a margin anterior to metaventral process; metaventral postcoxal lines USUALLY arcuate behind (Figs. 6f, 11f), sometimes angulate, but NEVER with a spur or with medial branch absent 33

32(31) Eye normally shaped, not extended posteriorly on ventral surface of head capsule (as in Fig. 2m); elytron without obvious rows of microsetae; metaventral postcoxal lines angulate posteriorly, often with a spur (Fig. 10f), medial branch sometimes absent; metatarsomeres I and II with flexible articulation (Fig. 10d); antenna with normal proportions (Fig. 10b) **. . . . . *Stilbus*** Seidlitz (p. 38)

- Eye extended posteriorly on ventral surface of head capsule (Fig. 2n); elytron with conspicuous rows of microsetae; metaventral postcoxal lines smoothly arcuate posteriorly, never with a spur or missing branch (Fig. 9f); metatarsomeres I and II with rigid articulation (Fig. 9d); antenna modified (more extreme in male), with funicle segments compressed and club elongate, longer than remainder of antenna (Fig. 9b). . . . . ***Nesiotus*** Guillebeau (p. 36)

33(31) Mandible with ventral ridge (Fig. 11a); ventral seta-lined ridge posterior to eye oriented obliquely (Fig. 2m); elytron, especially near suture, with rows of relatively distinct, rounded punctures; male pro- and mesotarsi with tarsomere II often expanded and elongated, much larger than tarsomere III (Fig. 11c); penis with spinose tri- or tetrapartite structure at apex (Fig. 11i); metaventral lines smoothly arcuate (Fig. 11f); prosternal process exceeding procoxae posteriorly, distinctly arcuate, with row of stout setae; body form generally elongate, pronotum more than half as long as wide; usually reddish in color . . . . . ***Xanthocomus*** Guillebeau (p. 42)

- Mandible without ventral ridge (Figs. 6a, 7a, 8a); ventral seta-lined ridge posterior to eye arcuate or oriented transversely (Fig. 2n); elytron with shallow crescentiform punctures, stronger laterally; penis with apex simple or with rod-like structures at apex; metaventral lines ranging from smoothly arcuate to acuminately pointed (Figs. 6i, 7i, 8i); prosternal process not or only barely exceeding procoxae posteriorly, truncate, often (but not always) with only one setae at each corner; body form usually shorter and more globose, pronotum less than half as long as wide; color variable**. . . . . *Acylomus*** Sharp (p. 28)

Genus group and generic accounts

PHAENOCEPHALUS-GROUP

Phaenocephalidae Matthews 1899: 205. Type genus: *Phaenocephalus* Wollaston.

Diagnosis. This group may be recognized by the posteriorly narrowed head capsule, the cylindrical antennal club, the elevated mesoventral disc, and the compressed metatarsi. The exposed portion of the metacoxae appears to extend less laterally than those of other Phalacridae, so that the metanepisternum and first abdominal ventrite are in broader contact. This group corresponds to the subfamily Phaenocephalinae proposed by Lawrence and Newton (1995).

Distribution and diversity. Nineteen recognized species, occurring in the Afrotropical, Oriental, and Australian regions.

Included genera (3). *Phaenocephalus* Wollaston, *Phalacrinus* Blackburn, *Ranomafanacrinus* Gimmel.

1. *Phaenocephalus* Wollaston, 1873

(Figs. 2i, j; 4; 37a, b)

Phænocephalus Wollaston 1873: 167. Type species: *Phaenocephalus castaneus* Wollaston 1873, fixed by monotypy.
Phalacratomus Scott 1922: 240. Type species: *Phalacratomus exiguus* Scott 1922, fixed by original designation. **Syn. nov.**
Heterostilbus Champion 1924*b*: 165. Type species: *Heterostilbus marginatus* Champion 1924, fixed by original designation. **Syn. nov.**

Type material. *Phaenocephalus castaneus* Wollaston: one syntype, only a single maxilla and labium remain (on an acetate card in Canada balsam, "Phanocephalus [*sic*] [black line dividing label] \ Maxilla, Labium of \ Aug 1885 [handwritten] // 759 // Matthews coll. \ 1904–120. [on underside of label]" (BMNH). The lectotype is not designated with the expectation that additional, intact specimens (Wollaston implied that there were multiples) will turn up from the syntype series.

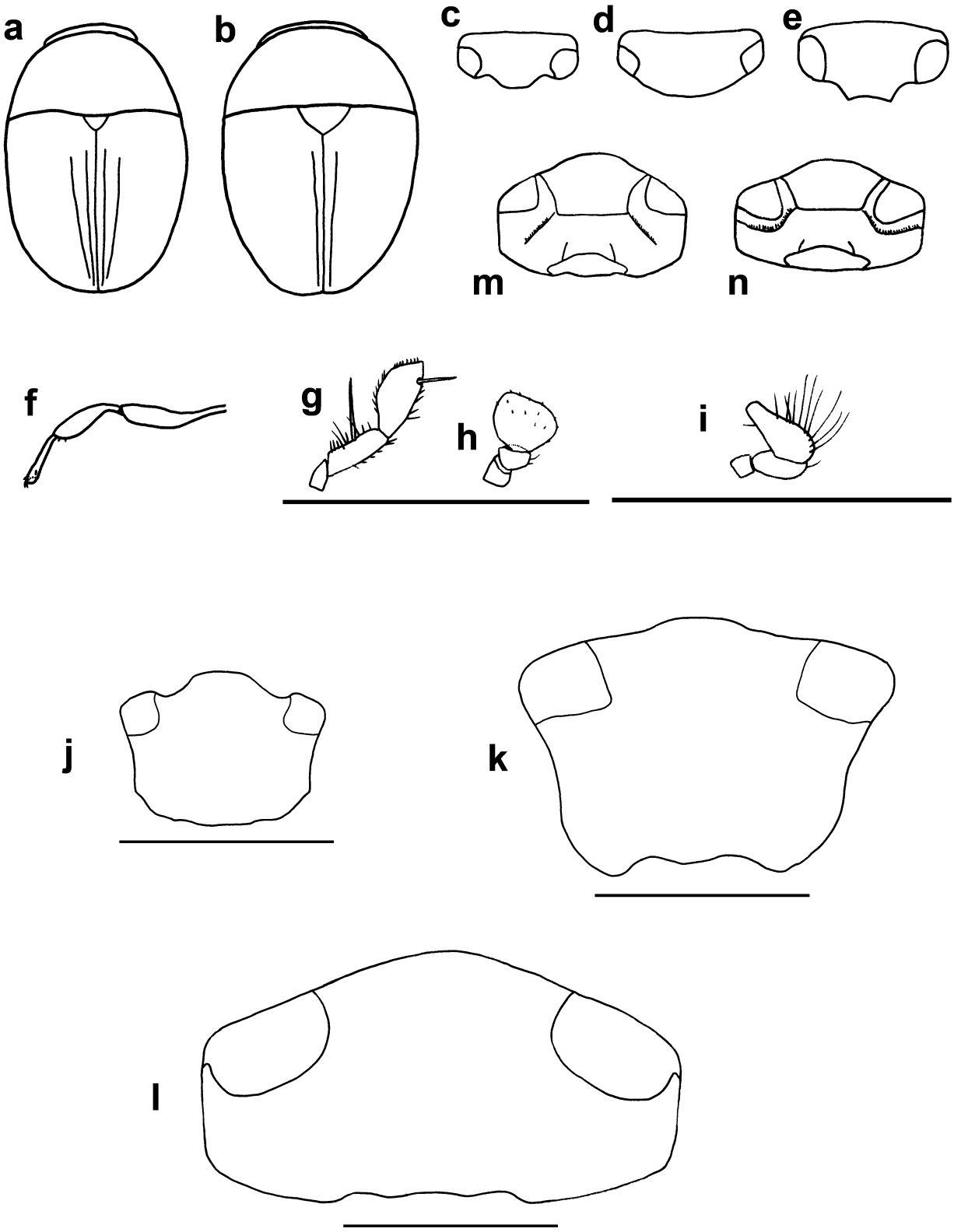

FIGURE 2. Key characters for Phalacridae. (a) Schematic of dorsal characters showing small scutellar shield and two sutural striae. (b) Schematic of dorsal characters showing large scutellar shield and one sutural stria. Frontal view of head capsule of (c) *Stilbus*; (d) *Phalacrus*; (e) *Tolyphus*. (f) Maxillary palpus of *Megistopalpus*. Labial palpus of (g) *Grouvelleus*; (h) *Phalacrinus* (scale bar = 0.5 mm); (i) *Phaenocephalus* (scale bar = 0.2 mm). Dorsal view of head capsule of (j) *Phaenocephalus*; (k) *Phalacrinus*; (l) *Acylomus* (scale bars = 0.5 mm). Ventral view of head capsule of (m) *Xanthocomus*; (n) *Nesiotus*.

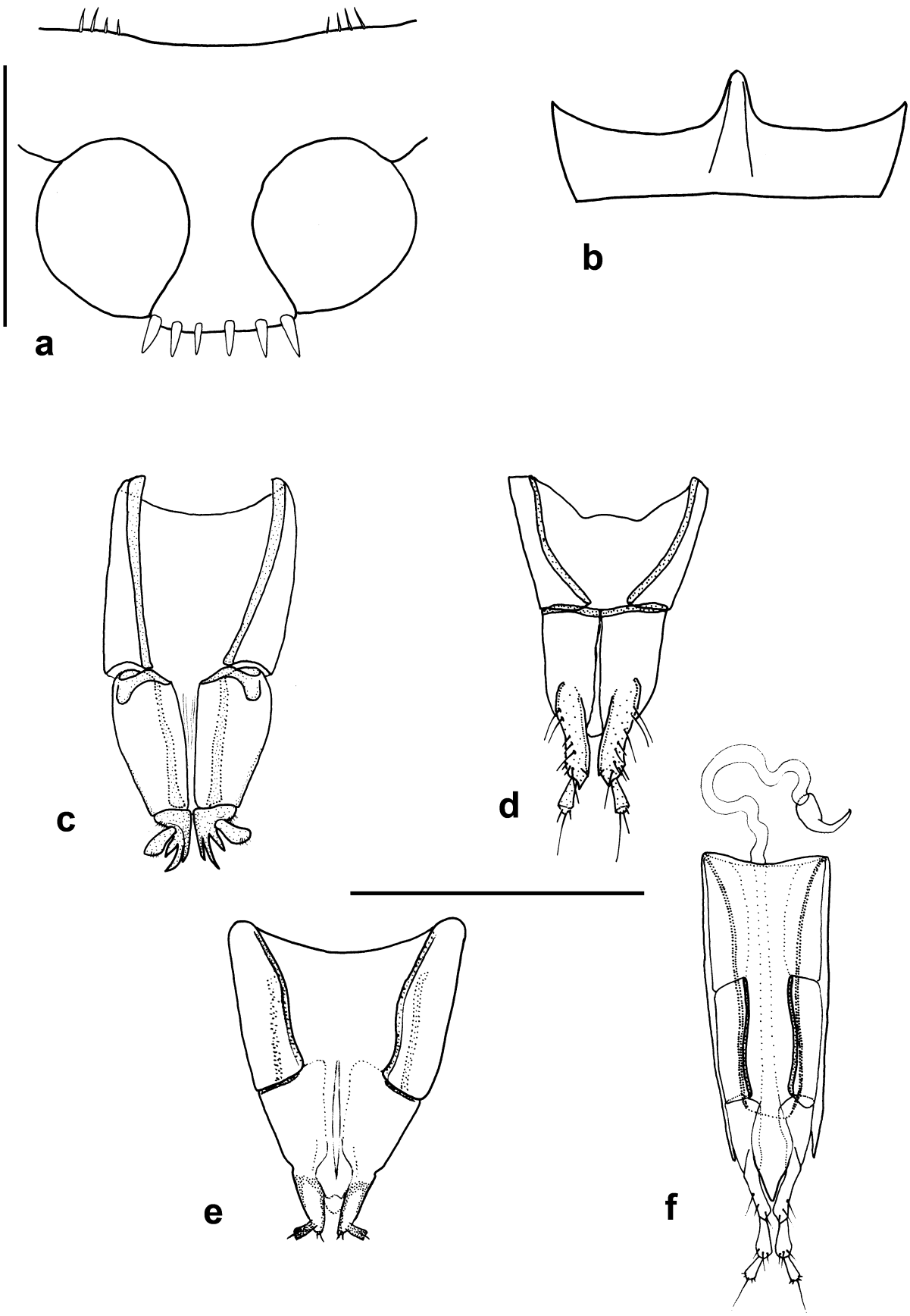

FIGURE 3. Key characters for Phalacridae. (a) Prosternal process of *Acylomus aciculatus* Sharp (scale bar = 0.5 mm). (b) First abdominal ventrite of *Malagophytus steineri* Gimmel. Ovipositor of (c) *Phalacrus* sp.; (d) *Phalacropsis dispar* (LeConte); (e) *Olibrus aeneus* (Fabricius); (f) *Litostilbus testaceus* (Fabricius) (scale bars = 0.5 mm).

Phalacratomus exiguus Scott: 10 syntypes found in BMNH, card mounted (plus one missing from card), the first specimen (with Scott's handwritten "TYPE" label) is chosen as the lectotype in order to stabilize the name, "19 [handwritten on card] // Type [red-bordered disc] // Silhouette, 1908 \ Seychelles Exp. // Seychelle Islands. Percy Sladen Trust Expedition. 1913–170. [on underside of label] // Phalacratomus exiguus \ TYPE. H. Scott [handwritten] // LECTOTYPE \ Phalacratomus \ exiguus Scott \ des. M.L. Gimmel 2011 [red label]" (BMNH). Nine syntypes from other localities in the Seychelles (including Mahé) were examined, each with label affixed "PARALECTOTYPE \ Phalacratomus \ exiguus Scott \ det. M.L. Gimmel 2011 [yellow label]".

Heterostilbus marginatus Champion: five syntypes in BMNH, first one (with Champion's "type" label) selected as the lectotype to stabilize the species name, "W. Almora Divn \ Kumaon U.P. \ June 1917. HGC. // 996 [handwritten] // Type H.T. [red-bordered disc] // Heterostilbus marginatus type Ch [handwritten] // Heterostilbus (n. gen.) marginatus, Ch. // Ent. Mo. Mag. 1924. \ G. C. C. det. [on underside of label] // G.C. Champion. \ Brit. Mus. \ 1924–63. [on underside of label] // LECTOTYPE \ Heterostilbus \ marginatus Champion \ des. M.L. Gimmel 2011 [red label]" (BMNH), card mounted. Four syntypes with labels reading "W. Almora" or "Bhatkot" were identified as paralectotypes, while two specimens with "Ranikhet" were excluded from the syntype series (only five specimens and the two former localities were listed in the original description). Each of the four received the label "PARALECTOTYPE \ Heterostilbus \ marginatus Champion \ det. M.L. Gimmel 2011 [yellow label]".

Diagnosis. May be readily recognized by the complete or almost complete lack of a sutural stria, elevated mesoventral disc, short tarsi with formula 4-4-4, and ovoid antennomere I.

Description. Very small to small, total length 1.1–1.8 mm. Dorsal surface from completely testaceous to completely black, often with lighter pronotum and elytral margins (Fig. 37a, b). Tibial spur formula 0-1-1, tarsal formula 4-4-4 in both sexes.

Head. Distinctly constricted behind eyes (Fig. 2j); without median endocarina. Eyes medium-sized; facets flat; interfacetal setae absent; not emarginate medially; without posterior emargination; periocular groove absent; without setose groove ventrally behind eye. Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennomere I ovoid; antennal club loosely 3-segmented, club symmetrical, nearly cylindrical, long, sometimes longer than remainder of antenna; antennomere XI not turbinate (Fig. 4b). Mandible (Fig. 4a) stout, with apex bidentate; without retinaculum; mandible without ventral ridge. Maxillary palpomere IV fusiform, inner edge slightly swollen medially; galea rounded; lacinia setose, without spines. Mentum with sides divergent toward apex; labial palpomere III constricted at apex (Fig. 2i). Labrum with apical margin arcuate. Gular sutures long, extending more than halfway to ventral mouthparts.

Thorax. Pronotum without obvious microsetae; with distinct scutellar lobe. Prosternum anteriorly with discontinuous row of marginal setae, a gap present medially, setae normal; procoxal cavity with anterolateral notchlike extension; prosternal process rounded in lateral view, not setose preapically, without spinelike setae at apex. Procoxae nearly contiguous; protrochanter without setae; protibia without ctenidium on kickface, apical spurs absent (Fig. 4c). Scutellar shield small, width at base less than length of eye. Elytron without spectral iridescence; sutural and discal striae completely absent; without transverse strigae; lateral margin without row of sawtooth-like setae. Mesoventral plate deeply notched anteriorly, not extending posteriorly to metaventrite, not forming procoxal rests; mesoventral disc elevated medially, forming a large plate anterior to metaventral process, not setose; mesanepisternum with complete transverse carina; mesocoxae separated by more than half width of a coxal cavity (Fig. 4f). Mesotarsomere III not bilobed. Metaventral process extending anteriorly just to halfway point of mesocoxae; metaventral postcoxal lines not separated from mesocoxal cavity margin (Fig. 4f); discrimen long, extending more than halfway to anterior margin of metaventral process; metendosternite with anterior tendons widely separated, ventral process intersecting ventral longitudinal flange at anterior margin (Fig. 4g). Anterior margin of metacoxa without emargination sublaterally; metacoxal plate without transverse line; metatibial foreface with apical ctenidium straight, perpendicular overall to long axis of tibia; apical spur cylindrical, distinctly shorter than width of tibial apex; metatarsomeres compacted, nearly identical to mesotarsomeres, joint between I and II flexible (Fig. 4d); metatarsomere III not bilobed. Hind wing (Fig. 4e) with distinct, straplike anal lobe; leading edge with incomplete row of long setae; AA_{3+4} not apparent; cubitoanal system not forked; CuA_2 and MP_{3+4} without distal remnants; r4 absent; apical field large, occupying well over half of wing, with large curved fleck and two smaller flecks present distal to rp-mp2; small transverse sclerite and small oval sclerite present just distal to end of radial bar.

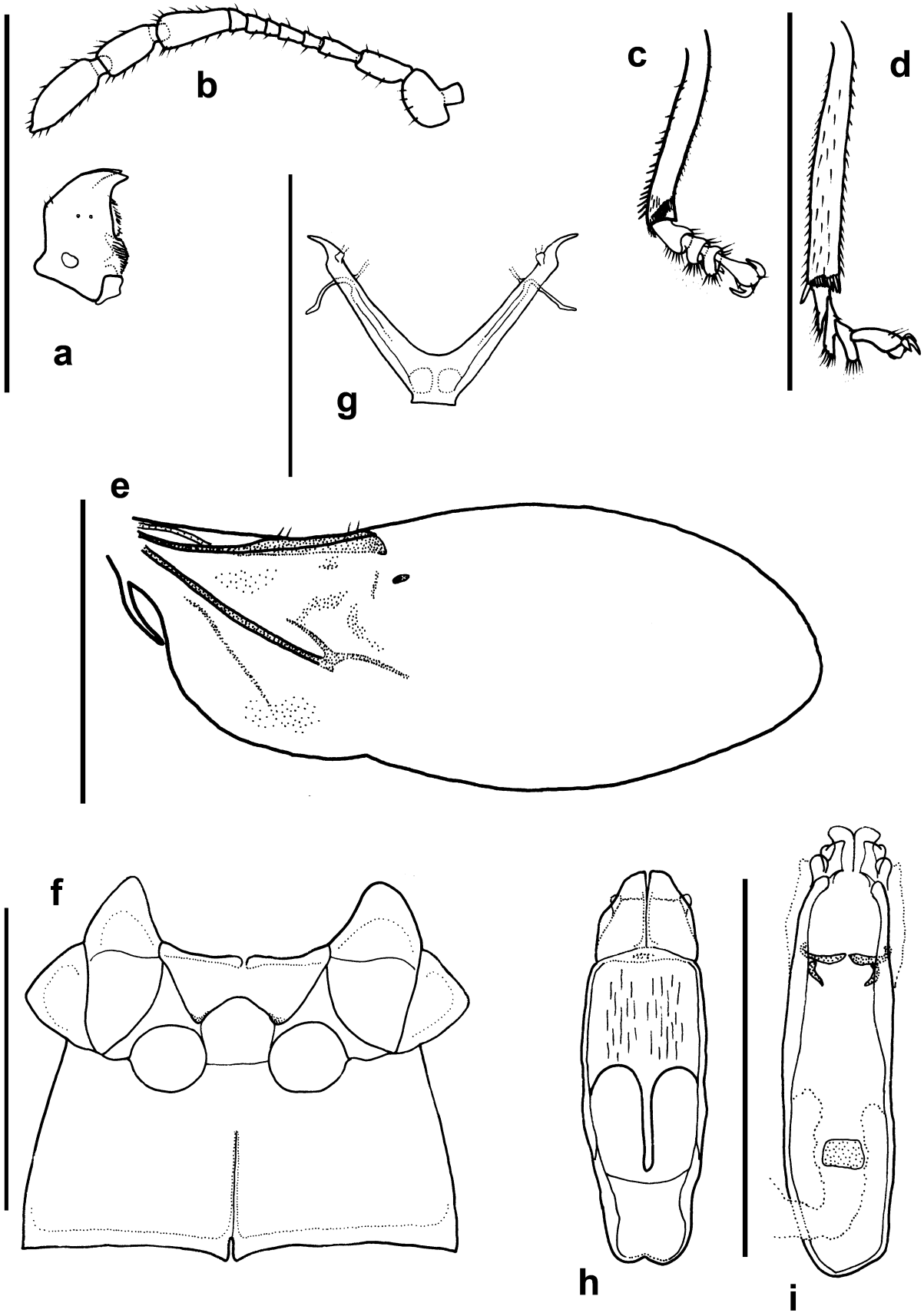

FIGURE 4. *Phaenocephalus* sp., male. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 0.5 mm). (h) Tegmen, ventral; (i) penis, ventral (scale bar = 0.5 mm).

Abdomen. Abdominal ventrite I without paired lines or calli; spiracles absent on segment VII. Male with aedeagus upright in repose; tegmen (Fig. 4h) with symmetrical anterior margin, parameres hinged to basal piece, parameres with medial longitudinal division; penis (Fig. 4i) parallel-sided, with fields of endophallic spicules, bilobed or complex apically; spiculum gastrale Y-shaped, with long basal rod. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. Specimens have been collected using diverse methods, including forest litter sifting (unusual for the family), Malaise traps, canopy fogging, pitfalls, and beating banana leaves.

Distribution and diversity. I have seen specimens from Africa as far west as Nigeria, Cameroon, and Angola, to Madagascar and the Seychelles (first records for the Afrotropical Region), eastward through the Indian Subcontinent to Japan and southeast Asia (including the Philippines), and into the Australian Region (first records for this region) from New Guinea and Australia (Northern Territory, Queensland, Western Australia, and Lord Howe Island). I have also seen specimens from Fiji (NZAC), where it appears to be the only phalacrid. Many species are undescribed.

Included species (8):

Phaenocephalus castaneus Wollaston, 1873 (Distribution: Japan) (type!)
Phaenocephalus coomani Paulian, 1950 (Distribution: Vietnam) (type!)
Phaenocephalus exiguus (Scott, 1922), **comb. nov.** (*Phalacratomus*) (Distribution: Seychelles) (type!)
Phaenocephalus kobensis (Champion, 1925), **comb. nov.** (*Heterostilbus*) (Distribution: Japan, Taiwan) (type!)
Phaenocephalus laevigatus (Champion, 1924), **comb. nov.** (*Heterostilbus*) (Distribution: India) (type!)
Phaenocephalus longiclava (Champion, 1925), **comb. nov.** (*Heterostilbus*) (Distribution: Malaysia, Philippines) (type!)
Phaenocephalus marginatus (Champion, 1924), **comb. nov.** (*Heterostilbus*) (Distribution: India) (type!)
Phaenocephalus minutulus (Champion, 1924), **comb. nov.** (*Heterostilbus*) (Distribution: Malaysia, Sri Lanka) (type!)

Discussion. This genus was first described as a member of the Corylophidae (Wollaston 1873), albeit with reservations. Matthews (1899) formally recognized its distinctness by erecting the monotypic family Phaenocephalidae. An additional species was added by Paulian (1950), but its family placement remained unchanged until Pakaluk (1991), who transferred it to Phalacridae based on a detailed examination of a range of anatomical features. My examination and analyses confirm that *Phaenocephalus* fits within the diagnosis of Phalacridae presented above.

Scott's genus *Phalacratomus* falls well within the concept of *Phaenocephalus* outlined in the diagnosis above, as does the Champion genus *Heterostilbus*, and I am newly proposing them as junior synonyms of *Phaenocephalus*.

2. *Phalacrinus* Blackburn, 1891

(Figs. 2h, k; 5; 37c)

Phalacrinus Blackburn 1891: 99. Type species: *Phalacrinus australis* Blackburn 1891, **here designated**.
Sphaerostilbus Champion 1924*b*: 164. Type species: *Sphaerostilbus dilatatus* Champion 1924, fixed by original designation. **Syn. nov.**

Type material. *Phalacrinus australis* Blackburn: holotype, "T \ 781 [handwritten] // Type \ H.T. [red-bordered disc] // Australia. [underlined with red] \ Blackburn Coll. \ B.M. 1910–236. // Phalacrinus \ australis, Blackb. // LECTOTYPE \ Phalacrinus \ australis Blackburn \ des. M.L. Gimmel 2012 [red label]" (BMNH), card mounted.

Sphaerostilbus dilatatus Champion: lectotype, here desginated, "W. Almora Divn \ Kumaon U.P. \ Oct. 1917. HGC // E 25 [handwritten] // Type \ H.T. [red-bordered disc] // Sphaerostilbus \ dilatatus, Ch \ type [handwritten] // Specimen \ figured // Sphaerostilbus \ (n. gen.) \ dilatatus, Champ. // Ent. Mo. Mag. 1924. \ G. C. C. det. // G.C. Champion. \ Brit. Mus. \ 1924–63. // SYN- \ TYPE [blue-bordered disc] // LECTOTYPE \ Sphaerostilbus \ dilatatus Champion \ des. M.L. Gimmel 2011 [red label]" (BMNH), card mounted. Paralectotypes from same

locality (1), Nilgiri Hills, India (3), and Mt. Matang, Sarawak, Borneo (2), each with label "PARALECTOTYPE \ Sphaerostilbus \ dilatatus Champion \ det. M.L. Gimmel 2011 [yellow label]" (BMNH).

Diagnosis. Perhaps the most distinctive genus of Phalacridae. The explanate pronotal and elytral margins, antennomere I flattened and triangular, terminal labial palpomere widest apically, elevated mesoventral disc, and constriction of the head behind the eyes serve to easily separate *Phalacrinus* from the rest of the family.

Description. Medium-sized, total length 2.0–3.0 mm. Pronotal and elytral margins distinctly explanate. Dorsal surface from completely testaceous to nearly black, often with nebulously lighter sutural area and elytral margins (Fig. 37c). Tibial spur formula 0-1-1, tarsal formula 4-4-4 in both sexes.

Head. Distinctly constricted behind eyes (Fig. 2k); with extremely short median endocarina at occiput. Eyes medium-sized; facets flat; interfacetal setae absent; not emarginate medially; without posterior emargination; periocular groove absent; with transverse setose groove ventrally behind eye. Frontoclypeus emarginate or not above antennal insertion; clypeal apex truncate. Antennomere I flattened, with antero-apical knob, appearing triangular; antennal club loosely 3-segmented, club symmetrical, nearly cylindrical, long, usually about as long as funicle; antennomere XI constricted on posterior face (Fig. 5b). Mandible (Fig. 5a) stout, with apex simple or sometimes bidentate, tip strongly bent medially and acuminate; without or with weak retinaculum; mandible without ventral ridge. Maxillary palpomere IV fusiform, relatively short, stout; galea securiform; lacinia with multiple spines. Mentum with sides divergent toward apex; labial palpomere III triangular, widest at apex (Fig. 2h). Labrum with apical margin slightly emarginate. Gular sutures long, strongly convergent, extending about halfway to ventral mouthparts.

Thorax. Pronotum without obvious microsetae; with weakly developed scutellar lobe. Prosternum anteriorly with continuous row of marginal setae, setae normal; procoxal cavity with anterolateral notchlike extension; prosternal process rounded in lateral view, not setose preapically, without spinelike setae at apex. Procoxae nearly contiguous; protrochanter with setae; protibia (Fig. 5c) without ctenidium on kickface, apical spurs absent. Scutellar shield small, width at base less than length of eye. Elytron without spectral iridescence; usually with nine more or less complete impressed striae, striae with distinct punctures; without transverse strigae; lateral margin without row of sawtooth-like setae. Mesoventral plate deeply notched anteriorly, not extending posteriorly to metaventrite, not forming procoxal rests; mesoventral disc elevated medially, forming a large plate anterior to metaventral process, setose; mesanepisternum with transverse carina present, incomplete; mesocoxae separated by less than half width of a coxal cavity (Fig. 5f). Mesotarsomere III not bilobed. Metaventral process (Fig. 5f) extending anteriorly just to halfway point of mesocoxae; metaventral postcoxal lines not separated from mesocoxal cavity margin; discrimen long, extending more than halfway to anterior margin of metaventral process; metendosternite (Fig. 5g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange at anterior margin. Anterior margin of metacoxa without emargination sublaterally; metacoxal plate without transverse line; metatibial foreface with apical ctenidium straight, perpendicular overall to long axis of tibia; apical spur cylindrical, distinctly shorter than width of tibial apex; metatarsomeres compacted, nearly identical to mesotarsomeres, joint between I and II flexible (Fig. 5d); metatarsomere III not bilobed. Hind wing (Fig. 5e) with distinct, ovate anal lobe; leading edge with complete row of long setae at level of RA+ScP; AA_{3+4} not apparent; cubitoanal system not forked; CuA_2 and MP_{3+4} with distal remnants; r4 absent; apical field with curved fleck present distal to rp-mp2; small transverse sclerite and small round sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines or calli; spiracles absent on segment VII. Male with aedeagus upright in repose; tegmen (Fig. 5h) with symmetrical anterior margin, parameres separated by suture from basal piece, parameres with medial longitudinal division; penis (Fig. 5i) wider posteriorly, with fields of endophallic spicules and sclerites, bilobed apically; spiculum gastrale V-shaped, arms free. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. Most specimens with capture data indicate that they were beaten from dry leaves, often of *Eucalyptus*. A few have been taken by litter sifting.

Distribution and diversity. Exclusively Indo-Australian, from India eastward to the Philippines and throughout Australia. Surprisingly, I have seen none from New Guinea.

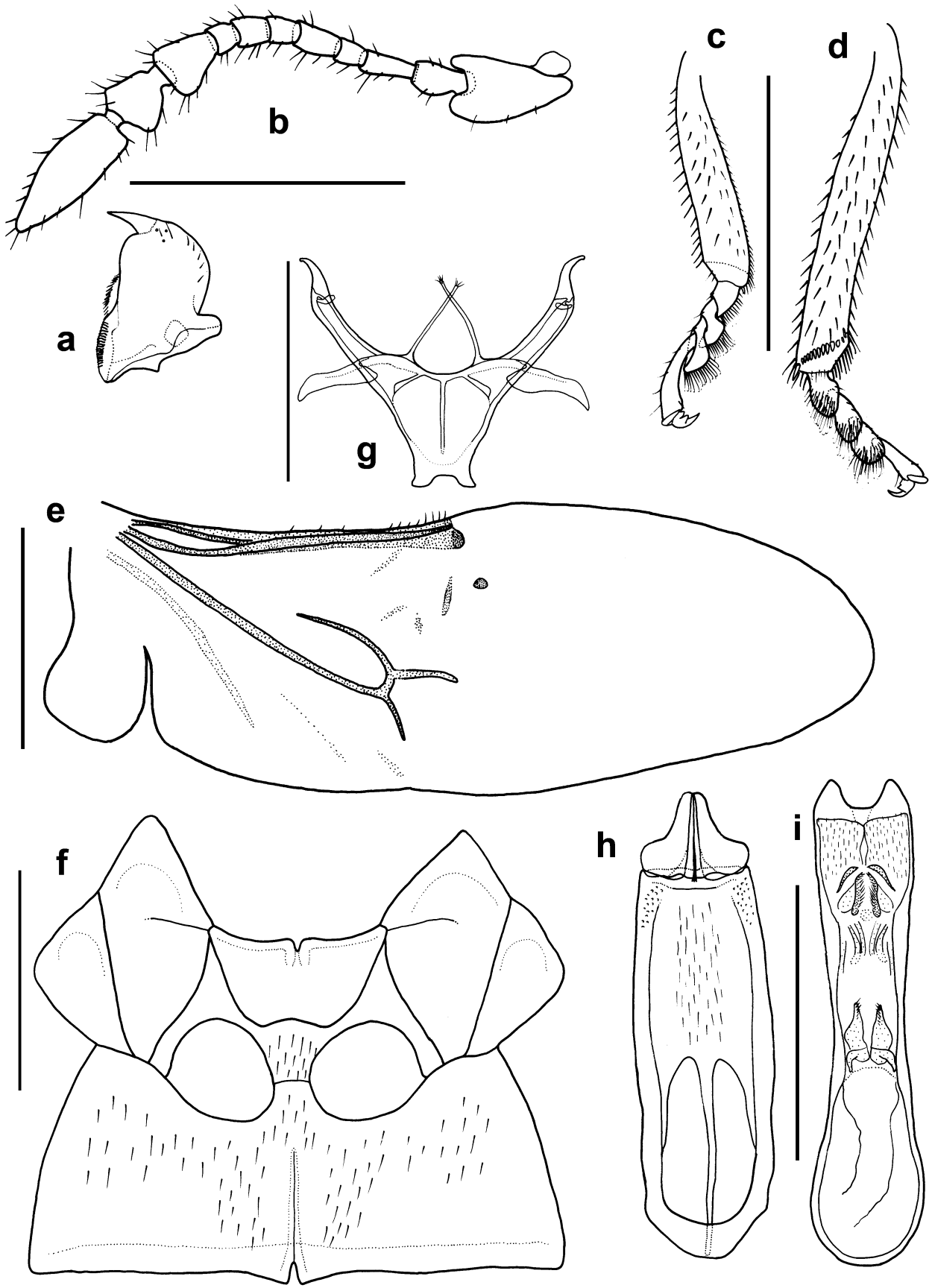

FIGURE 5. *Phalacrinus dilatatus*, male. (a) Right mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Right protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 0.5 mm). (h) Tegmen, ventral; (i) penis, ventral (scale bar = 0.5 mm).

Included species (10):

Phalacrinus australis Blackburn, 1891 (Distribution: Australia) (type!)
Phalacrinus comis Blackburn, 1895 (Distribution: Australia) (type!)
Phalacrinus compressus Blackburn, 1902 (Distribution: Australia) (type!)
Phalacrinus dilatatus (Champion, 1924), **comb. nov.** (*Sphaerostilbus*) (Distribution: India, Malaysia) (type!)
Phalacrinus navicularis Blackburn, 1902 (Distribution: Australia) (type!)
Phalacrinus nigriclavus Lea, 1932 (Distribution: Australia)
Phalacrinus notabilis Blackburn, 1895 (Distribution: Australia) (type!)
Phalacrinus obtusus Blackburn, 1891 (Distribution: Australia) (type!)
Phalacrinus rotundus Blackburn, 1891 (Distribution: Australia) (type!)
Phalacrinus umbratus Blackburn, 1902 (Distribution: Australia) (type!)

Discussion. Champion's genus *Sphaerostilbus* falls well within the concept of *Phalacrinus* outlined in the diagnosis above, and therefore I propose synonymy of the two here. Neither Blackburn nor subsequent authors have designated a type species for *Phalacrinus*. I have selected *P. australis* Blackburn to typify the genus name since it is the best described of the three available species treated in Blackburn's (1891) publication.

Only one specimen was discovered from the type series of *P. australis* in the BMNH. Although Blackburn did not enumerate the specimens he had in making his description, he did mention two localities in this context (Port Lincoln and Morgan, South Australia) necessitating two or more specimens. Damoiseau (1968: 29), in fact, indicated that an additional specimen from the syntype series was present in Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (IRSNB; not examined). I have therefore designated the BMNH specimen as the lectotype.

Champion's type series of *S. dilatatus* consists of seven specimens from multiple localities in India and Borneo. I have designated one specimen the lectotype in order to stabilize the identity of the species.

3. *Ranomafanacrinus* Gimmel, gen. nov.

(Figs. 37d, e, f)

Type species: *Ranomafanacrinus nigrinus* Gimmel, here designated.

Type material. See account of *R. nigrinus* below.

Diagnosis. Easily distinguished by its 4-4-4 tarsi in which the metatarsi are similar in form to the pro- and mesotarsi, the elongate-cylindrical antennal club, the prominent prosternal process, and the mesoventrite with a large hollow cavity for its reception.

Description. Medium-sized, total length 2.4 mm. Pronotal and elytral margins not explanate. Dorsal surface completely black, appendages paler (Figs. 37d, e, f). Tibial spur formula apparently 0-1-1, tarsal formula 4-4-4 in female (male unknown).

Head. Weakly constricted behind eyes. Eyes small; facets flat; not emarginate medially; without posterior emargination; periocular groove present, weak; without setose groove ventrally behind eye. Frontoclypeus not emarginate above antennal insertion; clypeal apex truncate. Antennomere I ovate; antennal club loosely 3-segmented, club weakly asymmetrical, nearly cylindrical; antennomere XI constricted on posterior face. Mandible with apex simple. Maxillary palpomere IV fusiform, stout, inner edge slighly swollen medially. Mentum with sides divergent; labial palpomere III triangular, widest at apex.

Thorax. Pronotum with scattered microsetae; with weakly developed scutellar lobe. Prosternum anteriorly with continuous row of marginal setae, setae normal; procoxal cavity with anterolateral notchlike extension; prosternal process angulate in lateral view, not setose preapically, without spinelike setae at apex. Procoxae moderately separated; protibia without ctenidium on kickface, apical spurs absent. Scutellar shield small, width at base about equivalent to length of eye. Elytron without spectral iridescence; lateral striae suggested, striae with distinct punctures; without transverse strigae; lateral margin without row of sawtooth-like setae. Mesoventral plate not extending posteriorly to metaventrite, forming procoxal rests; mesoventral disc with deep round depression

medially for reception of prosternal process; mesanepisternum with transverse carina absent; mesocoxae separated by less than half width of a coxal cavity. Mesotarsomere III not bilobed. Metaventral process extending anteriorly just to halfway point of mesocoxae; metaventral postcoxal lines not separated from mesocoxal cavity margin, but continuous (connected) across base of metaventral process; discrimen short, extending less than halfway to anterior margin of metaventral process. Anterior margin of metacoxa without emargination sublaterally; metacoxal plate with transverse line; metatibial foreface with apical ctenidium straight, perpendicular overall to long axis of tibia; apical spur cylindrical, distinctly shorter than width of tibial apex; metatarsomeres compacted, nearly identical to mesotarsomeres, joint between I and II flexible. Hind wing unstudied.

Abdomen. Abdominal ventrite I without paired lines or calli; spiracles present on segment VII. Female ovipositor weakly sclerotized, palpiform. Male genitalia unknown.

Immature stages. Unknown.

Bionomics. The only known specimen was captured in a Malaise trap in a small clearing in montane rainforest.

Distribution and diversity. Only one species, known from only one specimen collected in Ranomafana National Park, Madagascar.

Included species (1):

Ranomafanacrinus nigrinus Gimmel, **sp. nov.** (Distribution: Madagascar)

Discussion. Because this genus is known from only one specimen I did not perform a disarticulation. Accordingly, the above description lacks a number of internal and detailed external characters, and the genus was omitted from the phylogenetic analysis.

I have placed this genus within the *Phaenocephalus*-group because it shares numerous characters with *Phaenocephalus* and *Phalacrinus* (compacted tarsi, shape of the antennal club, the triangular terminal labial palpomere, slight narrowing of the head behind eyes, the short metaventral process). However, a number of significant characters are unique to this genus (the form of the mesoventrite, the large prosternal process, the unbroken connection of the metaventral lines across the base of the metaventral process), and it may deserve its own higher taxonomic category. Future investigations into this issue will require fresh material for both DNA work and detailed morphological analysis involving disarticulation.

Etymology. Named after the only known locality (Ranomafana National Park) of the only known specimen, plus the ending *-crinus* in allusion to its similarity to *Phalacrinus*. The gender of the name is masculine.

Ranomafanacrinus nigrinus Gimmel, sp. nov.

(Figs. 37d, e, f)

Holotype. Female, “MADAGASCAR: Prov. \ Fianarantsoa, 7 km \ W Ranomafana, 1100m \ 22–31 October 1988 \ W. E. Steiner // Malaise trap in \ small clearing, \ montane \ rain forest // HOLOTYPE ♀ \ Ranomafanacrinus \ nigrinus Gimmel \ des. M.L. Gimmel 2011 [red label]” (USNM), point mounted.

Paratypes. None.

Description. Total length 2.4 mm. Broadly ovate, highly convex dorsally. Dorsal color solid black; underside with hints of dark reddish-brown; femora brown; tibiae and tarsi yellowish-brown; antennae and mouthparts yellowish. Antennal club elongate, slender, not as long as funicle. Head and pronotum with extremely fine, evenly distributed punctation; pronotum with scattered recumbent microsetae; pronotum with dense, irregular microsculpture laterally, microsculpture lacking on median area. Elytron with dense, irregular microsculpture throughout, with six faint striae, medialmost three obsolete. Metaventrite weakly punctate, with long, sparse setae medially. Legs short, femora relatively narrow.

Spermatheca not observed. Male genitalia unknown.

Diagnosis. This species may be recognized by the characters given in the generic diagnosis.

Distribution. Known only from the type locality in east-central Madagascar.

Etymology. From the Latin *nigri-* (black), in reference to the solid pitch-black color of the cuticle, plus the ending *-inus*. The epithet is a noun in the nominative singular, standing in apposition.

STILBUS-GROUP

Eustilbini Guillebeau 1892*b*: 149. Type genus: *Eustilbus* Sharp.
Stilbini Jakobson 1915: 948. Type genus: *Stilbus* Seidlitz.

Diagnosis. This group may be recognized by the single elytral sutural stria, inner edge of the terminal maxillary palpomere swollen medially, the prosternal process projecting or step-like in lateral view, the metaventral process not surpassing the mesocoxae, the metaventral lines diverging from the mesocoxal cavities, the small scutellar shield, metatarsomere I shorter than II, and the absence of a protibial ctenidium. This group, in essentially its present constitution, was first characterized by Švec (2002).

Distribution and diversity. A total of 178 recognized species occurring nearly coextensively with the family as a whole.

Included genera (4). *Acylomus* Sharp, *Nesiotus* Guillebeau, *Stilbus* Seidlitz, *Xanthocomus* Guillebeau.

4. *Acylomus* Sharp, 1888

(Figs. 2l; 3a; 6–8; 37g–i)

Acylomus Sharp 1888: 256. Type species: *Acylomus aciculatus* Sharp 1889, fixed by monotypy.
Liophalacrus Sharp 1888: 255. Type species: *Liophalacrus bicolor* Sharp 1888, fixed by subsequent designation. **Syn. nov.**
Coelocoelius Guillebeau 1893*a*: 290. Type species: *Coelocoelius simoni* Guillebeau 1893, fixed by monotypy. [synonymized with *Acylomus* Sharp by Champion (1924*c*: 244)]
Ganyrus Guillebeau 1894*a*: 280. Type species: *Ganyrus rubellus* Guillebeau 1894, fixed by original designation. **Syn. nov.**
Podocesus Guillebeau 1894*a*: 281. Type species: *Eustilbus semirufus* Guillebeau 1893, fixed by original designation. **Syn. nov.**
Tinodemus Guillebeau 1894*a*: 282. Type species: *Tinodemus grouvellei* Guillebeau 1894, fixed by original designation. **Syn. nov.**
Dolerus Guillebeau 1894*a*: 282. Type species: *Dolerus limbatus* Guillebeau 1894, fixed by original designation.
Ledorus Guillebeau 1895: xxvii. Type species: *Dolerus limbatus* Guillebeau 1894, fixed by objective synonymy with *Dolerus* Guillebeau. [replacement name for *Dolerus* Guillebeau, 1894] [synonymized with *Podocesus* Guillebeau by Švec (2003: 117)] **Syn. nov.**
Astenulus Guillebeau 1896: 299. Type species: *Astenulus micropus* Guillebeau 1896, fixed by monotypy. [synonymized with *Tinodemus* Guillebeau by Švec (2002*b*: 220)]. **Syn. nov.**
Afronyrus Švec 2006: 106. Type species: *Afronyrus snizeki* Švec 2006, fixed by original designation. **Syn. nov.**

Type material. *Acylomus aciculatus* Sharp: 18 syntypes found in BMNH, one dissected male, point mounted, card containing left protibia/tarsus, right maxillary palp, and right antenna, tegmen and median lobe in glycerol-filled capsule, here designated as a lectotype to stabilize the species and generic name, "Sp. figured // Rio Hondo, \ B. Honduras. \ Blancaneau. // Acylomus aciculatus, Ch. [handwritten] // B.C.A.,Col.,II,(1). \ Acylomus aciculatus. // LECTOTYPE \ Acylomus \ aciculatus Sharp [binomial handwritten] \ W.E. Steiner, Jr. [red label, designation not published, turned over] // LECTOTYPE \ Acylomus \ aciculatus Sharp \ des. M.L. Gimmel 2011 [red label]" (BMNH). Paralectotypes: 17 (BMNH), with label attached "PARALECTOTYPE \ Acylomus \ aciculatus Sharp \ det. M.L. Gimmel 2011 [yellow label]".

Liophalacrus bicolor Sharp: eight syntypes found in BMNH, the card-mounted specimen with "Type" handwritten by David Sharp selected as the lectotype to stabilize the species and generic name, "Liophalacrus \ bicolor. \ Type D.S. \ Bugaba Champion. [handwritten on specimen card] // Type [red-bordered disc] // Bugaba, Panama. \ Champion // Sharp Coll. \ 1905.–313. // LECTOTYPE \ Liophalacrus \ bicolor Sharp \ des. M.L. Gimmel 2011 [red label]" (BMNH). Paralectotypes: 7 card-mounted specimens, with label attached "PARALECTOTYPE \ Liophalacrus \ bicolor Sharp \ des. M.L. Gimmel 2011 [yellow label]" (BMNH).

Coelocoelius simoni Guillebeau: two syntypes, card mounted, "San Esteban \ E. Simon III.88" (MNHN). Only two of the supposed four syntypes were found.

Ganyrus rubellus Guillebeau: holotype, female, "Abyss. \ Raffray [blue label] // 167 // Grouvelle [handwritten] // [handwritten label, illegible] // HOLOTYPE ♀ \ Ganyrus \ rubellus Guillebeau \ det. M.L. Gimmel 2009 [red label]" (MNHN), point mounted, genitalia in DMHF.

Eustilbus semirufus Guillebeau: holotype, male, card mounted, "Caracas \ 1 88 E S // Simon // TYPE // Museum Paris \ Coll. Générale // Lectotypus \ PODOCESUS SEMIRUFUS Guill. 1894 \ Z. Svec des. 1999 // GENITALIA IN WATER SOLUBLE MEDIUM—DMHF // semirufus Guilb." (MNHN). The lectotype designation is in error (the species was described from "1 exemplaire").

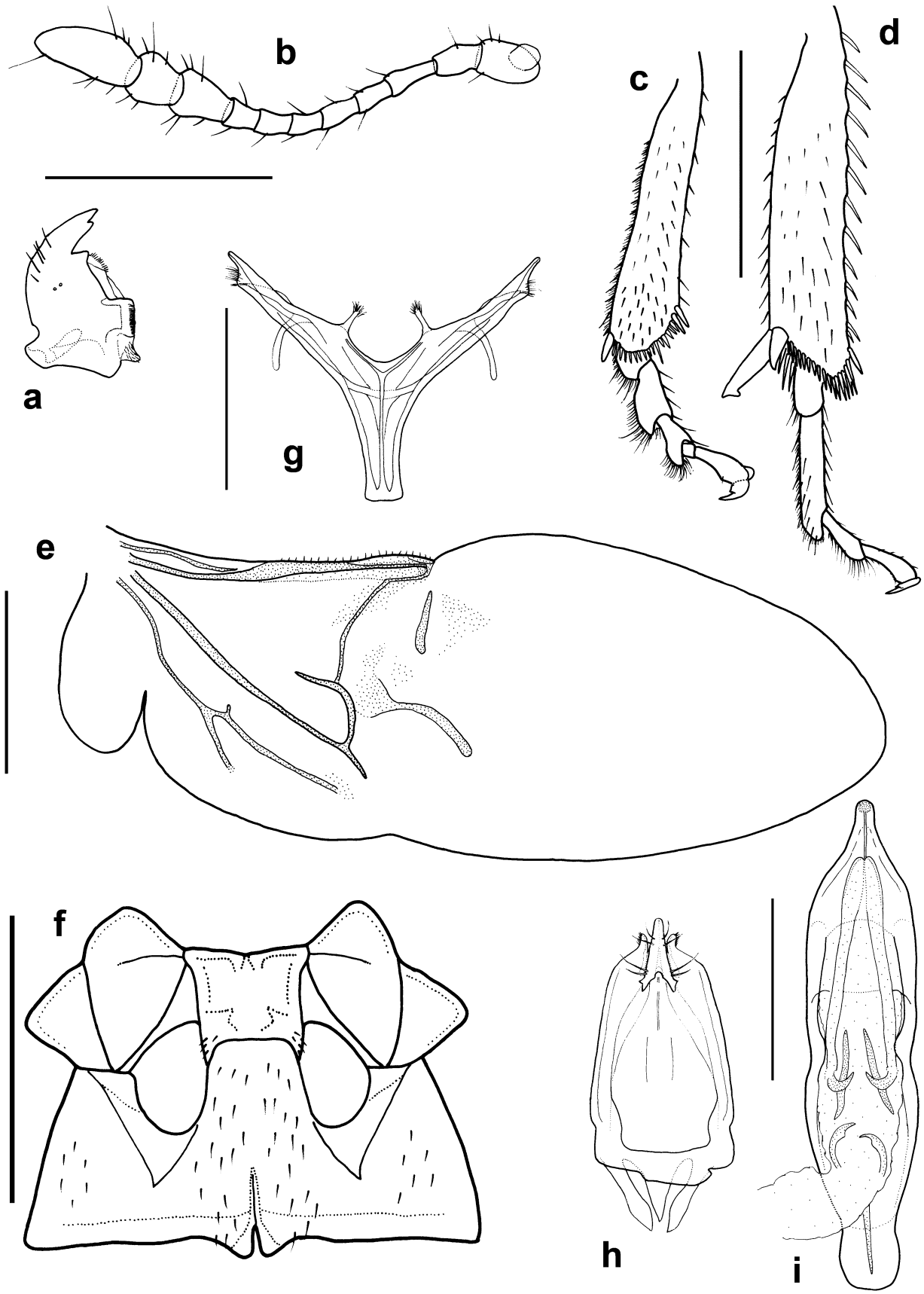

FIGURE 6. *Acylomus aciculatus*, male. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 1.0 mm). (g) Metendosternite (scale bar = 0.5 mm). (h) Tegmen, ventral; (i) penis, ventral (scale bar = 0.5 mm).

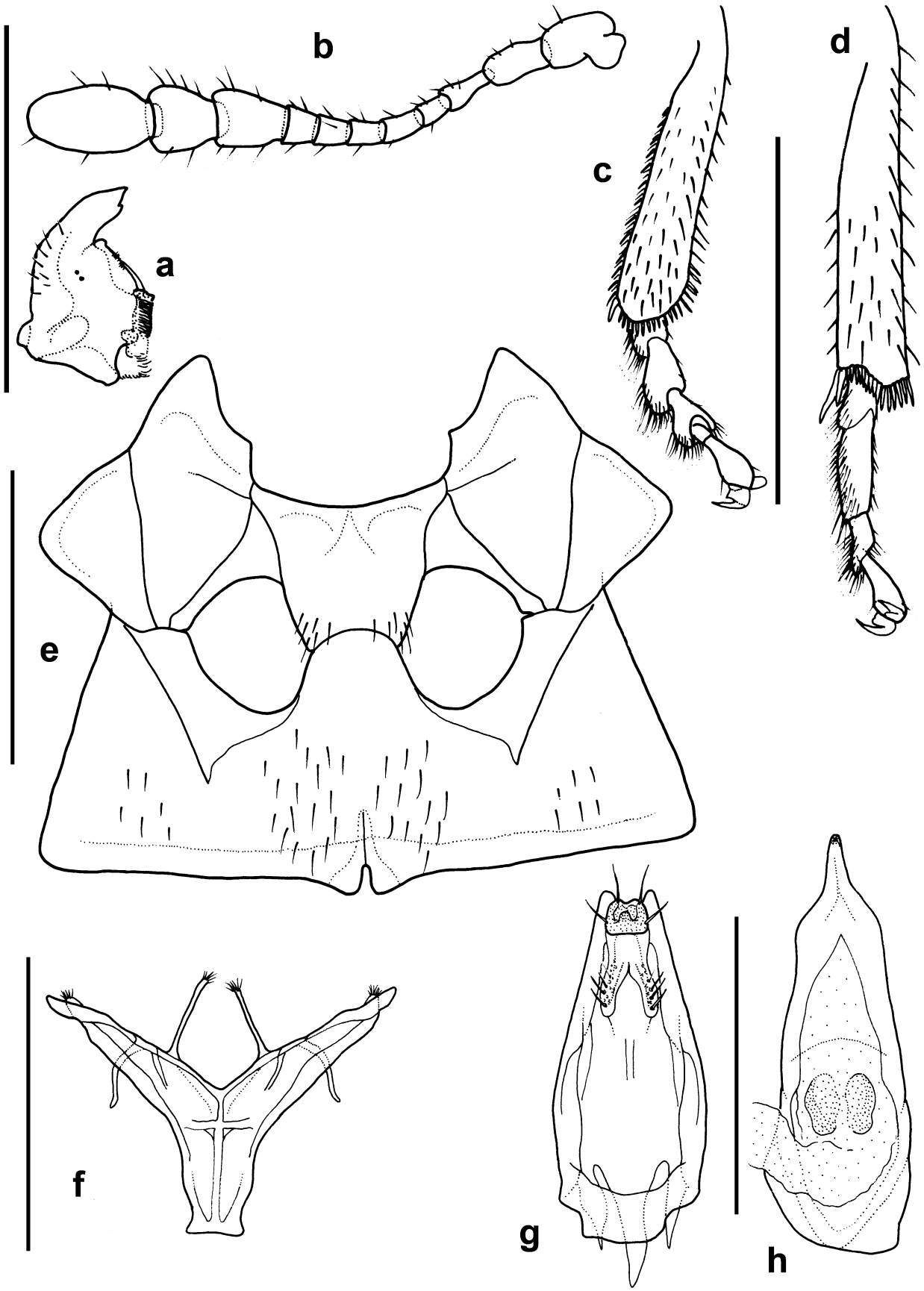

FIGURE 7. *Acylomus bicolor*, male. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (f) Metendosternite (scale bar = 0.5 mm). (g) Tegmen, ventral; (h) penis, ventral (scale bar = 0.5 mm).

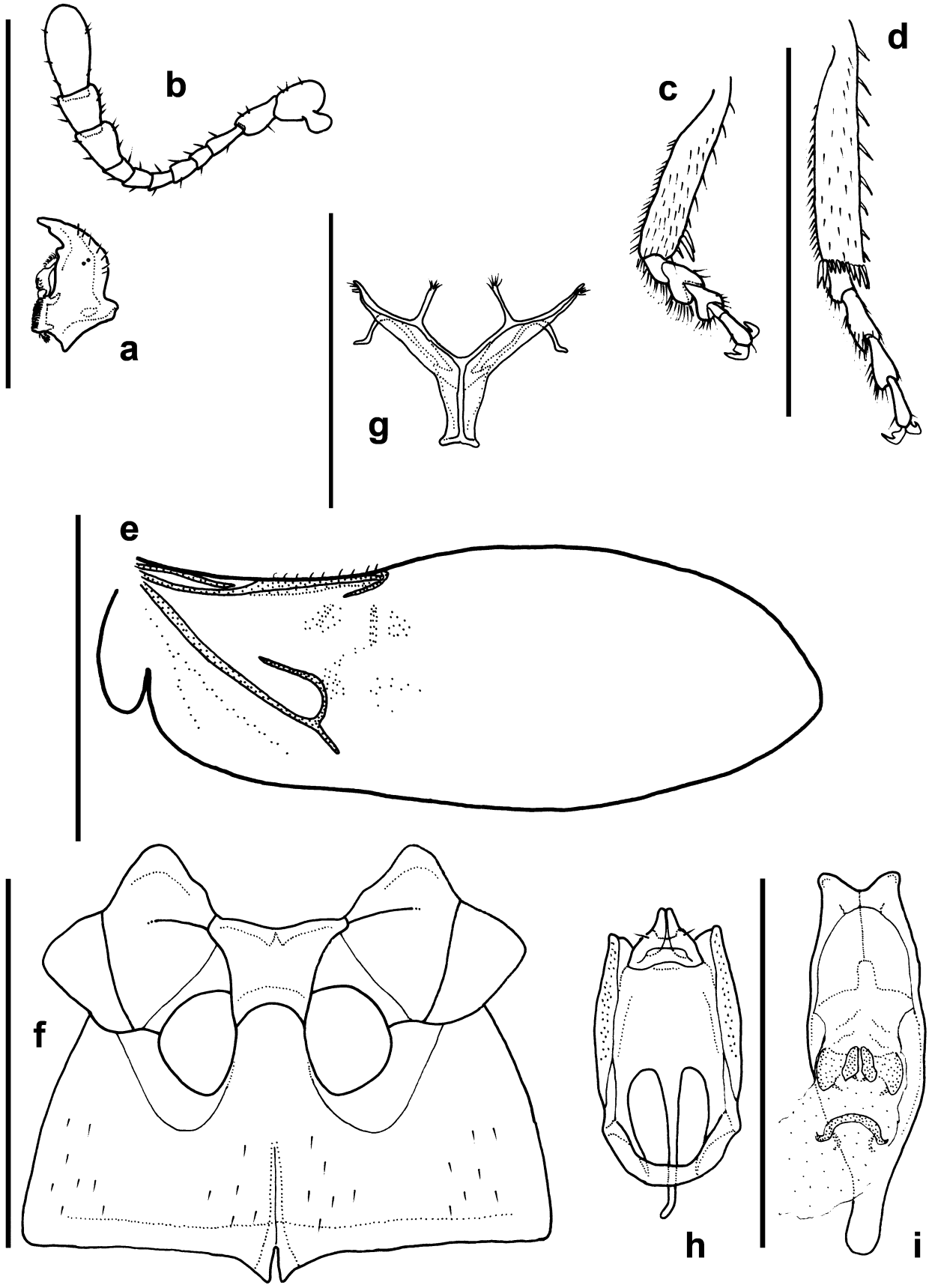

FIGURE 8. *Acylomus micropus*, male. (a) Right mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 0.5 mm). (h) Tegmen, ventral; (i) penis, ventral (scale bar = 0.5 mm).

Tinodemus grouvellei Guillebeau: lectotype, male, card mounted, genitalia dissected, "Michigan // Grouvelle // Museum Paris \ Coll. Générale // TYPE // Lectotypus TINODEMUS GROUVELLEI Guillebeau 1894 \ Z. Svec des. 1999 // GENITALIA IN DMHF—WATER SOLUBLE MED. // Grouvellei Guilb. // Acylomus \ ergoti Casey \ det. M. Gimmel 2008" (MNHN).

Dolerus limbatus Guillebeau: holotype, female, card mounted, "Grouvelle // Colombie // Museum Paris \ Coll. Générale // TYPE // Lectotypus DOLERUS LIMBATUS Guillebeau 1894 \ Z. Svec des. 1999 // ANTENNA IN DMHF—WATER SOLUBLE MEDIUM // limbatus Guilb. // Ledorus // Dolerus // limbatus Guilb." (MNHN). The lectotype designation is in error (the species was described from "1 exempl.").

Astenulus micropus Guillebeau: holotype, male, genitalia dissected, "Alluaud // Diego Suarez // Museum Paris \ Coll. Générale // HOLOTYPE" (MNHN).

Afronyrus snizeki Švec: type not accessible.

Diagnosis. May be recognized by the divergent metaventral postcoxal lines which may be arcuate or angulate, single elytral sutural stria, metatarsomere I shorter than II with joint between them more or less rigid, prosternal process angulate when viewed laterally and usually with row or pair of stiff setae at apex, ventral lobe of the eye not expanded posteriorly, mandible without a ventral ridge, and the tegmen with parameres hinged to basal piece.

Description. Very small to large, total length 1.3–3.5 mm. Dorsal color usually dark reddish-brown to piceous, sometimes with apex of elytra paler, or with pale maculations on disc (Fig. 37g–i). Tibial spur formula 2-2-2, tarsal formula 5-5-5 in females, 5-5-4 in males.

Head. Not constricted behind eyes (Fig. 2l). Eyes small to medium-sized; facets flat; interfacetal setae absent; strongly emarginate to straight medially; often with sharp posterior emargination; periocular groove present; with transverse setose groove ventrally behind eye. Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club 3-segmented, club symmetrical, antennomere XI not constricted (Figs. 6b, 7b, 8b). Mandible (Figs. 6a, 7a, 8a) with apex bidentate; with retinaculum; mandible without ventral ridge. Maxillary palpomere IV fusiform, inner edge swollen medially; galea short, rounded; lacinia with two stout spines, often with associated tuft of setae. Mentum with sides divergent toward apex; labial palpomere III fusiform. Labrum with apical margin arcuate to emarginate. Gular sutures short, barely evident, rarely long.

Thorax. Pronotum with or without obvious microsetae; with weakly to moderately developed scutellar lobe. Prosternum anteriorly with marginal setae distributed in two patches, setae normal; procoxal cavity with anterolateral notchlike extension; prosternal process angulate in lateral view, not conspicuously setose preapically, usually with row or pair of spinelike setae at apex (Fig. 3a). Protrochanter without setae; protibia without ctenidium on kickface (Figs. 6c, 7c, 8c). Scutellar shield small. Elytron usually without spectral iridescence, rarely present; one sutural stria present; discal striae absent or barely suggested; without or with weak transverse strigae; lateral margin usually with row of tiny, sawtooth-like setae. Mesoventral plate (Figs. 6f, 7e, 8f) notched anteriorly, extending posteriorly to metaventrite, dividing mesoventral disc in two, not forming or forming weak procoxal rests; mesanepisternum with incomplete transverse carina; mesocoxal cavities widely separate, separated by more than half width of a coxal cavity. Mesotarsomere III bilobed or not. Metaventral process (Figs. 6f, 7e, 8f) not extending anteriorly beyond anterior level of mesocoxae; metaventral postcoxal lines diverging from mesocoxal cavity margin, arcuate and smoothly rounded to acuminately pointed, branches always connected, never with a spur; discrimen short, extending less than halfway to anterior margin of metaventral process; metendosternite (Figs. 6g, 7f, 8g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange behind anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line present or absent; metatibial foreface with apical ctenidium roughly perpendicular overall to long axis of tibia; spurs cylindrical, longest spur subequal in length to or longer than width of tibial apex, spurs (Fig. 6d) and tibial apex sometimes modified in males; metatarsus slender, metatarsomere I distinctly shorter than metatarsomere II, joint between I and II rigid (Figs. 6d, 7d, 8d). Hind wing (Figs. 6e, 8e) with distinct, ovate anal lobe; leading edge with complete row of long setae at level of RA+ScP; AA_{3+4} not apparent; cubitoanal system often branched apically; CuA_2 and MP_{3+4} usually without distal remnants; r4 present or absent; flecks present in apical field just distal to rp-mp2; long to short transverse proximal sclerite and additional strong or moderate, irregular sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines or calli; spiracles apparently absent from segment VII. Male with aedeagus upright in repose; tegmen (Figs. 6h, 7g, 8h) with symmetrical anterior margin, parameres hinged to basal piece, parameres with or without medial longitudinal division; penis (Figs. 6i, 7h, 8i) variable, with

endophallic spicules, often with large sclerites, apex often pointed or tripartite; spiculum gastrale V-shaped, with arms free. Female ovipositor weakly sclerotized, palpiform.

Immature stages. The larva and pupa of *Acylomus pugetanus* Casey were described and illustrated by Steiner and Singh (1987).

Bionomics. Most members of this genus, at least in the Nearctic region, appear to be generalist ascomycete fungus grazers on dead vegetation as adults and larvae. Dead hanging leaf clusters, a habitat described in Steiner (1984), seems to be especially favored by a few eastern Nearctic species. I have observed one species, *A. elongatulus*, in large numbers on grass tussocks in Louisiana. Another species, *A. pugetanus*, develops within the sclerotia of *Claviceps* species (ergot) on grasses in northern North America (see Steiner and Singh 1987 for details). Most members are attracted to lights at night, often in large numbers.

Distribution and diversity. A widely distributed genus, well represented in most tropical and subtropical regions and in eastern North America, but absent over much of the Palearctic region. I have examined at least three species of this genus from Australia, with most specimens from the northern half of the continent; whether these are undescribed has not been determined. Although many synonyms apparently exist in the genus, a great many species are undescribed. Upon revision this will likely become the most species-rich phalacrid genus, should it prove to be monophyletic.

Included species (94):

Acylomus abjectus Casey, 1916 (Distribution: United States) (type!)
Acylomus aciculatus Sharp, 1889 (Distribution: Central America) (type!)
Acylomus acuminatus (Švec, 2002), **comb. nov.** (*Tinodemus*) (Distribution: Tanzania)
Acylomus acutangulus (Kirsch, 1873), **comb. nov.** (*Phalacrus*) (Distribution: Peru) (type!)
Acylomus ambagiosus (Lyubarsky, 2003), **comb. nov.** (*Stilbus*) (Distribution: Nepal)
Acylomus apicalis (Švec, 2002), **comb. nov.** (*Tinodemus*) (Distribution: Kenya)
Acylomus atomarius (Sharp, 1888), **comb. nov.** (*Olibrus*) (Distribution: Panama) (type!)
Acylomus bicolor (Sharp, 1888), **comb. nov.** (*Liophalacrus*) (Distribution: Panama) (type!)
Acylomus bicoloratus Gimmel, **nom. nov.** [for *Tinodemus bicolor* Švec, 2002, junior secondary homonym of *Acylomus bicolor* (Sharp, 1888)] (Distribution: Tanzania)
Acylomus bifurcus (Švec, 1992), **comb. nov.** (*Tinodemus*) (Distribution: Japan) (type!)
Acylomus borealis (Guillebeau, 1894) (Distribution: Canada) (type!)
Acylomus calcaratus Casey, 1890 (Distribution: Bahamas, Bermuda, United States) (type!)
Acylomus capriviensis (Lyubarsky, 1998), **comb. nov.** (*Podocesus*) (Distribution: southern Africa)
Acylomus carbonarius Casey, 1916 (Distribution: United States) (type!)
Acylomus championi (Hetschko, 1929), **comb. nov.** (*Tinodemus*) (Distribution: Namibia, South Africa) (type!)
Acylomus chinensis (Švec, 1992), **comb. nov.** (*Tinodemus*) (Distribution: China) (type!)
Acylomus claviger (Champion, 1925), **comb. nov.** (*Tinodemus*) (Distribution: subsaharan Africa) (type!)
Acylomus confusus Casey, 1916 (Distribution: United States) (type!)
Acylomus confusus (Švec, 1992), **comb. nov.** (*Tinodemus*) (Distribution: Japan) (type!) [junior secondary homonym not replaced since the older name is probably a synonym]
Acylomus cubensis Casey, 1916 (Distribution: Cuba) (type!)
Acylomus curvolineatus (Champion, 1924), **comb. nov.** (*Stilbus*) (Distribution: Oriental region) (type!) [see note on synonymy below]
Acylomus darwinii (Waterhouse, 1877) (Distribution: Ecuador) (type!)
Acylomus detractus Casey, 1916 (Distribution: Cuba) (type!)
Acylomus digestus Casey, 1916 (Distribution: United States) (type!)
Acylomus distinctus (Švec, 2002), **comb. nov.** (*Tinodemus*) (Distribution: southern Africa)
Acylomus ellipticus Casey, 1916 (Distribution: United States) (type!)
Acylomus elongatulus (Casey, 1890) (Distribution: United States) (type!)
Acylomus ergoti Casey, 1890 (Distribution: United States) (type!)
Acylomus eximius Casey, 1916 (Distribution: United States) (type!)
Acylomus extricatus Casey, 1890 (Distribution: United States) (type!)
Acylomus flaviceps (Guillebeau, 1894), **comb. nov.** (*Tinodemus*) (Distribution: Colombia) (type!)

Acylomus fortis Champion, 1925 (Distribution: Brazil) (type!)
Acylomus grouvellei (Guillebeau, 1894), **comb. nov.** (*Stilboides*) (Distribution: Brazil, Cuba) (type!)
Acylomus humilis Casey, 1916 (Distribution: United States) (type!)
Acylomus insularis (Guillebeau, 1894) (Distribution: Martinique) (type!)
Acylomus integer Casey, 1916 (Distribution: United States) (type!)
Acylomus interpositus (Švec, 1992), **comb. nov.** (*Podocesus*) (Distribution: Japan) (type!)
Acylomus latisternus (Guillebeau, 1894) (Distribution: ?Haiti) (type!)
Acylomus libidinosus (Lyubarsky, 2003), **comb. nov.** (*Stilbus*) (Distribution: Vietnam)
Acylomus limbatus (Guillebeau, 1894), **comb. nov.** (*Podocesus*) (Distribution: Colombia) (type!)
Acylomus lyubarskyi Gimmel, **nom. nov.** [for *Olibrus capriviensis* Lyubarsky, 1998, junior secondary homonym of *Acylomus capriviensis* (Lyubarsky, 1998)] (Distribution: Namibia)
Acylomus maruskae (Švec, 2002), **comb. nov.** (*Tinodemus*) (Distribution: Kenya, Tanzania, Uganda)
Acylomus mesomelas (Champion, 1925), **comb. nov.** (*Tinodemus*) (Distribution: South Africa, Tanzania, Zimbabwe) (type!)
Acylomus mexicanus (Sharp, 1888), **comb. nov.** (*Olibrus*) (Distribution: Belize, Guatemala, Mexico) (type!)
Acylomus micaceus Casey, 1916 (Distribution: Mexico) (type!)
Acylomus micropus (Guillebeau, 1896), **comb. nov.** (*Tinodemus*) (Distribution: Madagascar, Réunion) (type!)
Acylomus mifsudi (Švec, 2000), **comb. nov.** (*Tinodemus*) (Distribution: Malta)
Acylomus morosus Casey, 1916 (Distribution: United States) (type!)
Acylomus nebulosus Casey, 1890 (Distribution: United States) (type!)
Acylomus neglectus (Švec, 2002), **comb. nov.** (*Tinodemus*) (Distribution: Guinea, Zambia)
Acylomus oblongus (Guillebeau, 1894), **comb. nov.** (*Tinodemus*) (Distribution: Brazil) (type!)
Acylomus obsoletus (Švec, 2002), **comb. nov.** (*Tinodemus*) (Distribution: Kenya)
Acylomus obtusus (Švec, 2002), **comb. nov.** (*Tinodemus*) (Distribution: South Africa)
Acylomus orientalis Gimmel, **nom. nov.** [for *Stilbus similis* Švec, 1992, junior secondary homonym of *Acylomus similis* (Scott, 1922)] (Distribution: China, Japan) (type!)
Acylomus ornatus (Guillebeau, 1894), **comb. nov.** (*Tinodemus*) (Distribution: Mexico) (type!)
Acylomus ovalis (Švec, 2002), **comb. nov.** (*Tinodemus*) (Distribution: Tanzania, Uganda)
Acylomus ovulatus Casey, 1916 (Distribution: United States) (type!)
Acylomus partitus (Sharp, 1888), **comb. nov.** (*Olibrus*) (Distribution: Guatemala) (type!)
Acylomus parvulus (Boheman, 1858), **comb. nov.** (*Olibrus*) (Distribution: Peru)
Acylomus piceus Casey, 1890 (Distribution: United States) (type!)
Acylomus pictus (Horn, 1896), **comb. nov.** (*Litolibrus*) (Distribution: Mexico) (type!)
Acylomus polygramma (Flach, 1888), **comb. nov.** (*Tinodemus*) (Distribution: Mediterranean region)
Acylomus porrectus (Sharp, 1888), **comb. nov.** (*Olibrus*) (Distribution: Central America) (type!)
Acylomus pugetanus Casey, 1916 (Distribution: Canada, United States) (type!)
Acylomus pumilus (Guillebeau, 1894), **comb. nov.** (*Ganyrus*) (Distribution: Indonesia) (type!)
Acylomus quadrispinosus Casey, 1916 (Distribution: Cuba) (type!)
Acylomus reticulatus (Guillebeau, 1894), **comb. nov.** (*Ganyrus*) (Distribution: Indonesia) (type!)
Acylomus rotundus (Sharp, 1888), **comb. nov.** (*Liophalacrus*) (Distribution: Panama) (type!)
Acylomus rubellus (Guillebeau, 1894), **comb. nov.** (*Ganyrus*) (Distribution: Ethiopia) (type!)
Acylomus rubicundus (Champion, 1925), **comb. nov.** (*Tinodemus*) (Distribution: Namibia, Zimbabwe) (type!)
Acylomus ruficornis (Švec, 2002), **comb. nov.** (*Tinodemus*) (Distribution: Kenya)
Acylomus rufopunctatus (Lyubarsky, 1998), **comb. nov.** (*Podocesus*) (Distribution: Namibia, South Africa, Tanzania)
Acylomus sanderi (Švec, 2002), **comb. nov.** (*Tinodemus*) (Distribution: subsaharan Africa)
Acylomus sculpturatus (Švec, 2002), **comb. nov.** (*Tinodemus*) (Distribution: Guinea)
Acylomus secundus (Švec, 2002), **comb. nov.** (*Tinodemus*) (Distribution: subsaharan Africa)
Acylomus semirufus (Guillebeau, 1893), **comb. nov.** (*Podocesus*) (Distribution: Venezuela) (type!)
Acylomus similis (Scott, 1922), **comb. nov.** (*Nesiotus*) (Distribution: Seychelles) (type!)
Acylomus simoni (Guillebeau, 1893) (Distribution: Venezuela) (type!)
Acylomus snizeki (Švec, 2002), **comb. nov.** (*Tinodemus*) (Distribution: Guinea, Uganda)
Acylomus socialis Casey, 1916 (Distribution: United States) (type!)

Acylomus stilboides (Guillebeau, 1894) (Distribution: Brazil) (type!)
Acylomus strigillatus (Guillebeau, 1894), **comb. nov.** (*Ganyrus*) (Distribution: Mexico) (type!)
Acylomus subhemisphaericus (Guillebeau, 1894) (Distribution: Brazil) (type!)
Acylomus submaculatus (Sharp, 1888), **comb. nov.** (*Olibrus*) (Distribution: Central America) (type!)
Acylomus substrigosus (Sharp, 1888), **comb. nov.** (*Olibrus*) (Distribution: Guatemala) (type!)
Acylomus sveci Gimmel, **nom. nov.** [for *Tinodemus reticulatus* Švec, 2002, junior secondary homonym of *Acylomus reticulatus* (Guillebeau, 1894)] (Distribution: South Africa, Tanzania)
Acylomus teapensis (Sharp, 1888), **comb. nov.** (*Olibrus*) (Distribution: Mexico) (type!)
Acylomus texanus Casey, 1916 (Distribution: United States) (type!)
Acylomus tropicus (Scott, 1922), **comb. nov.** (*Tinodemus*) (Distribution: Réunion, Seychelles) (type!)
Acylomus vacivus Casey, 1916 (Distribution: United States) (type!)
Acylomus versicolor (Kirsch, 1873), **comb. nov.** (*Olibrus*) (Distribution: Peru) (type!)
Acylomus vicinus (Guillebeau, 1894) (Distribution: Brazil) (type!)
Acylomus vividus Casey, 1916 (Distribution: United States) (type!)
Acylomus zdeneki Gimmel, **nom. nov.** [for *Afronyrus snizeki* Švec, 2006, junior secondary homonym of *Acylomus snizeki* (Švec, 2002)] (Distribution: Kenya)

Discussion. Based on the original description (Boheman 1858), *Olibrus parvulus* cannot belong to *Olibrus*, for it has only a single sutural stria and the type is from Peru. It is likely a member of *Acylomus*, and I have tentatively transferred it to this genus.

Into this genus I have placed all New World *Stilbus*-group members with hinged parameres and without the characters of *Xanthocomus*. This includes the type species of *Podocesus*, *P. semirufus* Guillebeau (illustrated in Švec 2003: figs. 37–44), the type species of *Ledorus*, *Dolerus limbatus* Guillebeau (illustrated in Švec 2003: figs. 49, 50), and the type species of *Tinodemus*, *T. grouvellei* Guillebeau (illustrated in Švec 2002: figs. 9–16). In fact, *T. grouvellei*, described from "Michigan," is identical in aedeagal characteristics to a previously described form, *Acylomus ergoti* Casey. I therefore consider these two to be synonyms:

Acylomus ergoti Casey 1890 = *Tinodemus grouvellei* Guillebeau 1894, **syn. nov.**

Coelocoelius was synonymized with *Acylomus* by Champion (1924*c*). I have examined the type of the type species, *C. simoni*, and concur with this assessment.

The type of the type species of *Ganyrus*, *G. rubellus* Guillebeau (Ethiopia), falls well within my concept of *Acylomus*, and therefore I am synonymizing the two. Externally it is similar to *Acylomus sanderi* (Švec). I have seen the types of the three other species that were described in *Ganyrus*: *G. strigillatus* Guillebeau (Mexico), which obviously belongs in *Acylomus*; *G. pumilus* Guillebeau and *G. reticulatus* Guillebeau (both Sumatra), whose generic assignment to *Acylomus* is tentative given the condition of the types, whose ventral surfaces were obscured. Examination of the syntype series of *Nesiotus similis* Scott (1922: 239) has revealed that this species is more properly placed in *Acylomus*, based on the normally-proportioned antennal club and tarsal structure. Its metaventral postcoxal lines are arcuate, excluding the species from *Stilbus* Seidlitz.

Dissection of the lectotype (BMNH), here designated (complete label data: "Sarda, \ Bengal \ F. W. C. // G.C. Champion. \ Brit. Mus. \ 1925–42. // Stilbus \ curvolineatus, \ Champ. // E.M.M. 1924. \ det. G.C.C. // SYN- \ TYPE [blue-bordered disc] // LECTOTYPE ♂ \ Stilbus \ curvolineatus Champion \ des. M.L. Gimmel 2010 [red label]"), of *Stilbus curvolineatus* Champion (India) reveals an aedeagus much like that illustrated for both *Tinodemus meridianus* (Švec) (Afghanistan, Japan) and *Olibrus stuporatus* Lyubarsky (Java, Nepal) along with their original descriptions. I am considering these three names as synonymous, and *A. curvolineatus* assumes priority. The lectotype is designated to prevent future doubts about the identity of the species. The (one) paralectotype is female.

Acylomus curvolineatus (Champion 1924) = *Tinodemus meridianus* (Švec 1992) = *Olibrus stuporatus* Lyubarsky 1994, **syn. nov.**

I have been unable to examine the type of *Afronyrus snizeki* Švec located in Švec's private collection, but

based on the description and illustrations it falls within my broadened concept of *Acylomus*, based on the parameres hinged to the basal piece and modified tibial spurs of the male. Therefore I consider *Afronyrus* a junior synonym of *Acylomus*. This placement (and others in this genus) may be revised when detailed studies of the species and species groups of this complex genus are undertaken.

5. *Nesiotus* Guillebeau, 1896

(Figs. 2n; 9; 38a)

Nesiotus Guillebeau 1896: 298. Type species: *Nesiotus olibroides* Guillebeau 1896, fixed by monotypy.

Type material. *Nesiotus olibroides* Guillebeau: one specimen located in MNHN, male, card-mounted, genitalia dissected, here designated as a lectotype to stabilize the species and generic names, "Alluaud [handwritten] // Diego Suarez [handwritten] // MUSEUM PARIS \ COLL. GÉNÉRALE // HOLOTYPE [red label] // Nesiotus \ olibroides \ Guilb. [handwritten] // LECTOTYPE \ Nesiotus \ olibroides Guillebeau \ des. M.L. Gimmel 2009 [red label]" (MNHN). Although Guillebeau mentions "deux examples" in the original description, only one specimen was discovered in MNHN. The paralectotype may be located in BMNH (Scott 1922: 236).

Diagnosis. May be recognized by the divergent, smoothly arcuate metaventral postcoxal lines, single elytral sutural stria, rows of microsetae on the elytra, metatarsomere I shorter than II with joint between them rigid, prosternal process angulate when viewed laterally and with pair of stiff setae at apex, ventral lobe of the eye expanded posteriorly, mandible without a ventral ridge, and the tegmen with parameres fused to basal piece.

Description. Very small to small, total length 1.2–2.0 mm. Dorsal color reddish-testaceous to piceous, darker specimens often with reddish patches basally on elytra (Fig. 38a). Tibial spur formula 2-2-2, tarsal formula 5-5-5 in females, 5-5-4 in males.

Head. Not constricted behind eyes. Eyes medium-sized, with ventral lobe expanded posteriorly (Fig. 2n); facets slightly convex; interfacetal setae absent; distinctly emarginate medially; with sharp posterior emargination; periocular groove absent; with transverse setose groove ventrally behind eye (Fig. 2n). Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club 3-segmented, club weakly asymmetrical, as long as or longer than remainder of antenna (most extreme in male, Fig. 9b), antennomere XI not constricted. Mandible (Fig. 9a) with apex bidentate; without retinaculum; mandible without ventral ridge. Maxillary palpomere IV fusiform, inner edge swollen medially; galea short, rounded; lacinia with two stout spines. Mentum with sides divergent toward apex; labial palpomere III fusiform. Labrum with apical margin arcuate. Gular sutures long.

Thorax. Pronotum with distinct microsetae; with moderately well-developed scutellar lobe. Prosternum anteriorly with marginal setae distributed in two patches, setae normal; procoxal cavity with anterolateral notchlike extension; prosternal process angulate in lateral view, not conspicuously setose preapically, with pair of spinelike setae at apical corners. Protrochanter without setae; protibia without ctenidium on kickface (Fig. 9c). Scutellar shield small. Elytron with weak to moderate spectral iridescence; one sutural stria present; discal striae not impressed and apparently impunctate, but represented by rows of microsetae, irregular rows present in elytral intervals; with weak transverse strigae; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 9f) notched anteriorly, extending posteriorly to metaventrite, dividing mesoventral disc in two, procoxal rests absent; mesanepisternum with incomplete transverse carina; mesocoxal cavities widely separate, separated by more than half width of a coxal cavity. Mesotarsomere III not bilobed. Metaventral process (Fig. 9f) not extending anteriorly beyond anterior level of mesocoxae; metaventral postcoxal lines diverging from mesocoxal cavity margin, smoothly rounded behind, without a spur; discrimen short, extending less than halfway to anterior margin of metaventral process; metendosternite (Fig. 9g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange behind anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line; metafemur with subapical row of stout setae on posteroventral surface; metatibial foreface with apical ctenidium roughly perpendicular overall to long axis of tibia; spurs cylindrical, longest spur subequal to width of tibial apex; metatarsomere I shorter than metatarsomere II, joint between I and II rigid (Fig. 9d). Hind wing (Fig. 9e) with distinct, ovate anal lobe; leading edge with complete row of long setae at level of RA+ScP; AA_{3+4} not apparent; cubitoanal system unbranched apically; CuA_2 and MP_{3+4} with distal remnants; r4 present; flecks present in apical field just distal to rp-mp2; long transverse proximal sclerite and additional weak, irregular sclerite present just distal to end of radial bar.

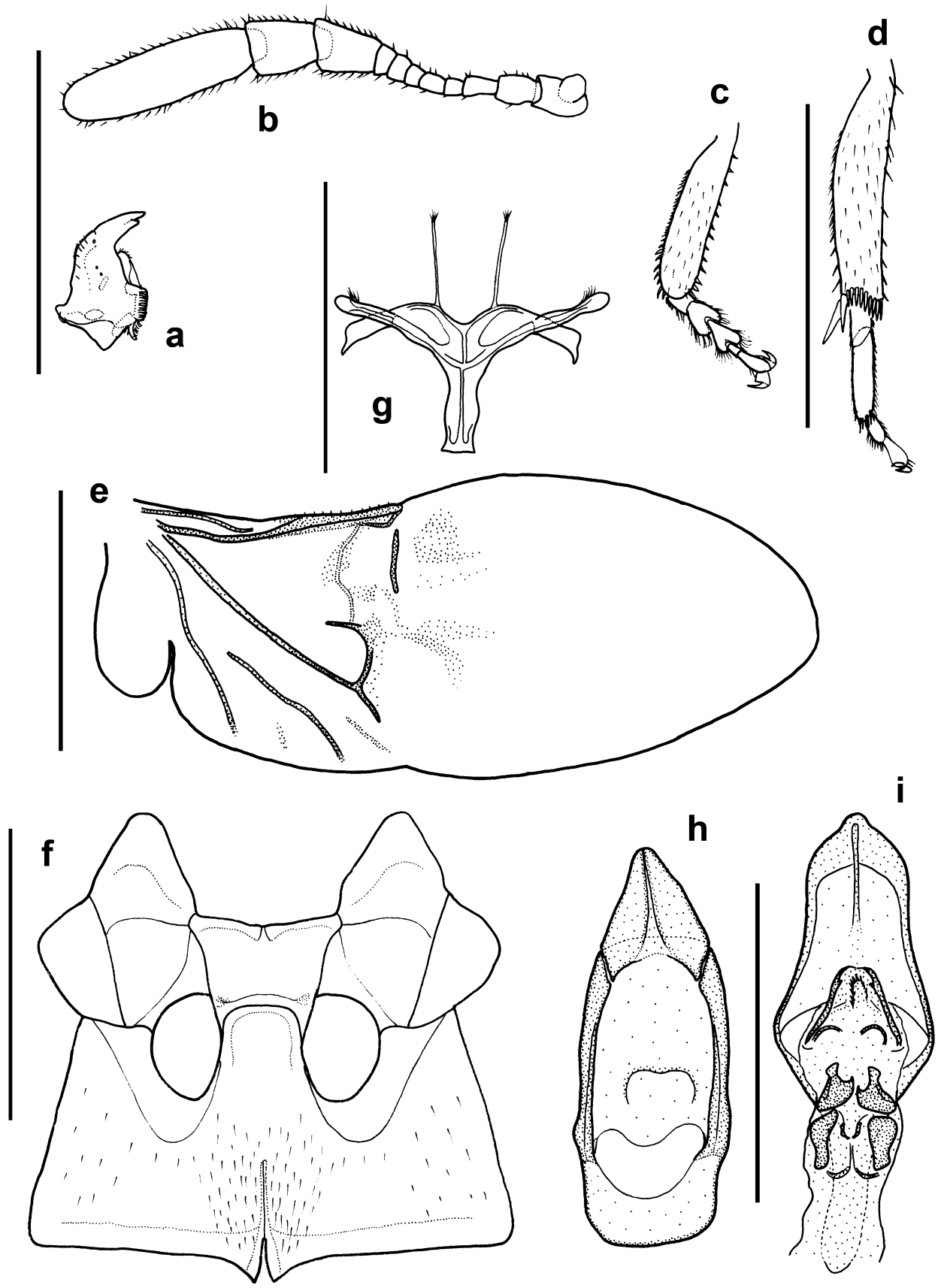

FIGURE 9. *Nesiotus* n. sp., male. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 0.5 mm). *Nesiotus olibroides* Guillebeau, lectotype male. (h) Tegmen, ventral; (i) penis, ventral (scale bar = 0.5 mm).

Abdomen. Abdominal ventrite I without paired lines or calli; spiracles apparently absent from segment VII. Male with aedeagus upright in repose; tegmen (Fig. 9h) with symmetrical anterior margin, parameres fused to basal piece, though separated by from it by a faint suture, parameres with medial longitudinal division; penis (Fig. 9i) somewhat wedge-shaped, with endophallic spicules, with large sclerites, apex weakly pointed; spiculum gastrale V-shaped, with arms free. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. Unknown.

Distribution and diversity. Apparently endemic to Madagascar. I have seen several new species of *Nesiotus* from that island.

Included species (1):

Nesiotus olibroides Guillebeau, 1896 (Distribution: Madagascar) (type!)

Discussion. See notes on the species originally described in *Nesiotus* by Scott (1922) in the *Acylomus* discussion.

6. *Stilbus* Seidlitz, 1872

(Figs. 2c; 10; 38b, c)

Olistherus Seidlitz 1872: 157. Type species: *Silpha atomaria* Linné 1767, fixed by subsequent designation. [junior homonym of *Olistherus* Agassiz, 1846]

Stilbus Seidlitz 1872: 35. Type species: *Anisotoma testacea* Panzer 1797, fixed by subsequent designation. [replacement name for *Olistherus* Seidlitz, 1872]

Eustilbus Sharp 1888: 253. Type species: *Anisotoma testacea* Panzer 1797, fixed by objective synonymy with *Stilbus* Seidlitz. [unjustified replacement name for *Stilbus* Seidlitz, 1872]

Stilboides Guillebeau 1894*a*: 282. Type species: *Stilboides sublineatus* Guillebeau 1894, fixed by original designation. [synonymized with *Stilbus* Seidlitz by Švec (2003: 101)]

Microstilbus Guillebeau 1894*a*: 283. Type species: *Phalacrus nitidus* Melsheimer 1844, fixed by original designation.

Type material. *Silpha atomaria* Linné: type in LSUK, not seen.

Anisotoma testacea Panzer: types not seen.

Stilboides sublineatus Guillebeau: syntype, male, genitalia dissected, "Grouvelle [handwritten] // St. Domingue [handwritten] // Museum Paris \ collection générale // HOLOTYPE [red label] // sublineatus Guilb. [handwritten] // Stilbus SUBLINEATUS (Guilb.) \ Svec det. 1992" (MNHN). Guillebeau mentioned four examples in his original description, and this specimen would probably best be considered a lectotype. This will be addressed in a future publication.

Phalacrus nitidus Melsheimer: 3 syntypes, lectotype here designated, with the following labels: "[blue disc] // nitidus \ M. \ Pa. [handwritten] // LECTOTYPE \ Phalacrus \ nitidus Melsheimer \ des. M.L. Gimmel 2010 [red label]" (MCZ). Three paralectotypes (MCZ): one belongs to Leiodidae (*Colenis*) with the labels "Melsh. // [red square, placed on pin by S. Henshaw]", and two paralectotypes are mounted on the same pin with the label "Melsh.", each with label added "PARALECTOTYPE \ Phalacrus \ nitidus Melsheimer \ det. M.L. Gimmel 2010 [yellow label]". The lectotype is designated to prevent future doubts about the name.

Diagnosis. May be recognized by the divergent, angulate or one-branched metaventral postcoxal lines, single elytral sutural stria, metatarsomere I shorter than II with joint between them flexible, prosternal process angulate when viewed laterally and with row of stiff setae at apex, ventral lobe of the eye not expanded, mandible without a ventral ridge, and the tegmen with parameres fused to basal piece.

Description. Very small to medium-sized, total length 1.1–2.5 mm. Dorsal color reddish-testaceous to piceous, often with elytral apices paler (Fig. 38b, c). Tibial spur formula 2-2-2, tarsal formula 5-5-4 in both sexes.

Head. Not constricted behind eyes. Eyes small to medium sized; facets flat; interfacetal setae absent; not emarginate medially; without sharp posterior emargination; periocular groove present; with transverse setose groove ventrally behind eye. Frontoclypeus (Fig. 2c) emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club 3-segmented, club weakly asymmetrical, antennomere XI not constricted (Fig. 10b). Mandible (Fig. 10a) with apex bidentate; with retinaculum; mandible without ventral ridge. Maxillary palpomere IV fusiform, inner edge swollen medially; galea short, rounded; lacinia with two stout spines, often with associated tuft of setae. Mentum with sides divergent toward apex; labial palpomere III fusiform. Labrum with apical margin arcuate to truncate. Gular sutures long.

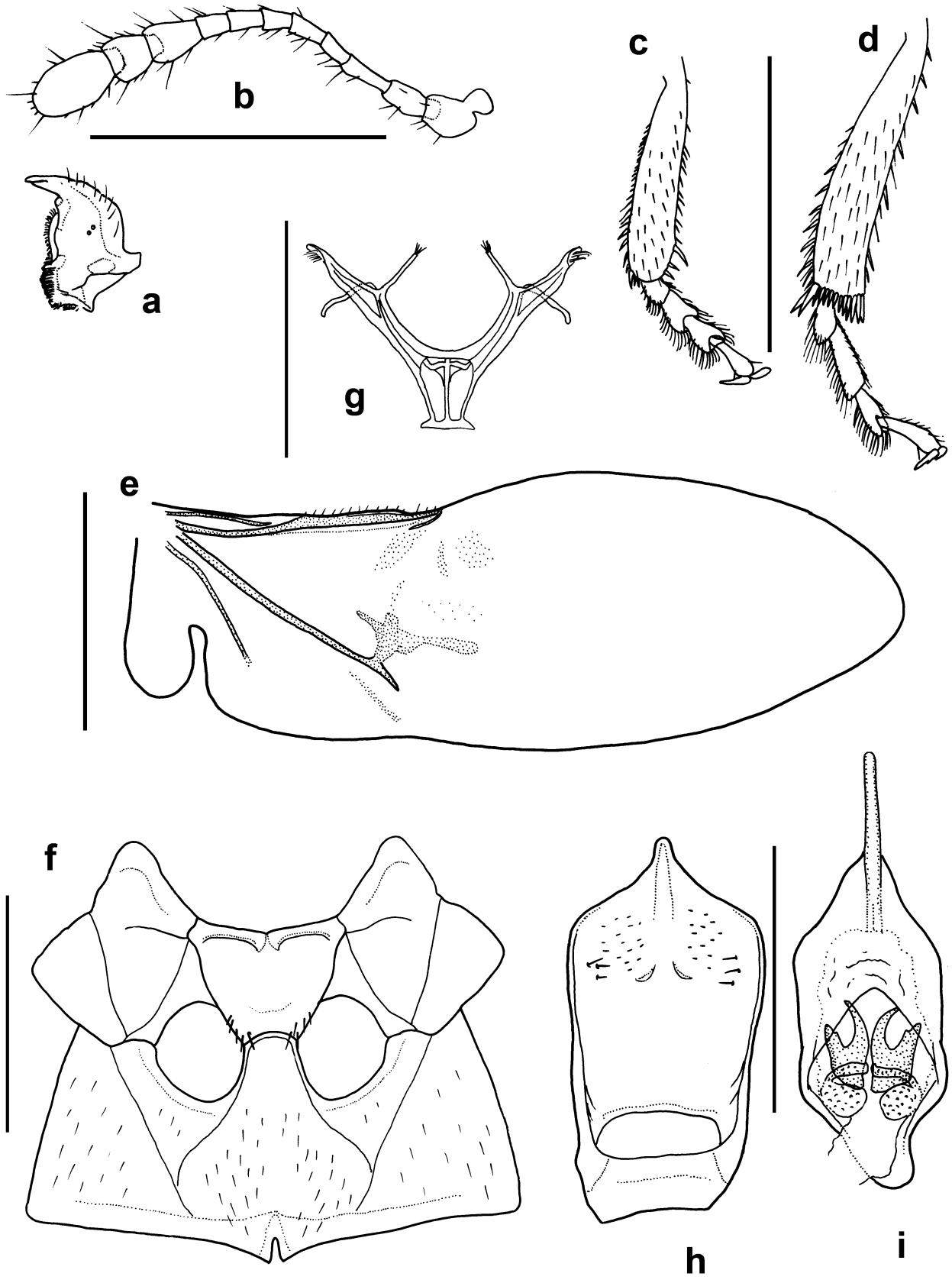

FIGURE 10. *Stilbus* nr. *apicalis*, male. (a) Right mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 0.5 mm). (h) Tegmen, ventral; (i) penis, ventral (scale bar = 0.5 mm).

Thorax. Pronotum with or without obvious microsetae; without or with weakly developed scutellar lobe. Prosternum anteriorly with marginal setae distributed in two patches, setae normal; procoxal cavity with anterolateral notchlike extension; prosternal process angulate in lateral view, not conspicuously setose preapically, with row of (often long) spinelike setae at apex. Protrochanter without setae; protibia without ctenidium on kickface (Fig. 10c). Scutellar shield small. Elytron without spectral iridescence; one sutural stria present; discal striae unimpressed, but sometimes represented by rows of faint, round punctures; without transverse strigae; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 10f) notched anteriorly, extending posteriorly to metaventrite, dividing mesoventral disc in two, procoxal rests indistinct or absent; mesanepisternum with incomplete transverse carina; mesocoxal cavities moderately widely separate, separated by less than half width of a coxal cavity. Mesotarsomere III bilobed. Metaventral process (Fig. 10f) not extending anteriorly beyond anterior level of mesocoxae; metaventral postcoxal lines diverging from mesocoxal cavity margin, usually angulate behind, often with a spur (Fig. 10f), branches occasionally not meeting or inner branch absent, rarely arcuate and smoothly rounded; discrimen short, extending less than halfway to anterior margin of metaventral process, or absent; metendosternite (Fig. 10g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange behind anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line absent; metatibial foreface with apical ctenidium roughly perpendicular overall to long axis of tibia; spurs cylindrical, longest spur distinctly shorter than width of tibial apex; metatarsomere I shorter than metatarsomere II, joint between I and II flexible (Fig. 10d). Hind wing (Fig. 10e) with distinct, ovate anal lobe; leading edge with complete row of long setae at level of RA+ScP; AA_{3+4} not apparent; cubitoanal system unbranched apically; CuA_2 and MP_{3+4} without distal remnants; r4 absent; flecks present in apical field just distal to rp-mp2; short transverse proximal sclerite and additional weak, irregular sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines or calli; ventrite III with toothed process medially in a few Nearctic forms; spiracles apparently absent from segment VII. Male with aedeagus upright in repose; tegmen (Fig. 10h) with symmetrical anterior margin, parameres fused to basal piece, parameres sometimes with medial longitudinal division; penis (Fig. 10i) variable, with endophallic spicules, often with large sclerites, apex with weak to strong median projection; spiculum gastrale V-shaped, with arms free. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Larval characters of *Stilbus* were illustrated and discussed in Steiner (1984) and Lawrence (1991).

Bionomics. Members of this genus are commonly swept from grassy areas. Specific feeding habits are unknown, but they probably are generalist mold feeders, much like members of *Acylomus*. They are strongly attracted to lights at night.

Distribution and diversity. A cosmopolitan genus, nearly coextensive with the distribution of the family as a whole, but apparently not well represented in the Australian region. This genus has been excellently treated for the Palearctic region (Švec 1992, including species now placed in *Acylomus*) and the Afrotropical region (Švec 2003), although much work still remains to be done, especially in the latter region. The exceedingly rich New World fauna has yet to receive a needed modern revision.

Included species (71):

Stilbus abbreviatus Casey, 1916 (Distribution: United States) (type!)
Stilbus aequalis (Sharp, 1888) (Distribution: Guatemala) (type!)
Stilbus angulatus Champion, 1925 (Distribution: subsaharan Africa) (type!)
Stilbus angulicaput (Scott, 1922) (Distribution: Seychelles) (type!)
Stilbus angustus Casey, 1916 (Distribution: United States) (type!)
Stilbus apertus Casey, 1916 (Distribution: United States) (type!)
Stilbus apicalis (Melsheimer, 1846) (Distribution: Canada, United States) (type!)
Stilbus apicipennis (Brèthes, 1924), **comb. nov.** (*Phalacrus*) (Distribution: Argentina) (type!)
Stilbus aquatilis (LeConte, 1856) (Distribution: United States) (type!)
Stilbus atomarius (Linné, 1767) (Distribution: Palearctic region)
Stilbus australis (Brèthes, 1922), **comb. nov.** (*Phalacrus*) (Distribution: Argentina)
Stilbus avunculus Flach, 1889 (Distribution: China, Japan)

Stilbus belfragei Casey, 1916 (Distribution: United States) (type!)
Stilbus bipustulatus Champion, 1925 (Distribution: Japan) (type!)
Stilbus brevisternus (Guillebeau, 1893) (Distribution: Vietnam) (type!)
Stilbus brunnescens (Motschulsky, 1858), **comb. nov.** (*Olibrus*) (Distribution: Sri Lanka)
Stilbus cinctus (Fauvel, 1903) (Distribution: New Caledonia)
Stilbus compactus Lyubarsky, 2003 (Distribution: Thailand)
Stilbus convergens Casey, 1890 (Distribution: United States) (type!)
Stilbus coxalis Švec, 1992 (Distribution: Japan)
Stilbus daublebskyorum Švec, 2003 (Distribution: Guinea)
Stilbus dollmani Champion, 1925 (Distribution: ?Zimbabwe) (type!)
Stilbus ferrugineus Švec, 1992 (Distribution: Azerbaijan)
Stilbus fidelis Casey, 1916 (Distribution: United States) (type!)
Stilbus finitimus Casey, 1916 (Distribution: United States) (type!)
Stilbus floridanus Casey, 1890 (Distribution: United States) (type!)
Stilbus galvestonicus Casey, 1916 (Distribution: United States) (type!)
Stilbus gossypii (Brèthes, 1912) (Distribution: Argentina)
Stilbus guillebeaui Hetschko, 1928 (Distribution: Indonesia) (type!)
Stilbus japonicus Švec, 1992 (Distribution: Japan)
Stilbus limatus Casey, 1916 (Distribution: United States) (type!)
Stilbus ludibundus Casey, 1916 (Distribution: United States) (type!)
Stilbus ludovicianus Casey, 1916 (Distribution: United States) (type!)
Stilbus merkli Švec, 1992 (Distribution: Russia)
Stilbus misellus (Guillebeau, 1894) (Distribution: Indonesia) (type!)
Stilbus modestus Casey, 1890 (Distribution: United States) (type!)
Stilbus mollis (Sharp, 1888) (Distribution: Guatemala) (type!)
Stilbus nanulus Casey, 1890 (Distribution: United States) (type!)
Stilbus nitidus (Melsheimer, 1846) (Distribution: United States) (type!)
Stilbus notabilis (Fall, 1901) (Distribution: United States) (type!)
Stilbus oblongus (Erichson, 1845) (Distribution: Palearctic region)
Stilbus obscurus Casey, 1890 (Distribution: United States) (type!)
Stilbus obtusus (LeConte, 1856) (Distribution: Mexico, United States) (type!)
Stilbus ochraceus Casey, 1916 (Distribution: United States) (type!)
Stilbus olearis Lyubarsky, 2003 (Distribution: Nepal)
Stilbus orbicularis Lyubarsky, 2003 (Distribution: Nepal)
Stilbus pallidus Casey, 1890 (Distribution: United States) (type!)
Stilbus pannonicus Franz, 1969 (Distribution: Palearctic region)
Stilbus piceus (Boheman, 1858), **comb. nov.** (*Olibrus*) (Distribution: United States)
Stilbus placidus (Sharp, 1888) (Distribution: Mexico) (type!)
Stilbus posticalis (Sharp, 1888), **comb. nov.** (*Olibrus*) (Distribution: Guatemala, Mexico) (type!)
Stilbus probatus Casey, 1916 (Distribution: United States) (type!)
Stilbus prudens Casey, 1916 (Distribution: United States) (type!)
Stilbus pubicoxis (Guillebeau, 1893) (Distribution: Vietnam) (type!)
Stilbus pusillus (LeConte, 1856) (Distribution: United States) (type!)
Stilbus seriatus (Guillebeau, 1894) (Distribution: ?Brazil) (type!)
Stilbus sharpi (Guillebeau, 1892) (Distribution: Africa, Middle East) (type!)
Stilbus shastanicus Casey, 1916 (Distribution: United States) (type!)
Stilbus simplex Lyubarsky, 1998 (Distribution: Namibia)
Stilbus sphaericulus Casey, 1916 (Distribution: United States) (type!)
Stilbus sternosetosus (Lyubarsky, 1998) (Distribution: Namibia)
Stilbus subalutaceus Casey, 1890 (Distribution: United States) (type!)
Stilbus sublineatus (Guillebeau, 1894) (Distribution: Haiti) (type!)
Stilbus substriatus (Guillebeau, 1894) (Distribution: Indonesia) (type!)

Stilbus testaceus (Panzer, 1797) (Distribution: Palearctic region)
Stilbus trisetosus Casey, 1916 (Distribution: United States) (type!)
Stilbus truncatus Švec, 1992 (Distribution: Morocco) (type!)
Stilbus univestis (Guillebeau, 1894) (Distribution: Cuba) (type!)
Stilbus viduus Casey, 1890 (Distribution: United States) (type!)
Stilbus yezoensis Hisamatsu, 1985 (Distribution: Japan)
Stilbus zotti Švec, 2003 (Distribution: Guinea)

Discussion. Based on the original description, *Olibrus piceus*, described from San Francisco, California, USA by Boheman (1858), possesses the characters of *Stilbus*, in particular the single sutural stria and rows of slight punctures on the elytra. I have tentatively moved it to this genus.

Enough characters were illustrated in Brèthes (1922: Fig. 2), including prosternal process apically with stiff setae, metaventral postcoxal lines with a single branch and extending to posterior margin, and hind tarsal structure to move his species *Phalacrus australis* to *Stilbus*.

The species decribed as *Stilbus libidinosus* Lyubarsky, 2003, cannot belong to this genus. The tegmen has hinged parameres (see Fig. 24, Lyubarsky 2003). Additionally, this species has arcuate metaventral postcoxal lines (see Fig. 23 in Lyubarsky 2003). I am provisionally transferring this species to *Acylomus*.

7. *Xanthocomus* Guillebeau, 1893

(Figs. 2m; 11; 38d, e)

Xanthocomus Guillebeau 1893*a*: 291. Type species: *Xanthocomus striatus* Guillebeau 1893, fixed by subsequent designation.
Leptostilbus Casey 1916: 71. Type species: *Leptostilbus rutilans* Casey 1916, fixed by subsequent designation (Gimmel 2011: 2). [synonymized with *Xanthocomus* Guillebeau by Gimmel (2011: 2)]

Type material. *Xanthocomus striatus* Guillebeau: two syntypes, including one dissected male, here designated as a lectotype to stabilize the species and generic names, "Caracas // Simon // Museum Paris, collection genérale // TYPE // [unpublished lectotype label, turned over] // GENITALIA IN DMHF—WATER SOLUBLE MEDIUM // striatus Guilb. // LECTOTYPE \ Xanthocomus \ striatus Guillebeau \ des. M.L. Gimmel 2011 [red label]" (MNHN). Paralectotype, also "Caracas // Simon…", with label attached "PARALECTOTYPE \ Xanthocomus \ striatus Guillebeau \ det. M.L. Gimmel 2011 [yellow label]" (MNHN).

Leptostilbus rutilans Casey: lectotype, point-mounted male with genitalia dissected out and mounted in DMHF on an acetate card on the same pin, "Brownsville \ Texas \ Wickham // CASEY \ bequest \ 1925 // rutilans 7 \ PARATYPE USNM \ 48982 [epithet and numbers handwritten] [red label] // LECTOTYPE \ Leptostilbus \ rutilans Casey \ des. M.L. Gimmel 2010 [red label]" (USNM).

Diagnosis. May be recognized by the divergent, arcuate metaventral postcoxal lines, single elytral sutural stria, metatarsomere I shorter than II and joint between them more or less rigid, prosternal process angulate when viewed laterally and with row of stiff setae at apex, mandible with a ventral ridge, the obliquely oriented setose groove behind eye ventrally, the tegmen with parameres hinged to basal piece, and the elongate, usually reddish-colored habitus.

Description. Small to large, total length 1.6–3.4 mm. Dorsal color dark reddish to reddish-testaceous (Fig. 38d, e). Tibial spur formula 2-2-2, tarsal formula 5-5-5 in females, 5-5-4 in males.

Head. Not constricted behind eyes. Eyes small to medium sized; facets flat; interfacetal setae absent; weakly emarginate medially; without sharp posterior emargination; periocular groove present; with obliquely oriented setose groove ventrally behind eye (Fig. 2m). Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club 3-segmented, club weakly asymmetrical, antennomere XI not constricted (Fig. 11b). Mandible (Fig. 11a) with apex bidentate; with retinaculum; mandible with ventral ridge and deep pocket. Maxillary palpomere IV fusiform, inner edge swollen medially; galea short, rounded; lacinia with two stout spines, often with associated tuft of setae. Mentum with sides divergent toward apex; labial palpomere III fusiform. Labrum with apical margin arcuate to truncate. Gular sutures long.

Thorax. Pronotum with or without obvious microsetae; with scutellar lobe absent or weakly developed. Prosternum anteriorly with marginal setae distributed in two patches, setae normal; procoxal cavity with

anterolateral notchlike extension; prosternal process angulate in lateral view, not conspicuously setose preapically, with row of spinelike setae at apex. Protrochanter without setae; protibia without ctenidium on kickface (Fig. 11c). Scutellar shield small. Elytron without or with moderate spectral iridescence; one sutural stria present; discal striae unimpressed, but usually represented by rows of distinct, round punctures; without transverse strigae; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 11f) notched anteriorly, extending posteriorly to metaventrite, dividing mesoventral disc in two, forming distinct procoxal rests; mesanepisternum with incomplete transverse carina; mesocoxal cavities widely separate, separated by more than half width of a coxal cavity. Mesotarsomere III bilobed. Metaventral process (Fig. 11f) not extending anteriorly beyond anterior level of mesocoxae; metaventral postcoxal lines diverging from mesocoxal cavity margin, arcuate and smoothly rounded; discrimen short, extending less than halfway to anterior margin of metaventral process; metendosternite (Fig. 11g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange behind anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line present or absent; metatibial foreface with apical ctenidium roughly perpendicular overall to long axis of tibia; spurs cylindrical, longest spur shorter than width of tibial apex, spurs sometimes weakly modified in males; metatarsomere I distinctly shorter than metatarsomere II, joint between I and II rigid (Fig. 11d). Hind wing (Fig. 11e) with distinct, ovate anal lobe; leading edge with complete row of long setae at level of RA+ScP; AA_{3+4} not apparent; cubitoanal system sometimes branched apically; CuA_2 and MP_{3+4} without distal remnants; r4 present or absent; flecks absent from apical field distal to rp-mp2; long transverse proximal sclerite and additional weak, irregular sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines or calli; spiracles apparently absent from segment VII. Male with aedeagus upright in repose; tegmen (Fig. 11h) with symmetrical anterior margin, parameres hinged to basal piece, parameres with medial longitudinal division; penis (Fig. 11i) slender, with endophallic spicules, often with large sclerites, apex with three or five small points; spiculum gastrale V-shaped, with arms free. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. Members of this genus have been swept from grassy meadows. They probably feed on microfungi growing on dead grasses.

Distribution and diversity. Occurring from the northern United States (Massachusetts to Michigan and Wisconsin) south to Argentina. They are a conspicuous faunal element in the West Indies.

Included species (11):

Xanthocomus attenuatus (Casey, 1890), **comb. nov.** (*Stilbus*) (Distribution: USA) (type!)
Xanthocomus badius Guillebeau, 1893 (Distribution: Venezuela) (type!)
Xanthocomus distinctus (Sharp, 1888), **comb. nov.** (*Leptostilbus*) (Distribution: Guatemala) (type!)
Xanthocomus floralis Guillebeau, 1894 (Distribution: Cuba) (type!)
Xanthocomus gracilis (Sharp, 1888), **comb. nov.** (*Stilbus*) (Distribution: Belize, Guatemala) (type!)
Xanthocomus grouvellei Guillebeau, 1894 (Distribution: Haiti)
Xanthocomus rufescens Guillebeau, 1894 (Distribution: Brazil) (type!)
Xanthocomus rufus Guillebeau, 1893 (Distribution: Venezuela) (type!)
Xanthocomus rutilans (Casey, 1916) (Distribution: USA, Central America, South America, West Indies) (type!)
Xanthocomus striatus Guillebeau, 1893 (Distribution: Venezuela) (type!)
Xanthocomus vicinus Guillebeau, 1893 (Distribution: Venezuela) (type!)

Discussion. The species of this genus were recently revised for North America (Gimmel 2011). Recent examination of types nominally described in *Stilbus* in the Casey collection has revealed three new synonymies:

Stilbus attenuatus Casey, 1890 = *Xanthocomus concinnus* (Casey, 1916); *Stilbus thoracicus* Casey, 1916; *Stilbus quadrisetosus* Casey, 1916, **syn. nov.**

The valid name for this species becomes *Xanthocomus attenuatus* (Casey, 1889).

The species of *Xanthocomus* from south of the United States are still in need of revision.

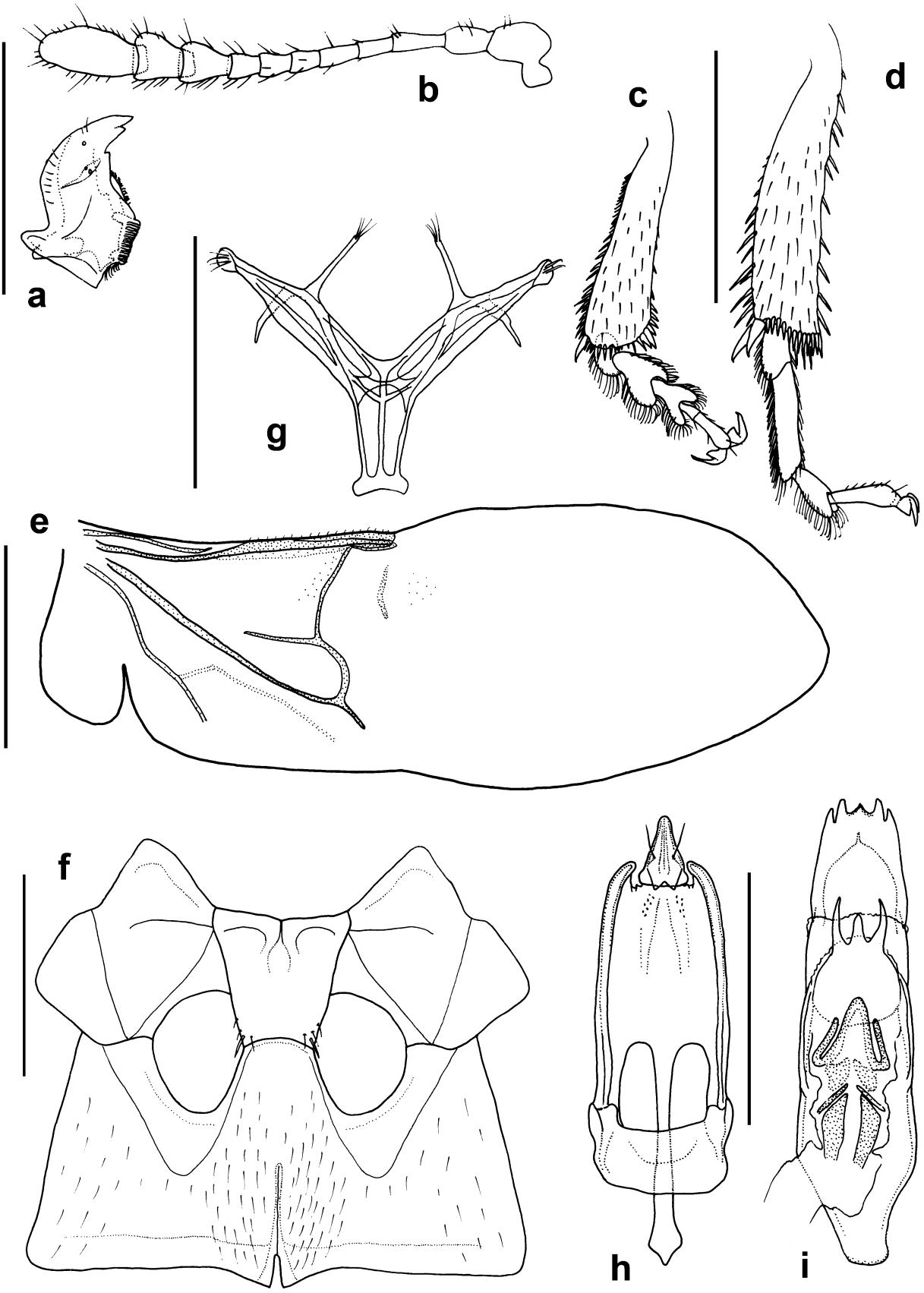

FIGURE 11. *Xanthocomus striatus*, male. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 0.5 mm). (h) Tegmen, ventral; (i) penis, ventral (scale bar = 0.5 mm).

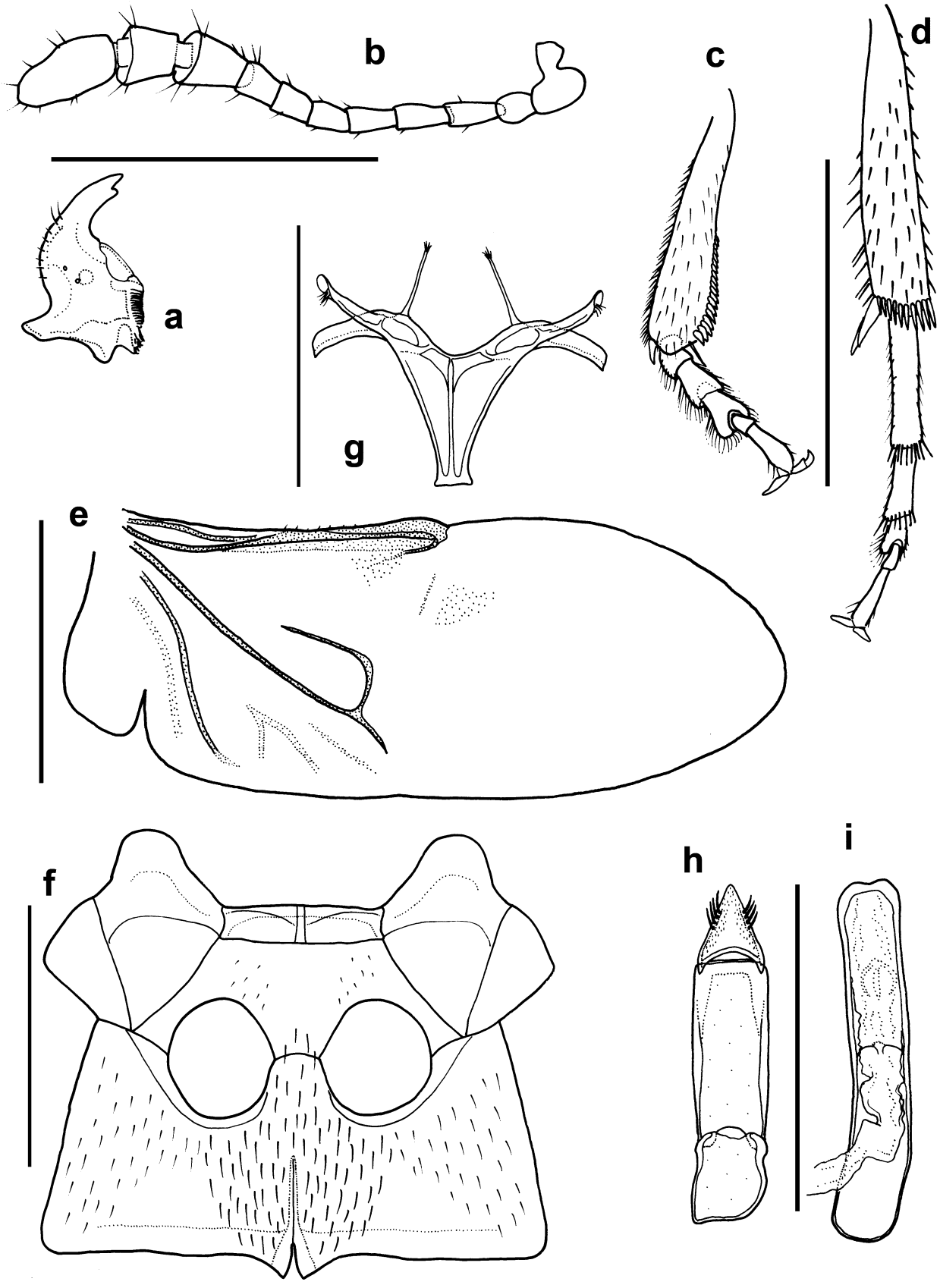

FIGURE 12. *Litostilbus testaceus*, male. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 0.5 mm). (h) Tegmen, ventral; (i) penis, ventral (scale bar = 0.5 mm).

PSEUDOLIBRUS-GROUP

Biophytini Guillebeau 1894*a*: 276. Type genus: *Biophytus* Guillebeau.
Megapalpini Guillebeau 1894*a*: 278. Type genus: *Megapalpus* Guillebeau (=*Megistopalpus* Guillebeau).

Diagnosis. This group may be recognized by the large scutellar shield, the presence of more than one elytral sutural stria, the metaventral process not surpassing the mesocoxae, and the presence of a protibial ctenidium.

Distribution and diversity. Eleven species, occurring in the Afrotropical, Oriental, and circum-Caribbean regions.

Included genera (3). *Litostilbus* Guillebeau, *Megistopalpus* Guillebeau, *Pseudolibrus* Flach.

8. *Litostilbus* Guillebeau, 1894

(Figs. 3f; 12; 38g–i)

Litostilbus Guillebeau 1894*a*: 283. Type species: *Sphaeridium testaceum* Fabricius 1792, fixed by original designation.
Pseudolitochrus Liubarsky 1993*a*: 16. Type species: *Phalacrus festivus* Motschulsky 1858, fixed by original designation. **Syn. nov.**

Type material. *Sphaeridium testaceum* Fabricius: three specimens associated with handwritten label "testaceum," one here designated lectotype to stabilize the species and generic name, sex unknown, right elytron missing, previous (unpublished) lectotype label turned upside down, label added "LECTOTYPE \ Sphaeridium \ testaceum Fabricius \ des. M.L. Gimmel 2010 [red label]" (ZMUC), straight pinned. Two paralectotypes, identified as Hydrophilidae and Cerylonidae by Warren E. Steiner, Jr., each with label "PARALECTOTYPE \ Sphaeridium \ testaceum Fabricius \ det. M.L. Gimmel 2010 [yellow label]" (ZMUC). All specimens are from "Americae meridionalis Insulis" (=Saint Thomas, Virgin Islands) and collected by "Dom. Smidt" according to original description.

Phalacrus festivus Motschulsky: holotype, sex unknown, "Phalacrus \ festivus \ Motsch. \ Ind. or. [handwritten, yellow label] // Pseudolitochrus \ festivus Mots. \ det. Lyubarsky 1993 // Holotype \ Phalacrus \ festivus Mots. \ det. Lyubarsky" (ZMUM), card mounted.

Diagnosis. Recognized by the large scutellar shield, elytron with one to three striae and spectral iridescence, presence of a protibial ctenidium, mesocoxal cavities not contiguous, and metatarsomere I longer than II.

Description. Small to large, total length 1.8–3.3 mm. Dorsal color testaceous to piceous, New World forms sometimes nebulously bicolored, a few southeast Asian forms strikingly so (Fig. 38g–i). Tibial spur formula 2-2-2, tarsal formula 5-5-5 in both sexes.

Head. Not constricted behind eyes. Eyes medium-sized; facets convex; interfacetal setae absent; weakly emarginate medially; without posterior emargination; periocular groove absent; with transverse setose groove ventrally behind eye. Frontoclypeus not or barely emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club 3-segmented, club symmetrical; antennomere XI weakly turbinate (Fig. 12b). Mandible (Fig. 12a) with apex tridentate; retinaculum absent; mandible without ventral ridge. Maxillary palpomere IV fusiform, elongate, nearly symmetrical; galea short, rounded; lacinia with two stout spines. Mentum with sides divergent toward apex; labial palpomere III fusiform. Labrum with apical margin arcuate. Gular sutures short, barely evident.

Thorax. Pronotum with microsetae present, distinct; with scutellar lobe absent or weakly developed. Prosternum anteriorly with continuous row of marginal setae, setae normal; procoxal cavity with anterolateral notchlike extension; prosternal process angulate in lateral view, conspicuously setose preapically, without row of spinelike setae at apex. Protrochanter without setae; protibia with ctenidium on kickface, extending from about one-half to three-quarters length of tibia (Fig. 12c). Scutellar shield large, width at base greater than length of eye. Elytron with spectral iridescence; with two or three sutural striae, rarely with one; disc with rudimentary striae or rows of punctures; with moderate to strong transverse strigae; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 12f) notched anteriorly, not extending posteriorly to metaventrite, forming procoxal rests; mesoventrite sunken medially, not setose; mesanepisternum with complete transverse carina; mesocoxal cavities separated by slightly less than half width of a coxal cavity. Mesotarsomere III not bilobed. Metaventral process

(Fig. 12f) not extending to anterior level of mesocoxae; metaventral postcoxal lines not separated from mesocoxal cavity margin; discrimen long, extending about halfway to anterior margin of metaventral process; metendosternite (Fig. 12g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange at anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line; metatibial foreface with apical ctenidium roughly perpendicular overall to long axis of tibia; spurs cylindrical, longest spur subequal to or distinctly longer than width of tibial apex; metatarsomere I longer than metatarsomere II, joint between I and II rigid (Fig. 12d). Hind wing (Fig. 12e) with distinct, ovate anal lobe; leading edge with incomplete row of long setae at level of RA+ScP; AA_{3+4} extremely weak, crossvein to Cu absent; cubitoanal system unbranched apically, but curving distally; CuA_2 and MP_{3+4} with distal remnants; r4 absent; flecks absent from apical field distal to rp-mp2; long transverse proximal sclerite and faint triangular sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines or calli; spiracles present and apparently functional on segment VII. Male with aedeagus upright in repose; tegmen (Fig. 12h) with asymmetrical anterior margin and parameres hinged to basal piece, parameres without medial longitudinal division; penis (Fig. 12i) long, slender, with small paired sclerites, apex bilobed; spiculum gastrale V- or U-shaped, arms connected by broad sclerotized lamina. Female ovipositor weakly sclerotized, palpiform (Fig. 3f).

Immature stages. Unknown.

Bionomics. These beetles have been taken by beating, in Malaise traps, and at lights. One long series from the Bahamas was collected from the trunk of *Coccoloba diversifolia* Jacq. (Polygonaceae) at night.

Distribution and diversity. Two described species from the West Indies and south Florida (probably synonymous), at least one undescribed species from Central and South America, and three described species from southeast Asia. The stunningly marked southeast Asian forms, like their New World counterparts, seem to show a high degree of intraspecific variation in both size and coloration, and the actual number of species will not be known until a careful taxonomic revision of this genus is undertaken.

Included species (5):

Litostilbus borneensis (Lyubarsky, 1994), **comb. nov.** (*Pseudolitochrus*) (Distribution: Indonesia)
Litostilbus festivus (Motschulsky, 1858), **comb. nov.** (*Pseudolitochrus*) (Distribution: southeast Asia) (type!)
Litostilbus malayanus (Champion, 1925), **comb. nov.** (*Pseudolitochrus*) (Distribution: Indonesia, Philippines) (type!)
Litostilbus testaceus (Fabricius, 1792) (Distribution: West Indies) (type!)
Litostilbus tristriatus (Casey, 1890), **comb. nov.** (*Ochrolitus*) (Distribution: USA (Florida)) (type!)

Discussion. While Liubarsky (1993*a*) was correct in separating Motschulsky's *Phalacrus festivus* from other Old World species by erecting a new genus for it (and later [Lyubarsky 1994*b*] two other species), he did not compare his genus to any New World forms. The New World *Litostilbus* are structurally almost identical to the southeast Asian *Pseudolitochrus*, and I have reflected this by synonymizing the two names. Casey's *Ochrolitus tristriatus* also belongs here, and may be synonymous with the Fabricius species.

9. *Megistopalpus* Guillebeau, 1895

(Figs. 2f; 39a, b)

Megapalpus Guillebeau 1893*b*: 297. Type species: *Megapalpus simoni* Guillebeau 1893, fixed by monotypy.
Megistopalpus Guillebeau 1895: xxvii. [replacement name for *Megapalpus* Guillebeau, 1893]

Type material. *Megapalpus simoni* Guillebeau: one syntype found, here designated as lectotype, point mounted, "Aden [handwritten] // Megapalpus \ Simoni \ Guilb. [handwritten] // LECTOTYPE \ Megapalpus \ simoni Guillebeau \ des. M.L. Gimmel 2009 [red label]" (MNHN). Two specimens were mentioned in the original description. The lectotype is designated in order to stabilize the generic and specific names.

Diagnosis. The only phalacrid whose maxillary palps approximate the length of the antennae. Otherwise quite similar to *Pseudolibrus*, with a protibial ctenidium, large scutellar shield, and nine nearly complete, distinct elytral striae, though members of the latter genus are smaller (2.7 mm or less).

Description. Large, total length 3.2 mm. Color solid testaceous (Fig. 39a). Tibial spur formula 2-2-2, tarsal formula 5-5-5 in female, male unknown.

Head. Not constricted behind eyes. Eyes medium-sized; facets convex; weakly emarginate medially; without posterior emargination; periocular groove absent. Frontoclypeus not emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club loosely 3-segmented, club weakly asymmetrical; antennomere XI weakly turbinate. Maxillary palp (Fig. 2f; Fig. 39b) extremely long, approaching length of antenna, palpomeres II–IV flattened, clavate, palpomere II longest. Labial palp unmodified, labial palpomere III elongate, fusiform.

Thorax. Pronotum with scattered microsetae; without scutellar lobe. Procoxal cavity with anterolateral notchlike extension; prosternal process weakly angulate in lateral view, somewhat setose preapically, without spinelike setae at apex. Protibia with ctenidium on kickface extending about one-third length of tibia. Scutellar shield large, about as long as greatest length of eye. Elytron without spectral iridescence; with nine distinct, more-or-less complete impunctate striae (including sutural), medialmost stria somewhat convergent apically, second stria (first discal) fusing with sutural stria before apex; with distinct transverse strigae, strongest laterally; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate notched anteriorly, not extending posteriorly to metaventrite, forming procoxal rests; mesoventral disc depressed medially, setose; mesanepisternum with complete transverse carina; mesocoxae approximate, separated by less than half width of a coxal cavity. Mesotarsomere III not bilobed. Metaventral process extending anteriorly just to halfway point of mesocoxae; metaventral postcoxal lines not separated from mesocoxal cavity margin; discrimen long, extending more than halfway to anterior margin of metaventral process. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line; metatibial foreface with apical ctenidium straight, perpendicular overall to long axis of tibia; spurs cylindrical, longest spur greater than width of tibial apex; metatarsomere I longer than metatarsomere II, but shorter than remainder of tarsus, joint between I and II rigid.

Abdomen. Abdominal ventrite I without paired lines.

Immature stages. Unknown.

Bionomics. Unknown.

Distribution and diversity. Known only from the lectotype collected in Yemen ("Aden") and from a Somali specimen (MSNG). The two may not be conspecific.

Included species (1):

Megistopalpus simoni (Guillebeau, 1893) (Distribution: Yemen) (type!)

Discussion. Since the genus is known only from two specimens, one a primary type, I did not disarticulate a member of this morphologically interesting genus for examination under a compound scope. Accordingly, the description above is relatively scanty and the genus was excluded from the phylogenetic analysis. However, based on external morphology it is quite similar to the genus *Pseudolibrus*, therefore I have included it in the *Pseudolibrus*-group.

10. *Pseudolibrus* Flach, 1889

(Figs. 13; 38f)

Pseudolibrus Flach 1889*a*: 270. Type species: *Pseudolibrus gestroi* Flach 1889, fixed by monotypy.
Biophytus Guillebeau 1894*a*: 279. Type species: *Biophytus grouvellei* Guillebeau 1894, fixed by original designation. **Syn. nov.**
Polyaloxus Guillebeau 1894*a*: 283. Type species: *Lithocrus pallidus* Wollaston 1867, fixed by original designation. **Syn. nov.**

Type material. *Pseudolibrus gestroi* Flach: holotype, "Bogos 1870 \ Sciotel [handwritten] \ O. Beccari. // Museo Civ. \ Genova // Olibrus \ pallescens \ m. [handwritten] // Olibrus \ pallescens \ n.sp. in litt. [handwritten] \ det.E.Reitter // ? TYPUS of \ Pseudolibrus \ gestroi Flach, 1889 \ R.Poggi [handwritten] [red label] // HOLOTYPE \ Pseudolibrus \ gestroi Flach \ det. M.L. Gimmel 2011 [red label]" (MSNG), card mounted.

Biophytus grouvellei Guillebeau: holotype, "Grouvelle [handwritten] // Zanzibar \ Raffray [green label] // HOLOTYPE [red label] // [illegible] // Museum Paris \ Coll. \ Générale // Grouvellei \ Guilb. // HOLOTYPE \ Biophytus \ grouvellei Guillebeau \ det. M.L. Gimmel 2009 [red label]" (MNHN), card mounted.

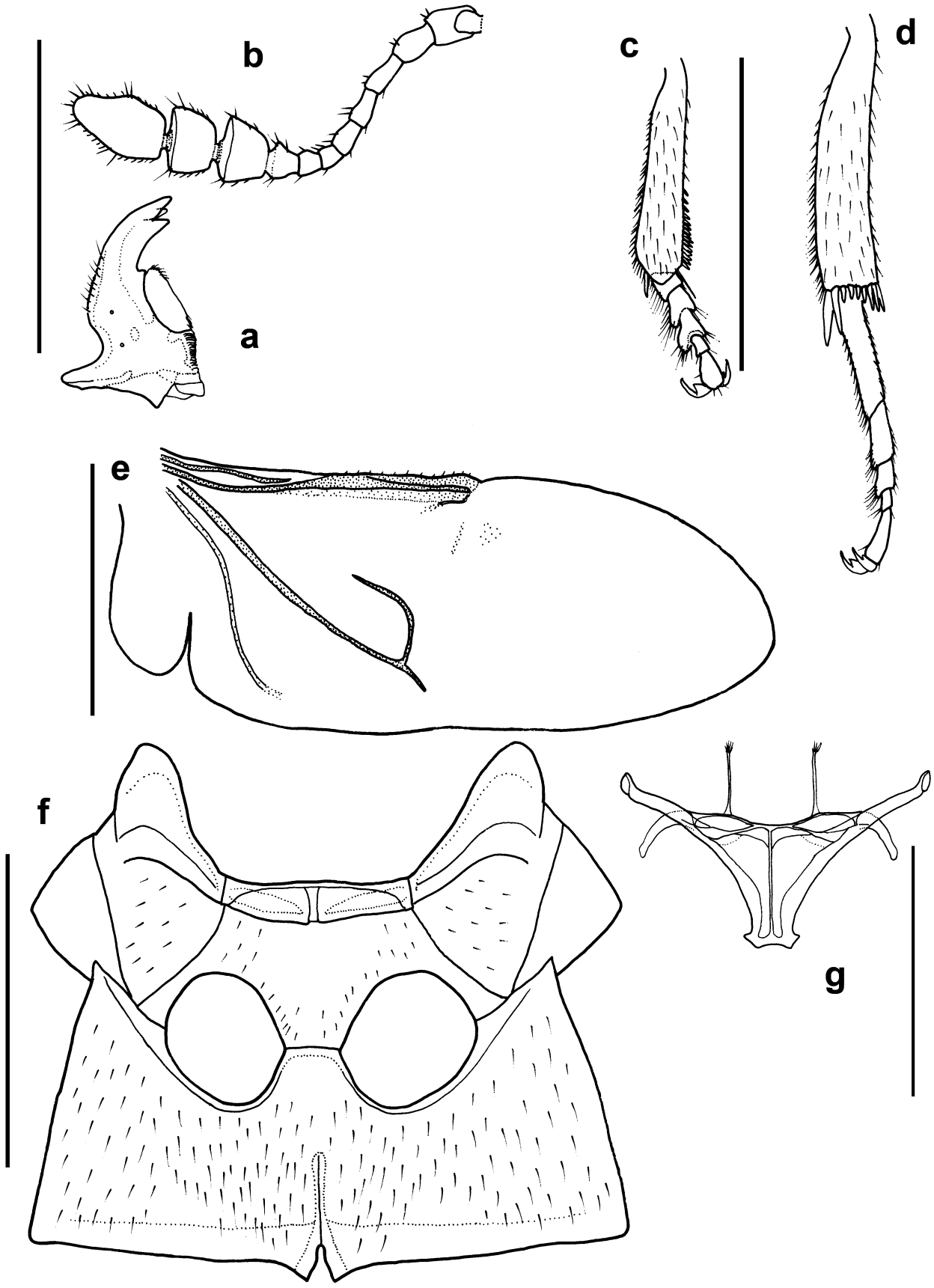

FIGURE 13. *Pseudolibrus* sp., female. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 0.5 mm).

Lithocrus pallidus Wollaston: lectotype, here designated, "Type [orange-bordered disc] // pallidus, Woll. [handwritten] // CAPE VERDE IS. \ S. Iago \ T.V. Wollaston Coll. \ B.M. 1867–82. // SYN- \ TYPE [blue-bordered disc] // Lithocrus \ pallidus W. [handwritten] // LECTOTYPE \ Lithocrus \ pallidus Wollaston \ des. M.L. Gimmel 2010 [red label]" (BMNH), card mounted. Three paralectotypes, with same data, with labels affixed "PARALECTOTYPE \ Lithocrus \ pallidus Wollaston \ det. M.L. Gimmel 2010 [yellow label]" (BMNH). The lectotype is here designated to stabilize the identity of the species and of the generic name *Polyaloxus* Guillebeau.

Diagnosis. Easily recognized by the combination of nine nearly complete elytral striae, large scutellar shield, and unmodified maxillary palps. Additional characters aiding in identification are lack of frontoclypeal emargination above antennal insertion, the presence of a protibial ctenidium, and metatarsomere I longer than II.

Description. Small to medium-sized, total length 1.5–2.7 mm. Color solid testaceous to solid black, darker specimens often with lighter elytral apices (Fig. 38f). Tibial spur formula 2-2-2, tarsal formula 5-5-5 in both sexes.

Head. Not constricted behind eyes. Eyes medium-sized; facets convex; interfacetal setae absent; weakly emarginate medially; without posterior emargination; periocular groove absent; with transverse setose groove ventrally behind eye. Frontoclypeus not emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club loosely 3-segmented, club weakly asymmetrical; antennomere XI weakly turbinate (Fig. 13b). Mandible (Fig. 13a) slender, with apex tridentate; with weak retinaculum; mandible without ventral ridge. Maxillary palpomere IV fusiform, nearly symmetrical; galea rounded; lacinia with two stout spines. Mentum with sides divergent toward apex; labial palpomere III elongate, fusiform. Labrum with apical margin arcuate. Gular sutures short, barely evident.

Thorax. Pronotum with distinct, scattered microsetae; without scutellar lobe. Prosternum anteriorly with continuous row of marginal setae, setae normal; procoxal cavity with anterolateral notchlike extension; prosternal process angulate in lateral view, usually conspicuously setose preapically, without spinelike setae at apex. Protrochanter without setae; protibia with ctenidium on kickface extending about one-third to one-half length of tibia (Fig. 13c). Scutellar shield large, about as long as or longer than length of eye. Elytron without spectral iridescence; with nine distinct, more-or-less complete striae, medialmost stria somewhat convergent apically, second stria (first discal) fusing with sutural stria before apex; with distinct transverse strigae, strongest laterally; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 13f) notched anteriorly, not extending posteriorly to metaventrite, forming procoxal rests; mesoventral disc depressed medially, setose; mesanepisternum with complete transverse carina; mesocoxae approximate, separated by less than half width of a coxal cavity. Mesotarsomere III not bilobed. Metaventral process (Fig. 13f) extending anteriorly just to halfway point of mesocoxae; metaventral postcoxal lines not separated from mesocoxal cavity margin; discrimen short, not quite extending halfway to anterior margin of metaventral process; metendosternite (Fig. 13g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange behind anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line; metatibial foreface with apical ctenidium straight, perpendicular overall to long axis of tibia; spurs cylindrical, longest spur subequal to width of tibial apex; metatarsomere I longer than metatarsomere II, but shorter than remainder of tarsus, joint between I and II rigid (Fig. 13d). Hind wing (Fig. 13e) with distinct, ovate anal lobe; leading edge without long setae; AA_{3+4} not apparent; cubitoanal system not forked; CuA_2 and MP_{3+4} without distal remnants; r4 absent; curved fleck present in apical field distal to rp-mp2; small transverse sclerite and medium-sized nebulous sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines or calli; spiracles present and apparently functional on segment VII. Male with aedeagus upright in repose; tegmen with symmetrical anterior margin and parameres hinged to basal piece, parameres without medial longitudinal division; penis parallel-sided, elongate, with small field of endophallic spicules, apex simple; spiculum gastrale with arms parallel, connected by broad lamina. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. Collection methods on labels are meager, but many were collected at lights and others were collected in Malaise traps. The gut of one dissected specimen contained large numbers of tripartite fungal spores.

Distribution and diversity. Exclusively Afrotropical, extending from Cape Verde and Liberia to Eritrea, Tanzania, Madagascar, Seychelles, and South Africa. A few undescribed species exist.

Included species (5):

Pseudolibrus gestroi Flach, 1889 (Distribution: Eritrea) (type!)
Pseudolibrus grouvellei (Guillebeau, 1894), **comb. nov.** (*Biophytus*) (Distribution: Tanzania) (type!)
Pseudolibrus pallidus (Wollaston, 1867), **comb. nov.** (*Polyaloxus*) (Distribution: Cape Verde) (type!)
Pseudolibrus snizeki (Švec, 2006), comb. nov. (*Biophytus*) (Distribution: Uganda)
Pseudolibrus striatus (Champion, 1925), **comb. nov.** (*Polyaloxus*) (Distribution: Angola, South Africa) (type!)

Discussion. The respective type species of *Pseudolibrus* Flach, *Biophytus* Guillebeau, and *Polyaloxus* Guillebeau are nearly identical, and the other included species in the latter two genera fit well within the generic concept described above. Unfortunately, the oldest genus-group name in this group of genera is *Pseudolibrus*, which had not been used since its original publication. *Biophytus* has been used as valid in the past 50 years, but apparently not by 10 or more authors in 25 works, so a reversal of precedence cannot occur without petition to the ICZN (see ICZN 1999, Article 23.9). This will have unpleasant consequences for any family-group name that may eventually apply to this group, since the two available are based on a synonymized (in the case of Biophytini Guillebeau) or on younger (in the case of Megapalpini Guillebeau) generic names.

PHALACRUS-GROUP

Phalacrurida Leach 1815: 116. Type genus: *Phalacrus* Paykull.

Diagnosis. This group may be recognized by the large scutellar shield, the shelflike frontoclypeus that is not emarginate over antennal insertions, the lack of divergent metaventral lines, aedeagus resting on its side in repose, metatarsomere I shorter than II, and lack of a protibial ctenidium.

Note. This is an extremely well-defined group based on adult characters. Its cohesion is further supported by a larval character unique among Coleoptera: the antennal sensorium is located on antennomere I rather than on antennomere II as in all other Phalacridae studied and all other Coleoptera.

Distribution and diversity. Ninety-six species, occurring throughout the range of Phalacridae.

Included genera (2). *Phalacropsis* Casey, *Phalacrus* Paykull.

11. *Phalacropsis* Casey, 1890
(Figs. 3d; 14; 39c)

Phalacropsis Casey 1890: 101. Type species: *Phalacrus dispar* LeConte 1879, fixed by monotypy.

Type material. *Phalacrus dispar* LeConte: holotype, "Veta Pass \ 21.6 [number handwritten] \ Col // 344 [handwritten] // P. dispar \ Lec. [handwritten] // Type \ 6644 [red label, number handwritten] // HOLOTYPE \ Phalacrus \ dispar LeConte \ det. M.L. Gimmel 2010 [red label]" (MCZ), point mounted.

Diagnosis. Recognized by the lack of a protibial ctenidium, large scutellar shield, lack of a sutural stria, protruded metaventral process, metatarsomere I shorter than II, and female ovipositor with gonocoxae not spiniform.

Description. Small to large, total length 1.7–3.2 mm. Dorsal color testaceous to brunneous (Fig. 39c). Tibial spur formula 2-2-2, tarsal formula 5-5-5 in both sexes.

Head. Not constricted behind eyes. Eyes small; facets flat; interfacetal setae absent; weakly emarginate medially; without posterior emargination; periocular groove absent; with transverse setose groove ventrally behind eye. Frontoclypeus not or barely emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club 3-segmented, club weakly asymmetrical; antennomere XI not constricted, often elongate (Fig. 14b). Mandible (Fig. 14a) with apex tridentate; retinaculum present, strong; mandible without ventral ridge. Maxillary palpomere IV cylindrical, elongate, narrower than palpomere III, nearly symmetrical; galea short, rounded; lacinia with two stout spines. Mentum with sides divergent toward apex; labial palpomere III fusiform. Labrum with apical margin truncate. Gular sutures short, barely evident.

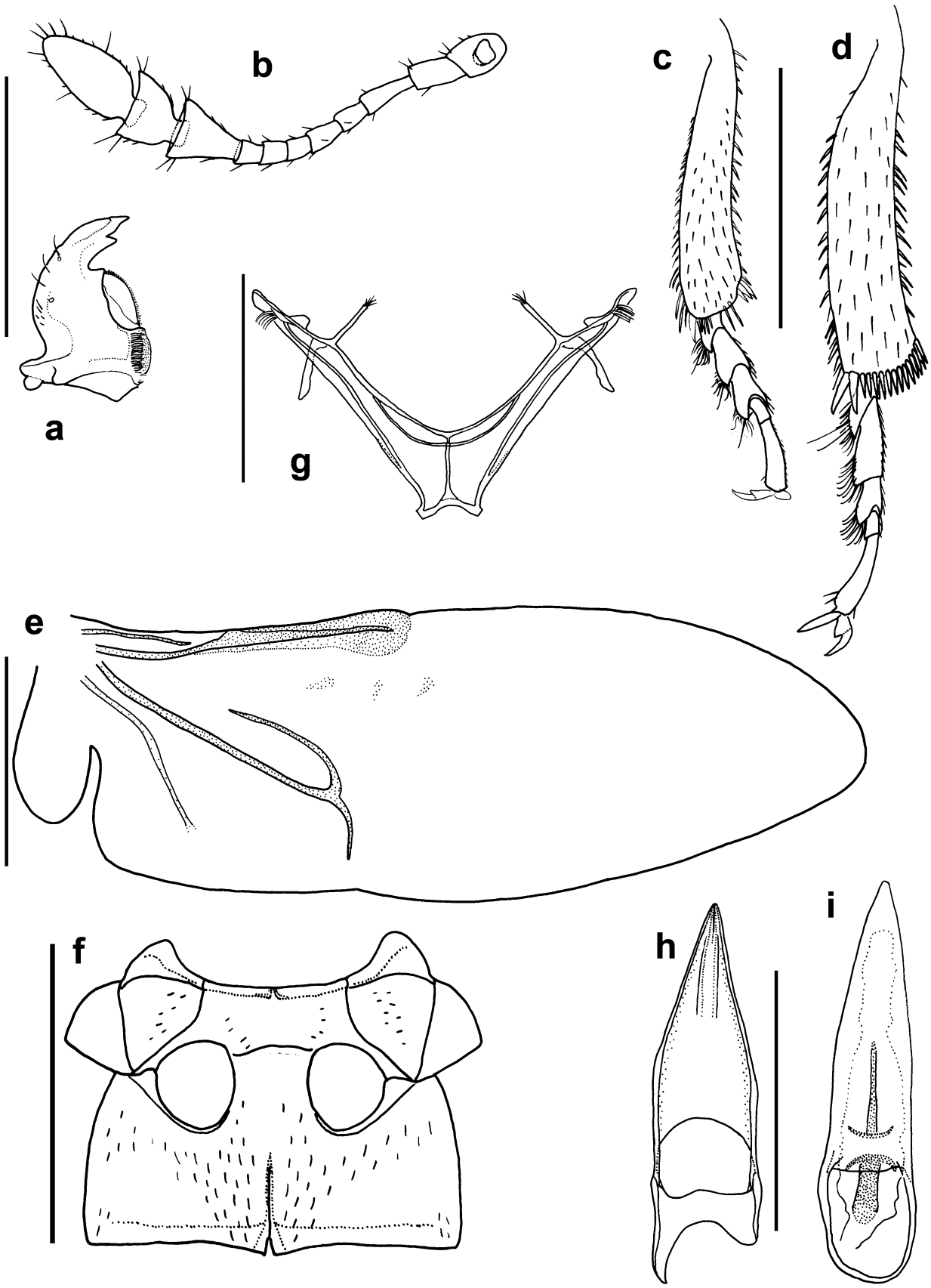

FIGURE 14. *Phalacropsis dispar*, female. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 1.0 mm). (g) Metendosternite (scale bar = 0.5 mm). Male. (h) Tegmen, ventral; (i) penis, ventral (scale bar = 0.5 mm).

Thorax. Pronotum without obvious microsetae; with scutellar lobe weakly developed. Prosternum anteriorly with continuous row of marginal setae, setae normal; procoxal cavity with anterolateral notchlike extension; prosternal process rounded in lateral view, not conspicuously setose preapically, without row of spinelike setae at apex. Protrochanter with setae; protibia without ctenidium on kickface (Fig. 14c). Scutellar shield large, width at base greater than length of eye. Elytron without spectral iridescence; without sutural stria; disc without even rudimentary striae or rows of punctures; without transverse strigae; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 14f) notched anteriorly, not extending posteriorly to metaventrite, forming procoxal rests; mesoventrite sunken medially, with scattered setae; mesanepisternum with complete transverse carina; mesocoxal cavities separated by much greater than half width of a coxal cavity. Mesotarsomere III bilobed. Metaventral process (Fig. 14f) extending beyond anterior level of mesocoxae, highly protruding and lobed anteriorly; metaventral postcoxal lines not separated from mesocoxal cavity margin; discrimen short, extending less than halfway to anterior margin of metaventral process; metendosternite (Fig. 14g) with anterior tendons widely separated, ventral process intersecting ventral longitudinal flange behind anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line; metafemur with subapical row of long setae on posteroventral surface; metatibial foreface with apical ctenidium roughly perpendicular overall to long axis of tibia; spurs cylindrical, longest spur much shorter than width of tibial apex; metatarsomere I shorter than metatarsomere II, joint between I and II flexible, tarsomeres with hairy pads similar to those of pro- and mesotarsus (Fig. 14d). Hind wing (Fig. 14e) with distinct, ovate anal lobe; leading edge without row of long setae at level of RA+ScP; AA_{3+4} not apparent; cubitoanal system unbranched apically; CuA_2 and MP_{3+4} without distal remnants; r4 absent; flecks absent from apical field distal to rp-mp2; extremely small flecks present in region just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines or calli; spiracles apparently absent from segment VII. Male with aedeagus rotated in repose, resting on its side; tegmen (Fig. 14h) with symmetrical anterior margin, with pair of acute struts, parameres fused to basal piece, parameres divided longitudinally; penis (Fig. 14i) with unpaired endophallic sclerites, apex simple; spiculum gastrale V-shaped, arms free. Female ovipositor (Fig. 3d) moderately sclerotized; gonocoxites not modified into spinose structures; gonostyli attached apically.

Immature stages. Larvae have not been formally described for this genus, although the mandible was illustrated in Steiner (1984: 441). The mandible possesses what appears to be a true mola, which is reflective of spore-mass-feeding habits.

Bionomics. The larvae of *Phalacropsis dispar* appear to be highly host specific, feeding on aeciospores and underlying sporogenous mycelium of native western pine stem rust fungi (*Peridermium* spp.) on various species of pines (*Pinus* spp.). The life cycle is completed in about 30 to 40 days, during which the larvae generally completely consume the contents of the aecia they infest, and appear to be highly effective in natural control of the rust fungus (Nelson 1982; Steiner 1984).

Distribution and diversity. The exact limits of this genus are unknown, and will require dissection of female genitalia to resolve. Occurring from Oregon and Idaho south to at least Venezuela and Bolivia. Apparently restricted to highland regions.

Included species (3):

Phalacropsis dispar (LeConte, 1879) (Distribution: United States) (type!)
Phalacropsis lucidus (Sharp, 1888), **comb. nov.** (*Phalacrus*) (Distribution: Guatemala) (type!)
Phalacropsis scutellaris (Sharp, 1888), **comb. nov.** (*Phalacrus*) (Distribution: Guatemala) (type!)

Discussion. Although *Phalacropsis* may render *Phalacrus* paraphyletic I am presently acknowledging their distinctness by maintaining them as separate genera. This includes the transfer of two Sharp species described from Guatemala in the genus *Phalacrus* to *Phalacropsis*. These new combinations are made explicit above.

12. *Phalacrus* Paykull, 1800

(Figs. 2d; 3c; 15; 39d, e)

Phalacrus Paykull 1800: 438. Type species: *Anisotoma corrusca* Panzer 1797, fixed by subsequent designation.
Glaurosoma Thomson 1859: 66. Type species: *Phalacrus substriatus* Gyllenhal 1813, fixed by original designation.

Type material. *Anisotoma corrusca* Panzer: types not seen.

Phalacrus substriatus Gyllenhal: types not seen.

Diagnosis. One of the few genera that may be unambiguously recognized in dorsal view based on structural characters. The scutellar shield is greatly enlarged relative to most other members of the family, and there is almost always a single sutural stria on the elytron (sometimes extremely reduced or absent). The spiniform ovipositor is an autapomorphy for the genus. Additionally, members have no emargination of the frontoclypeus above the antennal insertion, have metaventral postcoxal lines not separated from the coxal cavities, and have a group of long, stiff setae postero-ventrally near the apex of the femora.

Description. Very small to very large, total length 1.4–4.5 mm. Dorsal color usually pitch black, but a few forms rufotestaceous and some have reddish maculations on the elytra (Figs. 39d, e). Tibial spur formula 2-2-2, tarsal formula 5-5-5 in both sexes.

Head. Not constricted behind eyes. Eyes small; facets convex; interfacetal setae absent; weakly emarginate medially; without posterior emargination; periocular groove present or absent; with transverse setose groove ventrally behind eye. Frontoclypeus (Fig. 2d) not or barely emarginate above antennal insertion; clypeal apex arcuate-truncate, but often with asymmetrical emarginations. Antennal club 3-segmented, club symmetrical or weakly asymmetrical; antennomere XI not constricted, often elongate (Fig. 15b); males of some Greater Antillean forms with antennae longer than total body length. Mandible (Fig. 15a) with apex usually tridentate, middle cusp often quite long and slender, sometimes bidentate (upper cusp lacking) or simple (upper and lower cusps lacking), mandibles often asymmetrical; retinaculum present, strong; mandible without ventral ridge. Maxillary palpomere IV cylindrical, elongate, narrower than palpomere III, nearly symmetrical; galea short, rounded; lacinia with two stout spines. Mentum with sides divergent toward apex; labial palpomere III fusiform. Labrum with apical margin truncate. Gular sutures short, barely evident.

Thorax. Pronotum without obvious microsetae; with scutellar lobe weakly developed. Prosternum anteriorly with continuous row of marginal setae, setae normal; procoxal cavity with anterolateral notchlike extension; prosternal process rounded in lateral view, not conspicuously setose preapically, without row of spinelike setae at apex. Protrochanter with setae; protibia without ctenidium on kickface (Fig. 15c). Scutellar shield large, width of raised portion greater than length of eye. Elytron without spectral iridescence; with one sutural stria, stria rarely absent; disc often with rudimentary striae or rows of punctures; without transverse strigae; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 15f) notched anteriorly, not extending posteriorly to metaventrite, forming procoxal rests; mesoventrite sunken medially, not setose; mesanepisternum with complete transverse carina; mesocoxal cavities separated by much greater than half width of a coxal cavity. Mesotarsomere III bilobed. Metaventral process (Fig. 15f) extending at least to anterior level of mesocoxae, often highly protruding and lobed anteriorly; metaventral postcoxal lines not separated from mesocoxal cavity margin; discrimen short, extending less than halfway to anterior margin of metaventral process; metendosternite (Fig. 15g) with anterior tendons widely separated, ventral process intersecting ventral longitudinal flange at anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line; metafemur with subapical row of long setae on posteroventral surface; metatibial foreface with apical ctenidium roughly perpendicular overall to long axis of tibia; spurs cylindrical, longest spur much shorter than width of tibial apex; metatarsomere I shorter than metatarsomere II, joint between I and II flexible, tarsomeres with hairy pads similar to those of pro- and mesotarsus (Fig. 15d). Hind wing (Fig. 15e) with distinct, ovate anal lobe; leading edge without row of long setae at level of RA+ScP; AA_{3+4} not apparent except at base, crossvein to Cu absent; cubitoanal system unbranched apically; CuA_2 and MP_{3+4} without distal remnants; r4 absent; flecks absent from apical field distal to rp-mp2; flecks absent from region just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines or calli; spiracles apparently absent from segment VII; males of some New World forms with medial tufts of setae on some or all ventrites. Male with aedeagus rotated in repose, resting on its side; tegmen (Fig. 15h) with asymmetrical anterior margin and parameres either fused to basal piece or separated from (but not hinged to) basal piece by suture, parameres divided longitudinally; penis (Fig. 15i) with unpaired endophallic sclerites, apex simple; spiculum gastrale V-shaped, arms free. Female ovipositor (Fig. 3c) sclerotized, gonocoxites modified into cornified spinose structures, with 1–3 outwardly directed spines, gonostyli attached subapically.

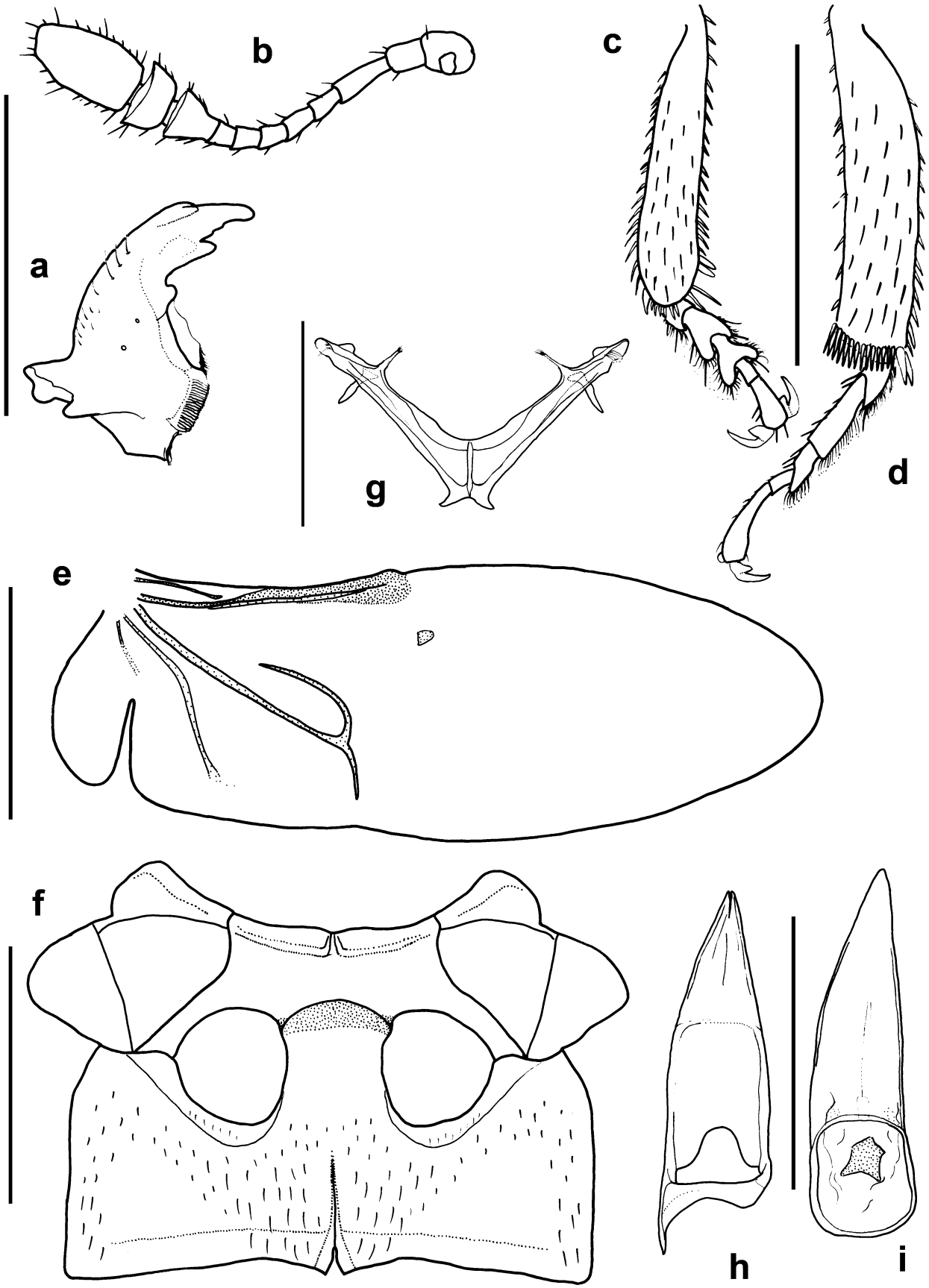

FIGURE 15. *Phalacrus* sp., female. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) right metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 0.5 mm). Male. (h) Tegmen, ventral; (i) penis, ventral (scale bar = 0.5 mm).

Immature stages. Friederichs (1908) described the larva of *Phalacrus corruscus* (Panzer). Emden (1928) described the larvae of *P. grossus* Erichson and *P. fimetarius* (Fabricius). d'Aguilar (1944) described the larva of *P. caricis* Sturm. Böving and Craighead (1931) illustrated the larva of the Nearctic *P. politus* Melsheimer, while the larva of the Australian *P. uniformis* (Blackburn) was described by Thompson and Marshall (1980).

Bionomics. Members of this genus are highly specialized feeders on smut fungi (Ustilaginales) and rust fungi (Pucciniales). Level of host specificity is unknown, but *Phalacrus* species have been recorded from *Ustilago* (including corn smut, *U. maydis* (DC.) Cda.), *Sporisorium* (including sugarcane smut, *S. scitamineum* (Sydow) M. Piepenbr., M. Stoll & Oberw.; see Agarwal [1956]), *Tilletia*, and *Cintractia*. Evidence exists (Agarwal 1956; Ericson *et al.* 1993) that smut-inhabiting beetles may be aiding in dispersal of their hosts. Adults and larvae of the Australian and introduced New Zealand species *Phalacrus uniformis* (Blackburn) feed on galls of the rust fungi *Uromycladium notabile* (Ludwig) McAlpine and *U. acaciae* (Cooke) Sydow, which infect *Acacia mearnsii* DeWildemann (see Thompson and Marshall 1980).

Among Australian specimens (mixture of species) with specific host data, *Phalacrus* specimens have been collected from: *Acacia brachybotrya* Benth. (Fabaceae), *A. dealbata* Link, *A. difformis* R.T.Baker, *A. implexa* Benth., *A. paradoxa* DC., *A. parramattensis* Tindale, *A. pendula* A.Cunn ex G.Don, *Eucalyptus*, *Melaleuca leucadendra* (L.) L. (Myrtaceae), and from *Sporisorium amphilophis* (H.Sydow) Langdon & Full. (Ustilaginales: Ustilaginaceae) on grass. Adults are also occasionally collected on flowers, including those of *Melaleuca ericifolia* Sm., *Leptospermum*, and *Eucalyptus* (all Myrtaceae) in Australia, and *Ligustrum sinense* Lour. (Oleaceae) in China. *Phalacrus substriatus* is often collected on *Narthecium ossifragum* (L.) Huds. (Nartheciaceae) in Europe. Flower-visiting is a somewhat common occurrence among (at least Palearctic) members of this genus.

Distribution and diversity. A morphologically isolated genus, similar only to the related *Phalacropsis* Casey, and one of only seven genera occurring in both the New and Old Worlds. The range of this genus is essentially coextensive with that of the family as a whole. In the New World, occurs from Alaska (specimens in USNM, certainly the northernmost record for the family in the Western Hemisphere) south to Argentina, including the Greater and Lesser Antilles, with the highest concentration of species in mountainous and xeric areas. In the Old World, it occurs in every region save for the Pacific Islands, though there is a report of a (probably introduced) *Phalacrus* species occurring in the Hawaiian Islands (Bowler *et al.* 1977; Ramsdale and Samuelson 2006). One introduced Australian species, *Phalacrus uniformis* (Blackburn), occurs in New Zealand, the only phalacrid known to be established there (Thompson and Marshall 1980), though a species of *Austroporus* may also be surviving there.

Included species (96):

Phalacrus acaciae Montrouzier, 1861 (Distribution: New Caledonia)
Phalacrus aethiops Gerstaecker, 1871 (Distribution: Tanzania)
Phalacrus affinis Motschulsky, 1866 (Distribution: Sri Lanka)
Phalacrus alluaudi Guillebeau, 1896 (Distribution: Madagascar) (type!)
Phalacrus americanus Guillebeau, 1894 (Distribution: United States) (type!)
Phalacrus apicalis Guillebeau, 1894 (Distribution: Tanzania) (type!)
Phalacrus arizonicus Casey, 1916 (Distribution: United States) (type!)
Phalacrus aterrimus Wollaston, 1867 (Distribution: Cape Verde, Senegal)
Phalacrus atrolucens Casey, 1916 (Distribution: United States) (type!)
Phalacrus atticus Guillebeau, 1894 (Distribution: Greece)
Phalacrus bataviensis Champion, 1925 (Distribution: Indonesia) (type!)
Phalacrus borealis Lafer, 1992 (Distribution: Russia)
Phalacrus brasiliensis Guillebeau, 1894 (Distribution: Brazil) (type!)
Phalacrus brevidens Champion, 1925 (Distribution: Japan) (type!)
Phalacrus brunnipes Brisout de Barneville, 1863 (Distribution: Mediterranean)
Phalacrus burrundiensis Blackburn, 1891 (Distribution: Australia to Africa) (type!)
Phalacrus californicus Casey, 1916 (Distribution: United States) (type!)
Phalacrus capax Casey, 1916 (Distribution: United States) (type!)
Phalacrus capreolus Švec, 2006 (Distribution: South Africa)
Phalacrus caricis Sturm, 1807 (Distribution: northern Europe to Mongolia)

Phalacrus caseyi Guillebeau, 1894 (Distribution: Brazil) (type!)
Phalacrus cervus Champion, 1925 (Distribution: South Africa) (type!)
Phalacrus championi Guillebeau, 1892 (Distribution: northern Europe)
Phalacrus conjunctus Casey, 1890 (Distribution: United States) (type!)
Phalacrus cooteri Švec, 2006 (Distribution: Kazakhstan)
Phalacrus corruscus (Panzer, 1797) (Distribution: throughout Palaearctic)
Phalacrus corvinus Guillebeau, 1894 (Distribution: India) (type!)
Phalacrus curticornis Švec, 2006 (Distribution: India)
Phalacrus exaluminatus Lyubarsky, 2003 (Distribution: Nepal)
Phalacrus fimetarius (Fabricius, 1775) (Distribution: western Palaearctic)
Phalacrus flavangulus Chevrolat, 1863 (Distribution: Cuba) (type!)
Phalacrus frater Flach, 1888 (Distribution: Caucasus, Turkey)
Phalacrus germanus Sharp, 1888 (Distribution: Guatemala) (type!)
Phalacrus grossus Erichson, 1845 (Distribution: throughout Palaearctic)
Phalacrus grouvellei Guillebeau, 1892 (Distribution: Tunisia)
Phalacrus havai Švec, 2006 (Distribution: Indonesia, Thailand)
Phalacrus illini Casey, 1916 (Distribution: United States) (type!)
Phalacrus immarginatus Champion, 1925 (Distribution: India, Nepal, Philippines) (type!)
Phalacrus incommodus Flach, 1888 (Distribution: Mediterranean)
Phalacrus indus Motschulsky, 1858 (Distribution: China, Indonesia, Sri Lanka)
Phalacrus insignis Lea, 1932 (Distribution: Australia)
Phalacrus insularis Guillebeau, 1892 (Distribution: Greece)
Phalacrus jejunus Casey, 1916 (Distribution: United States) (type!)
Phalacrus kuznetzovi Lafer, 1992 (Distribution: Japan, Russia)
Phalacrus lateralis Guillebeau, 1893 (Distribution: Yemen)
Phalacrus laticlava Champion, 1925 (Distribution: South Africa) (type!)
Phalacrus luteicornis Champion, 1924 (Distribution: Oriental Region) (type!)
Phalacrus mandibularis (Motschulsky, 1858) (Distribution: Sri Lanka)
Phalacrus maspalomensis Palm, 1975 (Distribution: Canary Islands)
Phalacrus maximus Fairmaire, 1852 (Distribution: Mediterranean)
Phalacrus mayeti Guillebeau, 1892 (Distribution: Algeria, Morocco, Spain)
Phalacrus mediocris Casey, 1916 (Distribution: United States) (type!)
Phalacrus mexicanus Hetschko, 1930 (Distribution: Mexico) (type!)
Phalacrus micans Guillebeau, 1893 (Distribution: Venezuela) (type!)
Phalacrus misellus Guillebeau, 1893 (Distribution: Venezuela)
Phalacrus montrouzieri Hetschko, 1928 (Distribution: New Caledonia)
Phalacrus oblongus Motschulsky, 1866 (Distribution: Sri Lanka)
Phalacrus obscurus Sharp, 1888 (Distribution: Mexico, Trinidad) (type!)
Phalacrus obsidianus Casey, 1916 (Distribution: United States) (type!)
Phalacrus ovalis LeConte, 1856 (Distribution: Guatemala, Mexico, United States) (type!)
Phalacrus penicillatus Say, 1824 (Distribution: Canada, United States)
Phalacrus perfusorius Lyubarsky, 2003 (Distribution: Nepal)
Phalacrus picipennis Champion, 1925 (Distribution: Uruguay) (type!)
Phalacrus politus Melsheimer, 1844 (Distribution: Bermuda, Canada, United States) (type!)
Phalacrus propinquus Guillebeau, 1894 (Distribution: United States) (type!)
Phalacrus pumilio LeConte, 1856 (Distribution: United States) (type!)
Phalacrus punctatus Champion, 1925 (Distribution: China, Japan) (type!)
Phalacrus raffrayi Guillebeau, 1894 (Distribution: Tanzania) (type!)
Phalacrus reticulosus Casey, 1916 (Distribution: Mexico) (type!)
Phalacrus rolciki Švec, 2006 (Distribution: Tanzania)
Phalacrus rubidus Motschulsky, 1858 (Distribution: Sri Lanka)
Phalacrus ruficornis Boheman, 1858 (Distribution: Argentina)

Phalacrus rufipes Motschulsky, 1866 (Distribution: Sri Lanka)
Phalacrus rufitarsis Motschulsky, 1858 (Distribution: Sri Lanka, Vietnam)
Phalacrus rufoguttatus Lyubarsky, 1994 (Distribution: Philippines)
Phalacrus rupimontis Casey, 1916 (Distribution: United States) (type!)
Phalacrus saueri Švec, 2006 (Distribution: India)
Phalacrus sayi Casey, 1889 (Distribution: United States) (type!)
Phalacrus seriatus LeConte, 1856 (Distribution: United States)
Phalacrus seriepunctatus Brisout de Barneville, 1863 (Distribution: Mediterranean)
Phalacrus sharpi Guillebeau, 1894 (Distribution: Tanzania) (type!)
Phalacrus simoni Guillebeau, 1893 (Distribution: Venezuela) (type!)
Phalacrus simplex LeConte, 1856 (Distribution: United States) (type!)
Phalacrus snizeki Švec, 2006 (Distribution: Kenya)
Phalacrus striatodiscus Champion, 1925 (Distribution: Uruguay) (type!)
Phalacrus striatus Hatch, 1962 (Distribution: United States)
Phalacrus subacutus Casey, 1916 (Distribution: United States) (type!)
Phalacrus substriatus Gyllenhal, 1813 (Distribution: western Palaearctic)
Phalacrus subtropicus Casey, 1916 (Distribution: Mexico, United States) (type!)
Phalacrus tarsalis Guillebeau, 1894 (Distribution: Colombia) (type!)
Phalacrus tenebrosus Guillebeau, 1894 (Distribution: Singapore) (type!)
Phalacrus tenuicornis Champion, 1925 (Distribution: Oriental Region) (type!)
Phalacrus uniformis (Blackburn, 1891) (Distribution: Australia, New Zealand) (type!)
Phalacrus validiceps Casey, 1916 (Distribution: United States) (type!)
Phalacrus vernicatus Casey, 1916 (Distribution: United States) (type!)
Phalacrus vicinus Guillebeau, 1894 (Distribution: United States) (type!)

Discussion. See comments under *Phalacropsis*.

OLIBROPORUS-GROUP

Diagnosis. This group may be recognized by the metaventral process not surpassing mesocoxae, non-divergent metaventral lines, small scutellar shield, metatarsomere I shorter than II, lack of a protibial ctenidium, and mesocoxal cavities separated by more than half their width.

Distribution and diversity. Forty-eight species occurring in the warm regions of the New World and the Australasian region.

Included genera (4). *Austroporus* Gimmel, *Olibroporus* Casey, *Platyphalacrus* Gimmel, *Pycinus* Guillebeau.

13. *Austroporus* Gimmel, gen. nov.
(Figs. 16; 39f)

Type species: *Austroporus victoriensis* (Blackburn), here designated.

Type material. *Olibrus victoriensis* Blackburn: holotype, "T. \ 3626 \ A7. [handwritten in red ink on specimen card] // Type \ H.T. [red-bordered disc] // Australia [underlined with red] \ Blackburn Coll. \ B.M. 1910—236. // Parasemus \ victoriensis, Blackb. [handwritten] // HOLOTYPE \ Olibrus \ victoriensis Blackburn \ det. M.L. Gimmel 2011 [red label]" (BMNH), card mounted.

Diagnosis. This genus is characterized by having a medially setose prosternum, metaventral process not produced and lobed anteriad of mesocoxae, metaventral postcoxal lines not separated from coxal cavities, metatarsomere I shorter than II, mandible tridentate or simple, with ventral ridge and without retinaculum, and elytra usually with spectral iridescence.

Description. Very small to large, total length 1.4–4.0 mm. Dorsal color completely testaceous to completely black, elytra often maculated with red or orange (Fig. 39f). Tibial spur formula 2-2-2, tarsal formula 5-5-5 in both sexes.

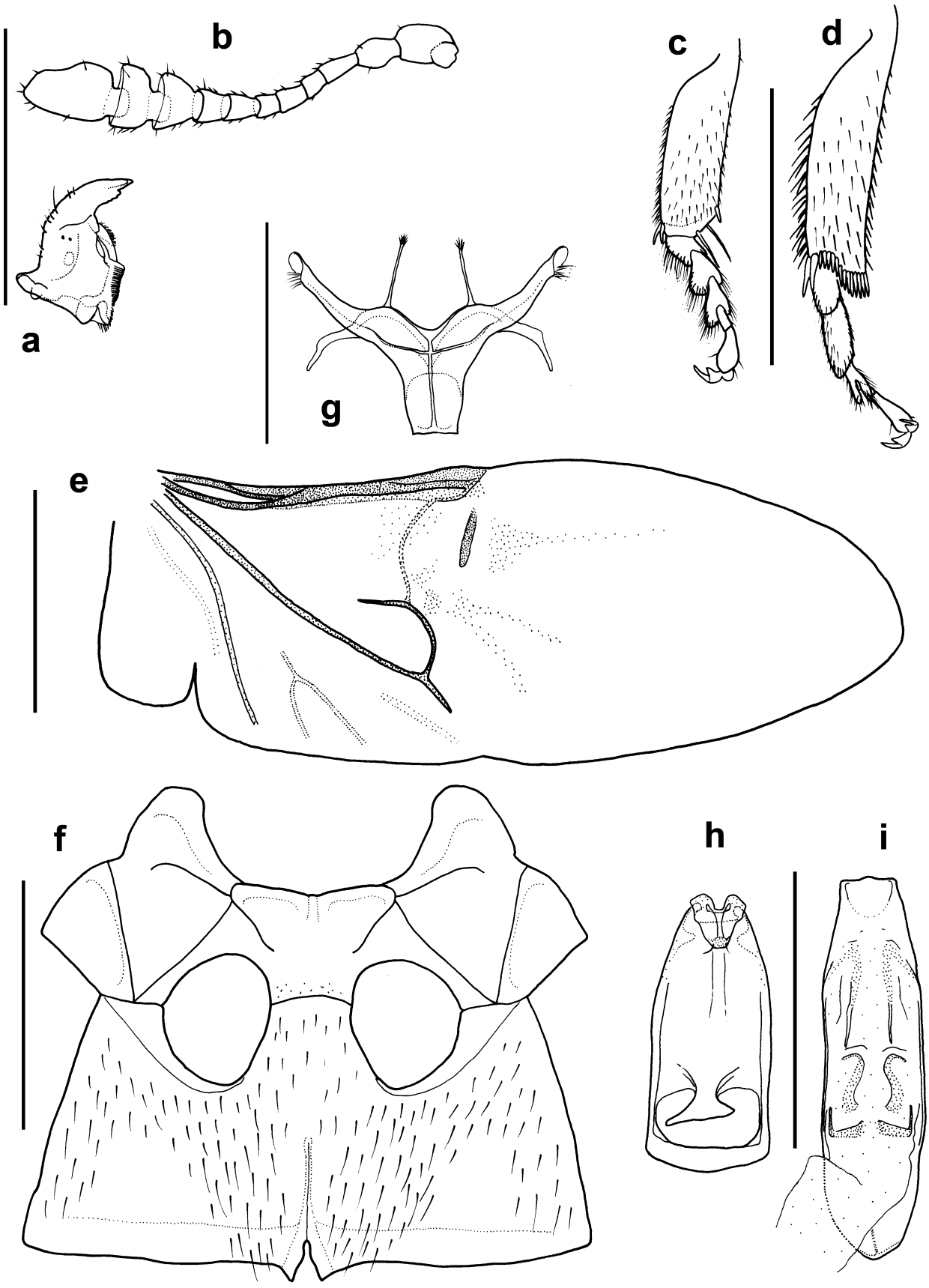

FIGURE 16. *Austroporus victoriensis*, male. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 0.5 mm). (h) Tegmen, ventral; (i) penis, ventral (scale bar = 0.5 mm).

Head. Not constricted behind eyes. Eyes medium-sized to large; facets convex; weak interfacetal setae present; weakly emarginate medially; without or (rarely) with acute posterior emargination; periocular groove present or (rarely) absent; with transverse setose groove ventrally behind eye. Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club 3-segmented, club weakly asymmetrical, antennomere XI turbinate or constricted on anterior edge only (Fig. 16b). Mandible (Fig. 16a) with apex tridentate, with dorsal tooth smallest, apex rarely simple; without retinaculum; mandible with ventral ridge. Maxillary palpomere IV fusiform, slender, nearly symmetrical; galea short, rounded; lacinia with two stout spines. Mentum with sides divergent toward apex; labial palpomere III fusiform. Labrum with apical margin arcuate. Gular sutures short, barely evident.

Thorax. Pronotum without obvious microsetae; with quite weakly developed scutellar lobe. Prosternum anteriorly with continuous row of marginal setae, setae flattened at base; procoxal cavity with anterolateral notchlike extension; prosternal process angulate in lateral view, usually conspicuously setose preapically, without spinelike setae at apex. Protrochanter with setae; protibia without ctenidium on kickface (Fig. 16c). Scutellar shield small. Elytron often with spectral iridescence; with one sutural stria; disc of elytra often with conspicuous rows of punctures; without transverse strigae; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 16f) notched anteriorly, not extending posteriorly to metaventrite, latero-posterior border obscured medially, forming procoxal rests; mesoventral disc depressed medially, not setose; mesanepisternum with incomplete transverse carina; mesocoxal cavities widely separate, separated by more than half width of a coxal cavity. Mesotarsomere III not bilobed. Metaventral process (Fig. 16f) extending to or nearly to anterior level of mesocoxae, truncate anteriorly; metaventral postcoxal lines not separated from mesocoxal cavity margin; discrimen long, extending about halfway to anterior margin of metaventral process; metendosternite (Fig. 16g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange behind anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line; metatibial foreface with apical ctenidium roughly perpendicular overall to long axis of tibia; spurs cylindrical, longest spur shorter than or subequal to width of tibial apex; metatarsomere I shorter than metatarsomere II, joint between I and II rigid (Fig. 16d); metatarsomere III not bilobed. Hind wing (Fig. 16e) with distinct, ovate anal lobe; leading edge without row of long setae at level of RA+ScP; AA_{3+4} very faintly indicated, crossvein to Cu absent; cubitoanal system unbranched apically; CuA_2 and MP_{3+4} with distal remnants; r4 developed and connected with RA_{3+4}; flecks present in apical field just distal to rp-mp2, with fainter curved flecks more distally; long transverse proximal sclerite and additional large triangular sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines, with calli; spiracles present and apparently functional on segment VII. Male with aedeagus upright in repose; tegmen (Fig. 16h) with symmetrical anterior margin and parameres hinged to basal piece, parameres without medial longitudinal division; penis (Fig. 16i) often with complex pairs of endophallic sclerites and spicules, apex truncate; spiculum gastrale V-shaped, with arms free. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. Many specimens have been captured in Malaise and flight intercept traps, at blacklights, and a few by beating. A series of *A. victoriensis* was collected under bark of fire-killed eucalyptus. A few specimens have been collected from fallen eucalyptus branches and moldy grass. One series from Northern Territory, Australia, was taken by beating *Ficus*. A series of specimens has been taken from *Uromycladium* galls on *Acacia*, both in Australia and in New Zealand (outside the native habitat of all three organisms involved). Interestingly, this habitat is identical to that of *Phalacrus uniformis* (Blackburn), another phalacrid species introduced from Australia to New Zealand. A number of specimens have been taken from flowers, and the plant species from those specimens with specific host data are *Alphitonia excelsa* (Fenzl) Benth. (Rhamnaceae) and *Acradenia euodiiformis* T.Hartley & F.Muell. (Rutaceae). Many of these records are likely accidental, and a more detailed study of the species and habits of the genus are required to definitively pronounce the preferences of members of *Austroporus*. However, a large series of an elongate species in Queensland has been collected from flower spikes of *Xanthorrhoea* (Xanthorrhoeaceae), indicating more than an incidental relationship between plant and beetle.

Distribution and diversity. A diverse group occurring throughout the Australian region, concentrated east of Wallace's line, although I have seen a few specimens from Borneo and Thailand.

Included species (33):

Austroporus adumbratus (Blackburn, 1902), **comb. nov.** (*Parasemus*) (Distribution: Australia) (type!)

Austroporus alpicola (Blackburn, 1891), **comb. nov.** (*Parasemus*) (Distribution: Australia) (type!)
Austroporus altus (Lea, 1932), **comb. nov.** (*Parasemus*) (Distribution: Papua New Guinea)
Austroporus apicipennis (Lea, 1932), **comb. nov.** (*Parasemus*) (Distribution: Australia)
Austroporus australiae (Lea, 1932), **comb. nov.** (*Parasemus*) (Distribution: Australia)
Austroporus bimaculiflavus (Lea, 1932), **comb. nov.** (*Parasemus*) (Distribution: Australia)
Austroporus comes (Blackburn, 1895), **comb. nov.** (*Parasemus*) (Distribution: Australia) (type!)
Austroporus compsus (Lea, 1932), **comb. nov.** (*Parasemus*) (Distribution: Australia)
Austroporus discoideus (Blackburn, 1895), **comb. nov.** (*Parasemus*) (Distribution: Australia) (type!)
Austroporus doctus (Blackburn, 1895), **comb. nov.** (*Parasemus*) (Distribution: Australia) (type!)
Austroporus fulgidus (Lea, 1932), **comb. nov.** (*Parasemus*) (Distribution: Australia)
Austroporus haploderus (Lea, 1932), **comb. nov.** (*Parasemus*) (Distribution: Australia)
Austroporus internatus (Blackburn, 1895), **comb. nov.** (*Parasemus*) (Distribution: Australia) (type!)
Austroporus iridipennis (Lea, 1932), **comb. nov.** (*Parasemus*) (Distribution: Australia)
Austroporus lateralis (Blackburn, 1891), **comb. nov.** (*Parasemus*) (Distribution: Australia) (type!)
Austroporus melas (Lea, 1932), **comb. nov.** (*Parasemus*) (Distribution: Australia)
Austroporus mitchelli (Blackburn, 1899), **comb. nov.** (*Parasemus*) (Distribution: Australia, Papua New Guinea) (type!)
Austroporus modestus (Blackburn, 1895), **comb. nov.** (*Parasemus*) (Distribution: Australia) (type!)
Austroporus moestus (Lea, 1932), **comb. nov.** (*Parasemus*) (Distribution: Papua New Guinea)
Austroporus montanus (Lea, 1932), **comb. nov.** (*Parasemus*) (Distribution: Papua New Guinea)
Austroporus noctivagus (Lea, 1932), **comb. nov.** (*Parasemus*) (Distribution: Australia)
Austroporus obliquiniger (Lea, 1932), **comb. nov.** (*Parasemus*) (Distribution: Australia)
Austroporus obsoletus (Blackburn, 1895), **comb. nov.** (*Parasemus*) (Distribution: Australia) (type!)
Austroporus pallens (Lea, 1932), **comb. nov.** (*Parasemus*) (Distribution: Papua New Guinea)
Austroporus pallidicornis (Lea, 1932), **comb. nov.** (*Parasemus*) (Distribution: Australia)
Austroporus pallidus (Blackburn, 1902), **comb. nov.** (*Parasemus*) (Distribution: Australia) (type!)
Austroporus quadrimaculatus (Lea, 1932), **comb. nov.** (*Parasemus*) (Distribution: Papua New Guinea)
Austroporus rufosuturalis (Lea, 1932), **comb. nov.** (*Parasemus*) (Distribution: Australia)
Austroporus suturellus (Blackburn, 1891), **comb. nov.** (*Parasemus*) (Distribution: Australia) (type!)
Austroporus tasmaniae (Lea, 1932), **comb. nov.** (*Parasemus*) (Distribution: Australia)
Austroporus terraereginae (Lea, 1932), **comb. nov.** (*Parasemus*) (Distribution: Australia)
Austroporus torridus (Blackburn, 1895), **comb. nov.** (*Parasemus*) (Distribution: Australia, Papua New Guinea) (type!)
Austroporus victoriensis (Blackburn, 1891), **comb. nov.** (*Parasemus*) (Distribution: Australia) (type!)

Discussion. This genus has been erected to accommodate those species left "orphaned" by the removal of the type species of *Parasemus* from the Australasian fauna (see account of *Olibroporus* for details). Although closely related to the New World genera *Olibroporus* and *Pycinus*, *Austroporus* has a number of features that I believe justify its separation from its New World counterparts, and provide evidence of its monophyly (mentioned in diagnosis above).

Etymology. From the prefix *austro-* (southern or Australian) plus the suffix *-porus*, in allusion to the related genus *Olibroporus*. The gender of the name is masculine.

14. *Olibroporus* Casey, 1890

(Figs. 17; 40a)

Olibroporus Casey 1890: 111. Type species: *Olibroporus punctatus* Casey 1890, fixed by monotypy.
Parasemus Guillebeau 1894*a*: 281. Type species: *Parasemus grouvellei* Guillebeau 1894, fixed by original designation. **Syn. nov.**

Type material. *Olibroporus punctatus* Casey: holotype, "Type // Fla // Pseudolibrus [*sic*] \ punctatus [handwritten]" (USNM).

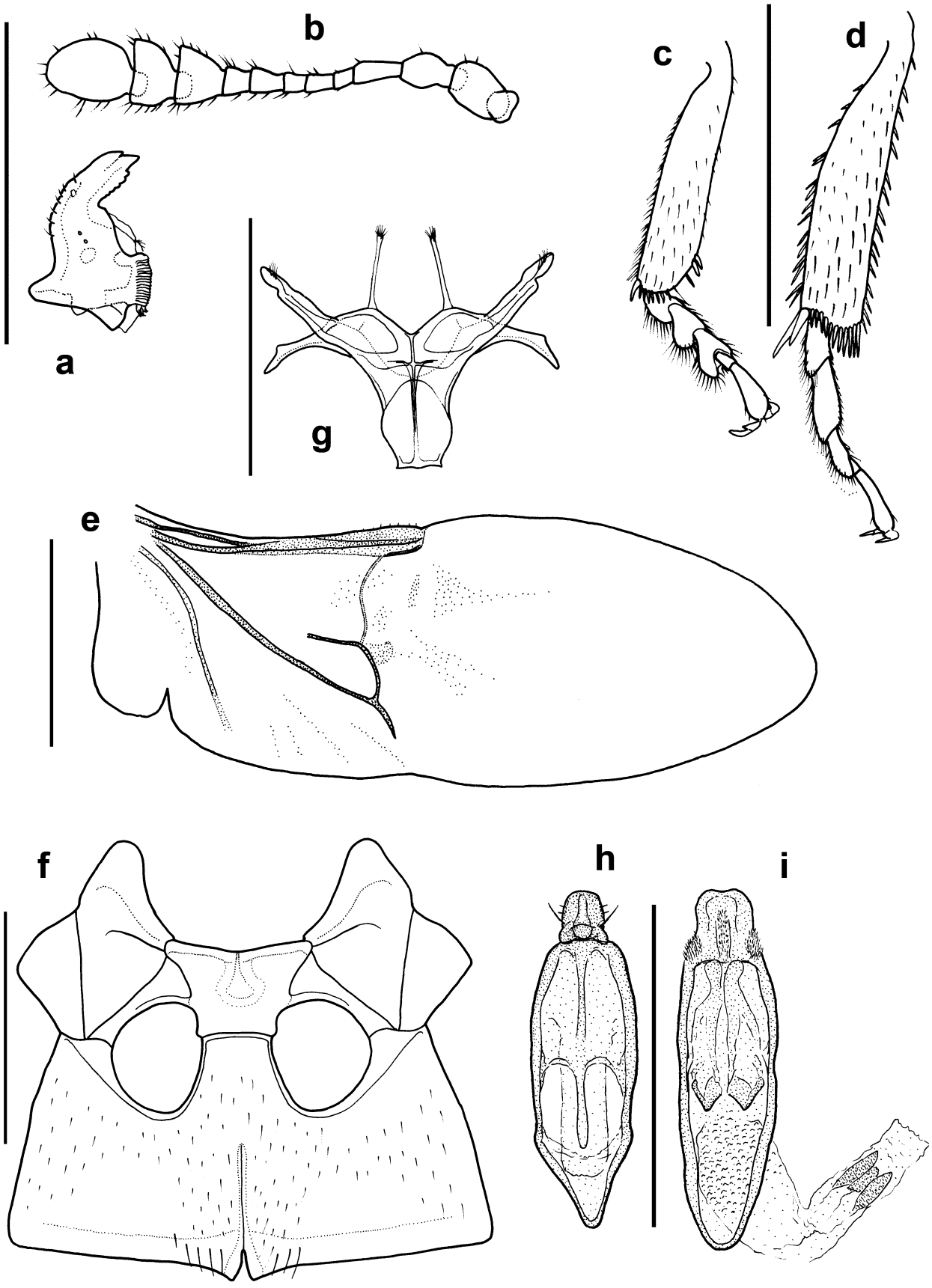

FIGURE 17. *Olibroporus punctatus*, male. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 0.5 mm). (h) Tegmen, dorsal; (i) penis, dorsal (scale bar = 0.5 mm).

Parasemus grouvellei Guillebeau: holotype, "Australia [handwritten, LOCALITY PROBABLY IN ERROR] // Grouvelle [handwritten] // HOLOTYPE \ Parasemus \ grouvellei Guillebeau \ det. M.L. Gimmel 2009 [red label]" (MNHN), point mounted.

Diagnosis. Recognized by the combination of lack of protibial ctenidium, metaventral process not protruding, metaventral postcoxal lines not separated from coxal cavities, small scutellar shield, metatarsomere I shorter than II, mandible with apex bidentate and with dorsal row of small, blunt teeth, and elytra without diffraction grating.

Description. Small to medium-sized, total length 1.7–2.5 mm. Color completely piceous to black (Fig. 40a). Tibial spur formula 2-2-2, tarsal formula 5-5-5 in both sexes.

Head. Not constricted behind eyes. Eyes large; facets convex; interfacetal setae absent; weakly emarginate medially; without posterior emargination; periocular groove present; with transverse setose groove ventrally behind eye. Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club 3-segmented, club weakly asymmetrical, antennomere XI slightly constricted on anterior edge (Fig. 17b). Mandible (Fig. 17a) with apex bidentate, with row of two or more small, rounded teeth on dorsal edge; without retinaculum; mandible without ventral ridge. Maxillary palpomere IV short, fusiform, nearly symmetrical; galea short, rounded; lacinia with two stout spines. Mentum with sides divergent toward apex; labial palpomere III fusiform. Labrum with apical margin arcuate. Gular sutures short, barely evident.

Thorax. Pronotum without obvious microsetae; with quite weakly developed scutellar lobe. Prosternum anteriorly with continuous row of marginal setae, setae flattened at base; procoxal cavity with anterolateral notchlike extension; prosternal process angulate in lateral view, not conspicuously setose preapically, without spinelike setae at apex. Protrochanter with setae; protibia without ctenidium on kickface (Fig. 17c). Scutellar shield small. Elytron without spectral iridescence; with one sutural stria; disc of elytra with conspicuous rows of punctures; without transverse strigae; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 17f) notched anteriorly, extending posteriorly to metaventrite, dividing mesoventral disc in two, forming procoxal rests; mesanepisternum with incomplete transverse carina; mesocoxal cavities widely separate, separated by more than half width of a coxal cavity. Mesotarsomere III bilobed. Metaventral process (Fig. 17f) extending nearly to anterior level of mesocoxae; metaventral postcoxal lines not separated from mesocoxal cavity margin; discrimen long, extending about halfway to anterior margin of metaventral process; metendosternite (Fig. 17g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange behind anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line; metatibial foreface with apical ctenidium roughly perpendicular overall to long axis of tibia; spurs cylindrical, longest spur shorter than width of tibial apex; metatarsomere I slightly shorter than metatarsomere II, joint between I and II rigid (Fig. 17d); metatarsomere III bilobed. Hind wing (Fig. 17e) with distinct, ovate anal lobe; leading edge without row of long setae at level of RA+ScP; AA_{3+4} very faintly indicated, crossvein to Cu absent; cubitoanal system unbranched apically; CuA_2 and MP_{3+4} with faint distal remnants; r4 weakly developed, connected with RA_{3+4}; conspicuous fleck present in apical field just distal to rp-mp2; long transverse proximal sclerite and additional small triangular sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines, with distinct calli; spiracles present and apparently functional on segment VII. Male with aedeagus upright in repose; tegmen (Fig. 17h) with symmetrical anterior margin and parameres hinged to basal piece, parameres without medial longitudinal division; penis (Fig. 17i) with pair of endophallic sclerites and spicules, apex weakly bilobed; spiculum gastrale V-shaped, with arms free. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. Habits of members of this genus are unknown. Specimens whose collection information is known have been collected using Malaise and blacklight traps. One Florida specimen was collected by "beating burned oaks."

Distribution and diversity. Occurring from New Jersey, USA, west to Baja California Sur, Mexico, and south to Brazil. From the West Indies I have seen specimens from Cuba and the Cayman Islands. Based on dissection of male genitalia, at least two species are present in this genus, but the association of the two currently valid names with these is unclear at present.

Included species (2):

Olibroporus grouvellei (Guillebeau, 1894), **comb. nov.** (*Parasemus*) (Distribution: unknown) (type!)

Olibroporus punctatus Casey, 1890 (Distribution: United States) (type!)

Discussion. The holotype of *Parasemus grouvellei*, although bearing the label "Australia," is identical to specimens of the New World *Olibroporus*. I have seen no additional specimens resembling *Olibroporus* outside of the New World and I strongly suspect *P. grouvellei* has an erroneous locality label. Regardless, the specimen matches Guillebeau's description and is certainly the true holotype. I therefore propose the synonymy of *Parasemus* with *Olibroporus*. I have created a new genus, *Austroporus* (see above), for most of the species attributed to *Parasemus* by Blackburn (1891, 1895, 1899, 1902) and later by Lea (1932). One species described in *Parasemus*, *P. uniformis* (Blackburn), has subsequently been moved to *Phalacrus* (see Thompson and Marshall 1980), while another (*P. parvopallidus* Lea) has been removed from Phalacridae altogether (see "Taxa removed from Phalacridae" below).

15. *Platyphalacrus* Gimmel, gen. nov.

(Figs. 18; 39g–i)

Type species: *Platyphalacrus lawrencei*, here designated.

Type material. See account of *Platyphalacrus lawrencei* below.

Diagnosis. This genus is characterized by having a medially setose prosternum, metaventral process not produced and lobed anteriad of mesocoxae, metaventral postcoxal lines not separated from coxal cavities, metatarsomere I shorter than II, mandible tridentate, without ventral ridge and with strong retinaculum, and the flattened body form when viewed laterally.

Description. Medium-sized, total length 2.7–2.9 mm. Dorsal color completely reddish-testaceous (Figs. 39g–i). Tibial spur formula 2-2-2, tarsal formula 5-5-5 in both sexes.

Head. Not constricted behind eyes. Eyes small; facets flat; interfacetal setae present; not emarginate medially; without posterior emargination; periocular groove present; with transverse setose groove ventrally behind eye. Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennae short, antennal club 3-segmented, club symmetrical, weakly developed, antennomere XI constricted on anterior edge only (Fig. 18b). Mandible (Fig. 18a) with apex tridentate, with dorsal tooth smallest; with distinct retinaculum; mandible without ventral ridge. Maxillary palpomere IV fusiform, short, slender, nearly symmetrical; galea short, rounded; lacinia with two stout spines. Mentum with sides divergent toward apex; labial palpomere III fusiform. Labrum with apical margin slightly emarginate. Gular sutures short, barely evident.

Thorax. Pronotum without obvious microsetae; with quite weakly developed scutellar lobe. Prosternum anteriorly with continuous row of marginal setae, setae flattened at base; procoxal cavity with anterolateral notchlike extension; prosternal process angulate in lateral view, not conspicuously setose preapically, without spinelike setae at apex. Protrochanter with setae; protibia without ctenidium on kickface (Fig. 18c). Scutellar shield small. Elytron without spectral iridescence; with one sutural stria; disc of elytron with conspicuous rows of punctures; without transverse strigae; lateral margin somewhat explanate, especially posteriorly, with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 18f) notched anteriorly, not extending posteriorly to metaventrite, latero-posterior border obscured medially, forming procoxal rests; mesoventral disc depressed medially, not setose; mesanepisternum with complete transverse carina; mesocoxal cavities widely separate, separated by more than half width of a coxal cavity. Mesotarsomere III bilobed. Metaventral process (Fig. 18f) extending nearly to anterior level of mesocoxae, truncate anteriorly; metaventral postcoxal lines not separated from mesocoxal cavity margin; discrimen long, extending about halfway to anterior margin of metaventral process; metendosternite with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange at anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line; metatibial foreface with apical ctenidium roughly perpendicular overall to long axis of tibia; spurs cylindrical, longest spur shorter than width of tibial apex; metatarsomere I shorter than metatarsomere II, joint between I and II rigid (Fig. 18d); metatarsomere III bilobed. Hind wing (Fig. 18e) with distinct, ovate anal lobe; leading edge with complete row of long setae at level of RA+ScP; AA_{3+4} present, faint, crossvein to Cu absent; cubitoanal system unbranched apically, fused with faint remnant of CuA_2; CuA_2 and MP_3

with separate and faint distal remnants; r4 developed and connected with RA_{3+4}; strong flecks present in apical field just distal to rp-mp2, with fainter flecks more distally; long transverse proximal sclerite and additional large, faint triangular sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines, with calli; spiracles present and apparently functional on segment VII. Male with aedeagus upright in repose; tegmen (Fig. 18g) with symmetrical anterior margin and parameres hinged to basal piece, parameres without medial longitudinal division; penis (Fig. 18h) with pairs of endophallic sclerites and spicules, apex truncate. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. Associated with male cones of *Macrozamia* cycads growing naturally in southwestern Australia. The beetles probably feed on the cycad pollen.

Distribution and diversity. Only one species so far known, restricted to the southwestern portion of Western Australia (Fig. 44e).

Included species (1):

Platyphalacrus lawrencei Gimmel, **sp. nov.** (Distribution: Australia)

Etymology. This genus is a combination of the Greek *platys* (flat) and the genus name *Phalacrus*, in reference to the flattened form of the type species, indeed the flattest known phalacrid. The gender of the name is masculine.

Platyphalacrus lawrencei Gimmel, sp. nov.

(Figs. 18; 39g–i)

Holotype. "33.51S 123.00E \ Thomas River \ 23 km NWbyW of \ Mt. Arid WA \ 4–7.xi.1977 \ J.F. Lawrence // J.F. Lawrence \ Lot No. 77-24 [number handwritten] // Male cones \ of \ Macrozamia [handwritten] // HOLOTYPE \ Platyphalacrus \ lawrencei Gimmel \ des. M.L. Gimmel 2011 [red label]" (ANIC), point mounted.

Paratypes (3). Same data as holotype, with "PARATYPE \ Platyphalacrus \ lawrencei Gimmel \ det. M.L. Gimmel 2011 [yellow label]" (1, USNM; 1, MLGC); "Lake Muir 60km \ SE Manjimup WA \ 6–10 Jul. 1980 \ S.&J. Peck SBP95 // berlesate \ rotted cones \ Macrozamia \ reidlei // PARATYPE \ Platyphalacrus \ lawrencei Gimmel \ det. M.L. Gimmel 2011 [yellow label]" (1, ANIC).

Description. Total length 2.7–2.9 mm; relatively elongate, nearly parallel-sided at middle one-third; dorsum abruptly flattened, sides of pronotum and (especially) elytra nearly vertical starting at about stria 7; lateral margins slightly explanate, especially posterior portion of elytra. Color testaceous to rufotestaceous throughout; without trace of diffraction grating, dorsal surface devoid of microsculpture. Antenna short, about as long as width of head; antennal club slightly more than half as long as funicle, weakly formed; antennomere XI short, nearly circular. Punctation of head extremely fine and dense; punctation of pronotum slighly coarser but less dense, with interspersed micropunctures; elytral punctation dense, even, slightly coarser than that of pronotum, becoming crescentiform laterally, appearing almost as transverse strigae at some angles; elytron with single engraved (sutural) stria, but with eight additional lightly impressed, punctate striae traceable nearly entire length of elytron. Prosternum somewhat setose medially, with pair of short, stout setae preapically on prosternal process. Mesoventrite punctate nearly throughout. Legs short, femora, tibia, and tarsus of all legs stout; tarsomeres 1–3 of all legs with dense pad of setae; metatarsus only slightly longer than mesotarsus. Protibia with two stout spines at outer apical angle. Metatarsomere I slightly shorter than II, about as long as III.

Tegmen of aedeagus with wide, spatulate dorsal strut; fused parameres with three pairs of lateral setae, proximal pair longest; penis slightly bisinuate at apex, with complex series of sclerites in internal sac. Female genitalia unstudied.

Diagnosis. This species may be recognized by the characters given in the generic diagnosis.

Distribution. Known only from southwestern Australia (Fig. 44e).

Etymology. This species is named in honor of Dr. John Lawrence of Gympie, Australia, who first brought to my attention and provided me with all known specimens of this distinctive new genus of Phalacridae. The epithet is a noun in the genitive case.

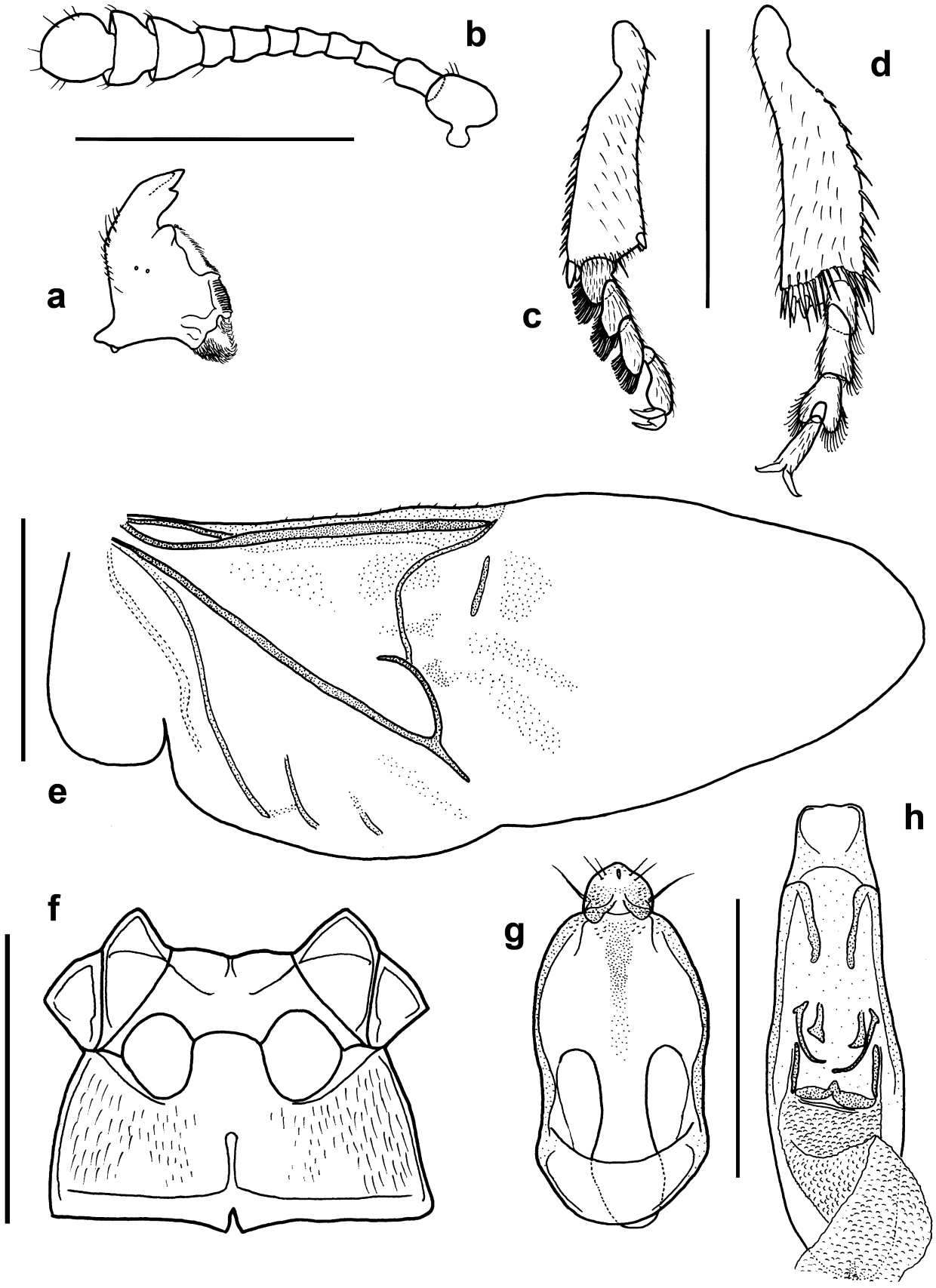

FIGURE 18. *Platyphalacrus lawrencei*, male. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) right metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 1.0 mm). (g) Tegmen, ventral; (h) penis, ventral (scale bar = 0.5 mm).

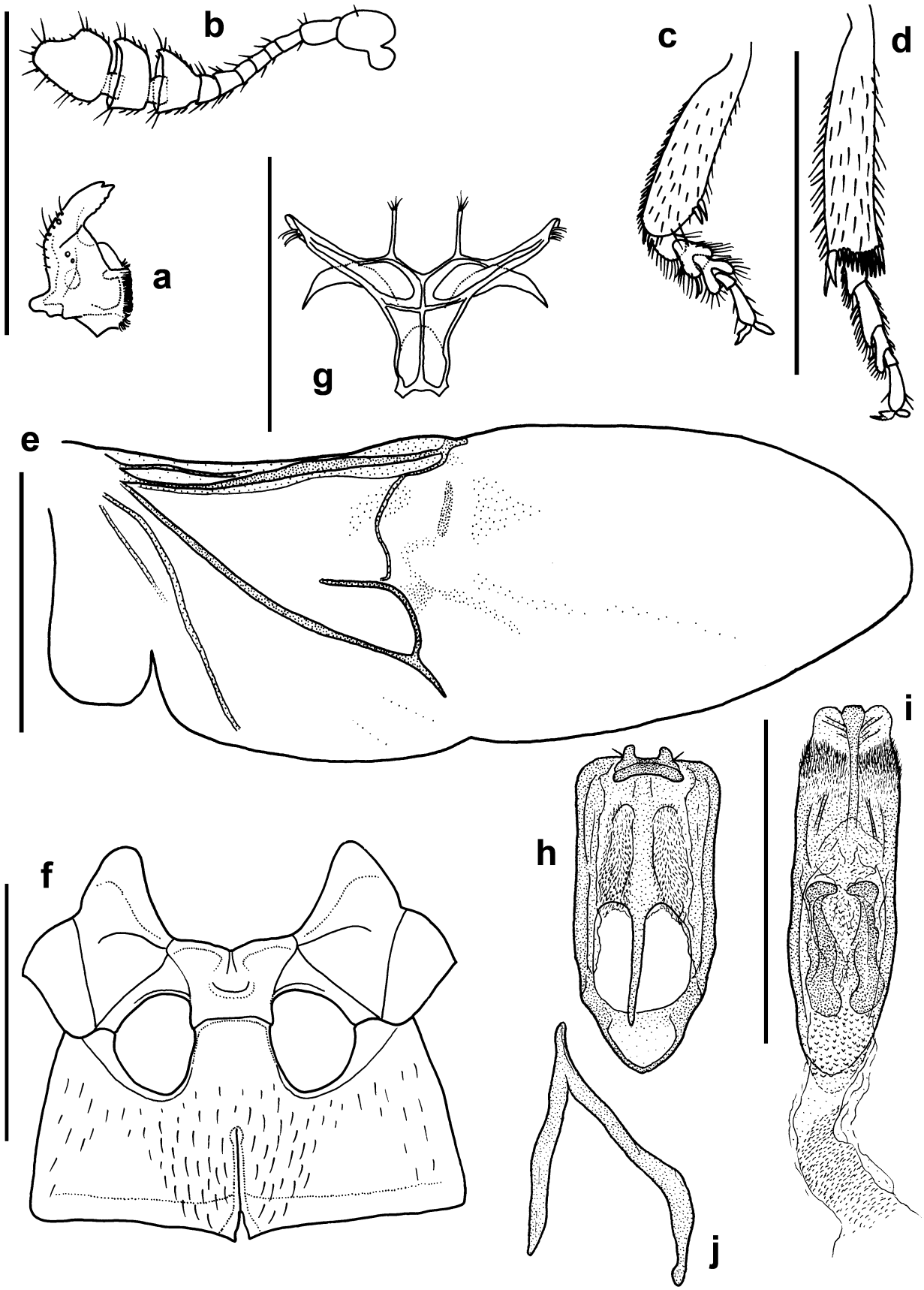

FIGURE 19. *Pycinus* sp., male. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 0.5 mm). *Pycinus politus*, lectotype male. (h) Tegmen, dorsal; (i) penis, dorsal; (j) spiculum gastrale (scale bar = 0.5 mm).

16. *Pycinus* Guillebeau, 1893
(Figs. 19; 40b, c)

Pycinus Guillebeau 1893*a*: 289. Type species: *Pycinus politus* Guillebeau 1893, fixed by subsequent designation.
Ochrodemus Guillebeau 1893*a*: 293. Type species: *Ochrodemus brevitarsis* Guillebeau 1893, fixed by monotypy. **Syn. nov.**
Radinus Guillebeau 1893*a*: 295. Type species: *Radinus latus* Guillebeau 1893, fixed by monotypy. **Syn. nov.**
Euphalacrus Champion 1925*b*: 608. Type species: *Euphalacrus crassipes* Champion 1925, fixed by original designation. **Syn. nov.**

Type material. *Pycinus politus* Guillebeau: two syntypes found (of five mentioned by Guillebeau 1893*a*: 289), one here designated lectotype, male, "Caracas [handwritten] // Simon [handwritten] // Muséum Paris \ Coll. Générale [green label] // Pycinus \ politus \ Guilleb. [handwritten] // LECTOTYPE ♂ \ Pycinus \ politus Guillebeau \ des. M.L. Gimmel 2009 [red label]" (MNHN), point mounted, genitalia dissected and mounted in DMHF. Paralectotype, female, "Caracas [handwritten] // Simon [handwritten] // Muséum Paris \ Coll. Générale [green label] // TYPE [red label] // politus \ Guilb. [handwritten] // PARALECTOTYPE ♀ \ Pycinus \ politus Guillebeau \ det. M.L. Gimmel 2009 [yellow label]" (MNHN), point mounted, genitalia dissected and mounted in DMHF. The lectotype is designated to prevent future doubts about the identity of this species and of the genus *Pycinus*.

Ochrodemus brevitarsis Guillebeau: holotype, "San Esteban \ E. Simon III.88 // Muséum Paris \ Coll. Générale [green label] // TYPE [red label] // [unpublished lectotype label, turned over] // brevitarsis \ Guilb. [handwritten] // HOLOTYPE ♀ \ Ochrodemus \ brevitarsis Guillebeau \ det. M.L. Gimmel 2009 [red label]" (MNHN), point mounted.

Radinus latus Guillebeau: holotype, "Caracas [handwritten] // Simon [handwritten] // Muséum Paris \ Coll. Générale [green label] // TYPE [red label] // latus \ Guilb. [handwritten] / HOLOTYPE ♀ \ Radinus \ latus Guillebeau \ det. M.L. Gimmel 2009 [red label]" (MNHN), point mounted.

Euphalacrus crassipes Champion: two syntypes found in BMNH, lectotype, here designated, "Fry \ Rio Jan. // Fry Coll. \ 1905.100. // Type \ H.T. [red-bordered disc] // Euphalacrus \ crassipes Ch. \ type [handwritten] // Specimen \ figured. // Ann. Mag. N.H. \ Ser. 9. XVI 1925. \ G.C.C. det. // SYN- \ TYPE [blue-bordered disc] // LECTOTYPE \ Euphalacrus \ crassipes Champion \ des. M.L. Gimmel 2010 [red label]" (BMNH), card mounted. Paralectotype, "[female symbol] // Ilha Santo Amaro \ nr. Santos, Brazil. \ G.E. Bryant. \ 23.IV.1912 [date handwritten] // G. Bryant Coll. \ 1919–147 // Euphalacrus \ crassipes Ch. \ Cotype. [handwritten] // Specimen \ figured. // Co- \ type [yellow-bordered disc] // Ann. Mag. N.H. \ Ser. 9. XVI 1925. \ G.C.C. det. // SYN- \ TYPE [blue-bordered disc] // PARALECTOTYPE \ Euphalacrus \ crassipes Champion \ det. M.L. Gimmel 2010 [yellow label]" (BMNH). The lectotype is designated in order to fix the identity and type locality of this taxon.

Diagnosis. This genus is characterized by having a medially setose prosternum, metaventral process not produced anteriad of mesocoxae, metaventral postcoxal lines not separated from coxal cavities, metatarsomere I shorter than II, mandible with ventral ridge and with dorsal row of small, blunt teeth, and elytra usually with spectral iridescence.

Description. Small to large, total length 1.6–3.2 mm. A few species (undescribed) are quite dorsoventrally flattened, while others are extremely globose. Dorsal color completely completely testaceous to completely black, ventral surface, appendages, and often pronotum much lighter in color (Figs. 40b, c); no maculated species are known. Tibial spur formula 2-2-2, tarsal formula 5-5-5 in both sexes.

Head. Not constricted behind eyes. Eyes small to large; facets flat; interfacetal setae absent; weakly to deeply emarginate medially; without posterior emargination; periocular groove present; with transverse setose groove ventrally behind eye. Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club 3-segmented (one undescribed Brazilian species with 5-segmented club), club weakly asymmetrical, antennomere XI slightly constricted on anterior edge (Fig. 19b). Mandible (Fig. 19a) with apex bidentate, with row of two or more small, rounded teeth on dorsal edge; without retinaculum; mandible with ventral ridge. Maxillary palpomere IV fusiform, nearly symmetrical; galea short, rounded; lacinia with two stout spines. Mentum with sides divergent toward apex; labial palpomere III fusifsorm. Labrum with apical margin truncate. Gular sutures short, barely evident.

Thorax. Pronotum without obvious microsetae; with quite weakly developed scutellar lobe. Prosternum anteriorly with continuous row of marginal setae, setae flattened at base; procoxal cavity with anterolateral notchlike extension; prosternal process angulate in lateral view, usually conspicuously setose preapically, without spinelike setae at apex. Protrochanter with setae; protibia without ctenidium on kickface (Fig. 19c). Scutellar shield

small. Elytron usually with spectral iridescence; with one sutural stria; disc of elytra often with conspicuous rows of punctures; without transverse strigae; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 19f) deeply notched anteriorly, extending posteriorly to metaventrite, dividing mesoventral disc in two, forming procoxal rests; mesanepisternum with incomplete transverse carina; mesocoxal cavities widely separate, separated by more than half width of a coxal cavity. Mesotarsomere III bilobed. Metaventral process (Fig. 19f) extending nearly to anterior level of mesocoxae; metaventral postcoxal lines not separated from mesocoxal cavity margin; discrimen long, extending about halfway to anterior margin of metaventral process; metendosternite (Fig. 19g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange at anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line; metatibial foreface with apical ctenidium roughly perpendicular overall to long axis of tibia; spurs cylindrical, longest spur shorter than or subequal to width of tibial apex; metatarsomere I shorter than metatarsomere II, joint between I and II rigid (Fig. 19d); metatarsomere III bilobed. Hind wing (Fig. 19e) with distinct, ovate anal lobe; leading edge without row of long setae at level of RA+ScP; AA_{3+4} apparent only basally, crossvein to Cu absent; cubitoanal system unbranched apically; CuA_2 and MP_{3+4} without distal remnants; r4 weak but connected with RA_{3+4}; conspicuous fleck present in apical field just distal to rp-mp2, with much fainter fleck more distally; long transverse proximal sclerite and additional small triangular sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines, without calli; spiracles present and apparently functional on segment VII. Male with aedeagus upright in repose; tegmen (Fig. 19h) with symmetrical anterior margin and parameres hinged to basal piece, parameres without medial longitudinal division; penis (Fig. 19g) with pair of endophallic sclerites and spicules, apex variable; spiculum gastrale V-shaped, with arms free. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. Many specimens have been collected by beating, Malaise traps, and flight intercept traps. Members of this genus do not appear to be strongly attracted to lights.

Distribution and diversity. Restricted to the Neotropics, from Mexico south to Argentina. Many undescribed species exist.

Included species (12):

Pycinus brevitarsis (Guillebeau, 1893), **comb. nov.** (*Ochrodemus*) (Distribution: Venezuela) (type!)
Pycinus crassipes (Champion, 1925), **comb. nov.** (*Euphalacrus*) (Distribution: Brazil) (type!)
Pycinus guatemalenus (Sharp, 1888), **comb. nov.** (*Olibrus*) (Distribution: Guatemala, Panama) (type!)
Pycinus hemisphaericus Guillebeau, 1893 (Distribution: Venezuela) (type!)
Pycinus latipes (Sharp, 1888), **comb. nov.** (*Olibrus*) (Distribution: Panama) (type!)
Pycinus latus (Guillebeau, 1893), **comb. nov.** (*Radinus*) (Distribution: Venezuela) (type!)
Pycinus microsternus (Sharp, 1888), **comb. nov.** (*Olibrus*) (Distribution: Panama) (type!)
Pycinus politus Guillebeau, 1893 (Distribution: Venezuela) (type!)
Pycinus rubiginosus (Sharp, 1888), **comb. nov.** (*Olibrus*) (Distribution: Guatemala, Mexico) (type!)
Pycinus subrotundatus Guillebeau, 1893 (Distribution: Venezuela) (type!)
Pycinus tropicus (Kirsch, 1870), **comb. nov.** (*Phalacrus*) (Distribution: Colombia) (type!)
Pycinus vulgaris (Sharp, 1888), **comb. nov.** (*Olibrus*) (Distribution: Guatemala) (type!)

Discussion. Guillebeau's genera *Pycinus*, *Ochrodemus*, and *Radinus*, all described in the same paper, do not display differences that warrant generic distinction. Interestingly, he described these three genera in two different tribes: *Pycinus* and *Ochrodemus* in his "Olibrini" and *Radinus* in his newly defined group "Heteromorphini" (with *Sphaeropsis* Guillebeau). The latter supposedly differs in having the "Bord apical médian du prosternum dépassant distinctement les hanches" (p. 295) (apical border of the prosternal process distinctly exceeding the coxae). Examination of the type specimens of the type species of all three genera reveals only the slightest variation in this and other character states. These generic synonymies result in two new combinations, listed above.

Euphalacrus Champion, as well, is clearly a superfluous name, as its type species falls well within the concept of *Pycinus*. Therefore I propose *Euphalacrus* as a new synonym of *Pycinus*.

After examination of types, I have determined that several of the Central American species described by Sharp (1888) in *Olibrus* belong to the genus *Pycinus*. Kirsch's (1870) *Phalacrus tropicus* also belongs here. These six new combinations are included above.

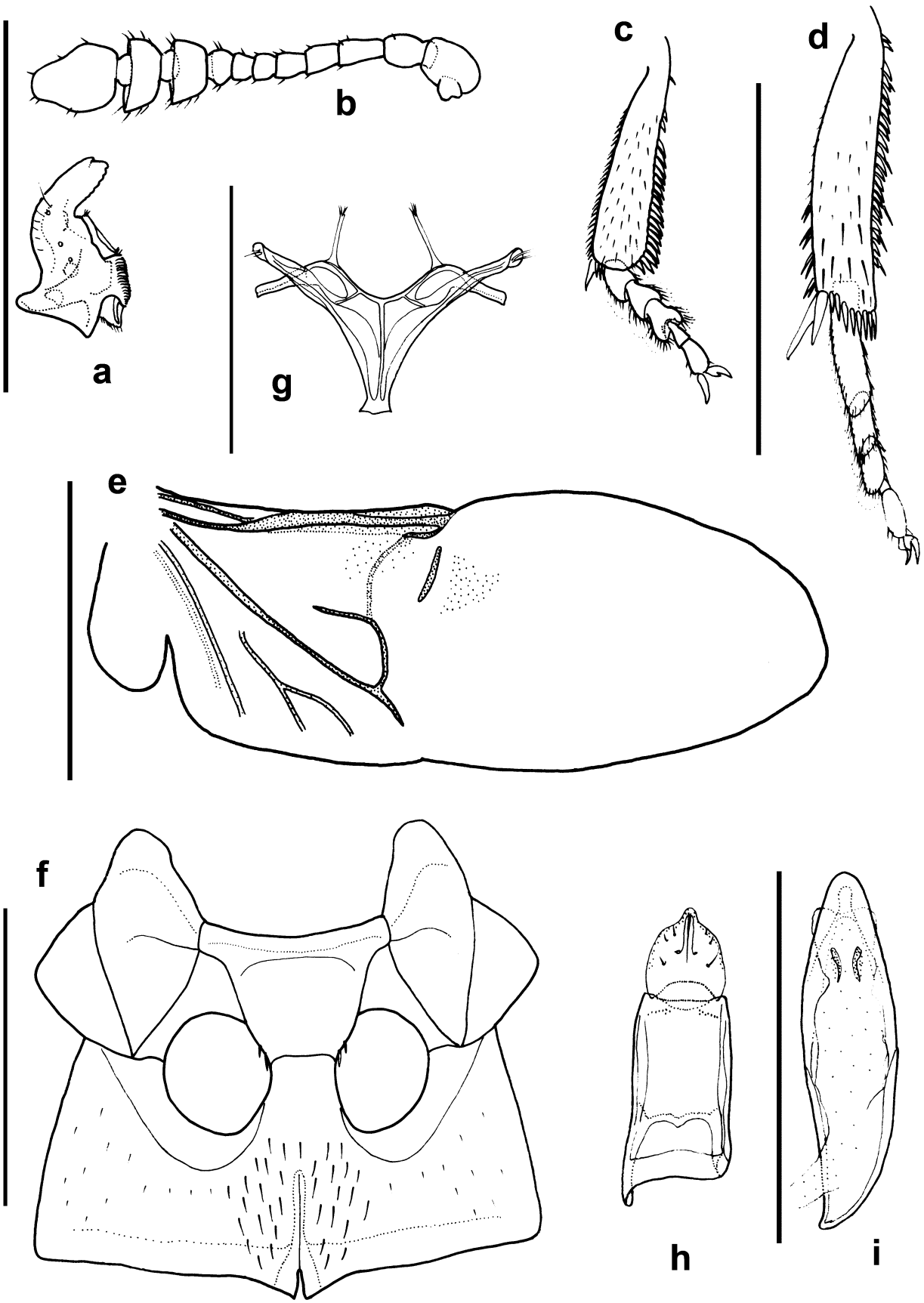

FIGURE 20. *Ochrolitus rubens*, male. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 0.5 mm). (h) Tegmen, dorsal; (i) penis, ventral (scale bar = 0.5 mm).

OCHROLITUS-GROUP

Ochrolitini Guillebeau 1894*a*: 278. Type genus: *Ochrolitus* Sharp.

Diagnosis. This group may be recognized the shelflike prosternal process (acute when viewed laterally), the mesoventral plate extending posteriorly to metaventral process, the metaventral process not surpassing the mesocoxae, the small scutellar shield, metatarsomere I as long as or longer than II, and presence of a protibial ctenidium.

Distribution and diversity. Three described species, known from the warm, wet regions of the New World and in the Australasian region.

Included genera (2). *Ochrolitus* Sharp, *Sveculus* Gimmel.

17. *Ochrolitus* Sharp, 1889

(Figs. 20; 40d, e)

Ochrolitus Sharp 1889: 264. Type species: *Ochrolitus optatus* Sharp 1889, fixed by subsequent designation.
Gorginus Guillebeau 1894*a*: 283. Type species: *Olibrus rubens* LeConte 1856, fixed by original designation. **Syn. nov.**
Erythrolitus Casey 1916: 85. Type species: *Olibrus rubens* LeConte 1856, fixed by monotypy.

Type material. *Ochrolitus optatus* Sharp: holotype, "Ochrolitus \ optatus \ Type D.S. \ Irazu 6-7000 ft. \ Rogers. [handwritten on specimen card] // Type [orange-bordered disc] // Sp. figured. // Irazu, \ 6-7000 ft. \ H. Rogers. // B.C.A.,Col.,II,(1). // HOLOTYPE \ Ochrolitus \ optatus Sharp \ det. M.L. Gimmel 2010 [red label]" (BMNH), card mounted.

Olibrus rubens LeConte: holotype, "[orange disc] // Type \ 6651 [red label, number handwritten] // O. rubens \ Lec. [handwritten] // HOLOTYPE \ Olibrus \ rubens LeConte \ det. M.L. Gimmel 2010 [red label]" (MCZ), point mounted.

Diagnosis. Recognized by the long protibial ctenidium, small scutellar shield, metaventral process not exceeding mesocoxae anteriorly, metaventral lines separated from mesocoxal cavities, two or three elytral striae, and prosternal process with row of spinelike setae at apex.

Description. Small to medium-sized, total length 1.5–2.5 mm. Dorsal color solid reddish-testaceous to reddish-piceous (Figs. 40d, e). Tibial spur formula 2-2-2, tarsal formula 5-5-5 in both sexes.

Head. Not constricted behind eyes. Eyes small to medium-sized; facets flat; interfacetal setae absent; weakly emarginate medially; without posterior emargination; periocular groove absent or present but weak; with transverse setose groove ventrally behind eye. Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club 3-segmented, club weakly asymmetrical; antennomere XI turbinate (Fig. 20b). Mandible (Fig. 20a) with apex bidentate, with row small, rounded teeth on dorsal edge; retinaculum absent; mandible without ventral ridge. Maxillary palpomere IV fusiform, short, nearly symmetrical; galea short, rounded; lacinia with two stout spines. Mentum with sides divergent toward apex; labial palpomere III fusiform. Labrum with apical margin truncate. Gular sutures short, barely evident.

Thorax. Pronotum with obvious microsetae present, distinct; with weakly to moderately developed scutellar lobe. Prosternum anteriorly with continuous row of marginal setae, setae flattened at base; procoxal cavity with anterolateral notchlike extension; prosternal process angulate and shelflike in lateral view, with narrow horizontal translucent apical process and row of spinelike setae at apex. Protrochanter without setae; protibia with ctenidium on kickface, extending about three-quarters length of tibia (Fig. 20c). Scutellar shield small. Elytron with spectral iridescence; with two or three sutural striae; disc with rudimentary striae or rows of punctures; with moderate to strong transverse strigae; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 20f) not notched anteriorly, extending posteriorly to metaventrite, dividing mesoventral disc in two, forming procoxal rests; mesanepisternum with incomplete transverse carina; mesocoxal cavities separated by about half width of a coxal cavity. Mesotarsomere III not bilobed. Metaventral process (Fig. 20f) extending not quite to anterior level of mesocoxae; metaventral postcoxal lines separated from mesocoxal cavity margin, smoothly arcuate; discrimen short, extending less than halfway to anterior margin of metaventral process; metendosternite (Fig. 20g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange at anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line; metatibial

foreface with apical ctenidium roughly perpendicular overall to long axis of tibia; spurs cylindrical, longest spur subequal to or longer than width of tibial apex; metatarsomere I longer than metatarsomere II, joint between I and II rigid (Fig. 20d). Hind wing (Fig. 20e) with distinct, ovate anal lobe; leading edge without row of long setae at level of RA+ScP; AA_{3+4} extremely weak, crossvein to Cu absent; cubitoanal system unbranched apically; MP_{3+4} and (possibly) CuA_2 with distal remnants; r4 present, weak, connecting RP to RA_{3+4}; flecks absent from apical field distal to rp-mp2; long transverse proximal sclerite and faint triangular sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines or calli; spiracles present and apparently functional on segment VII. Male with aedeagus upright in repose; tegmen (Fig. 20h) with asymmetrical anterior margin and parameres hinged to basal piece, parameres with medial longitudinal division; penis (Fig. 20i) with with paired sclerites and fields of endophallic spicules, apex simple; spiculum gastrale V-shaped, arms connected by broad sclerotized lamina, anterior portion oblique. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. Apparently scarce throughout most of its range, but most commonly collected at blacklights. Other methods of collection are flight intercept traps and fogging. This is one of the most abundantly collected phalacrids in Lindgren funnel traps in the southeastern United States.

Distribution and diversity. This genus contains two described species and at least one undescribed species, the latter of which is widespread in the Neotropical Region. I have seen specimens from New Jersey to Texas, south to Bolivia and Santa Catarina, Brazil. From the West Indies I have seen specimens only from Dominican Republic, and these may represent a new species.

Included species (2):

Ochrolitus optatus Sharp, 1889 (Distribution: Costa Rica) (type!)
Ochrolitus rubens (LeConte, 1856), **comb. nov.** (*Gorginus*) (Distribution: USA) (type!)

Discussion. Casey (1889–1890) described the species *Ochrolitus tristriatus* in this genus, without seeing Sharp's type of *O. optatus*. He believed the species to be congeneric based on the habitus drawing and short description in Sharp (1889). Guillebeau (1894*a*) erected a separate genus for *O. rubens*, *Gorginus*, in his world treatment of the family. Casey (1916) redundantly devoted a new genus, *Erythrolitus*, to *O. rubens* (without knowledge of Guillebeau's actions over twenty years previous), in recognition of the difference between the two Nearctic forms. However, after examination of all types involved, I am convinced that no significant structural differences exist between the type species of *Ochrolitus* and *Gorginus*, and therefore I propose their synonymy. This necessitates the formation of one new combination (see above). *Ochrolitus tristriatus* Casey actually belongs in the genus *Litostilbus* Guillebeau (see account of that genus).

18. *Sveculus* Gimmel, gen. nov.

(Figs. 21; 40f, g)

Type species: *Sveculus lewisi*, here designated.

Type material. See account of *Sveculus lewisi* below.

Diagnosis. This is the only genus of Phalacridae with the following combination of characters: protibia with long ctenidium, prosternal process with apical transparent laminar process, and metatarsomeres I and II subequal in length.

Description. Very small to small, total length 1.1–2.0 mm. Dorsal color solid testaceous to rufo-testaceous (Figs. 40f, g). Tibial spur formula 2-2-2, tarsal formula 5-5-5 in both sexes.

Head. Not constricted behind eyes. Eyes small to medium-sized; facets flat; interfacetal setae absent; weakly emarginate medially; without posterior emargination; periocular groove absent; with transverse setose groove ventrally behind eye. Frontoclypeus not or barely emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club 3-segmented, club weakly asymmetrical; antennomere XI constricted on anterior edge (Fig. 21b). Mandible (Fig. 21a) with apex bidentate; retinaculum absent; mandible without ventral ridge. Maxillary palpomere IV fusiform, short, nearly symmetrical; galea short, rounded; lacinia with two stout spines. Mentum with sides divergent toward apex; labial palpomere III fusiform. Labrum with apical margin arcuate. Gular sutures short, barely evident.

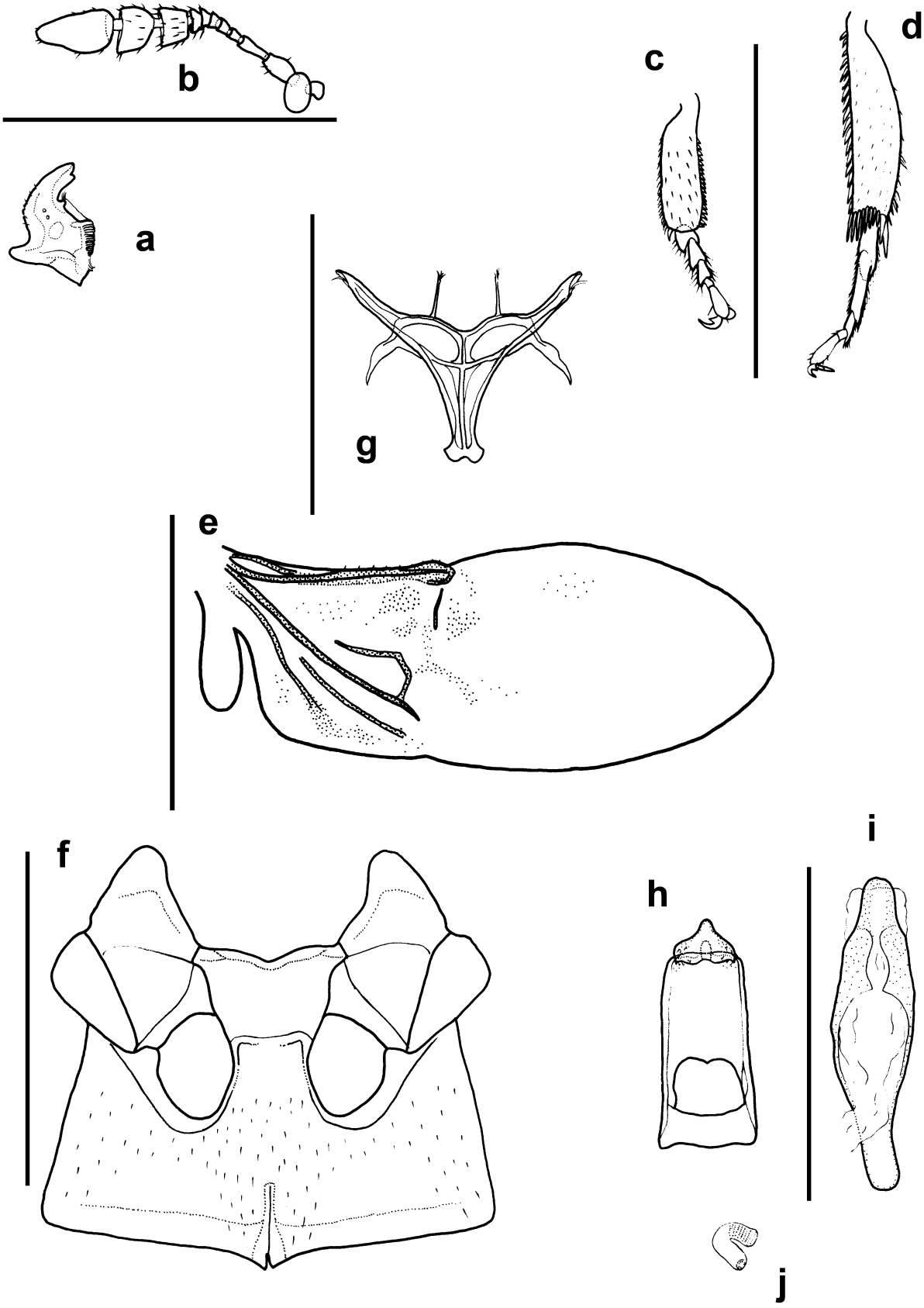

FIGURE 21. *Sveculus lewisi*, male. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) right metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 0.5 mm). (h) Tegmen, ventral; (i) penis, ventral (scale bar = 0.5 mm). Female. (j) Spermatheca (scale bar = 0.5 mm).

Thorax. Pronotum with microsetae present, distinct; with scutellar lobe weakly to moderately developed. Prosternum anteriorly with continuous row of marginal setae, setae flattened at base; procoxal cavity without anterolateral notchlike extension; prosternal process angulate in lateral view, sometimes conspicuously setose preapically, with broad horizontal translucent process at apex, apex without row of spinelike setae. Protrochanter without setae; protibia with ctenidium on kickface, extending about two-thirds length of tibia (Fig. 21c). Scutellar shield small. Elytron with spectral iridescence present or absent; with one weak sutural stria or stria absent; disc without even rudimentary striae or rows of punctures; with weak to strong transverse strigae, or strigae absent; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 21f) deeply notched anteriorly, extending posteriorly to metaventrite, not forming procoxal rests; mesanepisternum with complete transverse carina; mesocoxal cavities separated by slightly more than half width of a coxal cavity. Mesotarsomere III not bilobed. Metaventral process (Fig. 21f) not extending to anterior level of mesocoxae; metaventral postcoxal lines narrowly separated from mesocoxal cavity margin; discrimen short, extending less than halfway to anterior margin of metaventral process; metendosternite (Fig. 21g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange behind anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line; metatibial foreface with apical ctenidium roughly perpendicular overall to long axis of tibia, or slightly oblique; spurs cylindrical, longest spur subequal to width of tibial apex; metatarsomere I subequal to metatarsomere II or I slightly shorter, joint between I and II rigid (Fig. 21d). Hind wing (Fig. 21e) with distinct, ovate anal lobe; leading edge with incomplete row of long setae at level of RA+ScP; AA_{3+4} absent; cubitoanal system unbranched apically; MP_{3+4} with long, unbranched distal remnant; r4 absent; flecks present in apical field distal to rp-mp2; long transverse proximal sclerite and faint triangular sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines or calli; spiracles apparently absent from segment VII. Male with aedeagus upright in repose; tegmen (Fig. 21h) with symmetrical anterior margin and parameres hinged to basal piece, parameres without medial longitudinal division; penis (Fig. 21i) narrowed apically, with pair of endophallic sclerites, apex simple; spiculum gastrale V-shaped, arms free, with oblique anterior extension. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. Most specimens with ecological data were collected using Malaise or flight intercept traps or by fogging. Two Mindanao specimens were collected “under bark of log,” while one was collected “on decaying fleshy, gilled bracket fungus.” No material has been identified in the adult gut. None are known to have been collected at light.

Distribution and diversity. Southeast Asia from Thailand and the Malay Peninsula through Borneo, Sulawesi, and Mindanao, to Queensland, New South Wales, and Australian Capital Territory, Australia. This genus also occurs in Madagascar. Despite having examined a large amount of material from New Guinea, I have not seen specimens from that island. There are several morphospecies in collections, all apparently undescribed.

Included species (1):

Sveculus lewisi Gimmel, **sp. nov.** (Distribution: southeast Asia)

Etymology. This genus is named in honor of Dr. Zdeněk Švec of Prague, Czech Republic, in recognition of his significant contributions to understanding the phalacrid fauna of the Old World. The gender of the name is masculine.

Sveculus lewisi Gimmel, sp. nov.

(Figs. 21; 40f, g)

Holotype. Male, “TRAY \ 5 // Fog 7, 1200m. \ 18.ii.1985 \ Gng. Ambang F.R. \ nr. Kotamobagu // INDONESIA \ SULAWESI UTARA \ Gng. Ambang F.R. \ nr. Kotamobagu \ Feb. 1985 // 377 [gray label] // R. Ent. Soc. Lond. \ PROJECT WALLACE \ B.M. 1985-10 // HOLOTYPE ♂ \ Sveculus \ lewisi Gimmel \ des. M.L. Gimmel 2011 [red label]” (BMNH), point mounted, genitalia mounted on acetate card on same pin in DMHF (water and alcohol soluble).

Paratypes. "TRAY \ 8 // Fog 17, 1100m \ Danau Mooat, \ Pandanus, 31.vii.85 // INDONESIA \ SULAWESI UTARA \ Danau Mooat 1200m \ nr. Kotamobagu \ July 1985 // R. Ent. Soc. Lond. \ PROJECT WALLACE \ B.M. 1985-10" (1, BMNH); same but also with labels "Slide No. 469 \ E. Lewis 1989 [numbers handwritten] // ♀" (1, BMNH); same but with "Slide No. 468 \ E. Lewis 1989 [numbers handwritten] // ♀ // 29" (1, BMNH); "INDONESIA: \ SULAWESI UTARA, \ Dumoga-Bone N.P. \ 9–16 May 1985. // Malaise \ trap // Lowland forest \ ca. 200m. // R. Ent. Soc. Lond. \ PROJECT WALLACE \ B.M. 1985-10" (1, BMNH); "INDONESIA: \ SULAWESI UTARA, \ Dumoga-Bone N.P. \ 15–22 May 1985. // Malaise \ trap 1 // Plot A, ca 200m \ Lowland forest // R. Ent. Soc. Lond. \ PROJECT WALLACE \ B.M. 1985-10" (1 disarticulated, BMNH); same but date on first label "November 1985." (1 disarticulated, BMNH); same but date on first label "April 1985." and with label "82.4 [handwritten]" (1 disarticulated, BMNH); all with label added "PARATYPE \ Sveculus \ lewisi Gimmel \ det. M.L. Gimmel 2011 [yellow label]".

Description. Total length 1.5–1.8 mm. Color light reddish-testaceous throughout. Antennal club slightly longer than funicle; antennomere XI triangular, slightly longer than IX and X combined. Head punctation extremely fine and sparse; eyes separated on frons by about 2.5 times width of a single eye (in frontal view). Pronotal punctation almost nonexistent; posterior margin not bordered; with weak scutellar lobe; hind angles obtuse. Elytron devoid of microsculpture, without distinct punctures, without transverse strigae, with weak but evident diffraction grating; with sutural stria quite weak, extending about 2/3 length of elytron, without a trace of additional striae. Prosternal process (including translucent projection) extending well beyond procoxae; prosternum devoid of setae. Protibia with ctenidium extending about 2/3 length of tibia. Metaventral process (including mesoventral posterior margin) with slight depression, not appearing emarginate. Metaventrite without distinct punctures, densely setose medially; metaventral postcoxal lines smoothly arcuate, enclosing an area about 1/6 length of metaventrite behind coxae. Metatarsomere I slightly shorter than II; metatarsomeres I and II together much longer than remainder of tarsus (Fig. 21d).

Tegmen of aedeagus with fused parameres bluntly pointed, without median cleft (Fig. 21h). Penis widest at about middle, with smoothly rounded tip (Fig. 21i). Spermatheca as illustrated (Fig. 21j).

Diagnosis. This species may be recognized by the characters given in the generic diagnosis.

Distribution. Known only from North Sulawesi (Sulawesi Utara), Indonesia.

Etymology. Named in honor of the late Ernest S. Lewis (1924–2009) of Chagford, England, for his (mostly unpublished) contributions to the understanding of Phalacridae. The epithet is a noun in the genitive case.

OLIBRUS-GROUP

Idiobiidae Gistel 1856: 383. Type genus: *Idiobius* Gistel. [name not used as valid since original description]
Olibrini Guillebeau 1892*b*: 147. Type genus: *Olibrus* Erichson.
Tolyphini Guillebeau 1892*b*: 147. Type genus: *Tolyphus* Erichson.

Diagnosis. This group may be recognized by the metaventral process surpassing the mesocoxae, the non-divergent metaventral lines, the lack of a protibial ctenidium, the lack of an emargination on the posterior part of the eye, the small scutellar shield, and the ovipositor modified into a wedge-shaped organ.

Distribution and diversity. A total of 137 species, occurring nearly everywhere Phalacridae are found except the Neotropical region.

Included genera (2). *Olibrus* Erichson, *Tolyphus* Erichson.

19. *Olibrus* Erichson, 1845

(Figs. 3e; 22; 41a)

Olibrus Erichson 1845: 113. Type species: *Sphaeridium bicolor* Fabricius 1792, fixed by subsequent designation.
Idiobius Gistel 1856: 383. Type species: *Phalacrus flavicornis* Sturm 1807, designated by Pakaluk *et al.* (1994: 229). [synonymized with *Olibrus* by Pakaluk *et al.* 1994: 229]

Type material. *Sphaeridium bicolor* Fabricius: two syntypes, not seen (ZMUC).

Phalacrus flavicornis Sturm: type not seen.

Diagnosis. This genus may be recognized by metatarsomere I shorter than metatarsomere II, metaventral process protruding anteriorly, protibia without ctenidium (but with up to 4 spines), no spectral iridescence on elytra but rather with a greasy luster, antennomere 11 turbinate (sometimes weakly so), and female ovipositor distinctive (modified into a double-pointed wedge with styli arising subapically and pointing laterally).

Description. Very small to large, total length 1.1–3.9 mm. Color highly variable, from completely testaceous to completely black, often with metallic greenish or bluish luster, dark specimens sometimes with subapical yellow or red maculations (Fig. 41a). Tibial spur formula 2-2-2, tarsal formula 5-5-5 in females, 5-5-5 or 5-5-4 in males.

Head. Not constricted behind eyes. Eyes medium-sized; facets flat; interfacetal setae absent; weakly emarginate or straight medially; without posterior emargination; periocular groove present or absent; with transverse setose groove ventrally behind eye. Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club 3-segmented, club weakly asymmetrical, antennomere XI weakly to strongly turbinate (Fig. 22b). Mandible (Fig. 22a) slender; apex tridentate; without retinaculum; mandible without ventral ridge. Maxillary palpomere IV fusiform, nearly symmetrical; galea short, rounded; lacinia with two stout spines. Mentum with sides divergent toward apex; labial palpomere III fusiform, pointed or not apically. Labrum with apical margin truncate. Gular sutures short, barely evident.

Thorax. Pronotum without obvious microsetae; with moderately developed scutellar lobe. Prosternum anteriorly with continuous row of marginal setae, setae flattened at base; procoxal cavity with anterolateral notchlike extension; prosternal process rounded in lateral view, not conspicuously setose preapically, without spinelike setae at apex. Protrochanter with setae; protibia without ctenidium on kickface (Fig. 22c), but with group of up to four spines at outer apical angle; male protarsomere II sometimes expanded. Scutellar shield small. Elytron usually without spectral iridescence, often with brassy or aeneous luster, iridescent in some southern African species; usually two sutural striae present, sometimes only one, occasionally with quite short third stria in apical third; discal striae sometimes weakly developed, with parallel rows of punctures; without transverse strigae; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 22f) notched anteriorly, extending posteriorly to metaventrite, dividing mesoventral disc in two, not forming procoxal rests; mesanepisternum with complete or incomplete transverse carina; mesocoxal cavities widely separate, separated by more than half width of a coxal cavity. Mesotarsomere III bilobed. Metaventral process (Fig. 22f) extending at least to anterior level of mesocoxae, often protruding and arcuately lobed anteriorly; metaventral postcoxal lines not separated from mesocoxal cavity margin; discrimen quite short, extending much less than halfway to anterior margin of metaventral process; metendosternite (Fig. 22g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange behind anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate without transverse line; metatibial foreface with apical ctenidium roughly perpendicular overall to long axis of tibia; spurs cylindrical, longest spur subequal in length to width of tibial apex; metatarsomere I shorter than metatarsomere II, joint between I and II flexible (Fig. 22d); metatarsomere III bilobed. Hind wing (Fig. 22e) with distinct, ovate anal lobe; leading edge with complete row of long setae at level of RA+ScP; AA_{3+4} strong and complete, or faint, sometimes connected to Cu by AA_3; cubitoanal system branched apically; CuA_2 and MP_{3+4} with distal remnants; r4 absent or weakly developed, not connected with RA_{3+4}; conspicuous flecks absent from apical field distal to rp-mp2, or with extremely short fleck proximally; long transverse proximal sclerite and sometimes additional small oblique sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines or calli; spiracles present and apparently functional on segment VII. Male with aedeagus upright in repose; tegmen (Fig. 22h) with symmetrical or asymmetrical anterior margin and parameres separated by suture from basal piece, parameres with or without medial longitudinal division; penis (Fig. 22i) with subapical paired endophallic sclerites, apex simple or weakly bilobed; spiculum gastrale V-shaped, with arms free. Female ovipositor (Fig. 3e) sclerotized, gonocoxites together forming wedge, gonostyli attached subapically.

Immature stages. Laboulbéne (1868) described the larva of *O. affinis* (Sturm) and its habits. Urban (1926, 1930) described the larvae of *Olibrus aeneus* (Fabricius) and *O. millefolii* (Paykull). Löben Sels (1934) described the larva and pupa of a Nearctic *Olibrus* (as *Phalacrus politus* Melsheimer).

Bionomics. At least in the Holarctic region and southern Africa, members of this genus are diurnal and visit flowers of various plants (especially Asteraceae) as adults. As larvae, they are more host specific, developing within the flower heads of particular composites, including *Solidago*, *Symphyotrichum*, *Achillea*, *Chrysopsis*, *Helichrysum*, *Tragopogon*, *Senecio*, *Hypochaeris*, *Matricaria*, *Anthemis*, *Leontodon*, and *Crepis*. The larvae feed

with their heads pointed downward among the disc flowers of the flower head, and their presence is often evidenced by a tuft of pappus protruding above the level of the flower disc. They appear to feed only on fluids, as no particulate matter has been observed in the gut. In flower heads of *Symphyotrichum novae-angliae* (L.) G.L. Nesom, in Kansas, I discovered anywhere from four to nine larvae living inside each head. Members of *Olibrus* have been considered as biological control agents of certain weedy Asteraceae, including *O. aeneus* for the introduced European *Tripleurospermum perforatum* (Mérat) Wagenitz in Canada (see Freese and Günther 1991). Flower heads fed upon by the beetles tend to be destroyed, but the potential utility of the beetle is compromised by its oligophagous nature.

Among non-Asteraceae occurrences, specimens were collected by D. Habeck in Queensland (FSCA) on flowers and foliage of the cajeput tree, *Melaleuca linariifolia* Sm. (Myrtaceae). In South Africa, some were collected by beating a species of *Acacia*.

Distribution and diversity. One of the few genera occurring in both New and Old Worlds, it occurs in North America from southern Canada south to at least the Mexican states of México and Tlaxcala. I have seen no specimens of true *Olibrus* from the West Indies. In the Old World it occurs throughout the Palearctic Region, and also in eastern and southern Africa (excluding wet tropical regions), the Oriental Region, and at least to Queensland and Western Australia.

Olibrus is currently the largest genus in Phalacridae in terms of described species. Many (especially Oriental) species will probably be removed from this genus after the appropriate types are examined. The Nearctic fauna is probably severely over-described (notably by Thomas L. Casey) and many of the species names are likely to be synonyms. The South African *Olibrus* fauna is exceedingly rich, and if any lineage of the Phalacridae is to be regarded as an adaptive radiation, it is this one.

Included species (128):

Olibrus abstinens Casey, 1916 (Distribution: United States) (type!)
Olibrus aenescens Küster, 1852 (Distribution: western Mediterranean)
Olibrus aeneus (Fabricius, 1792) (Distribution: Palearctic)
Olibrus aeratus (Champion, 1925) (Distribution: South Africa) (type!)
Olibrus affinis (Sturm, 1807) (Distribution: Palearctic) (type!)
Olibrus albomaculatus Motschulsky, 1858 (Distribution: southeast Asia) [NOTE: may not belong in *Olibrus*]
Olibrus anthobius Guillebeau, 1894 (Distribution: Ethiopia) (type!)
Olibrus aridus Casey, 1916 (Distribution: United States) (type!)
Olibrus bakeri Casey, 1916 (Distribution: United States) (type!)
Olibrus baudueri Tournier, 1888 (Distribution: western Palearctic)
Olibrus bedeli Guillebeau, 1892 (Distribution: northern Africa)
Olibrus bevinsi Champion, 1925 (Distribution: South Africa) (type!)
Olibrus bicolor (Fabricius, 1792) (Distribution: Palearctic)
Olibrus bimaculatus Küster, 1848 (Distribution: Palearctic)
Olibrus bisignatus (Ménétries, 1849) (Distribution: Palearctic)
Olibrus bivulnerus Motschulsky, 1858 (Distribution: ?Sri Lanka) [NOTE: may not belong in *Olibrus*]
Olibrus blanditus Casey, 1916 (Distribution: United States) (type!)
Olibrus bohemani Champion, 1925 (Distribution: South Africa) (type!)
Olibrus brunneus (Motschulsky, 1858) (Distribution: Sri Lanka, Taiwan) [NOTE: may not belong in *Olibrus*]
Olibrus bullatus Casey, 1916 (Distribution: United States) (type!)
Olibrus calamis Casey, 1916 (Distribution: United States) (type!)
Olibrus callidus Casey, 1916 (Distribution: United States) (type!)
Olibrus calvosus Lyubarsky, 2003 (Distribution: Nepal) [NOTE: may not belong in *Olibrus*]
Olibrus camptoides Reitter, 1892 (Distribution: “Turkestan”)
Olibrus capensis (Guérin-Méneville, 1844), **comb. nov.** (*Tolyphus*) (Distribution: South Africa)
Olibrus caseyi Hetschko, 1930 (Distribution: United States) (type!)
Olibrus castaneus Baudi di Selve, 1870 (Distribution: Mediterranean region)
Olibrus caucasicus Tournier, 1889 (Distribution: Mediterranean region) (type!)
Olibrus cessus Casey, 1916 (Distribution: United States) (type!)

Olibrus cinerariae Wollaston, 1854 (Distribution: Madeira)
Olibrus collucens Casey, 1916 (Distribution: United States) (type!)
Olibrus congener Wollaston, 1864 (Distribution: Canary Islands)
Olibrus consanguineus Flach, 1889 (Distribution: Japan)
Olibrus corticalis (Panzer, 1797) (Distribution: western Palearctic)
Olibrus decoloratus Casey, 1916 (Distribution: United States) (type!)
Olibrus delicatulus Tournier, 1889 (Distribution: Russia) (type!)
Olibrus demarzoi Švec & Angelini, 1996 (Distribution: Italy, Turkey)
Olibrus desbrochersi Guillebeau, 1892 (Distribution: western Mediterranean)
Olibrus egenus Guillebeau, 1896 (Distribution: Madagascar) (type!)
Olibrus evanescens Champion, 1925 (Distribution: South Africa) (type!)
Olibrus fallaciosus Casey, 1916 (Distribution: United States) (type!)
Olibrus fallax Flach, 1888 (Distribution: Austria, Italy)
Olibrus festivus Lyubarsky, 2005 (Distribution: South Africa) (type!)
Olibrus firmus Lyubarsky, 2003 (Distribution: Nepal) [NOTE: may not belong in *Olibrus*]
Olibrus flachi Reitter, 1891 (Distribution: Kazakhstan, Uzbekistan)
Olibrus flavicornis (Sturm, 1807) (Distribution: Palearctic)
Olibrus florum Wollaston, 1854 (Distribution: Canary Islands)
Olibrus frustratus Casey, 1916 (Distribution: United States) (type!)
Olibrus gemma Wollaston, 1867 (Distribution: Cape Verde)
Olibrus gerhardti Flach, 1888 (Distribution: Europe)
Olibrus globiformis Tournier, 1894 (Distribution: Turkey) (type!)
Olibrus guttatus Tournier, 1889 (Distribution: western Palearctic) (type!)
Olibrus hervosus Lyubarsky, 1994 (Distribution: Borneo, India, Philippines) [NOTE: may not belong in *Olibrus*]
Olibrus igneus Fauvel, 1903 (Distribution: New Caledonia) [NOTE: probably does not belong in *Olibrus*]
Olibrus impotens Casey, 1916 (Distribution: United States) (type!)
Olibrus impressus Hatch, 1962 (Distribution: United States)
Olibrus irregularis Casey, 1916 (Distribution: United States) (type!)
Olibrus jelineki Švec & Ponel, 1999 (Distribution: Turkey)
Olibrus judaicus Sahlberg, 1913 (Distribution: Israel)
Olibrus kaszabi Medvedev, 1971 (Distribution: Mongolia)
Olibrus koltzei Flach, 1888 (Distribution: central Palearctic)
Olibrus laevisternus Guillebeau, 1897 (Distribution: Syria)
Olibrus latisternus (Guillebeau, 1893), **comb. nov.** (*Litochrus*) (Distribution: Vietnam) (type!)
Olibrus latisternus Guillebeau, 1894 (Distribution: Oriental) (type!) [junior secondary homonym not replaced, pending further investigation]
Olibrus lecontei Casey, 1890 (Distribution: United States) (type!)
Olibrus liquidus Erichson, 1845 (Distribution: western Palearctic)
Olibrus lubricatus Lyubarsky, 2004 (Distribution: Nepal) [NOTE: may not belong in *Olibrus*]
Olibrus lubricus Casey, 1916 (Distribution: United States) (type!)
Olibrus macropus Champion, 1925 (Distribution: South Africa) (type!)
Olibrus metallescens Flach, 1888 (Distribution: Mongolia, Russia)
Olibrus millefolii (Paykull, 1800) (Distribution: Palearctic)
Olibrus minusculus Motschulsky, 1866 (Distribution: Sri Lanka) [NOTE: may not belong in *Olibrus*]
Olibrus motschulskyi Lyubarsky, 1994 (Distribution: Sri Lanka) [NOTE: may not belong in *Olibrus*]
Olibrus multesimus Lyubarsky, 1994 (Distribution: Oriental) [NOTE: may not belong in *Olibrus*]
Olibrus nainiensis Champion, 1924 (Distribution: India, Indonesia, Philippines) (type!)
Olibrus namibiensis Lyubarsky, 1998 (Distribution: Namibia, South Africa)
Olibrus natalensis Champion, 1924 (Distribution: South Africa) (type!)
Olibrus neglectus Casey, 1890 (Distribution: United States) (type!)
Olibrus nigroclavatus Champion, 1925 (Distribution: South Africa) (type!)

Olibrus norvegicus Münster, 1901 (Distribution: Palearctic)
Olibrus notatus Wollaston, 1867 (Distribution: Cape Verde)
Olibrus obscuricornis Guillebeau, 1894 (Distribution: India) (type!)
Olibrus obscurus Guillebeau, 1892 (Distribution: Italy, Slovakia)
Olibrus ovalis Khnzorian, 1962 (Distribution: Armenia)
Olibrus pallidulus Motschulsky, 1858 (Distribution: Sri Lanka) [NOTE: may not belong in *Olibrus*]
Olibrus pallipes (Say, 1824) (Distribution: United States)
Olibrus particeps Mulsant & Rey, 1861 (Distribution: Palearctic)
Olibrus peringueyi Gimmel, **nom. nov.** [for *Olibrus consanguineus* Péringuey, 1892, junior primary homonym of *Olibrus consanguineus* Flach, 1889] (Distribution: South Africa)
Olibrus permicans Reitter, 1913 (Distribution: China)
Olibrus platycephalus Champion, 1924 (Distribution: India) (type!) [NOTE: may not belong in *Olibrus*]
Olibrus platysternus Champion, 1925 (Distribution: Namibia, South Africa) (type!)
Olibrus pondoensis Champion, 1925 (Distribution: Namibia, South Africa) (type!)
Olibrus pruddeni Casey, 1916 (Distribution: United States) (type!)
Olibrus punctatus Lyubarsky, 1994 (Distribution: Borneo) [NOTE: may not belong in *Olibrus*]
Olibrus pygmaeus (Sturm, 1807) (Distribution: western Palearctic)
Olibrus quadristriatus Champion, 1925 (Distribution: South Africa) (type!)
Olibrus raffrayi Guillebeau, 1894 (Distribution: Ethiopia) (type!)
Olibrus rasilis Lyubarsky, 2003 (Distribution: Nepal)
Olibrus reitteri Flach, 1888 (Distribution: Mediterranean)
Olibrus reyi Guillebeau, 1892 (Distribution: Greece)
Olibrus rufescens Motschulsky, 1858 (Distribution: Indonesia, Sri Lanka) [NOTE: may not belong in *Olibrus*]
Olibrus rufipes LeConte, 1856 (Distribution: Canada, United States) (type!)
Olibrus rufopiceus Motschulsky, 1858 (Distribution: Japan, Sri Lanka) [NOTE: may not belong in *Olibrus*]
Olibrus rufoplagiatus Champion, 1925 (Distribution: South Africa) (type!)
Olibrus rufosignatus Lyubarsky, 1998 (Distribution: Namibia)
Olibrus rufoterminatus Champion, 1925 (Distribution: Namibia, South Africa, Zimbabwe) (type!)
Olibrus seidlitzii Flach, 1888 (Distribution: Mongolia, Russia)
Olibrus selvei Guillebeau, 1892 (Distribution: Cyprus)
Olibrus semistriatus LeConte, 1856 (Distribution: Canada, United States) (type!)
Olibrus singularis Tournier, 1889 (Distribution: Morocco, Spain)
Olibrus snizeki Švec, 2005 (Distribution: Kenya)
Olibrus sternalis Casey, 1916, **resurrected name** (Distribution: United States) (type!)
Olibrus stictus Lyubarsky, 1994 (Distribution: Oriental) [NOTE: may not belong in *Olibrus*]
Olibrus stierlini Flach, 1888 (Distribution: western Palearctic)
Olibrus stlatarius Lyubarsky, 1994 (Distribution: Indonesia, Philippines) [NOTE: may not belong in *Olibrus*]
Olibrus stlembus Lyubarsky, 1994 (Distribution: Nepal, Philippines) [NOTE: may not belong in *Olibrus*]
Olibrus striatissimus Reitter, 1899 (Distribution: Azerbaijan, Iran)
Olibrus stuporatus Lyubarsky, 1994 (Distribution: Indonesia, Nepal) [NOTE: may not belong in *Olibrus*]
Olibrus subaereus Wollaston, 1864 (Distribution: Canary Islands)
Olibrus tangerianus Tournier, 1889 (Distribution: Morocco)
Olibrus tolyphoides Champion, 1925 (Distribution: South Africa) (type!)
Olibrus turcicus Švec & Ponel, 1999 (Distribution: Turkey)
Olibrus utealis Casey, 1916 (Distribution: United States) (type!)
Olibrus veteratus Lyubarsky, 2003 (Distribution: Indonesia, Vietnam) [NOTE: may not belong in *Olibrus*]
Olibrus viridescens Champion, 1925 (Distribution: South Africa) (type!)
Olibrus vittatus LeConte, 1863 (Distribution: Canada, United States) (type!)
Olibrus voraginalis Casey, 1916 (Distribution: United States) (type!)
Olibrus wickhami Casey, 1890 (Distribution: United States) (type!)

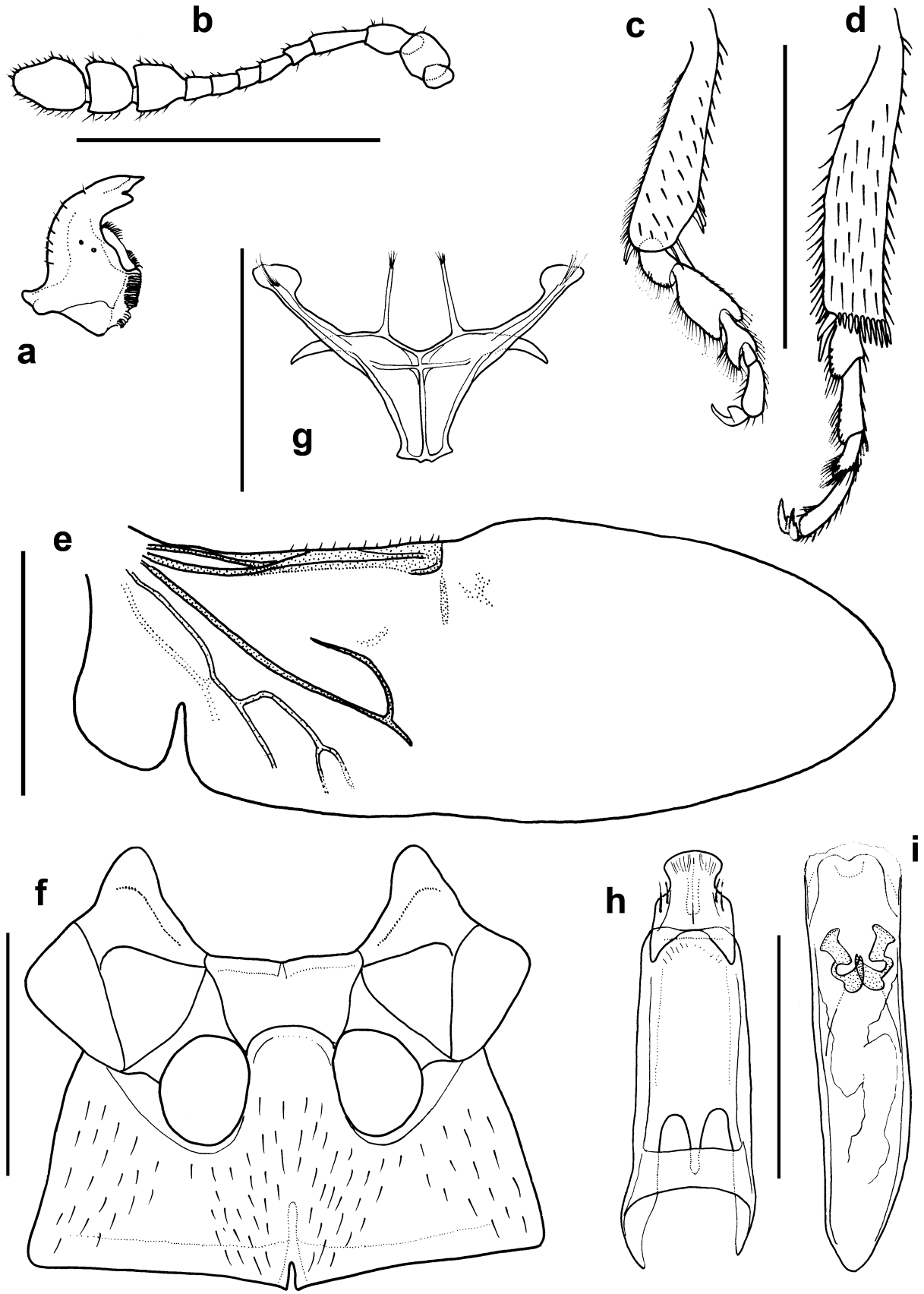

FIGURE 22. *Olibrus aeneus*, male. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 0.5 mm). (h) Tegmen, ventral; (i) penis, ventral (scale bar = 0.5 mm).

Discussion. Motschulsky's and Lyubarsky's Oriental species of *Olibrus*, treated by Lyubarsky (1993*a*, *b*, 1994*a*, 2003), have not been examined by me. Lyubarsky's concept of this genus was much broader than that presented here. Additionally, his drawings and descriptions tend to be sparse and schematic, and do not necessarily emphasize diagnostic characters. Therefore, species described by these authors are only provisionally retained in *Olibrus*, with the exception of one species, *Olibrus brunnescens* Motschulsky, 1858, which I have transferred to *Stilbus* Seidlitz based on the distinctive aedeagus illustrated in Lyubarsky (1993*b*). Lyubarsky's (1998, 2005) African species are more clearly illustrated, and certain of his species have been transferred out of *Olibrus* by Švec (2002, 2003). I have provisionally transferred *O. capriviensis* Lyubarsky, 1998 to *Acylomus* Sharp.

The large, striking species *Olibrus capensis* Guérin-Méneville, from South Africa, was transferred to *Tolyphus* (*Pharcisinus*) by Champion (1925*a*) without explanation. I have examined material of this species (BMNH, SANC) and it properly belongs in *Olibrus*.

Upon examination of the types of *Olibrus bullatus* Casey, 1916, and *O. sternalis* Casey, 1916, I have determined these are probably not synonymous. The elytra differ in the extent of microsculpture. While many of Casey's names in *Olibrus* are certainly junior synonyms, I have chosen to resurrect *O. sternalis* so that it may be properly placed in future.

20. *Tolyphus* Erichson, 1845

(Figs. 2e; 23; 40h, i)

Tolyphus Erichson 1845: 108. Type species: *Phalacrus granulatus* Guérin-Méneville 1834, fixed by monotypy.
Pharcisinus Guillebeau 1894*a*: 278. Type species: *Tolyphus punctulatus* Rosenhauer 1856, fixed by original designation.

Type material. *Phalacrus granulatus* Guérin-Méneville: types not seen.

Tolyphus punctulatus Rosenhauer: types not seen.

Diagnosis. Readily recognized by the parallel-sided habitus, emarginate frontoclypeus, distinct elytral striae, short antennae, tuberculate tibial kickface, apically expanded protibia, and broad, flattened metatibial spurs. The labral tormae are unlike others I have seen in the family, being convergent just posterior to the posterior labral margin.

Description. Medium-sized, total length 2.0–3.0 mm. Color solid piceous to black, often with metallic greenish or bluish luster (Fig. 40h). Tibial spur formula 2-2-2, tarsal formula 5-5-5 in females, 5-5-4 in males.

Head. Not constricted behind eyes. Eyes medium-sized; facets convex, dorsalmost facets often (subgenus *Tolyphus*) abruptly smaller than adjacent facets (Fig. 40i); interfacetal setae absent; weakly emarginate or straight medially; without posterior emargination; periocular groove absent; with transverse setose groove ventrally behind eye. Frontoclypeus emarginate above antennal insertion; clypeal apex broadly emarginate (Fig. 2e). Antennal club 3-segmented, club weakly asymmetrical, antennomere XI weakly to strongly turbinate (Fig. 23b). Mandible (Fig. 23a) slender; apex simple; with distinct retinaculum; mandible without ventral ridge. Maxillary palpomere IV fusiform, nearly symmetrical; galea short, rounded; lacinia with two stout spines. Mentum with sides divergent toward apex; labial palpomere III fusiform. Labrum with apical margin truncate or slightly emarginate. Gular sutures short, barely evident.

Thorax. Pronotum without obvious microsetae; with weakly developed scutellar lobe. Prosternum anteriorly with continuous row of marginal setae, setae normal; procoxal cavity with anterolateral notchlike extension; prosternal process rounded in lateral view, sometimes conspicuously setose preapically, without spinelike setae at apex. Protrochanter with setae; protibia without ctenidium on kickface, but outer apical angle expanded and with two stout spines (Fig. 23c). Scutellar shield small. Elytron without spectral iridescence, often with brassy or aeneous luster; with one or two engraved (sutural) striae present, usually with additional superficial striae on disc, accompanied by rows of punctures; without transverse strigae; lateral margin without row of sawtooth-like setae. Mesoventral plate (Fig. 23f) not notched anteriorly, extending posteriorly to metaventrite, dividing mesoventral disc in two, not forming procoxal rests; mesanepisternum with incomplete transverse carina; mesocoxal cavities widely separate, separated by more than half width of a coxal cavity. Mesotarsomere III bilobed. Metaventral process (Fig. 23f) extending at least to anterior level of mesocoxae, often protruding and slightly lobed anteriorly; metaventral postcoxal lines not separated from mesocoxal cavity margin; discrimen extremely short or absent; metendosternite (Fig. 23g) with anterior tendons narrowly separated, ventral process intersecting ventral

longitudinal flange behind anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line; metatibial foreface with apical ctenidium roughly perpendicular overall to long axis of tibia; spurs markedly flattened, longest spur distinctly shorter than width of tibial apex; metatarsomere I shorter than metatarsomere II, joint between I and II flexible (Fig. 23d); metatarsomere III bilobed. Hind wing (Fig. 23e) with distinct, ovate anal lobe; leading edge with complete row of long setae at level of RA+ScP; AA_{3+4} strong and complete, connected to Cu by AA_3; cubitoanal system branched apically; CuA_2 and MP_{3+4} with distal remnants; r4 absent; weak fleck present in apical field just distal to rp-mp2; long or short transverse proximal sclerite and additional small curved sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines or calli; spiracles present and apparently functional on segment VII. Male with aedeagus upright in repose; tegmen (Fig. 23h) with asymmetrical anterior margin and parameres separated by suture from basal piece, parameres without medial longitudinal division; penis (Fig. 23i) with pair of large endophallic sclerites, apex simple; spiculum gastrale V-shaped, with arms free or partially connected by sclerotized lamina. Female ovipositor sclerotized, gonocoxites together forming wedge, gonostyli attached subapically.

Immature stages. Unknown.

Bionomics. Apparently pollen-feeding on members of Asteraceae as adults. Numerous pollen grains were observed in the hindgut of dissected specimens. Peyerimhoff (1915) reports *T. granulatus* on *Crepis taraxacifolia* Thuil. [=*Crepis vesicaria* L.] (Asteraceae) in North Africa and southern France, and that the larvae may be found in April in the interior of the flower feeding on the tender seeds. Peyerimhoff (1926) reported *T. punctatostriatus* Kraatz [=*T. punctulatus* Rosenhauer] abundant in June on flowers of *Sonchus maritimus* L. in North Africa, and *T. punctulatus* in April on flowers of *Taraxacum inaequilobum* Pom. He concluded that members of the genus develop exclusively in the flower heads of composites, a hypothesis that I cannot refute.

Distribution and diversity. Eight described species, though a revision is necessary to confirm the validity of the names described during the 20th century. They occur exclusively in the warm, dry belt from the western Mediterranean eastward to at least Kazakhstan.

Included species (8):

Subgenus *Tolyphus* Erichson, 1845:

Tolyphus (s.str.) dubius Gridelli, 1930 (Distribution: Egypt, Libya)
Tolyphus (s.str.) granulatus (Guérin-Méneville, 1834) (Distribution: circum-Mediterranean)
Tolyphus (s.str.) rufescens Pic, 1914 (Distribution: Italy, Egypt)
Tolyphus (s.str.) sedilloti Guillebeau, 1892 (Distribution: Libya, Tunisia)

Subgenus *Pharcisinus* Guillebeau, 1894:

Tolyphus (Pharcisinus) bimaculatus Medvedev, 1963 (Distribution: Kazakhstan)
Tolyphus (Pharcisinus) jankovskii Skopin, 1951 (Distribution: Kazakhstan)
Tolyphus (Pharcisinus) punctulatus Rosenhauer, 1856 (Distribution: circum-Mediterranean)
Tolyphus (Pharcisinus) transcaspicus Reitter, 1913 (Distribution: Turkmenistan)

Discussion. This genus shares many character states with the much more widespread *Olibrus* Erichson, including a protruding metaventral process, turbinate antennomere 11, mesofemoral lines adhering to coxal cavity, female ovipositor modified into a highly sclerotized wedge-like organ, no protibial ctenidium, and metatarsomere I shorter than metatarsomere II. Guillebeau (1894*a*: 278) erected the genus *Pharcisinus* based on characters of the ommatidia, dorsal surface sculpturing, and form of abdominal ventrite V in the male. This group was relegated to a subgenus of *Tolyphus* by Ganglbauer (1899: 743), which is the arrangement I follow here.

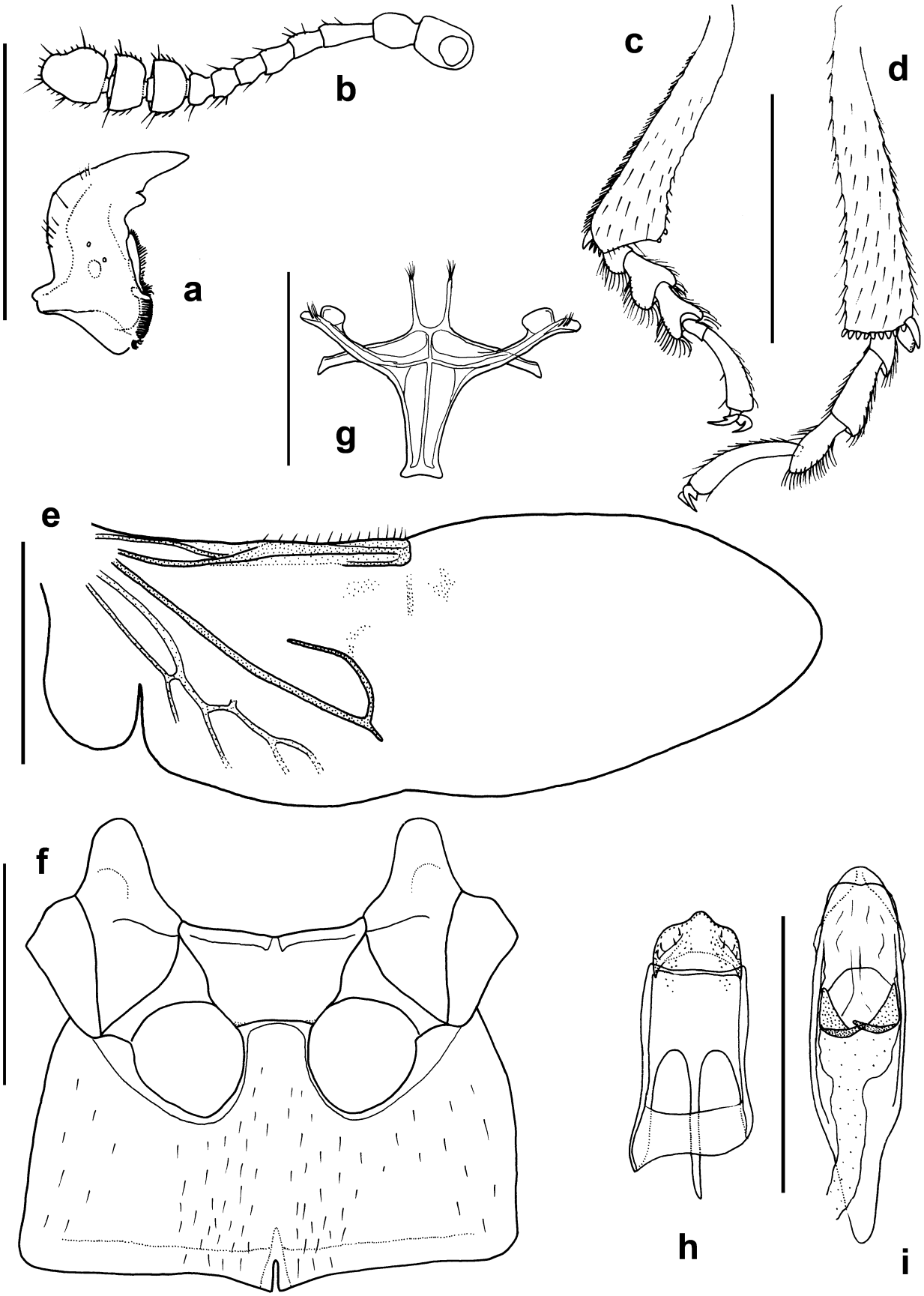

FIGURE 23. *Tolyphus* (*Tolyphus*) *granulatus*, male. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) right metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 0.5 mm). (h) Tegmen, ventral; (i) penis, ventral (scale bar = 0.5 mm).

Key to subgenera of *Tolyphus*:

1 Eyes with upper facets distinctly smaller than lower facets (Fig. 40i); last abdominal ventrite of male with median depression. . . . . *Tolyphus* (*Tolyphus* Erichson)
- Eyes with facets uniform; last abdominal ventrite of male without depression . . . . . *Tolyphus* (*Pharcisinus* Guillebeau)

The species *Olibrus capensis* (Guérin-Méneville) was moved to *Tolyphus* (*Pharcisinus*) by Champion (1925*a*: 37), but this is not justified, as that species clearly possesses characters of *Olibrus*, not *Tolyphus*.

OLIBROSOMA-GROUP

Diagnosis. This group may be recognized by the small scutellar shield, presence of a protibial ctenidium, the mesoventral plate not extending posteriorly to the metaventral process, and the metaventral process not surpassing the mesocoxae.

Distribution and diversity. Four species, occurring in the Afrotropical region and the Middle East.

Included genera (3). *Antennogasmus* Gimmel, *Malagasmus* Gimmel, *Olibrosoma* Tournier.

21. *Antennogasmus* Gimmel, gen. nov.

(Figs. 24; 41b)

Type species: *Antennogasmus cordatus* Gimmel, here designated.

Type material. See account of *A. cordatus* below.

Diagnosis. Recognized by small scutellar shield, metaventral postcoxal lines not separated from coxal cavities, short metaventral process, long protibial ctenidium, and one sutural stria. Males are readily recognized by their greatly enlarged and constricted antennomere XI.

Description. Medium-sized to large, total length 2.3–3.3 mm. Color highly variable, from completely testaceous to mostly piceous or black, often with lighter pronotum and/or bright maculations on elytra (Fig. 41b). Tibial spur formula 2-2-2, tarsal formula 5-5-5 in both sexes.

Head. Not constricted behind eyes. Eyes often large; facets convex; interfacetal setae absent; distinctly emarginate medially; without posterior emargination; periocular groove present or absent; with transverse setose groove ventrally behind eye. Frontoclypeus emarginate above antennal insertion; clypeal apex straight. Antennal club 3-segmented, club strongly asymmetrical, segment XI in males much longer than segments IX and X combined, sometimes as long as remainder of antenna, with anterior and posterior constriction (turbinate) (Fig. 24b). Mandible (Fig. 24a) with apex bidentate, with dorsal tooth small; without retinaculum; mandible without ventral ridge. Maxillary palpomere IV fusiform, slender, nearly symmetrical; galea short, rounded; lacinia with two stout spines. Mentum with sides divergent toward apex; labial palpomere III elongate, fusiform. Labrum with apical margin arcuate. Gula with medial internal rounded projection; gular sutures short, barely evident.

Thorax. Pronotum without obvious microsetae; with distinct scutellar lobe. Prosternum anteriorly with continuous row of marginal setae, setae normal; procoxal cavity with anterolateral notchlike extension; prosternal process angulate in lateral view, usually conspicuously setose preapically, without spinelike setae at apex. Protrochanter without setae; protibia with long ctenidium on kickface (Fig. 24c). Scutellar shield small. Elytron with moderate to strong spectral iridescence; one sutural stria present, discal striae weakly developed, sometimes with rows of weak punctation; without transverse strigae; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 24f) notched anteriorly, not extending posteriorly to metaventrite, forming procoxal rests; mesoventral disc depressed medially, not setose; mesanepisternum with complete transverse carina; mesocoxae approximate, separated by less than half width of a coxal cavity. Mesotarsomere III bilobed. Metaventral process (Fig. 24f) extending anteriorly beyond halfway point but not reaching anterior level of mesocoxae; metaventral postcoxal lines not separated from mesocoxal cavity margin; discrimen short, not quite extending halfway to anterior margin of metaventral process; metendosternite (Fig. 24g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange behind anterior margin. Anterior margin of metacoxa with

emargination sublaterally; metacoxal plate with transverse line; metatibial foreface with apical ctenidium procurved but perpendicular overall to long axis of tibia; spurs cylindrical, longest spur longer than width of tibial apex; metatarsomere I much longer than metatarsomere II, about as long as remainder of tarsus, joint between I and II flexible (Fig. 24d); metatarsomere III bilobed. Hind wing (Fig. 24e) with distinct, ovate anal lobe; leading edge without long setae; AA_{3+4} strong, anastomosing with Cu and without spur AA_4; cubitoanal system branching apically; CuA_2 and MP_{3+4} with distal remnants; r4 complete, connecting RP to apical hinge; conspicuous flecks present in apical field distal to rp-mp2; small transverse sclerite and large triangular sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines or calli; spiracles present and apparently functional on segment VII. Male with aedeagus upright in repose; tegmen (Fig. 24h) with symmetrical anterior margin and parameres hinged to basal piece, parameres with medial longitudinal division; penis (Fig. 24i) narrow in anterior half, with subapical endophallic sclerites, with long, complex series of sclerites and spicules within ejaculatory duct; spiculum gastrale V-shaped, with arms free. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. The bionomic information on labels is quite general to absent, but a number of specimens have been collected "at light" while another was collected in a flight intercept trap and another by canopy fogging. Habitat labels include "coastal dune forest" and "in forest."

Distribution and diversity. I have seen at least eight species in this genus, none previously described. Only the type species is described below, and the others must await a species-level revision. Collectively, they occur in the Afrotropical Region from Liberia to South Africa and Madagascar, including Ghana, Nigeria, Congo, Democratic Republic of the Congo, and Angola.

Included species (1):

Antennogasmus cordatus Gimmel, **sp. nov.** (Distribution: Madagascar, South Africa)

Discussion. The description above is based on several specimens representing new species within this genus, in addition to the species described below. These are the most strikingly colored phalacrids occurring in the Afrotropical region.

Etymology. From the Latin *antenno-* referring to the modified male antenna, and *-gasmus* in reference to its shared characters with the widespread genus *Augasmus*. The gender of the name is masculine.

Antennogasmus cordatus Gimmel, sp. nov.

(Figs. 24; 41b)

Holotype. Male, "SOUTH AFRICA: NATAL \ Leeukop, E of Pongola \ unable to trace coordinates \ 24.i.1992 Vogt & Holm // NATIONAL COLL. \ OF INSECTS \ Pretoria, S.Afr. // HOLOTYPE ♂ \ Antennogasmus \ cordatus Gimmel \ des. M.L. Gimmel 2011 [red label]" (SANC), card mounted.

Paratypes (3). "Mkuzi. \ Zululand. \ Dec., 1945. \ DDT Killed. \ DDT No. \ 0 // NATIONAL COLL. \ OF INSECTS \ Pretoria, S.Afr." (1 ♂, SANC); "MADAGASCAR: 45m elv. \ W. of Ft. Dauphin (Tolonaro) \ 25º01´12´´S, 46º38´59´´E \ 15NOV1994, M.A. Ivie & \ D. Pollock, in forest" (1 ♀, MAIC); "SOUTH AFRICA: Transvaal \ 13km, N. Louis Trichardt \ 10-XIII-1990 \ R. Miller & L. Stange" (1 ♂, FSCA [disarticulated]) all with "PARATYPE \ Antennogasmus \ cordatus Gimmel \ det. M.L. Gimmel 2011 [yellow label]".

Description. Total length 3.1–3.3 mm, ovate, evenly convex. Color piceous dorsally, becoming rufous along the extreme posterior and lateral borders of the pronotum, lateral and posterior borders of elytron, and clypeal region; appendages and ventral surface rufotestaceous; with reddish discal maculation on each elytron, variable in size but broadly connected across suture, appearing heart- or butterfly-shaped; strong diffraction grating present on scutellar shield and elytra, absent from pronotum. Antenna sexually dimorphic; in males with antennomere XI greatly elongate, padlike, with deep emargination on anterior border about halfway down length of antennomere, with small emargination on posterior border about 2/3 down length of antennomere, antennomere XI about as long as funicle (Fig. 24b); antennomeres IX and X short and transverse; antenna about as long as width of head capsule; in females antennomere XI weakly modified, without distinct emarginations, longer than IX and X combined,

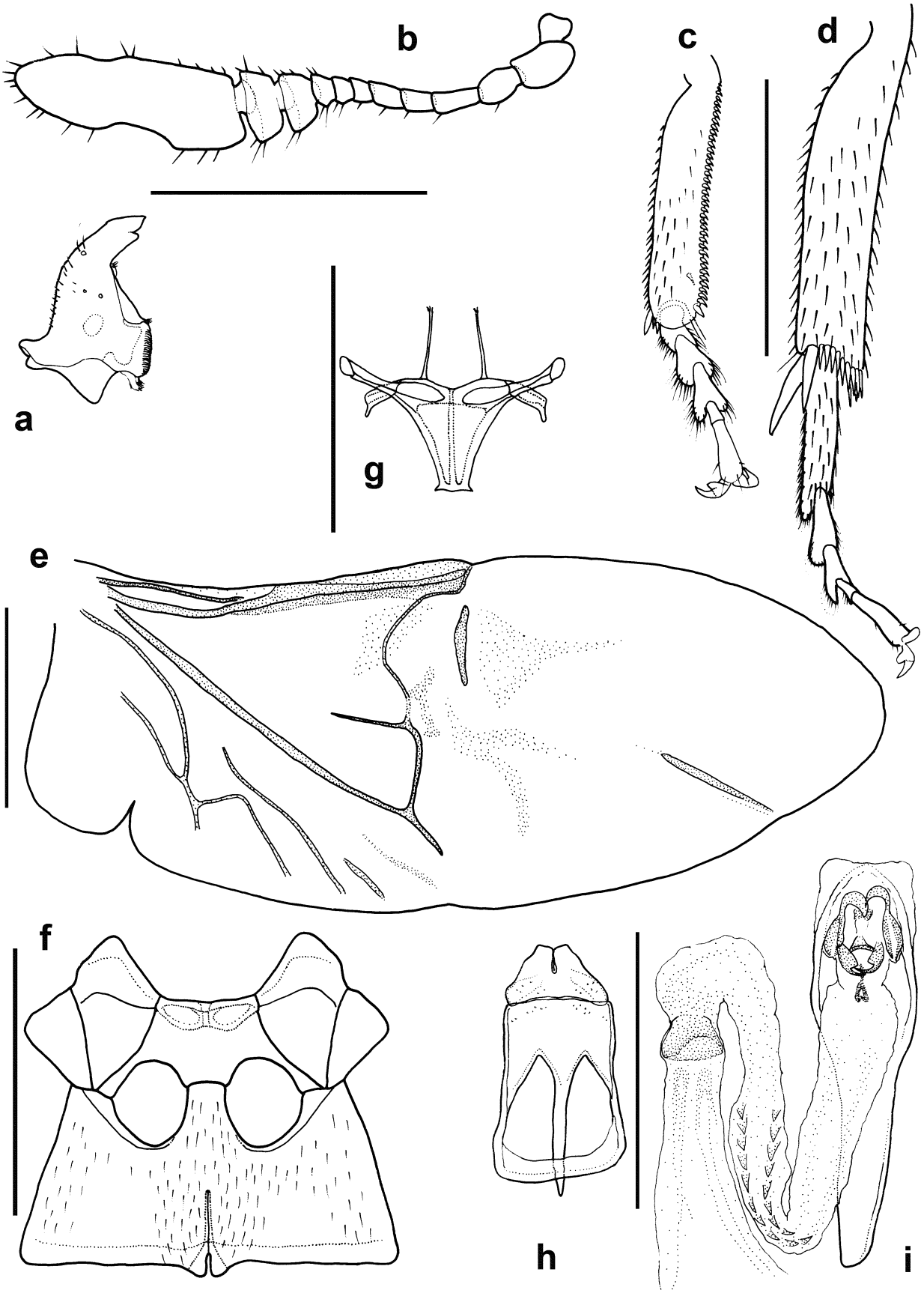

FIGURE 24. *Antennogasmus cordatus*, male. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 1.0 mm). (g) Metendosternite (scale bar = 1.0 mm). (h) Tegmen, ventral; (i) penis, ventral (scale bar = 0.5 mm).

about as long as funicle but total antennal length shorter than in male, less than width of head capsule. Head extremely finely, densely punctate; eyes large, separated on frons by about the width of a single eye. Pronotum with punctation finer and more sparse than that of head; with faint posterior border in about medial third; posterior angles slightly acute. Elytron with a single engraved sutural stria, other striae lightly impressed with distinct rows of punctures extending nearly to basal margin, punctures not crescentiform; intervals punctate, punctures smaller than those of striae, relatively dense. Microsculpture absent from dorsal surface. Prosternal process with a few hairlike preapical setae. Protibial ctenidium quite long, extending nearly entire length of tibia. Mesotibial spurs distinctly projecting beyond apical ctenidium; mesotarsomere II longer than I or II. Metaventrite densely, weakly punctate. Longest metatibial spur extending to about halfway point of metatarsomere I; metatarsomere I about as long as remainder of metatarsus (Fig. 24d).

Tegmen (Fig. 24h) of aedeagus short, with long, pointed dorsal strut; fused parameres with median sulcus extending about halfway from apex; median lobe (Fig. 24i) of aedeagus spatulate, distinctly wider in apical half, with complex series of internal sac sclerites, ductus with rows of spicules and a bulblike structure proximal of entry into median lobe. Female genitalia unstudied.

Diagnosis. This species may be recognized by the characters given in the generic diagnosis.

Distribution. Known from three localities in eastern South Africa and one locality in southern Madagascar (Fig. 44c).

Etymology. From the Latin *cordis* (heart), referring to the red heart-shaped marking on the elytra. The epithet is a noun in the nominative singular, standing in apposition.

22. *Malagasmus* Gimmel, gen. nov.

(Figs. 25; 41c, d)

Type species: *Malagasmus thalesi* Gimmel, here designated.

Type material. See account of *Malagasmus thalesi* below.

Diagnosis. Sharing many characters with *Augasmus*, including the oblique metatibial apical ctenidium and extremely long metatarsomere I, but readily distinguished by characters of the meso-metaventral region, including the truncate metaventral process not exceeding the mesocoxae anteriorly, and mesoventral plate not extending posteriorly and forming procoxal rests.

Description. Medium-sized to large, total length 2.7–3.7 mm. Dorsal color solid reddish-testaceous (Figs. 41c, d). Tibial spur formula 2-2-2, tarsal formula 5-5-4, presumably in both sexes (males unknown).

Head. Not constricted behind eyes. Eyes large; facets flat; interfacetal setae absent; deeply emarginate medially; without posterior emargination; periocular groove present; with transverse setose groove ventrally behind eye. Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club loosely 3-segmented, club weakly asymmetrical; antennomere XI weakly turbinate (Fig. 25b). Mandible (Fig. 25a) with apex simple; retinaculum absent; mandible without ventral ridge. Maxillary palpomere IV fusiform, elongate, nearly symmetrical; galea short, rounded; lacinia with two stout spines. Mentum parallel-sided; labial palpomere III triangular, expanded apically. Labrum with apical margin arcuate. Gular sutures short, barely evident.

Thorax. Pronotum without obvious microsetae; with distinct scutellar lobe. Prosternum anteriorly with row of marginal setae distributed evenly, setae normal; procoxal cavity without anterolateral notchlike extension; prosternal process angulate in lateral view, not distinctly setose preapically, without spinelike setae at apex. Protrochanter without setae; protibia with ctenidium on kickface extending about three-quarters length of tibia (Fig. 25c); apex of tibia with eversible pad (not usually visible in dry-mounted specimens). Scutellar shield small, width at base shorter than length of eye. Elytron with spectral iridescence; with one sutural stria; with transverse strigae; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 25f) notched anteriorly, not extending posteriorly to metaventrite, forming procoxal rests, mesoventral disc sunken medially, with scattered setae; mesanepisternum with complete transverse carina; mesocoxal cavities separated by less than half width of single coxal cavity. Mesotarsomere III not bilobed. Metaventral process (Fig. 25f) extending to about level of anterior margin of mesocoxae, truncate apically; metaventral postcoxal lines separated from mesocoxal cavity margin, following cavity borders; discrimen short, extending less than halfway to anterior margin of metaventral process; metendosternite (Fig. 25g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange behind

anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate without transverse line; metatibial foreface with apical ctenidium markedly oblique, oriented about 45° to long axis of tibia; spurs cylindrical, longest spur longer than width of tibial apex; metatarsus as long as metatibia, metatarsomere I much longer than metatarsomere II, longer than remainder of tarsus, joint between I and II rigid (Fig. 25d); metatarsomere III not bilobed. Hind wing (Fig. 25e) with distinct, ovate anal lobe; leading edge without row of long setae; AA_{3+4} faint, crossvein to Cu absent but two veins nearly anastomosing; cubitoanal system forked; CuA_2 and MP_{3+4} with distal remnants; r4 barely indicated, incomplete; complex of flecks present in apical field distal to rp-mp2; long transverse sclerite and large nebulous triangular sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines, with calli; spiracles present and apparently functional on segment VII. Male unknown. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. The type series of *M. thalesi* was collected in a Malaise trap.

Distribution and diversity. Known only from one species, occurring in Toliara Province, Madagascar (Fig. 44a).

Included species (1):

Malagasmus thalesi Gimmel, **sp. nov.** (Distribution: Madagascar)

Discussion. The protarsus of this genus was illustrated (Fig. 25c) with a membranous vesicle protruding from the first tarsomere, readily visible in the disarticulation but difficult to observe in dry-mounted specimens. It is unknown whether this morphological feature, which may function as an adhesive organ, is more widespread in Phalacridae. This issue deserves further investigation.

Etymology. From *malago-* (Malagasy) and *-gasmus*, in allusion to its similarity to the genus *Augasmus*. The gender of the name is masculine.

Malagasmus thalesi Gimmel, sp. nov.

(Figs. 25; 41c, d)

Holotype. Female, "MADAGASCAR: Prov. \ Toliara; Ifaty, \ 23°09'S, 43°37'E \ 17–22 Sept. 1993 // Malaise trap in \ desert scrub forest; \ collrs. W.E.Steiner; \ R. Andriamasimanana // HOLOTYPE ♀ \ Malagasmus \ thalesi Gimmel \ des. M.L. Gimmel 2011 [red label]" (USNM), point mounted.

Paratypes (8 females, USNM). Same data as holotype, with "PARATYPE ♀ \ Malagasmus \ thalesi Gimmel \ det. M.L. Gimmel 2011 [yellow label]".

Description. Total length 2.7–3.7 mm; elongate, flattened posteriorly. Color rufotestaceous dorsally, apex of elytra gradually lighter in color, ventral surface and appendages similar in color, or with ventrites slightly darker; moderate diffraction grating present on scutellar shield and elytra, absent from pronotum. Antennomeres IX and X projected anterolaterally, antennomere XI elongate; antennal club nearly as long as funicle (Fig. 25b). Punctation of head and pronotum quite dense, weak, punctures of two distinct sizes; elytra with a single sutural stria in apical 4/5, other striae faintly indicated, without distinct rows of punctures, background punctation weaker than that of pronotum, with distinct transverse strigae on apical 4/5, strongest laterally and apically; microsculpture absent. Prosternum not setose medially; apex of prosternal process with short, ventrally-directed, hairlike setae. Protibial ctenidium extending about ¾ length of tibia. Mesotibia with ctenidium on kickface with spines longer than those on protibia and directed more apically; spurs about as long as apex of tibia; mesotarsomere I elongate, longer than II and III combined. Metaventrite without strong punctures; moderately setose medially; with metaventral lines strong, arcuate, enclosing an area about 1/3 length of metaventrite behind mesocoxa (Fig. 25f). Metatibia (Fig. 25d) with ctenidium similar to that of mesotibia, but with a slight outward bend about 1/3 from apex; metatarsomere I longer than remainder of tarsus; metatarsomeres I and II with rows of strong spines.

Male genitalia unknown. Spermatheca as illustrated (Fig. 25h).

Diagnosis. This species may be recognized by the characters given in the generic diagnosis.

Distribution. Known only from the type locality in Toliara Province in southwestern Madagascar (Fig. 44a).

Etymology. Named in honor of the great Greek thinker, Thales of Miletus (c. 620–546 BCE), the first known philosopher to adopt a naturalistic, non-mystical view of existence. The epithet is a noun in the genitive case.

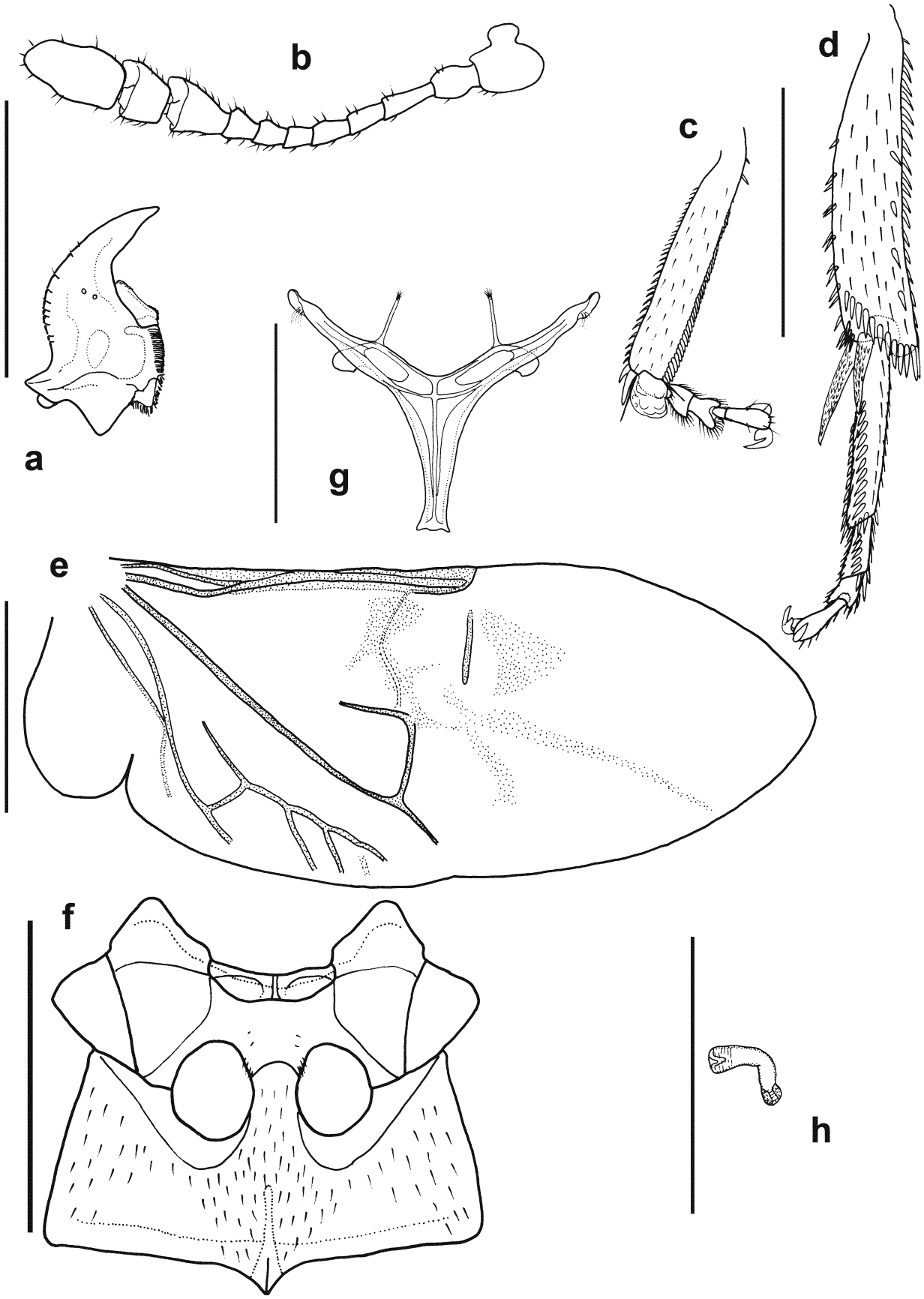

FIGURE 25. *Malagasmus thalesi*, female. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 1.0 mm). (g) Metendosternite (scale bar = 0.5 mm). (h) Spermatheca (scale bar = 0.5 mm).

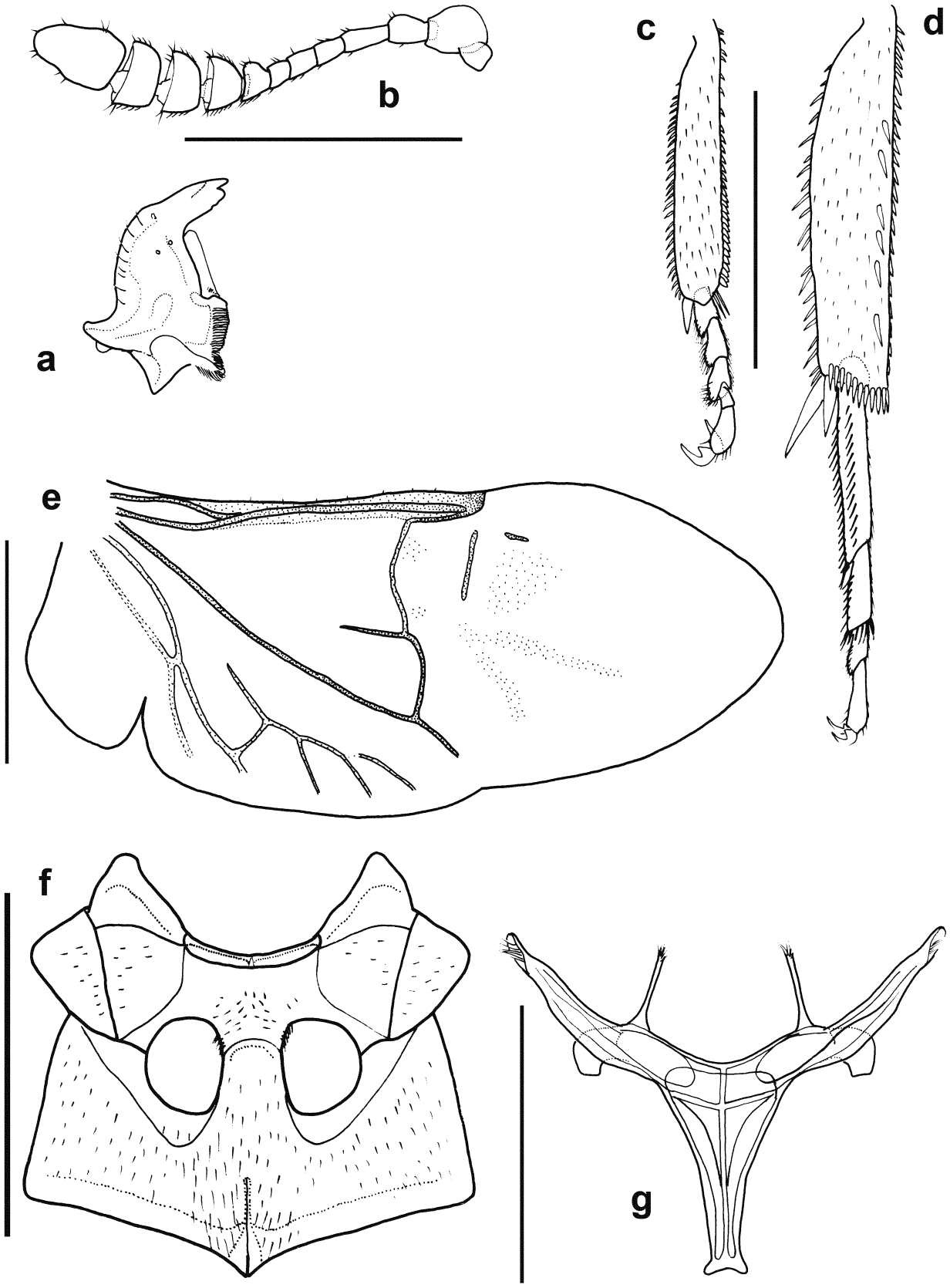

FIGURE 26. *Olibrosoma testacea*, female. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 1.0 mm). (g) Metendosternite (scale bar = 0.5 mm).

23. *Olibrosoma* Tournier, 1889

(Figs. 26; 41e)

Olibrosoma Tournier 1889: 83. Type species: *Olibrosoma testacea* Tournier 1889, fixed by monotypy.
Helectrus Guillebeau 1892*b*: 147. Type species: *Helectrus brisouti* Guillebeau 1892, fixed by original designation.
Pyracoderus Guillebeau 1892*b*: 148. Type species: *Pyracoderus lemoroi* Guillebeau 1892, fixed by original designation.
Litochroides Guillebeau 1892*b*: 148. Type species: *Litochroides sharpi* Guillebeau 1892, fixed by original designation.
Lichrotus Liubarsky 1993*a*: 17, as subgenus of *Litochrus* Erichson. Type species: *Litochrus strigosus* Reitter 1899, fixed by monotypy. **Syn. nov.**

Type material. *Olibrosoma testacea* Tournier: lectotype, male, "water soluble // Egypte // [illegible] // Olibrosoma testaceum // Peyer. vidi // TYPE // Museum Paris, \ collection genérale // Lectotypus \ OLIBROSOMA TESTACEA Tourn. 1889 \ Z. Svec des. 1999" (MNHN), genitalia dissected.

Helectrus brisouti Guillebeau: type not seen.

Pyracoderus lemoroi Guillebeau: type not seen.

Litochroides sharpi Guillebeau: type not seen.

Litochrus strigosus Reitter: type not seen.

Diagnosis. The only phalacrid (except for an undescribed species of *Pycinus* from Brazil) whose antennal club contains more than three segments. Additionally, metatarsomere I is much longer than metatarsomere II, the metaventral process reaches about the anterior level of the mesocoxae, and the scutellar shield is narrower than the width of an eye.

Description. Medium-sized to large, total length 2.0–3.5 mm. Dorsal color solid testaceous to piceous (Fig. 41e), darker specimens usually with lighter elytral apices. Tibial spur formula 2-2-2, tarsal formula 5-5-4 in both sexes.

Head. Not constricted behind eyes. Eyes large; facets convex; interfacetal setae absent; deeply emarginate medially; without posterior emargination; periocular groove present; with transverse setose groove ventrally behind eye. Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club 4-segmented, antennomere VII usually broadly triangular, so that club may appear 5-segmented, club weakly asymmetrical; antennomere XI weakly turbinate (Fig. 26b). Mandible (Fig. 26a) with apex simple or tridentate; retinaculum absent; mandible without ventral ridge. Maxillary palpomere IV fusiform, nearly symmetrical; galea short, rounded; lacinia with two stout spines. Mentum parallel-sided; labial palpomere III weakly triangular, with apex relatively broad. Labrum with apical margin truncate. Gular sutures short, barely evident.

Thorax. Pronotum without obvious microsetae; with distinct scutellar lobe. Prosternum anteriorly with row of marginal setae distributed evenly, setae normal; procoxal cavity without anterolateral notchlike extension; prosternal process angulate in lateral view, not distinctly setose preapically, without spinelike setae at apex. Protrochanter with setae; protibia with ctenidium on kickface extending two-thirds to three-quarters length of tibia (Fig. 26c). Scutellar shield small, width at base shorter than length of eye. Elytron with or without spectral iridescence; with one sutural stria; with weak transverse strigae; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 26f) notched anteriorly, not extending posteriorly to metaventrite, forming procoxal rests, mesoventral disc sunken medially, with scattered setae; mesanepisternum with complete transverse carina; mesocoxal cavities separated by slightly more than half width of single coxal cavity. Mesotarsomere III not bilobed. Metaventral process (Fig. 26f) extending to about level of anterior margin of mesocoxae, truncate apically; metaventral postcoxal lines separated slightly from mesocoxal cavity margin, following cavity borders; discrimen short, extending less than halfway to anterior margin of metaventral process; metendosternite (Fig. 26g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange behind anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate without transverse line; metatibial foreface with apical ctenidium markedly oblique, oriented about 45° to long axis of tibia; spurs cylindrical, longest spur longer than width of tibial apex; metatarsus about as long as metatibia, metatarsomere I much longer than metatarsomere II, about as long as remainder of tarsus, joint between I and II rigid (Fig. 26d); metatarsomere III not bilobed. Hind wing (Fig. 26e) with distinct, ovate anal lobe; leading edge with incomplete row of long setae; AA_{3+4} distinct, crossvein to Cu present; cubitoanal system forked apically; CuA_2 and MP_{3+4} with distal remnants; r4 present, connecting RP with RA_{3+4}; large fleck present in apical field distal to rp-mp2; long transverse sclerite, horizontal sclerite, and large nebulous triangular sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines, with calli; spiracles present and apparently functional on segment VII. Male with aedeagus upright in repose; tegmen with symmetrical anterior margin, parameres separated by suture from basal piece, parameres without medial longitudinal division; penis narrow, with pair of endophallic sclerites and fields of endophallic spicules, apex acutely pointed; spiculum gastrale with arms V-shaped, free apically, sometimes laminate basally, with short anterior extension. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. Peyerimhoff (1907) reports *O. testacea* from flowers of *Phelipaea* (=*Orobanche*, Orobanchaceae) in Sinai. Label data are meager for the specimens I have examined but a series from Botswana was taken in a Malaise trap.

Distribution and diversity. Interestingly, the type species of this genus ranges in the hottest, driest deserts of North Africa and the Middle East, from Mauritania and Mali east across the Sahara to Saudi Arabia and Iran. I have seen a few undescribed species from Subsaharan Africa, south to South Africa. I have not seen the Reitter species.

Included species (2):

Olibrosoma strigosa (Reitter, 1899), **comb. nov.** (Distribution: "Transcaspien")
Olibrosoma testacea Tournier, 1889 (Distribution: North Africa, Middle East) (type!)

Discussion. I have tentatively synonymized Liubarsky's (1993*a*) subgenus *Litochrus* (*Lichrotus*) based purely on his and Reitter's (1899) brief descriptions of the type species. The key character is a 4-segmented antennal club, which no other known Old World phalacrid possesses. The type species of *Olibrosoma* was redescribed by Švec (2010).

LITOCHROPUS-GROUP

Diagnosis. This group may be recognized by the head not constricted behind eyes, small scutellar shield, absence of a protibial ctenidium, metatarsomere I as long as or longer than metatarsomere II, and the metaventral lines separated from coxal cavities.

Distribution and diversity. Eleven species, occurring primarily in the New World, but with a few species known from the Indo-Australian region.

Included genera (2). *Litochropus* Casey, *Neolitochrus* Gimmel.

24. *Litochropus* Casey, 1890

(Figs. 27; 42c, d)

Litochropus Casey 1890: 140. Type species: *Litochropus scalptus* Casey 1890, fixed by monotypy.

Type material. *Litochropus scalptus* Casey: three syntypes, lectotype here designated to stabilize species name, male with genitalia dissected, "· N.C. [=Hot Spring, French Broad River, North Carolina] // CASEY \ bequest \ 1925 // scalptus 2 \ PARATYPE USNM \ 49013 [epithet and numbers handwritten] [red label] // LECTOTYPE ♂ \ Litochropus \ scalptus Casey \ des. M.L. Gimmel 2010 [red label]" (USNM). Paralectotypes (2 males, USNM), one with similar data to lectotype, another with locality "D.C.", each with label affixed "PARALECTOTYPE ♂ \ Litochropus \ scalptus Casey \ det. M.L. Gimmel 2010 [yellow label]".

Diagnosis. Recognized by the small scutellar shield, lack of protibial ctenidium, protruding metaventral process, metatarsomere I longer than II, mesoventral plate extending posteriorly to metaventral process, and (usually) distinct transverse strigae on elytra.

Description. Very small to medium-sized, total length 1.0–2.9 mm. Dorsal color solid brunneo-piceous to black (Figs. 42c, d), some darker forms with elytral apices lighter. Tibial spur formula 2-2-2 or 2-1-2, tarsal formula 5-5-5 in both sexes.

Head. Not constricted behind eyes. Eyes small to large; facets flat; interfacetal setae absent; weakly or (rarely) strongly emarginate medially; without posterior emargination; periocular groove absent or (rarely) present; with transverse setose groove ventrally behind eye. Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club 3-segmented, club weakly asymmetrical; antennomere XI not constricted (Fig. 27b). Mandible (Fig. 27a) with apex bidentate; retinaculum present; mandible without ventral ridge. Maxillary palpomere

IV fusiform, nearly symmetrical; galea short, rounded; lacinia with two stout spines. Mentum with sides divergent toward apex; labial palpomere III fusiform. Labrum with apical margin arcuate. Gular sutures short, barely evident.

Thorax. Pronotum with obvious microsetae present, distinct; with weakly to strongly developed scutellar lobe. Prosternum anteriorly with continuous row of marginal setae, setae normal; procoxal cavity with anterolateral notchlike extension; prosternal process rounded to angulate in lateral view, sometimes conspicuously setose preapically, without spinelike setae at apex. Protrochanter without setae; protibia without ctenidium on kickface (Fig. 27c). Scutellar shield small. Elytron without spectral iridescence; with one or (sometimes) two sutural striae; disc with rudimentary striae or rows of punctures; with weak to strong transverse strigae; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 27f) notched anteriorly, extending posteriorly to metaventrite, dividing mesoventral disc in two, usually forming procoxal rests; mesanepisternum with complete transverse carina; mesocoxal cavities widely separate, separated by more than half width of a coxal cavity. Mesotarsomere III not bilobed. Metaventral process (Fig. 27f) extending to or beyond anterior level of mesocoxae, sometimes protruding and arcuately lobed anteriorly; metaventral postcoxal lines narrowly or not at all separated from mesocoxal cavity margin, smoothly arcuate; discrimen short, extending less than halfway to anterior margin of metaventral process; metendosternite (Fig. 27g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange behind anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line; metatibial foreface with apical ctenidium roughly perpendicular overall to long axis of tibia; spurs cylindrical, longest spur shorter than or subequal in length to width of tibial apex; metatarsomere I longer than metatarsomere II, joint between I and II rigid (Fig. 27d). Hind wing (Fig. 27e) with distinct, ovate anal lobe; leading edge with complete row of long setae at level of RA+ScP; AA_{3+4} absent; cubitoanal system unbranched apically; CuA_2 and MP_{3+4} without distal remnants; r4 absent; flecks absent from apical field distal to rp-mp2; long transverse proximal sclerite and weak oblique sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines or calli; spiracles present and apparently functional on segment VII. Male with aedeagus upright in repose; tegmen with asymmetrical anterior margin and parameres hinged to basal piece, parameres with medial longitudinal division; penis with with paired sclerites and fields of endophallic spicules, apex simple; spiculum gastrale V-shaped, arms free. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Steiner (1977), in an unpublished thesis, illustrated and described the larva and pupa of *L. clavicornis*.

Bionomics. *Litochropus clavicornis* larvae, pupae, and adults have been collected and reared from *Daldinia fissa* C. G. Lloyd (Ascomycota: Xylariaceae) in Texas (Steiner 1984; Lawrence 1977, as *D. simulans* Child). *Litochropus scalptus* adults were collected from the stromata of *Daldinia concentrica* (Bolton) Cesati & de Notaris in Vermont (Lawrence 1977). Larvae feed on the corky tissue, while adults feed primarily on the spores. I have collected an undescribed species of *Litochropus* from another species of Xylariaceae (probably *Nemania*) in Tennessee.

Distribution and diversity. Most diverse in the New World, where it occurs from Quebec in the north to Bolivia in the south. I have seen specimens only from Cuba in the West Indies. This genus was revised for North America in an unpublished thesis (Steiner 1977), in which one new species is illustrated and characterized. I have seen a new species from the Great Smoky Mountains of the southern Appalachians, and a large number of species from the Neotropics are undescribed. *Litochropus* also occurs in eastern and northern Australia, New Guinea, and Borneo. The number of described Old World species is unknown (see discussion).

Included species (6):

Litochropus clavicornis Casey, 1916 (Distribution: USA) (type!)
Litochropus divergens (Lea, 1932), **comb. nov.** (*Litochrus*) (Distribution: Australia)
Litochropus globulus (Sharp, 1889), **comb. nov.** (*Litochrus*) (Distribution: Panama) (type!)
Litochropus moerens (Guillebeau, 1894), **comb. nov.** (*Merobrachys*) (Distribution: Brazil) (type!)
Litochropus reversus (Sharp, 1889), **comb. nov.** (*Litochrus*) (Distribution: Guatemala) (type!)
Litochropus scalptus Casey, 1890 (Distribution: Canada, USA) (type!)

Discussion. From the description (including the presence of two sutural striae) and illustrations (metatibia/tarsus, antenna) of Lea (1932) for his *Litochrus divergens*, I have determined that this species actually belongs to *Litochropus*. Additional species described in *Litochrus* by Arthur Lea (1932) may belong to this genus, but their generic identities will be unknown until examination of types is undertaken.

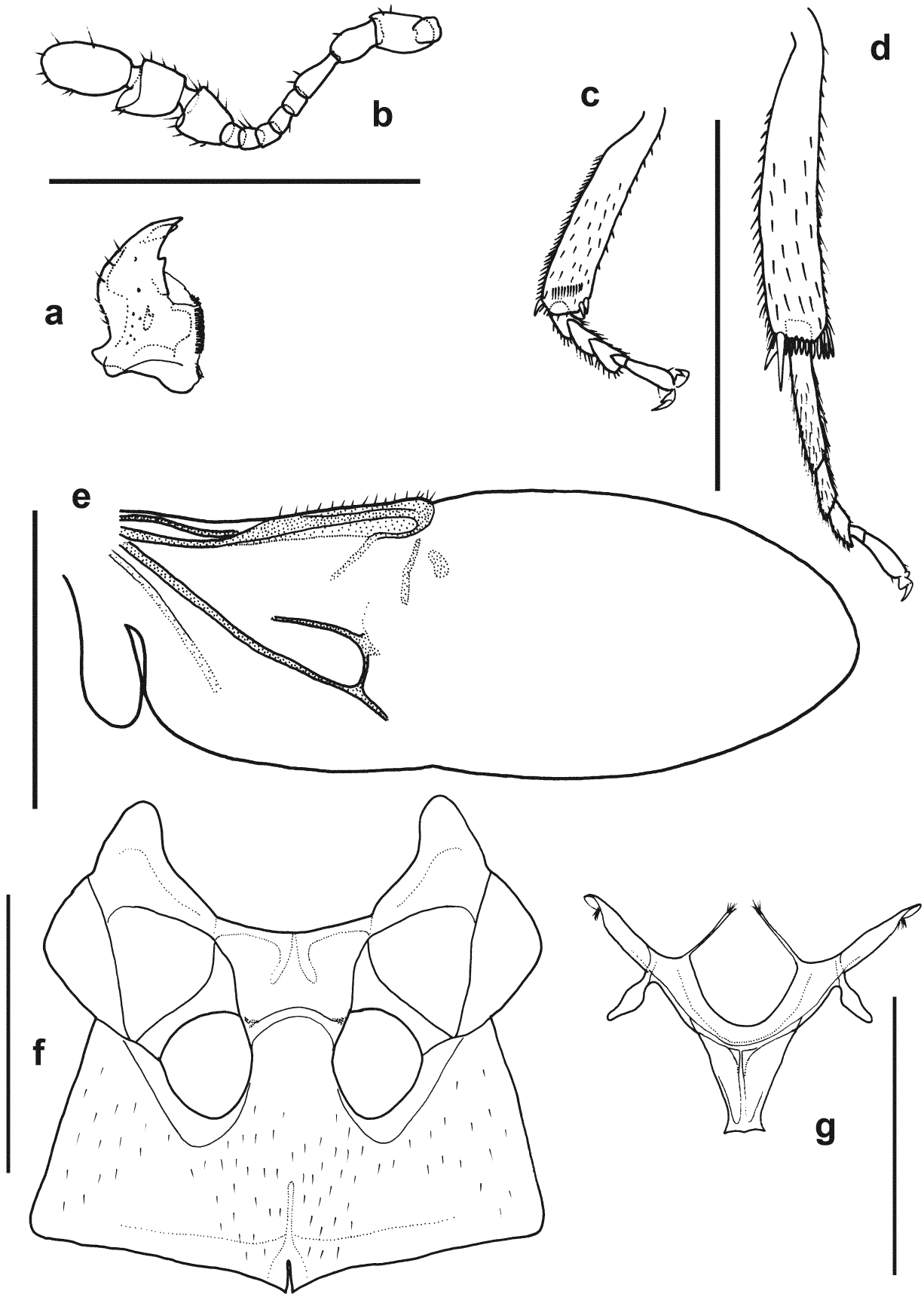

FIGURE 27. *Litochropus clavicornis*, female. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 0.5 mm).

25. *Neolitochrus* Gimmel, gen. nov.
(Figs. 28; 42h, i)

Type species: *Litochrus pulchellus* LeConte 1856, here designated.

Type material. *Litochrus pulchellus* LeConte: holotype, "[orange disc (=Southern states, Gulf states)] // Type \ 6657 [red label, number handwritten] // Litochrus \ pulchellus \ Lec. [handwritten] // HOLOTYPE \ Litochrus \ pulchellus LeConte \ det. M.L. Gimmel 2010 [red label]" (MCZ), point mounted.

Diagnosis. Recognized by the lack of a protibial ctenidium, presence of one or two elytral striae, small scutellar shield, metatarsomere I longer than II, lack of spectral iridescence on elytra, and metaventral plate not extending posteriorly to metaventral process.

Description. Very small to medium-sized, total length 0.9–2.3 mm. Dorsal color highly variable, some darker forms with yellowish or reddish maculations (Figs. 42h, i). Tibial spur formula 2-2-2 (appearing 1-1-1 in an undescribed species from Haiti), tarsal formula 5-5-4 in males, 5-5-5 in females.

Head. Not constricted behind eyes. Eyes medium-sized to large; facets convex; interfacetal setae absent; strongly emarginate medially; without posterior emargination; periocular groove absent or (rarely) present and weak; with transverse setose groove ventrally behind eye. Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club 3-segmented, club weakly asymmetrical; antennomere XI not constricted or constricted on anterior aspect only (Fig. 28b). Mandible (Fig. 28a) with apex bidentate; retinaculum absent; mandible without ventral ridge. Maxillary palpomere IV fusiform, short, nearly symmetrical; galea short, rounded; lacinia with two stout spines. Mentum with sides divergent toward apex; labial palpomere III extremely short, round, as wide as long to slightly longer than wide. Labrum with apical margin arcuate. Gular sutures short, barely evident.

Thorax. Pronotum with obvious microsetae present, distinct; with weakly to moderately developed scutellar lobe. Prosternum anteriorly with marginal row of setae discontinuous, with gap medially, setae normal; procoxal cavity with anterolateral notchlike extension; prosternal process rounded in lateral view, not conspicuously setose preapically, without spinelike setae at apex. Protrochanter without setae; protibia without ctenidium on kickface (Fig. 28c). Scutellar shield small. Elytron without spectral iridescence, though usually with microsculpture-induced iridescence; with two or (sometimes) one sutural striae; disc usually devoid of rudimentary striae or rows of punctures; sometimes with weak transverse strigae; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 28f) notched anteriorly, lateral borders becoming obscured posteriorly, incomplete, not extending to mesocoxal cavities or mesoventral process, not forming procoxal rests; mesoventral disc sunken medially, asetose; mesanepisternum with complete transverse carina; mesocoxal cavities widely separate, separated by more than half width of a coxal cavity. Mesotarsomere III bilobed. Metaventral process (Fig. 28f) extending beyond anterior level of mesocoxae, sometimes protruding and arcuately lobed anteriorly; metaventral postcoxal lines narrowly or not at all separated from mesocoxal cavity margin, smoothly arcuate; discrimen short, extending less than halfway to anterior margin of metaventral process; metendosternite (Fig. 28g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange behind anterior margin. Anterior margin of metacoxa without emargination sublaterally; metacoxal plate with transverse line; metatibial foreface with apical ctenidium roughly perpendicular overall to long axis of tibia; spurs cylindrical, longest spur distinctly longer than width of tibial apex; metatarsomere I longer than metatarsomere II, joint between I and II rigid (Fig. 28d). Hind wing (Fig. 28e) with distinct, ovate anal lobe; leading edge with complete row of long setae at level of RA+ScP; AA_{3+4} absent; cubitoanal system unbranched apically; CuA_2 and MP_{3+4} without distal remnants; r4 absent; flecks absent from apical field distal to rp-mp2; long transverse proximal sclerite and weak irregular sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines or calli; spiracles present and apparently functional on segment VII. Male with aedeagus upright in repose; tegmen (Fig. 28h) with asymmetrical anterior margin and parameres hinged to basal piece, parameres with or without medial longitudinal division; penis (Fig. 28i) with with paired sclerites and fields of endophallic spicules, apex simple or weakly bilobed; spiculum gastrale V-shaped, arms free. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. Members of this genus have been collected by beating and often come to lights at night in numbers. Their feeding habits remain poorly known, although they are probably feeders on ascomycete fungi.

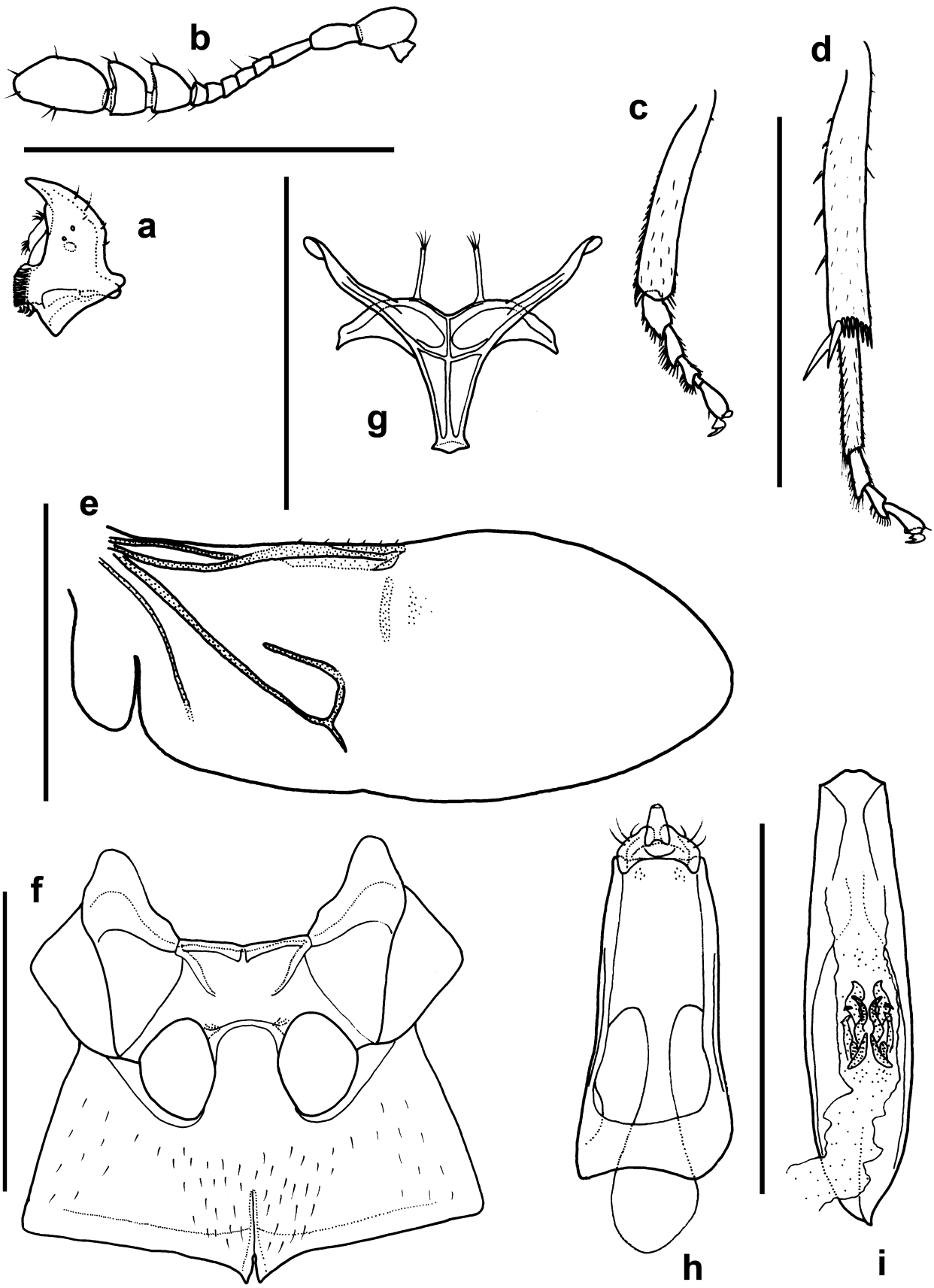

FIGURE 28. *Neolitochrus pulchellus*, male. (a) Right mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 0.5 mm). (h) Tegmen, ventral; (i) penis, ventral (scale bar = 0.5 mm).

Distribution and diversity. Occurring in the New World from at least New Jersey, Illinois, and Arizona in the north to Bolivia, Paraguay, and Brazil (Santa Catarina) in the south. I have seen specimens from the Bahamas, Cuba, and Hispaniola in the West Indies. The Neotropical region contains a large number of undescribed species. I have seen specimens from Thailand (HIC) that appear to belong to this genus.

Included species (5):

Neolitochrus aterrimus (Casey, 1890), **comb. nov.** (*Litochrus*) (Distribution: USA) (type!)
Neolitochrus crucigerus (Casey, 1890), **comb. nov.** (*Litochrus*) (Distribution: USA) (type!)
Neolitochrus immaculatus (Casey, 1890), **comb. nov.** (*Litochrus*) (Distribution: USA) (type!)
Neolitochrus mexicanus (Guillebeau, 1894), **comb. nov.** (*Heterolitus*) (Distribution: Mexico) (type!)
Neolitochrus pulchellus (LeConte, 1856), **comb. nov.** (*Litochrus*) (Distribution: USA) (type!)

Discussion. In the Neotropical Region some species (recognized dorsally by a nebulous transverse dark band across the elytra) exhibit body forms that are virtually opisthognathous. They also possess an abnormally acute metaventral process and a narrow prosternal process. Upon further study this group of species may warrant generic status. At 0.9 mm, *Neolitochrus* contains the smallest known phalacrids.

Etymology. Derived from the Greek *neos* (new) and the phalacrid genus *Litochrus*, with which this genus was formerly confused. The gender of the name is masculine.

INCERTAE SEDIS GENERA

Discussion. The genera in this assemblage were not consistently or convincingly placed within groups in the phylogenetic analyses, and are morphologically dissimilar from each other and from other groups. A few of them may truly deserve a monogeneric tribe or subfamily, but this determination awaits a future study with a denser taxon sampling and a molecular dataset.

Included genera (9). *Apallodes* Reitter, *Augasmus* Motschulsky, *Entomocnemus* Guillebeau, *Eulitrus* Gimmel, *Grouvelleus* Guillebeau, *Litochrus* Erichson, *Malagophytus* Gimmel, *Paracylomus* Gimmel, *Steinerlitrus* Gimmel.

26. *Apallodes* Reitter, 1873

(Figs. 29; 41f)

Apallodes Reitter 1873: 130. Type species: *Apallodes palpalis* Reitter 1873, fixed by monotypy.
Litolibrus Sharp 1889: 258. Type species: *Litolibrus obesus* Sharp 1889, fixed by subsequent designation. **Syn. nov.**
Sphaeropsis Guillebeau 1893*a*: 295. Type species: *Sphaeropsis simoni* Guillebeau 1893, fixed by monotypy. **Syn. nov.**
Gyromorphus Guillebeau 1894*a*: 283. Type species: *Sphaeropsis simoni* Guillebeau 1893, fixed by original designation. **Syn. nov.**

Type material. *Apallodes palpalis* Reitter: one syntype found, here designated as lectotype, female, "Parahyba \ [handwritten, illegible, green label] // Brazil [handwritten,green label] // [handwritten, illegible] // Type [handwritten] // 258 [handwritten, yellow label] // Apallodes \ palpalis m. [handwritten] // LECTOTYPE ♀ \ Apallodes \ palpalis Reitter \ des. M.L. Gimmel 2009 [red label]" (MNHN), card mounted on left side.

Litolibrus obesus Sharp: 31 syntypes seen in BMNH, card-mounted specimen with "Type" written on card by David Sharp selected as lectotype in order to stabilize the species name, "Litolibrus \ obesus \ Type \ D.S. \ V. de Chiriqui [handwritten on card] // Type [red-bordered disc] // V. de Chiriqui, 4,000–6,000 ft. Champion // Sharp Coll. \ 1905.–313. // LECTOTYPE \ Litolibrus \ obesus Sharp \ des. M.L. Gimmel 2011 [red label]" (BMNH). Paralectotypes (30, BMNH), including additional specimens from the Panama locality, plus specimens from multiple localities in Guatemala, each with label affixed "PARALECTOTYPE \ Litolibrus \ obesus Sharp \ det. M.L. Gimmel 2011 [yellow label]".

Sphaeropsis simoni Guillebeau: holotype, female, "Caracas [handwritten] // Simon [handwritten] // [handwritten, illegible] // HOLOTYPE ♀ \ Sphaeropsis \ simoni Guillebeau \ det. M. Gimmel 2009 [red label]" (MNHN), point mounted.

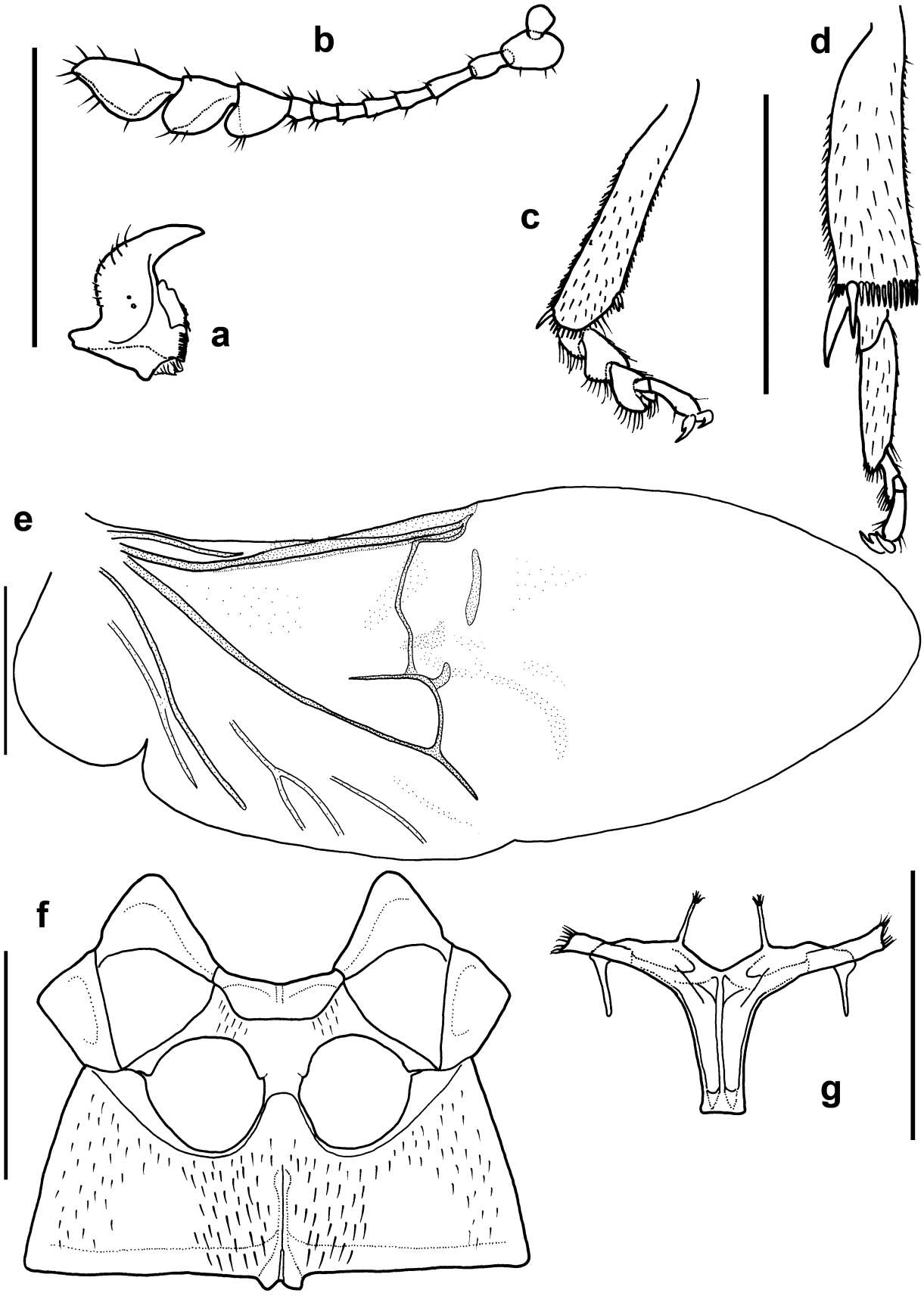

FIGURE 29. *Apallodes* sp., male. (a) Left mandible, dorsal; (b) left antenna (scale bar = 1.0 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 1.0 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 1.0 mm). (g) Metendosternite (scale bar = 1.0 mm).

Diagnosis. Members of this genus are readily recognized as such by the narrowly separated mesocoxae, the oblique articulation of metatarsomeres I and II, which are laterally compressed, the prosternal process extending posterior of the procoxae with an arcuate tip devoid of stiff setae, the strong spectral iridescence on the elytra, and the strongly asymmetrical club.

Description. Small to very large, 1.9–4.8 mm long, often highly globose. Color uniformly pale testaceous or rufous, head and pronotum often lighter in color, elytra and pronotum sometimes piceous with striking yellowish or reddish maculations; never uniformly piceous, always with at least apex of elytra pale (Fig. 41f). Tibial spur formula 2-2-2, tarsal formula 5-5-5 in both sexes.

Head. Not constricted behind eyes. Eyes large; facets flat; interfacetal setae absent; deeply emarginate medially; without posterior emargination; periocular groove present; with transverse setose groove ventrally behind eye. Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club 3-segmented, club strongly asymmetrical, antennomere XI triangular, sometimes constricted on anterior edge (Fig. 29b). Mandible (Fig. 29a) with apex simple; without retinaculum; mandible with ventral ridge. Maxillary palpomere IV fusiform, elongate, nearly symmetrical; galea (sometimes greatly) elongate, pointed apically; lacinia with two stout spines. Mentum with sides divergent toward apex; labial palpomere III fusiform. Labrum with apical margin arcuate. Gular sutures short, barely evident.

Thorax. Pronotum without obvious microsetae; with weakly developed scutellar lobe. Prosternum anteriorly with continuous row of marginal setae, setae flattened at base; procoxal cavity with anterolateral notchlike extension; prosternal process angulate in lateral view, usually conspicuously setose preapically, sometimes with ventrally-pointed spinelike setae at apex. Protrochanter without setae; protibia with or without ctenidium on kickface, from two spines (Fig. 29c) to row of about 12 spines; protarsomere II usually expanded in male. Scutellar shield small. Elytron with spectral iridescence; with one sutural stria; disc of elytra sometimes with weak rows of punctures; without transverse strigae; with subbasal band of coarse comblike ridges extending across base of scutellar shield; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 29f) notched anteriorly, not extending posteriorly to metaventrite, forming procoxal rests, mesoventral disc sunken medially, without setae; mesanepisternum with complete transverse carina; mesocoxal cavities narrowly separate, separated by much less than half width of a coxal cavity. Mesotarsomere III bilobed. Metaventral process (Fig. 29f) only extending to about halfway point of mesocoxae; metaventral postcoxal lines not separated from mesocoxal cavity margin; discrimen long, extending about halfway to anterior margin of metaventral process; metendosternite (Fig. 29g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange at anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line; metatibial foreface with apical ctenidium roughly perpendicular overall to long axis of tibia; male metatibia sometimes with oblique row of coarse setae on backface; spurs cylindrical, longest spur subequal to or longer than width of tibial apex; metatarsomere I shorter than metatarsomere II, joint between I and II rigid (Fig. 29d); metatarsomere III bilobed. Hind wing (Fig. 29e) with distinct, ovate anal lobe; leading edge without row of long setae at level of RA+ScP; AA_{3+4} present, not connected to Cu by crossvein; cubitoanal system unbranched apically; CuA_2 and MP_{3+4} with distal remnants; r4 developed, connected with RA_{3+4}; conspicuous flecks present in apical field just distal to rp-mp2, with much fainter fleck more distally; long transverse proximal sclerite and additional small triangular sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines, without calli; spiracles present and apparently functional on segment VII. Male with aedeagus upright in repose; tegmen with symmetrical anterior margin and parameres hinged to basal piece, parameres without medial longitudinal division, often with secondary projections; penis with pairs of endophallic sclerites and spicules, apex notched; spiculum gastrale Y-shaped, with arms free. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. Most specimens with method-of-capture data were collected with flight intercept traps, Malaise traps, beating, and blacklight traps. A series from Peru was collected from “smooth *Hypoxylon*” (Ascomycota: Xylariaceae).

Distribution and diversity. Restricted to the New World, this genus ranges from the southeastern United States (Louisiana, Mississippi, Oklahoma, Texas) and Sinaloa, Mexico, south through the Neotropics to at least Misiones Province, Argentina. It is also present disjunctly in southern Florida, Cuba, and the Cayman Islands, but apparently absent from the Lesser Antilles.

Included species (25):

Apallodes angularis (Champion, 1925), **comb. nov.** (*Litolibrus*) (Distribution: Brazil) (type!)
Apallodes argus (Champion, 1925), **comb. nov.** (*Litolibrus*) (Distribution: Brazil) (type!)
Apallodes bipupillatus (Champion, 1925), **comb. nov.** (*Litolibrus*) (Distribution: Brazil) (type!)
Apallodes championi Gimmel, **nom. nov.** [for *Litolibrus ocellatus* Champion, 1925, junior secondary homonym of *Apallodes ocellatus* Reitter, 1874] (Distribution: Brazil) (type!)
Apallodes cinctus (Sharp, 1889), **comb. nov.** (*Litolibrus*) (Distribution: Panama) (type!)
Apallodes erythropterus (Champion, 1925), **comb. nov.** (*Litolibrus*) (Distribution: Brazil) (type!)
Apallodes fulgens (Sharp, 1889), **comb. nov.** (*Litolibrus*) (Distribution: Guatemala) (type!)
Apallodes gibbus (Champion, 1925), **comb. nov.** (*Litolibrus*) (Distribution: Brazil) (type!)
Apallodes minor (Sharp, 1889), **comb. nov.** (*Litolibrus*) (Distribution: Guatemala) (type!)
Apallodes obesus (Sharp, 1889), **comb. nov.** (*Litolibrus*) (Distribution: Guatemala, Panama) (type!)
Apallodes obliqueguttatus (Champion, 1925), **comb. nov.** (*Litolibrus*) (Distribution: Brazil) (type!)
Apallodes obliteratus (Champion, 1925), **comb. nov.** (*Litolibrus*) (Distribution: Brazil) (type!)
Apallodes ocellatus Reitter, 1874 (Distribution: Brazil) (type!)
Apallodes octoguttatus (Champion, 1925), **comb. nov.** (*Litolibrus*) (Distribution: Brazil) (type!)
Apallodes palpalis Reitter, 1873 (Distribution: Brazil) (type!)
Apallodes pantherinus (Champion, 1925), **comb. nov.** (*Litolibrus*) (Distribution: Brazil) (type!)
Apallodes posticatus (Sharp, 1889), **comb. nov.** (*Litolibrus*) (Distribution: Guatemala, Panama) (type!)
Apallodes princeps (Schwarz, 1878), **comb. nov.** (*Litolibrus*) (Distribution: Cuba, USA) (type!)
Apallodes quadratus (Sharp, 1889), **comb. nov.** (*Litolibrus*) (Distribution: Guatemala) (type!)
Apallodes rufipennis (Sharp, 1889), **comb. nov.** (*Litolibrus*) (Distribution: Panama) (type!)
Apallodes sericeus (Kirsch, 1873), **comb. nov.** (*Phalacrus*) (Distribution: Peru) (type!)
Apallodes signatus (Sharp, 1889), **comb. nov.** (*Litolibrus*) (Distribution: Panama) (type!)
Apallodes simoni (Guillebeau, 1893), **comb. nov.** (*Sphaeropsis*) (Distribution: Venezuela) (type!)
Apallodes uniformis (Casey, 1890), **comb. nov.** (*Litolibrus*) (Distribution: USA) (type!)
Apallodes varians (Sharp, 1889), **comb. nov.** (*Litolibrus*) (Distribution: Guatemala, Panama) (type!)

Discussion. Reitter (1873: 132) mentioned two localities ("Parahyba" and "Columbia") in his original description of *Apallodes palpalis*, implying that there are at least two syntype specimens. Only one specimen from either of these localities (Parahyba) was located in MNHN, and this is designated the lectotype to stabilize future application of this name.

Sharp (1889) apparently knew nothing of Reitter's *Apallodes* (probably because the latter was originally described in Nitidulidae) when erecting the genus *Litolibrus*. The two genera are clearly synonyms, and this results in 20 new combinations and one new name (see list above). Guillebeau's *Sphaeropsis* (=*Gyromorphus* Guillebeau, see below) is also clearly within the limits of the genus *Apallodes* as defined above, and I propose that they become new generic synonyms. This results in one new combination.

Guillebeau (1894*a*: 283) designated as the genotype of his new genus *Gyromorphus* one "*Ochrolitus Simoni* Guillebeau (Ann. Soc. ent. Fr.)" indicating it had already been described. This is apparently a two-part error—he actually had previously described the species under *Sphaeropsis* with the comment "Ce genre est bien voisin du genre *Ochrolitus* Sharp [This genus is quite close to the genus *Ochrolitus* Sharp]", while the name *Gyromorphus* is an error for *Sphaeropsis* Guillebeau, and must have been a remnant of an alternate draft of his work. I consider *Sphaeropsis* and *Gyromorphus* to be objective synonyms.

The type (deposited in MTD) of *Phalacrus sericeus* Kirsch, 1873, clearly belongs in this genus.

At 4.8 mm, this genus includes the largest phalacrids in the New World. Some strongly resemble nitidulids of the genus *Pallodes* on superficial examination. Other species are strikingly patterned with ocellate spots, transverse maculations, or cordate markings and are arguably the most visually appealing members of the family.

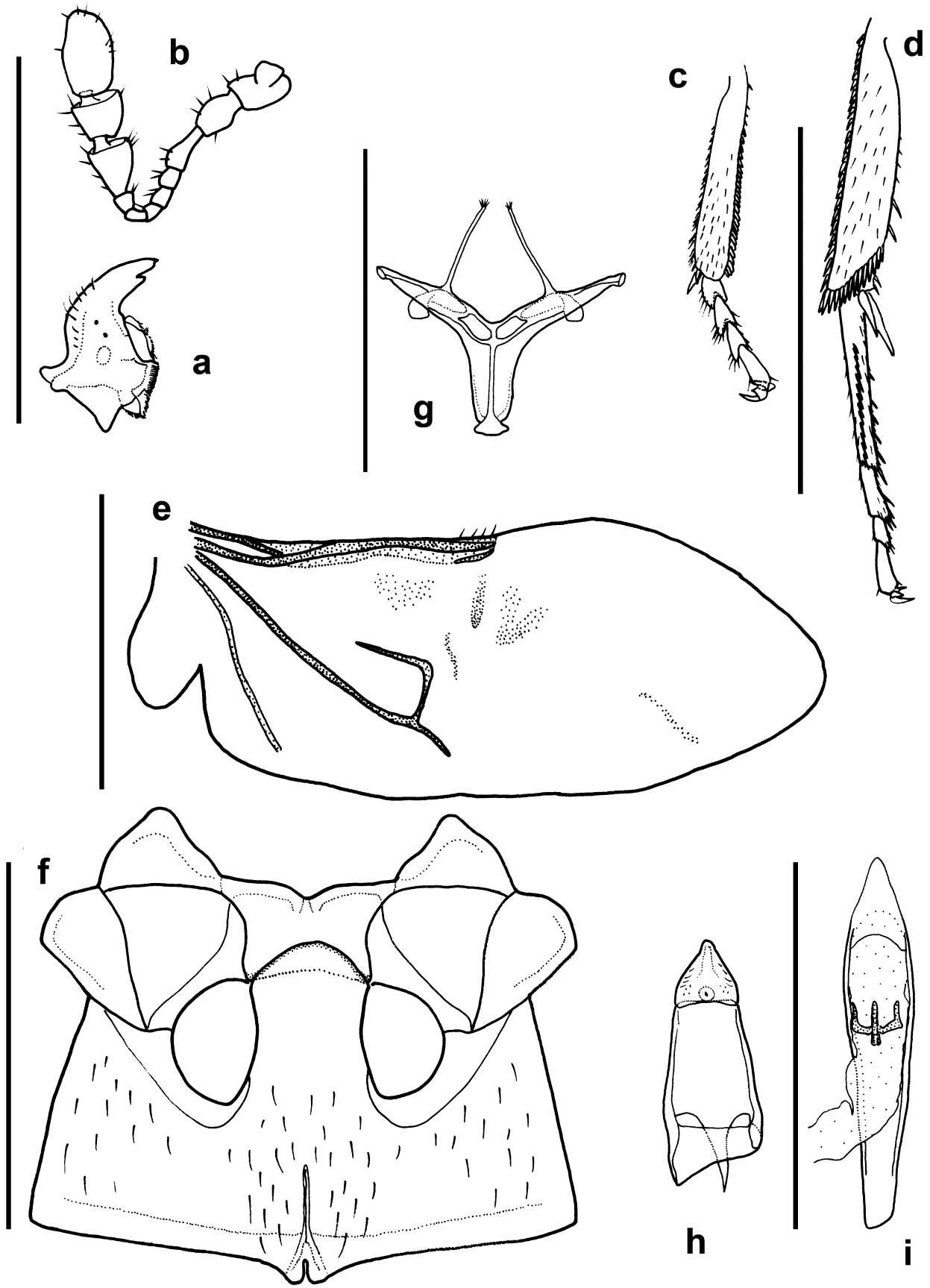

FIGURE 30. *Augasmus humilis*, male. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) right metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 0.5 mm). (h) Tegmen, ventral; (i) penis, ventral (scale bar = 0.5 mm).

27. *Augasmus* Motschulsky, 1858

(Figs. 30; 41g, h)

Augasmus Motschulsky 1858: 35. Type species: *Augasmus ligatus* Motschulsky 1858, fixed by subsequent designation.

Liocrus Flach 1889*b*: 271, as subgenus of *Litocrus*[*sic*] Erichson. Type species: *Litocrus coronatus* Flach 1889, fixed by monotypy.

Heterolitus Guillebeau 1893*c*: 375. Type species: *Heterolitus humilis* Guillebeau 1893, fixed by subsequent designation (Guillebeau 1894*a*: 280). [synonymized with *Augasmus* Motschulsky by Lyubarsky (1993*c*: 35)]

Parischius Guillebeau 1896: 297. Type species: *Parischius alluaudi* Guillebeau 1896, fixed by subsequent designation (Švec *in* Löbl and Smetana 2007: 64).

Megischius Guillebeau 1896: 298. Type species: *Megischius limbicollis* Guillebeau 1896, fixed by monotypy. **Syn. nov.**

Nematolibrus Sahlberg 1913: 21. Type species: *Nematolibrus filitarsis* Sahlberg 1913, fixed by monotypy. **Syn. nov.**

Type material. *Augasmus ligatus* Motschulsky: holotype, "Augasma \ ligata \ Motsh. \ Ind. or. [handwritten on yellow label] // Augasmus \ ligatus Motsch. \ Lectotype design. \ Lyubarsky // HOLOTYPE \ Augasmus \ ligatus Motschulsky \ det. M.L. Gimmel 2010 [red label]" (ZMUM), card-mounted with genitalia vial. Lyubarsky's lectotype designation was not published, but is unnecessary in any case.

Liocrus coronatus Flach: type not seen.

Heterolitus humilis Guillebeau: three syntypes, first with the labels "TONKIN (F.de B.) // Heterolitus humilis Grouv."; second with the label "Mt"; third with the labels "Hué // Litochrus humilis Grou \ ty. // Heterolitus humilis Grouv." (MNHN), all card mounted.

Parischius alluaudi Guillebeau: two syntypes, with the labels "Madagascar \ Diego Suarez \ Ch. Alluaud 1893 // Museum Paris \ Coll. Générale // SYNTYPE // Augasmus alluaudi (Guill.) \ Zd. Svec det. 1998" and "Madag. // Alluaud" (MNHN), card mounted.

Megischius limbicollis Guillebeau: type not located, but probably in MNHN.

Nematolibrus filitarsis Sahlberg: two syntypes, one here designated as lectotype with the labels "Tarsus // J.Sahlb. // Spec. typ. // 4417 // Mus. Zool. H:fors \ Spec. typ. No 1002 \ Nematolibrus \ filitarsis J.S. // Nematolibrus filitarsis n.sp. [handwritten] // SYNTYPE [red label] // Nematolibrus filitarsis J.Sahlb. [red label] // LECTOTYPE ♀ \ Nematolibrus \ filitarsis J.Sahlberg \ des. M.L. Gimmel 2010 [red label]" (MZH), point mounted. Paralectotype with the same data, female, with label affixed "PARALECTOTYPE ♀ \ Nematolibrus \ filitarsis J.Sahlberg \ det. M.L. Gimmel 2010 [yellow label]", card mounted. The lectotype is designated to enforce stability of its associated name.

Diagnosis. May be recognized by the long protibial ctenidium, anteriorly protruded metaventral process, oblique apical ctenidium on the metatibia, and extremely long metatarsomere I.

Description. Small to medium-sized, total length 1.5–2.6 mm. Dorsal color highly variable, often wholly testaceous but often with black patterns (Figs. 41g, h). Tibial spur formula 2-2-2, tarsal formula 4-5-4 or 5-5-4, sexes not differing in formula.

Head. Not constricted behind eyes. Eyes small to medium-sized to large; facets flat; interfacetal setae absent; weakly to deeply emarginate medially; without posterior emargination; periocular groove present or absent; with transverse setose groove ventrally behind eye. Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club loosely 3-segmented, club weakly asymmetrical; antennomere XI not constricted (Fig. 30b), widened subapically in certain African forms. Mandible (Fig. 30a) with apex bidentate; retinaculum absent; mandible without ventral ridge. Maxillary palpomere IV short, stout, nearly symmetrical; galea short, rounded; lacinia with two stout spines. Mentum with sides divergent toward apex; labial palpomere III expanded at midlength, pointed apically. Labrum with apical margin arcuate. Gular sutures long, extending over halfway to ventral mouthparts.

Thorax. Pronotum without obvious microsetae; with distinct scutellar lobe. Prosternum anteriorly with row of marginal setae discontinuous, with gap medially, setae flattened at base; procoxal cavity without anterolateral notchlike extension; prosternal process rounded in lateral view, not setose preapically, without spinelike setae at apex. Protrochanter without setae; protibia with ctenidium on kickface extending from about half to three-quarters length of tibia (Fig. 30c). Scutellar shield small, width at base shorter than length of eye. Elytron with spectral iridescence; with one sutural stria; with absent to strong transverse strigae; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 30f) deeply notched anteriorly, extending posteriorly to metaventrite (dividing mesoventral disc medially), not forming procoxal rests; mesanepisternum with complete transverse carina; mesocoxal cavities

separated by more than half width of single coxal cavity. Mesotarsomere III not bilobed. Metaventral process (Fig. 30f) exceeding level of anterior margin of mesocoxae, rounded apically; metaventral postcoxal lines separated slightly from mesocoxal cavity margin, following cavity borders; discrimen short, extending less than halfway to anterior margin of metaventral process; metendosternite (Fig. 30g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange behind anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate without transverse line; metatibial foreface with apical ctenidium markedly oblique, oriented about 45° to long axis of tibia (Fig. 30d); spurs cylindrical, longest spur longer than width of tibial apex; metatarsus as long as or longer than metatibia, metatarsomere I much longer than metatarsomere II, usually much longer than remainder of tarsus, joint between I and II rigid (Fig. 30d); metatarsomere III not bilobed. Hind wing (Fig. 30e) with distinct, ovate anal lobe; leading edge with incomplete row of long setae; AA_{3+4} absent; cubitoanal system unbranched apically; CuA_2 and MP_{3+4} without distal remnants; r4 absent; no flecks present in apical field distal to rp-mp2, or with faint fleck near posteroapical border; long transverse sclerite and large nebulous triangular sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines, with calli; spiracles present and apparently functional on segment VII. Male with aedeagus upright in repose; tegmen (Fig. 30h) with asymmetrical anterior margin, parameres separated by suture from basal piece, parameres without medial longitudinal division; penis (Fig. 30i) narrow, devoid of endophallic sclerites or prominent fields of endophallic spicules, apex acutely pointed; spiculum gastrale with arms V-shaped, free, with short, curved, anterior extension. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. Blacklight and Malaise trap are the most common methods by which members of this genus have been taken, but a few were collected by "beating hanging branch". A series from Java (ANIC) was collected from the flowers and leaves of *Castanopsis argentea* (Blume) A.DC. (Fagaceae) at the rainforest edge (1350 m elevation).

Distribution and diversity. A large and diverse group, this genus ranges throughout the tropical and some subtropical regions of the Old World, including islands in the Indian Ocean and near-continental islands.

Included species (36):

Augasmus borneensis Lyubarsky, 1994 (Distribution: Borneo)
Augasmus coloratus (Blackburn, 1895), **comb. nov.** (*Litochrus*) (Distribution: Australia) (type!)
Augasmus comptulus Lyubarsky, 2003 (Distribution: Nepal)
Augasmus concolor Lyubarsky, 1994 (Distribution: Indonesia, Philippines, Thailand)
Augasmus coronatus (Flach, 1889) (Distribution: Japan, Taiwan)
Augasmus distriatus Lyubarsky, 1994 (Distribution: Borneo)
Augasmus exquisitus Gimmel, **nom. nov.** [for *Litochrus pulchellus* Blackburn, 1895, junior primary homonym of *Litochrus pulchellus* LeConte, 1856] (Distribution: Australia) (type!)
Augasmus filitarsis (Sahlberg, 1913), **comb. nov.** (*Nematolibrus*) (Distribution: Turkey) (type!)
Augasmus gilbus Lyubarsky, 2003 (Distribution: Nepal, Vietnam)
Augasmus grouvellei (Guillebeau, 1894), **comb. nov.** (*Heterolitus*) (Distribution: Indonesia) (type!)
Augasmus humilis (Guillebeau, 1893) (Distribution: China, Taiwan, Vietnam)
Augasmus intactus (Lea, 1932), **comb. nov.** (*Litochrus*) (Distribution: Papua New Guinea)
Augasmus ligatus Motschulsky, 1858 (Distribution: Oriental Region) (type!)
Augasmus limbicollis (Guillebeau, 1896), **comb. nov.** (*Megischius*) (Distribution: Madagascar)
Augasmus longitarsis (Lea, 1932), **comb. nov.** (*Litochrus*) (Distribution: Papua New Guinea)
Augasmus luridus Lyubarsky, 2003 (Distribution: Nepal)
Augasmus nigromaculatus (Hisamatsu, 1985) (Distribution: Japan, Taiwan)
Augasmus nipponicus (Hisamatsu, 1985) (Distribution: Japan)
Augasmus noteroides (Blackburn, 1895), **comb. nov.** (*Litochrus*) (Distribution: Australia) (type!)
Augasmus obliquenotatus (Champion, 1925), **comb. nov.** (*Heterolitus*) (Distribution: South Africa) (type!)
Augasmus palleolus (Guillebeau, 1894), **comb. nov.** (*Heterolitus*) (Distribution: Indonesia) (type!)
Augasmus perparvulus (Guillebeau, 1896), **comb. nov.** (*Heterolitus*) (Distribution: Madagascar) (type!)
Augasmus perpolitus Lyubarsky, 2003 (Distribution: Nepal)
Augasmus picinus (Guillebeau, 1894), **comb. nov.** (*Heterolitus*) (Distribution: Tanzania) (type!)
Augasmus platycnemus (Champion, 1925) (Distribution: Namibia, South Africa, Zambia) (type!)
Augasmus pseudosinuatus Lyubarsky, 1994 (Distribution: Philippines)

Augasmus senegalensis (Guillebeau, 1894), **comb. nov.** (*Heterolitus*) (Distribution: Senegal) (type!)
Augasmus shirozui (Hisamatsu, 1959) (Distribution: Japan, Russia)
Augasmus strigellus (Guillebeau, 1894) (Distribution: Celebes) (type!)
Augasmus strigosus (Reitter, 1899), **comb. nov.** (*Litochrus*) (Distribution: "Transcaspien")
Augasmus subflavus Lyubarsky, 2003 (Distribution: Nepal)
Augasmus substrigosus (Champion, 1925) (Distribution: southern Africa) (type!)
Augasmus suturalis (Guillebeau, 1894), **comb. nov.** (*Heterolitus*) (Distribution: Indonesia) (type!)
Augasmus testaceus Motschulsky, 1858 (Distribution: India, Sri Lanka)
Augasmus thoracicus (Fleutiaux, 1887) (Distribution: Australia through southern Asia to Africa) (type!)
Augasmus v-niger (Lea, 1932), **comb. nov.** (*Heterolitus*) (Distribution: Papua New Guinea)

Discussion. Although a highly distinctive genus, *Augasmus* has a complex and composite taxonomic history, largely stemming from the poor original description of Motschulsky (1858) and historical inaccessibility of his types. The genus was subsequently described once by Flach (as a subgenus of *Litochrus*), once by Sahlberg, and at least two times by Guillebeau.

Although Lyubarsky (1993*c*: 35) rightly synonymized *Heterolitus* with *Augasmus*, he did not make the new combinations explicit. I have listed all of these above. The type of *Nematolibrus filitarsis* Sahlberg conforms well to the definition of *Augasmus* outlined above. I am proposing synonymy of these two genera. After examining the Blackburn types of *Litochrus coloratus*, *L. noteroides*, and *L. pulchellus*, I have concluded that all three fall within the concept of this genus. The new combinations are made explicit above (and *L. pulchellus*, a junior primary homonym, is given a replacement name).

Although I have not examined the types of Arthur Lea, a few of his *Litochrus* species whose hind legs are illustrated in the same work obviously belong here, based on their obliquely oriented apical ctenidia and extremely long apical spurs. The species are *L. longitarsis* Lea (1932: fig. 10), *L. intactus* Lea (1932: fig. 18), and *L. v-niger* Lea (1932: fig. 24). The new combinations are made explicit above.

Unfortunately I could not locate the types of *Megischius limbicollis* Guillebeau in MNHN. Based on Guillebeau's (1896) description, *Megischius* appears to be congeneric with *Augasmus*. He states that the genus is similar to *Parischius* Guillebeau (the type species of which clearly belongs in *Augasmus*) except that the first article of the posterior tarsi is only twice as long as the second and shorter than the following joined together. The size is small (1.5 mm) and the metaventral process presumably surpasses the mesocoxae (these two characters preclude it from being congeneric with *Malagasmus* Gimmel). There are no other phalacrids of which I have seen specimens or records from Madagascar that could fit this description other than species of *Augasmus*, and I am tentatively proposing synonymy of these two genera with the hope that the type of *M. limbicollis* will be located in the future.

28. *Entomocnemus* Guillebeau, 1894

(Figs. 31; 41i)

Entomocnemus Guillebeau 1894*a*: 307, as subgenus of *Eustilbus* Sharp. Type species: *Eustilbus (Entomocnemus) raffrayi* Guillebeau 1894, fixed by monotypy. [elevated to generic rank by Švec 2003: 125]
Stilbomimus Champion 1924*c*: 242. Type species: *Stilbomimus polymorphus* Champion 1924, fixed by original designation. **Syn. nov.**

Type material. *Eustilbus raffrayi* Guillebeau: holotype, card mounted, "Abyss. Raffray // Grouvelle // Museum Paris \ Coll. \ Générale // HOLOTYPE // Raffrayi Guilb." (MNHN).

Stilbomimus polymorphus Champion: seven syntypes found in BMNH, card-mounted specimen labeled "Type" by George Champion selected as a lectotype to stabilize the species name, "Ceylon \ G. E. Bryant. // Kandy. VI.1908 [handwritten] // G. Bryant Coll. \ 1919–147 [on underside of label] // Type \ H.T. [red-bordered disc] // Stilbomimus polymorphus type Ch. [handwritten] // Stilbomimus polymorphus, Champ. // E.M.M. 1924 \ det. G.C.C. [on underside of label] // LECTOTYPE \ Stilbomimus \ polymorphus Champion \ des. M.L. Gimmel 2011 [red label]" (BMNH). Paralectotypes (6, BMNH), from type locality in Sri Lanka and Nilgiri Hills, India, each with label affixed "PARALECTOTYPE \ Stilbomimus \ polymorphus Champion \ det. M.L. Gimmel 2011 [yellow label]". Champion's "varieties" were excluded from the syntype series.

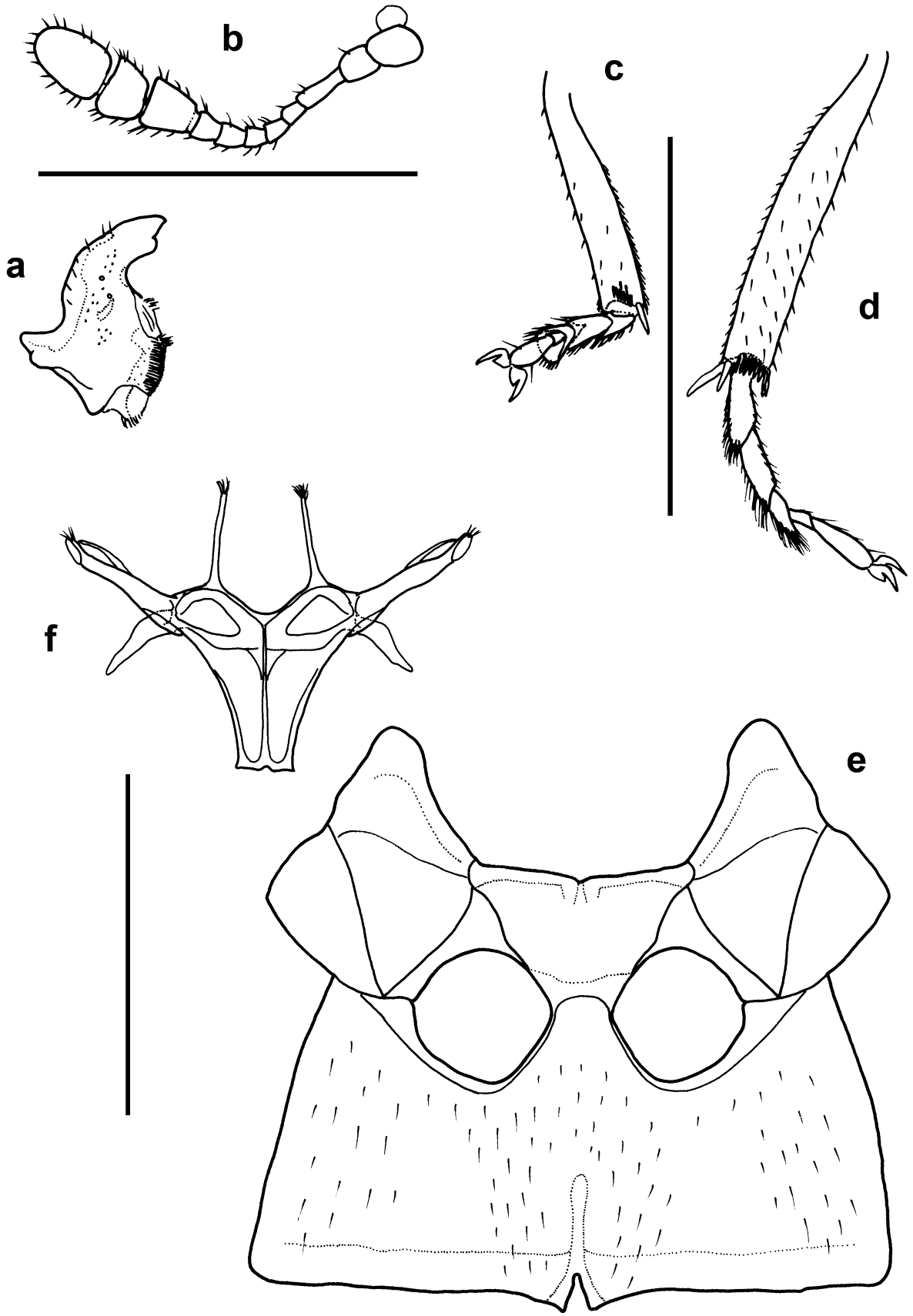

FIGURE 31. *Entomocnemus* sp., female. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Right protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Meso- and metaventrite, ventral; (f) metendosternite (scale bar = 0.5 mm).

Diagnosis. A difficult genus to recognize, but possessing the following diagnostic characteristics: meso-metaventral margin usually emarginate (but sometimes truncate) for reception of prosternal process (which may have apical translucent process), elytra with spectral iridescence, metaventral postcoxal lines not separated from coxal cavities, metatarsomeres I and II about equal, scutellar shield small, elytral striae (when present) more or less parallel to suture.

Description. Small to large, total length 1.6–3.5 mm. Dorsal color ranging from solid testaceous to solid black, some darker forms with red or yellow elytral maculations of various shapes and extent (Fig. 41i). Tibial spur formula 2-2-2 or 2-1-2, tarsal formula 5-5-5 in both sexes.

Head. Not constricted behind eyes. Eyes small to medium-sized; facets flat; interfacetal setae absent; weakly emarginate medially; without posterior emargination; periocular groove present or absent; with transverse setose groove ventrally behind eye. Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club 3-segmented, club weakly asymmetrical; antennomere XI not constricted (Fig. 31b). Mandible (Fig. 31a) with apex bidentate; retinaculum absent; mandible without ventral ridge. Maxillary palpomere IV short, fusiform, inner edge slightly swollen medially; galea short, rounded; lacinia with multiple spines. Mentum with sides divergent toward apex; labial palpomere III fusiform. Labrum with apical margin arcuate. Gular sutures short, barely evident.

Thorax. Pronotum without obvious microsetae; with weakly developed scutellar lobe. Prosternum anteriorly with continuous row of marginal setae, setae normal; procoxal cavity with anterolateral notchlike extension; prosternal process rounded to angulate in lateral view, not conspicuously setose preapically, without spinelike setae at apex, often with horizontal translucent process at apex. Protrochanter with setae; protibia usually without ctenidium on kickface (Fig. 31c), sometimes with short ctenidium extending about 1/5 length of tibia. Scutellar shield small. Elytron with spectral iridescence; with one or (occasionally) multiple striae, striae punctate; without transverse strigae; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 31e) deeply notched anteriorly, extending posteriorly to metaventrite, dividing mesoventral disc in two, forming procoxal rests; mesanepisternum with complete transverse carina; mesocoxal cavities moderately separate, separated by less than half width of a coxal cavity. Mesotarsomere III not bilobed. Metaventral process (Fig. 31e) extending beyond halfway point of mesocoxae, mesoventral lip on anterior edge usually emarginate, sometimes truncate; metaventral postcoxal lines not at all separated from mesocoxal cavity margin; discrimen short, extending less than halfway to anterior margin of metaventral process; metendosternite (Fig. 31f) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange behind anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate without transverse line; metatibial foreface with apical ctenidium roughly perpendicular overall to long axis of tibia; spurs cylindrical, longest spur subequal to or longer than width of tibial apex; metatarsomere I about equal to metatarsomere II, joint between I and II flexible (Fig. 31d). Hind wing with distinct, ovate anal lobe; leading edge with complete row of long setae at level of RA+ScP; AA_{3+4} absent; cubitoanal system unbranched apically; CuA_2 and MP_{3+4} without distal remnants; r4 absent; flecks present in apical field distal to rp-mp2; long transverse proximal sclerite and strong irregular sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines or calli; spiracles present and apparently functional on segment VII. Male with aedeagus upright in repose; tegmen with symmetrical anterior margin and parameres hinged to basal piece, parameres with medial longitudinal division; penis with with paired sclerites and fields of endophallic spicules, sometimes with long flagellum, apex trilobed; spiculum gastrale V-shaped, arms free. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. A series from Borneo was taken by beating the foliage of a downed *Cinnamomum* (Lauraceae) tree. Most other specimens from both southeast Asia and southern Africa with collection data have been taken by beating. A few have also been collected from Malaise traps.

Distribution and diversity. This genus occurs in two disjunct areas: subsaharan Africa and the Oriental region. There appear to be many undescribed species in southern Africa, but the actual number of species in southeast Asia, whose colorful species seem to be highly variable in appearance, is unknown at present.

Included species (8):

Entomocnemus borneensis (Champion, 1924), **comb. nov.** (*Stilbomimus*) (Distribution: Malaysia) (type!)
Entomocnemus diluticollis (Champion, 1924), **comb. nov.** (*Stilbomimus*) (Distribution: India) (type!)
Entomocnemus nyasanus (Champion, 1925) (Distribution: Malawi) (type!)
Entomocnemus polymorphus (Champion, 1924), **comb. nov.** (*Stilbomimus*) (Distribution: India, Indonesia, Sri Lanka) (type!)
Entomocnemus raffrayi (Guillebeau, 1894) (Distribution: Ethiopia) (type!)
Entomocnemus rhodesianus (Champion, 1925) (Distribution: Malawi, Zambia) (type!)
Entomocnemus triguttatus (Champion, 1925), **comb. nov.** (*Heterolitus*) (Distribution: South Africa) (type!)
Entomocnemus v-flavum (Champion, 1924) (Distribution: India) (type!)

Discussion. One of the most composite genera of those treated in this monograph, *Entomocnemus* as presently defined will likely require fracturing upon further study. The description given above is expanded to include a number of apparently undescribed species from both southern Africa and southeast Asia. Species I have examined tend to be represented by very few individuals, and this situation has made in-depth examination especially problematic. However, I believe Švec (2003) was correct in transferring the African species described in *Stilbomimus* to *Entomocnemus*. After examining types of all described species in question, I have concluded that the southeast Asian species (including the type species of *Stilbomimus*) are also congeneric. The species placed in *Entomocnemus* (and *Stilbomimus* prior to this study) form a relatively well-defined group with slender tibiae and no protibial ctenidium, but are variable with regard to the development of the mesoventral emargination.

29. *Eulitrus* Sharp, 1889
(Figs. 32; 43f)

Eulitrus Sharp 1889: 257. Type species: *Eulitrus estriatus* Sharp, 1889, fixed by subsequent designation.

Type material. *Eulitrus estriatus* Sharp: lectotype, here designated in order to fix the species name and type locality, “Eulitrus \ estriatus \ Type D.S. \ Panama \ Champion [handwritten on specimen card] // Type [red-bordered disc] // Panama. \ Champion. // Sharp Coll. \ 1905.—313. // SYN- \ TYPE [blue-bordered disc] // LECTOTYPE \ Eulitrus \ estriatus Sharp \ des. M.L. Gimmel 2010 [red label]” (BMNH), card mounted. Paralectotypes (3): “Eulitrus \ estriatus \ D.S. \ Chontales Janson [handwritten on specimen card] // ESL \ 19 // See slide Coll. \ No. 3 ESL 62, 63 [numbers handwritten] // Slide No. 380 381 \ E. Lewis 1988 [numbers handwritten] / / Chontales, \ Nicaragua. \ Janson. // Sharp Coll. \ 1905,–313. // SYN- \ TYPE [blue-bordered disc]”; “Eulitrus \ estriatus. D.S. \ Bugaba. [handwritten on specimen card] // ♀ // Bugaba, \ Panama. \ Champion. // B.C.A., Col., II, (1). // SYN- \ TYPE [blue-bordered disc]”; “Eulitrus \ estriatus \ D.S. \ Bugaba \ Champion [handwritten on specimen card] // Sp. figured. // Bugaba. \ Panama. \ Champion. // B.C.A., Col., II, (1). // ESL \ 20 // SYN- \ TYPE [blue-bordered disc]” (all BMNH), card mounted, with label attached “PARALECTOTYPE \ Eulitrus \ estriatus Sharp \ det. M.L. Gimmel 2010 [yellow label]”.

Diagnosis. The genus *Eulitrus* is readily recognizable and morphologically well delimited from other members of Phalacridae. The following characters diagnose members of the genus: protibia with ctenidium on kickface extending from one-half to two-thirds length of tibia, metaventral process greatly protruding anteriorly, surpassing mesocoxae and resting upon rounded prosternal process when beetle is in repose, metaventral lines narrowly separated from mesocoxal cavities, metatarsomere II about three to six times length of metatarsomere I, sutural stria of elytron completely absent, strong spectral iridescence present on elytra, median lobe of male genitalia spearhead-shaped with an acuminate tip, and spiculum gastrale heavily sclerotized, forming a delta-shaped plate.

Description. Very small to large, total length 1.2–4.0 mm. Dorsal color brunneous to black (Fig. 43f), often with reddish maculations. Tibial spur formula 2-2-2, tarsal formula 5-5-5 in both sexes.

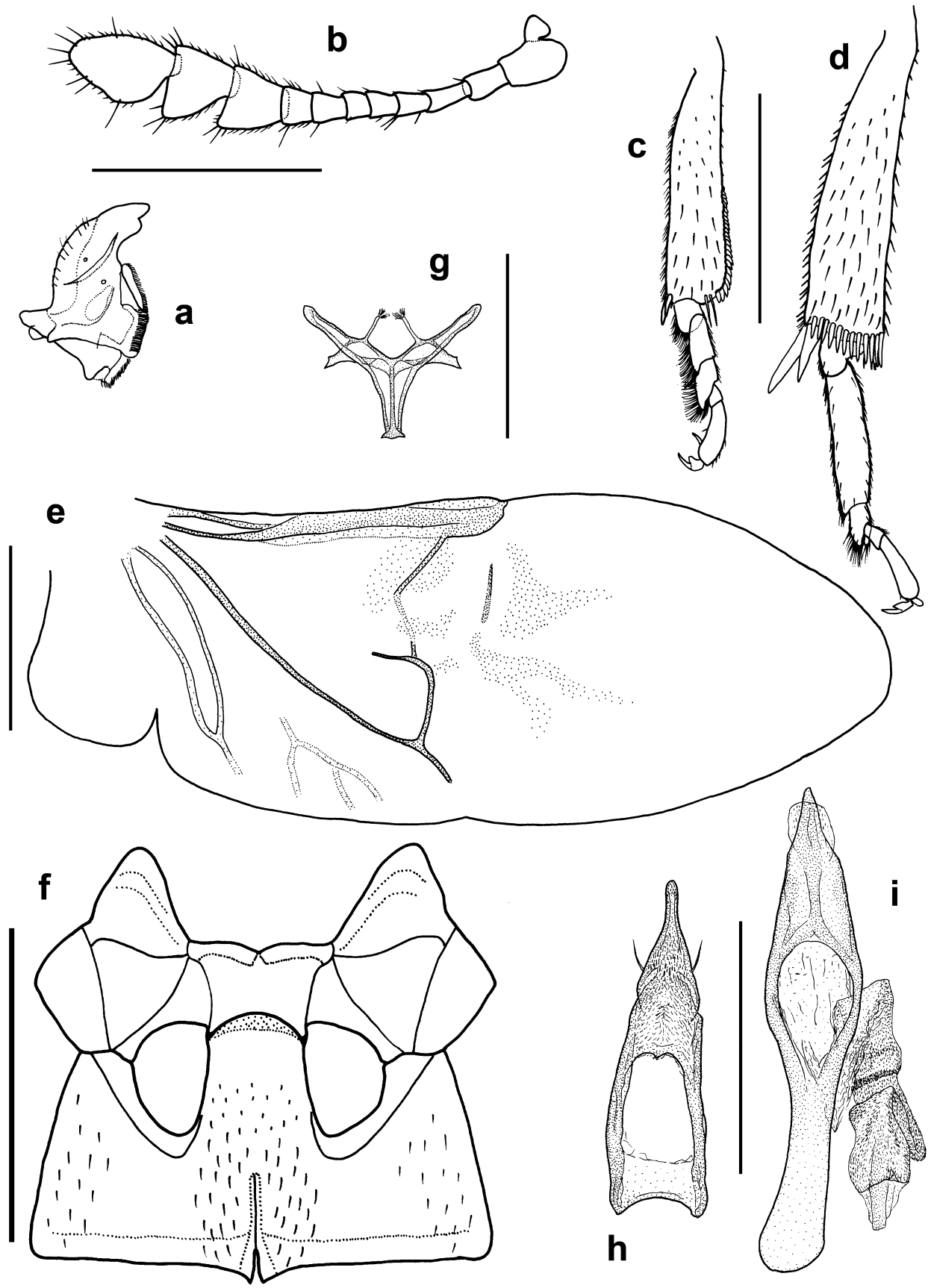

FIGURE 32. *Eulitrus estriatus*, male. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 1.0 mm). (g) Metendosternite (scale bar = 1.0 mm). (h) Tegmen, dorsal; (i) penis, dorsal (scale bar = 0.5 mm).

Head. Not constricted behind eyes. Eyes medium-sized to large; facets flat; interfacetal setae absent; strongly emarginate medially; without posterior emargination; periocular groove present; with transverse setose groove ventrally behind eye. Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club 3-segmented, club strongly asymmetrical, antennomere XI unconstricted or weakly turbinate (Fig. 32b). Mandible (Fig. 32a) with apex bidentate; without retinaculum; mandible with ventral ridge. Maxillary palpomere IV fusiform, nearly symmetrical; galea short, rounded; lacinia with two stout spines. Mentum with sides divergent toward apex; labial palpomere III fusiform. Labrum with apical margin arcuate. Gular sutures short, barely evident.

Thorax. Pronotum without obvious microsetae; with moderately developed scutellar lobe. Prosternum anteriorly with continuous row of marginal setae, setae flattened at base; procoxal cavity with anterolateral notchlike extension; hypomeron with weak to strong transverse carina originating along coxal cavity just posterior to notchlike extension; prosternal process rounded in lateral view, sometimes conspicuously setose preapically, without spinelike setae at apex. Protrochanter without setae; protibia with ctenidium on kickface, extending from about 1/3 to 2/3 length of tibia (Fig. 32c). Scutellar shield small. Elytron with distinct spectral iridescence; with sutural stria absent or barely indicated; disc devoid of striae or distinct rows of punctures; without transverse strigae; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 32f) notched anteriorly, extending posteriorly to metaventrite, dividing mesoventral disc in two, not forming procoxal rests; mesanepisternum with complete transverse carina; mesocoxal cavities widely separate, separated by more than half width of a coxal cavity. Mesotarsomere III bilobed. Metaventral process (Fig. 32f) extending beyond anterior level of mesocoxae, protruding and arcuately lobed anteriorly; metaventral postcoxal lines narrowly separated from mesocoxal cavity margin, smoothly arcuate; discrimen short, extending less than halfway to anterior margin of metaventral process; metendosternite (Fig. 32g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange at anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line; metatibial foreface with apical ctenidium roughly perpendicular overall to long axis of tibia; spurs cylindrical, longest spur subequal in length to width of tibial apex; metatarsomere I shorter, often much shorter than metatarsomere II, joint between I and II rigid (Fig. 32d). Hind wing (Fig. 32e) with distinct, ovate anal lobe; leading edge without row of long setae at level of RA+ScP; AA_{3+4} present, strong, anastomosing with Cu, spur AA_4 absent; cubitoanal system unbranched apically; CuA_2 and MP_{3+4} with distal remnants; r4 developed, connected with RA_{3+4}; with distinct curved flecks in apical field distal to rp-mp2; long transverse proximal sclerite and faint triangular sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines or calli; spiracles present and apparently functional on segment VII. Male with aedeagus upright in repose; tegmen (Fig. 32h) with symmetrical anterior margin and parameres fused to basal piece but separated from it by suture, parameres without medial longitudinal division; penis (Fig. 32i) lance-shaped, with basal strut widened, with distinct fields of endophallic spicules, apex acuminate; spiculum gastrale V-shaped with arms connected by broad lamina, or Y-shaped with long basal rod. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. Members of *Eulitrus* have been collected using a variety of generalized methods including beating, canopy fogging, blacklighting, Malaise traps, and flight intercept traps.

Distribution and diversity. Strictly Neotropical, occurring from Jalisco and Veracruz States in Mexico south to Paraguay and Misiones Province, Argentina. Known from Venezuela and Guyana but I have not seen specimens from the West Indies or islands of the South American continental shelf. Two described species are included in the genus, but many new species await description.

Included species (2):

Eulitrus anisotomus Sharp, 1889 (Distribution: Belize) (type!)
Eulitrus estriatus Sharp, 1889 (Distribution: Nicaragua, Panama) (type!)

Discussion. A well defined genus, *Eulitrus* probably has the least complex history of all previously described genera of Phalacridae.

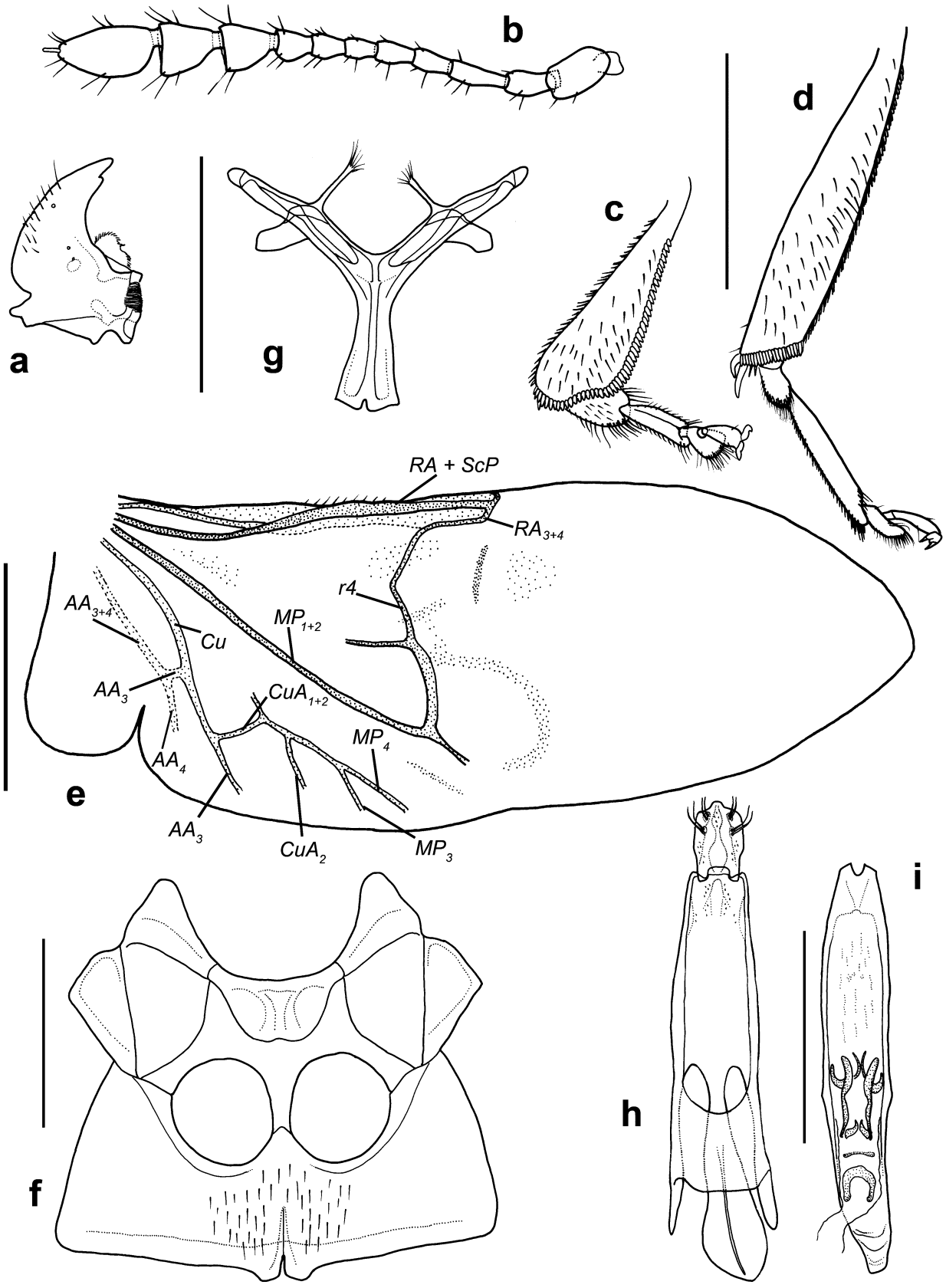

FIGURE 33. *Grouvelleus dilutus*, male. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 0.5 mm). (h) Tegmen, ventral; (i) penis, ventral (scale bar = 0.5 mm).

30. *Grouvelleus* Guillebeau, 1892

(Figs. 2g; 33; 42a, b)

Grouvelleus Guillebeau 1892*c*: cxxxiv. Type species: *Grouvelleus prosternalis* Guillebeau 1892, fixed by monotypy.
Ochrolitoides Champion 1924*c*: 245. Type species: *Ochrolitoides magister* Champion 1924, fixed by original designation. **Syn. nov.**
Litotarsus Champion 1925*b*: 615. Type species: *Litotarsus dilutus* Champion 1925, fixed by original designation. **Syn. nov.**

Type material. *Grouvelleus prosternalis* Guillebeau: holotype, female, "Saigon [handwritten] // Type // Grouvelleus \ prosternalis \ Guilb. [handwritten] // type ex \ Guillebeau \ Ann. Fr. 1893.378 [handwritten] \ Collection FLEUTIAUX // HOLOTYPE ♀ \ Grouvelleus \ prosternalis Guillebeau \ det. M.L. Gimmel 2009 [red label]" (MNHN), point mounted.

Ochrolitoides magister Champion: lectotype, here designated, male, "[male symbol] // Kandy, \ Ceylon // G.E. Bryant \ VI.1908 [handwritten] // G. Bryant Coll. \ 1919–147 // Ochrolitoides \ magister, \ Champ. // E.M.M. 1924. \ det. G.C.C. // See slide Coll. \ No. ESL 55 // Ochrolitoides \ magister \ type Ch [handwritten] // SYN- \ TYPE [blue-bordered disc] // LECTOTYPE ♂ \ Ochrolitoides \ magister Champion \ des. M.L. Gimmel 2010 [red label]" (BMNH), point mounted, genitalia removed from specimen and slide mounted by E.S. Lewis. Paralectotype: same data as lectotype, female, with label affixed "PARALECTOTYPE ♀ \ Ochrolitoides \ magister Champion \ det. M.L. Gimmel 2010 [yellow label]" (BMNH).

Litotarsus dilutus Champion: holotype, male, "Type \ H.T. // Specimen figured. // See slide Coll. \ No. ESL 89 // G. Bryant Coll. \ 1919–147 // Quop, \ W. Sarawak. \ III-IV.1914. \ G.E. Bryant. // prost. process \ forming rec. \ in mesost. // Gen. NOT \ Grouvelleus, \ 1892 Guill // Litotarsus \ dilutus, \ type Ch. // Ann. Mag. N.H. \ Ser 9. xvi.1925. \ G.C.C. det. // HOLOTYPE \ Litotarsus \ dilutus Champion \ det. M.L. Gimmel 2010 [red label]" (BMNH), point mounted, genitalia removed from specimen and slide mounted by E.S. Lewis.

Diagnosis. This genus has a number of bizarre features that readily separate it from the rest of the Phalacridae. The mesocoxae are nearly contiguous, and the meso-metaventral junction lies behind the midpoint of the coxae. From a ventral aspect the prosternal process appears as a spearpoint-shaped posterior projection, and the procoxal rests on the mesoventral plate are large. The maxillary galea is elongate and acuminate, and the terminal maxillary palpomere is long and knife-shaped. Additionally, the distinctly punctate elytral striae are among the most prominent in the family.

Description. Small to very large, total length 1.8–4.5 mm. Dorsal color solid reddish-testaceous (Figs. 42a, b) to solid black, some darker forms with bicolored elytra. Tibial spur formula 2-2-2, tarsal formula 5-5-5 in both sexes.

Head. Not constricted behind eyes. Eyes small to medium-sized; facets flat; interfacetal setae absent; weakly emarginate medially; without posterior emargination; periocular groove present or absent; with transverse setose groove ventrally behind eye. Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club loosely 3-segmented, club weakly asymmetrical; antennomere XI not or weakly constricted (Fig. 33b). Mandible (Fig. 33a) with apex bidentate; retinaculum absent; mandible without ventral ridge. Maxillary palpomere IV long, flattened and knife-shaped, inner edge swollen; galea elongate, tapered; lacinia with multiple stout spines. Mentum with sides divergent toward apex; labial palpomere III slightly expanded, triangular, labial palpomere II often with cluster of large stout setae (Fig. 2g), palpomere III with one or two stout setae on outer margin before apex. Labrum with apical margin slightly emarginate. Gular sutures short, barely evident.

Thorax. Pronotum without obvious microsetae; with weakly developed scutellar lobe. Prosternum anteriorly with continuous row of marginal setae, setae flattened at base; procoxal cavity with anterolateral notchlike extension; prosternal process angulate in lateral view, long and spearpoint-shaped in ventral view, usually conspicuously setose preapically, without spinelike setae at apex. Protrochanter without setae; protibia with ctenidium on kickface extending almost entire length of tibia, often extending around apex to level of apical spurs (Fig. 33c). Scutellar shield small, width at base subequal to length of eye. Elytron with spectral iridescence; with nine distinct, more-or-less complete striae, medialmost striae not convergent apically; without transverse strigae; lateral margin without row of sawtooth-like setae. Mesoventral plate (Fig. 33f) notched anteriorly, not extending posteriorly to metaventrite, forming deep procoxal rests; mesoventral disc depressed medially; mesanepisternum with complete transverse carina; mesocoxal cavities nearly contiguous, barely separated by a strip of cuticle. Mesotarsomere III not bilobed. Metaventrite short (Fig. 33f); metaventral process not quite reaching halfway point

of mesocoxae; metaventral postcoxal lines not separated from mesocoxal cavity margin, or separated only slightly but following cavity borders; discrimen short, not quite extending halfway to anterior margin of metaventral process; metendosternite (Fig. 33g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange behind anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line; metatibia sometimes greatly expanded (*G. tibialis*); metatibial foreface with apical ctenidium straight, roughly perpendicular overall to long axis of tibia; spurs cylindrical, longest spur shorter than or subequal to width of tibial apex; metatarsomere I much shorter than metatarsomere II, to subequal to metatarsomere II, joint between I and II rigid (Fig. 33d); metatarsomere III not bilobed. Hind wing (Fig. 33e) with distinct, ovate anal lobe; leading edge with incomplete row of long setae; AA_{3+4} present, connected by crossvein to Cu; cubitoanal system branched apically; CuA_2 and MP_{3+4} with distal remnants; r4 complete, connecting RP with RA_{3+4}; large curved fleck present in apical field distal to rp-mp2; small transverse sclerite and medium-sized nebulous sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines or calli; spiracles present and apparently functional on segment VII. Male with aedeagus upright in repose; tegmen (Fig. 33h) with symmetrical anterior margin and parameres hinged to basal piece, parameres without medial longitudinal division; penis (Fig. 33i) narrow, with fields of endophallic spicules and sclerites, apex with two truncate processes; spiculum gastrale with arms v-shaped, connected by broad lamina or not. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. Gut contents reveal unidentified fungal material. Information on labels is quite meager, but a long series of *G. dilutus* was collected by beating foliage.

Distribution and diversity. Members of this genus occur in the humid tropical belt of the Afrotropical Region (new record for this realm) from Sierra Leone to Uganda, south to Angola. I have seen no specimens from Madagascar. In the Oriental realm they occur from India and Sri Lanka to Vietnam to Borneo. The African fauna is entirely undescribed, and there are new species from southeast Asia.

Included species (7):

Grouvelleus anisotomoides (Champion, 1925), **comb. nov.** (*Litotarsus*) (Distribution: Myanmar) (type!)
Grouvelleus dilutus (Champion, 1925), **comb. nov.** (*Litotarsus*) (Distribution: Malaysia) (type!)
Grouvelleus magister (Champion, 1924), **comb. nov.** (*Ochrolitoides*) (Distribution: Sri Lanka) (type!)
Grouvelleus magnus (Motschulsky, 1866), **comb. nov.** (*Litotarsus*) (Distribution: Sri Lanka)
Grouvelleus prosternalis Guillebeau, 1892 (Distribution: Vietnam) (type!)
Grouvelleus siamensis (Champion, 1924), **comb. nov.** (*Ochrolitoides*) (Distribution: Thailand) (type!)
Grouvelleus tibialis (Švec, 2006), **comb. nov.** (*Litotarsus*) (Distribution: Malaysia)

Discussion. The previously described species of *Grouvelleus*, *Litotarsus*, and *Ochrolitoides* share a number of important characters (mentioned in the diagnosis), and I have synonymized them here. Their type species differ principally in body size and length ratios of metatarsomeres I and II, but there are other species in this group that exhibit intermediate character states. The tarsal configuration was the primary criterion Champion (1925*b*) used in justifying his new genus *Litotarsus*, so I believe his comment written on a label attached to the holotype of *L. dilutus* (see above) carries no weight.

31. *Litochrus* Erichson, 1845

(Figs. 34; 42e, f)

Litochrus Erichson 1845: 108. Type species: *Phalacrus brunneus* Erichson 1842, fixed by subsequent designation.
Lithocrus[lapsus calami]: Lacordaire 1854: 286.
Micromerus Guillebeau 1892*b*: 148. Type species: *Stilbus koltzei* Reitter 1887, fixed by original designation. **Syn. nov.**
Merobrachys Guillebeau 1895: xxvi. Type species: *Stilbus Koltzei* Reitter 1887, fixed by objective synonymy with *Micromerus* Guillebeau. [replacement name for *Micromerus* Guillebeau, 1892] **Syn. nov.**

Type material. *Phalacrus brunneus* Erichson: type not seen.
Stilbus koltzei Reitter: type not seen.

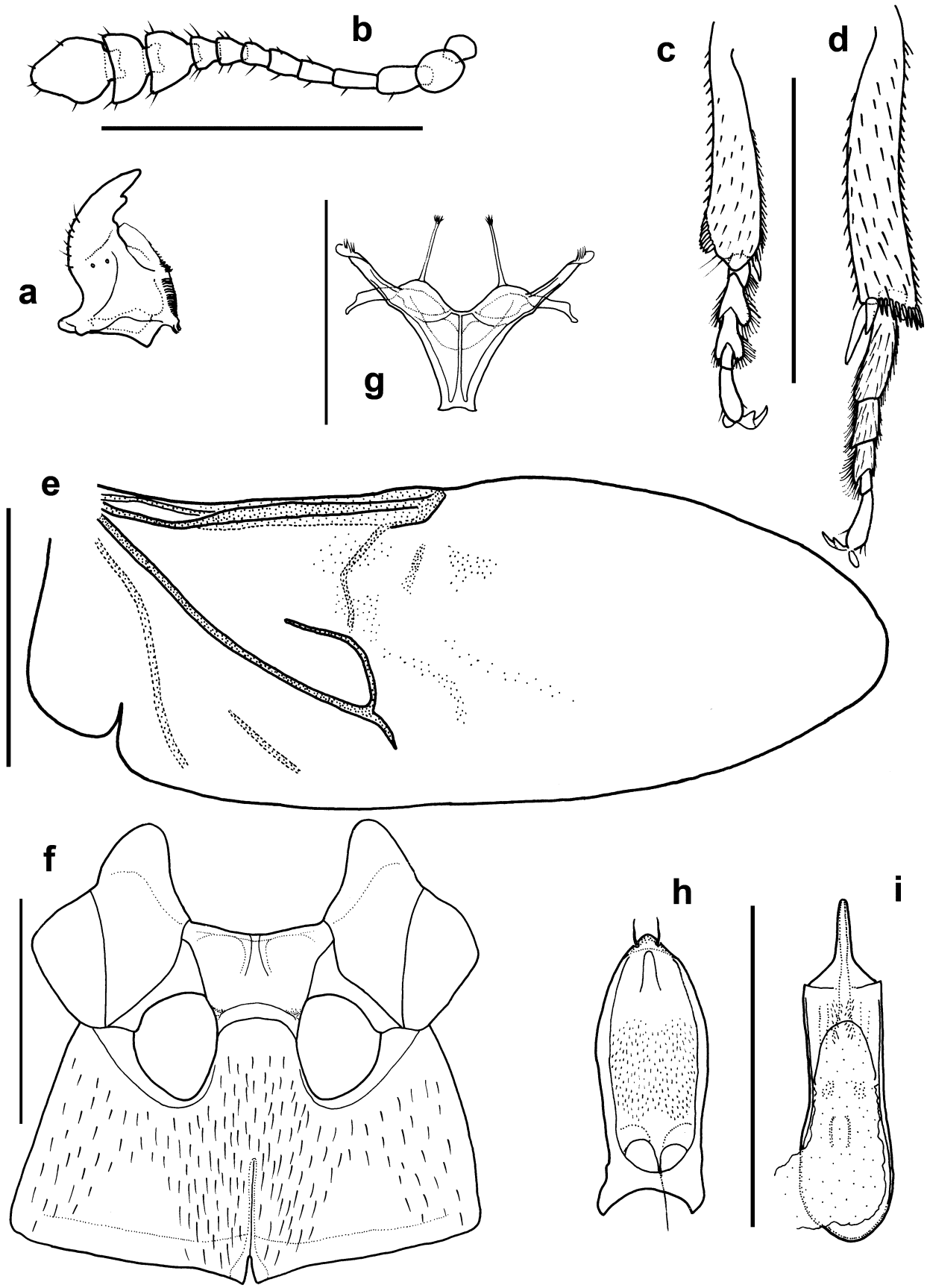

FIGURE 34. *Litochrus brunneus*, male. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Right protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 0.5 mm). (h) Tegmen, ventral; (i) penis, ventral (scale bar = 0.5 mm).

Diagnosis. Distinguished from most other members of the family by the short subapical protibial ctenidium, which extends much less than half the distance of the tibia, and by the apical process of the median lobe which is acuminate and often terminates in a ventrally directed hook. Additionally, in all species metatarsomere I is longer than metatarsomere II, the metaventral process protrudes well anteriad the mesocoxae, the metaventral lines are not separate from the mesocoxal cavities, the terminal antennal segment is typically quite short and transverse, and all have distinct spectral iridescence on the elytra and are often marked with yellow or reddish maculations.

Description. Very small to very large, total length 1.3–4.4 mm. Color variable, from completely yellowish-testaceous to completely piceous, dark specimens often with extensive yellow or red maculations on the elytra (Figs. 42e, f). Tibial spur formula 2-2-2, tarsal formula 5-5-5 in both sexes.

Head. Not constricted behind eyes. Eyes medium-sized to large; facets flat; interfacetal setae absent; weakly to strongly emarginate medially; without posterior emargination; periocular groove absent; with transverse setose groove ventrally behind eye. Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club 3-segmented, club symmetrical, antennomere XI strongly turbinate (Fig. 34b). Mandible (Fig. 34a) with apex bidentate; without retinaculum; mandible with ventral ridge. Maxillary palpomere IV fusiform, slender, nearly symmetrical; galea short, rounded; lacinia with two stout spines. Mentum with sides divergent toward apex; labial palpomere III fusiform, narrowly truncate apically. Labrum with apical margin truncate. Gular sutures short, barely evident.

Thorax. Pronotum without obvious microsetae; with moderately developed scutellar lobe. Prosternum anteriorly with continuous row of marginal setae, setae normal; procoxal cavity with anterolateral notchlike extension; prosternal process rounded in lateral view, often conspicuously setose preapically, without spinelike setae at apex. Protrochanter without setae; protibia with short ctenidium on kickface, with group of five or more spines at outer apical angle (Fig. 34c). Scutellar shield small. Elytron with distinct spectral iridescence; with one sutural stria; discal striae sometimes weakly developed, often consisting of weak rows of punctures; without transverse strigae; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 34f) notched anteriorly, extending posteriorly to metaventrite, dividing mesoventral disc in two, forming procoxal rests; mesanepisternum without transverse carina; mesocoxal cavities widely separate, separated by more than half width of a coxal cavity. Mesotarsomere III bilobed. Metaventral process (Fig. 34f) extending at least to anterior level of mesocoxae, protruding and often arcuately lobed anteriorly; metaventral postcoxal lines not separated from mesocoxal cavity margin; discrimen long, extending about halfway to anterior margin of metaventral process; metendosternite (Fig. 34g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange at anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line; metatibial foreface with apical ctenidium roughly perpendicular overall to long axis of tibia; spurs cylindrical, longest spur subequal in length to width of tibial apex; metatarsomere I longer than metatarsomere II, joint between I and II rigid (Fig. 34d); metatarsomere III bilobed. Hind wing (Fig. 34e) with distinct, ovate anal lobe; leading edge without row of long setae at level of RA+ScP; AA_{3+4} absent; cubitoanal system unbranched apically; CuA_2 or MP_{3+4} with floating distal remnant; r4 developed, connected with RA_{3+4}; with faint fleck in apical field distal to rp-mp2; long transverse proximal sclerite and faint triangular sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines or calli; spiracles present and apparently functional on segment VII. Male with aedeagus upright in repose; tegmen (Fig. 34h) with symmetrical anterior margin and parameres hinged to basal piece, parameres without medial longitudinal division; penis (Fig. 34i) with endophallic sclerites and spicules, apex acuminate, often terminating in ventrally directed hook; spiculum gastrale V- or Y-shaped, arms connected by broad sclerotized lamina. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. Species of *Litochrus* have been collected from a wide variety of habitats using a wide variety of methods. One specimen from Lord Howe Island was collected from rotted wood, and a series from New South Wales was collected by pyrethrin fogging of fungus-covered logs. A number of series from Australia were collected under bark of *Eucalyptus*. A few Papua New Guinean specimens were collected by Berlese funnel from forest litter of various types. A number of collections suggest that at least some members of *Litochrus* are strongly attracted to flowers of varying types. A series from the Russian Far East was collected "on flowers." A long series of *L. brunneus* was collected in Tasmania "beating tea trees" (Myrtaceae: *Leptospermum*), while a series from Queensland was collected beating flowers and foliage of *Melaleuca linariifolia* Sm. A series from Western

Australia was collected from blooming *Acacia platycarpa* F.Muell. (Fabaceae). Members of the genus in various localities in Australia were collected from the blooms of the following: *Rhodomyrtus psidioides* (G.Don.) Benth., *Syzygium smithii* (Poir.) Nied., and *Tristaniopsis laurina* (Sm.) Peter G.Wilson & J.T.Waterh. (all Myrtaceae); *Alphitonia excelsa* (Fenzl) Benth. (Rhamnaceae); *Elaeocarpus reticulatus* Sm. (Elaeocarpaceae); *Cuttsia viburnea* F.Muell. (Rousseaceae); *Schizomeria ovata* D.Don (Cunoniaceae); *Cryptocarya microneura* Meisn. (Lauraceae); and *Euroschinus falcata* Hook. (Anacardiaceae). A large number of specimens have been collected at light or in Malaise / flight intercept traps. A long series from Queensland was collected by pyrethrin fogging of tree ferns, while series from Tasmania were collected by a similar method from *Atherosperma moschatum* Labill. (Atherospermataceae) and *Nothofagus* (Fagaceae).

Distribution and diversity. The dominant genus in the Australian region and adjacent lands, *Litochrus* contains a wealth of body forms and color patterns. Species occur from at least the Far East of Russia in the north through Japan, China, the Philippines, and New Guinea to Tasmania (Australia) in the south, and from the Solomon Islands, New Caledonia, and Lord Howe Island in the east to at least Sri Lanka and Pakistan in the west.

Included species (43):

Litochrus alternans Blackburn, 1891 (Distribution: Australia) (type!)
Litochrus amabilis (Guillebeau, 1894), **comb. nov.** (*Merobrachys*) (Distribution: Australia) (type!)
Litochrus apiciflavus Lea, 1932 (Distribution: Australia)
Litochrus baccaeformis Blackburn, 1902 (Distribution: Australia) (type!)
Litochrus basipennis Lea, 1932 (Distribution: Australia)
Litochrus bicolor (Lyubarsky, 1996), **comb. nov.** (*Augasmus*) (Distribution: New Guinea)
Litochrus bimaculatus (Matsumura, 1914), **comb. nov.** (*Merobrachys*) (Distribution: Japan)
Litochrus binotatus Lea, 1932 (Distribution: Australia)
Litochrus bipustulatus (Lyubarsky, 1996), **comb. nov.** (*Augasmus*) (Distribution: New Guinea)
Litochrus blackburni Lea, 1932 (Distribution: New Guinea)
Litochrus brunneus (Erichson, 1842) (Distribution: Australia)
Litochrus burgersi (Lyubarsky, 1996), **comb. nov.** (*Augasmus*) (Distribution: New Guinea)
Litochrus caeruleotinctus Lea, 1932 (Distribution: Australia, New Guinea)
Litochrus flavonotatus Lea, 1932 (Distribution: New Guinea)
Litochrus frigidus Blackburn, 1891 (Distribution: Australia) (type!)
Litochrus fumatus Lea, 1932 (Distribution: Australia)
Litochrus fuscoguttatus (Champion, 1924), **comb. nov.** (*Merobrachys*) (Distribution: India) (type!)
Litochrus grouvellei (Guillebeau, 1894), **comb. nov.** (*Merobrachys*) (Distribution: “Sunésie”) (type!)
Litochrus koltzei (Reitter, 1887), **comb. nov.** (*Merobrachys*) (Distribution: Russia) (type!)
Litochrus laeticulus Blackburn, 1891 (Distribution: Australia) (type!)
Litochrus lautus Blackburn, 1902 (Distribution: Australia) (type!)
Litochrus maculatus Blackburn, 1891 (Distribution: Australia) (type!)
Litochrus major Blackburn, 1891 (Distribution: Australia) (type!)
Litochrus majorinus Lea, 1932 (Distribution: Australia)
Litochrus maritimus Blackburn, 1903 (Distribution: Australia) (type!)
Litochrus minutus Hisamatsu, 1985 (Distribution: Japan)
Litochrus nigritus (Lyubarsky, 1996), **comb. nov.** (*Augasmus*) (Distribution: New Guinea)
Litochrus obscuricollis Blackburn, 1902 (Distribution: Australia) (type!)
Litochrus obscuripes Lea, 1932 (Distribution: New Guinea)
Litochrus pallidicollis Lea, 1932 (Distribution: New Guinea)
Litochrus pallidipes Lea, 1932 (Distribution: New Guinea)
Litochrus palmerstoni Blackburn, 1891 (Distribution: Australia) (type!)
Litochrus parvoniger Lea, 1932 (Distribution: New Guinea)
Litochrus perparvus Blackburn, 1902 (Distribution: Australia) (type!)
Litochrus piceus (Lyubarsky, 1996), **comb. nov.** (*Augasmus*) (Distribution: New Guinea)
Litochrus plagiatus Blackburn, 1902 (Distribution: Australia) (type!)
Litochrus pronotalis Gimmel, **nom. nov.** [for *Augasmus bimaculatus* Lyubarsky, 1996, junior secondary homonym of *Litochrus bimaculatus* (Matsumura, 1914)] (Distribution: New Guinea)

Litochrus ruficollis Lea, 1932 (Distribution: Australia)
Litochrus rufoguttatus Champion, 1925 (Distribution: Japan) (type!)
Litochrus ryukyuensis Hisamatsu, 1985 (Distribution: Japan)
Litochrus sydneyensis Blackburn, 1892 (Distribution: Australia) (type!)
Litochrus tinctus Blackburn, 1895 (Distribution: Australia) (type!)
Litochrus triangulus (Fauvel, 1903), **comb. nov.** (*Olibrus*) (Distribution: New Caledonia) (type!)

Discussion. This genus had an inauspicious beginning that certainly contributed to the worldwide confusion over its limits and composition. Erichson (1845) described it in a footnote and mentioned, almost in passing, the two previously described species that should be included in it. The identity of these species was not elaborated on until Blackburn (1891), who did not see the types of the Australian species *L. brunneus* (which would become the type species), and Guillebeau (1894*a*), who misdiagnosed the genera *Litochrus* and *Micromerus* (=*Merobrachys*) with regard to the hind tarsi. Blackburn (1891–1903), although correctly divining the identity of the Erichson species, had a broader concept of this genus that includes my concept of *Augasmus* Motschulsky. Examination of the types of Blackburn has resulted in the removal of three species to the latter genus. Examination of the detailed illustrations of metatibiae, metatarsi, and antennae in Lea (1932) has resulted in the removal of an additional three species to *Augasmus* (see account of that genus for details on these six species), and one species to *Litochropus* (see account of that genus). However, after examination of illustrations and non-type material, I have determined that all of the species newly described by Lyubarsky (1996) in *Augasmus* actually belong to *Litochrus*. In other publications Lyubarsky's concept of *Augasmus* is essentially in agreement with mine.

Casey (1889) applied Erichson's concept of *Litochrus* to a few North American forms, despite admitting that Erichson's genus is probably a composite of genera, and despite enumerating differences between the North American forms and Erichson's description. As I have defined the genus above, true *Litochrus* differs in a large number of structural details from superficially similar forms in the New World, and all species described from that region previously under this name have been transferred to *Litochropus* Casey or *Neolitochrus* Gimmel (see accounts of those genera for details).

Guillebeau's (1893*c*) species that he tentatively described in *Litochrus*, *L. latisternus*, I have determined to probably belong in *Olibrus* after a cursory examination of the type (MNHN). I have tentatively transferred it to the latter genus.

I have examined specimens of *Merobrachys koltzei* (Reitter) from the Far East of Russia and there are no essential differences between this form and those included in my definition of *Litochrus*. Therefore I propose synonymy of these two genera. This synonymy results in four new combinations, made explicit above. I have also examined the type of *Olibrus triangulus* Fauvel (MNHN) and it falls easily within the concept of *Litochrus* presented above in the diagnosis.

32. *Malagophytus* Gimmel, gen. nov.

(Figs. 3b; 42g)

Type species: *Malagophytus steineri* Gimmel, here designated.

Type material. See account of *M. steineri* below.

Diagnosis. Distinguished by the separated mesocoxal cavities, lack of a protibial ctenidium, large scutellar shield, four convergent elytral discal striae, and paired postcoxal lines on abdominal ventrite I.

Description. Very small, total length 1.3–1.5 mm. Color solid rufotestaceous (Fig. 42g). Tibial spur formula 2-2-2, tarsal formula 5-5-5.

Head. Not constricted behind eyes. Eyes medium-sized; weakly emarginate medially; with broad posterior emargination; periocular groove absent. Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club 3-segmented, club weakly asymmetrical; antennomere XI constricted on posterior edge. Mandible with apex tridentate; with weak retinaculum. Maxillary palpomere IV fusiform, short, nearly symmetrical. Labial palpomere III fusiform, pointed. Gular sutures long, extending at least halfway to ventral mouthparts.

Thorax. Pronotum with distinct, scattered microsetae; with weakly developed scutellar lobe. Procoxal cavity with anterolateral notchlike extension; prosternal process angulate in lateral view, with preapical setae, with broad

translucent horizontal apical process, without spinelike setae at apex. Protibia without ctenidium on kickface. Scutellar shield large, about as wide as length of eye. Elytron without spectral iridescence; with one distinct sutural stria, plus four more-or-less complete striae, all striae convergent on sutural stria apically, with rudiments of additional striae; without transverse strigae. Mesoventral plate notched anteriorly, extending posteriorly to metaventrite, forming procoxal rests, with a moderately deep, circular, median depression for reception of prosternal process; mesanepisternum with complete transverse carina; mesocoxae approximate, separated by less than half width of a coxal cavity. Mesotarsomere III not bilobed. Metaventral process extending anteriorly just to halfway point of mesocoxae; metaventral postcoxal lines narrowly separated from mesocoxal cavity margin, arcuate; discrimen short, not extending halfway to anterior margin of metaventral process. Metatibial foreface with apical ctenidium straight, perpendicular overall to long axis of tibia; spurs cylindrical, longest spur subequal to width of tibial apex; metatarsomere I longer than metatarsomere II, but shorter than remainder of tarsus, joint between I and II rigid.

Abdomen. Abdominal ventrite I (Fig. 3b) with paired lines extending from metacoxal process posteriorly about 2/3 of the way to suture between ventrites I and II, divergent posteriorly. Genitalia unstudied.

Immature stages. Unknown.

Bionomics. Only one of the specimens has any collection information: "on reed litter."

Distribution and diversity. Known so far only from two specimens (representing one species) from southeastern Madagascar (Fig. 44b).

Included species (1):

Malagophytus steineri Gimmel, **sp. nov.** (Distribution: Madagascar)

Discussion. Because this genus is known from only two specimens I did not perform a disarticulation. Accordingly, the above description lacks a number of internal and detailed external characters, and the genus was excluded from the phylogenetic analysis.

Etymology. From *malago*-, referring to its Malagasy homeland, and Greek *phyton* (a creature). The gender of the name is masculine.

Malagophytus steineri Gimmel, sp. nov.

(Figs. 3b; 42g)

Holotype. "MADAGASCAR \ Fianarantsoa Prov., \ Namarona River 7 km \ W Ranomafana, 900 m \ 8–21 October 1988 \ W. E. Steiner // HOLOTYPE \ Malagophytus \ steineri Gimmel \ des. M.L. Gimmel 2011 [red label]" (USNM), point mounted.

Paratype (1, BMNH). "Madagascar [underlined in purple] \ 20 kms. N. of \ Ft. Dauphin \ 18.x.1970 // ex \ reed \ litter // Coll. \ P. Hammond \ B.M. 1970-603 // PARATYPE \ Malagophytus \ steineri Gimmel \ det. M.L. Gimmel 2011 [yellow label]", card mounted.

Description. Total length 1.3–1.5 mm. Color brunneous, margins of head, pronotum, and elytra tending toward testaceous; appendages and underside testaceous, meso- and metaventral regions darker. Antennal club shorter than funicle; antennomere XI ovate. Head and pronotum with extremely sparse, weak punctation, latter with sparse recumbent microsetae. Elytron with distinct transverse microsculpture throughout, with sparse recumbent microsetae; with sutural stria (parallel to margin) extending about 2/3 length of elytron, with four additional engraved striae, striae beginning in basal 1/3 of elytron and extending obliquely to almost meet sutural stria at well-spaced intervals, last stria nearing sutural stria at about 1/6 from apex of elytron, additional striae faintly indicated. Prosternal process (with translucent projection) extending well beyond procoxae; with pair of short, stiff setae positioned subapically. Metaventrite without distinct punctures, setose medially; metaventral postcoxal lines narrowly arcuate, enclosing an area about ¼ length of metaventrite behind coxae. Metatarsomere I slightly longer than II.

Male and female genitalia unknown.

Diagnosis. This species may be recognized by the characters given in the generic diagnosis.

Distribution. Known only from two localities in southeastern Madagascar (Fig. 44b).

Etymology. Named for Warren E. Steiner, Jr. (Cheverly, MD), primary collector of three new genera of phalacrids from Madagascar, including this one. The epithet is a noun in the genitive case.

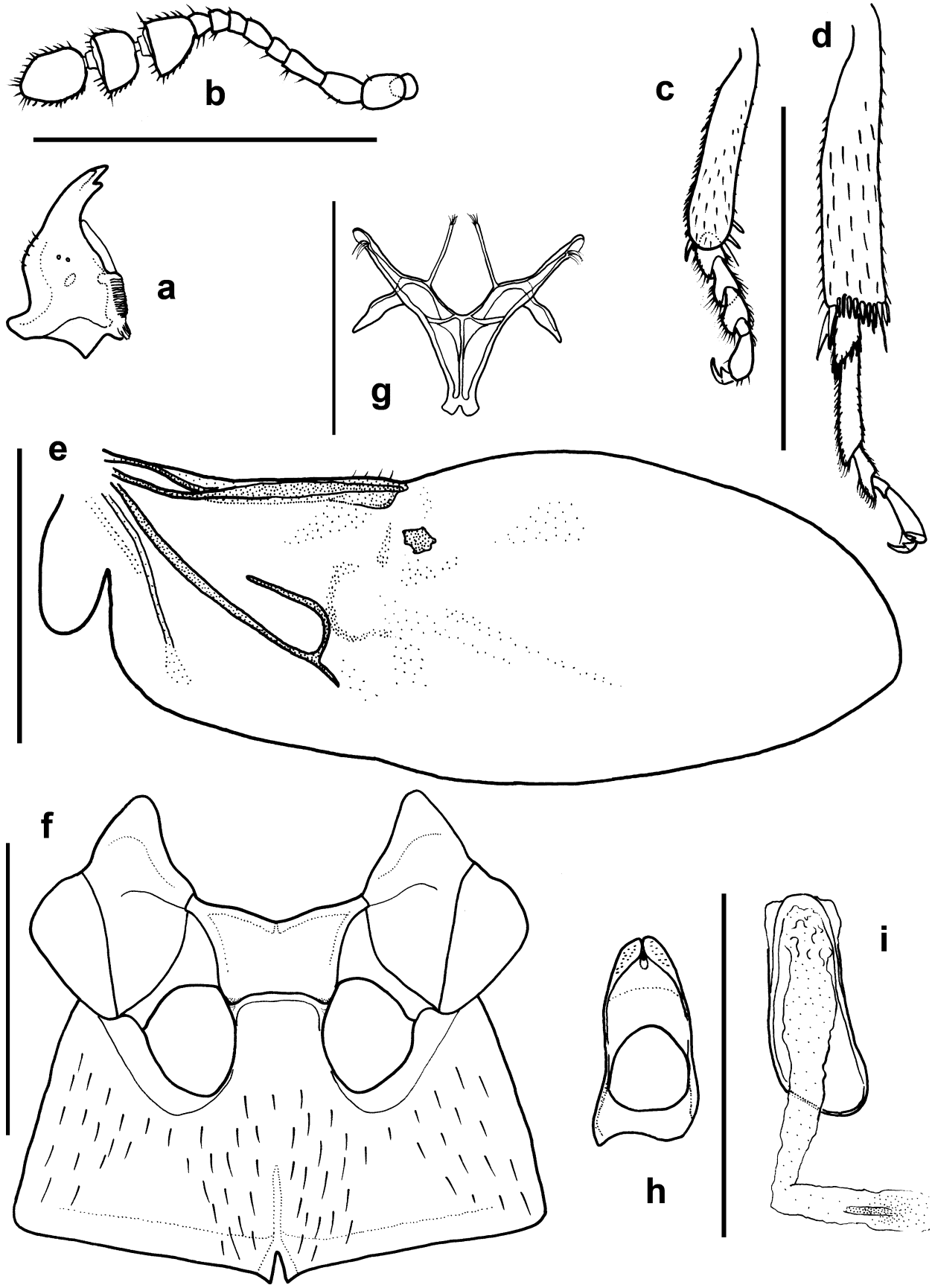

FIGURE 35. *Paracylomus asiaticus*, male. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 0.5 mm). (h) Tegmen, ventral; (i) penis, ventral (scale bar = 0.5 mm).

33. *Paracylomus* Gimmel, gen. nov.

(Figs. 35; 43a, b)

Type species: *Acylomus asiaticus* Champion, here designated.

Type material. *Acylomus asiaticus* Champion: lectotype, here designated in order to stabilize the species and new genus name, "Ceylon [underlined with yellow] \ G. Lewis. \ 1910—320. // Horton Plains. \ 6,000 ft. \ 18-20.III.82. // 20.3.82 [handwritten] // Type \ H.T. [red-bordered disc] // Acylomus \ asiaticus \ type Ch. [handwritten] // cox. lines angular \ + sterna as in \ S. geminus [handwritten] // Acylomus \ asiaticus, \ Champ. // E.M.M. 1924. \ det. G.C.C. // SYN- \ TYPE [blue-bordered disc] // LECTOTYPE \ Acylomus \ asiaticus Champion \ des. M.L. Gimmel 2011 [red label]" (BMNH). Paralectotype card-mounted upside down, with same locality labels, label added "PARALECTOTYPE \ Acylomus \ asiaticus Champion \ det. M.L. Gimmel 2011 [yellow label]" (BMNH).

Diagnosis. Recognized by a combination of the following features: elytra with two engraved sutural striae, metaventral process lobed and extending anteriorly beyond mesocoxae, metaventral postcoxal lines separated from mesocoxal cavities, protibia without ctenidium, and metatarsomere I shorter than II.

Description. Small, total length 1.7–1.9 mm. Dorsal color dark reddish-testaceous (Figs. 43a, b). Tibial spur formula 2-2-2, tarsal formula 5-5-5 in both sexes.

Head. Not constricted behind eyes. Eyes small; facets flat; interfacetal setae absent; weakly emarginate medially; without posterior emargination; periocular groove absent; with transverse setose groove ventrally behind eye. Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club 3-segmented, club weakly asymmetrical, antennomere XI weakly turbinate (Fig. 35b). Mandible (Fig. 35a) with apex tridentate; without retinaculum; mandible without ventral ridge. Maxillary palpomere IV fusiform, short, nearly symmetrical; galea short, rounded; lacinia with two stout spines. Mentum with sides divergent toward apex; labial palpomere III fusiform. Labrum with apical margin arcuate. Gular sutures short, barely evident.

Thorax. Pronotum without obvious microsetae; with weakly developed scutellar lobe. Prosternum anteriorly with continuous row of marginal setae, setae flattened at base; procoxal cavity with anterolateral notchlike extension; prosternal process rounded in lateral view, not conspicuously setose preapically, without spinelike setae at apex. Protrochanter without setae; protibia without ctenidium on kickface. Scutellar shield small. Elytron with weak spectral iridescence; two sutural striae present, convergent in apical fourth of elytron; discal striae barely suggested; without transverse strigae; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 35f) notched anteriorly, extending posteriorly to metaventrite, dividing mesoventral disc in two, not forming procoxal rests; mesanepisternum with incomplete transverse carina; mesocoxal cavities widely separate, separated by more than half width of a coxal cavity. Mesotarsomere III not bilobed. Metaventral process (Fig. 35f) extending beyond anterior level of mesocoxae, protruding and arcuately lobed anteriorly; metaventral postcoxal lines relatively weak, diverging from mesocoxal cavity margin, arcuate; discrimen short, extending less than halfway to anterior margin of metaventral process; metendosternite (Fig. 35g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange at anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line; metatibial foreface with apical ctenidium roughly perpendicular overall to long axis of tibia; spurs cylindrical, longest spur subequal in length to width of tibial apex; metatarsus long and slender, metatarsomere I shorter than metatarsomere II, joint between I and II rigid (Fig. 35d); metatarsomere III not bilobed. Hind wing (Fig. 35e) with distinct, ovate anal lobe; leading edge with incomplete row of long setae at level of RA+ScP; AA_{3+4} apparent only basally, without crossvein to Cu; cubitoanal system unbranched apically; CuA_2 and MP_{3+4} without distal remnants; r4 absent; flecks present in apical field just distal to rp-mp2; long transverse proximal sclerite and additional strong, irregular sclerite present just distal to end of radial bar.

Abdomen. Abdominal ventrite I without paired lines or calli; spiracles apparently absent from segment VII. Male with aedeagus upright in repose; tegmen (Fig. 35h) with asymmetrical anterior margin and parameres separated by weak suture from basal piece, parameres with medial longitudinal division; penis (Fig. 35i) short, wide, with endophallic spicules, no large sclerites, apex simple; spiculum gastrale V-shaped, with arms free. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. One series was collected from a Malaise trap.

Distribution and diversity. Only one species, known from Horton Plains National Park, Sri Lanka, and a specimen simply labeled "Ceylon" (see map, Fig. 44d).

Included species (1):

Paracylomus asiaticus (Champion, 1924), **comb. nov.** (*Acylomus*) (Distribution: Sri Lanka) (type!)

Discussion. Despite Champion's notes to the contrary, the type species does possess (albeit weak) metaventral postcoxal lines that diverge from the coxal cavities, though they are smoothly and evenly arcuate. This species was originally described in *Acylomus*, but the anteriorly lobed metaventral process and two sutural striae on each elytron make it quite distinctive.

Etymology. From the Greek prefix *para-* (near) plus the genus *Acylomus*, with which this genus shares a number of characters and has been confused in the past. The gender of the name is masculine.

34. *Steinerlitrus* Gimmel, gen. nov.

(Figs. 36; 43c–e)

Type species: *Steinerlitrus warreni* Gimmel, here designated.

Type material. See account of *Steinerlitrus warreni* below.

Diagnosis. Readily distinguised from other Phalacridae by the greatly anteriorly protruded metaventrite, lack of a protibial ctenidium, metatarsomere II longer than I, small scutellar shield, acute notch on the posterior margin of the eye, and a reduced or absent elytral sutural stria.

Description. Very small to medium-sized, total length 1.2–2.4 mm. Color generally piceous, often with yellow maculations (Figs. 43d, e). Tibial spur formula 2-2-2, tarsal formula 5-5-5 in both sexes.

Head. Not constricted behind eyes. Eyes small; facets flat; interfacetal setae absent; not emarginate medially; with acute posterior emargination (Fig. 43c); periocular groove absent; lacking distinct setose groove ventrally behind eye. Frontoclypeus emarginate above antennal insertion; clypeal apex arcuate-truncate. Antennal club 3-segmented, club strongly symmetrical, antennomere XI strongly turbinate (Fig. 36b). Mandible (Fig. 36a) with apex tridentate; without retinaculum; mandible with ventral ridge. Maxillary palpomere IV fusiform, nearly symmetrical; galea short, rounded; lacinia with two stout spines. Mentum with sides divergent toward apex; labial palpomere III fusiform, pointed apically. Labrum with apical margin arcuate, with tuft of inwardly curved setae at each corner. Gular sutures short, barely evident.

Thorax. Pronotum with scattered, distinct microsetae; with weakly developed scutellar lobe. Prosternum anteriorly with continuous row of marginal setae, setae flattened at base; procoxal cavity with anterolateral notchlike extension; prosternal process rounded in lateral view, often conspicuously setose preapically, without spinelike setae at apex. Protrochanter without setae; protibia without ctenidium (Fig. 36c). Scutellar shield small. Elytron without or with weak spectral iridescence; without or with one weak sutural stria; elytral disc with weak rows of punctures; without transverse strigae; lateral margin with row of tiny, sawtooth-like setae. Mesoventral plate (Fig. 36f) notched anteriorly, extending posteriorly to metaventrite, dividing mesoventral disc in two, not forming procoxal rests; mesanepisternum with complete transverse carina; mesocoxal cavities widely separate, separated by more than width of a coxal cavity. Mesotarsomere III not bilobed. Metaventral process (Fig. 36f) extending beyond anterior level of mesocoxae, protruding and arcuately lobed anteriorly; metaventral postcoxal lines not separated from mesocoxal cavity margin; discrimen extremely short, extending much less than halfway to anterior margin of metaventral process; metendosternite (Fig. 36g) with anterior tendons moderately separated, ventral process intersecting ventral longitudinal flange at anterior margin. Anterior margin of metacoxa with emargination sublaterally; metacoxal plate with transverse line; metatibial foreface with apical ctenidium roughly perpendicular overall to long axis of tibia; spurs cylindrical, quite short, distinctly shorter than width of tibial apex; metatarsomere I shorter than metatarsomere II, joint between I and II rigid (Fig. 36d). Hind wing (Fig. 36e) with distinct, ovate anal lobe; leading edge with complete row of long setae at level of RA+ScP; AA_{3+4} evident only basally, without crossvein to Cu; cubitoanal system unbranched apically; CuA_2 and MP_{3+4} without distal remnants, though faint flecking is often present; r4 absent; with strong fleck in apical field just distal to rp-mp2; short transverse proximal sclerite and faint triangular sclerite present just distal to end of radial bar.

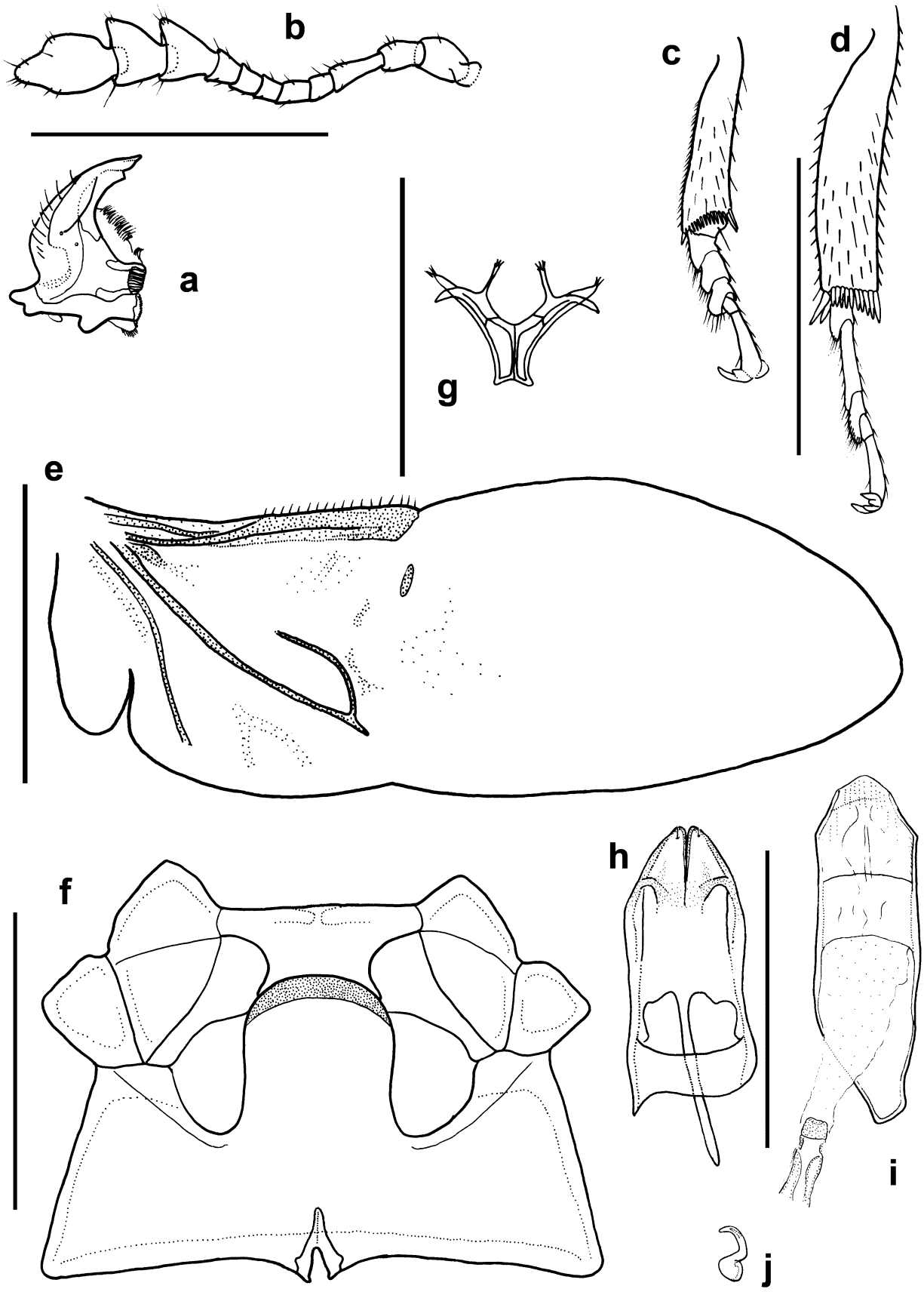

FIGURE 36. *Steinerlitrus warreni*, male. (a) Left mandible, dorsal; (b) left antenna (scale bar = 0.5 mm). (c) Left protibia and tarsus, dorsal; (d) left metatibia and tarsus, ventral (scale bar = 0.5 mm). (e) Hind wing (scale bar = 1.0 mm). (f) Meso- and metaventrite, ventral (scale bar = 0.5 mm). (g) Metendosternite (scale bar = 1.0 mm). (h) Tegmen, ventral; (i) penis, ventral (scale bar = 0.5 mm). Female. (j) Spermatheca (scale bar = 0.5 mm).

Abdomen. Abdominal ventrite I without paired lines, with calli; spiracles present and apparently functional on segment VII. Male with aedeagus upright in repose; tegmen (Fig. 36h) with asymmetrical anterior margin and parameres completely fused to basal piece or partially separated by suture, parameres with medial longitudinal division; penis (Fig. 36i) with endophallic spicules in cylindrical arrangement, apex truncate; spiculum gastrale V-shaped, distorted, arms free. Female ovipositor weakly sclerotized, palpiform.

Immature stages. Unknown.

Bionomics. Large series of both an undescribed species and *S. warreni* were collected from the trunk of a living *Macrolobium* sp. (Fabaceae) at night. One specimen of an undescribed species was sifted from a statary-phase colony of *Eciton burchelli* Westwood (Formicidae), but the presence of the phalacrid was likely accidental.

Distribution and diversity. One species described below, but other, undescribed, species are known from northern South America east of the Andes, all from the Amazon Basin and Guiana Shield.

Included species (1):

Steinerlitrus warreni Gimmel, **sp. nov.** (Distribution: Venezuela)

Discussion. Although at least five undescribed species are known to me, I have described only one species in this publication to meet ICZN requirements. The genus will receive a dedicated treatment in the future.

Etymology. This genus is named in honor of Warren E. Steiner, Jr., of Cheverly, Maryland, USA, the world's greatest phalacrid collector, together with the ending *-litrus* because of its superficial similarity to members of *Eulitrus*. The gender of the name is masculine.

Steinerlitrus warreni Gimmel, sp. nov.

(Figs. 36; 43c–e)

Holotype. Male, "VENEZUELA: Amazonas \ Cerro de la Neblina, basecamp \ 0º50'N 66º10'W 140m 22Feb1985 \ trunk of live Macrolobium at night \ coll. W.E. Steiner // HOLOTYPE ♂ \ Steinerlitrus \ warreni Gimmel \ des. M.L. Gimmel 2011 [red label]" (USNM), point mounted.

Paratypes (86)**.** Same data as holotype (45, USNM); same data as holotype except 25Feb1985 (36, USNM; 5, MLGC); all with label added "PARATYPE \ Steinerlitrus \ warreni Gimmel \ det. M.L. Gimmel 2011 [yellow label]".

Description. Total length 2.0–2.2 mm. Color dark brown, often with nebulous lighter areas along base of elytra, around elytral suture in basal half, and along the lateral margins of the pronotum and elytra; appendages testaceous. Antenna slightly longer than width of head capsule; antennal club about as long as funicle; antennomere XI markedly turbinate, slightly shorter than IX and X combined (Fig. 36b). Head punctation extremely fine and dense. Pronotal punctation similar to that of head; posterior margin not bordered; with weak scutellar lobe; hind angles obtuse. Elytron devoid of microsculpture, with quite weak diffraction grating; sutural stria weak but evident in apical 1/3, additional striae indicated by rows of weak punctures, striae not impressed, intervals with row of punctures similar in size to those of striae; elytral posterior angle sharp, acute. Prosternal process setose medially. Metaventrite densely setose medially. Metatarsomere I about half as long as II; metatarsomeres I and II together about as long as remainder of tarsus (Fig. 36d).

Tegmen of aedeagus with fused parameres partially set off from basal piece (Fig. 36h). Penis narrowed in apical 1/5 (Fig. 36h). Spermatheca as illustrated (Fig. 36j).

Diagnosis. This species may be recognized by the characters given in the generic diagnosis.

Etymology. The specific epithet is a further monument to Warren E. Steiner, Jr., collector of the holotype and the entire type series. The epithet is a noun in the genitive case.

Taxa removed from Phalacridae

I have removed the following genera and species from the family Phalacridae, through examination of both types and original illustrations. Additional species currently described in Phalacridae are probably misplaced with regard to family, but these will not be discovered until all type specimens have been examined.

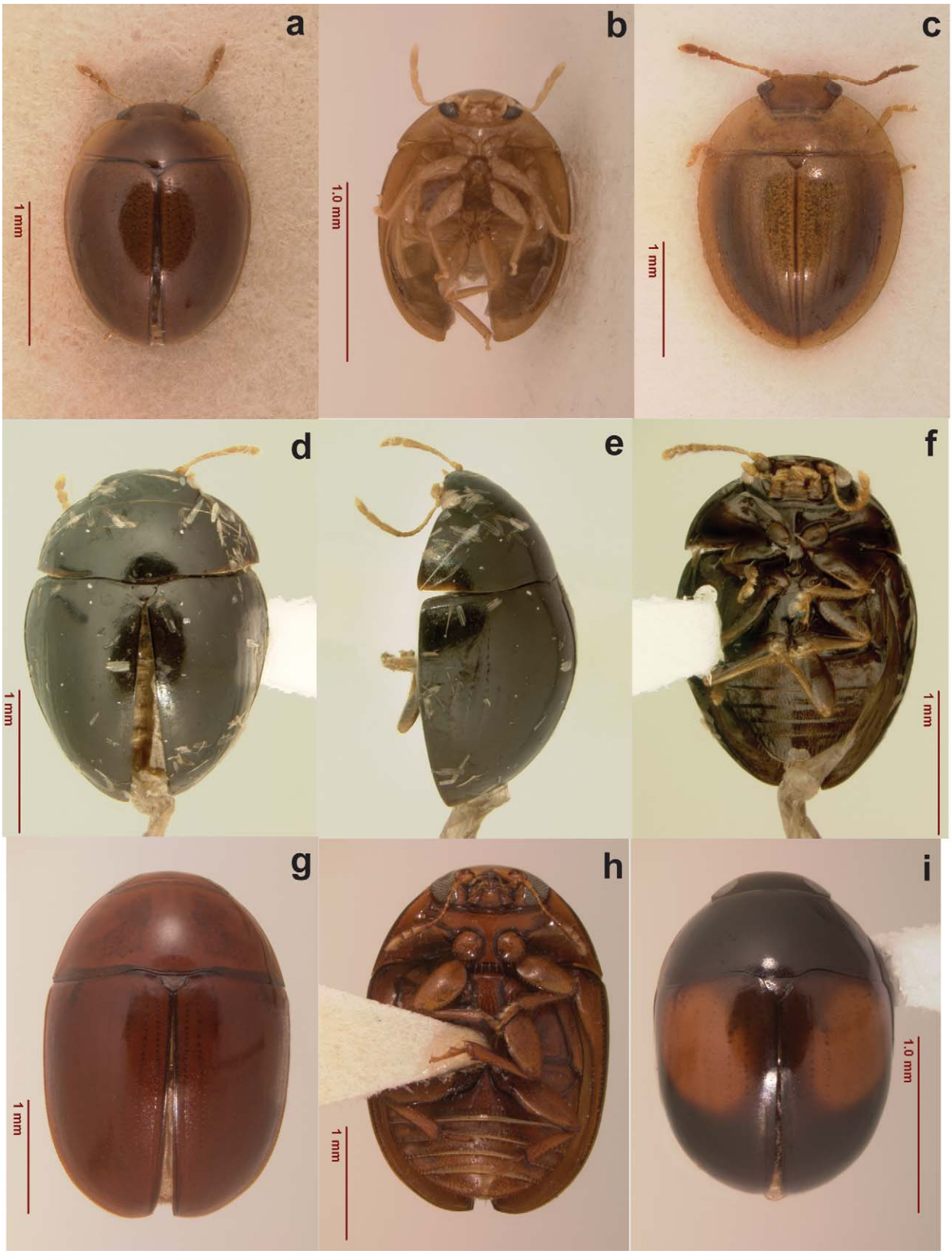

FIGURE 37. Photographs. *Phaenocephalus* sp.: (a) dorsal; (b) ventral. *Phalacrinus* sp.: (c) dorsal. *Ranomafanacrinus nigrinus*, holotype: (d) dorsal; (e) lateral; (f) ventral. *Acylomus aciculatus*: (g) dorsal; (h) ventral. *Acylomus bicolor*: (i) dorsal.

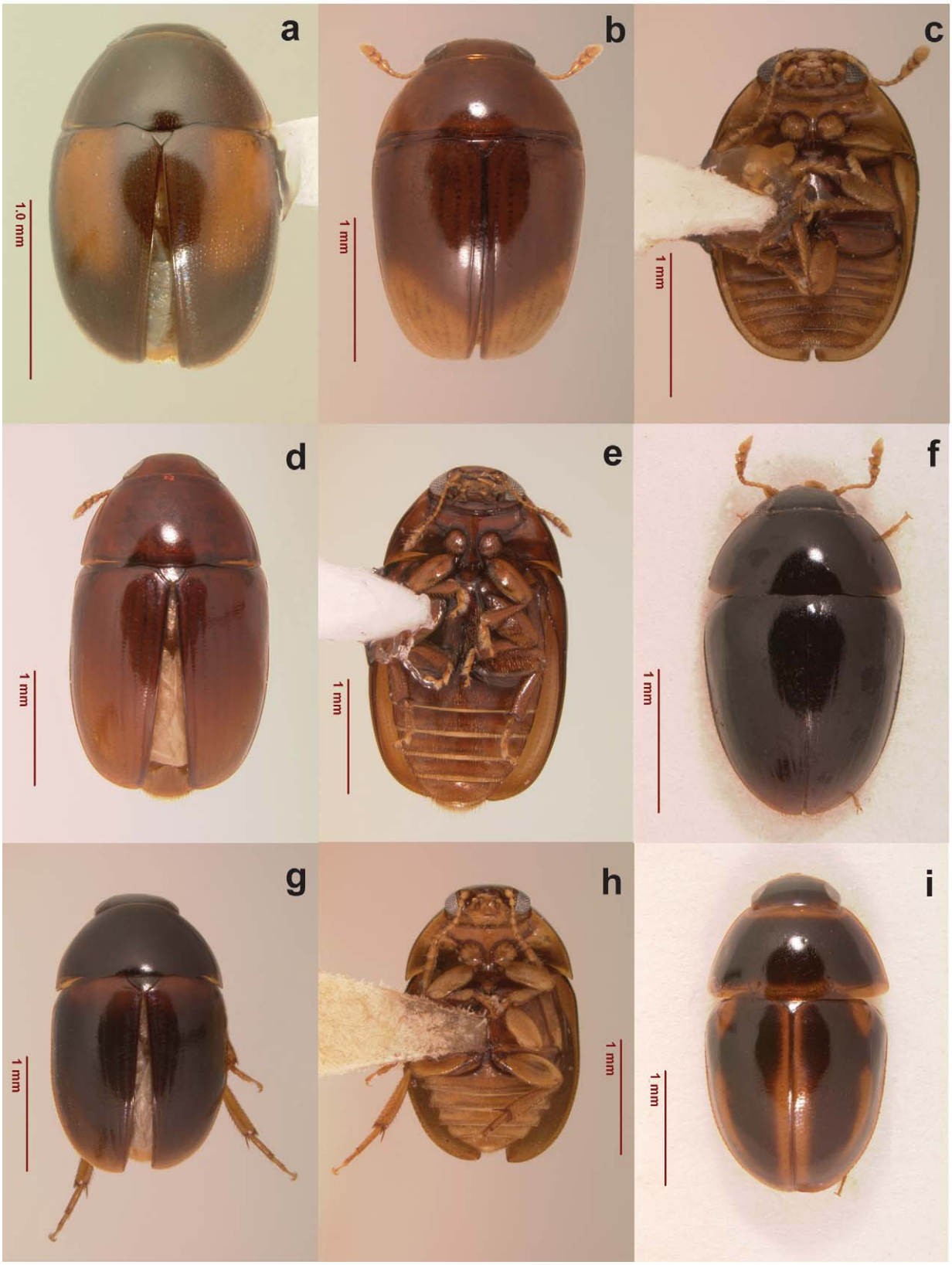

FIGURE 38. Photographs. *Nesiotus* n.sp.: (a) dorsal. *Stilbus* nr. *apicalis*, male: (b) dorsal; (c) ventral. *Xanthocomus* sp.: (d) dorsal; (e) ventral. *Pseudolibrus* sp.: (f) dorsal. *Litostilbus testaceus*: (g) dorsal; (h) ventral. *Litostilbus* sp., southeast Asia: (i) dorsal.

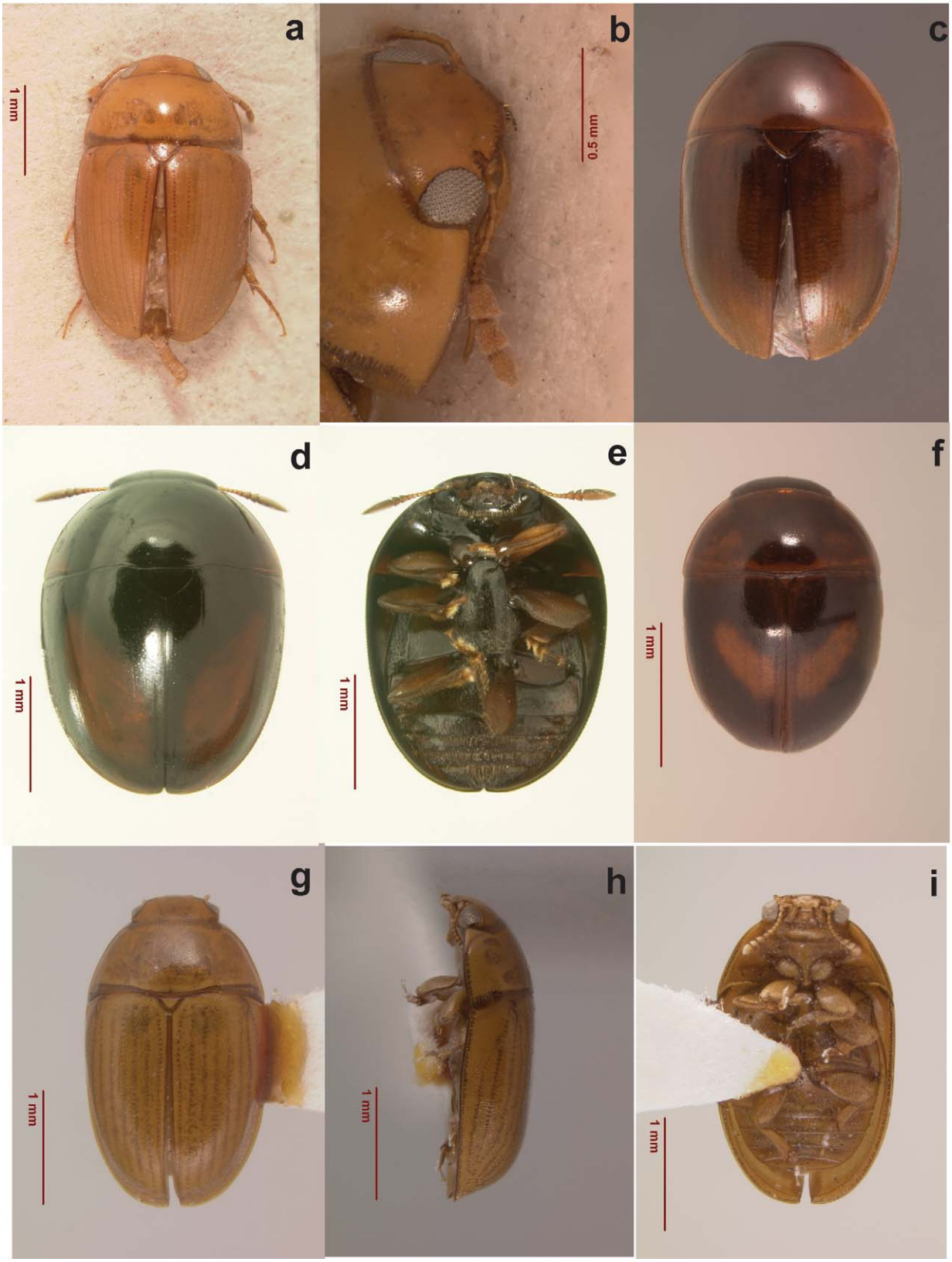

FIGURE 39. Photographs. *Megistopalpus simoni*, lectotype: (a) dorsal; (b) view of antenna and maxillary palp. *Phalacropsis dispar*: (c) dorsal. *Phalacrus rufoguttatus*: (d) dorsal; (e) ventral. *Austroporus* sp.: (f) dorsal. *Platyphalacrus lawrencei*: (g) dorsal; (h) lateral; (f) ventral.

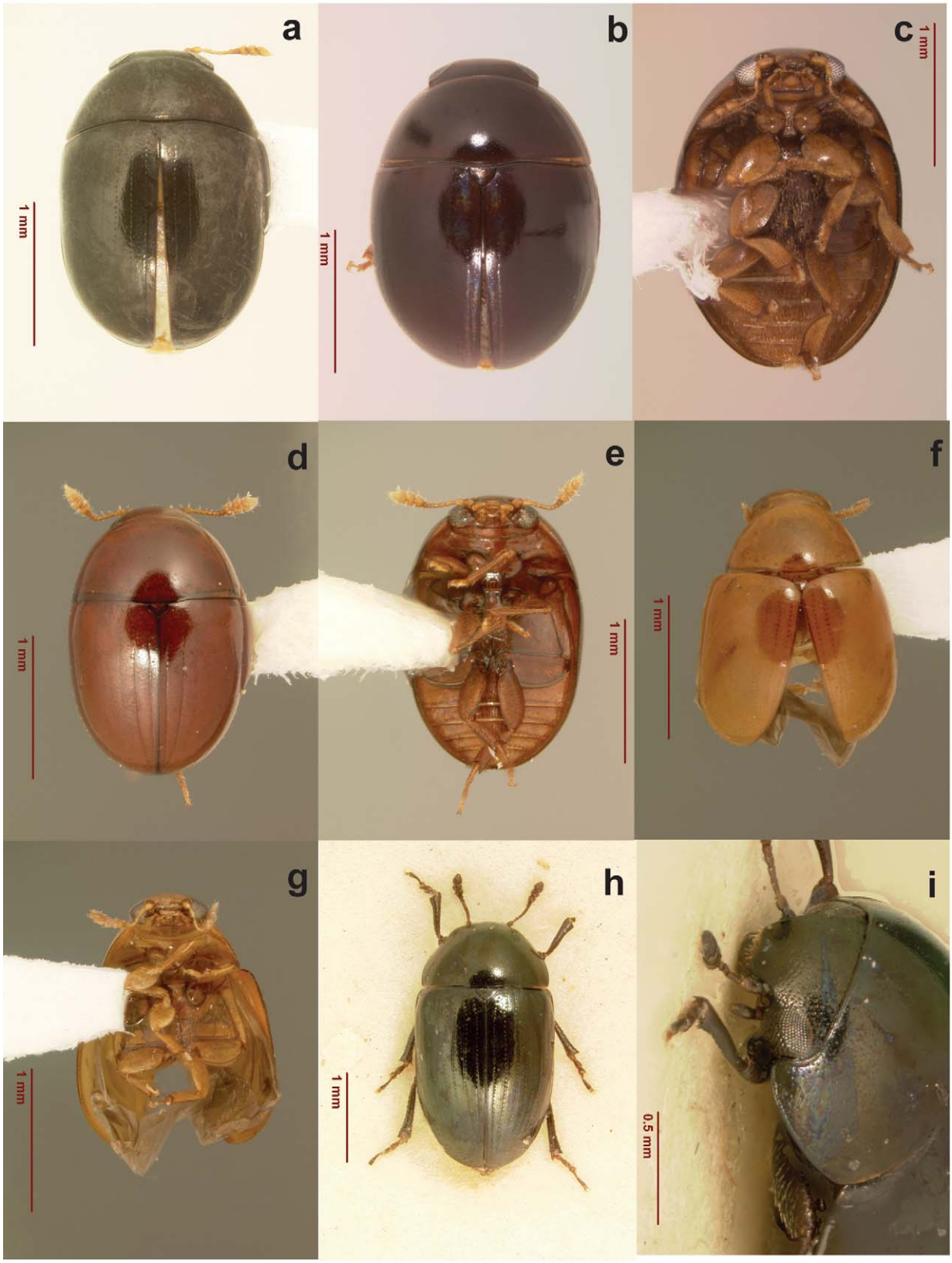

FIGURE 40. Photographs. *Olibroporus punctatus*: (a) dorsal. *Pycinus* sp.: (b) dorsal; (c) ventral. *Ochrolitus rubens*: (d) dorsal; (e) ventral. *Sveculus lewisi*, holotype: (f) dorsal; (g) ventral. *Tolyphus* (*Tolyphus*) *granulatus*: (h) dorsal; (i) head and pronotum laterally, showing eye facets.

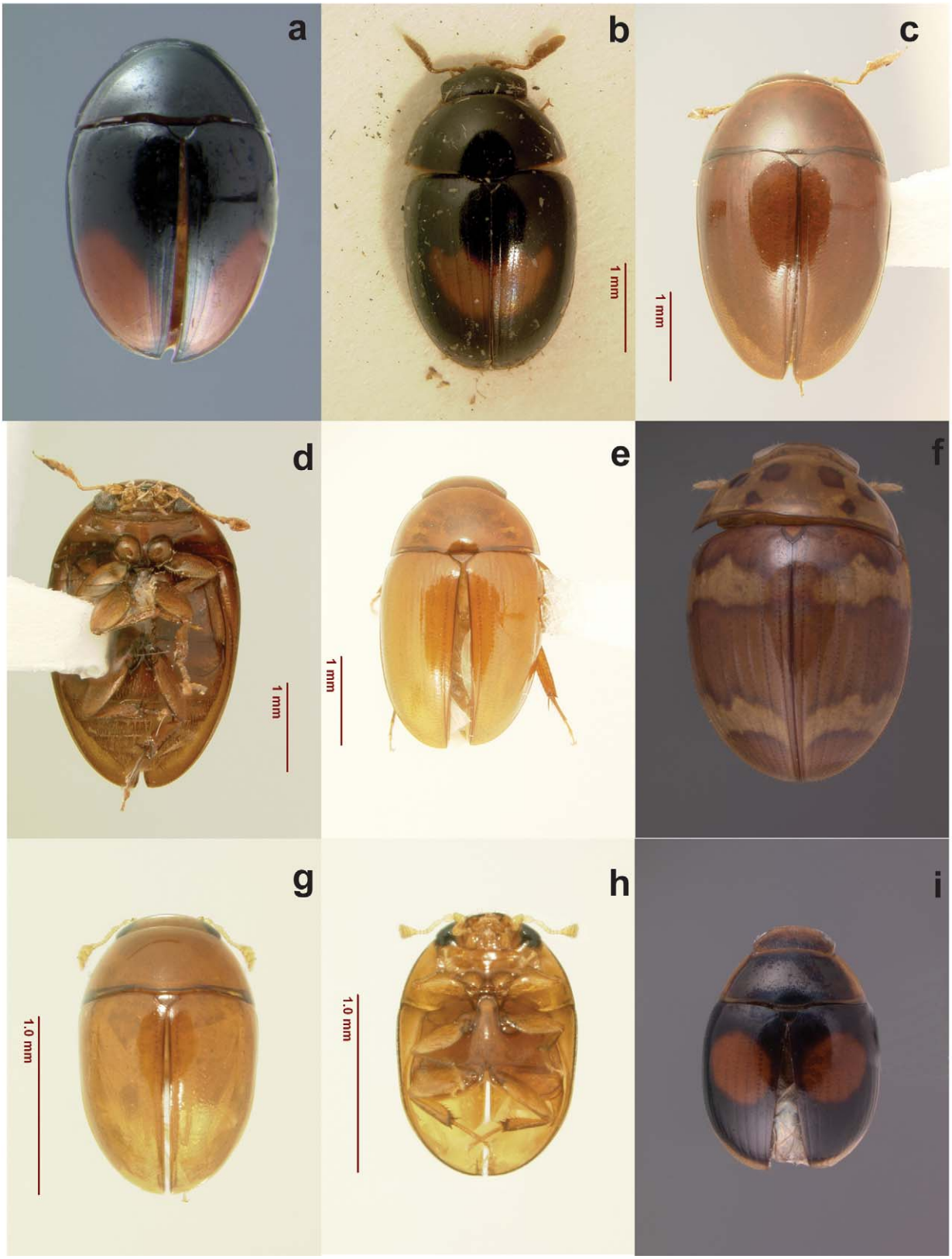

FIGURE 41. Photographs. *Olibrus* sp.: (a) dorsal. *Antennogasmus cordatus*, holotype: (b) dorsal. *Malagasmus thalesi*, holotype: (c) dorsal; (d) ventral. *Olibrosoma testacea*: (e) dorsal. *Apallodes* sp.: (f) dorsal. *Augasmus humilis*: (g) dorsal; (h) ventral. *Entomocnemus* sp., southeast Asia: (i) dorsal.

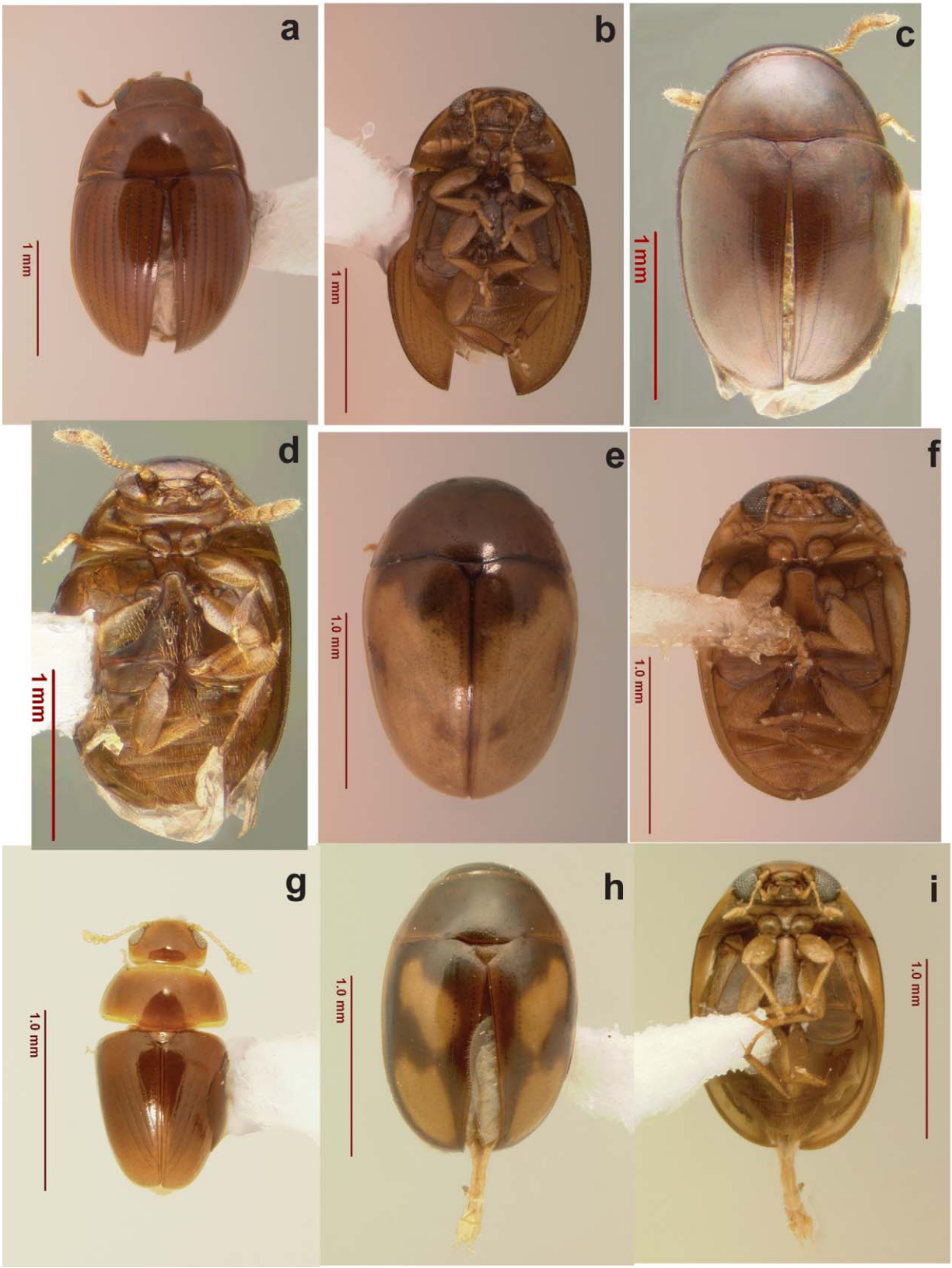

FIGURE 42. Photographs. *Grouvelleus* n.sp., Africa: (a) dorsal; (b) ventral. *Litochropus* n.sp.: (c) dorsal; (d) ventral. *Litochrus* sp.: (e) dorsal; (f) ventral. *Malagophytus steineri*, holotype: (g) dorsal. *Neolitochrus pulchellus*: (h) dorsal; (i) ventral.

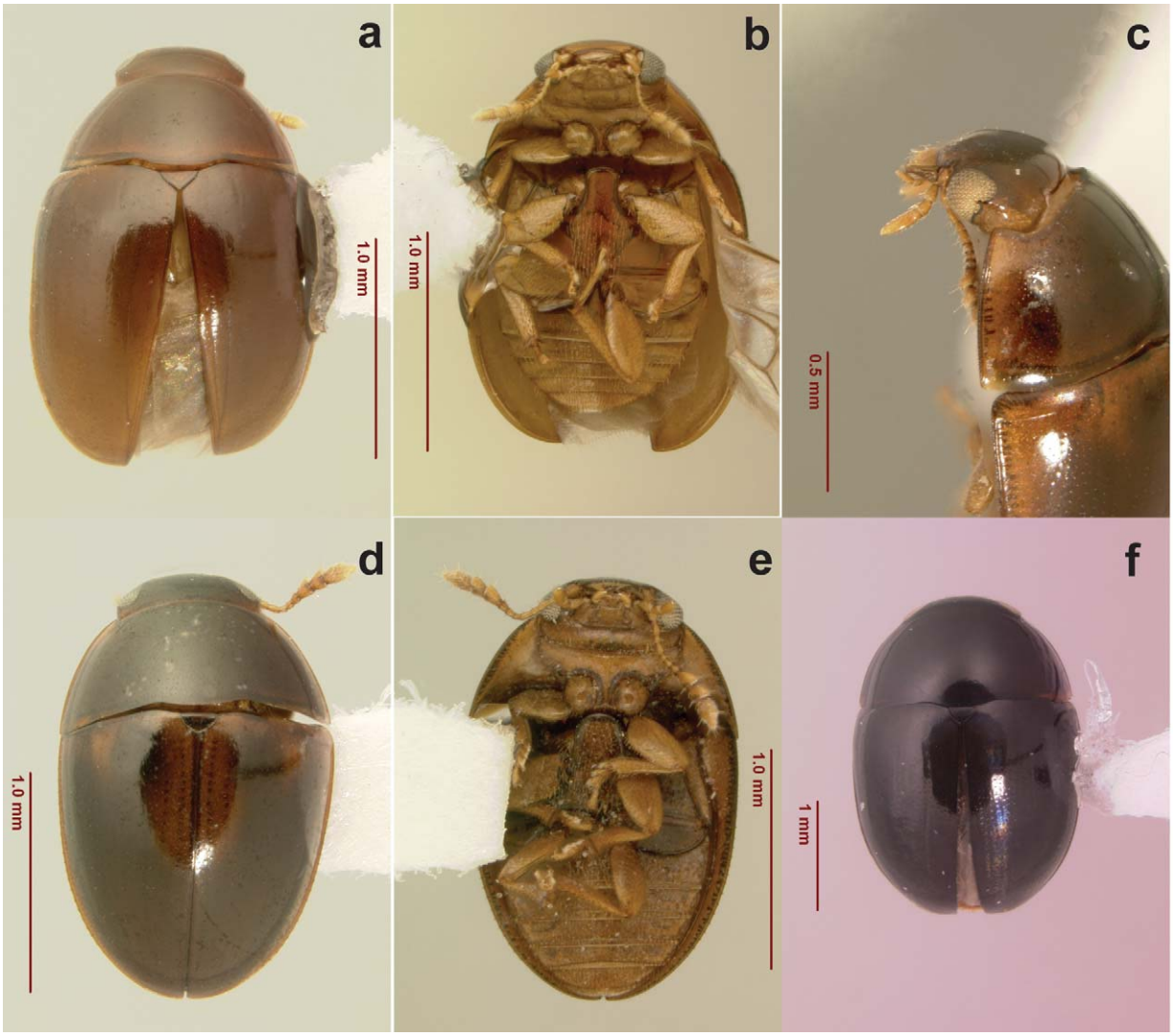

FIGURE 43. Photographs. *Paracylomus asiaticus*: (a) dorsal; (b) ventral. *Steinerlitrus warreni*: (c) head and pronotum laterally, showing posterior eye emargination; (d) dorsal; (e) ventral. *Eulitrus estriatus*: (f) dorsal.

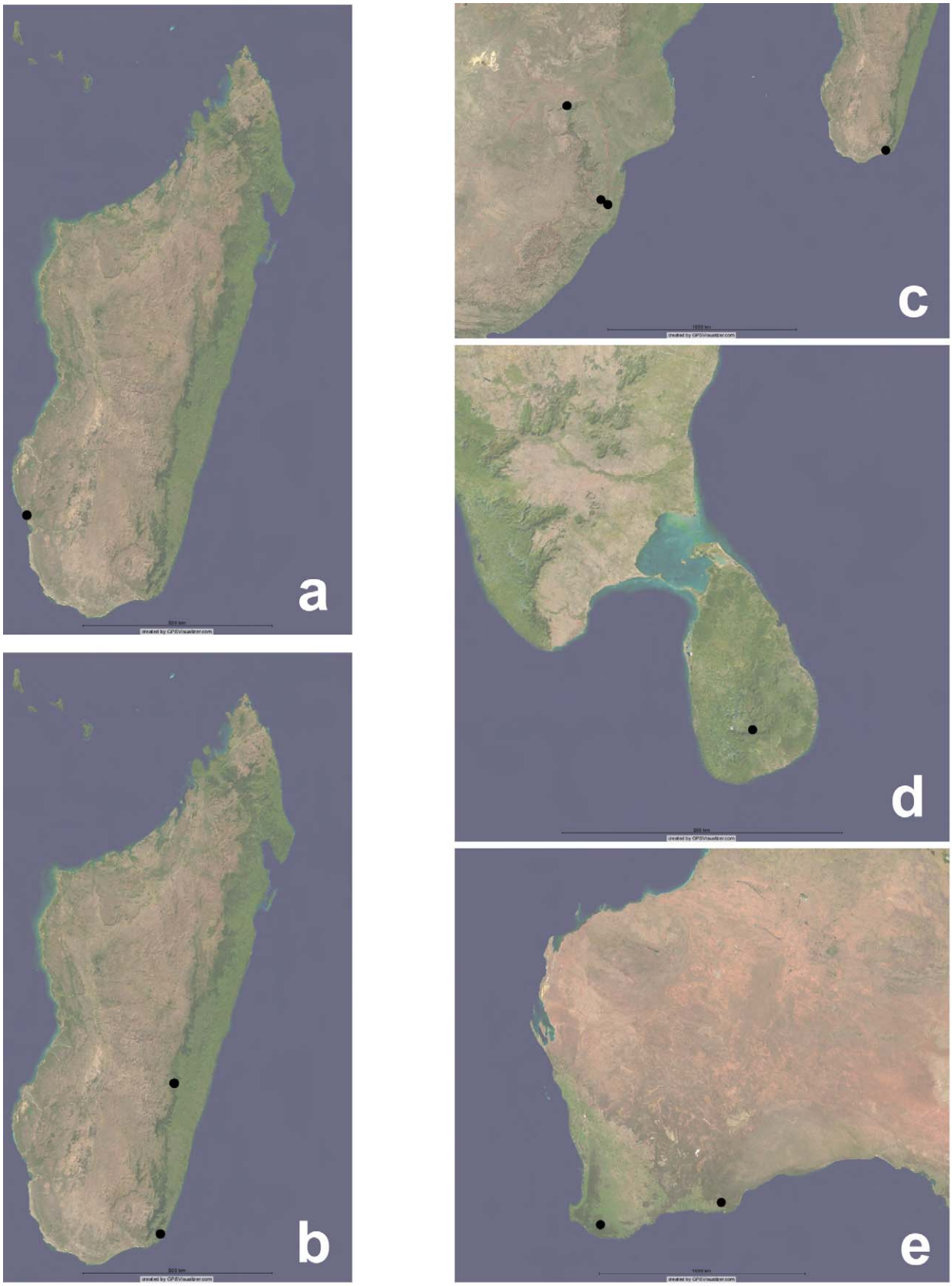

FIGURE 44. Collection localities. (a) *Malagasmus thalesi* distribution in Madagascar; (b) *Malagophytus steineri* distribution in Madagascar; (c) *Antennogasmus cordatus* distribution in southern Africa and Madagascar; (d) *Paracylomus asiaticus* distribution in Sri Lanka; (e) *Platyphalacrus lawrencei* distribution in Western Australia.

MORPHOLOGICAL CHARACTER MATRIX

	1111111111	2222222222	3333333333	4444444444	5555555555	6666666666	7777777777	8888888888	999999999
	123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	012345678
Brachypterus	000000001	0000022000	1020200000	0001000000	1000001100	0000010001	0100100100	0100-00001	0101200001	011000000
Cyclaxyra	110000000	0000000000	0000001100	1001000000	0000000000	0000002010	2000010100	0000000020	100???????	010120100
Propalticus	000100001	0000010000	0010100000	0000000000	0000000000	0300010000	101000000-	1000000000	1000000000	100001000
Placonotus	000100000	0000120010	0010101010	0000000000	0000000000	010000010-	000000000-	1100000000	1000000000	100000010
Acylomus aciculatus	110011100	1100101010	0300001101	0101001001	0000001001	010101111-	1010112110	0110000110	1001001020	010001010
Acylomus bicolor	110010100	1100101010	0300100101	1101001001	0000001011	010100111-	1010112110	0100000110	1001001020	010001010
Acylomus calcaratus	110021100	1100101010	0300201101	0101001001	0000001001	010101110-	1010011110	0110000110	1001001100	010001010
Acylomus micropus	110001100	1100101010	0000101101	1101001000	0000001001	010101110-	1010021110	0100000010	1001000000	010000010
Antennogasmus	100020100	1100221000	0000010101	0001001000	0100001011	0101011011	2110110110	0110000221	1101211120	000000010
Apallodes	110020100	1100202001	1000000101	0011001000	0000011011	1101011011	2110100010	1110000110	1101200120	000001000
Augasmus	110010000	1100001000	0001001101	0101011100	0101001011	010101210-	2010021110	0100100220	1011100001	100111110
Austroporus	100110100	1100010001	0000000101	0011001000	1000001011	1101011211	1010010010	0110000010	1101200120	100001010
Entomocnemus	110010000	1100001000	0200000101	0001001000	1000001011	010101211-	2110010110	0100000101	1101000000	000000010
Eulitrus	110020100	1100201001	0000000101	0011101100	0100001011	000101110-	2010121110	1110000110	1101210120	000011120
Grouvelleus	110010000	1100001000	1201200101	0011001000	0100101011	0501001011	2210000110	0110000010	1101111120	000001020
Litochropus	110010000	1100001010	0000000101	1001001000	0000001001	011101111-	2011021110	0110000120	1101000001	000100010
Litochrus	110010000	1100121001	0000100101	0001001100	0100001011	010101111-	0010120010	1110000120	1101200120	000011020
Litostilbus	100010010	1100120000	0000000101	1001001000	0100001111	0311011011	2110000010	1110000220	1101100101	000101020
Malagasmus	110020100	1100022000	0011000101	0001011000	01000?1011	0111011011	2110011110	0100100220	1011201110	100110010
Neolitochrus	100020000	1100011000	0001000101	1101001100	0000001001	0201011201	2010121110	0010000220	1001000001	000101010
Nesiotus	100021000	1100001000	0000001101	1101001001	0000001011	011101110-	1010011110	0111000110	1001000120	010020010
Ochrolitus	110010100	1100021100	0000100101	1011001011	0100001011	021101011-	1110011110	1110000120	1101200121	000100020
Olibroporus	100010100	1100011100	0000000101	0011001000	1000001001	110101111-	1010110010	0110000010	1101100120	100001010
Olibrosoma	100020100	1101010000	0011110101	0001011000	1100001001	0111011011	2010021110	0100100220	1011111120	100011010
Olibrus aeneus	110010000	1100020000	0000100101	0011001100	1000011001	020101110-	2010120110	0100000111	1001001101	000010011
Olibrus sp. 1	110010100	1100020000	0000100101	0011001100	1000001001	020101110-	1010120110	0100000111	1101011110	000111011
Paracylomus	110010000	1100020000	0000000101	0011001100	0000001011	020101110-	1010021110	1111000110	1101100000	010110110
Phaenocephalus	010000000	0100101000	0102001101	0101001100	0011001001	0001002000	2011000011	1000010001	0102100000	010000100
Phalacrinus	010000000	1110032000	2201201111	0001001100	1011001001	0501102000	1111000010	1000010001	0101000100	010000010
Phalacropsis	110010010	1100000010	0000100101	0001001100	1000001101	0001011011	2010120111	0111000011	1101200001	011020010
Phalacrus	100010010	1100100010	0000100101	0001001100	1000001101	0101011011	2010120111	1111000011	1101200001	011110012
Platyphalacrus	110100100	1100110010	0000200101	00?1001000	1000001001	1101111211	2010110010	1110000010	0101000120	100001???
Pseudolibrus	100010010	1100020010	0000000101	1001001000	0100001101	0511011011	2110000110	0110000120	1101200000	000001120
Pycinus sp. 1	110010100	1100011101	0000100101	0011001000	1000001011	110101211-	1010110010	0110000110	1101200020	000001010
Pycinus sp. 2	100000100	1100011101	0000100101	0011001000	1000001001	110101211-	1010110010	0110000010	1101000000	000001110
Steinerlitrus	110001000	0100220001	0000000101	1011001100	0000001001	010101110-	2010020110	1110000010	1101000000	100120010
Stilbus	110000100	1100001010	0300001101	1101001001	0000001001	010101110-	1110112210	0100000011	1011000000	010021010
Sveculus	110010000	1100011000	0000000101	1011011010	0100001001	011101210-	2010011110	0110000100	1101100100	010000000
Tolyphus (Pharcisinus)	100000001	1100022010	0000100101	0001001100	1000001001	010000010-	1010120110	0110001011	1001011100	000111021
Tolyphus (Tolyphus)	101010001	1100022010	0000200101	0001001100	1000001001	020000010-	1010120210	0110001011	1001011100	000111011
Xanthocomus rutilans	110010100	2100001011	0000101101	0101001001	0000001001	010101111-	1010111110	0100000010	1001000001	010000010
Xanthocomus striatus	110010100	2100001011	0300001101	1101001001	0000001011	010101111-	1010111110	0110000010	1001001021	010000010

FIGURE 45. Character matrix of 98 morphological characters for 38 taxa of Phalacridae and 4 outgroup taxa.

Species

Parasemus parvopallidus Lea, 1932 (Distribution: Australia [Queensland])

Examination of the hind leg illustration accompanying the original description of this species (Lea 1932: fig. 53) revealed a tibial and tarsal structure not found in the Phalacridae. It is, however, quite similar to some Hydrophilidae (especially species currently described in *Paracymus*), and so I am tentatively transferring it to that family.

Genera

Sternosternus Guillebeau 1894*c*: ccvii. Type species: *Sternosternus grouvellei* Guillebeau 1894, fixed by monotypy.

My examination of the type specimen (from Sumatra) of the only included species, *S. grouvellei*, revealed that it belongs to the family Hydrophilidae. Based on an identification made from a dorsal habitus photograph, it belongs to the tribe Coelostomatini (subfamily Sphaeridiinae), probably the genus *Dactylosternum* Wollaston (Andrew E.Z. Short, personal communication).

Phylogenetic treatment

The attempt at formulation of a higher classification in the family Phalacridae is beset with difficulties. Surveying the genera in a pre-phylogenetic context, one finds no overt structural syndromes upon which to divide up the family into mutually exclusive units. Instead, one is presented with an exasperating number of permutations of mostly binary characters. Even the would-be constructor of a purely phenetic classification would be stymied by the amount of convergent evolution that has apparently occurred within the group, since no one character system or systems in combination seem to emerge above the rest to aid in creation of stable subdivisions.

In order to tackle this problem I have conducted a phylogenetic analysis based on a detailed morphological study of the family. Application of cladistic methodology in light of the above issues is problematic for many of the same reasons, but at least has the advantage of being more statistically sound.

Taxon sampling. An effort was made to study at least one representative of each described genus that was not obviously a junior synonym, as well as putative undescribed genera. Additionally, two or more species were examined from particularly large, widespread, or polymorphic genera. Certain genera were represented only by singletons (*Ranomafanacrinus* Gimmel) or doubletons (*Malagophytus* Gimmel, *Megistopalpus* Guillebeau), were not disarticulated and accordingly were excluded from the phylogenetic analysis. In cases where one of the sexes was not disarticulated, the genitalia of the non-disarticulated sex was examined from a dissected specimen (see Materials and Methods section for details). Choice of outgroups was based on previously hypothesized sister taxa and select other "lower" cucujoids. These were Laemophloeidae (*Placonotus* Macleay), Propalticidae (*Propalticus* Sharp), Kateretidae (*Brachypterus* Kugelann), and Cyclaxyridae (*Cyclaxyra* Broun).

The following exemplar taxa and specimens were disarticulated for the morphological phylogenetic analysis (* = outgroups; *ND* = not disarticulated):

Taxon	♂	♀
**Brachypterus urticae* (Fabricius)	Tennessee, USA	Tennessee, USA
**Cyclaxyra politula* (Broun)	New Zealand	New Zealand
**Propalticus* sp.	Malaysia	Malaysia
**Placonotus zimmermani* (LeConte)	Louisiana, USA	Louisiana, USA
Acylomus aciculatus Sharp	Colombia	Panama
Acylomus bicolor (Sharp)	Puntarenas, Costa Rica	*ND*
Acylomus calcaratus Casey	Louisiana, USA	Louisiana, USA
Acylomus micropus (Guillebeau)	Tuleár, Madagascar	Tuleár, Madagascar
Antennogasmus cordatus n.sp.	Transvaal, South Africa	*ND*
Apallodes sp.	Peru; Mexico	*ND*
Augasmus humilis (Guillebeau)	Luzon, Philippines	Songkhla, Thailand
Austroporus victoriensis (Blackburn)	Queensland, Australia	ACT, Australia
Entomocnemus sp.	*ND*	South Africa
Eulitrus estriatus Sharp	Panama; Costa Rica	*ND*
Grouvelleus dilutus (Champion)	Sabah, Malaysia	Sabah, Malaysia
Litochropus clavicornis Casey	Louisiana, USA	Louisiana, USA
Litochrus brunneus (Erichson)	Tasmania, Australia	Tasmania, Australia
Litostilbus testaceus (Fabricius)	Andros, Bahamas	Andros, Bahamas
Malagasmus thalesi n.sp.	*ND*	Toliara, Madagascar
Neolitochrus pulchellus (LeConte)	Louisiana, USA	Louisiana, USA
Nesiotus undescribed sp.	Madagascar	Madagascar
Ochrolitus rubens (LeConte)	Louisiana/Florida, USA	Louisiana, USA
Olibroporus punctatus Casey	Louisiana, USA	Louisiana, USA
Olibrosoma testacea Tournier	*ND*	Mauritania
Olibrus aeneus (Fabricius)	Luxembourg	Luxembourg
Olibrus sp.	Louisiana, USA	Louisiana, USA
Paracylomus asiaticus (Champion)	Sri Lanka	Sri Lanka
Phaenocephalus sp.	Sabah, Malaysia	Sabah, Malaysia
Phalacrinus dilatatus (Champion)	Kelantan, Malaysia	Kelanton, Malaysia
Phalacropsis dispar (LeConte)	California, USA	California, USA
Phalacrus sp.	Oklahoma, USA	New Mexico, USA
Platyphalacrus lawrencei n.sp.	Western Australia	*ND*
Pseudolibrus sp.	*ND*	Iringa, Tanzania
Pycinus sp. 1	El Paraiso, Honduras	Panama
Pycinus sp. 2 (flattened form)	*ND*	Panama
Steinerlitrus warreni n.sp.	Amazonas, Venezuela	Amazonas, Venezuela
Stilbus sp. near *apicalis* (Melsheimer)	New Mexico, USA	New Mexico, USA
Sveculus lewisi n.sp.	Sulawesi, Indonesia	Sulawesi, Indonesia
T. (Pharcisinus) punctulatus Rosenhauer	Nouasser, Morocco	*ND*
T. (Tolyphus) granulatus (Guérin)	Algeria	*ND*
Xanthocomus rutilans (Casey)	Texas, USA	*ND*
Xanthocomus striatus Guillebeau	enezuela	*ND*

Character analysis. No *a priori* assumptions about character polarity were made for any of the characters utilized. Since outgroup character distribution is polymorphic for many characters, I have avoided specifying polarity and instead have simply included the four outgroup taxa in the analysis.

Disarticulated specimens were examined and character states of each of 98 morphological characters were scored into a matrix using WinClada 1.00.08 (Nixon 2002) (see Fig. 45). Larval characters were omitted since larvae are known or described for only a handful of genera (ca. 15%). Characters were all discrete and were treated as unordered and unweighted. Following is a list of characters scored for phylogenetic analysis. In the interest of clarity I have included annotations, since I have introduced a few new characters and since morphological terms are far from standardized. I have also shown the length, consistency index, and retention index (from the strict consensus tree) for individual characters in square brackets.

1. *Head capsule width at tempora*. (0) narrower than width at eyes; (1) as wide as width at eyes. The head is narrowed posteriorly in the *Phaenocephalus*-group (Figs. 2j, k) and in most outgroups (except *Cyclaxyra*). [*L* = 2; *ci* = 0.50; *ri* = 0.75]
2. *Eye facet surface*. (0) convex; (1) flat. This character was coded under the compound microscope only; it is not easily visible under a dissecting microscope. The facets are convex in most outgroups (except *Cyclaxyra*) and in many phalacrid genera. [*L* = 11; *ci* = 0.09; *ri* = 0.28]
3. *Eye facet size*. (0) uniform; (1) dorsal facets abruptly smaller. In S1 (Fig. 40i) approximately the dorsal third of the eye is composed of facets about half the diameter of those in the ventral two-thirds of the eye. This state is found only in *Tolyphus* (*s.str.*). [*L* = 1; uninformative]
4. *Eye interfacetal setae*. (0) absent; (1) present. Interfacetal setae are present most visibly in *Platyphalacrus*, but a few setae are present in *Austroporus*. This state also occurs in the laemophloeid and propalticid outgroups. [*L* = 2; *ci* = 0.50; *ri* = 0.66]
5. *Eye medial emargination*. (0) absent; (1) weak; (2) distinct. S2 is expressed as a rounded notch at the point of intersection with the frontoclypeal margin. S1 is represented by a shallow embayment of the eye margin, while in S0 there is no detectable embayment. The medial emargination is absent in all outgroups. [*L* = 13; *ci* = 0.15; *ri* = 0.38]
6. *Eye posterior sharp emargination*. (0) absent; (1) present. S1 is typified by *Steinerlitrus* (Fig. 43c) and some of the *Stilbus*-group. All outgroups lack the posterior emargination. [*L* = 5; *ci* = 0.20; *ri* = 0]
7. *Eye dorsal margin periocular groove*. (0) absent; (1) present. This is a slight groove usually deepest along the medio-posterior portion of the dorsal eye margin. It is seen most easily in dry-mounted specimens using reflected light. The groove is present in about half the phalacrid taxa coded, and absent in all outgroups. [*L* = 6; *ci* = 0.16; *ri* = 0.72]
8. *Frontoclypeal emargination above antennal insertion.* (0) present; (1) absent. When the frontoclypeal emargination is absent, the frontoclypeal margin forms a continuous arcuate shelf between the eyes (Fig. 2d). The emargination is absent in the *Pseudolibrus*-group and *Phalacrus*-group. [*L* = 2; *ci* = 0.50; *ri* = 0.66]
9. *Frontoclypeal margin above labrum*. (0) straight to slightly arcuate; (1) weakly emarginate. Emarginate in *Tolyphus* (Fig. 2e) and two of the outgroups (*Brachypterus* and *Propalticus*). [*L* = 3; *ci* = 0.33; *ri* = 0.33]
10. *Head capsule ventral seta-lined ridge behind eye*. (0) absent; (1) present, transverse; (2) present, oblique. This is a carina on the gena separating the anterior portion of the gena (postocular area) from the posterior portion, the latter of which is on a slightly higher plane. It contains a row of decumbent anteriorly-directed setae. The carina usually runs from the ventral mouthparts to the lateral portion of the gena (Fig. 2n), often quite close to the eye margin but sometimes quite distant from it. In many genera, the more medial portion of the carina is obliquely oriented, but becomes transverse laterally (behind the eye). These are scored as having a transverse ridge (S1). In those scored as having an oblique ridge (species of *Xanthocomus*), the ridge is oblique for its entire length (Fig. 2m). In some taxa (*Phaenocephalus*, *Ranomafanacrinus*, *Steinerlitrus*, and outgroups) the ridge is entirely absent. [*L* = 4; *ci* = 0.50; *ri* = 0.66]
11. *Antennomere I attachment to head capsule*. (0) arising from base of antennomere I; (1) arising midlaterally from antennomere I. The lateral attachment of the antennal scape (see Fig. 8b) to the head is a putative synapomorphy for Phalacridae. [*L* = 1; *ci* = 1.0; *ri* = 1.0]
12. *Antennomere I shape*. (0) ovoid; (1) triangular. The triangularly lobed scape (Fig. 5b) is found only in *Phalacrinus*. [*L* = 1; uninformative]
13. *Antennal club number of segments*. (0) three; (1) four or five. The four- to five-segmented antennal club (Fig. 26b) is found only in *Olibrosoma*. An undescribed species of *Pycinus* from Brazil possesses a 5-segmented club but it was not included in this analysis. All outgroups possess the 3-segmented condition (the antennal club present only in female of *Placonotus zimmermani*; the female state is coded for this and the following character). [*L* = 1; uninformative]
14. *Antennal club symmetry.* (0) weakly asymmetrical; (1) symmetrical; (2) strongly asymmetrical. The antennal club is considered symmetrical (Fig. 7b) if the flattened portions of the club segments are approximately equal on both sides of the antennal axis. The asymmetry is considered weak if the flattened portion on one side is more prominent (Fig. 21b), and strong if the flattened portion is only present on one side of the axis (Fig. 29b). The club is weakly asymmetrical in most outgroups (except *Placonotus* in which it is symmetrical) and most phalacrid genera. The club is strongly asymmetrical in *Antennogasmus*, *Apallodes*, *Eulitrus*, and *Steinerlitrus*. [*L* = 12; *ci* = 0.16; *ri* = 0.16]
15. *Antennomere XI subapical constriction*. (0) absent; (1) present, on anterior aspect only; (2) present, on both anterior and posterior aspects. The complete constriction is most extreme in the *Olibrus*-group (Figs. 22b, 23b). Outgroups are variable in regard to this character. [*L* = 13; *ci* = 0.23; *ri* = 0.52]
16. *Mandibular apex*. (0) tridentate; (1) bidentate; (2) simple. A mandibular tooth is considered apical if it is distal to the prosthecal region. Most outgroups (except *Brachypterus*, whose mandibular apex is simple) possess the tridentate condition. [*L* =

10; *ci* = 0.20; *ri* = 0.55]

17. *Mandible dorsal blade subapical series of teeth*. (0) absent; (1) present. These are small, blunt denticles just proximal to the dorsalmost tooth of the mandibular apex along the dorsal blade (Fig. 17a). They are present in *Ochrolitus*, *Olibroporus*, and *Pycinus*. [*L* = 3; *ci* = 0.33; *ri* = 0.33]
18. *Mandibular retinaculum*. (0) absent; (1) present. The retinaculum, when present, is adjacent to the anterior portion of the prostheca (Fig. 6a). It is absent in most outgroups (but present in *Placonotus*). [*L* = 7; *ci* = 0.14; *ri* = 0.57]
19. *Mandibular ventral ridge*. (0) absent; (1) present. This is a ridge of cuticle of unknown function (see Fig. 11a). It is present in *Apallodes*, *Austroporus*, *Eulitrus*, *Litochrus*, *Pycinus*, *Steinerlitrus*, and *Xanthocomus*. [*L* = 6; *ci* = 0.16; *ri* = 0.37]
20. *Galea shape*. (0) rounded; (1) acute; (2) securiform. All outgroups (except *Brachypterus*, with an acute galea) possess a rounded galea. *Apallodes* and *Grouvelleus* possess an acute galea, while in *Phalacrinus* it is securiform. [*L* = 4; *ci* = 0.50; *ri* = 0]
21. *Lacinial apex*. (0) with two small, stout spines; (1) with setae only; (2) with multiple spines; (3) with two spines plus tuft of setae. Most taxa of Phalacridae (and outgroups) have only two stout spines. *Phaenocephalus* possesses only setae, while most of the *Stilbus*-group have a tuft of setae in addition to the spines. [*L* = 7; *ci* = 0.42; *ri* = 0.33]
22. *Mentum laterally.* (0) pointed (sides divergent); (1) parallel-sided. In most phalacrids the sides of the mentum diverge apically, but in *Malagasmus* and *Olibrosoma* (and in the outgroups *Placonotus* and *Propalticus*) the sides are parallel. In one outgroup (*Brachypterus*) the sides are convergent apically. [*L* = 3; *ci* = 0.66; *ri* = 0.66]
23. *Labial palpomere III shape*. (0) fusiform; (1) nearly triangular, widest at apex; (2) constricted at apex. The terminal labial palpomere is fusiform (Fig. 2g) in most taxa (including the outgroups), widest at apex (Fig. 2h) in a few (almost circular in *Phalacrinus*), and constricted at apex (Fig. 2i) in one (*Phaenocephalus*). [*L* = 5; *ci* = 0.40; *ri* = 0.40]
24. *Labrum apical margin.* (0) arcuate; (1) truncate; (2) emarginate. Since the setae are dense and the character state differences slight, this character usually requires disarticulation and viewing under a compound microscope for proper observation. This character is variably distributed among the outgroups. [*L* = 16; *ci* = 0.12; *ri* = 0.26]
25. *Gular median internal tubercle*. (0) absent; (1) present. This is an internal round, raised area medially at the front of the gula, visible only in thoroughly cleared specimens. Apparent only in *Antennogasmus* and *Olibrosoma*. [*L* = 2; *ci* = 0.50; *ri* = 0]
26. *Gular sutures*. (0) short, barely evident; (1) long, extending at least halfway to ventral mouthparts. The gular sutures are short to absent in the majority of Phalacridae and in two of the outgroups (*Brachypterus* and *Propalticus*). [*L* = 6; *ci* = 0.16; *ri* = 0.54]
27. *Transverse occipital ridge*. (0) present; (1) absent. Present only in outgroups (all except *Cyclaxyra*). [*L* = 1; *ci* = 1.0; *ri* = 1.0]
28. *Head capsule median endocarina*. (0) absent; (1) present. The endocarina, when present (in *Phalacrinus* and the outgroup *Placonotus*), occurs at the occiput, and may be quite short. [*L* = 2; *ci* = 0.50; *ri* = 0]
29. *Corpotentorium.* (0) sclerotized; (1) membranous (appearing absent). The membranous corpotentorium is a putative synapomorphy for Phalacridae. [*L* = 1; *ci* = 1.0; *ri* = 1.0]
30. *Pronotal disc scattered microsetae*. (0) absent or indistinct; (1) present, distinct. Visible only in clean, non-abraded, dry-mounted specimens, these setae are quite short, completely recumbent, and longitudinally oriented. [*L* = 11; *ci* = 0.09; *ri* = 0.16]
31. *Prosternum anterior marginal row of setae*. (0) distributed evenly along margin; (1) with gap medially. Although the forward-directed setae along the anterior margin of the prosternum may be abraded, the bases are still visible in disarticulations. A few phalacrid taxa have a medial gap in the distribution of setae, notably in the *Stilbus*-group (Fig. 3a). The setae are distributed evenly in most phalacrid genera and in outgroups. [*L* = 3; *ci* = 0.33; *ri* = 0.80]
32. *Prosternum anterior margin setae shape*. (0) normal; (1) flattened at base, lanceolate. The lanceolate condition of the marginal setae is present in a number of phalacrid taxa. The setae are normal in most phalacrid taxa and outgroups. [*L* = 8; *ci* = 0.12; *ri* = 0.41]
33. *Notosternal suture*. (0) incomplete or absent; (1) complete. The notosternal suture appears to be absent only in outgroups (*Placonotus* and *Propalticus*). [*L* = 1; *ci* = 1.0; *ri* = 1.0]
34. *Hypomeron*. (0) without transverse carina; (1) with transverse carina originating at procoxa. Because of the usual position of the front legs in mounted specimens, this character is most easily observed in disarticulations. S1 occurs only in *Eulitrus*. [*L* = 1; uninformative]
35. *Procoxal cavity extension at anterolateral corner.* (0) present; (1) absent. When present there is a physical gap in the cuticle, not merely a suture, often partially exposing the trochantinopleuron. Disarticulation is generally required to properly assess this character. The gap is present in all outgroups and most phalacrids, but absent in *Augasmus*, *Malagasmus*, *Olibrosoma*, and *Sveculus*. [*L* = 3; *ci* = 0.33; *ri* = 0.33]
36. *Prosternal process vertical foramen*. (0) absent; (1) present. This structure may be conceptualized as an internal, dorsal extension of the apex of the prosternal process that loops and connects back to the main portion of the prosternum. When both procoxae are removed, a complete circular hole can be observed through the prosternum from a lateral aspect. This foramen is not known to occur in any beetle groups except Phalacridae, where it occurs in all genera. [*L* = 1; *ci* = 1.0; *ri* = 1.0]
37. *Prosternal process apical shape*. (0) angulate in lateral view; (1) rounded in lateral view. A rounded prosternal process is often (but not always) associated with a strongly projecting metaventral process that rests upon the prosternal process when the beetle is in repose. [*L* = 4; *ci* = 0.25; *ri* = 0.76]
38. *Prosternal process apical process*. (0) without transparent process; (1) with transparent process. This is a horizontally flattened, arcuate projection that is an extension of the apical margin of the prosternal process (Fig. 40g). It is present in *Ochrolitus*, *Sveculus*, and a few *Entomocnemus* (though not in the species coded). The projection may or may not possess spinelike setae (character 39). [*L* = 2; *ci* = 0.50; *ri* = 0]
39. *Prosternal process apical setae*. (0) without spinelike setae; (1) with series of spinelike setae. These setae, when present, are

always rigid and socketed (not hairlike) and present along the margin of the apex of the prosternal process (Fig. 3a). Series may contain as few as two small setae, placed near the corners (some *Acylomus*), or upwards of 10 extremely prominent setae. These setae abrade easily, so examination of setal sockets under the compound scope may be necessary. Present in *Ochrolitus* and virtually all *Stilbus*-group members. [*L* = 3; *ci* = 0.33; *ri* = 0.71]

40. *Protrochanter*. (0) without setae; (1) with setae. The protrochanter may contain one to two setae arising from about midway along the posterior margin. Setae are present in one of the outgroups (*Brachypterus*) and a few phalacrids. [*L* = 6; *ci* = 0.16; *ri* = 0.64]
41. *Protibial ctenidium*. (0) absent; (1) present. This is a close-set row of short, stout, spinelike setae on the external edge of the protibia. These may extend virtually the entire length of the tibia (Fig. 33c), or may be present as a short row of 5–10 spines (Fig. 34c) (*Litochrus*, some *Apallodes*). In the S0 condition up to 3 spines are present at the outer apical angle of the protibia (Fig. 35c), but these do not form a close-set row. Besides those taxa mentioned above, the ctenidium occurs in the *Pseudolibrus*-group, *Ochrolitus*-group, *Olibrosoma*-group, *Augasmus*, *Eulitrus*, and *Grouvelleus*. It does not occur in any of the outgroups. [*L* = 5; *ci* = 0.20; *ri* = 0.60]
42. *Protibial spurs*. (0) present; (1) absent. Protibial spurs are absent (Fig. 4c) in the *Phaenocephalus*-group. [*L* = 1; *ci* = 1.0; *ri* = 1.0]
43. *Protarsomere number*. (0) five; (1) four. Only four protarsomeres are present (Fig. 4c) in *Phaenocephalus*-group and *Augasmus*. The tarsomere that has been fused or disintegrated is the fourth (nodiform) tarsomere. [*L* = 2; *ci* = 0.50; *ri* = 0.50]
44. *Protarsomere I modification in male*. (0) unmodified; (1) modified. S1 has only been observed in *Grouvelleus*, in which the male protarsomere I is enlarged and densely setose ventrally (Fig. 33c). [*L* = 1; uninformative]
45. *Protarsomere II modification in male*. (0) unmodified; (1) modified. In the modified state, the segment is enlarged with dense setae ventrally. Present in *Apallodes* and a few *Olibrus*. [*L* = 2; *ci* = 0.50; *ri* = 0]
46. *Pretarsal claw basal tooth or angulation*. (0) absent; (1) present. The pretarsal claws of all tarsi have a basal angulation in all Phalacridae and one outgroup (*Brachypterus*). [*L* = 2; *ci* = 0.50; *ri* = 0.50]
47. *Scutellar shield size*. (0) width at base less than longitudinal length of eye; (1) width at base more than longitudinal length of eye. The relative size of the scutellar shield has a bimodal distribution, with a large scutellar shield (Fig. 2b) occurring in the *Pseudolibrus*-group, *Phalacrus*-group, and *Malagophytus* (latter not included in analysis). The outgroup *Brachypterus* also possesses a large scutellar shield. All other outgroups and phalacrid genera studied have a "normal-sized" scutellar shield (Fig. 2a). [*L* = 3; *ci* = 0.33; *ri* = 0.50]
48. *Elytral spectral iridescence*. (0) absent; (1) present. Spectral iridescence (the presence of ordered spectra that change position based on the angle of observation; see Seago *et al.* 2009) is present on the elytra of about half of the genera of Phalacridae (see Fig. 43f), and in none of the outgroups. Hinton and Gibbs (1969) described the structural mechanism of this iridescence. This character is probably highly plastic evolutionarily, since a few genera contain species both with and without these diffraction gratings. [*L* = 12; *ci* = 0.08; *ri* = 0.26]
49. *Elytral subbasal line at level of posterior extent of pronotum*. (0) absent; (1) present. This is a smooth, shelflike line anteriorly on the elytron (visible chiefly on the lateral portion of the elytron) that separates the smooth, polished region at the base of the elytron from the (usually) more sculptured and/or punctate elytral disc. It corresponds with the posteriormost extent of the pronotum. This character is a putative synapomorphy for Phalacridae. [*L* = 1; *ci* = 1.0; *ri* = 1.0]
50. *Elytral subbasal transverse band of comblike grooves*. (0) absent; (1) present. Positionally, this band may be considered a medial extension of the subbasal line (C49). The comblike grooves are oriented longitudinally and correspond with minute teeth on the posterior margin of the prontoum. They are present in both the *Olibroporus*-group and in *Apallodes*, but slightly coarser in the latter group. [*L* = 2; *ci* = 0.50; *ri* = 0.80]
51. *Elytral engraved striae number*. (0) zero; (1) one (sutural); (2) two; (3) three; (4) five; (5) more than five. An engraved elytral stria is sharply visible in slide mounts, unlike a simple impressed puncture row, which may superficially appear to be a stria in dry-mounted specimens. Engraved striae may be identified in dry specimens by positioning the specimen such that the reflected light from the elytron is at a shallow angle (the impressed "striae" will become invisible, but the engraved striae will appear as sharp lines). Engraved striae, when present, always populate the elytron starting with the sutural stria and proceeding laterally. I have seen no instances of "skipped" striae. The majority of phalacrids possess a single sutural stria (Fig. 2b), but striae are completely absent in *Eulitrus*, *Phaenocephalus*, and *Phalacropsis*. A smattering of genera have two striae (Fig. 2a) per elytron, even fewer have three striae, only *Malagophytus* (not analyzed) has exactly five striae (Fig. 42g), while *Pseudolibrus*, *Grouvelleus*, and *Phalacrinus* each have a full complement of nine striae (Fig. 42a). [*L* = 14; *ci* = 0.28; *ri* = 0.16]
52. *Elytral transverse strigae*. (0) absent; (1) present. These appear as well-spaced fine transverse striae on the elytra, usually more prominent laterally and apically. Present in several genera of Phalacridae. [*L* = 6; *ci* = 0.16; *ri* = 0.28]
53. *Elytral epipleuron*. (0) roughly horizontal; (1) vertical. This character refers to the level of reflexion of the epipleuron. I consider a vertically reflected elytral epipleuron to be a putative synapomorphy for Phalacridae (it is horizontally reflected in all outgroups), but *Tolyphus* possesses a horizontal epipleuron. [*L* = 2; *ci* = 0.50; *ri* = 0.80]
54. *Elytral lateral margins*. (0) not or barely explanate; (1) distinctly explanate. In this context, "explanate" refers to a margin that is deflected laterally in cross-section (in another context phalacrids could be said to have "vertically explanate" elytra). Under this restricted definition, only *Phalacrinus* and *Platyphalacrus* are considered to have explanate elytral margins (Fig. 37c). [*L* = 2; *ci* = 0.50; *ri* = 0]
55. *Elytron lateral margin row of minute, sawtooth-like setae*. (0) absent; (1) present. The bases of these small spinelike setae lie in the marginal bead of the elytron and are only reliably observed under a compound microscope. They are present in most of the genera of Phalacridae and in two outgroups (*Brachypterus* and *Propalticus*). [*L* = 6; *ci* = 0.16; *ri* = 0.28]
56. *Mesoventral plate anterior edge*. (0) simple; (1) notched vertically; (2) notched horizontally and vertically. The "mesoventral

plate" here refers to a delimited region of the mesoventrite whose anterior margin is always coextensive with that of the mesoventrite, and is bordered laterally and posteriorly by a distinct ridge of cuticle (ridge sometimes obliterated posteromedially, see C57). The remainder of the mesoventrite is referred to as the "mesoventral disc." When procoxal rests are present, the mesoventral plate alone is involved in their formation (see C58). The notch is considered vertical when there is simply a break in the anterior bead of the mesoventrite, while the notch is considered horizontal when there is a notch in the outline of the mesoventrite from a ventral aspect (Fig. 30f). A horizontal notch is always accompanied by a vertical notch. This notch apparently receives the dorsal part of the prosternal process when the beetle is in repose. The anterior margin is simple in three outgroups (*Brachypterus*, *Placonotus*, and *Propalticus*), *Ochrolitus*, and *Tolyphus*. [*L* = 9; *ci* = 0.22; *ri* = 0.41]

57. *Mesoventral plate posterior border.* (0) not extending posteriorly to metaventrite; (1) extending posteriorly to metaventrite, dividing mesoventral disc in two; (2) obscured medially. The mesoventral plate is discussed under C56. In a majority of phalacrid genera the mesoventral plate divides the mesoventral disc into two parts (Fig. 7e), while in a fair number of genera (and in all outgroups except *Placonotus*) the disc is contiguous behind the plate (Fig. 12f). The posterior border of the plate is obliterated (Fig. 16f) in *Austroporus*, *Neolitochrus*, and *Platyphalacrus*. [*L* = 9; *ci* = 0.22; *ri* = 0.53]
58. *Mesoventral plate procoxal rests*. (0) absent; (1) present. If the plate has a median or paramedian ridge, a sulcus, or has distinct paired depressions (Fig. 19f), it is considered to have procoxal rests. [*L* = 9; *ci* = 0.11; *ri* = 0.55]
59. *Mesoventral disc medially.* (0) elevated, on same plane as metaventral process; (1) sunken. For those taxa whose mesoventral plate divides the mesoventral disc, this character is coded as "-" (gap). The disc is on the same plane as the mesoventrite (Fig. 4f) only in the *Phaenocephalus*-group and in outgroups. [*L* = 2; *ci* = 0.50; *ri* = 0.66]
60. *Mesanepisternum transverse carina*. (0) absent; (1) present, incomplete; (2) present, complete. This ridge of cuticle corresponds with the posteriormost extent of the prothorax when the beetle is in repose. It is absent (Fig. 34f) in *Litochrus* and two outgroups (*Brachypterus* and *Placonotus*). It is considered incomplete (Fig. 35f) if the carina does not reach the lateral margin of the mesanepisternum (the carina always originates at the medial margin). [*L* = 10; *ci* = 0.20; *ri* = 0.60]
61. *Mesocoxal cavity separation*. (0) greater than half width of coxal cavity; (1) less than half width of coxal cavity; (2) nearly contiguous. The mesocoxal cavities are nearly contiguous (Fig. 33f) only in *Grouvelleus*. [*L* = 9; *ci* = 0.22; *ri* = 0.22]
62. *Mesocoxal cavity closure by meso- and metaventrite*. (0) open; (1) closed. The mesocoxal cavities are closed in all Phalacridae and in one outgroup (*Propalticus*). [*L* = 2; *ci* = 0.50; *ri* = 0.50]
63. *Mesotibial spurs*. (0) two; (1) one. The number of mesotibial spurs is reduced to one in *Phaenocephalus*-group and in *Litochropus*. [*L* = 2; *ci* = 0.50; *ri* = 0.50]
64. *Mesotarsomere III lobe*. (0) with a single lobe; (1) distinctly bilobed. Mesotarsomere III is unilobed in most outgroups (except *Brachypterus*). [*L* = 10; *ci* = 0.10; *ri* = 0.55]
65. *Metaventral process apically.* (0) not exceeding halfway point of mesocoxae; (1) exceeding halfway point but not reaching anterior level of mesocoxae; (2) reaching or exceeding anterior level of mesocoxae. In all outgroups (except *Cyclaxyra*) the metaventral process does not exceed the halfway point of the mesocoxae (as in Fig. 13f). [*L* = 11; *ci* = 0.18; *ri* = 0.59]
66. *Metaventral postcoxal lines*. (0) closely tracing mesocoxa; (1) diverging from mesocoxa, smoothly rounded; (2) diverging from mesocoxa, angulate. These lines, which are often referred to as "femoral lines" in other taxa, are neither located on the femora nor do they seem to correlate with the sweep of the femora against the metaventrite. I have therefore adopted a more literal terminology here. The lines are angulate (Figs. 6f, 10f) only in *Stilbus* and a few *Acylomus*. Character state 0 (Fig. 13f) is found in all outgroups. [*L* = 11; *ci* = 0.18; *ri* = 0.40]
67. *Metaventral discrimen*. (0) long, at least half length of metaventrite at midline; (1) short, less than half length of metaventrite at midline; (2) absent. The extent of the discrimen can only be properly observed in cleared specimens. The discrimen is long in two outgroups (*Placonotus* and *Propalticus*) and short in the other two outgroups. The discrimen is absent (Fig. 10f) in *Stilbus apicalis* and *Tolyphus* (*s.str.*). [*L* = 8; *ci* = 0.25; *ri* = 0.50]
68. *Metacoxal separation*. (0) moderately to widely separated; (1) narrowly separated, nearly contiguous. The narrowly separated condition is a putative synapomorphy for Phalacridae. This character is correlated with the width of the metendosternite at its base. [*L* = 1; *ci* = 1.0; *ri* = 1.0]
69. *Metendosternite anterior tendons*. (0) approximate, arising about halfway or less than halfway down furcal arms; (1) widely separated, arising more than halfway down furcal arms. The widely separated condition is correlated with a short, triangular metendosternite. The tendons are widely separated (Fig. 14g) in *Phaenocephalus*, and the *Phalacrus*-group. Tendons are not apparent in two outgroups (*Propalticus*, *Placonotus*), while they are approximate (as in Fig. 7f) in the other two (*Brachypterus*, *Cyclaxyra*). [*L* = 2; *ci* = 0.50; *ri* = 0.50]
70. *Metendosternite ventral process*. (0) intersecting ventral longitudinal flange behind anterior margin of metendosternite; (1) intersecting ventral longitudinal flange at anterior medial margin of metendosternite. The ventral process (transverse) and the ventral longitudinal flange (longitudinal) are transverse phragmata on the ventral surface of the metendosternite. CS0 may be observed in Fig. 6g, while CS1 may be observed in Fig. 5g. The two character states are evenly distributed among outgroups. [*L* = 9; *ci* = 0.11; *ri* = 0.33]
71. *Metacoxa anterior margin*. (0) without emargination; (1) with emargination. The emargination occurs sublaterally on the anterior margin of the metacoxal plate. It is absent in two of the outgroups (*Cyclaxyra* and *Propalticus*), *Neolitochrus*, and the *Phaenocephalus*-group. [*L* = 4; *ci* = 0.25; *ri* = 0.25]
72. *Metacoxa transverse line*. (0) absent; (1) present. This is a shelflike line demarcating approximately the anterior third of the metacoxal plate. It is absent in all of outgroups but present in a majority of the genera of Phalacridae. [*L* = 10; *ci* = 0.10; *ri* = 0.40]
73. *Metafemur posteroventral surface subapical row of long setae*. (0) absent; (1) present. These setae, when present, occur on both the meso- and metafemora, but are most prominent on the latter. They are present in *Nesiotus*, *Paracylomus*, and the

Phalacrus-group. [*L* = 3; *ci* = 0.33; *ri* = 0.33]

74. *Metatibial foreface apical ctenidium*. (0) perpendicular to long axis of tibia; (1) oblique to long axis of tibia. The apical crown of spines in *Augasmus*, *Malagasmus*, and *Olibrosoma* extends obliquely up the metatibia (Fig. 30d). [*L* = 2; *ci* = 0.50; *ri* = 0.50]
75. *Metatibial spur number*. (0) two; (1) one. Character state (1) is found only in the *Phaenocephalus*-group (Fig. 4d). [*L* = 1; *ci* = 1.0; *ri* = 1.0]
76. *Metatibial spur shape*. (0) cylindrical; (1) flattened. The flattened metatibial spurs (Fig. 23d) are found only in *Tolyphus*. [*L* = 1; *ci* = 1.0; *ri* = 1.0]
77. *Metatibial spur (longest)*. (0) distinctly shorter than tibial apex; (1) subequal to tibial apex; (2) distinctly longer than tibial apex. In taxa with sexes dimorphic with regard to spur development, this character is coded for the female ("normal" condition). The spurs are shorter than the tibial apex in all outgroups. [*L* = 13; *ci* = 0.15; *ri* = 0.45]
78. *Metatarsomere I relative to metatarsomere II*. (0) tarsomeres subequal; (1) metatarsomere I shorter; (2) metatarsomere I longer. The tarsomeres are subequal in most outgroups (except *Cyclaxyra*). [*L* = 10; *ci* = 0.20; *ri* = 0.50]
79. *Metatarsomere I articulation with metatarsomere II*. (0) rigid; (1) movable. The flexibility of the joint between the tarsomeres can generally be assessed by examining the tarsi under a compound microscope. When movable, the joint is typically narrow and oblique; when rigid, it is typically thick and transverse. The joint is rigid in most outgroups (except *Brachypterus*). [*L* = 6; *ci* = 0.16; *ri* = 0.54]
80. *Metatarsomere II with ventral setal pad*. (0) present; (1) absent. The ventral setal pad (similar to that of metatarsomere III of most taxa) is present (Fig. 5d) in *Platyphalacrus* and the *Phaenocephalus*-group. [*L* = 3; *ci* = 0.33; *ri* = 0.33]
81. *Metatarsus of male number of tarsomeres*. (0) one fewer than in mesotarsus; (1) same as that in mesotarsus. Since the tarsomere that is eliminated (or fused) when reduction occurs is the tiny, nodiform fourth tarsomere, this character may be quite difficult to observe in dried specimens. This male heteromerous condition (Fig. 8d) is typical of the *Stilbus*-group, *Augasmus*, *Malagasmus*, *Olibrosoma*, most *Olibrus*-group members, and most outgroups (except *Brachypterus*). [*L* = 7; *ci* = 0.14; *ri* = 0.64]
82. *Metatarsus of female number of tarsomeres*. (0) same as that in mesotarsus; (1) one fewer than in mesotarsus. This female heteromerous condition occurs in *Augasmus*, *Malagasmus*, *Olibrosoma*, and *Stilbus*. The females are homomerous in all outgroups. [*L* = 3; *ci* = 0.33; *ri* = 0.33]
83. *Hind wing anal lobe*. (0) not set off by notch; (1) set off by notch, ovate; (2) set off by notch, straplike. A straplike anal lobe (Fig. 4e) is present in *Phaenocephalus*, while the anal lobe is completely absent in the outgroup *Propalticus*. [*L* = 2; *ci* = 1.0; *ri* = 1.0]
84. *Hind wing row of distinct setae on leading edge at level of RA+ScP*. (0) present, complete; (1) present, incomplete; (2) absent. Although these setae may be abraded, this character is remarkably reliable. [*L* = 13; *ci* = 0.15; *ri* = 0.38]
85. *Hind wing AA_3 connecting AA_{3+4} with Cu*. (0) absent; (1) present. See Fig. 33e for a diagram of wing veins in Phalacridae. [*L* = 5; *ci* = 0.20; *ri* = 0.33]
86. *Hind wing AA_3 branching*. (0) absent; (1) present. This character was coded as present if the cubitoanal system (Cu + AA_3) showed a bi- or multifurcation (sometimes joined to MP_{3+4}). When branched, often the distal branch (CuA_{1+2}) is longest and extends transversely across the medial field (as in Fig. 33e). [*L* = 7; *ci* = 0.14; *ri* = 0.45]
87. *Hind wing distal remnants of CuA_2 and/or MP_{3+4}*. (0) absent; (1) present. This character was coded as present if segments were observed in the medial field between the distal portion of AA_3 and the medial bar, roughly parallel to both, either "floating" segments (Fig. 32e) or segments joined (Fig. 33e) to crossvein CuA_{1+2} (see C86). [*L* = 9; *ci* = 0.11; *ri* = 0.57]
88. *Hind wing r4*. (0) absent; (1) developed, not connected with RA_{3+4}; (2) developed, connected with RA_{3+4}. In S2 the radial bar and medial bar have an unbroken connection (Fig. 33e). In *Malagasmus* and some *Olibrus* the vein is clearly developed, but does not connect the two bars (Fig. 25e). [*L* = 9; *ci* = 0.22; *ri* = 0.53]
89. *Hind wing fleck(s) beyond rp-mp2 in apical field*. (0) present; (1) absent. This character generally correlates with the total amount of sclerotization of the hind wing (fleck is present when wing is well sclerotized). [*L* = 8; *ci* = 0.12; *ri* = 0.30]
90. *Abdominal ventrite I calli*. (0) absent; (1) present. This character was described in Leschen (2003) in erotylid beetles. The abdominal calli are consistently visible only in cleared specimens under the compound microscope. They are present in *Augasmus*, *Austroporus*, *Malagasmus*, *Olibroporus*, *Olibrosoma*, *Platyphalacrus*, and *Steinerlitrus*, and in two of the outgroups (*Placonotus* and *Propalticus*). [*L* = 6; *ci* = 0.16; *ri* = 0.37]
91. *Abdominal spiracles on segment VII*. (0) present; (1) absent. Segment VII spiracles are present in a majority of phalacrid genera and half of the outgroups (*Placonotus* and *Propalticus*). The absent condition is typical of the *Stilbus*-group, *Phalacrus*-group, and the *Phaenocephalus*-group. In a few of the latter taxa, tiny, apparently nonfunctional rudiments were observed which lack a trachea. [*L* = 6; *ci* = 0.16; *ri* = 0.66]
92. *Aedeagus orientation in repose*. (0) upright; (1) resting on side. The aedeagus rests on its side in the *Phalacrus*-group and one outgroup (*Brachypterus*). In this condition there is a concomitant difference in the plane of compression of the aedeagus (dorsoventrally flattened in taxa with aedeagus upright, laterally flattened in taxa with aedeagus resting on side). [*L* = 2; *ci* = 0.50; *ri* = 0.50]
93. *Tegmen anterior margin*. (0) symmetrical; (1) asymmetrical. This refers to the outline of the basal ring of the tegmen as seen in a straight dorsoventral aspect. [*L* = 9; *ci* = 0.11; *ri* = 0.33]
94. *Paramere articulation*. (0) hinged to basal piece; (1) fused to basal piece, but separated by suture; (2) completely fused with basal piece. The parameres in Phalacridae are fused into a single structure (but sometimes divided, see C95), but may be variously fused (Fig. 15h) or hinged (Fig. 6h) with the basal piece. [*L* = 9; *ci* = 0.22; *ri* = 0.50]
95. *Paramere division*. (0) divided longitudinally; (1) undivided. If there is a longitudinal suture or incision medially in the (fused) parameres, this character was coded as divided (Fig. 9h). [*L* = 10; *ci* = 0.10; *ri* = 0.52]
96. *Endophallus sclerites*. (0) present; (1) absent. This character was coded as present only if there were large sclerites in the

endophallus (Fig. 24i), not just fields of spicules (Fig. 32i). [*L* = 7; *ci* = 0.14; *ri* = 0]

97. *Spiculum gastrale*. (0) Y-shaped, with long basal rod; (1) V- or U-shaped, arms free; (2) connected by a broad sclerotized lamina. In three of the outgroups (*Brachypterus*, *Cyclaxyra*, and *Propalticus*) the spiculum gastrale is Y-shaped with a long basal rod. [*L* = 9; *ci* = 0.22; *ri* = 0.36]

98. *Ovipositor sclerotization*. (0) weak, palpiform; (1) strong, with wedge-shaped gonocoxae; (2) strong, with toothed gonocoxae. A weak, palpiform ovipositor is typical of the outgroups and most genera of Phalacridae (Fig. 3f). A wedge-shaped ovipositor (Fig. 3e) is typical of the *Olibrus*-group, while a toothed ovipositor (Fig. 3c) occurs only in *Phalacrus*. [*L* = 2; *ci* = 1.0; *ri* = 1.0]

Cladistic methods. The morphological data set presented above was analyzed using parsimony. Of the 98 morphological characters compared, 93 were parsimony informative (5 autapomorphies). The autapomorphies were retained in the matrix, however, to allow visualization of long branches on the tree for more derived taxa and as potential "ready-made" characters as more taxa are added to the analysis in the future. WinClada 1.00.08 (Nixon 2002) was used to display and manipulate matrices and resulting trees. The morphological character matrix was analyzed using NONA version 2.0 (Goloboff 1999), in which a heuristic search was performed using multiple TBR + TBR (hold: 1000; mult*n: 500; hold/: 10). Bootstrap support values were calculated for the resulting topologies. Trees were rooted to the outgroup *Brachypterus urticae*.

Results

Phylogenetic results. Parsimony analysis of the morphological data resulted in 116 most parsimonious trees (*L* = 489, *CI* = 0.26, *RI* = 0.54). These are summarized with a strict consensus tree (*L* = 550, *CI* = 0.23, *RI* = 0.46) with characters and support values mapped (Fig. 46). Red node numbers in Fig. 46 refer to the node numbers below.

Node 1. In the analysis the family Phalacridae is monophyletic with only moderate bootstrap support, but with five unique and unreversed synapomorphies: head capsule attachment knob of antennomere I arising midlaterally (C11-S1); corpotentorium membranous (C29-S1); prosternal process with vertical foramen (C36-S1); elytron with subbasal line (C49-S1); metacoxae nearly contiguous (C68-S1). The vertical elytral epipleuron (C53-S1), unique to Phalacridae in this study, is reversed in *Tolyphus*. With *Propalticus*, all Phalacridae share the closed mesocoxal condition (C62-S1). Sister-group relationships are poorly resolved in this study, with *Cyclaxyra* weakly supported as sister to Phalacridae.

Node 2. Within the Phalacridae, the proposed subfamily Phaenocephalinae (*sensu* Lawrence and Newton 1995), *Phaenocephalus* + *Phalacrinus*, was recoved as strongly monophyletic. This grouping is supported by two unique and unreversed synapomorphies: protibial spurs absent (C42-S1); one metatibial spur (C75-S1). The independence of these two characters, however, is questionable. Additionally, they are the only phalacrids with a 4-4-4 tarsal formula and a posteriorly narrowed head capsule. However, its placement as sister to the remaining Phalacridae was quite weakly supported. Additional molecular data (18S rDNA; Gimmel, unpublished data) suggest placement of "Phaenocephalinae" higher in the phalacrid tree. Within the historical "Phalacrinae" (all phalacrid taxa except "Phaenocephalinae") deep relationships were unrecovered. However, a number of clades were moderately to strongly recovered (see below).

Node 3. *Stilbus*-group. This group consists of the genera *Acylomus*, *Nesiotus*, *Stilbus*, and *Xanthocomus*. It was only weakly supported in this analysis, but these genera possess a suite of unreversed characters that render them a cohesive group, including: prosternum with anterior marginal setal row with medial gap (C31-S1); prosternal process with apical row or pair of spinelike setae (C39-S1) (though not apparent in some small Old World members of the group, including *Acylomus micropus*); mesanepisternum with incomplete transverse carina (C60-S1); male with heteromerous tarsi (C81-S0); abdominal spiracles absent from segment VII (C91-S1). All have metaventral postcoxal lines that diverge from the mesocoxal cavity (C66-S1,S2), but these vary widely in their divergence and shape. Within-group relationships are obscure, but *Xanthocomus* appears to be a monophyletic group, with oblique ventral post-ocular setal ridge behind eye (C10-S2) being a synapomorphy. Reciprocal monophyly of the large genera *Acylomus* and *Stilbus* is in question, but these genera are diagnosable using an aedeagal character (see key for details).

Habits of this group have been observed to be mostly surface-mold grazing on dead vegetation; however, at least one species develops in ergot fungus.

Node 4. *Phalacrus*-group. Although not possessing unique synapomorphies in the context of this analysis, this group of two genera, *Phalacropsis* and *Phalacrus*, is one of the most well-defined in the family. Its members possess a suite of characters (each of which can be found in other genera of Phalacridae or in one or more of the

outgroups): frontoclypeus not emarginate above antennal insertion (C8-S1); mandibular retinaculum present (C18-S1); scutellum large (C47-S1); mesoventral plate not extending to metaventrite (C57-S0); metendosternite with anterior tendons widely separated (C69-S1); metafemur with subapical row of long setae (C73-S1); abdominal spiracles absent from segment VII (C91-S1); aedeagus rotated 90° (on side) in repose (C92-S1). This last character state is found only in the distant outgroup, *Brachypterus urticae*, in this analysis.

Habits of this group are unique among Phalacridae: all complete their life cycle within the galls of rust and smut fungi. These are the only phalacrids known to be associated with basidiomycete fungi.

Node 5. *Olibrus*-group. This group of two genera, *Olibrus* and *Tolyphus*, is another highly cohesive group both morphologically and behaviorally, despite comments by Crowson (1955: 108) regarding the apparently "primitive" nature of the genus *Tolyphus* in relation to other Holarctic Phalacridae (including *Olibrus*). Although these are grouped with only moderate support, they possess one unique and unreversed synapomorphy, the strongly sclerotized ovipositor with wedge-shaped gonocoxae (C98-S1). There are also two (non-unique) synapomorphies found in the hind wing: cubitoanal system branched apically (C86-S1); distal remnants of CuA_2 and/or MP_{3+4} present (C87-S1). Within the genus group, the two subgenera of *Tolyphus* are placed as sister groups, with a number of synapomorphies, one of them unique: metatibial spurs flattened (C76-S1). *Tolyphus* also possesses an emarginate clypeus (C9-S1), otherwise found only in two outgroups (*Brachypterus urticae* and *Propalticus*). The possibility exists that *Tolyphus* is nested within the large and diverse genus *Olibrus*, but this problem must be addressed by a much more thorough sampling within this genus group.

As with the previous group, habits of this group are unique among Phalacridae: all are pollen-feeding flower visitors, primarily on the flower heads of Asteraceae. Known larvae (*Tolyphus* are still unknown) develop among the disc flowers and feed on fluid material.

Node 6. *Pseudolibrus*-group. The two genera *Litostilbus* and *Pseudolibrus* are grouped together with moderate support in this analysis. These share a suite of characters, though none individually are unique synapomorphies in this analysis: frontoclypeus not emarginate above antennal insertion (C8-S1); mandibular apex tridentate (C16-S0); scutellum large (C47-S1); elytra with transverse strigae (C52-S1); mesoventral plate not extending to metaventrite (C57-S0); metaventral process not exceeding halfway point of mesocoxae (C65-S0); r4 absent from hind wing (C88-S0). To this group may be safely added the genus *Megistopalpus*, which is known only from two specimens and so could not be coded. It is quite similar to *Pseudolibrus* but larger and with extremely modified maxillary palpi.

Habits are essentially unknown for this group, but dissected specimens of *Pseudolibrus* had septate fungal spores in their hindguts.

Node 7. *Olibrosoma*-group. This group of three genera, *Antennogasmus*, *Malagasmus*, and *Olibrosoma*, received poor support in this analysis with the inclusion of *Antennogasmus*, but moderately high support with that genus excluded. There are no unique synapomorphies that define either grouping, but the three-genus unit is readily diagnosable (see key to genera for details). Non-unique synapomorphies that help define the group are: mesoventral plate not extending posteriorly to metaventrite (C57-S0); and hind wing with cubitoanal system branched (C86-S1).

Habits for members of the group are virtually unknown, but *Olibrosoma* has been collected from flowers of *Orobanche*.

Node 8. *Olibroporus*-group. This group of four genera, *Austroporus*, *Olibroporus*, *Platyphalacrus*, and *Pycinus*, received relatively low support in this analysis. There is no unique unreversed synapomorphy for this group in the family-level context. Non-unique synapomorphies include the elytral subbasal band of grooves (C50-S1) which is shared with *Apallodes*. However, the condition in *Apallodes* is of a slightly different nature (coarser grooves) and the condition of this genus and the *Olibroporus*-group may not be homologous. Together the members of the *Olibroporus*-group represent a diagnostic unit (see key to genera for details).

Habits for the group are poorly known, but *Platyphalacrus* occurs on male cycad cones, and members of *Austroporus* have been collected from a variety of flowers.

FIGURE 46. Strict consensus tree of the genera of Phalacridae from maximum parsimony analysis of morphological matrix of 98 characters (*L* = 550, *CI* = 0.23, *RI* = 0.46). Bootstrap values are shown (in black) above branches with >49% support. Red numbers near nodes correspond with node numbers in text.

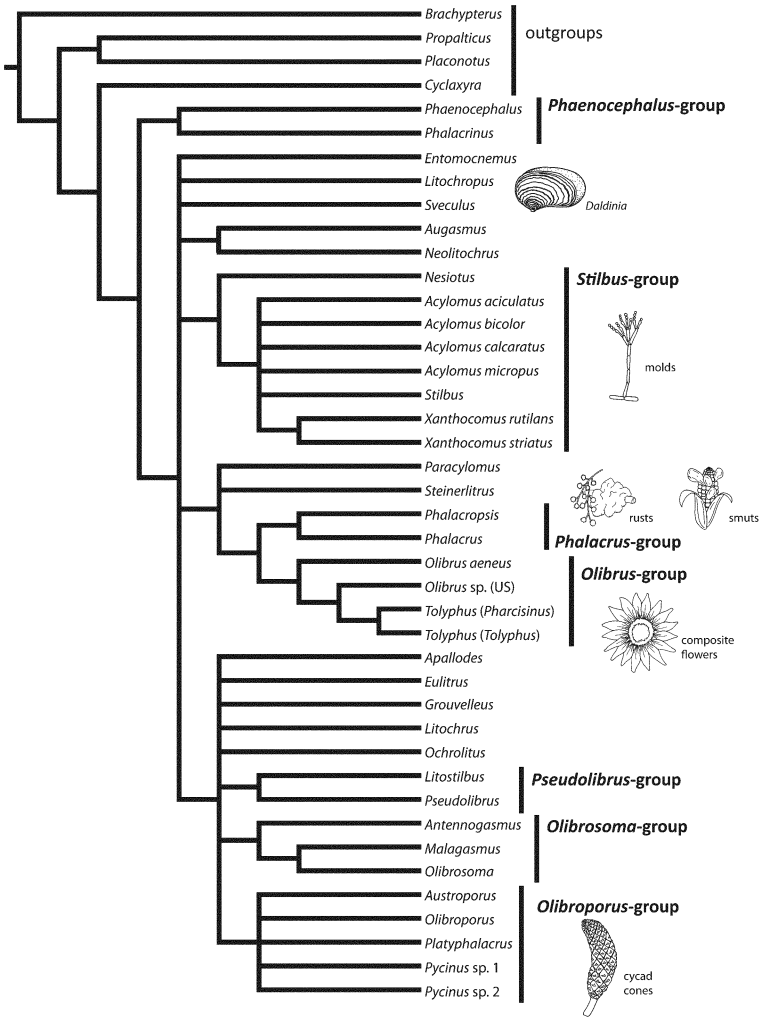

FIGURE 47. Phylogenetic hypothesis of Phalacridae, with genus groups and habits mapped on tree.

Other genera. The level of resolution from this phylogenetic analysis was inadequate to place the remaining genera convincingly into groups. However, some of these genera may deserve generic groups of their own. For instance, members of the bizarre genus *Grouvelleus* possesses two autapomorphies, including: 1) protarsomere I enlarged and densely setose in male and 2) mesocoxal cavities nearly contiguous. Two pairs of genera, *Litochropus* + *Neolitochrus* (*Litochropus*-group) and *Ochrolitus* + *Sveculus* (*Ochrolitus*-group), though not recovered as sister groups in this analysis, represent a diagnostic unit (see key) and together possess a unique character state, the transparent apical process on the prosternal process. This relationship is supported by molecular data (18s rDNA; Gimmel, unpublished).

A summary tree is presented with genus-groups and their feeding habits, where known (Fig. 47).

Discussion

This study is the first in over 100 years to treat the world fauna of Phalacridae in detail, providing a firm foundation for modern investigations into the evolutionary history of the group. The family as presently constituted is monophyletic and well-defined. A few well-supported internal clades have been identified within the family based on morphological data. Types and museum holdings of all of the described genera have been critically examined and reconciled and a large number of synonymies and new genera have been proposed. A thorough morphological analysis of adults and world key to genera have been presented, allowing identification by non-specialists and providing a framework for all future studies on the family.

Since the genera were not conclusively placed into higher groups with the morphological analysis, additional effort will be required to rectify this situation. This will involve expanded phylogenetic analyses with the addition of multiple genetic markers (including nuclear and mitochondrial protein-coding genes) and a broader sampling of taxa. Discovery and detailed study of the immature stages of more genera will certainly add a rich morphological character set from which to draw alternative phylogenetic hypotheses.

In order to achieve a comprehensive, systematic understanding of the group, species-level revisions of most of the genera defined and described in this work are sorely needed. Dissection and examination of male genitalia will be required, although not necessarily sufficient, in nearly all cases to define species boundaries. Based on the definitions of genera provided in this work, these revisions may be undertaken with confidence at the world level, although work at the regional level in the case of the larger genera (*Acylomus*, *Olibrus*, *Phalacrus*, *Stilbus*) may be more feasible. Examination of types will also be essential, and a large portion of the background work investigating type localities, type depositories, and primary type status is nearly complete (Gimmel, world catalogue MS).

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