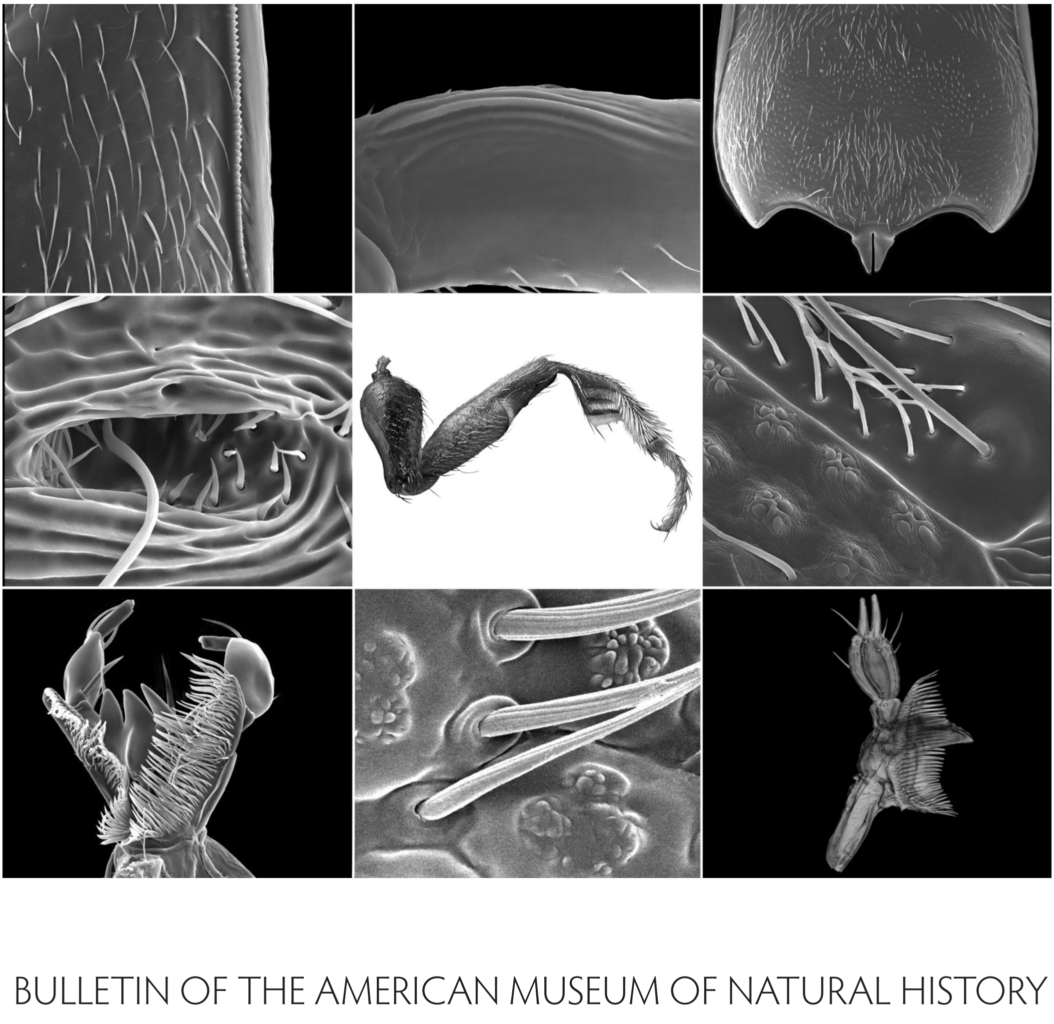
Generic Revisions of the Scopaeina and the Sphaeronina

(COLEOPTERA: STAPHYLINIDAE: PAEDERINAE: LATHROBIINI)

LEE HERMAN



BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

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ABSTRACT

The generic classifications of the paederine subtribes Scopaeina Mulsant and Rey, 1878, and Sphaeronina Casey, 1905, are revised. Sphaeronina, **revised status**, is resurrected from synonymy. Keys to the included genera of both subtribes are included. Newly discovered characters in both subtribes are discussed and illustrated.

The Scopaeina now includes *Scopaeus*, *Hyperscopaeus*, *Micranops*, *Orus*, and *Trisunius*. The account for each genus includes its diagnostic characters, a description, summary of the general distribution, and list of the included species and specimens examined.

Scopaeus Erichson, 1839, has a **revised definition** and is now restricted to species that have not only a constricted neck and a trichobothrium adjacent to and at about the middorsal margin of the eye, but also a metathoracic/mesofemoral stridulum comprised of a lateral, metaventral file and mesofemoral plectral ridges, slender, apically acute, metakatepisternal processes, and a middorsally fused median lobe of the aedeagus. The stridulum, redefined herein as a file and plectrum that when rubbed together produce stridulation in insects. The metaventral file and mesofemoral plectral ridges of *Scopaeus*, is, heretofore, unknown in the Staphylinidae or perhaps, even the Coleoptera. Variations of the stridulum and metakatepisternal processes are illustrated and described for each species group. Five genus-group names in the Western Hemisphere, *Scopaeomerus* Sharp, 1886, and *Euscopaeus* Sharp, 1886, are **new synonyms** of *Scopaeus*; *Scopaeodera* Casey, 1886, *Scopaeoma* Casey, 1905, and *Scopaeopsis* Casey, 1905, are **revised status junior synonyms** of *Scopaeus*. The species in those generic groups are now included in species groups of *Scopaeus*.

Hyperscopaeus Coiffait, 1984, **new status**, is elevated to genus from subgeneric status in *Scopaeus*. *Trisunius* Assing, 2011**, new subtribal assignment**, is moved from the Medonina to the Scopaeina. *Typhloscopaeus* Jarrige, 1951, **incertae sedis**, formerly a subgenus of *Scopaeus*, is of unknown placement, but the species and generic names are retained in *Scopaeus* awaiting study of the type.

Orus cervicula Casey, 1905, **revised combination**, is returned to *Orus* from *Scopaeus*. *Orus femoralis* (Sharp, 1887), **new combination**, is transferred from *Scopaeus*. There are now three named species of *Orus* with narrow necks.

Scopaeus chiriquensis (Sharp, 1886), *S. guatemalensis* (Sharp, 1886), *S. obscurus* (Sharp, 1886), and *S. palmatus* (Sharp, 1886), **new combinations**, are transferred to *Scopaeus* from *Scopaeomerus*. *Medon mexicanus* (Bernhauer, 1910), **new combination**, is transferred to *Medon* from *Scopaeomerus*.

Scopaeus crassitarsis (Sharp, 1886), *S. gracilicornis* (Sharp, 1886), *S. impar* (Bierig, 1935), **new combinations,** are transferred to *Scopaeus* from *Euscopaeus*.

The following names are transferred from *Scopaeus* to *Hyperscopaeus* **as new combinations:** *Hyperscopaeus admixtus* (Fagel, 1973), *H. albertvillensis* (Fagel, 1973), *H. allardianus* (Fagel, 1973), *H. andrewesi* (Cameron, 1931), *H. angolanus* (Fagel, 1973), *H. bamaniaensis* (Fagel, 1973), *H. borneensis* (Cameron, 1941), *H. bredoanus* (Fagel, 1973), *H. calidus* (Bernhauer, 1932), *H. confusoides* (Fagel, 1973), *H. confusus* (Fagel, 1973), *H. consimilis* (Fagel, 1973), *H. convexiceps* (Bernhauer, 1932), *H. corpulentus* (Fagel, 1973), *H. decelleanus* (Fagel, 1973), *H. dolosus* (Fagel, 1973), *H. endrodyanus* (Fagel, 1973), *H. errans* (Fagel, 1973), *H. erraticus* (Fagel, 1973), *H. fageli* (Levasseur, 1981), *H. fallaciosus* (Fagel, 1973), *H. filicornis* (Fagel, 1973), *H. flavidulus* (Fagel, 1973), *H. flavocastaneus* (Lea, 1923), *H. fluviatilis* (Fagel, 1973), *H. fossiceps* (Eppelsheim, 1885), *H. fuliginosus* (Fagel, 1973), *H. fulvescens* (Motschulsky, 1858), *H. fusculus* (Motschulsky, 1858), *H. gigantulus* (Bernhauer, 1929), *H. girardianus* (Fagel, 1973), *H. hova* (Fauvel, 1905), *H. hulstaertianus* (Fagel, 1973), *H. intermixtus* (Fagel, 1973), *H. kaszabianus* (Fagel, 1973), *H. katanganus* (Fagel, 1973), *H. kivuanus* (Fagel, 1973), *H. lamtoensis* (Fagel, 1973), *H. leleupianus* (Fagel, 1973), *H. leopoldvillensis* (Fagel, 1973), *H. lescuyeri* (Delaunay, Coache, and Rainon, 2019), *H. levasseuri* (Lundgren, 1982), *H. longiusculus* (Fagel, 1973), *H. machadoanus* (Fagel, 1973), *H. major* (Eppelsheim, 1885), *H. methneri* (Bernhauer, 1932), *H.*

minutulus (Fagel, 1973), *H. mulongoensis* (Fagel, 1973), *H. nitidiceps* (Fagel, 1973), *H. nitidicollis* (Fagel, 1973), *H. opacicollis* (Bernhauer, 1942), *H. overlaetianus* (Fagel, 1973), *H. parvicornis* (Fauvel, 1900), *H. procerus* (Kraatz, 1859), *H. pruinosulus* (Eppelsheim, 1885), *H. pseudomethneri* (Fagel, 1973), *H. puberulus* (Kraatz, 1859), *H. reduncus* (Fagel, 1973), *H. ripicola* (Fagel, 1973), *H. rubricollis* (Fagel, 1973), *H. rubrotestaceus* (Kraatz, 1859), *H. ruguliceps* (Fagel, 1973), *H. ruziziensis* (Fagel, 1973), *H. semifuscus* (Kraatz, 1859), *H. senegalensis* (Fagel, 1973), *H. seydeli* (Cameron, 1952), *H. simillimus* (Fagel, 1973), *H. simulator* (Fagel, 1973), *H. spathiferus* (Coiffait, 1970), *H. spinosophallatus* (Frisch, 2012), *H. subconfusus* (Fagel, 1973), *H. subprocerus* (Coiffait, 1978), *H. surdus* (Fagel, 1973), *H. suspectus* (Fauvel, 1907), *H. tchapembanus* (Fagel, 1973), *H. thoracicus* (Motschulsky, 1858), *H. tristis* (Bernhauer, 1929), *H. vagans* (Fagel, 1973, and *H. voltae* (Fagel, 1973).

Sphaeronina, **revised status**, is resurrected from synonymy and now includes *Sphaeronum* Sharp, 1876, *Tripectenopus* Lea, 1918, *Typhloleleupius* Fagel, 1964, and *Coecoscopaeus* Coiffait, 1982; the last three genera are new assignments to the subtribe. Sphaeronina is redefined by the presence of a hypopharyngeal peg, an enlarged protibial concavity with combs, a ventral denticle on the left mandible, and a groove on the outer edge of the mandibles; additional possible diagnostic characters are discussed.

Sphaeronum, *Tripectenopus*, *Typhloleleupius*, and *Coecoscopaeus* are redescribed; the genera are found, respectively, in the American tropical and subtropical regions, Australia, southern Africa and perhaps Madagascar, and Tunisia. Few African and Australian were available for study.

Scopaeodracus Scheerpeltz, 1935, is a **new synonym** of *Tripectenopus*. *Tripectenopus handschini* (Scheerpeltz, 1935), **new combination**, is transferred from *Scopaeodracus*; *Tripectenopus australiae* (Fauvel, 1878), *T. microps* (Lea, 1923), *T. pectinatrix* (Lea, 1923), and *T. torrensensis* (Blackburn, 1891), **new combinations**, are transferred from *Domene*.

INTRODUCTION

The present article examines the generic classification of two unrelated subtribes of the Paederinae. Their inclusion in the same work was unplanned, but investigation of one led to the other. The article begins with a revision of the generic classification of the Scopaeina and follows with review of the excluded genera and generic classification of the Sphaeronina.

Upon beginning studies of the generic classification of the Scopaeina Mulsant and Rey, 1878, a group of more than 500 species, most of which were in *Scopaeus* Erichson, 1839, the questions to be resolved seemed so few and relatively simple that anticipation was high that the work would be completed in short order. However, the task was far more complex, challenging, and time consuming, but ultimately, more fruitful and interesting than expected.

Immediately prior to the present work the Scopaeina included five valid genera, *Euscopaeus* Sharp, 1886, *Micranops* Cameron, 1913, *Orus* Casey, 1885, *Scopaeomerus* Sharp, 1886, and *Scopaeus*. The most recent addition, *Micranops*, had been overlooked by nearly everyone after its original description and no one studied it until this century (Frisch et al., 2002a: 46). Frisch, in long series of publications, reconstructed *Micranops* and the classification of most of the Eurasian species of *Scopaeus*. However, several small and one large question remained. The definition of the subtribe required reexamination. The three species of *Euscopaeus* were so similar to the five in *Scopaeus* (*Scopaeopsis*) Casey, 1905, that the two clusters of species warranted comparison. Another genus, *Trisunius* Assing, 2011, erroneously placed in the Medonina, required transfer to the Scopaeina. That genus, however, had a paucity of characters separating it from some other scopaeine genera. Few exclusive characters defined the scopaeine genera. However, the crux of the entire exploration of the subtribe was understanding *Scopaeus*; therein lay the largest, most challenging question. Among the species of the Eastern Hemisphere the diversity of habitus of *Scopaeus* seems relatively minor. On the other hand, species of the subtropical and tropical Americas appear to exhibit far greater variation of habitus than those of Eurasia. Even David Sharp (1876: 248) remarked that three of seven of the Brazilian species he described "depart[ed] widely in facies from the ordinary [European] species of the genus." That external variation begged deeper examination.

Finding unique, derived characters to delimit *Scopaeus* proved a major challenge. It seemed improbable that major, new, unique characters would be discovered in a genus that had been collected, observed, and identified by a few hundred coleopterists for nearly two centuries. For most of that time the narrow neck was the main diagnostic character; the tricuspidate ligula reported by Erichson (1839) was rarely used. A third character, the paraocular trichobothrium, was discovered in the Scopaeina during last third of the 20th century but was unused for *Scopaeus* until the early years of the 2000s. However, these three structures are all present in other paederine and/or scopaeine genera. There lay the conundrum to be addressed: seek unique characters to hold this huge cluster of species together or split it into multiple genera defined by unique, derived features, without rendering the resulting *Scopaeus* paraphyletic. Finding and documenting the answer was a journey of more than 10 years.

Initially, the goal of the present work was defining the Scopaeina and its included genera. However, based on the possession of a narrow neck, a few other genera had been associated with—considered to be near—*Scopaeus*. Although those ideas had been rejected by other authors, the genera were in limbo, so I decided to examine them and to write a short paragraph for each discussing their distinction from *Scopaeus* and suggesting subtribal placements. That serendipitous decision resulted in resurrection and enlargement of the Sphaeronina to include five generic names, two of which I had never examined before and a third I had seen, but not studied.

In the next section Scopaeina and its included genera are redescribed. *Scopaeus* is redefined. Following that, Sphaeronina is resurrected and redefined to include four genera, three newly assigned. Keys to the genera and descriptions and illustrations for the genera of both subtribes are presented.

ABBREVIATIONS FOR SPECIES ASSIGNMENTS

Each of these abbreviations and their related definition was discussed in detail in Herman, 2010: 6–7.

H	Holotype
L	Lectotype
Lit. Att. []	Literature Attribution [Country]
P	Paratype
Pl	Paralectotype
Sp	Specimen
Syn	Syntype

ABBREVIATIONS FOR COLLECTIONS

AMNH	American Museum of Natural History, New York
ANIC	Australian National Insect Collection, Canberra
BMNH	The Natural History Museum, London
CASC	California Academy of Sciences, San Francisco, California
CUMC	Cornell University Museum, Ithaca, New York
FMNH	Field Museum of Natural History, Chicago, Illinois
IRSN	Institut Royal des Sciences Naturelles, Brussels
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, MA
MHNG	Muséum d'Histoire Naturelle, Geneva
MNHN	Muséum National d'Histoire Naturelle, Paris
MNKB	Museum für Naturkunde, Berlin
MRAC	Musée Royal des l'Afrique Centrale, Tervuren
NHMB	Naturhistorisches Museum, Basel
NHMW	Naturhistorisches Museum, Vienna

SAMA	South Australian Museum, Adelaide
SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg
TMCB	Természettundomanyi Muzeum, Budapest
USNM	National Museum of Natural History, Washington, DC
ZMUM	Zoological Museum, University of Moscow

Methods

Descriptions: Although the formal descriptions include pubescence, macrosetae, surface microsculpturing and punctation, no effort was made to illustrate those features because they are of marginal importance for the identification and placement of the species into genera. Far more emphasis was placed on illustrating structural characters that defined genera and features rarely illustrated or newly discovered. Each generic account includes a diagnosis, description, and paragraphs concerning distribution, habitat, synonyms, and discussions of a variety of topics as dictated by information known about the genus.

Illustrations: In my earlier publications most images were pen-and-ink or pen-and-charcoal illustrations with, beginning in 1970, some scanning electron microscope (SEM) photos. By contrast most—hundreds—of the illustrations in the present work are photographs from the SEM. A smaller number of photos were made with a Canon EOS 70D, DSLR using transmitted light for slide mounted specimens with a Wild M20 compound microscope (figs. 9, 10, 95–103, 154–164, 167, 205–210, 240–243, 272–275, 318, 320, 323–325, 342–348, 351, 367–380, 383–391, 393–403) or reflected light with a Leitz binocular dissecting microscope or a Nikon SMZ18 (figs. 1–8, 256–258, 349, 362–366, 381, 382, 392). Images using reflected or transmitted light are stacks of multiple photographs assembled with Helicon Focus. Figure 350 was produced with the Visionary Digital photomicrographic apparatus with Infiniti optics and a Canon 70D DSLR camera (ViDPA). Only 69 pen-and-ink line drawings are included. All the illustrations were edited with Affinity Photo software, an equally robust, but far less expensive, available for purchase, rather than rental, alternative to Adobe Photoshop, now available only to lease.

Measurements: Elytral length (EL) – posterior edge of scutellum, along elytral suture, to line across posterior most edges of elytra

Pronotal length (PL) – along midlongitudinal line from anterior margin to posterior margin

Neck width (NW) – across the narrowest point of the nuchal groove

Head width (HW) – across the widest postocular width of the head capsule

Material examined and species included: At the end of each generic account is a list of the species included. In that list, valid names are in bold italic type and flush left. Invalid synonyms are in italics and indented under the valid name. So that the disposition of all species-group names is clear to the reader, species transferred to other genera in the present work are in italics and flush left, with the name of the genus to which it is transferred in the same line. Each species-group name includes its author and date of publication; these data are not necessarily cited elsewhere in this article, but their presence in the list will satisfy recommendations 22A.1 and 51A of the ICZN. The status of the specimens, holotypes, paratypes, etc., upon which generic assignments were based is indicated by an abbreviation as noted above under Abbreviations for Species Assignments. Unexamined species were assigned to genus by literature attribution. The distribution cited for the species that were examined is based only on the specimens examined, the known distribution may be greater. For species assigned to the genus by literature attribution, the distribution was extracted from publications.

Genus-group names cited in text: The ICZN (recommendations 22A.1, 51A) suggests that the author and date of publication be cited at least once in works citing the taxon indicated by that name. In the section on the Sphaeronina and in discussions of the stridula of various genera of beetles, dozens of genera are cited, many only once, in discussions of the distribution of characters in the Paederinae. Following is an alphabetical list of those genus-group names, each with their respective author and original date of publication. For genera with subgenera, the nominotypical generic name is cited first, followed by the subgeneric name in parentheses, then the author and date of the subgeneric name. The list is an effort to both comply with the ICZN recommendation and provide paragraphs of text with less clutter and better flow by removing the authors and dates of the names cited.

Acalophaena Sharp, 1886, *Acanthoglossa* Kraatz, 1959, *Achenium* Leach, 1819, *Achenomorphus* Motschulsky, 1858, *Apatetica* Westwood, 1848, *Asemobius* Horn, 1895, *Astenus* Dejean, 1833, *Bolbophites* Fauvel, 1904, *Brachynetes* Bernhauer, 1922, *Cephalochaetus* Kraatz, 1859, *Charichirus* Sharp, 1889, *Chetocephalus* Cameron, 1944, *Cicindela* Linnaeus, 1758, *Dacnochilus* LeConte, 1861, *Deroderus* Sharp, 1886, *Dibelonetes* R. Sahlberg, 1844, *Dibelophacis* Bierig, 1933, *Dolicaon* Laporte, 1835, *Domene* (*Domene*) Fauvel, 1873, *Domene* (*Canariomene*) Oromí and Hernández, 1986, *Domene* (*Lathromene*) Koch, 1938, *Domene* (*Lobramene*) Assing, 2021, *Domene* (*Spelaeomene*) Español, 1977, *Echiaster* Erichson, 1839, *Ecitocleptis* Borgmeier, 1949, *Ecitonides* Wasmann, 1894, *Euetheola* Bates, 1888, *Eurysunius* Reitter, 1909, *Eustilicus* Sharp, 1886, *Haplonazeris* Coiffait and Saiz, 1968, *Heteroleucus* Sharp, 1886, *Homaeotarsus* Hochhuth, 1851, *Lathrobium* Gravenhorst, 1802, *Lobrathium* Mulsant and Rey, 1878, *Medon* Stephens, 1833, *Megastilicus* Casey, 1889, *Micrillus* Raffray, 1873, *Mimophites* Fauvel, 1904, *Monista* Sharp, 1876, *Monocrypta* Casey, 1904, *Myrmecosaurus* Wasmann, 1909, *Nanobius* Herman, 1977, *Nazeris* Fauvel, 1873, *Neolindus* Scheerpeltz, 1933, *Neomedon* Sharp, 1886, *Nicrophorus* Fabricius, 1775, *Nodynus* Waterhouse, 1876, *Ochthephilum* Stephens, 1829, *Oedichirus* Erichson, 1839, *Ophitodum* Fagel, 1977, *Ophryomedon* Wasmann, 1916, *Opithes* Blackwelder, 1952, *Oxyporus* Fabricius, 1775, *Pachymedon* Cameron, 1931, *Paederus* Fabricius, 1775, *Panscopaeus* Sharp, 1889, *Pinobius* MacLeay, 1873, *Pinophilus* Gravenhorst, 1802, *Procirrus* Latreille, 1829, *Pseudastenus* Bernhauer, 1933, *Pseudolathra* Casey, 1905, *Pseudopsis* Newman, 1834, *Pseudoxyporus* Nakane and Sawada, 1956, *Ronetus* Blackwelder, 1943, *Rugilus* Leach, 1819, *Scopaeodes* Sharp, 1876, *Scopobium* Blackwelder, 1939, *Scymbalium* Erichson, 1839, *Serrolabis* Fagel, 1958, *Stamnoderus* Sharp, 1886, *Stilicastenus* Coiffait, 1975, *Stilicoderus* Sharp, 1889, *Stilicopsis* Sachse, 1852, *Stiliphacis* Bierig, 1938, *Stilomedon* Sharp, 1886, *Stilosaurus* Blackwelder, 1943, *Sunesta* Blackwelder, 1939, *Synecitonides* Reichensperger, 1936, *Throbalium* Mulsant and Rey, 1878, *Zalobius* LeConte, 1874.

TAXONOMY

Scopaeina Mulsant and Rey

Figures 1–8, 11–348

Scopaeina Mulsant and Rey, 1878.
— Seidlitz, 1889a: 92, 93, 371 (latinized use; characters; key to genera and species). — Seidlitz, 1889b: 92, 93, 395 (latinized use; key to genera and species). — Jakobson, 1909: 486 (characters; key to genera). — Hatch, 1957: 150 (characters; key to genera of Pacific Northwest). — Blackwelder and Arnett, 1974: 57 (checklist; North America; Central America; West Indies). — Campbell and Davies, 1991: 114 (checklist; Canada). — Newton and Thayer, 1992: 62 (subtribe of Paederini). — Newton, Thayer, Ashe, and Chandler, 2000: 326, 327, 386 (characters; key to genera in North America; notes). — Ádám and Hegyessy, 2001: 110 (notes). — Frisch et al., 2002a: 27 (phylogeny and biogeography of Western Palaearctic species). — Navarrete-Heredia et al., 2002: 279 (characters; notes; genera and species of Mexico). — Smetana, 2004: 615 (Palaearctic catalog).

Scopéates Mulsant and Rey, 1878: 178 (genera included: *Scopaeus*, *Stilicus*). Type genus: *Scopaeus* Erichson, 1839.

— Ganglbauer, 1895: 494 (characters). — Newton and Thayer, 1992: 62 (not latinized, available?; type genus; synonym of Scopaeina).

Polyodontidos Solier, 1849: 303 (cited as Poliodontidos; genera included: *Physognathus*, *Stenus*, *Rugilus*, *Polyodontus*). Type genus: *Polyodontus* Solier, 1849.

— Lacordaire, 1854: 151 (cited as Polyodontides; characters). — Newton and Thayer, 1992: 62 (based on preoccupied generic name; not latinized, available?; synonym of Scopaeina).

Scopaeina Seidlitz, 1889a: 92, 93, 371 (characters; genera included: *Scopaeus*, *Stilicus*; key to species). Type genus: *Scopaeus* Erichson, 1839.

— Newton and Thayer, 1992: 62 (may be first latinized use; type genus).

Scopaei Casey, 1905: 20, 190 (genera included: *Leucorus*, *Pycnorus*, *Orus*, *Scopaeus*, *Scopaeoma*, *Scopaeopsis*, *Scopaeodera*). Type genus: *Scopaeus* Erichson, 1839.

— Coiffait, 1982: 9 (characters; Western Palaearctic genera: *Scopaeus*; *Coecoscopaeus*).

Diagnosis: The Scopaeina can be separated from all other subtribes by the cephalic trichobothrium that is contiguous with the dorsal margin of the eye (figs. 13, 15, 245, 297, 333) in a rounded depression or canal or in a short cavity behind and nearly touching the eye (fig. 282) or moderately, but distinctly separated from it (figs. 12, 266), and the tripartite ligular lobe (figs. 160, 187, 248, 317, 339, 343), absence of the pronotal marginal ridge (figs. 52, 54, 56, 330), long, posteriorly tapered profurcasternum (fig. 98, 345), and trilobed anterior margin of abdominal sternite II (figs. 179, 255, 284, 211, 338). Each of these characters is homoplasic and found in other genera of the Paederinae. No other genus or subtribe possesses them all.

Description

Body length 1.8–6.6 mm.

Head longer than wide, lateral margins nearly straight to strongly rounded (figs. 1–5, 47–50, 240, 259, 286, 342).

Cephalic trichobothrium in ovoid or elongate depression, present on lateral side adjacent to dorsal margin of eye (figs. 11, 15, 297, 333) or displaced posteriorly to temple (figs. 267, 282); trichoid sensillum (fig. 194, 266, 309, 333) long, thin, slightly tapered from base to apex, and with straight fluting for most of length (fig. 108).

Neck with nuchal groove shallow (figs. 258, 272) to deep (fig. 240) and without longitudinal carinae. Nuchal ridge present (figs. 161, 193, 266, 333).

Eyes with setae between corneal lenses (except species with few corneal lenses) (figs. 17, 18, 20, 22, 25, 240, 334); corneal lenses with (figs. 19, 20, 247) or without sensilla (figs. 23–46).

Gular sutures well separated (figs. 47, 286, 326) to contiguous or nearly so (fig. 49, 244). Gula without pubescence or punctures.

Antennae not geniculate, first antennomere of normal length, not overly elongated.

Mandible moderately long, moderately broad, and dentate; ventral surface without denticle; outer edge without groove; prostheca evident as cluster of cuticular processes at base of mandible (figs. 67, 263).

Labrum bidentate, quadridentate, or edentate; median emargination present (figs. 6, 100, 159, 319).

Epipharyngeal surface (figs. 169, 186, 249, 319, 340) with curved, diagonal ridge near median groove extending from laterad of middle of base to anterior margin and marking lateral edge of median groove; epipharynx with large, dense cluster of cuticular processes.

Maxillary palpomere 4 small, cylindrical, slightly swollen basally, and asetate; palpomere 3 moderately compressed and gradually expanded apically.

Labium with sclerotized ligula; anterior margin with broad, flattened, wider than thick, apically tapered, subacute, tripartite lobe (figs. 160, 168, 187, 248, 318, 343); paraglossa with large brush comprised of mesial row of stout setae and dense cluster of cuticular processes diverging from base to apex.

Prothorax (figs. 1–5, 7, 8, 51, 53, 256–258) longer than wide; anterolateral angle well developed to poorly developed; widest at anterolateral margin or near middle of lateral margin; lateral margins approximately parallel to gradually convergent posteriorly from middle or anterolateral angles; surface without trichobothria. Pronotal marginal ridge absent (figs. 52, 56, 330). Prohypomeron with postprocoxal lobe long or short; transverse hypomeronal ridge present (fig. 52) or absent (figs. 54, 56); submarginal ridge present (figs. 52, 54, 56, 330).

Profurcasternum (figs. 51, 98, 345) long, tapered posteriorly, widely separated from hypomeron, wide between prosternal apophyseal invaginations; anterior portion of furcasternum fused with median piece of probasisternum; apex acute in ventral view, rounded in lateral view and reaching to near anterior margin of mesoventrite.

Intercoxal carina long and with acute, knifelike, ventral edge (figs. 53, 345).

Procoxal cavity open posteriorly (figs. 98, 287, 345).

Mesospiracular peritreme small, moderately sclerotized, separated from furcasternum, postprocoxal lobe of hypomeron, and each other (fig. 345).

Scutellum pubescent.

Mesoventrite without midlongitudinal carina; surface with microsculptured network of fine microridges; network dense, strongly to moderately developed, less well developed medially; microsculpturing present anteriorly (figs. 9, 82, 93, 176, 198, 250, 276) and weakly developed (figs. 109, 124, 148) or absent posteriorly (figs. 96, 114, 122, 166, 154); basisternum with oval, median depression present and well developed to moderately developed (fig. 82, 174, 250) to broad and shallow (fig. 93) to absent and replaced by broad, feeble impression (fig. 276); microsculpturing of depression weaker than surrounding surface (figs. 93, 250, 341) or absent (figs. 148, 188); depression with (fig. 181) or without pores (fig. 93, 188). Mesofurcasternum (figs. 9, 93, 250) short, wide, and without or with weak microsculpturing. Prepectal ridge strongly curved and separated medially (figs. 9, 82). Mesanapleural suture present anteriorly and posteriorly (fig. 250) or absent posteriorly (figs. 9, 82, 109). Mesotransventral ridge long to short and strongly to shallowly curved (figs. 9, 93, 276) to weakly developed to absent (figs. 122, 181, 188, 276).

Elytra with or without setae on posterior margin; elytral epipleural ridge absent; submarginal ridge present.

Protibia with diagonally to longitudinally transverse combs extending for most of tibial length; combs in shallow depression; tibia not strongly expanded medially, more or less parallel sided for most of length except at tapered base.

Protarsomere, mesotarsomere, and metatarsomere 4 not expanded beneath 5.

Mesotibia and metatibia without spinelike setae along length.

Metatibia with comb on inside or on both sides of apex; comb on inner side large, with numerous teeth; comb on outer side small and with fewer teeth.

Abdominal segments III to VII with tergite and sternite separated; segments III to VII with two pairs of lateroventrites.

Sternite I absent.

Sternite II short; anterior margin bisinuate (figs. 147, 179); posterior margin with (figs. 116, 140, 204, 303, 338) or without (figs. 86, 255, 284) small median lobe or “point.”

Sternite III with basally rounded (figs. 128, 140) or acute (figs. 179, 204, 311) midlongitudinal carina or carina absent (fig. 147); basal transverse ridge present (figs. 147, 179); basal transverse ridge with short lobe or point (figs. 57, 106, 145, 255, 284) or moderately long to long, narrow carina (figs. 179, 204, 321, 338) extending posteriorly or without lobe or point (figs. 147, 192); sublateral carina absent (figs. 147, 179).

Tergite IX with posterior margin deeply emarginate; base of emargination wide and broadly rounded or flat (figs. 261, 331) or narrow and acute (figs. 73, 76, 77); emargination occupied by tergite X; anterior margin broadly concave; middorsal base fused (figs; 261, 292, 331) or partly (figs. 72, 73, 76, 77) to completely divided (figs. 74, 75, 289); lateral side, in lateral view, with lateroapical process gradually tapered to slender, acute apex (see Frisch, 2002: figs. 30–34; lateroapical process with apex straight to slightly to strongly curved dorsally (see Frisch et al., 2002a: figs. 37–39) and extending to about posterior margin of tergite X.

Tergite X (figs. 72–77, 261, 289, 292, 331) elliptical, trapezoidal, or long and tapered anteriorly; tergite X exposed except for narrow anterior and lateral edges covered by tergite IX.

Male: Sternite VII with posterior margin emarginate or unmodified and with or without setae; surface unmodified or modified variously with depressions, elevations; setae scattered or clustered; modifications usually species specific.

Sternite VIII with shallow to deep, narrow to wide emargination; emargination with or without median extension or ventrally directed teeth; surface with or without depression(s) and clusters of setae.

Tergite IX symmetrical (figs. 72, 74, 76) or asymmetrical (figs. 261, 292, 331).

Sternite IX long and slender to moderately wide (figs. 79, 291, 329).

Aedeagus with paramere present as short, flat lobe appressed to median lobe near median foramen or paramere absent.

Female: Sternites VII and VIII with unmodified surface and posterior margin. Tergite IX symmetrical (figs. 73, 75, 77, 289, 347). Gonocoxal plate divided into two long, moderately wide, lateral plates (figs. 78–80, 264, 290, 332); lateral plate not divided into distal and proximal gonocoxites.

Discussion

Nomenclature: The subtribal name was originally published in the vernacular, Scopéates, by Mulsant and Rey (1878: 178). Seidlitz (1889a: 92, 93; 1889b: 92, 93) made the name available when he latinized the name as Scopaeina (ICZN, 1999: Article 11.7.2; Newton and Thayer, 1992: 62). The subtribe was accepted as valid by some subsequent authors who used a subtribal classification for the Paederinae. Some used the vernacular name (Ganglbauer, 1895: 494), others the latinized form Scopaeina (Seidlitz, 1889a: 92; Herman, 1991: 6; Smetana, 2004: 616; Frisch et al., 2002a) or Scopaei (Casey, 1905: 20, 190; Leng, 1920: 104; Coiffait, 1982: 9).

Composition: Initially *Scopaeus* (or *Polyodontus* Solier, 1849, = *Scopaeus*) and *Stilicus* Berthold, 1827 (= *Rugilus* Leach, 1819) were included in the same subtribal group (Solier, 1849: 303–311; Mulsant and Rey, 1878: 178; Seidlitz, 1889a: 93; Ganglbauer, 1895: 494). Sharp (1886: 538–549) did not use subtribes but published *Scopaeomerus*, *Scopaeus*, *Euscopaeus*, and *Orus* in sequence and alluded to their affinity to one another; he provided no supporting characters defining a group. Casey (1905: 20) was the first to formally classify, characterize, and publish the Scopaei (= Scopaeina) as a group now regarded as monophyletic. He (1905: 20) also removed *Stilicus* (= *Rugilus*) from the Scopaei to establish the Stilici (= Stilicina). Casey (1905: 191–192) included in the Scopaeina seven genus-group names which were later consolidated into two genera, *Scopaeus* and *Orus* (Blackwelder, 1939a: 98, 105–106). At the inception of the present work 26 genus-group names, 12 as valid genera or subgenera, comprised the Scopaeina.

Four other genera, *Coecoscopaeus*, *Parascopaeus*, *Scopaeodracus*, and *Typhloleleupius*, have been considered near *Scopaeus* or in the Scopaeina. They have been excluded from Scopaeina by other authors. The characters that segregate them from the Scopaeina are discussed herein in a separate section along with hypotheses concerning their subtribal assignment.

Characters: An early character defining the Scopaeina was the narrow neck (Mulsant and Rey, 1878: 2; Seidlitz, 1889a: 92; Ganglbauer, 1895: 494); this is a widespread feature in the Paederinae.

The first use of the tripartite ligula [glossa] to define *Scopaeus* was by Erichson (1839: 29; 1840: 604). David Sharp used it 36 years later. Buried in a long paragraph introducing the species of *Scopaeus* in the Amazonian valley Sharp (1876: 248) noted that the tricuspid ligular margin was characteristic of the genus and that it persuaded him to combine in *Scopaeus* some Amazonian region species that "depart widely in facies from the ordinary species of the genus." Although he cited no characters to justify the opinion, Sharp noted that his *Scopaeus chloroticus* "may ultimately give rise to the establishment of a separate genus." He was correct, the species is now in *Micranops* (Frisch and Herman, 2014: 69). The tricuspid ligula was used by Casey (1905: 20) to provide the first strong character for delimiting the Scopaeina and permitted inclusion of genera with wide necks. Some authors who accepted subtribal level groups did not endorse Scopaeina (or Scopaei) as valid and included *Scopaeus* and related genera in a more inclusive group (Blackwelder, 1944: 116–122, in the Lathrobii).

Trichobothria, cited as a furrow with a long seta [in the present work as a "trichoid sensillum"] or furrow with a setigerous tubercule, were discovered in the Scopaeina and published first for *Orus* and *Nivorus* (= *Micranops*) (Herman, 1965a, 1965b) and a few years later for *Scopaeus* (Fagel, 1973: 18). Frisch et al., (2002a: 35) defined the subtribe by the slender neck, oblong pronotum strongly tapered toward the anterior margin, quadridentate labrum, unidentate laterotergite of tergite IX, and two-piece spermatheca, but omitted mention of the trichobothrium and tripartite ligula.

As recognized now the Scopaeina is one of the easily and robustly defined, monophyletic groups of the Paederinae. The subtribe is defined and its monophyly supported by the tripartite ligula, presence of the cephalic trichobothria contiguous with the dorsal margin of the eye or on the temple just posterior to the eye, absence of the pronotal marginal ridge, long, tapered profurcasternum, and trilobed anterior margin of sternite II.

Prior to the present work only a few authors defined the Scopaeina by the presence of a cephalic trichobothrium near the eye (Herman, 1991: 6; Frisch and Oromi, 2006: 24). Until then the structure was described but incorrectly named with a phrase. The first mention of the structure in the Scopaeina, species of *Orus* (including subgenus *Nivorus* [= *Micranops*]) were reported to have a "postorbital furrow with setigerous tubercle," "setigerous furrow present above or behind eye," or "furrow containing a long seta" (Herman, 1965a, 1965b). Fagel (1973: 18) described the structure for *Scopaeus* as "un fort pore supra-oculaire d'où naît une très longue soie pâle." Later the structure was referred to in *Micranops* as a "setiferous furrow behind the eye" (Frisch et al., 2002a: 35).

That character seemed sufficient and unique for the Scopaeina until Johannes Frisch (in litt., May 20, 2015) pointed out that *Domene* (*Lathromene*) *lusitanica* Reboleira and Oromi, 2011, appeared to have the same attribute. In the description of *D. lusitanica* the authors described and depicted, in a line drawing, a "long and thin seta inserted in a supraocular, small semicircular depression" (Reboleira et al., 2011: 50, fig. 3a). Serrano et al., (2015: 404, fig. 3b) published an SEM image of the identical structure for *Domene* (*Lathromene*) *viriatoi* Serrano and Boieiro, 2015. Neither of those species were available for examination for the present work. However, according to figure 3a (Reboleira et al., 2011), *D. lusitanica* lacks the tripartite ligular lobe which eliminates it from the Scopaeina. For the description of *D. viriatoi* the authors (Serrano et al., 2015: 405, fig. 3e) do not include an image of the mouthparts, but they do illustrate the protibia with the enlarged grooming apparatus that is characteristic of many species of *Domene*, but not those of the Scopaeina. I surmise it unlikely the tripartite ligular lobe will be discovered in *D. viriatoi*.

Although cephalic trichobothria have been reported for adults in three other subtribes of the Paederinae, including the Scopaeina (Herman, 1991: 6), the work of Reboleira et al., 2011, immediately raised the question of how widespread paraocular trichobothria are in *Domene* Fauvel, 1873. At this writing only nine species of

Domene were available to me for examination. Two of them, *D.* (*Lathromene*) *scopaeella* Fauvel, 1873, and *D.* (*Canariomene*) *jonayi* Hernández and Medina, 1990, have a paraocular trichobothrium. None of the remaining seven species of the genus available for examination, five in *Domene* (*Domene*) and two in *Domene* (*Macromene*), had a cephalic trichobothrium either near the eye or elsewhere.

For *Domene* (*Lathromene*), in addition to *D. lusitanica*, *D. scopaeella*, and *D. viriatoi*, but based only on published descriptions and/or illustrations of the 11 species of the subgenus, a paraocular trichobothrium is or appears to be present in *D. barraganensis* Outerelo and Gamara (2012: fig. 2), *D. bergidi* Salgado and Outerelo (1991: fig. 2), and *D. caurelensis* Outerelo, Gamara, and Salgado (2000: fig. 5). The illustration for *D. hispanica* Outerelo (1985: fig. 2a), displays a short, stout seta near the position that would normally bear a trichobothrium. It is unclear whether this thick seta was meant to represent the normally slender trichoid sensillum or whether the trichobothrium was overlooked, omitted, or absent. For the remaining four species of *D.* (*Lathromene*), *D. cantabrica* Coiffait (1973: 118), *D. gallaeciana* Feldmann and Hernando (2005: 401), *D. gridelliana* Fagel (1967: 201), *D. subiasi* Outerelo (1977: 28), the literature is unclear, there is neither mention nor illustration of a supraocular trichobothrium in the original descriptions. Although I examined only *D. jonayi* of the subgenus *Canariomene*, based on this cursory survey, I postulate it is likely that all the correctly assigned species of *D.* (*Lathromene*) and *D.* (*Canariomene*) Oromí and Hernández, 1986, have a trichobothrium adjacent to the eye. Furthermore, because, among the species examined or reported in the literature, no species of *Domene* s.s. and *D.* (*Macromene*) have cephalic trichobothria, it appears likely they are absent in these two subgenera. For the five species of *D.* (*Spelaeomene*), all from Morocco, no specimens were available for examination. A published image of the head of *D.* (*Spelaeomene*) *aurouxi* Español, 1970, displays what appears to be a blurry image of a slender trichoid sensillum of a trichobothrium (Hernando and Comas, 2014: fig. 2a). This putative sensillum is on the right side of the head where it extends from about the position of the tiny eye toward and crossing antennomere 1 at about the apical third. Literature for the remaining four species of *D.* (*Spelaeomene*) provided neither mention, illustration, nor hint of cephalic trichobothria; nevertheless, I suspect they are present. A deeper examination and search for overlooked characters in *Domene* might result in dividing the group, based in part on the presence or absence of the cephalic trichobothrium.

With the taxonomic value of cephalic trichobothia slightly tainted as a "perfect" derived feature for the Scopaeina and with no other known characters unique to the group another obstacle was added to the study. Although homoplasic features are entirely acceptable for defining taxa in different clades, the discovery of unique, derived characters would be invaluable and preferable. However, it should be noted that the location (or position), form, and setation, of the integumental depression which surrounds and in which the bothrium is located differ both within the Scopaeina and between that and *Domene*. The paucity of material available to me for *Domene* and because nearly all my drawings are made using specimens disarticulated for slide mounting and examination and illustration by compound microscope, it was impossible for me to portray the trichobothria of *Domene*. However, the published illustrations cited in the present discussion differ from those included herein for the Scopaeina. Small differences between the trichobothria of the two taxa would appear to support regarding the trichobothria as synapomorphic, independent developments for the Scopaeina and for *Domene*. To date cephalic trichobothria in adult Paederinae are reported in Scopaeina and some genera of the Cryptobiina, Cylindroxystina, and Lathrobiina. Characteristic positions of trichobothria, not their mere existence, on the head and the modifications of the surface that accommodates the structures can be regarded as potentially defining characters. Only in the Scopaeina do all members have cephalic trichobothria near the eye; among four genera the trichobothrial impression is contiguous with the dorsal margin of the eye; for *Micranops*, the outlier fifth genus, the trichobothrium is temporal and near, but separated from the eye. Cephalic trichobothria are present near the eye in some genera of the Cryptobiina, *Neolindus* Scheerpeltz, 1933, of the Cylindroxystina, and now two, perhaps three, subgenera of *Domene* of the Lathrobiina (see further discussion in Noteworthy Morphological Features of the Scopaeina). However, for none of them is the trichobothrial depression contiguous with margin of the eye. Furthermore, this trichobothrial depression lacks setae in *Neolindus* and *Domene*, and is round and margined with a ridge.

Enallagium, *Medome*, and *Ecitomedon* have a tripartite ligular lobe. I have too few specimens of these genera to dissect and so was unable to determine if the structures are the same or only similar. However, the three genera all lack the cephalic trichobothrium and are omitted from the Scopaeina.

Genera Included: *Micranops* Cameron, 1913, *Orus* Casey, 1885, *Hyperscopaeus* Coiffait, 1984, *Scopaeus* Erichson, 1839, and *Trisunius* Assing, 2011.

Noteworthy Morphological Features of the Scopaeina

Included in this section are remarks on a few significant, newly discovered structures, or diagnostic characters, used in the present examination of the Scopaeina.

Head

Trichobothrium (pl. trichobothria): As used herein, a sensory organ comprised of a bothrium, a bump, pit, or depression, from which arises a trichoid sensillum, a long, hairlike seta (figs. 11, 15; see also Nichols, 1989). Trichobothria are widely present in arthropods and a variety of functions, but commonly that of a mechanoreceptor, have been ascribed to them. Bothria (sg. bothrium) exhibit some variation in structure and form, the sensilla (sg. sensillum), apparently not so much, at least in the Paederinae. Addressing trichobothrial variants outside the Scopaeina is beyond the intended scope of the present work, but they have been briefly discussed and referenced for other taxa by other authors (see, for example, Schuh, 1975, and Opitz, 2004: 19). Additional descriptive details of trichobothria are presented in the accounts for the subtribe and included genera (figs. 11–16, 108, 297, 298, 344) and briefly in this section.

Steyskal (1991) denounced use of trichobothrium to discuss and describe the seta [sensillum]. He wrote "Trichobothrium…is a well formed word if used with reference to the receptacle which is at the base of all setae." He wrote that most uses of the word incorrectly referred to the seta. According to Steyskal, in 1917 Hansen wrote that the term was "well composed as it signifies a hair in a pit." Steyskal responded that the definition was untrue because the term actually means "a pit into which a hair is inserted." Perhaps a hairsplitting complaint? Because application of trichobothrium did not conform to its formation he proposed that bothriotrix (pl. bothriotricha) replace it to discuss the "unusually thin, flexible, elongate setae, found in characteristic positions."

Steyskal's objection is not to the word *trichobothrium*, but to its application to the "seta." If investigators referred to a trichobothrium as a "cuplike integumental receptacle into which the seta is inserted." he would have no objection. Most, perhaps all, uses of *trichobothrium* pertain to the sensory organ that consists of a pit (bothrium) and sensory "hair" (sensillum). It is probable that one first notices the long, fine, hairlike "seta," not the receptacle. One might describe the position of the organ, the condition of the bothrium, or sensillum, depending on which exhibits more informative variation. By general use and understanding a trichobothrium has both a bothrium and sensillum. It seems improbable that anyone thinks a pit without a sensillum or a sensillum without a bothrium is either a trichobothrium or bothriotrix.

According to Steyskal, from the time of its fabrication "trichobothrien" was used for the hair, not the pit. Similarly, many uses of *trichobothrium* I have seen in the literature referred to the seta [sensillum]; few discussed the receptacle or pit, but it was described if it varied. A Google search for the singular and plural of "trichobothria" and "bothriotricha" yielded 36 times more uses of the former than latter. *Trichobothria* is used in a variety of arthropod taxa, bothriotricha primarily, perhaps only, in the Collembola. Should we replace a commonly used term with a more rarely used one?

Since all words are made-up inventions, defined first by the originator and then by consensus of use, it makes little sense to replace *trichobothrium* simply because its etymological pedigree is questioned, rather than according to how it is used by (nearly) everyone. How many words would we be compelled to abandon if we used only those that were properly formed?

Scopaeine trichobothria. Species of the Scopaeina have either dorsal, paraocular (figs. 11, 15, 194, 206, 315, 333, 344) or temporal (figs. 267, 282) trichobothria. The bothrium is included in a supraocular depression (figs. 11, 15, 23, 27, 245, 333, 334) adjacent to and near the middle of the dorsal margin of the eye, supraocular canal (figs. 13, 297, 309, 316) adjacent to and near the posterodorsal margin of the eye, or a temporal, postocular cavity (figs. 12, 267, 282) behind and separated from the eye. The paraocular trichobothrial depression and canal are shallow and lack sculpturing; short setae may be present in the canal (fig. 13, 297, 316) or adjacent to the depression (figs. 11, 14–16, 108). The depression is ovoid, the posterior and dorsal margins are well developed, the anterior margin less well formed so the depression gradually merges with the cephalic surface anteriorly. The trichobothrial canal is long, anteriorly tapered, deeper posteriorly, and gradually shallower anteriorly; the bothrium is at the deeper, posterior end of the canal where the marginal edges are well developed; just anterior to the bothrium is a cluster of setae. The canal gradually fades away anteriorly. In addition to the setae in the trichobothrial receptacle, setae tend to cluster near the trichobothrial depression and canal, dorsally and posteriorly near the depression (fig. 14–16) and posteriorly near the canal (fig. 13, 297, 316). The temporal bothrium is in a deep, short, sharply margined cavity, behind and separated from the eye (figs. 12, 266, 267, 282, 283); the cavity is setate.

For the Scopaeina trichoid sensilla are flexible, long, thin, imperceptibly and gradually tapered from base to apex (figs. 11–16, 194, 245, 267, 309, 333), have a shiny, silky appearance under reflected light and originate from low, rounded bothria located in depressed areas near the eye. The sensillum of at least some species is fluted (figs. 27, 40, 81, 108, 269); however, that feature was not explored and perhaps is common to trichoid sensilla for all species. Trichoid sensilla might be overlooked because they are so very thin and may be plastered against the cuticular surface on pinned, pointed, or card-mounted specimens.

The function of trichobothria in the Scopaeina is unknown. Species of the subtribe are primarily ground-dwelling animals that live cryptically in the debris of upper layers of sandy or gravelly soil in moist habitats with organic detritus. They are typically collected near streams and rivers in leaf litter and debris and under stones or in gravel on damp, sandy soil of sunny or moderately shaded banks, and far less commonly on shaded forest floors in moist leaf litter and organic ground debris or in caves (Frisch et al., 2002a; 28; Frisch and Oromi, 2006; Herman, 1965a, 1965b; personal obs.). How trichobothria, how trichoid sensilla function in the perhaps restricted space of these upper layers of gravel, sand, debris, slightly moist leaf litter is difficult to fathom. One can only guess that many or most individuals are on or near the surface or in the loose upper layers of organic debris where the interstices in the litter, debris, sand, and gravel are far more commodious for tiny beetles to move about than might be imagined, ample for tiny beetles to move comfortably, and for long, slender trichoid sensilla to operate effectively. Among the various functions predicated for trichobothria one plausible possibility for litter-dwelling beetles is the disturbance of the sensillum by movement of air made by prey or predators (Crowson, 1981: 258, 463).

Although trichobothria are regarded as typical of paederine larvae and found on the head, stipes, and pronotum (Thayer, 2005: 317, 330), they are known for adults of rather few genera of the subfamily. Although common in larvae of the Paederinae, it is unclear whether all larvae of the subfamily have them. In addition to the Scopaeina, cephalic trichobothria occur (personal obs.) in *Neolindus* (Cylindroxystina), two, perhaps three, subgenera of *Domene* (Lathrobiina), and *Ababactus*, *Biocrypta*, *Cryptobiella*, *Homaeotarsus*, *Lissobiops*, *Monocrypta*, *Ophitodum*, *Opithes*, *Pycnocrypta*, *Scopaeodes* (Cryptobiina). Not only will subtribal characters of the Cryptobiina, Cylindroxystina, and Lathrobiina separate these genera from the Scopaeina, but the absence of a pronotal marginal ridge, bisinuate anterior margin of sternite II, tricuspidate ligular lobe, and dorsal paraocular or temporal, postocular position of the trichobothrium will separate the Scopaeina from these genera.

VESTITURE. The vestiture is of two types of setae, pale, short, fine pubescence and longer, thicker, pigmented macrosetae. Herein pubescence and macrosetae replace the terms primary and secondary setae respectively as used by Frisch in his many publications on *Scopaeus*. Pubescence is furlike, comprised of small, fine, decumbent or recumbent setae, is dense to sparse, and covers most of the body of most species. Macrosetae are the larger, longer, often pigmented, erect or suberect setae, are scattered, and are far less common. The density of both varies.

GULAR SUTURES are narrowly separated to nearly contiguous in *Hyperscopaeus* (fig. 244) and some *Scopaeus* (fig. 49). The sutures are moderately widely separated in the adults of most species of the subtribe. Extrapolating from work by Evans (1965a), Naomi (1987) proposed the function of the closely aligned sutures was to provide for attachment of more powerful and thicker adductor muscles among predatory species that feed on living prey and for species that burrow. Among the Scopaeina, *Hyperscopaeus* and the more robust species of *Scopaeus* (for example, those of the *S. opacus* species group) have narrowly separated to contiguous gular sutures. We don't know much about what scopaeine species eat. However, might the larger species be eating larger and active prey than do smaller species, which might be feeding on eggs and prey with softer outer integument? That hypothesis remains to be tested. The condition of the gular sutures may help to define some species groups of *Hyperscopaeus* and *Scopaeus*.

LABRAL DENTICLES: The anterior labral margin of most species of the Scopaeina has one (fig. 159) or two (figs. 6, 100, 169, 186, 249, 319, 340) pairs of slender, apically acute, or broader and apically rounded processes or lobes. Only the *S. chiriquensis* species group lacks denticles (fig. 59) or have a median lobe (fig. 58); the latter might be considered an apically rounded denticle by some or a lobe by others; in either case it is more easily seen using a compound microscope. That process or lobe or denticle was seen and illustrated only by using a compound microscope for a slide-mounted specimen. Herein, the slender, tapered, apically acute, labral processes are referred to as denticles, as they would be by most authors; the broader, apically rounded projections or processes are more open to interpretation as lobes or broadly rounded denticles. To my way of seeing and thinking, strongly tapered, apically acute protrusions are denticles, whereas the broadly rounded ones that effectively do not taper are lobes. Marginal enlargements of the labrum such as the broad, apically rounded, submedial ones of figure 59 or the tiny, sublateral ones of figure 319 might be referred to by one author as lobes, as I do, and by another as denticles on a labrum. However, almost certainly both, if on the posterior margin of an abdominal sternal segment, would be described by most authors as lobes. This dilemma of wording is best resolved by illustrations. The species group lacking denticles presently includes only a few named species, but others exist in collections, and more are certainly to be discovered in the wild. The submedial labral denticle of scopaeines is always longer than the sublateral. Many species, in place of an apically acute denticle, have a broad, apically rounded lobe in the position of the sublateral denticle; the lobe is small to moderately large. Frisch (in litt., 23 August 2018) regards the sublateral lobe as a denticle and describes the labrum of the Scopaeina as quadridentate (Frisch et al., 2002a: 35). Frisch (personal commun.) considers, probably correctly, the quadridentate state to be synapomorphic for the Scopaeina and accurately observes that the sublateral denticle is smaller and more variable in form than the submarginal denticle. Herein, the subtribe is regarded to be edentate, unidentate, bidentate, or quadridentate. Although a minor point, readers should be aware of the differences of interpretation of the labral margin between the present article and the works of Frisch. Our difference of language does not mean we disagree about the structure or evolution of the labrum. The rounded, labral lobe may have given rise to the acute, labral denticle or vice versa. However, labral denticulation is a relatively poor character for defining genera in the Scopaeina.

LIGULA: The paraglossae (fig. 317), the lateral elements of the ligula, are dorsad of the labial palps, broadly curved medially, and covered with a mesial row of stout setae and a dense mass of cuticular processes laterally (figs. 168, 248, 310, 317, 339; Snodgrass, 1935: 145–150, 156; Matsuda, 1965). The paraglossal setae and cuticular processes extend proximally along the lateral side of the hypopharynx and converge posteriorly near the entrance of the mouth. Among the Scopaeina, the glossa, which may be modified to what is referred to herein as a tripartite ligular lobe (figs. 160, 187), tricuspidate ligula, or tricuspid ligula, is a prominent, sporklike row of three glabrous, long, wide, tapered lobes centered between the paraglossae. Proximad of the trilobed glossa is the hypopharynx which can have cuticular processes (fig. 187) or not (figs. 248, 310, 318, 339). The tricuspid ligula was discovered in *Scopaeus* more than 180 years ago (Erichson, 1839: 29; 1840: 605), used to synonymize *Polyodontus* with *Scopaeus* (Kraatz, 1857: 701), referred to as a tricuspidate ligula (Sharp, 1876: 248), and used later in the classification of the Paederinae (Casey, 1905: 20). More recently Assing (2011: 197, fig. 60) illustrated and cited it in *Trisunius*. It is one of the defining characteristics of the Scopaeina. The lobes are sclerotized, wide basally, tapered to subacute apices, flattened, and lack vestiture or other adornment. But alas, the structure may not be unique to the Scopaeina. Although absent in most genera it occurs in *Ecitomedon* (Medonina), *Medome*, and *Enallagium* (Lathrobiina). A comparative morphological study of the tripartite ligula of these four genera and those of the Scopaeina may or may not reveal the origins to have been homoplasic.

The function of the tripartite glossa is unknown, but perhaps worth speculation because it is a unique structure. If, as suggested by some authors (Evans, 1965b: 92, 108, 106; Crowson, 1981: 163, 165; Thayer, 2005: 299), extraoral digestion is general among the Staphylinidae, including the Paederinae, the ligular lobes of the Scopaeina may be part of a blocking and filtering apparatus designed to maintain prey in a preoral cavity until it is essentially a liquified soup.

According to Evans (1965b) among morphological structures used in preoral digestion by *Philonthus decorus* (Gravenhorst) are: a median emargination and ventral groove of the labrum; densely setate medial edge of the maxillary lacinia and galea; anteriorly and anteromedially oriented setae and spicules on the surfaces of the epipharynx, paraglossa, hypopharynx, and mandibular mesial base; along with a chamber, an empty space, where prey animals, or parts of, can be held and converted to a dense chyme of particles and tiny lumps of flesh mixed with digestive enzymes. Evans (1965b) provided a vivid, detailed account of preoral digestion by *P. decorus*. He wrote that the prey animal is captured with the mandibles which hold and pulverize the animal, that the setal brushes of the lacinia and galea rotate rapidly to move the mass of flesh upward and anteriorly to prevent cuticle and large bits of tissue from entering the mouth. All the while digestive enzymes are supplied, so the bolus gradually becomes a dense liquid of fine particles as cuticular pieces and indigestible tissue are moved forward, upward, and out of the preoral macerational cavity. The resultant emulsion of enzymes and animal tissues is drawn through the oral opening into the proventriculus then mesenteron.

The genera of the Scopaeina have all the requisite structures for preoral digestion. The labrum (figs. 169, 186, 249, 319, 340) has a median, marginal notch and deep channel on the ventral surface; the epipharynx is covered with anteromedially directed setae and cuticular processes (figs. 169, 249). The ventral labral groove (fig. 169) provides the roof for a preoral digestion chamber, the dorsal surface of the hypopharynx (fig. 187) provides the floor, and the massive collection of anteromedially directed, hypopharyngeal and paraglossal setae and cuticular processes form the lateral walls of the chamber. The microsculptured surface of the labral groove (*Scopaeus*, figs. 169, 186, 249) may hinder the posterior flow of pieces of sclerites and overly large clumps of tissue. The bolus is ground to a pulp in this digestion chamber. The cluster of epipharyngeal spicules, cuticular processes, and setae along with the mass of paraglossal setae create a posteriorly converging pathway (figs. 168, 169) that corrals and guides the liquified mass backward toward the oral opening as pieces of cuticle and large lumps are ejected anteriorly. The anteroventral position of the tripartite ligular lobe may make it an entryway gate to help maintain the mass in the digestive chamber yet permit sifting and ejection of unwanted tissue.

In contrast to *Scopaeus*, microsculpturing of the labral groove is evident only posteriorly in *Orus* (fig. 319) and absent in *Trisunius* (fig. 340); those variations may reflect dietary differences.

If the tripartite ligular lobe is important for processing and digesting prey, might the organ reflect the diet of the species?

PETIOLATE NECK refers to the neck of staphylinids with a longer than usual, abruptly constricted, narrow, nuchal groove (figs. 99, 161, 240). Behind is the nuchal ridge (figs. 161, 193). This configuration occurs in *Hyperscopaeus* and *Scopaeus*, but not the other scopaeine genera, *Micranops*, *Orus*, and *Trisunius*, which, like most paederines, have a moderately constricted, wide neck and short nuchal groove (figs. 256–258). Petiolate necks are scattered throughout the Paederinae and found in some speciose genera, for example *Rugilus*, but is not especially common otherwise (personal obs.). That infrequency may be the reason a narrow neck has long been considered a defining feature of *Scopaeus*. However, used alone, the pinched neck created a polyphyletic group for *Scopaeus* that masked monophyletic entities within. Some narrow-necked species were regarded as related to *Scopaeus*; discussion of these genera is included in another section of this work.

The nuchal ridge is a strong ridge in *Scopaeus* and *Hyperscopaeus* (figs. 193, 240) that crosses the dorsal surface of the neck onto the sides where it ends before reaching the ventral surface. In dorsal view the ridge is evident as a small projection or nuchal bump (fig. 99) on each side of the neck and is more prominent on some species than others. The neck of *Micranops*, *Orus*, and *Trisunius* is wide, not strongly constricted or petiolate, and the nuchal ridge is merely a low, modestly developed ridge on the dorsal and lateral sides (figs. 266, 333).

EYES: The eyes of most species of the subtribe have setae between the corneal lenses of the compound eyes (figs. 13, 17–22). Those with only one corneal lens lack corneal seta; whether those with few lenses have or lack setae requires further study.

The corneal lenses of *Hyperscopaeus* (fig. 17) and some species of *Micranops* (fig. 19) and *Orus* (fig. 20) have a corneal sensillum on the surface of lens of the first two or three rows of lenses along the dorsal edge of the eye. These sensilla vary among the three genera. These sensilla were not found in *Scopaeus* (figs. 23–46) or *Trisunius* (fig. 22), but there was no particular search for them since they can only be found with SEM examination. The surface of the corneal lens of some species of *Micranops* (fig. 18) and *Scopaeus* (figs. 23, 29, 34, 35, 37, 38, 40, 46) are wrinkled. Whether this corneal wrinkling is a precursor to or remnant of sensilla or represents something altogether different is unknown. Alternatively, the wrinkling may be an artifact created by the vacuum of the SEM; understanding this wrinkling requires further investigation. The structures on the corneal surface of a species of *Orus* (fig. 21) and some of the lenses on *Hyperscopaeus* (figs. 11, 17) look defunct. The function of corneal sensilla needs investigation. The reason for or function of these corneal sensilla is unknown. The surface modification of the corneal lens cannot be seen with binocular dissecting or compound microscopes; they were discovered and illustrated with SEM photographs.

Most species of the subtribe have presumably functional, large, well-developed eyes. Four known species of *Micranops* are eyeless; *M. brunneus* has a white, ocelluslike eye spot. At least three undescribed species of *Orus* have reduced eyes and are flightless (personal obs.). Absence of eyes is usually associated with species that live in caves or deep in the soil; some species that live at high elevation also lack eyes and are flightless. Eyeless species of *Micranops* have been found in caves, under deeply embedded rocks at 2450 m elevation, and up to 35 cm deep in the soil (Frisch and Oromí, 2006); *M. brunneus*, known from one specimen, is flightless and collected at 3000 ft elevation in Jamaica (Cameron, 1913: 351), perhaps in soil. Flightless species all have reduced eyes. Many specimens of *Orus rubens* have been collected from numerous caves in arid regions of the United States and Mexico, but none have been found without or with reduced eyes (personal obs.).

Thorax

PROTHORAX: The lack of a pronotal marginal ridge in the Scopaeina also occurs in some Procirrina, Cryptobiina, Stilicina, Monista, Stilicopsina, Astenina, and Echiasterina.

The PROFURCASTERNUM extends posteriorly from the sternacostal suture (fig. 345), which connects the apophyseal invaginations of the proendosternites. The probasisternum is the entire sclerite that extends anteriorly from the sternacostal suture to the anterior proventral margin and anterolaterally to the notosternal sutures. In the Scopaeina the profurcasternum is moderately long to long, strongly tapered posteriorly to an acute apex, and includes the extension of the median, intercoxal ridge from the basisternum (figs. 98, 345).

The demarcation of the rarely referred to profurcasternum has been misinterpreted in some recent works. The probasisternum (fig. 345) has an unnamed ridge across the posterior portion that is confluent with the anterior margin of the procoxal cavity. That ridge is not the sternacostal ridge as so interpreted in an earlier, influential work (Smetana and Davies, 2000: 10–11, fig. 2). In that article figure 2 depicts a hypothetical species. The two spots labelled “fossa” almost certainly represent the apophyseal invaginations for the proendosternites. When carefully examined, between those invaginations one would find an internal ridge and an external suture (though perhaps faint) connecting the invaginations. The internal ridge and external suture would be the sternacostal suture and the anterior demarcation of the profurcasternum, which would be a short, wide sclerite in the Smetana and Davies hypothetical example. One recently published example of the Smetana and Davies interpretation is Solodovnikov (2005: fig. 64); other articles have employed the same interpretation.

MESOVENTRITE: Terms were needed for discussion of variation of the ventral surface of the mesothorax. Neither Blackwelder (1936) nor Naomi (1988) discussed in detail the ridges on the mesoventrite. The terms applied herein were derived from my understanding of Snodgrass (1935) and the dense, difficult-to-understand work of Matsuda (1970). The terms used herein reflect extension of previous interpretations (Herman, 2013: 17–25, figs. 20, 21) and are summarized in figure 9. Of potential taxonomic interest are the conditions of the prepectal, mesanepisternal, and transventral ridge, the distribution of the microsculpturing, and details of the median depression. Whether any of these ridges will have any value for identification, classification, or phylogeny is yet to be determined. Perhaps old-timers from decades past explored these ridges and found their use wanting, but since there is no record of that examination, they may be worth testing.

The prepectal ridge is separated and the medial end of each half strongly curved in all genera and species groups (figs. 82, 181, 198, 250, 276, 346). Despite the condition of the prepectal ridges for *S. ooderes* shown in figure 176, the prepectal ridges of this species group do not touch. The depiction of the left prepectal ridge in figure 176 is aberrant and was not found in other specimens of the species. The mesotransventral ridge (fig. 9) is present in all scopaeine genera, short in *Micranops* (fig. 276), well developed and strongly curved in *Hyperscopaeus*, *Orus*, and *Trisunius* (figs. 250, 299, 341). Among the species groups of *Scopaeus*, the mesotransventral ridge (fig. 9) varies in curvature (figs. 93, 103, 166) and length (figs. 96) and, for a few, the ridge is absent or difficult to detect (figs. 122, 181, 188). The anterior portion of the mesanapleural suture (fig. 9) is present in most scopaeines (fig. 93, 176, 250, 276, 299, 241), but may be absent (figs. 96, 122) or its condition difficult to assuredly determine (figs. 166, 188) in a few species groups of *Scopaeus*. The posterior segment of the mesanapleural suture (fig. 250) was found only in *Hyperscopaeus*.

The scopaeine mesobasisternum has a median, oval depression (figs. 9, 82, 250, 308, 341). For most scopaeines the depression is deep and narrow (figs. 82, 250) or broad and shallow (fig. 93). The depth, size, and shape of the median depression varies; the smallest appears to be in the *S. opacus* and *S. nitidus* species groups (figs. 166, 181). For *Micranops* (fig. 276) it is broad, shallow, and barely evident, perhaps nonexistent. Most surprising is the dense cluster of, possibly, secretory pores in the median depression of *Scopaeus opacus* (*S. opacus* species group) (figs. 181–182). It is yet to be determined if other species of the *S. opacus* species group have these pores or if they are found elsewhere in *Scopaeus*.

The mesoventral surface of *Micranops*, *Hyperscopaeus*, *Orus*, and *Trisunius* is covered (figs. 250, 276, 299, 341) with a microsculptured mesh of fine microridges, the strength of which is reduced medially. For *Scopaeus* the network is present anteriorly in all groups. For some the mesh is present everywhere, but slightly to moderately diminished posteriorly (figs. 82, 93, 141, 211), for others it is partially (figs. 109, 124) or entirely absent posteriorly (figs. 122, 166, 188). For most groups of *Scopaeus* the network of microsculpturing is present and moderately to well developed (figs. 82, 93, 102, 141) to weakly developed or absent and the surface glabrous (figs. 96, 122, 156, 166, 181, 188) on the vertical section of the posterior mesobasisternum (fig. 9) that borders the mesocoxal cavity and touches the anterior margin of the mesofurcasternum.

MESOFURCASTERNAL APOPHYSIS: A species of the *S. chiriquensis* species group has a long, slender, internal, posteriorly extended spike, the mesofurcasternal apophysis (fig. 82). No muscles or tendons were found to be attached to the apophysis. To date this apophysis has been found in no other species of *Scopaeus*, but a species of the *S. nevermanni* species group (fig. 156) has a tiny nubbin in the same position that may represent a remnant or precursor or may have no connection to the mesofurcasternal apophysis. This apophysis is found in at least one species of *Hyperscopaeus* (fig. 241, 250), but is absent in at least one other. The function and distribution of the apophysis are unknown.

Visible in most of the illustrations of the mesothorax are two, small, black holes on each side of the intercoxal carina, the mesosternal apophyseal invaginations (figs. 9, 96) of the mesendosternites. In illustrations of slide-mounted specimens, the endosternite is visible as a long, slender, dark shadow extending anteriorly from the invagination (figs. 9, 96, 156). The invaginations and the suture extending between them mark the anterior margin of the mesofurcasternum and posterior margin of the mesobasisternum (fig. 9); anteriorly are the variously fused or divided mesobasisternal, mesoanepisternal, and mesoepisternal sclerites.

Metaventrite: The terms used in the present work (fig. 10) come directly from an earlier discussion of the metaventrite (Herman, 2013: 17–25, figs. 20, 21) that had been derived from my understanding of Snodgrass (1935) and Matsuda (1970). The structures related to description of the stridulum, metaventral sublateral ridge, and metakatepisternal processes are new.

Although the terms applied to structures of the pterothorax are based on the current interpretation of Ferris and his students (see Herman, 2013, for references) I remain skeptical of the validity of Ferris's lost-sternum hypothesis. The current deployment of his hypothesis seems to have appeared suddenly and without preamble, discussion, or any more than the minimal data published by Ferris and a few of his students. Those who promulgate the Ferris hypothesis have produced no new data to support their contention. Indubitably, hypotheses can be proposed based on minimal or zero evidence, thought experiments, even dreams, but they should be falsifiable and so tested. Matsuda (1970), in a dense, difficult to read, 400-page treatise on the evolution of the insect thorax, rejected the Ferris hypothesis after studying numerous species across the orders of Insecta. This rejection does not seem to have been refuted or even considered by those who now promote the lost-sternum hypothesis. If—as demonstrated by Matsuda and herein—identifiable sternal elements remain, then the lost-sternum hypothesis requires testing rather than acceptance without comment. More morphological and possibly embryological study and discussion is required to resolve this conundrum. At a bare minimum, Matsuda's work, though challenging to read and understand, requires careful consideration before accepting Ferris's lost-sternum hypothesis.

Two heretofore unrecognized characters unique to *Scopaeus* and important for defining the genus, the stridular file and metakatepisternal processes, are found on the metaventrite. The file, one half of the stridulum, is difficult to see using our standard binocular dissecting microscopes; the light must reflect from it at just the right angle for it to be seen or the metaventrite must be viewed using diffused light. Even when viewing slide-mounted specimens with a compound microscope it can be overlooked. However, the file can be seen with both instruments if one knows where to look and does so with properly adjusted light. Herein, numerous images show and discussions describe where to find the file. Most species of *Scopaeus* are small to tiny and the file in most is tucked tightly against the submarginal ridge of the metaventrite (figs. 86, 89, 90, 101, 102). The file was a serendipitous discovery on one of the relatively few species for which the file is exposed and partly separated from the metaventral submarginal ridge (figs. 163, 164). Illustrations of the file are from both SEM images and photographs of slide preparations. Although the SEM images show more detail, the slide images are included both in part to demonstrate that the file can be seen and interpreted without the SEM.

The second new character is the pair of long, tapered metakatepisternal processes (fig. 97), which is discussed in more detail following discussions of the metathoracic and mesofemoral elements of the stridulum.

Stridulum (pl. stridula; adj. stridular; nominalized from the neuter form of the Latin adjective *stridulus*, "that which makes a shrill or high-pitched sound"): a sound-producing structure consisting of a file (also called a rasp or pars stridens) (fig. 105) and plectrum (or scraper) (fig. 106), which are rubbed together to produce sound, i.e., to stridulate. The term is proposed as a synonymic replacement for the clumsy "stridulatory structure" or "stridulatory organ". Stridulum has been used for the stridular file in Orthoptera (Nichols, 1989). However, since at least three other terms are already available and used for the file and there is no one-word synonym for the two stridulatory structures together, a better use of the word "stridulum" would be to fill that vacancy.

Since some species of insects that are known to stridulate have structures resembling those in *Scopaeus*, the hypothesis herein is that species of *Scopaeus* also stridulate. Throughout the present work, discussions of the stridulum for *Scopaeus* all assume stridulation; that idea remains a hypothesis until shown otherwise.

STRIDULAR FILE**:** Stridula of *Scopaeus* are comprised of a file, a row of many tiny, contiguous bumps or ridges or "teeth" near the lateral edge of the metathorax and plectral ridges, a cluster of ridges on the mesial or posterior base of the mesofemur. In the Scopaeina stridula are unique to *Scopaeus* and help define the genus. Their discovery forced abandonment of a nearly finished manuscript with copious illustrations and required a complete rewrite and reillustration for the present one. That discovery also permitted detection of two other previously unnoticed features that are diagnostic for the genus. The stridular file is a long row of many, short, rounded or keeled (fig. 90) bumps, ridges, or teeth (fig. 151). The bumps are contiguous in most groups (fig. 105) or slightly separated in one (figs. 164, 165). The teeth of the file tend to be smaller anteriorly (figs. 90, 150), then large through the long midsection, then smaller again posteriorly until they fade away (figs. 105, 111, 126, 151, 178, 196). The file occupies about half to two-thirds of the length of the metaventrite (fig. 104, 142, 154). For most species groups and perhaps most species, the file hugs, that is, it is contiguous with the metaventral submarginal ridge (figs. 10, 105, 110, 111); for a few the file is against the submarginal ridge for most of its length and bends slightly away near the distal end (figs. 131, 133) or sweeps medially from about the basal third of the submarginal ridge onto the mediolateral region of the metaventrite (figs. 119, 154, 163). The teeth of the file vary among species in size, number, form, ventral surface, and separation from one another. Understanding the diversity and function of those details requires new research, larger samples of individuals and species, and work with living animals.

MESOFEMORAL PLECTRAL RIDGES are a series of ridges aligned with the longitudinal axis, near the base of the mesial or inner surface of the mesofemur (fig. 106). The number of ridges varies from one (fig. 85) to perhaps 12 (figs. 132, 203) or more. The *S. chiriquensis* species group seems to have only one plectral ridge (fig. 85); that number requires confirmation with additional species and specimens. The ridges, although near the middle, begin slightly closer to the ventral edge of the femur in some species (fig. 239), and closer to the dorsal margin in others (fig. 92, 107, 127). For a few species the cluster of plectral ridges touches the dorsal margin (fig. 113, 121). For each set of plectral ridges, at least one ridge is more prominent and larger than the others (figs. 106, 112, 113, 121).

The plectral ridges are a realignment of the existing microsculptured surface. For scopaeine species that lack plectral ridges the entire mesial mesofemoral surface, from base to apex and ventral to dorsal margin, is covered with strong, transverse, dorsoventrally aligned microsculpturing (figs. 253, 277, 279, 302, 312, 337). For *Scopaeus* the more distant microsculpturing surrounding the plectral ridges is also arranged dorsoventrally (figs. 146, 197, 219). The microsculpturing nearest the plectral ridges, particularly that ventrad of the ridges, is aligned in transitional angles (figs. 92, 107). The plectral ridges are arranged nearly in line with the long axis of the mesofemur.

Obviously, the plectral ridges are rubbed or slid along the length of the file to produced sound. The stridulum is present in both males and females. Many questions surround this stridulum. No one knows whether sounds are produced by species of *Scopaeus*, the structures are suggestive, but no sound has been heard … yet.

Species of *Scopaeus* are not found in the open, but rather live under stones, in gravel on damp, sandy, sparsely vegetated banks exposed to sun and covered with organic debris near rivers and streams (Frisch et al., 2002: 28) or can be collected from the uppermost layers of moist, sunny to partially shaded soil with ground litter and debris and near streams.

Many obvious questions about stridula can be asked. If *Scopaeus* spp. live in such confined habitats, why would sound be produced? In close quarters how far would the sound travel? What would be the function of the sound? Who hears the sound? Do conspecifics hear the sound and, if so, what and where are the auditory structures? If heard, what do the recipients do? What prompts stridulation? The challenge of finding auditory structures is discussed below. Are there tympanal or subgenual organs or some other type of chordotonal organs, if so, where and how would they be recognized? Are there antennal auditory structures? Are the sounds defensive or attractive or are they notifications? Since trichobothria are mechanoreceptors that might sense the movement of molecules of air, might the trichoid sensillum detect movements of predators or prey? If sound vibrates the trichoid sensillum, why do other genera of the subtribe, which do not have stridula, have trichobothria? Or asked another way, why don't other scopaeine genera have stridula? Do these other scopaeine genera have different, unrecognized structures for producing sound? Since species of *Scopaeus* are so small, would recording the sound of one individual even be possible? Could several or many specimens in a container be recorded and might the resultant sound be organized or mere chaotic sound or noise? To be able to hear and record the sound of these minute beetles, might one gather specimens of one of the larger species, and put them, male or female or both, into a terrarium with recording equipment sensitive to ultrasound? Are the stridula and sounds species specific?

Because among species of *Scopaeus* the files vary in length, shape, and position on the metaventrite, and the teeth vary in number, size, separation, surface, and form, and because the plectral ridges also vary in number, length, curvature, prominence, and position on the mesofemur, there is little doubt the sounds, whether "songs" or mere chirps, will vary. If they vary among species, might the differences suggest conspecific signaling, notifications, between the males and females of location and availability for mating? If the variations of chirps are associated with mating, might that be a barrier between species?

Stridula, widespread in the Coleoptera (Crowson, 1981), have been found in four families of the Adephaga and up to 26 families of the Polyphaga according to Wessel (2006). Since stridula are usually found serendipitously rather than by systematic searches, it is likely that many more genera and families will be discovered to have them. Crowson (1981: 340) listed nine possible functions of sound production among insects. Four of them were directly related to mating, two were said to be restricted to social insects, and one each to disturbance/alarm, pair formation/aggregation, and aggression. Wessel (2006) wrote that at least 14 types of stridula occur on various structures in adult beetles, three in larvae, and one in a pupa. According to Wessel's table 30.2, the metaventrite/mesofemur of *Scopaeus*, unknown in the Coleoptera until now, would be the 15th type.

Prior to the present article, stridula were reported in the Staphylinidae for nine genera of four subfamilies: the Apateticinae, Oxyporinae, Pseudopsinae, and Silphinae. A fifth subfamily, the Paederinae, and the 10th and 11th genera with stridula are reported herein. For *Nicrophorus*, of the Silphinae, the plectrum is a subapical ridge on the ventral side of each elytron and a file is on two ridges, one on each side of the midline of the fourth or fifth abdominal tergites (Lane and Rothschild, 1965: figs. 1, 2; Ward, 2022). Stridula for *Nicrophorus* were discovered as long ago as 1869 by Hermann Landois and, thereafter, reported upon in at least 11 more articles by various authors, including Charles Darwin (Hall et al., 2013: 662). Both genera of the Apateticinae are stated to have a stridulatory file on the lateral margin of abdominal sternite II, *Apatetica* by Madge (1980: 312) and *Nodynus* by Thayer (2005: 328). Neither author illustrated the file nor described nor pointed to a possible plectrum (= scraper). Stridulatory files were discovered by Newton (1982) who, in the first classificatory use of stridula in the Staphylinidae, redefined the Pseudopsinae to include *Pseudopsis*, *Zalobius*, *Asemobius*, and *Nanobius*. Each of the four genera have a file on the lateral side of tergite IX. SEM images of the stridulatory file were provided for *Pseudopsis* and *Nanobius*. For the plectrum, "the apex of the inflexed sides of tergum VIII" was suggested (Newton, 1982: 9). More recently, stridula were found on species of *Oxyporus* and *Pseudoxyporus* of the Oxyporinae (Navarrete-Heredia et al., 2021). The stridula for both genera are on the legs. For both *Oxyporus* and *Pseudoxyporus*, the stridulatory file is on the ventral surface of the mesocoxae. Although the plectrum of *Oxyporus* is on the basal quarter of the posterior surface of the profemur, for *Pseudoxyporus* it is on the distal half to three quarters of the posterior surface of the procoxa. All the species of *Oxyporus* examined had stridula. For Old World species of *Pseudoxyporus* some had stridula, some did not. In the Paederinae, all the species of *Scopaeus* have stridula. To date, *Scopaeus*, with nearly 400 named species, is by far the most speciose staphylinid genus with stridula. At least one other genus of the Paederinae has an abdominal stridulum (personal obs.; Herman, in prep.).

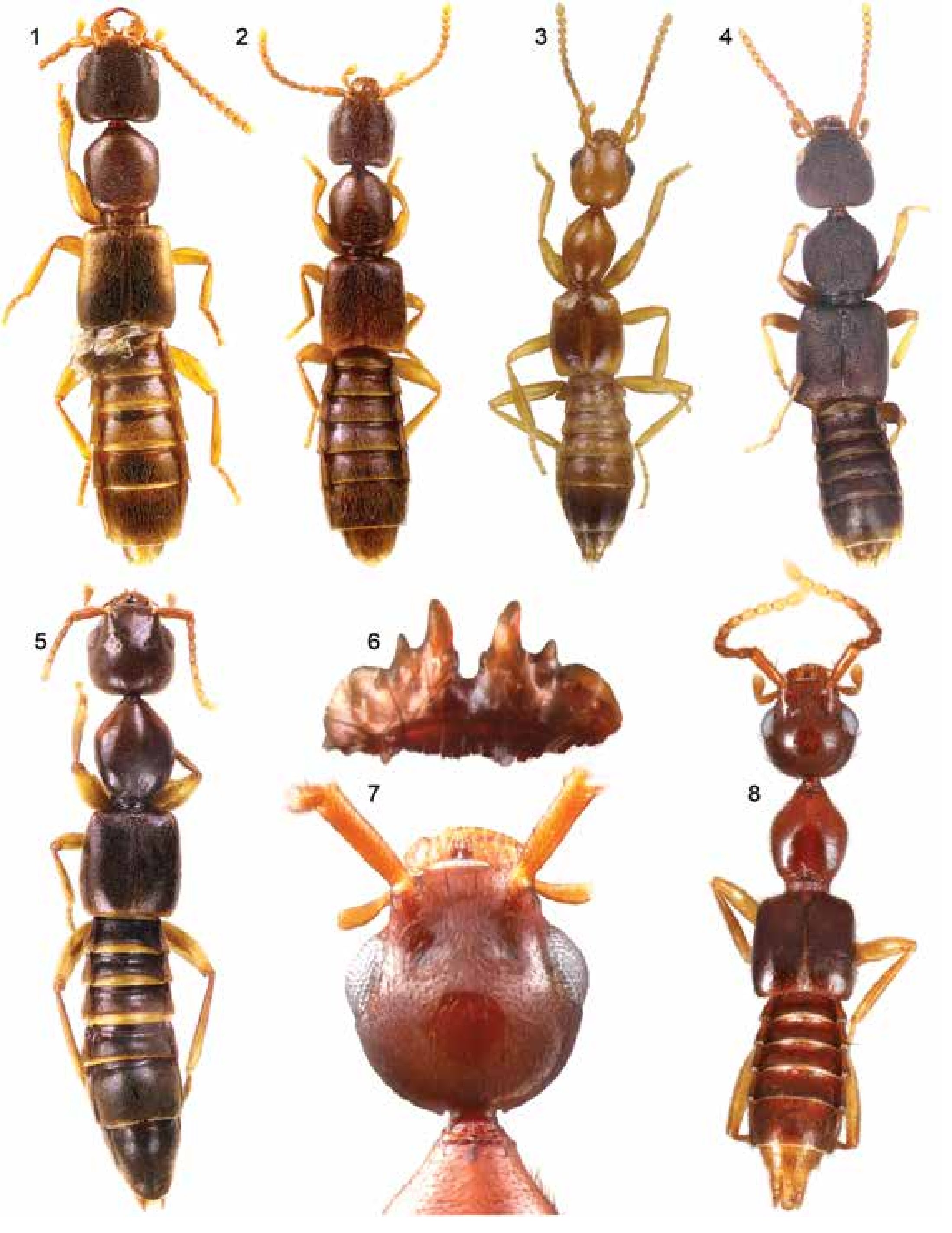
Among the 11 genera of the Staphylinidae, stridulation has been demonstrated, recorded, and hypotheses of the function of the chirps have been proposed and tested only for some species of *Nicrophorus* (Lane and Rothschild, 1965; Hall et al., 2013; Ward, 2022). Stridulation has been heard in no other of the Staphylinidae.

Although auditory structures, such as ears, have been described for few beetles, it would not be rash to assume that if a species has a structure specifically for producing sound, it can also hear the sounds so produced. Audition in insects can be through the air or substrate. Airborne sounds can be detected by tympana. Insect ears function primarily to detect sounds by conspecifics or sounds produced by predators or prey (Forrest et al., 1997). It might be assumed that stridulation would produce airborne sounds.

The rather easily recognized stridula have been found in many groups of beetles but reports of hearing organs in the Coleoptera are far less common and detecting them seems a significantly greater challenge. Tympanic auditory structures include three general components: a spot or area of thinner cuticle that responds to airborne vibrations, the tympanic membrane, that is associated with an expansion of the tracheal system, an air sac, and a chordotonal sensory organ to convert vibrations of the membrane into neural signals (Forrest et al., 1997). Among the Coleoptera, tympana have been reported on the first abdominal tergite for the tiger beetle, *Cicindela marutha* Dow, 1911 (see Yager and Spangler, 1995, 1997), the cervical membrane for the scarab beetle, *Euetheola humilis* (Burmeister, 1847) (Forrest et al., 1997), and the clypeus for *Nicrophorus americanus* Olivier, 1790, and *Nicrophorus marginatus* Fabricius, 1801 (Ward, 2002).

The beetles for which tympana have been found are all large animals. *Scopaeus* are all small, about 2 to 5 mm long. Finding tympana or some other sort of ear will be an exceptionally difficult task.

The METAKATEPISTERNAL PROCESSES are diagnostic for *Scopaeus* (fig. 142). For *Hyperscopaeus* (fig. 241), *Orus* (fig. 300), and *Trisunius* (fig. 335) they are short and apically rounded or blunt. For *Micranops* they are wide with a diagonally truncate apical margin (figs. 270, 280). Those of *Scopaeus* are apically acute, slender, and short (fig. 137, 195, 227) to moderately long (figs. 110, 183) to long (figs. 83, 119). The condition of this structure is a more convenient character to identify *Scopaeus* than is trying to see the stridular file or plectral ridges. However, *Scopaeus filiformis* (*S. debilis*



FIGS. 1–8. *Scopaeus*. Figs. 1–4. habitus. **1.** *S. chiriquensis* sp. grp., *S.* sp. **2.** *S. frater*. **3.** *nitidus* sp. grp., *S. laxus*. **4.** *S.* “reticulate” sp. grp., *S.* sp. **5, 6.** *S. opacus* sp. grp., *S. elaboratus*. **5.** Habitus. **6.** Labrum, dorsal, setae omitted. **7, 8.** *S. nevermanni* sp. grp., *S.* sp. **7.** Head, dorsal, marginal setae omitted. **8.** Habitus, prolegs not visible.

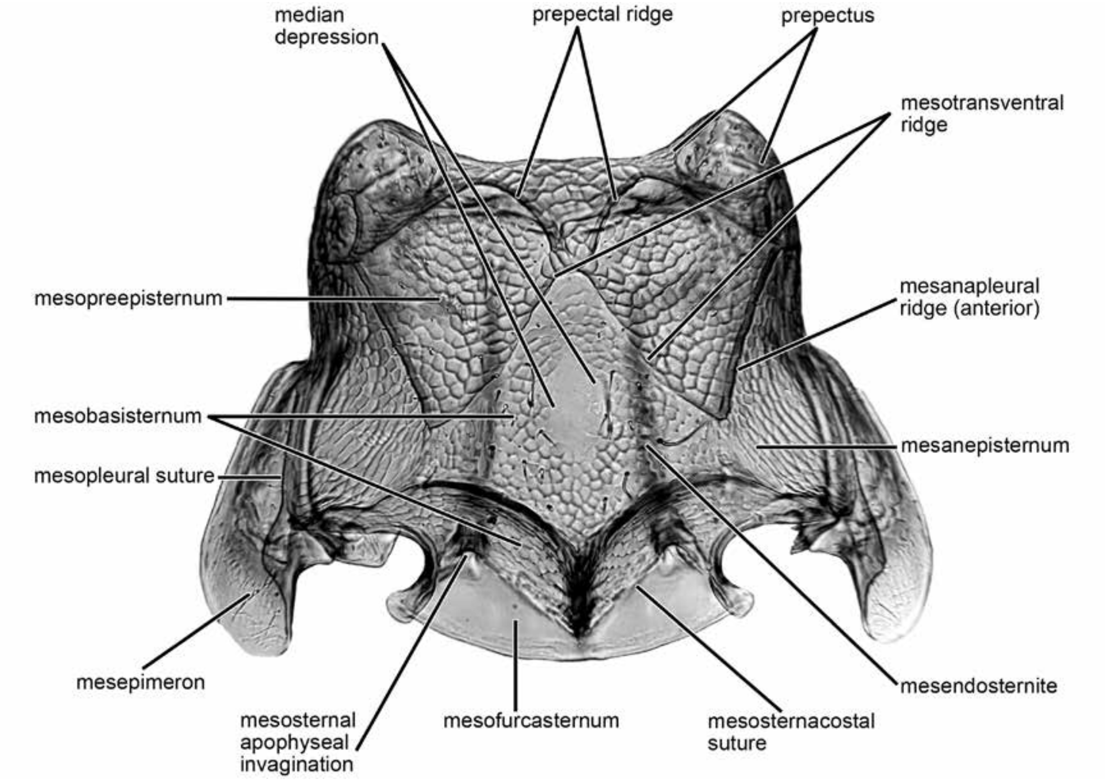


FIG. 9. *Orus rubens*. Mesoventrite, structural features.

species group) is an outlier with short, broad metakatepisternal processes (figs. 89, 94). Since the specimen depicted was the only one available to me for dissection, it is impossible to ascertain whether the specimen I dissected is aberrant or if the images accurately depict the species. All other examples of *S. filiformis* were examined at European museums before this character was discovered. By contrast, the processes of *S. debilis* and *S. udus*, both in the *S. debilis* species group, is moderately long and tapered to an acute point. If figures 89 and 94 are accurate, it would be interesting to explore what is different about *S. filiformis* that its metakatepisternal processes diverge from those of other *Scopaeus*. However, that exploration might be fruitless without knowing the function of the metakatepisternal processes. The short, wide metakatepisternal processes of *Micranops* (figs. 270, 280) are similar to those of *S. filiformis*. The lateral margin is straight for *Micranops* (figs. 270, 280) and notched in the *S. filiformis* (fig. 89). The processes vary in *Scopaeus*, but whether the variation is among the species groups or among the species in the groups or both is unknown. The function of the metakatepisternal processes is unknown as is the reason for the variation.

Abdomen

STERNITES II AND III are little used for classification or identification, but for the Scopaeina there are a few potentially useful characters. Excepting the Oxytelinae, sternite II is much reduced in the family, often a mere narrow fringe of sclerite along the anterior edge of sternite III. For the Scopaeina the bisinuate anterior margin of II (figs. 179, 284, 338) is characteristic of and helps define the subtribe, despite its occurrence

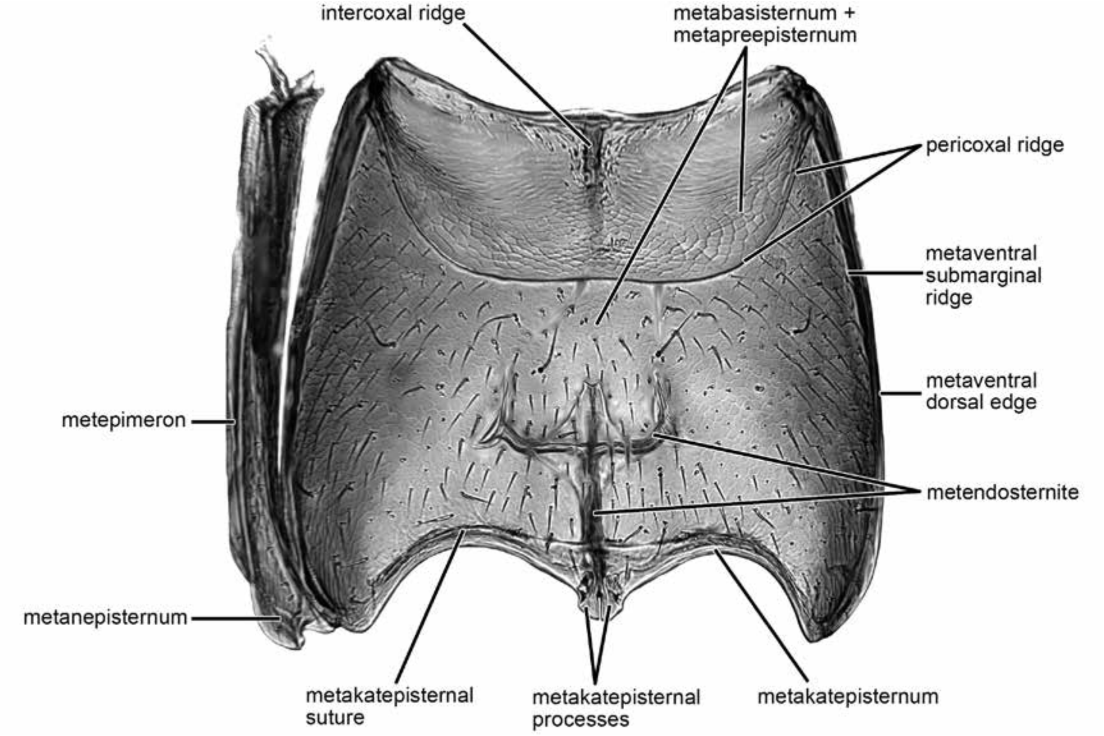


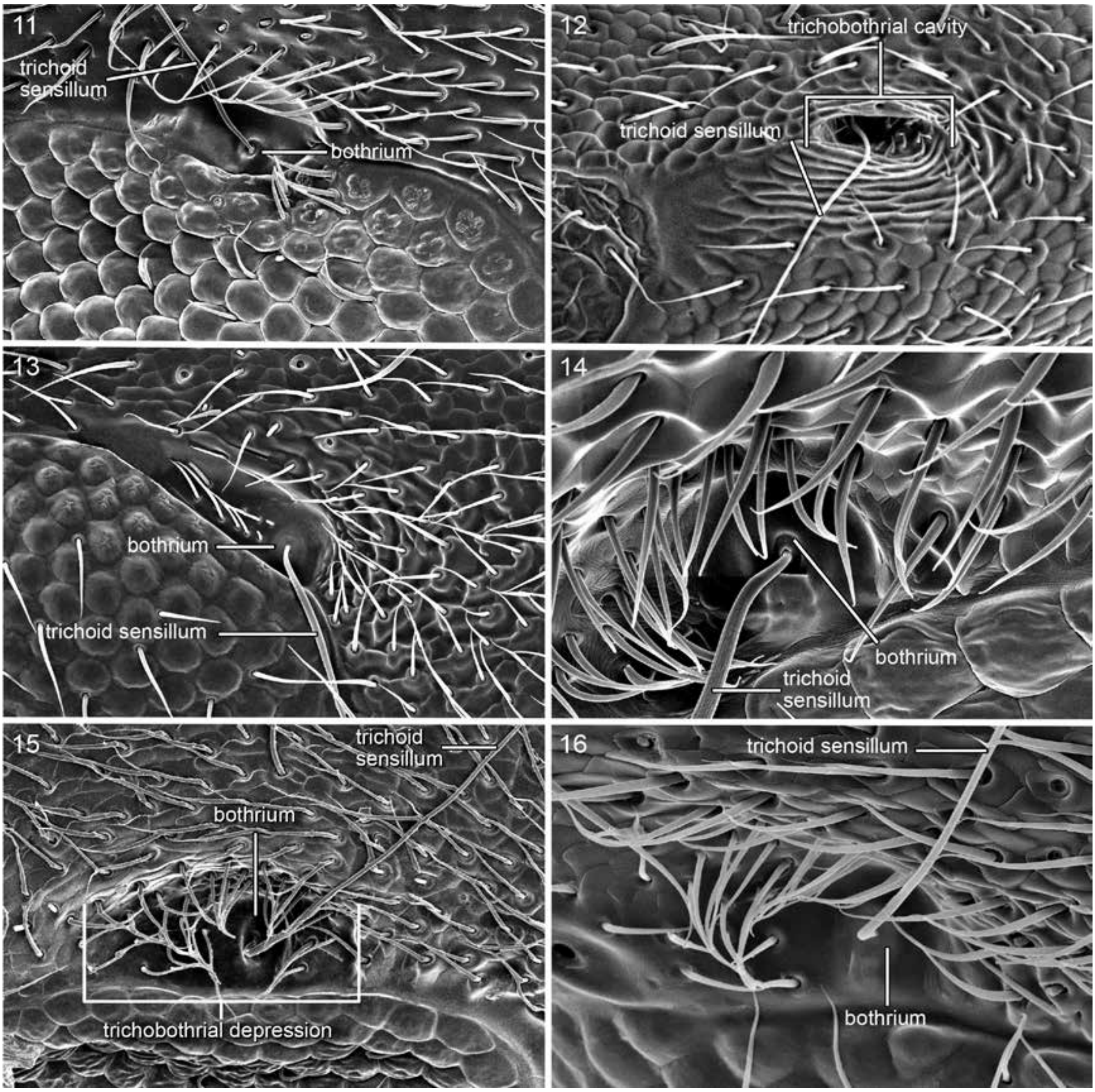
FIG. 10. *Orus rubens*. Metaventrite, structural features.

in some other subtribes. Sternite II may have a median point extending from the middle of the posterior margin and a median ridge (figs. 179, 204) or lack both (fig. 86).

Similarly, sternite III may have (fig. 179) or lack (fig. 147) a median ridge or the ridge may be short, poorly developed, and reduced to a small median point extending from the transverse basal ridge (fig. 145) or both the median point and ridge might be absent (fig. 192). The length of the median ridge of III, the presence or absence of the median point of the transverse basal ridge, and the curvature of the latter vary among the species groups. Some of these variations may help define species groups, some may be species specific.

STERNITE IV of some species of *Scopaeus* have a minute, median pore near the anterior margin (figs. 180, 199–200, 232–233) that might be an opening for glandular secretions; that uncertainty is the reason for the question mark beside the label "glandular" in the illustrations. Some species have a large depression with a nearby, apparently associated pore (figs. 87–88, 134–135, 152–153). Some species have a large depression, but no evident pore (figs. 129–130, 216). One species has a large pore (fig. 123); another of the *S. rotundiceps* species group also has a large pore, but the segment was too damaged to illustrate the glandular opening.

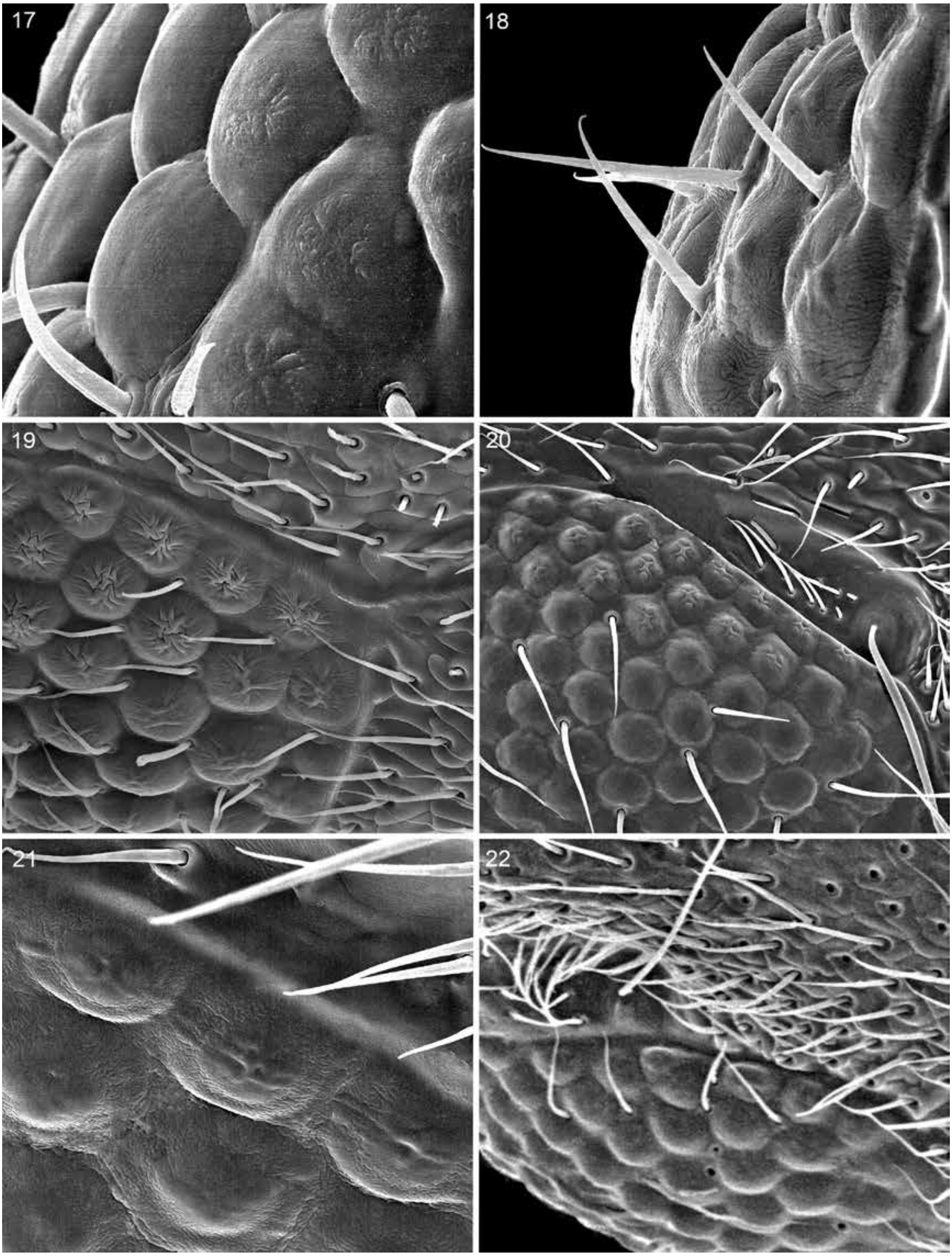
STERNITES VII AND VIII of males are variously modified, VII more than VIII. These features are largely species specific. Sternite VII is variously modified. The posterior margin may be emarginate, have posteriorly directed lobes that take various forms, have one or more large, thick setae or setae that may or may not be arranged in clusters; the surface may have clusters of setae, or they may be more scattered, may have depressions or elevations of varying position, size, and depth. Alternatively, sternite VII is unmodified in some species. For sternite



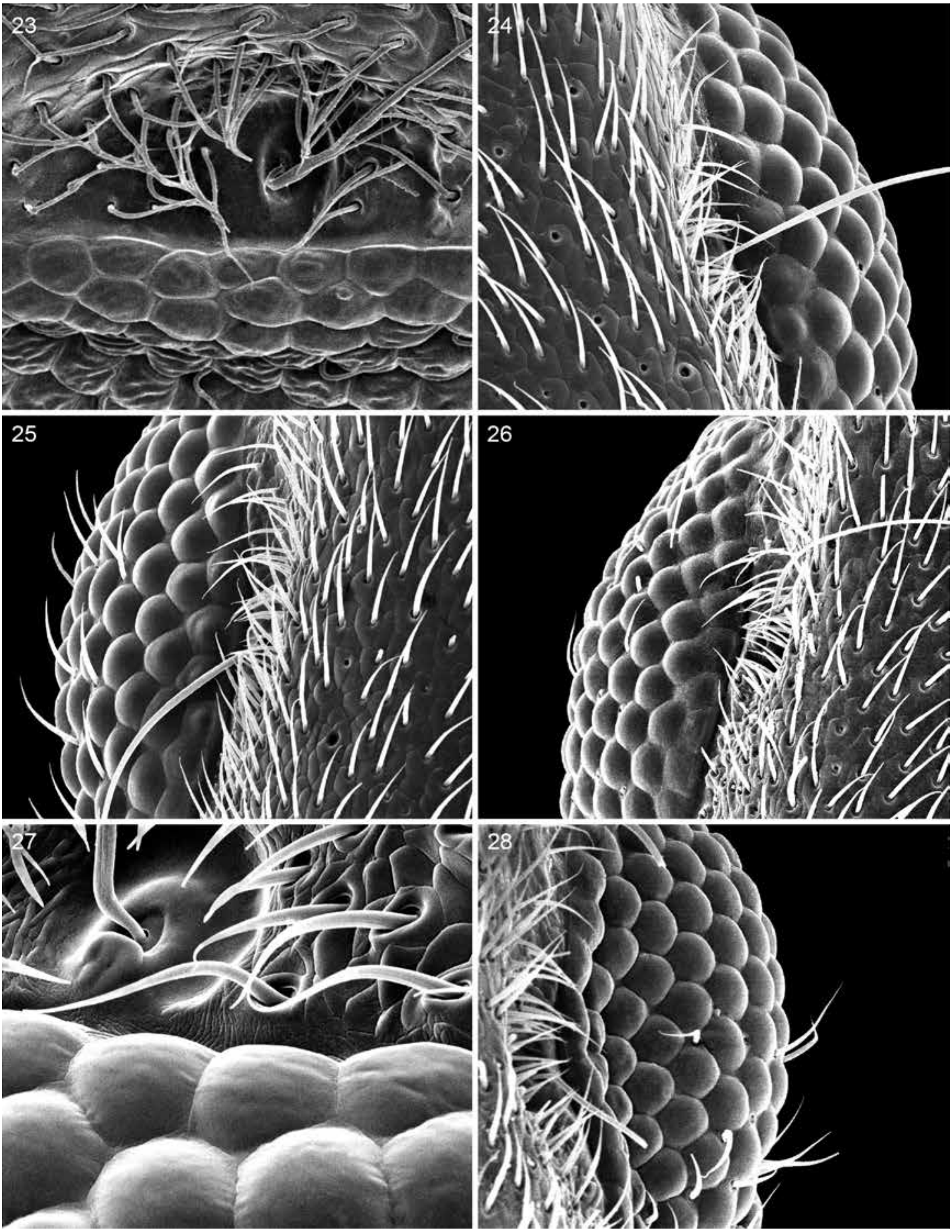
FIGS. 11–16. Scopaeina. Head, trichobothrial variation. **11.** *Hyperscopaeus* sp. **12.** *Micranops* sp. **13.** *Orus punctatus*. **14.** *Scopaeus* "reticulate" sp. grp. **15.** *Scopaeus chiriquensis* sp. grp. **16.** *Trisunius spathulatus*.

VIII the posterior margin has a shallow to deep, wide to narrow median emargination, which may have or lack a median extension or ventrally directed teeth. The surface of sternite VIII may or may not have one or more depressions and the setae may be evenly distributed or some may be arranged in clusters.

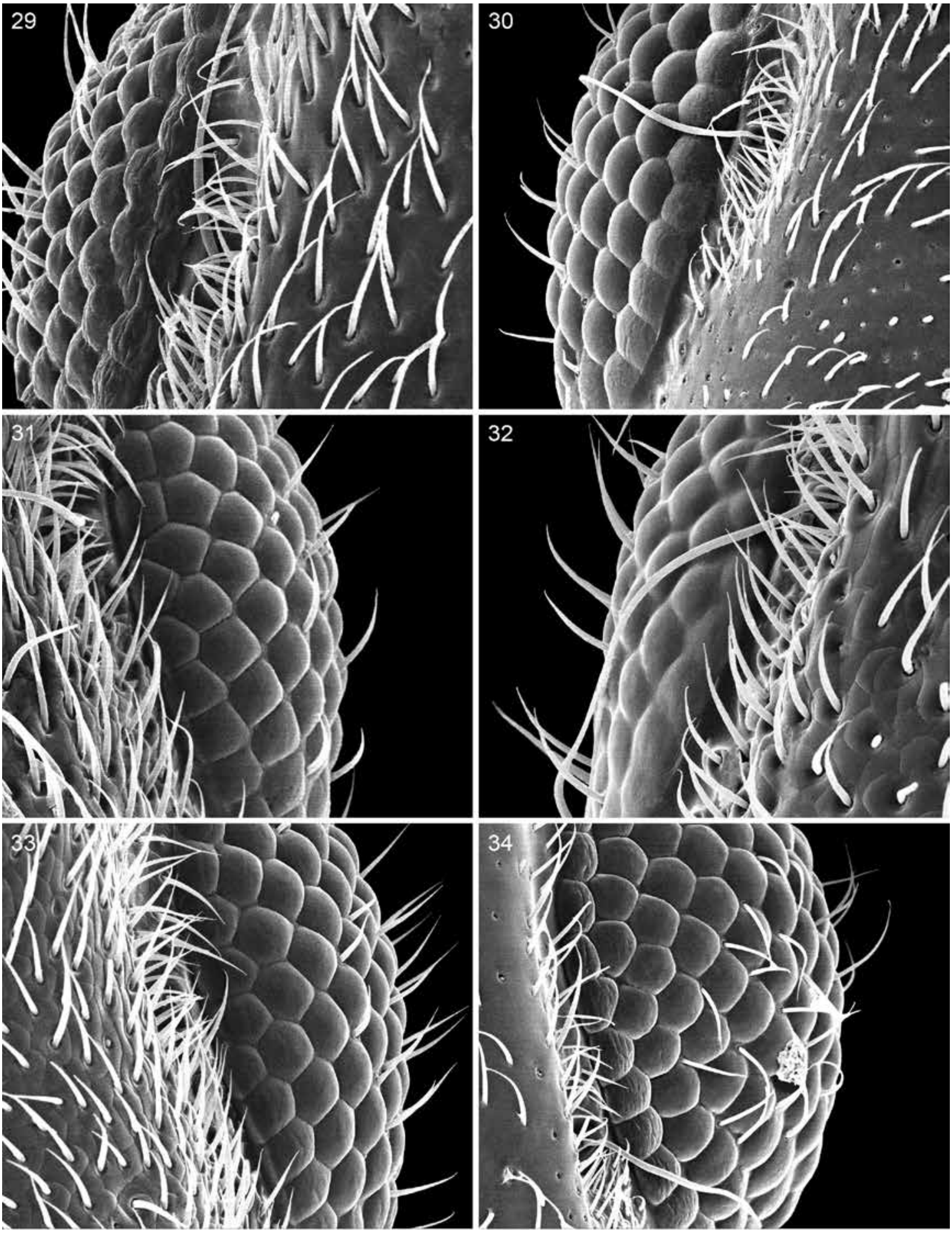
Aedeagus: The dorsal surface of the median lobe of *Hyperscopaeus* (fig. 243) has a midlongitudinal, membranous split. The dorsal surface of the medial lobe of *Scopaeus* (fig. 158) is solid and lacks a midlongitudinal split, thereby separating it from *Hyperscopaeus*. For the other scopaeine genera, the dorsal surface of the medial lobe also has a midlongitudinal split, except for *Orus* (*Leucorus*) for which there is a median, oval sclerite surrounded by membrane (Herman, 1965a: 113, figs. 2d, 3d; erroneously stated as ventral view).



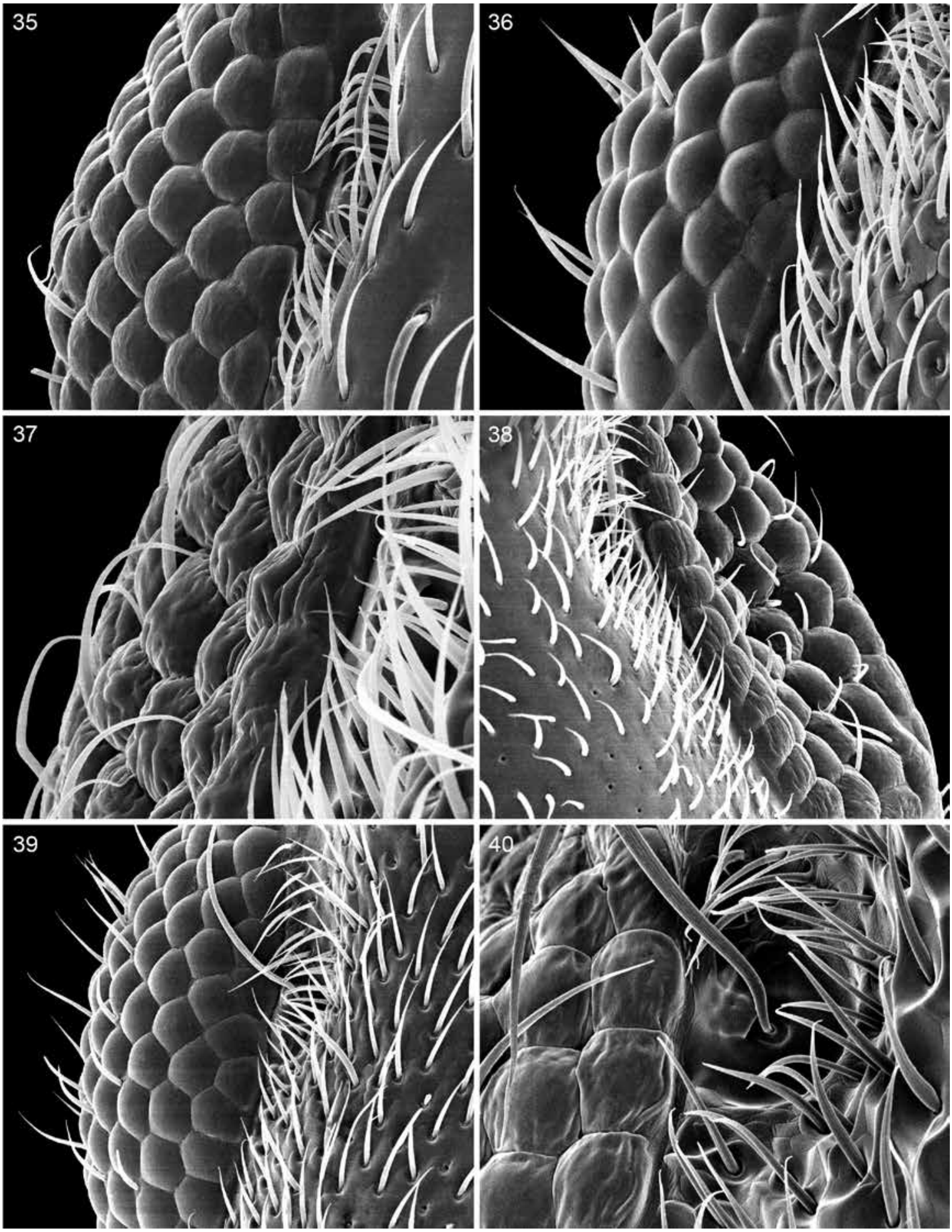
FIGS. 17–22. Compound eyes, corneal surface. **17.** *Hyperscopaeus* sp. **18.** *Micranops* sp., Bimini. **19.** *Micranops* sp., Burkina Faso. **20.** *Orus punctatus*. **21.** *Orus rubens*. **22.** *Trisunius spathulatus*.



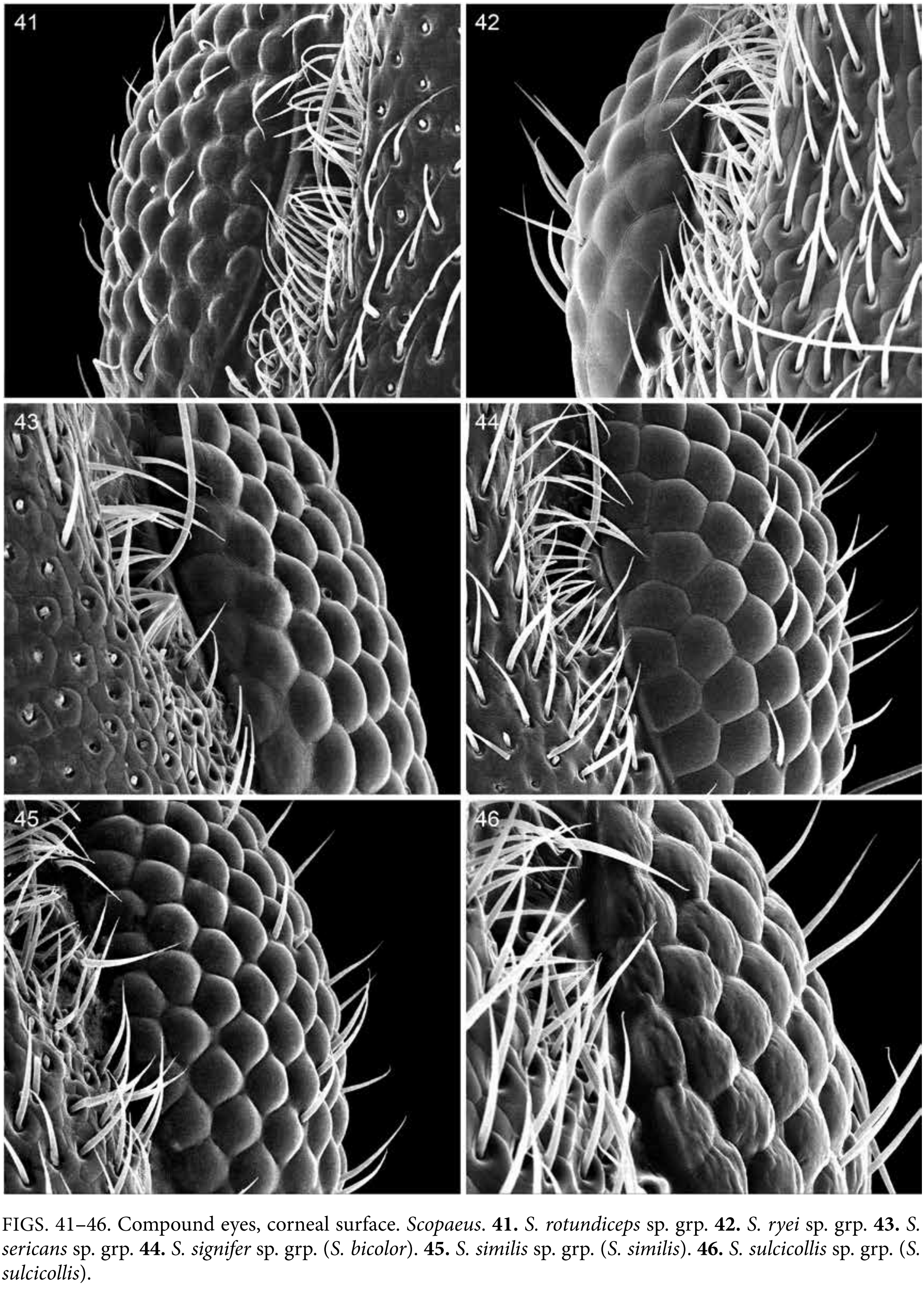
FIGS. 23–28. Compound eyes, corneal surface. *Scopaeus*. **23.** *S. chiriquensis* sp. grp. **24.** *S. debilis* sp. grp. (*S. debilis*). **25.** *S. debilis* sp. grp. (*S. filiformis*). **26.** *S. elegans* sp. grp. (*S. cameroni*). **27.** *S. elegans* sp. grp. (*S. persicus*). **28.** *S. gracilis* sp. grp. (*S. gracilis*).



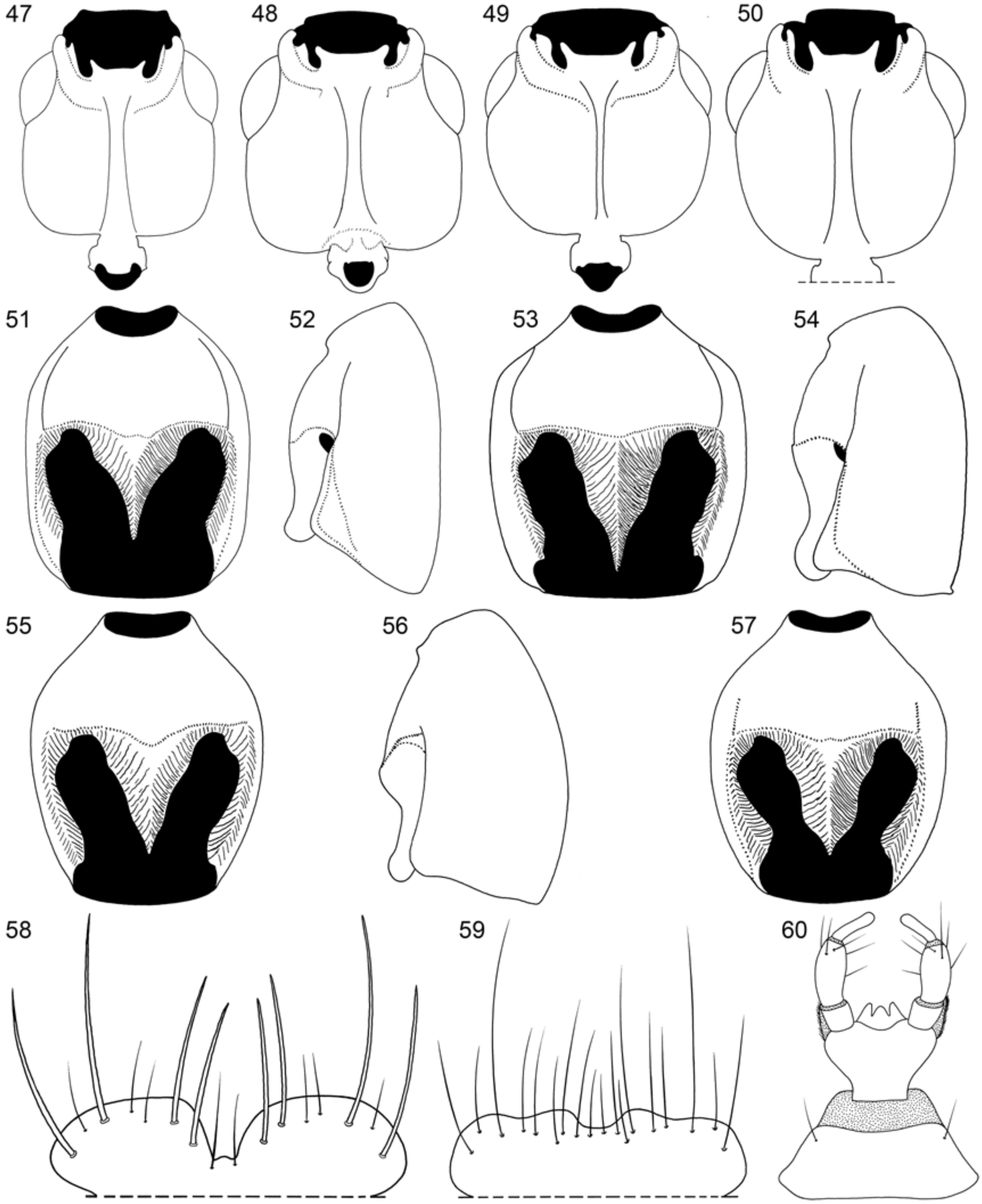
FIGS. 29–34. Compound eyes, corneal surface. *Scopaeus*. **29.** *S. laevigatus* sp. grp. (*S. laevigatus*). **30.** *S. limbatus* sp. grp. **31.** *S. longicollis* sp. grp. **32.** *S. minutus* sp. grp. (*S. chalcodactylus*). **33.** *S. mutatus* sp. grp. **34.** *S. nevermanni* sp. grp.



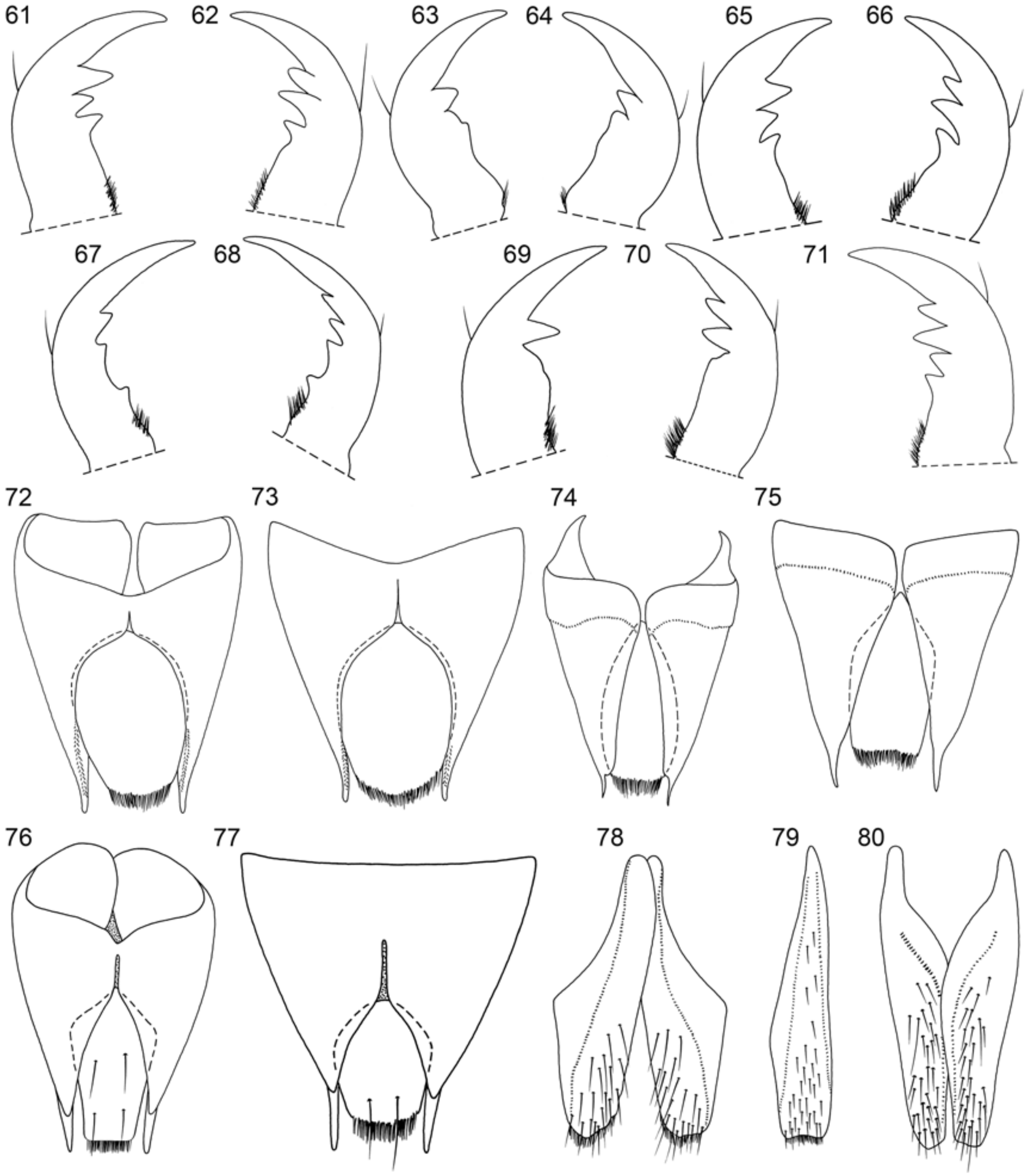
FIGS. 35–40. Compound eyes, corneal surface. *Scopaeus*. **35.** *S. nitidus* sp. grp. **36.** *S. obscuripes* sp. grp. (*S. likovskyi*). **37.** *S. ooderes* sp. grp. (*S. ooderes*). **38.** *S. opacus* sp. grp. (*S. opacus*). **39.** *S. punctatellus* sp. grp. (*S. punctatellus*). **40.** *S.* "reticulate" sp. grp.



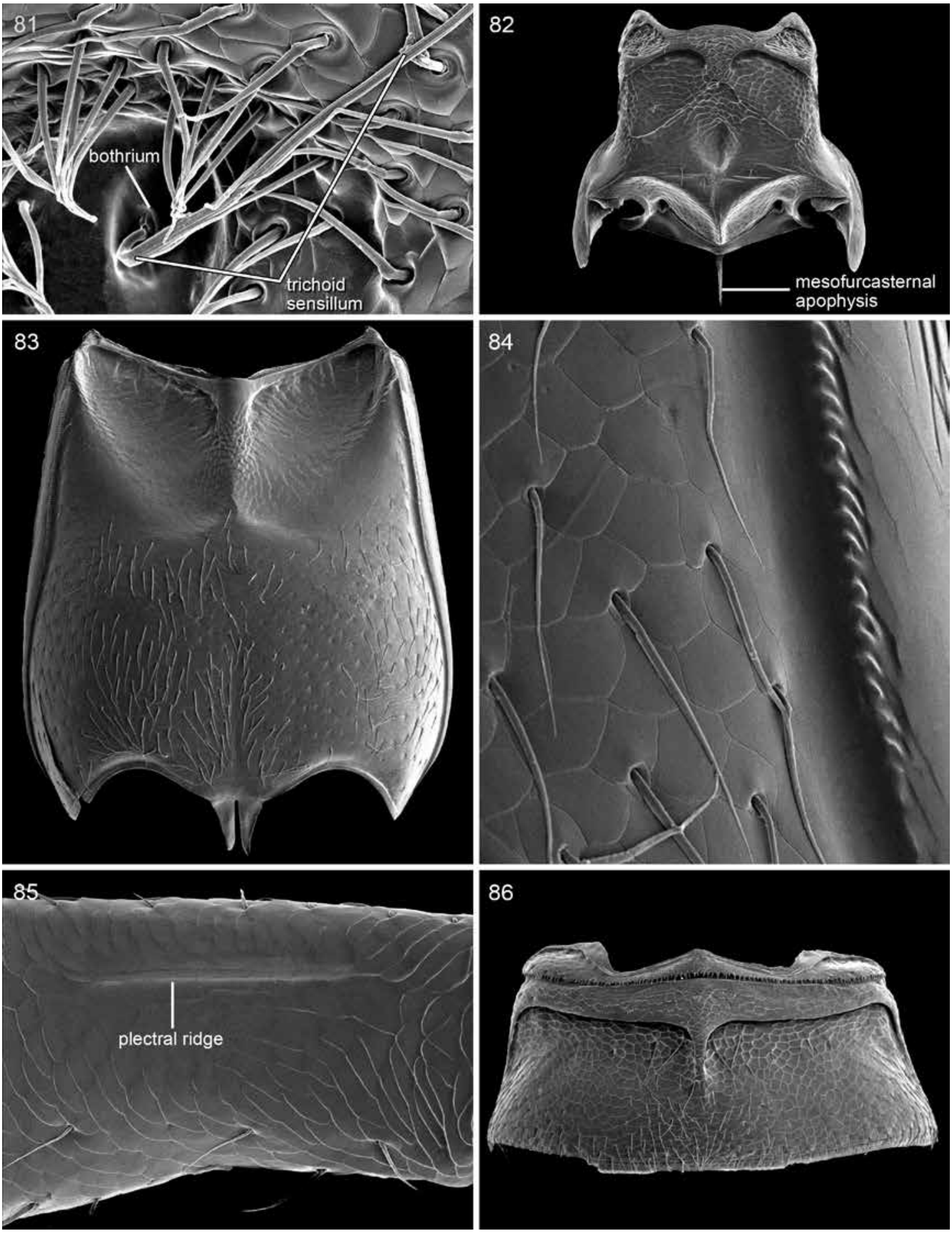
FIGS. 41–46. Compound eyes, corneal surface. *Scopaeus*. **41.** *S. rotundiceps* sp. grp. **42.** *S. ryei* sp. grp. **43.** *S. sericans* sp. grp. **44.** *S. signifer* sp. grp. (*S. bicolor*). **45.** *S. similis* sp. grp. (*S. similis*). **46.** *S. sulcicollis* sp. grp. (*S. sulcicollis*).



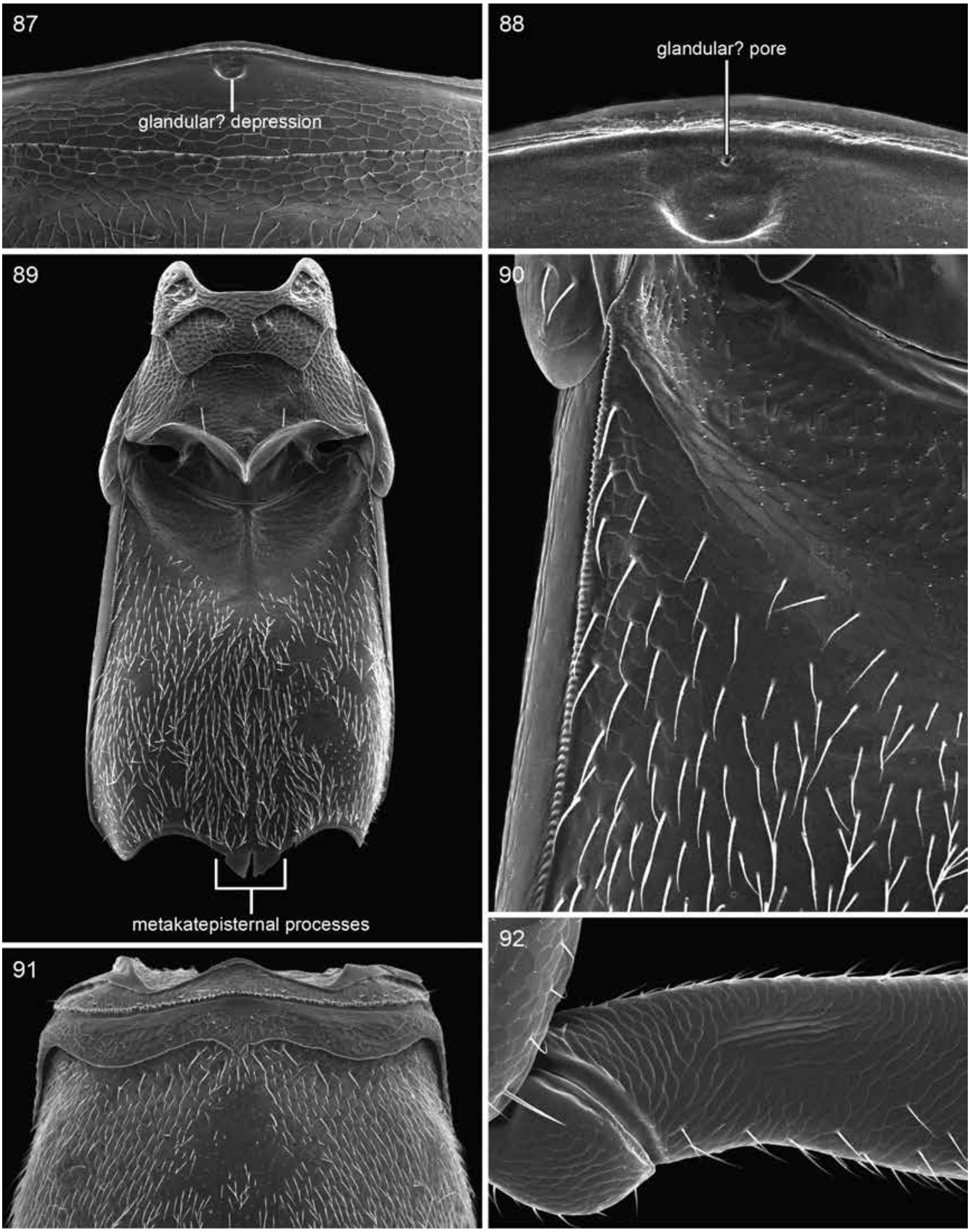
FIGS. 47–60. *Scopaeus*. Head, Prothorax, Mouthparts. **47–50**. Head. **47.** *S. picipes*. **48.** *S. chiriquensis* sp. grp. (*S.* sp.). **49.** *S. opacus* sp. grp. (*S.* sp.). **50.** *S. nitidus* sp. grp. (*S.* sp.). **51–57**. Prothorax. **51, 52**. *S. picipes*. **51.** Ventral. **52.** Lateral. **53, 54.** *S. chiriquensis* sp. grp. (*S.* sp.). **53.** Ventral. **54.** Lateral. **55–57**. *S. nitidus* sp. grp. (*S.* sp.). **55.** Ventral. **56.** Lateral. **57.** *S. opacus* sp. grp. (*S.* sp.), ventral. **58–60**. *S. chiriquensis* sp. grp. (*S.* sp.). **58.** Labrum. **59.** Labrum. **60.** Labium, ventral.



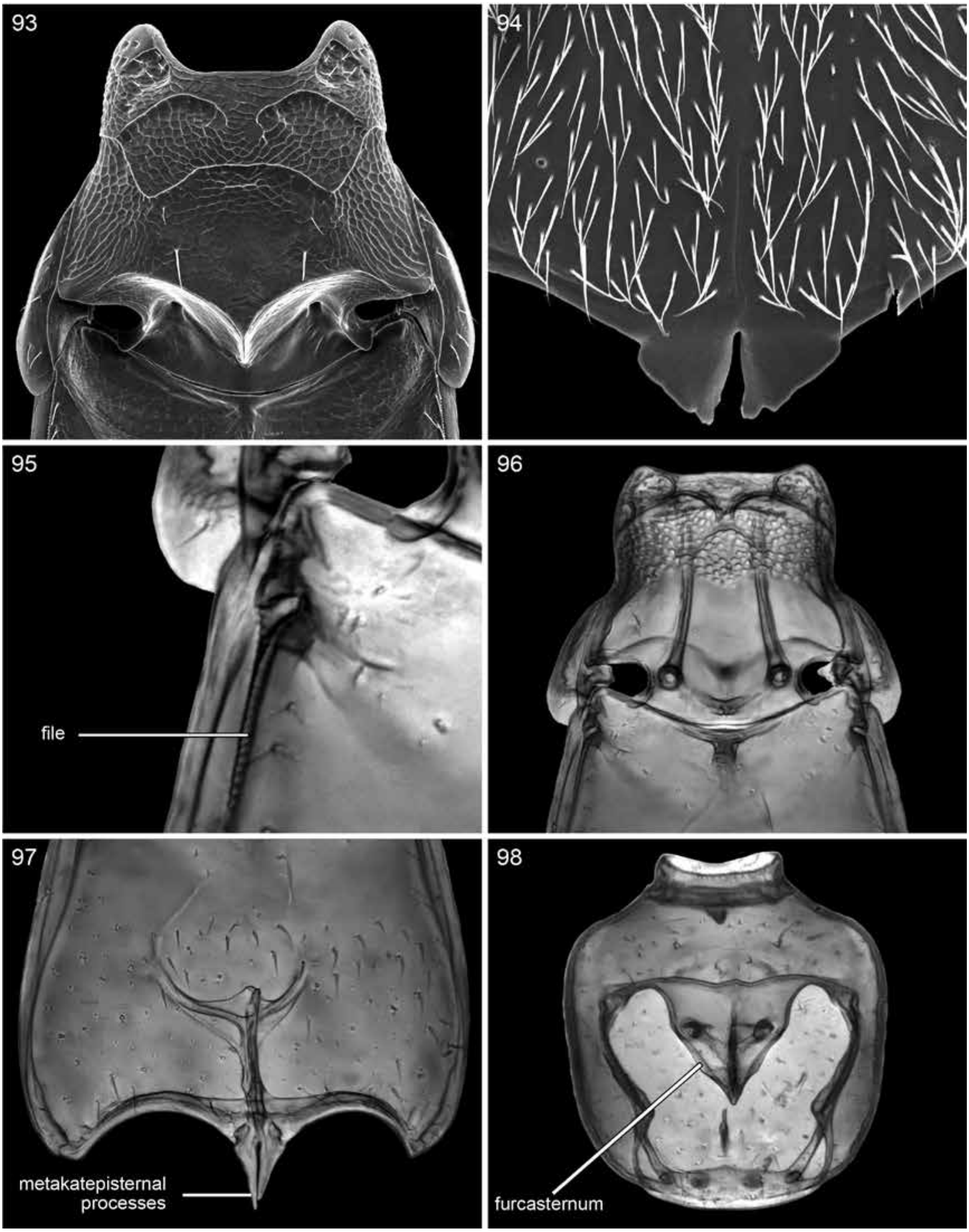
FIGS. 61–80. *Scopaeus.* Mandibles, Genital segments. **61–71**. Mandibles, dorsal. **61, 62**. *S. picipes.* **63, 64**. *S. chiriquensis* sp. grp. (*S.* sp.). **65, 66**. *S. nitidus* sp. grp. (*S.* sp.). **67–71**. *S. opacus* sp. grp. (*S.* spp.). **72–77**. Tergites IX, X. **72, 73**. *S. picipes.* **72.** Male. **73.** Female. **74, 75**. *S. nitidus* sp. grp. (*S.* sp.). **74.** Male. **75.** Female. **76–79**. *S. chiriquensis* sp. grp. (*S.* sp.). **76.** Male. **77.** Female. **78.** Lateral gonocoxal plates. **79.** Sternite IX, male. **80.** *S. picipes*, Lateral gonocoxal plates.



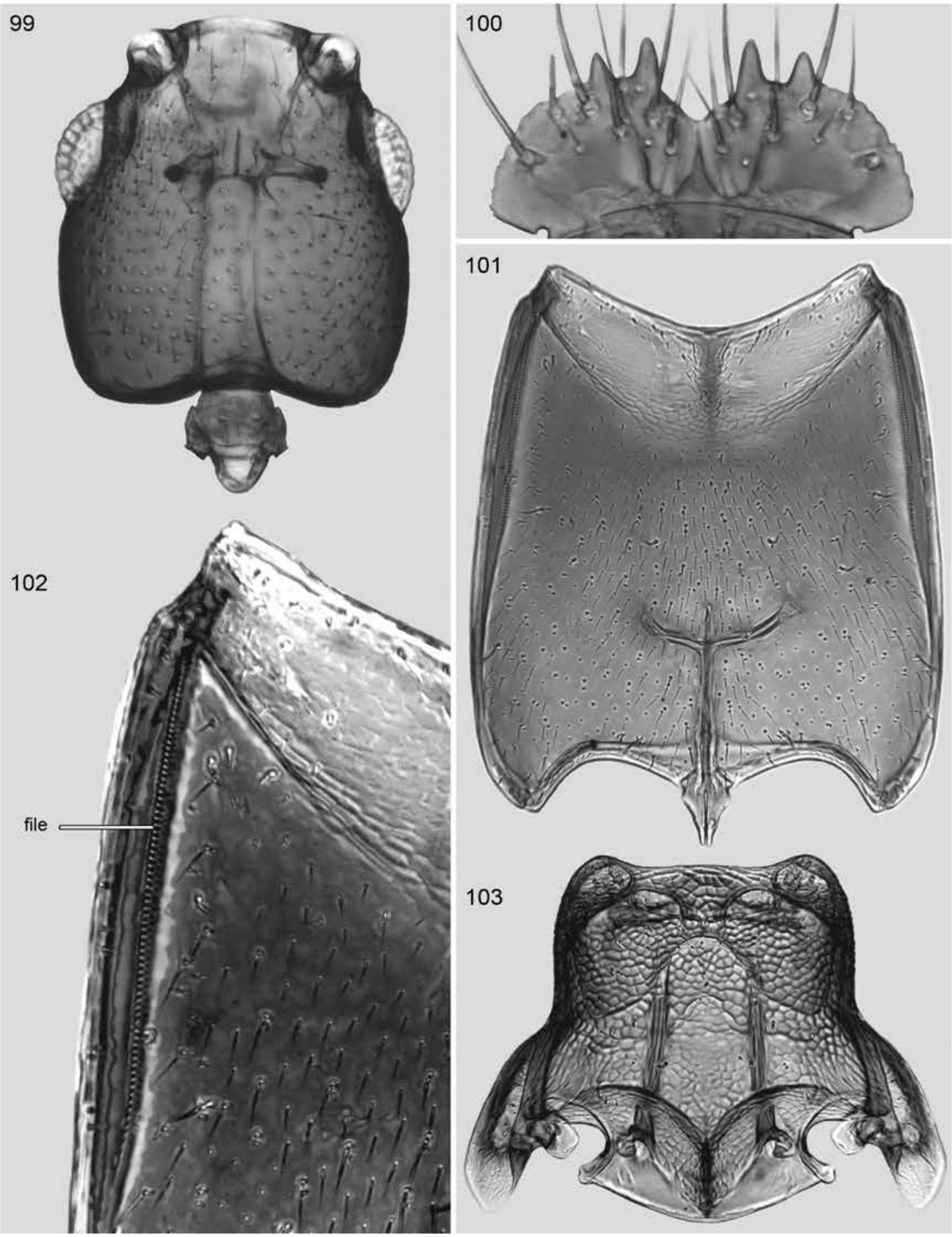
FIGS. 81–86. *Scopaeus*. *S. chiriquensis* sp. grp., (*S.* sp.). **81.** Head, trichobothrium. **82.** Mesoventrite. **83.** Metaventrite. **84.** Metaventrite, left file. **85.** Mesofemur, left base, plectral ridge. **86.** Sternites II and III.



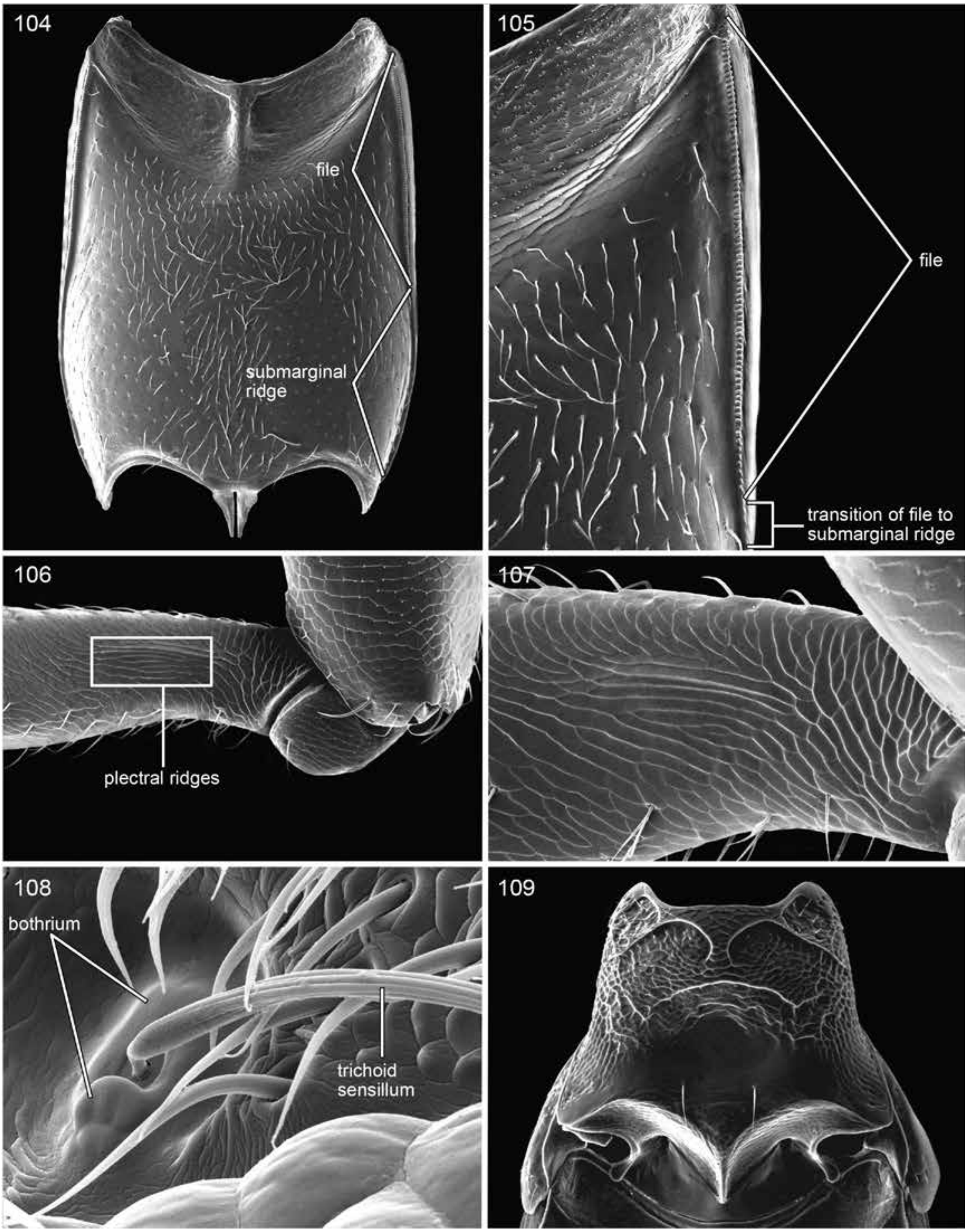
FIGS. 87–92. *Scopaeus*. **87–88.** *S. chiriquensis* sp. grp., (*S.* sp.), Sternite IV. **87.** Midanterior margin. **88.** Midanterior margin enlarged, glandular(?) depression. **89–92.** *S. debilis* sp. grp., (*S. filiformis*). **89.** Pteroventrites. **90.** Metaventrite, right file. **91.** Sternites II and III. **92.** Mesofemur, right base, plectral ridges.



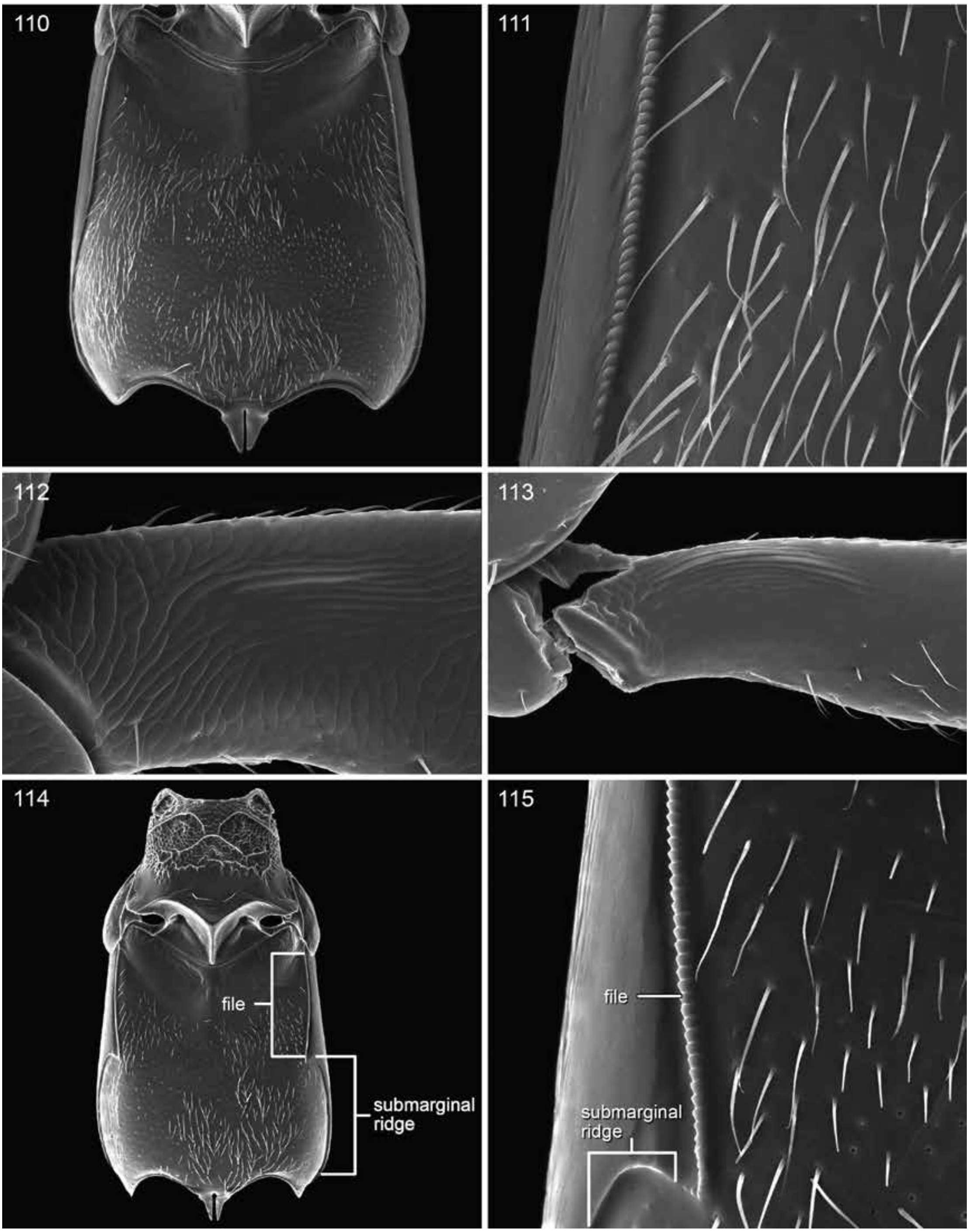
FIGS. 93–98. *Scopaeus*. **93–94.** *S. debilis* sp. grp., (*S. filiformis*). **93.** Mesoventrite and anterior metaventrite. **94.** Metaventrite, midapex, metakatepisternal processes. **95–98.** *S. dissimilis* sp. grp., (*S.* sp.). **95.** Metaventrite, right file. **96.** Mesoventrite and anterior metaventrite. **97.** Metaventrite, posterior, metakatepisternal processes. **98.** Prothorax, ventral.



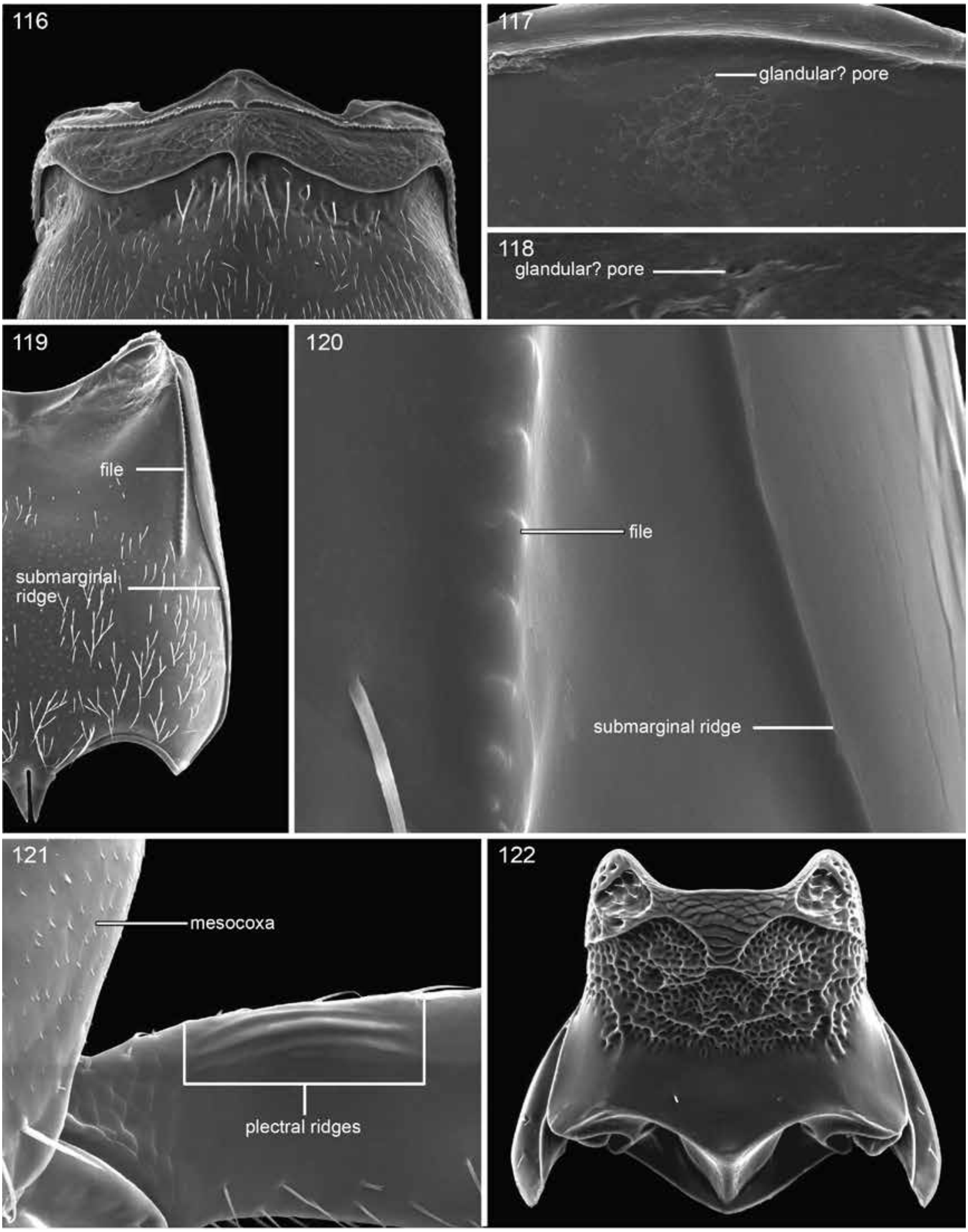
FIGS. 99–103. *Scopaeus*. **99–100.** *S. dissimilis* sp. grp., (*S.* sp.) **99.** Head, dorsal. **100.** Labrum. **101–103.** *S. elegans* sp. grp., (*S. cameroni*). **101.** Metaventrite. **102.** Metaventrite, right file. **103.** Mesoventrite.



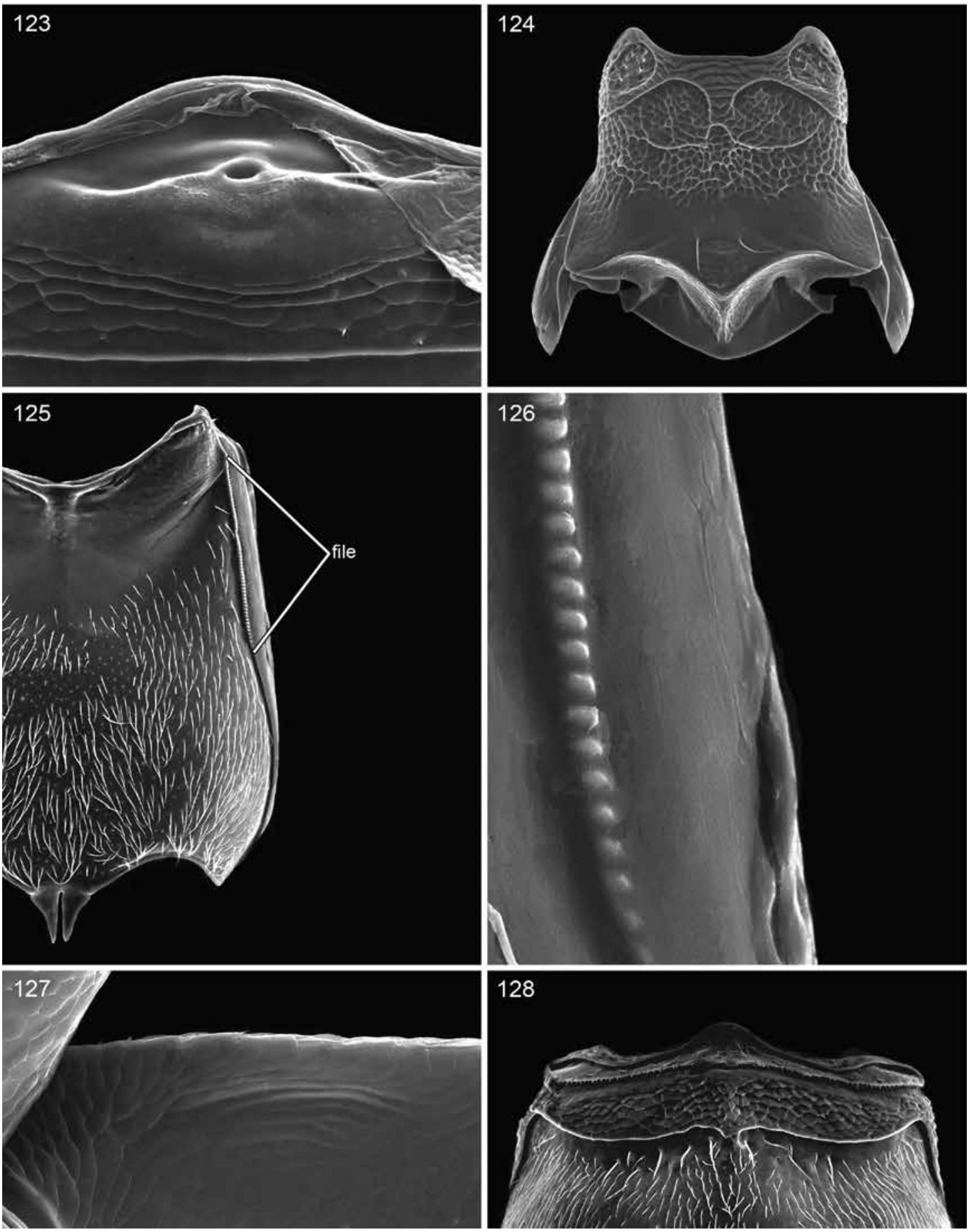
FIGS. 104–109. *Scopaeus*. **104–106.** *S. elegans* sp. grp., (*S. cameroni*). **104.** Metaventrite. **105.** Metaventrite, left file. **106.** Mesofemur, left base, plectral ridges. **107–108.** *S. elegans* sp. grp., (*S. persicus*). **107.** Mesofemur, left base, plectral ridges. **108.** Trichobothrium, head. **109.** *S. gracilis* sp. grp., (*S. gracilis*), Mesoventrite.



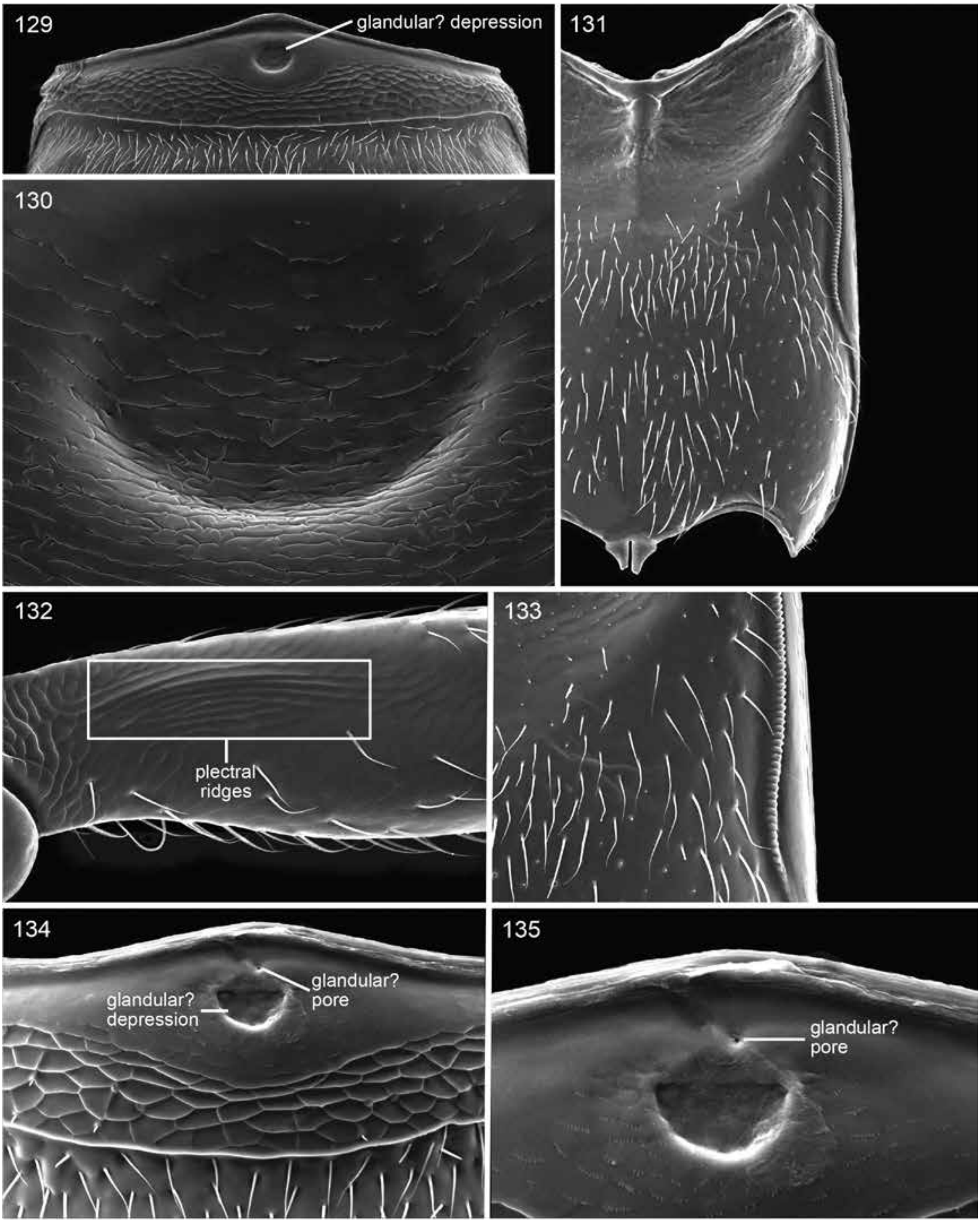
FIGS. 110–115. *Scopaeus*. **110–112.** *S. gracilis* sp. grp., (*S. gracilis*). **110.** Metaventrite and apex of mesoventrite. **111.** Metaventrite, right file. **112.** Mesofemur, right base, plectral ridges. **113–115.** *S. laevigatus* sp. grp., (*S. laevigatus*). **113.** Mesofemur, right base, plectral ridges. **114.** Pteroventrites. **115.** Metaventrite, right file, enlarged.



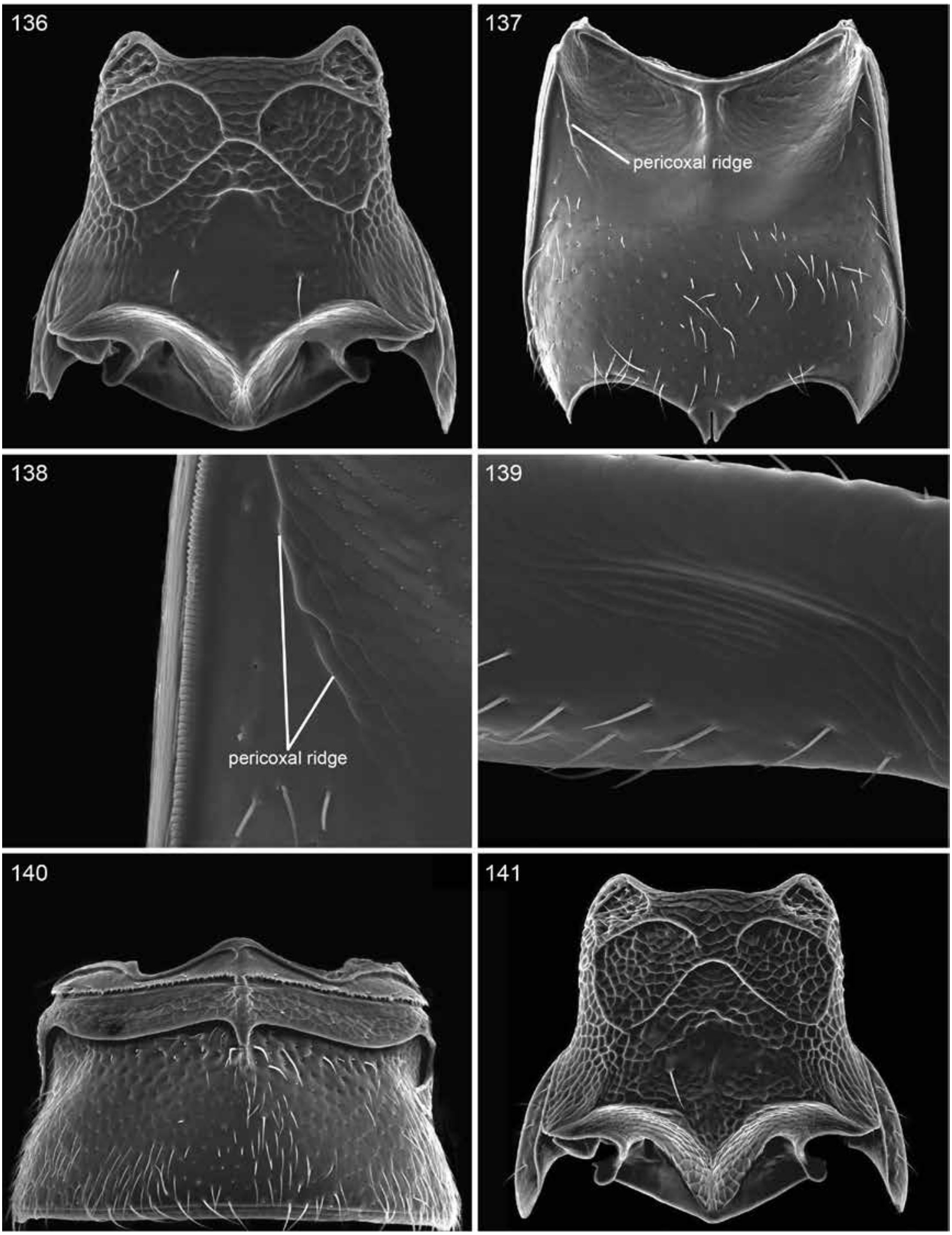
FIGS. 116–122. *Scopaeus*. *S. laevigatus* sp. grp. **116–118.** (*S. laevigatus*). **116.** Sternites II and III. **117, 118.** Sternite IV, midanterior margin. **117.** Glandular(?) region. **118.** Glandular(?) pore. **119–122.** (*S. subfasciatus*). **119.** Metaventrite. **120.** Metaventrite, enlarged section of left file. **121.** Mesofemur, right base, plectral ridges. **122.** Mesoventrite.



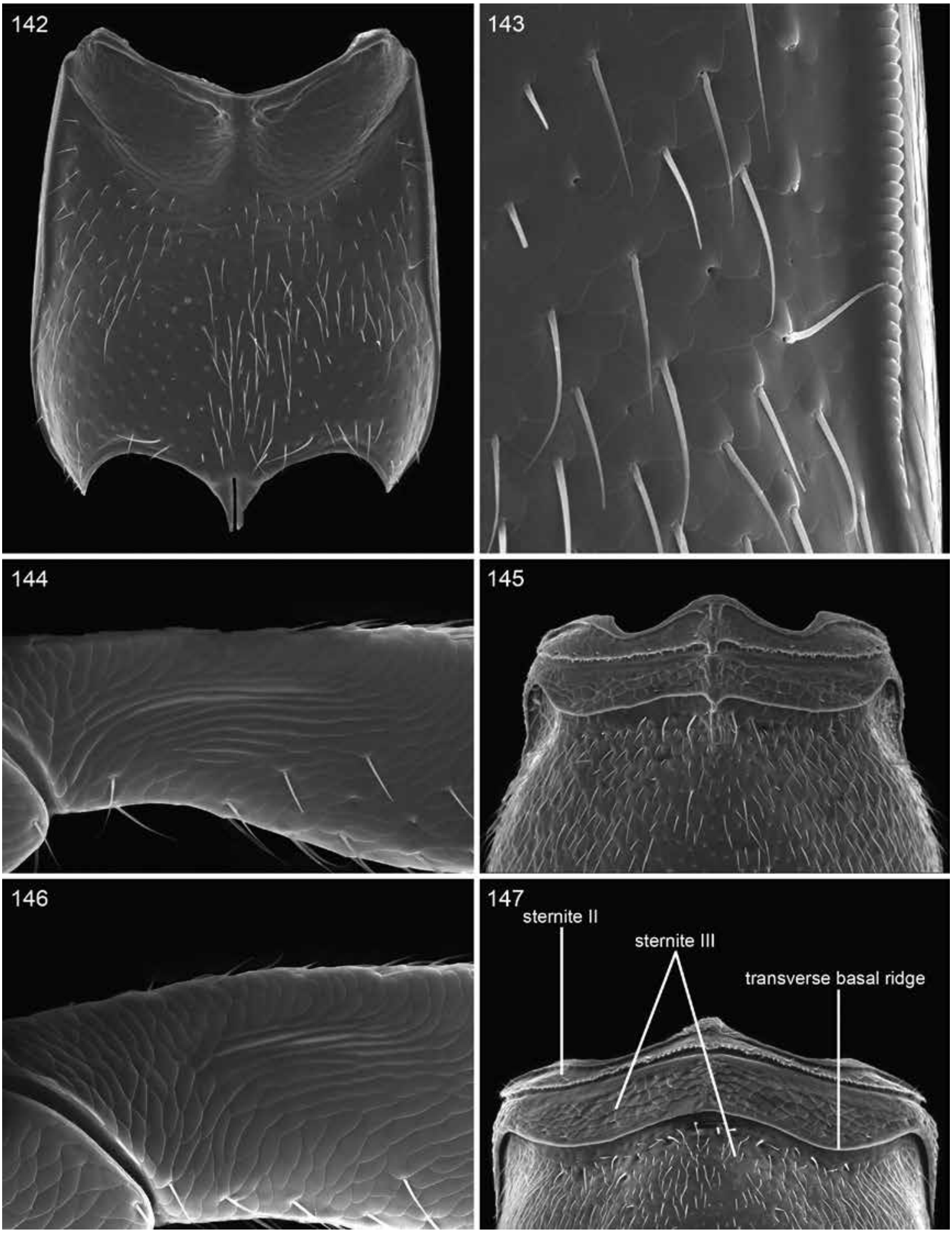
FIGS. 123–128. *Scopaeus*. **123.** *S. laevigatus* sp. grp. (*S. subfasciatus*), Sternite IV, midanterior enlarged, glandular(?) opening. **124–128.** *S. limbatus* sp. grp., (*S.* sp.). **124.** Mesoventrite. **125.** Metaventrite. **126.** Metaventrite, enlarged section of left file. **127.** Mesofemur, right base, plectral ridges. **128.** Sternites II and III.



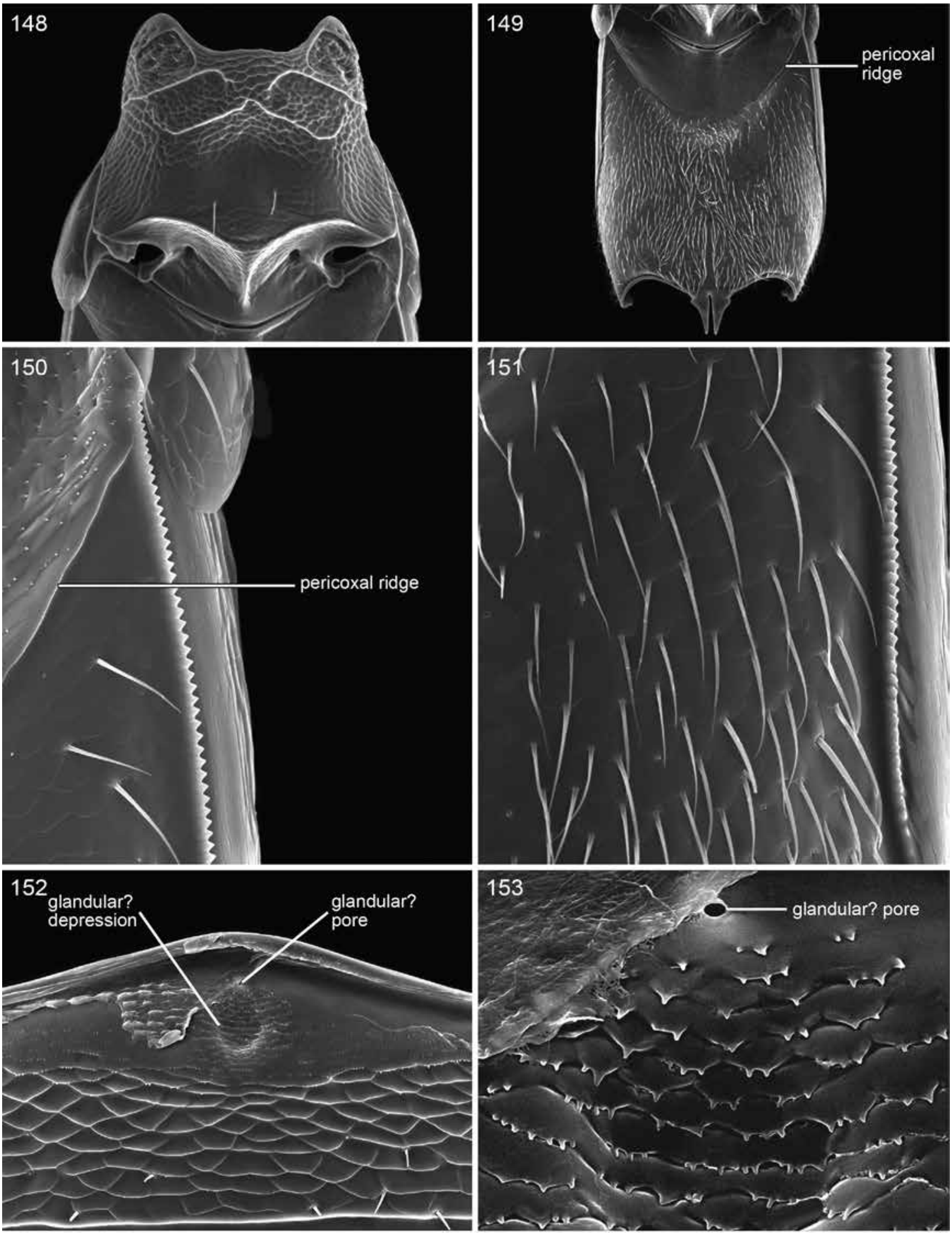
FIGS. 129–135. *Scopaeus*. **129–130.** *S. limbatus* sp. grp. (*S.* sp.). **129.** Sternite IV, anterior. **130.** Sternite IV, midanterior, enlarged glandular(?) depression. **131–133.** *S. longicollis* sp. grp. (*S.* sp.). **131.** Metaventrite. **132.** Mesofemur, right base, plectral ridges. **133.** Metaventrite, left file. **134–135.** *S. minimus* sp. grp. (*S. minimus*). **134.** Sternite IV, midanterior. **135.** Sternite IV, midanterior enlarged, glandular(?) depression and pore.



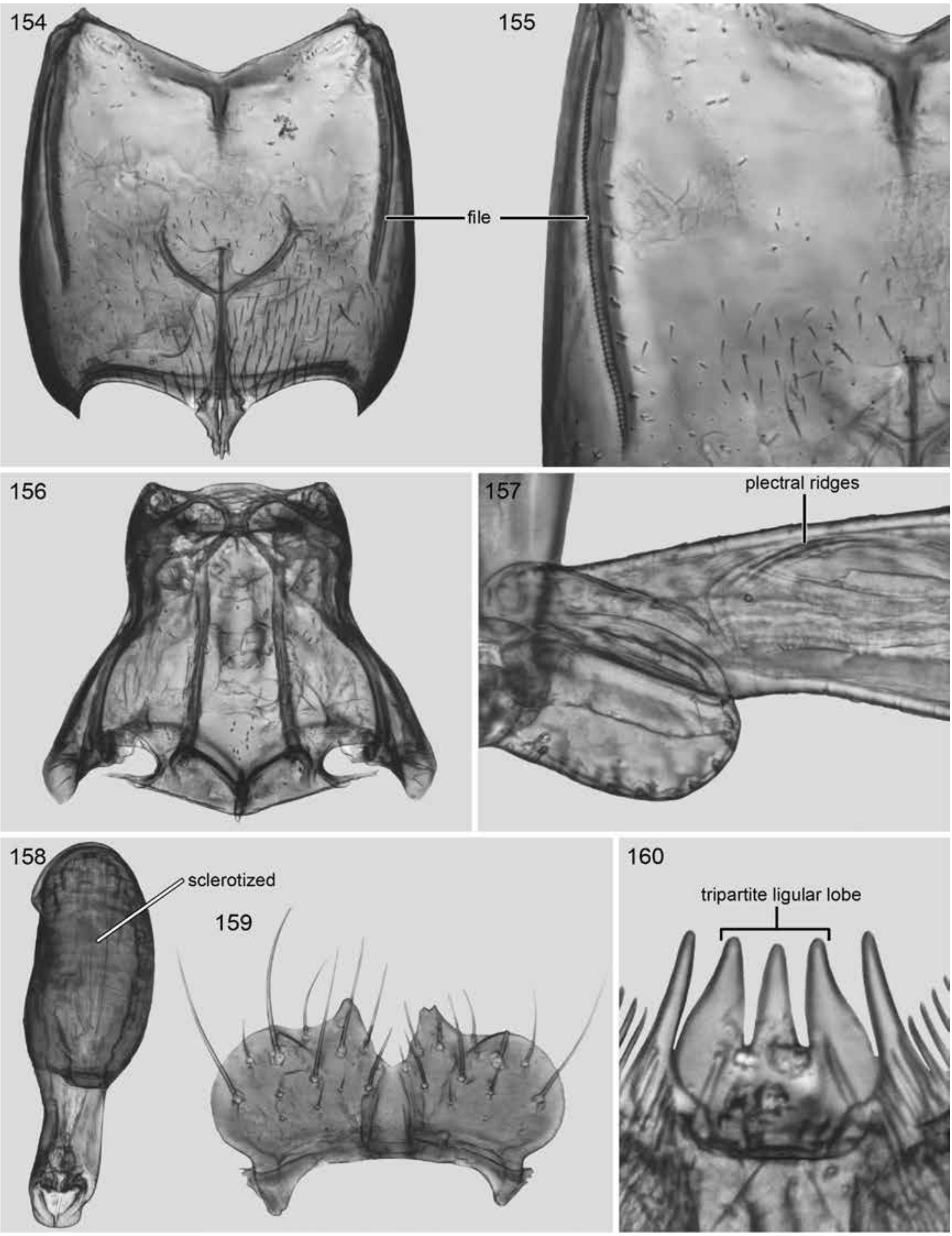
FIGS. 136–141. *Scopaeus*. **136–140.** *S. minimus* sp. grp. (*S. minimus*). **136.** Mesoventrite. **137.** Metaventrite. **138.** Metaventrite, right file. **139.** Mesofemur, left base, plectral ridges. **140.** Sternites II and III. **141.** *S. minutus* sp. grp. (*S. pusillus*), Mesoventrite.



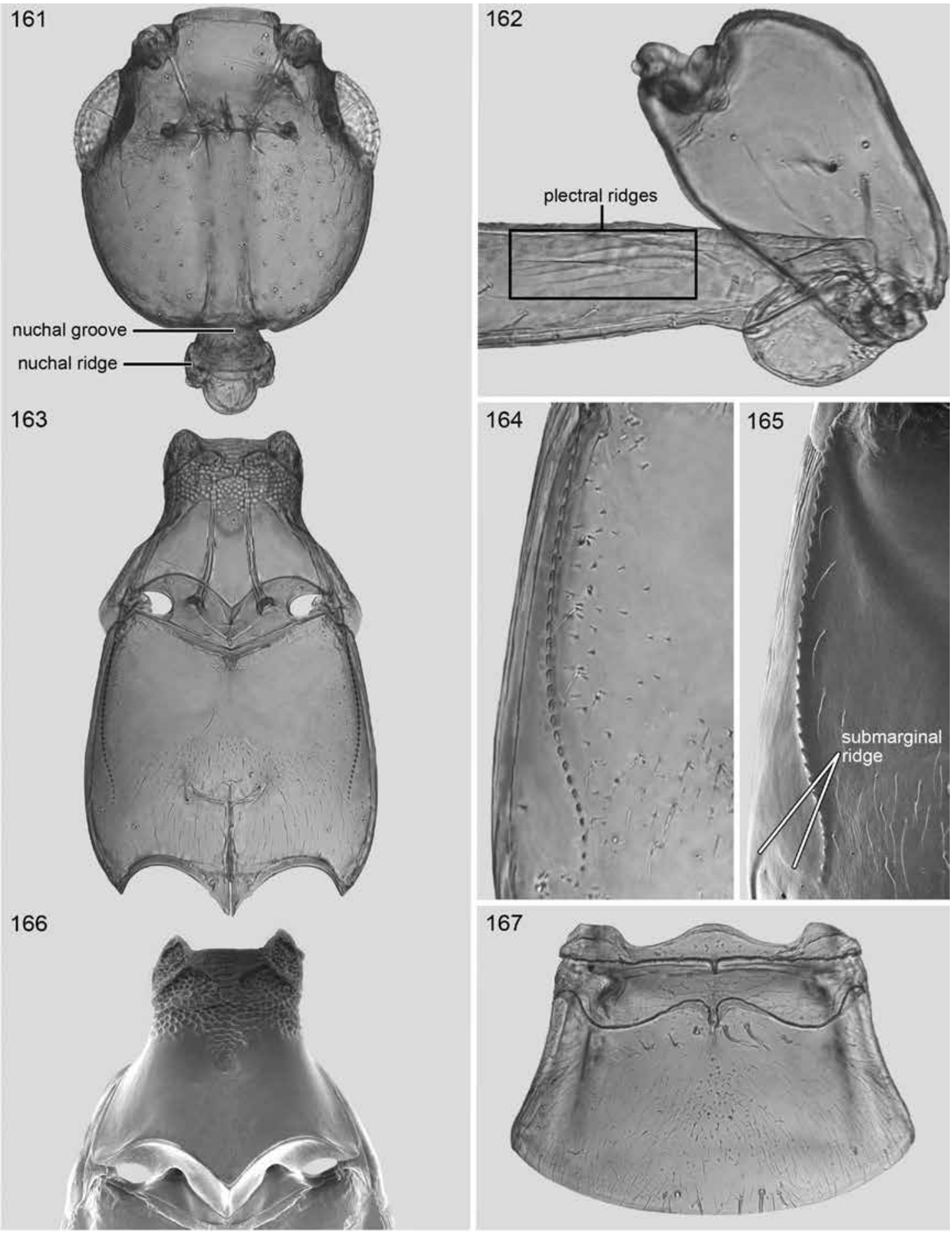
FIGS. 142–147. *Scopaeus*. **142–145.** *S. minutus* sp. grp. (*S. pusillus*). **142.** Metaventrite. **143.** Metaventrite, left file. **144.** Mesofemur, right base, plectral ridge. **145.** Sternites II and III. **146–147.** *S. mutatus* sp. grp. (*S.* sp.). **146.** Mesofemur, right base, plectral ridges. **147.** Sternites II and III.



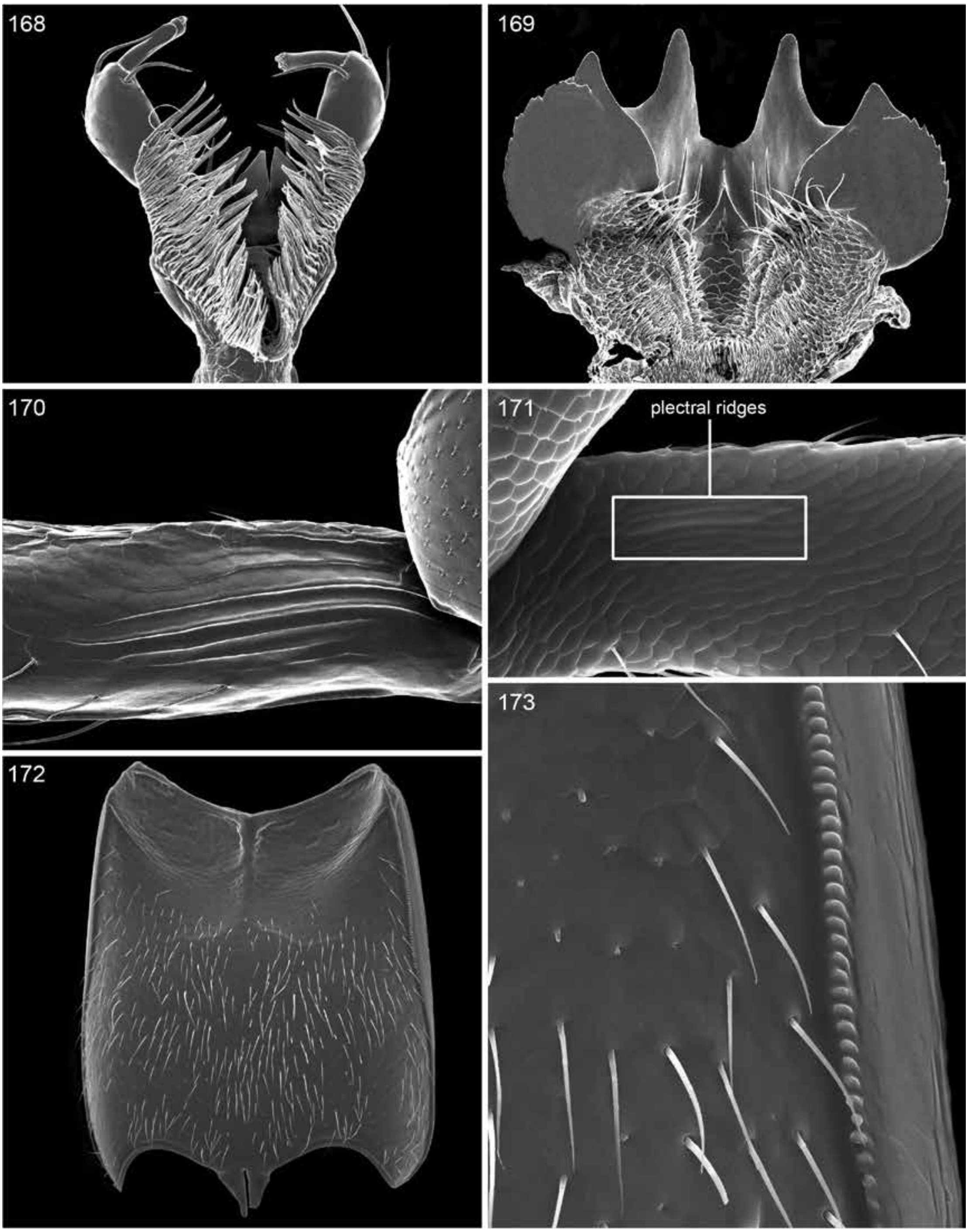
FIGS. 148–153. *Scopaeus*. *S. mutatus* sp. grp. (*S*. sp.). **148.** Mesoventrite. **149.** Metaventrite. **150.** Metaventrite, anterior left file. **151.** Metaventrite, posterior left file. **152.** Sternite IV, midanterior. **153.** Sternite IV, midanterior enlarged, glandular(?) depression and pore.



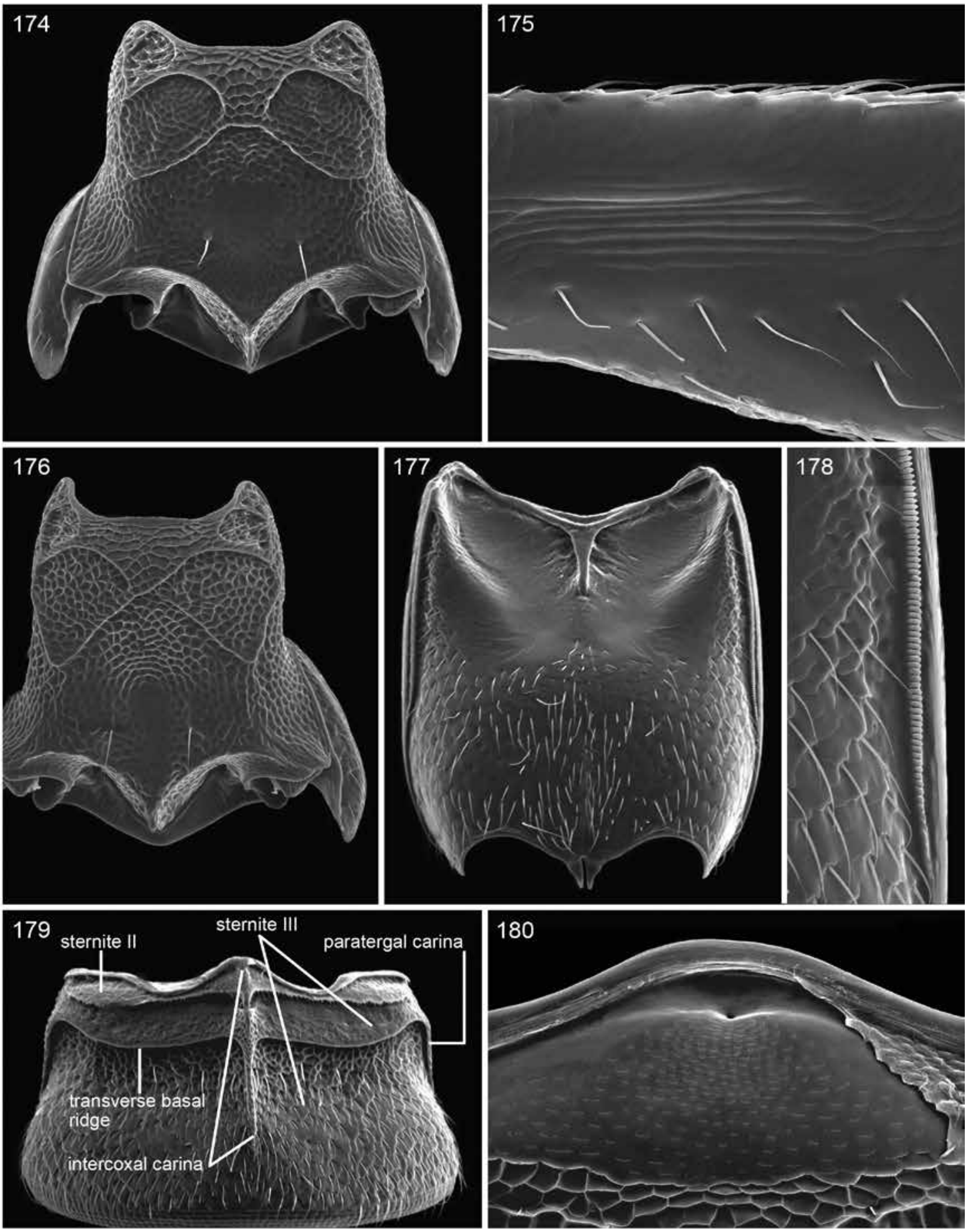
FIGS. 154–160. *Scopaeus*. *S. nevermanni* sp. grp. (*S.* sp.). **154.** Metaventrite. **155.** Metaventrite, right file. **156.** Mesoventrite. **157.** Mesofemur, right base, plectral ridges. **158.** Aedeagus, dorsal. **159.** Labrum. **160.** Labium, hypopharynx, tripartite ligular lobe.



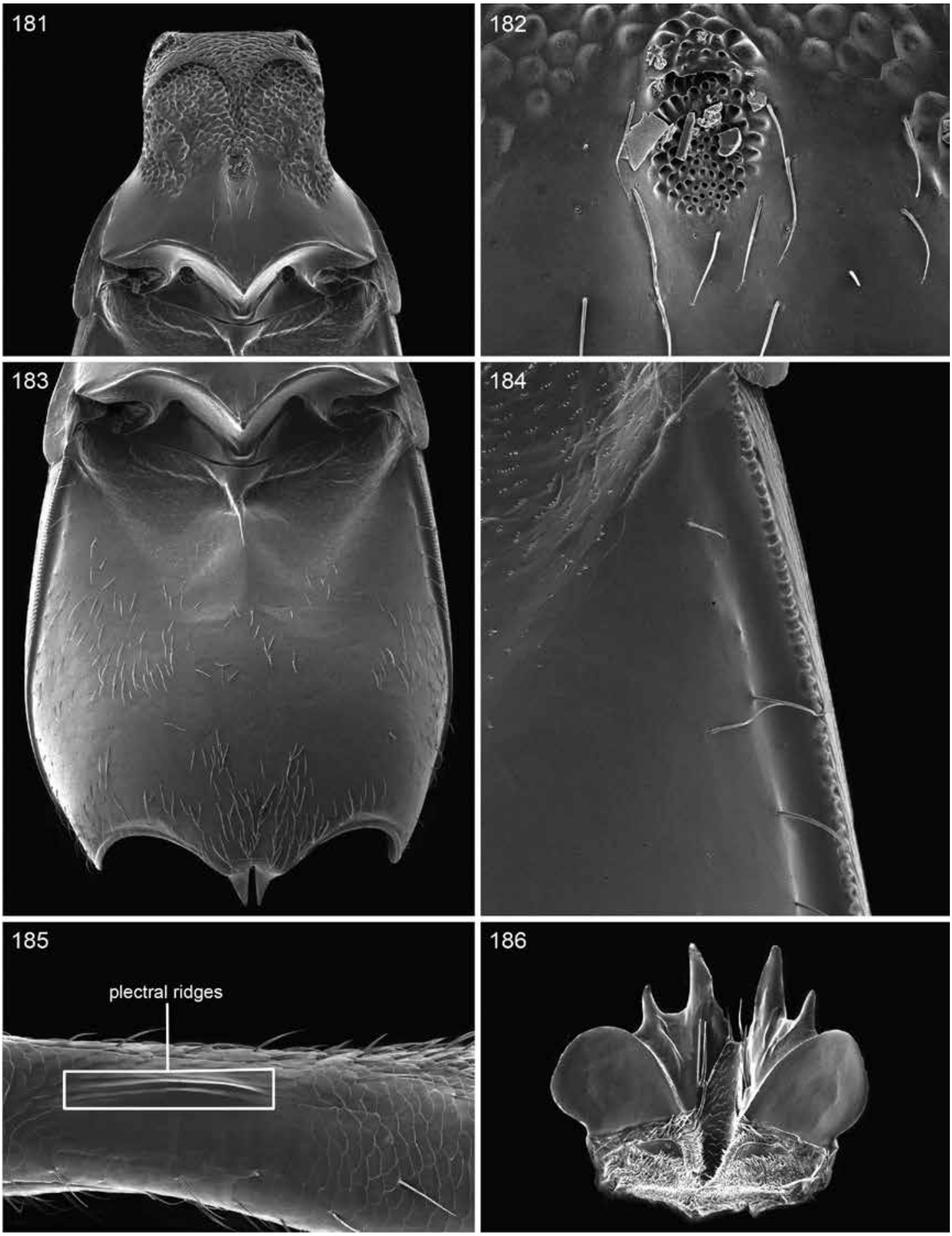
FIGS. 161–167. *Scopaeus*. *S. nitidus* sp. grp. (*S.* sp.). **161.** Head. **162.** Mesofemur and coxa, plectral ridges. **163.** Pteroventrites. **164, 165.** Metaventrite, right file. **166.** Mesoventrite. **167.** Sternites II and III.



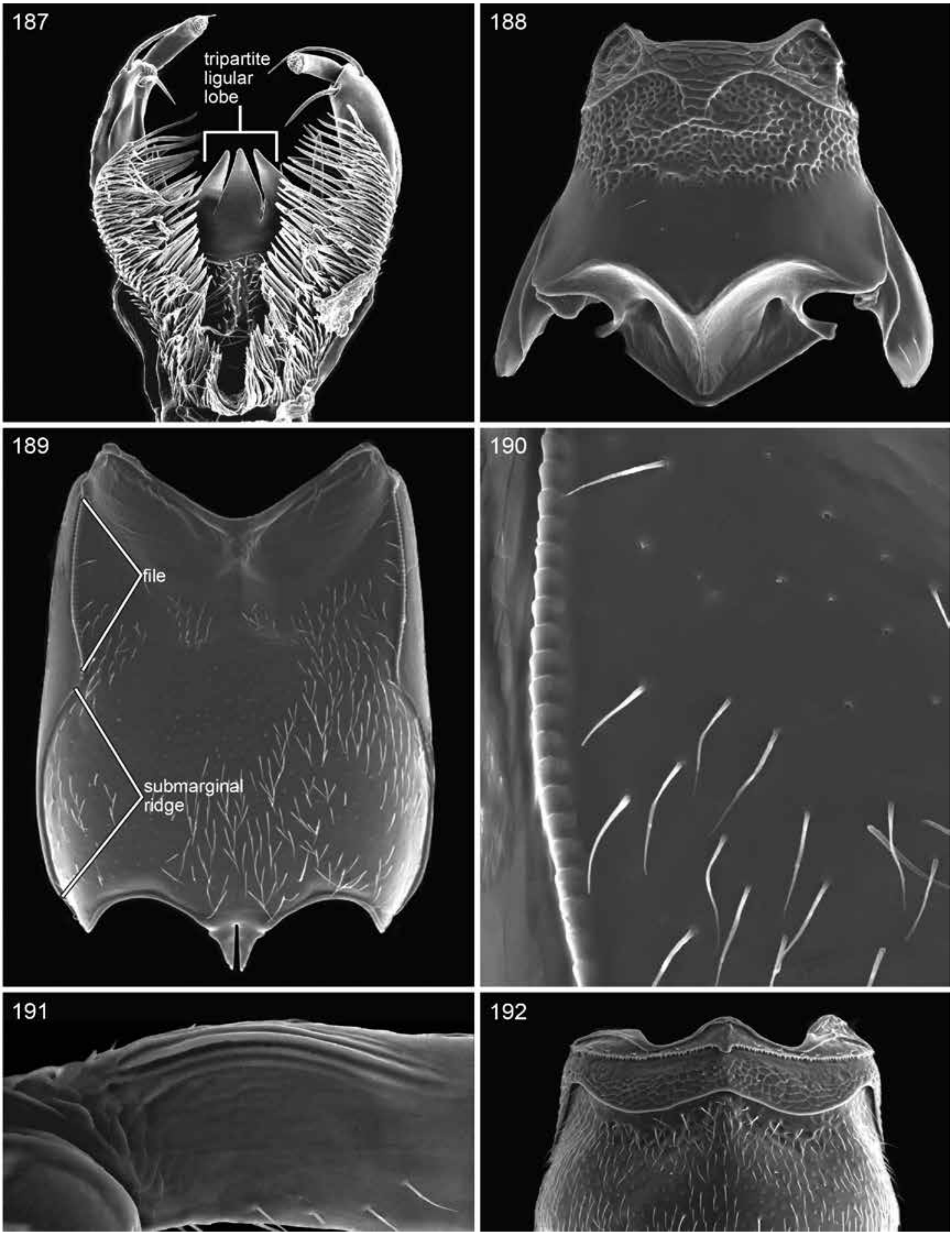
FIGS. 168–173. *Scopaeus*. **168–170.** *S. nitidus* sp. grp. (*S.* sp.). **168.** Labium, hypopharynx. **169.** Labrum, epipharynx. **170.** Mesofemur, left base, plectral ridges. **171–173.** *S. obscuripes* sp. grp. (*S. likovskyi*). **171.** Mesofemur, right base, plectral ridges. **172.** Metaventrite. **173.** Metaventrite, left file.



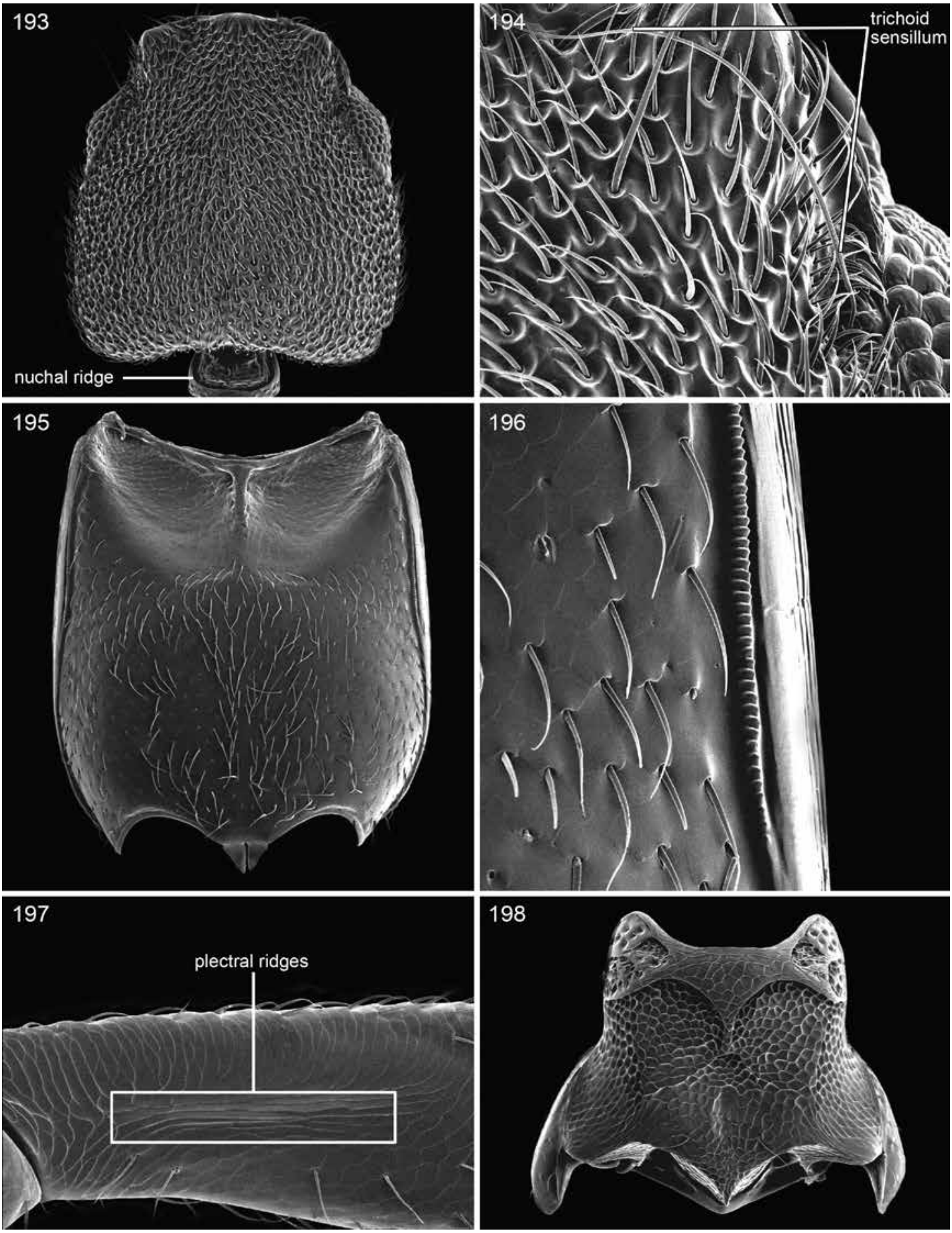
FIGS. 174–180. *Scopaeus*. **174.** *S. obscuripes* sp. grp. (*S. likovskyi*). Mesoventrite. **175–180.** *S. ooderes* sp. grp., (*S. ooderes*). **175.** Mesofemur, right base, plectral ridges. **176.** Mesoventrite. **177.** Metaventrite. **178.** Metaventrite, left file. **179.** Sternites II and III. **180.** Sternite IV, midanterior enlarged, glandular(?) pore.



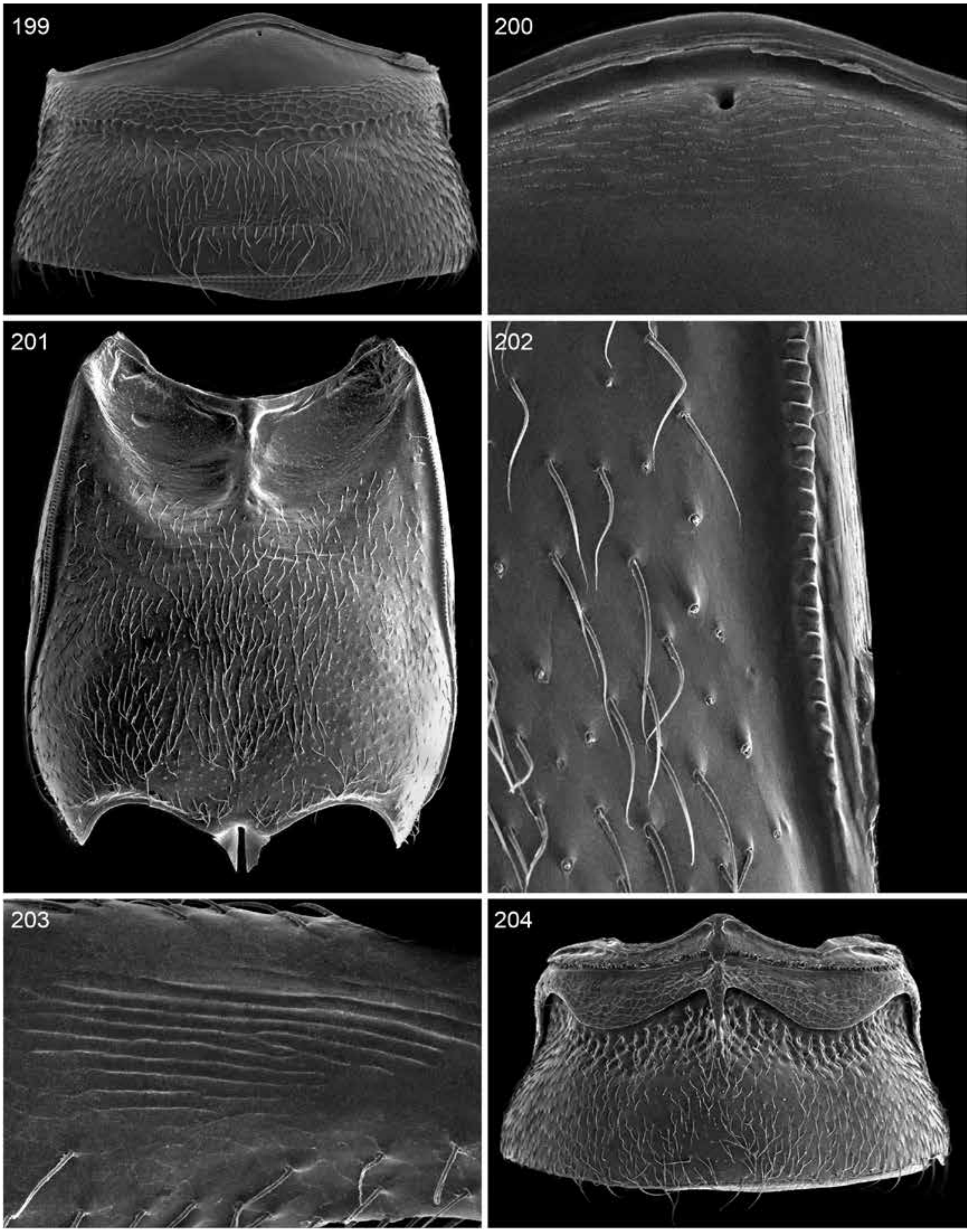
FIGS. 181–186. *Scopaeus*. *S. opacus* sp. grp., (*S. opacus*). **181.** Mesoventrite. **182.** Mesoventrite, median depression, enlarged. **183.** Metaventrite. **184.** Metaventrite, left file. **185.** Mesofemur, right base, plectral ridges. **186.** Labrum, epipharynx.



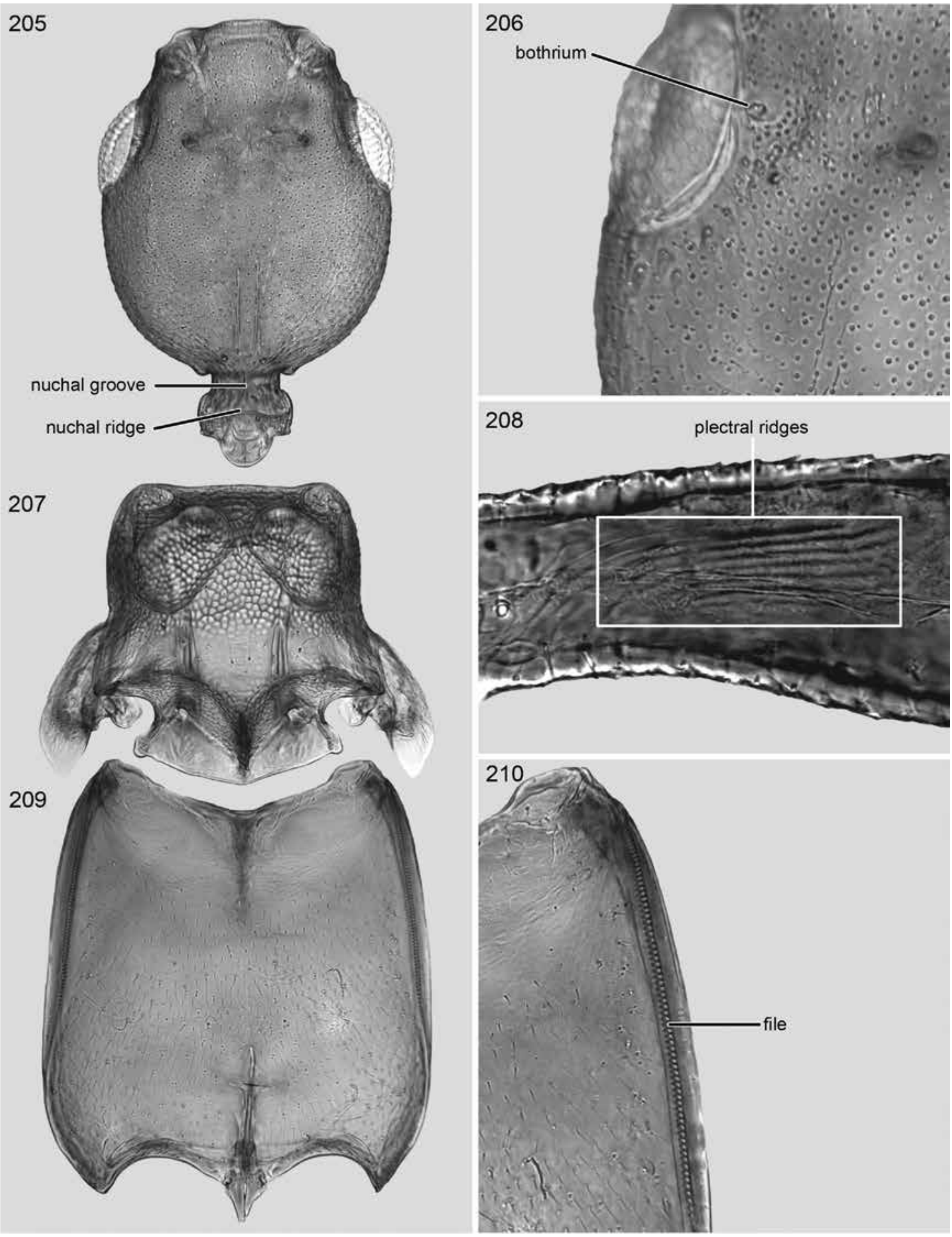
FIGS. 187–192. *Scopaeus*. **187.** *S. opacus* sp. grp., (*S. opacus*). Labium, hypopharynx. **188–192.** *S. punctatellus* sp. grp.; *S. punctatellus*. **188.** Mesoventrite. **189.** Metaventrite. **190.** Metaventrite, right file. **191.** Mesofemur, right base, plectral file. **192.** Sternites II and III.



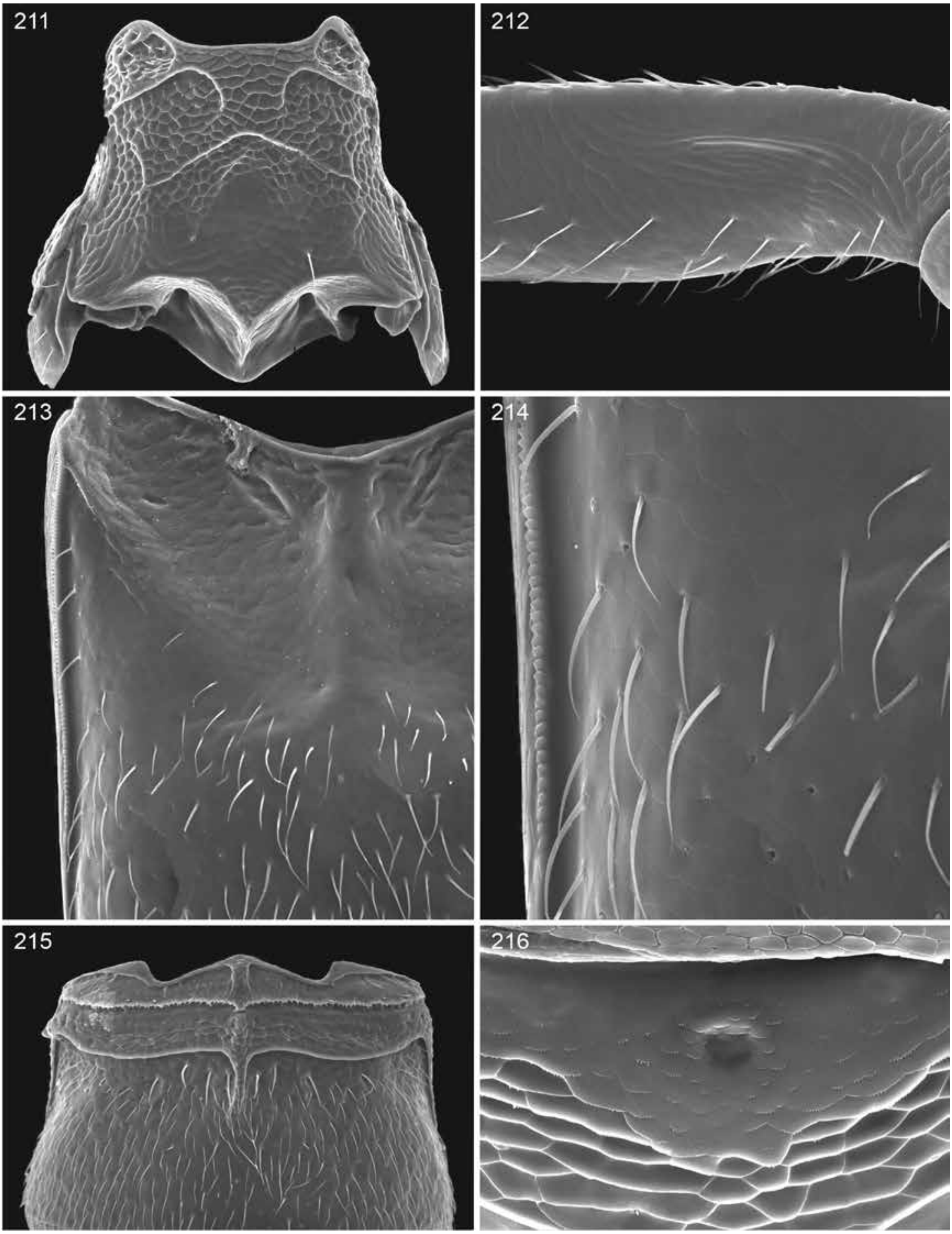
FIGS. 193–198. *Scopaeus*. *S.* “reticulate” sp. grp. (*S.* sp.). **193.** Head. **194.** Head, right, anterolateral, trichobothrium. **195.** Metaventrite. **196.** Metaventrite, left file. **197.** Mesofemur, right base, plectral ridges. **198.** Mesoventrite.



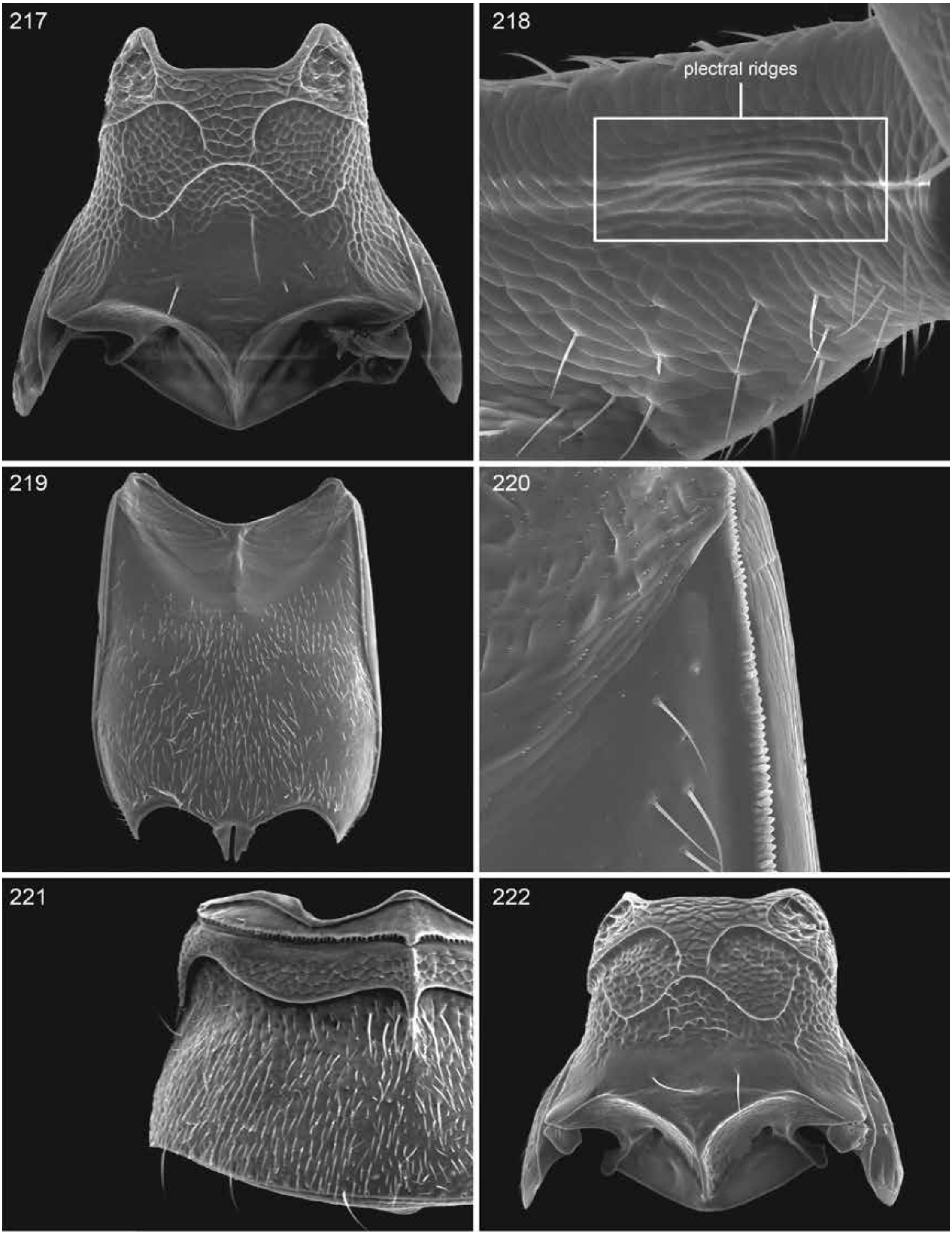
FIGS. 199–204. *Scopaeus*. **199–200.** *S.* “reticulate” sp. grp. (*S.* sp.). **199.** Sternite IV. **200.** Sternite IV, enlarged midanterior, glandular(?) pore. **201–204.** *S. rotundiceps* sp. grp. (*S.* sp.). **201.** Metaventrite. **202.** Metaventrite, left file. **203.** Mesofemur, left base, plectral ridges. **204.** Sternites II and III.



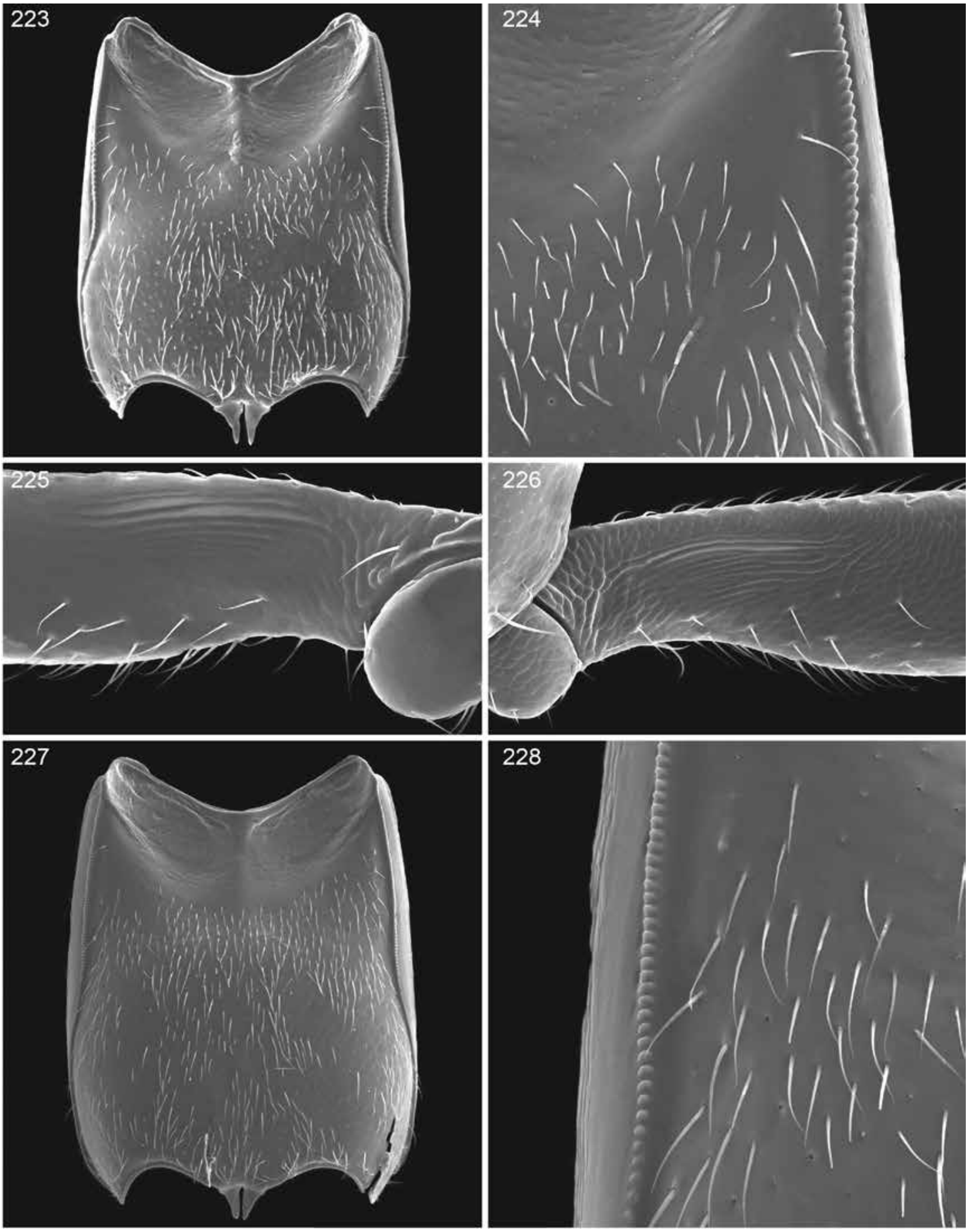
FIGS. 205–210. *Scopaeus*. *S. rotundiceps* sp. grp. (*S.* sp.). **205.** Head. **206.** Head, dorsal, left lateral, bothrium. **207.** Mesoventrite. **208.** Mesofemur, right base, plectral ridges. **209.** Metaventrite. **210.** Metaventrite, left file.



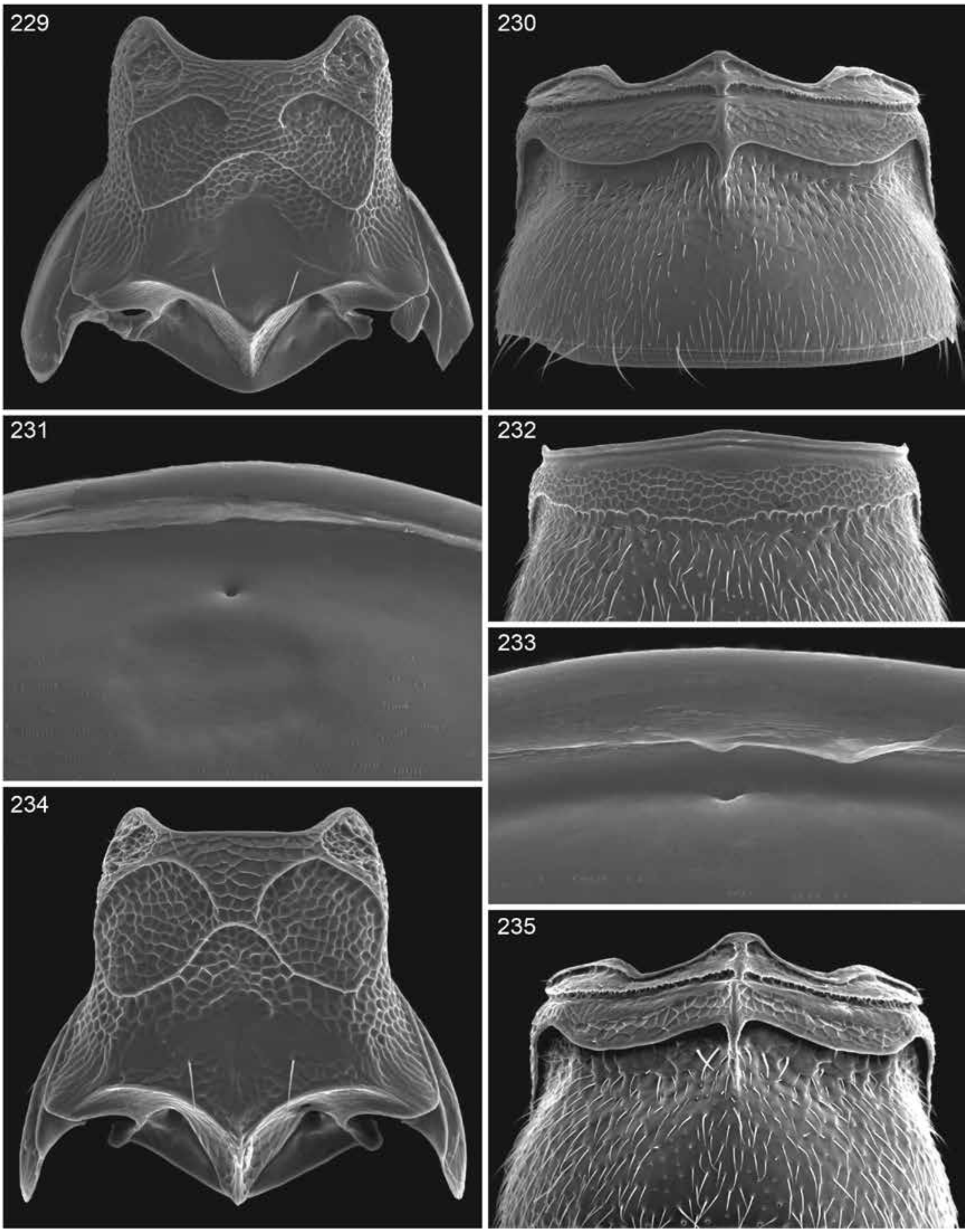
FIGS. 211–216. *Scopaeus*. *S. ryei* sp. grp. (*S.* sp.). **211.** Mesoventrite. **212.** Mesofemur, left basal, plectral ridges. **213.** Metaventrite, anterior right side and middle. **214.** Metaventrite, right file. **215.** Sternites II and III. **216.** Sternite IV, midanterior enlarged, glandular(?) depression.



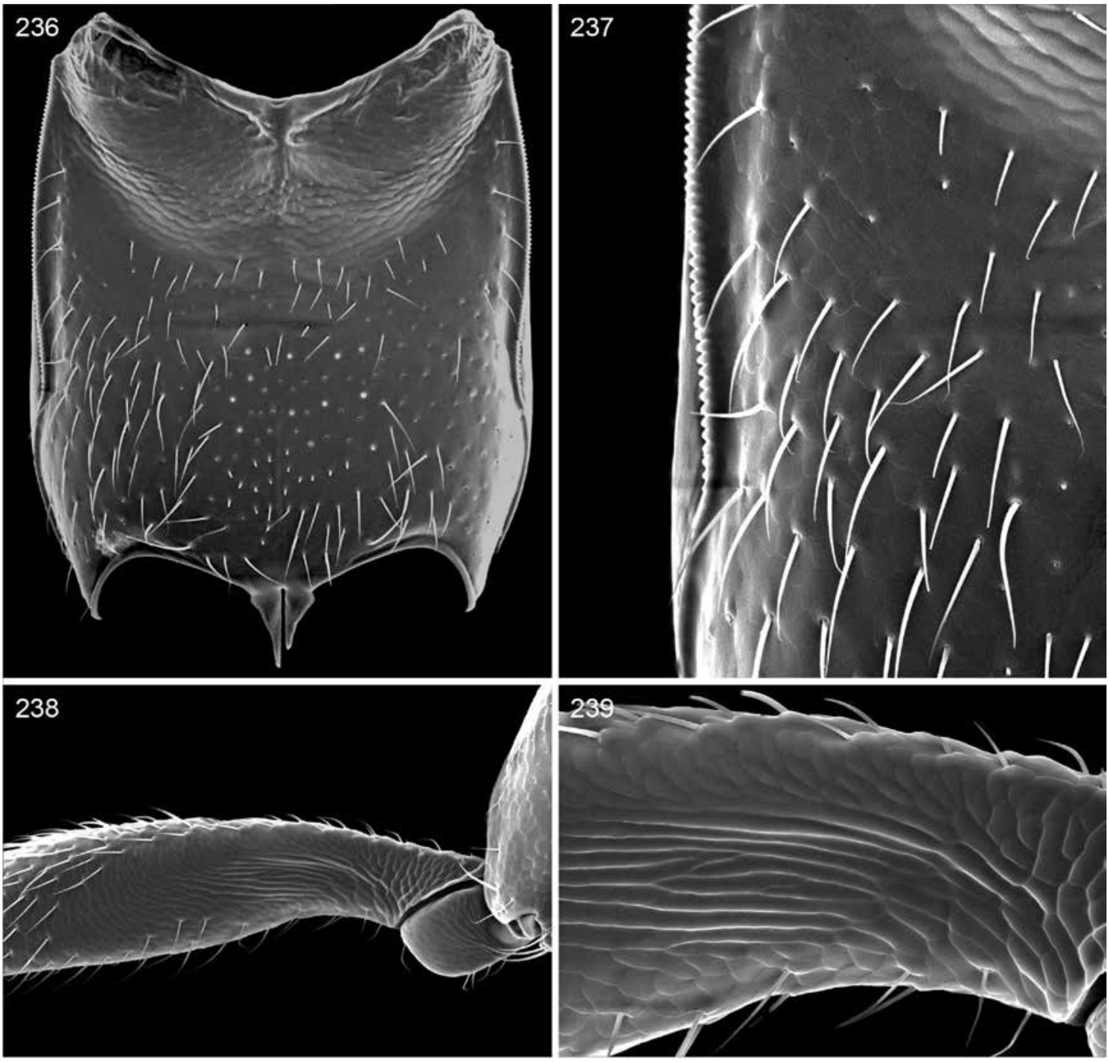
FIGS. 217–222. *Scopaeus*. **217–221.** *S. sericans* sp. grp. (*S.* sp.). **217.** Mesoventrite. **218.** Mesofemur, left base, plectral ridges. **219.** Metaventrite. **220.** Metaventrite, left file. **221.** Sternites II and III, cropped. **222.** *Scopaeus signifer* sp. grp. (*S. bicolor*). Mesoventrite.



FIGS. 223–228. *Scopaeus*. **223–225.** *S. signifer* sp. grp. (*S. bicolor*). **223.** Metaventrite. **224.** Metaventrite, left file. **225.** Mesofemur, left base, plectral ridges. **226–228.** *S. similis* sp. grp., (*S. similis*). **226.** Mesofemur, right base, plectral ridges. **227.** Metaventrite. **228.** Metaventrite, right file.



FIGS. 229–235. *Scopaeus*. **229–231.** *S. similis* sp. grp. (*S. similis*). **229.** Mesoventrite. **230.** Sternites II and III. **231.** Sternite IV, midanterior enlarged, glandular(?) pore. **232–235.** *S. sulcicollis* sp. grp., (*S. sulcicollis*). **232.** Sternite IV. **233.** Sternite IV, midanterior enlarged, glandular(?) pore. **234.** Mesoventrite. **235.** Sternites II and III.



FIGS. 236–239. *Scopaeus*. *S. sulcicollis* sp. grp. (*S. sulcicollis*). **236.** Metaventrite. **237.** Metaventrite, right file. **238.** Mesofemur, left. **239.** Mesofemur, left base, plectral ridges.

KEY TO GENERA OF THE SCOPAEINA

1. Head with trichobothrium in cavity on temple, behind and separated from margin of eye (figs. 267, 282); tropical and subtropical regions of World.............................*Micranops*

– Head with trichobothrium in canal or depression and touching dorsal margin of eye (figs. 13–16, 245, 297, 333, 334).............2

2(1).Metakatepisternal process apically acute (figs. 89, 97), longer than wide (figs. 83, 101, 154) or rarely with length and width about equal (fig. 94); metaventrite with stridular file (figs. 104, 115, 119); mesofemur with plectral ridges (figs. 85, 121, 132, 157, 197); widespread in all temperate, subtropical, and tropical regions.................................*Scopaeus*

– Metakatepisternal process short, wide, and apically blunt or rounded (figs. 241, 300, 335); metaventrite without stridular file (figs. 251–252, 300–301, 335–336); mesofemur without plectral ridges (figs. 253, 279, 302, 337)..3

3(2).Trichobothrium adjacent to posterodorsal margin of eye (figs. 297, 309, 315); Canada to Guatemala..*Orus*

– Trichobothrium adjacent to (fig. 245) or slightly ahead of (figs. 333–334) middorsal margin of eye...4

4(3).Neck petiolate, nuchal groove narrow, about one eighth to one sixth as wide as greatest postocular width of head (fig. 240); Tropical and subtropical regions of Africa, India, southern Asia, Australia.........*Hyperscopaeus*

– Neck not petiolate, nuchal groove wide, about one third to two fifths as wide as greatest postocular width of head (fig. 342); China, Nepal, India, Thailand, Borneo..*Trisunius*

Scopaeus Erichson, Revised Definition

Figures 1–8, 14, 15, 23–239

Scopaeus Erichson, 1839: 29. Type species: *Paederus laevigatus* Gyllenhal, 1827: 483, fixed by Duponchel (1841: 57) by subsequent designation.

— Erichson, 1840: 604 (first included species: *laevigatus*, *didymus*, *minutus*, *minimus*, *infirmus*, *exiguus*, *pygmaeus*, *fasciatellus*, *pulchellus*; characters). — Redtenbacher, L., 1849: 61, 717 (key; characters). — Schaum, 1852: 27 (list of species; Europe). — Lacordaire, 1854: 95 (characters; notes; list of species). — Mulsant and Rey, 1855a: 161 [= Mulsant and Rey, 1855b: 49] (characters; notes). — Fairmaire and Laboulbène, 1856: 558 (characters). — Kraatz, 1857: 667, 701 (characters; key). — Jacquelin du Val, 1857: 46 (characters). — Redtenbacher, L., 1857: 213 (characters). — Thomson, 1858: 40 (characters). — Waterhouse, G., 1858: 27 (catalog; British species). — Thomson, 1859: 28 (characters; type species: *laevigatus*). — Schaum, 1859: 28 (catalog; European species). — Thomson, 1860: 207 (characters). — LeConte, 1861: 66 (key). — Gredler, 1863: 110 (list of species from Tirol). — LeConte, 1863b: 25 (list of North American species). — Crotch, 1863: 35 (catalog; British species). — Wencker and Silbermann, 1866: 32 (list of species; collecting notes; France). — Rye, 1866: 249 (catalog of British species). — Fauvel, 1867: 2, 5 [= 1868: 7, 10] (key; characters). — Thomson, 1867: 180 (key). — Gemminger and Harold, 1868: 618 (catalog; 46 species). — Jacquelin du Val, 1868: 72 (catalog; Europe). — Sharp, 1871: 12 (list of British species). — Fauvel, 1873a: 292, 307 [= 1873b: 134; 1873c: 21] (key; characters). — Crotch, 1873: 32 (checklist; North American species). — Cox, 1874: 277, 283 (characters; key to British species). — Redtenbacher, L., 1874: 230 (characters; 9 species). — Fauvel, 1875a: xix [= 1875b: 221] (catalog; 15 species). — Sharp, 1876: 248 (notes; 7 Brazilian species). — Mulsant and Rey, 1878: 179 (characters; 12 French species). — LeConte, 1880: 178 (notes; two species). — Heyden, 1880: 76 (list of species of Siberian region). — Duvivier, 1883: 168 (catalog). — Lynch Arribálzaga, 1884: 245 (characters; notes; three Argentine species). — Casey, 1886a: 38 (characters). — Casey, 1886b: 217, 229 (characters). — Sharp, 1886: 540 (notes; 20 Mesoamerican species). — Sharp, 1887: 795 (notes). — Fowler, 1888: 310 (notes; key to three British species). — Fauvel, 1889: 255 (notes). — Heyden, E. Reitter and J. Weise, 1891: 108 (list of species of Europe and Caucasus region). — Seidlitz, 1889a: 93, 371 (characters; key to some European species). — Seidlitz, 1889b: 93, 395 (characters; key to some European species). — Sharp and Fowler, 1893: 13 (catalog; British species). — Heyden, 1893: 45 (list of species of Siberian region). — Ganglbauer, 1895: 526 (characters; key to 11 European species). — Heyden, 1896: 34 (list of species of Siberian region). — Casey, 1905: 191, 203 (characters; notes; key to species). — Heyden, E. Reitter and J. Weise, 1906: 154 (list of species of Europe and Caucasus region). — Reitter, 1909: 140, 147 (key; key to German species). — Saint Claire Deville, 1910: 139 (notes; key to and annotated list of species of Seine Basin, France). — Kuhnt, 1912: 218 (key to German species). — Bernhauer and Schubert, 1912: 245 (catalog). — Petri, 1912: 65 (list of species of Siebenbürgen). — Johansen, 1914: 442, 460 (characters; key to Danish species). — Bruch, 1915: 496 (catalog; Argentina). — Chagnon, 1917: 192 (checklist; Quebec). — Leng, 1920: 104 (catalog of American species). — Cameron, 1921: 353, 373, 403 (characters; key and catalog for species of Singapore). — Cameron, 1925: 44 (catalog; species of British India). — Winkler, 1925: 364 (catalog; Palearctic region). — Porta, 1926: 68, 72 (characters; key to Italian species). — Leng and Mutchler, 1927: 20 (catalog; American species). — Bruch, 1928: 442 (catalog; Argentina). — Portevin, 1929: 384, 385 (characters; French species). — Beare, 1930: 16 (catalog; British species). — Roubal, 1930: 354 (catalog; Slovakia). — Cameron, 1931: 31, 169 (characters; key to Indian species). — Joy, 1932: 136 (key to British species). — Scheerpeltz, 1933: 1264 (catalog). — Binaghi, 1935 (key and characters for some species). — Saint-Claire Deville, 1935: 96 (catalog; French species). — Blackwelder, 1939a: 100, 105, 121 (key; checklist; type species). — Blackwelder, 1939b: 24 (catalog of American species). — Glick, 1939: 31 (high aerial capture). — Hansen, V., Hellén, Jansson, Munster, and Strand, 1939: 33 (checklist; northern Europe). — Tottenham, 1940: 53 (correction of type species). — Blackwelder, 1943: 230, 279 (key; characters; key to West Indian species; notes; type species). — Blackwelder, 1944: 119 (checklist of species, Latin America). — Kloet and Hincks, 1945: 164 (checklist; British species). — Porta, 1949: 144 (notes; key to Italian species). — Tottenham, 1949: 367, 415 (type species: *laevigatus* Gyllenhal; checklist of British species). — Blackwelder, 1952: 347 (type species; synonyms). — Adachi, 1955: 15, 25 (characters; key to Japanese species). — Hatch, 1957: 151, 161 (characters; key to subgenera and species of N.W. United States). — Kocher, 1958: 127 (checklist of species; Morocco). — Coiffait, 1960: 284 (characters; key to subgenera). — Hansen, V., Klefbeck, Sjöberg, Stenius, and Strand, 1960: 134–137 (checklist; northern Europe). — Fagel, 1961a: 273 (notes). — Fagel, 1961b: 200 (notes). — Ferreira, 1962: 15 (catalog; Portuguese species). — Arnett, 1963: 244, 269 (characters; notes). — Székessy, 1963: 42 (characters). — Palm, 1963: 14 (characters; key to species of Sweden). — Fagel, 1963: 355 (notes). — Lohse, 1964: 143 (characters; key to central European species). — Szujecki, 1965: 34 (characters; key to Polish species). — Fagel, 1965: 209 (notes). — Coiffait, 1968 (notes; characters). — Coiffait and Saiz, 1968: 380, 389 (key; characters; key to Chilean species). — Scheerpeltz, 1968: 52 (catalog; Austrian species). — Allen, 1969: 198 (British species; notes; key). — Fagel, 1973 (revision of African species; characters; key to species and to species groups; catalog of African species). — Shibata, 1973: 51 (catalog; Taiwanese species). — Tikhomirova, 1973: 177 (checklist of species of USSR). — Moore and Legner, 1974: 558 (characters). — Blackwelder and Arnett, 1974: 57 (checklist; North America; Central America; West Indies). — Moore and Legner, 1975: 137 (catalog; American species). — Pope, 1977: 27 (checklist; British species). — Shibata, 1977: 58 (catalog; Japanese species). — Moore and Legner, 1979: 114 (characters; notes). — Burakowski, Mroczkowski, and Stefańska, 1979: 219 (catalog; Poland). — Muona, 1979: 17 (list of Scandinavian species). — Uhlig, 1979: 249 (some species collected in Germany). — Dvořák, 1979: 114 (some species collected in Slovakia). — Uhlig, Vogel, and Sieber, 1980: 243 (some species collected in Germany). — Spahr, 1981: 96 (references to specimens from amber and copal). — Coiffait, 1982: 11 (characters in key). — Matthews, 1982: 8 (notes; Australia). — Tóth, 1983: 2, 20 (characters; key to Hungarian species). — Coiffait, 1984: 148 (key to subgenera and species; characters; distribution). — Hammond, 1984: 204 (checklist; Borneo). — Boháč, 1985: 453 (characters; notes; key to Czechoslovakian species). — Outerelo and Gamarra, 1985: 35 (characters). — Frank, 1986: 369 (checklist; Florida species). — Segers, 1986: 38 (catalog; Belgian species). — Silfverberg, 1992: 19 (list of species of Fennoscandia, Denmark, and the Baltic States). — Navarrete-Heredia and Márquez-Luna, 1993 (cave collections; Mexico). — Boháč, 1993: 46 (list of species of Czech Republic). — Frisch, 1994: 4 (aedeagal morphology). — Terlutter, 1995: 68 (list of some species of Germany). — Ciceroni and Zanetti, 1995: 21 (list of species of Italy). — Biswas and Biswas, 1995: 279 (key to species of West Bengal). — Hansen, M., 1996: 103 (list of Danish species). — Hansen, M., Mahler, Palm, and Pedersen, 1996: 242 (additions to list of Danish species). — Downie and Arnett, 1996: 405 (characters; key to species of Northeastern North America). — Frisch, 1997a (revision of western Palaearctic species). — Frisch, 1998 (revision of some West Palaearctic species). — Lundgren, 1998: 49 (list of species from Florida; records for other States listed for each species). — Hansen, M., Palm, Pedersen, and Runge, 1998: 71 (list of species collected in 1997; Denmark). — Frisch, 1999a (characters and discussion of and key to species of *debilis* species group). — Frisch, 1999b (characters and discussion of species of *S. obscuripes* species group). — Frisch, 1999c (characters and discussion of species of *S. sulcicollis* species group). — Newton, Thayer, Ashe, and Chandler, 2000: 386 (42 North American species; characters in key; notes). — Assing and Schülke, 2001: 132 (checklist of central European species). — Frisch, Burckhardt, and Wolters, 2002a: 27 (taxonomic history; summary of natural history; anatomy; characters; species-group characters and classification; phylogeny and biogeography of species of Western Palaearctic; character evolution; classification; type species). — Frisch, Burckhardt, and Wolters, 2002b: 2 (catalog; Western Palaearctic). — Frisch, Burckhardt, and Wolters, 2002c: 1 (data matrix for cladistic analysis). — Navarrete-Heredia, Newton, Thayer, Ashe, and Chandler, 2002: 280 (characters in key to genera for Mexico; general notes; list of Mexican species). — Frisch, 2003: 649 (revision of *Scopaeus laevigatus* species group). — Smetana, 2004: 615 (Palaearctic catalog). — Frisch, 2005: 73

(characters of *S. limbatus* species group and revision of species). — Stan, 2004: 99 (checklist; Romania). — Frisch, 2006a: 20 (checklist of species of Iran). — Frisch, 2007a: 195 (revision of and characters for *S. gracilis* species group; discussion of biogeography). — Frisch, 2009: 271 (characters and revision of species of *Scopaeus mutatus* group; discussion of designation of lectotypes; discussion of phylogeography). — Jiménez-Sánchez, Zaragoza-Caballero, and Noguera, 2009: 167 (seasonal abundance; Morelos, Mexico). — Frisch, 2011: 363 (revision of and characters for *S. paliferus* species group). — Frisch, 2012a: 277 (revision of and characters for *S. sericans* species group). — Assing, 2012b: 322 (characters). — Frisch, 2012b: 370 (characters; comments; key to species of Central Europe). — Frisch, 2014: 201 (revision of and characters for *S. similis* species group). — Frisch, 2015a: 139 (revision of and characters for *obscuripes* species group; distribution; notes; key to species; phylogeography). — Frisch, 2016: 56-88 (revision of types of Australian species).

Polyodontus Solier, 1849: 310. (preoccupied by Eysenhardt, 1818). Type species: *Polyodontus angustatus* Solier, 1849: 312, fixed by monotypy.

— Lacordaire, 1854: 95 (characters; notes; list of species). — Kraatz, 1857: 701 (synonym of *Scopaeus*; notes). — Kraatz, 1859: 4, 12 (synonym of *Scopaeus*). — Fauvel, 1867: 2 [= 1868: 10] (synonym of *Scopaeus*). — Gemminger and Harold, 1868: 618 (synonym of *Scopaeus*). — Fauvel, 1873a: 307 [= 1873c: 21] (synonym of *Scopaeus*). — Fauvel, 1875a: xix [= 1875b: 221] (synonym of *Scopaeus*). — Mulsant and Rey, 1878: 194 (characters; group of *Scopaeus*; key). — Lynch Arribálzaga, 1884: 245 (synonym of *Scopaeus*). — Seidlitz, 1889a: 372 (subgenus of *Scopaeus*; key to some European species). — Seidlitz, 1889b: 395 (subgenus of *Scopaeus*; key to some European species). — Heyden, Reitter, and Weise, 1891: 109 (catalog; subgenus of *Scopaeus*; Europe). — Ganglbauer, 1895: 526 (subgenus of *Scopaeus*). — Heyden, Reitter, and Weise, 1906: 154 (catalog; subgenus of *Scopaeus*; Europe). — Bernhauer and Schubert, 1912: 245 (synonym of *Scopaeus*). — Cameron, 1931: 169 (synonym of *Scopaeus*). — Scheerpeltz, 1933: 1264 (subgenus of *Scopaeus*; catalog). — Binaghi, 1935: 85, 87 (characters). — Blackwelder, 1939a: 105, 121 (synonym of *Scopaeus*; type species). — Blackwelder, 1943: 279 (synonym of *Scopaeus*; type species). — Blackwelder, 1944: 119 (synonym of *Scopaeus*). — Tottenham, 1949: 368, 415 (type species: *angustatus* Solier; subgenus of *Scopaeus*; checklist of British species). — Coiffait, 1952: 8 (subgenus of *Scopaeus*; list of and key to species). — Blackwelder, 1952: 318 (type species; preoccupied name; synonym of *Scopaeus*). — Coiffait, 1968: 407 (notes; preoccupied name). — Coiffait and Saiz, 1968: 389 (synonym of *Scopaeus*). — Saiz, 1969: 8 (synonym of *Scopaeus*). — Blackwelder and Arnett, 1974: 57 (synonym of *Scopaeus*). — Coiffait, 1984: 148 (synonym of *Scopaeus*). — Outerelo and Gamarra, 1985: 35 (characters). — Newton, Thayer, Ashe, and Chandler, 2000: 386 (synonym of *Scopaeus*). — Frisch, Burckhardt, and Wolters, 2002a: 45 (homonym; notes; position uncertain). — Frisch, Burckhardt, and Wolters, 2002b: 2 (synonym of *Scopaeus*). — Smetana, 2004: 615 (synonym of *Scopaeus*).

Scoponeus Motschulsky, 1858: 641. Type species: *Scoponeus testaceus* Motschulsky, 1858: 642, fixed by Blackwelder (1939a: 121) by subsequent designation.

— Gemminger and Harold, 1868: 618 (synonym of *Scopaeus*). — Fauvel, 1873a: 307 [= 1873c: 21] (synonym of *Scopaeus*). — Fauvel, 1875a: xix [= 1875b: 221] (synonym of

Scopaeus). — Lynch Arribálzaga, 1884: 245 (synonym of *Scopaeus*). — Ganglbauer, 1895: 526 (synonym of *Polyodontus*). — Bernhauer and Schubert, 1912: 245 (synonym of *Scopaeus*). — Cameron, 1931: 169 (synonym of *Scopaeus*). — Blackwelder, 1939a: 105, 121 (synonym of *Scopaeus*; type species). — Blackwelder, 1943: 279 (synonym of *Scopaeus*; type species). — Blackwelder, 1944: 119 (synonym of *Scopaeus*). — Blackwelder, 1952: 348 (type species, date of genus cited as 1857; synonym of *Scopaeus*). — Blackwelder and Arnett, 1974: 57 (synonym of *Scopaeus*). — Coiffait, 1984: 148 (synonym of *Scopaeus*). — Smetana, 2004: 615 (synonym of *Scopaeus*).

Euscopaeus Sharp, 1886: 548. Type species: *Euscopaeus crassitarsis* Sharp, 1886: 548, fixed by Lucas (1920: 290) by subsequent designation. **New synonym**.

— Bernhauer and Schubert, 1912: 252 (catalog). — Blackwelder, 1939a: 118 (type species). — Blackwelder, 1944: 121 (checklist of species, Latin America). — Blackwelder, 1952: 161 (type species). — Blackwelder and Arnett, 1974: 62 (checklist; North America; Central America; West Indies).

Scopaeomerus Sharp, 1886: 538. Type species: *Scopaeomerus chiriquensis* Sharp, 1886: 539, fixed by Lucas (1920: 587; cited as "*Sc. chiriguensis*") by subsequent designation. **New synonym**.

— Bernhauer and Schubert, 1912: 252 (catalog). — Blackwelder, 1939a: 121 (type species). — Blackwelder, 1944: 120 (checklist of species, Latin America). — Blackwelder, 1952: 347 (type species). — Blackwelder and Arnett, 1974: 59 (checklist; North America; Central America; West Indies). — Navarrete-Heredia, J.L., A.F. Newton, M.K. Thayer, J.S. Ashe, and D.S. Chandler. 2002: 280 (characters in key to genera for Mexico; general notes; list of Mexican species).

Leptorus Casey, 1886b: 220. Type species: *Scopaeus exiguus* Erichson, 1840: 608, fixed by Blackwelder (1939a: 119) by subsequent designation.

— Casey, 1905: 203 (synonym of *Scopaeus*). — Bernhauer and Schubert, 1912: 245 (synonym of *Scopaeus*). — Cameron, 1931: 169 (synonym of *Scopaeus*). — Blackwelder, 1939a: 119 (synonym of *Scopaeus*; type species). — Blackwelder, 1943: 279 (synonym of *Scopaeus*; type species). — Blackwelder, 1944: 119 (synonym of *Scopaeus*). — Blackwelder, 1952: 217 (type species; synonym of *Scopaeus*). — Blackwelder and Arnett, 1974: 57 (synonym of *Scopaeus*). — Campbell and Davies, 1991: 114 (synonym of *Scopaeus*). — Newton, Thayer, Ashe, and Chandler, 2000: 386 (synonym of *Scopaeus*). — Smetana, 2004: 615 (synonym of *Scopaeus*).

Scopaeodera Casey, 1886b: 220. Type species: *Echiaster nitidus* LeConte, 1863a: 47, fixed by monotypy. **Revised status junior synonym**.

— Casey, 1905: 192, 217 (characters; notes; key to species). — Bernhauer and Schubert, 1912: 245 (subgenus of *Scopaeus*). — Leng, 1920: 104 (catalog of American species). — Cameron, 1931: 169 (synonym of *Scopaeus*). — Blackwelder, 1939a: 100, 106, 121 (key; subgenus of *Scopaeus*; checklist; type species). — Blackwelder, 1943: 279 (subgenus of *Scopaeus*; type species). — Blackwelder, 1944: 119 (subgenus of *Scopaeus*). — Blackwelder, 1952: 346 (type species; subgenus of *Scopaeus*). — Blackwelder and Arnett, 1974: 57 (synonym of *Scopaeus*). — Newton, Thayer, Ashe, and Chandler, 2000: 386 (subgenus of *Scopaeus*). — Navarrete-Heredia, Newton, Thayer, Ashe, and Chandler, 2002: 280 (subgenus of *Scopaeus*).

Scopaeoma Casey, 1905: 211. Type species: *Scopaeus rotundiceps* Casey, 1886b: 217, fixed by Blackwelder (1939a: 121) by subsequent designation. **Revised status junior synonym**.

— Bernhauer and Schubert, 1912: 245 (subgenus of *Scopaeus*). — Leng, 1920: 104 (catalog of American species). — Leng and Mutchler, 1927: 20 (catalog; American species). — Cameron, 1931: 169 (synonym of *Scopaeus*). — Blackwelder, 1939a: 100, 106, 121 (key; subgenus of *Scopaeus*; checklist; type species). — Blackwelder, 1943: 279 (subgenus of *Scopaeus*; type species). — Blackwelder, 1944: 119 (subgenus of *Scopaeus*). — Blackwelder, 1952: 347 (subgenus of *Scopaeus*; type species). — Hatch, 1957: 160 (subgenus of *Scopaeus*; characters). — Blackwelder and Arnett, 1974: 57 (synonym of *Scopaeus*). — Campbell and Davies, 1991: 114 (subgenus of *Scopaeus*). — Newton, Thayer, Ashe, and Chandler, 2000: 386 (subgenus of *Scopaeus*). — Navarrete-Heredia, J.L., A.F. Newton, M.K. Thayer, J.S. Ashe, and D.S. Chandler. 2002: 280 (subgenus of *Scopaeus*).

Scopaeopsis Casey, 1905: 214. Type species: *Echiaster opacus* LeConte, 1863a: 46, fixed by Blackwelder (1939a: 121) by subsequent designation. **Revised status junior synonym**.

— Bernhauer and Schubert, 1912: 245 (subgenus of *Scopaeus*). — Leng, 1920: 104 (catalog of American species). — Cameron, 1931: 169 (synonym of *Scopaeus*). — Blackwelder, 1939a: 100, 106, 121 (key; subgenus of *Scopaeus*; checklist; type species). — Blackwelder, 1943: 279 (subgenus of *Scopaeus*; type species). — Blackwelder, 1944: 119 (subgenus of *Scopaeus*). — Blackwelder, 1952: 347 (type species; subgenus of *Scopaeus*). — Blackwelder and Arnett, 1974: 58 (synonym of *Scopaeus*). — Campbell and Davies, 1991: 114 (subgenus of *Scopaeus*). — Newton, Thayer, Ashe, and Chandler, 2000: 386 (subgenus of *Scopaeus*). — Navarrete-Heredia, Newton, Thayer, Ashe, and Chandler, 2002: 280 (subgenus of *Scopaeus*).

Pseudorus Casey, 1910: 190. (preoccupied by *Pseudorus* Walker, 1851). Type species: *Pseudorus prolixipennis* Casey, 1910: 191, fixed by Blackwelder (1939a: 121) by subsequent designation.

— Leng, 1920: 104 (catalog of American species). — Scheerpeltz, 1933: 1264 (subgenus of *Scopaeus*; catalog). — Blackwelder, 1939a: 105, 121 (synonym of *Scopaeus*; type species). — Blackwelder, 1943: 279 (synonym of *Scopaeus*; type species). — Blackwelder, 1944: 119 (synonym of *Scopaeus*). — Blackwelder, 1952: 330 (type species; synonym of *Scopaeus*). — Blackwelder and Arnett, 1974: 58 (synonym of *Scopaeus*). — Campbell and Davies, 1991: 114 (synonym of *Scopaeus*). — Newton, Thayer, Ashe, and Chandler, 2000: 386 (synonym of *Scopaeus*). — Smetana, 2004: 615 (synonym of *Scopaeus*).

Stilpon Coiffait, 1952: 6. (preoccupied by *Stilpon* Loew, 1859). Type species: *Scopaeus baudrimonti* Coiffait, 1952: 6, fixed by original designation.

— Coiffait, 1984: 148 (synonym of *Scopaeus*). — Frisch, Burckhardt, and Wolters, 2002a: 45 (synonym of *Scopaeus*). — Smetana, 2004: 615 (synonym of *Scopaeus*).

Euscopaeus Coiffait, 1960: 285. [preoccupied by *Euscopaeus* Sharp, 1886]. Type species: *Scopaeus didymus* Erichson, 1840: 606, fixed by original designation.

— Coiffait, 1968: 415 (homonym of *Euscopaeus* Sharp, 1886; synonym of *Alloscopaeus* Coiffait, 1968). — Coiffait, 1984: 148 (synonym of *Alloscopaeus*). — Frisch, Burckhardt, and Wolters, 2002a: 46 (synonym of *Scopaeus*; type species). — Smetana, 2004: 615 (synonym of *Scopaeus*).

Geoscopaeus Coiffait, 1960: 284. (replacement name for *Stilpon* Coiffait). Type species: *Scopaeus baudrimonti* Coiffait, 1952: 6, fixed by objective synonymy with *Stilpon* (ICZN: 1999: Article 67.8).

— Fagel, 1973: 18 (characters). — Coiffait, 1984: 148 (synonym of *Scopaeus*; erroneous type species corrected). — Frisch, Burckhardt, and Wolters, 2002a: 45, 46 (synonym of *Scopaeus*; notes; type species). — Frisch, Burckhardt, and Wolters, 2002b: 2 (synonym of *Scopaeus*). — Smetana, 2004: 615 (synonym of *Scopaeus*).

Heteroscopaeus Coiffait, 1960: 285. Type species: *Scopaeus sericans* Mulsant and Rey, 1855a: 168, fixed by original designation.

— Coiffait, 1968: 418 (synonym of *Hyposcopaeus*). — Outerelo and Gamarra, 1985: 36 (characters). — Frisch, Burckhardt, and Wolters, 2002a: 46 (synonym of *Scopaeus*; type species). — Frisch, Burckhardt, and Wolters, 2002b: 2 (synonym of *Scopaeus*). — Smetana, 2004: 615 (synonym of *Scopaeus*).

Hyposcopaeus Coiffait, 1960: 285. Type species: *Scopaeus scitulus* Baudi di Selve, 1857: 103, fixed by original designation.

— Coiffait, 1984: 148 (subgenus of *Scopaeus*; key to species). — Outerelo and Gamarra, 1985: 36 (characters). — Ádám, 1987: 144 (list of two species with collecting notes; Hungary). — Frisch, Burckhardt, and Wolters, 2002a: 46 (synonym of *Scopaeus*; type species). — Frisch, Burckhardt, and Wolters, 2002b: 2 (synonym of *Scopaeus*). — Smetana, 2004: 615 (synonym of *Scopaeus*).

Alloscopaeus Coiffait, 1968: 414. [replacement name for *Euscopaeus* Coiffait]. Type species: *Scopaeus didymus* Erichson, 1840: 606, fixed by objective synonymy with *Euscopaeus* and original designation (ICZN, 1999: Article 67.8).

— Coiffait, 1984: 148 (subgenus of *Scopaeus*; key to species). — Outerelo and Gamarra, 1985: 36 (characters). — Frisch, Burckhardt, and Wolters, 2002a: 46 (synonym of *Scopaeus*; type species). — Frisch, Burckhardt, and Wolters, 2002b: 2 (synonym of *Scopaeus*). — Smetana, 2004: 615 (synonym of *Scopaeus*).

Anomoscopaeus Coiffait, 1968: 426. Type species: *Xantholinus gracilis* (Sperk, 1835: 152), fixed by original designation.

— Coiffait, 1984: 148 (subgenus of *Scopaeus*; key to species). — Outerelo and Gamarra, 1985: 36 (synonym of *Heteroscopaeus*). — Frisch, Burckhardt, and Wolters, 2002a: 46 (synonym of *Scopaeus*; type species). — Frisch, Burckhardt, and Wolters, 2002b: 2 (synonym of *Scopaeus*). — Smetana, 2004: 615 (synonym of *Scopaeus*).

Asiascopaeus Coiffait, 1984: 152. Type species: *Scopaeus asiaticus* Bernhauer, 1915: 265, fixed by original designation.

— Smetana, 2004: 615 (subgenus of *Scopaeus*; Palaearctic catalog). — Frisch, 2015a: 139 (synonym of *Scopaeus*).

Typhloscopaeus Jarrige, 1951: 333. (Described as a subgenus of *Scopaeus*; Incertae sedis). Type species: *Scopaeus pauliani* Jarrige, 1951: 333, fixed by original designation and monotypy. [Note: The status of this name is discussed below under "Synonymy".]

Diagnosis: Unique to *Scopaeus* are a metathoracic/mesofemoral stridulum (figs. 119, 121) and the long, tapered, apically acute, metakatepisternal processes (figs. 83, 97, 110) extending between the metacoxae; these two features separate the genus from all other Scopaeina and Paederinae. The stridular file is on the lateral (figs. 102, 104, 105) or submarginal (figs. 114, 119, 154, 155) surface of the metaventrite; the stridular plectral ridges (figs. 85, 106, 121) are on the mesial base of the mesofemur. Other scopaeine genera lack a stridulum and the metakatepisternal process is short and rounded or diagonally truncate apically (figs. 241, 270, 300, 334), not long and acute. An outlier of *Scopaeus* with respect to the metakatepisternal processes is *S. filiformis* for which the processes are similar to those of species of *Micranops* (cf. figs. 89, 270); the former has a stridulum, that is, a file and plectral ridges (figs. 90, 92), the latter does not (figs. 270, 271, 277); the two also differ by the position of their trichobothrium. The metakatepisternal process is more easily seen than is the stridulum, therefore more accessible for identification, but must be used with caution for species such as *S. filiformis* but is easily put aside by the position of the trichobothrium. The metakatepisternal process of *S. filiformis* (figs. 89, 94), unlike other species of the *S. debilis* species group, is short, the lateral margin extends diagonally to an acute apex and has a subapical notch. That notch is absent from the similar metakatepisternal processes of *Micranops* (figs. 270, 280).

Ancillary characters aid in separating *Scopaeus* from others of the subtribe.

The slender, constricted neck of *Scopaeus* (figs. 7, 47, 49, 99, 161, 205) will separate it from *Trisunius* (figs. 258, 342), most species of *Orus* (fig. 257), and the Western Hemisphere species of *Micranops* (fig. 256). The neck/head width ratio of *Scopaeus* is one sixth to one quarter as wide as the head; for *Orus* and the Eastern Hemisphere species of *Micranops* is it about one fifth to two fifths, and for *Hyperscopaeus* it is one eighth to one sixth. So, there is a small overlap among some species of these genera with species of *Scopaeus*. The position of the trichobothrium differs among *Orus*, *Micranops*, and *Scopaeus*. For *Orus* (figs. 297, 315) the trichobothrium is in a long canal beginning at the posterodorsal edge of the tapered eye, whereas that of *Micranops* (figs. 267, 282) is in a short, deep cavity behind and separated from the margin of the eye. The trichobothrium of *Hyperscopaeus* (fig. 245), *Scopaeus* (figs. 15, 26, 39, 206), and *Trisunius* (fig. 274) is above and contiguous with and near the middle of the dorsal edge of the eye.

The gular sutures of *Hyperscopaeus* (fig. 244) are narrowly separated. For most *Scopaeus* (figs. 47, 48, 50) the sutures are moderately widely separated or narrowly so in some (fig. 49).

The dorsal surface of the aedeagal median lobe of *Scopaeus* is sclerotized (fig. 158) and the midlongitudinal surface is fused for the entire length; the whole length of the sclerotized dorsal surface of the median lobe of *Hyperscopaeus* is divided by a median membranous strip (fig. 243).

Tergite IX of *Scopaeus* males (figs. 72, 74, 76), unlike that of the other genera of the Scopaeina, is symmetrical. For *Hyperscopaeus*, *Orus* (figs. 292, 323), and *Trisunius* (fig. 331) tergite IX is notably asymmetrical; the left anteroventral side is larger, more broadly rounded, and wraps medially more than does the right anteroventral side. *Micranops* differs from the preceding three genera in that the left anteroventral side is only slightly larger than the right (fig. 261).

Description: Body length 1.9–4.9 mm.

Head (figs. 1–5, 7, 8) with postocular lateral margin broadly rounded; basal angles distinct and well developed to absent; basal margin broadly and shallowly to moderately emarginate, to truncate, to rounded and continuous with gradually and broadly rounded lateral margins; basal margin without median tumescence; basal margin with or without shallow, vertical sulcus; posteroventral surface without small to minute tubercle laterad of neck.

Neck petiolate (figs. 1–5, 7, 99); nuchal groove deep and strongly constricted, and base of neck abruptly expanded (figs. 99, 161, 205); neck width across nuchal constriction one sixth to one fourth as wide as greatest postocular width of head; nuchal ridge present dorsally and laterally (figs. 161, 193).

Dorsal cephalic surface with dense, minute to fine to moderately strong to coarse, setate punctation (most species) or dense, strong, setate, reticulo-umbilicate punctation (some species; fig. 193) or dense, setate, micropunctate microtubercles (some species), or much less dense, hardly discernible, setate punctation (some species); surface with (most species) or without (some species) interpunctational microsculpturing; surface with dull shine (most species) or polished (some species); pubescence (fine setae) dense (most species) to sparse (some species) dorsally and laterally, less dense ventrally; macrosetae short to long, sparsely distributed, frequently present peripherally, present dorsally in some species.

Cephalic trichobothrium near midpoint of dorsal margin of eye (figs. 15, 26, 39, 205, 206);

bothrium in rounded to moderately elongated depression (figs. 14, 15, 23, 39, 40); surface near depression with setae, particularly dorsad of depression (figs. 14, 15, 23, 40).

Eyes with posterior margin broadly rounded; corneal lenses without sensilla (figs. 23–46); corneal lens with smooth (figs. 24, 26, 31–33, 36, 39, 42, 43–45), slightly to strongly wrinkled (figs. 27, 29, 30, 34, 35, 37, 38, 40,46) or slightly altered surface (figs. 23, 25, 41).

Gular sutures moderately widely (most species) (figs. 47, 48, 50, [99, 161 sutures visible through the cuticle as shadows]) to narrowly (fig. 49) separated.

Mandibles, denticular number: left/right respectively, 1/3, 2/2, 2/3, 3/3, or 3/4 (figs. 61–71).

Labrum quadridentate (figs. 6, 100, 169, 186) for most species, edentate (fig. 59), unidentate (fig. 58) or bidentate (fig. 159) for some.

Pronotum broadly and shallowly to moderately strongly convex (figs. 1–5, 8, 52, 54, 56); surface with dense, minute to fine to moderately strong to coarse, setate punctation (most species) or dense, strong, setate, reticulo-umbilicate punctation (some species, fig. 193) or dense, setate, micropunctate microtubercles (some species), or much less dense, hardly discernible, setate punctation (some species); surface with (most species) or without (some species) interpunctational microsculpturing; midlongitudinal strip with or without punctation and with (most species) or without microsculpturing (some species); surface with dull shine (most species) or polished (some species); pubescence of fine setae dense to sparse dorsally and laterally, less dense ventrally; macrosetae short to long, sparsely distributed, frequently present peripherally, present dorsally in some species; median groove absent or absent medially, but present and shallow anteriorly and posteriorly or posteriorly only; posterior median groove of some species replaced by slightly raised ridge.

Prohypomeron with postprocoxal lobe separated from remainder of hypomeron by prohypomeronal transverse ridge (fig. 52) or transverse ridge absent (figs. 54, 56); prohypomeronal submarginal ridge present (figs. 52, 54) or absent (fig. 56); lobe with or without setae. Notosternal suture present (figs. 51–54), absent (figs. 55, 56), or partially developed (fig. 57).

Elytra longer to shorter than pronotum; surface with dense microtuberculation or with dense to sparse punctation; pubescence dense to sparse; posterior edge with or without row of setae.

Mesoventrite with large, deep, oval to rounded, median depression (figs. 82, 93, 176); surface entirely or partially covered with reticulate microsculpturing (figs. 93, 109, 122, 141, 166, 188, 198).

Mesofurcasternum with (fig. 82) or without (figs. 103, 122) internal, furcasternal apophysis on posteromedial margin.

Mesofemur with one to at least 12 plectral ridges at basal of posterior (mesial) surface usually nearer dorsal than ventral edge (figs. 85, 92, 106, 113, 121, 132, 139, 144, 185, 191, 197, 203).

Mesocoxal acetabulum margined anterolaterally by short (figs. 114, 195, 201, 213), moderately long (figs. 110, 125, 131, 137), to long (figs. 101, 104, 149) pericoxal ridge or without ridge (figs. 83, 177).

Metaventrite with stridular file (figs. 104, 105, 119, 133, 155, 165); file extending posteriorly from near mesocoxa and parallel to submarginal ridge (figs. 104, 105, 172, 173) or parallel to submarginal ridge anteriorly and diverging and increasingly separated from ridge posteriorly (figs. 119, 195, 165); submarginal ridge parallel to or slightly diverging from dorsolateral margin of metaventrite or gradually curved medially near middle then bent abruptly and curved to become parallel to dorsal margin again in some species (figs. 119, 165, 188).

Metakatepisternal process long, slender, and apically tapered to acute point (figs. 97, 154, 183) or short and broad with lateral margin approaching median margin diagonally to apical point; diagonal margin notched near apex (figs. 89, 94).

Sternite II with anterior margin bisinuate (figs. 167, 179, 215); median point of posterior margin present (figs. 116, 145, 167, 179) or absent (figs. 86, 128); median ridge present (figs. 116, 145, 179 215).

Sternite III with (figs. 179, 204) or without (figs. 147, 192) intercoxal carina; intercoxal carina long (fig. 179), short (fig. 86, 140), or reduced to median point extending from transverse basal ridge (fig. 91, 128, 145); transverse basal ridge strongly (fig. 192, 204), moderately (figs. 140, 215), or subtly bisinuate (fig. 86).

Sternite IV with small (figs. 87–88, 134–135, 152–153, 199–200) to large (fig. 123), apparently, glandular pore near anterior margin or pore apparently absent (figs. 129–130, 216); depression present (figs. 87–88, 129–130, 134–135) or absent (figs. 199–200, 232–233) (depression might be an artifact; see more above in section on morphology of the Scopaeina).

MALE: Sternite VII unmodified or with variously emargination of posterior margin, depressions of surface, and clusters of macrosetae.

Sternite VIII with wide to narrow, deep to shallow median, variously configured emargination of posterior margin and with or without median extension or teeth.

Tergite IX symmetrical: left and right anteroventral sides of approximately equal size and form (figs. 72, 74, 76); base fused (figs. 72, 76) with medial incision or separated (fig. 74) into right and left portions of tergite IX.

Tergite X (see Frisch, 2002: figs. 40–44) elongate, ovoid or pentagonoid; anterior margin rounded with slight to distinct apically rounded, median point (figs. 72, 74, 76).

Aedeagus with dorsal surface of median lobe fully sclerotized, without midlongitudinal membranous split (fig. 158); parameres present as tiny lobes appressed to surface on each lateral side of median foramen.

FEMALE: Sternite VII with unmodified posterior margin.

Sternite VIII with rounded posterior margin.

Tergite IX symmetrical (figs. 73, 75, 77): left and right anteroventral sides of approximately equal size and form; middorsal base fused with median incision extending anteriorly from posterior margin (figs. 73, 77) or entirely divided medially (figs. 75).

Tergite X (figs. 73–75) long, ovoid, and anteriorly tapered with rounded anterior margin; anterior margin with or without rounded median point.

Spermatheca bipartite with elongate extension/process of hollow chamber segment (see Frisch et al., 2002a: 30, figs. 22–29).

DISTRIBUTION AND HABITAT: The species of *Scopaeus* are widely distributed in temperate, subtropical, and tropical regions throughout the world but most species occur in subtropical and tropical areas and have been collected at 150 meters below sea level in Sri Lanka (label data from specimens in AMNH) to as high as 3500 meters, for *S. likovskyi*, in Afghanistan (Frisch, 2008a: 283). The genus remains unknown from arctic or subarctic regions or very high elevations.

Frisch et al. (2002a: 28), wrote that most species are found under stones, in gravel on damp sandy shores of rivers and streams that are more or less sunny, sparsely vegetated, with ground litter and other organic debris. They are not found in wet gravel that lacks vegetation or organic debris near the shoreline. Species frequently colonized narrow banks or larger banks if the conditions are appropriate. Some species live in marshy habitats such as wet meadows, bogs, and swamps and some are found in barrens, grasslands, even dry grasslands, and forest steppes.

In accordance with the observations and experience of Frisch, label data show that most specimens collected by others were found in litter at the edge of gravelly and sandy rivers, streams, and seeps. In Zimbabwe specimens were taken from marshy ground near streams, marshy turf near or separated from streams. In some instances, in Vietnam, for example, *Scopaeus* were found even when the streams were reduced to mere trickles or reduced to scattered drying pools and puddles, lined with abundant organic debris along the edges (also seen commonly by Frisch, personal commun.). Although in more moist regions increasingly fewer specimens and decreasing species diversity are probable as one moves farther from the preferred habitat of *Scopaeus* spp. along streams and rivers, in arid/semiarid regions specimens are found only near stream, lakes, and other moist areas.

However, labels for specimens collected in moist regions record specimens from deep forests in damp depressions, from under the barks of logs, in log mold, epiphytic debris, moss, humus, litter under ferns, moss near cascading streams, tree-fall and fruit-fall litter, and decaying leaves or fruit. It is possible, perhaps likely, that many of these records are the result of sifting litter and debris thereby making the actual habitat difficult to discern and Frisch (personal commun.) regards such records as atypical for *Scopaeus*. Moreover, specimen number and species diversity rapidly diminish as one moves further from streamside habitats. Species and many specimens have been collected at lights and flight intercept and malaise traps; these collections simply indicate the presence of the species and that they can fly.

Nothing is known of the feeding habits of *Scopaeus* species nor have their larval or pupal stages been described (Frisch et al., 2002a), but they probably eat smaller arthropods, and their small size suggests they may eat eggs, small immature stages, and small non-arthropods.

SYNONYMY: Historical and new. Because *Scopaeus* is so speciose and so many modifications of the infrageneric classification have been published, particularly in the past 50 years, it seems befitting to summarize the historical synonymy and discuss the newly recognized ones.

Erichson (1840: 604) described *Scopaeus* to include four European, one North African, one Nearctic, and three Neotropical species. Two of the European species, *Paederus laevigatus* Gyllenhal and *Lathrobrium minimus* Erichson, were already known.

Polyodontus Solier (1849: 310, 311), a junior homonym, was described for one, presumably Chilean species, *P. angustatus*, though no locality was cited nor was the number of specimens examined stated. Kraatz (1857: 701) combined the name with *Scopaeus*, perhaps because, according to the original description of *Polyodontus*, the "lengüeta" [tongue = labium?] is tridentate as is the ligular margin of *Scopaeus*. Whether Kraatz saw a type of *Polyodontus* is uncertain. After Kraatz moved *Polyodontus* to *Scopaeus* subsequent authors considered it to be either a synonym or subgenus. As a subgenus most of the species placed in *Polyodontus* were European or Eurasian along with one from New Zealand. The location of the type specimen(s) of *P. angustatus* is currently unclear; it was not found in Paris and a specimen labelled as "type" in Brussels is almost certainly not part of the type series. It is unknown which, if any, investigators who used *Polyodontus* for European species examined specimens of the original series (see Mulsant and Rey, 1878: 194; Ganglbauer, 1895: 529; Binaghi, 1935: 95–107; Coiffait, 1952: 8). The name was not used after 1952.

Motschulsky (1858: 641) proposed *Scoponeus* for one Asian species; without comment; Gemminger and Harold (1868: 618) synonymized the name with *Scopaeus*.

Casey (1886b: 220) named two genera. The first, *Scopaeodera*, was named for a North American species he transferred from *Echiaster*. He wrote that the genus would perhaps include some of Sharp's South American species and his "Group 4" of the Central American species, together with *S. pulchellus* Erichson. However, only *Echiaster nitidus* LeConte was an originally included in the genus because Casey's use of "perhaps" lends doubt to the inclusion of the others. *Scopaeodera* was cited previously as a junior synonym of *Scopaeus* in at least two publications and as a subgenus in others (see synonymic list for *Scopaeus*). The placement herein as a junior synonym is a revised status for the name.

The second genus, *Leptorus*, Casey (1886b: 220) included 13 North American species. Later Casey (1905: 203) revised his opinion and synonymized *Leptorus* with *Scopaeus* because his renewed scrutiny of the European species of *Scopaeus* led him to conclude he was unable to find characters of sufficient importance or consistency to separate the two faunas.

In the same publication Casey (1905: 222, 214) named two more genera for American species, *Scopaeopsis* and *Scopaeoma*. Without stated reasons, those two genera, along with *Scopaeodera*, were reduced to subgenera (Bernhauer and Schubert, 1912: 245; Blackwelder, 1939a: 100, 106) or junior synonyms (Cameron, 1931: 169) of *Scopaeus* and have been listed as subgenera by many other authors (see synonymic list for *Scopaeus*). In the present work both *Scopaeopsis* and *Scopaeoma* are revised status junior synonyms of *Scopaeus*.

Pseudorus, proposed for three American species (Casey (1910: 190) was reduced to a subgenus (Scheerpeltz, 1933: 1264), then a junior synonym (Blackwelder, 1939a: 119) of *Scopaeus*; both demotions were made without comment.

Coiffait (1952: 6; 1960: 285) described two subgenera, *Stilpon* and *Euscopaeus*, both junior homonyms, that he later replaced with *Geoscopaeus* and *Alloscopaeus* respectively (Coiffait (1960: 284; 1968: 414). Along with the replacement names Coiffait (1960: 284, 285; 1968: 426; 1984: 150) established five more subgenera for *Scopaeus*: *Heteroscopaeus*, *Hyposcopaeus*, *Anomoscopaeus*, *Asiascopaeus*, and *Hyperscopaeus*.

Jarrige (1951: 333) described a new subgenus, *Typhloscopaeus*, for one specimen of a Madagascan species. See below for details of its disposition as a name of unknown placement.

By 2001 *Scopaeus* had grown from nine species in 1840 to over 400 distributed among 12 subgenera. However, that division was massively lopsided; the vast bulk of the species remained in the nominate subgenus, rather few were assigned to other subgenera. That disparity suggested *Scopaeus* s.s., that is without the subgenera, was likely to be a paraphyletic group; although the other subgenera were separated by denoted characters, none were proposed to support definition of the nominate group. In a landmark publication (Frisch et al., 2002a) for the genus most of the Eurasian subgenera were regarded by the authors as polyphyletic and synonymized with *Scopaeus* (s.l.) and a classification of species groups, complementing those of Fagel (1973), was established. The subgenera *Geoscopaeus*, *Alloscopaeus*, *Heteroscopaeus*, *Hyposcopaeus*, *Anomoscopaeus* and later, *Asiascopaeus*, were synonymized with *Scopaeus* (Frisch et al., 2002a: 46; Frisch, 2015a: 139, 146).

Among the remaining subgenera were the American *Scopaeodera* Casey, 1886, *Scopaeoma* Casey, 1905, and *Scopaeopsis* Casey, 1905, the Madagascan *Typhloscopaeus* Jarrige, 1951, and the African, Asian, and Australian *Hyperscopaeus* Coiffait, 1984. Whether or not these names represented monophyletic groups, their valid status clearly rendered *Scopaeus* either polyphyletic, paraphyletic, or both.

Frisch steadfastly maintained in publication, correspondence, and in person that *Hyperscopaeus* should be separated from *Scopaeus* (Frisch et al., 2002a: 38, 45; personal commun.). His opinion was based on derived external, aedeagal, and spermathecal features of *Hyperscopaeus* that separated it from *Scopaeus* and the derived characters that supported the monophyly of *Scopaeus* (Frisch et al., 2002a: 38). Most of the characters used to support this contention were genitalic features of the males and females that seemed difficult to access or understand or seemed not very strong. Nonetheless, his careful work and informed opinion created a strong incentive to painstakingly study the intersection of the two groups. I feared removing *Hyperscopaeus* would render *Scopaeus* paraphyletic and so continued searching both groups for other characters that might either support or refute Frisch's hypothesis. In the end his contention was well supported, but with more accessible, new characters, and *Hyperscopaeus* is elevated to genus in the present work (see Discussion for *Hyperscopaeus* for a more complete explanation).

Typhloscopaeus was originally published as a subgenus of *Scopaeus* for one species, *Scopaeus* (*Typhloscopaeus*) *pauliani*, represented by a single female from Madagascar (Jarrige, 1951: 333). None of the characters included in the description either persuasively support its assignment to or exclude it from *Scopaeus* or the Scopaeina, so, I think there is no supportable reason for removing it or doing anything more than recognizing its indeterminate status as incertae sedis and leaving it where it is and as it was originally added to *Scopaeus* until the type can be studied. According to the description (Jarrige, 1951: 333), the unique type specimen was deposited in the Muséum National d'Histoire Naturelle, Paris. The specimen was not found by curator Azadeh Taghavian-Azari after an extensive search of the Jarrige and the general collections.

Finally, remaining are the American *Scopaeodera* Casey, 1886, *Scopaeoma* Casey, 1905, and *Scopaeopsis* Casey, 1905, described as genera and reduced to subgenera (Bernhauer and Schubert, 1912: 245; Blackwelder, 1939a: 100, 106; Newton et al., 2000: 386; Navarrete-Heredia et al., 2002: 280) or synonyms (Cameron, 1931: 169) of *Scopaeus*. Along with these three names two others recognized as genera for American species, *Scopaeomerus* Sharp (1886: 538) and *Euscopaeus* Sharp (1886: 548), are added to *Scopaeus* as species groups in the present work. Among these five groups *Euscopaeus* and *Scopaeopsis* are indistinguishable; they were never compared with each other until now. The species of *Euscopaeus-Scopaeopsis* are among the largest of *Scopaeus*, the head, pronotum, and elytra are coated with dense, fine pubescence and lack or have few macrosetae (fig. 5). The integument of the species of *Scopaeodera* is polished, the pubescence is sparse, macrosetae are notable, and the prothorax is more or less ovoid (fig. 3). *Scopaeomerus* is easily recognized by its bold form and edentate (or unidentate) labrum (figs. 1, 58, 59). None of these five groups can be separated from *Scopaeus* as herein redefined. *Euscopaeus* and *Scopaeomerus* are new synonyms of *Scopaeus*; *Scopaeodera*, *Scopaeoma*, and *Scopaeopsis* are revised status junior synonyms of *Scopaeus*; all possess a stridulum and have long, tapered metakatepisternal processes.

Even with all the species assigned to the Eurasian, African, and New World species groups, the large cluster of unassigned species remaining in *Scopaeus* represent a paraphyletic group. This paraphyly will continue so until the currently included species are studied and distributed among existing and newly proposed species groups and the species remaining in the nominate group share the same unique, derived features. When done, it might then make sense to develop a subgeneric classification.

Discussion: In 1840, a year after Erichson (1839) described *Scopaeus* without included species, he added four European, one North African, three North American, and one South American species. Since then, hundreds more have been discovered and the infrageneric groupings have multiplied. Some were described as genera and later reduced to subgenera or synonyms of *Scopaeus* while others were described as subgenera. To date 20 genus-group names have been used for species of *Scopaeus* (table 1).

Among the Eastern Hemispheric subgeneric names five were applied to the fauna of Europe, two to Asia, and two to Africa; two names are junior homonyms (see table 1 and synonymic list for *Scopaeus*). Prior to the present work all but two of the subgenera of *Scopaeus* in the Palaearctic region were reduced to synonyms and the species distributed among various species groups by Frisch. Fagel moved all the sub-Saharan species to species groups. Now most of the named, Old World species reside in species groups.

Among the genus-group names for the Western Hemisphere seven were named for North American species and one for a South American species. Three of the names were synonymized with *Scopaeus*, in the mid-19th and 20th centuries. No named species groups were proposed for the New World species.

As yet no comprehensive infrageneric classification has been proposed for *Scopaeus* nor will there be one in the present publication. Despite the former subgeneric classification of *Scopaeus* and the currently developing efforts to organize species groups, *Scopaeus* s.s. was and may still be a paraphyletic group until either an infrageneric classification has been universally applied to the genus or entirely abandoned.

INFRAGENERIC CLASSIFICATION

History and Discussion: The following extended discussion is intended to bring attention to the range of variation of some previously unexplored, external features within *Scopaeus*. It is most conveniently organized and discussed in the context of species groups and geographically by Eastern and Western hemispheres and sub-Saharan Africa. The Eurasian species groups have been well established by Frisch in numerous articles published in the last 30 years. Frisch's species groups are based largely on detailed morphology of the aedeagus and spermatheca along secondary sexual characters of the abdomen of males. The present discussion of species groups presents suggestions of external structures that might be explored henceforth. The structures highlighted are newly noted in the present work. Whether any of them will be of taxonomic or phylogenetic importance will be determined by subsequent investigators. The major drawback of this presentation of potential characters is the paucity of material available to me for study. However, these structures, as is always the case for any character, are hypotheses for examination of species and groups.

A revised infrageneric classification, which is currently an ongoing project of Frisch, is beyond the intended scope of the present work. However, the existing classification of *Scopaeus* s.l. is discussed as a summary of work to date. Except for one incertae sedis name, subgenera will no longer exist in the Old World. To place the infrageneric classification of the New World species on the same level as the preponderance of the Old World species, the subgeneric names used in the New World are replaced with species-group names. About a third of the species of *Scopaeus* remain without species-group assignments. For most of the history of the genus the infrageneric classification of *Scopaeus* has been evolving from subgenera to species groups. Until we understand the range and the depth of variation in *Scopaeus*, until all species are included in monophyletic groups, continuation and elaboration of species-group classifications seem appropriate, efficient, and fruitful.

Prior to publication of the present work 459 valid species were included in the genus. As a result of the present work, *Scopaeus* now includes 380 valid species with many others to be discovered. Most species appear to be easily separated by the intriguingly complex aedeagus and the external secondary sexual structures of the males. The females are usually difficult or impossible to identify; modest headway toward their identification has been made by Frisch using features of segment IX and the spermatheca, but still the females of many species are not easily identified or are identified by collecting-association with the male. Long ago, Frisch (1998: 90; Frisch et al., 2002a: 30) determined that the spermatheca is of little use for identifying species but may provide characters that help diagnose species groups. Attempts have been made to distribute the species into subgenera or species groups, but these classifications are regional, incomplete, and restricted to Eurasia or Africa or North America. Study of infrageneric groups between the Eastern and Western hemispheres is needed; for the Indo-Australian region and China the work is currently underway. Subgenera were rejected as polyphyletic for Eurasia by Frisch (1997–2015) and abandoned in Africa by Fagel (1973), who did so for somewhat aesthetic reasons. Both opted for a species-group classification. That initiative is supported herein, so the genus-group taxa of the Western Hemisphere are synonymized with *Scopaeus*. The classification of *Scopaeus* for Eurasia has been explored far more thoroughly and by many more investigators than for the Americas. Species of the Americas are in desperate need of study. Frisch (personal commun.) has dissected many North American species and to date expects the Nearctic and Palearctic faunas to be distinct and without any overlap of species groups. His results have not been published. The faunas for the Eastern and Western hemispheres are discussed separately.

TABLE 1

Scopaeus: Distribution of Type Species among Species Groups

Subgenus group name[1]	**Type species**[2]	***Scopaeus* sp. grp.**[3]
Eastern Hemisphere		
Scopaeus	*Paederus laevigatus*	*laevigatus* grp.
Scoponeus	*Scoponeus testaceus*	*laevigatus* grp.
Geoscopaeus[4]	*Scopaeus baudrimonti*	*ryei* grp.
Stilpon[4]	*Scopaeus baudrimonti*	*ryei* grp.
Alloscopaeus[5]	*Scopaeus didymus*	*minutus* grp.
Euscopaeus[5]	*Scopaeus didymus*	*minutus* grp.
Heteroscopaeus	*Scopaeus sericans*	*sericans* grp.
Anomoscopaeus	*Xantholinus gracilis*	*gracilis* grp.
Hyposcopaeus	*Scopaeus scitulus*	*debilis* grp.
Asiascopaeus	*Scopaeus asiaticus*	*obscuripes* grp.
Typhloscopaeus[6]	*Scopaeus pauliani*	(Incertae sedis)
Hyperscopaeus[7]	*Scopaeus spathiferus*	(Elevated)
Western Hemisphere		
Polyodontus	*Polyodontus angustatus*	(sp. incert. sed.)
Euscopaeus	*Euscopaeus crassitarsis*	*opacus* grp
Scopaeomerus	*Scopaeomerus chiriquensis*	*chiriquensis* grp
Leptorus[8]	*Scopaeus exiguus*	= *Scopaeus* (s.l.)
Scopaeodera	*Echiaster nitidus*	*nitidus* grp
Scopaeoma	*Scopaeus rotundiceps*	*rotundiceps* grp
Scopaeopsis	*Echiaster opacus*	*opacus* grp
Pseudorus[9]	*Scopaeus prolixipennis*	= *Scopaeus* (s.l.)
__________[10]	*Scopaeus nevermanni*[11]	*nevermanni* grp
__________[10]	______________________[12]	*reticulate* grp

[1] For author and date of each genus-group name, see synonymic list at beginning of account for *Scopaeus*. Names listed chronologically for the two geographical groupings.

[2] For author and date of each species group name, see "Species included and material examined" at end of account for *Scopaeus*.

[3] Species groups assignments according to Frisch et al., 2002a: 37.

[4] *Stilpon*, junior homonym, replaced by *Geoscopaeus*.

[5] *Euscopaeus*, junior homonym, replaced by *Alloscopaeus*.

[6] Genus incertae sedis; see "Synonymy" in account for *Scopaeus*.

[7] Elevated in present work.

[8] Name synonymized with *Scopaeus* (s.s.) by Casey (1905).

[9] Name synonymized with *Scopaeus* (s.s.) by Blackwelder (1939).

[10] No subgenus name proposed.

[11] An included species, not a type species

[12] No known named species included.

Eastern Hemisphere Species Groups

To this writing 35 African and Eurasian species groups have been proposed and characterized; some groups extend into the South Asian, Indonesian, and Australian regions. Following is a list of the groups along with brief comments for each.

Eurasian Species Groups

The species groups discussed in this section are primarily Eurasian, but a few groups include some African species.

Perhaps the first among various attempts to segregate groups of species in *Scopaeus* was by Fauvel (1873a: 308, 311), who, based on the shape of the head and a few other external features, placed 10 French species in two groups, group 1 "*Scopaeus*" and group 2 "*Polyodontus*," each with five species. Group 2 referred to Solier's *Polyodontus*, a genus based on a species from the other side of the globe in Chile. Other Europeans, but not all, used the same system (see, for example, Mulsant and Rey, 1878: 182, 194; Ganglbauer, 1895: 526; Reitter, 1909: 148; Binaghi, 1935; Tottenham, 1949: 368, 415; Coiffait, 1952: 8; among others).

Once *Polyodontus* Solier, 1849, was revealed to be a junior homonym of Eysenhardt, 1818 (Blackwelder, 1952: 318), its use abruptly ended, but there's been no discussion about the disposition of the species that had been assigned to it by Binaghi, Coiffait, and others. The most complete list of the species included in *Polyodontus* is by Binaghi (1935: 95–107), the most recent by Coiffait (1952: 5–8). Coiffait (1984) assigned the 20 names in Binaghi's list to five subgenera, one of which is now a genus; the 14 names in Coiffait, 1952, were assigned to four subgenera. In Frisch's classification the species formerly assigned to *Polyodontus* are distributed among six species groups of *Scopaeus* and another genus (see table 2). Unsurprisingly, according to those assignments *Polyodontus* Solier is not only a junior homonym but was also a polyphyletic group as constructed in Europe. Remaining is the type species, *P. angustatus*, which has not been assigned to either the nominate or any other species group. Its assignment will depend on accurate identification or examination of the type specimens, if they are found. Cameron (1950: 23) described *S.* (*Polyodontus*) *apterus* from New Zealand; Frisch (2016: 60) redescribed and reassigned it to the nominate subgenus of *Scopaeus*. *Polyodontus* is revisited in the section concerning the species groups of the Western Hemisphere.

Beginning in the mid-1990s and continuing to the present writing, Frisch has been intensely exploring the infrageneric classification of *Scopaeus* of the Eastern Hemisphere and the identity, distribution, and phylogeny of its species. Initially Frisch included species in subgenera (1994) or used no infrageneric classification (1996, 1997a, 1997b, 1998). Later he (Frisch, 1997a: 524) wrote that the subgenera would no longer be used because those in current use were not monophyletic and in 1999 he began carefully developing a species-group classification. Since beginning his work, in a series of elegantly executed publications, Frisch has synonymized all but two of the subgenera of the Eastern Hemisphere, assigned 155 species, about 40% of the known species, to 16 species groups, described 90 new species, synonymized 53 nominal species, and proposed hypotheses of phylogenetic placements among and within the species groups. The species of these groups are distributed across the Palaearctic region. The type species of the synonymized Eurasian subgenera are distributed among seven of his species groups (table 1). Remaining to be studied are other Eurasian species as well as those from China, India, Southeast Asia, the Indo-Australia region, New Zealand, and the Pacific region. Frisch (2016) revised the known species for Australia and New Zealand; he described no new species nor recognized any species groups. Currently Frisch (personal commun.) is revising the known species and describing new species of the Scopaeus of Indonesia and adjacent Southeast Asia but said he will propose no additional species groups for now. The Afri-

TABLE 2

Current Assignment of Eurasian Species Formerly Included in *Polyodontus*

Species	Genus group[6]	Assignment[7]
ampliatus[1]	*Hyposcopaeus*	*S. sulcicollis* grp.
anxius[2]	not included	*S. longicollis* grp.
bordei[1, 8]	*incertae sedis*	*S. ryei* grp.
brevicuspis[1, 2]	*Hyposcopaeus*	*S. ryei* grp.
chalcodactylus[4]	not included	*S. minutus* grp.
championi[1]	*Alloscopaeus*	*S. minutus* grp.
cognatus[1, 2, 9]	*Scopaeus* (s.s.)	*S. sulcicollis* grp.
cordifer[1, 10]	*Scopaeus* (s.s.)	*S. longicollis* grp.
didymus[1, 2]	*Alloscopaeus*	*S. minutus* grp.
furcatus[1, 11]	*Hyposcopaeus*	*S. minimus* grp.
gladifer[1]	*Alloscopaeus*	*S. minutus* grp.
gracilipes[3, 12]	*Alloscopaeus*	*S. minutus* grp.
hispanicus[1]	*Alloscopaeus*	*S. longicollis* grp.
ibericus[2, 13]	*Alloscopaeus*	*S. debilis* grp.
lanceolatus[1, 2]	*Alloscopaeus*	*S. minutus* grp.
laneyriei[2, 8]	*Hyposcopaeus*	*S. ryei* grp.
littoralis[5]	*Hyposcopaeus*	*S. ryei* grp.
microphthalmus[1]	*Microscopaeus*	*Micranops*
micropterus[1, 2]	*Alloscopaeus*	*S. minutus* grp.
minimus[1, 2, 3]	*Hyposcopaeus*	*S. minimus* grp.
minutus[1, 2, 3]	*Alloscopaeus*	*S. minutus* grp.
mitratus[1]	*Alloscopaeus*	*S. minutus* grp.
pilicornis[1]	not included	*Micranops*
portai[1, 2]	*Hyposcopaeus*	*S. ryei* grp.
pusillus[1, 2, 3]	*Alloscopaeus*	*S. minutus* grp.
rubidus[1, 2]	*Anomoscopaeus*	*S. sulcicollis* grp.
ryei[2]	*Hyposcopaeus*	*S. ryei* grp.
sulcicollis[3]	*Scopaeus* (s.s.)	*S. sulcicollis* grp.
temperei[3, 8]	*Hyposcopaeus*	*S. ryei* grp.

[1] Name from Binaghi (1935).
[2] Name from Tottenham (1949).
[3] Name from Coiffait (1952).
[4] Name from Ganglbauer (1895).
[5] Name from Ochs (1958: 276).
[6] Genus group assignment by Coiffait, 1984.
[7] Species groups assignments from Frisch (1999--2015) and summarized in Discussion for *Scopaeus*.
[8] Junior synonym of *S. portai* Luze.
[9] Junior synonym of *S. sulcicollis* (Stephens).
[10] Junior synonym of *S. proculus* Normand.
[11] Junior synonym of *S. minimus* (Erichson).
[12] Junior synonym of *S. minutus* Erichson.
[13] Junior synonym of *S. debilis* Hochhuth.

can and Eurasian species groups require integration. Doubtless many more species will be discovered. The two subgenera of the Eastern Hemisphere that Frisch did not synonymize, *Hyperscopaeus* and *Typhloscopaeus*, are discussed above in the section on synonyms; in the present work the former is elevated, the latter is incertae sedis.

Frisch's classification is scattered among dozens of articles. To access his species groups, their definitions, and compositions more efficiently, the following is a short summary of each group and an index, by species group, to his publications to 2016. For every group a list of the species included to date is provided along with a general statement of each group's distribution extracted from an unpublished catalog of the subfamily. Frisch defined the groups by detailed characters of the aedeagus and spermatheca and some external characters. To understand these complex genitalic characters careful explanation and precise illustrations are required; these are published in the articles that define the groups. Rather than attempt to summarize herein those characters and furnish the images necessary to understand them, the reader is provided with citations to the previously published descriptions and figures for each group.

For most of the Eurasian species groups, a few heretofore-unused characters are included in a paragraph of Additional characters; for several groups some characters were not included for want of specimens for dissection. The account of each species group includes a paragraph headed by the words "Additional characters," which begins with the name, if known, and includes the sex and country of origin of the specimen examined. For all the species groups discussed in this section, the only specimens listed as examined are those dissected for detailed study and illustration; the descriptions are based on only those dissected specimens. The additional characters are hypotheses for further study. Reference may be made to additional specimens, but that are not included among the specimens dissected or included as examined.

The additional characters are suggestions for exploration, they are not proposed as definitive supporting features of the group. The structures are presented as hypotheses to support the grouping of species and are intended to be refuted or found useful for defining groups.

The species groups are presented alphabetically rather than phylogenetically.

The ***S. debilis* group** includes five species (*S. debilis*, *S. filiformis*, *S. madagascarensis*, *S. mendosus*, *S. udus*). The type species of *Hyposcopaeus*, *S. scitulus* resides in this species group as a junior synonym of *S. debilis*.

The group was first recognized by Fagel (1973: 38), who used *S. tenuis*, a junior synonym of *S. filiformis*, to name the group. Frisch (1999a: 362) replaced *S. tenuis* with the better-known, valid species *S. debilis*. The group was defined by Fagel (1973: 38) and Frisch (1999a: 363; Frisch et al., 2002a: 39). The group is widespread, occurring in western, central, eastern, and southern Europe through southwestern Asia, including the Arabian Peninsula, through central, southern, and eastern Asia, including East Siberia (Frisch, 2010: 162) to Japan and from North Africa through most of the countries of Africa to South Africa and in Madagascar.

ADDITIONAL CHARACTERS: *S. filiformis* (figs. 25, 89–94; one female: Kenya); *S. debilis* (fig. 24; one female: Spain).

Head without tentorial depression. Corneal lenses (figs. 24, 25) without sensilla or wrinkles and with (fig. 25) or without median tumescence.

Mesoventrite (fig. 93) covered with microsculpturing, midapical surface with moderately developed sculpturing; apical vertical portion of basisternum with moderately developed microsculpturing; prepectal ridge separated medially; mesanapleural ridge with anterior segment present, posterior segment absent; mesotransventral ridge present and broadly curved; median depression present and without pores; mesofurcasternum without median apophysis on posterior margin.

Mesofemoral plectral ridges (seven in fig. 92) straight and just above middle of femoral base.

Pericoxal ridge (figs. 89, 90) present near anterolateral margin of mesocoxal cavity; ridge short.

Metaventral submarginal ridge (fig. 89) slightly enlarged mesially near middle and parallel to metaventral dorsal margin anteriorly and converging posteriorly.

Stridular file straight, contiguous with submarginal ridge (fig. 90).

Metakatepisternal process moderately long and acute apically (*S. debilis; S. udus*) or about as wide as long and apical margin directed diagonally to meet mesial margin (*S. filiformis*, fig. 89, 94).

Sternite II without median point on posterior margin (fig. 91).

Sternite III (fig. 91) broadly rounded midlongitudinally; intercoxal carina evident only as small point at middle of transverse basal ridge; transverse basal ridge moderately sinuate.

Sternite IV not examined.

The ***S. elegans*** **group** includes 35 species (*S. alborzensis*, *S. anlasi*, *S. assingi*, *S. bilaminulatus*, *S. bituberculatus*, *S. borumandi*, *S. cameroni*, *S. cariensis*, *S. creticus*, *S. cyprius*, *S. efesi*, *S. elegans*, *S. fagelianus*, *S. femursetosus*, *S. graecus*, *S. haemusensis*, *S. heinzi*, *S. hercegovinensis*, *S. iranensis*, *S. kermanensis*, *S. korelli*, *S. korgei*, *S. kurdistanicoides*, *S. kurdistanus*, *S. mariae*, *S. menteshensis*, *S. persicus*, *S. puthzi*, *S. qohrudensis*, *S. schillhammeri*, *S. serriae*, *S. tauricus*, *S. trifurcatus*, *S. ulughdaghensis*, *S. zagrosensis*).

This was Frisch's first formally established and defined group (1994: 4). Further definition, discussion, biogeographic consideration, and additional species were published (Frisch, 1997b, 1999d; 2002; 2006a; 2006b; 2008b; 2010; Frisch and Wolters, 1999; Frisch et al., 2002a: 37, 41; Anlaş and Frisch, 2014). The group occurs in southwestern Asia and southeastern Europe in the vicinity of the Caspian, Black, and Mediterranean seas.

Additional characters: *S. cameroni* (figs. 26, 101–106; one female: Iran); *S. persicus* (figs. 27, 107, 108; one female: Iran).

Head without tentorial depression. Corneal lens without sensilla and with or without slight wrinkles (figs. 26, 27, 108).

Mesoventrite (fig. 103) covered with microsculpturing, slightly less strong medially; apical vertical portion of basisternum with well-developed microsculpturing; prepectal ridge separated medially; mesanapleural ridge with anterior segment present, posterior segment absent; mesotransventral ridge present and strongly curved medially; median depression without pores; mesofurcasternum without median apophysis on posterior margin.

Mesofemoral plectral ridges (about eight in figs. 106, 107) slightly curved, and near dorsal edge of femur.

Pericoxal ridge (figs. 101, 104, 105) long and present at anterolateral margin of mesocoxal cavity and extending posteromedially.

Metaventral submarginal ridge (figs. 101, 104) more or less straight basally, convergent with dorsal margin posteriorly.

Stridular file (figs. 101, 104, 105) straight and contiguous with submarginal ridge.

Metakatepisternal process (figs. 101, 104) longer than wide, slender, tapered, and apically acute.

Sternite II with median point on posterior margin.

Sternite III with acute intercoxal carina; transverse basal ridge bisinuate and with median point.

Sternite IV not examined.

The ***S. gracilis*** **group** includes 10 species (*S. asirensis*, *S. flavofasciatus*, *S. gracilis*, *S. longicornis*, *S. meridioafricanus*, *S. pakistanensis*, *S. poggii*, *S. siculus*, *S. socotrensis*, *S. stramineus*). *Scopaeus gracilis* is the type species of *Anomoscopaeus*. (Definition and composition: Frisch et al., 2002a: 37; Frisch, 2007a; 2015b.)

Frisch (1998: 95) published the first characters for the *S. gracilis* species group in a discussion of *S. siculus*, expanded the definition (Frisch et al., 2002a: 39), then revised it in a review of the group (Frisch, 2007a: 196). The review also resulted in a new composition of the group. Not only was a new subgroup clade with five species added, but two species, *S. crassipes* and *S. sinaicus*, that had been included in 2002 were eliminated, but not assigned to another species group. Frisch (personal commun.) intends to return the two species to a subgroup of the *S. gracilis* group. The group occurs in the Canary Islands, North Africa, western, southern, central, and southeastern Europe across Syria, Turkey, the Caucasus, Iran, Pakistan, the Arabian Peninsula, Madagascar, and southern and southwestern Africa. In yet to be published work, Frisch told me (personal commun.) that this species group is huge, that he will redefine it, describe many new species, add more previously described species, and report the group to occur widely in Africa, Asia, and the southeastern Palaearctic regions.

Additional characters: *S. gracilis* (figs. 28, 109–112; one female: Germany).

Head without tentorial depression.

Corneal lenses (fig. 28) without sensilla or wrinkles.

Mesoventrite (fig. 109) with most of surface covered by microsculpturing, weakly covered to absent midposteriorly; apical vertical portion of basisternum with moderately developed microsculpturing; prepectal ridge separated medially; mesanapleural ridge partially developed to absent; mesotransventral ridge present; median depression without pores; mesofurcasternum without median apophysis on posterior margin.

Mesofemoral plectral ridges (about nine in fig. 112) nearly straight, and nearer to dorsal femoral margin.

Pericoxal ridge (fig. 110) present near anterolateral margin of mesocoxal cavity and moderately long.

Metaventral submarginal (fig. 110) ridge more or less straight and parallel to metaventral dorsal margin basally and medially, then convergent posteriorly. Stridular file (fig. 111) contiguous with submarginal ridge.

Metakatepisternal process (fig. 110) longer than wide, slender, tapered, and apically acute.

Sternite II with small median point.

Sternite III with weakly developed median carina; transverse basal ridge shallowly curved medially and without median point.

Sternite IV apparently with median glandular(?) depression.

The ***S. laevigatus* group** includes 22 species (*S. azerbaidzhanus*, *S. biskrensis*, *S. ebneri*, *S. hermani*, *S. laevigatus*, *S. muehlei*, *S. naomii*, *S. nipponensis*, *S. nitidulus*, *S. philippinensis*, *S. schuelkei*, *S. subfasciatus*, *S. sumbaensis* (= *S. ivani*), *S. tahitiensis*, *S. testaceipes*, *S. testaceus*, *S. trapeziceps*, *S. unifasciatus*, *S. viriliformis*, *S. virilis*, *S. viriloides*, *S. wunderlei*; Frisch et al. 2002a: 37; Frisch, 2003; Frisch, 2016). The type species for *Scopaeus* s.s., *S. laevigatus*, and *Scoponeus*, *S. testaceus*, are included in this group. (Definition: Frisch et al., 2002a: 38–39; Frisch, 2003: 651; 2016: 79.)

The group, proposed in 2002, was revised in detail in 2003. In that revision the group was divided into three subgroups, 10 new species were described, and 10 names were seen as junior synonyms. Most of the species are scattered from the western edge of Europe across Asia to Japan, Korea, and including India, peninsular Malaysia, Indonesia, the Philippines, and Polynesia to Australia. One species, *S. subfasciatus*, is found across southern and southwestern Asia, the Arabian Peninsula, and is widespread from northern to southern Africa.

Additional characters: *S. laevigatus* (figs. 29, 113–118; one female: Bulgaria; two males: France, Austria; *S. subfasciatus* (figs. 119–123; one female: Kenya).

Head without tentorial depression.

Corneal lenses (figs. 29) without sensilla, surface wrinkled; dorsal rows more strongly wrinkled than those farther away.

Mesoventrite (figs. 114, 122) with microsculpturing on most of basal two thirds, mesanepisternum and apical mesobasisternum without microsculpturing; apical vertical portion of basisternum with feebly to moderately developed microsculpturing; prepectal ridge separated medially; mesanapleural ridge absent; mesotransventral ridge present and moderately strongly curved (fig. 114) or absent (fig. 122); median depression without pores; mesofurcasternum without median apophysis on posterior margin.

Mesofemoral plectral ridges (about four and nine in figs. 113, 121) strongly curved, and near dorsal femoral margin.

Pericoxal ridge (fig. 119) short and present at anterolateral margin of mesocoxal cavity.

Metaventral submarginal ridge enlarged at about basal third (fig. 119) or half (fig. 114), then convergent posteriorly with metaventral dorsal margin.

Stridular file strongly curved medially, contiguous with submarginal ridge basally and slightly separated apically (figs. 114, 115) or nearly contiguous with submarginal ridge basally then gradually and increasingly separated posteriorly (fig. 119).

Metakatepisternal process (figs. 114, 119) longer than wide, tapered apically, and with acute apex.

Sternite II with median point on posterior margin (figs. 116).

Sternite III with moderately developed intercoxal carina (fig. 116); transverse basal ridge strongly sinuate and with long moderately long intercoxal carina.

Sternite IV with tiny (figs. 117, 118) to large (fig. 123) midbasal pore.

The ***S. limbatus* group** includes 14 species: (*S. australiensis*, *S. baliensis*, *S. ceylonensis*, *S. fulvus*, *S. gustavkraatzi*, *S. indiensis*, *S. janaki*, *S. limbatus*, *S. sarawakensis*, *S. siamensis*, *S. solomonensis*, *S. sundaensis*, *S. vietnamensis*, *S. weigeli*). (Definition: Frisch, 2005: 74, provided a detailed description of the group.)

The group is widespread from the Seychelles and Mascarenes across southern Asia to as far north as Afghanistan, Nepal, Bhutan, to India, Sri Lanka, peninsular Malaysia, Indonesia, New Guinea, northern Australia to the Solomon Islands, French Polynesia, through the southeastern third of China to Taiwan and Japan. *Scopaeus limbatus* occupies most of this range. So far, the *limbatus* group is represented in Australia by only *S. australiensis*.

ADDITIONAL CHARACTERS: *S. limbatus* group (figs. 30, 124–130; one unidentified female: India).

Head without tentorial depression.

Corneal lenses without sensilla, lenses adjacent to dorsal margin slightly wrinkled (fig. 30).

Mesoventrite (fig. 124) covered with microsculpturing, absent from midapical mesobasisternum; apical vertical portion of basisternum with microsculpturing; prepectal ridge separated medially; mesanapleural ridge partially present anteriorly, posterior portion absent; mesotransventral ridge present; median depression without pores; mesofurcasternum without median apophysis on posterior margin.

Mesofemoral plectral ridges (about eight in fig. 127) moderately curved, and near dorsal margin of femur.

Pericoxal ridge (fig. 125) moderately long on anterolateral margin of mesocoxal cavity; ridge long.

Metaventral submarginal ridge (fig. 125) slightly enlarged near middle, posteriorly convergent with metaventral dorsal margin.

Stridular file (fig. 125, 126) contiguous with submarginal ridge.

Metakatepisternal process (fig. 125) longer than wide, tapered, and apically acute.

Sternite II (fig. 128) without median point on posterior margin.

Sternite III (fig. 128) with intercoxal carina poorly developed, mostly reduced to acute median point extending from transverse basal ridge.

Sternite IV (figs. 129, 130) with round glandular(?) depression; pore absent.

The ***S. longicollis* group** includes seven species: *S. anxius*, *S. bertiae*, *S. franzi*, *S. hispanicus*, *S. kovaci*, *S. longicollis*, *S. proculus* (Frisch et al., 2002a: 37). (Definition: Frisch, 1999e: 164; Frisch et al., 2002a: 40.)

The group lives in North Africa, the Iberian Peninsula into France, Germany, Switzerland, and Italy.

ADDITIONAL CHARACTERS: *S. longicollis* group; some characters not included for lack of specimens (figs. 31, 131–133; one unidentified female: Spain).

Head without tentorial depression.

Corneal lenses (fig. 31) smooth, without sensilla or wrinkles.

Mesoventrite not examined.

Mesofemoral plectral ridges (about nine in fig. 132) moderately curved, and near dorsal margin of femur.

Pericoxal ridge (fig. 131) moderately long and present at anterolateral margin of mesocoxal cavity.

Metaventral submarginal ridge (figs. 131, 133) moderately enlarged near middle then narrowed and convergent with metaventral dorsal margin.

Stridular file (figs. 131, 133) contiguous with submarginal ridge, curved slightly medially near subapex, then laterally at apex.

Metaketepisternum (fig. 131) moderately longer than wide, tapered, and apically acute (apex damaged in image).

Sternites III and IV not examined.

The ***S. minimus*** **group** includes only two species (*S. minimus*, *S. palaestinus*; Frisch et al., 2002a: 37). (Definition: Frisch, 1998: 101; Frisch et al., 2002a: 40.)

The group is widespread in central, southeastern, and southern Europe to Israel, Turkey, Iran, and southwestern Russia. Frisch (2010: 196) published comments on the habitat and distribution of *S. minimus*. He cited the species in the *S. minimus* group, but accidentally included in the group three species he had previously assigned to the *S. ryei* species group (Frisch, personal commun.); both the *minimus* and *ryei* groups are treated here separately as he originally published them.

Additional characters: *S. minimus* (figs. 134–140; one male: Austria).

Head without tentorial depression.

Corneal lenses not examined.

Mesoventrite (fig. 136) with microsculpturing basally and laterally, absent from midapical region of mesobasisternum; apical vertical portion of basisternum with microsculpturing; prepectal ridge separated medially; mesanapleural ridge with anterior segment present, posterior segment absent; mesotransventral ridge present, strongly curved medially; median depression without pores; mesofurcasternum without median apophysis on posterior margin.

Mesofemoral plectral ridges (about nine in fig. 139) slightly curved, and approximately equidistant from dorsal and ventral femoral margins.

Pericoxal ridge (figs. 137, 138) beginning at anterolateral margin of mesocoxal cavity; ridge long.

Metaventral submarginal ridge (fig. 137) more or less straight, posteriorly convergent with metaventral dorsal margin. Stridular file straight, contiguous with submarginal ridge (figs. 137, 138).

Metakatepisternal process longer than wide, tapered, and apically acute (fig. 137).

Sternite II with median point extending from posterior margin (fig. 140).

Sternite III (fig. 140) with short, well-developed intercoxal ridge; transverse basal ridge moderately sinuate with median point.

Sternite IV with moderately large semicircular depression and tiny pore (figs. 134, 135).

The ***S. minutus*** **group** includes 19 species (*S. alaschiacus*, *S. binaghii*, *S. chalcodactylus*, *S. championi*, *S. didymus*, *S. fageli*, *S. farsensis*, *S. gladifer*, *S. hyrcanus*, *S. lanceolatus*, *S. loebli*, *S. micropterus*, *S. minutoides*, *S. minutus*, *S. mitratus*, *S. perroti*, *S. pusilloides*, *S. pusillus*, *S. subopacus*; Frisch et al., 2002a: 37; Frisch, 2006c: 269; Frisch, 2007b). The type species, *S. didymus*, of *Euscopaeus* Coiffait and its replacement name, *Alloscopaeus*, are part of this group. (Definition: Frisch et al., 2002a: 40; Frisch, 2007a: 196.)

The group is widespread in most parts of Europe, Russia, Turkey, the Caucasus, Iran, and North Africa. Two species, *S. minutus* and *S. pusillus*, have wide, overlapping distributions in Europe and Russia; the former has been introduced to Quebec and Ontario, Canada, and although not so reported, the species may have entered the United States. The others have more limited distributions.

Additional characters: *S. chalcodactylus* (fig. 32; one female: Azerbaijan; *S. pusillus* (figs. 141–145; one female: Russia).

Head without tentorial depression.

Corneal lenses without sensilla or wrinkles (figs. 32).

Mesoventrite (fig. 141) with strong microsculpturing, weaker at median depression; apical vertical portion of basisternum with microsculpturing; prepectal ridge separated medially; mesanapleural ridge with anterior segment present, posterior segment absent; mesotransventral ridge present and strongly curved medially; median depression without pores; mesofurcasternum without median apophysis on posterior margin.

Mesofemoral plectral ridges (about 10 in fig. 144) slightly curved proximally, and straight distally; ridges equidistant between dorsal and ventral femoral margins.

Pericoxal ridge (fig. 142) present at anterolateral margin of mesocoxal cavity, ridge moderately long.

Metaventral submarginal ridge (fig. 142) more or less parallel to metaventral dorsal margin basally, convergent with margin posteriorly. Stridular file (figs. 142, 143) contiguous with submarginal ridge.

Metakatepisternal process (fig. 142) longer than wide, tapered, apically acute.

Sternite II (fig. 145) with median point extending from posterior margin.

Sternite III (fig. 145) with moderately developed intercoxal carina, posterior end reduced to median point extending from transverse basal ridge.

Sternite IV not examined.

The ***S. mutatus* group** includes six species (*S. alaniensis*, *S. gusarovi*, *S. imbecillus*, *S. khnzoriani*, *S. meridioanatolicus*, *S. mutatus*; Frisch et al., 2002a: 37). (Definition: Frisch et al., 2002a: 38; Frisch, 2009: 272.)

Frisch et al. (2002a: 37) included three species. A more complete description was published (Frisch, 2009), and four more species were added, three of which were new species, and one was synonymized. The group is found across Turkey, the Caucasus (including southwestern Russia), Syria, Iran into Turkmenistan.

ADDITIONAL CHARACTERS: *S. mutatus* group (figs. 33, 146–153; one unidentified female: Iran).

Head without tentorial depression.

Corneal lenses without sensilla, lenses along dorsal margin with feeble wrinkles (figs. 33).

Mesoventrite (fig. 148) with strong microsculpturing basally and laterally, weaker midapically; apical vertical portion of basisternum with microsculpturing; prepectal ridge separated medially; mesanapleural ridge with anterior segment partially present, posterior segment absent; mesotransventral ridge present; median depression without pores; mesofurcasternum without median apophysis on posterior margin.

Mesofemoral plectral ridges (about nine in fig. 146) nearly straight, and on midbase nearer to dorsal than to ventral femoral margin.

Pericoxal ridge (figs. 149, 150) present on lateral margin of mesocoxal cavity; ridge long, extending to midventral region, but well separated medially.

Metaventral submarginal ridge (fig. 149) slightly enlarged just past middle then convergent to dorsal margin.

Stridular file (figs. 149–151) straight, contiguous with submarginal ridge.

Metakatepisternal process (fig. 149) longer than wide, tapered, and apically acute.

Sternite II (fig. 147) without median point extending from posterior margin.

Sternite III with low, barely discernible intercoxal carina (fig. 147); transverse basal ridge sinuate and without median point remnant of median carina.

Sternite IV (figs. 152, 153) with oval, median, basal depression and with tiny pore between depression and anterior margin.

The ***S. obscuripes* group** includes 11 species (*S. apiculatus*, *S. asiaticus*, *S. caspius*, *S. chatkalensis*, *S. kabakovi*, *S. klapperichi*, *S. likovskyi*, *S. milkoi*, *S. moriturus*, *S. obscuripes*, *S. schawalleri*). The type species of *Asiascopaeus*, *S. asiaticus*, is assigned to the group. (Definition and composition: Frisch, 1999b: 47; 2008a; 2015a: 139.)

The species are from the Caucasus, northern India and Pakistan, Afghanistan, and central Asia.

ADDITIONAL CHARACTERS: *S. likovskyi* (figs. 36, 171–174; one female: Kyrgyzstan).

Head without tentorial depression.

Corneal lenses (fig. 36) without sensilla or wrinkles.

Mesoventrite (fig. 174) with strong microsculpturing, weaker in vicinity of median depression; apical vertical portion of basisternum with microsculpturing; prepectal ridge separated medially; mesanapleural ridge with anterior segment present, posterior segment absent; mesotransventral ridge present; median depression without pores; mesofurcasternum without median apophysis on posterior margin.

Mesofemoral plectral ridges (about six in fig. 171) slightly curved, and on midbasal surface closer to dorsal femoral margin than to ventral margin.

Pericoxal ridge (fig. 172) present at anterolateral margin; ridge moderately long.

Metaventral submarginal ridge (fig. 172) straight basally and convergent posteriorly with metaventral dorsal margin.

Stridular file (figs. 172, 173) straight, contiguous with submarginal ridge.

Metakatepisternal process (fig. 172) longer than wide, tapered, and apically acute. Sternites II, III, and IV not examined.

The ***S. paliferus* group** includes two species (*S. chinensis*, *S. paliferus*). (Definition: Frisch, 2011: 362.)

The group is known from eastern Siberia, eastern China to Japan. No specimens were available for study and dissection.

The ***S. ryei* group** comprises four species (*S. brevicuspis*, *S. littoralis*, *S. portai*, *S. ryei*). The type species of *Stilpon* and its replacement name, *Geoscopaeus*, is *S. baudrimonti*; it is included in this species group as a junior synonym of *S. ryei*. (Definition and composition: Frisch et al., 2002a: 37, 40.)

Fagel (1973: 18–37) cited the correct type species for *Geoscopaeus* when he added 12 species to the group. However, that type species is a member of *Scopaeus*, whereas the species Fagel added belong in *Micranops* and were transferred (Frisch and Herman, 2014; see the discussion in the account for *Micranops*). The species of the *S. ryei* group are found in Europe and North Africa. *Scopaeus ryei* occurs in central and southeastern Europe; the others are in more southern and western European locales and two of them also occur in North Africa. Frisch (2010: 196) accidently listed three species of this group, *S. brevicuspis*, *S. portai*, and *S. ryei*, in the *S. minimus* group (Frisch, personal commun.).

ADDITIONAL CHARACTERS: *S. ryei* group (figs. 42, 211–216; one unidentified female: Italy).

Head without tentorial depression.

Corneal lenses (fig. 42) without sensilla or wrinkles.

Mesoventrite (fig. 211) with strong microsculpturing except near and in median depression; apical vertical portion of basisternum with microsculpturing; prepectal ridge separated medially; mesanapleural ridge with anterior segment partially developed, posterior segment absent; mesotransventral ridge present; median depression without pores; mesofurcasternum without median apophysis on posterior margin.

Mesofemoral plectral ridges (about nine fig. 212) moderately curved, and nearer dorsal femoral margin than ventral.

Pericoxal ridge (fig. 213) short and present at anterolateral margin of mesocoxal cavity.

Metaventral submarginal ridge straight (fig. 213). Stridular file (figs. 213, 214) straight, contiguous with submarginal ridge.

Metakatepisternal processes longer than wide, tapered, apically acute.

Sternite II (fig. 215) with median point on posterior margin; median carina distinct.

Sternite III (fig. 215) with moderately developed intercoxal carina; transverse basal ridge moderately sinuate and with median point.

Sternite IV (fig. 216) with moderately large median depression; pore absent.

The ***S. sericans* group** has five species (*S. cylindricus*, *S. kastcheevi*, *S. sareptanus*, *S. sericans*, *S. turkestanicus*). The type species of *Heteroscopaeus*, *S. sericans*, is included here. (Definition and composition: Frisch et al., 2002a: 37, 40; Frisch, 2012a: 278.)

A more thorough description of the group was published by Frisch (2012a) along with the addition of two species. The group is known from western, central, and into eastern Europe, western Russia, and central Asia.

Additional characters: *S. sericans* group (figs. 43, 217–221; one unidentified female: Kazakhstan).

Head without tentorial depression.

Corneal lenses (fig. 43) without sensilla or wrinkles.

Mesoventrite (fig. 217) with strong microsculpturing, but weak midapically in and near median depression; apical vertical portion of basisternum with microsculpturing; prepectal ridge separated medially; mesanapleural ridge with incomplete anterior segment and posterior segment absent; mesotransventral ridge present and strongly curved; median depression without pores; mesofurcasternum without median apophysis on posterior margin.

Mesofemoral plectral ridges (about nine in fig. 218) moderately to more strongly curved just above middle of femoral base.

Pericoxal ridge (figs. 219, 220) present at anterolateral margin of mesocoxal cavity; ridge moderately long.

Metaventral submarginal ridge (fig. 219) more or less straight, slightly enlarged just distad of middle, then converging to dorsal margin.

Stridular file (figs. 219, 220) straight and contiguous with submarginal ridge.

Metakatepisternal process (fig. 219) longer than wide, tapered, and apically acute.

Sternite II (fig. 221) with median point on posterior margin.

Sternite III (fig. 221) with intercoxal carina; transverse basal ridge with median point and strongly sinuate.

Sternite IV not examined with SEM.

The ***S. signifer* group** has three species (*S. bicolor*, *S. galinae*, *S. signifer*). (Definition: Frisch, 1997a: 539; Frisch et al., 2002a: 37, 39.)

Frisch proposed the group for two species in 1997, a third, *S. bicolor*, was added in 2002. The group is spread throughout south-central and southeastern Europe and North Africa across Israel, Turkey, Iraq, and Iran to central Asia.

Additional characters: *S. bicolor* (figs. 44, 222–225; one female: Bulgaria).

Head without tentorial depression.

Corneal lenses (fig. 44) without sensilla or wrinkles.

Mesoventrite (fig. 222) with strong microsculpturing anteriorly and laterally, weaker or absent across apical third; apical vertical portion of basisternum with microsculpturing; prepectal ridge separated medially; mesanapleural ridge with anterior segment present, posterior segment absent; mesotransventral ridge present and strongly curved; median depression without pores; mesofurcasternum without median apophysis on posterior margin.

Mesofemoral plectral ridges (about nine in fig. 225) slightly curved, and near dorsal margin of femur.

Pericoxal ridge (fig. 223) short and present at anterolateral margin of mesocoxal cavity.

Metaventral submarginal ridge (fig. 223) slightly enlarged at about middle.

Stridular file (figs. 223, 224) contiguous with submarginal ridge; file slightly bent away from submarginal ridge subapically.

Metakatepisternal process (fig. 223) longer than wide, tapered, apically acute.

Sternite II with median point on posterior margin.

Sternite III with moderately developed intercoxal carina; transverse basal ridge with long median point and strongly sinuate.

Sternite IV not examined.

The ***S. similis* group** has six species (*S. ferganensis*, *S. gissarensis*, *S. hiekei*, *S. longilobatus*, *S. similis minor*, *S. similis similis*, *S. triangularis*). (Definition: Frisch, 2014: 201.)

The group is known from Central Asia and adjacent Middle Eastern and south Asian countries.

Additional characters: *S. similis* (figs. 45, 226–231; one female: Kyrgyzstan).

Head without tentorial depression.

Corneal lenses (fig. 45) without sensilla or wrinkles.

Mesoventrite (fig. 229) with strong microsculpturing anteriorly and laterally, but poorly developed midapically; apical vertical portion of basisternum with microsculpturing; prepectal ridge separated medially; mesanapleural ridge with anterior segment present, posterior segment absent; mesotransventral ridge present and moderately strongly curved; median depression without pores; mesofurcasternum without median apophysis on posterior margin.

Mesofemoral plectral ridges (about 13 in fig. 226) long, slightly curved, and occupying most of middle of basal region.

Pericoxal ridge (fig. 227) moderately long and present at anterolateral margin of mesocoxal cavity.

Metaventral submarginal ridge (fig. 227) straight to about middle then curved toward dorsal metaventral margin.

Stridular file (figs. 227, 228) straight then slightly curved at apical third, contiguous with submarginal ridge.

Metakatepisternal process (fig. 227) longer than wide, tapered, and apically acute.

Sternite II (fig. 230) with median point on posterior margin.

Sternite III (fig. 230) with moderately developed intercoxal carina; transverse basal ridge strongly sinuate and with moderately long median point.

Sternite IV (fig. 231) with shallow, transversely oblong depression basally and with tiny pore between depression and anterior margin.

The ***S. sulcicollis*** **group** includes five species: (*S. ampliatus*, *S. argonauta*, *S. ponticus*, *S. rubidus*, *S. sulcicollis*. (Definition: Frisch, 1999c: 540; Frisch et al., 2002a: 37.)

Frisch (1997a: 537) proposed the *sulcicollis* group for two species, *argonauta* and *sulcicollis*. Later he revised the group, added three more species, and provided a more explicit definition of the group (Frisch, 1999c: 540). The group is widespread in Europe to Turkey, the Caucasus, and southwestern Russia.

Additional characters: *S. sulcicollis* (figs. 46, 232–239; one female: Germany).

Head without tentorial depression. Corneal lenses (fig. 46) without sensilla, with wrinkled surface.

Mesoventrite (fig. 234) with strong microsculpturing anteriorly and laterally, weaker midapically in and near median depression; apical vertical portion of basisternum with microsculpturing; prepectal ridge separated medially; mesanapleural ridge partially developed anteriorly, absent posteriorly; mesotransventral ridge present and strongly curved; median depression without pores; mesofurcasternum without median apophysis on posterior margin.

Mesofemoral plectral ridges (about 11 in figs. 238, 239) nearly straight to curved, and at about middle of femoral base extending to near ventral margin.

Pericoxal ridge (fig. 236) at anterolateral margin of mesocoxal cavity; ridge short.

Metaventral submarginal ridge (figs. 236, 237) slightly enlarged at about apical third.

Stridular file (figs. 236, 237) contiguous with submarginal ridge, straight for most of length, with apical portion curved medially.

Metakatepisternal process (fig. 236) longer than wide, tapered, and apically acute.

Sternite II (fig. 235) with median point on posterior margin.

Sternite III (fig. 235) with well-developed intercoxal carina; transverse basal ridge strongly sinuate and with long median point.

Sternite IV (fig. 233) with tiny median pore near anterior margin.

Australian Species Group

The ***S. ooderes*** **group**. Because I was able to study a series of *Scopaeus ooderes*, this species group is proposed to discuss the species in the context of a species-group classification. *Scopaeus ooderes* was discussed, redescribed, and illustrated by Frisch (2016), who revised the known species and assigned none to species groups. Doing so here provides a seed for an Australian species-group classification of the genus.

Additional characters: *S. ooderes* (figs. 37, 175–180; one male: Australia).

Head without tentorial depression.

Corneal lenses (fig. 37) without sensilla, surface strongly wrinkled.

Mesoventrite (fig. 176) with strongly microsculpturing on most of surface, slightly less strong in and adjacent to median depression; apical vertical portion of basisternum with microsculpturing; prepectal ridge separated medially (note: the prepectal ridges of fig. 176 touch medially, which is aberrant; examination of other specimens of the species group do not confirm the ridges touching); mesanapleural ridge with anterior segment present, posterior segment absent; mesotransventral ridge present and strongly curved; median depression without pores; mesofurcasternum without median apophysis on posterior margin.

Mesofemoral plectral ridges (about eight in fig. 175) long, straight, and about equidistant from dorsal and ventral femoral margins.

Pericoxal ridge absent from margin of mesocoxal cavity (fig. 177).

Metaventral submarginal ridge (fig. 177) straight, not swollen or enlarged near middle.

Stridular file (figs. 177, 178) contiguous with submarginal ridge with apical half moderately separated from ridge.

Metakatepisternal process (fig. 177) slightly longer than wide, tapered, and apically acute.

Sternite II with median point on posterior margin (fig. 179).

Sternite III (fig. 179) with well-developed intercoxal carina; transverse basal ridge moderately sinuate, with moderately long median point.

Sternite IV (fig. 180) with small, median pore basally.

African Species Groups

In Africa, prior to Fagel's (1973) work on the *Scopaeus* there were 41 species recorded for all of Africa. Fagel, in that one publication, described or redescribed 124 species and illustrated characters for each. For practical and preferential reasons Fagel (1973) shunned subgenera and proposed 19 species groups for the sub-Saharan *Scopaeus*. He omitted the species of North Africa and embraced both external and aedeagal characters to define the groups.

Since all of Fagel's work on the African *Scopaeus* is in one book and the species of each group are included in a checklist (Fagel, 1973: 10–14) it seems superfluous to list them here. To simplify access, the species groups are listed alphabetically here with the number of species included and a citation of the page on which the group is described. The following 19 groups of African species were recognized by Fagel (1973) as *Scopaeus*. However, nearly half of the species, those in the *S. gigantulus*, *S. pseudomethneri*, *S. nitidicollis*, and *S. tristis* groups, a total of 61 species, are transferred in the present work to the genus *Hyperscopaeus*. The remaining 63 Afrotropical species are distributed among 15 species groups of *Scopaeus*.

The ***S. celisianus* group**: two species; description (Fagel, 1973: 10, 45).

The ***S. crassipes* group**: 17 species; description (Fagel, 1973: 13, 211).

The ***S. gigantulus* group**: one species; description (Fagel, 1973: 10, 49). The species of this group is transferred to *Hyperscopaeus* in the present work.

The ***S. punctatellus* group** was not included in Fagel's 1973 monograph, but is cited here for one interesting species, *S. punctatellus*, described from Madagascar and reported from tropical central Africa to southern Africa and north to the Arabian Peninsula. Fagel (1973: 13, 177) included *S. punctatellus* and *S. laetus* together with three other species in the *S. laetus* group. When Frisch (2003: 680) synonymized *S. laetus* with *S. subfasciatus* the species became part of the *S. laevigatus* group and Fagel's *S. laetus* group no longer had a name. So, a new group name *S. punctatellus* is proposed here to include one of the species. The other three species are excluded because I don't know them, and they may or may not be related to either *S. laetus* or *S. punctatellus*; they are no longer assigned to any species group. However, Frisch (personal commun.) has begun a manuscript on the *S. punctatellus* group, a group he proposed independent of the present work.

A Zambian specimen of *S. punctatellus* was available for dissection. The species shares the form and position of the mesofemoral plectral ridges (fig. 191) with those of the *S. laevigatus* species group (figs. 113, 121). The species (fig. 189) shares with *S. laevigatus* (figs. 114, 115) the more mesial position of the apical portion of the stridular file while still maintaining contact with the submarginal ridge and as with *S. subfasciatus* the absence of the mesotransventral ridge (cf. figs. 122, 188). Unlike *S. laevigatus* (fig. 116), sternite III of *S. punctatellus* lacks a median point extending from the transverse basal ridge (fig. 192). Based on the overlap of stridular characters of *S. punctatellus* it seemed possible that with additional study of *S. punctatellus* species group and the *S. laevigatus* species group might be combined. However, Frisch (personal commun.) told me that the habitus and characters of the aedeagus and the sternite VIII of the males of *S. punctatellus* differ greatly from those of the males of species of the *S. laevigatus* group and that he will not include *S. punctatellus* in the *S. laevigatus* group.

Additional characters: *S. punctatellus* (figs. 39, 188–192; one female: Zambia).

Head without tentorial depression.

Corneal lenses (fig. 39) without sensilla or wrinkles.

Mesoventrite (fig. 188) covered with microsculpturing anteriorly, devoid of microsculpturing posteriorly; apical vertical portion of basisternum with feeble microsculpturing; prepectal ridge separated medially; mesanapleural ridge absent; mesotransventral ridge absent; median depression without pores; mesofurcasternum without median apophysis on posterior margin.

Mesofemoral plectral ridges (about five in fig. 191) strongly curved, and at dorsal edge of femur.

Pericoxal ridge (fig. 189) short, at anterolateral margin of mesocoxal cavity.

Metaventral submarginal ridge strongly extended medially just proximad of middle, then strongly curved posterodorsally.

Stridular file (figs. 189, 190) contiguous with submarginal ridge and with apical portion extending mesially.

Metakatepisternal process (fig. 189) longer than wide, tapered, and apically acute.

Sternite II (fig. 192) with median point on posterior margin.

Sternite III (fig. 192) with weakly developed intercoxal carina; transverse basal ridge strongly sinuate and without median point.

Sternite IV not examined.

The ***S. leleupi* group**: three species; description (Fagel, 1973: 12, 139).

The ***S. nicanor* group**: three species; description (Fagel, 1973: 12, 144).

The ***S. nitidicollis* group**: 15 species; description (Fagel, 1973: 11, 103). The species of this group are transferred to *Hyperscopaeus* in the present work.

The ***S. paludicola*** group: five species; description (Fagel, 1973: 12, 167).

The ***S. pellionis* group**: one species; description (Fagel, 1973: 12, 125).

The ***S. peregrinus* group**: eight species; description (Fagel, 1973: 13, 196).

The ***S. pseudomethneri* group**: 38 species; description (Fagel, 1973: 10, 52). The species of this group are transferred to *Hyperscopaeus* in the present work.

The ***S. rugosulus* group**: one species; description (Fagel, 1973: 12, 128).

The ***S. scotti* group**: three species; description (Fagel, 1973: 13, 243).

The ***S. summicola* group**: five species; description (Fagel, 1973: 12, 130).

The ***S. tenuis* group**: four species; description (Fagel, 1973: 10, 38). The *tenuis* group and the *debilis* group of Frisch (see above) are the same.

The ***S. tristis* group**: seven species; description (Fagel, 1973: 12, 151). The species of this group are transferred to *Hyperscopaeus* in the present work.

The ***S. tshuapaensis* group**: one species; description (Fagel, 1973: 12, 165).

The ***S. vilhenai* group**: four species; description (Fagel, 1973: 13, 190).

The ***S. witteanus* group**: one species; description (Fagel, 1973: 13, 187).

Geoscopaeus Coiffait. Although the title of Fagel's publication referred only to *Scopaeus* he also revised the African species of *Geoscopaeus*. He included 12 species, nine of them new, and characterized the genus (Fagel, 1973: 18). Although he cited the correct type species for *Geoscopaeus*, he misidentified the genus and all the African species he included were transferred to *Micranops* by Frisch and Herman (2014). A dozen years earlier Frisch et al. (2002a: 45) published the synonymy of *Micranops* Cameron, 1913, *Nivorus* Herman, 1965, and *Microscopaeus* Coiffait, 1980; *Geoscopaeus* was correctly synonymized with *Scopaeus*. However, since Frisch et al. (2002a; personal commun.) was a study of the western Palaearctic fauna, the transfer of the species Fagel (1973) added to *Geoscopaeus* were not then reassigned to *Micranops*.

Western Hemisphere Species Groups

The species of *Scopaeus* of the Americas have not been assigned to named species groups. Infrageneric groups all existed as numbered groups or as subgenera after first having been described as genera. Erichson (1840: 605–609) described the first four species for the Western Hemisphere, one from the United States, two from Puerto Rico, and one from Colombia. A fifth New World species was added after the genus *Polyodontus*, described for a Chilean species by Solier (1849: 312), was synonymized with *Scopaeus* (Kraatz, 1857: 701; 1859: 4, 12).

A Cuban species was added by Fauvel (1863: 436). LeConte (1863a: 46–47) described two species from the United States in *Echiaster* that were later transferred to *Scopaeodera* and *Scopaeopsis* by Casey (1886a: 220; 1905: 215), both of which were moved to *Scopaeus* long ago. Sharp (1876: 248–253) added seven from Brazil and later (Sharp, 1886: 540–548) described 20 species from Mexico and Central America and distributed them to four numbered, but unnamed, species groups; he also named two genera that are synonymized with *Scopaeus* in the present work. Although many other species were described in the Americas by various authors, Lynch Arribálzaga (1884), Fauvel (1891), Fall (1901), Schubert (1909), Cameron (1913), Bernhauer (1910, 1927, 1934, 1939), Notman (1919, 1920, 1921), Bierig (1934), Blackwelder (1943), and Hatch (1957), no one but Casey (1905, 1910), proposed names that became subgenera of *Scopaeus*. All the American subgenera, *Scopaeodera* Casey, *Scopaeopsis* Casey, and *Scopaeoma* Casey, as well as two genera, *Scopaeomerus* Sharp and *Euscopaeus* Sharp, are synonyms with *Scopaeus* herein (see discussion of synonyms above); the included species are assigned to species groups. Most of these species groups are likely monophyletic, but that question will be addressed by others. Named species of the Americas lacking subgeneric assignment are not assigned to species groups in the present work. Included are those of Casey's *Leptorus* and *Pseudorus* along with most of the species described after his work (see remarks for *Leptorus* and *Pseudorus* below).

Treated herein as species groups in the Americas are only the notable standouts, those with derived features that separate them from other species groups of *Scopaeus*. It is among these groups that particular and intense effort was expended searching unsuccessfully for derived characters to separate them from a *Scopaeus* that remained monophyletic. Included among those groups are the *S. chiriquensis*, *S. nevermanni*, *S. nitidus*, and *S. opacus* groups along with the Reticulate group. The conundrum was the elevation of all or even one of the species groups to generic level would have rendered *Scopaeus* without defining characters. The task was to detect apomorphic characters that would define *Scopaeus* if or when autapomorphic species groups were extracted. Resolving this puzzle devoured years of search and study.

Each of these collections of species, formerly genera or subgenera, are treated as species groups of *Scopaeus* (table 1). Each group will provide less daunting starting points for revisions of the American species than if the entire

American fauna of *Scopaeus* were tackled at one go. Some of the American species are among the most elegant and beautiful of the genus (see figs. 3, 5, 8). In addition to groups based on former subgenera there are other easily and notably defined groups that had not been named as subgenera or for which there are no named species. The New World *Scopaeus* fauna has not been discussed with nearly the remarkable detail, vigor, and careful study as has been provided by Frisch for the Eurasian fauna. The present discussion of the American fauna merely touches obvious highlights of the available variation and brings attention to an exquisite fauna ripe for study. The treatment herein is basic and certainly additional groups and details of structure will be revealed in new research. Without doubt there are other species groups that can be identified among the described species, but none are as obvious as six of the following seven groups. Recognition of other potential groups will be the task of subsequent investigators. Among conspicuous and unambiguous species groups in the Nearctic and Neotropical regions the following seven are listed alphabetically. But first a discussion of *Polyodontus*.

Polyodontus. Before discussing the *Scopaeus* species groups of the Americas questions regarding an early addition to the South American fauna must be addressed. Solier (1849: 310–312) described the new genus and species, *Polyodontus angustatus*. In his description he also cited published illustrations of the habitus, labrum, maxillary palpus, and antenna.

The only identified specimen of *P. angustatus* I have examined is one labelled as "Type" in Brussels (IRSN). However, it is unlikely to be a part of the type series and may or may not be correctly identified. In the original description Solier cited no locality, not continent, country, town, nor region. The species is presumed to be from Chile because it was published in a work about plants and animals of that country. The specimen in Brussels, labelled from Concepción, was probably the specimen to which Fauvel referred in his 1867 article, and is apparently part of his collection, not Solier's. The collections of Solier and Gay are said to be in the Muséum National d'Histoire Naturelle, Paris (Horn and Kahle, 1935–37: 87). Others have reported specimens of *S.* (*P.*) *angustatus* from Chile: Santiago (Fairmaire and Germain, 1862: 437) and Concepción (Fauvel, 1867: 5) and Argentina: Chacabuco (Lynch Arribálzaga, 1884: 247). Besides Solier, no one who has published anything about the species appears to have examined type material.

Two provisos concern *Polyodontus* Solier, 1849. First, the name is a junior homonym of Eysenhardt, 1818, and as such a new genus-group name will be required if the genus group is recognized as distinct. Second, the published habitus image of the species referred to by Solier, Lamina 6, figure 1, bears little resemblance to any *Scopaeus* I have seen. However, Solier's images of the labrum (Lamina 6, fig. 1a), in particular, and maxillary palpus (fig. 1b) do resemble those of *Scopaeus*. Lacordaire (1854: 95) referred to the species as near *Scopaeus* because Solier described *P. angustatus* as having a trilobed labial margin and near *Lithocharis* by its form. Kraatz (1857) synonymized it with *Scopaeus* for the possession of the tridentate ligular margin. To settle the question of its identity and position within the Paederinae I requested the syntype(s) of *P. angustatus* Solier from Paris. The curator of the beetle collection first told me the General Director of the Museum no longer permitted loans of any type material, but that photographs of types could be sent. When photographs were requested, I was told the type(s) could not be found. So, the identity of *P. angustatus* remains hidden.

Once *Polyodontus* was combined with *Scopaeus* it was cited as a subgenus and, surprisingly for a group based on a western South American species, soon used to park various European species that differed from the nominate *Scopaeus*. The use of the name for some European species is discussed above in the groups of the Eastern Hemisphere.

The ***S. chiriquensis* group** includes four named species [*S. chiriquensis*, *S. guatemalensis*, *S. obscurus*, *S. palmatus*]. The type species of *Scopaeomerus*, *S. chiriquensis*, is in this group. This group is formerly the genus *Scopaeomerus* Sharp, 1886, and is herein a **new synonym** of *Scopaeus*. There are additional, unnamed species.

Diagnosis: *S. chiriquensis* group (figs. 1, 15, 23, 48, 53, 54, 58–60, 63, 64, 76, 77, 81–88; one male and female: Costa Rica). The species have an edentate labral margin (fig. 58, perhaps interpreted as unidentate by some; fig. 59), a vertical sulcus on the basal edge of the head adjacent to the nuchal groove, and the prohypomeronal ridge is absent. The species have a mesofurcasternal apophysis (fig. 82), a slender, posteriorly directed, spiniform process on the middle of the internal edge of the posterior margin of the mesofurcasternum.

Description: Head shining dully; punctation and pubescence moderately dense; setae of pubescence moderately long; punctures tiny; dorsum without tentorial depression; interpunctational microsculpture present; corneal lenses without sensilla, but lenses near dorsal margin of eye with small tumescence (fig. 23); basal angles strongly developed (figs. 1, 48); basal margin (fig. 1) sinuatotruncate to emarginate, and with shallow, median groove; labrum edentate (fig. 58 [median lobe, if considered a denticle, would make this a unidentate labrum]), but some with lobiform denticle (fig. 59) and with wide, deeply to shallowly emarginate margin; gular sutures (fig. 48) narrowly to somewhat widely separated.

Pronotum shining dully; punctation and pubescence moderately dense; pubescence moderately long; punctures tiny; interpunctational microsculpture present; notosternal suture (figs. 53, 54) present, more strongly developed posteriorly than anteriorly; prohypomeronal transverse ridge absent (cf. figs. 54 and 52); submarginal ridge (cf. figs. 54 and 52) well separated from margin; prohypomeron lobe without setae.

Elytra shining dully; punctation and pubescence dense; puncture tiny and atop microtubercle; setae of pubescence short; posterior edge with a few small setae.

Mesoventrite (fig. 82) with microsculpturing strong anteriorly, weaker laterally and near median depression; apical vertical portion of basisternum with microsculpturing; prepectal ridge separated medially; mesanapleural ridge with anterior segment present and weakly developed, posterior segment absent; mesotransventral ridge present; median depression without pores; mesofurcasternum with long, slender, tapered mesofurcasternal process extending posteriorly.

Mesofemoral plectral ridges (perhaps three or four in fig. 85) straight, and nearer dorsal femoral margin than ventral.

Pericoxal ridge (fig. 83) short and weakly developed at anterolateral margin of mesocoxal cavity.

Metaventrite (fig. 83) with submarginal ridge gradually narrower posteriorly from about middle; stridular file (figs. 83, 84) contiguous with metaventral submarginal ridge; metakatepisternal process longer than wide, tapered, and apically acute.

Abdominal sternite II (fig. 86) without median point on posterior margin. Sternite III (fig. 86) with weak intercoxal carina; basal transverse ridge feebly sinuate and with long median point. Sternite IV (figs. 87, 88) with midbasal depression and with tiny pore proximad of depression. Sternites IV–V with modest, transverse, basal impression.

Discussion: The described species are from Guatemala and Panama, but specimens and other species are known from Costa Rica, Venezuela, Ecuador, Peru, and Bolivia. Specimens have been collected from forest floor and streamside leaf litter and debris at 760 to 1825 m elevation, a few were collected at flight intercept traps, and one in an “exposed termite nest.” It is highly improbable any species of this group are termitophiles.

Also included in this species group are species from Peru, Brazil, French Guiana, and Costa Rica with a truncate, edentate labral margin with an abrupt, narrow, shallow to moderately deep, median emargination; some have a small, submedial, lobiform denticle at the lateral margin of the emargination (fig. 59). These species are retained in this species group because the labrum is edentate and the few specimens that were disarticulated possess the mesofurcasternal apophysis. Further studies might exclude some of them from this species group.

Scopaeomerus mexicanus Bernhauer (1910: 373) is transferred herein to *Medon* as a **new combination**. This transfer is made with the recognition that no diagnostic, synapomorphic states have been identified for either *Medon* or the Medonina. The species has a moderately deep emarginate labrum and an evidently small denticle adjacent to the labral emargination, lacks a supraocular, cephalic trichobothrium, and has a wide neck, the anteocciput or nuchal groove of which is almost three tenths as wide as the postocular width of the head, and the pronotum is nearly square, only slightly longer than wide.

The ***S. dissimilis*** **group** includes one species (*S. dissimilis*). This was designated by Sharp (1886: 544) as species group 2. Specimens of a Panamanian species are similar and are the basis for the following characters.

Diagnosis: *S. dissimilis* group (figs. 95–100; one female: Panama). The group can be recognized by the strong basal angles and broad emargination of the basal margin of the head (fig. 99), the squarish prothorax (fig. 98) that is slightly longer than wide, and moderately dense pubescence of the head and pronotum and denser elytral pubescence. The integument is polished, the head and pronotum has fine, moderately dense pubescence. The head lacks tentorial depressions. Sharp reported the tarsi to be short, but the basal metatarsomere appears to be slightly longer than the second.

Description: Head polished; punctation and pubescence moderately dense and moderately long, absent medially and from clypeus; macrosetae near or on margin; punctures moderately large; corneal lenses not examined; dorsum without tentorial depression; microsculpture absent; basal angles (fig. 99) well developed, strongly rounded; basal margin (fig. 99) strongly emarginate and with moderately wide and deep, vertical, median impression; labrum quadridentate (fig. 100); gular sutures (fig. 99, visible as through integument) moderately separated.

Pronotum (fig. 98) slightly longer than wide; surface polished; punctation and pubescence sparser than on head and absent medially; punctures absent to tiny and scarcely discernible; macrosetae on margin; microsculpture absent; notosternal suture weak; prohypomeronal transverse ridge absent; prohypomeronal submarginal ridge present; postprocoxal lobe with a few setae.

Elytra polished, with moderately dense punctation and pubescence and denser than on head; punctures small, moderately developed; posterior edge without or with a few minute setae.

Mesoventrite (fig. 96) with strong microsculpture basally, absent on apical half; apical vertical portion of basisternum without microsculpturing; prepectal ridge separated medially; mesanapleural ridge absent; mesotransventral ridge present medially; median depression without pores; mesofurcasternum without median mesofurcasternal apophysis on posterior margin.

Mesofemur with several long plectral ridges (based on examination of mounted specimen and viewed with reflected light using dissecting microscope).

Pericoxal ridge short and present only at anterolateral margin of mesocoxal cavity (fig. 95).

Metaventrite (fig. 97) with metaventral submarginal ridge slightly enlarged near middle; stridular file (figs. 95, 96) contiguous with metaventral submarginal ridge and not deflected mesially. Metakatepisternal process (fig. 97) longer than wide, tapered, and apically acute.

Metatarsus with first tarsomere slightly longer than second.

Abdominal tergites and sternites III–VI each with moderately deep, transverse, basal impression; sternite III with intercoxal carina; sternite IV not examined.

Discussion: The one female syntype (FMNH) available for examination was covered with fine coating of glue making it difficult to properly study; for safety of the specimen, it was not removed from the card and cleaned. The syntype had only a few macrosetae along the margin, but the others were probably broken off. Sharp (1886: 544) wrote that the four specimens of the type series were "in very decayed condition." Four Panamanian female specimens that appear to be similar to or conspecific with *S. dissimilis* were available for detailed study; a fifth specimen was dissected but not examined using the SEM.

The ***S. nevermanni* group** includes two named species (*S. chapini* Blackwelder and *S. nevermanni* Bierig). The named species are from Jamaica and Costa Rica respectively.

Diagnosis: *S. nevermanni* group (figs. 7, 8, 34, 154–160; male and female: Costa Rica). This group is readily recognized by the large, prominent, tentorial depression (fig. 7). The general form, integumental sheen, absence of punctation, polished, glabrous apical three fifths of the mesoventrite (fig. 156), and position and form of the stridular file are shared with the *S. nitidus* group. For the *S. nevermanni* group, the labrum is bidentate, the trichobothrium is behind the middle of the dorsal margin of the eye, the integument is moderately densely pubescent, the pronotum lacks and the head has a few, hardly noticeable, marginal macrosetae, the prohypomeronal ridge is present, and the base of the pronotum has a broad, basal depression bisected by a short, midlongitudinal ridge. By contrast, for the *S. nitidus* group, the labrum is quadridentate (fig. 169), the trichobothrium is near the middle of the dorsal margin of the eye, the integument is far less pubescent, both the head and the pronotum have prominent, marginal macrosetae, the prohypomeronal ridge is absent (fig. 56), and the base of the pronotum lacks both a depression and acute, midlongitudinal ridge.

Description: Head orbiculate (figs. 7, 8) or trapezoidal; surface strongly shining to subnitid; punctation and pubescence moderately dense; pubescence moderately long; macrosetae present but inconspicuous; punctures absent; corneal lenses without sensilla, dorsal row with wrinkles (fig. 34); dorsum with broad, rounded tentorial depression (fig. 7); microsculpture absent; lateral margin gradually curved to broadly rounded basal angles or lateral margin gradually rounded from eye to neck (figs. 7, 8); basal angles present or absent; basal margin without median groove; labrum (fig. 159) bidentate, labral margin laterad of denticle broadly rounded; gular sutures moderately widely separated and parallel; gula depressed for most of length, depression deeper basally than anteriorly.

Pronotum elliptical (fig. 8), base with broad depression with midlongitudinal, dorsally acute ridge; integument strongly shining to subnitid; punctation and pubescence moderately dense; pubescence moderately long; macrosetae absent; punctures fine; microsculpturing absent; notosternal suture absent; prohypomeronal transverse ridge present; prohypomeronal submarginal ridge present; prohypomeronal lobe with a few setae.

Elytra strongly shining to subnitid; punctation and pubescence moderately dense; punctures absent; setae of pubescence moderately long; posterior edge with a few tiny setae.

Mesoventrite (fig. 156) without microsculpturing on apical three fifths; apical vertical portion of basisternum without microsculpturing; prepectal ridge fused medially; mesanapleural ridge absent; mesotransventral ridge present; median depression without pores; mesofurcasternum with minute median mesofurcasternal apophysis on posterior margin (fig. 156).

Mesofemoral plectral ridges (perhaps four in fig. 157) strongly curved and near dorsal margin of femur.

Pericoxal (fig. 154) ridge absent.

Metaventrite with metaventral submarginal ridge weakly developed, strongly enlarged near middle, and extending mesially, then abruptly curved dorsally; stridular file contiguous with submarginal ridge, apical portion strongly curved mesially (figs. 154, 155).

Metakatepisternal process longer than wide, tapered, and apically acute.

Metatarsus with first tarsomere longer than second.

Abdominal tergites and sternites III–VI with prominent, transverse, basal impression.

Terga III and IV with short, basal, midlongitudinal ridge.

Sternite II with median point on posterior margin.

Sternite III with acute intercoxal carina; transverse basal ridge sinuate and with median point.

Sternite IV not examined.

Discussion: Based on external, secondary sexual characters of the males from Guatemala, Costa Rica, Panama, Suriname, and Peru all appear to be one species. However, because the terrain between Nicaragua and Peru is so diverse and mountainous, examination of the aedeagus might reveal this apparently widespread species to be a species complex. Peru also harbors a quite different species that varies from others by aedeagal and external abdominal characters. The head of most of the species is orbiculate, but that of the Peruvian species is trapezoidal.

The group is known from Jamaica, Belize, Guatemala, Costa Rica, Panama, Guyana, Suriname, and Peru. Unexpectedly, in the Bierig collection (FMNH) four specimens covered with fungal hyphae are from Florida, USA; this record is the only report of the species group from the United States; the record requires corroboration.

Specimens have been collected from leaf litter and debris in swampy areas, at the edge of streams, the forest floor litter; they were also collected from rotten figs and at lights.

The ***S. nitidus* group** includes 10 species (*S. delicatulus*, *S. discoidalis*, *S. distans*, *S. filitarsis*, *S. laxus*, *S. nitidus*, *S. politus*, *S. pulchellus*, *S. semicornis*, *S. sonoricus*). The type species of *Scopaeodera* Casey, *S. nitidus* (LeConte), is included here. *Scopaeodera* is a revised status junior synonym of *Scopaeus*.

Diagnosis: *S. nitidus* group (figs. 35, 50, 55–56, 65, 66, 74, 75, 161–170; *S. laxus* fig. 3). The integument is polished, has sparse pubescence with prominent, marginal macrosetae on the head and pronotum, and lacks punctures; the prohypomeronal transverse ridge is absent (fig. 56) and tergites and sternites IV and V each have a deep, transverse, basal depression.

Description: Head polished; punctation absent; pubescence sparse laterally, absent medially; macrosetae near or on margin; dorsum without tentorial depression; microsculpture absent; corneal lenses (fig. 35) without sensilla, dorsal row of lenses weakly wrinkled; basal angles broadly rounded (figs. 50, 161); basal margin truncate and with broad, shallow, medial impression; labrum quadridentate (fig. 169); gular sutures (figs. 50, 161; sutures of latter figure visible through integument) moderately separated and diverging moderately to weakly posteriorly from near submentum.

Pronotum polished; pubescence sparse laterally, absent medially; punctures absent; macrosetae on margin; notosternal suture absent (fig. 55); prohypomeronal transverse ridge absent (fig. 56); prohypomeronal submarginal ridge absent (fig. 56); postprocoxal lobe with a few setae.

Elytra polished, with sparse pubescence; punctures barely discernible; posterior edge without setae.

Mesoventrite (figs. 163, 166) with strong microsculpturing on basal two fifths, without microsculpturing on apical three fifths; apical vertical portion of basisternum with or without feeble microsculpturing; prepectal ridge separated medially; mesanapleural ridge absent; mesotransventral ridge present; median depression without pores; mesofurcasternum without median mesofurcasternal apophysis on posterior margin.

Mesofemoral plectral ridges (about 5 to 10 in figs. 162, 170) straight to moderately curved and ridges covering most of femoral base.

Pericoxal ridge absent (fig. 165).

Metaventrite (figs. 163–165) with metaventral submarginal ridge strongly enlarged near middle and extending mesially, then abruptly curved dorsolaterally; stridular file contiguous with submarginal ridge, apical portion strongly deflected mesially. Metakatepisternal process longer than wide, tapered, and apically acute.

Metatarsus with first tarsomere longer than second.

Abdominal tergites and sternites III–VI each with deep, transverse, basal impression. Sternite II (fig. 167) with median point on posterior margin.

Sternite III with acute intercoxal carina; transverse basal ridge strongly sinuate and with median point (fig. 167). Sternite IV not examined.

Discussion: Most of the named species in this group comprise the Central American Group 4 of Sharp (1886: 546) along with two others previously described by him from Brazilian Amazonia (Sharp, 1876: 252). Casey (1886b: 220) named the genus *Scopaeodera* for *Echiaster nitidus* LeConte and later (1905: 217) described a second species, *S. sonorica*.

Before finding the stridulum, this group of species, (along with the *S. nevermanni* and *S. opacus* groups), seemed a strong contender for separation from *Scopaeus*. However, it was impossible to distinguish two groups despite a prolonged, intensive search for characters that differentiated *Scopaeodera* while maintaining the remaining species of *Scopaeus* as a monophyletic group.

Specimens of the group were collected in leaf litter and ground debris near streams, from vegetated, shaded banks of streams in Argentina and the sandy shore of streams in Costa Rica. Individuals attracted to lights have been collected at numerous localities in various countries. Species have been collected in Argentina, Ecuador, Brazil, French Guiana, Suriname, Guyana, Panama, Costa Rica, Nicaragua, Guatemala, Mexico, and the United States.

The ***S. opacus* group** includes 13 species (*S. antoniensis*, *S. crassitarsis*, *S. duryi*, *S. elaboratus*, *S. gracilicornis*, *S. grandicollis*, *S. impar*, *S. mollis*, *S. opacus*, *S. ornatus*, *S. pallens*, *S. rambouseki*, *S. ventralis*). The type species of *Euscopaeus* Sharp, 1886, *E. crassitarsis* Sharp, and *Scopaeopsis*, *S. opacus* (LeConte), are placed in this species group. *Scopaeopsis* Casey, 1905, is a revised status junior synonym of *Scopaeus* and *Euscopaeus* Sharp, 1886, is a new synonym of *Scopaeus*. Doubtless additional species will be described.

Diagnosis: *S. elaboratus* (figs: 5, 6; one male: United States); *S. opacus* (figs. 38, 181–187; males and females: USA); *S. opacus* sp. group (figs. 49, 57, 67–71). The species have a moderately robust to robust build, the surface of the head and pronotum is covered with fine, dense pubescence, the punctation is tiny and barely visible, and there are few large, marginal macrosetae. The gular sutures (fig. 49) are slightly separated and parallel for most of their length. The first metatarsomere is longer than the second.

Description: Head and pronotum with fine, dense pubescence and without or with a few prominent, marginal macrosetae; head, pronotum, and elytra strongly shining to seminitid, but not polished; head and pronotal with dense microtuberculation or fine, hardly discernible punctation.

Head (figs. 5, 49) without tentorial depression; basal angles of head strongly to broadly rounded to absent; basal margin of head slightly emarginate to truncate to broadly rounded. Labral denticles (figs. 6, 186) long, especially submedial denticle, submedial denticle with inner margin cleft or with slight to strong, asetate or setate swelling. Gular sutures (fig. 49) parallel and narrowly to moderately widely separated.

Pronotum (fig. 5, 57) ovate, anterior pronotal angles poorly developed; notosternal suture present or absent; prohypomeronal transverse ridge present; postprocoxal lobe setate.

Elytral surface with dense microtuberculation or tiny punctures.

Mesoventrite (fig. 181) with strong microsculpturing on anterior two thirds, without microsculpturing on apical third; apical vertical portion of basisternum without or with feeble microsculpturing; prepectal ridge separated medially; mesanapleural ridge absent; mesotransventral ridge absent; median depression with dense cluster of pores (figs. 181, 182); mesofurcasternum without median mesofurcasternal apophysis on posterior margin.

Mesofemoral plectral ridges (about 5 in fig. 185) weakly curved, and near dorsal margin of femur.

Mesoventral pericoxal ridge (figs. 183, 184) at anterolateral margin of mesocoxal cavity; ridge short.

Metaventral submarginal ridge straight (fig. 183). Stridular file (figs. 183, 184) contiguous with submarginal ridge.

Metakatepisternal process (fig. 183) longer than wide, tapered, and apically acute.

Metatarsus with first tarsomere longer than second.

Sternite II with median point on posterior margin.

Sternite III with moderately developed intercoxal carina; transverse basal ridge moderately sinuate and with long, median point.

Sternite IV not examined.

Discussion: *Euscopaeus* Sharp, 1886, was erected for two Guatemalan species, *E. crassitarsis* and *E. gracilicornis*. Bierig added a third species, *E. impar*, from Panama. These species are similar to those originally included in *Scopaeopsis* Casey, 1905: *S. duryi*, *S. elaborata*, *S. opaca*, *S. pallens*, *S. ventralis*. The two genus-group names are synonymized herein. This group of species was one of the three that I thought might represent a separate genus from *Scopaeus*.

As mentioned in the discussion of the *S. nitidus* species group, before discovery of the stridulum, this group of species was seemed to represent a genus separate from *Scopaeus* and significant effort was expended seeking characters that would separate it from *Scopaeus*.

This group of moderately large bodied species occurs from North America to Argentina. Specimens have been collected from leaf litter on the edge of streams, swamps, and ponds in Argentina and Ecuador and the United States.

The **"Reticulate" group** includes no known described species. The informal name for this group is merely a descriptive word referring to the densely, reticulately, sculptured surface (figs. 4, 193) of the dorsum of the head and the pronotum. The name is used to be able to refer to the group.

Diagnosis: "Reticulate" group (figs. 4, 14, 40, 193–200). The group is most notably identified by the dense umbilicate to reticuloumbilicate punctation (figs. 193, 194) and dense pubescence of moderately long, coarse setae. No other species of the genus are so coarsely and densely punctate. The density and type of punctation along with the narrow neck is reminiscent of species of *Rugilus*.

Description: Head (fig. 193) rectangular; surface with dull sheen (fig. 4); dorsum without tentorial depression; punctation and pubescence dense; interpunctational microsculpture absent; basal angles well developed; basal margin feebly to strongly emarginate and with shallow, vertical, median sulcus.

Corneal lenses without sensilla, surface wrinkled (fig. 40).

Labrum bidentate.

Gular sutures slightly to moderately diverging posteriorly from near submentum.

Pronotum with dull luster (fig. 4); punctation and pubescence dense; setae moderately long; surface with reticuloumbilicate to umbilicate punctation; interpunctational microsculpture absent; notosternal suture present, moderately developed; prohypomeronal transverse ridge present; submarginal ridge moderately well separated from margin; postprocoxal lobe with a few setae.

Elytra shining dully; punctation and pubescence dense; punctures moderately large and more or less open posteriorly; setae moderately long; posterior edge with a few small, well-spaced setae.

Mesoventrite covered with microsculpturing (fig. 198); apical vertical portion of basisternum with microsculpturing; prepectal ridge narrowly separated medially; mesanapleural ridge absent; mesotransventral ridge moderately to weakly developed; mesofurcasternum (fig. 198) without median mesofurcasternal apophysis on posterior margin.

Median mesobasisternal depression without pores.

Mesoventral pericoxal ridge (fig. 195) at anterolateral edge of mesocoxal cavity small and poorly evident.

Mesofemoral plectral ridges (about seven in fig. 197) curved at base and slightly closer to ventral femoral margin than to dorsal.

Metaventrite (fig. 195) with submarginal ridge straight.

Stridular file (fig. 196) straight and contiguous with metaventral submarginal ridge.

Metakatepisternal process (fig. 195) moderately longer than wide, tapered, apically acute.

Abdominal segments IV and V with base of terga modestly impressed, base of sterna IV and V strongly impressed.

Sternite II with median point on posterior margin.

Sternite III with well-developed intercoxal carina; transverse basal ridge weakly sinuate, with long, median point.

Sternite IV (figs. 199–200) with small, midbasal pore.

Discussion: After having examined or seen images of the type specimens of *Scopaeus* or read the description of all the named species of the genus from the Americas, no named species were found that would fall into this group. The species are tiny, but the group is widespread in South and Central America, which presents the possibility that a species of the group might have been described in another genus. Since the pronotum is squarish a species might have been described in one of the genera of the Medonina. Prior to discovery of the stridulum this group was another that seemed clearly separate from *Scopaeus*. However, the slender neck, presence of the supraocular trichobothrium, tripartite ligula, stridulum, tapered, slender, apically acute metakatepisternal processes, and sclerotized, undivided dorsal surface of the aedeagus clearly anchor the group in *Scopaeus*.

Species were examined from Guadeloupe, Costa Rica, Panama, Venezuela, Peru, and Argentina. Among the limited material examined were at least five species: one in Costa Rica, two in Panama, and two in Argentina. Specimens from Guadeloupe, Venezuela, and Peru were females and might represent additional species.

According to the label data on the specimens examined, examples of the Reticulate group have been collected from debris on the forest floor, near streams, in dry, moist, and wet leaf litter, in log debris and under bark, from mosses and epiphytes of a downed limb, from ground litter in cloud forests, and from an opened termite nest. It is unclear whether the samples were from Berlese samples or siftate from randomly sampled litter and debris on the forest floor, so not much can be gleaned from the collections about the actual habitat of any of the species. However, few specimens are known in total and from each collecting event.

The ***S. rotundiceps*** **group** includes seven species (*S. angusticeps*, *S. brunnipes*, *S. caseyi*, *S. notmani*, *S. puritanus*, *S. rotundiceps*, *S. truncaticeps*). The type species of *Scopaeoma*, *S. rotundiceps*, is part of this group. Only the types of each of the seven species assigned to the group and two unidentified AMNH specimens were examined for this group. The characters provided here are based on Casey's description (Casey, 1905: 191) and features of the two dissected specimens.

Diagnosis: *S. rotundiceps* group (figs. 41, 201–210; one female: United States). According to Casey (1905: 191, 211) this group, described as *Scopaeoma*, is distinguished by the short basal metatarsomere that is "never more than slightly longer than the second," the oval prothorax, narrowly separated gular sutures, and punctation of head and pronotum that is small, but distinctly visible.

In addition, macrosetae are apparently absent from the head, prothorax, and elytra, the pronotum is ovoid and the anterior angle absent and the prohypomeronal transverse ridge is present. The metakatepisternal process is tapered, longer than wide, and apically acute and the stridular file is contiguous with the metaventral submarginal ridge.

Description: Head and pronotum with fine, dense pubescence; punctation dense and fine; macrosetae apparently absent.

Head (fig. 205) without tentorial pit; basal angles absent, lateral margin broadly rounded from eye to neck.

Corneal lenses (fig. 41) without sensilla or wrinkles.

Labral denticles with long submedial denticle, inner margin of submarginal denticle straight and unmodified.

Gular sutures narrowly to moderately widely separated.

Pronotum ovoid, anterior angles absent; notosternal suture feebly developed; prohypomeronal transverse ridge present.

Mesoventrite (fig. 207) with strong microsculpturing on anterior two thirds and weak to absent on transverse, anterior swatch of posterior third; apical vertical portion of basisternum with microsculpturing; prepectal ridge separated medially; mesanapleural ridge with anterior segment present, posterior segment absent; mesotransventral ridge present and strongly curved; median depression without pores; mesofurcasternum without median mesofurcasternal apophysis on posterior margin.

Mesoventral pericoxal ridge (fig. 201) at anterolateral margin of mesocoxal cavity; ridge short.

Mesofemur with numerous plectral ridges (about eight to 12 in figs. 203, 208); ridges straight for most of length, feebly curved on proximal ends.

Metaventrite (figs. 201, 209) with metaventral submarginal ridge straight. Stridular file straight and contiguous with submarginal ridge (figs. 201, 202, 209, 210).

Metakatepisternal process (fig. 201, 209) longer than wide, tapered, and apically acute.

Metatarsus with first tarsomere slightly longer than second.

Sternite II (fig. 204) with moderately developed median carina; posterior margin with median point.

Sternite III (fig. 204) with intercoxal carina moderately well developed; transverse basal ridge strongly sinuate and with long, median point.

Sternite IV with "glandular lobe" on anterior margin.

The *S. rotundiceps* group is known from Canada and the United States.

Two remaining named species clusters of *Scopaeus* in the Western Hemisphere, *Leptorus* and *Pseudorus*, were both synonymized with *Scopaeus* s.s. more than a hundred years ago (see history of use of both names above in the synonymic listings for *Scopaeus*). The second time Casey (1905: 203) referred to *Leptorus* he placed it as a junior synonym of *Scopaeus* and all authors since have so regarded it. *Pseudorus* was used by Casey only in the original description. The name was used once as a subgenus in a catalog (Scheerpeltz, 1933: 1264) and thereafter cited by all authors as synonymous with *Scopaeus*. Unlike the American species discussed in the preceding paragraphs, the type specimens of *Leptorus* and *Pseudorus* reveal no notable characters that distinguish them. Their habitus is generally similar to that of the Eurasian species of *Scopaeus*.

SCOPAEUS: CHECKLIST OF SPECIES INCLUDED AND MATERIAL EXAMINED

380 species

abyssinicus Fagel, 1956 - H (BMNH) — Ethiopia

admixtus Fagel, 1973, transferred to *Hyperscopaeus*

alaniensis Coiffait, 1969 - Sp (MNKB) — Turkey

alaschiacus Frisch, 1998 - P (MNKB) — Cyprus

albertvillensis Fagel, 1973, transferred to *Hyperscopaeus*

alborzensis Frisch, 2010 - H, P (MNKB) — Iran

aliiceps Fairmaire, 1892 - L (IRSN), Sp (FMNH) — Eritrea, Djibouti

allardianus Fagel, 1973, transferred to *Hyperscopaeus*

amos Fagel, 1973 - H (MRAC) — D.R. Congo

amphionis Fagel, 1973 - H (MRAC) — D.R. Congo

ampliatus Binaghi, 1935 - Sp (BMNH, MNKB) — Corsica

andrewesi Cameron, 1931, transferred to *Hyperscopaeus*

angolanus Fagel, 1973, transferred to *Hyperscopaeus*

angustatus (Solier, 1849) - Syn? (IRSN) — Chile (The specimen in the IRSN labelled as "type" is from Concepción. Solier cited no locality and described the species from an unstated number of specimens that are presumably in the collection of C. Gay, or perhaps that of Solier, both of which Horn and Kahle [1935–37: 87, 262] reported to be in the Muséum National d'Histoire Naturelle, Paris. I doubt the specimen in Brussels is part of the type series of *S. angustatus*.)

angusticeps (Casey, 1905) - Syn (USNM) — United States
angusticollis Cameron, 1913 - Syn (BMNH) — West Indies
angustissimus Casey, 1905 - Syn (USNM) — United States
anlasi Frisch, 2010 - Lit. Att — Turkey]
annuliphallus Coiffait, 1975 - H (NHMW) — Nepal
antennalis Cameron, 1913 - Syn (BMNH), Sp (FMNH) — Cuba, Haiti
antoniensis Sharp, 1886 - Syn (BMNH), Syn, Sp (FMNH) — Guatemala, Panama
anxius Mulsant and Rey, 1861 - Sp (BMNH, MNKB) — France, Spain

  pourtoyi Coiffait, 1960
  balazuci Coiffait, 1968
  revestensis Coiffait, 1968 - P (BMNH) — France

apterus Sharp, 1886 - H (BMNH) — Guatemala
apiculatus Frisch, 2015 - Lit. Att. — [Kyrgyzstan]
apterus Cameron, 1950 - Lit. Att. — [New Zealand]
arcuatus Hatch, 1957 - H (USNM) — United States
arena Blackwelder, 1943 - H (USNM) Saint Lucia
argonauta Gusarov, 1992 - Sp (NHMW, MNKB) — Georgia, Caucasus
arizonae Casey, 1905 - Syn (USNM) — United States
asiaticus Bernhauer, 1915 - Syn (FMNH, BMNH), Sp (MNKB) — Uzbekistan, Tajikistan
asirensis Frisch, 2007 - Lit. Att. — [Saudi Arabia, Yemen]
assingi Frisch, 2010 - Lit. Att. — [Turkey]
auripilis Cameron, 1913 - Syn (BMNH) — West Indies
australiensis Frisch, 2005 - P (MNKB) — Australia
azerbaidzhanus Gusarov, 1994 - Sp (NHMW, SDEI, MNKB) — Azerbaijan/Iran
baliensis Frisch, 2005 - Sp (NHMW) — Indonesia
bamaniaensis Fagel, 1973, transferred to *Hyperscopaeus*
beesoni Cameron, 1931 - Syn (BMNH), Syn, Sp (FMNH) — India
beieri Scheerpeltz, 1963 - Lit. Att. — [Sudan]
bertiae Frisch, 1999 - P (BMNH) — Morocco
bicolor Baudi, 1848 - Sp (BMNH, SDEI) — Italy, Libya
bicuspis Kraatz, 1859 - Syn (SDEI), Sp (FMNH) — India orientale, Vietnam
bilaminulatus Scheerpeltz, 1958 - Pl (NHMW) — Turkey
binaghii Frisch, 2001 - Lit. Att. — [Morocco]
bingervillensis Fagel, 1973 - H (MRAC), P (BMNH) — Ivory Coast, Nigeria
biskrensis Fagel, 1957 - P (IRSN), Sp (NHMW, SDEI, MNKB) — Algeria, Spain, Italy
bituberculatus Frisch, 2002 - H, P (MNKB) — Turkey
blackburni Bernhauer and Schubert, 1912 — [replacement name]

  femoralis Blackburn, 1892 - T (BMNH) — Australia

borbonicus Lecoq, 1987 - Lit. Att. — [Réunion]
borneensis Cameron, 1941, transferred to *Hyperscopaeus*
borumandi Frisch, 2010 - H, P (MNKB) — Iran
boxi Blackwelder, 1943 - H (USNM), P (FMNH) — Saint Lucia
brachypterus Casey, 1905 - Syn (USNM), Sp (FMNH) — United States
brasiliensis Bernhauer, 1934 - Syn (FMNH, BMNH) — Brazil
bredoanus Fagel, 1973, transferred to *Hyperscopaeus*
brevicuspis Binaghi, 1935 - Sp (BMNH, SDEI) — Corsica, Sardinia
brevipennis Sharp, 1886 - H (BMNH) — Guatemala
brunnescens Fagel, 1956 - H (BMNH), P (IRSN) — Ethiopia
brunnipes LeConte, 1880 - Sp (AMNH) — United States
burgeonianus Fagel, 1973 - H (MRAC) — D.R. Congo
calidus Bernhauer, 1932, transferred to *Hyperscopaeus*

californicus (Fall, 1901) - Lit. Att. — [United States]
camelaensis Fagel, 1973 - H (MRAC), P (BMNH) — Angola, Zambia
cameroni Coiffait, 1968 - H (BMNH), Sp (NHMW, SDEI, MNKB) — Bulgaria, Turkey

lemnicus Coiffait, 1968 - H, P (BMNH) — Greece
turcicus Coiffait, 1968
armeniacus Coiffait, 1968
ectypus Coiffait, 1971
illyricus Frisch, 1997 - H (NHMW) —Albania

cariensis Frisch, 2002 - H, P (MNKB) — Turkey
carissimus Sharp, 1886 - H (BMNH) — Guatemala
carolinae Casey, 1905 - Syn (USNM), Sp (FMNH) — United States
caseyi Scheerpeltz, 1933 - [replacement name] *procerus* (Casey, 1905) - Syn (USNM) — United States
caspius Frisch, 2015 - Lit. Att. — [Azerbaijan]
celisianus Fagel, 1973 - H (MRAC) — D.R. Congo
ceylonensis Frisch, 2005 - P (MNKB) — Sri Lanka
chalcodactylus (Kolenati, 1846) - Sp (MNKB, SDEI) — Turkey, Caucasus
championi Binaghi 1935 - Sp (MNKB) — Austria
chapini Blackwelder, 1943 - H (USNM) — Jamaica
chatkalensis Frisch, 2015 - Lit. Att. — [Kyrgyzstan]
chinensis Frisch, 2011 - P (MNKB) — China
chiriquensis Sharp, 1886 - H (BMNH) — Panama

New combination, transferred from *Scopaeomerus*

cinctipennis Jarrige, 1970 - Lit. Att. — [Madagascar]
complex Sharp, 1874 - Syn (BMNH), Sp (FMNH) Japan
concavus Hatch, 1957 - H (USNM) — United States
concolor Sharp, 1886 - Syn (BMNH), Syn, Sp (FMNH) — Mexico, Guatemala, Brazil
confusoides Fagel, 1973, transferred to *Hyperscopaeus*
confusus Fagel, 1973, transferred to *Hyperscopaeus*
consimilis Fagel, 1973, transferred to *Hyperscopaeus*
convexiceps Bernhauer, 1932, transferred to *Hyperscopaeus*
coriaceus (Cameron, 1932) - Syn (BMNH) — Malaysia
corpulentus Fagel, 1973, transferred to *Hyperscopaeus*
courtoisi Lecoq, 1987 - Lit. Att. — [Mauritius]
crassipes crassipes Wollaston, 1867 - Lit. Att — [Ivory Coast, Cape Verde Islands, Mauritania, Algeria, Egypt, "East Africa," Tanzania, Rwanda]

tassiliensis Jarrige, 1958
mauretanicus Coiffait, 1960

crassipes angolensis Fagel, 1973 - Lit. Att. — Angola, D.R. Congo]
crassitarsis (Sharp, 1886) - H (BMNH) — Guatemala

New combination, transferred from *Euscopaeus*

crassulus Casey, 1905 - Syn (USNM) — United States
creticus Frisch, 1994 - P (MNKB), Sp (NHMW) — Greece
ctenocryptus Lea, 1923 - Syn (SAMA), Sp (FMNH) — Australia
cupiens Blackwelder, 1943 - H (USNM) — Jamaica
currax Sharp, 1889 - Syn (BMNH), Sp (FMNH, MNKB) — China, Japan
curraxoides Adachi, 1955 - Lit. Att. — [Japan]
curtipennis Schubert, 1909 - Syn (FMNH) Mexico
cylindricus Ochs, 1953 - Lit. Att. — [France, Spain]
cyprius Frisch, 1997 - P (MNKB) — Cyprus
darlingtoni Blackwelder, 1943 - Lit. Att. — [Cuba]
debilis Hochhuth, 1851 - Sp (FMNH) — Tunisia, Israel, Saudi Arabia, Ethiopia

scitulus Baudi, 1857 - Pl (SDEI) — Italy
boops Scheerpeltz, 1931
ibericus Coiffait, 1952
afghanicus Scheerpeltz, 1960

decelleanus Fagel, 1973, transferred to *Hyperscopaeus*
degener Casey, 1905 - Syn (USMN), Sp (FMNH) — United States

delicatissimus Bernhauer, 1937 - H (FMNH) — Tanzania

trivialis Cameron, 1951 - H (BMNH) — Sierra Leone

delicatulus Sharp, 1886 - Syn (BMNH, FMNH) — Panama

delicatus Casey, 1905 - Syn (USNM) — United States

densicollis Cameron, 1932 - Syn (BMNH) — Malaysia

desaegerianus desaegerianus Fagel, 1973 - H (MRAC), P, Sp (BMNH) — South Africa, Zimbabwe, D.R. Congo

desaegerianus secludatus Fagel, 1973 - H (MRAC) — South Africa

didymus Erichson, 1840 - L (MNKB), Sp (FMNH, SDEI, MNKB) — Corsica, Sardinia, Sicily, Italy, Spain

mateui Coiffait, 1953

digitalis Fauvel, 1878 - T (BMNH) — Australia

dilutus Motschulsky, 1858 - Syn (ZMUM), Sp (FMNH) — China, Java, Philippines, Sri Lanka, Sumatra, Vietnam, "Indes orientales"

discoidalis Sharp, 1886 - Syn (BMNH, FMNH) — Guatemala

dissentaneus Fagel, 1973 - [replacement name] Sp (MRAC) — Angola

gratellus Cameron, 1951 - Syn (BMNH), Sp (MRAC) — Angola

dissimilis Sharp, 1886 - Syn (BMNH, FMNH) — Panama

distans Sharp, 1876 - Syn (BMNH), Syn, Sp (FMNH) — Brazil

diversiceps Bernhauer, 1939 - H (FMNH) — Argentina

dolosus Fagel, 1973, transferred to *Hyperscopaeus*

dominicanus Blackwelder, 1943 - Lit. Att. — [Dominican Republic]

dubius Blackburn, 1891 - Sp (FMNH), Syn (BMNH; note: head and prothorax missing; generic assignment uncertain) — Australia

durus Fagel, 1973 - H (IRSN) — Eritrea

duryi (Casey, 1905) - Syn (USNM) — United States

ebneri Scheerpeltz, 1929 - Sp (MNKB) — Cyprus, Lebanon

efesi Frisch, 2002 - H, P (MNKB) — Turkey

effundatus Fagel, 1973 - H (MRAC) — D.R. Congo

elaboratus (Casey, 1905) - Syn (USNM), Sp (FMNH) — United States

elegans Luze, 1910 - H, P (NHMW), Sp (MNKB) — Lebanon, Turkey

pseudoelegans Bordoni, 1980

elegantulus Cameron, 1930 - H (BMNH) — Malaysia

elgonensis Levasseur, 1981 - Lit. Att. — [Kenya]

elisabethvillensis Fagel, 1973 - Sp (BMNH, MRAC) — Zambia, D.R. Congo

endrodyanus Fagel, 1973, transferred to *Hyperscopaeus*

errans Fagel, 1973, transferred to *Hyperscopaeus*

erraticus Fagel, 1973, transferred to *Hyperscopaeus*

evagatus Fagel, 1973 - Lit. Att. — [Congo Republic]

exiguus Erichson, 1840 - Syn (MNKB), Sp (FMNH) — United States

fageli Coiffait, 1960 - Sp (SDEI) — Morocco

kerdousensis Coiffait, 1973

fageli Levasseur, 1981, transferred to *Hyperscopaeus*

fagelianus Coiffait, 1969 - Sp (MNKB) — Turkey

fallaciosus Fagel, 1973, transferred to *Hyperscopaeus*

farsensis Frisch, 2007 - H, P (MNKB) — Iran

fasciatellus Erichson, 1840 - Lit. Att. — [Puerto Rico]

fauveli Fagel, 1956 - Lit. Att. — [Ethiopia]

femineus (Moore and Legner, 1975) - Lit. Att. — [United States]

femoralis Sharp, 1887, transferred to *Orus*

femursetosus Frisch, 2006 - H (MNKB) — Iran

ferganensis Frisch, 2014 - Lit. Att. — [Kyrgyzstan, Uzbekistan]

filicornis Fagel, 1973, transferred to *Hyperscopaeus*

filiformis Wollaston, 1867 - Sp (BMNH, SDEI, MNKB) — Aden, Angola, Botswana, Cape Verde, Egypt, Ethiopia, Gambia, Nigeria, South Africa, Sudan, Uganda, Indonesia, Thailand, Laos

tenuis Eppelsheim, 1885
sutteri Scheerpeltz, 1957
richteri Scheerpeltz, 1961
schaeuffelei Scheerpeltz, 1961
schremmeri Scheerpeltz, 1963

filitarsis Sharp, 1886 - Syn (BMNH, FMNH) — Guatemala, Mexico

filum Sharp, 1886 - Syn (BMNH, FMNH) — Guatemala

flavidulus Fagel, 1973, transferred to *Hyperscopaeus*

flavocastaneus Lea, 1923, transferred to *Hyperscopaeus*

flavofasciatus Frisch, 1998 - P (MNKB) — Cyprus

fluviatilis Fagel, 1973, transferred to *Hyperscopaeus*

fossiceps Eppelsheim, 1885, transferred to *Hyperscopaeus*

franzi Coiffait, 1968 - Sp (MNKB) — Portugal
tricuspis Outerelo, 1978

frater Lynch Arribálzaga, 1884 - Sp (BMNH, FMNH) — Argentina, Brazil

frommeri (Moore and Legner, 1972) - Lit. Att. — [United States]

fuliginosus Fagel, 1973, transferred to *Hyperscopaeus*

fulvescens (Motschulsky, 1858), transferred to *Hyperscopaeus*

fulvus Cameron, 1931 - L, Pl (BMNH), Sp (MNKB) — India, Thailand, Laos, Vietnam

fusculus (Motschulsky, 1858), transferred to *Hyperscopaeus.*

galapagosus Coiffait, 1981 - Lit. Att. — [Galapagos Islands]

galinae Gusarov, 1991 - Sp (MNKB) — Uzbekistan, Turkmenistan

gangtokensis Biswas, 2003 - Lit. Att. — [India]

garambanus Fagel, 1973 - Sp (MRAC) — D.R. Congo

germanus Cameron, 1931 - Syn (BMNH), Sp (FMNH) — India

gigantulus Bernhauer, 1929, transferred to *Hyperscopaeus*

gilensis Casey, 1905 - Syn (USNM) — United States

girardi Levasseur, 1981 - Lit. Att. — [Ivory Coast]

girardianus Fagel, 1973, transferred to *Hyperscopaeus*

gissarensis Frisch, 2014 - Lit. Att. — [Uzbekistan]

giulianii (Moore and Legner, 1972) - Lit. Att. — [United States]

gladifer Binaghi, 1935 - Sp (NHMW, MNKB) — Bulgaria, Ukraine
bulgaricus Coiffait, 1971

gomyi Lecoq, 1987 - Lit. Att. — [Mauritius]

gracilicornis (Sharp, 1886) - Syn (BMNH) — Guatemala

New combination, transferred from *Euscopaeus.*

gracilis (Sperk, 1835) - N (MNKB), Sp (FMNH, SDEI) — Austria, Czechoslovakia, Italy, Poland, Yugoslavia, Greece

erichsonii Kolenati, 1846 - L (MNKB) — Transcaucasus
apicalis Mulsant and Rey, 1855
trossulus Wollaston, 1864
koestlinianus Scheerpeltz, 1970

graecus Frisch, 1994 - P (MNKB), Sp (NHMW, SDEI) — Albania, Greece, Montenegro

grandicollis Bernhauer, 1910 - H (FMNH) — Mexico

grandipennis Bernhauer, 1941 - H (FMNH) — Peru

graskopensis Fagel, 1973 - P (BMNH) — South Africa

guatemalensis (Sharp, 1886) - H (BMNH) — Guatemala

New combination, transferred from *Scopaeomerus*

gusarovi Frisch, 2009 - H, P (MNKB) — Georgia, Azerbaijan

gustavkraatzi Frisch, 2005 - Lit. Att. — [Myanmar]

haemusensis Frisch, 1997 - H, P (NHMW), P (MNKB) — Bulgaria

heinzi Korge, 1971 - Lit. Att. — [Turkey]

hercegovinensis Frisch, 1998 - Lit. Att. — [Bosnia Herzegovina]

hermani Frisch, 2003 - P (BMNH, MNKB) — Solomon Islands

hiekei Frisch, 2014 - Lit. Att. — [Kazakhstan]

hispanicus Binaghi, 1935 - Sp (NHMW, MNKB) — Spain

gredensis Coiffait, 1968

hova Fauvel, 1905 - transferred to *Hyperscopaeus*

hudsonicus Casey, 1905 - Syn (USNM), Sp (FMNH) — United States

hulstaertianus Fagel, 1973, transferred to *Hyperscopaeus*

humidulus Cameron, 1932 - Syn (BMNH) — Malaysia

humilis Cameron, 1931 - Sp (FMNH) — India

hyrcanus Frisch, 2006 - H, P (MNKB) — Iran

illustris Fauvel, 1863 - Syn (IRSN) — Venezuela

imbecillus Frisch, 2009 - H, P (MNKB) — Turkey

impar (Bierig, 1935) - H (FMNH) — Panama **New Combination**, transferred from *Euscopaeus.*

indiensis Frisch, 2005 - P (BMNH) — India

insidiosus Fagel, 1973 - P (MRAC) — South Africa

intermixtus Fagel, 1973, transferred to *Hyperscopaeus*

interocularis Lea, 1912 - Syn (SAMA) — Australia

iranensis Frisch, 2006 - H, P (MNKB) — Iran

jacobsoni Cameron, 1930 - H (BMNH) — Indonesia

janaki Frisch, 2005 - H (MNKB), P (MNKB, BMNH) — India, Sri Lanka, Reunion

japonicus Cameron, 1933 - H (BMNH), Sp (FMNH) — China, Japan, Taiwan

javanus Cameron, 1936 - Syn (BMNH) — Indonesia

jeanneli Levasseur, 1981 - Lit. Att. — [Kenya]

kabakovi Gusarov, 1994 - Sp (MNKB) — Austria

kasongensis Fagel, 1973 - H (MRAC), P (BMNH) — D.R. Congo, Sierra Leone

kastcheevi Frisch, 2012 - H, P (MNKB) — Kazakhstan

kaszabianus Fagel, 1973, transferred to *Hyperscopaeus*

katanganus Fagel, 1973, transferred to *Hyperscopaeus*

kermanensis Frisch, 2010 - H, P (MNKB) — Iran

khnzoriani Coiffait, 1968 - Sp (MNKB) — Turkey

kivuanus Fagel, 1973, transferred to *Hyperscopaeus*

kivuensis Fagel, 1973 - H (MRAC) — D.R. Congo

klapperichi Frisch, 2008 - Lit. Att. — [Afghanistan]

kokodanus Cameron, 1938 - H (BMNH) — Papua New Guinea

korelli Frisch, 1999 - H (MNKB) — Turkey

korgei Frisch, 2006 - Lit. Att. — [Turkey]

kovaci Frisch, 1996 - P (NHMW, SDEI, MNKB), Sp (BMNH) — Spain, Morocco, Algeria

kurdistanicoides Frisch, 2002 - H, P (MNKB) — Turkey

kurdistanus Korge, 1971 - Sp (MNKB) — Turkey, Iran

laevigatus (Gyllenhal, 1827) - Sp (FMNH, SDEI, MNKB) — France, Germany, Czech Republic, Austria, Greece, Cyprus

schneideri Bernhauer, 1900 - L, Pl, Sp (FMNH)

laevis Sharp, 1876 - H (BMNH) — Brazil

lamtoensis Fagel, 1973, transferred to *Hyperscopaeus*

lanceolatus Binaghi, 1935 - P (NHMW) Sp (SDEI, MNKB) — Austria, Italy, France

latebricola Blackburn, 1888 - T (BMNH), Sp (FMNH) — Australia

laticollis Cameron, 1925 - Syn (SDEI) — Indonesia

latitarsis Sharp, 1886 - H (BMNH), Sp (FMNH) — Panama, Costa Rica

laxus Sharp, 1876 - Syn, Sp (BMNH, FMNH) — Argentina, Brazil, Chile

leleupi Cameron, 1952 - Syn (MRAC, BMNH) — D.R. Congo

leleupianus Fagel, 1973, transferred to *Hyperscopaeus*

leopoldvillensis Fagel, 1973, transferred to *Hyperscopaeus*

lescuyeri Delaunay, Coache, and Rainon, 2019, transferred to *Hyperscopaeus* *levasseuri* Lundgren, 1982, transferred to *Hyperscopaeus*

ligulifer Sharp, 1886 - Syn (BMNH); Sp (FMNH) — Panama

likovskyi Boháč, 1988 - Sp (SDEI) — Tajikistan

limbatus Kraatz, 1859 - Sp (FMNH, MNKB) — Taiwan, Philippines, Sri Lanka

linearis Notman, 1919 - Sp (AMNH) — Canada

littoralis Ochs, 1958 - Lit. Att. — [France]

loebli Frisch, 1997 - P (NHMW, MNKB) — Turkey, Syria

longicollis Fauvel, 1873 - L (IRSN), Sp (MNKB) — France, Switzerland

longicornis Fauvel, 1905 - Sp (FMNH, MNKB) — Madagascar, Tanzania

longilobatus Frisch, 2014 - Lit. Att. — [Kyrgyzstan]

longipennis (Fall, 1901) - Sp (FMNH) — United States

longiusculus Fagel, 1973, transferred to *Hyperscopaeus*

loxias Fagel, 1973, - Lit. Att. — [D.R. Congo]

lucidus Cameron, 1931 - Syn (BMNH) — India

luctuosus Bernhauer, 1932 - Syn, Sp (FMNH, MRAC) — Cameroon, D.R. Congo

  bernhaueri Cameron, 1951 - H (BMNH) — D.R. Congo

ludificatorius Fagel, 1973 - Lit. Att. — [Eritrea]

ludificatus Fagel, 1973 - P (MRAC) — South Africa

lugubris Lynch Arribálzaga, 1884 - Sp (FMNH) — Argentina

lungwensis Fagel, 1973 - H (MRAC) — D.R. Congo

luzonicus Cameron, 1941 - Syn (BMNH) — Philippines

machadoanus Fagel, 1973, transferred to *Hyperscopaeus*

macilentus Casey, 1905 - Syn (USNM), Sp (FMNH) — United States

madagascarensis Frisch, 1999 - P (MNKB), Sp (NHMW) — Madagascar

major Eppelsheim, 1885, transferred to *Hyperscopaeus*

marginalis Cameron, 1932 - Syn (BMNH) — Malaysia

marginatus Cameron, 1913 - Syn (BMNH) — Jamaica

mariae Frisch, 2002 - H (MNKB) — Iran

masaicus Fagel, 1973 - H (MRAC) — Tanzania

mendosus Fagel, 1973 - H (MRAC), Sp (IRSN, MNKB) — D.R. Congo, Namibia

menteshensis Anlaş and Frisch, 2014 - Lit. Att. — [Turkey]

meridioafricanus Frisch, 2007 - H (MNKB), P (MNKB) — Namibia, South Africa

meridioanatolicus Frisch, 2009 - H, P (MNKB) — Turkey

methneri Bernhauer, 1932, transferred to *Hyperscopaeus*

micropterus Fauvel, 1873 - Sp (NHMW, MNKB, SDEI) — Italy

micros Kraatz, 1859 - Syn (SDEI), Sp (FMNH) — Java, Philippines, Sri Lanka

milkoi Frisch, 2015 - Lit. Att. — [Kyrgyzstan]

minimus (Erichson, 1839) - L, Pl (MNKB), Sp (FMNH, MNKB) — France, Germany, Austria

  furcatus Binaghi, 1935
  pamphylicus Coiffait, 1969

minutoides Coiffait, 1969 - Sp (BMNH, SDEI, MNKB) — Turkey

minutulus Fagel, 1973, transferred to *Hyperscopaeus*

minutus Erichson, 1840 - [*Nomen protectum*] - L, Pl (MNKB), Sp (FMNH, SDEI, MNKB) — France, Germany, Austria, Bosnia Herzegovina

  pumilus (Heer, 1839) - [*Nomen oblitum*, see Herman, 2003: 15]
  debilis Mulsant and Rey, 1855
  intermedius Mulsant and Rey, 1844 - Sp (FMNH) — Austria
  gracilipes Edmonds, 1933

miscellus (Cameron, 1932) - Lit. Att. — [Malaysia]

mitratus Binaghi, 1935 - H (MSNG), Sp (SDEI, MNKB) — Italy

mixtus Cameron, 1941 - Syn (BMNH) — Malaysia

moerens Lea, 1923 - Syn (SAMA) — Australia

mollis Sharp, 1886 - Syn (BMNH), Sp (FMNH) — Guatemala, Costa Rica, Panama

molo Fagel, 1973 - P (MRAC) — Congo

montalbanensis Bernhauer, 1912 - Syn, Sp (FMNH) — Philippines

monticola Cameron, 1931 - Syn (BMNH) — India

***morituru*s** Frisch, 2015 - Lit. Att. — [Kyrgyzstan]

muehlei Frisch, 1994 - H, P (MNKB) — Crete

muhiensis Fagel, 1973 - H (MRAC) — D.R. Congo

mulongoensis Fagel, 1973, transferred to *Hyperscopaeus*

mutatus Gemminger and Harold, 1868 - [Replacement name] Sp (MNKB) — Iran, Georgia

pusillus Hochhuth, 1849
talyschensis Coiffait, 1968
koestlini Scheerpeltz, 1970

myrmecocephalus Lea, 1927 - H (SAMA) — Fiji

naomii Frisch, 2003 - P (MNKB) — Japan

nepalensis Scheerpeltz, 1976 - Lit. Att. — [Nepal]

nepalicus Coiffait, 1975 - H (NHMW) — Nepal

nevermanni Bernhauer, 1942 - Syn (FMNH) — Costa Rica

nicanor Fagel, 1973 - P (MRAC) — D.R. Congo

nicetius Fagel, 1973 - H (MRAC) — D.R. Congo

nigellus Wollaston, 1864 - Lit. Att. — [Canary Islands]

niger Cameron, 1918 - Syn (BMNH) — Singapore

nigerrimus Cameron, 1945 - H (BMNH) — South Africa

nimius Fagel, 1973 - H (MRAC) — D.R. Congo

nipponensis Frisch, 2003 - Lit. Att. — [Japan]

nitidiceps Fagel, 1973, transferred to *Hyperscopaeus*

nitidicollis Fagel, 1973, transferred to *Hyperscopaeus*

nitidipennis Cameron, 1950 - Lit. Att. — [South Africa]

nitidulus Motschulsky, 1858 - Sp (FMNH, NHMW, MNKB) — India, Thailand, Malaysia, Indonesia, Philippines

nitidus (LeConte, 1863) - Sp (FMNH) — United States

notangulus Casey, 1905 - Syn (USNM) — United States

notmani Scheerpeltz, 1933 - [Replacement name]

pallidus (Notman, 1921) - Lit. Att. — [United States]

obscuripennis Blackburn, 1891 - Syn (BMNH), Syn? (SAMA) — Australia

obscuripes Cameron, 1931 - L, Pl, Sp (BMNH) — India

obscurus Sharp, 1886 - Syn (BMNH, FMNH), Sp (FMNH) — Guatemala, Mexico

obscurus (Sharp, 1886) - H (BMNH) — Panama **New combination**, transferred from *Scopaeomerus*

ooderes Lea, 1923 - H (SAMA) — Australia

opaciceps Cameron, 1932 - Syn (BMNH) — Malaysia

opacicollis Bernhauer, 1942, transferred to *Hyperscopaeus*

opacus (LeConte, 1863) - Sp (FMNH) — United States

orbiceps Cameron, 1931 - Syn (BMNH) — India

ornatus Sharp, 1876 - Syn (BMNH, FMNH) — Brazil

orophilus Fagel, 1973 - H (MRAC) — D.R. Congo

overlaetianus Fagel, 1973, transferred to *Hyperscopaeus*

oviceps Bernhauer, 1920 - Syn (FMNH) — Australia

pakistanensis Frisch, 2007 - P (MNKB) — Pakistan

palaestinus Frisch, 1998 - P (MNKB) — Israel

paliferus Frisch, 2011 - P (MNKB) — Russia

pallens (Casey, 1905) - Syn (USNM) — United States

palmatus (Sharp, 1886) - Syn (BMNH) — Panama

New combination, transferred from *Scopaeomerus*

paludicola Cameron, 1945 - Syn (BMNH) — South Africa

pallipes Cameron, 1945 - Syn (BMNH) — South Africa

parvicornis Fauvel, 1900, transferred to *Hyperscopaeus*

parvipterus Coiffait, 1980 - Lit. Att. — [French Polynesia]

pauliani Jarrige, 1951 - Lit. Att.(incertae sedis) — [Madagascar]

pauper Sharp, 1876 - H (BMNH), Sp (FMNH) — Brazil, Trinidad

pellionis Fagel, 1973 - H (MRAC) — D.R. Congo

penangensis Cameron, 1950 - Syn (BMNH) — Malaysia

peregrinus Fauvel, 1907 - P (MRAC), Sp (FMNH) — South Africa

perroti Ochs, 1955 - H (MHNG), Sp (NHMW, SDEI, MNKB) — Morocco, Algeria, Tunisia

persicus Frisch, 1994 - Sp (MNKB) — Iran

persimilis Cameron, 1951 - H (BMNH) — Angola

philippinensis Frisch, 2003 - P (BMNH, NHMW, MNKB) — Philippines

piceolus Sharp, 1886 - Syn (BMNH) — Guatemala

picipes (Casey, 1885) - Syn (USNM), Sp (FMNH) — United States

poggii Frisch, 2007 - Lit. Att. — [Italy]

politus Sharp, 1886 - Syn (BMNH, FMNH) — Guatemala

ponticus Frisch, 1999 - P (MNKB), Sp (NHMW) — Turkey

portai Luze, 1910 - L, Pl (NHMW), Sp (SDEI, MNKB) — Italy, Menorca, Morocco

bordei Peyerimhoff, 1914
laneyriei Coiffait, 1952
temperei Coiffait, 1952
lusitanicus Coiffait, 1968
marocanus Coiffait, 1970

potamus Blackwelder, 1943 - H (USNM), P (FMNH) — Saint Lucia

procerus Kraatz, 1859, transferred to *Hyperscopaeus*

proculus Normand, 1935 - Sp (FMNH) — Tunisia

cordifer Binaghi, 1935

prolixipennis (Casey, 1910) - Syn (USNM) — United States

pruinosulus Eppelsheim, 1885, transferred to *Hyperscopaeus*

pseudomethneri Fagel, 1973, transferred to *Hyperscopaeus*

puberulus Kraatz, 1859, transferred to *Hyperscopaeus*

pulchellus Erichson, 1840 - Syn (MNKB), Sp (FMNH) — Grenada, Guatemala, Venezuela

apicipennis Sharp, 1886 - Syn (BMNH, FMNH)

punctatellus Fauvel, 1905 - L (IRSN), Sp (BMNH, FMNH, MRAC, SDEI, MNKB) — South Africa, Botswana, Zimbabwe, Zambia, Madagascar, Tanzania, Kenya, D.R. Congo, Ivory Coast, Guinea

sharpi Cameron, 1912 - Syn (BMNH)
gratellus Cameron, 1950 - H (BMNH)

puncticeps Kraatz, 1859 - Syn (SDEI), Sp (FMNH) — India orientale, Philippines

punctithorax Bernhauer, 1927 - Syn (FMNH) — Argentina

puritanus (Casey, 1905) - Syn (USNM) — United States

pusilloides Frisch, 1997 - H (NHMW) — Spain

pusillus Kiesenwetter, 1843 - L (SDEI), Sp (MNKB) — Germany, Russia, Greece

abbreviatus Mulsant and Rey, 1855

puthzi Frisch, 1994 - H (MNKB) — Greece

pygmaeus Erichson, 1840 - Sp (FMNH) — West Indies

simplicicollis Cameron, 1913 - Syn (BMNH) — West Indies

qohrudensis Frisch, 2008 - H, P (MNKB) — Iran

quadriceps Notman, 1920 - Lit. Att. — [United States]

quadripennis Casey, 1905 - Syn (USNM) — United States

rambouseki (Bierig, 1934) - H, P (FMNH) — Cuba

reduncus Fagel, 1973, transferred to *Hyperscopaeus*

ripicola Fagel, 1973, transferred to *Hyperscopaeus*

rivularis Blackwelder, 1943 - H (USNM), P (FMNH) — Jamaica

rotundiceps Casey, 1886 - Syn (USNM) — United States

ruandensis Fagel, 1973 - H (MRAC) — Rwanda

rubidus Mulsant and Rey, 1855 - Sp (FMNH, SDEI, MNKB) — Austria, Italy, Spain
  subcylindricus Scriba, 1868
rubricollis Fagel, 1973, transferred to *Hyperscopaeus*
rubrotestaceus Kraatz, 1859, transferred to *Hyperscopaeus*
rudis Fauvel, 1891 - Syn (IRSN) — Venezuela
ruficollis Fauvel, 1877 - H (IRSN), Sp (FMNH) — Australia
rufulus (Kraatz, 1859) - Syn (SDEI) — India orientale
rugegensis Fagel, 1973 - H (MRAC) — Rwanda
rugosulus Fagel, 1973 - H (MRAC) — D.R. Congo
ruguliceps Fagel, 1973, transferred to *Hyperscopaeus*
rulomus Blackwelder, 1943 - H (USNM) — Jamaica
ruwenzoriensis Fagel, 1973 - H (MRAC) — D.R. Congo
ruziziensis Fagel, 1973, transferred to *Hyperscopaeus*
ryei Wollaston, 1872 - Sp (BMNH, SDEI, MNKB) — Austria, France, Germany

  baudrimonti Coiffait, 1952
  jarrigei Coiffait, 1953
  forcipis Ochs, 1955

saginellus Casey, 1905 - Syn (USNM) — United States
salvini Sharp, 1886 - Syn (BMNH, FMNH) — Guatemala
sarawakensis Frisch, 2005 - Lit. Att. — [Malaysia]
sareptanus Gusarov, 1992 - H (ZISP), Sp (MNKB) — Russia, Kazakhstan
satricus satricus Fagel, 1973 - H (MRAC), P (BMNH) — D.R. Congo
satricus meges Fagel, 1973 - H (MRAC) — South Africa
schawalleri Frisch, 2015 - Lit. Att. — [Kyrgyzstan]
schillhammeri Frisch, 1994 - H (NHMW), Sp (MNKB) — Turkey, Iran
schuelkei Frisch, 2003 - P (BMNH, NHMW, SDEI, MNKB) — Japan, Taiwan, China
schusteri Scheerpeltz, 1965 - Syn (NHMW), Sp (MNKB) — Greece

  cerrutii Coiffait, 1976

scotti Fagel, 1956 - H (BMNH), Sp (IRSN) — Ethiopia, D.R. Congo
semicornis Bernhauer, 1942 - Syn (FMNH) — Costa Rica
semifuscus Kraatz, 1859, transferred to *Hyperscopaeus*
senegalensis Fagel, 1973, transferred to *Hyperscopaeus*
sericans Mulsant and Rey, 1855 - Syn (IRSN), Sp (FMNH, SDEI) — .France, Italy
serriae Frisch, 2006 - H (MNKB) — Iran
seydeli Cameron, 1952, transferred to *Hyperscopaeus*
siamensis Frisch, 2005 - H, P (MNKB), P (BMNH, NHMW) — Thailand, China
siculus Binaghi, 1935 - Lit. Att. — [Italy]
signifer Fauvel, 1899 - L (IRSN), Sp (BMNH, MNKB) — Libya, Tunisia, Iraq, Iran

  kochi Binaghi, 1935
  remsensis Coiffait, 1973

similaris Fagel, 1973 - H (MRAC) — D.R. Congo, Congo Republic
similis similis Eppelsheim, 1892 - L, Pl (NHMW), Sp (FMNH, MNKB) — Uzbekistan, Kyrgyzstan
similis minor Frisch, 2014 - Lit. Att. — [Iran, Turkmenistan]
simillimus Fagel, 1973, transferred to *Hyperscopaeus*
simulator Fagel, 1973, transferred to *Hyperscopaeus*
sinaicus Coiffait, 1970 - Lit. Att. — [Egypt, Israel]

  saoudiensis Coiffait, 1981 - H (NHMB) — Saudi Arabia

socotrensis Frisch, 2015 - Lit. Att. — [Yemen]
solomonensis Frisch, 2005 - H, P (BMNH), P (MNKB) — Solomon Islands
sonoricus (Casey, 1905) - Syn (USNM) — United States
spathiferus Coiffait, 1970, transferred to *Hyperscopaeus*

spectralis (Casey, 1910) - Syn (USNM) — United States

spinosophallatus Frisch, 2012, transferred to *Hyperscopaeus*

stramineus Frisch, 2007 - H, P (MNKB) — Iran

subconfusus Fagel, 1973, transferred to *Hyperscopaeus*

subfasciatus Kraatz, 1859 - L, Pl (SDEI), Sp (BMNH, NHMW, MNKB) — Nigeria, Sudan, Zaire, Zambia, Botswana, Namibia, India, Sri Lanka, Thailand, Laos

laetus Eppelsheim, 1885 - Syn, Sp (FMNH, NHMW), Sp (MRAC) — Ghana, Ivory Coast, Sudan, D.R. Congo
nitiduloides Cameron, 1931 - L, Pl (BMNH) — India
collarti Cameron, 1935
mirei Jarrige, 1968

subopacus Wollaston, 1860 - Lit. Att. — [Madeira]
maderae Coiffait, 1960

subprocerus Coiffait, 1978, transferred to *Hyperscopaeus*

sulcicollis (Stephens, 1833) - Sp (FMNH, SDEI, MNKB) — Austria, Czechoslovakia, Germany, Hungary, Italy, USSR, Yugoslavia

cognatus Mulsant and Rey, 1855

sumbaensis Scheerpeltz, 1957 - Sp (MNKB) — Indonesia

ivani Frisch, 2003 - P (MNKB) — Indonesia

summicola Fagel, 1973 - H (MRAC) — D.R. Congo

sundaensis Frisch, 2005 - P (BMNH, MNKB) — Indonesia, Reunion

surdus Fagel, 1973, transferred to *Hyperscopaeus*

suspectus Fauvel, 1907, transferred to *Hyperscopaeus*

tahitiensis Coiffait, 1977 - H (MNHN), Sp (BMNH) — Society Islands

tarsalis Sharp, 1876 - H (BMNH) — Brazil

tauricus Frisch, 1997 - Sp (MNKB) — Turkey

tchapembanus Fagel, 1973, transferred to *Hyperscopaeus*

testaceipes Lea, 1923 - Syn (SAMA) — Australia
gracilis Oke, 1933
okei Herman, 2003

testaceus (Motschulsky, 1858) - Lit. Att. — [Japan, Taiwan, China, Vietnam, Laos, Cambodia, Indonesia, Singapore, Malaysia, Thailand, "India orientali," India, Sri Lanka, France]

suturalis Kraatz, 1859
quadraticeps Bernhauer, 1938
rufescens Adachi, 1955
pseudolaevigatus Ochs, 1955
loeffleri Scheerpeltz, 1971

texanus (Casey, 1886) - Syn (USNM), Sp (FMNH) — United States

thoracicus (Motschulsky, 1858), transferred to *Hyperscopaeus*

tibialis Coiffait and Saiz, 1968 - Lit. Att. — [Chile]

tigreanus Bernhauer, 1939 - H (FMNH) — Argentina

tonkinensis Cameron, 1946 - P? (BMNH, MNHN) — Vietnam

transvaalensis Fagel, 1973 - P (MRAC) — South Africa

trapeziceps Frisch, 2003 - P (MNKB), Sp (BMNH) — China, Japan

triangularis Luze, 1904 - L, Pl (NHMW) — Uzbekistan

trifurcatus Frisch, 2002 - H, P (MNKB) — Turkey

tristis Bernhauer, 1929, transferred to *Hyperscopaeus*

truncaticeps Casey, 1886 - Syn (USNM) — United States

tsaratananus Jarrige, 1970 - Lit. Att. — [Madagascar]

tshuapaensis Fagel, 1973 - H (MRAC) — D.R. Congo

tucumanensis Bernhauer, 1939 - H (FMNH) — Argentina

tumbaensis Fagel, 1973 - H (MRAC) — D.R. Congo

turkestanicus Frisch, 2012 - H, P (MNKB) — Kazakhstan

udus Fagel, 1973 - H, P, Sp (BMNH), P (MRAC, SDEI, MNKB) — Zambia, Zimbabwe, Botswana, Namibia, Angola, South Africa

ulughdaghensis Frisch, 2010 - H (MNKB) — Iran

uluguruensis Fagel, 1965 - H (MRAC) — Tanzania

umbra Sharp, 1886 - H (BMNH) — Guatemala (The holotype of *S. umbra* is in *Scopaeus*. Other specimens in the BMNH and FMNH identified as *S. umbra* are an unidentified species of *Micranops*.)

unifasciatus Fauvel, 1889 - Sp (NHMW) — Papua New Guinea, Australia

basicollis Lea, 1923

vagans Fagel, 1973, transferred to *Hyperscopaeus*

velutinus Motschulsky, 1858 - Syn (ZMUM), Sp (FMNH) — "Indes orientales," Philippines, Sri Lanka

decipiens Kraatz, 1859 - Syn (SDEI)

ventralis (Casey, 1905) - Syn (USNM), Sp (FMNH) — United States

versicolor (Casey, 1886) - Syn (USNM) — United States

bicolor (Casey, 1886)

vietnamensis Frisch, 2005 - Lit. Att. — [Vietnam]

vilhenai Cameron, 1951 - Syn (BMNH) — Angola

vilis Sharp, 1886 - H (BMNH) — Panama

viriliformis Frisch, 2003 - P (MNKB) — Japan

virilis Sharp, 1874 - L (BMNH), Sp (FMNH, MNKB) — Japan

kreyenbergi Bernhauer, 1928 - L, Pl (SDEI), Pl (FMNH) — China

viriloides Frisch, 2003 - P (BMNH) — India

voltae Fagel, 1973, transferred to *Hyperscopaeus*

weigeli Frisch, 2005 - H (BMNH), P (MNKB) — India, Nepal

witteanus Fagel, 1973 - H (MRAC) — D.R. Congo

wunderlei Frisch, 2003 - H, P (NHMW), P (BMNH, SDEI, MNKB) — Indonesia

yoshidai Adachi, 1955 - Lit. Att. — [Japan]

zagrosensis Frisch, 2006 - H, P (MNKB) — Iran

UNDETERMINED SPECIMENS: Albania, Antigua, Argentina, Australia, Austria, Bahama Islands, Bolivia, Brazil, Cameroon, Canada, Chile, China, Colombia, Corfu, Corsica, Costa Rica, Cuba, Czech Republic, Dahomey, D.R. Congo, D'Entrecasteaux Islands, Dominica, Dominican Republic, Ecuador, Egypt, Elba Island, France, French Guiana, Greece, Guadeloupe, Guatemala, Honduras, Hungary, India, Indonesia , Iran, Italy, Ivory Coast, Japan, Liberia, Madagascar, Malaysia, Mariana Islands, Mexico, Morocco, Mozambique, Myanmar, Namibia, Nepal, Netherlands, Nigeria, Norway, Pakistan, Palau Islands, Panama, Papua New Guinea, Paraguay, Peru, Philippines, Poland, Puerto Rico, Ryukyu Islands, Sardinia, Senegal, Sicily, Sierra Leone, Slovakia, Solomon Islands, South Africa, Sri Lanka, Sudan, Surinam, Taiwan, Tanzania, Thailand, Tunisia, Turkey, Uganda, Upper Volta, United States, Russia, Venezuela, Vietnam, Yap Islands, Yugoslavia, and Zimbabwe.

DISSECTIONS: Disarticulations: *Scopaeus bicolor* (female), *Scopaeus cameroni* (female), *Scopaeus chalcodactylus* (female), *Scopaeus debilis* (female), *Scopaeus elegans* (female), *Scopaeus filiformis* (female), *Scopaeus gracilis* (female), *Scopaeus laevigatus* (female, male), *Scopaeus laxus* (female, male), *Scopaeus likovskyi* (female), *Scopaeus limbatus* group (female), *Scopaeus longicollis* group (female), *Scopaeus minimus* (female), *Scopaeus mutatus* group (female), *Scopaeus ooderes* (male), *Scopaeus opacus* (female, male), *Scopaeus persicus* (female), *Scopaeus picipes* (female, male), *Scopaeus punctatellus* (female), *Scopaeus pusillus* (female), *Scopaeus ryei* group (female), *Scopaeus sericans* group (female), *Scopaeus similis* (female), *Scopaeus subfasciatus* (female), *Scopaeus sulcicollis* (female), *Scopaeus udus* (female), and unidentified males and females of various Neotropical morphotypes including species described in *Scopaeus* (*Scopaeodera*), *Scopaeus* (*Scopaeoma*), *Scopaeus* (*Scopaeopsis*), and *Scopaeomerus* and undescribed species unassignable to any named subgenus or species group.

Hyperscopaeus Coiffait, New Status

Figures 11, 17, 240–255

Hyperscopaeus Coiffait, 1984: 150. Type species: *Scopaeus spathiferus* Coiffait, 1970: 106, fixed by monotypy.

— Frisch, Burckhardt, and Wolters, 2002a: 45, 46 (may be distinct genus). — Frisch, Burckhardt, and Wolters, 2002b: 2 (subgenus of *Scopaeus*). — Smetana, 2004: 615 (subgenus of *Scopaeus*; Palaearctic catalog). — Frisch, 2016: 65 (subgenus of *Scopaeus*; characters for Australian species).

DIAGNOSIS: *Hyperscopaeus* is separated from *Scopaeus* by the short, apically rounded to diagonally truncate metakatepisternal process (figs. 241, 251) and by the absence of a stridulum, which includes mesofemoral plectral ridges (fig. 253) and a metaventral file near the submarginal ridge (fig. 250, 251). For *Scopaeus* the metakatepisternal process is long, tapered and apically acute (fig. 104) or short, wide, and apically acute (fig. 94) and a stridulum is present (figs. 90, 92; 104–107). The dorsal side of the median lobe of *Hyperscopaeus* (fig. 243) has a midlongitudinal division, but for *Scopaeus* (fig. 158) it is entirely sclerotized and without medial separation.

Hyperscopaeus is separated from *Micranops* by the position of the trichobothrium, a supraocular trichobothrial depression in the former (fig. 245), and an ovoid postocular trichobothrial cavity in the latter (figs. 266, 282). Similarly, the position of the supraocular trichobothrium adjacent to the middorsal margin of the eye for *Hyperscopaeus* (fig. 245) separates it from *Orus* with its trichobothrial canal at the posterior margin of the posteriorly tapered eye (figs. 297, 315, 316). The neck of *Hyperscopaeus* is exceedingly narrow (fig. 240), about an eighth to a sixth as wide as the postocular width of the head; the neck of *Trisunius* (fig. 342) is about a third to two fifths as wide as the postocular width of head. The neck of most species of *Orus* (fig. 286) is about a third as wide as the postocular width of the head; the neck of a few species is narrower, about a fifth as wide as the head. The gular sutures of *Hyperscopaeus* are narrowly separated to nearly contiguous for most of their length (fig. 244), whereas they are moderately widely separated in *Trisunius* and *Orus* (figs. 286, 326). The posterior margin of the head of some species of *Hyperscopaeus* has a tumescence with a shallow to moderately deep median groove, neither *Trisunius* nor *Orus* have this cephalic tumescence. *Orus* is North American; *Hyperscopaeus* is from Africa, southern Asia, and Australia.

DESCRIPTION: Body length 2.3–6.6 mm.

Head (fig. 240) with postocular lateral margin nearly straight to broadly and shallowly rounded to basal angle; basal angle sharply rounded; basal margin slightly to strongly sinuo-emarginate, interrupted by small to moderately large median tumescence in some species; tumescence with shallow to moderately deep midlongitudinal groove or sulcus; posteroventral surface (figs. 244, 246) with one or two moderately large to tiny tubercles laterad of lateral margin of neck or tubercles coalescent forming low, elongate ridge or tubercles absent; tubercles, if present, visible (fig. 240) or hidden from dorsal view.

Neck (fig. 240) strongly petiolate; nuchal groove deep and strongly constricted, and base of neck abruptly expanded; neck width across nuchal groove one eighth to one sixth as wide as postocular width of head; nuchal ridge strongly to moderately developed dorsally and laterally.

Dorsal cephalic surface with fine, dense, simple punctation or with tiny puncture on peak of microtubercle; punctation or microtuberculation uniform, but slightly less dense between supra-antennal bosses; surface without microsculpturing; surface with dull shine, not polished; pubescence fine, dense, and uniform; macrosetae moderately long, peripheral, and scattered.

Cephalic trichobothrium adjacent to middle of dorsal margin of eye; bothrium in rounded or ovoid trichobothrial depression (fig. 245); trichobothrial depression without setae, but with setae along dorsal margin.

Eyes with posterior margin rounded to slightly flattened to slightly emarginate; corneal lenses of dorsal two or three rows with corneal sensilla (fig. 17, 247).

Gular sutures (fig. 244) narrowly separated, nearly contiguous in some species, and parallel for most of length.

Mandibles: left mandible with three denticles; right mandible with four denticles, basal (third) and subbasal (fourth) denticles well separated or both denticles present as part of large, broad, flat, basal lobe on which third and fourth denticles vary from small to moderately large.

Labrum quadridentate (fig. 249).

Pronotum broadly and shallowly convex to nearly flat; surface with fine, uniform, dense punctation; surface without microsculpturing; midlongitudinal strip moderately punctate or narrow and impunctate; surface with dull shine, not polished; pubescence fine, dense, and uniform; macrosetae present, moderately long, and peripheral or absent; median groove present or absent; midlongitudinal line marked by posteriorly directed setae; posterior margin broadly and shallowly to moderately emarginate; surface with dull shine, not polished; pubescence fine, dense, and uniform; macrosetae moderately long and scattered.

Prohypomeron with postprocoxal lobe separated from remainder of hypomeron by well-developed transverse ridge; lobe with a few setae.

Notosternal suture present.

Elytra longer than or subequal to pronotum; surface with microtubercles; microtubercles with minute, dorsal puncture; surface with fine, dense pubescence; posterior margin with row of setae.

Mesoventrite (fig. 250) with deep, ovoid, median depression.

Mesofurcasternum with internal, median mesofurcasternal apophysis on posteromedial margin present (figs. 241, 250) or absent.

Mesofemur without stridular plectral ridges (fig. 253).

Mesocoxal acetabulum margined by long pericoxal ridge and well developed to more weakly developed near middle (figs. 241, 251).

Metaventrite without stridular file (figs. 251, 252).

Metakatepisternal process short and with rounded to diagonally truncate apex (fig. 241, 251).

Sternite III (fig. 255) without median carina; transverse basal ridge moderately sinuate and with broad, median point.

Sternite IV without apparent glandular pore (fig. 254).

MALE: Sternite VII with surface and posterior margin unmodified or variously modified.

Sternite VIII with emargination of posterior margin of variable width and depth (Frisch, 2016: fig. 59).

Tergite IX asymmetrical: left anteroventral side larger, more broadly rounded, and wrapping medially more than right; posterior margin with U-shaped emargination; middorsal base divided medially from anterior to posterior margin of Tergite IX or for most of length but not reaching tergite X. Sternite IX elongate.

Tergite X elliptical; anterior margin rounded and without median point.

Aedeagus (fig. 243) with dorsal surface of median lobe midlongitudinally divided; median lobe darkly pigmented black medially, beginning near base of ventral process and extending posteriorly; parameres present and appressed to surface laterad of median foramen.

FEMALE: Sternite VII unmodified.

Sternite VIII (fig. 242) with posterior margin moderately deeply to shallowly to feebly emarginate to flattened to broadly rounded and not emarginate.

Tergite IX symmetrical: left and right anteroventral sides of approximately equal size; posterior margin with U-shaped emargination; middorsal base fused medially.

Tergite X elliptical; anterior margin broadly rounded and without median point.

DISTRIBUTION AND HABITAT: *Hyperscopaeus* is speciose and widely distributed in Africa; although with fewer known species, the distribution extends eastward across southern Asia to Australia. The paucity of Asian and Australian species and specimens is an artifact of collecting and doubtless more will be found there. Of the 77 described species included in the genus, 65 are from Africa where they are known from most countries. To now, none have been recorded from Algeria, Botswana, Burundi, Central African Republic, Ethiopia, Libya, Malawi, Mauritania, Morocco, Namibia, Rwanda, South Africa, South Sudan, and Zambia. No species have been reported from Madagascar.

Among the 12 remaining species, three are Sri Lankan, one is from India, another from Bhutan, four from Myanmar, one from Guam, and two are Australian. Unidentified species have been collected from Indonesia (Sumatra, Java), Pakistan, Singapore, Vietnam, and Papua New Guinea (Normanby Island) and, according to Frisch (personal commun.), Malaysia, Thailand, Laos, and Sri Lanka. The two Australian species are from New South Wales, Queensland, and Northern Territory.

Certainly, many more species will be discovered, and the genus will probably be reported from all countries of Africa, Madagascar, and across southern Asia, including China and India, Indonesia, the Philippines, and the island of New Guinea and Australia. Frisch (personal commun.) affirms this opinion.

Little is known of the habitat of species of *Hyperscopaeus*. Fagel (1973: 50–125) cited label data from species he described or redescribed. He reported some species as having been collected at lights. Others were collected from forest litter or soil in marshy or inundated forest or from sandy shores of rivers. One species, *H. convexiceps*, was collected from among roots of a species of Cyperaceae in a swampy area (Fagel, 1973: 125).

Frisch (2012c: 298) reported nothing definitive about the habitat of *H. spinosophallatus* and said (Frisch, personal commun.) he knows nothing about the habitat of *Hyperscopaeus*, but thinks it differs from that for *Scopaeus*. Frisch (personal commun.) found no specimens of *Hyperscopaeus* in gravel or sandy banks of streams, habitats typical for *Scopaeus*. In three expeditions to Java and Sulawesi Frisch (personal commun.) found many species and specimens of *Scopaeus* on riverbanks, but not a single specimen of *Hyperscopaeus*.

Most of the specimens in the AMNH collection were collected at lights. A couple of specimens from Sri Lanka were found in the bed of a stream.

Discussion: *Hyperscopaeus*, originally proposed by Coiffait (1984: 150) as a subgenus of *Scopaeus* for the Egyptian species, *Scopaeus spathiferus*, is herein raised to generic rank. Only aedeagal characters were originally cited to separate it from other species of *Scopaeus*; the absence of a cephalic "fossette" (= trichobothrial cavity), a small, postocular pit, distinguished it from *Microscopaeus* (= *Micranops*). Of note, the trichobothrium was not cited, perhaps overlooked, by Coiffait (1984) for either *Scopaeus* or *Hyperscopaeus*.

Eleven years before Coiffait established *Hyperscopaeus* for one species, Fagel (1973) described or redescribed 126 African species of *Scopaeus*, which he assigned to 19 species groups. Sixty-one of those species are congeneric with *H. spathiferus*, the type species of *Hyperscopaeus*. Fagel assigned those species to four groups: *H. gigantulus* with one species, *H. nitidicollis* with 15, *H. pseudomentheri* with 38 (Fagel 1973: 49–125), and *H. tristis* with seven species (Fagel, 1973: 151–164). Species of those groups are all moved herein to *Hyperscopaeus*.

Frisch et al. (2002a, 2002b) continued to define this subgenus of *Scopaeus* by features of the aedeagus, but also wrote that it might be a distinct genus based on many external and sexual apomorphies (Frisch et al., 2002a: 45). Among the external characters with which Frisch et al. (2002a: 38) defined *Hyperscopaeus* are the: (1) slender neck (one eighth the width of the head), (2) elongate, parallel-sided head, (3) concave posterior margin of the head, (4) parallel lateral margins of the pronotum, (5) wide protarsomeres (about three times wider than long), (6) emarginate sternite VIII of the female, and (7) more deeply (than for *Scopaeus*) emarginate sternite VIII of males. Accentuating details of the aedeagus, Frisch et al. (2002a: 38 and figs. 7–9) further characterized *Hyperscopaeus* by the: (8) large aedeagus, (9) long, membranous, unipartite apical portion of the median lobe with distinct apical lobes, (10) broad sclerotized ring of the median lobe, and (11) proximal position of the median foramen on the median lobe.

Despite the list of characters published by Frisch et al. (2002a: 38) *Hyperscopaeus* seemed to me uncertainly defined. Based on aedeagal characters, *Hyperscopaeu*s appeared to be a monophyletic group, other characters were somewhat nebulous differences of degree. Although the image of the spermatheca (Frisch et al., 2002a: fig. 23) of *Hyperscopaeus* is strikingly distinct from the other spermathecae on the same page, no apomorphic feature was pointed to for *Hyperscopaeus*, on the image or in the text, for distinction from *Scopaeus*. However, Frisch et al. (2002a: 44) thought the loss of the process of the spermathecal chamber in *Hyperscopaeus* and its presence in *Scopaeus*, reflected an apomorphic feature for the latter. Some of the defining characters listed in the previous paragraph faded away as more species were examined; that was particularly true among the Asian species. Frisch, based primarily on aedeagal characters, published—and stated to me in person—that he thought the subgenus *Hyperscopaeus* should be recognized separately from *Scopaeus*. When he and I discussed the idea, I was unconvinced that it should be carved from *Scopaeus* solely based on aedeagal and spermathecal divergences. My misgivings centered on how a genus of more than 400 species might be defined by derived features if the species of *Hyperscopaeus* were removed. Although, I had no doubt that *Hyperscopaeus* was a monophyletic group, as are the (other) species groups of *Scopaeus*, as a matter of practicality, I was (and am) resistant to forcing people to dissect the genitalia just to identify a genus if that group clearly fits within another. *Scopaeus* with *Hyperscopaeus* had been defined by the position of paraocular trichobothrium adjacent to the middle of the dorsal margin of the eye, quadridenticulate labral margin, and skinny neck, characters that circumscribed a genus of approximately 450 species from all other Paederinae. Removing *Hyperscopaeus* from *Scopaeus* because of autapomorphic characters detected in the former would leave no characters that defined the much larger, remaining cluster of species, *Scopaeus*. Removing *Hyperscopaeus* demanded finding derived characters that defined *Scopaeus*. Without those characters, *Hyperscopaeus* appeared to be simply a monophyletic group of robust species within *Scopaeus*.

My opinion was abruptly transformed upon the sudden, surprising discovery of a stridulum in *Scopaeus* (figs. 105, 106) and its absence in the species now assigned to *Hyperscopaeus* (figs. 251–253). This new view solidified on finding the pair of long, slender, apically acute metakatepisternal processes in *Scopaeus* (fig. 97) in contrast to the shorter, apically rounded processes in *Hyperscopaeus* (fig. 241), and the dorsally sclerotized and fused midlongitudinal strip of the aedeagal median lobe of *Scopaeus* (fig. 158) in contrast to the membranous median separation for *Hyperscopaeus* (fig. 243). All these characters are unique and derived for *Scopaeus*. Unfortunately, *Hyperscopaeus*, despite its monophyly based on aedeagal features, remains deficient for the presence of external apomorphic features to distinguish it from *Scopaeus*.

Most of the characters suggested by other investigators or explored herein to define *Hyperscopaeus* disappear in a fog of variation. Among proposed defining structures are the following.

The slender neck of *Hyperscopaeus* is one eighth to one sixth as wide as the head and overlaps with some species of *Scopaeus* that also have a neck a sixth as wide as the head.

The head and prothorax of some species of *Hyperscopaeus* are each approximately parallel sided, but the lateral sides of others are moderately convergent or broadly and shallowly rounded and akin to species of *Scopaeus*.

The concave (or emarginate) posterior margin of the head of *Hyperscopaeus* is found in some species of *Scopaeus* (fig. 1).

The basal four protarsomes of *Hyperscopaeus* are three times wider than long according to

Frisch et al. (2002a: 38) and might be useful as a defining feature of the genus. However, in the same paper the authors (p. 30) appeared to report overlapping variation of the width of the protarsomeres for some species groups of *Scopaeus* with the following statement: "In *Scopaeus*, the protarsomeres are also dilated (chars. 8:2, 8:3) ... in a few species groups." Characters 8:2 and 8:3 are "about twice as wide as long" and "three times as long as wide" respectively (Frisch et al., 2002a: 51). However, even if the difference is diagnostic, Frisch and his colleagues did not appear to explore or employ the character further or state the relative width of the protarsomeres of any species groups of *Scopaeus*. My exploration of the relative length-to-width ratio of *Hyperscopaeus* and *Scopaeus* revealed considerable variation, including variation among the basal four tarsomere of individuals. The width of the basal four protarsomeres of *Hyperscopaeus* varies from about three times the length, to twice the length, to subequal length and width. Similar results were seen for *Scopaeus*, the protarsomeres varied from somewhat greater than twice as wide as long to twice the length to subequal length and width.

The posterior margin of sternite VIII of *Hyperscopaeus* females varies from moderately deeply to shallowly to feebly emarginate to straight and without emargination to rounded.

Among suggested aedeagal characters, the position of the median foramen is more proximal, closer to the anterior margin of the median lobe, for *Hyperscopaeus* in contrast to the more distal position of the median foramen of *Scopaeus* (cf. Frisch, 2012c: fig. 2, and Frisch et al., 2002a: fig. 20). However, for some species of *Scopaeus*, for example *S. ooderes*, the median foramen is quite close to the rounded base of the aedeagus (see Frisch, 2016: fig. 39). This feature may be plesiomorphic for *Hyperscopaeus*.

Other structures to define *Hyperscopaeus* and discriminate it from *Scopaeus*, but that ultimately proved too variable, were explored. Some of these features may be species specific.

The posterior cephalic margin of *Hyperscopaeus* has a median tumescence that is medially divided by a shallow to moderately deep depression with a black, vertical, median sulcus; the depression is feeble in some species, but a black line or modest sulcus remains. A similar, but feeble, tumescence with depression and sulcus is found in some species of *Scopaeus*. However, although a possible, but poor, defining feature, it is too inconsistent to be useful.

The posteroventral surface of the head is strongly sloped and broadly concave in many species of *Hyperscopaeus*, but not all.

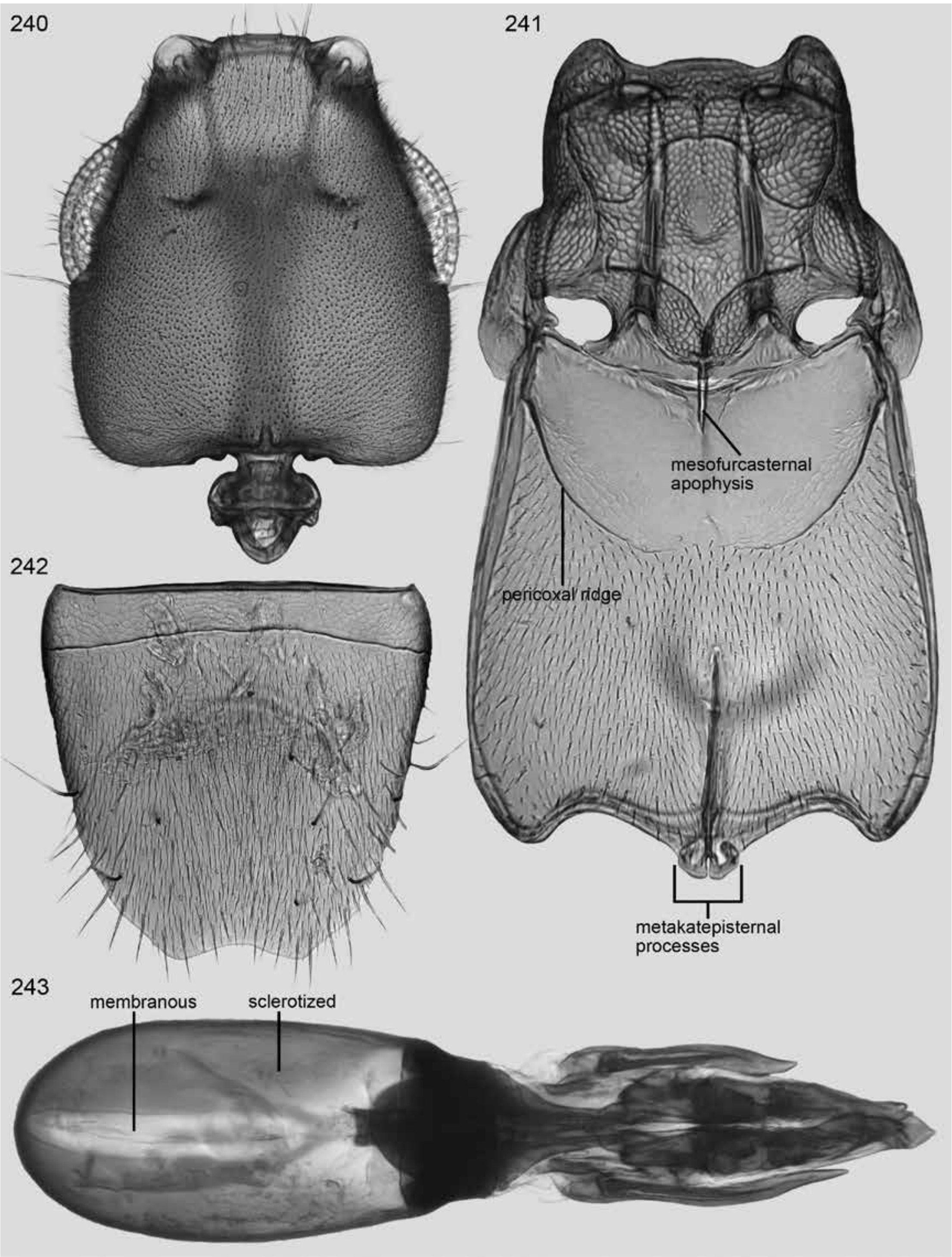
Most African species of *Hyperscopaeus* have a pair of tubercles on the ventral base of the head near each side of the neck (figs. 240, 244, 246); the tubercles of some species are large, in others tiny; the tubercles coalesce to form a short ridge in some; two tubercles are reduced to one in others. Among Asian species the ventrobasal tubercles are small or absent.

The cephalic and pronotal surfaces of most species of *Hyperscopaeus* are covered with dense, small to minute punctation. For some Asian species the simple cephalic and pronotal punctures are replaced by microtubercles, each with a tiny setate puncture on the peak. Among the named Asian species with setate microtubercles are *H. rubrotestaceus* and *H. semifuscus*.

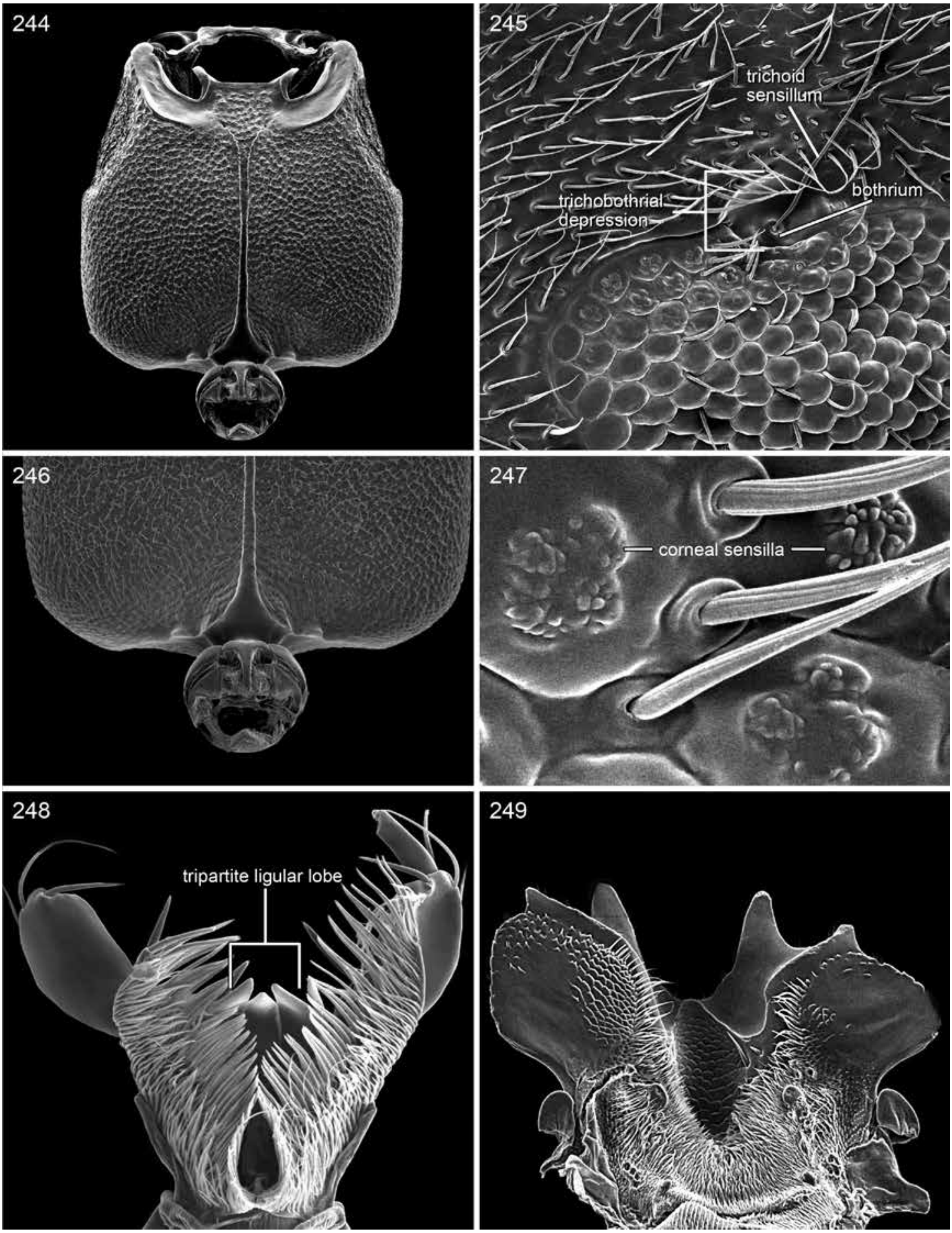
The right mandible of *Hyperscopaeus* has four denticles; the fourth is separated and distinct from the third in some species, in others it is part of a large, broad, basal lobe with two denticles, a large third and small to tiny fourth; the basal denticulate lobe, although not found in other scopaeine genera, is not found in all species of *Hyperscopaeus*.

The neck has a shallow to moderately deep nuchal groove adjacent and anterior to the nuchal ridge in some, but not all species of *Hyperscopaeus*.

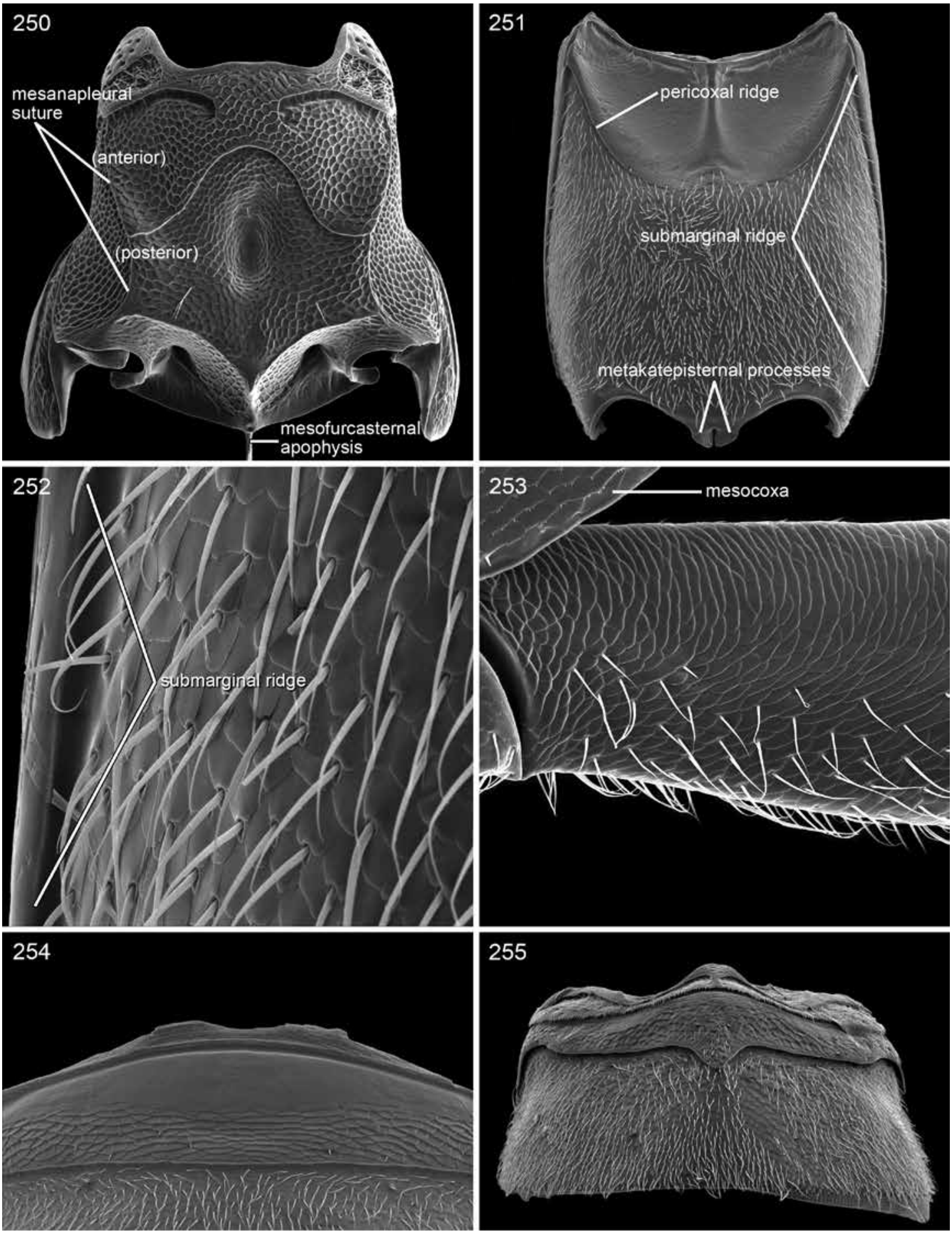
A newly discovered structure, of unknown function, is the long, slender, internal apophysis extending posteriorly from the midline of the mesofurcasternum (figs. 241, 250); at least a few species of *Hyperscopaeus* lack that apophysis and



FIGS. 240–243. *Hyperscopaeus* sp. **240.** Head. **241.** Pteroventrites. **242.** Sternite VIII, female. **243.** Aedeagus, dorsal.



FIGS. 244–249. *Hyperscopaeus* sp. **244.** Head, ventral (eyes collapsed). **245.** Head, laterodorsal, trichobothrium. **246.** Head, basal third. **247.** Eye, anterodorsal, corneal sensilla. **248.** Labium, hypopharynx. **249.** Labrum, ephipharynx.



FIGS. 250–255. *Hyperscopaeus* sp. **250.** Mesoventrite. **251.** Metaventrite. **252.** Metaventrite, right lateral margin. **253.** Mesofemur, right base. **254.** Sternite IV, midanterior margin. **255.** Sternites II and III.

a few species of the *Scopaeus chiriquensis* species group possess it (fig. 82). Furthermore, use of this potential character will require a dissection that separates the mesothorax from the metathorax or treatment that makes them transparent.

Tergite IX of females of *Hyperscopaeus* is medially fused basally, but this may be less derived than a divided base.

Among external features that might support the monophyly of *Hyperscopaeus* are the following.

The gular sutures of *Hyperscopaeus* are narrowly separated, virtually contiguous in some species, and parallel for most of their length (fig. 244); for most species of *Scopaeus* the gular sutures are moderately to widely separated but are narrowly separated for species of the *S. opacus* species group and for some species of the *S. chiriquensis* species groups.

Some species of *Hyperscopaeus*, especially the large ones, have a strong ridge on the probasisternum that extends from the anterior, basisternal margin that connects with the intercoxal carina of the probasisternum/profurcasternum. The ridge is present and distinct but shorter and not reaching the intercoxal carina in most species; for at least a few species the ridge appears to be absent. No species of *Scopaeus* were found with the ridge. However, few species and specimens of *Hyperscopaeus* were available to me, so this feature might yet be further investigated as diagnostic for *Hyperscopaeus* and *Scopaeus*.

Tergite IX of males lacks apodemes on the ventroanterior angle; the posterior margin of sternite VIII of males has a deep, wide, triangular emargination; the aedeagus is large, the median foramen proximal, and the median lobe darkly pigmented, black, beginning at the base of the ventral process and extending posteriorly.

Although, in the present work no external characters unique to *Hyperscopaeus* were found, perhaps someone else will find an overlooked structure. After all, look at *Scopaeus*.

On reflection, it is worth noting that despite the energy and time expended in the intense search for unique, external characters to define *Scopaeus*, the result was to eject *Hyperscopaeus* as a plesiomorphic group from *Scopaeus* and to then remember that more than 20 years ago, Frisch et al. (2002a: 38, figs. 40, 41) had hypothesized the *Scopaeus* subgenus, *Hyperscopaeus*, to be the sister group of the hundreds of remaining species of *Scopaeus*.

SPECIES INCLUDED AND MATERIAL EXAMINED

78 species

admixtus (Fagel, 1973) - H (IRSN) — D.R. Congo
New combination, transferred from *Scopaeus*
albertvillensis (Fagel, 1973) - H (MRAC) — D.R. Congo
New combination, transferred from *Scopaeus*
allardianus (Fagel, 1973) - H (MNHN) — D.R. Congo
New combination, transferred from *Scopaeus*
andrewesi (Cameron, 1931) - Syn (BMNH) — India
New combination, transferred from *Scopaeus*
angolanus (Fagel, 1973) - H (MRAC) — Angola
New combination, transferred from *Scopaeus*
bamaniaensis (Fagel, 1973) - H (MRAC), P (BMNH) — D.R. Congo
New combination, transferred from *Scopaeus*
borneensis (Cameron, 1941) - H (BMNH) — Indonesia
New combination, transferred from *Scopaeus*
bredoanus (Fagel, 1973) - H (IRSN) — D.R. Congo
New combination, transferred from *Scopaeus*
calidus (Bernhauer, 1932) - Syn, Sp (FMNH), Syn (MRAC) — Tanzania, Mozambique, D.R. Congo
New combination, transferred from *Scopaeus*
confusoides (Fagel, 1973) - P (MRAC, MNHN), Sp (FMNH, MNHN) — Ivory Coast, Niger
New combination, transferred from *Scopaeus*
confusus (Fagel, 1973) - H (IRSN) — D.R. Congo
New combination, transferred from *Scopaeus*

consimilis (Fagel, 1973) - P (MRAC) — Congo Republic

New combination, transferred from *Scopaeus*

convexiceps (Bernhauer, 1932) - Syn (MRAC, FMNH), Sp (MNHN) — D.R. Congo

New combination, transferred from *Scopaeus*

corpulentus (Fagel, 1973) - H (MRAC), P (NHMW, MNHN) — Ivory Coast, Chad

New combination, transferred from *Scopaeus*

decelleanus (Fagel, 1973) - H (MRAC), P (MNHN) — Senegal, Ivory Coast

New combination, transferred from *Scopaeus*

dolosus (Fagel, 1973) - H (MRAC), Sp (MNHN) — Ivory Coast

New combination, transferred from *Scopaeus*

endrodyanus (Fagel, 1973) - Sp (MRAC) — Congo Republic

New combination, transferred from *Scopaeus*

errans (Fagel, 1973) - H (MRAC) — D.R. Congo

New combination, transferred from *Scopaeus*

erraticus (Fagel, 1973) - H (MRAC) — D.R. Congo

New combination, transferred from *Scopaeus*

fallaciosus (Fagel, 1973) - P (MRAC), P, Sp (NMHN) — D.R. Congo

New combination, transferred from *Scopaeus*

filicornis (Fagel, 1973) - H (MRAC) — Equatorial Guinea, Ivory Coast

New combination, transferred from *Scopaeus*

flavidulus (Fagel, 1973) - H (MRAC) — D.R. Congo

New combination, transferred from *Scopaeus*

flavocastaneus (Lea, 1923) - H, P (SAMA) — Australia

New combination, transferred from *Scopaeus*

fluviatilis (Fagel, 1973) - H (MRAC), P (BMNH) — D.R. Congo

New combination, transferred from *Scopaeus*

fossiceps (Eppelsheim, 1885) - Syn (NHMW, IRSN), Syn, Sp (FMNH) — D.R. Congo, Ghana

New combination, transferred from *Scopaeus*

fuliginosus (Fagel, 1973) - H (MRAC), P, Sp (MNHN) — Ivory Coast

New combination, transferred from *Scopaeus*

fulvescens (Motschulsky, 1858) - Syn (ZMUM) — ”Indes orientales”

New combination, transferred from *Scopaeus*

fusculus (Motschulsky, 1858) - Syn (ZMUM), Sp (FMNH) — Indonesia (Java, Sumatra), “Indes orientales”

New combination, transferred from *Scopaeus*-*procerus* (Kraatz, 1859) - Syn (SDEI) — India Orientali

New combination, transferred from *Scopaeus*

gigantulus (Bernhauer, 1929) - Syn (FMNH, MRAC) — D.R. Congo, Gabon, Cameroon

New combination, transferred from *Scopaeus*

girardianus (Fagel, 1973) - P (MRAC, MNHN) — Ivory Coast

New combination, transferred from *Scopaeus*

hova (Fauvel, 1905) - Sp (IRSN) — Madagascar

New combination, transferred from *Scopaeus*

hulstaertianus (Fagel, 1973) - H (MRAC) — D.R. Congo

New combination, transferred from *Scopaeus*

intermixtus (Fagel, 1973) - H (MRAC) — D.R. Congo

New combination, transferred from *Scopaeus*

kaszabianus (Fagel, 1973) - P (MRAC, MNHN) — Congo Republic

New combination, transferred from *Scopaeus*

katanganus (Fagel, 1973) - H (MRAC) — D.R. Congo

New combination, transferred from *Scopaeus*

kivuanus (Fagel, 1973) - H (MRAC) — D.R. Congo

New combination, transferred from *Scopaeus*

lamtoensis (Fagel, 1973) - P (MRAC) — Ivory Coast

New combination, transferred from *Scopaeus*

leleupianus (Fagel, 1973) - H (MRAC) — D.R. Congo

New combination, transferred from *Scopaeus*

leopoldvillensis (Fagel, 1973) - H (MRAC), P, Sp (MNHN) — D.R. Congo

New combination, transferred from *Scopaeus*

lescuyeri (Delaunay, Coache, and Rainon, 2019) - Lit. Att. — [Benin]

New combination, transferred from *Scopaeus*

levasseuri (Lundgren, 1982) - (replacement name for *fageli*) — Ivory Coast

New combination, transferred from *Scopaeus*

fageli (Levasseur, 1981) - H (MNHN)

New combination, transferred from *Scopaeus*

longiusculus (Fagel, 1973) - H (MRAC), P (FMNH) — D.R. Congo

New combination, transferred from *Scopaeus*

machadoanus (Fagel, 1973) - H (MRAC) — Angola

New combination, transferred from *Scopaeus*

major (Eppelsheim, 1885) - Syn (NHMW, IRSN), Sp (FMNH, MRAC, MNHN) — Guinea-Bissau, Ghana, Chad, Tanzania

New combination, transferred from *Scopaeus*

methneri (Bernhauer, 1932) - Syn (FMNH) — Tanzania

New combination, transferred from *Scopaeus*

minutulus (Fagel, 1973) - P (MRAC) — Congo Republic

New combination, transferred from *Scopaeus*

mulongoensis (Fagel, 1973) - H (MRAC), P, Sp (FMNH), Sp (IRSN)… D.R. Congo

New combination, transferred from *Scopaeus*

nitidiceps (Fagel, 1973) - H (MRAC), P, Sp (MNHN) — Ivory Coast

New combination, transferred from *Scopaeus*

nitidicollis (Fagel, 1973) - H (MRAC) — D.R. Congo

New combination, transferred from *Scopaeus*

opacicollis (Bernhauer, 1942) - Syn (FMNH, abdomen missing) — Guam

New combination, transferred from *Scopaeus*

overlaetianus (Fagel, 1973) - H (MRAC), Sp (BMNH) — D.R. Congo, Zambia

New combination, transferred from *Scopaeus*

parvicornis (Fauvel, 1900) - Syn (MNKB), Sp (IRSN, FMNH, MRAC, MNHN) — Congo Republic, D.R. Congo

New combination, transferred from *Scopaeus*

pruinosulus (Eppelsheim, 1885) - Syn (NHMW, IRSN), Syn, Sp (FMNH, MNHN) — D.R. Congo, Ghana

New combination, transferred from *Scopaeus*

pseudomethneri (Fagel, 1973) - H (MRAC), P, Sp (FMNH), Sp (IRSN) — D.R. Congo

New combination, transferred from *Scopaeus*

puberulus (Kraatz, 1859) - Syn (IRSN), Sp (FMNH) — Myanmar, India

New combination, transferred from *Scopaeus*

reduncus (Fagel, 1973) - H (MRAC) — D.R. Congo, Congo Republic, Gabon

New combination, transferred from *Scopaeus*

ripicola (Fagel, 1973) - H (MRAC), P (MNHN) — D.R. Congo

New combination, transferred from *Scopaeus*

rubricollis (Fagel, 1973) - H (MRAC), P (IRSN) — D.R. Congo

New combination, transferred from *Scopaeus*

rubrotestaceus (Kraatz, 1859) - Sp (FMNH, SDEI) — Sri Lanka

New combination, transferred from *Scopaeus*

ruguliceps (Fagel, 1973) - H (MRAC) — Ivory Coast

New combination, transferred from *Scopaeus*

ruziziensis (Fagel, 1973) - H (MRAC) — D.R. Congo

New combination, transferred from *Scopaeus*

semifuscus (Kraatz, 1859) - Syn (SDEI), Sp (FMNH) — Sri Lanka, Indonesia

New combination, transferred from *Scopaeus* (note: Frisch doubts occurrence in Indonesia, in litt., December 20, 2018)

senegalensis (Fagel, 1973) - H (IRSN) — Mali

New combination, transferred from *Scopaeus*

seydeli (Cameron, 1952) - Syn (MRAC, BMNH) — D.R. Congo, Congo Republic

New combination, transferred from *Scopaeus*

simillimus (Fagel, 1973) - H (MRAC), P (MNHN) — D.R. Congo

New combination, transferred from *Scopaeus*

simulator (Fagel, 1973) - H, P (BMNH), P (MRAC) — Zambia

New combination, transferred from *Scopaeus*

spathiferus (Coiffait, 1970) - H (MNHN) — Egypt

New combination, transferred from *Scopaeus*

spinosophallatus (Frisch, 2012) - H (ANIC) — Australia

New combination, transferred from *Scopaeus*

subconfusus (Fagel, 1973) - H (MRAC), Sp (MNHN) — Ivory Coast

New combination, transferred from *Scopaeus*

subprocerus (Coiffait, 1978) - H, P (NHMB) — Bhutan

New combination, transferred from *Scopaeus*

surdus (Fagel, 1973) - H (MRAC) — D.R. Congo

New combination, transferred from *Scopaeus*

suspectus (Fauvel, 1907) - L (IRSN) — Kenya

New combination, transferred from *Scopaeus*

tchapembanus (Fagel, 1973) - H (MRAC) — Angola

New combination, transferred from *Scopaeus*

thoracicus (Motschulsky, 1858) - Syn (ZMUM) — Indes orientales

New combination, transferred from *Scopaeus*

tristis (Bernhauer, 1929) - Syn, Sp (FMNH), Sp (MNHN) — D.R. Congo

New combination, transferred from *Scopaeus*

vagans (Fagel, 1973) - H (MRAC), P (MNHN), Sp (BMNH) — Ivory Coast, Gabon, Congo Republic

New combination, transferred from *Scopaeus*

voltae (Fagel, 1973) - H, P (MNHN), P (MRAC, NHMW) — Chad

New combination, transferred from *Scopaeus*

UNDETERMINED SPECIMENS: Africa: Benin, Burkina Faso, D.R. Congo, Ivory Coast, Liberia, Nigeria, Sierra Leone. Asia: Malaysia (Sabah), Pakistan, Papua New Guinea (Normanby Island), Sri Lanka, Vietnam.

DISSECTIONS: Disarticulations: Undetermined males and females of several species (D.R. Congo, Liberia, Sri Lanka, Vietnam); aedeagal dissections: (*H. longiusculus*, *H. mulongoensis*, and *H. pseudomentheri*)

Micranops Cameron

Figures 12, 18, 19, 256, 259–285.

Micranops Cameron, 1913: 350. Type species: *Micranops brunneus* Cameron, 1913: 350, fixed by monotypy.

— Cameron, 1923: 400 (correction of original description). — Scheerpeltz, 1933: 1271 (catalog). — Blackwelder, 1939a: 98, 105, 119 (key; checklist; type species). — Blackwelder, 1944: 119 (checklist of species, Latin America). — Blackwelder, 1952: 243 (type species). — Blackwelder and Arnett, 1974: 57 (checklist; North America; Central America; West Indies). — Frisch, Burckhardt, and Wolters, 2002a: 35, 45, 46 (characters; included in phylogenetic analysis of Scopaeina species of Western Palaearctic; notes; synonymy). — Frisch, Burckhardt, and Wolters, 2002b: 1 (catalog). — Smetana, 2004: 615 (Palaearctic catalog). — Frisch and Oromí, 2006: 23 (characters; discussion; taxonomic history; three new species; discussion of endogean and troglobitic species). — Frisch and Herman, 2014: 67 (checklist, original reference and distribution of species; one new species).

Nivorus Herman, 1965a: 119. Type species: *Orus cameroni* Blackwelder, 1943: 278, fixed by original designation.

— Blackwelder and Arnett, 1974: 57 (synonym of *Orus*). — Newton, Thayer, Ashe, and Chandler, 2000: 386 (subgenus of *Orus*). — Navarrete-Heredia et al., 2002: 279 (subgenus of *Orus*; unnamed species known from Mexico). — Frisch, Burckhardt, and Wolters, 2002a: 45, 46 (synonym of *Micranops*; type species). — Frisch, Burckhardt, and Wolters, 2002b: 1 (synonym of *Micranops*; type species). — Smetana, 2004: 615 (synonym of *Micranops*). — Frisch and Herman, 2014: 68 (synonym of *Micranops*).

Microscopaeus Coiffait, 1981: 19. Type species: *Scopaeus microphthalmus* Eppelsheim, 1888: 409, fixed by original designation.

— Coiffait, 1984: 148 (subgenus of *Scopaeus*; key to species). — Frisch, Burckhardt, and Wolters, 2002a: 45, 46 (synonym of *Micranops*; type species). — Frisch, Burckhardt, and Wolters, 2002b: 1 (synonym of *Micranops*; type species). — Smetana, 2004: 615 (synonym of *Micranops*). — Frisch and Herman, 2014: 68 (synonym of *Micranops*).

DIAGNOSIS: *Micranops* is separated from all other Scopaeina by the unique form and position of the trichobothrial cavity on the lateral side of the head behind and separated from the posterior margin of the eye (figs. 266, 267, 282). The trichobothrial depression or canal of all other genera of the Scopaeina touches the dorsal margin of the eye (figs. 11, 13–15, 334).

DESCRIPTION: Body length 1.8–5.1 mm.

Head with postocular lateral margin broadly and shallowly (fig. 259, 272, 282) to strongly curved to basal angles; basal angles broadly (Frisch and Oromí, 2006: figs. 1, 2) to sharply (fig. 259, 272, 282) rounded or head elongate with broadly rounded lateral margins (Frisch and Oromí, 2006: fig. 4a); basal margin truncate to broadly and shallowly emarginate (fig. 272) to slightly rounded and without median tumescence; posteroventral surface without tubercles.

Neck wide, moderately constricted at nuchal groove and gradually expanded at occiput and not petiolate (fig. 272) or petiolate and strongly constricted at nuchal groove and abruptly expanded at occiput (species of Eastern Hemisphere); nuchal groove moderately deep to deep; neck width across nuchal constriction one to two fifths as wide as greatest postocular width of head; nuchal ridge present dorsally and laterally (fig. 266).

Dorsal surface of head with fine, dense to moderately dense punctation; punctation denser laterally than medially and punctation most sparse midanteriorly; punctation distinct or obscured by strong microsculpturing; microsculpturing dense and uniform to present only near margins; surface dull to strongly shining to polished; pubescence fine and dense, moderately dense; macrosetae short, peripheral, and few.

Cephalic trichobothrium present as small, deep cavity on lateral side of head behind and separated from eye (figs. 267, 282); for eyeless species, behind normal position of eye; trichobothrial cavity with setae around periphery of inner surface (figs. 268, 269); bothrium positioned near middle of cavity (fig. 269).

Eyes with posterior margin broadly to more narrowly rounded; corneal lenses with (fig. 19) or without (fig. 18) sensilla.

Gular sutures moderately widely separated (fig. 272, sutures visible through integument as diffuse, gray shadows).

Mandibles: right mandible with three or four denticles, left with three (fig. 263).

Labrum bidentate (fig. 265; some might regard as denticles the rounded lobes laterad of submedial denticles).

Pronotum broadly and shallowly convex to nearly flat; surface with fine to moderately coarse punctation; punctation dense to moderately dense, uniform, and obscured by microsculpturing in many species; microsculpturing dense and uniform or present near margins; midlongitudinal strip impunctate; surface dull to moderately shiny to polished; pubescence fine and dense to moderately dense; macrosetae short, peripheral, and few; median groove present on posterior half and distinct to feeble; posterior margin straight to slightly emarginate.

Prohypomeron without transverse, prohypomeronal ridge; postprocoxal lobe with few setae.

Notosternal suture present (fig. 260) or absent.

Elytra longer or shorter than pronotum; surface punctate; pubescence dense to moderately dense; posterior margin with row of setae.

Mesoventrite with broad, shallow, median, basisternal depression (fig. 276); prepectal ridges medially separated; mesotransventral ridge present medially only; mesanapleural ridge with anterior segment present, posterior segment poorly developed.

Mesofurcasternum without (figs. 273, 276) internal, median apophysis on posteromedial margin.

Mesofemur without plectral ridges (fig. 277).

Mesocoxal acetabulum margined by pericoxal ridge (figs. 270, 280).

Metaventrite without stridular file (figs. 270, 271; 280, 281).

Metakatepisternal process short, about as wide as long, apically acute, lateral margin diagonally directed to meet medial margin and sharply rounded apically (fig. 270).

Sternite II (fig. 284) without median point on posterior margin.

Sternite III without median carina; transverse basal ridge weakly sinuate, and with moderately long, triangular, median point (fig. 284).

Sternite IV without glandular opening or lobe (fig. 278).

Male: Sternite VII with surface variously modified or unmodified; posterior margin with median emargination of varying depth, width, configuration.

Sternite VIII with wide to narrow, shallow to deep median emargination (see Frisch and Oromí, 2006: figs. 12, 14)

Tergite IX (fig. 261) slightly asymmetrical: left anteroventral side slightly larger and wrapping medially slightly more than right; posterior margin with basal edge of emargination flat to shallowly to strongly curved; middorsal base fused medially (fig. 261).

Tergite X (fig. 261, 285) trapezoidal; anterior margin wide and moderately rounded to nearly straight and without median point.

Aedeagus (figs. 274, 275; see Frisch and Oromí, 2006: figs. 7, 10) with dorsal surface of median lobe midlongitudinally divided; parameres absent.

Female: Sternite VII unmodified.

Sternite VIII with rounded posterior margin.

Tergite IX (see Frisch and Oromí, 2006: figs. 15, 18) symmetrical, left and right anteroventral sides of approximately equal size; posterior margin with deep U-shaped emargination, anterior margin of emargination strongly to more gradually rounded; middorsal base fused medially.

Tergite X (see Frisch and Oromí, 2006: figs. 15, 18) with anterior margin slightly concave or slightly to strongly rounded to lateral margin; anterior margin without median point.

Distribution and Habitat: *Micranops* is known from tropical and subtropical regions around the world with one species, *M. pilicornis*, reaching the periphery of more temperate locales (see Frisch and Herman, 2014: 70). New World species are found across the southern United States south through the West Indies and Mexico south into northern Argentina. In the Caribbean species are known on four West Indian islands: Cuba, Jamaica, Hispaniola, and Grenada. In the Old World species have been collected from the Canary Islands eastward to Italy and southern Europe and across the Middle East and the Caucasus to Turkmenistan on to India, Sri Lanka, the Malay Peninsula, the Philippines, Taiwan, and Australia, and in Africa from Egypt to tropical and southern Africa. Most species are known from one or a few localities and most specimens in collections are unnamed. *Micranops pilicornis*, found from Italy east to the Balkans, Cyprus, Turkey, the Middle East, Iran, southern Russia, and Turkmenistan, has the widest known distribution of any in the genus (Frisch and Oromí, 2006: 24; Frisch and Herman, 2014: 70). As of this writing, to my knowledge, *M. pilicornis* has not been reported from mainland Spain.

Based on specimen label data and published accounts, the following is known about the potential habitat for species of *Micranops*. Species have been found in the lowlands and high montane regions, some to as high as 2000 and 2200 meters in the Democratic Republic of the Congo for *M. lwiroensis* (Fagel, 1973) and *M. aborensis* (Fagel, 1973: 32, 33) and 2450 meters on Tenerife, Canary Islands, for *M. mlejneki* (Frisch and Oromí, 2006: 30). According to label data, they have been collected from forest-floor leaf litter and humus, near streams, from epiphytic humus, log mold and debris, flood debris, and at light traps. Specimens of *M. cameroni* were collected from under seaweed in Jamaica (Blackwelder, 1943: 279). Frisch and Oromí (2006: 35) wrote that most species of *Micranops* inhabit the interstices of the upper layers of moist sandy or gravelly soil, often near streams. Frisch and Oromí (2006: 35) reported *Micranops pilicornis*, a widespread southwest Eurasian species, has been repeatedly collected near running water under deeply embedded stones or up to about 20 cm deep in sandy or gravelly banks. In the same article they described or redescribed three endogean and one troglobitic species. *Micranops spelaeus* Frisch and Oromí, 2006, the only troglobitic species reported for the Scopaeina and represented by a single specimen, was collected from the Canary Islands on Tenerife; at 5.1 mm, it is also the largest known species of the genus. Two other species described from the Canaries, *M. bifossicapitatus* Outerelo and Oromí, 1987, and *M. mlejneki* Frisch and Oromí, 2006, were collected in caves, the latter also from under an embedded rock. Both are considered endogean species and in caves only because of the aridity of the islands (Frisch and Oromí, 2006). Frisch wrote that he regards species of *Micranops* to be inhabitants of humid, sandy soil on riverbanks and creeks with sparse vegetation, that the species live in the interstices of soil, and exhibit adaptations to an endogean mode of life (Frisch and Herman, 2014: 68). *Micranops myrmecophilus* was collected in Argentina with *Acromyrmex lundii* Guérin-Méneville, 1838, (Bernhauer, 1921: 103) and *M. pilicornis* was collected from the nest of *Messor concolor* Santschi, 1927, in Turkey (Frisch, 1997c: 100). It seems highly improbable that either *M. myrmecophilus* or *M. pilicornis* are myrmecophiles. No scopaeine species are known to live with ants. The preceding records likely merely reflect that these species, like many other paederines, were simply collected from habitats that also included ants. Only further collecting and observation will resolve the question. If the specimens were collected with a sifter, little can be deduced about their true habitat. The few specimens I collected in Panama and Argentina were sifted from leaf litter near a stream and one within the entrance of a mammal burrow. (Note: The names of both species of ants above were corrected by consulting a pdf of Bolton's, 2016, online General Catalogue to the Ants of the World.[1]) *Acromyrmex lundii* was corrected from *A. lundi* and *M. concolor* is a junior synonym of *Messor wasmanni* Krausse, 1910.)

SYNONYMY: *Nivorus* was described as a subgenus of *Orus* (Herman, 1965a: 119). Both *Nivorus* and *Micranops* share the short, deep, trichobothrial cavity on the lateral side of the head; no known characters distinguish the two generic groups. The type species of *Micranops*, *M. brunneus* (fig. 256), which I first saw in London in 1983 and recognized that it and species of *Nivorus* were congeneric, has reduced eyes, elytra, humeral angles, metathorax, and flying wings and is much larger; these reductions and size differential are insufficient reasons to recognize two genera. The type locality of *M. brunneus* is the Newcastle District at 3000 feet elevation, Jamaica.

Microscopaeus, described by Coiffait (1981: 19) as a subgenus of *Scopaeus*, was distinguished by the presence of an oblong pit, "fossette," behind the eye (fig. 282). Although the localities cited in the original description of *Scopaeus microphthalmus*, the type species of *Microscopaeus*, included various sites of the Levant, Frisch's (1997c: 96) lectotype designation fixed the type locality as Crete.

In correspondence with Frisch, I suggested the Eastern and Western Hemisphere species with the postocular trichobothrial cavity were congeneric. He published that synonymy (Frisch et al., 2002a: 46; 2002b: 1), but in correspondence a few years later professed misgivings about the synonymy. Only recently have SEM images of the trichobothrial cavity (figs. 266–268, 282, 283) revealed small differences of the position of the cavity relative to the eye and interesting structural variations of some details of the trichobothrial cavity between the New and Old World groups. Furthermore, the specimen from Burkina Faso has sensilla on some corneal lenses (fig. 19), that from Bimini does not (fig. 18). Both the eye and trichobothrial variations require detailed scrutiny of more specimens and species of both hemispheres.

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[1] Bolton, B. 2016. The general catalogue of the ants of the world. Word files of Barry Bolton, 3 May 2016. For taxonomic reference purposes. This is not a publication. Online resource (www.antwiki.org/wiki/images/d/dd/NGC_January_2016.pdf). (Using this address in a browser does not take one directly to the catalog, nor does going directly to www.antwiki.org make the catalog easy to find. Finding it is a bit of a scramble.)

The width of the neck compared with the width of the head differs between the groups of the two hemispheres, but that difference overlaps within one standard deviation (table 3). See the Discussion for further information on the overlap of the relative width of the head and neck.

Few species of both regions were available for study in the present work so the question could not be fully addressed here. Additional discussion of variation between the species of the two hemispheres follows below in the Discussion. The synonym of the two groups requires further study with, but more specimens and a larger sampling to the species of both regions.

FLIGHT AND SIGHT: "As far as known presently, most species of *Micranops* are able to fly" (Frisch and Oromí, 2006: 35). Many species of the genus have normally developed eyes, elytra, metathorax, and wings. Some have reduced eyes and wings.

The first eyeless species was *Micranops bifossicapitatus* (Outerelo and Oromí, 1987) from the Canary Islands. Two decades later Frisch and Oromí (2006) described three more eyeless species, *M. subterraneus*, *M. mlejneki*, and *M. spelaeus*, from the Canaries. To date these four are the only known eyeless species of *Micranops*. As is typical for eyeless species, all of them also have reduced elytra with broadly rounded elytral humeral angles, reduced metathorax and wings, and lack a palisade fringe on tergite VII.

Micranops brunneus was the first species of the genus reported to be eyeless. In the original description Cameron (1913: 350) wrote that eyes were "absent, their position marked by a round whitish depression," but he erred. I examined the holotype in London in 1983 and again in 2007. The eye of *M. brunneus* is a single, small, white corneal lens with a smooth, shiny surface. In line with the diminished eyes, the elytra are reduced, and the elytral humeral angle is broadly rounded, the metathorax and wings are reduced, and the palisade fringe of tergite VII is absent. I have examined four unnamed species from Australia, Malaysia, Costa Rica, and Peru with small or tiny eyes comprised of a few corneal facets and similarly reduced elytra, wings, metathorax, and without a palisade fringe.

Some of the corneal lenses of a specimen from Burkina Faso have sensilla (fig. 19). The sensilla are well developed and clustered on the posterodorsal two or three rows of lenses (fig. 282). A few lenses ventrad of those have poorly developed sensilla that may not be functional. The corneal lenses of an undescribed species from Bimini lack those sensilla, but the surface has some tiny bumps and ridges (fig. 18) that may be precursors, remnants of sensilla, or represent something different. Distribution of these sensilla among species of the genus requires further investigation. Of significant interest would be the geographical and taxonomic distribution of these ocular sensilla. Their function is unknown.

At least one species displays wing-dimorphic populations with both flying and flightless individuals. Frisch (in litt.: 2018 October 24, November 7) wrote that most of the dozens of specimens of *M. pilicornis* he collected in Anatolia are wingless, but that some have longer elytra with well-developed humeral angles and that at least one of them had fully developed wings exposed. He also stated that for flying specimens the palisade fringe is present and that the fringe is poorly developed or absent on flightless ones. Earlier he and his coauthor reported a flying specimen of the species had been collected in Italy and that the species is microphthalmic (Frisch and Oromí, 2006: 35). I have seen only one specimen of the species; the elytra appeared to be fully developed and the eyes are well developed.

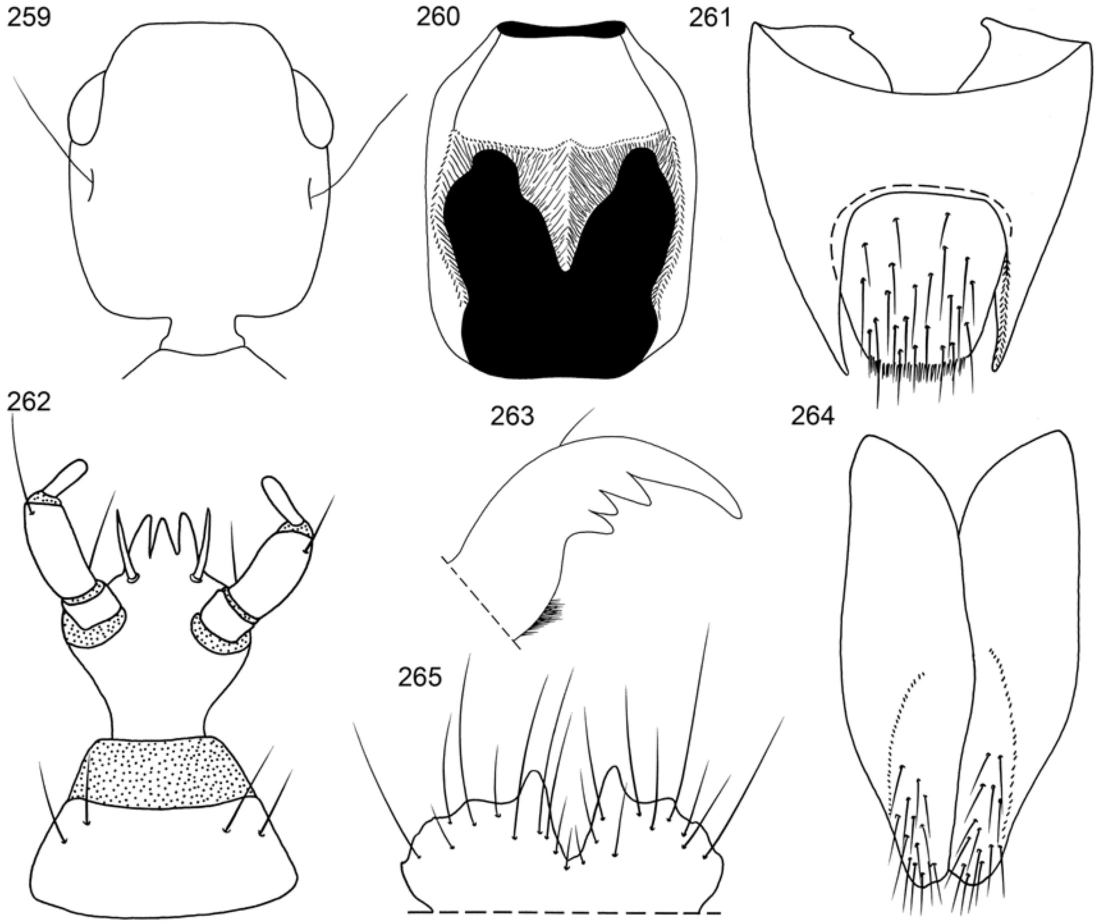
For another species I examined just over 100 specimens from 10 localities of an unnamed North American species nearly all of which have reduced elytra, but for which the eyes appear normal, albeit slightly smaller, with numerous facets, than those of some congeners. The elytra and metathorax of all the males (40 specimens) were reduced and the wings were mere small pads; the palisade fringe of tergite VII was present. Nearly all the 64 females of this North American species had similarly reduced wings;

FIGS. 256–258. Habitus. **256.** *Micranops brunneus*, syntype. **257.** *Orus rubens*. **258.** *Trisunius* sp.

nine females had what appeared to be fully developed elytra and metathorax and I assume fully developed wings. The winged females were all from localities from which I had no males, so the conspecificity of the winged and wing-reduced specimens is uncertain as is the dimorphism of the species. However, the presence of a palisade fringe of tergite VII suggests there are flying individuals of the species. Certainly, there are other species with both flying and flightless populations.

Discussion: *Micranops* was based on one specimen of *M. brunneus*, found in the Jamaican highlands at about 900 meters that, according to the author (Cameron, 1913: 350), lacked eyes and was apterous. Blackwelder (1939a: 98), who studied no specimens of *Micranops*, but based on the original description used the absence of eyes to identify this genus in his key. However, the one known specimen has one white, corneal lens remaining; the eye may be nonfunctional or perhaps only light sensitive. In Blackwelder's monograph of the West Indian Staphylinidae (1943) *Micranops* was neither addressed nor even mentioned. The genus remained effectively unknown until the works of Frisch and his coauthors (Frisch et. al, 2002a, 2002b; Frisch and Oromí, 2006; Frisch and Herman, 2014).

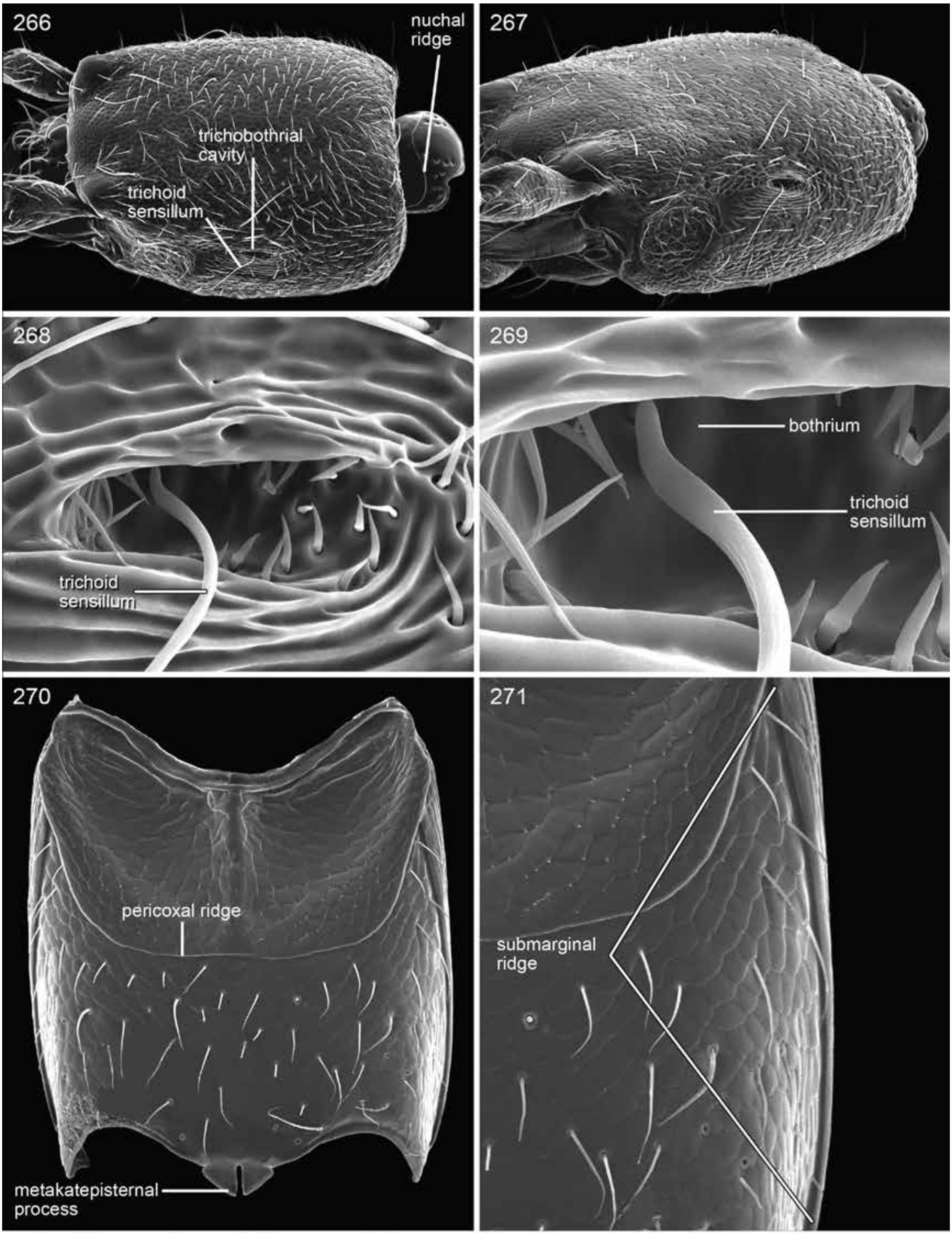
Herman (1965a: 119), unaware of the existence of *Micranops*, described *Nivorus*, type species *Orus cameroni*, as a subgenus of *Orus*, based on the presence of a furrow with a long "seta," or



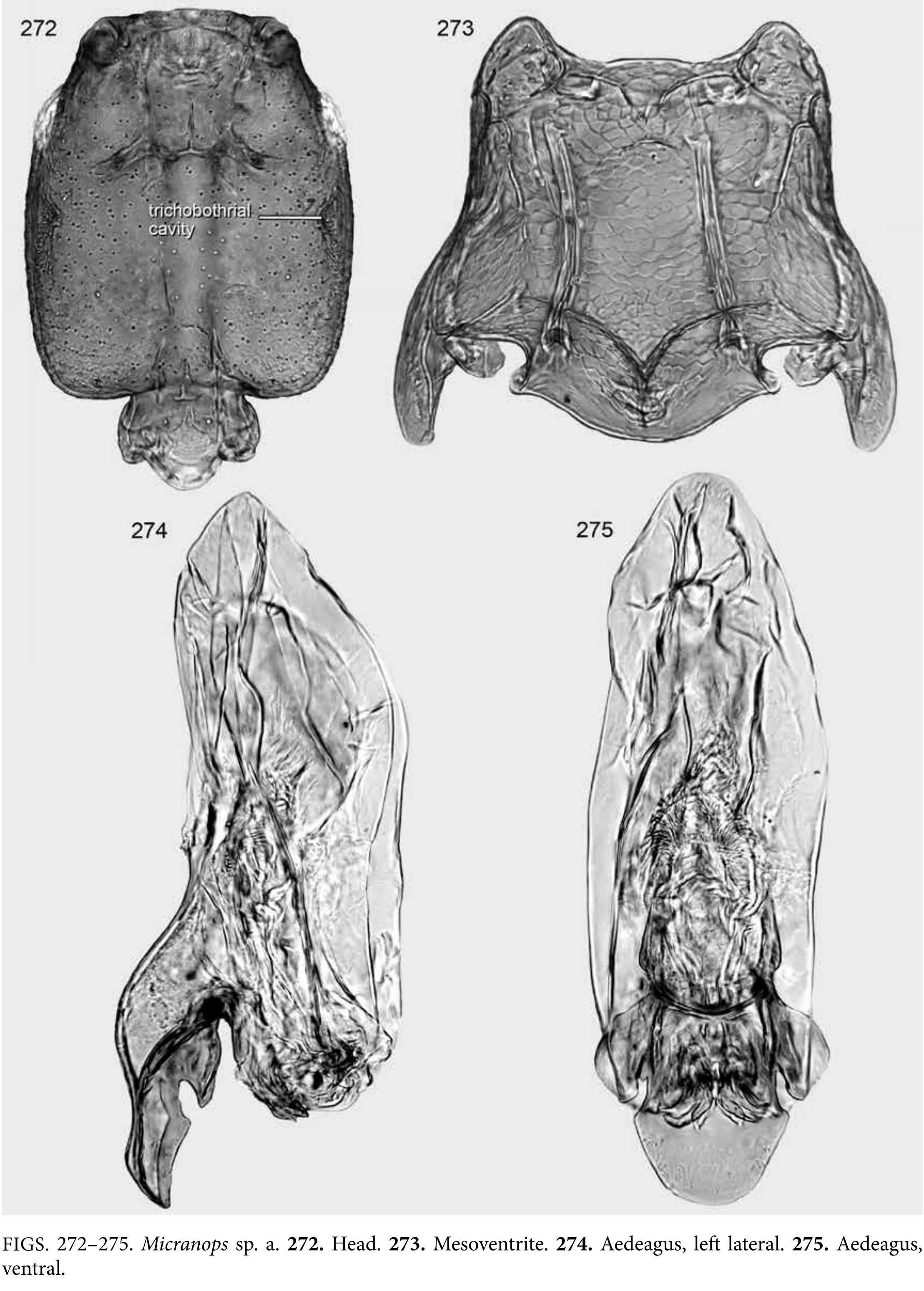
FIGS. 259–265. *Micranops.* sp. a. **259.** Head. **260.** Prothorax. **261.** Tergites IX, X, male. **262.** Labium, ventral. **263.** Mandible, left. **264.** Lateral gonocoxal plates. **265.** Labrum.

as we now know, the sensory seta or trichoid sensillum of a trichobothrium, on the lateral side of the head. Two Caribbean species described by Blackwelder (1943: 277, 278) in *Orus* (*Leucorus*), were the initial species included in *Orus* (*Nivorus*); a Surinamese species was added later (Herman, 1965a, 1968b).

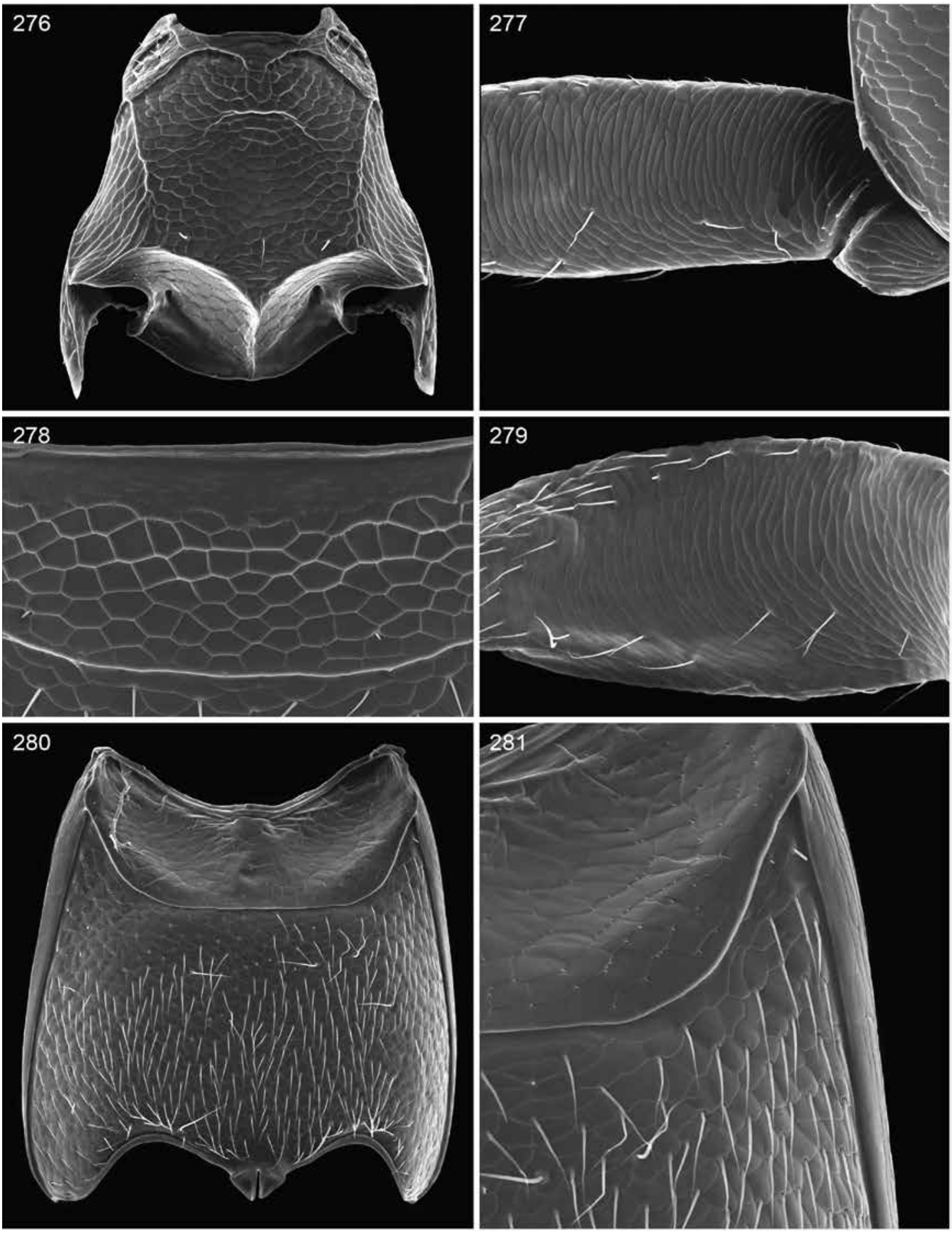
Coiffait (1952: 6) described *Stilpon* with three species (*S. baudrimonti*, *S. bordei* [= *S. portai*], and *S. microphthalmus*), as a subgenus of *Scopaeus* with reduced eyes. The designated type species, *Scopaeus baudrimonti*, a junior synonym of *Scopaeus ryei* Wollaston, 1872 (Frisch, 1998: 101), has a supraocular trichobothrium, as does *S. portai*; both species belong in *Scopaeus*. Later Coiffait (1960: 284) proposed *Geoscopaeus* to replace *Stilpon*, a junior homonym of Loew, 1859, and elevated the group to generic level, but incorrectly cited *Scopaeus microphthalmus*, which has a postocular trichobothrium, as type species of *Geoscopaeus*. Fagel (1973: 14, 18), in a monograph on African *Scopaeus*, continued to treat *Geoscopaeus* at the generic level, corrected the type species, but characterized the genus as having a large, cephalic, postocular pore with a long seta (= trichobothrium) on the temple. Fagel (1973: 21–36) then included 12 African species in *Geoscopaeus*, all with a postocular



FIGS. 266–271. *Micranops* sp. a. **266.** Head, right laterodorsal (eye collapsed). **267.** Head, right anterolateral (eye collapsed). **268.** Head, lateral, trichobothrial cavity enlarged. **269.** Trichobothrial cavity enlarged to show trichobothrium. **270.** Metaventrite. **271.** Metaventrite, left lateral.



FIGS. 272–275. *Micranops* sp. a. **272.** Head. **273.** Mesoventrite. **274.** Aedeagus, left lateral. **275.** Aedeagus, ventral.



FIGS. 276–281. *Micranops*. **276–278.** *M.* sp. a. **276.** Mesoventrite. **277.** Mesofemur, left base. **278.** Sternite IV, midanterior margin, enlarged. **279–281.** *M.* sp. b. **279.** Mesofemur, left. **280.** Metaventrite. **281.** Metaventrite, lateral margin.

trichobothrium; later all were transferred to *Micranops* (Frisch and Herman, 2014). In his introductory remarks for *Geoscopaeus*, Fagel (1973: 18) indicated that along with the three species originally included by Coiffait (1952: 6), two Asian (*Scopaeus pallidulus* Kraatz, 1859, and *Scopaeus planiusculus* Kraatz, 1859) and one New World (*Scopaeus umbra* Sharp, 1886) species should be added. However, although Fagel characterized the genus as possessing a setate postocular pore (= trichobothrium) only three (*S. microphthalmus*, *S. pallidulus*, and *S. planiusculus*) of the six included non-African species have postocular trichobothria; the trichobothrium of the others, including the type species of *Geoscopaeus*, is supraocular. It is unclear what specimens he examined for his assignments. The trichobothrium of the holotype of *S. umbra* is supraocular, so it remains in *Scopaeus*. All the specimens (that I've seen) subsequently identified as *S. umbra* in the Field (FMNH) and British (BMNH) Museums have a postocular trichobothrium and represent an unidentified species of *Micranops*.

Coiffait (1981: 19) removed *G. microphthalmus* Eppelsheim from *Geoscopaeus* and made it the type species of *Microscopaeus*, a new subgenus of *Scopaeus* that included one other species, *S. yemenicus*. This subgenus was defined by the presence of an oblong pit behind the eye. Finally, Coiffait (1984: 148) cited *Geoscopaeus* as a junior synonym of *Scopaeus* and continued to list *Microscopaeus* as a subgenus.

The type localities of *Micranops* and *Microscopaeus*, Jamaica and Crete respectively (see Synonymy above for details), are of note to the following two paragraphs concerning variation of the New and Old World species of the genus.

The neck of most Old World species of *Micranops* is narrow, but there is a wide range of variation that overlaps the wider neck of the New World species (table 3). In the Old World the ratio ranges from 0.18 to 0.40 (mean: 0.25; sample: 49; standard deviation: +/-0.05) and in the New World 0.28 to 0.40. (mean: 0.32; sample: 63; standard deviation: +/-0.03). As shown in table 3 the range of variation of the species of the two hemispheres overlaps at one standard deviation. The mean ratio of the neck width to head width of the Old World species is about one quarter and about one third for the New World species. However, the range of variation of this metric encompasses the entire range in the Old World species, from about one fifth to two fifths the width of the head. For the New World species, the neck ranges from about a quarter to two fifths the width of the head; there are no known specimens with a very narrow neck. In the Old World species with the narrower necks are nearly all Asian, while most of the African species have the wider neck found in the Americas. As can be seen in table 3, there are specimens that link the clusters of narrow-neck and wide-neck species.

The surface of the head and pronotum of most species, both New World and Old, have dense microsculpturing that dominates the punctation and is best viewed with diffused light. The punctation of the head and pronotum of *M. brunneus*, the type species of *Micranops*, is distinct and clearly visible and the microsculpturing is strong and well developed. I have examined a species from Australia and another from Malaysia in which the distribution of the microsculpturing is restricted, portions of the integument are polished, and the punctation is strongly developed and clearly visible. The illustration of *M. bifossicapitatus* appears to show—and is confirmed in the description—clearly visible cephalic and pronotal punctation (Frisch and Oromí, 2006: 27).

Frisch and Herman (2014) transferred 21 species to *Micranops* from *Scopaeus* and *Lathrobium* thereby making *Micranops* a moderately speciose genus with 33 described species. The authors included bibliographic references and a summary of the distribution for each species. However, the genus is far more widely distributed and speciose than their checklist indicated. Both authors have examined a significant number of undescribed species throughout the range of the genus. It is probable that many more of these tiny

TABLE 3

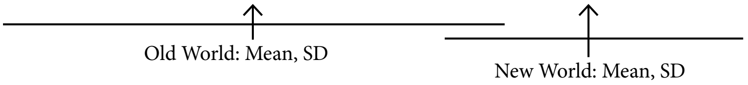
Micranops **spp.: Geographical Distribution of Ratio: Neck Width/Head Width**

Boldface abbreviations of the histogram represent countries of the Old World; Roman abbreviations are for New World countries. Each country abbreviation in the histogram represents one individual. The numbers across the bottom of the histogram, 0.18 to 0.40, are the ratios of the neck width divided by the postocular head width. The two lines below the row of ratios represent the mean, the upward pointing arrow, and plus and minus one standard deviation for Old World and New World respectively

Old World samples: **Au,** Australia; **BF,** Burkina Faso; **SL,** Sri Lanka; **EG,** Egypt; **ER,** Eritrea; **IC,** Ivory Coast; **IN,** India; **ML,** Malaysia; **MY,** Myanmar; **NG,** New Guinea; **PP,** Philippines; **TH,** Thailand; **TK,** Turkey; **TW,** Taiwan; **VL,** Lake Victoria; **VN,** Vietnam; **ZM,** Zambia.

New World samples: AG, Argentina; BM, Bimini; BV, Bolivia; BZ, Brazil; CO, Colombia; CR, Costa Rica; CU, Cuba; JM, Jamaica; MX Mexico; PM, Panama; PR, Peru; UR, Uruguay; US, United States; VZ, Venezuela; WI, West Indies.

												BV	BZ									
												CO	US									
		MY										CO	US				US					
		NG									PR	PR	CO		US		US					
	EG	**PP**									CR	BZ	BZ	MX	US		BZ					
	IN	**VN**									CR	JM	JM	MX	US	US	MX	MX				
	PP	**SL**									CR	JM	JM	US	BM	US	PR	MX				
	VN	**TH**					**ML**	**ML**	**TK**		CR	CU	JM	UR	BM	MX	BZ	BM				
	VN	**TH**		**TK**			**ML**	**ML**	**TW**	VZ	CR	WI	US	AG	BM	BM	BZ	US				
	VN	**TH**	**TH**	**TK**	**IN**	**TK**	**ML**	**BF**	**ER**	CR	**TW**	JM	**TW**	CU	CU	PR	CU	PM			AG	AG
IN	**VN**	**VN**	**TH**	**IC**	**VL**	**ZM**	**BF**	**BF**	**BF**	**TW**	**TW**	JM	**BF**	**ZM**	**ZM**	PR	**ZM**	**ZM**	**ZM**		MX	**AU**
0.18	0.19	0.20	0.21	0.22	0.23	0.24	0.25	0.26	0.27	0.28	0.29	0.30	0.31	0.32	0.33	0.34	0.35	0.36	0.37	0.38	0.39	0.40



beetles will be discovered throughout the tropical and subtropical world and that *Micranops* will be one of the speciose genera of the Scopaeina.

The principal species-diagnostic features for the males of *Micranops* are the length, width, and form of the ventral process of the aedeagus and surfaces and posterior margins of sternites VII and VIII. Identification of the females is more difficult.

Species Included and Material Examined

33 species

aborensis (Fagel, 1973) - H (MRAC) — D.R. Congo

bartolozzii Frisch and Herman, 2014 - Lit. Att. — [Tanzania]

bifossicapitatus (Outerelo and Oromí, 1987) - Lit. Att. — [Canary Islands]

brachyceroides (Fagel, 1973) - H (MRAC), P (IRSN, NHMW) — Ivory Coast, Mali

brachycerus (Fauvel, 1900) - L (IRSN), Sp (BMNH) — D.R. Congo, Angola

brunneus Cameron, 1913 - Syn (BMNH), sp (FMNH, AMNH) — Jamaica

caelebs (Fagel, 1973) - H (MRAC), P (NHMW) — D.R. Congo, Congo Republic

cameroni (Blackwelder, 1943) - H, Sp (USNM), P (FMNH) — Cuba, Grenada, Haiti, Jamaica

chloroticus (Sharp, 1876) - H (BMNH) — Brazil

hoyoensis (Fagel, 1973) - H (MRAC) — D.R. Congo

hustachei (Coiffait, 1987) - Replacement name

franzi (Coiffait, 1982) - H (NHMW) — Nepal

lacustris (Bernhauer, 1937) - Syn (FMNH) — Uganda

fragilis (Cameron, 1947) - Syn (BMNH) — Eritrea

longiceps (Casey, 1886) - H (USNM) — United States

lwiroensis (Fagel, 1973) - H (MRAC) — D.R. Congo

mabalianus (Fagel, 1973) - H (MRAC) — D.R. Congo

mediicollis (Lea, 1923) - Syn (SAMA) — Australia

mlejneki Frisch and Oromí, 2006 - P (MNKB) — Canary Islands

myrmecophilus (Bernhauer, 1921) Syn (FMNH), Sp (AMNH) — Argentina

obscurellus (Cameron, 1932) - Syn (BMNH) — Malaysia

pallidulus (Kraatz, 1857) - H (SDEI), Sp (FMNH) — Ethiopia, India, Philippines, Vietnam

pilicornis (Baudi di Selve, 1870) - Pl (SDEI), Sp (BMNH) — Cyprus, Greece

microphthalmus (Eppelsheim, 1888) - Pl (SDEI, MNKB), Sp (FMNH) — Lebanon, Turkey, Albania

planiusculus (Kraatz, 1859) - Syn (SDEI) — India orientale

pokharensis (Coiffait, 1981) - Lit. Att. — [Nepal]

ruwenzoricus (Fagel, 1973) - H (MRAC) — D.R. Congo

spelaeus Frisch and Oromí, 2006 - Lit. Att. — [Canary Islands]

subapterus (Cameron, 1951) - Syn (BMNH, MRAC) — Angola

subterraneus Frisch and Oromí, 2006 - P (MNKB) — Canary Islands

surinamensis (Herman, 1965) - H (CUMC) — Suriname

upembanus (Fagel, 1973) - H (MRAC) — D.R. Congo

viti Assing, 2021 - Lit. Att. — [Pakistan]

volans (Blackwelder, 1943) - H (USNM) — Jamaica

yemenicus (Coiffait, 1981) - H, P (TMCB), Sp (MNKB) — Yemen

zambezianus (Fagel, 1973) - H (MRAC) — Zambia

UNDETERMINED SPECIMENS: Eastern Hemisphere: Australia (New South Wales), Burkina Faso, Egypt, Ivory Coast, Malaysia, Myanmar, Sri Lanka, Taiwan, Thailand, Turkey, Vietnam, Zambia.

Western Hemisphere: Argentina (Tucumán), Bolivia, Brazil (Pará, Santa Catarina), Colombia, Costa Rica, Cuba, Mexico (Chiapas, Michoacán, Nayarit, San Luis Potosí, Vera Cruz), Panama, Peru, The Bahamas (Bimini), Uruguay, United States (Arizona, Texas, Oklahoma, Florida), Venezuela (Barinas).

DISSECTIONS: Disarticulation: Undetermined males and females (Bimini, Burkina Faso, Taiwan).

Orus Casey

Figures 9, 10, 13, 20, 21, 257, 286–325

Orus Casey, 1885: 136. Type species: *Orus punctatus* Casey, 1885: 138, fixed by Blackwelder (1939a: 120) by subsequent designation.

— Casey, 1886a: 36, 38 (characters; notes). — Casey, 1886b: 217, 226, 229 (characters). — Sharp, 1886: 549 (notes; one Mesoamerican species). — Fall, 1901: 222 (distribution; notes). — Casey, 1905: 191, 196 (characters; notes; key to species). — Bernhauer and Schubert, 1912: 245 (subgenus of *Scopaeus*). — Leng, 1920: 104 (catalog of American species). — Cameron, 1931: 169 (synonym of *Scopaeus*). — Blackwelder, 1939a: 98, 105, 120 (key; checklist; type species). — Blackwelder, 1939b: 24 (catalog of American species). — Blackwelder, 1943: 230, 277 (key; characters; key to West Indian species; notes; type species).

— Blackwelder, 1944: 119 (checklist of species, Latin America). — Blackwelder, 1952: 278 (type species). — Hatch, 1957: 151 (characters; key to subgenera and species of N.W. United States). — Arnett, 1963: 244, 269 (characters; notes). — Herman, 1965a (revision of two subgenera; key to subgenera). — Herman, 1965b (revision of two subgenera; type species; key to species; characters; distribution; checklist of species). — Blackwelder and Arnett, 1974: 57 (checklist; North America; Central America; West Indies). — Moore and Legner, 1974: 559 (characters). — Moore and Legner, 1975: 128 (catalog; American species). — Moore and Legner, 1979: 110 (characters; notes). — Downie and Arnett, 1996: 405 (characters; key to species of Northeastern North America). — Newton, Thayer, Ashe, and Chandler, 2000: 386 (North American species; characters in key; notes). — Frisch, Burckhardt, and Wolters, 2002a: 46 (discussion). — Navarrete-Heredia et al., 2002: 279 (characters in key to genera for Mexico; general notes; unnamed species known from Mexico). — Jiménez-Sánchez, Zaragoza-Caballero, and Noguera, 2009: 167 (seasonal abundance; Morelos, Mexico).

Leucorus Casey, 1905: 192. Type species: *Leucorus rubens* Casey, 1905: 194, fixed by Blackwelder (1939a: 119) by subsequent designation. Subgenus of *Scopaeus*. — Bernhauer and Schubert, 1912: 245 (subgenus of *Scopaeus*). — Leng, 1920: 104 (catalog of American species). — Cameron, 1931: 169 (subgenus of *Scopaeus*). — Blackwelder, 1939a: 98, 105, 119 (key; subgenus of *Orus*; checklist; type species). — Blackwelder, 1943: 277 (subgenus of *Orus*; type species). — Blackwelder, 1944: 119 (subgenus of *Orus*). — Blackwelder, 1952: 220 (type species; subgenus of *Orus*). — Herman, 1965a: 113 (key; characters; key to species; notes; type species; subgenus of *Orus*). — Blackwelder and Arnett, 1974: 57 (synonym of *Orus*). — Newton, Thayer, Ashe, and Chandler, 2000: 386 (subgenus of *Orus*). — Navarrete-Heredia et al., 2002: 279 (subgenus of *Orus*).

Pycnorus Casey, 1905: 194. Type species: *Scopaeus dentiger* LeConte, 1880: 179, fixed by Blackwelder (1939a: 121) by subsequent designation. Subgenus of *Scopaeus*. — Bernhauer and Schubert, 1912: 245 (subgenus of *Scopaeus*). — Leng, 1920: 104 (catalog of American species). — Cameron, 1931: 169 (subgenus of *Scopaeus*). — Blackwelder, 1939a: 98, 105, 121 (key; subgenus of *Orus*; checklist; type species). — Blackwelder, 1943: 277 (subgenus of *Orus*; type species). — Blackwelder, 1944: 119 (synonym of *Orus*). — Blackwelder, 1952: 333 (type species; synonym of *Orus*). — Hatch, 1957: 159 (subgenus of *Orus*; characters). — Herman, 1965a: 113 (key; subgenus of *Orus*). — Herman, 1965b: 74, 81, 87 (subgenus of *Orus*; key; characters; key to species; type species; notes; distribution). — Blackwelder and Arnett, 1974: 57 (synonym of *Orus*). — Campbell and Davies, 1991: 114 (subgenus of *Orus*). — Newton, Thayer, Ashe, and Chandler, 2000: 386 (subgenus of *Orus*). — Navarrete-Heredia et al., 2002: 279 (subgenus of *Orus*).

Diagnosis: *Orus* can be separated from the other genera of Scopaeina by the position of the cephalic trichobothrium adjacent to the dorsoposterior edge of the posteriorly tapered margin of the eye (figs. 297, 309, 315). The trichobothrium is at the posterior end of an elongate trichobothrial canal, which extends along the dorsal margin of the eye anteriorly from the posterior margin; the canal has a cluster of setae in front of the bothrium. Among other genera of the Scopaeina, the trichobothrium touches at or near the middorsal edge of the eye in *Scopaeus*, *Hyperscopaeus*, and *Trisunius*; for *Micranops*, the trichobothrium is in a deep cavity behind and separated from the posterior margin of the eye. The neck (fig. 286) of most species of *Orus* is about one third to two fifths the width of the postocular width of the head, but is narrower, about a fifth as wide, in *O. cervicula*, *O. femoralis*, and *O. montanus*. Species of *Orus* lack a stridulum (figs. 300–302; 305–307; 312–314) and the apex of the metakatepisternal process is rounded (figs. 300, 305, 313); *Scopaeus* possesses a stridulum (figs. 142–144) and the metakatepisternal process is acute apically (fig. 142).

Description: Body Length 2.5–4.4 mm.

Head with postocular lateral margin gradually rounded to basal angle (fig. 286); basal angle strongly rounded; basal margin more or less truncate and without or with weak, broad emargination; basal margin without median tumescence, sulcus, or groove; posteroventral surface with minute tubercle laterad of neck.

Neck wide, gradually expanded for most species, strongly to moderately petiolate for a few (see *O. cervicula* and *O. montanus*); nuchal groove strongly to moderately constricted and base of neck abruptly expanded; neck width across nuchal groove about one third (fig. 286) to about one fifth as wide as postocular width of head (*O. cervicula* and *O. montanus*; see Discussion below); nuchal ridge present dorsally and laterally.

Dorsal surface with fine, moderately dense to dense punctation; punctation distinct, strong to fine, and uniform to less dense or absent from median strip; microsculpturing present or absent and surface polished except for fine microsculpturing on clypeal region; pubescence fine, moderately dense to dense; macrosetae moderately long, peripheral, and few.

Cephalic trichobothrium (figs. 297, 309, 315) in elongate, trichobothrial canal adjacent to tapered posterior margin of eye; trichobothrial canal deeper posteriorly and increasingly shallow and tapered anteriorly; surface of canal setate anterior to bothrium; trichobothrium present posteriorly in deepest part of trichobothrial canal.

Eyes tapered posteriorly and with posterior margin strongly and narrowly rounded to nearly pointed (fig. 297); corneal lenses with sensilla well developed (figs. 20, 298) or evident as remnants (figs. 21, 316).

Gular sutures moderately widely separated (fig. 286).

Mandibles: Left mandible with three denticles (fig. 294), right mandible with four denticles (fig. 295).

Labrum bidentate (figs. 293, 319) or quadridentate (fig. 296), or denticles reduced to small, rounded lobes (fig. 288).

Pronotum broadly and moderately convex; surface with moderately dense to dense punctation; midlongitudinal strip usually without punctation but present occasionally; microsculpturing absent or present; midlongitudinal strip with or without microsculpturing; surface moderately shiny to polished; pubescence fine and moderately dense to dense; macrosetae moderately long, peripheral, and few; median groove present and shallow or absent.

Prohypomeron with lobe separated from remainder of hypomeron by well-developed to weakly developed transverse, prohypomeronal ridge; lobe with a few setae anteriorly. Notosternal suture present (fig. 287).

Elytra longer to shorter than pronotum; punctation and pubescence moderately dense to dense; posterior margin with row of setae.

Mesoventrite with broad, rounded, moderately deep, basisternal, median depression (figs. 9, 299, 308, 320); prepectal ridges medially separated; mesotransventral ridge strongly curved; mesanapleural ridge with anterior segment present, posterior segment absent (fig. 9) or with possible remnant (figs. 299, 308).

Mesofurcasternum without (fig. 299, 308) internal median apophysis on posteromedial margin.

Mesofemur without stridular plectral ridges (figs. 302, 307, 312).

Mesocoxal acetabulum margined by pericoxal ridge and well developed throughout (fig. 10, 313) or well developed laterally and poorly developed or absent posteriorly (figs. 300, 305).

Metaventrite without stridular file (figs. 300, 301; 305, 306; 313, 314).

Metakatepisternal process short and apically rounded (figs. 300, 305, 313).

Sternite II (figs. 303, 311, 321) with median point on posterior margin.

Sternite III (figs. 303, 311, 321) with well-developed median carina; transverse basal ridge sinuate and with median point.

Sternite IV without glandular lobe or pore (figs. 304, 322).

Male: Sternite VII with variously modified median surface and posterior margin.

Sternite VIII with wide and moderately deep to shallow or narrow and deep emargination of posterior margin.

Tergite IX (figs. 292, 323) asymmetrical; left anteroventral side larger than right or with large, medially directed lobe; right anteroventral side without medially directed lobe and not enlarged anteriorly or medially (fig. 323); posterior margin with broadly U-shaped emargination; mid-dorsal base fused (fig. 292) or divided medially.

Sternite IX elongate (fig. 291).

Tergite X (fig. 292) trapezoidal or elliptical; anterior margin without median point; anterior margin straight to sharply rounded lateral angles or strongly rounded to lateral angles.

Aedeagus with dorsal surface of median lobe divided midlongitudinally or with oval, median sclerite surrounded by membrane; paramere present as small lobe on lateral side of median foramen (fig. 324).

Female: Sternite VII with unmodified posterior margin.

Sternite VIII with posterior margin rounded, but otherwise unmodified.

Tergite IX (fig. 289) symmetrical; left and right anteroventral sides of approximately equal size; posterior margin broadly U-shaped; mid-dorsal base divided.

Tergite X (fig. 289) with anterior margin with subacute, median point and strongly rounded to lateral margin or anterior margin with median point then sloping and rounded to lateral margin.

Distribution and Habitat: Most of the species of *Orus* are known only from the United States and most occur between the eastern edge and Front Range of the Rocky Mountains to the Pacific Coastal Range. Although most specimens and species have been collected in California, Oregon, and Washington, the genus is found throughout the western mountains. Only two species have been collected in the United States and Canada, *O. dentiger* in the east and *O. punctatus* in the west, but *O. parallelus* might occur in the west of both countries. In the United States, only *O. dentiger* and *O. rubens* occur east of the Rocky Mountains, the latter as far east as Ohio. One named species (*O. ferrugineus*) occurs in Mexico and the southwestern United States. One described species, *O. guatemalenus*, is known from Guatemala and Mexico and another, *O. femoralis*, is described from Mexico City. I have examined several undescribed species from Mexico and others from the United States. Surely more will be found in the United States, but it seems likely that many more species will be discovered in Mexico, particularly on the Mexican Plateau and forests of the bordering Sierra Madre Oriental and Occidental ranges. A specimen of *O. dentiger* from Mexico in the Field Museum is erroneously labeled.

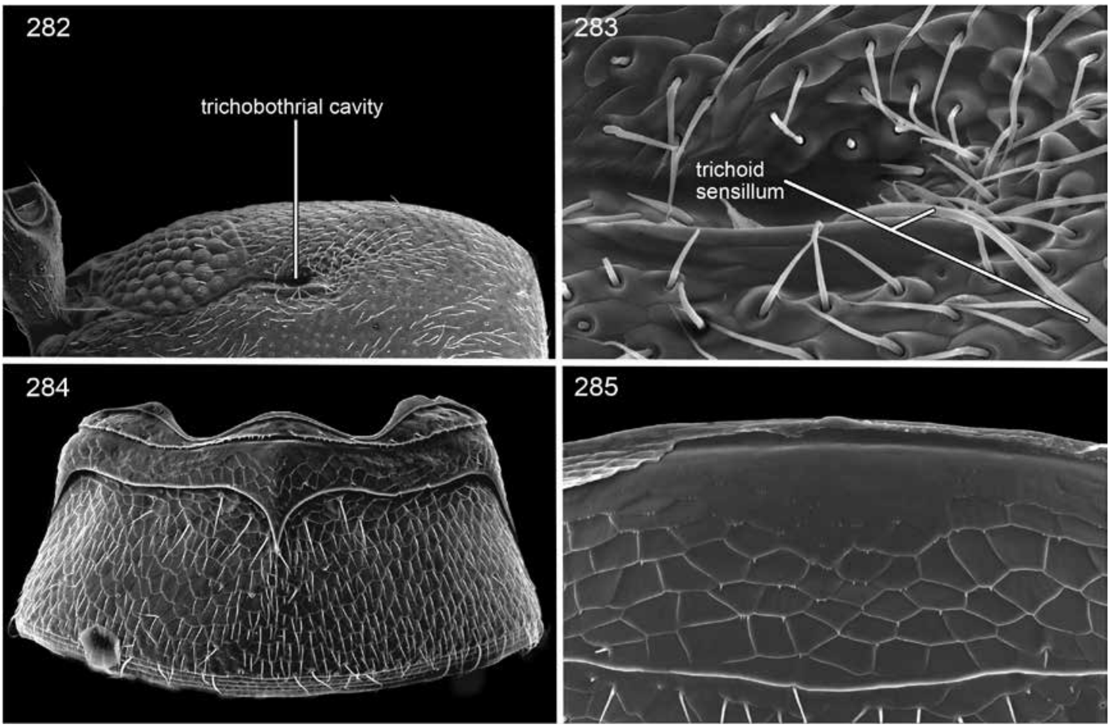
Species have been collected from leaf litter and other organic debris near streams, ponds, and marshes, but some are occasionally reported from fungus, under bark, and in tree-stump debris. Two species have been collected in caves. *Orus rubens* is commonly found in caves of Texas and is one of the several most frequently collected staphylinid species of those caves. The other, *O. ferrugineus*, appears to be a sometime cave inhabitant in north central Mexico; I have seen only a few such individuals. Neither species is cave adapted; both are primarily surface dwellers. It is likely they moved into caves of the southwestern United States and north central region of the Mexican Plateau (Chihuahua and Coahuila) to survive the aridity of the region. Those species along with all others of *Orus* live on the surface in organic debris and leaf litter in more humid habitats and regions. Most species have been collected in the mountains at about 600 to 1800 meters elevation; one, *O. rubens*, has been collected at 2500 meters in Arizona and in the lowlands of the Midwest. Some species are found in litter at the edge of lowland streams and marshes.

Specimens of *O. punctatus* collected at about 1000 m from the Sweetwater River near Descanso, San Diego County, California harbored an unidentified species of the parasitic fungi Laboulbeniales. *Orus punctatus* was reported to eat the eggs of the anthomyiid cabbage maggot, *Hylemya brassicae* (Bouché) (see Herman, 1965b: 77, 90, for citations).

SUBGENERA: Casey described three genera, *Orus* in 1885, and *Pycnorus* and *Leucorus* in 1905. Soon after, the names were listed, without discussion, either as subgenera of *Scopaeus* (Berhauer and Schubert, 1912: 245; Cameron, 1931: 169) or genera (Leng, 1920: 104). In his key to the genera of the Paederini, Blackwelder (1939a: 98, 105) treated *Orus*, *Pycnorus* and *Leucorus* as subgenera; a few years later he (1944: 119; 1952: 278) listed *Leucorus* and *Orus* as subgenera with *Pycnorus* a synonym of *Orus*. In a revision of *Orus*, the three were treated as subgenera (Herman, 1965a, 1965b). Blackwelder and Arnett (1974: 57) listed *Leucorus* and *Pycnorus* as junior synonyms of *Orus*. More recently others have listed both names as subgenera of *Orus* (Campbell and Davis, 1991: 114; Newton et al., 2000: 386; Navarrete-Heredia et al., 2002: 279).

Casey (1885, 1905) provided characters for each genus-group name, as did Blackwelder (1939a) and Herman (1965a, 1965b), but the question of rank and grouping was not explicitly addressed.

Orus, *Pycnorus*, and *Leucorus* each have characters that distinguish them from the others, but elevating even one of the groups to genus or subgenus results in at least one group without unique, derived characters. *Orus* as a group that includes three clusters of species can be separated from all other Scopaeina by the posteriorly tapered form of the eye and the position of the trichobothrium on the dorsoposterior edge of the eye and from *Scopaeus* and *Hyperscopaeus* by the wide neck. The characters that separate *Orus*, *Pycnorus*, and *Leucorus* include modifications of the labrum, gula, metafemur, tergite VIII, and aedeagus. *Leucorus* has several derived characters to separate it from *Orus* and *Pycnorus*. The subgenera vary in the number of labral denticles (0, 2, or 4). Species of *Orus* and *Pycnorus* have 4 labral denticles. Males of *Pycnorus* have a pointed, gular tubercle reduced to a small, rounded bump on females, the gular surface is broadly impressed and strongly microsculptured, and males have a row of spines on the enlarged, strongly curved metafemur; *Orus* and *Leucorus* have neither the gular nor femoral modifications. The dorsal surface of the median lobe of the aedeagus of both *Orus* and *Pycnorus* is membranous (Herman, 1965b: 21). Species of *Leucorus* have two labral denticles (female, fig. 293) or none or two submedial lobes (male, fig. 288); the aedeagus has a hooked process at the distal end of the basal foramen (fig. 325; Herman, 1965a: figs. 1b–3b) and the dorsal surface has an oval sclerite surrounded by membrane (Herman, 1965a: figs. 2d, 3d) that may be a compression plate that when drawn inward helps evert the internal sac, and males have a deep, narrow emargination of tergite VIII (Herman, 1965a: figs. 1a–3a). The pericoxal ridge is well developed posteriorly and laterally in *Leucorus* (figs. 10, 313), but well developed laterally and weakly developed posteriorly in *Pycnorus* and *Orus* (figs. 300, 305). Tergite IX of the males (figs. 292, 323) is strongly asymmetrical with the left anterior side larger than the right. The medially directed lobe of the medioventral edge of tergite IX is lobed (fig. 323); the lobe is more strongly developed in *Leucorus* than in the other two groups. Modifications of the gula and metafemur of *Pycnorus* males and the labrum, aedeagus, and tergite VIII *Leucorus* are unique in the Scopaeina. As a subgenus, *Orus* is basically left over and without derived features to define it. The quadridentate labrum is shared by *Orus* and *Pycnorus*, but that feature is found throughout the subtribe. Likewise, a group including *Orus* and *Pycnorus* has no defining derived characters.

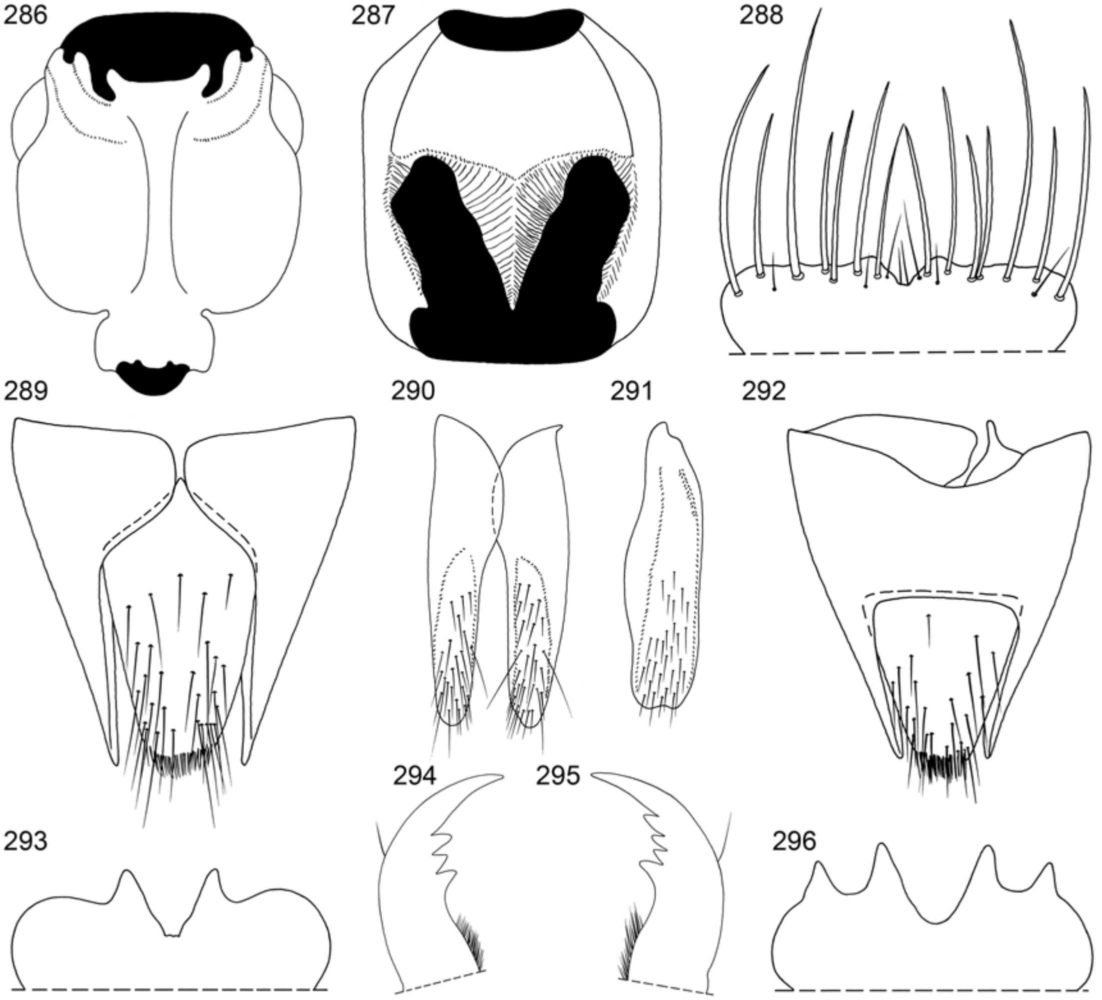


FIGS. 282–285. *Micranops* sp. b. **282.** Head, right lateral, eye and trichobothrial cavity. **283.** Trichobothrial cavity, enlarged. **284.** Sternites II and III. **285.** Sternite IV, midanterior margin, enlarged.

Although the temptation to synonymize *Leucorus* and *Pycnorus* with *Orus* was great and in earlier drafts I had so done, I understood, and one reviewer so agreed, that action did nothing to change our understanding of the three groups and their relationship with one another. Discussions with others and review comments persuaded me to let well enough alone.

Discussion: *Narrow-necked species*: For most species of *Orus* the width of the neck is about a quarter to a third as wide as the widest portion of the postocular head. For a few, *O. cervicula* Casey, *O. femoralis*, and *O. montanus* Fall, the neck is slightly more to slightly less than a fifth as wide as the head. A few years ago, Frisch asked me why in 1965 had I included the slender-necked *O. montanus* in *Orus* rather than *Scopaeus*. The following is a more complete answer than I gave him then.

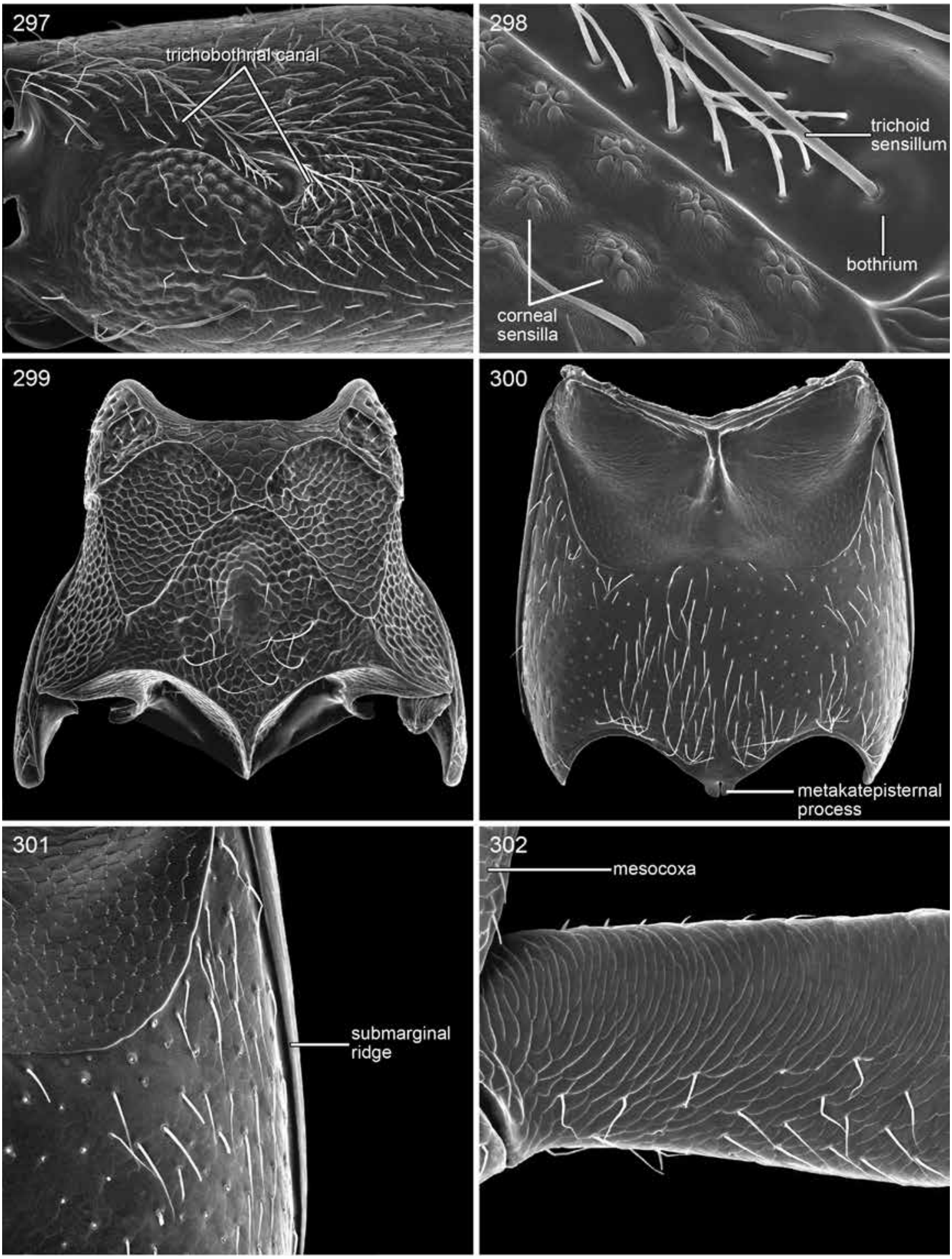
Both species were described in *Orus*. Later *O. cervicula* was moved to *Pseudorus* (Casey, 1910: 190), then to *Scopaeus* (Bernhauer and Schubert, 1912: 246; Blackwelder, 1939a: 105; Moore and Legner, 1975: 138), where it remained until the present work. When Casey redescribed *Orus* he (1905: 191) wrote in the first couplet of the key that the neck was “a fourth to nearly a third as wide as the head.” By contrast, the neck of *Scopaeus* was ambiguously described as “extremely slender.” Casey (1905: 198) included *O. montanus* in *Orus* despite its narrow neck. Furthermore, in Casey’s key (1905: 196) to species of *Orus* the second option of the first couplet, “Neck very slender as in *Scopaeus*,” led to *O. cervicula*. Subsequently, Casey (1910: 190) moved *O. cervicula* to *Pseudorus* (later a subgenus, then synonym, of *Scopaeus*) because the neck “is very minute and thin as in *Scopaeus*.” The first half of the couplet 25 of Blackwelder’s key (1939a: 98),



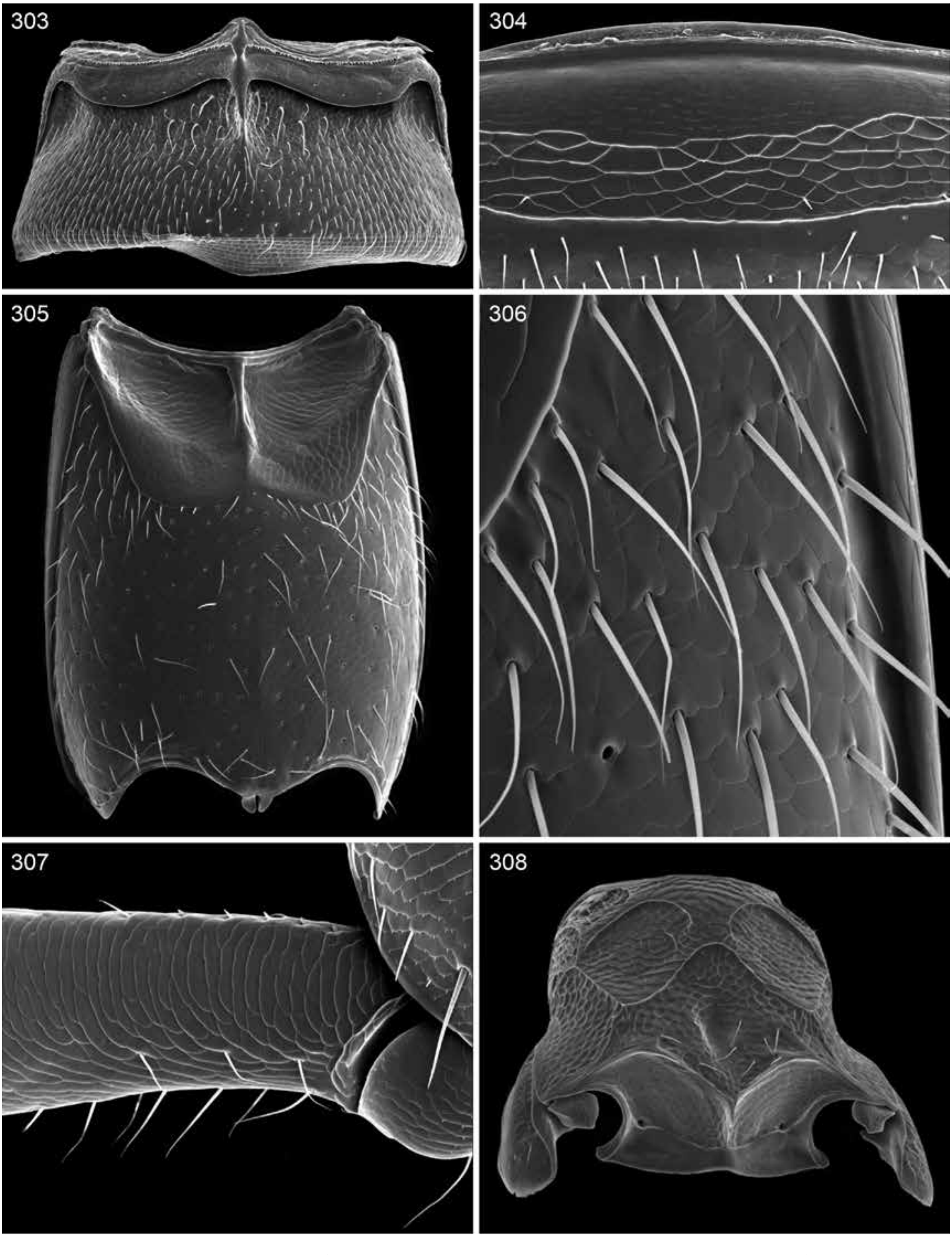
FIGS. 286–296. *Orus*. **286–295**. *Orus rubens*. **286.** Head. **287.** Prothorax. **288.** Labrum, male. **289.** Tergites IX, X, female. **290.** Lateral gonocoxal plates. **291.** Sternite IX, male. **292.** Tergites IX, X, male. **293.** Labrum, female. **294–295**. Mandibles, dorsal. **296.** *Orus dentiger*, labrum, female.

the neck is "one-fourth as wide as head, or more" which led to *Orus* and the second half, "one-fifth to one-eighth as wide as head" to *Scopaeus*. Blackwelder (1939a: 105) included *O. montanus* in *Orus* and *O. cervicula* in *Scopaeus*. No defense for the inclusion of the skinny-necked *O. montanus* in *Orus* was presented by either author.

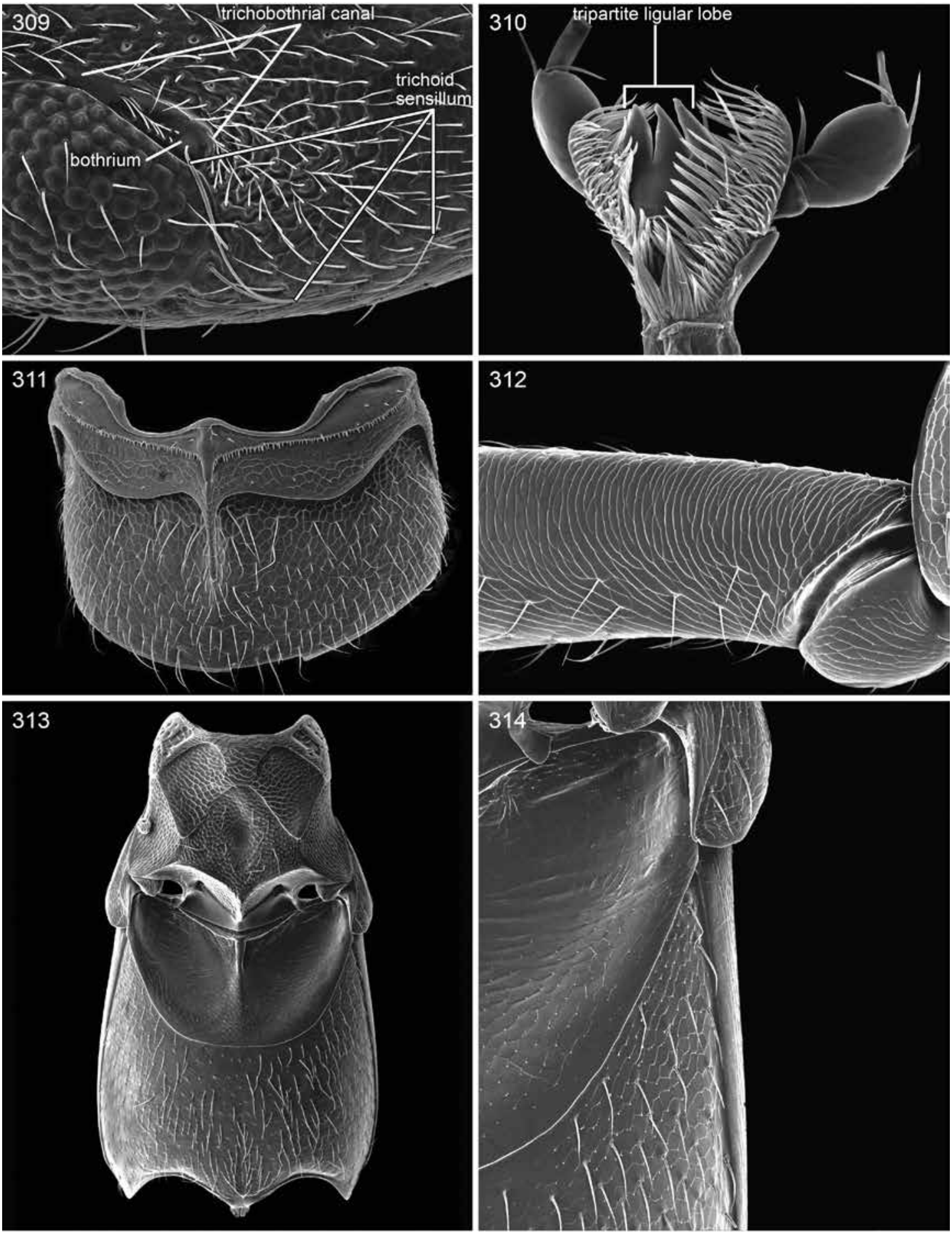
In a revision of *Orus*, the then newly discovered cephalic trichobothrial characters provided a more explicit definition of the genus (figs. 315, 316; Herman, 1965a: fig. 2e). The eye of *Orus* is tapered posteriorly (fig. 297), the trichobothrial canal touches the dorsoposterior edge of the eye, and the trichoid sensillum is inserted near the posterior edge of the eye. For *Scopaeus* the posterior margin of the eye is rounded and the trichobothrium and the sensillum are adjacent to the middle of the dorsal margin of the eye. *Orus montanus* was included in *Orus* because of the tapered eye and position of the trichobothrium (Herman, 1965b). For the present work and with consideration of newly discovered characters for *Scopaeus*,



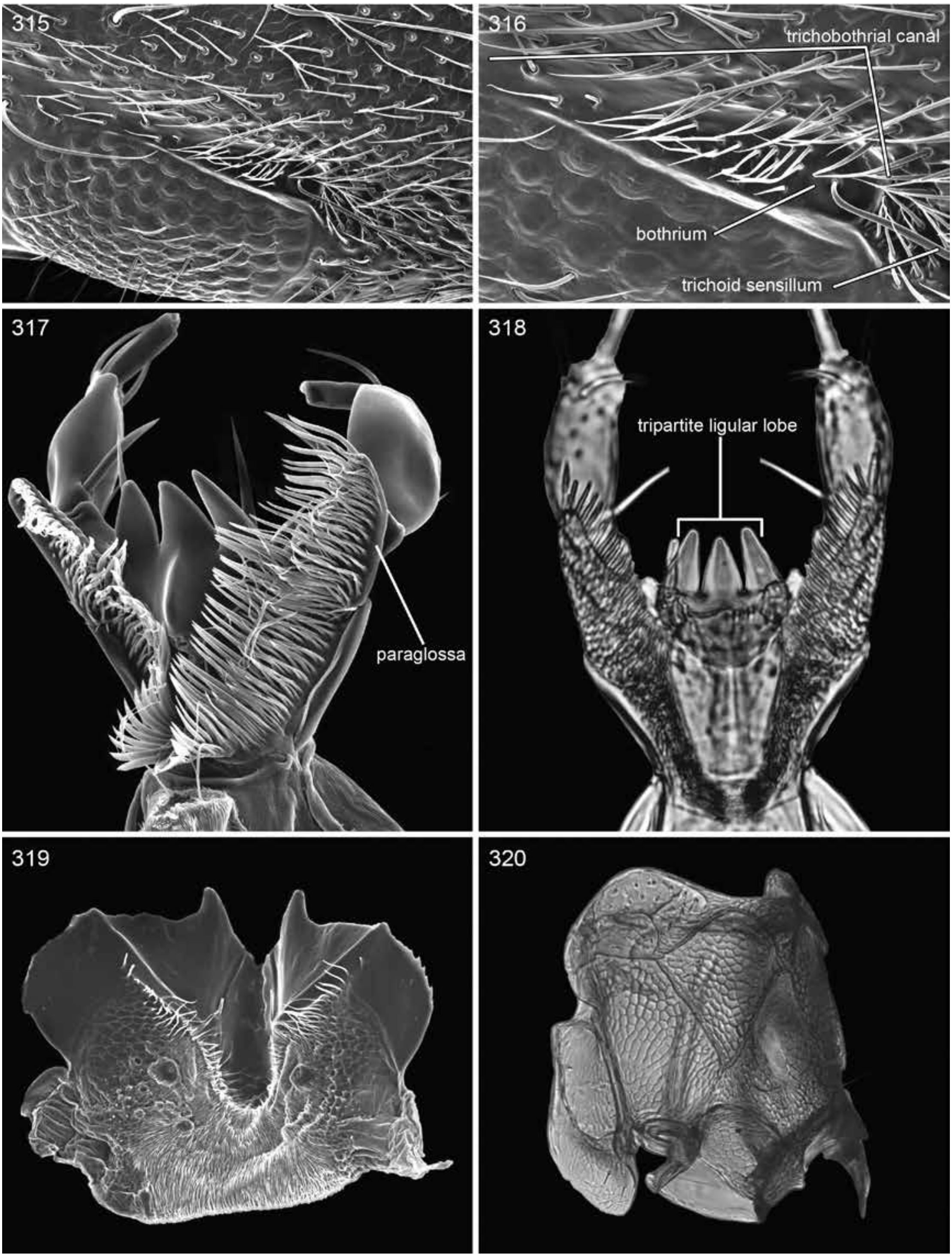
FIGS. 297–302. *Orus dentiger*. **297.** Head, left lateral. **298.** Trichobothrium, enlarged. **299.** Mesoventrite. **300.** Metaventrite. **301.** Metaventrite, left lateral margin. **302.** Mesofemur, right base.



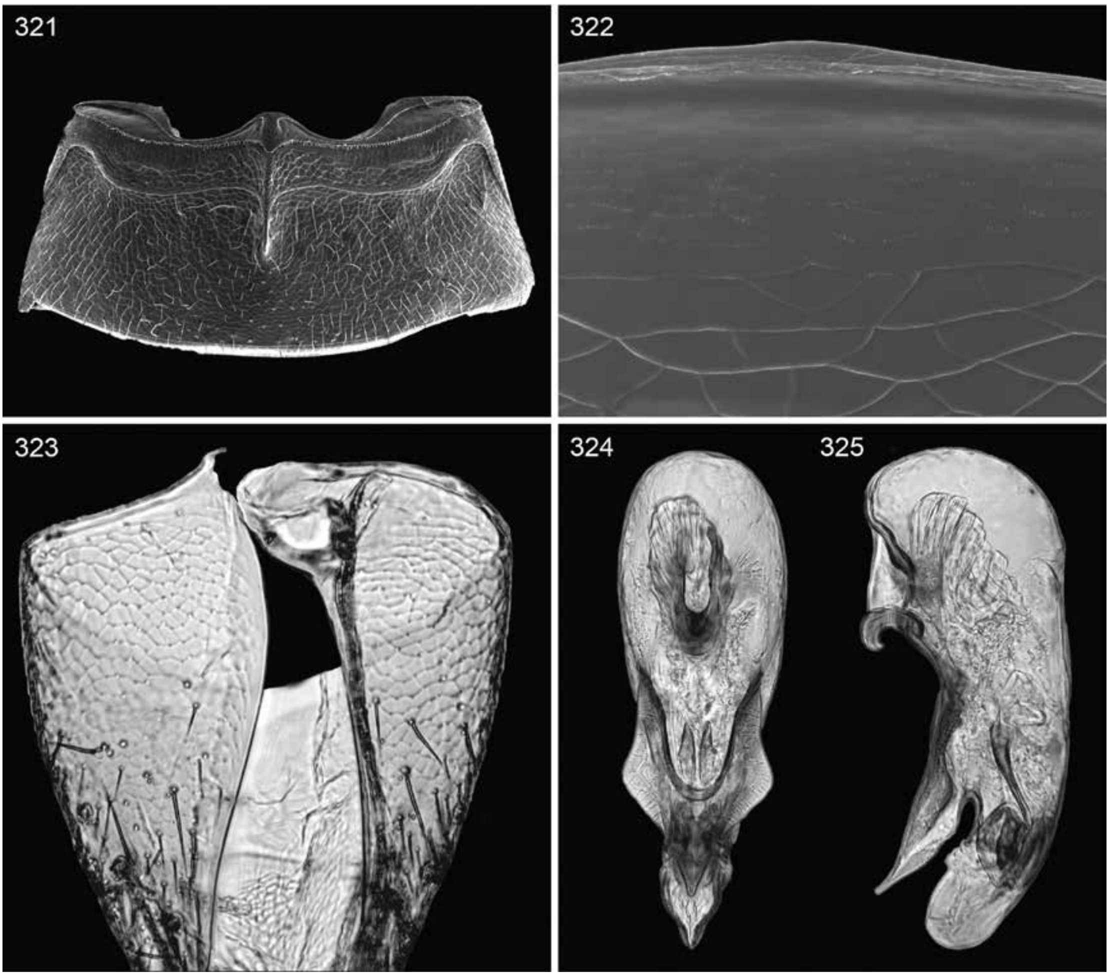
FIGS. 303–308. *Orus*. **303–304.** *O. dentiger*. **303.** Sternites II and III. **304.** Sternite IV, midanterior margin. **305–308.** *O. punctatus*. **305.** Metaventrite. **306.** Metaventrite, left lateral margin. **307.** Mesofemur, left base. **308.** Mesoventrite, posteroventral.



FIGS. 309–314. *Orus*. **309–311.** *O. punctatus*. **309.** Head, dorsolateral, trichobothrium. **310.** Labium, hypopharynx. **311.** Sternites II and III. **312–314.** *O. rubens*. **312.** Mesofemur, left base. **313.** Pteroventrites. **314.** Metaventrite, left anterolateral margin.



FIGS. 315–320. *Orus rubens*. **315.** Head, dorsolateral, trichobothrium. **316.** Trichobothrium. **317, 318.** Labium, hypopharynx. **319.** Labrum, epipharynx. **320.** Mesoventrite, lateroventral.



FIGS. 321–325. *Orus rubens*. **321.** Sternites II and III. **322.** Sternite IV, midanterior margin. **323.** Tergite IX, ventral, male. **324.** Aedeagus, ventral. **325.** Aedeagus, left lateral.

the type series of *O. montanus* was reexamined corroborating the earlier assignment of the species to *Orus*. Neither the male nor female syntype of *O. montanus* exhibit a stridulum, the metaventral stridulatory file and mesofemoral plectral ridges are absent and the metakatepisternal processes are rounded apically rather than acute. Furthermore, for the male, the dorsal surface of the aedeagal median lobe is entirely membranous in contrast to the entirely sclerotized median lobe of *Scopaeus*. Since in 1965 *O. cervicula* had been excluded from the genus for 55 years (Casey, 1910: 190) the species was not even considered in the revision of *Orus* (Herman, 1965a, 1965b). However, the species also bears both features that in 1965 defined *Orus*. Furthermore, as for *O. montanus*, new characters defining *Scopaeus* support excluding *O. cervicula* from it because it lacks a stridulum and the apex of the metakatepisternal processes are rounded rather than acute. Although the aedeagus of *O. cervicula* was not examined, it is virtually certain that the dorsal surface of the median lobe is membranous. The slender-necked *Orus femoralis* is transferred from *Scopaeus* because it too shares the defining features of *Orus* and rather than those of *Scopaeus*.

Flight: For only one species is there nearly direct evidence of flight. No individuals have been collected or observed in flight, but specimens of one species were collected at a black light, to which they presumably flew, not walked. In lieu of such observations the only compelling evidence would be exceptionally reduced wings. No effort was made to lift an elytron of mounted specimens to see the wings, but by happenstance, wings of some individuals of species were partially or fully visible. Without evidence of the wing length, conjecture herein of flightlessness is circumstantial based on possession of abnormally abbreviated elytra, broadly rounded, elytral humeral angles, and absence or poor quality of the palisade fringe of abdominal tergite VIII. In addition, the metathorax of flightless species is usually reduced; the mesocoxae and metacoxae often nearly touch, and the eyes can be reduced.

Three unnamed species of *Orus* cannot fly. The elytra of two are 30% shorter than the pronotum, the elytral humeral angle is more broadly rounded than for other congenerics, the palisade fringe of tergite VIII is absent, the eyes and metathorax are reduced; for neither are wings exposed. The third species looks more or less normal. The elytra are only 15% shorter than the pronotum, the humeral angle is narrowly rounded, like congenerics for which flight is presumed, and the palisade fringe is present and both it and the metathorax seem normally developed. However, the exposed wings of several specimens are so reduced that they barely extend beyond the elytral margin.

For only *O. rubens* is there any evidence of flight. Specimens of the species were taken at a black light at about 1650 m in the Chiricahua Mountain of southeastern Arizona (Herman, 1965a: 114). Among the many hundreds of collecting records available to me, no other specimens were collected at lights, and none were collected in flight.

Among the remaining species, described and undescribed, evidence of flight or lack thereof is ambiguous. They all have well-developed humeral angles, the metathorax is normally developed, and the palisade fringe is present. The elytral length varies from 20% shorter to 30% longer than the pronotum. The elytral and pronotal length was measured for 17 species. Of these the elytral length varied from 20% shorter than to 6% longer than the pronotum for only *O. dentiger*. For only one of the 22 specimens of *O. dentiger* sampled were the elytra slightly longer than the pronotum; several disarticulated specimens had significantly reduced wings that were longer than mere pads. The elytra of *O. rubens*, of which at least some individuals may fly, vary from 10% shorter to 10% longer than the pronotum; most were within 5% of the pronotal length. The length of the elytra and pronotum for most individuals of *O. ferrugineus*, was subequal ranging from -8% to +13%. The elytra of all the individuals of *O. punctatus* were 20%–30% longer than the pronotum. The elytral length of all the remaining species measured was longer (+6%–27%).

Species Included and Material Examined

18 species

cervicula Casey, 1905 - Syn (USNM) — United States
Revised combination, transferred from *Scopaeus*

deceptor Casey, 1905 - Syn (USNM) — United States

dentiger (LeConte, 1880) - Syn (MCZC), Sp (AMNH, FMNH, USNM)….Canada, United States

iowanus (Casey, 1905)
humile (Notman, 1919)

distinctus Casey, 1905 - Syn (USNM), Sp (AMNH) — United States

femoralis (Sharp, 1887) - H (BMNH) — Mexico

New combination, transferred from *Scopaeus* [Note: On examining the type I neglected to record features for subgeneric assignment]

femoratus Fall, 1901 - H (MCZC) — United States

ferrugineus (Casey, 1905) - L (USNM), Sp (AMNH, FMNH, USNM) — Mexico, United States

luridus (Casey, 1905) - Syn (USNM)
ochrinus (Casey, 1905) - L, Pl (USNM)

fraternus Fall, 1901 - Syn (MCZC) — United States

guatemalenus Sharp, 1886 - L, Pl (BMNH, FMNH) — Guatemala

hemilobatus Herman, 1965 - H (CASC) — United States

montanus Fall, 1901 - Syn (MCZC) — United States

parallelus Casey, 1886 - Syn (USNM), Sp (AMNH, FMNH) — United States

armiger (Fall, 1901) - H (MCZC)
boreellus Casey, 1905 - L (USNM)
longicollis Casey, 1905 - Syn (USNM)
provensis Casey, 1910 - H (USNM)
caseyianus (Scheerpeltz, 1933)

pinalinus Casey, 1905 - Syn (USNM) — United States

punctatus Casey, 1885 - H (USNM), Sp (USNM, CASC, AMNH) — Canada, United States

sonomae Casey, 1905 - L (USNM)
pallidus Casey, 1905 - Syn (USNM)
filius Casey, 1905 - L (USNM)

robustulus Casey, 1905 - Syn (USNM) — United States

rubens (Casey, 1905) - H (USNM), Sp (AMNH, FMNH) — United States

shastanus Casey, 1905 - Syn (USNM), Sp (FMNH) — United States

pugetanus Casey, 1905 - L (USNM)

sinuatus Herman, 1965 - H (CASC), P (FMNH) — United States

Undetermined specimens: Canada, United States, Mexico.

Dissections: Disarticulation: *Orus rubens* (male, female); *Orus dentiger* (male, female); *Orus punctatus* (male, female).

Trisunius Assing, New Subtribal Assignment

Figures 16, 22, 258, 326–348

Trisunius Assing, 2011: 196. Type species: *Trisunius spathulatus* Assing, 2011: 198, fixed by original designation.

— Assing, 2012a: 210 (partially revised key to species). — Assing, 2013: 1539 (checklist of species with general distribution). — Assing, 2014 (new records and species). — Assing, 2015 (new records and species).

Diagnosis: *Trisunius* is separated from *Scopaeus* by a wide neck (fig. 342), absence of a stridulum (figs. 335–337), apically rounded metakatepisternal process (fig. 335), and presence of the pericoxal ridge around the mesocoxal acetabulum (fig. 335). The wide neck of *Trisunius* will separate it from *Hyperscopaeus* (fig. 240); the neck of the former is about a third to two fifths as wide as the postocular width of head, the latter about one eighth to one sixth. *Orus* and *Micranops* are both separated from *Trisunius* by the position of the cephalic trichobothrium. The trichobothrium of *Trisunius* is in a trichobothrial depression near or just forward of the middle of the dorsal edge of the eye, and the sensillum is near the middle of the eye (figs. 344, 333); for *Orus* it is in a trichobothrial canal that begins at the dorsoposterior edge of the eye, which tapers posteriorly and the sensillum is adjacent to the posterior margin of the eye; for *Micranops* the trichobothrium is in a short trichobothrial cavity behind and separated from the eye.

Description: Body length 2.0–4.1 mm.

Head (fig. 342) with postocular lateral margin broadly and shallowly rounded; basal angles well developed and strongly rounded; basal margin shallowly emarginate medially and without median tumescence, groove, or sulcus; posteroventral surface without tubercles.

Neck (fig. 342) not petiolate; nuchal groove moderately deep; neck width across nuchal constriction a third to two fifths as wide as postocular width of head; nuchal ridge present dorsally and laterally (figs. 333, 342).

Dorsal surface of head with fine to moderately strong, moderately dense to dense punctation (fig. 333); midlongitudinal strip without or with less dense punctation; microsculpturing fine, strong, and dense to feeble to absent; surface with dull to polished luster; pubescence fine and moderately dense to dense; macrosetae moderately long, peripheral, and few.

Cephalic trichobothrium in trichobothrial depression adjacent dorsal margin of eye near or just forward of middle of eye (fig. 334); trichobothrial depression (fig. 334) with small cluster of setae in front of bothrium and with dense cluster of setae along dorsal margin.

Eyes with broadly rounded posterior margin.

Gular sutures moderately widely separated and divergent posteriorly (fig. 326).

Mandibles: left mandible with three (Assing, 2011: fig. 71) or four denticles (fig. 327); right mandible with three (Assing, 2011: fig. 72) or five denticles (fig. 328).

Labrum quadridentate (figs. 340).

Pronotum broadly and moderately convex; surface with moderately dense to dense punctation; microsculpturing well developed, poorly developed, or absent and uniform to present laterally and/or anteriorly; surface moderately shiny to polished; pubescence moderately dense to dense; macrosetae moderately long, peripheral, and few; midlongitudinal strip impunctate and without microsculpturing or with weak to feeble microsculpturing anteriorly; median groove absent or present posteriorly and moderately strong to weak; midlongitudinal ridge present and weak posteriorly or absent; posterior margin weakly emarginate to straight.

Prohypomeron without transverse hypomeronal ridge or ridge present, weakly developed, and incomplete; submarginal ridge present; lobe with or without setae or with a few (fig. 330).

Notosternal suture present (fig. 330, 345).

Elytra longer to shorter than pronotum; surface with moderately dense punctation and pubescence; posterior margin with row of setae.

Mesoventrite with large, rounded, deep, median, basisternal depression (fig. 341); prepectal ridges separated medially; mesotransversal ridge broadly curved; mesanapleural ridge with anterior segment present, posterior segment absent.

Mesofurcasternum without (fig. 346) internal, median apophysis on posteromedial margin.

Mesofemur without stridular plectrum (figs. 335–337).

Mesocoxal acetabulum margined by pericoxal ridge (fig. 335) or present only laterally.

Metaventrite without stridular file (fig. 336). Metakatepisternal process short and apically rounded (fig. 335).

Sternite II with median point on posterior margin (fig. 338).

Sternite III with well developed median carina; transverse basal ridge moderately sinuate and with long median point.

Male. Sternite VII with or without slightly to moderately modified surface and with or without shallow emargination of posterior margin (see Assing, 2011: figs. 6, 13, 23, 30, 37, 43, 48, 54, 63, 77).

Sternite VIII with emargination of posterior margin of variable width and depth (see Assing, 2011: figs. 7, 14, 24, 31, 38, 44, 49, 55, 64, 78).

Tergite IX (fig. 331) asymmetrical; left anteroventral side larger, more broadly rounded, and wrapping ventromedially more than right; posterior emargination more or less U-shaped; middorsal base fused. Sternite IX (fig. 329) elongate and moderately wide.

Tergite X elliptical; anterior margin without median point, strongly rounded medially, then sloped and slightly rounded to lateral margin (figs. 331).

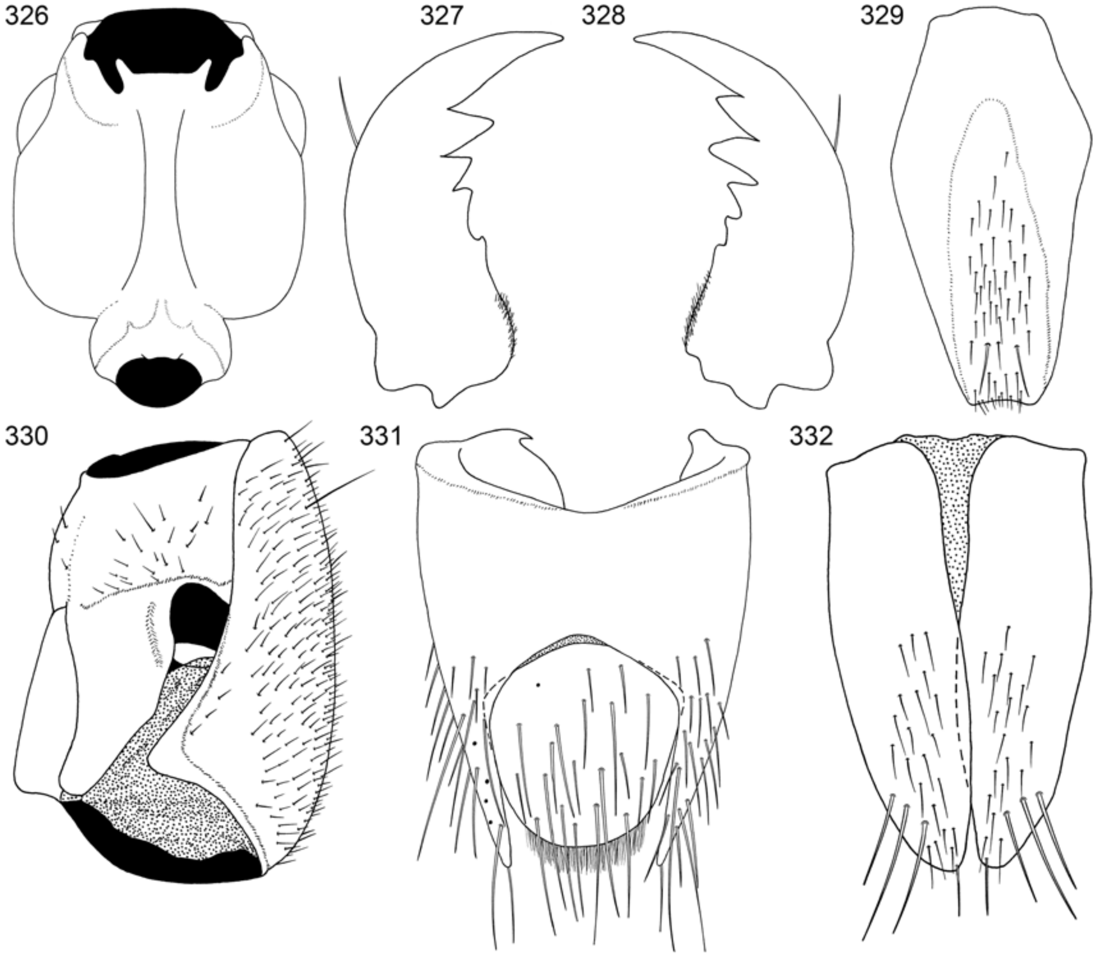
Aedeagus with dorsal surface of median lobe midlongitudinally divided.

Female. Sternite VII unmodified.

Sternite VIII with unmodified surface and posterior margin.

Abdominal sternite VIII with rounded posterior margin.

Tergite IX (fig. 347) symmetrical; left and right anteroventral sides of approximately



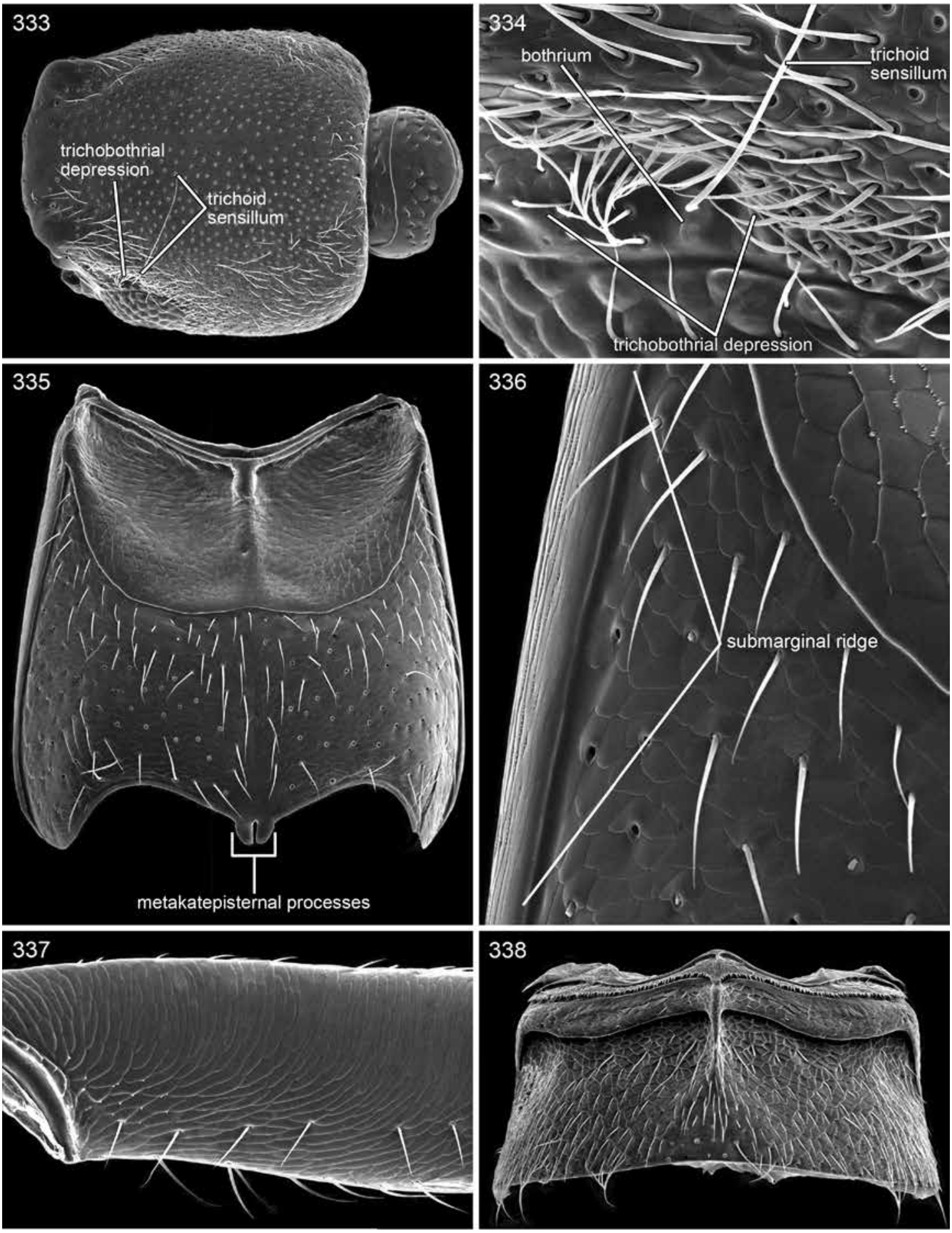
FIGS. 326–332. *Trisunius spathulatus.* **326**. Head. **327–328**. Mandibles, dorsal, female. **329**. Sternite IX, male. **330**. Prothorax, lateroventral. **331**. Tergites IX, X, male. **332**. Lateral gonocoxal plates.

equal size; posterior emargination wide, deep posteriorly, narrow anteriorly, and extending to anterior margin of tergite; middorsal base medially divided.

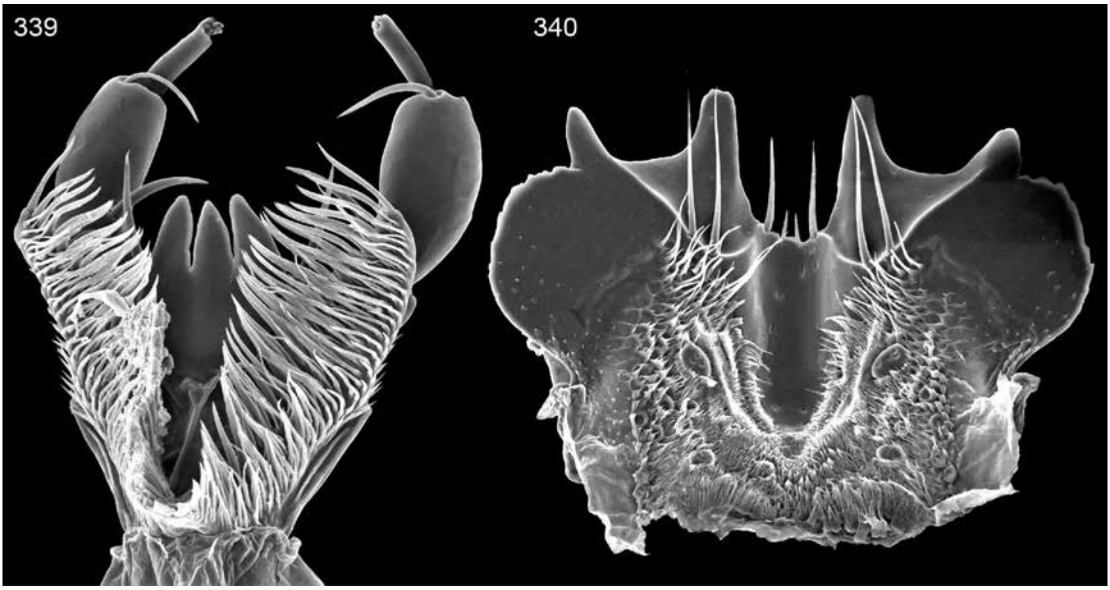
Tergite X (fig. 347) with anterior margin strongly rounded medially, then sloped and slightly rounded to lateral margin.

Distribution and Habitat: At this writing all the named species are from the Asian mainland. Ten of the 22 described species are from China. The genus is also known from Nepal, India, Thailand, and Vietnam. In China the genus is known from Yunnan, Hubei, and Shaanxi. Unnamed species from Vietnam, Malaysia, Nepal, the Philippines, and South Africa were examined.

Reflecting the intensity of collecting, most of the Chinese species are represented by many specimens; only one is known by just the holotype and two others by the holotype and one paratype. By contrast, most of the species from Nepal and Thailand are known by only the holotype and for India by a few specimens. Since species are found in Hubei and Shaanxi provinces perhaps other more northern and eastern species are yet to be discovered. Based on the occurrence



FIGS. 333–338. *Trisunius spathulatus*. **333.** Head. **334.** Head, left anterolateral, trichobothrium. **335.** Metaventrite. **336.** Metaventrite, right margin. **337.** Mesofemur, right base. **338.** Sternites II and III.



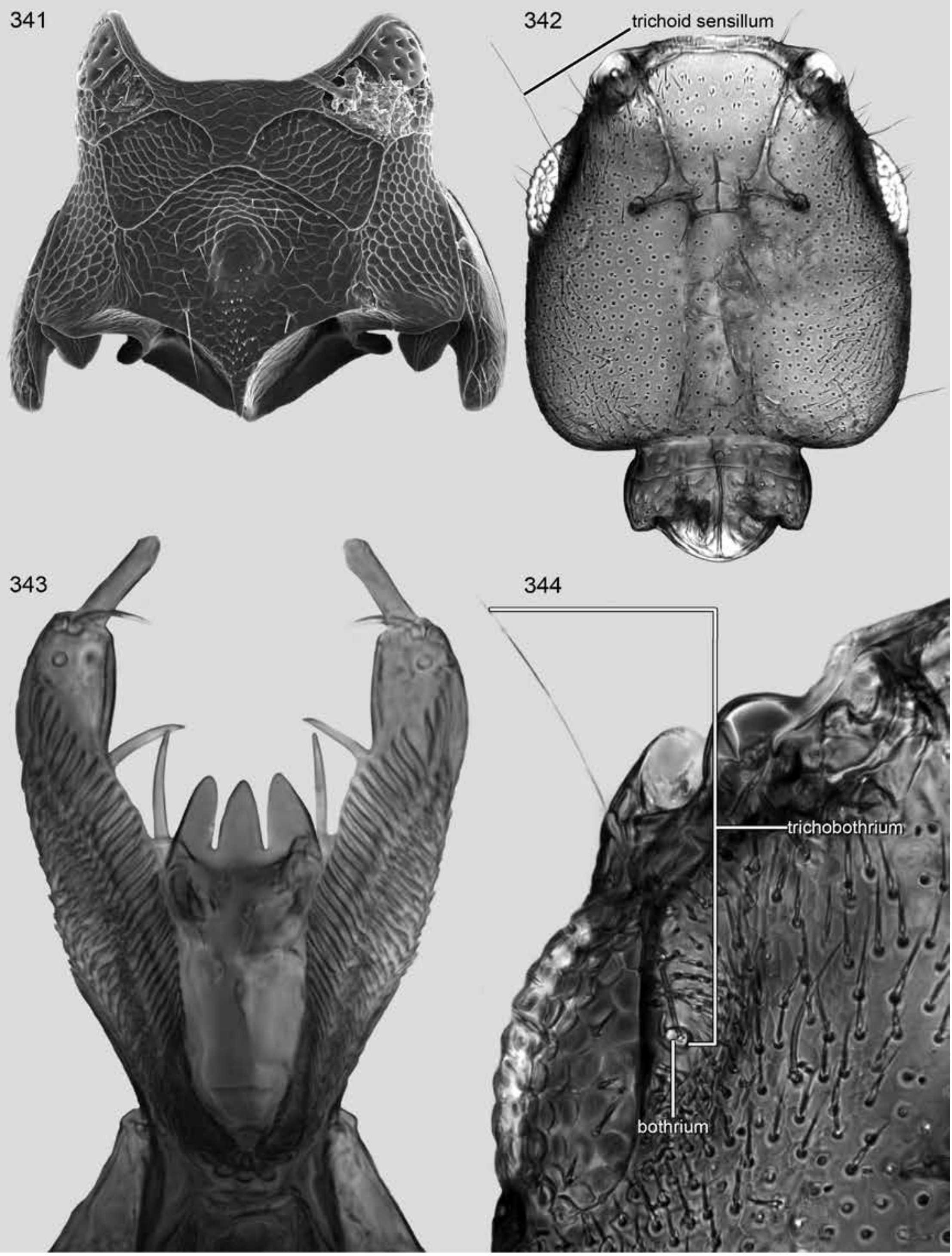
FIGS. 339–340. *Trisunius spathulatus*. **339.** Labium, hypopharynx. **340.** Labrum, epipharynx.

of described species along with the data for a few unnamed species, it is plausible that many more species will be described and that the known geographic range of *Trisunius* will be significantly enlarged. The genus probably occurs throughout central and southern China, Southeast Asia, the Indian subcontinent, Maritime Southeast Asia, Africa, and perhaps Australia.

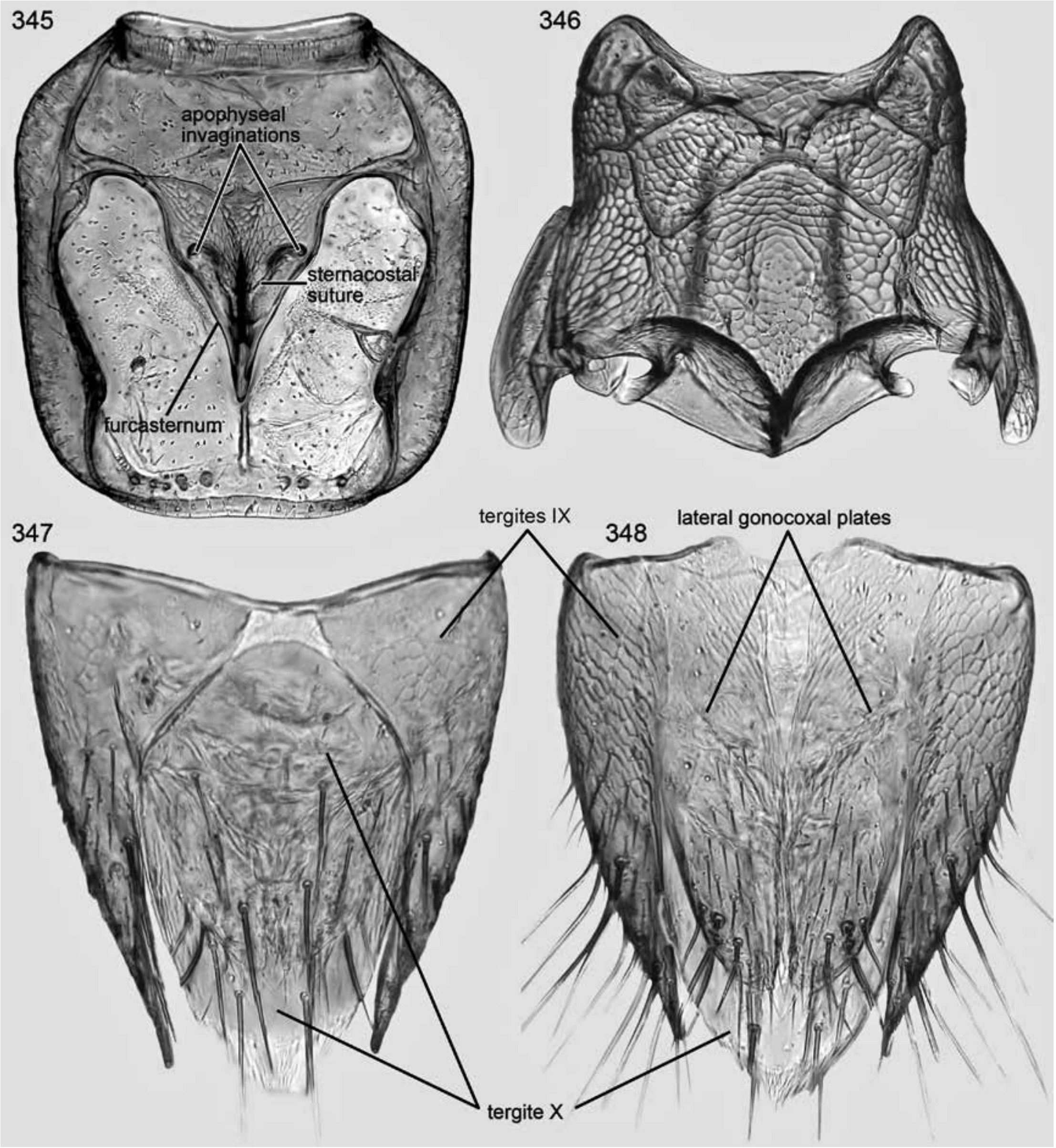
According to label data published by Assing (2011–2015) specimens have been collected primarily in forest litter, deep humus, wet debris near a waterfall at 850 m elevation, near snowfields, and occasionally in open grassland or shrub habitats. Species have been collected at elevations of 270 to 3600 m. The genus appears to be primarily montane. A specimen of *T. spathulatus* was collected at 850 m, but the species was generally found at elevations between 2000 and 2600 m. Most species and specimens were collected at elevations between 2000 and 2900 m. Individuals of 11 species were collected below 2000 m. High mountain species collected above 3000 m include *T. perpusillus* (3100 m), *T. monticola* (3470 m), and *T. alesi* (3600 m). Unnamed Vietnamese specimens were collected from near a forest stream at 270 m and from a drying stream at 1150 m and one from Borneo was found at 1500 m.

Discussion: When Assing (2011) described *Trisunius* he included 10 species, only one of which was already known. To date Assing has described 20 of the 22 species; two were described in other genera. When Assing (2011: 214) proposed the genus he transferred the Indian species, *Medon monticola* Cameron, 1931, to *Trisunius* and a year later added *Lathrobium perpusillus* Coiffait, 1982 (Assing, 2012a: 210).

Subtribal assignment. Assing (2011) included *Trisunius* in the inadequately defined Medonina. That subtribe is effectively an accumulation of leftover genera with a squarish pronotum that cannot be included in other subtribes and that may or may not be related. *Trisunius* has a supraocular trichobothrium, one of the principal defining features of the Scopaeina. However, some impalpable feature also suggests Scopaeina. When I first saw a specimen of the type species in Berlin I immediately thought "*Orus*" then looked for the trichobothrium. Since most of the species of the Scopaeina, most notably the speciose *Scopaeus*, have a narrow, petiolate neck, many workers simply do not consider the Sco-



FIGS. 341–344. *Trisunius spathulatus*. **341.** Mesoventrite. **342.** Head. **343.** Labium, hypopharynx. **344.** Head, left anterolateral, trichobothium.



FIGS. 345–348. *Trisunius spathulatus*. **345.** Prothorax. **346.** Mesoventrite. **347.** Tergites IX, X, female. **348.** Tergite IX and lateral gonocoxal plates, female.

paeina to be home to species with a wide neck. Not only does *Trisunius* share the paraocular cephalic trichobothrium with other scopaeines, but it also bears the tripartite ligular lobe, trilobed abdominal sternite II, and it lacks a pronotal marginal ridge.

Flight: Of the 22 species presently described nearly half are reported to have shortened elytra with weakly developed humeral angles, wings that are reduced or “completely” reduced, and a palisade fringe of tergite VII that is present, rudimentary, or absent. Four species, *T. cultellatus*, *T. discrepans*, *T. ligulatus*, and *T. spathulatus*, have a palisade fringe and are considered dimorphic for elytral and wing length (Assing, 2011: 198, 202, 203, 206). Furthermore, the eyes are reduced for those species. Assing (2011: 198) wrote, not only do dimorphic species have modifications of the elytra and wings, but the head of the micropterous and macropterous individuals differ. The modified head of the two forms was most clearly illustrated for *T. cultellatus*; the head of the micropterous morph is weakly dilated behind the eyes, whereas the head of the macropterous form is subparallel to narrowed posteriorly (Assing, 2011: 203, cf. figs. 18, 19). Three species, *T. alesi*, *T. rastratus*, and *T. smetanai*, are reported to have a narrow or rudimentary palisade fringe; these species may have yet undiscovered flying individuals (Assing, 2012a; 2013; 2014: 446). On the other hand, because they lack a palisade fringe, three species, *T. borailicus*, *T. manasluensis*, and *T. perpusillus*, flying individuals may be uncommon; for each the wings are completely reduced, however, each is known only by the holotype (Assing, 2012a: 211, 214; 2013: 1535).

Species Included and Material Examined

22 species

alesi Assing, 2012 - Lit. Att. — [Nepal]
appendiculatus Assing, 2011 - Lit. Att. — [China]
borailicus Assing, 2013 - Lit. Att. — [India]
conlectus Assing, 2015 - Lit. Att. — [Thailand]
cultellatus Assing, 2011 - P (MNKB) — China
discrepans Assing, 2011 - P (MNKB) — China
iaculatus Assing, 2011 - P (MNKB) — China
ligulatus Assing, 2011 - P (MNKB) — China
manasluensis Assing, 2012 - Lit. Att. — [Nepal]
monticola (Cameron, 1931) - Lit. Att. — [India]
opaciceps Assing, 2012 - Lit. Att. — [Nepal]
penicillatus Assing, 2015 - Lit. Att. — [Thailand]
perpusillus (Coiffait, 1982) - Lit. Att. — [Nepal]
rastratus Assing, 2014 - Lit. Att. — [China]
scaphiformis Assing, 2015 - Lit. Att. — [Thailand]
schuelkei Assing, 2011 - Lit. Att. — [China]
smetanai Assing, 2014 - Lit. Att. — [China]
spathulatus Assing, 2011 - P (MNKB) — China
tenuincisus Assing, 2013 - Lit. Att. — [India]
thiacus Assing, 2011 - Lit. Att. — [Thailand]
truncatus Assing, 2011 - P (MNKB) — China
volans Assing, 2013 - Lit. Att. — [Nepal]

Undetermined specimens: Nepal, Vietnam, Malaysia, Philippines, South Africa.

Dissections: Disarticulation: *Trisunius spathulatus* (female) and genital segments of male.

GENERA EXCLUDED FROM THE SCOPAEINA

This section discusses six genera that some authors at various times have suggested are near *Scopaeus* and begins with a revision of the generic classification of the Sphaeronina.

The decision to revise the generic classification of the Sphaeronina in the context of studying the Scopaeina was completely serendipitous. Initially I planned only to write a paragraph for each of six genera to supply characters—reasons for why they were not near or part of *Scopaeus*—and to propose hypotheses for their subtribal assignments. Of the six I had seen a paratype of *Typhloleleupius doryloides* Fagel in Brussels. In the AMNH collection I had tentatively identified a specimen of *Scopaeodracus* and had about 100 specimens of *Sphaeronum*. I knew *Tripectenopus* and *Coecoscopaeus* only as literature entities. *Sphaeronum* was the only genus of the five that had been dissected prior to the present work. Presented with the necessity and opportunity of examining these genera I was able to borrow examples of the two unknown genera. Once viewed I was gobsmacked to see that five of the six not only resembled one another, but shared unique, derived characters that defined a group for which a subtribal name, Sphaeronina, existed to house them.

Sphaeronina Casey

Figures 349–403

Sphaeronina Casey, 1905: 54. [Cited as Sphaeronia; Genera included: *Scopaeodes* Sharp, 1876, *Sphaeronum* Sharp, 1876, cited as *Sphaeronium* nomen nudum]. Type genus: *Sphaeronum* Sharp, 1876.

— Newton and Thayer, 1992: 61 (cited as synonym of Lathrobiina).

Diagnosis. Sphaeronina can be separated from all other subtribes and genera by the wide, triangular, deep, ctenidial concavity of the protibia that has three, wide, diagonally transverse combs (figs. 350, 351), the large, heavily sclerotized, dorsally directed, basally wide, apically tapered and obtuse hypopharyngeal peg (figs. 370–372, 386–388, 397–398), the denticle arising from the ventral surface of the left mandible (figs. 374, 390–391, 400), and the groove on the outer edge of the mandibles. The hypopharyngeal peg and ventral mandibular denticle appear to be unique features. In addition to the preceding characters, the genera of the Sphaeronina are explicitly excluded from the Scopaeina by the absence of cephalic paraocular trichobothria and tripartite ligular lobes.

Although occurring elsewhere in the Paederinae, eight other homoplasic features aid recognition and support definition of the subtribe. The (1) neck is narrow, about one ninth to one sixth as wide as the head (figs. 349, 364, 381, 382, 392, 403), (2) gular sutures are confluent (fig. 403), (3) gena has a hollowed surface, (4) pronotum is ovoid (fig. 349, 355, 363, 381), (5) pronotal marginal ridge is absent, (6) probasisternum is long, moderately to strongly rounded with the surface adjacent to the procoxae slightly to moderately swollen (fig. 355, 393), (7) procoxa has a carina on the mesial surface (figs. 380, 385, 394), (8) exposed surface of the scutellum lacks or has few setae and is wide basally and notably slender apically (fig. 378), and (9) slender, acute tip of the lateroapical process of tergum IX is strongly bent dorsally (figs. 360, 379).

The head of *Sphaeronum*, *Typhloleleupius* Fagel, 1964, and *Coecoscopaeus* Coiffait, 1982, has a submarginal, postocular groove (figs. 365, 366, 403) on the lateroventral surface. Some species of *Tripectenopus* Lea, 1918, have a short, feeble groove or ridge in the same position and some have only a hint of a groove or ridge or lack it entirely. The profurcasternum of *Typhloleleupius*, *Tripectenopus*, and *Coecoscopaeus* is long, slender, tapered posteriorly, and widely separated from the hypomeron (fig. 393), while for *Sphaeronum* the profurcasternum is long and wide and touches the hypomeron (fig. 355). All the genera have a deep, wide subantennal hollow on the gena between the eye and the mandibular base.

Description. Body length 2.7–12 mm.

Head (figs. 349, 362, 364, 381, 392) elongate, longer than wide; lateral margin long and broadly rounded. Cephalic trichobothria absent.

Neck petiolate (figs. 362, 382); nuchal groove abruptly and strongly constricted and proximad occiput strongly enlarged; nuchal groove about one ninth to one sixth as wide as greatest width of head; nuchal groove without longitudinal carinae; nuchal ridge absent.

Gular sutures confluent (fig. 403).

Submentum with medial surface broad, flat, and delimited laterally by submarginal ridge.

Antenna not geniculate; flagellar antennomeres tending to moniliform.

Gena, between eye and mandibular base, with wide, deep subantennal hollow.

Mandibles strongly dentate (figs. 373–376, 389–391, 399–402); mandibular denticles not in dorsoventral alignment along mesial edge, arranged on two planes (see denticles on left of fig. 390); left mandible with large denticle on ventral surface (figs. 374, 390, 400) and with more denticles than right; right mandible with small to tiny denticle on ventral surface or ventral denticle absent and marked by slight tumescence.

Maxillary palpus with second palpomere gradually expanded apically; third palpomere (figs. 356, 383, 396) slightly flattened dorsoventrally and pedunculate, with slender, curved base and expanded, clavate to capitate, apically; fourth palpomere asetate and conical to nipple-like, with broad base.

Labium with first palpomere shorter than second and slightly less thick; second palpomere long and stout (figs. 370, 387, 398); third palpomere slender and without setae; mentum small and transverse (fig. 354); dorsal surface with comb of contiguous setae extending from apex of paraglossa onto and reaching base of hypopharynx; anteromedial surface with hypopharyngeal peg; hypopharyngeal peg large, strongly sclerotized, dorsally directed, with wide base and tapered apically to obtuse apex (figs. 370–372, 386–388, 397–398; tripartite, ligular lobe absent; no specimens of *Coecoscopaeus* available for dissection).

Prothorax ovoid and longer than wide (figs. 349, 355, 363, 382, 393); widest at anterolateral angles or near middle of lateral margin; anterolateral angle moderately to poorly developed; lateral margins gradually convergent posteriorly from middle or anterolateral angles.

Pronotal marginal ridge absent.

Probasisternum (figs. 355, 393) long and moderately to strongly rounded; surface anterior to procoxae slightly to moderately swollen; transverse prosternal carina in front of procoxae at posterior margin of acclivity; midlongitudinal ridge absent.

Length of probasisternum, measured from its anterior margin to anterior edge of procoxal cavity, greater than the distance between anterior margin of profurcasternum and posterior margin of notum.

Notosternal suture present or absent.

Prohypomeron with short to long postprocoxal lobe; hypomeronal transverse ridge present; submarginal ridge absent.

Intercoxal carina well developed, with acute, knifelike ventral edge.

Profurcasternum long, tapered posteriorly and widely separated from hypomeron (fig. 393) or long, expanded laterally, and touching hypomeron (fig. 355); apex reaching to anterior margin of mesoventrite.

Procoxal cavity open or closed.

Mesospiracular peritreme small, moderately sclerotized, separated from hypomeron and each other, and separated from or partially covered by furcasternum.

Elytral epipleural ridge absent; submarginal ridge present; posterior margin with densely to sparsely populated row of setae.

Scutellum without or with few setae; base wide, apical half slender (fig. 378).

Mesoventrite without midlongitudinal carina; mesoventrite with deep to feeble median depression; surface without ridges (fig. 368) or with remnants of prepectal, mesanapleural, and mesotransventral ridges; suture separating pteroventrites present or absent (figs. 367, 368).

Procoxa with mesial carina near base (figs. 380, 385, 394).

Protibia (figs. 350, 351) with large, triangular lobe on basal half; mesial surface of lobe deeply, broadly concave; ctenidial concavity with three, wide, diagonally transverse combs.

Profemur with large, diagonal ridge on anteroventral edge; ridge with comb of closely spaced setae on ventral edge.

Protarsomere with setae ventrally, but without densely setose pad. Protarsomere, mesotarsomere, and metatarsomere 4 not expanded beneath metatarsomere 5.

Metatibial apex with one or two apical combs.

Abdominal segments III to VII with tergum and sternum of each segment separated; segments III to VII with two pairs of lateroventrites.

Sternum II short and trilobed.

Sternum III with basal, midlongitudinal, rounded or acute carina extending posteriorly; basal transverse ridge present; sublateral carina absent.

Sternite IV without glandular opening.

Tergum IX (figs. 357, 358, 377; see Janák, 2013: figs. 41, 45, 55) with posterior margin deeply emarginate; middorsal base fused or divided; emargination occupied by tergum X; lateroapical process (figs. 360, 377, 379) tapered gradually to acute apex with apical portion slender and strongly (most species) to gradually curved dorsally (a few species), apical portion long (most species) to short (few species).

Tergum X (figs. 357, 358, 377; see Janák, 2013: figs. 41, 45, 55) more or less trianguloid or trapezoidal and exposed with basal margin slightly covered by IX.

Aedeagus symmetrical (fig. 356); parameres absent; basal piece absent (examined only for one species of *Sphaeronum* and one of *Typhloleleupius*).

Segment IX (fig. 359) of female with median or lateral gonocoxal plate; "vulvar apparatus" proximad of gonocoxal plate(s) (examined only for one species of *Sphaeronum* and one of *Typhloleleupius*).

Spermatheca not examined.

Discussion. *Coecoscopaeus*, *Tripectenopus*, and *Typhloleleupius*, all have a tapered profurcasternum (fig. 393) widely separated from the prohypomeron, whereas *Sphaeronum* has a wide profurcasternum (fig. 355) contiguous with the prohypomeron. Despite that major distinction, the four genera share two characters found nowhere else and many others found in few paederine genera. The four genera share so many characters that scarcely any remain to distinguish them from each other. Unique to the subtribe is the massive, heavily sclerotized, hypopharyngeal peg (figs. 370, 386, 397) and prominent denticle arising on the ventral surface of the left mandible (figs. 374, 390, 400).

Casey (1905: 54) proposed Sphaeronina (cited as Sphaeronia) for two Neotropical genera described by Sharp (1876), *Sphaeronum* and *Scopaeodes*, with six and two species respectively, all from Brazil. Thereafter, the subtribal name was ignored for more than a century. Bernhauer and Schubert (1912: 278) and Blackwelder (1939a: 114) placed *Scopaeodes* among paederine genera now in the Cryptobiina. In a checklist, Blackwelder (1944: 126) included *Scopaeodes* in the Cryptobiina (cited as Cryptobii). There is ample support for that placement. *Sphaeronum* was included, without subtribal assignment, in lists of genera by Bernhauer and Schubert (1912: 276) and Blackwelder (1939a: 116). Later (Blackwelder, 1944: 128; Blackwelder and Arnett, 1974: 76) *Sphaeronum* was included in the Echiasterina Casey, 1905 (cited as Echiasteres) or between *Echiaster* Erichson, 1839, and *Pinophilus* Gravenhorst, 1802 (Blackwelder, 1943: 374). The name Sphaeronina (or Sphaeronia) evaporated from the literature until Newton and Thayer (1992: 61) cited it without comment as a synonym of the Lathrobiina. Twenty years later, *Sphaeronum*, the type genus of Sphaeronina, was again included in the Echiasterina (Navarrete-Heredia et al., 2002: 285); the name Sphaeronina was not cited.

In the present work Sphaeronina is resurrected, redefined, and reconstituted with three genera that had been associated with or thought to be similar to *Scopaeus*, or listed as incertae sedis. More than 35 years ago in the AMNH collections I brought the South American *Sphaeronum* and Australian *Scopaeodracus* Scheerpeltz together in the Sphaeronina. In 2007 after briefly examining undissected paratypes of the type species of the African *Typhloleleupius* I concluded that it and *Scopaeodracus* were probably synonyms because they shared so many characters, and no obvious features separated them. However, my tentative identification of *Scopaeodracus* was based on Scheerpeltz's (1935) description; I had and have seen neither type material of the taxon nor reliably identified specimens. Until the present work I had seen no specimens of *Tripectenopus* or *Coecoscopaeus*.

Since Al Newton had collected in South Africa and Australia, I wrote to him seeking specimens of *Coecoscopaeus, Scopaeodracus*, *Typhloleleupius*, and *Tripectenopus*. He responded by lending seven specimens of an unnamed species of *Typhloleleupius* and a specimen of each of two species of *Tripectenopus*, and by generously providing a list of Australian species originally assigned to *Domene* that belonged in *Tripectenopus*. In this work these transfers are based on his examination of the relevant types. Britton (1974: 87) suggested *Tripectenopus* and *Typhloleleupius* might be synonyms. Newton (in litt., June 27, 2009) considered *Tripectenopus* and *Scopaeodracus* to be synonyms. Although Newton did not know *Coecoscopaeus*, Frisch did. He had borrowed a syntype of the only known species and helped arrange a loan of that specimen to me. Once able to study specimens of *Coecoscopaeus*, *Tripectenopus*, and *Typhloleleupius*, I was astonished by the remarkable number of characters shared with *Scopaeodracus* and *Sphaeronum* and the overall similarity of appearance of the five genera. That discovery and the availability of relevant examples of the five genera lead me to explore their morphology to try to determine their subtribal affiliation.

Although no reasons, no characters, were offered to support moving *Sphaeronum* to Echiasterina (Blackwelder, 1944: 128; Blackwelder and Arnett, 1974: 76) the assignment may have been based on the laterally expanded profurcasternum that touched the hypomeron, a feature typical of genera of Echiasterina. However, the profurcasternum is enlarged and touches the prohypomeron in, for example, *Astenus*, *Brachynetes*, *Cephalochaetus*, *Haplonazeris*, *Nazeris*, *Pachymedon*, *Sunesta*, and, along with other genera of the Astenina and Stilicopsina, as well as some species of *Rugilus*. So, although a wide, hypomeron-contiguous profurcasternum is a useful apomorphy, it is homoplasic and alone insufficient for generic placement. *Sphaeronum* is excluded from Echiasterina because the labrum in that subtribe is strongly dentate and has a ridge across the base, and the third and fourth maxillary palpomeres are fusiform and acicular respectively. *Sphaeronum* lacks the preceding features. Furthermore, the Echiasterina differs from the Sphaeronina as follows: the outer surface of the mandibles lacks a groove, the left mandible lacks a ventral denticle, the hypopharyngeal peg is absent, the anterior margin of the hypopharynx has a row of small, spinelike setae, the two protibial ctenidia or combs are arranged longitudinally, the protibia lacks the enlarged ctenidial concavity, and the anterior portion of the probasisternum is short and wide.

Coecoscopaeus, *Scopaeodracus*, *Sphaeronum*, *Tripectenopus*, and *Typhloleleupius* comprise a clade, a hypothesis of a monophyletic group, a subtribal taxon supported by characters stated above in the Diagnosis. Most of those characters are homoplasic in the Paederinae except for the hypopharyngeal peg, ventral denticle of the left mandible, and form of the scutellum. The defining characters presented in the diagnosis are discussed in the following paragraphs. Although some are homoplasic they, nonetheless, help to define the group.

LABIUM: The hypopharyngeal peg (fig. 397, 398) is unique in the Paederinae. I have seen it in none of approximately 150 disarticulated paederine genera. Among the Lathrobiina some genera (for example *Acalophaena*, *Achenium*, *Domene*, *Lathrobium*, *Lobrathium*, *Pseudolathra*, *Throbalium*, and scattered among a few genera of other subtribes) have, near the anterior margin of the hypopharynx, a minute, apically acute, anterodorsally directed spine. It is unclear whether this spine has anything to do with the hypopharyngeal peg of Sphaeronina. Is it a precursor or does it just happen to be in roughly the same position? For Sphaeronina a specimen of one species of *Sphaeronum*, *Tripectenopus*, and *Typhloleleupius*, was dissected. For *Coecoscopaeus coecus* I examined only one syntype and could neither dissect nor move the mouthparts nor was I unable to see dorsal structures on the labium. However, the left mandible of *C. coecus* has a large ventral denticle; on the strength of the unique mandibular character the genus is included in the Sphaeronina. That placement is supported by the homoplasic characters cited in the diagnosis for the subtribe.

MANDIBLES: A denticle originating on the ventral surface in the Sphaeronina appears to be unique in the Paederinae. All but one of the denticles of the mandibles of the Sphaeronina are on the medial edge where they are slightly out of alignment (fig. 390). The left mandible of *Coecoscopaeus*, *Sphaeronum*, *Tripectenopus*, and *Typhloleleupius* has a large denticle originating on the ventral surface (figs. 389–391). The right mandible may or may not have a small denticle or bump arising from the ventral surface. The outer margin of both mandibles of the sphaero-

FIG. 349. *Sphaeronum pallidum*. Habitus.

nine genera has a groove that begins near the base and extends toward the mandibular apex. The mandibular denticles of the mesial edge of most paederines are aligned with the medial edge of the mandible; for some few, the denticles are only slightly out of alignment with the medial edge (see, e.g., *Astenus*, *Echiaster*, *Ectocleptis*, *Nazeris*, *Pinophilinus*, *Scopaeodes, Serrolabis*, *Throbalium*, etc.); none were found with a denticle arising from the ventral surface. For most other genera the outer surface of the mandibles lacks a well-defined groove. Some genera have a feeble to shallow groove on the outer surface (e.g., *Achenomorphus*, *Charichirus*, *Deroderus*, *Dolicaon*, *Eustilicus*, *Medon*, *Pseudolathra*, *Scopobium*, *Scymbalium*, *Serrolabis*, *Stilicoderus*, *Rugilus*), but none of those examined have the deep, well developed groove featured in Sphaeronina.

Neck: The neck of genera of Sphaeronina is about a ninth to a sixth as wide as the head (figs. 349, 382). A modest number of paederine genera have a slender neck. If a slender neck is defined as less than a fourth as wide as the head this feature occurs in the subtribes Astenina, Cryptobiina, Echiasterina, Medonina, Scopaeina, and Stilicina in, for example, such genera as *Acanthoglossa*, *Echiaster*, *Eustilicus*, *Opithes, Panscopaeus*, *Ronetus*, *Rugilus*, *Scopaeodes*, *Scopaeus, Stilicastenus*, *Stilomedon*, etc. Although not unique, it clearly supports the definition of Sphaeronina.

Gular sutures: The gular sutures are confluent along their entire length in the Sphaeronina (fig. 403). This homoplasic condition is widely scattered in the subfamily. The species of *Domene* (*Spelaeomene*) and *Domene* (*Canariomene*) have partly confluent gular sutures. Among other paederine entirely or partially confluent gular sutures are found in the Astenina, Cryptobiina, Echiasterina, Procirrina, Stilicina, and Stilicopsina. Example genera with confluent gular sutures include: *Astenus*, *Bolbophites*, *Brachynetes*, *Deroderus*, *Dibelonetes*, *Dibelophacis*, *Echiaster*, *Ecitonides*, *Eurysunius*, *Eustilicus*, *Haplonazeris*, *Megastilicus*, *Mimophites*, *Monocrypta*, *Myrmecosaurus*, *Nazeris*, *Ophitodum*, *Ophryomedon*, *Procirrus*, *Ronetus*, *Rugilus*, *Stamnoderus*, *Stilicoderus*, *Stilicopsis*, *Stiliphacis*, *Stilosaurus*, *Sunesta*, and *Synecitonides*.

Prothorax: The probasisternum (figs. 355, 393) of the genera of Sphaeronina lacks a midlongitudinal ridge and is notably long, strongly rounded transversely and, for all but *Coecoscopaeus*, swollen near the procoxae. The probasisternum among other paederines is short, flat, or slightly rounded transversely, and may or may

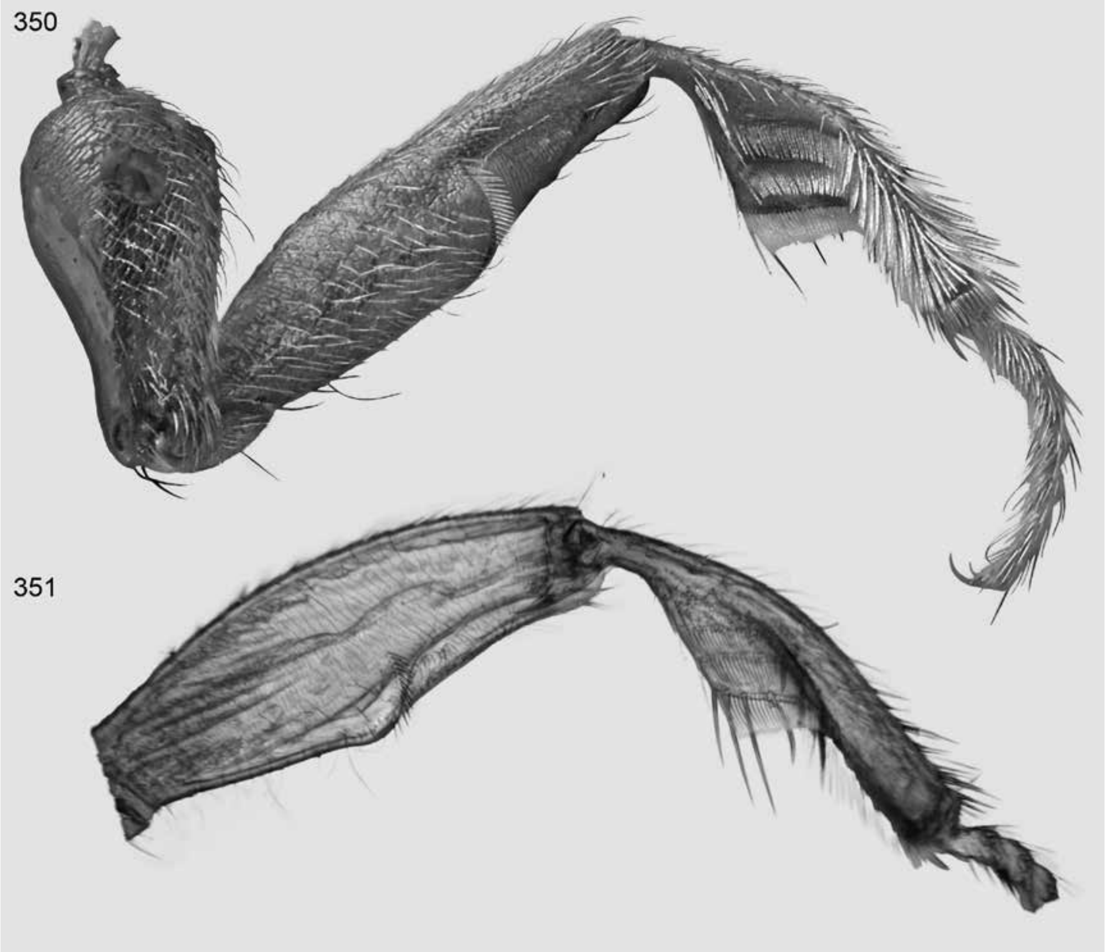


FIG. 350–351. Proleg, left. **350.** *Sphaeronum* sp. a. **351.** *Tripectenopus* sp.

not have a midlongitudinal ridge. The probasisternum of genera of the Sphaeronina (fig. 393) is distinctly longer than in other paederines (figs. 98, 345; also see *Acanthoglossa*, *Astenus*, *Domene*, *Echiaster*, *Neolindus*; *Neomedon*, *Ochthephilum*, *Oedichirus*, *Paederus*, *Pinobius*, *Pinophilus*, *Rugilus*, *Stilicopsis*, and many others).

The pronotum of Sphaeronina lacks a pronotal marginal ridge. This homoplasic character is scattered throughout the Paederinae and found in some genera of most subtribes. Examples of a few genera in which all or some species lack the ridge are *Astenus*, *Chetocephalus*, *Echiaster*, *Monista*, *Orus*, *Paederus*, *Procirrus*, *Rugilus*, *Scopaeus* and *Stilicopsis*.

Procoxa: The base of the procoxa has a small, transverse carina on the mesial surface. This carina seems to conveniently fit under the lateral edge of the long, tapered basisternum/furcasternum. I have seen this feature elsewhere in the Paederinae and have wondered if it was a means of stabilizing coxal rotation when the leg is in use.

Protibia: Protibial grooming combs and, opposite it, a femoral ridge with a comb, are characteristic of the Paederinae. In the subfamily, the protibial ctenidia or combs are arranged across (see, e.g., *Astenus*, *Dolicaon*, *Domene*, *Homaeotarsus*, *Lobrathium*, *Micrillus*, *Paederus*, *Pinophilus*, *Procirrus*, *Rugilus*, and many others) or extend along most of the length (a few examples: *Cepha-*

lochaetus, *Echiaster*, *Eustilicus*, *Neolindus*, *Pseudastenus*, *Ronetus*, *Stamnoderus*, *Stilicopsis*, *Stilomedon*, and many others) of the protibia. For most genera with transverse combs the depression is slight to moderate; species with longitudinal protibial combs lack or have a feeble to weak depression; some genera lack a ctenidial depression (see, for example, most genera of the Cryptobiina, also *Dacnochilus*, *Paederus*, *Neolindus*, etc.) and the combs are on the unmodified surface. For most species the depression is feeble to shallow to moderately deep and the tibia is not expanded or is slightly to moderately enlarged in the vicinity of the combs. Among the subtribes the range of variation of the transverse protibial grooming combs is greatest in the Lathrobiina. The protibial grooming structure is particularly notable for *Domene* where, perhaps, all the species have a large, deep, protibial, ctenidial concavity. I have examined specimens of only 13 of the 86 species and protibial illustrations for perhaps a dozen more (see illustrations in: Peyerimhoff, 1949: 82; Español, 1970: 371; 1972: 52; Outerelo, 1985: 105; Oromí and Hernández, 1986: 131, 137; Hernández and Medina, 1990: 289, 291; Salgado and Outerelo, 1991: 211; Wunderle, 1992: 147; Hernández and Oromí, 1993: 67; Hernando and Comas, 2014: 106; and Serrano et al., 2015: 405). The protibia of all of them has an enlarged, deep, ctenidial concavity that is presumably characteristic of the genus. Outside of *Domene* the only other paederine taxa with the dramatically wide, deep, "scooped-out," ctenidial concavity of the protibia are the genera of Sphaeronina (figs. 350, 351; Scheerpeltz, 1935: 641; Britton, 1974: 86). This homoplasic feature is one of the defining traits of the Sphaeronina and suggests possible affinity between it and elements of the Lathrobiina, a poorly defined subtribe in serious need of careful morphological study.

Scutellum: The exposed dorsal surface of the scutellum of Sphaeronina is wide basally; the lateral margins are sinuate, then abruptly constricted at about the apical third to form a tapered lobe apically (fig. 378; see Britton, 1974: fig. 2). This configuration does not seem to occur in other genera of the subfamily. The scutellum of species in most other genera is wide to moderately wide gradually tapering to the apex.

Domene: Few of the 86 valid species currently included in *Domene* (extracted from my unpublished catalog of the Paederinae) were available for study; among those available each was represented by only a couple of specimens of which only one could be dissected. That deficit has prevented proposing a suitable definition of the genus. Only two specimens of one species of *Domene* (*Canariomene*) *jonayi* Hernández and Medina, 1990, were available for study, but not dissection. No examples of *Domene* (*Spelaeomene*) or *Domene* (*Lobramene*) were available. Few species and few specimens of *Domene* (*Lathromene*) were examined. Only one male and female of *Domene* (*Domene*) *scabricollis* Erichson, 1840, could be dissected. That species lacks the hypopharyngeal peg and the ventral denticle of the left mandible and is omitted from Sphaeronina. There exists the potential that one or more species currently assigned to *Domene* might belong in Sphaeronina. That possibility awaits availability of material for dissection.

Genera Included: *Coecoscopaeus* Coiffait, 1982, *Sphaeronum* Sharp, 1876, *Tripectenopus* Lea, 1918, and *Typhloleleupius* Fagel, 1964.

KEY TO GENERA OF THE SPHAERONINA

1. Metatibia with one apical comb....................2
– Metatibia with two apical combs, one on each side..3
2(1) Pronotum with postprocoxal lobe nearly vertical; profurcasternum apically tapered and widely separated from prohypomeron (as in fig. 393); head without basal extension (see figs. 362, 364); Tunisia............*Coecoscopaeus*
– Pronotum with postprocoxal lobe strongly bent medially and lying or nearly lying on surface of profurcasternum; profurcasternum expanded laterally and touching prohypomeron (fig. 355); head (of most species) with rectangulate basal extension

(figs. 362, 364); Mexico and Cuba south to Argentina..................................*Sphaeronum*

3(1)Species from southern Africa or Madagascar; anterior margin of labrum with large to small denticles (fig. 395; Janák, 2013: fig. 21)................................*Typhloleleupius*

– Species from Australia; labrum edentate and deeply emarginate (fig. 384; Scheerpeltz, 1935: fig. 4a)..............................*Tripectenopus*

Sphaeronum Sharp

Figures 349, 350, 352–380

Sphaeronum Sharp, 1876: 224 (species included: *opacum*, *depressifrons*, *carinifrons*, *elongatum*, *carinicolle*, *pallidum*). **Type species:** *Sphaeronum pallidum* Sharp, fixed by Casey (1905: 55) by subsequent designation.

— Duvivier, 1883: 167 (catalog). — Casey, 1905: 55 (characters). — Bernhauer and Schubert, 1912: 276 (catalog). — Blackwelder, 1939a: 101, 116, 121 (key; checklist; type species). — Blackwelder, 1943: 231, 374 (key; characters; type species). — Blackwelder, 1944: 128 (checklist of species, Latin America). — Blackwelder, 1952: 355 (type species). — Blackwelder and Arnett, 1974: 76 (checklist; North America; Central America; West Indies). — Navarrete-Heredia, Newton, Thayer, Ashe, and Chandler, 2002: 285 (characters in key to genera for Mexico; general notes; unnamed species in Mexico).

Sphaerinum Sharp, 1876: 36, 224 (**Nomen nudum**. See discussion below under "Synonymy").

— Blackwelder, 1943: 374 (synonym of *Sphaeronum*). — Blackwelder, 1952: 355 (synonym of *Sphaeronum*; type species). — Blackwelder and Arnett, 1974: 76 (synonym of *Sphaeronum*).

Diagnosis: The head of most species of *Sphaeronum* has a rectangulate "basal extension" of the posterior margin; the extension is small (fig. 364) to moderately large (fig. 362) to large, easily separating the genus from all other Sphaeronina. A few species of the genus lack the extension.

Sphaeronum also can be separated from *Tripectenopus* and *Typhloleleupius* by the presence of the mesial, apical, metatibial comb and the short, medially bent postprocoxal lobe. The profurcasternum of *Sphaeronum* is expanded and contiguous with the prohypomeron (fig. 355). With these characters the species of *Sphaeronum* that lack the basal cephalic extension can be distinguished from other sphaeronines. *Tripectenopus* and *Typhloleleupius* both have two apical, metatibial combs, a deep depression with a midlongitudinal furrow on the mesoventral basisternum, and a nearly vertical postprocoxal lobe. The profurcasternum of both *Tripectenopus* and *Typhloleleupius* (fig. 393) is wide basally, tapers posteriorly, and is well separated from and does not touch the hypomeron. Species of *Sphaeronum* have a prominent, submarginal, subocular groove on the lateroventral margin of the head that extends from the hypostomal ridge (figs. 365, 366), near the base of the mandibles, to the neck. *Typhloleleupius* has a lateroventral, submarginal, cephalic groove that is less strongly developed than for *Sphaeronum*. Some species of *Tripectenopus* lack the submarginal groove and some have a short, shallow, poorly developed groove and others have a modest ridge in the same vicinity. The eyes of *Sphaeronum* lack setae, whereas the eyes are setate for species of *Tripectenopus* with multifaceted eyes.

The Neotropical *Sphaeronum* is separated from the North African *Coecoscopaeus* by the short, medially bent postprocoxal lobe and the wide, laterally expanded, profurcasternum that touches the prohypomeron. Although most species of *Sphaeronum* have a cephalic extension, at least two do not, nor does *Coecoscopaeus*. The neck of *Sphaeronum* of species with the cephalic basal extension is attached to the ventral surface, just below the posterior margin (fig. 365). The neck of *Coecoscopaeus* is attached to the midhorizonal plane of the posterior margin of the head.

Description: Body length 2.7–12 mm.

Head (figs. 362, 364) with lateral margin gradually rounded to basal angle or cephalic basal extension; basal angle broadly to strongly rounded or absent and head gradually tapered to cephalic basal extension; basal margin slightly emarginate or with wide, medial, apically truncate, cephalic basal extension; species with emarginate basal margin with slight to moderate medial swelling in place of basal extension.

Cephalic basal extension (figs. 362, 364, 365) present or absent; basal extension wide to moderately wide and with long to short, straight to emarginate lateral margin; dorsal edge of lateral margin carinate or rounded; posterolateral angle tumescent; surface with middorsal carina or tumescence.

Lateroventral surface of head with deep, narrow, submarginal, subocular groove extending posteriorly from hypostomal ridge near base of mandible to posterior margin of head and to neck.

Dorsal surface (fig. 362, 364) with moderately dense to dense, fine to coarse punctation; midline with or without punctation or partially punctate; microsculpturing feeble and sparse or absent; pubescence moderately dense to dense.

Clypeal margin (fig. 362) without or with small bump or tumescence mesiad of supraantennal hump.

Eyes present and with many ommatidia; eyes without setae.

Neck width across nuchal groove one ninth to one sixth as wide as greatest width of head.

Maxillary palpomere four (fig. 353) small, nipple shaped, broad basally then strongly tapered and short, compressed, truncate apically.

Labrum (fig. 352) with anterior margin truncate and with abrupt median emargination or broadly emarginate and emargination beginning near lateral margin and continuing to middle; anterior margin with or without lobe like denticle.

Prothorax with length about twice width.

Pronotum (fig. 363) with simple, fine to coarse punctation; punctation moderately dense to dense, more or less uniform, but absent from midline; microsculpturing present, strong and dense to sparse and weaker, or absent; surface with low, midlongitudinal ridge from near base extending anteriorly for half to two thirds of length; ridge without punctation and with or without fine median groove.

Notosternal suture absent (fig. 355) or represented by faint, feeble ridge or narrow, shiny strip or disruption of microsculpturing; remnant of suture present as short groove extending posteriorly from lateroventral edge of anterior margin of probasisternum.

Prohypomeron with anterior surface sparsely to densely and finely to coarsely punctate; postprocoxal lobe short, acute apically, pubescence sparse to dense or absent, and strongly bent medially and leaning toward profurcasternum; prohypomeronal transverse ridge strongly developed and bordered dorsally by distinct hypomeronal groove; submarginal ridge absent.

Profurcasternum (fig. 355) broad, extending to and touching, but not fused to hypomeron; profurcasternal intercoxal keel extending beyond posterior margin as tricarinate, apically acute lobe.

Procoxal cavity (fig. 355) closed posteriorly by expanded profurcasternum.

Elytra shorter than or subequal to pronotum.

Mesoventral basisternum (fig. 368) without midlongitudinal carina; surface with shallow to barely discernible median depression.

Metaventrite (fig. 367) with mesopericoxal ridge present laterally; metakatepisternal processes (fig. 369) short and rounded apically.

Meso-metaventral junction absent or possibly evident as slightly pale diagonal strips (figs. 367, 368).

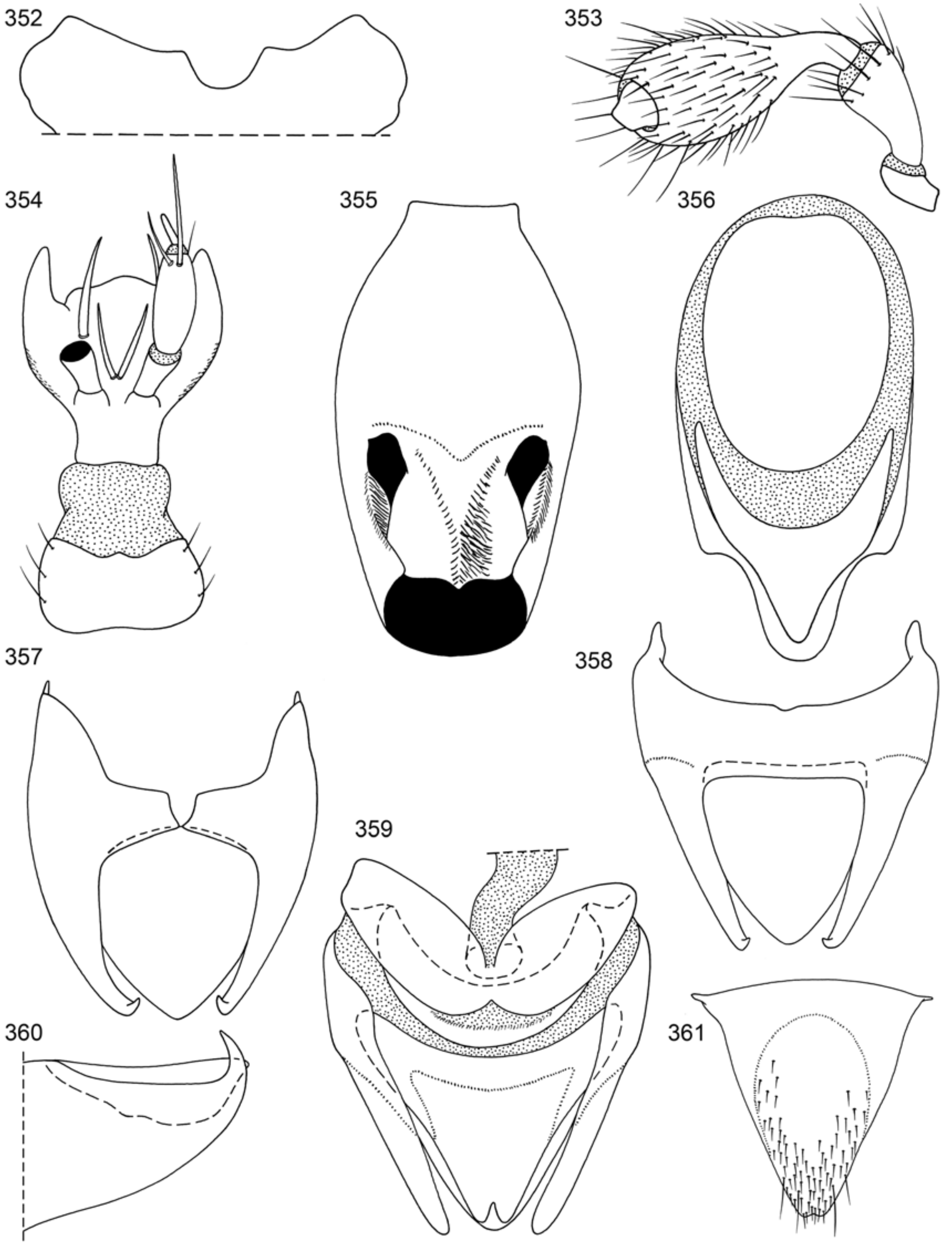
Metatrochanter without spines on posterior margin.

Metafemur without spinelike setae on inner edge.

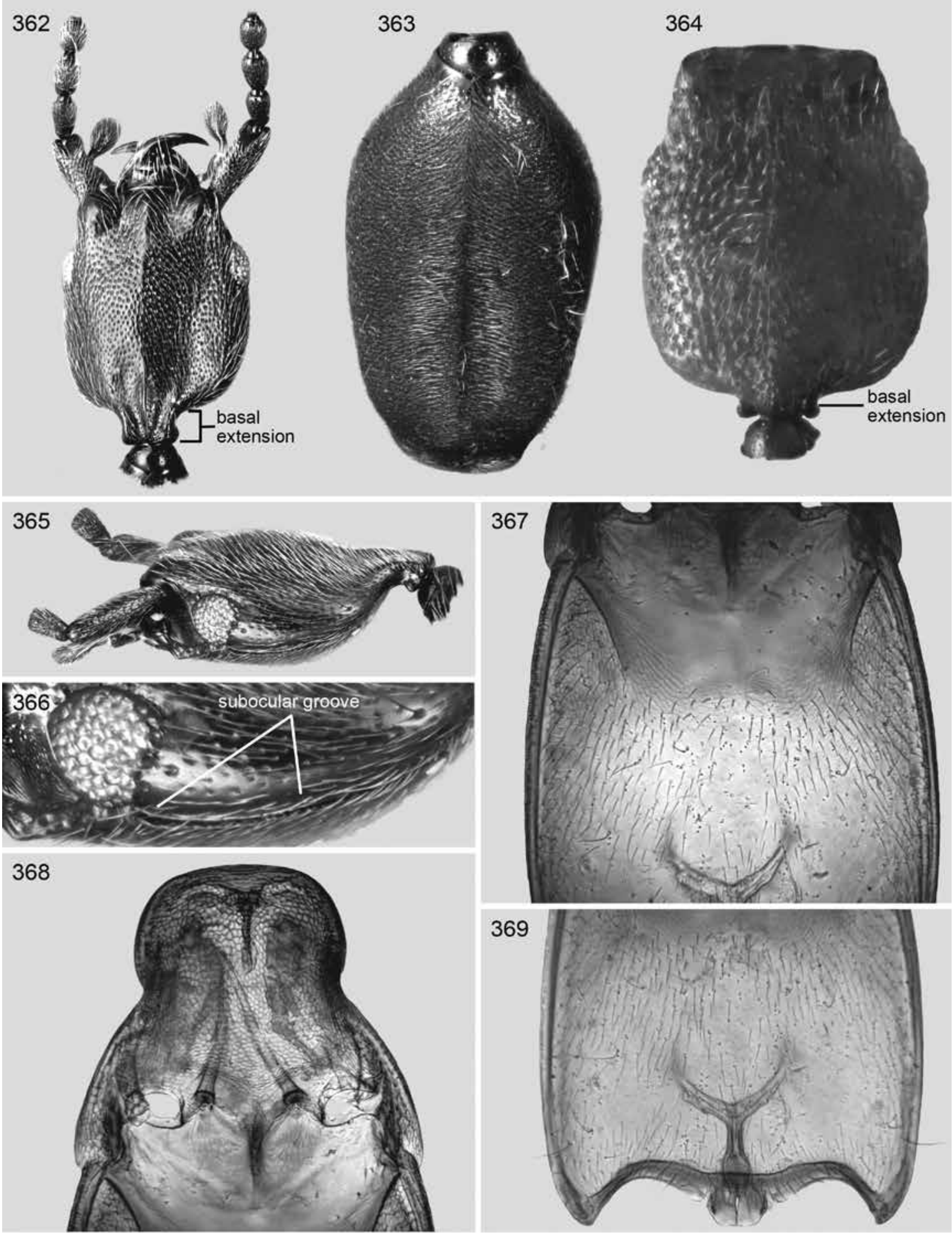
Metatibia without spinelike setae on inner edge; apex with comb on inner side.

Tergum VIII with palisade fringe on posterior margin.

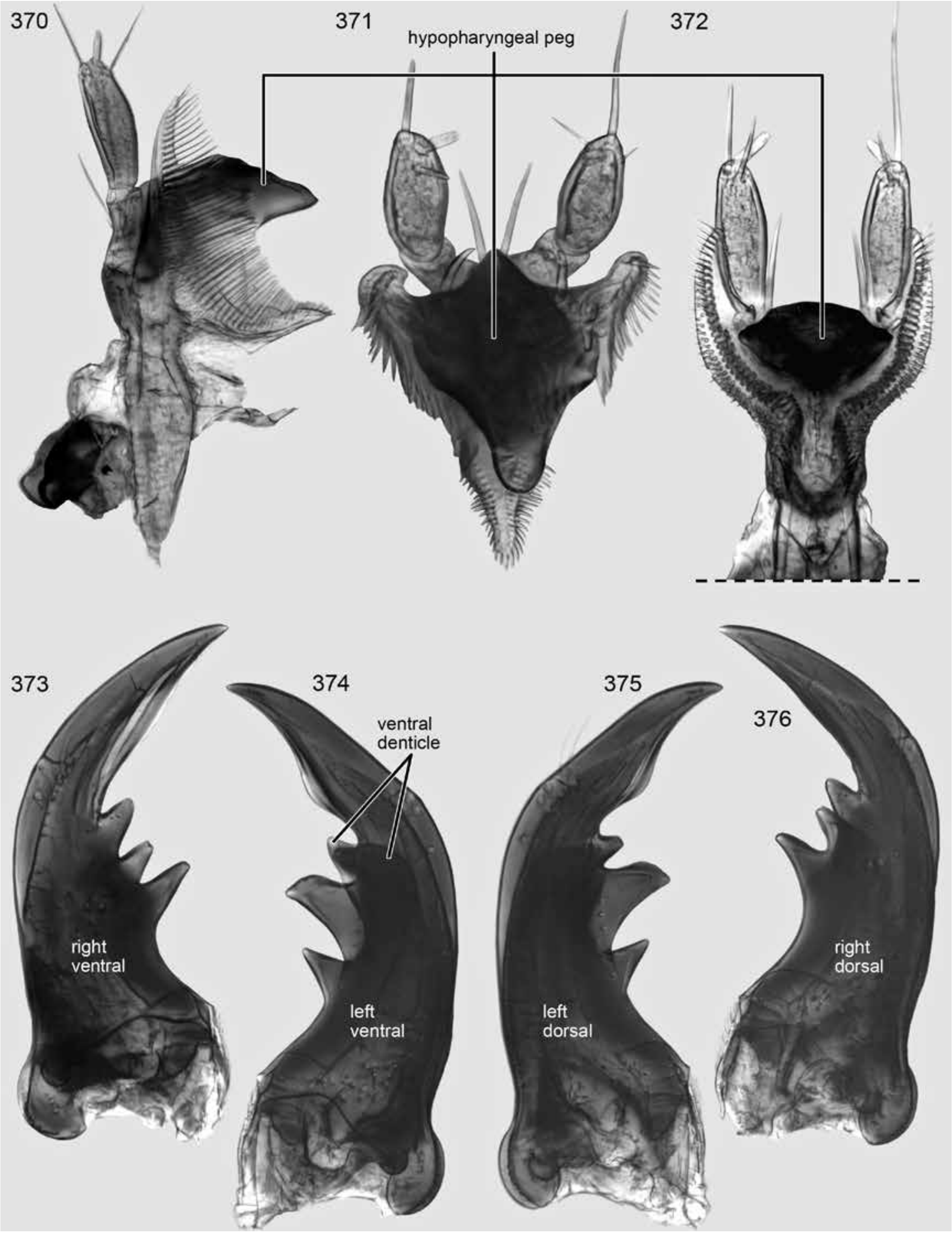
Tergite IX with lateroapical process sharply (figs. 360, 379) to gradually bent dorsally.



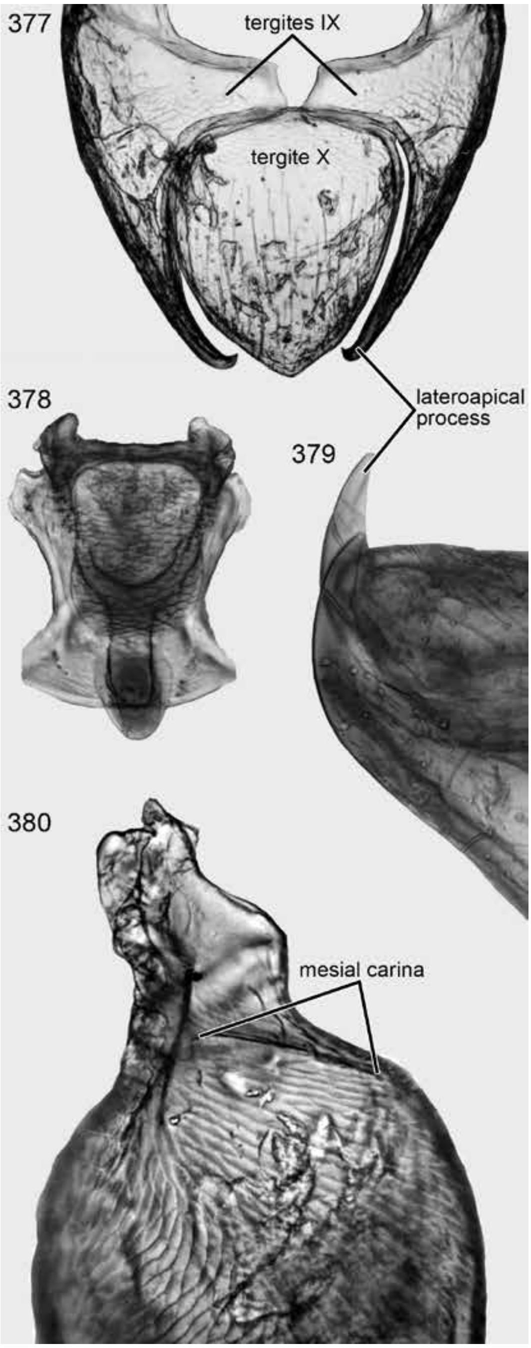
FIGS. 352–361. *Sphaeronum* sp. c. **352.** Labrum. **353.** Maxillary palpus. **354.** Labium, ventral. **355.** Prothorax. **356.** Aedeagus, dorsal. **357.** Tergites IX, X, male. **358.** Tergites IX, X, female. **359.** Genital segments, ventral, female. **360.** Tergites IX, X, lateral. **361.** Sternite IX, male.



FIGS. 362–369. *Sphaeronum* spp. a, b, c. **362.** Head. **363.** Pronotum. **364.** Head. **365.** Head, left lateral. **366.** Head, enlarged, left lateral. **367.** Metaventrite, anterior with posterior mesoventrite. **368.** Mesoventrite and anterior metaventrite. **369.** Metaventrite, posterior.



FIGS. 370–376. *Sphaeronum* sp. c. **370–372.** Labium, hypopharynx. **370.** Lateral. **371.** Anterior. **372.** Dorsal. **373–376.** Mandibles. **373.** Ventral, right. **374.** Ventral, left. **375.** Dorsal, left. **376.** Dorsal, right.



FIGS. 377–380. *Sphaeronum*. sp. c. **377.** Tergites IX, X, male. **378.** Scutellum, female. **379.** Tergite IX, lateroapical process, lateral, female. **380.** Procoxa, dorsal end, male.

Male: Tergum IX of male with middorsal base divided (figs. 357, 377).

Sternite IX (fig. 361) of male triangular with emargination of posterior margin.

Aedeagus (in ventral view) oval, symmetrical, with ventral process; parameres absent; basal piece absent.

Female: Tergite IX (fig. 358) of female with middorsal base fused; median gonocoxal plate (fig. 359) triangular and apical margin with narrow notch.

Spermatheca not examined.

Distribution and Habitat: *Sphaeronum* is known from Paraguay and Bolivia north to Mexico and Cuba. Most specimens examined and six of the seven described species are from Brazil, one is from Cuba. I have examined unidentified specimens from Bolivia, Peru, Venezuela, and Mexico. It is possible the genus will be found in the northern provinces of Argentina from Misiones to Salta and Jujuy.

The species seem to be infrequently collected. Of the six Brazilian species described by Sharp (1876: 225–229), four were based on one specimen each, one on two specimens, and the sixth on 10 specimens; the Cuban species was also based on one specimen (Blackwelder, 1943: 375). For none of the described species was the collecting habitat stated. Nearly all the specimens for which collecting data were available were taken at lights. One specimen was taken in "human dung" (Brazil), another from forest floor litter (Brazil), and a third from a rotten fig (Peru). The paucity of specimens and dearth of habitat information may hamper discovery of new specimens.

Nomenclature: In the first of his two-part work on the Staphylinidae of the Amazonian Valley, Sharp (1876: 36) proposed *Sphaerinum* for six species but described neither the genus nor species. Had at least one of the species been characterized, *Sphaerinum* would have been an available name (ICZN, 1999: Article 12.2.5). In the second part Sharp (1876: 224–229) described the seven taxa, including the genus, abandoned the name *Sphaerinum* and replaced it with *Sphaeronum* because he erroneously decided the former was preoccupied by *Sphaerina* Erichson. Sharp (1876: 224) cited *Sphaerinum* as a synonym of *Sphaeronum*, but neither use of the former made it available.

Discussion: Only seven named species are named in the genus, but among the rather limited material I've examined are at least several more undescribed ones. Most of these specimens were collected at lights and, as seems commonly the case, most are females. For several species no males are represented among the samples.

The cephalic "basal extension" of most species is large and prominent with a strongly developed midlongitudinal carina or tumescence. Two species lack the cephalic extension, for one there is a tumescence in its place, and for a few the cephalic extension is distinct, but short. The carina of the lateral edge is absent in some species, the median carina is a tumescence in some and absent in a few. All the species have a postocular (or slightly subocular), lateroventral, submarginal, cephalic groove that extends the length of the head from the eye. The neck (fig. 365) is attached just below the dorsal edge of the posterior margin of the cephalic basal extension so the nuchal groove is covered and can be viewed only by tilting the head downward. The neck of those without the extension is attached normally.

Some species have a supraocular groove that extends to just beyond the posterior margin of the eye and in one the groove reaches nearly to the base of the head; the ridge along the ventral edge of the groove reaches the neck in all species examined. The postprocoxal lobe of *Sphaeronum* is one of the shortest I've seen in the entire subfamily. Sharp (1876: 225, fn.) observed the ligula appeared to be "entirely corneous" but was unsure about that because the structure had become distorted during dissection. He may have seen the ventral surface of the hypopharyngeal peg, which, until now, was not used or mentioned again.

Species Included and Material Examined

7 species

berberum Blackwelder, 1943 - Lit. Att. — [Cuba]
carinicolle Sharp, 1876 - H (BMNH), Sp (FMNH) — Argentina, Brazil, Paraguay
carinifrons Sharp, 1876 - H (BMNH) — Brazil
depressifrons Sharp, 1876 - H (BMNH, FMNH) — Brazil
elongatum Sharp, 1876 - H (BMNH), Sp (FMNH) — Brazil
opacum Sharp, 1876 - Syn (BMNH) — Brazil
pallidum Sharp, 1876 - Syn (BMNH, FMNH) — Brazil

Undetermined specimens: Bolivia, Brazil, Mexico, Peru, Venezuela.

Dissections: *Sphaeronum* sp. (Bolivia; disarticulated male and female).

Coecoscopaeus Coiffait

Coecoscopaeus Coiffait, 1982: 11 [characters in key and type species in footnote]. Type species: *Scopaeus coecus* Peyerimhoff, 1906: 56. Fixed by original designation and monotypy.

— Coiffait, 1984: 209 (description; distribution). — Frisch, Burckhardt, and Wolters, 2002a: 45 (removed from Scopaeina; notes). — Smetana, 2004: 622 (Palaearctic catalog; incertae sedis). — Janák, 2013: 81 (cited as *Caecoscopaeus*; differs from *Typhloleleupius*).

Diagnosis: The North African *Coecoscopaeus* has one apical metatibial comb and the mesobasisternum has a shallow, barely discernible, median depression. The Australian *Tripectenopus* and southern African *Typhloleleupius* have two apical, metatibial combs and the mesobasisternum of both has a deep, median depression with a strong midlongitudinal furrow.

Like *Coecoscopaeus*, *Sphaeronum* also has an apical metatibial comb on the inner apex, the ventral submarginal groove extends from the mandibular base to the neck, and the mesobasisternum has a shallow to feeble median depression. The postprocoxal lobe is moderately long and nearly vertical for *Coecoscopaeus* but is very short and strongly bent medially for *Sphaeronum*. The profurcasternum of *Coecoscopaeus* tapers posteriorly (as in fig. 393) and is well separated from the hypomeron; the profurcasternum of *Sphaeronum* is wide and contiguous with the hypomeron (fig. 355).

The male's metafemur and metatibia of *Coecoscopaeus* each have a row of three and four, respectively, short, thick, spiniform setae, each well separated from the next. The metatrochanter of the males has spines. Males of the other three genera lack these setae or spines. No female specimen was available.

Description: Body length: 3.7 mm.

Head with lateral margin gradually rounded to basal angle; basal angle well developed and strongly rounded; basal margin shallowly emarginate; anterolateral surface without temporal ridge extending posteriorly from lateral surface of supraantennal hump onto temple; lateroventral surface with submarginal groove extending from near base of mandible to neck.

Dorsal cephalic surface polished; microsculpturing absent; punctation moderately dense and moderately coarse; punctation absent from midlongitudinal strip and anterior portion of clypeus.

Clypeal margin without small, conical horn or tumescence mesiad of supraantennal hump.

Eyes absent; ommatidial eyespot absent.

Neck across nuchal groove about one sixth as wide as width of head.

Maxillary palpomere four small, conical.

Labrum with deep emargination; emargination with rounded base (broadly rounded, not V-shaped as illustrated in Coiffait, 1984: 209, fig. 58a); anterior margin with small, rounded denticle on each lobe of labrum.

Prothorax about onethird longer than wide.

Pronotal punctation moderately dense but absent from midlongitudinal strip; surface polished; microsculpturing absent; surface flattened to lateral margin then strongly convex; surface slightly depressed just behind middle to just before posterior margin; midlongitudinal line with slight ridge on posterior quarter.

Notosternal suture presence or absence ambiguous; surface microsculpturing strong.

Prohypomeron with postprocoxal lobe moderately long, nearly vertical, rounded apically, and without setae.

Profurcasternum long, narrow, tapered posteriorly, widely separated from hypomeron.

Procoxal cavity open posteriorly.

Elytra shorter than pronotum; posterior margin with sparse row of setae.

Mesoventrite without midlongitudinal carina; surface with weak, shallow median depression.

Metatrochanter (of male) with two small spines on posterior margin.

Metafemur (of male) with three, thick, spinelike setae on posterior margin.

Metatibia with four, small, spinelike setae on anterior margin (of male only?); apex with comb on inner side.

Tergum VII without palisade fringe on posterior margin.

Tergum IX with middorsal base of male fused.

Segments IX and X of female not examined.

Aedeagus not examined.

Spermatheca not examined.

Distribution and Habitat: *Coecoscopaeus* is known only from Tunisia where the four only known specimens of *C. coecus* were collected from crevices in clay and said to be adapted to subterranean life (Peyerimhoff, 1906: 56).

Nomenclature: Coiffait (1982: 9) first cited the name *Coecoscopaeus*, without characters and in the Scopaeina (written as Scopaei), in a key to paederine subtribes and again (Coiffait, 1984: 5) in the Sommaire. Several pages further on, in a key to Palaearctic paederine genera Coiffait (1982: 11) provided differentiating characters and designated *Scopaeus coecus* Peyerimoff as the type species for the genus, which then made the name available (ICZN, 1999: Articles 13.1.1, 13.3). Later he formally, and in more detail, redescribed the genus and species (Coiffait, 1984: 209–210).

Discussion: Coiffait (1982: 11; 1984: [5], 209) established the monotypic *Coecoscopaeus* for the anophthalmic, flightless, Tunisian species, *Scopaeus coecus* Peyerimhoff (1906: 56). He placed it in the Scopaeina (cited as Scopaei) with *Scopaeus* because of the narrow neck of both. However, a slender neck is widespread in the subfamily and does not alone define *Scopaeus* or any other paederine genus. Frisch et al. (2002a: 45) correctly excluded *Coecoscopaeus coecus* from the Scopaeina but neglected to cite characters that led to that conclusion. Thus, *Coecoscopaeus* lacks the paraocular, cephalic trichobothrium (see figs. 309, 333) and the tripartite ligular lobe (see figs. 160, 187)—both characteristic of the Scopaeina, and lacks the apomorphic stridulum (see figs. 105, 106) of *Scopaeus.*

Coecoscopaeus has features entirely absent in the Scopaeina but that are found in three other genera all of which are now assigned to Sphaeronina. These genera, *Typhloleleupius*, *Tripectenopus*, and *Sphaeronum*, are found in Africa, Australia, and South America respectively.

Beyond the syntypic series of three males and one female, apparently, no other specimens of *C. coecus* have been collected. I was able to study a male syntype. However, since the species is rarely collected and there are few specimens in collections, I was uncomfortable with dissecting or even manipulating the mouthparts to see the hypopharyngeal peg, one of two characters that permit definitive subtribal assignment. The ventral side of the presumed hypopharyngeal peg could be seen between the labial palpomeres.

In addition to the likely presence of a hypopharyngeal peg, the species is assigned to the Sphaeronina because it shares the following features with the other three included genera: (1) the mandibular denticles of each mandible are out of alignment with one another; (2) the mandibles have a groove on the anterolateral surface and the left mandible has a denticle on the ventral surface; (3) the labrum has a deep emargination with a rounded base; (4) the submarginal, lateroventral, cephalic surface has a long groove extending from near the base of the mandibles to the neck; (5) the gular sutures are confluent; (6) the neck is narrow, about one sixth as wide as the greatest width of the head; (7) below the antennal insertion is a prominent subantennal hollow on the gena; (8) the probasisternum is long; (9) the pronotal marginal ridge is absent; (10) the protibia has a large lobe with a deep concavity lined with three diagonally transverse combs; (11) the profemur has a large ridge with a comb on the apex; (12) the slender, acute tip of the lateroapical process of tergum IX is strongly bent dorsally.

All but one of the preceding 12 characters are homoplasic. Among those 12, the large denticle arising from the ventral surface of the left mandible is the only unique character that places *Coecoscopaeus* in the Sphaeronina.

The spines on the metatrochanter and spinelike setae on the metafemur and metatibia of the males are notable. However, since no females were available for study it is uncertain whether they also have these spines and spinelike setae, so the character is not offered as a diagnostic feature of the genus or even species.

The elytra may be fused along the elytral suture, the scutellum appears to be fused to the elytral base, and the wings may be entirely absent.

The illustration of the protibia by Coiffait (1984: 209, fig. 58d) is entirely misleading. As shown there the protibia seems to have a deep notch when in fact the protibia of *Coecoscopaeus* has a large triangular lobe as illustrated herein for *Sphaeronum* and *Tripectenopus* (figs. 350, 351).

Species Included and Material Examined

1 species

The account for *Coecoscopaeus* was based on examination of one male syntype of the type series.

coecus (Peyerimhoff, 1906) - Syn (IRSN) — Tunisia

Undetermined specimens: None.
Dissections: None.

Tripectenopus Lea

Figures 351, 381–391

Tripectenopus Lea, 1918: 83 (species included: *caecus*). Type species: *Tripectenopus caecus* Lea, fixed by monotypy.

— Scheerpeltz, 1933: 1270 (catalog). — Blackwelder, 1939a: 122 (type species). — Blackwelder, 1952: 397 (type species).

Scopaeodracus Scheerpeltz, 1935: 638. Type species: *Scopaeodracus handschini* Scheerpeltz, 1935: 646, fixed by original designation and monotypy. **New synonym**.

— Blackwelder, 1952: 347 (type species).

DIAGNOSIS: *Tripectenopus* has two apical, metatibial combs; both *Sphaeronum* and *Coecoscopaeus* have one. *Tripectenopus* has a deep, longitudinally furrowed, mesobasisternal depression; the mesobasisternal depression of both *Sphaeronum* and *Coecoscopaeus* is barely discernible. The prohypomeron and profurcasternum of *Tripectenopus* are separated (Britton, 1974: fig. 6); they touch in *Sphaeronum* (fig. 355). These three characters do not distinguish *Tripectenopus* from *Typhloleleupius*.

Tripectenopus and *Typhloleleupius* are most conveniently and clearly separated by the Indian Ocean; the former is confined to Australia, the latter to southern Africa and Madagascar. Few morphological features separate them. The labrum of *Tripectenopus* is deeply emarginate and edentate (fig. 384; Scheerpeltz, 1935: 4a). The labrum of *Typhloleleupius* has a large, submedial, apically acute (Janák, 2013: fig. 21) to small, apically rounded denticle (fig. 394) submedially on the anterior margin. None of the articles published on *Typhloleleupius* and *Tripectenopus* present characters or discussion to aid separation. Until now the two genera have never been compared or associated with each other.

Other possibly distinguishing characters, two of which have been cited as diagnostic for *Tripectenopus*, are all subtribal features that permit separation from other Paederinae. They include the confluent gular sutures (Scheerpeltz, 1935: fig. 3a), absence of the pronotal marginal ridge, presence of the hypomeronal ridge of the postprocoxal lobe, the trilobed anterior margin of sternum II, the strongly sclerotized, dorsally directed, hypopharyngeal peg (figs. 386–388), and the enlarged grooming concavity of the protibia (fig. 351; Scheerpeltz, 1935: fig. 4h).

DESCRIPTION: Body length 3.2–11.0 mm (from Lea, 1918: 85, 1923: 29–31; Scheerpeltz, 1935: 647; Britton, 1974: 86).

Head (figs. 381, 382; Scheerpeltz, 1935: fig. 1a; Britton, 1974: fig. 5) with lateral margin gradually rounded to basal angles or to neck; basal angle broadly to strongly rounded or absent; basal margin slightly to strongly rounded and slightly to strongly emarginate medially or with small median lobe; anterolateral surface with or without temporal ridge; temporal ridge, when present, fine, short, and extending posteriorly from lateral surface of supraantennal hump onto temple; lateroventral surface with or without submarginal furrow or ridge; furrow or ridge, when present, moderately long, posteriorly extended, and well separated from basal angle of head.

Dorsal cephalic surface (fig. 382) with dense to moderately dense punctation; punctation distinct and moderately coarse; punctation present or absent from midlongitudinal strip; microsculpturing present and distinct to feeble; pubescence fine and with scattered coarse, long, macrosetae.

Clypeal margin of males with large (Britton, 1974: fig. 5), apically rounded, conical horn mesiad of supraantennal hump or horn replaced by tumescence (fig. 382); female with small to slight tumescence in place of horn.

Labrum deeply emarginate and edentate (fig. 384).

Eyes present and with many ommatidia, reduced to one ommatidium (fig. 382, evident as small, ocelluslike bump on right side), or absent (Britton, 1974: 86); multifaceted eyes with setae.

Neck width across nuchal groove about one sixth as wide as greatest width of head.

Maxillary palpomere 4 small, conical (fig. 383).

Labrum deeply emarginate and edentate (fig. 384).

Prothorax about one fifth to one third longer than wide.

Pronotum (fig. 382) with punctation moderately dense to dense and uniform, but absent from midline; microsculpturing distinct, weak, or absent; surface with low, midlongitudinal ridge; median ridge moderately developed basally, weak or absent medially, absent anteriorly; median ridge with or without slight groove.

Notosternal suture present and weakly developed (Britton, 1974: fig. 6).

Prohypomeron moderately densely punctate; postprocoxal lobe moderately long, nearly vertical, apex rounded, surface without setae; transverse hypomeronal ridge present and broadly curved.

Profurcasternum long, narrow, tapered posteriorly, widely separated from hypomeron (Britton, 1974: fig. 6).

Procoxal cavity open posteriorly.

Elytra shorter to longer than pronotum.

Mesoventrite without midlongitudinal carina; mesobasisternum with broad, median depression; basisternal depression with strong, midlongitudinal furrow.

Procoxa with mesial carina near base (fig. 385).

Metatrochanter without spines on posterior margin.

Metafemur without spinelike setae on inner edge.

Metatibia without spinelike setae on inner edge; apex with comb on inner and outer sides.

Tergum VIII with or without palisade fringe.

Tergum IX with apex of lateroapical process long to short; tergum IX of male with middorsal base fused (female not examined).

Segments IX and X not examined.

Aedeagus not examined (illustrated for *T. occultus*: Britton, 1974: 85).

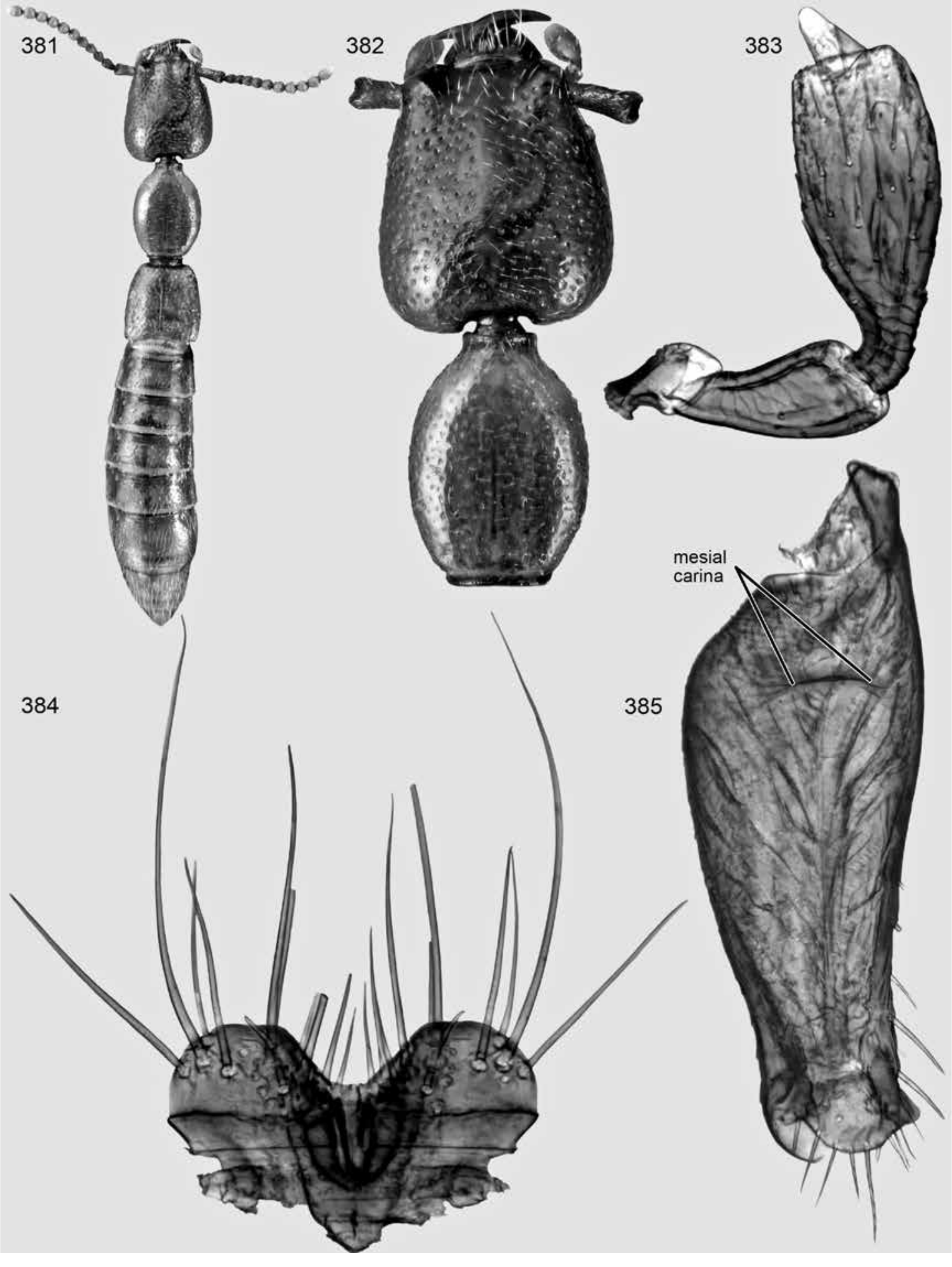
Spermatheca not examined.

Distribution and Habitat: Although *Tripectenopus* is widespread in Australia and has been collected in New South Wales, Northern Territory, Queensland, South Australia, and Western Australia, the genus is known by few specimens from few localities. Although specimens of the genus have been rarely collected, but it is anticipated that more, perhaps many more, species will be described.

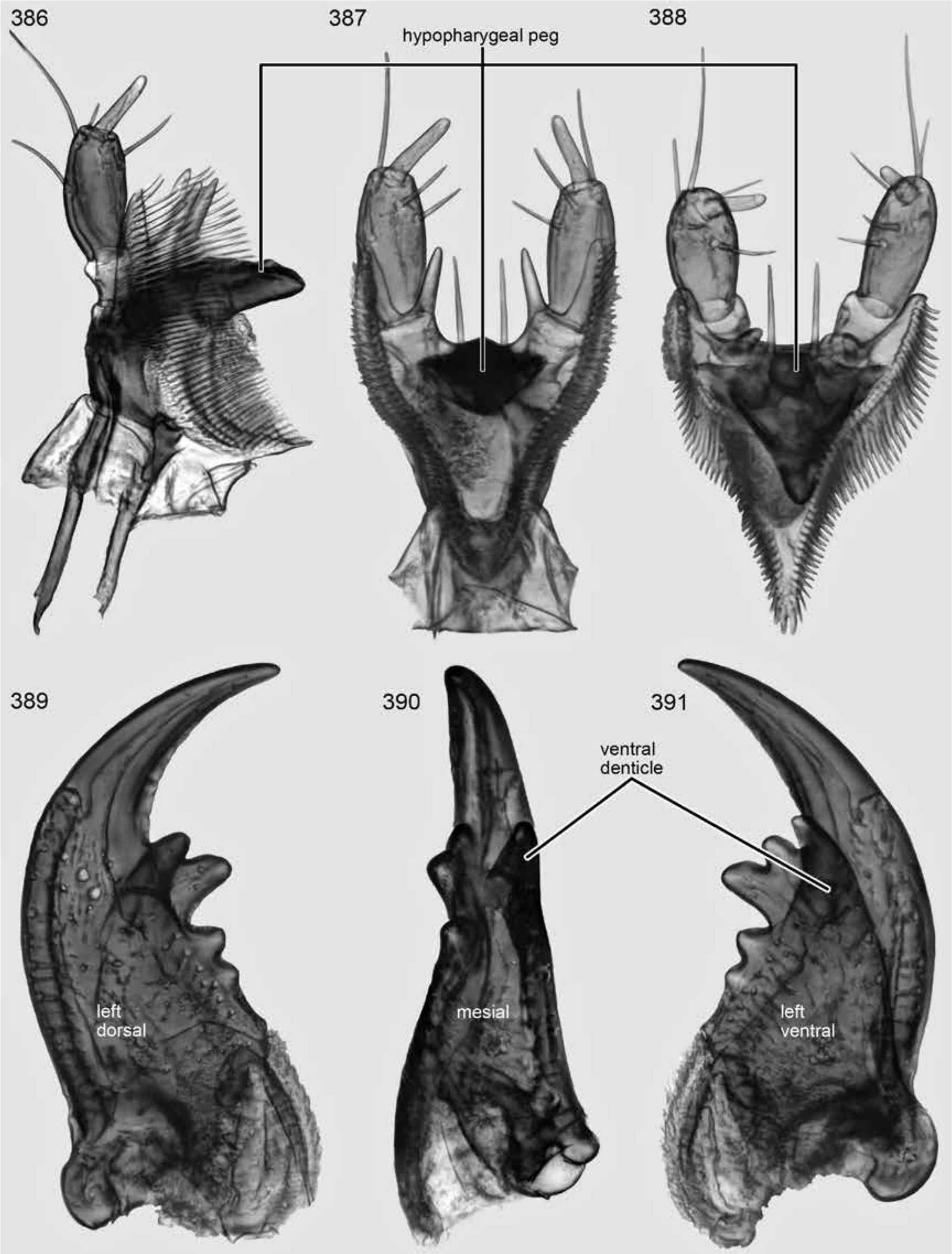
Little is known about the habitat or where specimens and species might be found, but the few data available suggest deep litter of the forest floor for at least some species. Specimens of *Tr. torrensensis* were collected from river debris (Blackburn, 1891: 75) and from a flooding river in Queensland (Lea, 1923: 29). *Tripectenopus occultus* was taken from a cave in Western Australia (Britton, 1974: 85); both species lack eyes. Among unidentified specimens I examined, two were attracted to lights and one was collected from forest floor leaf and log debris. The only known elevational record is 1580 meters for an unidentified specimen collected in New South Wales. Three species were collected near rivers.

Discussion: When Lea (1918: 83) described the monotypic, Australian *Tripectenopus* he included many of the essentials that define the subtribe Sphaeronina: the ovate head, moniliform antennomeres, narrow neck, elongate prothorax, enlarged protibial grooming lobe, and small scutellum. His illustrations depict several of these diagnostic features. Lea also noted that *Tripectenopus caecus* was apterous and eyeless. He did not state the sex of the type, but since he described none of the external features typical of males, the specimen may be a female. He placed the genus near *Domene* and thought *Tr. caecus* looked like an exaggerated *Domene torrensensis* Blackburn, 1891; he separated the two by the presence or absence of eyes.

Scheerpeltz (1935: 638) published a detailed eight-page description with 10 illustrations permitting recognition of the Australian monotypic *Scopaeodracus*, but not separation from *Tripectenopus*. Among noteworthy characters are the form of the head and pronotum, the confluent



FIGS. 381–385. *Tripectenopus* spp. **381.** Habitus, legs omitted. **382.** Head and prothorax, legs omitted. **383.** Maxillary palpus. **384.** Labrum. **385.** Procoxa, mesial surface.



FIGS. 386–391. *Tripectenopus* sp. **386–388.** Labium, hypopharynx. **386.** Lateral. **387.** Dorsal. **388.** Anterior. **389–391.** Mandibles, left. **389.** Dorsal. **380.** Mesial. **391.** Ventral.

gular sutures, bilobed labrum, narrow neck, large grooming structures of the protibia and profemur, and ventral denticle of the mandibles; all are features of the subtribe. Scheerpeltz did not refer to *Tripectenopus* and placed his new genus near *Scopaeus*.

Tripectenopus occultus Britton, 1974, was the second species described in the genus. Britton included most of the same diagnostic features for the genus relevant to the gular sutures, protibiae, eyes, antennae, and procoxal concavity, cited by Lea and Scheerpeltz. Britton listed the narrow neck as a feature of the Paederinae, but, though widespread, it is neither a defining nor the more common condition of the subfamily. This species was the first among the three genera for which males were known and described. After studying the type species of *Typhloleleupius*, Britton opined that it and *Tripectenopus* might be synonyms. Except for male specific features and the anophthalmy, the characters Britton used to define *Tripectenopus* are those that distinguish the subtribe.

Omitting a brief comment by Britton (1974: 87), *Tripectenopus*, *Scopaeodracus*, and *Typhloleleupius* were not compared with or considered in the context of one another by anyone. Many of the published characters for each are either found widely among paederines or are possessed by each of the three genera and are considered herein to define the Sphaeronina. Among the Australian species I find no characters to suggest there are two genera. I agree with Newton's supposition (in litt., June 27, 2009) that the two are synonyms and hereby formally synonymize *Tripectenopus* and *Scopaeodracus*.

For the Australian *Tripectenopus* and southern African and Madagascan *Typhloleleupius* there appear to be no characters that separate them as clearly as their respective geographical locations. The structural diagnostic features distinct to each are few and variable. Some characters are present in one genus but are whispers in the other. The two genera share most characters. Britton (1974: 87), who studied the type species of *Typhloleleupius*, thought the two might be synonyms because he found no distinguishing features, but most of the characters he used are subtribal and shared by the four, now included genera. Some possible discriminatory features published by Janák (2013) or discovered during the present study are considered in the following six paragraphs.

(1) All known species of *Typhloleleupius* are eyeless (*Ty. doryloides*, *Ty. minutus*, *Ty. podocarpus*) or have one ommatidium (*Ty. capensis*, *Ty. elongatus*). Among *Tripectenopus* there are eyeless species (*Tr. caecus*, *Tr. occultus*) and species with multifaceted eyes (*Tr. microps*, *Tr. pectinatrix*, *Tr. handschini*, *Tr. torrensensis*). The presence, reduction, or absence of eyes is strongly correlated with the habitat and is insufficient as a generic level characteristic.

(2) The anterolateral portion of the head of *Typhloleleupius* has a fine temporal ridge on the side of the head that originates on the side of the supraantennal hump and extends posteriorly onto the temple. The surface below this ridge was described as a "longitudinal furrow" by Janák (2013: 82 and fig. 4; in litt., August 28, 2019). However, as the ridge is more evident than the furrow emphasis is placed on the "temporal ridge." In dorsal view images of *Ty. doryloides*, *Ty. minutus*, and *Ty. podocarpus* (Janák, 2013: figs. 9, 10, 15, 16) the temporal ridge can be seen as a black line along the lateral periphery of the head beginning near the antennal insertion. Both the type of *Ty. doryloides* and *Typhloleleupius* near *minutus* have a temporal ridge. An Australian species of *Tripectenopus* with one corneal lens has an identical, but shorter, temporal ridge. Lea (1918: 84) mentioned a feeble, oblique ridge on the side of the head of *Tripectenopus caecus*. Species of *Tripectenopus* with eyes lack a temporal ridge, which suggests it may be confined to eyeless or reduced-eye species. The presence of these ridges and grooves in species of both regions make them unsuitable generic features.

(3) The clypeal margin of males of *Typhloleleupius* has a small, conical, apically rounded horn mesiad of the antennal insertion (Janák, 2013: figs. 8, 10, 14); the horn is smaller in the females (Janák, 2013: figs. 14, 16). In the same position on the clypeus of males of *Tripectenopus*

the horn is large (Britton, 1974: fig. 5) or reduced to a small bump and on females a slight tumescence is present (fig. 382).

(4) According to the illustration of the labrum of *Typhloleleupius doryloides* (Janák, 2013: fig. 21) the anterior margin is emarginate medially with a broad denticle on each side. Janák's (2013) descriptions of all the species indicate a rather prominent "denticle" or "lobe" adjacent to the median emargination. In my notes for the type of *Ty. doryloides*, the labrum has a broad, apically rounded denticle adjacent to the median emargination. The labrum of *Typhloleleupius* near *minutus* is deeply emarginate and the anterior margin has a small boss, bump, lobe, or denticle (fig. 395), but lacks longer, larger, more apically pointed denticles. The labrum of four unidentified species of *Tripectenopus* and *Tr. handschini* (Scheerpeltz) (1935: fig. 4a) has a deeply emarginate, bilobed anterior margin (fig. 384) and none has a denticle or lobe adjacent to the emargination.

(5) The submarginal lateroventral region of the head of the type of *Ty. doryloides* has a furrow or groove extending from near the base of the mandible posteriorly (as in figs. 365, 366). This groove was not recorded by Fagel (1964) or Janák (2013). The groove is present in *Typhloleleupius* near *minutus* (as in figs. 365, 366). The dark shadow near the ventral edge of Janák's (2013) figure 4 is in the correct position and was affirmed to be a furrow by Jiri Janák (in litt., September 1, 2019); Janák also reported that he has an undescribed species with a similar furrow. Among the four unidentified species of *Tripectenopus* the submarginal, lateroventral groove is absent from three. One species has a weak ridge with an adjacent feeble impression, one has a short, shallow, barely perceptible impression, one has neither a ridge nor impression, and the fourth has a shallow, distinct furrow passing beneath and beyond the eye.

(6) Based on the published lateral view images of the two genera, *Tripectenopus* (Britton, 1974: fig. 4) and *Typhloleleupius* (Janák, 2013: figs. 25, 31, 33, 46), the aedeagus appears to offer no differential characters.

In summary, I am deeply skeptical that the species of these two regions should be assigned to separate genera. Not one of the preceding characters supports recognition of two genera. Two genera are maintained here only because they are separated by about 10,400 kilometers of ocean. No morphological characters have been found to support recognition. The presence, reduction, or absence of eyes is largely habitat related. The temporal and submarginal grooves and ridges are variable and found on species in both regions. The clypeal "horns" are mere variable bumps and might not even distinguish species. The labral dentition might separate species, but in some the denticles are the slightest of "bumps." Even in *Scopaeus*, a genus of many species with highly developed, large, long, apically acute denticles, includes species with lobes that are regarded denticles only by a stretch of imagination. The aedeagus offers no help.

Species Included and Material Examined

7 species

I examined none of the identified species of this genus except one Cape York peninsular Australian specimen I identified as *Scopaeodracus* sp. The transferred names are based on information provided by A.F. Newton who studied the relevant types. The diagnosis, description, and discussions of the genus were based on examination of one specimen each of four unidentified species, two females and two males, and extraction of information from published works and which are cited where necessary.

australiae (Fauvel, 1878) — [Australia]
 New combination, transferred from *Domene*
caecus Lea, 1918 - Lit. Att. — [Australia]
handschini (Scheerpeltz, 1935) - Lit. Att. — [Australia]
 New combination, transferred from *Scopaeodracus*
microps (Lea, 1923) — [Australia]

New combination, transferred from *Domene*
occultus Britton, 1974 - Lit. Att. — [Australia]
pectinatrix (Lea, 1923) — [Australia]
New combination, transferred from *Domene*
torrensensis (Blackburn, 1891) — [Australia]
New combination, transferred from *Domene*

Undetermined specimens: Australia, (two males, two females).

Dissections: Australia (unidentified female, head and prothorax).

Typhloleleupius Fagel

Figures 392–403

Typhloleleupius Fagel, 1964: 390. Type species: *Typhloleleupius doryloides* Fagel, 1964: 391, fixed by original designation and monotypy.
— Janák, 2013: 81 (characters; revision of and key to species; excluded from Scopaeina; subtribe placement not known incertae sedis).

Diagnosis: The prohypomeron and profurcasternum of *Typhloleleupius* (fig. 393) do not touch, in contrast to *Sphaeronum* (fig. 355). The basisternum of the mesoventrite of *Typhloleleupius* has a deep, midlongitudinal depression; *Sphaeronum* and *Coecoscopaeus* have a barely discernible mesobasisternal depression. *Typhloleleupius* has two metatibial apical combs; *Sphaeronum* and *Coecoscopaeus* each have one. The anterior margin of the labrum of *Typhloleleupius* is emarginate and has an adjacent lobe or apically rounded to acute denticle (fig. 395; Janák, 2013: fig. 21); the labrum of *Tripectenopus* is bilobed and edentate (fig. 384); the former is confined to southern Africa and Madagascar, the latter to Australia.

Other important characters of *Typhloleleupius*, all subtribal features, include confluent gular sutures; absence of the pronotal marginal ridge; presence of the hypomeronal ridge of the postprocoxal lobe; trilobed anterior margin of sternum II; strongly sclerotized, dorsally directed, hypopharyngeal peg; and enlarged grooming concavity of the protibia.

Description: Body length 3.4–5.9 mm (from Janák, 2013).

Head (figs. 392, 403) with lateral margin gradually rounded to neck or to basal angles (Janák, 2013: 85, 86); basal angle absent or broadly to strongly rounded; basal margin strongly to slightly emarginate to slightly rounded medially; anterolateral surface with fine, short to long, temporal ridge extending posteriorly from lateral surface of supraantennal hump onto temple (fig); lateroventral surface with long submarginal, subocular groove (fig. 403) extending from near base of mandibles posteriorly toward basal angle of head.

Dorsal surface of head with dense to moderately dense punctation; punctation distinct and coarse, absent from midlongitudinal line; microsculpturing present and distinct to feeble; pubescence fine and with scattered, longer macrosetae.

Clypeal margin of males with small to large, anteriorly directed, conical horn mesiad of supraantennal hump; females with smaller horn.

Eyes absent or reduced to one or a few ommatidia (Janák, 2013: 82).

Neck width across nuchal about one eighth to one sixth as wide as greatest width of head.

Maxillary palpomere 4 small, conical. Labrum deeply (fig. 395) to moderately deeply emarginate (Janák, 2013: fig. 21); anterior margin with small to moderately large, submedial lobe or denticle (Janák, 2013: fig. 21). (Note: Janák, 2013, described considerable variation of the anterior labral margin among the five species.)

Prothorax about one fourth to one third longer than wide.

Pronotum (fig. 392) with moderately dense to dense and uniform punctation, but absent from median strip; microsculpturing distinct, weak, or absent; surface with low, midlongitudinal ridge; median ridge moderately developed basally, weak medially, absent anteriorly; median ridge with slight median groove.

Notosternal suture present, evident as narrow polished line through microsculptured surface.

Prohypomeron moderately densely punctate and pubescent; postprocoxal lobe moderately long, nearly vertical, apex rounded, surface without setae; transverse hypomeronal ridge present and sinuate.

Profurcasternum (fig. 393) long, narrow, tapered posteriorly, widely separated from hypomeron.

Procoxal cavity open posteriorly.

Elytra shorter than pronotum.

Mesoventrite without midlongitudinal carina; mesobasisternum with broad, median depression; depression with strong, midlongitudinal furrow.

Procoxa (fig. 394) with mesial carina near base.

Metatrochanter without spines on posterior margin.

Metafemur without spinelike setae on inner edge.

Metatibia without spinelike setae on inner edge; apex with comb on inner and outer sides.

Tergum VIII without palisade fringe.

Tergum IX with middorsal base fused. Segment IX of female with lateral gonocoxal plate, wide basally and tapered apically.

Aedeagus symmetrical and broad in ventral view; ventral process present; parameres absent; basal piece absent.

Spermatheca not examined.

Distribution and Habitat: *Typhloleleupius* is known from South Africa (Natal and Eastern and Western Cape Provinces), and Lesotho. Janák (2013: 98) reported several undescribed species are in Madagascar.

Collections have been made in scrubland vegetation, in forest litter and humus among roots of trees at a depth of 10 to 40 cm, and under stones at elevations of between 970 to 2000 meters (Janák, 2013). *Typhloleleupius* near *minutus* was collected from *Buddleia* leaf litter at 1800 meters elevation.

Discussion: Few characters distinguish *Typhloleleupius* and *Tripectenopus*. I am unconvinced these names represent different genera; their alleged separation is considered in more detail in the Discussion for *Tripectenopus*.

The South African *Typhloleleupius* was described by Fagel (1964: 390) for a new species represented by five females. He affiliated the genus with *Scopaeus*. The diagnostic characters, which can be sifted from the description, are essentially those cited for *Tripectenopus* and *Scopaeodracus*. Fagel described the anterior labral margin as having a fairly deep notch limited by two obtuse projections ("avec encoche assez profonde, limitée par deux saillies obtuses").

Typhloleleupius was revised by Janák (2013). He redescribed the genus, illustrated characters, provided a key for identification, recognized four new species, and described the males for three of them. Because the genus lacked the supraocular trichobothrium Janák excluded it from Scopaeina and labeled it incertae sedis in the Paederinae. *Typhloleleupius* was compared with *Coecoscopaeus*.

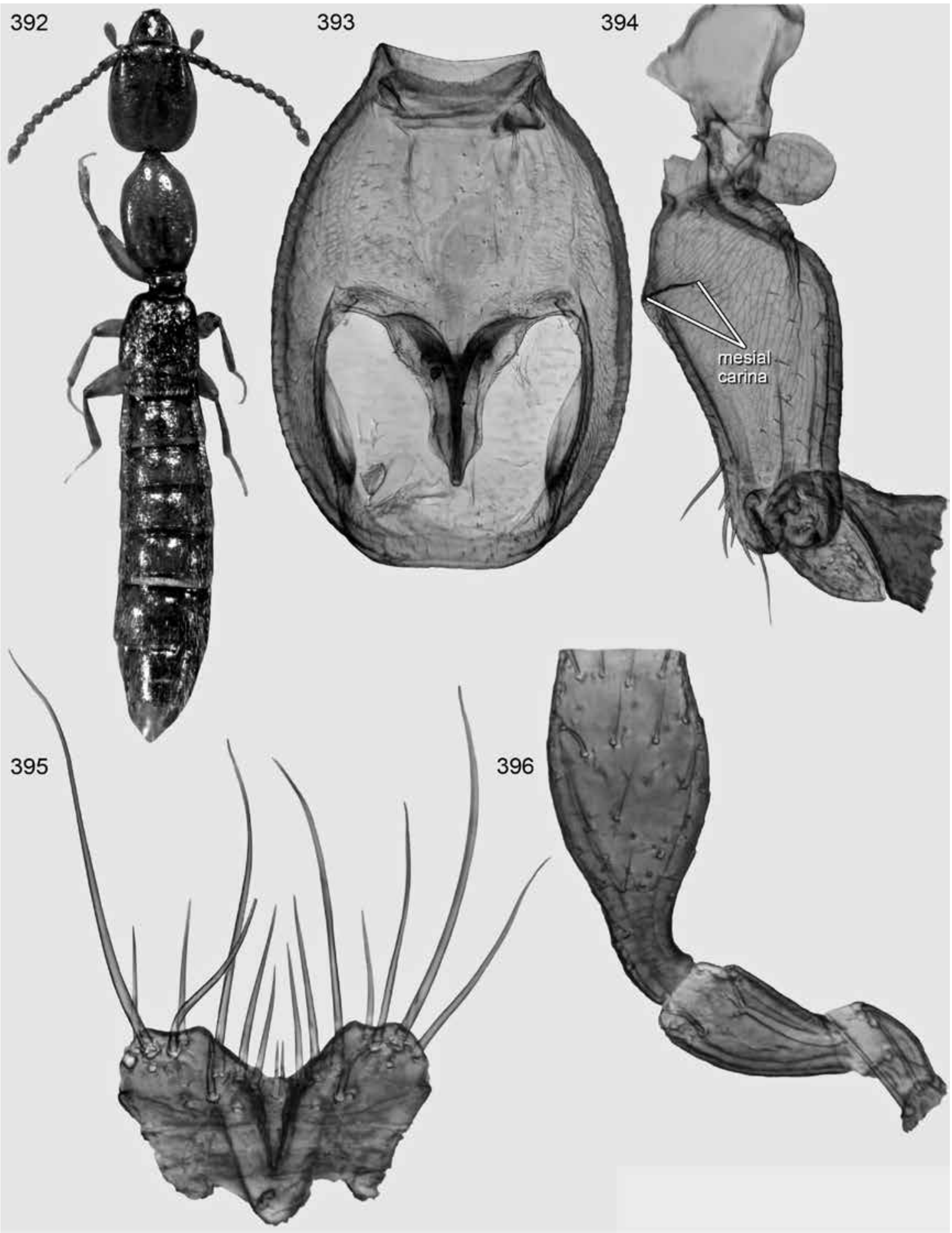
Three of the five named South African species lack eyes, two have one corneal lens (Janák, 2013; in litt., September 1, 2019). Janák (2013: 82) described the fourth and fifth metatarsomeres as having a bilobed posterior margin. For neither the slide-mounted specimens nor the point-mounted specimens of *Typhloleleupius* near *minutus*, were those tarsomeres bilobed, but rather the margin was broadly rounded. According to Janák (2013) the longitudinal furrow, below the fine temporal ridge, of the head varies in length among the five species. The males have a small, conical horn on the anterior margin of the clypeus mesiad of the antennae; the horn is reduced in females.

Species Included and Material Examined

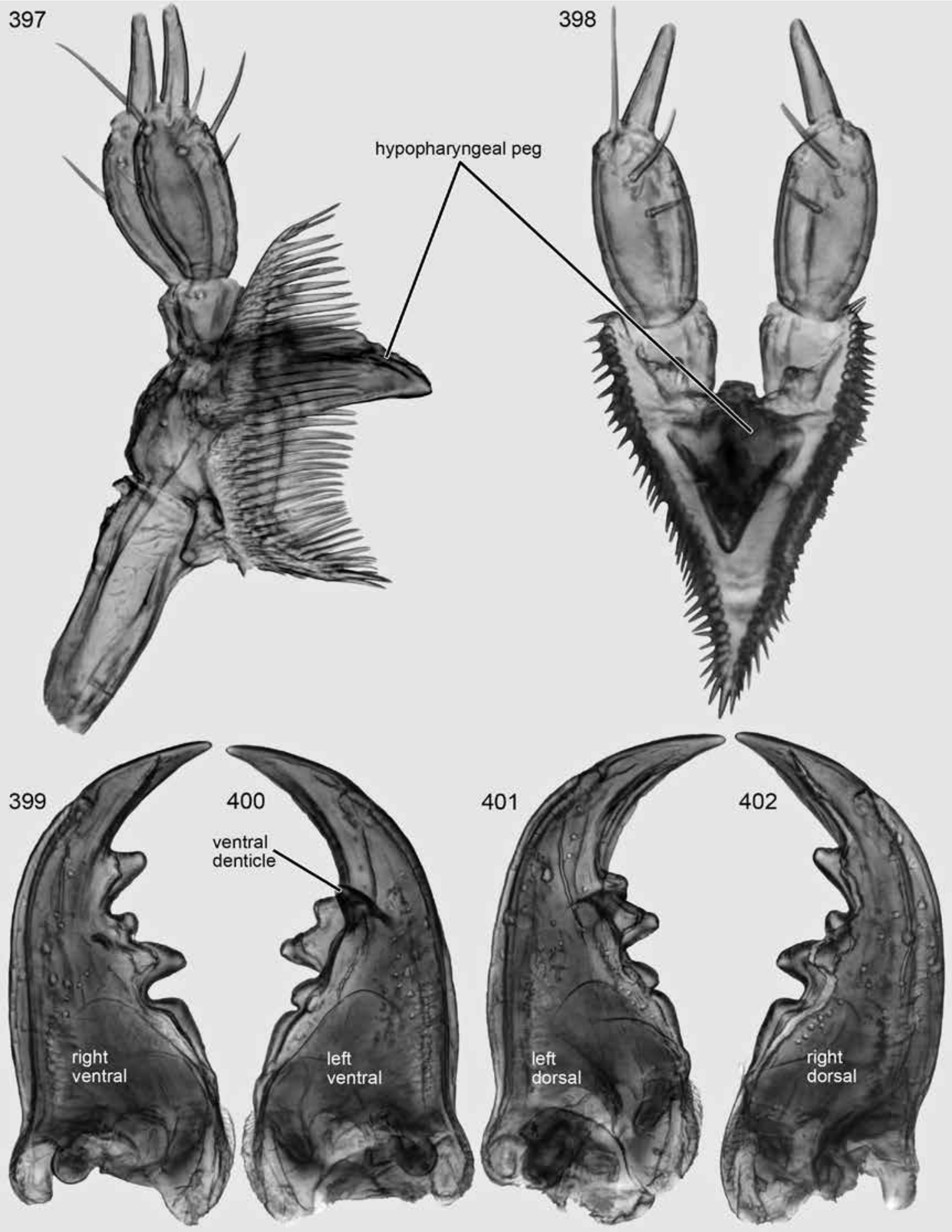
5 species

The account for *Typhloleleupius* was based on study of specimens of *Typhloleleupius* nr. *minutus*, descriptions and images in Janák, 2013, and 2019 email correspondence with J. Janák.

capensis Janák, 2013 - Lit. Att. — [South Africa]



FIGS. 392–396. *Typhloleleupius*. **392.** *T. doryloides*, right proleg omitted. **393–396.** *T.* nr. *minutus*. **393.** Prothorax. **394.** Procoxa, anteromesial. **395.** Labrum. **396.** Maxillary palpus, fourth palpomere missing.



FIGS. 397–402. *Typhloleleupius* nr. *minutus*. **397–398.** Labium, hypopharynx. **397.** Lateral. **398.** Anterior. **399–402.** Mandibles.

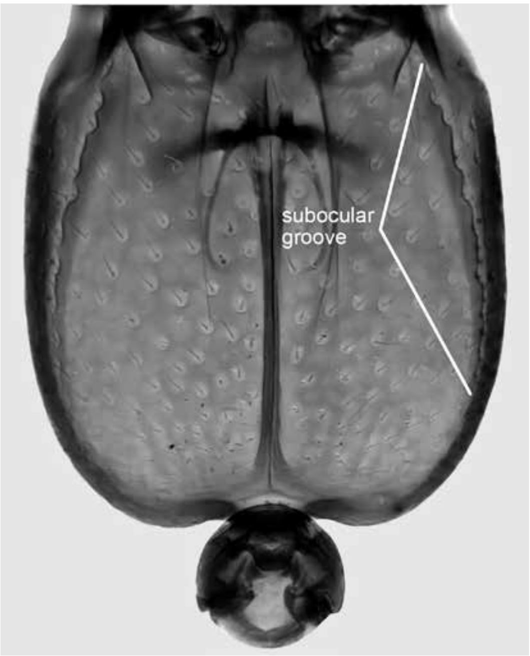


FIG. 403. *Typhloleleupius* nr. *minutus*. Head, ventral.

doryloides Fagel, 1964 - P (MRAC) — South Africa
elongatus Janák, 2013 - Lit. Att. — [South Africa]
minutus Janák, 2013 - Lit. Att. — [Lesotho]
podocarpus Janák, 2013 - Lit. Att. — [South Africa]

Undetermined specimens: South Africa (*Typhloleleupius* nr. *minutus*).

Dissections: *Typhloleleupius* nr. *minutus* (South Africa; male; cleared, partially dissected, slide mounted male and female).

Medonina Casey

Parascopaeus Cameron

Parascopaeus Cameron, 1918: 76 (species included: *nitidus*). Type species: *Parascopaeus nitidus* Cameron, fixed by monotypy. — Cameron, 1921a: 353, 373, 403 (cited [erroneously] as a new subgenus of *Medon* on p. 403; characters; key and catalog for species of Singapore). — Scheerpeltz, 1933: 1264 (catalog). — Blackwelder, 1939: 120 (type species). — Blackwelder, 1952: 293 (type species).

Discussion: *Parascopaeus* is not a member of the Scopaeina. Although never actually included in the Scopaeina, *Parascopaeus* was marginally associated with the subtribe when it was first described by being placed between *Scopaeus* and *Dacnochilus* (Cameron, 1918: 76), *Medon* and *Scopaeus* (Cameron, 1921: 373, 403), or *Acalophaena* and *Scopaeus* (Scheerpeltz, 1933: 1264). Almost certainly by erroneous oversight, Cameron (1921: 403) listed it as a subgenus of *Medon*, which is closer than *Scopaeus* to its apparent affinity. On two other pages of the same article Cameron (1921: 353, 373) clearly cited it as a genus. For now, *Parascopaeus* should be placed in the Medonina, presently a subtribe-awaiting-correct-placement genera.

I have seen only a single, card-mounted specimen of *Parascopaeus nitidus* Cameron, 1921, the holotype of the type species, in the Natural History Museum, London. The species is small and similar to species of *Scopaeus*. The following is based on the original description and my notes from a 2007 examination of the dorsal side of the undissected holotype and as described by Cameron (1918: 76, 77). A better understanding of the affinities of *Parascopaeus* would require detailed examination and perhaps dissections of males and females.

Nonetheless, two features definitively purge it from the Scopaeina. Most notably, the type lacks the paraocular trichobothrium, which is characteristic of the Scopaeina (see figs. 309, 333), and it has a pronotal marginal ridge, which is absent in the Scopaeina. Except for the males of *Orus ferrugineus* and species of the *Scopaeus chiriquensis* species group, the Scopaeina have one or two pairs of labral denticles; the labrum of *Parascopaeus* is edentate. The width of the neck of *Parascopaeus* is slightly more than a quarter of the postocular width of the head, a character that varies from one eighth to two thirds the width of the head in the Scopaeina. *Parascopaeus* has a slender neck, but that alone does not support inclusion in *Scopaeus* or the Scopaeina. Among other defining features of the Scopaeina are the labial tripartite ligular lobe (fig. 187), and the trilobed anterior margin of abdominal sternum II. Both characters are ventral and could not be examined without removing the specimen from the mounting card, which I did not do.

For now, the practical reason for placing *Parascopaeus* in the Medonina is the nearly square pronotum, the absence of characters that place it elsewhere, and Cameron's (1921: 403), perhaps erroneous citation of it as a subgenus of *Medon*.

Species Included and Material Examined

1 species

nitidus Cameron, 1918 - H (BMNH) — Singapore

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I am much indebted to Johannes Frisch (MNKB) for gifting me with determined representative species of most of the Eurasian species groups he recognized in *Scopaeus*. Without those specimens, an organized discussion of the depth and breadth of the variation within the genus would have been difficult or impossible. During one of my visits to the Museum für Naturkunde to study types deposited there, Johannes permitted me to review the many types of *Scopaeus* that he had borrowed from other collections. I am deeply grateful for that access; without it most of those species would have remained invisible to me. Frisch and I have had many fruitful discussions over many topics in addition to scopaeines and for those I remain indebted. I thank him for reading various drafts of this manuscript; his comments and sharing his wide knowledge of *Scopaeus* led to discussions of various facets of the life and structure of *Scopaeus*. These discussions significantly improved the manuscript.

Steve Thurston (AMNH), who normally edited my illustrations, both photos and drawings, for publication, spent hours teaching me the basics of editing and preparing digital illustrations for the present publication. For his patience, knowledge, generosity, time, and effort I am genuinely obligated.

Many appreciative thanks to Corey Smith (AMNH), the highly, diversely talented collection assistant for the beetle collection, who helped me with some of the Scanning Electron Microscope imaging.

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During the too many years spent working on this project I visited several major collections to examine the type specimens of as many species as possible. I thank each of the curators and assistants of those collection as follows: The Natural History Museum, London; Institut Royal des Sciences Naturelles, Brussels; and Musée Royal des l'Afrique Centrale, Tervuren. I thank Terry Erwin at the National Museum of Natural History, Washington, D.C., for permitting me on-site examination of the collections. I especially thank Crystal Maier and Rachael Hawkins for sending me the holotype of *Orus montanus* Fall permitting corroboration of the generic assignment of the species based on new characters.

I thank Jiri Janák for his willingness to share, via email, some of his knowledge of the genus *Typhloleleupius*.

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