GENERIC REVISION OF THE PROCIRRINA (COLEOPTERA: STAPHYLINIDAE: PAEDERINAE: PINOPHILINI)

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ABSTRACT

The paederine subtribe Procirrina is redescribed, the morphology, phylogenetic relationships, and distribution are discussed, and a key to the eight genera is presented. In the section on morphology, the female genital sclerites are discussed and terms are proposed for the fused sclerites. *Neoprocirrus*, *Oedichirus*, *Oedodactylus*, *Palaminus*, *Paraprocirrus*, *Procirrus*, and *Pseudoprocirrus* are redescribed and a list of the included species and examined species is included for each. *Stylokyrtus*, **new genus**, is described for *Oedodactylus errans* Sharp, 1876, **new combination**. *Parapalaminus* Bierig, 1943, *Procirrinus* Koch, 1934, and *Oedichiranus* Reitter, 1906, described as subgenera, are **new synonyms** of *Palaminus*, *Procirrus*, and *Oedichirus* respectively. The sister group of Procirrina is Pinophilina. The basal genus of the Procirrina is *Oedodactylus*; *Pseudoprocirrus* is the sister group to the remainder of the genera, which are clustered in two clades. *Palaminus* + *Oedichirus* comprise one of the two clades with *Paraprocirrus* and *Procirrus* + *Neoprocirrus* as its sister. As *Stylokyrtus* is known by only one specimen, most of the characters important to phylogenetic placement of the genus were unavailable for study and its position within the subtribe is ambiguous.

INTRODUCTION

As part of a comprehensive examination of the classification of the Paederinae, presented here is a discussion of the classification, morphology, distribution, and phylogeny of the paederine subtribe Procirrina. First cited as Procirri, Procirrina was proposed and made available (ICZN, 1999: Article 12.2.4) in a catalog (Bernhauer and Schubert, 1912: 197). At that time no characters were provided for the group, which included five genera, *Procirrus, Eucirrus, Oedodactylus, Palaminus*, and *Oedichirus*, with 148 species of which over 100 were in *Palaminus*.

The first characters for the group were published 51 years after the group was recognized. This belated description is not surprising since the species dwell primarily in tropical and subtropical regions. Only four species are in Europe and those species barely reach the continent. The first characterization and all the following were brief, usually presented in keys, and confined to statements that the abdominal segments lacked paratergites and maxillary palpomere 4 is enlarged (Arnett, 1963: 243, 267; Coiffait, 1978b: 323; Outerelo and Gamarra, 1985: 20; Fagel, 1971: 11; Newton et al., 2000: 328, 389; Navarrete-Heredia et al., 2002: 393). Unexpectedly, Fagel (1971: 11), in his massive revision of the African Procirrina, presented characters for the subtribe in no more depth than did other authors.

The first genus of the group was described in 1829 and included one European species; thereafter, from 1832 through 1952, 13 more genus-group names were added, nine of which were first established with only one species. When the subtribe was segregated in 1912 only 148 species were known for the group. At the present writing the number of species has more than quadrupled to 648 (excluding synonymic names). The preponderance of species is in *Oedichirus* and *Palaminus* with 303 and 306 respectively; *Procirrus* has 29 species, and each of the remaining has one, two, or four. Europeans, normally the first to describe and know well their regional taxa, have published on their species of procirrines, but little on the subtribe. Doubtless that neglect is explained by the fact that the five species in the group (one *Procirrus* and four *Oedichirus*) are North African species that in Europe are confined to the southern edge.

The purpose of this work is to redescribe and illustrate the genera, present a key for their identification, corroborate species assignments, discuss the general morphology of the subtribe, propose a phylogeny of generic relationships, and bring to one place a summary of what is known about the group. No special efforts were made to solve problems concerning particular species. Generally, resolution of such questions needs to be addressed in the context of revising the species. The most disappointing aspect and the major impediment to this work was the paucity of specimens for dissection and for comparative morphological study. The poverty of specimens means that detail and

refinement of the generic classification of the group will come with revisionary studies of the species and genera.

METHODS AND MATERIAL EXAMINED: Insofar as possible, I completely dissect a male and female of a species of each genus and for genera with significant variation additional species are dissected. A complete dissection, also referred to herein as a disarticulation, is the separation of the major body regions and removal of the appendages, genital segment, aedeagus, and the female genital sclerites. More limited dissections are designated with the structure dissected, for example, abdominal dissection. Disarticulations were performed on a species only if there were a sufficient number of specimens in the series. In general, for this generic study, I dissected for genitalic features only if I had several (three or more) specimens. If the species was represented by only the type I did not dissect it. I reserve such dissections for revisions of species. In the Procirrina, material for complete dissections was available only for *Procirrus*, *Oedichirus*, *Palaminus*, and *Oedodactylus*; the first three genera are fairly uniform and few species were represented by significant series so few were dissected. *Oedodactylus* is more heterogeneous, but only one specimen was available for disarticulation and two for abdominal dissection. For *Neoprocirrus*, *Paraprocirrus*, *Pseudoprocirrus*, and *Stylokyrtus* few specimens are known, so structures that, to be seen, require dissection were not studied and other features were partly visible because only minimal manipulation was possible. In the descriptions unexamined characters are cited with a double asterisk and enclosed in square brackets.

MEASUREMENTS

In the present work a few structures are compared in size with others; the comparison is informal and no measurements are published. Measured are the following.

Head width: measured from the outer margin of one eye across to the outer margin of the other, even for the few species that are wider across the temples;

Head length: measured from the anterior margin of the frontoclypeus to the anterior margin of the nuchal groove;

Neck width: measured across the narrowest part of the nuchal constriction (= nuchal groove);

Pronotal length: measured midlongitudinally from the anterior to the posterior margin;

Pronotal width: measured across the widest place, usually at about the anterior third;

Elytral length: measured from the posterior edge of the scutellum to a line across the posterior most portion of the posterior margin of the elytra;

Tergum IX length: measured midlongitudinally from the anterior margin of the tergum to the anterior margin of the emargination between the bases of the lateroapical processes (fig. 25);

Tergum IX emargination (length of lateroapical processes): measured from the anterior margin of the emargination (base of lateroapical processes) to a line across the apices of the lateroapical processes (fig. 25).

Most commonly, synonyms are the result of two or more groups sharing the same nominal type genus or type species, or holotype, lectotype, or neotype (objective synonyms) or, alternatively, are two or more named groups that cannot be separated by any known character in the opinion of investigators (subjective synonyms). Objective synonyms are based on shared types and are immutable. Subjective ones are opinions usually based on discovering that presumed distinguishing characters intergrade or are linked by transitional specimens or species or genera, or that no characters separating them were found. However, subjective synonyms can also be based on the discovery that a paraphyletic group was created from a monophyletic one when another group with autapomorphic features was named and separated as either a subgenus or genus and the group that remained after the separation then had no synapomorphic characters to define it. To maintain monophyletic genera, autapomorphic groups are best retained within a genus, perhaps as species groups, pending study of the entire classification of the genus. Without revising all the species, it is possible to study a large genus, establish its monophyly, examine all the species in search of monophyletic species groups, and forget about a subgeneric classification. In the same sort of investigation it is possible to recognize

that autapomorphic subgenera render the group of species that remain in the nominate subgenus a paraphyletic group if a new character to support it is not found. A current ongoing example of this species-group approach are the numerous publications on *Scopaeus* (see, for example, Frisch, 2005, 2009).

Specimens were sorted, studied, dissected, and measured using a Leitz Stereoscopic Microscope. Measurements were made using an ocular grid. A Wild M20 compound microscope was used for detailed examination of disarticulated, slide-mounted specimens embedded in glycerin jelly and line drawings were made aided by a drawing tube attached to the same microscope. Scanning electron microscope (SEM) images were made using a Hitachi S-4700 cold field emission scanning electron microscope with a secondary electron detector. Specimens were prepared for dissection and for viewing with the SEM by clearing them in warm KOH or lactic acid. For viewing with the SEM, after dissection specimens were critical-point dried in a carbon dioxide medium using a Bal-Tec CPD030 and sputter coated with gold-palladium. Habitus photographs 1–8 were made at the AMNH with a Microptic-USA photomicrographic apparatus, equipped with Infinity K2 optics and a Nikon DIX digital camera. Figure 9 was taken at the Museum of Natural History, London, using a 7.1 megapixel Canon Powershot SD800 IS Digital ELPH mounted on a Leitz stereoscopic microscope. Because most staphylinids are so flexible the tagmata are rarely in perfect alignment, with either camera, photographs were taken of each region of the body and the habitus assembled using Adobe Photoshop CS3. For the phylogenetic analysis the matrix of characters was analysed using Winclada 1.00.08 (Nixon, 1999–2002).

Species Assignments: To assign species to genus my original intention was to examine all the species of each genus; type specimens were preferred, but in lieu of those, identified specimens were used. Logistically and financially that goal became impossible. In the lists of Species Included and Material Examined, I specify with abbreviations, defined below, whether the generic assignment is based on a holotype, lectotype, syntype, neotype, paratype, paralectotype, or a subsequently identified specimen. Repositories of specimens of each species examined are denoted by abbreviations, also defined below. Species for which I saw no specimens are included in the genera to which they are currently assigned in the literature and those species are so annotated; the accuracy of literature assignments and those based on subsequently identified specimens need verification.

Species-group synonyms cited in the lists of Species Included and Material Examined are based on published synonymies; verification of the synonymy of species is beyond the intended scope of the present work. Type material of any of those synonyms that I saw is indicated in the lists. For species I examined, the stated country records are based only on those specimens; if in the literature the species was reported from other countries, those records are not included in the lists. For literature-assigned species (Lit. Att.), all the published country records are included.

Here I emphasize three general points about all putative name-bearing types. First and most important, it is essential that data in the original description be compared with the data accompanying the presumed type(s). The next two points follow from the first. Second, just because a specimen is labeled as a type does not make it so. The act of designating a type is accomplished only in publication and the code specifies the requirements of that act (ICZN, 1999: Articles 73–75). A specimen labeled ''holotype'' might be a syntype. Third, when deciding whether a specimen belongs to the type series, one should ascertain that the data (i.e., locality, date, collector, sex, characters, etc.) in the original description and that accompanying the specimen are concordant. If they are not, reconciliation or explanation of the discrepancies is appropriate. This last point seems to be overlooked in some lectotype designations wherein the lectotypic locality differs from that in the original description. However, having stated this, it is also the case that for species described long ago, in the 1700s and much of the 1800s, the types are often poorly labeled and the task of identifying them

objectively as the original specimens is often formidable. Johannes Frisch (2009) published a cautionary essay concerning the difficulty of determining the syntypes of a species described by Hochhuth in 1849 and that discussion serves as an example of some of the problems encountered in historical collections.

Abbreviations for Species Assignments (alphabetical order)

H Holotype

Holotypes are designated only by the author in the original publication (Article 73.1). A specimen labeled as holotype or type and stated to be such in the original description is the holotype by original designation (Article 73.1.1). A specimen stated or implied in the original publication to be the only specimen examined is the holotype by monotypy (Article 73.1.2), but the provision that a specimen implied to be the only one examined can be difficult to apply. The last sentence of Article 73.1.2, which states that for a taxon "established before 2000 evidence derived from outside the work itself may be taken into account to help identify the specimen" [on which the species is based], can be similarly fraught with difficulty. Furthermore, if an author states that a specified individual is the type or that only one specimen is known or was studied, but in the depository that specimen is not labeled as type it is nonetheless the type, one need only find and authenticate that specimen. The code includes two other means by which a holotype is designated (articles 73.1.4 and 73.1.5) that were not used herein. Caution is advisable whenever one finds specimens, particularly historical ones, labeled as a name-bearing type. The fact that a specimen has a type label does not conclusively make it part of the type series. Similarly a specimen with a holotype label is not necessarily validly designated. Long ago some curators of some collections attached a holotype (or type) label to the first specimen of the presumed type series, but if the type was not designated in the original description it is not a holotype; it may be a syntype. In some collections all of the specimens of a species are grouped together, both original ones and those collected subsequently, so distinguishing the type series is mandatory, but difficult to do if the specimens are not labeled or are poorly labeled. A curator might publish a list of types in their care with some names stated to be represented by holotypes. If examination of the original description for such a name reveals no such designation then the use of the word "holotype" may be an inadvertent lectotype designation under provisions of Article 74.6.

L Lectotype

A syntype selected after the original description as the name-bearing specimen is a lectotype, but simply labeling a specimen as lectotype is insufficient; the designation must be published. After 1999 a valid lectotype designation must include an explicit statement of deliberate designation (ICZN, 2003: 263). To emphasize an earlier point, the label data with the specimen should be concordant with the originally published data; if it is not, then the discrepancies need be discussed.

Lit. Att. [ ]
Literature Attribution ["Country distribution cited within brackets"]

Species that I have not examined are included in the lists of Species Included and Material Examined, but the generic assignment is based on the most recent attribution in the literature. These articles were often published by specialists with broad, deep knowledge of staphylinids, but nonetheless the placements should be corroborated by examination of type material. Included in the square brackets are the countries from which the unexamined species are reported in the literature.

P Paratype
Pl Paralectotype
sp Specimen

It was impossible to examine types of all species so specimens identified subsequent to the original description are included here. Most of these specimens were determined by knowledgeable staphylinid specialists; however, the placements should be verified by examination of name-bearing types.

Syn Syntype

Syntypes are the specimens of a type series for which no holotype was designated; they remain syntypes until a lectotype is designated (Article 73.2). They are often labeled as cotypes or types. If they are not labeled as types, but it can be determined that they are part of the type series, then they are syntypes. A single specimen of a species labeled "Type" or "Typus" and not stated in the original description to be the only

specimen examined is a syntype. Even a specimen labeled as holotype or unique is a syntype if in the original publication there was no designation or statement that it was the only specimen. To emphasize the point, the label data with the specimen(s) should be concordant with the originally published data.

Syn? Syntype?

Specimens labeled as type or cotype for which the label and published data differ and thereby their status as part of the type series is uncertain.

Abbreviations for Collections

AMNH	American Museum of Natural History, New York
BMNH	The Natural History Museum, London
FMNH	Field Museum of Natural History, Chicago
GdRC	Guillaume de Rougemont Collection, Londinières, France
IRSN	Institut Royal des Sciences Naturelles, Brussels
MNHB	Museum für Naturkunde, Berlin
NHMW	Naturhistorisches Museum, Wien
MRAC	Musée Royal de l'Afrique Centrale, Tervuren
SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg

TAXONOMY

Procirrina Bernhauer and Schubert

Procirrina Bernhauer and Schubert, 1912.

— Arnett, 1963: 243, 267 (characters; genera of the United States). — Fagel, 1971: 11 (characters; revision of African species). — Blackwelder and Arnett, 1974: 48 (checklist; North America, Central America, West Indies). — Newton and Thayer, 1992: 62 (subtribe of Pinophilini). — Newton et al., 2000: 328, 389 (characters; genera in North America; notes). — Navarrete-Heredia et al., 2002: 293 (characters; general notes; genera and species of Mexico). — Smetana, 2004: 623 (Palaearctic catalog).

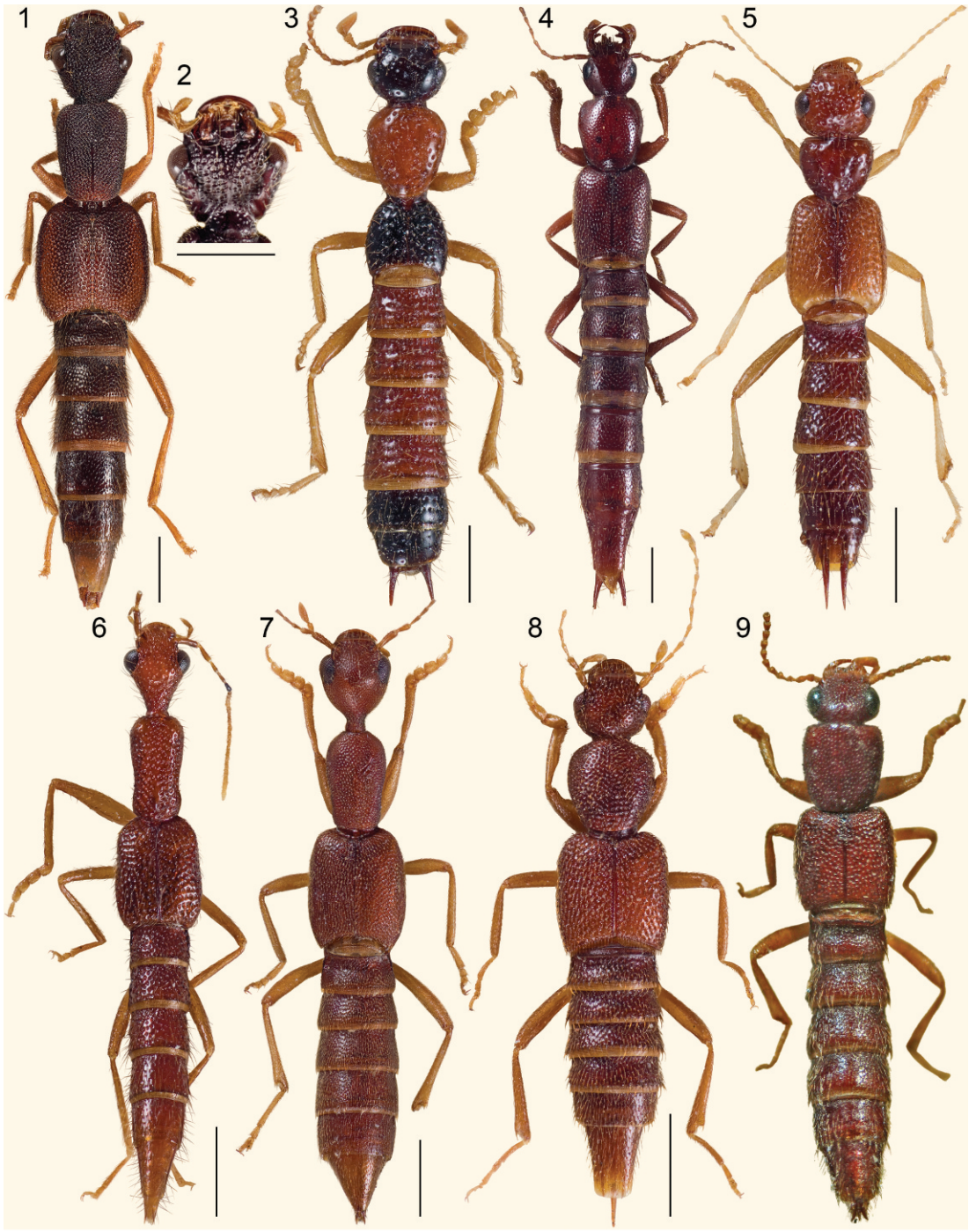
Procirri Bernhauer and Schubert, 1912: 197 (genera included: *Procirrus, Eucirrus, Oedodactylus, Palaminus, Oedichirus*). Type genus: *Procirrus* Latreille, 1829: 436.

— Leng, 1920: 100 (North American catalog). — Blackwelder, 1944: 130 (checklist for Latin America). — Coiffait, 1978b: 323 (characters; genera and species of Palaearctic Region). — Newton and Thayer, 1992: 62 (type genus). — Outerelo and Gamarra, 1985: 20, 21 (characters; key to genera of Iberia Peninsula).

DIAGNOSIS: The Procirrina are separated from all other Paederinae except the Pinophilina by the enlarged, securiform (fig. 71) or fusiform (fig. 56) maxillary palpomere 4. The genera of the Procirrina have the first three (fig. 89) or four (figs. 59, 92) tarsomeres inflated and that character will separate them from the Pinophilina and all other genera of the subfamily. Abdominal segments IV to VII lack paratergites in the Procirrina (fig. 26). The tergum and sternum of each of segments IV to VI are fused and each segment is cylindrical in the Procirrina. In the Pinophilina segments IV to VI each have paratergites and the tergum and sternum of each segment are separated.

Other features that help define the Procirrina are the emargination of the posterior margin of the conjoined elytra (figs. 1, 3, 5) and the apically expanded metatibia (fig. 39), which has a comb on both sides of the apex. The procoxae are long and strongly exserted from the procoxal cavity. Finally, the mesospiracular peritremes are enlarged and fused medially, forming a large plate (figs. 17, 19, 54, 80) that is fused to the furcasternum and to the hypomeron, so the procoxal cavities are closed posteriorly.

DESCRIPTION: Head elongate (figs. 6, 7) to transverse (fig. 77). Neck not petiolate, nuchal constriction shallow to moderately deep. Occiput gradually expanded posteriorly, without longitudinal carinae. Gena not expanded laterally. Eyes without setae (figs. 10, 15); posterior margin rounded; posteroventral margin rounded to slightly flattened. Dorsal surface without carinae. Head without trichobothria. Antennomere 1 straight, not geniculate, and slightly shorter to slightly longer than antennomeres 2 and 3 combined. Mandibles with one denticle near middle (figs. 56, 98); prostheca present (figs. 56, 79, 98). Maxillary palpomeres 2 and 3 gradually



Figs. 1–9. Habitus, scale bar = 1 mm. **1.** *Neoprocirrus* sp. **2.** *Neoprocirrus* sp., Head, ventral. **3.** *Oedichirus paederinus*. **4.** *Oedodactylus fuscobrunneus*. **5.** *Palaminus nigrosuturalis*. **6.** *Paraprocirrus miricornis*. **7.** *Procirrus lefebvrei*. **8.** *Pseudoprocirrus arrowi*. **9.** *Stylokyrtus errans*.

expanded apically (figs. 57, 95); palpomere 4 enlarged, securiform (fig. 81, 95) to fusiform (fig. 57), compressed, pubescent, without transverse suture, and longer than palpomere 2 or 3. Labial palps three, segmented (figs. 13, 69, 83, 94). Ligular sclerite present (figs. 83, 94). Mentum (figs. 69, 83) transverse; surface without tumescence. Labrum not fused to frontoclypeal margin; anterior margin emarginate (figs. 55, 84); surface without median carina; denticles and lobes without spinelike setae.

Prothorax widest anteriorly. Pronotum without trichobothria; surface without carinae. Postprocoxal lobe without row of setae on ventral edge. Basisternum narrow anterior to coxae, without transverse carina, and with intercoxal carina. Furcasternum moderately long; apicolateral margin fused to mesospiracular peritreme (figs. 17, 19, 54); surface with median, intercoxal carina. Mesothoracic spiracular peritremes enlarged, strongly sclerotized, fused medially to one another, anteromedially to furcasternum, and laterally to hypomeron (figs. 17, 19). Procoxal cavity closed posteriorly by enlarged mesospiracular peritreme (figs. 70, 80). Elytral epipleural ridge absent; punctation uniform, not arranged in rows (figs. 11, 14); posterior margin of conjoined elytra emarginate (figs. 1, 3, 5). Mesosternal-metasternal suture present and poorly to moderately developed. Mesendosternite straight and slender. Metendosternite forked.

Procoxa elongate, nearly as long as femur, and strongly exserted from cavities. Profemur without comb of closely spaced setae on ventral edge; ventral edge with ridge or fissure near middle (figs. 36, 40). (Note: It may be that all procirrines have a slit or fissure, but because the slit is usually closed in dried specimens and because of the small size of the animals, the slit is difficult to see and the ridge may have a fissure.) Protibia with diagonally transverse combs on ventral surface (fig. 35); ctenidial depression feeble or absent. Protarsomeres 1–3 (fig. 89) or 1–4 (fig. 59) inflated; ventral surface of enlarged protarsomeres without setose pad, but with slits, setae, and processes (figs. 41–43, 45, 46); tarsomere 4 not expanded beneath 5 and apical margin entire, not bilobed (figs. 76, 89); tarsomere 5 of normal form, slender basally and expanded apically (figs. 59, 92). Mesotibia without spinelike setae. Metatibia expanded apically; spinelike setae absent along length; apex with comb on both sides (fig. 39); combs long and diagonally oriented. Mesotarsomeres and metatarsomeres 1–4 slender, not bulbous (fig. 50); mesotarsomere and metatarsomere 1 longer than others, as long as to longer than combination of tarsomeres 2 and 3, 2–4, or 2–5; tarsomeres 1–3 pubescent beneath, but without setose pad; tarsomere 4 extending beneath tarsomere 5, apical margin entire to feebly emarginate, dorsal surface deeply impressed medially (figs. 50, 51), and ventral surface with setose pad (figs. 48, 49); tarsomere 5 inserted at base of tarsomere 4 (fig. 51, arrow).

Abdominal segment III with or without paratergites; paratergal carina present in absence of paratergite (figs. 23, 26); tergum and sternum fused (fig. 23) or separated. Segments IV to VI without paratergites (fig. 26); tergum and sternum of each segment fused. Segment VII without paratergites; tergum and sternum separated or fused (fig. 33); palisade fringe of posterior margin absent (fig. 33). Segment VIII without paratergites and tergum and sternum separated. Sternum II (fig. 22) narrow, fused to III, and with midlongitudinal ridge; posterior margin with row of setae. Sternum III (figs. 22, 27) with median intercoxal carina; base with transverse ridge; surface with sublateral ridge extending posteriorly from transverse ridge (figs. 22, 27). Tergum IX fused medially (figs. 61, 65, 99, 103). Tergum X (figs. 73, 103) present and largely exposed, covered only slightly laterally and basally by tergum IX; fused to tergum IX in one genus (fig. 87).

DISCUSSION: This distinct, easily identified group has been segregated for only about 100 years. Initially nine genus-group names, five valid genera (including a homonym replaced later), one valid subgenus, and three synonyms were included in the Procirrina. After 1912 only five more names were added, a replacement name, two genera, and two subgenera. In the last 100 years the number of species has increased by more than four times and many more remain to be described. Few specimens of most species are known. The habitat of the group is poorly known,

but most species are probably collected from leaf litter and ground debris and some are found in bushes and trees.

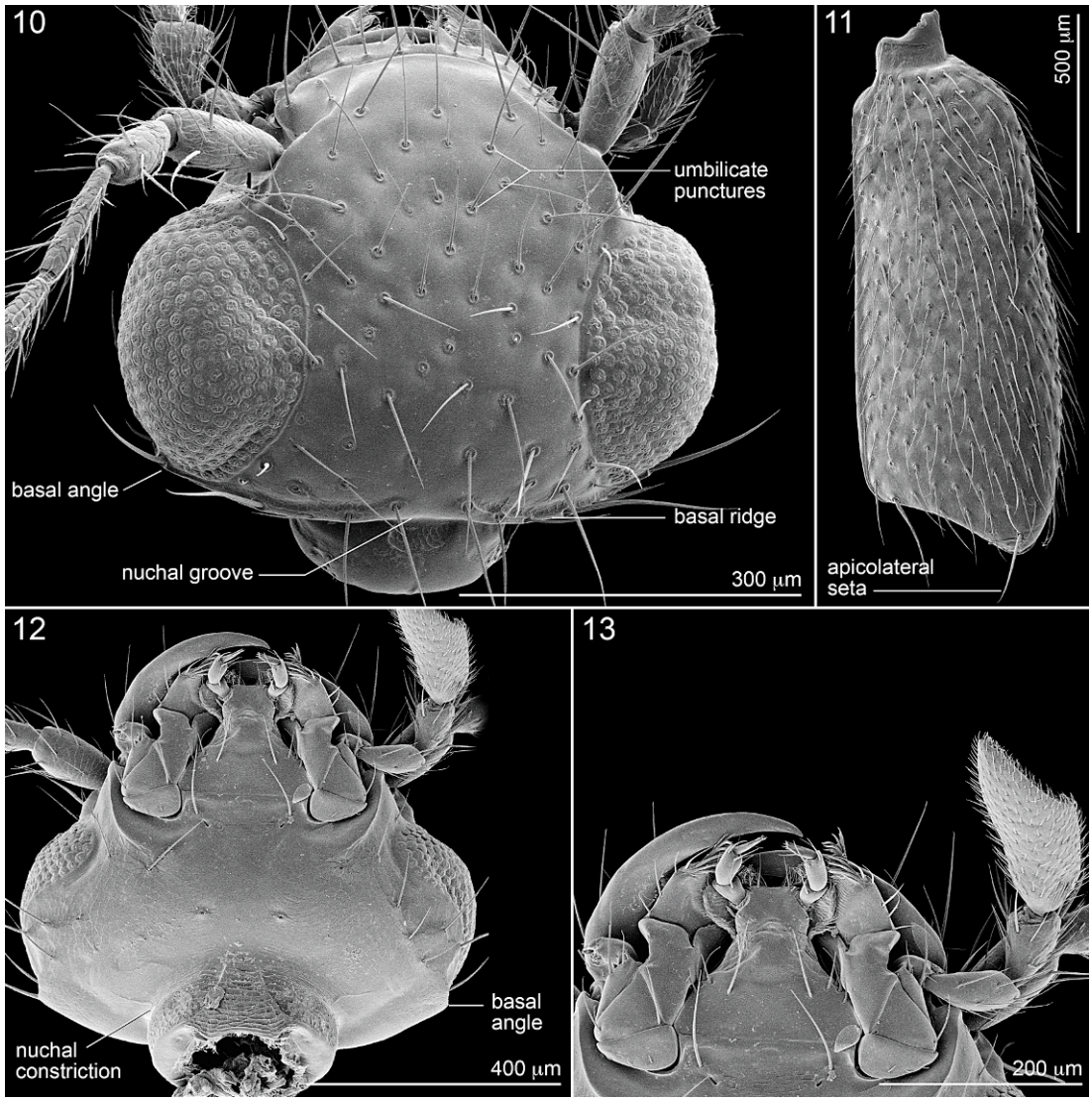
Morphology of the Procirrina

The following is a general discussion of the morphology of the Procirrina. A few structures require a slightly more general treatment to orient the reader or because they have been misinterpreted.

COLOR: Among all the Procirrina only some species of *Oedichirus* and one or two of *Procirrus*, *P. bicolor* and perhaps *P. allardianus* (see Fagel, 1971: 42), have "colorful" bodies. Many of those species resemble a color pattern common to many species of *Paederus* with the head, elytra, and apical abdominal segments black and the prothorax and basal abdominal segments orange to reddish orange (fig. 3); they are possibly mimics of *Paederus*, some of which carry toxins produced by an endosymbiotic bacterium of the genus *Pseudomonas* (i.e., Kellner, 2002a, 2002b; 2003). Many species of *Oedichirus* have dark tibiofemoral maculations, others do not. Most species of *Oedichirus* and those of the other procirrine genera run the gamut from black to brown to reddish brown to yellowish brown in various combinations.

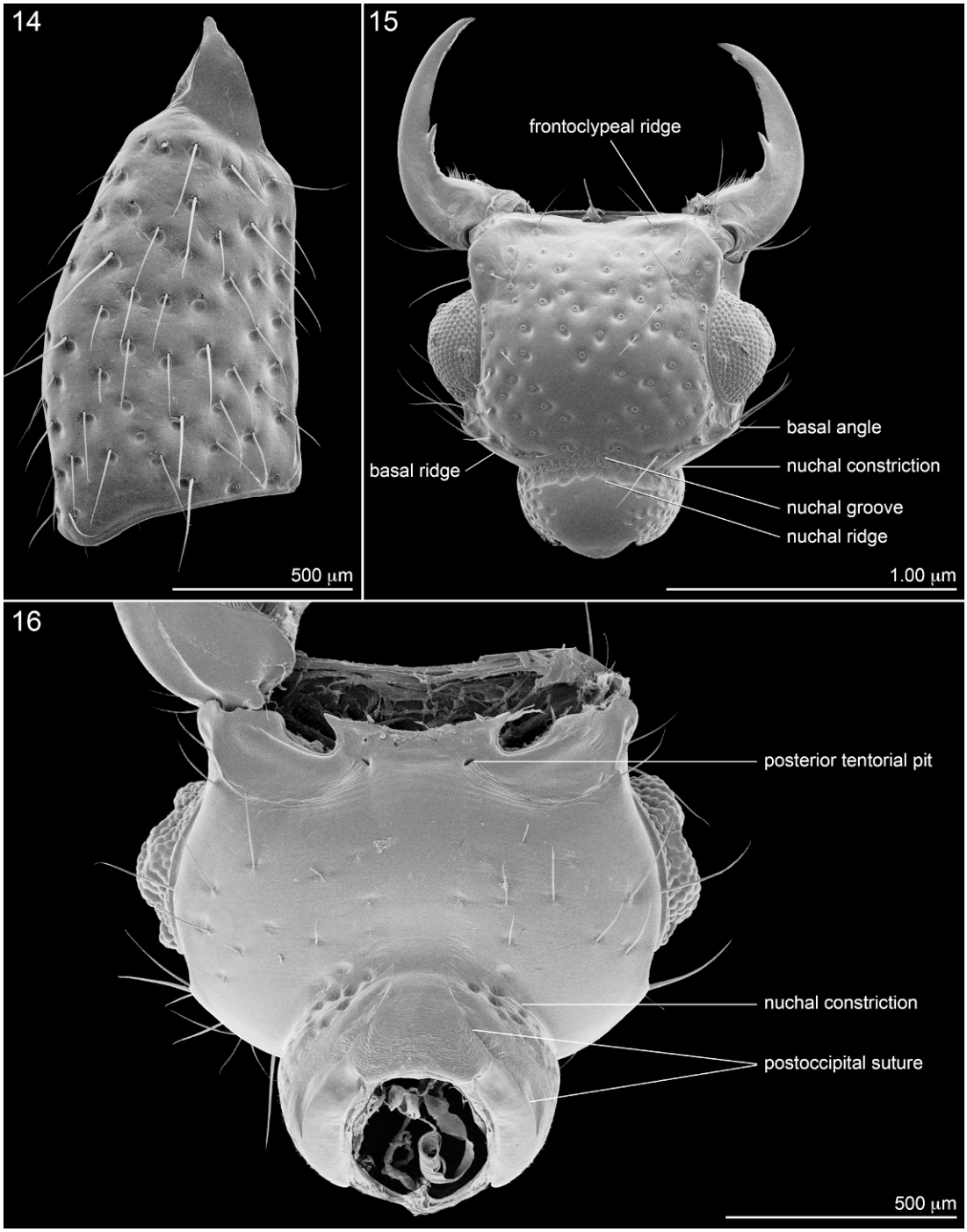
PUNCTATION: Punctation is significant and diverse within the Paederinae. Procirrina punctational types may be asetate or setate and the latter are simple or umbilicate. In the revisions of other subtribes other types of punctures will be described and illustrated. Setate punctures have a seta, asetate punctures have none (fig. 17). Simple punctures are depressions, without walls, with a seta that extends from a socket, usually near the center. Umbilicate punctures are depressions without walls from which arise a seta that is on a bump or surrounded by a microridge; each puncture resembles a navel, is well separated from others, and the seta is near the center (fig. 18). Reticulate punctures are close together, have a seta near the middle of a depression, and are bordered by a vertical wall or ridge that is shared with adjacent punctures; the puncture varies from shallow to moderately deep. These types of punctures can intergrade and individuals can have more than one type. Simple punctures are found on the head of *Stylokyrtus* and umbilicate punctures on the head and pronotum of most other genera (figs. 10, 15, 18). Reticulate punctation, which is not illustrated for the Procirrina, but will be for other subtribes, is mixed with umbilicate punctures on the head of *Paraprocirrus*. Most punctures are setate, but asetate ones are common. The size and depth of punctures vary. Coarse punctation is comprised of large, deep punctures, fine punctures are shallow and small. Punctational density varies, but density is difficult to quantify. Large, coarse punctation includes fewer punctures per unit area than fine punctation. The seta is at or near the center (figs. 10, 15, 18) or at the anterior of the puncture (figs. 14, 22, 23), but the latter position is difficult to discern in small individuals without using the SEM.

HEAD: The head of most of the procirrine genera is wider than long, the postocular lateral margins are moderately long and curved to rounded basal angles (*Oedodactylus*; fig. 77), short and nearly straight to strongly angulate basal angles (*Oedichirus*; fig. 15), or broadly rounded to the neck (*Oedodactylus fuscobrunneus*, *Pseudoprocirrus arrowi*; figs. 4, 8). The head of *Pseudoprocirrus arrowi* is more or less orbicular (fig. 8). The postocular lateral margins of many *Palaminus* are short (fig. 90), in some species barely discernible (fig. 10), and straight, and the basal angles sharply angulate in most species (fig. 12); the acute basal angles are the lateral ends of a transverse carina or ridge (figs. 10, 12) along the basal margin of the head. In *Paraprocirrus* the head is longer than wide and the postocular lateral margins are long and converge to the neck (fig. 6). *Procirrus* has a pedunculate head (figs. 7, 52, 53) that is wide anteriorly and tapers from the eyes directly to the neck, but before reaching the neck the constriction is more gradual and the head appears to be on a slender, slightly tapered pedicel. The head of *Neoprocirrus* is about as long as wide and the postocular lateral margins are long and converge posteriorly to poorly developed basal angles (fig. 1). The gular sutures are separated in all genera except *Procirrus* in which they are confluent posteriorly (fig. 53); some species of *Oedichirus* and *Palaminus* lack them or they are feeble (figs. 12, 16).



Figs. 10–13. *Palaminus* sp. (Costa Rica). **10.** Head, dorsal. **11.** Elytron, right. **12.** Head, ventral. **13.** Labium and maxilla, ventral.

The neck, the constricted base of the head, is comprised of an occiput, occupying most of the neck, and postocciput. The postocciput is a narrow sclerite surrounding the occipital foramen and separated from the occiput by the postoccipital suture that continues ventrally and extends anteriorly as the gular sutures (figs. 16, 91). The neck is separated from the head anteriorly by a transverse groove or constriction (figs. 15, 16). Generally the Paederinae, including the Procirrina, lack the abundance of cephalic ridges described by Smetana and Davies (2000), but many paederines do have a transverse carina or ridge on the dorsal surface that extends onto the lateral surface. Smetana and Davies (2000: 5, 8) discussed and illustrated a similar carina that they referred to as the *nuchal ridge*. They go on to explain that in most Quediina the nuchal ridge joins with the infraorbital ridge, which extends to near the mandibular articulation (Smetana and Da-

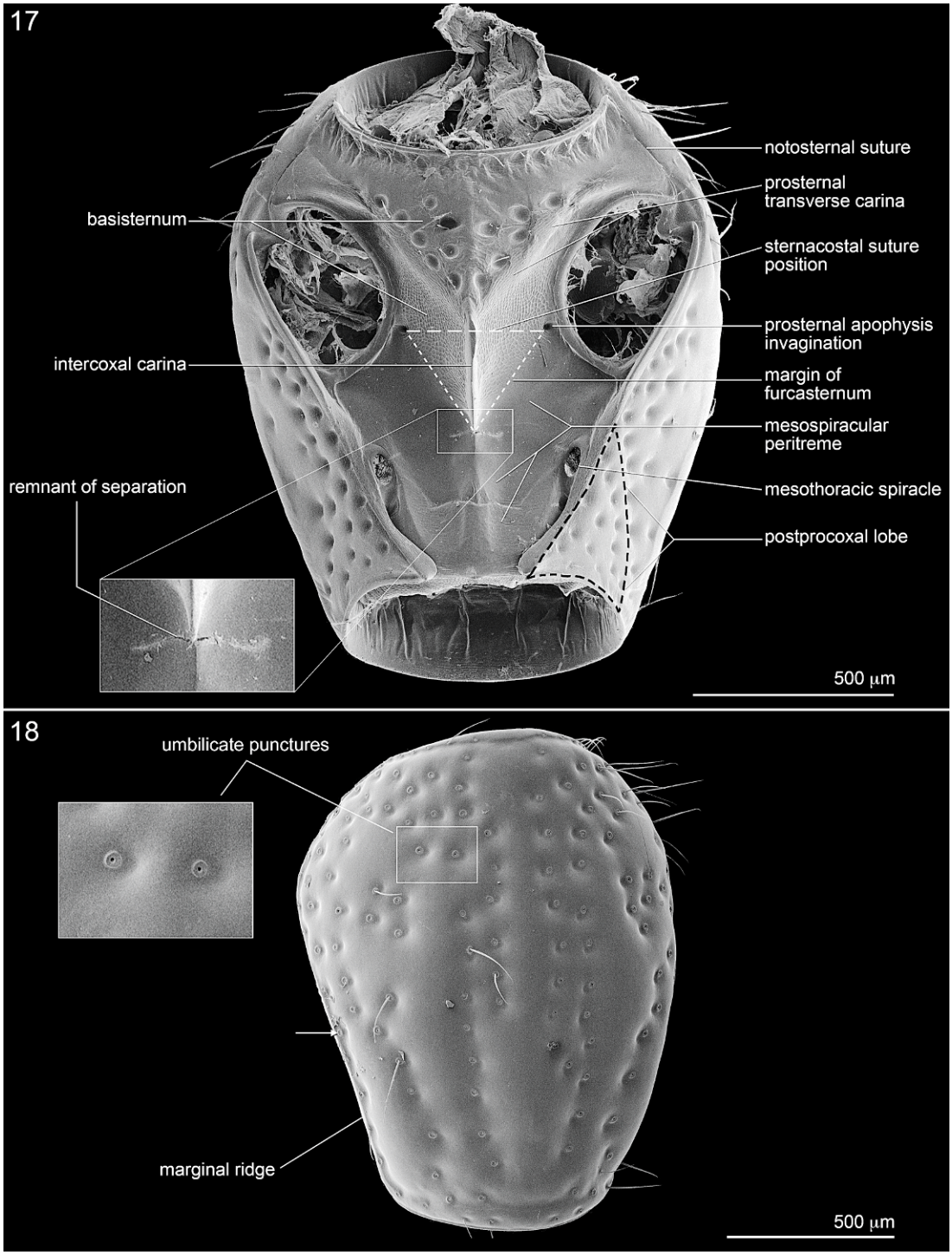


Figs. 14–16. *Oedichirus geniculatus*. **14.** Elytron, left. **15.** Head, dorsal. **16.** Head, ventral.

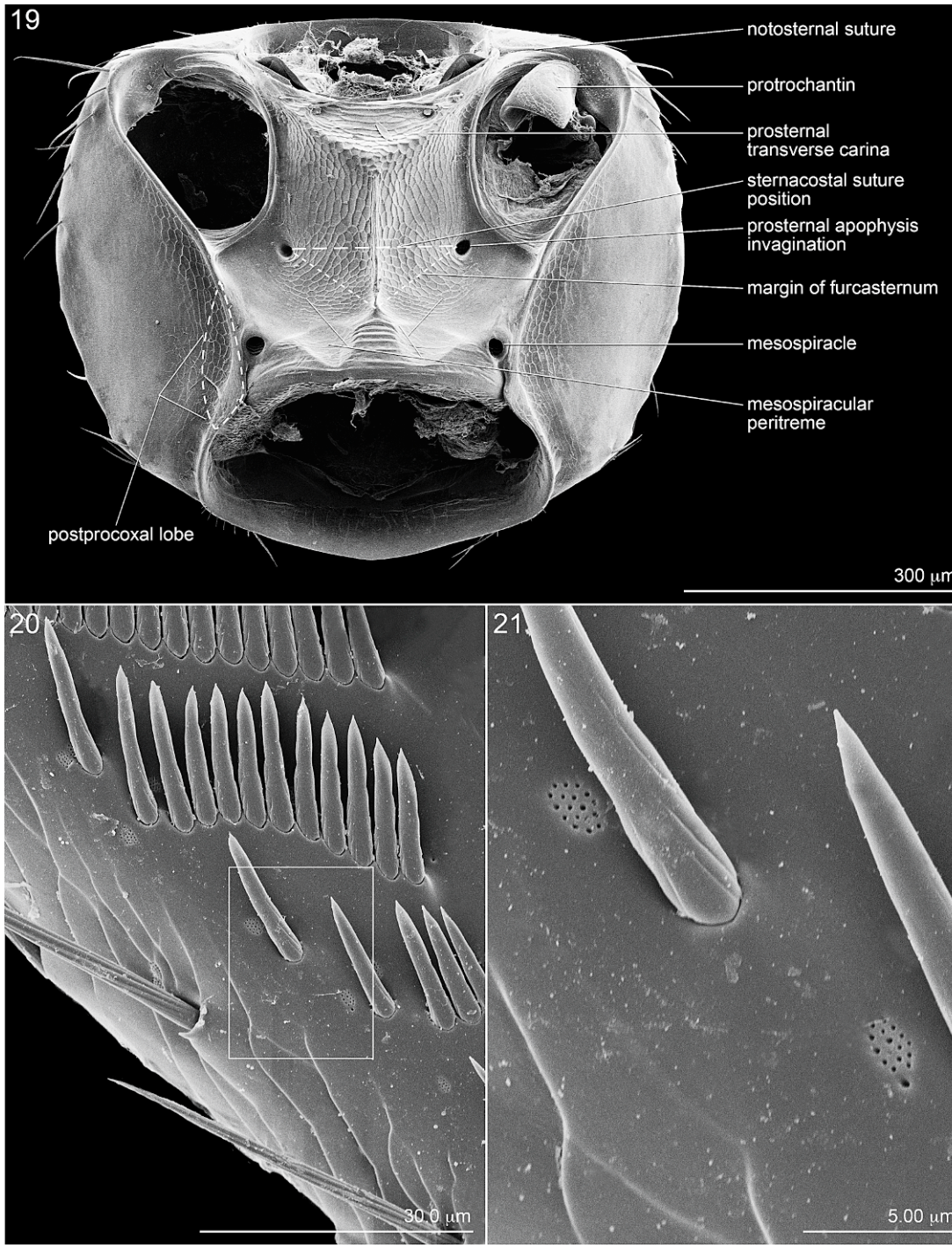
vies, 2000: 8 and fig. 1). The ridge that results from the merging of the nuchal and infraorbital ridges fits a definition of an occipital suture (Snodgrass, 1935: 128), so it is possible that this transverse ridge on the neck of paederines is a remnant of the occipital suture. However, *nuchal ridge* has a continuing history of use for this carina in the family and is a neutral, descriptive term that does not suggest homology with the occipital suture. Since the position and form of the ridge in the Paederinae is similar to that in the Staphylininae and since no particular evidence is known that the carina is in fact part of the occipital suture, the carina is referred to as the *nuchal ridge* or *carina* for the Paederinae (fig. 15). The constriction that separates the neck from the head has been referred to as the *nuchal constriction* (Smetana and Davies, 2000: fig. 1). The nuchal constriction is present dorsally (fig. 15) as a transverse groove that often extends laterally and ventrally (fig. 16). The transverse dorsal groove is absent to shallow, feeble to deep, strongly developed in the Paederinae, and referred to herein both as the *nuchal groove* and *nuchal constriction* (fig. 15). The width of the neck, measured across the nuchal constriction, is diagnostic in some Paederinae. In the Procirrina the neck is narrow (*Paraprocirrus*, *Procirrus*; figs. 6, 7) to wide (*Oedichirus*, *Oedodactylus*; figs. 66, 78), the nuchal constriction is shallow to moderately deep, and the nuchal ridge is present or absent.

In most Paederinae, maxillary palpomere 4 is glabrous, short, less than the length of palpomere 3, slender, and conical, or acicular and parallel sided, and in some taxa, minute. In the Procirrina, maxillary palpomere 4 is robust, enlarged, pubescent, compressed, and securiform (figs. 71, 81, 95) or fusiform (fig. 57). The surface across the transverse apex of a species of *Oedichirus* is covered with stubby, blunt sensilla, possibly sensilla basiconica (fig. 30 and inset). No specimens of the other genera were available for SEM study of the fourth palpomere. The anterior margin of the labrum has a median emargination and one to three pairs of denticles (figs. 72, 97) or a submedial lobe on each side of the emargination (fig. 84). The antennae are long and slender. Unique to *Oedichirus*, antennomere 11 has a spiniform pencil of stout, flattened setae apically (fig. 31); this pencil may function to wick a secretion from the surface, but as yet there is no evidence that secretory glands exist in the antennomere. The members of the pencil can separate (fig. 32). The pencil was first reported by Sahlberg (1847: 803) and later discussed by Sharp (1876: 338, 339), who wrote that the pencil was partly ''retracted'' into the body of the antennomere. Sharp studied dried specimens and indeed the pencil can be found retracted in some dried specimens, but it is unclear, perhaps doubtful, whether this withdrawal occurs in living individuals. If found only in dried specimens and not in live ones, then the retraction is an artifact of the drying and collapse of the less strongly sclerotized apex of the antennomere. The apex of antennomere 11 also has basiconic-like sensilla (fig. 32 and inset). Antennomere 11 is elongate in *Paraprocirrus* and *Neoprocirrus*; in the former it is as long as the preceding three to nine antennomeres combined and in the latter as long as the preceding two to seven. Elongation of antennomere 11 in the subfamily is uncommon.

THORAX: With the exception of *Palaminus*, the prothorax is longer than wide (figs. 54, 66) in most species. In *Palaminus* it is wider than long (fig. 90) to slightly longer than wide (fig. 5); in some *Oedodactylus* it is as wide as long (fig. 77), in other species longer than wide (fig. 4). In most genera the width is greatest near the anterior third or fourth and the lateral margins converge posteriad. In *Paraprocirrus* the lateral margins are sinuate and only modestly convergent posteriorly (fig. 6). Punctation among and within genera varies in distribution and density, as does the surface texture. The pronotal marginal ridge (fig. 18) is absent in *Procirrus*, most species of *Palaminus*, and some of *Oedichirus*. Species of the other genera, including most of *Oedichirus*, have a marginal ridge and in most punctures touch the ridge (fig. 18, arrow). Ventrad of the marginal ridge is the hypomeron, which extends from the anterior to the posterior prothoracic margins. Anteriorly the hypomeron is narrow and limited ventrally and anteriad of the procoxal cavity by the notosternal suture, which is moderately to poorly developed or absent; in *Palaminus* it is



Figs. 17–18. *Oedichirus geniculatus*. **17.** Prothorax, ventral; inset: apex of intercoxal carina. **18.** Pronotum; arrow to punctures contiguous with marginal ridge; inset: enlargment of punctures, setae missing.



Figs. 19–21. *Palaminus* sp. (Costa Rica). **19.** Prothorax, ventral. **20.** Protibia, ctenidial surface. **21.** Protibia, ctenidial surface, enlargement of boxed area in figure 20.

short and anterior to the procoxae (fig. 19). Posteriorly, from beside and behind the procoxal cavity, the hypomeron extends ventrally. The ventral edge reaches the posterior margin of the prothorax and that juncture is pointed (figs. 17, 80) or rounded (fig. 19). The postprocoxal lobe (figs. 17, 19) is the ventral half or third of the large, more or less triangular sclerite formed by the piece of the hypomeron behind the procoxa. The form of this lobe varies in the Paederinae and presents a few characters that help define taxa. In *Palaminus* the surface of the postprocoxal lobe is impunctate (fig. 19) and in *Oedichirus* it has dense to moderately dense asetate punctation (fig. 17). The lobe is usually long and apically acute (figs. 17, 80), but is short and the apex rounded in *Palaminus* (figs. 19, 93). In *Procirrus* and *Paraprocirrus* the lobes extend strongly toward the midsagittal line and their apices nearly touch (fig. 54), but in most genera they are moderately to widely separated (figs. 17, 70, 80, 93).

The ventral surface of the prothorax of the Procirrina (figs. 17, 19) is a strongly sclerotized amalgam of four sclerites: a basisternum, furcasternum, and two mesospiracular peritremes. The basisternum extends the width of the ventroanterior surface from one notosternal suture to the other, is narrow in front of the procoxal cavities, and medially, it is long, V-shaped, and extends between (fig. 17), in some species far between (fig. 54), the coxae. An intercoxal carina extends posteriorly from the V-shaped apex of prosternal transverse carina. A short basisternum anterior to the procoxae is common in the subtribe.

The prosternal transverse carina (figs. 17, 19) (= sternacostal suture of Blackwelder [1936: 19], which he erroneously labeled as the prosternal suture in figure 3A; = sternacostal ridge of Smetana and Davies [2000: 5, 11, fig. 54]), borders the anterior and part of the medial edge of the procoxal acetabulum. From that carina the basisternum is inflexed to form the concave, sclerotized sides and partial roof of the coxal acetabulum; it was referred to as the cryptosternum (Hlavac 1972: 126) and erroneously identified as the furcasternum (Blackwelder, 1936: 19; Herman, 1981: 344; Naomi, 1988: 507; Smetana and Davies, 2000: 5, 11; Solodovnikov, 2005: 89, 90). This inflexed region, part of the basisternum, extends posteriorly to and ends at the true sternacostal suture, which, when present, connects the two prosternal apophyses. Paederines usually lack the suture, but the bases of the prosternal apophyses are found at the two pits or fossae or invaginations or prosternal aphophyseal pits on each side of the middle line adjacent to the coxal cavity (figs. 17, 19). They appear as a pair of dark spots on slide-mounted material and line illustrations herein (figs. 70, 80), but as pits in SEM images (figs. 17, 19). Blackwelder (1936: figs. 22, 23) presents them as a pair of black spots and Smetana and Davies (2000: fig. 2) label them as fossae and they are shown, but unlabeled, in their figures 42 and 54.

The prosternal apophyses connected by the sternacostal suture separate the basisternum anteriorly from the furcasternum or sternellum posteriorly (Snodgrass, 1935: 191, 192). The furcasternum is variably developed in the Paederinae, but in most species it is moderately long and tapers to a point. In the Procirrina the apicolateral margins of the furcasternum are indistinguishable because the furcasternum is fused to the mesothoracic peritremes. The limits of the furcasternum can be estimated by drawing a line between the invaginations of the prosternal apophyses (shown by horizontal broken line in figs. 17, 19) and by drawing two others diagonally (shown by the diagonal broken lines in figs. 17, 19), one on each side of the midsagittal line, from the invaginations to the end of the intercoxal carina, which in some species has an incision that appears to be a remnant of the separation of the furcasternum and mesospiracular peritreme (fig. 17, inset). The resulting triangle is the estimated procirrine furcasternum (figs. 17, 19). The furcasternum of most Paederinae is long, but short in most Staphylininae.

The large, strongly sclerotized plate behind the furcasternum and to which it is fused, is formed by the fusion of the medial margins of enlarged mesospiracular peritremes. The plate usually has a broad, low, rounded, median ridge that extends from the apex of the intercoxal carina almost to the posterior margin. The spiracles are in the sclerite near

the hypomeron. The plate is fused laterally to the hypomeron and anteromedially to the furcasternum. Because of the development of the mesospiracular plate, the procoxal cavities are closed posteriorly, a relatively unusual condition in the Staphylinidae. In most staphylinids the mesospiracular peritremes are small sclerites that encircle the spiracles.

The elytra of all species of Procirrina lack an epipleural ridge and the posterior margin of the conjoined elytra is emarginate (figs. 1, 3, 5, 7). Species of *Procirrus*, *Oedodactylus*, *Stylokyrtus*, *Neoprocirrus*, and *Pseudoprocirrus* have a row of setae on the edge of the posterior margin; those of *Oedichirus*, *Palaminus*, and *Paraprocirrus* do not (figs. 11, 14). Species of *Neoprocirrus*, *Pseudoprocirrus*, *Oedodactylus*, most species of *Procirrus* and *Palaminus*, and a few species of *Oedichirus* have fully developed elytra, well-developed humeral angles, presumably fully developed wings, and perhaps can fly. The elytra of species of *Paraprocirrus*, most species of *Oedichirus*, and a few of *Palaminus* are reduced and the humeral angles are absent or diminished, the metathorax is reduced, the flying wings are short, reduced to small pads, or absent, and the species are flightless. The pterothorax is discussed in an article on New World *Oedichirus* (Herman, in prep.).

LEGS: Two notable features of the prothoracic legs are common to all the procirrine species. First, the procoxae are long, about as long as the femora, and strongly exserted from the coxal cavities. Second, the basal three or four protarsomeres are inflated (figs. 44, 59, 89). Some, for example, *Oedichirus*, have an arc-shaped slit on the ventral surface (figs. 45–47) from which extend setae and membranous structures that, despite critical-point drying, remained partly hidden. In others, such as *Palaminus*, the ventral surface revealed little more than a complex, compact cluster of blunt tipped setae and processes; a slit, if present, did not open and the cluster of processes was so impenetrable that other feature could not be seen (figs. 41–43). The ventral protarsal structure of the other genera could not be studied with the SEM. The first four tarsomeres of *Oedichirus* (figs. 44, 76) are large, bulbous, and decrease in size slightly from the first to the last tarsomere. For other genera the more apical tarsomeres tend to be smaller than the basal ones (figs. 89, 92) and in *Pseudoprocirrus* are more elongate, flattened, and narrowed from the basal tarsomere to the third one. *Oedodactylus* (fig. 89) and *Pseudoprocirrus* have three enlarged tarsomeres; the other genera have four. The most apical of the swollen tarsomeres, either the third or fourth, of all genera is asymmetrical and the more slender, distal tarsomere is inserted laterad of the midlongitudinal line. No other paederines have such enlarged tarsomeres. Although I was unable to see the detail desired, based on the variation revealed for *Oedichirus* and *Palaminus*, it is clear that the protarsi are complex, vary among genera, and may provide taxonomic and phylogenetic characters. Of interest would be the examination of the details of variation among and within the genera and what these protarsal modifications have to do with the lifestyle of the animals. Protarsomere 5 of *Palaminus* and *Oedichirus* is densely pubescent ventrally (figs. 42, 45, 47), but sparsely to moderately pubescent in the other genera.

The profemur of Procirrina lacks the comb of closely spaced setae on the ventral edge found in some Paederinae. *Oedichirus geniculatus* has what appears to be a carina or ridge on the ventral profemoral edge, but is a slit that, in dried specimens, is narrow and barely noticeable with a light microscope or not evident at all without a scanning electron microscope (fig. 36). In a specimen of *O. geniculatus* treated for weeks in lactic acid the slit opened to reveal a wide cleft covered by a membrane packed with micropores that may provide exits for secretory glands whose secretions may aid cleansing the antennae and mouthparts. The slit of the first preparation closed during the critical-point drying procedure. Other attempts to prepare specimens to maintain the slit open failed and the slit closed or the membrane broke and internal tissue, muscles, etc., erupted through the gap (fig. 37). In one preparation the slit remained open, the membrane burst, but a piece of it with micropores was visible along the edge of the gap (fig. 38, inset). A slit, found by using the SEM, is also present in *Palaminus* (fig. 40), but was closed; with a

light microscope, only a ridge was visible. The other genera may also have a profemoral slit, but the insufficiency of specimens prevented a search by SEM.

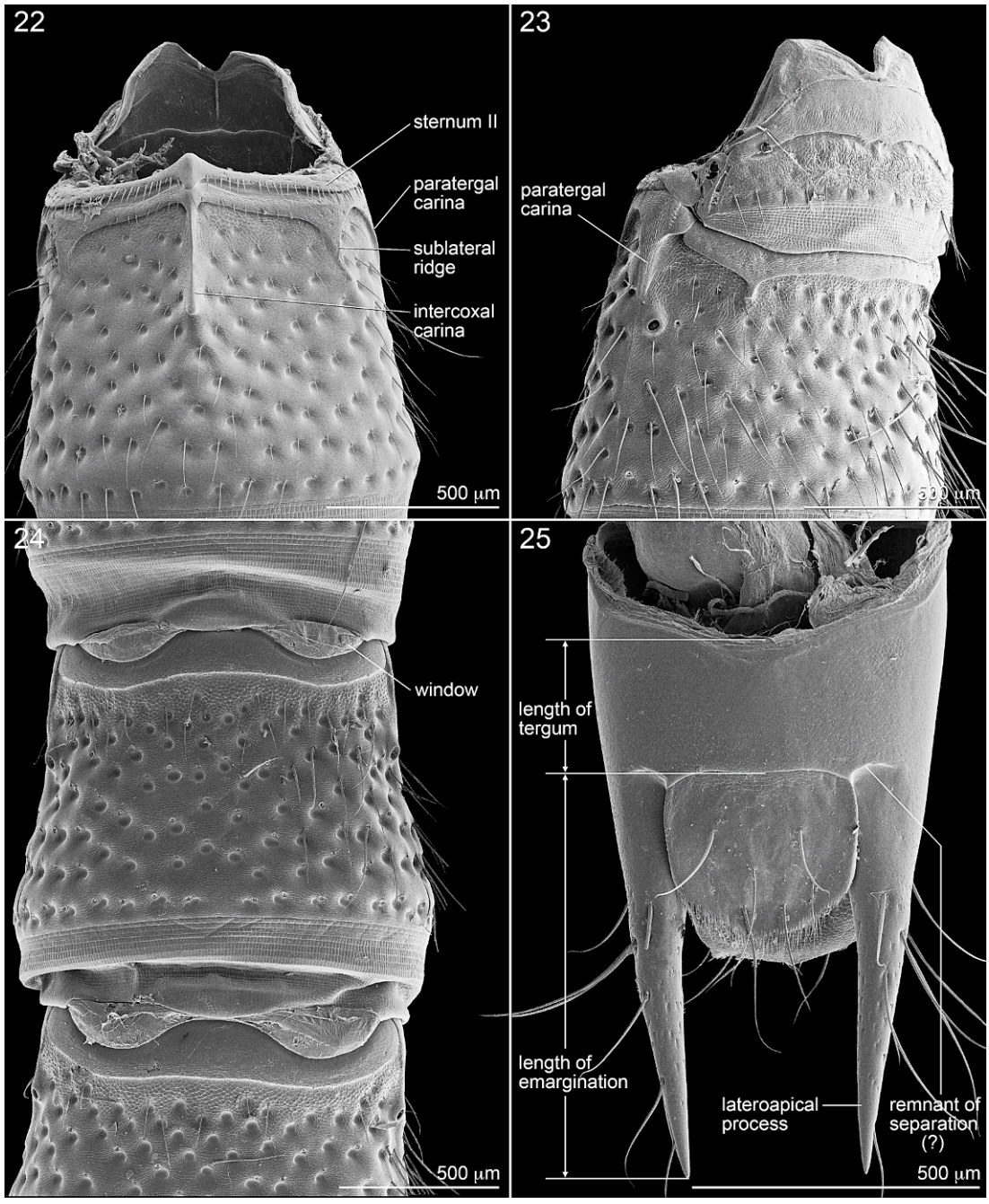
The protibiae of most procirrine species have numerous, diagonally transverse, toiletry combs distributed from near the base to near the apex. Adjacent to one end of these combs in a species of *Palaminus* are clusters of micropores (figs. 20, 21) that were not found in *O. geniculatus* (fig. 35). These pores may also provide secretions for cleaning. The ctenidial surface of the protibia lacks (fig. 35) or has a shallow to feeble (fig. 41) depression. The apical region of the tibia is slender and the diameter more or less similar to the remainder of the tibia in most genera. In *Palaminus* the protibia is gradually expanded apically, so the diameters of the tibial apex and base of tarsomere 1 are approximately the same (fig. 41).

The mesotibia and metatibia are both long and slender, but the latter is expanded and flattened apically. Along the apex of both sides of the metatibia are combs of slender spiniform setae (fig. 39); the combs are diagonally oriented and may be used for both cleaning and wing-folding. The inner comb is shorter than the outer, but both are well developed and the size difference is small. The mesotarsomeres and metatarsomeres are slender and more or less typical of many paederines, but the basal tarsomere of both the middle and hind legs is elongate, longer than tarsomeres 2 or 3 or all of the remaining tarsomeres combined. Tarsomere 4 extends beneath the last tarsomere because tarsomere 5 originates at the base of tarsomere 4 rather than the apex (fig. 51, arrow). The apical margin of tarsomere 4 is feebly emarginate (fig. 51) or entire and the ventral surface has a dense pad of specialized setae in *Oedichirus* (figs. 48, 49).

ABDOMEN: Except for *Palaminus* the abdominal surface of most genera is covered with punctures and fine, hardly visible microsculpturing (figs. 23, 24). *Palaminus* is unique in that the surface of segments III to VI is covered with triangular or diamond-shaped ''cells'' that appear to overlap one another like shingles on a roof (figs. 26–28); this macrosculpturing is referred to as *imbricate* (see Erichson, 1840: 682; Casey, 1910: 197; Cameron, 1931: 1, 21). The surface of each diamond-shaped cell is usually polished, slightly tumescent, and has one apical seta.

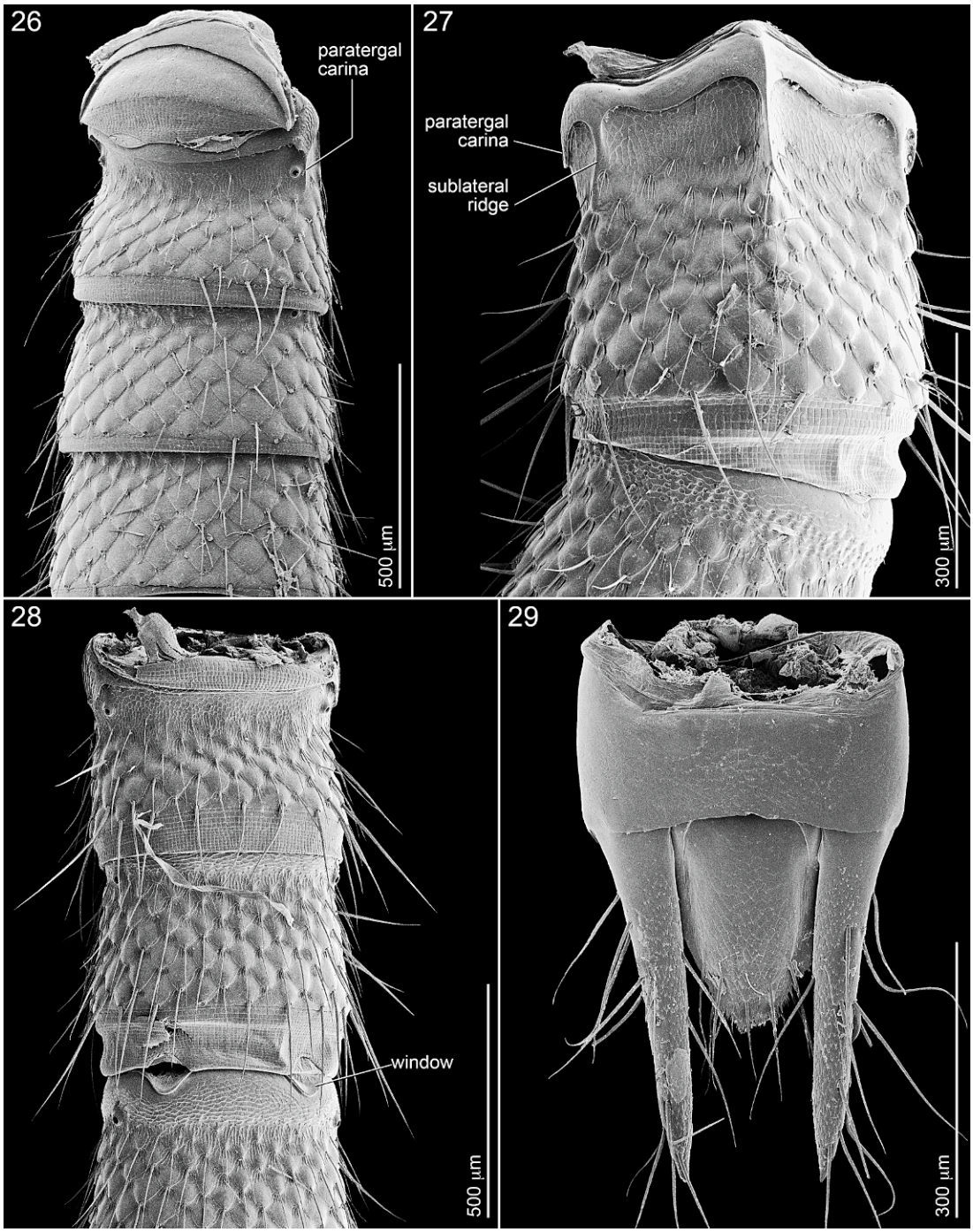
The sclerites of the abdomen have been referred to as *tergite* and *sternite* for the large dorsal and ventral sclerites and paratergites for the narrow sclerites between the dorsal and ventral sclerite by many, perhaps most authors on the Staphylinidae and recently as *tergum* and *sternum* or *tergite* and *sternite* in the same paper (Grebennikov and Newton, 2009: 300). Snodgrass (1935), in his discussion of these sclerites for insects, concluded that the tergal and sternal sclerites are composite structures comprised of the primary, ancestral, median portion along with pieces of the sclerotized intersegmental region, and lateral sclerites. Nonetheless, Snodgrass (1935: 76–78, 82) referred to the ventral sclerite as the *sternum* and the dorsal as the *tergum,* a convention followed herein. Between the tergum and sternum are pleural and other secondary sclerites of the tergal and sternal regions (Snodgrass, 1935: 78–79, 250–251) and following this interpretation of the source of the sclerites between the tergum and sternum, those found there in the Staphylinidae could be part of the sternum or tergum or pleural sclerites. Based on a possible transformation series, it was reasoned that these sclerites were part of the sternum (Herman, 1970: 350). Staphylinid workers often refer to these sclerites as *paratergites* (Blackwelder, 1936; Uhlig, 1989, and numerous taxonomic works), but others have used *lateral plates* (Naomi, 1989a), *parasclerites* (Grebennikov and Newton, 2009), or *paratergite* and *parasternite* based on the position relative to the tergum or sternum (Herman, 1970: 350). Snodgrass (1935: 82, fig. 139) used *paratergite* and *laterotergite* for lateral sclerotization of the dorsum separate from the median sclerite. Inasmuch as the origin of the sclerites between the tergum and sternum in the Staphylinidae is unclear and since the commonly used term *paratergite* simply signifies they are ''beside the tergum,'' it is reasonable to continue using it.

In the Procirrina only segment III has paratergites, one on each side, and then only in *Oedodactylus*, *Pseudoprocirrus*, and some

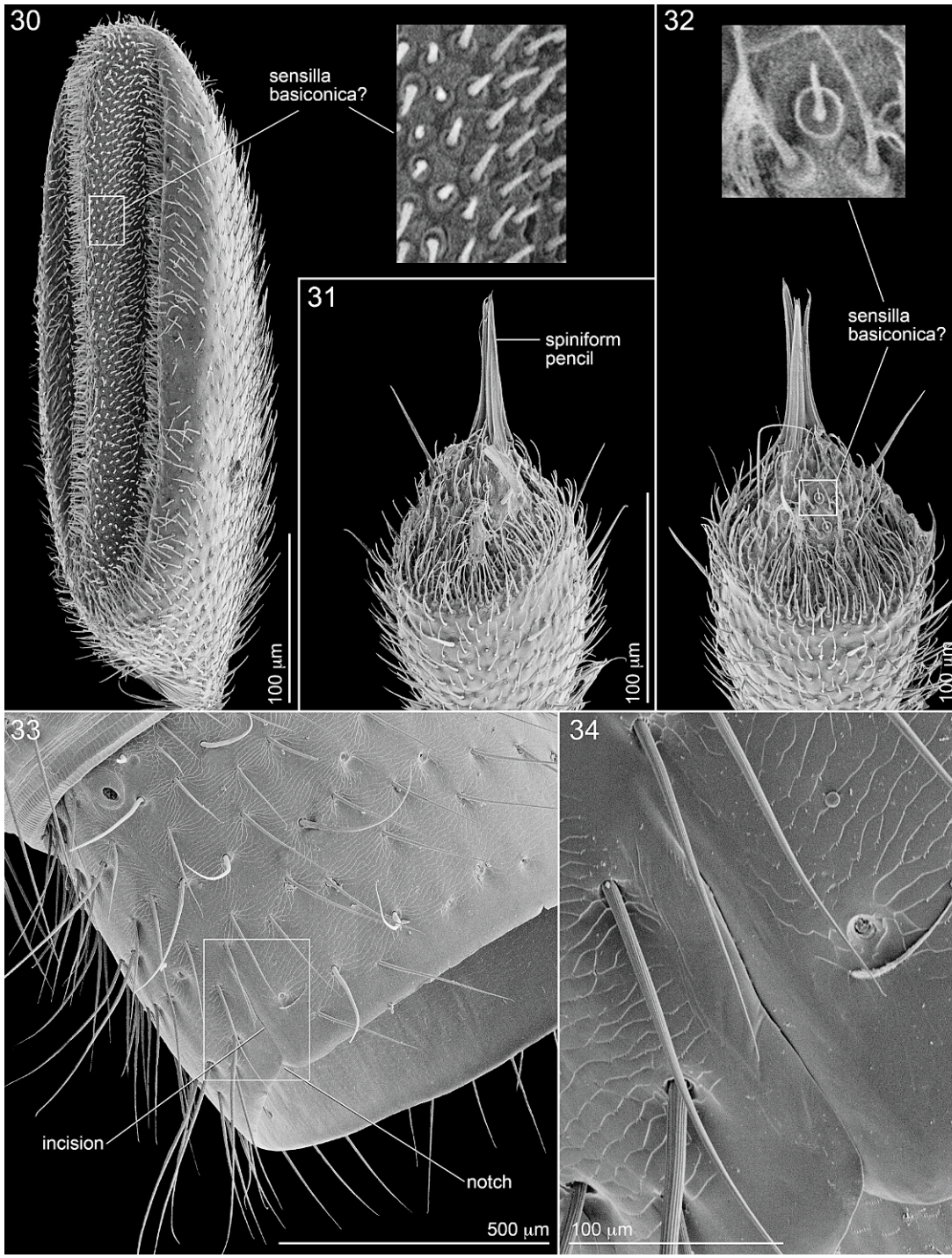


Figs. 22–25. *Oedichirus geniculatus*. **22.** Sterna II and III. **23.** Terga II and III, laterodorsal. **24.** Terga IV and V. **25.** Terga IX and X, male.

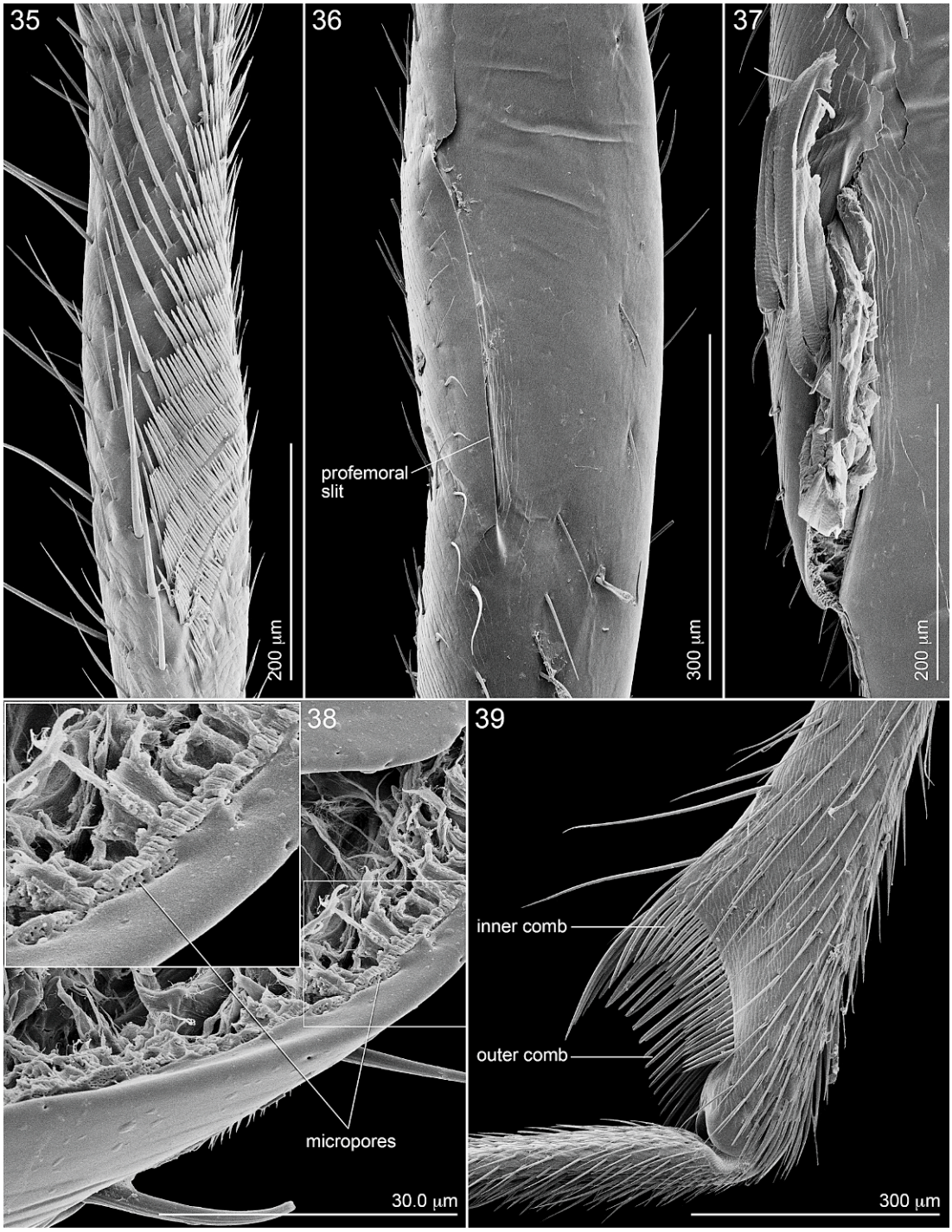
species of *Oedichirus*. Paratergite III is absent in species of the other genera and in most species of *Oedichirus*, which all have instead a paratergal carina (figs. 23, 26). The paratergal carina is adjacent to and ventrad or laterad of the spiracle in the same position as would be the paratergite were it present; it is likely a remnant of the paratergite and/or



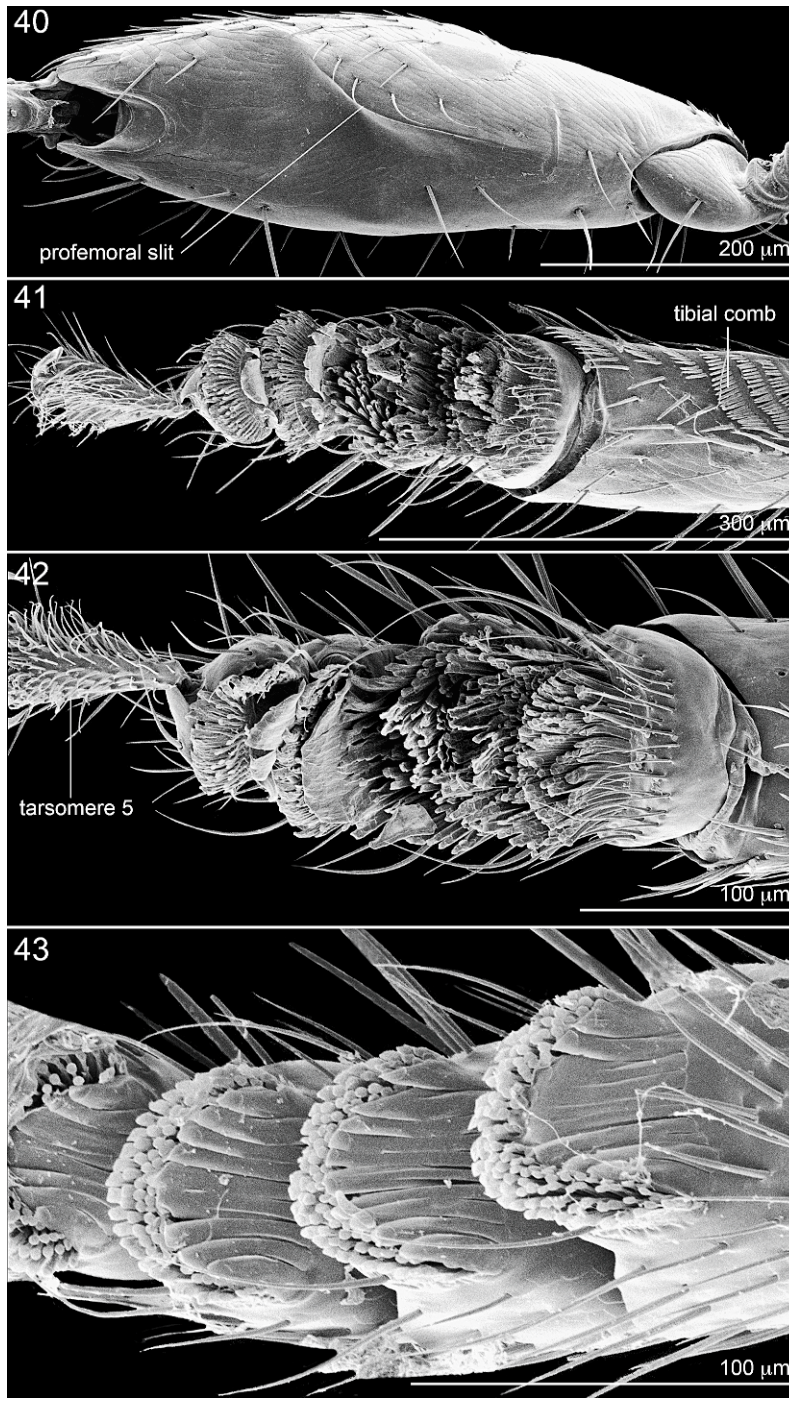
Figs. 26–29. *Palaminus* sp. (Costa Rica). **26.** Terga II–V, laterodorsal. **27.** Sterna II–IV. **28.** Terga IV–VI. **29.** Terga IX and X.



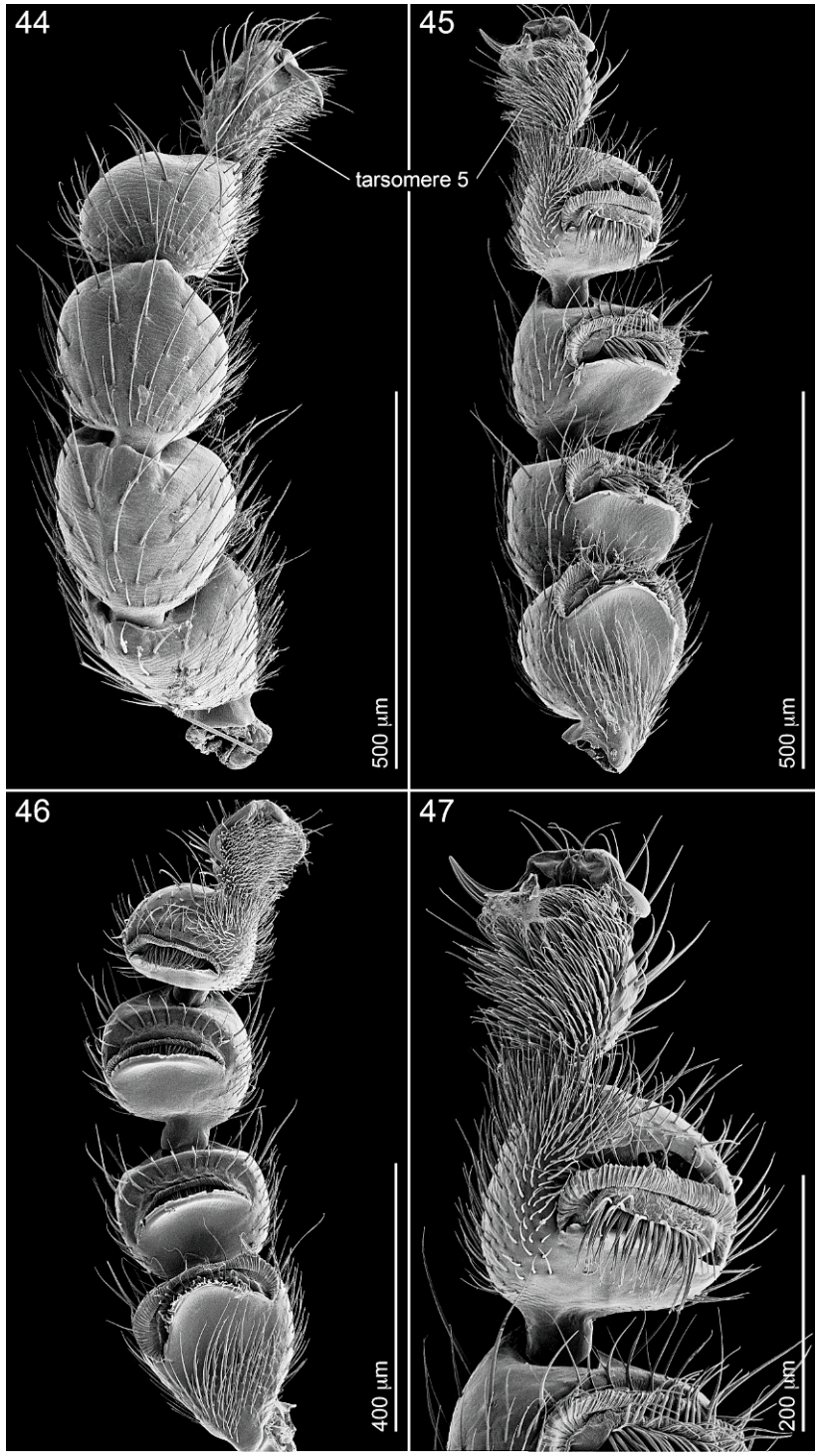
Figs. 30–34. *Oedichirus geniculatus*. **30.** Maxillary palpomere 4, apical surface; inset, sensilla basiconica (?) enlarged. **31, 32.** Antennomere 11; inset: sensilla basiconica (?) enlarged. **33.** Segment VII, laterodorsal. **34.** Segment VII, enlargement of notch and incision in boxed area of figure 33.



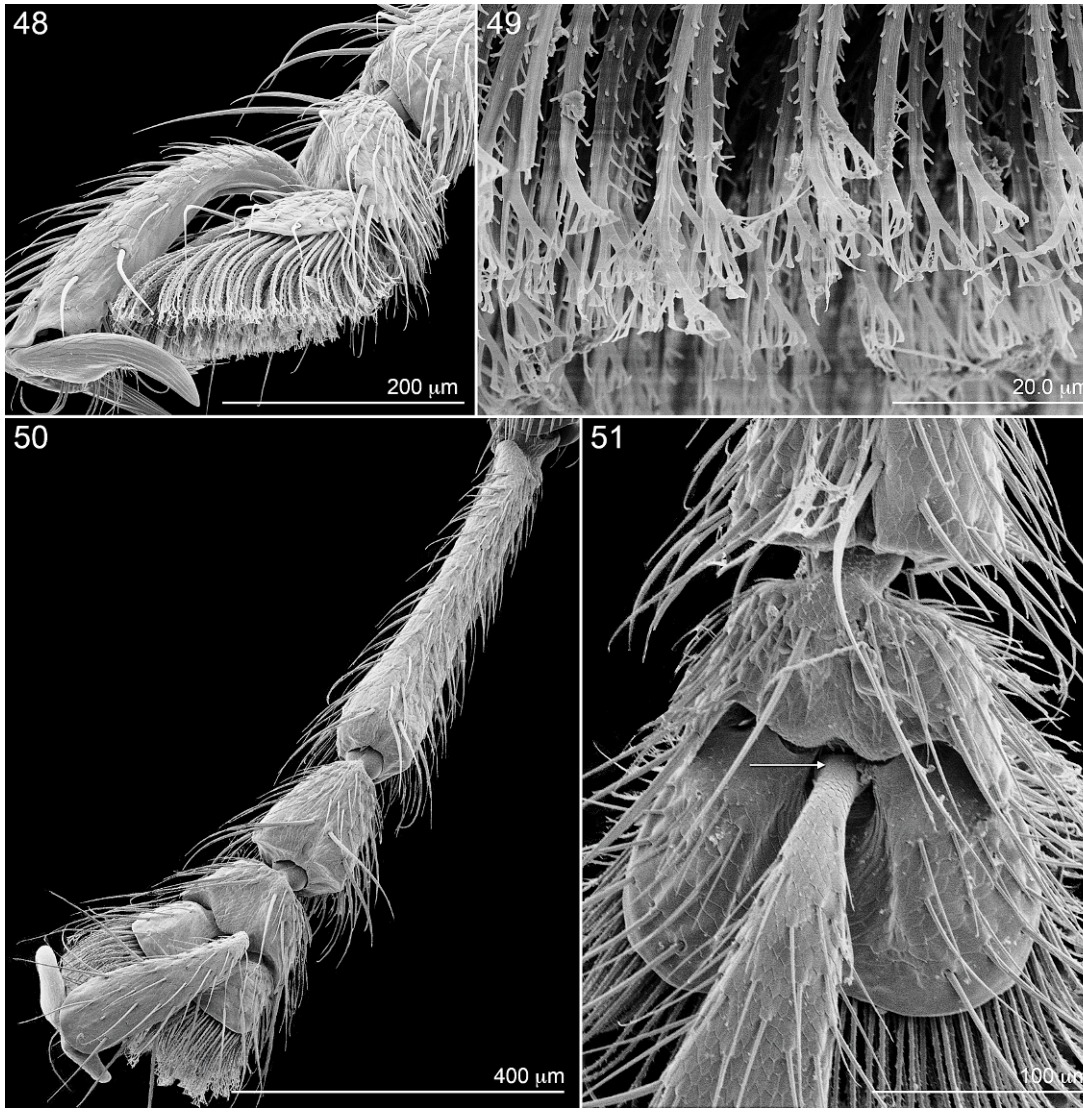
Figs. 35–39. *Oedichirus geniculatus*. **35.** Protibia, ctenidial surface. **36, 37.** Profemur, ventral. **38.** Profemoral slit, opened, ventral. **39.** Metatibia, apex.



Figs. 40–43. *Palaminus* spp. (Costa Rica, U.S.A.). **40.** Profemur, ventral. **41, 42.** Protarsus, ventral. **43.** Protarsomeres 1–4.



Figs. 44–47. *Oedichirus geniculatus*. **44.** Protarsus, right, dorsal. **45, 46.** Protarsus, ventral. **47.** Protarsomeres 4 and 5, ventral.



Figs. 48–51. *Oedichirus geniculatus*. **48.** Metatarsomeres 2 (partial) through 5, lateral. **49.** Metatarsomere 4, setal pad, lateral. **50.** Metatarsus. **51.** Metatarsomeres 2 (partial), 3, 4, and 5 (partial), arrow to origin of 5.

edge of the sternum. The length of the paratergal carina varies from short (fig. 23) to extending just past spiracle III (fig. 26) or reaching to more than half the length of the segment in some *Oedichirus,* and the carina can be fine to coarse.

Most staphylinids have two paratergites between the tergum and sternum. Because the species of some of the less-derived subfamilies of the Staphylinidae have only one paratergite (for example, Oxytelinae: *Deleaster*, *Syntomium,* and Omaliinae) the presence of one paratergite may be the plesiomorphic state, two sclerites would be derived, and their loss and the fusion of the tergum and sternum would be more derived yet. There may be reversals, so that by contrast, in the Paederinae in which most taxa have two paratergites, the presence of one would be derived, the loss of that is more derived, the

presence of a paratergal carina is derived, its loss further derived, and again, fusion of the tergum and sternum would be most derived. Where present in the Procirrina, paratergite III is narrow and strongly tapered and tergum and sternum III are separated. Paratergite III is replaced by a paratergal carina in most Procirrina.

Segments IV to VI lack paratergites and paratergal carinae, the tergum and sternum of each segment are fused, and each segment is cylindrical (fig. 26). Segment VII lacks paratergites and the tergum and sternum are separated in all but two genera. Tergum and sternum VII are fused in *Palaminus*. In *Oedichirus* tergum and sternum VII are fused basally, but the apical, lateral side of the segment has an incision that extends a short distance from the notch of the posterior margin (figs. 33, 34); it is unique in the subtribe. This incision notch presumably represents a remnant of the division of the tergum and sternum. Species that fly usually have a palisade fringe, a wing-grooming device (Hammond, 1979: 134, 137), on the posterior margin of tergum VII and those that lack flight usually lack the fringe; this is true for most Paederinae and most other Staphylinidae. However, in the Procirrina the posterior margin of tergum VII lacks the palisade fringe whether or not the species can fly.

Unique in the Paederinae to *Oedichirus* (fig. 24) and *Palaminus* (fig. 28) are a dorsal and a ventral pair of oval ''cells'' or ''windows'' in the intersegmental membrane adjacent to the anterior margin of terga and sterna III to VII. The windows are covered with an opaque, white membrane. No glands are associated with these cells and their function is obscure, but they might facilitate lateral flexibility of the abdomen (Peter Hammond, personal commun.).

Tergum and sternum VIII for all genera and species of the subtribe are separated. The posterior margin of sternum VIII of males is usually emarginate and the subapical and median surfaces can be elaborated with depressions, setae, tumescences, etc., useful for diagnosing species. In some species sterna VI and VII are similarly modified in the males. Sterna VI to VIII are usually unmodified in female procirrines.

Like other staphylinids, segment IX of the Procirrina differs from all the preceding ones. Tergum IX is fused medially in the Procirrina (figs. 99, 103), extends laterally to cover the lateral side (fig. 100, 104), then ventrally where the edges may touch medially (fig. 85) or are separated by the male sternum IX or the female genital sclerites. The middorsal length varies from short (some *Palaminus*; fig. 99) to long (*Procirrus*, *Neoprocirrus*; figs. 61, 65). The lateral, apical portion of tergum IX extends posteriorly as a short to long lateroapical process, which is cylindrical or subcylindrical in most genera, but laterally compressed in *Procirrus*, and tapered, apically acute, long (some *Oedichirus*) to short (*Procirrus*), and straight to slightly (*Palaminus*) to strongly deflexed (some *Oedichirus*, *Stylokyrtus*). This process is fused to the transverse base of the tergum in all but *Palaminus* (figs. 29, 99, 100), in which it is separated and may be mobile. The separation in *Palaminus* is secondary and derived. Some species of *Oedichirus* have a short groove (fig. 25) or partial suture on the dorsal surface at the juncture of the transverse sclerite of IX and base of the lateroapical process; other species apparently do not, but the suture is difficult to see without the SEM. The form and structure of tergum IX varies throughout the Paederinae and will be discussed as the other subtribes are revised.

Sternum IX of procirrine males, typical of most paederines, is elongate, moderately wide, and more or less symmetrical. In other male Paederinae the size and symmetry may vary significantly and can be useful to identify species.

In staphylinids, the female ventral sclerites of segment IX differ in form, number, and origin from that of the male. The three paired ventral sclerites, the genital sclerites of female staphylinids, have been referred to as the *valvifer* or *hemisternite, coxite,* and *stylus* (Blackwelder, 1936; Naomi, 1989b) and as the *proximal, basal,* or *first* and *distal, apical,* or *second gonocoxites*, and *stylus* (Solodovnikov, 2006). Blackwelder's (1936) morphology of the female genital segment followed Tanner's (1927: figs. 36, 37) interpretation. Naomi (1989b: 727–731), who followed Matsuda (1976: fig. 77b, c), used hemisternite

in place of *valvifer,* but that term is still rarely used. Use of the second set of terms was in place by at least 1979 (Thayer and Newton, 1979: figs. 66, 67), but the reason for renaming the sclerites was not discussed; since then other authors writing on the family have used the terms (Smetana, 1988: 170; Solodonikov, 2005: 89). Using *gonocoxite* suggests appendicular origin of the basal genital sclerite; *hemisternite* and, perhaps, *valvifer* suggest sternal origin. Although Mickoleit (1973) and Deuve (1988, 1993) advance the idea of appendicular origin of the female genital sclerites, the issue remains unsettled. There seems to have been no direct refutation of one or the other of the hypotheses of the origin of the female genital sclerites for the Coleoptera.

The ventral sclerites of segment IX of female paederines are notably variable; their manifestations and taxonomic distribution will be discussed for other subtribes as revisions are published. However, the immediate difficulty is terminology and homology for some of these sclerites in paederines. Excluding the stylus, which appears to be absent in paederines (Herman, personal obs.), the base number of female genital sclerites in the Paederinae is four sclerites, a basal and apical pair. In addition, among paederines there may also be 1 sclerite or 3–6 or more female genital sclerites (Herman, 1981, various figures). Many paederines have one pair of midlongitudinally separated genital sclerites and in *Stereocephalus*, because of the partial, transverse ''suture'' near the middle, it was suggested that the suture marked the fusion of the basal and apical sclerites (Herman, 1979: 4 and fig. 19). A similar partial suture is found in a few other paederine genera (Herman, personal obs.). Some species have two genital sclerites, one anterior to the other (Herman, 1981: fig. 34) which suggests the basal pair are fused as one sclerite and the apical as another (Herman, 1981: 348). Species with one sclerite (Herman, 1981: fig. 29) may result from the medial fusion of the basal and apical pairs as one or the medial fusion of the basal or apical pair and loss of the other. In species with more sclerites (fig. 101; Herman, 1981: figs. 190, 362, 369, 376, 389, 407, 424, 432, 446, 456), the additional ones may result from fragmentation of the basal sclerite or the appearance of new sclerites.

Hypotheses for the homology for the preceding arrangements of ventral sclerites in the Paederinae are as follows. Two pairs of sclerites would be the *proximal* (= valvifer and hemisternite) *and distal gonocoxites* (fig. 86). Two midlongitudinally separated sclerites, the result of fusion of the two gonocoxites on each side, would be a pair of *lateral gonocoxal plates* (Frisch, 2009: fig. 29, = hemisternites). A median anterior and median posterior plate, resulting from the medial fusion of the proximal and distal gonocoxites respectively, would be the *proximal gonocoxal plate* and *distal gonocoxal plate*. A single median plate, the result of the fusion of the basal and apical gonocoxites or the loss of one or the other of the pairs of gonocoxites and medial fusion of the remaining, would be the *median gonocoxal plate* (fig. 74).

Among the Procirrina, *Oedodactylus* (fig. 86) and *Pseudoprocirrus* (fig. 105) have two paired ventral sclerites, the proximal and distal gonocoxites, and lack a stylus. *Procirrus* (fig. 64) and *Oedichirus* have one sclerite, the median gonocoxal plate (fig. 74). For *Oedichirus* the vulva is incorporated into (Herman, in prep.) or proximad of (fig. 74) the median gonocoxal plate. The genital sclerites of the species of *Palaminus* (fig. 101) depicted herein are comprised of a proximal gonocoxal plate, which has a divided base and includes the vulva, and and a distal gonocoxal sclerite, which is partly fused to the proximal sclerite. Laterally the line of fusion of the two gonocoxal plates can be seen as a low ridge and medially the separation is complete. Although far more study is required, preliminary examination suggests that the variation of the gonocoxal plates and vulva in *Palaminus* is as great as it is for *Oedichirus*, that it may provide phylogenetic information, and that it will be useful for identification of females.

Tergum X is embedded in the space between the lateroapical processes of IX in *Procirrus*, *Oedichirus*, and *Palaminus*, and is largely to fully exposed; the edge of the basal margin and perhaps lateral margin is covered by tergum IX (figs. 60, 73). Tergum X is fused to IX in *Oedodactylus*

(fig. 87) and attached to IX only along the anterior margin in *Pseudoprocirrus* (fig. 103). Tergum X is large (fig. 73) to small (fig. 61), shield shaped, and the posterior margin is broadly rounded (fig. 73), truncate (fig. 65), or attenuate with lateral margins that converge to an apical point (fig. 87). The posterior margin of X has many long cuticular processes.

The procirrine aedeagus is asymmetrical. *Procirrus* has a divided basal piece (fig. 62) which is absent in the other genera (fig. 88). Parameres are present in *Procirrus*, *Oedichirus*, and *Palaminus* (figs. 62, 75, 102), but absent in *Oedodactylus* (fig. 88). Fagel (1971: 49–50) reported that *Pseudoprocirrus abyssincus* has only one paramere. The form of the median lobe varies. A sclerotized spermatheca was not found.

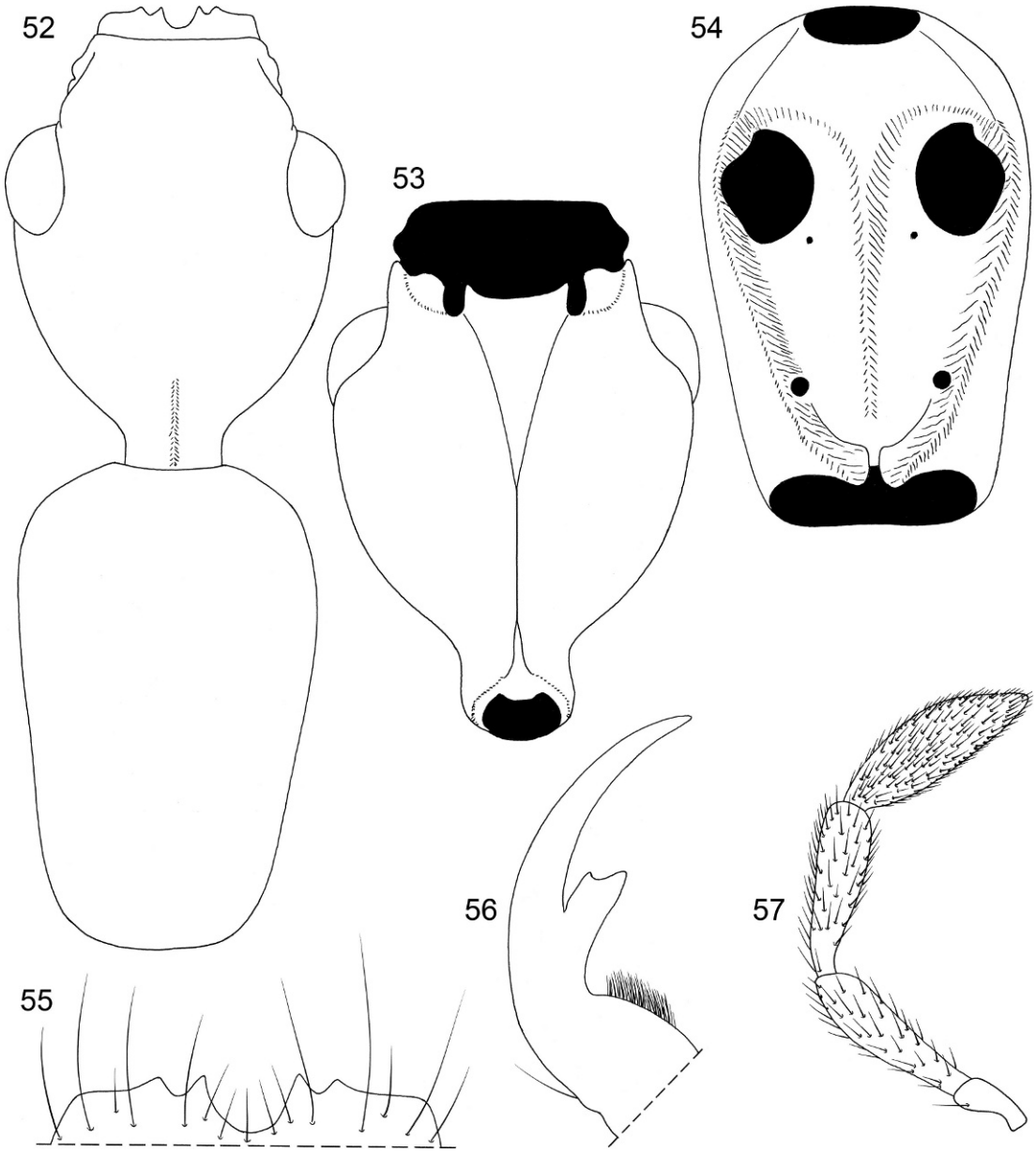
KEY TO GENERA OF THE PROCIRRINA

1. Abdominal segment VII with tergum and sternum partially (figs. 33, 34) or completely fused; abdominal segments IV to VI with pair of windows in intersegmental membrane adjacent to tergum and sternum (figs. 24, 28) 2
– Abdominal segment VII with tergum and sternum separated; abdominal segments IV to VI without windows in intersegmental membrane 3
2. Abdomen without imbricate macrosculpturing, surface strongly punctate (fig. 24); tergum and sternum VII fused at base and with apical incision (figs. 33, 34); elytra without long, prominent seta on lateroapical angle (fig. 14); (Mexico and Caribbean to Brazil; southern Europe and Africa, southern Asia to Japan, and Australia) . . . . . *Oedichirus*
– Abdomen with diamond-shaped, imbricate macrosculpturing, surface without noticeable punctation (figs. 27, 28); tergum and sternum VII completely fused, without incision; elytra with long, prominent, thicker seta on lateroapical angle (fig. 96); (Canada to Argentina; Africa, India, southeastern Asia to Japan, and Australia) . . . *Palaminus*
3 (1). Protarsomeres 1–4 inflated (fig. 59). . . . 4
– Protarsomeres 1–3 inflated (fig. 89). . . . 7
4 (3). Elytra without row of setae on posterior edge 5
– Elytra with row of setae on posterior edge . . . 6
5 (4). Head pedunculate, postocular region strongly tapered to narrow, nearly parallel-sided pedicel (figs. 7, 52); labrum quadridentate (fig. 55); antennomere 11 slightly longer to shorter than 9 and 10 combined; (Canary Islands, southern Europe, Africa, southern Asia to Japan, and Australia) . . . *Procirrus*
– Head gradually tapered to neck (fig. 6); labrum bidentate; antennomere 11 slightly shorter to longer than 8–10 combined; (Singapore, Malaysia) . . . . . *Paraprocirrus*
6 (4). Head with groove on ventral surface extending from neck to eye (fig. 2); (Indonesia, Malaysia) . . . . . *Neoprocirrus*
– Head without groove on ventral surface; (Brazil). . . . . *Stylokyrtus*
7 (3). Tergum and sternum VIII with transverse basal ridge; tergum X fused to tergum IX (fig. 87); (southern Mexico to Argentina and Chile) . . . . . *Oedodactylus*
– Tergum and sternum VIII without transverse basal ridge; tergum X separated from tergum IX (fig. 103); (Ethiopia, Zanzibar, Zambia) . . . . . *Pseudoprocirrus*

Procirrus Latreille
Figures 7, 52–64

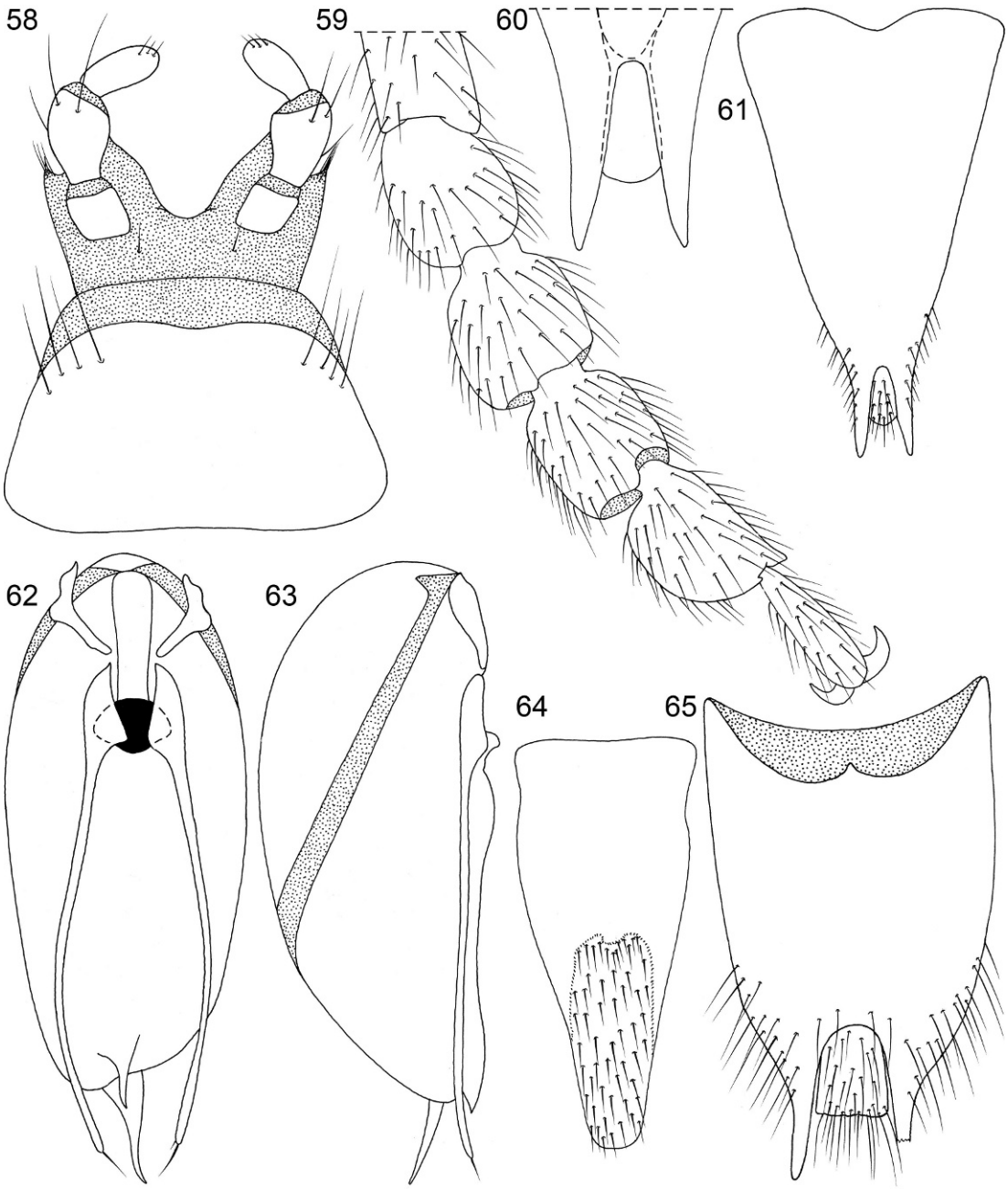
Procirrus Latreille, 1829: 436. Type species: *Procirrus lefebvrei* Latreille, 1829: 436, fixed by monotypy.

— Laporte, 1835: 123 (characters). — Erichson, 1840: 685 (characters). — Laporte, 1840: 184 (characters). — Schaum, 1852: 28 (list of species; Europe). — Lacordaire, 1854: 108 (characters; notes; list of species). — Kraatz, 1857: 667, 668 (notes; key). — Jacquelin du Val, 1857: 50 (characters). — Redtenbacher, 1857: 217 (characters). — Jacquelin du Val, 1859: 74 (catalog; Europe). — Schaum, 1859: 29 (catalog; European species). — Gemminger and Harold, 1868: 630 (catalog). — Redtenbacher, 1874: 236 (characters). — Fauvel, 1875a: 219 (catalog). — Fauvel, 1875b: xvii (catalog). — Duvivier, 1883: 176 (catalog). — Heyden et al., 1891: 110 (list of species of Europe and Caucasus Region). — Heyden et al., 1906: 152 (list of species of Europe and Caucasus Region). — Bernhauer and Schubert, 1912: 197 (catalog). — Lea, 1923: 8 (characters). — Cameron, 1925: 33 (catalog; species of British India). — Porta, 1926: 67 (characters). — Winkler, 1925: 358 (catalog; Palaearctic Region). — Cameron, 1931: 1, 18 (characters). — Scheerpeltz, 1933: 1212 (catalog). — Blackwelder, 1952: 322 (type species). — Adachi, 1955: 13, 14 (characters;



Figs. 52–57. *Procirrus lefebvrei*. **52.** Head and pronotum. **53.** Head, ventral. **54.** Prothorax, ventral. **55.** Labrum. **56.** Mandible, left. **57.** Maxillary palpus.

key). — Kocher, 1958: 117 (checklist of species; Morocco). — Fagel, 1971: 11, 22 (characters; key to African species; type species). — Tikhomirova, 1973: 175 (checklist of species of USSR). — Bordoni, 1975: 419 (characters). — Shibata, 1977: 19 (catalog; Japanese species). — Coiffait, 1978b: 323 (characters; key to western Palaearctic species; distribution). — Hammond, 1984: 204 (checklist; Borneo). — Outerelo and Gamarra, 1985: 21 (characters). — Ciceroni and Zanetti, 1995: 19 (list of species of Italy). — Smetana, 2004: 624 (Palaearctic catalog).



Figs. 58–64. *Procirrus lefebvrei*. **58.** Labium. **59.** Protarsus, dorsal. **60.** Tergum IX, apex, and tergum X, female. **61.** Terga IX and X, female. **62.** Aedeagus, ventral. **63.** Aedeagus, right lateral. **64.** Median gonocoxal plate, female. Fig. 65. *Neoprocirrus* sp. (Malaysia). Terga IX and X, male, right lateroapical process apex broken.

Procirrus Gray, 1832: 294 (species included: *lefebvrei*, cited as *lefeburi*). Type species: *Procirrus lefebvrei* Gray, 1832: 294, fixed by monotypy. Objective synonym of *Procirrus*.

— Blackwelder, 1952: 322 (synonym of *Procirrus*). — Smetana, 2004: 624 (synonym of *Procirrus*).

Microphius Chevrolat, 1846: 201. Type species: *Procirrus lefebvrei* Latreille, fixed by monotypy. Objective synonym of *Procirrus*.

— Blackwelder, 1952: 322 (type species; synonym of *Procirrus*).

Procirrinus Koch, 1934: 79. Type species: *Procirrus saulcyi* Fauvel, 1873: 291, fixed by monotypy. **New synonym**.

— Blackwelder, 1952: 322 (type species). — Smetana, 2004: 624 (subgenus of *Procirrus*).

DIAGNOSIS: *Procirrus* is separated from other Procirrina by the four inflated protarsomeres (fig. 59), pedunculate base of the head (figs. 7, 52), quadridentate labrum (fig. 55), elongate pronotum (figs. 7, 52), and absence of a pronotal marginal ridge. Abdominal segment III has a paratergal carina laterally (as in fig. 23), the tergum and sternum are fused, and the segment is cylindrical. Tergum and sternum VII are separated. The quadridentate labrum will separate *Procirrus* from *Paraprocirrus*. The absence of a ventral cephalic groove (cf. fig. 2) that extends diagonally from the margin of the eye to the neck distinguishes *Procirrus* from *Neoprocirrus*. The absence of setae on the edge of the posterior margin of the elytra will separate *Procirrus* from *Neoprocirrus*, *Oedodactylus*, *Pseudoprocirrus*, and *Stylokyrtus*.

DESCRIPTION: Head (figs. 7, 52) pedunculate, elongate, longer than wide, tapered from posterior margin of eyes to neck; frontoclypeus with subapical, interantennal, transverse ridge; postocular lateral (fig. 52) margin strongly rounded to neck; postocular margin long; basal angle absent (fig. 52); basal margin of head indistinguishable from lateral margin, without marginal ridge, and feebly distinct from occiput. Neck across nuchal constriction one fourth to three tenths as wide as greatest postocular width of head; nuchal groove feeble, indistinct; nuchal ridge absent. Eye length less than postocular length of head (fig. 52). Dorsal surface with dense umbilicate punctation. Ventral surface without postocular groove (fig. 53). Gular sutures (fig. 53) separated anteriorly and confluent posteriorly, some species with sutures separated nearly to neck; sutures most approximate posteriorly. Gula with minute to moderately long pubescence. Antennomere 11 slightly longer than to slightly shorter than 9 and 10 combined; apex without apical spinelike pencil of setae. Mandibles with apically bifid denticle (fig. 56); prostheca evident as cluster of cuticular processes at base (fig. 56). Maxillary palpus (fig. 57) with palpomere 4 shorter than second and subequal to third, symmetrically to asymmetrically fusiform, moderately compressed. Labium (fig. 58) with glossae large, widely separated, and with narrowly rounded apex. Hypopharynx without lobes or cluster of spinelike setae on anterior margin; lateral region with dense cluster of cuticular processes. Labrum (fig. 55) with two pairs of denticles on anterior margin. Epipharynx with two small setae near anterior margin laterad of middle; surface with dense cluster of cuticular processes on curved ridge adjacent to median groove; median groove present; epipharynx not visible along anterior labral margin in dorsal view.

Prothorax (fig. 52) trapezoidal, longer than wide; widest near anterior fourth and lateral margins broadly rounded to slightly sinuate and gradually convergent posteriorly. Pronotum with dense umbilicate punctation; punctation uniform and with or without impunctate, narrow, midlongitudinal ridge on posterior third or half. Pronotal marginal ridge poorly developed or absent. Notosternal suture poorly developed. Hypomeron densely punctate. Postprocoxal lobe long and punctate; transverse ridge present proximad of apex; apex of each lobe nearly touching one another medially (fig. 54). Probasisternum without median carina (fig. 54); surface with coarse, dense punctation. Mesospiracular peritreme (fig. 54) with anteromedial margin fused to furcasternum. Elytra slightly longer to shorter than pronotum; humeral angles present (fig. 7) or absent; posterior edge without row of setae; subapical region (cf. fig. 96) without long, prominent, medioposteriorly directed seta near lateroapical corner. Scutellum pubes-

cent. Mesosternum without median carina. Mesocoxal acetabulum with marginal carina laterally and posteriorly. Intersternal suture feebly developed.

Profemur with carina on distal half of anteroventral surface. Protibia with many (12 in a specimen of *P. lefebvrei*) combs extending from near base to apex; tibia with feeble, indistinct depression on ctenidial surface; apical portion neither constricted nor enlarged. Protarsomeres (fig. 59) 1–4 inflated; base of tarsomere 1 not surrounded by cupulate protibial apex; apical margin of tarsomere 4 not expanded beneath tarsomere 5 and not bilobed; tarsomere 5 unmodified and inserted laterad of middle of asymmetrical tarsomere 4; tarsomere 5 with moderately dense pubescence ventrally. Mesotarsomere 1 about as long as or longer than remaining tarsomeres. Metatarsomere 1 longer than remaining tarsomeres combined.

Abdominal segments without imbricate macrosculpturing (cf. fig. 26). Segment III without paratergites; paratergal carina present at base laterad of spiracle; tergum and sternum III fused. Segment VII with tergum and sternum separated. Segments IV to VII without oval "windows" in intersegmental membrane (cf. fig. 24). Sternum I absent. Sterna IV to VII without glandular lobe or slit along anterior margin. Tergum IX (fig. 61) of male and female fused medially; emargination shallow, about one seventh of length of tergum, and narrow; lateroapical process (fig. 61) short, slender, slightly curved ventrally, and extending slightly beyond apical margin of tergum X; lateroapical process fused basally to remainder of segment. Tergum X (fig. 60) with apical margin rounded; base separated from tergum IX.

Genital sclerites fused to form broad, long median gonocoxal plate (fig. 64).

Aedeagus (figs. 62, 63) asymmetrical; parameres present, long, slender, with one or more apical setae, and separated from median lobe; basal piece present and divided into two sclerites at base of median lobe.

DISTRIBUTION AND HABITAT: *Procirrus* is a modest size group of 29 species found on the Canary Islands, across southernmost Europe and in Africa, eastward through southern Asia to Australia and Japan. Four fifths of the species are recorded from Africa (18) and Australia (6). In Africa 14 sub-Saharan species were described by Fagel (1971: 22–47) and in Australia four species are known from New South Wales, Victoria, and South Australia (Lea, 1923: 8–10; Fauvel, 1878a: 509) and two from northwestern Western Australia (Lea, 1923: 9–10). The remaining five species occur across southern Asia from Lebanon to Japan as follows. *Procirrus hermani* Drugmand occurs in Israel (Drugmand, 1989: 108); *P. saulcyi* Fauvel in Israel (Fauvel, 1873: 291), Lebanon (Smetana, 2004: 624), and Turkey (Assing, 2004: 683); *P. feae* Fauvel in India (Cameron, 1931: 19), Myanmar (Fauvel, 1895: 215), and Java (Cameron, 1936: 42); *P. fusculus* Sharp in Bangladesh (Sharp, 1889: 324); and *P. lewisii* Sharp in Thailand (Last, 1961: 305), Hong Kong (Rougemont, 2001: 43), and Japan (Sharp, 1889: 324). *Procirrus fusculus*, originally described from Bangladesh and later reported in Japan (Adachi, 1955: 14), was omitted from the most recent checklist of Japanese species of the genus (Shibata, 1977: 19). Although Japan and Hong Kong share the species, none have been collected in mainland China. Note that in southwestern Asia the genus is reported only from sites near the Mediterranean; from there it next appears in India.

One of 18 African species, *P. lefebvrei*, is the only one of the genus in Europe and has been found only in southern Spain and southern Italy. Described originally from Sicily, it has since been recorded from Sardinia (Porta, 1926: 67; Koch, 1934: 78), Calabria, Italy (Porta, 1926: 67), Cádiz, Spain (Outerelo, 1984: 291), the Canary Islands (Fauvel, 1897: 270; Koch, 1934: 78; Machado and Oromi, 2000: 46), Algeria (P. Lucas, 1846: 122; Fauvel, 1873: 291; Koch, 1934: 78; Jarrige, 1952: 118), Morocco (Fauvel, 1886: 32; Jarrige, 1952: 118), Tunisia (Fauvel, 1902: 80; Normand, 1935: 365), Egypt (Motschulsky, 1851: 656 [as *P. niloticus*]; Koch, 1934: 77 [as *P. lefebvrei macrops*]), Ethiopia (Fauvel, 1876: 65), Sudan (Scheerpeltz, 1974: 10 [as *P. lefebvrei macrops*]), Java (Fauvel, 1886: 32), and Borneo (Scheerpeltz, 1933: 1212). The Ethiopian record is *P. abyssinicus*, which Fagel (1971: 30) described from a female deposited in the Fauvel collection and which Fagel

stated that Fauvel (1876: 65) had confused with *P. lefebvrei*.

Little has been published concerning the habitat of species of *Procirrus*. Cameron (1931: 19) collected one specimen of an unnamed species in India in damp leaves, Fagel (1971: 27–47) cited African species collected in forest humus, leaf litter in the forest and near streams, plant detritus and at lights, Rougemont (2001: 43) reported *P. lewisi* from Hong Kong in damp leaf litter near a stream and in forest floor litter, and Assing (2004: 683) collected specimens of *P. saulcyi* in Turkey from oak and laurel litter. Species have been collected at elevations from 950 m (*P. strictus*) to as high as 1950 m (*P. bacillus*) in Africa, but most species were reported without elevational data (Fagel, 1971: 45, 46); *P. saulcyi* was recorded at 400 and 920 m elevation in Turkey and 700 m in Israel (Assing, 2004: 683).

SYNONYMY: Koch (1934: 79) described *Procirrinus* as a new subgenus for *Procirrus saulcyi*. To distinguish the monotypic subgenus from other species of the genus he relied on three elytral characters. The humeral angles are absent, the elytra are shorter than the pronotum, and they are narrower than the width of the apical region of the abdomen. Such reductions of the elytra are common to most staphylinid species that lack or have reduced wings. Species without wings tend to have more extreme reductions than those with merely shortened wings. Species are known in many genera with loss-of-flight reductions of the elytra and pterothorax and, although some authors have recognized genus-group taxa based solely on such adaptations, these features alone usually do not, perhaps never, define a monophyletic group. As there is only one species in *Procirrus* (*Procirrinus*), the monophyly of the subgenus is a moot point. Because the stated features are unlikely to define a monophyletic group and I can find no others that do, the subgeneric name *Procirrinus* is placed as a junior synonym of *Procirrus*.

Procirrus Gray (1832: 294) is a junior synonymic homonym. His description of the genus and the only included species, *P. lefebvrei* (cited as *P. lefeburi*), is an exact translation of the description by Latreille (1829: 436) and is partly the rationale for listing Gray's name as a junior synonymic homonym of Latreille's name (Blackwelder, 1952: 322; Smetana, 2004: 624). The senior species-group name was originally spelled as *P. lefeburi*. Laporte (1840: 184, pl. 13, fig. 1) cited the name as *P. lefeburi* in the text, but as *P. lefebvrei* for the illustration. Thereafter, nearly all authors cited the name as *Procirrus lefebvrei* and that name was declared correct (Herman, 2003: 3). Since Laporte and others used the name "*lefebvrei*" for the species, it is probable that the species was named for Monsieur A.L. Lefebvre, a well-known French entomologist of that era. Latreille cited the collector's name as "Lefèvre."

Microphius Chevrolat (1846: 201) was published as a junior synonym of *Procirrus*, but was cited as "*Microphius*, Dejean" with reference to the third edition of Dejean's catalog (1836: 74), in which the generic name is listed with two unavailable species-group names. The generic name was cited by other authors thereafter, but without characters or available species (see Blackwelder, 1952: 246, for list of other citations of name). Finally, Chevrolat (1846: 201) listed it as a junior synonym of *Procirrus*, with the type species *Procirrus lefebvrei* Latreille, by objective synonymy (Blackwelder, 1952: 322).

DISCUSSION: Most of the species have been described from one or a few individuals from one or a few localities. Specimens of the genus appear to be rarely collected. New records of some known species were usually published without access to the relevant type specimens. It is probable that revision of published material will reveal some misidentifications and the unpublished specimens and new collections will result in the discovery of additional African, Asian, and Australian species.

Fagel (1971: 27) presented a species group classification of five groups for 15 tropical African species, plus *P. lefebvrei*, based on the number and condition of the setae on the parameres. The classification has not been applied to non-African species.

Procirrus lefebvrei is currently comprised of two subspecies, the nominate from Italy, Spain, Morocco, Algeria, and Tunisia (Fauvel, 1902: 80; Koch, 1934: 77–79; Outerelo, 1984: 291) and *P. lefebveri macrops* Koch, from the Canary Islands, Morocco, Algeria,

Egypt, and Sudan (Koch, 1934: 79; Jarrige, 1952: 118; Scheerpeltz, 1974: 10; Outerelo, 1984: 291–292). The species was recorded improbably from Java (Fauvel, 1886: 32) and Borneo (Scheerpeltz, 1933: 1212), but is almost certainly one or more other species. Most of the records for the species require confirmation and the species needs revision, both to evaluate the validity and distribution of the two subspecies, which are based largely on the size of the eyes, and to determine which species are represented in Java and Borneo. Fagel (1971) reported neither subspecies in Sudan. Only Jarrige (1952) reported the *P. l. macrops* from Morocco and Algeria; most authors who cited it reported it from Egypt and the Canaries (Koch, 1934: 77–79; Coiffait, 1978b: 326; Smetana, 2004: 624). Outerelo (1984), who also listed it from Morocco and Algeria, was only summarizing the published records for the subspecies. If these two forms are subspecies and if Jarrige is erroneous in reporting it from Morocco and Algeria, then the curious disjunct distribution needs explanation. But if those records are accurate, then more details need be elicited about the distribution of both subspecies across North Africa.

Keys to species were published for the Mediterranean Region, including North Africa, by Coiffait (1978b: 325) and modified to include another species by Drugmand (1989). African species, except those of North Africa, can be identified with the key published by Fagel (1971: 25). The two species from India and Bangladesh were compared by Cameron (1931: 19). Fauvel (1878a: 509) provided a key for two of the Australian species and Lea (1923) described four more with comparisons among them, but published no key. Japan has only one species, which is also reported in China and Thailand.

Procirrus bicolor has *Paederus*-like coloration; the head, elytra, and apical abdominal segment are black, the pronotum and basal four abdominal segments are red. The color pattern of *Procirrus allardianus* may be similar (Fagel, 1971: 42).

Species Included and Material Examined

abyssinicus Fagel – Lit. Att. [Ethiopia]
allardianus Fagel – Lit. Att. [D.R. Congo]
antiquus Lea – Lit. Att. [Australia]
aristidis Fauvel – sp (FMNH) . . . . . Egypt
hybridus Koch
bacillus Fagel – H (MRAC). . . . . Tanzania
bicolor Fagel – H (MRAC) . . . . . D.R. Congo
castelnaui Fauvel – Syn (IRSN, BMNH) . . . . . Australia
congoensis Fagel – H (MRAC) . . . D.R. Congo
crocodilus Bernhauer – Syn (FMNH) . . . . . Zimbabwe
dolichoderes Lea – sp (BMNH) . . . . . Australia
feae Fauvel – Syn (IRSN), sp (BMNH) . . . . . Myanmar, India
ferrugineus Lea – Lit. Att. [Australia]
filiformis Fagel – Lit. Att. [Kenya]
fusculus Sharp – Syn (BMNH). . . . . India
garambanus Fagel – H (MRAC) . . . D.R. Congo
hermani Drugmand – Lit. Att. [Israel]
iti Drugmand – Lit. Att. [Gabon]
keanus Fagel – Lit. Att. [D.R. Congo]
kwangensis Fagel – H (MRAC) . . . D.R. Congo
latipennis Fagel – H (MRAC) . . . . . Rwanda
lefebvrei Latreille – sp (FMNH, SDEI). . . . . Algeria, Corsica, Egypt, Italy, Tunisia
lefebvrei Gray
niloticus Motschulsky
macrops Koch
lewisii Sharp – H (BMNH), sp (FMNH) . . . . . Japan, China, Taiwan
nimbaensis Fagel – sp (MRAC) . . . . Ivory Coast
opacus Lea – Lit. Att. [Australia]
saulcyi Fauvel – Syn (IRSN), sp (USNM, SDEI) . . . . . Israel
senegalensis Fagel – Lit. Att. [Senegal]
strictus Fagel – H (MRAC). . . . . D.R. Congo
uniformis Fagel – H (MRAC) . . . . D.R. Congo
victoriae Fauvel – H (BMNH). . . . . Australia

Undetermined Specimens: Australia, Malaysia, Nepal, Tanzania, Zaire, Zimbabwe.

Dissections: Complete dissection: *Procirrus lefebvrei* (2 females, Tunisia); Abdominal dissection: (1 male, Egypt).

Neoprocirrus Blackwelder
Figures 1, 2, 65

Neoprocirrus Blackwelder, 1952: 260. Type species: *Neoprocirrus drescheri* Cameron, 1936: 42, fixed by subsequent designation by Blackwelder (1952). (Note: Blackwelder's designation of type species made the generic name available, so he is the author [ICZN, 1999: Article 50.1].)

— Cameron, 1936: 42 (Note: Cameron proposed *Neoprocirrus*, but the name was unavailable because he failed to designate a type species [Article 13.3]; species included: *drescheri*, *bor-*

neensis; characters). — Hammond, 1984: 203 (checklist; Borneo).

DIAGNOSIS: *Neoprocirrus* is separated from *Paraprocirrus* by the deep postocular grooves (fig. 2) on the venter of the head in the former and their absence in the latter and all other procirrine genera. *Neoprocirrus* has moderately developed basal angles on the head (figs. 1, 2); they are indistinct in *Paraprocirrus*. Antennomere 11 is about as long as the preceding three to seven antennomeres combined. The presence of setae on the edge of the posterior margin of the elytra will separate *Neoprocirrus* from *Procirrus*, *Oedichirus*, *Palaminus*, and *Paraprocirrus*.

DESCRIPTION: Head (figs. 1, 2) not pedunculate, slightly wider than long, with postocular margins convergent to basal angles; frontoclypeus with interantennal, transverse ridge along anterior margin; postocular lateral margin (fig. 2) slightly to moderately rounded and moderately convergent to basal angle; postocular margin moderately long; basal angle (figs. 1, 2) moderately developed; basal margin with weak marginal ridge laterad of neck and moderately emarginate across neck. Neck across nuchal constriction about half as wide as greatest postocular width of head; nuchal groove shallow; nuchal ridge absent. Eye length about equal to postocular length of head. Dorsal surface with reticulate punctation. Ventral surface with deep subocular groove (fig. 2). Gular sutures separated; sutures most approximate posteriorly. Gular surface punctate and with tiny setae anteriorly. Antennomere 11 longer than preceding three to seven antennomeres; apex without spiniform pencil of setae. Mandibles with apically bifid denticle; [**prostheca].[1] Maxillary palpus with fourth palpomere about as long as or longer than third, asymmetrically fusiform or securiform. [**Labium, glossae]. [**Hypopharynx]. Labrum with or without two pairs of denticles on anterior margin. [**Epipharynx].

Prothorax (fig. 1) trapezoidiform, elongate, longer than wide; widest near anterior margin and lateral margins gradually curved and moderately convergent to base. Pronotum with dense, coarse, reticulate punctation; punctation uniform and absent only from narrow, polished midlongitudinal strip extending for most of length from near anterior margin to near basal margin. Pronotal marginal ridge poorly developed, evident less as ridge and more as change in surface sculpturing with surface dorsad of ridge punctate, but impunctate and polished ventrad. Notosternal suture poorly developed, evident as shallow groove in broad depression; suture and marginal ridge separated. Prohypomeron polished and densely punctate. Postprocoxal lobe moderately long and punctate; transverse ridge absent; apex of each lobe moderately widely separated from each other. Probasisternum with median carina near coxae; surface densely punctate. Mesospiracular peritreme with anteromedial margin fused to furcasternum and with or without feeble suture near apex of furcasternum. Elytra (fig. 1) slightly shorter to longer than pronotum; humeral angles present; posterior edge with row of setae; subapical region without long, thicker, mediposteriorly directed seta near lateral corner. Scutellum with a few setae. Mesosternum without median carina. Mesocoxal acetabulum with marginal carina laterally and posteriorly. [**Intersternal suture].

Profemur with ridge near middle of anteroventral surface. Protibia with numerous combs extending from near base to near apex; tibia without depression on ctenidial surface; apical region neither constricted nor enlarged. Protarsomeres 1–4 inflated and ventral surface without setose pad; base of tarsomere 1 not surrounded by cupulate protibial apex; apical margin of tarsomere 4 not expanded beneath tarsomere 5 and not bilobed; tarsomere 5 unmodified and inserted laterad of middle of asymmetrical tarsomere 4; tarsomere 5 sparsely pubescent ventrally. Mesotarsomere and metatarsomere 1 longer than remaining tarsomeres combined.

Abdominal segments without imbricate macrosculpturing (cf. fig. 26). Segment III without paratergites; paratergal carina present and laterad of spiracle (as in fig. 23); tergum and sternum III fused. Segment VII with tergum and sternum separated. Segments IV to VII without oval ''windows'' in intersegmental membrane (cf. fig. 24).

[1] This structure and other similarly cited structures were unavailable for study.

[**Sternum I]. [**Sterna IV to VI, glandular lobes]. Tergum IX (fig. 65) with base fused medially; apical emargination (fig. 65) shallow, about two fifths the length of tergum and narrow; lateroapical process (fig. 65) short, slender, curved ventrally, and extending beyond apical margin of tergum X; lateroapical process fused to remainder of segment. Tergum X (fig. 65) with apical margin truncate to shallowly rounded; base separated from tergum IX.

[**Female genital sclerites].

[**Aedeagus – glued to card but seemly too fragile to remove].

DISTRIBUTION AND HABITAT: Species of this genus are found on Java, Sumatra, and Malaysian Borneo. One, *N. drescheri*, was collected at an elevation of 4000 to 5000 feet (Cameron, 1936: 42) and the other, *N. borneensis*, at 6000 feet (Cameron, 1928: 439). More recently, three specimens of *N. borneensis* were taken from a moss forest at 1790 m (5907 feet) elevation in Mulu National Park, Sarawak, Malaysia. Guillaume de Rougemont (in litt., July 2007) found an undescribed species by sifting leaf litter in northern Sumatra. These sketchy data are all that are known about the habitat of the species.

The two described species of *Neoprocirrus* are known from only five specimens, four of them are *N. borneensis*. Little is known of the habitat. Undoubtedly other species will be found in mountainous regions of Indonesia and Malaysia. Guillaume de Rougemont (in litt., August 2007) reported that he collected perhaps 10 undescribed species in Borneo, Thailand, and Sri Lanka belonging to *Neoprocirrus* or to an undescribed genus.

DISCUSSION: Cameron (1936) described *Neoprocirrus* and included two species, but the genus was a nomen nudum because no type species was designated (ICZN, 1999: Article 13.3); the name became available when Blackwelder (1952) designated the type species. However, although Cameron's use of the generic name was unavailable, the species-group name, *drescheri*, which was described in the article with *Neoprocirrus*, was available as neither the validity nor availability of a genus-group name is required for an included species-group name to be available (ICZN, 1999: Article 11.9.3.1). *Neoprocirrus borneensis*, originally placed in *Paraprocirrus*, was transferred by Cameron (1936: 42).

The two known species of *Neoprocirrus* can be separated by the length of the last antennomere and labral dentition. Antennomere 11 is about as long as antennomeres 8–10 in *N. drescheri* and about as long as 4–10 in *N. borneensis*; the former has a pair of labral denticles, the latter lacks them.

Neoprocirrus and *Paraprocirrus* are linked by the long apical antennomere, the subapical carina on the anterior margin of the frontoclypeus, and the inflated basal four protarsomeres. The procoxae of both genera are long, nearly as long as the profemora.

SPECIES INCLUDED AND MATERIAL EXAMINED

borneensis (Cameron) – H, sp (BMNH) . . . Malaysia
drescheri Cameron – H (BMNH) . . . . Indonesia

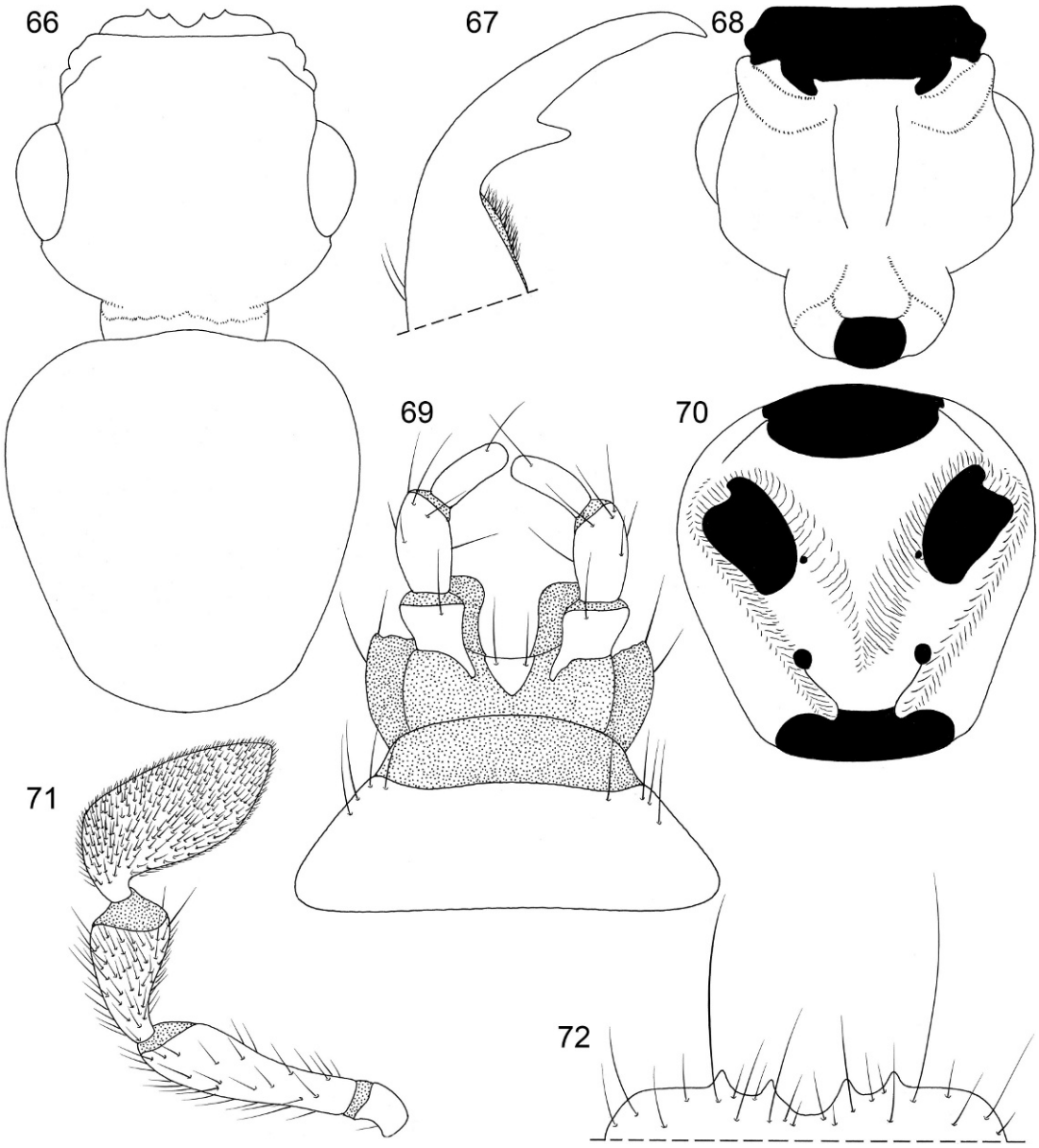
UNDETERMINED SPECIMENS: Indonesia (Sumatra); Malaysia (Sabah).

DISSECTIONS: Abdominal dissection: *Neoprocirrus* sp. (1 male, Malaysia: Sabah).

Oedichirus Erichson
Figures 3, 14–18, 22–39, 44–51, 66–76

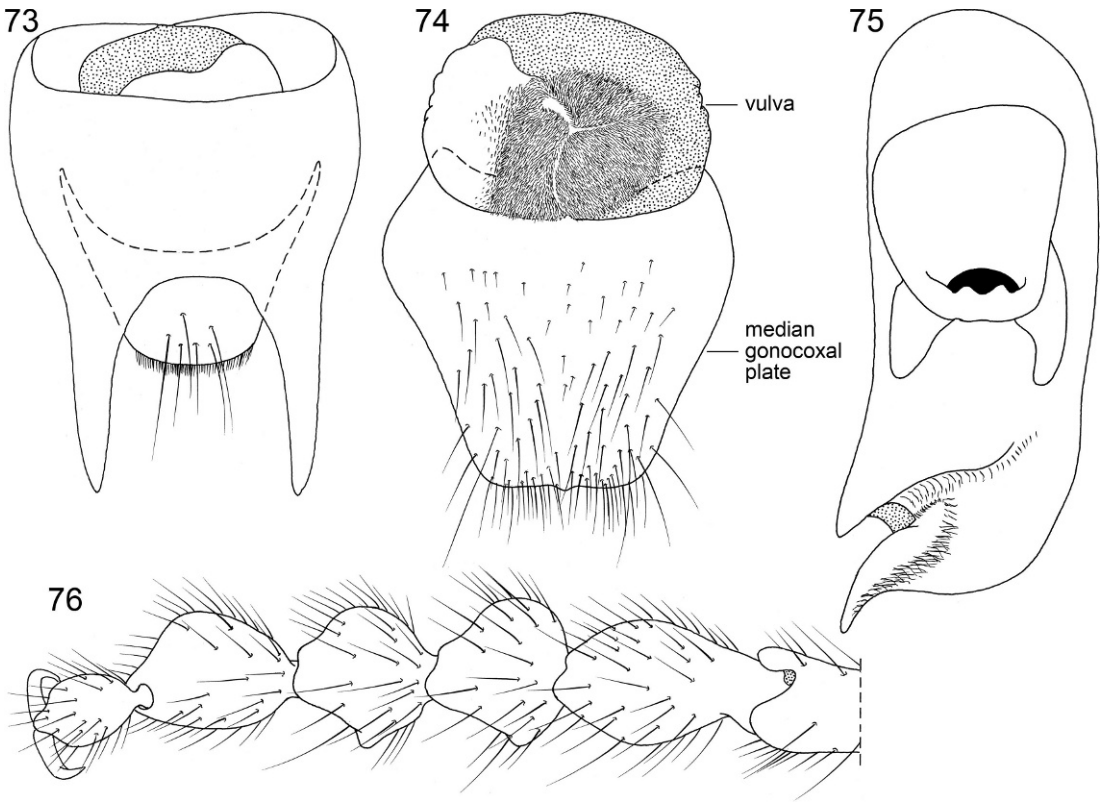
Oedichirus Erichson, 1839: 29. Type species: *Oedichirus paederinus* Erichson, 1840: 685, fixed by Erichson, 1840: 685, by subsequent monotypy.

— Erichson, 1840: 684 (characters; first included species: *paederinus*). — Schaum, 1852: 28 (list; Europe). — Lacordaire, 1854: 104 (characters; notes; list of species). — Kraatz, 1857: 666, 668 (notes; key). — Jacquelin du Val, 1857: 49 (characters). — Redtenbacher, 1857: 217 (characters). — Jacquelin du Val, 1859: 73 (catalog; Europe). — Schaum, 1859: 29 (catalog; Europe). — Gemminger and Harold, 1868: 629 (catalog; world). — Redtenbacher, 1874: 235 (characters). — Fauvel, 1875a: 219 (catalog; France). — Fauvel, 1875b: xvii (catalog; France). — Sharp, 1876: 338 (notes; synonyms; Brazil). — Duvivier, 1883: 176 (catalog). — Fauvel, 1889: 253 (notes). — Heyden et al., 1891: 110 (list; Europe and Caucasus Region). — Heyden et al., 1906: 152 (list; Europe and Caucasus Region). — Bernhauer and Schubert, 1912: 201 (catalog; world). — Cameron, 1925: 34, 106 (catalog; British India). — Winkler, 1925: 358 (catalog; Palaearctic Region). — Porta, 1926: 67 (characters). — Cameron,



Figs. 66–72. *Oedichirus* near *pictipes*. **66.** Head and pronotum. **67.** Mandible, left. **68.** Head, ventral. **69.** Labium. **70.** Prothorax, ventral. **71.** Maxillary palpus. **72.** Labrum.

1931: 1, 25 (characters; key to Indian species). — Scheerpeltz, 1933: 1217 (catalog; world). — Blackwelder, 1944: 131 (checklist; Latin America). — Blackwelder, 1952: 269 (type species). — Fagel, 1955: 194 (characters). — Adachi, 1955: 14 (characters; key). — Kocher, 1958: 117 (checklist; Morocco). — Fagel, 1963: 342 (notes). — Fagel, 1971: 11, 126, 196, 369 (characters; notes; key to species; type species). — Tikhomirova, 1973: 175 (checklist; USSR). — Bordoni, 1975: 419 (characters). — Shibata, 1977: 21 (catalog; Japan). — Coiffait, 1978b: 327 (characters; key to western Palaearctic species; distribution). — Hammond, 1984: 203 (checklist; Borneo). — Outerelo and Gamarra, 1985: 22 (characters). — Lecoq, 1986: 7



Figs. 73–76. *Oedichirus* near *pictipes*. **73.** Terga IX and X, female. **74.** Median gonocoxal plate and vulva. **75.** Aedeagus, ventral. **76.** Protarsus, left, dorsal.

(characters; key to Madagascar species; discussion). — Ciceroni and Zanetti, 1995: 20 (checklist; Italy). — Navarrete-Heredia et al., 2002: 293 (characters in key to genera for Mexico; general notes; unnamed species in Mexico). — Janák, 2003: 253 (list; Madagascar). — Smetana, 2004: 623 (Palaearctic catalog).

Elytrobaeus Sahlberg, 1847: 801. Type species: *Elytrobaeus geniculatus* Sahlberg, 1847: 802, fixed by monotypy.

— Gemminger and Harold, 1868: 629 (catalog). — Fauvel, 1875a: 219 (synonym of *Oedichirus*). — Fauvel, 1875b: xvii (synonym of *Oedichirus*). — Sharp, 1876: 338 (synonym of *Oedichirus*). — Bernhauer and Schubert, 1912: 201 (synonym of *Oedichirus*). — Cameron, 1931: 25 (synonym of *Oedichirus*). — Blackwelder, 1952: 147 (type species). — Smetana, 2004: 623 (synonym of *Oedichirus*).

Oedichiranus Reitter, 1906: 263. Type species: *Oedichirus dimidiatus* Reitter, 1906: 263, fixed by monotypy. **New Synonym**.

— Bernhauer and Schubert, 1912: 201 (subgenus of *Oedichirus*). — Blackwelder, 1952: 269 (subgenus of *Oedichirus*; type species). — Smetana, 2004: 623 (subgenus of *Oedichirus*).

DIAGNOSIS: *Oedichirus* can be separated from all other Procirrina by the spiniform pencil of setae on antennomere 11 (figs. 31, 32) and from all other genera except *Palaminus* by the "windows" (fig. 24) at the edge of the anterior margin of terga and sterna III to VII. The abdomen of *Oedichirus* is punctate (fig. 24) and lacks imbricate macrosculpturing and the lateroapical edge of the elytra lacks a long, stout seta (fig. 14). The abdomen of *Palaminus* lacks punctation and has imbricate sculpturing (fig. 28) and the elytra have a long, stout seta on the lateroapical corner (fig. 11, 96). Unlike other genera of the Procirrina, both *Oedichirus* and *Palaminus* have a dense cluster of setae on the ventral surface of protarsomere 5 (figs. 45,

47) and tergum and sternum VII are fused, basally in *Oedichirus* (figs. 33, 34) and completely in *Palaminus*. The absence of setae on the edge of the posterior margin of the elytra will separate *Oedichirus* from *Neoprocirrus*, *Oedodactylus*, *Pseudoprocirrus*, and *Stylokyrtus*.

DESCRIPTION: Head (fig. 66) not pedunculate, wider than long; frontoclypeus with subapical, interantennal, transverse ridge (fig. 15); subapical ridge curved or sinuate and complete, extending from one antennal fossa to other, or incomplete, extending from each antenna fossa and absent medially; postocular lateral margin rounded to neck or to poorly to well-developed basal angle of head (figs. 15, 66); postocular lateral margin (fig. 15) short to moderately long; basal margin of head distinct to indistinguishable from postocular lateral margin; base of head with (fig. 15) or without ridge extending laterally from neck to near eye. Neck across nuchal constriction half to two thirds as wide as greatest postocular width of head; nuchal groove moderately well developed (fig. 15); nuchal ridge present and well developed (figs. 15, 66). Eye length greater than postocular length of head. Dorsal surface with umbilicate punctation (fig. 15). Ventral surface (fig. 16) without postocular groove. Gular sutures absent or present, moderately to feebly developed, and separated (fig. 68); sutures most approximate near middle. Gular pubescence absent. Antennomere 11 subequal to 10; apex with spiniform pencil of setae (figs. 31, 32). Mandibles (fig. 67) with apically acute denticle; prostheca (fig. 67) evident as cluster of cuticular processes at base. Maxillary palpus (fig. 71) with palpomere 4 longer than second or third, securiform, and moderately compressed. Labium (fig. 69) with glossae broad, widely separated, and apically truncate. Hypopharynx with long submedial seta on anterior margin, but without lobes or cluster of spinelike setae; lateromedial surface covered densely with cuticular processes; sublateral surface with row of coarse setae. Labrum (fig. 72) with one to three pairs of denticles on anterior margin. Epipharynx without setae; median region with transverse, dense cluster of cuticular processes; median groove present; epipharynx not visible along anterior margin in dorsal view.

Prothorax (fig. 66) trapezoidiform, longer than wide in most species, rarely wider than long; widest near anterior third and with lateral margins strongly convergent anteriorly and gradually convergent posteriorly. Pronotum (fig. 18) with umbilicate punctation; punctation sparse to moderately dense, and absent from midline; punctation confused, arranged in straight or curved rows, or more or less evenly distributed. Pronotal marginal ridge present (fig. 18) and well developed, poorly developed, incomplete, or absent. Notosternal suture present (figs. 17, 70); marginal ridge, when present, and suture separated. Hypomeron polished, with or without punctation, and without microsculpturing. Postprocoxal lobe moderately long; punctation present and asetate (fig. 17); transverse ridge absent; apices (fig. 70) moderately widely separated from each other. Probasisternum (fig. 17) with median carina absent in most species, some with short carina; surface with punctures. Mesospiracular peritreme (fig. 17) with anteromedial margin fused to furcasternum. Elytra shorter to longer than pronotum; humeral angles absent (fig. 14) or present; posterior edge (fig. 14) without row of setae; subapical region without long, thicker, medioposteriorly directed seta near lateral corner (fig. 14). Scutellum without pubescence. Mesosternum without median carina. Mesocoxal acetabulum with marginal carina laterally; carina poorly developed to absent posteriorly and position marked by row of punctures. Intersternal suture present, incomplete, and weakly developed.

Profemur with ridge and slit near middle of ventroanterior surface (fig. 36). Protibia with multiple (14 in an Australian species) combs extending from proximad of middle to near apex; tibia without or with feeble depression on ctenidial surface; apical portion slender and slightly tapered to nearly parallel. Protarsomeres (fig. 76) 1–4 inflated and ventral surface without setose pad (figs. 45, 46); base of tarsomere 1 not surrounded by cupulate protibial apex; tarsomere 4 not expanded beneath tarsomere 5 and apical margin entire or weakly emargin-

ate (figs. 47, 76), not bilobed; tarsomere 5 unmodified and inserted laterad of middle of asymmetrical tarsomere 4; tarsomere 5 with dense pubescence ventrally (figs. 45, 47). Mesotarsomere and metatarsomere 1 (fig. 50) longer than combination of tarsomeres 2 and 3, 2–4, or 2–5.

Abdominal segments without imbricate macrosculpturing (fig. 24). Segment III with or without one paratergite, if paratergite absent then paratergal carina present basally (figs. 22, 23); tergum and sternum III fused or separated by paratergite. Segment VII with tergum and sternum fused basally and with incision leading to small notch at midlateral edge of posterior margin (figs. 33, 34). Segments III to VII with membranous "windows" or "cells" covered with white, opaque membrane in intersegmental membrane at anterior edge of sterna and terga (fig. 24). Sternum I absent. Sterna IV to VII without glandular lobe on anterior margin. Tergum IX (fig. 73) of male and female fused medially; emargination moderately deep, slightly shorter than length of tergum to more than twice length of tergum; lateroapical process (fig. 25) long, slender, moderately strongly curved ventrally, and extending beyond apex of tergum X; lateroapical process fused basally to remainder of segment, but with possible remnant of separation in some species (fig. 25). Tergum X (fig. 73) of male and female with apical margin broadly rounded; base separated from tergum IX.

Gonocoxites fused into large, broad median gonocoxal plate (fig. 74); vulva proximad of (fig. 74) or embedded in gonocoxal plate.

Aedeagus (fig. 75) asymmetrical; parameres present and appressed to median lobe for entire length of paramere, or appressed basally and free distally; basal piece absent.

DISTRIBUTION AND HABITAT: Most species of *Oedichirus* are found in tropical and subtropical regions, a few are known from more temperate regions. In the Old World, *Oedichirus* occurs from southern Europe to South Africa, east to Madagascar and across southern Asia through India, southeastern Asia, to Indonesia, the Philippines, Papua New Guinea, and Australia, China, and Japan. One central Asian species is known (Tajikistan), one is reported from Tasmania, and two from New Caledonia. New World species are known from Mexico and the Caribbean Islands south to Brazil, but have not been found in all the intervening countries.

Collections of *Oedichirus* have been made from leaf litter on the forest floor and moist litter near streams, swamps, or springs. Some species have been collected by sweeping lowland forest vegetation at night. Species are found in lowland forests, many live in montane forests, and occur to as high as 3500 m. Of the 175 species for which elevational data are available, 150 are found at elevations between 1000 and 2999 meters. At least 10 species have been collected at or above 3000 meters elevation; they include: *O. celisianus*, *O. ericeticola*, *O. flavifrons*, *O. luberensis kenyacus*, *O. meruensis*, *O. microphthalmus*, *O. omoanus*, *O. orophilus*, *O. ruwenzoricus*, and *O. uviraensis* (see Fagel, 1971). Two specimens of *Oedichirus simoni* were collected from pine/oak litter in Turkey (Assing, 2004: 683; 2006: 227). Many species are known from few specimens and often only one specimen is collected at a site.

Since so many species of *Oedichirus* are flightless it would seem unlikely to find species in trees or bushes and in fact many specimens were taken from ground litter (see Fagel, 1971). However, Borys Malkin, who for several decades travelled to many remote sites and villages of indigenous peoples in Central and South America after the Second World War, collected 10 specimens, all flightless, of three species of *Oedichirus* in Brazil by sweeping vegetation.

SYNONYMY: *Oedichiranus* was originally described as and has remained a subgenus. The characters for *Oedichiranus* listed by Reitter (1906: 264) to distinguish the subgenus from *Oedichirus* include long elytra, well-developed humeral angles, and a deep depression adjacent to the suture. These features are present in species with fully developed elytra and those species presumably can fly. The depth of the sutural depression and the height of the sutural ridge vary. Examples of species with a shallow to moderately developed sutural depression and sutural ridge include *O. arrowi*, *O. dollmani*, *O. idae*, *O. lewisius*, *O. segmentarius*, *O. strandi*, and *O. zumpti*; included among

examples of species with a strongly developed depression and sutural ridge are *O. latipennis*, *O. longipennis*, *O. oneili*, *O. pendleburyi*, *O. reitteri*, and *O. rhodesianus*. Most species with poorly developed humeral angles lack the sutural depression, or it is poorly developed and the sutural ridge is indistinct or weakly developed. Other than species diagnostic features, no characters unrelated to the possession of wings can be found that distinguish *O. reitteri* from other species of *Oedichirus*, so *Oedichiranus* is herewith synonymized with *Oedichirus*.

Elytrobaeus was described for one Brazilian species by Sahlberg (1847: 801, 802). Fauvel (1875a: 219; 1875b: xvii) and Sharp (1876: 338) synonymized the name with *Oedichirus*; Fauvel did so without comment. Sharp pointed out that the characters purporting to separate it from *Oedichirus* appeared to be "very indefinite." Sharp further stated that Sahlberg placed emphasis "on the last joint of the antennae terminating in a spine." To understand this spine Sharp studied specimens of *Oedichirus paederinus* and found that the terminal antennomere of two females was truncate whereas in the male it was terminated by a slender, long spine or seta. He also observed that the apex of the antennomere appears to be membranous and that the spine can be retracted and so the antennomere is apparently truncate. Sharp's observations are basically correct. Although the "spine" is actually a compact, spiniform pencil of stout, flat setae (fig. 31), it is found in both sexes of all species of *Oedichirus* and, in dried specimens, is retracted into the apex of the antennomere when the dried apex of the antennomere collapses. The length of the pencil may vary. This spiniform pencil is unique to *Oedichirus* and supports the monophyly of the genus and the synonymy of *Elytrobaeus* with *Oedichirus*.

DISCUSSION: Nearly 98% of the 303 described species of *Oedichirus* occur in the Old World. As a result of the intense work of Fagel (1971), Lecoq (1986), and Janák (2003), over 80% of the species are found in subsaharan Africa (147 species) and Madagascar (107 species). The remaining Old World species are in southern Europe (Spain, Italy, and Greece) and North Africa (six species), the western edge of southwestern Asia (two species), India (four species), Sri Lanka (three species), Indochina and Indonesia (five species), China (two species), Japan (four species), Papua New Guinea (eight species), Australia (11 species), and New Caledonia (two species). Only one species is in central Asia (Tajikistan) and two in China (Taiwan, Zhejiang). The four species reported in southern Europe also occur in North Africa. It is probable that the paucity of species outside Africa is an artifact of collecting and that with additional collecting more, perhaps many more, species will be found in all areas except temperate ones. New Caledonia has only two described species, but there are at least six others. Only eight species are known for all of the New World, but there are at least 12 others among a limited number of unidentified specimens.

Certainly more species are to be found for all the tropical and subtropical regions. However, with the exception of Europe, Africa, and Madagascar, the species from the remainder of the world need revision. Although the New World species are being revised (Herman, in prep.), few specimens from few localities are available, so many more species await discovery. Species continue to be described from Madagascar and undoubtedly more will be found in Africa.

Whether more species will be found at the periphery of the distribution of the genus is an open question, so these edges are discussed below. The *Oedichirus* fauna for most of the world is poorly understood and most identifications beyond the type series are suspect and need verification. The preponderance of flightless species in the genus makes likely a large number of species with restricted distributions.

Four North African species are in southern Europe in Italy (*O. oedypus* and *O. paederinus*), Spain (*O. paederinus* and *O. unicolor*), and Greece (*O. terminatus*). Two other species, *O. pardoi* Outerelo and Gamarra from Morocco, and *O. simoni* Eppelsheim from Israel, Lebanon, and Turkey; additional collecting may extend the range of these species. The species in Europe are the northern edge of the range of North African species.

The northernmost central Asian record for the genus is in Tajikistan (*O. reitteri*); the

species also occurs in Afghanistan, Turkey, and Cyprus.

Five species are reported from Japan (*O. chapmani*, *O. idae*, *O. kiuchii*, *O. kuroshio*, and *O. lewisius*). Only *O. lewisius* is recorded from Korea. For Japan the species are reported from the southernmost islands (Iriomote and Ishigaki; Hayashi, 1989) north to Kyushu, Shikoku, and southern Honshu and various islands between. Hayashi (1989) identified specimens from southern islands of Japan as *O. chapmani* Cameron, a species originally reported from Vietnam. Nothing in the discussion or redescription of *O. chapmani* suggests that Hayashi studied the type of the species, or had available reliably identified material. Furthermore, Cameron's description of *O. chapmani*, which was based on one specimen, is terse, including no illustrations, no description of the aedeagus or male external secondary sexual characteristics, nor even a statement as to the sex of the individual. For the preceding reasons and because of the great distance between Japan and Vietnam, records of *O. chapmani* from Japan need verification.

For China only *O. flammeus* (Zhejiang) and *O. kuroshio* (Taiwan) are known; the latter species is also in Japan and the former is the only record of the genus on mainland China. Given that most species of the genus occur in tropical and subtropical regions, additional species might be found in such areas of China.

Eleven species are reported from Australia and, as one would expect, all are along the periphery of the continent. Based only on the type localities, six species are from the tropical and subtropical regions of the north in Queensland (*O. cribricollis*, *O. cribriventer*, *O. grandis*, *O. intricatus*, and *O. paederoides*) and Western Australia (*O. terminalis*). Four are from the more temperate south in South Australia (*O. andersoni*), New South Wales (*O. pictipes*), Victoria (*O. cribripennis*), and Victoria and Tasmania (*O. tricolor*). The type locality of the eleventh species (*O. rubricollis*) is simply Australia.

Five Australian species (*O. cribricollis*, *O. cribripennis*, *O. cribriventer*, *O. pictipes*, and *O. terminalis*) are known only from the type locality. The remaining species are known from additional sites. The Australian species have not been revised and since perhaps 90% of the species of the genus are flightless and tend to have restricted distributions, the same is likely to be true of the Australian species. Some species reported from multiple, widely separated localities may be misidentified. For example, the syntypes of *O. tricolor* Lea are reported from both Victoria and Tasmania, but the species is stated to be apterous (Lea, 1904), so the syntypes may be different species. *Oedichirus andersoni* Blackburn is listed from both Western Australia (Swan River, which is near Perth) (Lea, 1904: 63) and South Australia (Port Lincoln) (Blackburn, 1888: 10); these localities are about 1800 km apart, so if *O. andersoni* is flightless then these specimens may be different species. *Oedichirus paederoides* is said to be from southern Queensland (Gayndah, NNW of Brisbane) (MacLeay, 1873: 147) and from New South Wales (Clarence River); the species is said to be winged, so these records, which are separated by about 480 km, may be correct. The Australian species are in great need of revision.

All the New World species are restricted to the Neotropical Region, but only eight have been described, one from Costa Rica, the others from Brazil. The poverty of species is the result of the lack of collecting. In a forthcoming article 10 new species will be described from Brazil, Bolivia, Peru, Ecuador, Mexico, and Dominican Republic (Herman, in prep.), but all are represented by few specimens and for most species only one locality is known. Collections of more specimens from more localities will result in discovery of many more new Neotropical species.

As is found in species of a number of staphylinid genera, some *Oedichirus* mimic a color pattern seen in many species of *Paederus* in which the head, elytra, and abdominal apex are black or metallic dark blue and the remaining regions are orange to reddish orange. Among some of the *Oedichirus* species with this color pattern are: *O. arrowi*, *O. bicolor*, *O. cameronianus*, *O. desaegerianus*, *O. eppelsheimianus*, *O. fortepunctatus*, *O. garambanus*, *O. idae*, *O. katanganus*, *O. kivuensis*, *O. lamotteanus*, *O. latipennis*, *O. leleupianus*, *O. lewisius*, *O. longipennis*, *O. nimbaensis*, *O. obscuripes*, *O.*

oneili, *O. paederinus*, *O. problematicus*, *O. reitteri*, *O. rhodesianus*, *O. segmentarius*, *O. strandi*, *O. terminatus*, *O. uelensis*, *O. villiersi*, and *O. zumpti*. All but four of these species are from Africa; two are from Japan, one is from India, one is from Central Asia; one of the African species is also found in southern Europe. All but one of these species, *O. paederinus*, have fully developed elytra and may be capable of flight. All of the species fall into "Section III" (species lacking the pronotal marginal ridge) of the three groupings proposed by Fagel (1971: 129–130). There are certainly other species with this color pattern, but I recorded this feature inconsistently and have not seen all the species. According to Coiffait (1978b: 330, 332) two species from the Mediterranean Region, *O. oedypus* and *O. simoni*, have this color pattern. I have seen no Australian species so colored, but the head and apical abdominal segments of *O. paederoides* are reported to be black and the basal three abdominal segments reddish. The color of the elytra was not stated (MacLeay, 1873: 147), but the name is suggestive and the species may fly. As yet no New World species are known that mimic the *Paederus* color pattern, although *O. neotropicus* is close.

Few keys to species have been published. Fagel (1971) published a key to the sub-Saharan African species. Lecoq (1986) published another for the species known to then for Madagascar, but many others have been described since. Coiffait (1978b: 329–330) published one for the six species of the Western Palaearctic Region and Cameron (1931: 25) for eight Indian species.

Species Included and Material Examined

abdominalis Boheman – sp (FMNH) . . . . . .South Africa
abyssinicus Fagel – Lit. Att. [Ethiopia]
aethiopopygus Fagel – H (MRAC). . . D.R. Congo
alatus Nietner – sp (BMNH) . . . . . Sri Lanka
ampamoho Janák – Lit. Att. [Madagascar]
analis Lecoq – Lit. Att. [Madagascar]
andapanus Lecoq – Lit. Att. [Madagascar]
andersoni Blackburn – Syn (BMNH). . . Australia
andringitra Janák – Lit. Att. [Madagascar]
andringitranus Jarrige – Lit. Att. [Madagascar]
angavokeliensis Lecoq – Lit. Att. [Madagascar]
angolensis Fagel – H (MRAC). . . . . Angola
anosibensis Lecoq – Lit. Att. [Madagascar]
anosyanus Lecoq – Lit. Att. [Madagascar]
antitra Janák – Lit. Att. [Madagascar]
anularis Lecoq – Lit. Att. [Madagascar]
appendiculatus Lecoq – Lit. Att. [Madagascar]
arrowi Bernhauer – Syn (FMNH) . . . . . Zambia
bacillus Fagel – H (MRAC). . . . . D.R. Congo
balarombe Janák – Lit. Att. [Madagascar]
balazuci Lecoq – Lit. Att. [Madagascar]
baloghi Last – Lit. Att. [Papua New Guinea]
bambusicola Fagel – H (MRAC) . . . . . Kenya
bara Janák – Lit. Att. [Madagascar]
barbertonensis Fagel – P (MRAC) . . . South Africa
basilewskyanus Fagel – H (MRAC) . . . Rwanda
beltermanni Bernhauer – H, sp (FMNH) . . . . . Cameroon
bertiae Lecoq – Lit. Att. [Madagascar]
betschi Jarrige – Lit. Att. [Madagascar]
betsileo Janák – Lit. Att. [Madagascar]
bicolor Fagel – H (MRAC) . . . . . D.R. Congo
bifidus Lecoq – Lit. Att. [Madagascar]
biguttatus Fauvel – Lit. Att. [Mozambique]
birmanus Fauvel – Syn (IRSN) . . . . . Myanmar
biroi Last – Lit. Att. [Papua New Guinea]
blukwaensis Fagel – H (MRAC) . . . . D.R. Congo
boehmi Bernhauer – H, sp (FMNH). . . . . Brazil
bonibona Janák – Lit. Att. [Madagascar]
bonsae Jarrige – Lit. Att. [Madagascar]
brachelytratus Lecoq – Lit. Att. [Madagascar]
brunneicolor Fagel – H (MRAC) . . . . D.R. Congo
brunneus Wendeler – Syn (MNHB) . . . . . Brazil
bulirschi Janák – Lit. Att. [Madagascar]
burgeoni Bernhauer – Syn (FMNH, MRAC). . . . . D.R. Congo
cameronianus Fagel – H (MRAC) . . . D.R. Congo
camerounensis Fagel – Lit. Att. [Cameroon]
capensis Fagel – P (MRAC) . . . . . South Africa
capicola Fagel – P (MRAC) . . . . . South Africa
carayoni Lecoq – Lit. Att. [Madagascar]
carolinorum Janák – Lit. Att. [Madagascar]
celisianus Fagel – H (MRAC) . . . . D.R. Congo
chapmani Cameron – H (BMNH) . . . . Vietnam
clementi Lecoq – Lit. Att. [Madagascar]
congoensis Bernhauer – Syn (FMNH). . . . . D.R. Congo
conspicuus Fagel – H (MRAC) . . . D.R. Congo
crebrepunctatus Fagel – H (MRAC) . . . . . D.R. Congo
cribricollis Lea – Lit. Att. [Australia]
cribripennis Lea – Lit. Att. [Australia]
geniculatus Lea
cribriventer Lea – Lit. Att. [Australia]
curticornis Fagel – Lit. Att. [D.R. Congo]
curtipennis Fagel – H (MRAC) . . . D.R. Congo
curtulus Lecoq – Lit. Att. [Madagascar]
densoides Fagel – Lit. Att. [South Africa]
densus Bernhauer – H (FMNH). . . South Africa
denticulatus Lecoq – Lit. Att. [Madagascar]

depressipennis Lecoq – Lit. Att. [Madagascar]
desaegerianus Fagel – H (MRAC) . . . D.R. Congo
descarpentriesi Jarrige – Lit. Att. [Madagascar]
didyanus Janák – Lit. Att. [Madagascar]
dimidiatus Eppelsheim – Lit. Att. [India]
elegans Cameron
dollmani Bernhauer – Syn (FMNH) . . . . Zambia
dubius Jarrige – Lit. Att. [Madagascar]
duflosi Lecoq – Lit. Att. [Madagascar]
dunayi Janák – Lit. Att. [Madagascar]
elgonensis Fagel – H (MRAC) . . . . . Kenya
ensifer Lecoq – Lit. Att. [Madagascar]
epiphyticola Janák – Lit. Att. [Madagascar]
eppelsheimianus Fagel – H (MRAC) . . . . . Mali
ericeticola Fagel – H (MRAC) . . . . D.R. Congo
excellens Cameron – sp (BMNH) . . . . Indonesia
fageli Lecoq – Lit. Att. [Madagascar]
femoralis Lecoq – Lit. Att. [Madagascar]
filicornis Fagel – H (MRAC) . . . . . D.R. Congo
fitorahana Janák – Lit. Att. [Madagascar]
flammeus Koch – Lit. Att. [China]
flavifrons Fagel – H (MRAC) . . . . D.R. Congo
flavipes Lecoq – Lit. Att. [Madagascar]
foveicollis Quedenfeldt – sp (FMNH) . . . . . Madagascar
fortepunctatus Fagel – H (MRAC) . . . D.R. Congo
franzi Lecoq – sp (BMNH) . . . . . Madagascar
furcatus Lecoq – Lit. Att. [Madagascar]
garambanus Fagel – H (MRAC) . . . . D.R. Congo
geniculatus (R. Sahlberg) – sp (FMNH) . . . Brazil
gladiatus Lecoq – sp (BMNH) . . . . . Madagascar
gracilis Fagel – H (MRAC) . . . . . D.R. Congo
grandis Bernhauer – Syn (FMNH) . . . . Australia
graskopensis Fagel – P (MRAC) . . . South Africa
griveaudi Lecoq – Lit. Att. [Madagascar]
hammondi Lecoq – H (BMNH) . . . . Madagascar
hanglipbosensis Fagel – Lit. Att. [South Africa]
haribe Janák – Lit. Att. [Madagascar]
hewitti Bernhauer – H (FMNH) . . . South Africa
histrio Lecoq – Lit. Att. [Madagascar]
humansdorpensis Fagel – P (MRAC) . . . . . .South Africa
humicola Fagel – Lit. Att. [South Africa]
idae Sharp – Syn (BMNH), sp (FMNH) . . . Japan
ingogoensis Fagel – Lit. Att. [South Africa]
insolitus Fagel – H (MRAC) . . . . . D.R. Congo
insularis Lecoq – Lit. Att. [Madagascar]
intermixtus Fagel – H (MRAC) . . . D.R. Congo
intricatus Fauvel – H (IRSN) . . . . . Australia
itombwensis Fagel – H (MRAC) . . . . D.R. Congo
ivohibensis Jarrige – Lit. Att. [Madagascar]
janae Janák – Lit. Att. [Madagascar]
jarrigei Lecoq – Lit. Att. [Madagascar]
jenisi Janák – Lit. Att. [Madagascar]
jocquei Lecoq – Lit. Att. [Comoros]
kaboboensis Fagel – H (MRAC) . . . . D.R. Congo
kahololoensis Fagel – H (MRAC) . . . D.R. Congo
kahuziensis Fagel – H (MRAC) . . . D.R. Congo
incertus Fagel [ssp] – H (MRAC) . . D.R. Congo
kalamba Janák – Lit. Att. [Madagascar]
kalehensis Fagel – H (MRAC) . . . . D.R. Congo
katanganus Fagel – H (MRAC) . . . D.R. Congo
katbergensis Fagel – H (BMNH), P (MRAC) . . . . . .South Africa
keanus Fagel – Lit. Att. [D.R. Congo]
kidundaensis Fagel – H (MRAC) . . . . . Tanzania
kilimanjarensis Fagel – H (MRAC) . . . Tanzania
kimbiensis Fagel – H (MRAC) . . . . D.R. Congo
kirunguensis Fagel – H (MRAC) . . D.R. Congo
kiuchii Sawada – Lit. Att. [Japan]
kivuensis Fagel – H (MRAC) . . . . . D.R. Congo
kolbei Fauvel – L, Pl (IRSN), sp (BMNH) . . . . . Madagascar
kolwezienus Fagel – Lit. Att. [D.R. Congo]
kuroshio Hayashi – Lit. Att. [Japan, Taiwan]
kyandolirensis Fagel – H (MRAC) . . . D.R. Congo
lamotteanus Fagel – sp (MRAC) . . . . . Guinea
laticeps Lecoq – Lit. Att. [Madagascar]
latipennis Bernhauer – Syn (FMNH) . . . Zambia
lecoqi Janák – Lit. Att. [Madagascar]
leleupianus Fagel – H (MRAC) . . . D.R. Congo
levasseuri Lecoq – Lit. Att. [Madagascar]
lewisius Sharp – H (BMNH), sp (FMNH) . . . . . .Japan
loksai Last – Lit. Att. [Papua New Guinea]
longicornis Lecoq – Lit. Att. [Madagascar]
longipennis Kraatz – L (SDEI), sp (FMNH) . . . . . "India orientali", Indonesia
longipilis Fagel – H (MRAC) . . . . D.R. Congo
luberensis Fagel – H (MRAC), sp (BMNH) . . . . . D.R. Congo
kalongensis Fagel [ssp] – H (MRAC) . . . . . D.R. Congo
obscurellus Fagel [ssp] – H (MRAC) . . . . . D.R. Congo
nigrinus Fagel [ssp] – Lit. Att. [D.R. Congo]
kenyacus Fagel [ssp] – H (MRAC) . . . . Kenya
imitator Fagel [ssp] – H (MRAC) . . . . . Kenya
lucidiceps Fagel – P (MRAC) . . . . South Africa
lugubris Fagel – H (MRAC) . . . . . D.R. Congo
luikoensis Fagel – H (MRAC) . . . . D.R. Congo
luvubuensis Fagel – H (MRAC) . . . D.R. Congo
lwiroensis Fagel – H (MRAC) . . . . D.R. Congo
madagascariensis Bernhauer – H (FMNH) . . . . . Madagascar
madegassus Fagel – Lit. Att. [Madagascar]
mafana Janák – Lit. Att. [Madagascar]
magnus Last – Lit. Att. [Papua New Guinea]
mahasoa Janák – Lit. Att. [Madagascar]
malalaka Janák – Lit. Att. [Madagascar]
mandibularis Lecoq – Lit. Att. [Madagascar]
mangabensis Lecoq – Lit. Att. [Madagascar]
manarivo Janák – Lit. Att. [Madagascar]
mariepskopensis Fagel – P (MRAC) . . . . . .South Africa
mavo Janák – Lit. Att. [Madagascar]

melanurus Eppelsheim – Lit. Att. [Cape Verde Islands, Guinea, Ghana, Ethiopia, Tanzania, Namibia]
meruensis Fagel – H (MRAC) . . . . . Tanzania
microcephalus Fagel – P (MRAC). . . South Africa
microphthalmus Fagel – Lit. Att. [Kenya]
minimus Bernhauer –Syn (FMNH) . . . South Africa
minor Cameron – Syn (BMNH). . . . . Sri Lanka
minutus Fagel – P (MRAC). . . . . South Africa
miskoi Janák – Lit. Att. [Madagascar]
mokotoensis Fagel – H (MRAC) . . . D.R. Congo
moloensis Fagel – H (MRAC) . . . . . Kenya
montanus Last – Lit. Att. [Papua New Guinea]
monticola Fagel – H (MRAC) . . . . D.R. Congo
surdus Fagel [ssp] – H (MRAC) . D.R. Congo
montishoyoensis Fagel – H (MRAC). . . . . D.R. Congo
moraveci Janák – Lit. Att. [Madagascar]
muscorum Jarrige – Lit. Att. [Madagascar]
mwengensis Fagel – H (MRAC). . . D.R. Congo
natalensis Fagel – Lit. Att. [South Africa]
neotropicus Blackwelder
pictipes Bierig – Syn (FMNH) . . . Costa Rica
newtonianus Fagel – H (MRAC) . . . South Africa
niger Cameron – Syn (BMNH), Syn, sp (FMNH) . . . . . India
nigriceps Fagel – H (MRAC). . . . . D.R. Congo
nigrolineatus Lecoq – Lit. Att. [Madagascar]
nimbaensis Fagel – sp (MRAC) . . . . Ivory Coast
nitidiventris Fagel – Lit. Att. [Kenya]
nodieri Lecoq – Lit. Att. [Madagascar]
nordicus Lecoq – sp (BMNH) . . . . . Madagascar
nosykombanus Lecoq – Lit. Att. [Madagascar]
novaeguineae Wendeler – Lit. Att. [Papua New Guinea]
novus Jarrige – Lit. Att. [Madagascar]
noyesi Lecoq – H (BMNH) . . . . . Madagascar
nyakageraensis Fagel – H (MRAC). . . D.R. Congo
nyalengwensis Fagel – H (MRAC) . . . D.R. Congo
obscuripes Fagel – H (MRAC). . . . D.R. Congo
obscurus Fagel – P (MRAC) . . . . . South Africa
obsoletus Lecoq – Lit. Att. [Madagascar]
occipitopunctatus Lecoq – Lit. Att. [Madagascar]
oedypus Rottenberg – Syn (SDEI) . . . . . Italy
walkeri Fauvel
ohausi Wendeler – Syn (MNHB) . . . . . Brazil
oldeaniensis Fagel – H (MRAC). . . . . Tanzania
omoanus Fagel – P (MRAC) . . . . . Kenya
oneili Péringuey – sp (FMNH). . . . . Zimbabwe?
opacus Lecoq – Lit. Att. [Madagascar]
optatus Sharp – Syn (BMNH), sp (FMNH) . . . . . Brazil
orophilus Fagel – H (MRAC) . . . . D.R. Congo
proximus Fagel [ssp] – H (MRAC) . . . . . D.R. Congo
oundaensis Last – Lit. Att. [New Caledonia]
paederinus Erichson – sp (FMNH) . . . . . Algeria, Italy, Morocco, Spain, Tunisia
quedenfeldtii Schaufuss
paederoides W.J. MacLeay – Lit. Att. [Australia]
papanganus Lecoq – Lit. Att. [Madagascar]
papuanus Cameron – Syn (BMNH) . . . . . Papua New Guinea
pardoi Outerelo and Gamarra – Lit. Att. [Morocco]
parviceps Fagel – Lit. Att. [South Africa, Zanzibar]
parvus Lecoq – Lit. Att. [Madagascar]
pauliani Lecoq – Lit. Att. [Madagascar]
pearceanus Fagel – H (MRAC) . . . . . Zimbabwe
pendleburyi Cameron – Syn (BMNH), sp (FMNH) . . . . . Malaysia, Singapore
penicillatus Jarrige – Lit. Att. [Madagascar]
pictipes Oke – Lit. Att. [Australia]
pietersburgensis Fagel – P (MRAC) . . . . . South Africa
problematicus Fagel – H (MRAC) . . . . . D.R. Congo
profundepunctatus Fagel – H (MRAC) . . . . . D.R. Congo
pubescens Lecoq – Lit. Att. [Madagascar]
puguensis Bernhauer – H, sp (FMNH) . . . . . Tanzania
pumilus Lecoq – Lit. Att. [Madagascar]
puncticollis Fagel – H (MRAC) . . . D.R. Congo
pyricollis Lea – Lit. Att. [Papua New Guinea]
radama Janák – Lit. Att. [Madagascar]
ranavalona Janák – Lit. Att. [Madagascar]
ranomafanus Janák – P (MNHB) . . . Madagascar
reitteri Bernhauer – Syn, sp (FMNH). . . . . Iraq, Tajikistan
dimidiatus Reitter
reticulatus Fagel – H (MRAC). . . . D.R. Congo
rhodesianus Bernhauer – Syn, sp (FMNH), sp (MRAC) . . . . . Zambia, D.R. Congo
elegantulus Fagel [ssp] – H (MRAC) . . . . . D.R. Congo
ruandaensis Fagel – H (MRAC). . . . . Rwanda
rubricollis Fauvel – H (BMNH) . . . . . Australia
ruficeps Kraatz – L (SDEI) . . . ''India orientali''
rufitarsis Fauvel – H (IRSN) . . . . . Madagascar
rufotestaceus Bernhauer – H (FMNH). . . Sri Lanka
(Note: Holotype missing head and prothorax.)
rufus Fauvel – Lit. Att. [Zanzibar]
rugegensis Fagel – H (MRAC). . . . . Rwanda
ruteri Lecoq – Lit. Att. [Madagascar]
ruwenzoricus Fagel – H (MRAC). . . D.R. Congo
sambavanus Lecoq – Lit. Att. [Madagascar]
sanctamariae Lecoq – Lit. Att. [Madagascar]
satyrus Lecoq – Lit. Att. [Madagascar]
schultheissi Fauvel – Syn (IRSN),sp (SDEI) . . . . . Indonesia
sedilloti Fauvel – Syn (IRSN) . . . New Caledonia
segmentarius Bernhauer – Pl, sp (FMNH), L (MRAC) . . . . . D.R. Congo
(Note: Fagel [1971: 417] cited the specimen he examined from Ituri as ''type,'' but it is a

lectotype designation under ICZN, 1999: Article 74.5.)
senegalensis (Laporte) – Lit. Att. [Senegal, Cape Verde Islands]
serrulatus Lecoq – Lit. Att. [Madagascar]
silvestris Lecoq – Lit. Att. [Madagascar]
similis Fagel – H (MRAC) . . . . . D.R. Congo
simillimus Fagel – Lit. Att. [South Africa]
simoni Eppelsheim – Lit. Att. [Israel, Lebanon, Turkey]
simplex Lecoq – Lit. Att. [Madagascar]
sogai Jarrige – Lit. Att. [Madagascar]
sparsepunctatus Fagel – H (MRAC) . . . . . D.R. Congo
sparsipennis Bernhauer – Syn (FMNH). . . Brazil
sparsutus Fagel – H (MRAC) . . . . . Rwanda
spectabilis Fagel – H (MRAC). . . . D.R. Congo
speculifrons Bernhauer – Syn, sp (FMNH) . . . . . .Brazil
splendidus Lecoq – Lit. Att. [Madagascar]
stilicinus Gerstaecker – Lit. Att. [Ethiopia, Tanzania, Zanzibar]
ignicollis Fauvel
strandi Bernhauer – H (FMNH) . . . . . Tanzania
strictus Fagel – H (MRAC). . . . . D.R. Congo
subdensus Fagel – Lit. Att. [South Africa]
summicola Fagel – H (MRAC) . . . . . Tanzania
tenuis Fagel – P (MRAC) . . . . . South Africa
terminalis Lea – sp (BMNH) . . . . . Australia
terminatus Erichson – Syn (MNHB), sp (BMNH) . . . . . Nigeria, Sierra Leone
rubronotatus Pic
testaceus Fagel – Lit. Att. [South Africa]
tigrinus Lecoq – Lit. Att. [Madagascar]
transvaalensis Fagel – P (MRAC). . . . South Africa
triangulipennis Fagel – H (MRAC). . . D.R. Congo
tricolor Lea – sp (FMNH, BMNH, SDEI) . . . . . Australia
tronqueti Lecoq – Lit. Att. [Madagascar]
tshiaberimuensis Fagel – H (MRAC) . . . . . D.R. Congo
tshuruyagaensis Fagel – H (MRAC) . . . Rwanda
turneri Bernhauer – Syn (FMNH) . . . South Africa
uelensis Fagel – H (MRAC) . . . . . D.R. Congo
uhligi Janák – Lit. Att. [Madagascar]
uluguruensis Fagel – H (MRAC) . . . . . Tanzania
uncinatus Lecoq – Lit. Att. [Madagascar]
unicolor Aubé – sp (FMNH, SDEI) . . . . . Spain
unicus Fagel – H (MRAC) . . . . . Tanzania
uniformis Fagel – H (MRAC) . . . . D.R. Congo
usambarae Bernhauer – H (FMNH), sp (MRAC) . . . . . Tanzania
uviraensis Fagel – H (MRAC) . . . . D.R. Congo
vadoni Lecoq – Lit. Att. [Madagascar]
variabilis Fagel – H (MRAC) . . . . D.R. Congo
variegatus Fagel – sp (BMNH, MRAC). . . . . South Africa
variipennis Fagel – H (MRAC) . . . D.R. Congo
varius Lecoq – Lit. Att. [Madagascar]
vaovao Janák – Lit. Att. [Madagascar]
ventralis Fauvel – Lit. Att. [Madagascar]
villiersi Cameron – Pl (BMNH), sp (MRAC) . . . . . Senegal, Chad
vohitrosa Janák – Lit. Att. [Madagascar]
witteanus Fagel – H (MRAC) . . . . D.R. Congo
woodbushensis Fagel – P (MRAC) . . . South Africa
yangambiensis Fagel – H (MRAC) . . . D.R. Congo
zanzibaricus Fagel – Lit. Att. [Zanzibar]
zumpti Bernhauer – Syn (FMNH) . . . Cameroon

UNDETERMINED SPECIMENS: Old World: Australia, Borneo, China, Indonesia, Madagascar, Malaysia, New Caledonia, Philippines, Zambia, Zimbabwe, Singapore, South Africa, Zaire.

New World: Brazil, Costa Rica, Ecuador, Mexico, Peru.

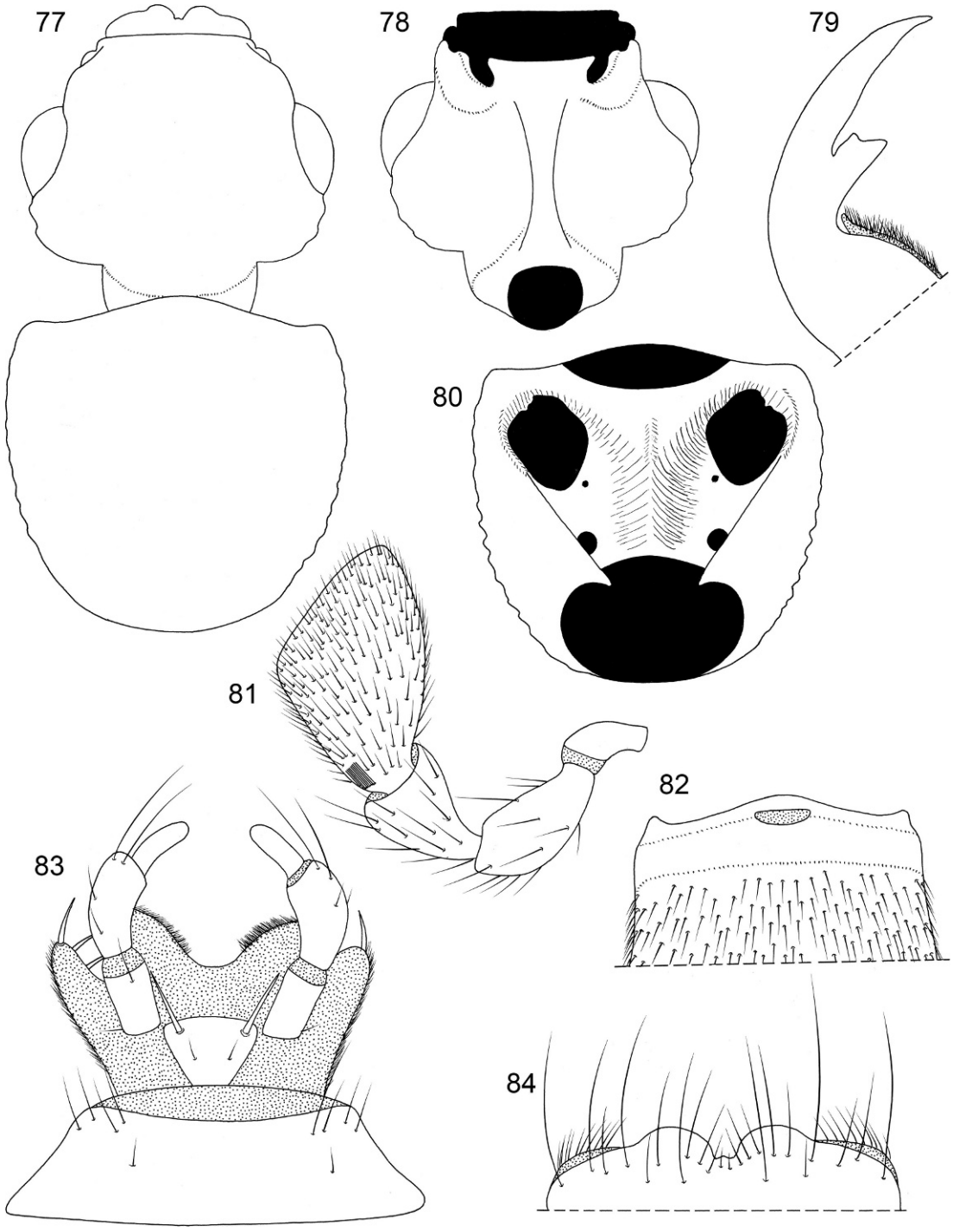
DISSECTIONS: Complete dissection: *Oedichirus* nr. *pictipes* (1 male, 1 female); *Oedichirus geniculatus* (1 male, 1 female).

Oedodactylus Fairmaire and Germain
Figures 4, 77–89

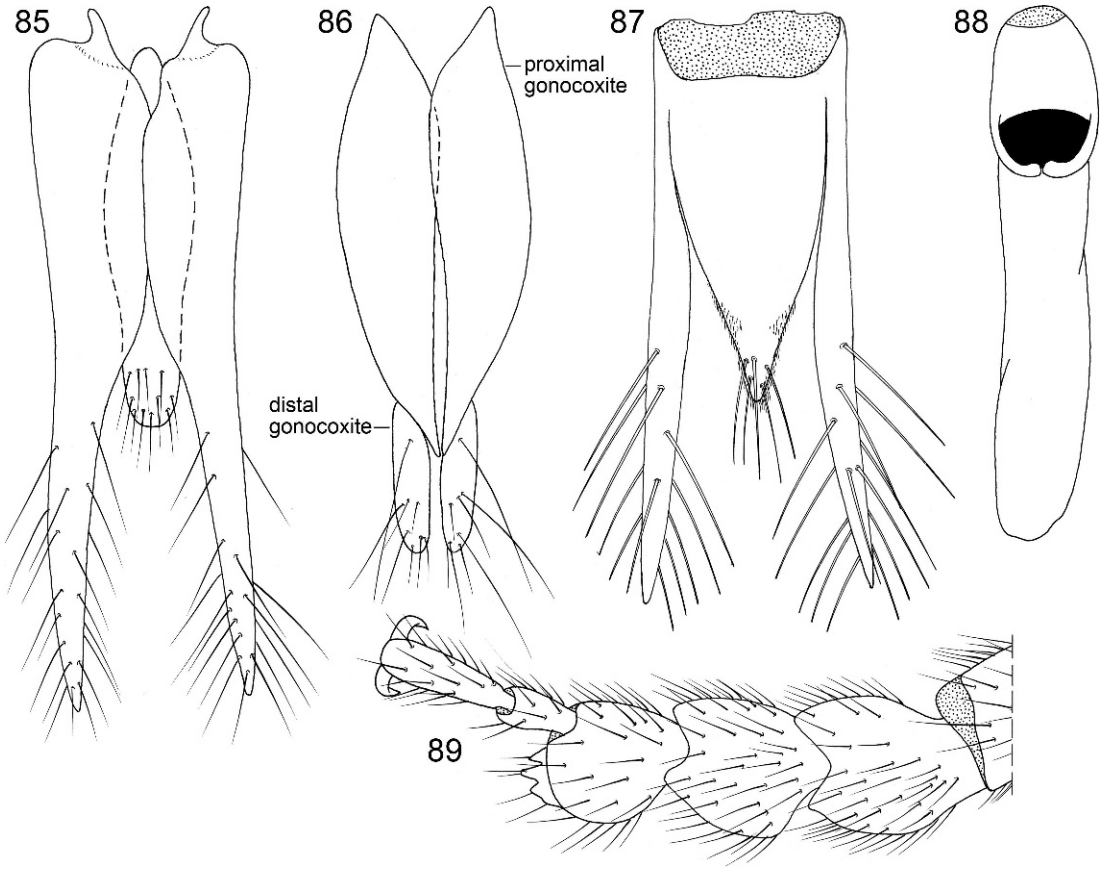
Oedodactylus Fairmaire and Germain, 1861: 441. Type species: *Oedodactylus fuscobrunneus* Fairmaire and Germain, 1861: 441, fixed by R. Lucas (1920: 452) by subsequent designation when he cited only one of the two originally included species.

— Fauvel, 1867: 2, 16 (key; characters). — Fauvel, 1868: 7, 21 (key; characters). — Gemminger and Harold, 1868: 629 (catalog; world). — Sharp, 1876: 337 (notes; Brazilian species). — Duvivier, 1883: 176 (catalog). — Sharp, 1886: 630 (Mexican species). — Bernhauer and Schubert, 1912: 198 (catalog; world). — Bruch, 1915: 493 (catalog; Argentina). — Bruch, 1928: 440 (catalog; Argentina). — Scheerpeltz, 1933: 1213 (catalog; world). — Blackwelder, 1944: 130 (checklist; Latin America). — Blackwelder, 1952: 270 (type species). — Coiffait and Saiz, 1968: 369 (characters; Chilean species; cited as *Aedodactylus*). — Navarrete-Heredia et al., 2002: 293 (characters; notes; list of Mexican species).

DIAGNOSIS: *Oedodactylus* can be separated from all other Procirrina except *Pseudoprocirrus* by the inflated basal three protarsomeres (fig. 89); the basal four are swollen in other genera (fig. 92). Both *Oedodactylus* and *Pseudoprocirrus* have a paratergite on each



Figs. 77–84. *Oedodactylus* near *anceps*. **77.** Head and pronotum. **78.** Head, ventral. **79.** Mandible, left. **80.** Prothorax, ventral. **81.** Maxillary palpus. **82.** Sternum IV, base. **83.** Labium. **84.** Labrum.



Figs. 85–89. *Oedodactylus* near *anceps*. **85.** Tergum and sternum IX, ventral, male. **86.** Proximal and distal gonocoxites. **87.** Terga IX and X, female. **88.** Aedeagus, ventral. **89.** Protarsomeres 1–5, right, dorsal.

side of abdominal segment III. *Oedodactylus* lacks an interantennal, transverse frontoclypeal ridge, the gular sutures are most approximate just proximad of the middle (fig. 78), tergum and sternum VIII have a transverse, basal ridge, and terga IX and X are fused (fig. 87). *Pseudoprocirrus* has a transverse, interantennal, frontoclypeal ridge, the gular sutures are most approximate medially, tergum and sternum VIII lack a transverse, basal ridge, and terga IX and X are separate (fig. 103). *Oedodactylus* is a New World tropical genus and *Pseudoprocirrus* is African. Some species of *Oedichirus* have paratergites on abdominal segment III, but in *Oedichirus* the tergum and sternum of segment VII are fused basally whereas in *Oedodactylus* they are separated. The presence of setae on the edge of the posterior margin of the elytra will separate *Oedodactylus* from *Procirrus*, *Oedichirus*, *Palaminus*, and *Paraprocirrus*.

DESCRIPTION: Head not pedunculate, wider than long (fig. 77); frontoclypeus without subapical, interantennal, transverse ridge; postocular lateral margin broadly rounded to basal angles or to neck; postocular lateral margin moderately long; basal angle present and strongly rounded (fig. 77) or absent (fig. 4); basal margin of head truncate or indistinguishable from lateral margin, with or without marginal ridge, and with median portion feebly to moderately emarginate anterior to neck. Neck across nuchal constriction one half to two thirds of greatest postocular width of head; nuchal

groove shallow to moderately deep; nuchal ridge present (fig. 77). Eye length longer (fig. 77) to slightly shorter than postocular length of head. Dorsal surface with moderately dense to dense umbilicate punctation. Ventral surface without postocular groove (cf. fig. 2). Gular sutures (fig. 78) separated and present basally; sutures most approximate just proximad of middle. Gula without pubescence. Antennomere 11 about as long as or slightly longer than 10; apex without spinelike pencil of setae. Mandibles with apically bifid denticle (fig. 79); prostheca digitiform apically and with cluster of cuticular processes medially (fig. 79). Maxillary palpus (fig. 81) with palpomere 4 longer than second or third, securiform, broad apically, slightly longer than wide, and compressed. Labium (fig. 83) with glossae separated, apically rounded, long, broad, and with a few cuticular processes on medial margin. Hypopharynx without spinelike setae or lobes on anterior margin; laterodorsal margin with dense cluster of setae; median groove present. Labrum without denticles on anterior margin, but with broad lobe adjacent to emargination (fig. 84). Epipharynx with dense, transverse cluster of cuticular processes across anterior portion and with five setae on lateral portion near anterior margin; median groove present; epipharynx slightly visible anterolaterally in dorsal view.

Prothorax rounded trapezoidal, as long as (fig. 77) to longer than wide (fig. 4); widest near anterior third and with lateral margins rounded and gradually convergent anteriad and posteriad from widest point. Pronotum with umbilicate punctation; punctation dense to moderately dense, uniform, and present on midline in most species, but absent in one. Pronotal marginal ridge present and entire. Notosternal suture absent. Hypomeron with fine microsculpturing and with a few punctures in some species. Postprocoxal lobe long and with a few to many punctures; transverse ridge present or absent; apices widely separated from each other. Probasisternum with median carina present (fig. 80) or absent; surface punctate. Mesospiracular peritreme (fig. 80) with anteromedial margin fused to furcasternum. Elytra longer than pronotum; humeral angles present; posterior edge with row of setae; subapical region without long, thicker, posteromediad directed seta near lateroapical corner. Scutellum with a few setae. Mesosternum with short median carina extending from mesosternal process. Mesocoxal acetabulum with marginal carina laterally and posteriorly. Intersternal suture present and well developed.

Profemur with rounded ridge on proximal half of anteroventral surface. Protibia with multiple (11 in a Venezuelan species) combs extending from near base to tibial apex; tibia with feeble depression on ctenidial surface; apical portion not constricted or enlarged. Protarsomeres 1–3 inflated (fig. 89); base of tarsomere 1 not surrounded by cupulate protibial apex; tarsomere 4 not expanded beneath tarsomere 5, apical margin entire, not bilobed, and with setae ventrally, but without setose pad; tarsomere 4 inserted laterad of middle of apex of asymmetrical third segment; tarsomere 5 sparsely pubescent ventrally. Mesotarsomere 1 longer than 2. Metatarsomere 1 longer than 2–4 combined.

Abdominal segments without imbricate macrosculpturing (cf. fig. 28). Segment III with one paratergite; paratergal carina absent; sternum and tergum III separated by paratergite. Segment VII with tergum and sternum separated. Segments IV to VII without oval ''windows'' in intersegmental membrane. Sternum I present, lightly sclerotized, and medially divided. Sterna IV (fig. 82) through VII with small, median, membrane covered, possibly glandular, slit on anterior margin. Tergum IX with transverse base narrow and fused middorsally (fig. 87); lateroapical process of IX (fig. 85, 87) long, slender, gradually curved ventrally, and extending well beyond apex of tergum X; lateroapical process fused basally to remainder of segment. Tergum X with base fused to base of tergum IX (fig. 87); apical margin attenuate, long, slender, and narrowly rounded apically.

Female genital sclerites separated medially; proximal gonocoxite long, broad, apically acute, and separated from short, setate, apically rounded distal gonocoxite (fig. 86).

Aedeagus (fig. 88) slightly asymmetrical; parameres absent; basal piece absent.

DISTRIBUTION AND HABITAT: *Oedodactylus* is a Neotropical genus collected at scattered localities from Mexico (Morelos and Veracruz States) south to Argentina (Buenos Aires Province) and Chile (Santiago District). I have seen specimens from Mexico, Costa Rica, Venezuela, Guyana, Brazil, Paraguay, Argentina, and Chile, but few specimens from any one place and few in total.

Almost nothing has been reported about the habitat of the species and the species are rarely collected. *Oedodactylus fuscobrunneus* was reported to have been collected from under stones in humid places (Fairmaire and Germain, 1861: 442) and, according to the locality labels, a few specimens of an unnamed Venezuelan species (near *anceps*) were collected at lights.

DISCUSSION: *Oedodactylus* is the only genus in the subtribe with terga IX and X fused (fig. 87). This fusion is unusual in the subfamily.

The similarity of some species of *Oedodactylus* and those of *Pseudoprocirrus* is remarkable, but features of abdominal segments III, IX, and X distinguish them. I dissected only the apical segments of the abdomen of a female of *Pseudoprocirrus arrowi* and only three specimens of two species of *Oedodactylus*. Nonetheless, these few dissections reveal tergum IX of *P. arrowi* to be fused midbasally, the lateroapical processes to be attached to IX despite an incision (fig. 104), and tergum X to be fully separated from IX (fig. 103). Fagel (1971: 49) wrote that *Pseudoprocirrus abyssinicus* possesses a single paramere; he had no males of *P. arrowi*. I have insufficient material of the genus to corroborate Fagel's observation and was unable to study his dissection of *P. abyssinicus*.

The largest, most robust species in the genus is *O. fuscobrunneus* (fig. 4), but the species also differs in other ways. The cephalic and pronotal punctation is not as coarse as for other species, the postocular lateral margin of the head is gradually curved to the neck, the basal angles of the head are absent, the pronotum is long, and the anterior angles are broadly rounded; the neck is about two thirds as wide as the postocular width of the head, but for other species the neck is about half the width. The basal angles of the head and the anterior angles of the pronotum are acute in most species, but rounded in *O. fuscobrunneus*. *Oedodactylus fauveli* is similar to *O. fuscobrunneus*, but the anterior pronotal angles of the former are moderately angulate and the pronotal midline is impunctate.

Revision of the genus is needed, in part to assess the variation described above. Only four species are currently in the genus, but among the few specimens I examined there appear to be additional ones.

SPECIES INCLUDED AND MATERIAL EXAMINED

anceps Sharp – H (BMNH) . . . . . Brazil
aper Sharp – Syn (BMNH) . . . . . Mexico
errans Sharp, transferred to *Stylokyrtus*
fauveli Sharp – Syn (BMNH, FMNH) . . . Mexico
fuscobrunneus Fairmaire and Germain – L (IRSN), Pl? (BMNH), sp (FMNH) . . . Chile, Argentina (Note: It is unclear whether the specimen designated as lectotype is part of the original series. Coiffait and Saiz [1968: 370] designated the lectotype, cited it from Rancagua, and wrote that Fauvel [1868: 22] added the locality to the original locality of "Santiago." These two cities are in different provinces now, but I don't know whether, when the species was collected, both were in the province of Santiago. This discrepancy needs reconciliation.)

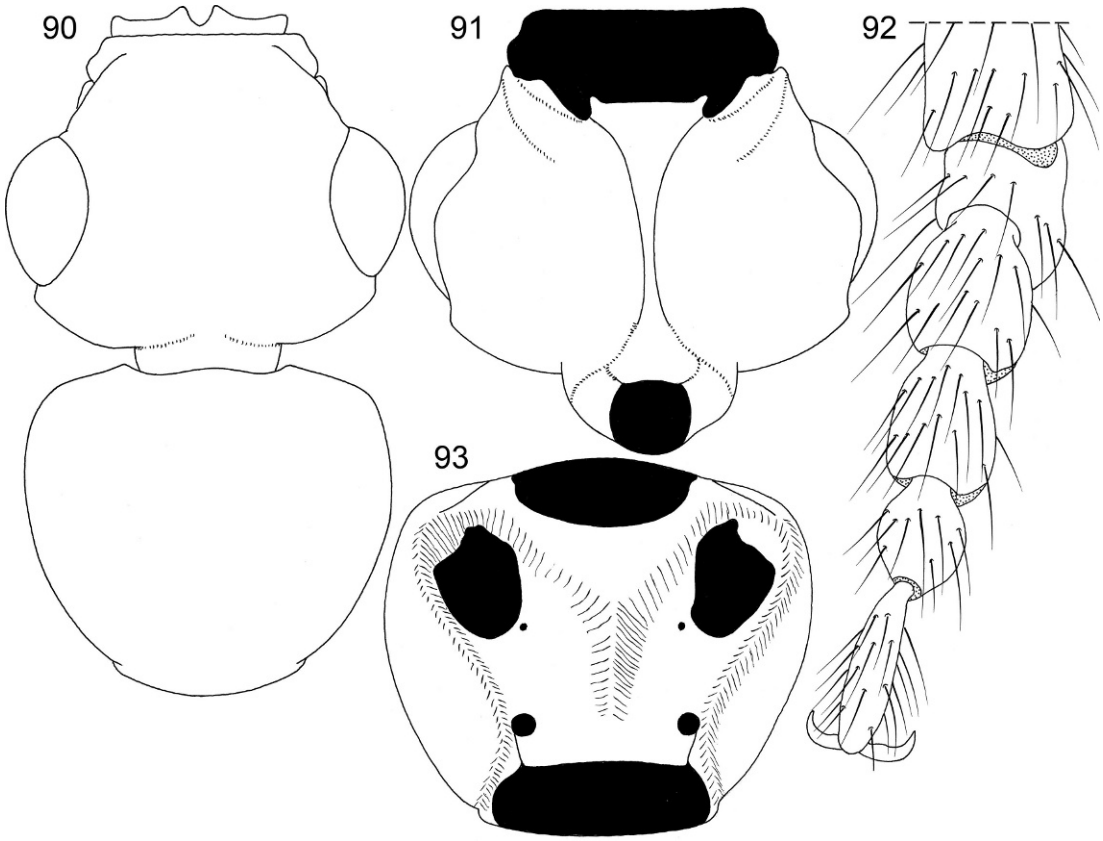
UNDETERMINED SPECIMENS: Argentina, Brazil, Costa Rica, Paraguay, Guyana, Venezuela.

DISSECTIONS: Disarticulation: Undetermined species near *O. anceps* (1 female, Venezuela) and abdominal dissection (1 male, Venezuela); Abdominal dissection *Oedodactylus* near *fauveli* (1 male, Paraguay).

Palaminus Erichson
Figures 5, 10–13, 19–21, 26–29, 40–43, 90–102

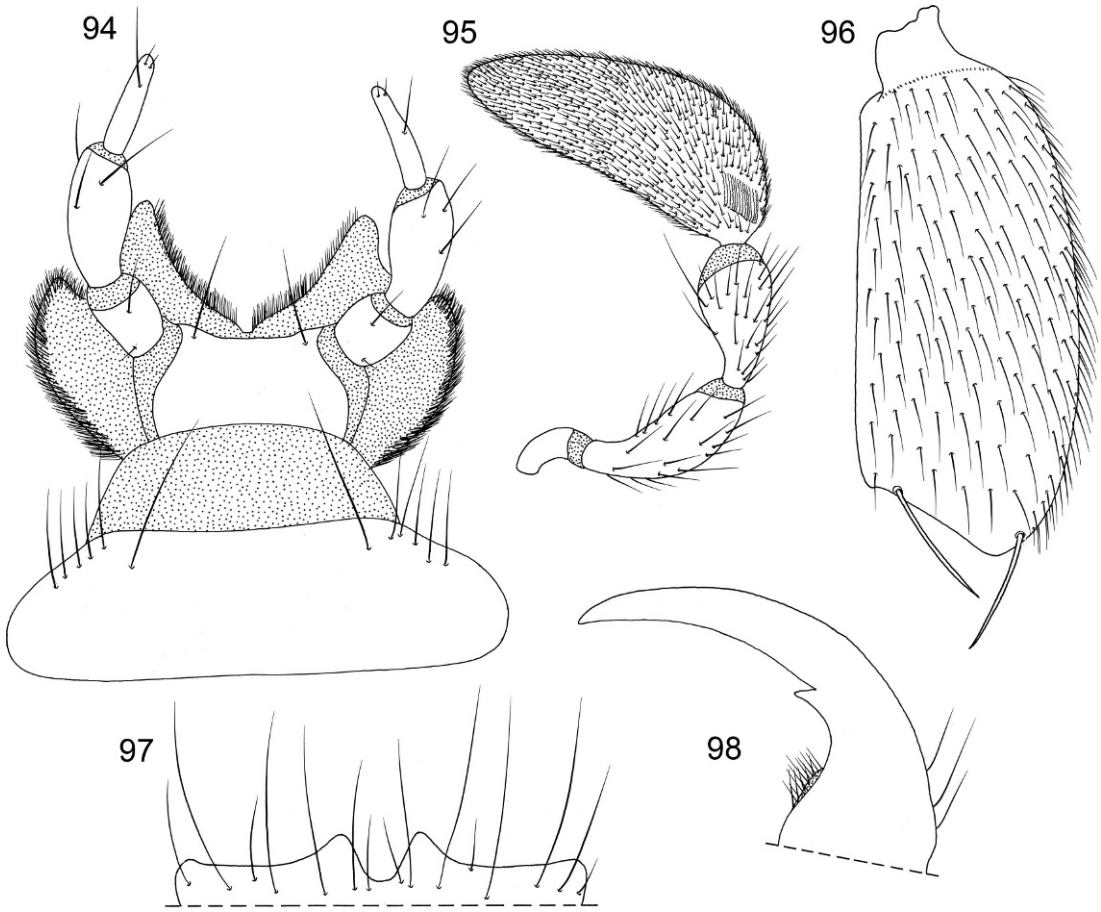
Palaminus Erichson, 1839: 29. Type species: *Palaminus pilosus* Erichson, 1840: 682, fixed by Duponchel (1841: 57) by subsequent designation.

— Erichson, 1840: 681 (characters; first included species: *pilosus*, *piceus*, *variabilis*, *testaceus*). — Lacordaire, 1854: 104 (characters; notes; list of species). — Kraatz, 1857: 666, 668 (notes; key). — LeConte, 1861: 66 (key). — LeConte,



Figs. 90–93. *Palaminus* sp. (Peru). **90.** Head and pronotum. **91.** Head, ventral. **92.** Protarsus, left, dorsal. **93.** Prothorax, ventral.

1863: 25 (list of species; North America). — Gemminger and Harold, 1868: 629 (catalog; world). — Crotch, 1873: 33 (checklist; North America). — Sharp, 1876: 340 (notes; Brazilian species). — Fauvel, 1878b: 225 (characters; notes; New Guinea species). — Duvivier, 1883: 175 (catalog). — Lynch Arribálzaga, 1884: 327 (characters; notes; Argentina). — Sharp, 1886: 631 (notes; Mexico and Central America). — Fauvel, 1891: 95 (key; Venezuela). — Blackburn, 1891: 75 (notes). — Casey, 1910: 192, 197 (characters; notes; key North America). — Blatchley, 1910: 440, 441 (characters). — Bernhauer and Schubert, 1912: 198 (catalog; world). — Bruch, 1915: 493 (catalog; Argentina). — Leng, 1920: 100 (catalog; U.S.A.). — Cameron, 1921: 352, 370, 402 (characters; key and catalog; Singapore). — Lea, 1923: 12 (notes). — Cameron, 1925: 33, 106 (catalog; British India). — Bruch, 1928: 440 (catalog; Argentina). — Notman, 1929: 2 (key; world). — Cameron, 1931: 1, 20 (characters; key; India). — Scheerpeltz, 1933: 1213 (catalog; world). — Bierig, 1935: 31 (natural history notes). — Glick, 1939: 31 (high aerial capture). — Blackwelder, 1943: 229, 388 (characters; notes; type species). — Bierig, 1943: 154 (notes). — Blackwelder, 1944: 130 (checklist; Latin America). — Blackwelder, 1952: 187 (type species). — Adachi, 1955: 14 (characters; key). — Arnett, 1963: 243, 267 (characters; notes). — Fagel, 1971: 11, 52 (characters; type species; Africa). — Seevers, 1971: 84 (amber fossil; late Oligocene to early Miocene; Mexico). — Shibata, 1973: 42 (catalog; Taiwan). — Moore and Legner, 1974: 555 (characters). — Blackwelder and Arnett, 1974: 48 (checklist; North America; West Indies). — Bordoni, 1975: 418 (characters). — Moore and Legner, 1975: 151 (catalog; U.S.A.). — Shibata, 1977: 20 (catalog; Japan).



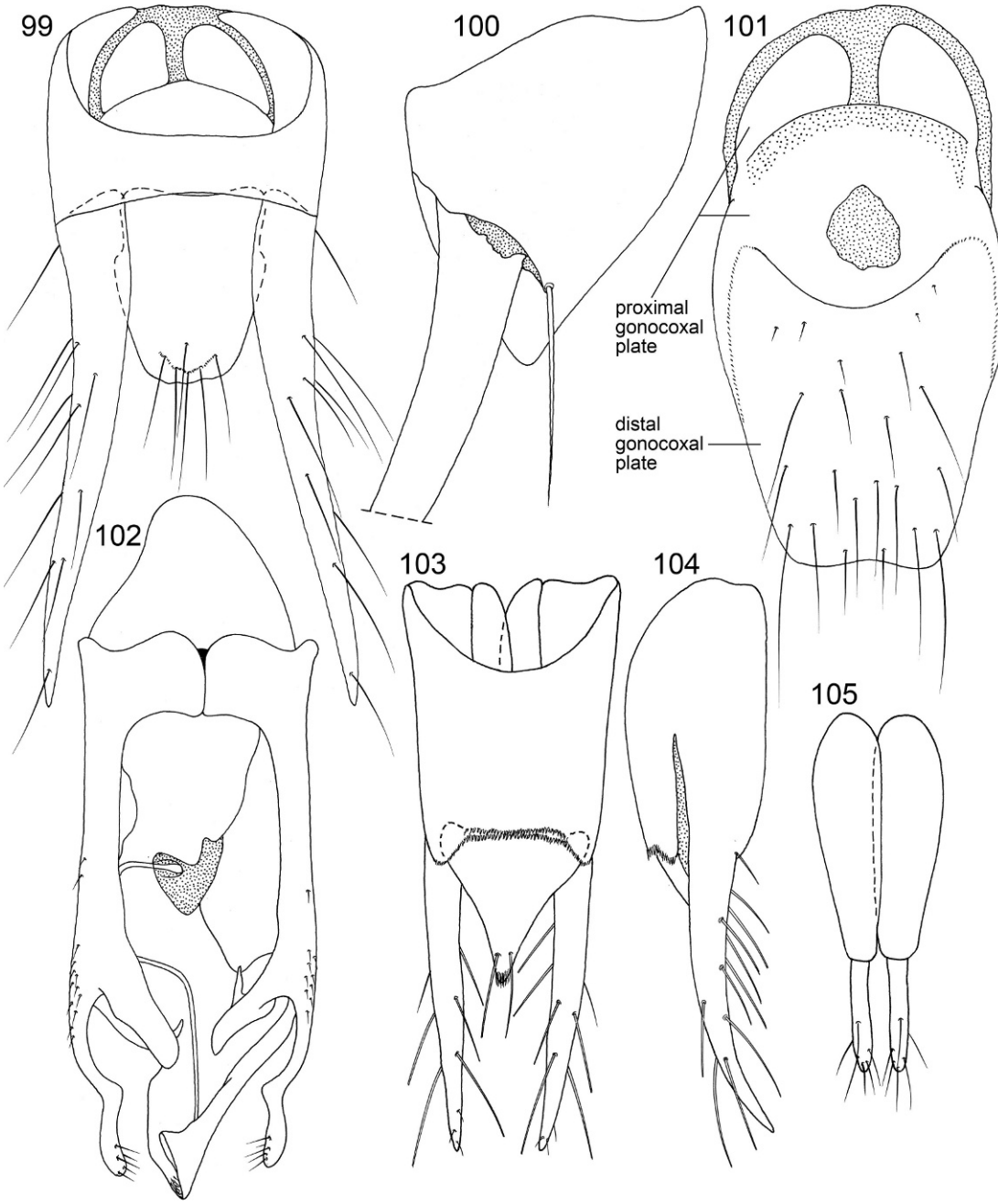
Figs. 94–98. *Palaminus* sp. (Peru). **94.** Labium. **95.** Maxillary palpus. **96.** Elytron, right. **97.** Labrum. **98.** Mandible, right.

— Moore and Legner, 1979: 122 (characters; notes). — Spahr, 1981: 96 (references to specimens from amber and copal). — Frank, 1982: 27 (parasites). — Hammond, 1984: 203 (checklist; Borneo). — Frank, 1986: 367 (checklist; Florida). — Lecoq, 1986: 81 (characters; discussion). — Biswas and Biswas, 1995: 266 (key to species of West Bengal). — Downie and Arnett, 1996: 424 (characters; key to species of Northeastern North America). — Lundgren, 1998: 48 (list of species from Florida; records for other States listed for each species). — Newton et al., 2000: 389 (characters in key; notes; U.S.A. and Canada). — Navarrete-Heredia et al., 2002: 294 (characters in key to genera for Mexico; general notes; list of species; Mexico). — Smetana, 2004: 624 (Palaearctic catalog).

Parapalaminus Bierig, 1943: 155. Type species: *Palaminus symphylus* Bierig, 1943: 155, fixed by original designation. **New Synonym**.

— Blackwelder, 1952: 292 (type species; subgenus of *Palaminus*). — Blackwelder and Arnett, 1974: 48 (synonym of *Palaminus*). — Navarrete-Heredia et al., 2002: 294 (subgenus of *Palaminus*).

DIAGNOSIS: *Palaminus* is one of the most recognizable genera in the subfamily; it is distinguished from all other paederines (and other staphylinids) by the imbricate abdominal macrosculpturing (figs. 26–28). Unlike other genera of the Procirrina, the elytron of *Palaminus* has a long, thick, medially directed



Figs. 99–102. *Palaminus* sp. (Peru). **99.** Terga IX and X, female. **100.** Tergum IX, lateral, female. **101.** Proximal and distal gonocoxal plates. **102.** Aedeagus. Figs. 103–105. *Pseudoprocirrus arrowi*. **103.** Terga IX and X, female. **104.** Terga IX and X, lateral, female. **105.** Proximal and distal gonocoxite.

seta near the apicolateral margin with a similar laterally directed seta near the apicomedial margin (figs. 11, 96); the protibia is gradually expanded apically from the base to the apex, which is about the same diameter as the base of tarsomere 1 (fig. 41), which appears to nest into the tibial apex. Like most genera of the subtribe abdominal segment III of *Palaminus* lacks paratergites (fig. 26). Only *Oedodactylus*, *Pseudoprocirrus*, and some species of *Oedichirus* have paratergites on segment III. Tergum and sternum VII are fused basally and separated apically in *Oedichirus* (figs. 33, 34), entirely fused in *Palaminus*, but separated in the other genera. Abdominal segments III–VII of *Palaminus* (fig. 28) and *Oedichirus* have a pair of ''cells'' or ''windows'' in the intersegmental membrane at the anterior edge of the segment on both the dorsal and ventral surfaces; these structures are lacking in the other genera. The absence of a row of setae on the edge of the posterior margin of the elytra (fig. 96) will separate *Palaminus* from *Neoprocirrus*, *Oedodactylus*, *Pseudoprocirrus*, and *Stylokyrtus*.

DESCRIPTION: Head not pedunculate, wider than long (fig. 90); frontoclypeus with or without subapical, interantennal, transverse ridge; postocular lateral margins short and straight (fig. 90); basal angle strongly angulate (fig. 90) to strongly rounded (fig. 5); basal margin of head gradually curved to neck (fig. 5) or to basal angle with marginal ridge extending from basal angle to neck (figs. 10, 90), and with median portion slightly to moderately emarginate anterior to neck. Neck across nuchal constriction about two fifths to half as wide as greatest postocular width of head; nuchal groove well developed; nuchal ridge moderately to poorly developed or absent. Eye length shorter to longer than postocular length of head. Dorsal surface with umbilicate punctation (fig. 10), some species with barely discernible punctation. Ventral surface without postocular groove. Gular sutures present (fig. 91) and distinct to barely visible (fig. 12) to absent; sutures moderately widely separated and most approximate near or proximad of middle to narrowly separated and most approximate posteriorly. Gula without pubescence. Antennomere 11 shorter than 9 and 10 combined, constricted subapically and tapered to narrowly rounded apex, and without apical, spinelike pencil of setae. Mandibles with apically acute denticle (fig. 98), not bifid; prostheca evident as cluster of cuticular processes at base (fig. 98). Maxillary palpus (fig. 95) with palpomere 4 transverse, securiform, and greatest length longer than third palpomere, and compressed. Labium (fig. 94) with glossae separated, apically rounded and tapered and with cuticular processes on medial margin. Hypopharynx without lobes or cluster of spinelike setae on anterior margin; lateral region with dense cluster of cuticular processes. Labrum (fig. 97) with one pair of submedial denticles on anterior margin. Epipharynx with seta near anterior margin laterad of middle and with small cluster of setae near lateral base; lateral region with long, cuticular processes; median groove present; epipharynx not visible along anterior margin of labrum in dorsal view.

Prothorax (fig. 90) curved trapezoidal, wider than long to slightly longer than wide; widest near anterior margin or anterior third and with lateral margins curved and gradually convergent posteriad. Pronotum with moderately dense umbilicate punctation; punctation weak in some species; punctation absent from midline basally. Pronotal marginal ridge absent or present. Notosternal suture present distad of procoxa (fig. 18). Hypomeron polished and impunctate. Postprocoxal lobe (figs. 19, 93) short to poorly developed, impunctate, and with curved ridge near ventral edge; transverse ridge absent; apices widely separated from one another. Probasisternum (fig. 93) short, without median carina, and without punctation. Mesospiracular peritreme (fig. 19) with anteromedial margin fused to furcasternum; suture absent. Elytra (fig. 5) longer to shorter than pronotum; humeral angles present or absent; posterior edge without row of setae; subapical region with one prominent, long, thicker, posteromediad-directed seta near lateroapical corner and another posterolaterad one near medioapcial corner (figs. 11, 96). Scutellum with scattered setae. Mesosternum with short, median carina extending from mesosternal process. Mesocoxal acetabulum with marginal carina laterally and partly posteriorly. Intersternal suture present medially but feebly developed.

Profemur with ridge and slit (fig. 40) on ventral edge extending from near middle toward base. Protibia with multiple (8 and 9 in species from U.S.A. and Peru respectively) combs (fig. 41); surface without (fig. 41) or with feeble depression on ctenidial surface; tibia widest apically, gradually expanded from base to apex. Protarsomeres 1–4 inflated (fig. 92); base of tarsomere 1 approximately same diameter as apex of expanded tibia (fig. 41); tarsomere 4 not expanded beneath tarsomere 5 and apical margin entire, not bilobed; tarsomere 5 unmodified and inserted laterad of middle of asymmetrical tarsomere 4; tarsomere 5 densely pubescent ventrally. Mesotarsomere and metatarsomere 1 as long as to longer than combination of tarsomeres 2 and 3 through 2–5.

Abdominal segments III to VI with imbricate macrosculpturing (figs. 26–28), VII without or with feeble imbricate macrosculpturing, and VIII and IX without it. Segment III without paratergites; paratergal carina present, short, and at base ventrad of spiracle (figs. 26, 27); tergum and sternum III fused. Segment VII with tergum and sternum completely fused and without notch at midlateral edge of posterior margin. Segments IV to VII with ''windows'' or ''cells'' covered with white, opaque membrane in intersegmental membrane at anterior edge of tergum and sternum (fig. 28). Sternum I absent. Sterna IV–VII without glandular lobe or slit on anterior margin. Tergum IX (figs. 29, 99) fused basally; emargination deep, three or more times deeper than length of tergum, and wide; lateroapical process (fig. 99) long, slender, straight to slightly curved ventrally, and extending well beyond tergum X; lateroapical process separated basally from remainder of segment (figs. 99, 100). Tergum X of male and female with apical margin rounded; base separated from tergum IX.

Female genital sclerites fused to form broad, distal gonocoxal plate partially fused to basally divided, proximal gonocoxal plate and vulva embedded in proximal region (fig. 101) in some species and in others to form one median gonocoxal plate.

Aedeagus (fig. 102) asymmetrical; parameres long, complex, and separated from median lobe for most of length; basal piece absent.

DISTRIBUTION AND HABITAT: The first four species were described by Erichson (1840: 682, 683) the year after he made the name *Palaminus* available. Three of the species, *P. piceus*, *P. pilosus*, and *P. variabilis*, were from Colombia; the latter was also reported from the West Indies and the fourth, *P. testaceus*, from the U.S.A. The most recently described species was from the Comoros (Lecoq, 1996: 138). In contrast to the sharply skewed Old versus New World distribution of *Oedichirus*, *Palaminus* is more evenly distributed with 141 New World and 165 Old World species. Madagascar, with 55 species, has more than any other country and the next closest is Brazil with 38. The genus is mostly a tropical and subtropical group with few species in temperate and semiarid regions.

In the New World the genus reaches north to the southern edge of Ontario, Canada (Campbell and Davies, 1991: 113), on the north shore of Lake Erie at 42.28°N (Anthony Davies, personal commun.) and extends south through eastern, southeastern, and southwestern United States and West Indies and Mexico to Argentina. For the United States, I have seen material for most of the eastern states to Arkansas, Missouri, Kansas, and Oklahoma, and species are recorded in Texas, New Mexico, and Arizona. The only far-western species was described from the southern Arizona/California border along the Colorado River. No species are reported in the northern Plains, central and northern Rockies, Great Basin, or western coastal states from southern California (except near Arizona) to British Colombia. In the West Indies I have seen specimens or species have been reported in the literature for the Bahamas, Greater Antilles (Cuba, Jamaica, Dominican Republic, Puerto Rico), and Lesser Antilles (Dominica, Trinidad). The genus is known in most countries from Mexico to Argentina where it reaches the north and central provinces of Jujuy (23°S), Salta (22°S), Tucumán, Misiones, San Luis (32°S), and Buenos Aires (33°S). The genus may be absent from most of Canada, the western half of the United States (except southern

California, Arizona, New Mexico, and Texas), southern Argentina, and Chile.

Most of the 165 Old World species are described from Africa and Madagascar and nearby islands (117 spp.). In Asia species are known from India, Sri Lanka, Myanmar, Singapore, Malaysian Borneo, Indonesia, Philippines, China, and Japan. Further south *Palaminus* is known from New Guinea and Australia, and in the Pacific from New Caledonia, Vanuatu, Fiji, Samoa, and Guam.

In Africa no species are reported north of the Sahel. The genus is unknown in Europe, Turkey, and the Levant west through Pakistan, central Asia, Russia, and New Zealand. All of the continental Asian species are in India, Bhutan, Myanmar, and China. It is found in Singapore and insular China in Hong Kong and Taiwan; the only record for mainland China is in Zhejiang. The species reported (Rougemont, 2001: 43) from Hong Kong (*P. parvus*) was described from Singapore. The species from Zhejiang (*P. truncatus*; Zheng, 2001: 324) was described from Coonoor in Tamil Nadu, southern India. The three other Chinese species are from Taiwan and two of those are the only representatives in Japan. The northernmost Old World locality is at almost 35°N (Kobe, Japan; *P. japonicus*) and the most southerly is an unspecified locality in Victoria, Australia (*P. australiae*). In India seven of the 10 species are reported from the south in Tamil Nadu and one of those is also from West Bengal. Only two species are reported in the north, one in Sikkim (*P. rufulus*) and one, the more northern species, at about 30°N in Arunachal Pradesh (*P. morosus*). *Palaminus indicus* Kraatz is reported from the Indian states of Tamil Nadu, West Bengal, and Sikkim (Biswas, 2003: 259) and may also be in Myanmar. The type locality of the species is "India orientali" (Kraatz, 1859: 153). Many of the species reported from that site by Kraatz were from what is now Myanmar (see Herman, 2001: 7, and Frisch, 2005: 77, for discussion and references).

In the New World the genus is distributed between approximately 42°N and 33°S and in the Old World about 35°N and perhaps to 38°S. At the northern and southern edges few species are known. The regions from which it appears to be unknown may be too arid, too cool, or both.

Collections have been made in lowland and tropical forests and in montane regions to elevations as high as 2500 meters (*P. kaboboensis*; Fagel, 1971: 63). Species are found on shrubs, trees, and overhanging vegetation, and may be collected by sweeping or by using a beating sheet, or in forest leaf litter, decaying litter, litter near streams, and ground debris. I have collected and/or have seen specimens of both flightless and flying specimens from leaf litter and from beating trees and bushes. It is unclear whether the winged species found on the ground live there or have fallen there from the vegetation, but I have seen many specimens collected from both habitats. Fagel (1971: 55), in his revision of the African species, thought that individuals collected from ground litter probably fell from vegetation. Bierig (1935: 32) wrote that flightless species were solitary vagabonds that lived in humus ("formas ápteras terrícolas… pueblan en terrenos húmedos el humus de boscajes, son seres solitarios y vagamundos"). Species have been collected in the upper tree canopy in Panama and probably occur there in most tropical regions.

SYNONYMY: Considering that *Palaminus* includes more than 300 species, there is surprisingly little external variation. This uniformity of external features is reflected in the lack of subgenera. Bierig (1943: 155) described one subgenus, *Parapalaminus*, for nine species (*P. barbiellinii*, *P. bifidus*, *P. bruchianus*, *P. coriaceus*, *P. diffinis*, *P. peralutaceus*, *P. pusillus*, *P. scitulus*, and *P. symphylus*) with alutaceous microsculpturing on the cephalic dorsum and pronotum. Bierig presented no other characters to support recognition of a subgenus. Another species, *P. erichsoni*, also has alutaceous sculpturing, but whereas the species cited by Bierig are small and yellowish brown, this species is larger and reddish brown with yellowish-brown elytral maculations. At least four species (*P. bifidus*, *P. grandicollis*, *P. parvipennis*, *P. scitulus*) have this microsculpturing only on the pronotum. The head (dorsal surface) and pronotum of the great majority of species of *Palaminus*, including its type species, are polished and lack microsculpturing. A few others have feeble cephalic and pronotal microsculpturing, so it appears that this sculpturing defines no group and *Parapalaminus* should be synony-

mized. It is doubtful that the stated sculpturing defines a monophyletic group. Furthermore, by separating a subgenus, *Parapalaminus*, a paraphyletic group, with 296 species, is created because there are no unique characters common to all the remaining species of *Palaminus* that are not also shared by those of *Parapalaminus*. If description or recognition of a subgenus results in the remaining species becoming a paraphyletic group then the subgenus should not be described or, if it already exists, should be synonymized, so as to maintain a genus defined by synapomorphic features. *Parapalaminus* is hereby synonymized with *Palaminus*.

DISCUSSION: *Palaminus* species are small, slender, elegant beetles with polished integument. Externally the species are similar, differing in color and size, but with beautiful, imbricate macrosculpturing (triangular or diamond shaped) (figs. 26–28) on the cylindrical abdomen. Most species are honey-colored yellowish brown, but others are black or reddish brown and some have maculations. The subterminal abdominal sterna of the males may exhibit elaborate secondary sexual characteristic, but the most striking variation occurs in the aedeagus which has rich, complex structure in many species (fig. 102) and is one of the principal, most reliable means of defining species of *Palaminus* with use of the males (see for example the illustrations in Fagel, 1971: 52–126). Preliminary studies suggest that the female genital sclerites also offer a rich unexploited resource that may be useful for species identification of females and for phylogenetic hypotheses. As yet no infrageneric classification exists for *Palaminus*, so it is unclear that aedeagal characters or female genitalic sclerites will determine groups. Because of the dearth of external characters, I expect that many specimens identified without reference to the aedeagus are misidentified and that some are synonyms or complexes of cryptic species.

The number of named species for the New and Old World differs only slightly. However, during the 117-year interval between when the first four species were described (Erichson, 1840) and 1956, when the most recent six were added (Wendeler, 1956a, 1956b), all of the 142 species known for *Palaminus* in the New World were described. It was not until 1859 that the first two Old World species were described (Kraatz, 1859: 153) and by 1952 only 60 species had been described for the entire hemisphere, so by 1956 more than two thirds of the named species were in the New World. During the 26 years from 1971–1996, Fagel (1971), Jarrige (1974, 1978), and Lecoq (1984, 1986, 1991, 1996) described 102 more species from Africa and Madagascar. Five others were described from Bhutan (Coiffait, 1978a: 114), Myanmar (Scheerpeltz, 1965: 103, 172), and Indonesia (Scheerpeltz, 1957: 260–262). Considering the external uniformity of the species and the fact that the most diagnostic features are associated with the aedeagus, the male terminal abdominal segments, and the female genital sclerites, there are surely many species awaiting discovery. By contrast, during the nearly 170 years the genus has been known, only one name has been listed as a synonym, one as a synonym and valid name in the same publication, two were published as varieties, one as a subspecies, and five names are homonyms and were replaced. Since in the New World and in the eastern part of the Old World the aedeagus was not used to distinguish species, it is probable that some synonymy will be discovered in those regions. Since in Africa and Madagascar the aedeagus and the terminal abdominal segments were employed extensively, it is less likely that heretofore unnoted synonyms will be found.

Palaminus requires revisionary study in nearly all parts of its range. The Nearctic species are being revised by Larry Watrous at this writing. Among some of the important and more or less recent taxonomic studies on *Palaminus* are a review of and key to the species of India (Cameron, 1931: 20), a revision and illustrations of the species for Africa (Fagel, 1971: 52) and description and illustrations for Madagascar (Lecoq, 1984, 1986, 1991, 1996; Jarrige, 1974, 1978). No keys were published for Africa or Madagascar and identification relies on comparison of specimens with descriptions and aedeagal illustrations. Downie and Arnett (1996: 424) provide a key and diagnoses for the species of northeastern North America, but without aedeagal characters or illustrations. Notman (1929) published a key to the 144 species then

known; the number of species has more than doubled since. All of the characters Notman uses are external (color, form, punctation), he does not indicate whether the key was based on characters from the literature or from actual specimens, and no use was made of the aedeagus or secondary sexual characteristics of the male abdomen, so the accuracy of identification using the key is limited. Many other articles present a list of species for a region or include isolated descriptions of new ones.

By beating bushes, trees, lianas, and so on, one can relatively easily collect *Palaminus* and large numbers of individuals can be quickly accumulated. Many of the identified *Palaminus* I examined were represented by few specimens, but many collections often have large accumulations of undetermined specimens. Obviously, any given species can be uncommon at a site and for that reason might be rare in museum collections, but the paucity of specimens of *Palaminus* may also partly reflect the lack of revisionary study that develops the tools needed to identify these masses of similar specimens.

Most species of *Palaminus* can fly. A few species (*P. apterus*, *P. larvalis*, *P. rosariensis*, plus other unidentified species from various regions) have shorter elytra that lack humeral angles and may be incapable of flight.

A specimen of an unidentified species of *Palaminus* was reported in Oligocene/Miocene amber from Mexico (Seevers, 1971: 84) and at least nine specimens of approximately the same age in Dominican amber are known in collections (Herman, personal obs.). The most diagnostic characters for species are the aedeagus and the female genital sclerites. The males of some living species have especially elaborate modifications of the abdominal sterna, but most do not, so identity often requires dissections. The extant species of the genus are far too poorly known for most parts of the world, but especially for the New World, to defend naming any of these fossils species. If and when the New World species are revised, describing and naming the fossil might be warranted.

Over a period of five years flights were made over Tallulah, Louisiana, in a biplane fitted with an aerial plankton net in an effort to gather information on dispersal and migration of insects, spiders, and mites. Flights were made during the day and night, at various elevations. During five years there were over 1300 flights. Over 4400 beetles were collected of which 19 were *Palaminus* spp.; of these 19 species, 16 were collected at night at about 500 feet altitude (Glick, 1939: 31), and which only shows that the species are more apt to fly at night when it is more humid.

Species Included and Material Examined

aequicollis Bernhauer – L (MRAC), Pl, sp (FMNH) . . . . . D.R. Congo
africanus Fagel – H (MRAC) . . . . . Guinea
allocerus Fauvel – L (IRSN) . . . . . Madagascar
alluaudi Jarrige – H (IRSN). . . . . Mauritius
aluticollis Bernhauer – H (FMNH). . . . . Brazil
amplipennis Fall – Lit. Att. [U.S.A.]
anacoreta Bierig – H, sp (FMNH) . . . . . Cuba
anceps Sharp – H (BMNH) . . . . . Brazil
andapanus Lecoq – Lit. Att. [Madagascar]
andohahelo Lecoq – Lit. Att. [Madagascar]
andrewesi Cameron – Syn (BMNH), sp (FMNH) . . . . . India
angolensis Fagel – sp (BMNH)
(Note: No locality with specimen; known from Angola.)
anjavidilavanus Jarrige – Lit. Att. [Madagascar]
ankazobensis Lecoq – Lit. Att. [Madagascar]
proximus Lecoq
anosyanus Lecoq – Lit. Att. [Madagascar]
apicalis Sharp – H (BMNH) . . . . . Brazil
apicatus Bernhauer – Syn (FMNH) . . . . Colombia
apicipennis Sharp – Syn (BMNH), Syn, sp (FMNH) . . . . . Guatemala, Mexico
apterus Bernhauer – H (FMNH) . . . Guadeloupe
armatus Fagel – H (MRAC) . . . . . D.R. Congo
assimilis Lecoq – Lit. Att. [Madagascar]
asymmetricus Bernhauer – Syn (FMNH) . . . . . Costa Rica
atriventris Bernhauer – Syn (FMNH) . . . . . Fiji
lateralis Cameron – P (BMNH) . . . . . Fiji
australiae Fauvel – H (BMNH), sp (FMNH, IRSN) . . . . . Australia, Loyalty Islands
hebridensis Cameron – H (BMNH). . . . . New Hebrides
bafianus Fagel – Lit. Att. [Cameroon]
balzani Bernhauer – Syn (FMNH) . . . . . Bolivia
barbiellinii Bernhauer – H, sp (FMNH). . . . . Brazil
barombiensis Fagel – Lit. Att. [Nigeria]
bermudezi Bierig – H (FMNH) . . . . . Cuba
betschi Jarrige – Lit. Att. [Madagascar]
bicolor Cameron – H (BMNH) . . . . . Papua New Guinea

bifidus Notman – H, P (AMNH), P (FMNH) . . . . Puerto Rico
biguttatus Fauvel – Syn (IRSN), sp (FMNH). . . . . Venezuela
biimpressus Bernhauer – Syn (FMNH) . . . . . Costa Rica
bipustulatus Bernhauer – Syn (FMNH). . . . . Colombia
birmanus Cameron – H (BMNH). . . . . Burma
bivittatus Cameron – Syn (BMNH), sp (FMNH) . . . . . New Guinea
obliteratus Cameron – Syn (BMNH). . . . . New Guinea
bivittipennis Lea – Lit. Att. [New Guinea]
blanci Jarrige – Lit. Att. [Madagascar]
bolivianus Bernhauer – Syn, sp (FMNH) . . . . . Bolivia, Brazil
bonariensis Lynch Arribálzaga – Syn? (IRSN), sp (FMNH) . . . . . Argentina
(Note: Lynch Arribálzaga [1884: 330] wrote "El ejemplar que poseo lo coleccioné en Chacabuco,…" which suggests that he examined only one specimen. Since he collected the specimen it is probable that it is deposited with his collection in Buenos Aires and it seems unlikely that type material is in the IRSN.)
borneenis Cameron – H (BMNH), sp (FMNH) . . . . . Malaysia
brachelytratus Lecoq – Lit. Att. [Madagascar]
brachypterus Lecoq – Lit. Att. [Madagascar]
breviceps Sharp – H (BMNH), sp (FMNH) . . . . . Brazil
brevicollis R. Sahlberg – sp (FMNH) . . . . Brazil
brevipennis Bernhauer–H,sp(FMNH)… Argentina
bruchi Bernhauer – H (FMNH) . . . . . Argentina
bruchianus Bierig – Syn (FMNH). . . . . Cuba
brunneus Fauvel – H (IRSN) . . . . . Madagascar
bryanti Cameron – Syn (BMNH). . . . Singapore
buehleri Scheerpeltz – Syn (NHMW) . . . Indonesia
capitalis Lecoq – Lit. Att. [Madagascar]
carayoni Lecoq – Lit. Att. [Madagascar]
carinatus Lecoq – Lit. Att. [Madagascar]
ceylanensis Kraatz – Syn (SDEI), sp (BMNH) . . . . . Sri Lanka
cheesmani Cameron – H (BMNH) . . . . . Papua New Guinea
chiriquensis Sharp – H (BMNH), sp (FMNH) . . . . . Panama
circumflexus Fauvel – L (IRSN), sp (FMNH) . . . . . Madagascar
cognatus Sharp – Syn (BMNH, FMNH). . . . . Panama
collaris Bernhauer – Syn (FMNH). . . Costa Rica
columbinus Bernhauer – Syn (FMNH) . . . . . Colombia
compressiventris Bernhauer – Syn (FMNH) . . . . . Mexico
concolor Sharp – Syn (BMNH), sp (FMNH). . . . . Guatemala, Mexico
confusus Fagel – H (BMNH), P (MRAC). . . . . D.R. Congo, Angola
congoensis Cameron – Syn (BMNH, MRAC) . . . . . D.R. Congo
(Note: Fagel [1971: 125] considers species to be incertae sedis for lack of a male.)
consimilis Lecoq – Lit. Att. [Madagascar]
continentalis Bernhauer – Syn, sp (FMNH). . . . . South Africa
contortus LeConte – Lit. Att. [U.S.A.]
coriaceus Cameron – Syn (BMNH), sp (FMNH). . . . . Haiti, Jamaica
crassus Sharp – H (BMNH), sp (FMNH). . . . . Brazil
crenatus Sharp – H (BMNH). . . . . Guatemala
crenulatus Lecoq – Lit. Att. [Madagascar]
cribratus LeConte – Lit. Att. [U.S.A.]
debilis Sharp – H (BMNH), sp (FMNH) . . . . . Mexico, Nicaragua
decorus Lecoq – Lit. Att. [Madagascar]
decussatus Wollaston – Syn (BMNH) . . . Madeira
deformis Sharp – Syn (BMNH, FMNH). . . . . Guatemala, Mexico
depressus Lecoq – Lit. Att. [Madagascar]
densicollis Bernhauer – H (FMNH) . . . . Mexico
descarpentriesi Jarrige – Lit. Att. [Madagascar]
dieganus Jarrige – Lit. Att. [Madagascar]
difficilis Cameron – P (BMNH) . . . . . Fiji
diffinis Sharp – H (BMNH), sp (FMNH) . . . . . Nicaragua, Costa Rica
discretus Sharp – H (BMNH) . . . . . Brazil
distans Sharp – H (BMNH). . . . . Brazil
dubius Notman – H (AMNH) . . . . . Guadeloupe
elegans Wendeler – H, P (MNHB) . . . . . Brazil
erichsoni Bernhauer – H (FMNH) . . . . . Bolivia
evansi Bernhauer – Syn (FMNH). . . . . Fiji
exiguus Lecoq – Lit. Att. [Madagascar]
fageli Jarrige – H (IRSN) . . . . . Madagascar
falsus Fagel – H (MRAC). . . . . D.R. Congo
fauveli Jarrige – H (IRSN) . . . . . Madagascar
ferrugineus R. Sahlberg – sp (FMNH) . . . Brazil
fijiensis Cameron – P (BMNH) . . . . . Fiji
filicornis Fagel – H (MRAC). . . . . D.R. Congo
filum Sharp – Syn (BMNH), Syn, sp (FMNH) . . . . . Costa Rica, Mexico, Nicaragua
fiziensis Fagel – H (MRAC) . . . . . D.R. Congo
flavescens Fagel – Lit. Att. [Guinea]
flavipennis LeConte – Lit. Att. [U.S.A.]
flavocinctus Lecoq – Lit. Att. [Madagascar]
flavoguttatus Cameron – Syn (BMNH). . . . . Philippines
flavus Fagel – H (MRAC). . . . . D.R. Congo
formosae Cameron – P (BMNH) . . . . . Taiwan
foutadjallonensis Fagel – P (MRAC). . . . Guinea
fragilis Sharp – H (BMNH). . . . . Brazil
fraternus Casey – Lit. Att. [U.S.A.]

freyianus Fagel – Lit. Att. [Guinea]
fuscatus Lecoq – Lit. Att. [Madagascar]
fuscipes Sharp – H (BMNH), sp (FMNH) . . . . . Brazil
fusciventris Sharp – H (BMNH), sp (FMNH) . . . . . Nicaragua, Costa Rica
fuscus Lecoq – Lit. Att. [Madagascar]
gabonicus Fagel – Lit. Att. [Gabon]
garambanus Fagel – H (MRAC) . . . . . D.R. Congo
germanus Cameron – P (BMNH) . . . . . Malaysia
gracilipes Sharp – Syn (BMNH), Syn, sp (FMNH) . . . . . Panama, Costa Rica, Mexico
gracilis Sharp – H (BMNH), sp (FMNH) . . . . . Brazil, Colombia, Peru
grandicollis Notman – H, P (AMNH), P (FMNH) . . . . . Puerto Rico
grandis Lecoq – Lit. Att. [Madagascar]
griveaudi Jarrige – Lit. Att. [Madagascar]
guineensis Fagel – Lit. Att. [Guinea, Ivory Coast]
heraldicus Fauvel – Syn (IRSN), sp (FMNH) . . . . . Venezuela, Colombia
hudsonicus Casey – Lit. Att. [U.S.A.]
hylaeus Bierig – Syn, sp (FMNH) . . . . . Cuba
illotus Lecoq – sp (BMNH) . . . . . Madagascar
implicatus Lecoq – Lit. Att. [Madagascar]
incertus Fagel – H (MRAC) . . . . . D.R. Congo
inconspicuus Lecoq – Lit. Att. [Madagascar]
indicus Kraatz – Syn (SDEI), sp (FMNH) . . . . . India, "India orientali, Indonesia, Philippines, Singapore, Vietnam
infuscatus Bernhauer – Syn, sp (FMNH) . . . . . Mexico
insignis Sharp – H (BMNH), sp (FMNH) . . . . . Panama, Costa Rica
insularis Cameron – Syn (BMNH), sp (FMNH) . . . . . Jamaica, Guadeloupe
invidus Casey – sp (FMNH) . . . . . Mexico
isthmianus Casey – Lit. Att. [Panama]
japonicus Cameron – H (BMNH) . . . . . Japan
jarrigei Lecoq – Lit. Att. [Madagascar]
jocquei Lecoq – Lit. Att. [Comoros]
kaboboensis Fagel – H (MRAC) . . . . . D.R. Congo
ruwenzoricus Fagel – H (MRAC) . . . D.R. Congo
kamerunensis Bernhauer–Pl(FMNH) . . . Cameroon
kasaiensis Fagel – H (MRAC) . . . . D.R. Congo
katanganus Fagel – H (MRAC) . . . D.R. Congo
kivuensis Fagel – H (MRAC) . . . . . D.R. Congo
kokodanus Cameron – H (BMNH) . . . . . Papua New Guinea
kundelungensis Fagel – H (MRAC) . . . D.R. Congo
kwangensis Fagel – H (MRAC) . . . D.R. Congo
lacertinus Sharp – Syn (BMNH) . . . Guatemala
lancifer Fauvel – Syn (IRSN) . . . . . Venezuela
larvalis LeConte – sp (FMNH) . . . . . United States (North Carolina, Texas).
lateripennis Bernhauer – Syn (FMNH) . . . . . Costa Rica
laticollis Wendeler – H (MNHB) . . . . . Brazil
latior Bernhauer – Syn (FMNH) . . . Costa Rica
lengi Notman – H (AMNH) . . . . . Puerto Rico
liberiensis Fagel – Lit. Att. [Liberia]
ligulifer Lecoq – Lit. Att. [Madagascar]
limbifer Fauvel – H (BMNH), sp (IRSN) . . . . . New Guinea
(Note: The collection of the IRSN has a specimen with a "type" label, but according to the original description [Fauvel, 1879: 82] the species was described from one specimen collected by Wallace and that specimen is in the BMNH.)
lividus LeConte – Lit. Att. [U.S.A.]
lobiventris Bernhauer – Syn (FMNH) . . . . . Costa Rica
longelytratus Lecoq – Lit. Att. [Madagascar]
longicollis Sharp – H (BMNH) . . . . . Panama
longicornis Sharp – H (BMNH), sp (FMNH) . . . . . Brazil
luteus Casey – Lit. Att. [Canada, U.S.A.]
luberensis Fagel – H (MRAC) . . . . D.R. Congo
lumiventris Herman – Lit. Att. [Taiwan]
spiniventris Bernhauer
(Note: Holotype missing from FMNH collection.)
maculatus Bernhauer – Syn (FMNH) . . . Australia
madecassa Fauvel – L (IRSN), sp (FMNH) . . . . . Madagascar
magniceps Bernhauer – H, sp (FMNH) . . . . . Argentina
magnipennis Bernhauer – Syn (FMNH) . . . . . Costa Rica
malaisei Scheerpeltz – Lit. Att. [Type not found in Vienna – May 2006]
malandanus Bernhauer – Syn (BMNH, FMNH) . . . . . Australia
masoalaensis Lecoq – Lit. Att. [Madagascar]
difficilis Lecoq
mexicanus Sharp – Syn (BMNH), sp (FMNH) . . . . . Mexico
milloti Lecoq – Lit. Att. [Comoros]
minor Bernhauer – Syn (FMNH) . . . . . Mexico
minutissimus Bernhauer – Syn (FMNH) . . . Guam
minusculus Lecoq – Lit. Att. [Madagascar]
minutulus Lecoq – Lit. Att. [Madagascar]
minutus Fagel – Lit. Att. [D.R. Congo]
mohelianus Lecoq – Lit. Att. [Comoros]
motoensis Fagel – H (MRAC) . . . . D.R. Congo
modestus Sharp – H (BMNH) . . . . . Brazil
molestus Jarrige – Lit. Att. [Madagascar]
montanus Cameron – H (BMNH) . . . Mauritius
monticola Cameron – Syn (BMNH), sp (FMNH) . . . . . Sri Lanka
morosus Cameron – Syn (BMNH) . . . . . India
multifidus Lecoq – Lit. Att. [Madagascar]
nevermanni Bernhauer – Syn (FMNH) . . . . . Costa Rica

niger Sharp – Syn (BMNH), sp (FMNH) . . . . . .Bolivia, Brazil
nigropiceus Cameron – Syn (BMNH), sp (FMNH) . . . . . India
nigrosuturalis Bernhauer – Syn (FMNH) . . . . . .Argentina
nilgiriensis Cameron – Syn (BMNH) . . . . India
nimbaensis Fagel – Lit. Att. [Guinea]
nitidulus Fagel – H (MRAC) . . . . . D.R. Congo
normalis LeConte – Lit. Att. [U.S.A.]
nossibianus Fauvel – L (IRSN), sp (FMNH) . . . . . .Madagascar, Tanzania
novaeguineae Fauvel – sp (FMNH) . . . . Indonesia
occidentalis Lecoq – Lit. Att. [Madagascar]
oculatus Fagel – H (MRAC) . . . . . D.R. Congo
ogloblini Bernhauer – H (FMNH) . . . Argentina
omissus Lecoq – Lit. Att. [Madagascar]
opaculus Bernhauer – H (FMNH) . . . . . Bolivia
ophtalmicus Lecoq – sp (BMNH) . . . Madagascar
pallidus R. Sahlberg – sp (FMNH). . . . . Brazil
pallipes LeConte – sp (FMNH) . . . . . United States (Florida)
palmatus Sharp – H (BMNH) . . . . . Panama
papuanus Cameron – H (BMNH). . . . . .Papua New Guinea
parcus Sharp – H (BMNH) . . . . . Brazil
pauliani Lecoq – Lit. Att. [Madagascar]
parviceps Sharp – H (BMNH) . . . . . Mexico
parvipennis Notman – H, P (AMNH), P (FMNH) . . . . . Puerto Rico
parvulus Sharp – Syn (BMNH), sp (FMNH). . . . . Mexico
parvus Cameron – Syn (BMNH) . . . . Singapore
pauloensis Bernhauer – H, sp (FMNH). . . Brazil
pellax Sharp – H (BMNH) . . . . . Brazil
pennifer Fauvel – L (IRSN), sp (FMNH) . . . . . India, Indonesia, Philippines, Seychelles
peralutaceus Bierig – Syn (FMNH). . . . . Cuba
perforatus Wendeler – H (MNHB) . . . . . Brazil
pertusus Lecoq – Lit. Att. [Madagascar]
peyrierasi Lecoq – Lit. Att. [Madagascar]
philippinus Bernhauer – Syn, sp (FMNH) . . . . . Philippines, Singapore
piceus Erichson – H (MNHB) . . . . . Colombia
pictus Bernhauer – Syn (FMNH, IRSN). . . . . .Bolivia
pilosus Erichson – Syn (MNHB) . . . . Colombia
pilum Bierig – H, P (FMNH). . . . . Cuba
plagiatus Fauvel – Syn (IRSN) . . . . . Venezuela
problematicus Fagel – H (MRAC) . . . D.R. Congo
procerus Notman – H (AMNH). . . . Puerto Rico
productus Schubert – Syn (MNHB) . . . Tanzania
prolongatus Jarrige – P (IRSN) . . . . Madagascar
propinquus Lecoq – Lit. Att. [Madagascar]
proximus Cameron – H, P (BMNH). . . . . .New Hebrides
pubescens Lecoq – Lit. Att. [Madagascar]
pullus Lecoq – Lit. Att. [Madagascar]
pulvereus Lecoq – Lit. Att. [Madagascar]
pumilus LeConte – Lit. Att. [U.S.A.]
puncticeps Sharp – H (BMNH), sp (FMNH). . . . . .Brazil
puncticollis Fagel – H (MRAC) . . . D.R. Congo
pusillus Notman – H (AMNH) . . . . Puerto Rico
quadriguttatus Fauvel – Syn (IRSN). . . . . .Venezuela
quadripustulatus Bernhauer – H, sp (FMNH). . . . . Bolivia, Colombia
rejectus Lecoq – Lit. Att. [Madagascar]
robustusSharp – H (BMNH) . . . . . Brazil
rosariensis Bierig – Syn (FMNH). . . . . Cuba
rotundicollis Wendeler – H (MNHB) . . . . Brazil
rubripennis Sharp – Syn (BMNH, FMNH) . . . . . Panama
rufotestaceus Lecoq – Lit. Att. [Madagascar]
rufulus Coiffait – Lit. Att. [Nepal, India, Bhutan]
rufus Cameron – Syn (BMNH), sp (FMNH). . . . . India
rugicollis Fauvel – Syn (IRSN) . . . . . Venezuela
sambavanus Lecoq – Lit. Att. [Madagascar]
samoensis Cameron – P (BMNH) . . . . . Samoa
saopaoloanus Wendeler – H (MNHB). . . . Brazil
schirmi Wendeler – H (MNHB) . . . . . Brazil
scitulus Notman – H, P (AMNH) . . Puerto Rico
sellatus Sharp – Syn (BMNH) . . . . . Brazil
sharpi Bernhauer – H (FMNH) . . . . . Peru
signifer Casey – Lit. Att. [U.S.A.]
silvestris Jarrige – Lit. Att. [Madagascar]
similis Fagel – H (MRAC) . . . . . D.R. Congo
simoni Fauvel – Syn (IRSN, BMNH). . . . . .Sri Lanka, India
simplex Sharp – Syn (BMNH), sp (FMNH) . . . . . .Brazil
sinuatus Sharp – H (BMNH). . . . . Brazil
sobrinus Sharp – Syn (BMNH) . . . . . Brazil
sogai Jarrige – Lit. Att. [Madagascar]
solitus Lecoq – Lit. Att. [Madagascar]
sordidus Sharp – Syn (BMNH) . . . . . Mexico
spiniventris Bernhauer – Syn (FMNH) . . . Brazil
stipes Sharp – H (BMNH). . . . . Brazil
strigosus Bierig – Syn (FMNH) . . . . Costa Rica
sumbaensis Scheerpeltz – Syn (NHMW) . . . . . .Indonesia
sutteri Scheerpeltz – Syn (NHMW) . . Indonesia
suturalis Fauvel – L (IRSN) . . . . . Madagascar
swezeyi Bernhauer – Syn (FMNH). . . . . Guam
symphylus Bierig – H, sp (FMNH). . . Costa Rica
tanalensis Jarrige – H (IRSN) . . . . . Madagascar
tegulatus Casey – Lit. Att. [Nicaragua]
tener Bernhauer – H (FMNH). . . . . Brazil
tenuis Lecoq – Lit. Att. [Madagascar]
testaceus Erichson – sp (FMNH) . . . . . U.S.A. (Florida, Georgia, Illinois, Kansas, New Jersey, North Carolina, Tennessee)
thiemei Bernhauer – Syn, sp (FMNH) . . . . . .Colombia

timidus Casey – Lit. Att. [U.S.A.]
tortilis Casey – Lit. Att. [Nicaragua]
transmarinus Fauvel – Syn (IRSN), sp (FMNH) . . . . . Tanzania
trapezicollis Fauvel – H (IRSN). . . . . Colombia (Note: No type label is attached to this specimen, but Fauvel [1901: 76] wrote that the species was based on one specimen.)
trapezimorphus Herman
trapezicollis Bernhauer – H (FMNH). . . Brazil
trifidus Lecoq – Lit. Att. [Madagascar]
trinotatus Fauvel – Syn (IRSN) . . . . . Venezuela (Note: The species was described in a key and no locality was cited. In the IRSN collection the type is labeled from "Colonia Tovar".)
trivittipennis Lea – Lit. Att. [Fiji]
truncatus Fauvel – Syn (IRSN), sp (FMNH). . . . . India
tsaratananus Lecoq – Lit. Att. [Madagascar]
tucumanensis Bernhauer – Syn (FMNH). . . . . Argentina
uncinatus Lecoq – Lit. Att. [Madagascar]
unicus Lecoq – Lit. Att. [Madagascar]
uniformis Cameron – H (BMNH) . . . . . Papua New Guinea
validus Sharp – Syn (BMNH) . . . . . Panama
variabilis Erichson – Syn (MNHB), sp (FMNH) . . . . . Brazil, Colombia, Grenada
variiventris Bernhauer – Syn (FMNH) . . Bolivia
varipennis Cameron – Syn (BMNH). . . . . New Guinea
veronicae Lecoq – Lit. Att. [Madagascar]
maculatus Lecoq
villiersi Lecoq – Lit. Att. [Madagascar]
vitiensis Fauvel – Syn (IRSN) . . . . . Fiji
vittatus Sharp – Syn (BMNH), sp (FMNH) . . . . . Costa Rica, Mexico
humeralis Sharp – H (BMNH) . . . . . Mexico
vittiger Bernhauer – Syn (FMNH) . . . . . Bolivia, Peru
volans Lecoq – Lit. Att. [Madagascar]
volitans Lecoq – Lit. Att. [Madagascar]
yangambiensis Fagel – H (MRAC), P (FMNH). . . . . D.R. Congo

UNDETERMINED SPECIMENS: Africa: Liberia, Rhodesia.

Asia: Borneo, India, Indonesia, Japan, Malaysia, Taiwan.

Australian and Pacific Region: Australia, Caroline Islands, Marianna Islands, New Caledonia, Papua New Guinea, Philippines.

South America: Argentina, Bolivia, Brazil, Colombia, Ecuador, French Guiana, Paraguay, Peru, Surinam, Venezuela.

North America: Bahamas, Belize, Costa Rica, Cuba, Dominica, Dominican Republic, El Salvador, Guatemala, Honduras, Jamaica, Mexico, Nicaragua, Panama, Puerto Rico, Trinidad, United States (Alabama, Arizona, Arkansas, Connecticut, Florida, Georgia, Illinois, Indiana, Kansas, Kentucky, Louisiana, Maryland, Michigan, Mississippi, Missouri, New Jersey, New York, North Carolina, Ohio, Oklahoma, Pennsylvania, South Carolina, Virginia).

DISSECTIONS: Disarticulation: *Palaminus* sp. (1 male, 1 female, Peru); (1 male, 1 female, U.S.A.).

Paraprocirrus Bernhauer
Figure 6

Paraprocirrus Bernhauer, 1923: 63 (replacement name for *Eucirrus* Fauvel). Type species: *Eucirrus miricornis* Fauvel, fixed by objective synonymy with *Eucirrus* (ICZN, 1999: Article 67.8).

— Scheerpeltz, 1933: 1212 (catalog; world). — Blackwelder, 1952: 292 (type species).

Eucirrus Fauvel, 1895: 215 (preoccupied by Melly, 1832). Type species: *Eucirrus miricornis* Fauvel, 1895: 216, fixed by monotypy.

— Bernhauer and Schubert, 1912: 198 (catalog; world). — Cameron, 1921: 352, 369, 402 (characters; key and catalog for species of Singapore). — Scheerpeltz, 1933: 1212 (synonym of *Paraprocirrus*). — Blackwelder, 1952: 154 (type species; synonym of *Paraprocirrus*).

DIAGNOSIS: *Paraprocirrus* is separated from *Neoprocirrus* by the bidentate labral margin, the subbasal constriction of the pronotum (in dorsal view) (fig. 6), the indistinct basal angles on the head (fig. 6), and the absence of ventral cephalic grooves (compare to fig. 2). The eleventh antennomere is elongate and the postocular portion of the head is elongate and gradually tapered to the neck (fig. 6). An undescribed species of *Paraprocirrus* has feebly developed basal angles at the juncture with the neck. The neck of *Paraprocirrus* is slightly less than two fifths the width of the widest postocular width of the head as compared to *Neoprocirrus* in which the neck is half as wide as the postocular width of the head. Protarsomeres 1–4 are swollen (fig. 6). The absence of setae on the edge of the posterior margin of the elytra will separate *Paraprocirrus* from *Neo-*

procirrus, *Oedodactylus*, *Pseudoprocirrus*, and *Stylokyrtus*.

DESCRIPTION: Head (fig. 6) not pedunculate, elongate, longer than wide, with postocular region tapered to neck; frontoclypeus with uninterrupted, subapical, interantennal, transverse ridge; postocular lateral margin broadly and shallowly rounded and strongly convergent to neck; postocular margin long; basal angle indistinct; basal margin broadly rounded, evident only anterior to nuchal constriction, and without marginal ridge. Neck across nuchal constriction slightly less than two fifths as wide as greatest postocular width of head; nuchal groove shallow; [**nuchal ridge].[2] Eye length shorter than postocular length of head. Dorsal surface with reticulate punctation anteriorly and umbilicate punctation medially and posteriorly. Ventral surface without postocular groove. Gular sutures separated; sutures most approximate posteriorly. Gula without pubescence. Antennomere 11 elongate, nearly as long as 8–10 combined to slightly longer than 2–10 combined; apex without spiniform pencil of setae. [**Mandibles, denticle]; [**prostheca]. Maxillary palpus with palpomere 4 longer than third, robust, fusiform, and compressed. [**Ligular region]. [**Labium, glossae]. [**Hypopharynx]. Labrum with submedial denticle on anterior margin. [**Epipharynx].

Prothorax (fig. 6) rectanguliform, longer than wide; widest near anterior margin then mildly to weakly constricted just distad of middle then slightly expanded to base. Pronotum with dense, coarse, umbilicate punctation; punctation uniform, surface without midlongitudinal carina, and with short impunctate midlongitudinal strip just proximad of base. Pronotal marginal ridge poorly and irregularly developed, margined dorsally by row of punctures and lateroventrally by impunctate, polished surface. Notosternal suture poorly developed, evident as weak ridge in broad depression; suture and marginal ridge separated. Hypomeron polished and densely punctate. Postprocoxal lobe moderately long and punctate; transverse ridge absent; apex of each lobe only moderately separated from one another medially. Probasisternum without median carina, but with ridge on each side of median tumescence; surface impunctate. Mesospiracular peritreme with anteromedial margin fused to furcasternum. Elytra shorter than pronotum; humeral angles absent; posterior edge without row of setae; subapical region without long, thicker, posteromediad directed seta near apicolateral corner. Scutellum with a few setae. Mesosternum without median carina. [**Mesocoxal acetabulum]. [**Intersternal suture].

Profemur with ridge near middle on anteroventral surface. Protibia with numerous combs [**number of combs] extending for most of length; tibia with shallow depression on ctenidial surface; apical portion neither constricted nor enlarged. Protarsomeres (fig. 6) 1–4 inflated, ventral surface without setose pad; base of tarsomere 1 not surrounded by cupulate protibial apex; tarsomere 4 not expanded beneath tarsomere 5 and apical margin entire, not bilobed; tarsomere 5 unmodified and inserted laterad of middle of asymmetrical tarsomere 4; tarsomere 5 with moderately dense pubescence ventrally. Mesotarsomere and metatarsomere 1 longer than remaining articles combined.

Abdominal segments without imbricate macrosculpturing (cf. fig. 28). Segment III without paratergites; paratergal carina present at base laterad of spiracle; tergum and sternum III fused. Segment VII with tergum and sternum separated. [**Segments IV–VI, ''windows'']. [**Sternum I]. [**Sternum IV]. Tergum IX fused basally; posterior margin deeply emarginate; lateroapical process short, slender in dorsal view and wider and apically tapered in lateral view, feebly curved ventrally, and extending beyond posterior margin of tergum X; [**base of lateroapical process]. Tergum X with apical margin rounded; base separated from tergum IX.

[**Female genital sclerites].

[**Aedeagus].

DISTRIBUTION AND HABITAT: I examined specimens of *P. miricornis* from Singapore, the type locality, and G. Rougemont (correspondence, July 2007) collected a specimen from Negri Sembilan, Malaysia, a new record for the species. He collected the Malaysian specimen and another from Singapore by

[2] This structure and other similarly cited structures were unavailable for study.

sifting forest floor litter. I examined one specimen of an undescribed species from Malaysia.

DISCUSSION: The genus was originally described as *Eucirrus* (Fauvel, 1895: 215), a preoccupied name replaced with *Paraprocirrus* (Bernhauer, 1923). Fauvel (1895: 216) described the species from one specimen; a second, slightly damaged one is in the Natural History Museum, London, and a third in the collection of Guillaume Rougemont, Londinières, France. Cameron (1928: 439) added *P. borneensis*, but later moved it to *Neoprocirrus* (Cameron, 1936: 42).

Paraprocirrus miricornis is rarely encountered and known by only three specimens. The fourth antennomere of the species is black while the others are reddish to yellowish brown.

The genus is linked to *Neoprocirrus* by the elongate terminal antennomere. Fauvel (1895: 216) placed the genus between *Procirrus* and *Oedichirus*. The specimens I examined are elongate and slender with long legs and antennae, pale reddish brown, and with coarse, umbilicate punctation on the head and pronotum.

Beyond the descriptions, the localities, and a little bit of collecting data nothing is known about the species.

SPECIES INCLUDED AND MATERIAL EXAMINED

miricornis (Fauvel) – H (IRSN), sp (BMNH, GdRC). . . . . Malaysia, Singapore (Note: The species appears to have been described from a single specimen. In the original description Fauvel, 1895: 216, wrote: "Je n'ai vu que l'exemplaire de ma collection,..." so that specimen is the holotype ICZN, 1999: Article 73.1.2], not a syntype. In the online list of types in Institut Royal des Sciences Naturelles, Brussels, the type is listed as a lectotype.)

UNDETERMINED SPECIMENS: Malaysia.
DISSECTIONS: None.

Pseudoprocirrus Bernhauer
Figures 8, 103–105

Pseudoprocirrus Bernhauer, 1934: 506. Type species: *Pseudoprocirrus arrowi* Bernhauer, 1934: 506, fixed by original designation and monotypy. — Blackwelder, 1952: 329 (type species). — Fagel, 1971: 11, 47 (characters; key to species; type species).

DIAGNOSIS: Only *Pseudoprocirrus* and *Oedodactylus* among the Procirrina have just three inflated protarsomeres (fig. 8 and as in fig. 89) and are therewith separated from the other six genera that have four (see fig. 92). In both genera abdominal segment III has a paratergite on each side, the third protarsomere is highly asymmetrical, and the posterior edge of the elytra has a row of setae. The two genera can be separated as follows. The African genus *Pseudoprocirrus* has a transverse, interantennal, frontoclypeal ridge, the gular sutures are most approximate near the middle, tergum and sternum VIII lack a transverse basal ridge, and tergum IX and tergum X are separated and distinct (fig. 103). The New World genus *Oedodactylus* lacks the frontoclypeal ridge, the gular sutures are most approximate basally, tergum and sternum VIII have a transverse basal ridge, and tergum IX is fused to tergum X (fig. 87). The presence of setae on the edge of the posterior margin of the elytra will separate *Pseudoprocirrus* from *Procirrus*, *Oedichirus*, *Palaminus*, and *Paraprocirrus*.

DESCRIPTION: Head (fig. 8) not pedunculate, wider than long; frontoclypeus with subapical, interantennal, transverse ridge; postocular lateral margin broadly rounded to neck; postocular lateral margin moderately long; basal angle absent; basal margin of head indistinguishable from lateral margin, without marginal ridge, and with median portion broadly and shallowly rounded anterior to neck. Neck across nuchal constriction about half as wide as greatest postocular width of head; [**nuchal groove][3]; [**nuchal ridge]. Eye length shorter than postocular length of head. Dorsal surface with dense umbilicate punctation. Ventral surface without postocular groove. Gular sutures separated and present basally; sutures most approximate at about middle. Gula without pubescence. Antennomere 11 about as long as 10; apex without spinelike pencil of setae. [**Mandibles]; [**prostheca]. Maxil-

[3] This structure and other similarly cited structures were unavailable for study.

lary palpus with palpomere 4 longer than second or third, elongate securiform, and compressed. [**Labium, glossae]. [**Hypopharynx]. Labrum without denticles on anterior margin, but with broad lobe adjacent to emargination. [**Epipharynx].

Prothorax (fig. 8) trapezoidal with rounded margins and longer than wide; widest near anterior third and with lateral margins broadly rounded and gradually convergent anteriorly and more strongly convergent posteriorly. Pronotal punctation umbilicate; punctation dense, uniform and present on midline. Pronotal marginal ridge present and entire. Notosternal suture absent. Postprocoxal lobe long and with few punctures; transverse carina absent; apices widely separated from each other. Probasisternum without median carina; surface punctate. Mesospiracular peritreme with anteromedial margin fused, without suture, to furcasternum. Elytra longer than pronotum; humeral angle broadly rounded; posterior edge with row of setae; subapical region without long, thicker, posteromediad-directed seta near lateroapical corner. [**Scutellum, setae covered]. [**Mesosternum, median carina covered]. Mesocoxal acetabulum with marginal carina laterally, absent posteriorly. [**Intersternal suture present and well developed].

Profemur with ridge on anteroventral surface. Protibia with multiple combs extending from near base to tibial apex; tibia with shallow depression on ctenidial surface; apical portion not constricted or enlarged. Protarsomeres (fig. 8) 1–3 swollen; tarsomeres 1–3 tapered and smaller from 1–3; base of tarsomere 1 not surrounded by cupulate protibial apex; tarsomere 4 not expanded beneath tarsomere 5 and apical margin entire, not bilobed, [**ventral setae covered]; tarsomere 4 inserted laterad of middle of apex of asymmetrical third segment; tarsomere 5 with sparse pubescence ventrally. Mesotarsomere 1 longer than tarsomere 2. Metatarsomere 1 longer than tarsomeres 2–4 combined.

Abdominal segments without imbricate macrosculpturing (cf. fig. 28). Segment III with one paratergite; paratergal carina absent; sternum and tergum III separated by paratergite. Segment VII with tergum and sternum separated. Segments IV–VII without oval "windows" in intersegmental membrane. [**Sternum I]. [**Sterna IV–VII, glandular lobes]. Tergum IX (fig. 103) with base fused medially; lateroapical process long, slender, curved ventrally (fig. 104), and extending well beyond apex of tergum X; base of lateroapical process fused to tergal base and with incision laterally (fig. 104). Tergum X with lateral margin attenuate (fig. 103) to narrowly rounded apex; base separated from tergum IX.

Female genital sclerites separated medially; proximal gonocoxite long, broad, flattened, apically truncate, and separated from shorter, setate, cylindrical, apically rounded distal gonocoxite (fig. 105).

[**Aedeagus] (according to Fagel, 1971: 49–50, *Pseudoprocirrus abyssinicus* has one paramere).

DISTRIBUTION AND HABITAT: The genus is recorded from Ethiopia, Zambia, Mozambique, and Zanzibar. No information about the habitat of the species has been published, nor was any on labels attached to specimens I examined.

DISCUSSION: Beyond characters used in descriptions virtually nothing is known about this genus. Bernhauer (1934: 506) described both the genus and the first included species from Zambia without illustrations. Fagel (1971: 47–52) described a second species from Ethiopia and illustrated silhouettes of the head, pronotum, and elytra of *P. arrowi* and *P. abyssinicus* and the underside of the head, the maxillary palpus, and aedeagus of the latter, and redescribed the genus.

Pseudoprocirrus and *Oedodactylus* share most features. Species of both genera have a pair of broad, rounded labral lobes, and enlarged first, second, and third protarsomeres (figs. 8, 89). Segment III of both genera has one paratergite on each side; the paratergite of *Oedodactylus* is moderately large, that of *Pseudoprocirrus* is narrow and difficult to see clearly. In the Procirrina only *Pseudoprocirrus*, *Oedodactylus*, and some species of *Oedichirus* have paratergites on III. Segments IV–VI lack paratergites and the tergum and sternum of each segment are fused. Segment VII also lacks paratergites, but the tergum and sternum are separated. The third protarsomere is strongly asymmetrical and the fourth tarsomere is inserted laterad of the middle of the apex of tarsomere

3, and the fourth maxillary palpomere of both is obliquely truncate.

The two genera have few external differences other than those already noted. The strongest features that differentiate *Pseudoprocirrus* and *Oedodactylus* are the separation of tergum IX and tergum X (fig. 103) in the former and fusion of these terga in the latter (fig. 87). The other strong differential feature is distribution: *Pseudoprocirrus* is in eastern Africa and *Oedodactylus* is Neotropical. The differentiating characters are few and the shared features many, but more detailed morphological study of the species may reveal others. *Pseudoprocirrus* includes only two species and *Oedodactylus* only four. Few specimens are known for *Pseudoprocirrus*, only four for *P. arrowi* and two for *P. abyssinicus*, and few dissections were possible.

Fagel (1971: 49) was aware that *Pseudoprocirrus* and *Oedodactylus* shared most characters, but continued to recognize two genera because he believed, based on his dissection of *P. abyssinicus*, that *Pseudoprocirrus* possessed a single paramere, whereas species of *Oedodactylus* have none. I examined a male and female syntype of *P. arrowi* and dissected the abdomen of the female, but not the one male, and was unable to verify Fagel's observation. However, one paramere is unusual. Because so few specimens were available, I could dissect the abdomen of only one specimen of each of two of the four species of *Oedodactylus* and so, was unable to corroborate that all the species lack parameres. Fagel (1971: 47) stated that the penultimate five to six antennal segments of *Pseudoprocirrus* are compressed; this is untrue for the two syntypes of *P. arrowi* that I examined. Because the base of the head of *P. arrowi* lacks basal angles and the pronotum has strongly rounded anterior angles, it differs from some species of *Oedodactylus*, but both features are found in *O. fuscobrunneus*. The form of the head of a syntype of *P. arrowi* shown herein (fig. 8) differs significantly from Fagel's (1971: 50, fig. 38) line drawing.

Species Included and Material Examined

abyssinicus Fagel – Lit. Att. [Ethiopia, Zanzibar]
arrowi Bernhauer – Syn (FMNH, BMNH) . . . . . Zambia

Undetermined Specimens: None.

Dissections: Abdominal dissection: *Pseudoprocirrus arrowi* (1 female, Zambia).

Stylokyrtus, new genus
Figure 9

Type species: *Oedodactylus errans* Sharp, 1876: 337, designated here.

Diagnosis: *Stylokyrtus* has four swollen protarsomeres, segment III has a paratergal carina and lacks paratergites, and tergum and sternum III are fused, but see Discussion for this genus. The preceding characters will separate *Stylokyrtus* from *Oedodactylus,* which has three inflated protarsomeres, paratergites on segment III, and tergum and sternum III separated. Tergum and sternum VII are separated in *Stylokyrtus,* which will distinguish the genus from *Oedichirus* and *Palaminus* in which tergum and sternum VII are partially or completely fused. The long lateroapical processes of tergum IX of *Stylokyrtus* will separate it from *Procirrus*, *Neoprocirrus*, and *Paraprocirrus,* which all have short lateroapical processes. Maxillary palpomere 4 is broad and obliquely truncate in *Stylokyrtus*, but symmetrically to asymmetrically fusiform in *Procirrus* and *Paraprocirrus* and fusiform to securiform in *Neoprocirrus*. The presence of setae on the edge of the posterior margin of the elytra will separate *Stylokyrtus* from *Procirrus*, *Oedichirus*, *Palaminus*, and *Paraprocirrus*.

Description: Head (fig. 9) not pedunculate, wider than long; frontoclypeus without subapical, interantennal ridge; postocular lateral margin strongly converging to neck; postocular lateral margin short; basal angles absent; basal margin of head indistinguishable from lateral margin. Neck across nuchal constriction about seven tenths as wide as greatest postocular width of head; [**nuchal groove][4]; [**nuchal ridge]. Eye length longer than postocular length of head. Dorsal surface with deep simple punctation. Ventral surface without postocular groove. Gular sutures separated. [**Gular pubescence and punctation]. Antennomere 11 about as long as 10; apex without spiniform pencil of setae. Man-

[4] This structure and other similarly cited structures were unavailable for study.

dibles with apically bifid denticle; [**prostheca]. Maxillary palpus with fourth palpomere longer than third, securiform, compressed. [**Labium, glossae]. [**Hypopharynx]. Labrum without denticles on anterior margin, but with poorly developed, broad lobe adjacent to emargination. [**Epipharynx].

Prothorax (fig. 9) trapezoidal, longer than wide; widest near anterior margin then broadly rounded and moderately strongly convergent to rounded basal margin. Pronotum with simple, dense, moderately coarse punctation; punctation uniform, but for impunctate midlongitudinal strip. Pronotal marginal ridge present. Notosternal suture poorly developed, evident as weak ridge in broad depression; suture and marginal ridge separated. Hypomeron polished and densely punctate. Postprocoxal lobe long and punctate; transverse carina absent; apex of lobes moderately widely separated from one another. Probasisternum with median carina; surface impunctate. Mesospiracular peritreme with anteromedial margin fused to furcasternum. Elytra slightly shorter than pronotum; humeral angle present; posterior edge with row of setae; subapical region without long, thicker, posteromediad directed seta near lateroapical corner. [**Scutellum, setae covered]. Mesosternum without median carina. [**Mesocoxal acetabulum]. [**Intersternal suture].

Profemur with carina near middle of anteroventral surface. Protibia with three combs near middle; tibia without depression on ctenidial surface; apical portion neither constricted or enlarged. Protarsomeres 1–4 inflated; [**ventral setae]; base of tarsomere 1 not surrounded by cupulate protibial apex; [**symmetry of insertion of tarsomere 5 on tarsomere 4]; [**pubescence on ventral surface of tarsomere 5]. Mesotarsomere 1 longer than second and third combined. Metatarsomere 1 about as long as tarsomeres 2–4.

Abdominal segments without imbricate macrosculpturing. Segment III without paratergites; paratergal carina present basally and laterad of spiracle; tergum and sternum III fused. Segment VII with tergum and sternum separated. [**Segments IV to VI, "windows"]. [**Sternum I]. [**Sterna IV–VI, glandular lobes]. Tergum IX [**base]; lateroapical process long, strongly curved ventrally, and extending well beyond apex of posterior margin of tergum X; [**base of lateroapical process]. [**Tergum X covered].

[**Female genital sclerites].

[**Aedeagus].

ETYMOLOGY: *Stylokyrtus,* from the Greek for "pillar" or "column" (*stylos*) and "curved" (*kyrtos*), refers to the strongly curved lateroapical processes of abdominal segment IX. The generic name is masculine.

DISTRIBUTION AND HABITAT: The genus is found in Brazil, but nothing is known about the habitat of the only species.

DISCUSSION: *Stylokyrtus errans* was originally described in *Oedodactylus*, but is removed from that genus because, unlike species in the latter, *S. errans* has four inflated protarsomeres, abdominal segment III lacks paratergites and has a basal paratergal carina, and tergum and sternum III are fused. The species of *Oedodactylus* have three inflated protarsomeres and abdominal segment III has a pair of paratergites and the tergum and sternum are separated. The male holotype of the type species was not dissected.

Note, however, that the paratergal carina of *S. errans* is strongly and coarsely developed and similar to the paratergite of species of *Oedodactylus*. I cannot see the sutures that delimit a paratergite for segment III and without dissection I am uncertain whether this structure is a carina or a paratergite or if the tergum and sternum are separated or fused. As the species is known only by the holotype, the needed dissection was impossible. Nonetheless, *S. errans* has four inflated protarsomeres and species of *Oedodactylus* have only three.

SPECIES INCLUDED AND MATERIAL EXAMINED

errans (Sharp) – H (BMNH) . . . . . Brazil
[**Newcombination**, transferred from *Oedodactylus*]

UNDETERMINED SPECIMENS: None.

DISSECTIONS: None.

DISCUSSION

GENERAL COMMENTS: In the Paederinae only the Procirrina, Cylindroxystina, and some species of Dolicaonina (*Gnathymenus*) and Paederina (*Paederus*) have lost the

abdominal paratergites and have a cylindrical abdomen. The fourth segment of the maxillary palpus is enlarged in only Procirrina and Pinophilina. The mesothoracic peritremes form a large sclerite and close the procoxal cavities posteriorly only in Procirrina, Dolicaonina, and some Paederina. The sister group of the Procirrina is Pinophilina; evidence suggests (Herman, unpubl.) that the sister of this clade includes the Dolicaonina and Paederina.

The Procirrina are known to most by one or more of the three most speciose genera, *Palaminus*, *Procirrus*, and *Oedichirus*. The other genera are obscure, have only a few species each, are found only in tropical regions, and are poorly represented in collections. Most of the species of all the genera are found in the tropics. *Oedichirus* and *Palaminus* are found in both the Old World and the New; *Oedodactylus* and *Stylokyrtus* are restricted to the New World tropics and *Procirrus*, *Neoprocirrus*, *Paraprocirrus*, and *Pseudoprocirrus* to the Old World tropics. A small number of species of *Oedichirus, Palaminus, and Procirrus* reach temperate regions.

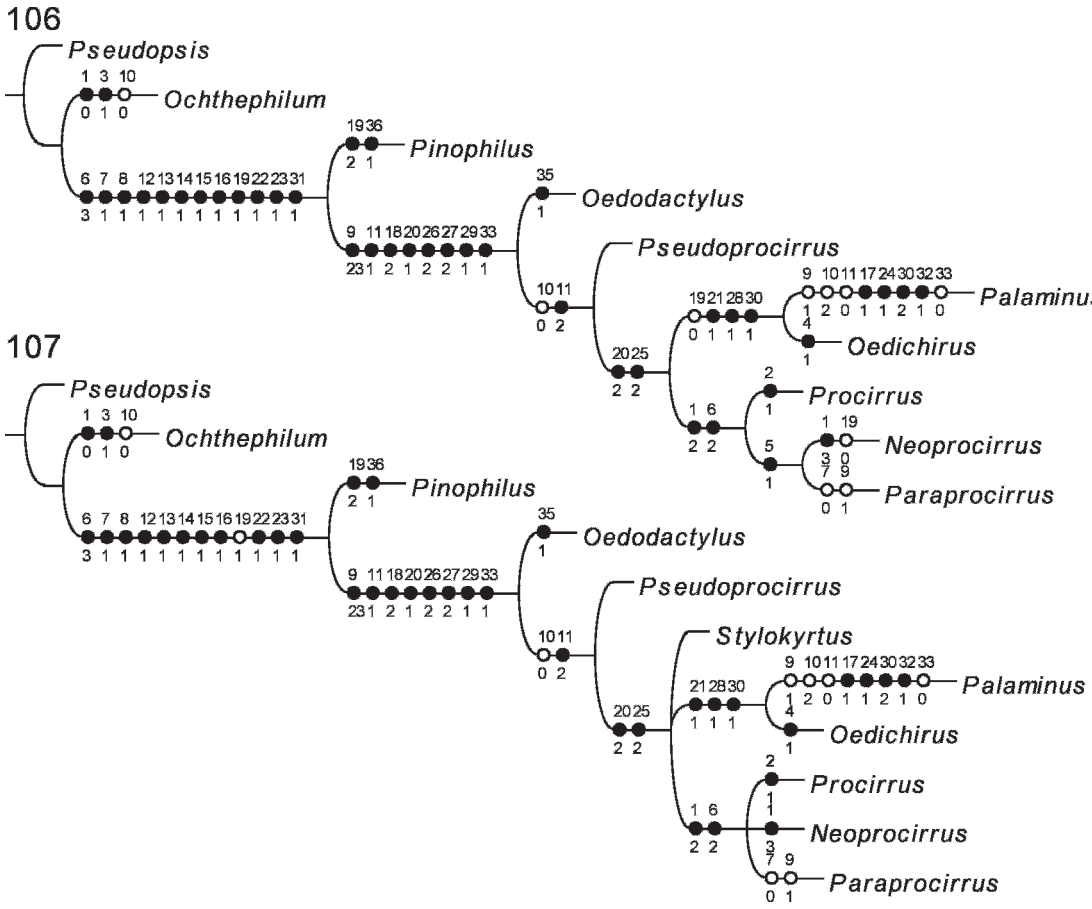
In the New World, one genus, *Palaminus*, reaches Canada and the United States; *Oedichirus*, *Oedodactylus*, and *Stylokyrtus* are only in the Neotropical Region. In the Old World only one species of *Procirrus* and five of *Oedichirus* are reported for Europe and those are all African species reaching only to the southern edge of the continent. The subtribe is absent from most of southwestern Asia, where only *Oedichirus* and *Procirrus* are known from the Levant countries and a female of *Oedichirus reitteri* was reported in Afghanistan (Scheerpeltz, 1961: 251). Species of *Oedichirus*, *Palaminus*, and *Procirrus*, are known from southern Asia: India to Vietnam through Indonesia to New Guinea; *Neoprocirrus* and *Paraprocirrus* are known from Indonesia and Malaysia. In eastern Asia, whereas one species of *Procirrus*, five of *Palaminus*, and two of *Oedichirus* are reported for Hong Kong and Taiwan and while two species of *Palaminus* and five of *Oedichirus* are in Japan, only two species of the subtribe reach mainland China (Zhejiang), one a species of *Palaminus* and the other one of *Oedichirus*. Eleven species of *Oedichirus*, four of *Palaminus*, and six of *Procirrus* are known for Australia and most of those are in the north. Although *Procirrus*, *Palaminus*, and *Oedichirus* occur in southern to eastern Asia and Australia the vast majority of the species are described from Madagascar and tropical Africa. Many species more are known for the Ethiopian Region than for the New World tropics, but that in part is the result of works by Fagel, Janák, Jarrige, and Lecoq. There have been few studies of the Neotropical fauna of the Procirrina and none recently.

It is probable that more species of Procirrina will be found in China, particularly in the tropical south, and in tropical regions of Australia and New Guinea through Indonesia and tropical Asia to Madagascar and Africa thence to the Neotropical Region. At this writing there are eight procirrine genera with 648 species—certainly many others will be found.

PHYLOGENY: To examine the phylogenetic relationships among the genera of the Procirrina a matrix of 37 characters was constructed for 11 taxa, including three outgroups, *Pseudopsis* (Pseudopsinae), *Ochthephilum* (Paederinae: Cryptobiina), and *Pinophilus* (Paederinae: Pinophilina). The characters examined for the analysis are listed in the appendix. The distribution of the characters states among taxa is summarized in the matrix (appendix 1). The discussion on morphology includes additional comments concerning these and other structures.

Because *Stylokyrtus* was represented by only the holotype, it was not dissected and characters critical to the placement of the genus in the subtribe were unavailable for examination; these characters are indicated in the matrix by question marks. To get a firm sense of the relationship of the genera for which all the characters were examined two matrices were analyzed; one excluded, the other included, *Stylokyrtus*.

Omitting *Stylokyrtus* resulted in one tree (fig. 106) of 68 steps, with 0.76 and 0.76 as the consistency index (CI) and retention index (RI) respectively. When the nine "uninformative" characters were deactivated and the revised matrix analyzed the tree was shorter (length = 61; CI = 0.73; RI = 0.76). Because the uninformative characters are all



Figs. 106–107. Cladograms for genera of Procirrina. **106.** Tree without *Stylokyrtus*. **107.** Strict consensus tree of three with *Stylokyrtus* included.

synapomorphic features that define the terminal taxa (genera), they remain in the matrix and analysis. Including *Stylokyrtus* in the analysis produced three trees (length = 69; CI = 0.75; RI = 0.75). For two trees *Stylokyrtus* was the sister of the clade that includes *Palaminus*, *Oedichirus*, *Procirrus*, *Neoprocirrus*, and *Paraprocirrus* and for one of the two trees that clade had the same topology as shown in figure 106, but in the other *Neoprocirrus* was the sister of *Procirrus* + *Paraprocirrus*. In the third tree *Stylokyrtus* was the sister of *Oedichirus* + *Palaminus* and, as in figure 106, *Procirrus* was the sister of *Neoprocirrus* + *Paraprocirrus*. The strict consensus tree of the clade is illustrated in figure 107 (length = 71; CI = 0.73; RI = 0.72).

Pinophilus and the Procirrina form a clade strongly supported by features of the maxillary palpus (6, 7, 8), mesospiracular peritreme (12, 13, 14, 15), metatibia (22), and abdominal sternum III (31). The monophyly of the Procirrina is supported by the emargination of the posterior margin of the contiguous elytra (character state: 18.2), the bulbous protarsomeres that include tarsomeres 1–3 (20.1) for the two basal genera and tarsomeres 1–4 (20.2) for the clade that includes *Palaminus* and *Oedichirus* and *Procirrus* plus *Neoprocirrus* and *Paraprocirrus*, the absence of paratergites on abdominal segments IV–VII (26.2, 27.2), the fused abdominal terga and sterna of segments IV–VI (29.1), and the ventrally curved lateroapical process of tergum IX (34.1). *Palaminus*

and *Oedichirus* are linked by the pubescence on the ventral surface of protarsomere 5 (21.1), the intersegmental abdominal "windows" (28.1), and fusion of tergum and sternum VII. *Palaminus* is defined by the macroseta on the apicolateral edge of the elytra (17.1), the imbricate abdominal sculpturing (24.1), the fused tergum and sternum VII (30.2), and the detached lateroapical process of tergum IX (33.1). *Oedichirus* is defined by the apical spiniform pencil of setae at the apex of antennomere 11 (4.1) and the basal fusion and apical incision of abdominal tergum and sternum VII (30.1). The clade with *Procirrus*, *Neoprocirrus*, and *Paraprocirrus* is defined by the elongate head (1.2) and long, fusiform fourth maxillary palpomere (6.0). The head of *Procirrus* is pedunculate (2.1) and *Neoprocirrus* and *Paraprocirrus* are sisters based on the elongate antennomere 11 (5.1).

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REFERENCES

Adachi, T. 1955. Systematic study on the subfamily Paederinae of Staphylinidae of Japan. Journal of the Tôyô University (Tokyo) 7: 11–36. [in Japanese, English summary of descriptions of new species].

Arnett, R.H. 1963. The beetles of the United States. (A manual for identification). Washington, DC: Catholic University of America, xi + 1112 pp.

Assing, V. 2004. New species and records of Staphylinidae from Turkey III (Insect: Coleoptera). Linzer Biologische Beiträge 36 (2): 669–733.

Assing, V. 2006. New species and records of Staphylinidae from Turkey VI, with six new synonymies (Coleoptera: Staphylinidae). Koleopterologische Rundschau 76: 223–276.

Bernhauer, M. 1923. Synonymische Bemerkungen bezüglich mehrfach beschriebener Staphylinidengattungen und Arten. Wiener Entomologische Zeitung 40: 63.

Bernhauer, M. 1934. The staphylinid fauna of South Africa. Annals of the South African Museum 30 (4): 481–509.

Bernhauer, M., and K. Schubert. 1912. Staphylinidae III. Pars 40. *In* S. Schenkling (editor), Coleopterorum catalogus…. Vol. 5, 191–288. Berlin: Junk.

Bierig, A. 1935. Pinophilini y Paederini (Col. Staph.) nuevos de la Isla de Cuba. Memorias de la Sociedad Cubana de Historia Natural ''Felipe Poey'' 9 (1): 29–42.

Bierig, A. 1943. Algunos estaphylinidae (Col.) nuevos de Costa Rica. Revista Chilena de Historia Natural 45 (1941): 154–163.

Biswas, D.N. 2003. Insecta: Coleoptera: Staphylinidae. *In* J.R.B. Alfred (editor), State Fauna Series 9. Fauna of Sikkim. Part 3: 237–281. Kolkata: Zoological Survey of India.

Biswas, D.N., and S. Biswas. 1995. Insecta: Coleoptera: Staphylinidae. *In* State Fauna Series 3. Fauna of West Bengal. Part 6A (Insecta: Coleoptera): 201–361. Calcutta: Zoological Survey of India.

Blackburn, T. 1888. Descriptions of twenty new species of South Australian Coleoptera. Transactions and Proceedings and Report of the Royal Society of South Australia 10: 1–11.

Blackburn, T. 1891. Further notes on Australian Coleoptera, with descriptions of new genera and species. Transactions and Proceedings and Report of the Royal Society of South Australia 14: 65–153.

Blackwelder, R.E. 1936. Morphology of the coleopterous family Staphylinidae. Smithsonian Miscellaneous Collections 94 (13): 1–102.

Blackwelder, R.E. 1943. Monograph of the West Indian beetles of the family Staphylinidae. Bulletin of the United States National Museum 182: i–viii + 1–658.

Blackwelder, R.E. 1944. Checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America. Part 1. Bulletin of the United States National Museum 185: xii + 1–188.

Blackwelder, R.E. 1952. The generic names of the beetle family Staphylinidae, with an essay on genotypy. United States National Museum Bulletin 200: i–iv + 1–483.

Blackwelder, R.E., and R.H. Arnett. 1974. Staphylinidae. *In* North American Beetle Fauna Project. Checklist of the beetles of Canada, United States, Mexico, Central America and the West Indies. 1 (2). The water beetles, rove beetles, and related groups. (Red Version): 1–188. Latham, NY: Biological Research Institute of America.

Blatchley, W.S. 1910. An illustrated descriptive catalogue of the Coleoptera or beetles (exclusive of the Rhynchophora) known to occur in Indiana…. Indianapolis: W. S. Blatchley, 1385 pp.

Bordoni, A. 1975. Morfologia cefalica e addominale della sottotribu Medina nov. e del genere *Medon* Stephens in particolare e suoi rapporti con la sistematica (Col. Staphylinidae). Redia 56: 417–445.

Bruch, C. 1915. Catálogo sistemático de los coleópteros de la República Argentina. Pars II. Familias: Halipidae, Dytiscidae, Gyrinidae, Hydrophilidae y Staphylinidae. Revista del Museo de La Plata 19: 471–526.

Bruch, C. 1928. Suplemento al catálogo sistemático de los coleópteros de la República Argentina. III. (Addenda, corrigenda y lista de especies). Boletín de la Academia Nacional de Ciencias (Córdoba) 29: 419–452.

Cameron, M. 1921. New species of Staphylinidae from Singapore. Part IV. (Conclusion). Transactions of the Entomological Society of London 1920: 347–413.

Cameron, M. 1925. Catalogue of the Indian insects. Part 6 — Staphylinidae. Calcutta: Government of India, 126 pp.

Cameron, M. 1928. New species of Staphylinidae from Borneo. Sarawak Museum Journal 3 (iv) (11): 423–451.

Cameron, M. 1931. The fauna of British India including Ceylon and Burma. Coleoptera. Staphylinidae. Vol. 2: viii + 1–257. London: Taylor and Francis.

Cameron, M. 1936. Fauna Javanica. The Staphylinidae (Col.) collected by Mr. F. C. Drescher. Tijdschrift voor Entomologie 79: 25–54.

Campbell, J.M., and A. Davies. 1991. Family Staphylinidae. Rove beetles. *In* Y. Bousquet (editor), Checklist of beetles of Canada and Alaska. Publication 1861/E: 86–124. Ottawa: Agriculture Canada.

Casey, T.L. 1910. Synonymic and descriptive notes on the Paederini and Pinophilini. Memoirs on the Coleoptera Vol. 1: 184–205. Lancaster, PA: New Era Printing Co.

Chevrolat, L.A.A. 1846. *Microphius*. *In* C. D'Orbigny (editor), Dictionnaire universel d'histoire naturelle. Vol. 8: 201. Paris: Renard, Martinet et C.

Ciceroni, A., A. Zanetti 1995. Genera 47–61 and 79–147: 10–14, 19–33. *In* A. Ciceroni, V. Puthz, and A. Zanetti, Fasc. 48. Coleoptera Polyphaga III. (Staphylinidae), *in* A. Minelli, S. Ruffo, and S. La Posta, Checklist delle specie della fauna italiana. Bologna: Calderini.

Coiffait, H. 1978a. Ergebnisse der Bhutan-Expedition 1972 des Naturhistorischen Museums in Basel. Coleoptera: fam. Staphylinidae subfam. Paederinae, Euaesthetinae, Piestinae, Osoriinae et Omalinae [sic]. Entomologica Basiliensia 3: 109–150.

Coiffait, H. 1978b. Coléoptères staphylinides de la région paléarctique occidentale III. Sous famille Staphylininae, Tribu Quediini. Sous famille Paederinae, Tribu Pinophilini. Nouvelle Revue d'Entomologie. Supplément. 8 (4): 3–364.

Coiffait, H., and F. Saiz. 1968. Les Staphylinidae (sensu lato) du Chile. *In* C. Delamare Deboutte-

ville and E. Rapoport (editors), Biologie de l'Amérique Australe. Études sur la faune du sol. Vol. 4: 339–468. Paris: Centre National de la Recherche Scientifique.

Crotch, G.R. 1873. Check list of the Coleoptera of America north of Mexico. Salem: Salem Press, 136 pp.

Dejean, P.F.M.A. 1836. Catalogue des Coléoptères de la collection de M. le Comte Dejean. Fasc 1–4: 1–384. Paris: Méquignon-Marvis.

Deuve, T. 1988. Les sternites VIII et IX de l'abdomen sont-ils visibles chez les imagos des Coléoptères et des autres insectes holométaboles? Nouvelle Revue d'Entomologie (n.s.) 5 (1): 21–34.

Deuve, T. 1993. L'abdomen et les genitalia des femelles de Coléoptères Adephaga. Mémoires du Muséum National d'Histoire Naturelle (Série A, Zoologie) 155: 1–184.

Downie, N.M., and R.H. Arnett, Jr. 1996. The beetles of northeastern North America. Vol. 1. Introduction; suborders Archostemata, Adephaga, and Polyphaga, thru superfamily Cantharoidea. Gainesville, FL: Sandhill Crane Press, 880 pp.

Drugmand, D. 1989. Contribution à la connaissance des Staphylinidae d'Israël (Coleoptera) I. Sous-familles des Paederinae Ganglbauer, 1895 et des Xantholininae Jeannel et Jarrige, 1849 [sic]. Bulletin and Annales de la Société Royale Belge d'Entomologie 125: 103–113.

Duponchel, P.A.J. 1841. Analyses d'ouvrages nouveaux. Genera et species Staphylinorum insectorum coleopterorum, auctore F. Erichson…. Revue Zoologique par la Société Cuvierienne 1841: 52–57.

Duvivier, A. 1883. Énumération des Staphylinides, décrits depuis la publication du catalogue de M. M. Gemminger et de Harold. Annales de la Société Entomologique de Belgique 27: 91–215.

Erichson, W.F. 1839. Genera et species Staphylinorum insectorum coleopterorum familiae., 1 (1): viii + 1–400. Berlin: F.H. Morin.

Erichson, W.F. 1840. Genera et species Staphylinorum insectorum coleopterorum familiae., 1 (2): 401–954. Berlin: F.H. Morin.

Fagel, G. 1955. Contribution à la connaissance des Staphylinidae XXXII. Notes sur le genre *Oedichirus* Erichson. Mémoires de la Société Royale d'Entomologie de Belgique 27: 194–206.

Fagel, G. 1963. Coleoptera Staphylinidae (Piestinae, Osoriinae, Oxytelinae, Paederinae). *In* La réserve naturelle intégrale du Mont Nimba. fasc. 5. Mémoire de l'Institut Français d'Afrique Noire 66: 337–356.

Fagel, G. 1971. Revision des genres *Procirrus* Latreille, *Palaminus* Erichson, *Oedichirus* Erichson et voisins de la faune africaine (Coleoptera, Staphylinidae, Paederinae). Musée Royal de l'Afrique Centrale Annales (serie in 8°). Sciences Zoologiques 186 (1970): 1–444.

Fairmaire, L., and P. Germain. 1861. Révision des Coléoptères du Chili. Annales de la Société Entomologique de France (4) 1: 405–456.

Fauvel, A. 1867. Faune du Chili. Insectes Coléoptères. Staphylinides (Suite et fin). Notices Entomologiques 5: 1–61.

Fauvel, A. 1868. Faune du Chili. Insectes Coléoptères. Staphylinides. (Suite et fin). Bulletin de la Société Linnéenne de Normandie (2) 1: 6–67.

Fauvel, A. 1873. Faune Gallo-Rhénane ou species des insectes qui habitent la France, la Belgique, la Hollande, le Luxembourg, la prusse Rhénane, la Nassau et la Valais avec tableaux synoptiques et planches gravées, vol. 3, part 4: 215–390. Caen: Le Blanc-Hardel.

Fauvel, A. 1875a. Faune Gallo-Rhénane … Catalogue systématique des staphylinides de la Faune Gallo-Rhénane avec l'addition synonymique des espèces européennes, sibériennes, caucasiques et Mediterranéennes et descriptions nouvelles. Bulletin de la Société Linnéenne de Normandie (2) 9: 202–236.

Fauvel, A. 1875b. Fauna Gallo-Rhénane … Catalogue systématique des staphylinides de la Faune Gallo-Rhénane avec l'addition synonymique des espèces européennes, sibériennes, caucasiques et Mediterranéennes et descriptions nouvelles, vol. 3, part 6: i–xxxviii. Caen: Le Blanc-Hardel.

Fauvel, A. 1876. Faune Gallo-Rhénane … 3rd supplément aux staphylinides, vol. 3, part 6: 47–82. Caen: Le Blanc-Hardel.

Fauvel, A. 1878a. Les staphylinides de l'Australie et de la Polynésie. Annali del Museo Civico di Storia Naturale di Genova 13: 465–598.

Fauvel, A. 1878b. Les staphylinides des Moluques et de la Nouvelle Guinée. Annali del Museo Civico di Storia Naturale di Genova 12: 171–315.

Fauvel, A. 1879. Les staphylinides des Moluques et de la Nouvelle Guinée. (2e. Memoire). Annali del Museo Civico di Storia Naturale di Genova 15: 63–121.

Fauvel, A. 1886. Les Staphylinides du nord de l'Afrique. Revue d'Entomologie 5: 9–100.

Fauvel, A. 1889. Les Coléoptères de la Nouvelle-Calédonie et dépendances avec descriptions, notes et synonymies nouvelles. Revue d'Entomologie 8: 242–271.

Fauvel, A. 1891. Voyage de M. E. Simon au Vénézuela (Décembre 1887–Avril 1888). 11e Mémoire. Revue d'Entomologie 10: 87–127.

Fauvel, A. 1895. Staphylinides nouveaux de l'Inde et de la Malaisie. Revue d'Entomologie 14: 180–286.

Fauvel, A. 1897. Catalogue des staphylinides de Barbarie et des îles Açores, Madères, Salvages et Canaries. 4th ed. Revue d'Entomologie 16: 237–371.

Fauvel, A. 1901. Voyage de M. le Dr. Ed. Bugnion au Venezuela, en Colombie et aux Antilles. Staphylinides. Revue d'Entomologie 20: 69–91.

Fauvel, A. 1902. Catalogue des staphylinides de la Barbarie de la Basse-Egypte et des Iles Açores, Madères, Salvages et Canaries. Revue d'Entomologie 21: 45–189.

Frank, J.H. 1982. The parasites of the Staphylinidae (Coleoptera). A contribution towards an encyclopedia of the Staphylinidae. University of Florida Agricultural Experiment Station Bulletin 824: vii + 1–118.

Frank, J.H. 1986. A preliminary checklist of the Staphylinidae (Coleoptera) of Florida. The Florida Entomologist 69 (2): 363–382.

Frisch, J. 2005. "*Scopaeus limbatus* Kraatz" of ancient authors — a monophyletic species group distributed in the Mascarene Islands, the South-East Palaearctic, the Oriental and Australian regions (Coleoptera, Staphylinidae, Paederinae). Deutsche Entomologische Zeitschrift 52 (1): 73–96.

Frisch, J. 2009. A revision of the *Scopaeus mutatus* species group (Staphylinidae, Paederinae), with description of new species from Anatolia and the Caucasus. Deutsche Entomologische Zeitschrift 56 (2): 271–287.

Gemminger, M., and E. Harold. 1868. Catalogus Coleopterorum hucusque descriptorum synonymicus et systematicus. Vol. 2: 425–752 + 6. Monachii: E. H. Gummi.

Glick, P.A. 1939. The distribution of insects, spiders, and mites in the air. U.S. Department of Agriculture Technical Bulletin 673: 1–150.

Gray, G. 1832. Notices of new genera and species. *In* E. Griffith and E. Pidgeon, The Class Insecta arranged by the Baron Cuvier, with supplementary additions to each order. Insecta. Vol. 1: viii + 570, *in* E. Griffith, The animal kingdon arranged in conformity with its organization, by the Baron Cuvier…with supplementary additions to each order. Vol. 14. London: Whittaker, Treacher.

Grebennikov, V.V., and A.F. Newton. 2009. Good-bye Scydmaenidae, or why the ant-like stone beetles should become megadiverse Staphylinidae sensu latissimo (Coleoptera). European Journal of Entomology 106: 275–301.

Hammond, P.M. 1979. Wing-folding mechanisms of beetles, with special reference to investigations of Adephagan phylogeny (Coleoptera). *In* T.L. Erwin, G.E. Ball, and D.R. Whitehead (editors), Carabid beetles: their evolution, natural history, and classification, 113–180. The Hague: W. Junk.

Hammond, P.M. 1984. An annotated check-list of Staphylinidae (Insecta: Coleoptera) recorded from Borneo. Sarawak Museum Journal (n.s.) 33 (54): 187–218.

Hayashi, Y. 1989. Two species of the genus *Oedichirus* (Coleoptera, Staphylinidae) from Japan and Taiwan. Kanagawa-Chûhô 90: 161–166.

Herman, L.H. 1970. Phylogeny and reclassification of the genera of the rove-beetle subfamily Oxytelinae of the World (Coleoptera, Staphylinidae). Bulletin of the American Museum of Natural History 142 (5): 343–454.

Herman, L.H. 1979. Revision of *Stereocephalus* (Coleoptera, Staphylinidae, Paederinae). American Museum Novitates 2683: 1–13.

Herman, L.H. 1981. Revision of the subtribe Dolicaonina of the New World, with discussions of phylogeny and the Old World genera (Staphylinidae, Paederinae). Bulletin of the American Museum of Natural History 167 (6): 327–520.

Herman, L.H. 2001. Catalog of the Staphylinidae (Insecta: Coleoptera). 1758 to the end of the Second Millennium. I. Introduction, history, biographical sketches, and Omaliine group. Bulletin of the American Museum of Natural History 265 (1): 1–650.

Herman, L.H. 2003. Nomenclatural changes in the Paederinae (Coleoptera: Staphylinidae). American Museum Novitates 3416: 1–28.

Herman, L.H. In prep. Revision of the New World species of *Oedichirus* (Coleoptera: Staphylinidae: Paederinae).

Heyden, L. von., E. Reitter, and J. Weise. 1891. Catalogus Coleopterorum Europae, Caucasi et Armeniae rossicae. Berlin: R. Friedländer, viii + 420 pp.

Heyden, L. von., E. Reitter, and J. Weise. 1906. Catalogus Coleopterorum Europae, Caucasi et Armeniae rossicae. Berlin: R. Friedländer, 774 pp.

Hlavac, T.F. 1972. The prothorax of Coleoptera: origin, major features of variation. Psyche 79 (3): 123–149.

ICZN (International Commission on Zoological Nomenclature), International code of zoological nomenclature. 1999. 4th ed. London: International Trust for Zoological Nomenclature, xxix + 306 pp.

ICZN. 2003. Declaration 44. Amendment of Article 74.7.3. Bulletin of Zoological Nomenclature 60 (4): 263.

Jacquelin Du Val, P.N.C. 1857. Famille des staphylinides. *In* Manuel Entomologique. Genera des Coléoptères d'Europe…. Vol. 2, 41–128. Paris: Deyrolle.

Jacquelin Du Val, P.N.C. 1859. Catalogue de la famille de staphylinides. *In* Manuel Entomologique. Genera des Coléoptères d'Europe…. Vol. 2: 53–83. Paris: Deyrolle.

Janák, J. 2003. Neue Arten neue Funde der Gattung *Oedichirus* aus Madagaskar IV. (Coleoptera: Staphylinidae: Paederinae: Pinophilini). Klapalekiana 39: 229–255.

Jarrige, J. 1952. Brachélytres nouveaux ou mal connus de la faune circaméditerranéenne. Annales de la Société Entomologique de France 119 (1950): 117–139.

Jarrige, J. 1974. Sur les types de *Palaminus* malgaches décrits par A. Fauvel. (Col. Staphylinidae). Annales de la Société Entomologique de France (n.s.) 10 (4): 865–874.

Jarrige, J. 1978. Contribution à l'étude des Coleoptera Brachelytra Staphylinidae du massif de l'Andringitra (Madagascar centre). Bulletin du Muséum National d'Histoire Naturelle Zoologie 353: 245–296.

Kellner, R.L.L. 2002a. Interspecific transmission of *Paederus* endosymbionts: relationship to the genetic divergence among the bacteria associated with pederin biosynthesis. Chemoecology 12: 133–138.

Kellner, R.L.L. 2002b. Molecular indentification of an endosymbiotic bacterium associated with pederin biosynthesis in *Paederus sabaeus* (Coleoptera: Staphylinidae). Insect Biochemistry and Molecular Biology 32: 389–395.

Kellner, R.L.L. 2003. Stadium-specific transmission of endosymbionts needed for pederin biosynthesis in three species of Paederus rove beetles. Entomologia Experimentalis et Applicata 107: 115–124.

Koch, C. 1934. Wissenschaftliche Ergebnisse der entomologischen Expeditionen seiner Durchlaucht des Fürsten Alessandro C. della Torre e Tasso nach Aegypten und auf die Halbinsel Sinai. IV. Staphylinidae (Coleoptera). Bulletin de la Société Royale Entomologique d'Égypte 18: 33–91.

Kocher, L. 1958. Catalogue commenté des Coléoptères du Maroc. Fascicule II. Hydrocanthares, Palpicornes, Brachelytres. Travaux de l'Institut Scientifique Chérifien, Série Zoologique 14: 1–246.

Kraatz, G. 1857. Naturgeschichte der Insecten Deutschlands. Abt. 1. Coleoptera. Zweiter Band. Lief. 3–6: 377–1080. Berlin: Nicolai.

Kraatz, G. 1859. Die Staphylinen-Fauna von Ostindien, insbesondere der Insel Ceylan. Archiv für Naturgeschichte 25 (1): 1–196.

Lacordaire, J.T. 1854. Histoire des insectes. Genera des coléoptères ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes. Vol. 2. Paris: Librairie Encyclopédique de Roret, 548 pp.

Laporte, F.L. (Castelnau). 1835. Études entomologiques, ou description d'insectes nouveaux, et observations sur leur synonymie. Paris: Méquignon-Marvis, 159 pp.

Laporte, F.L. (Castelnau). 1840. Histoire naturelle des insectes coléoptères. Vol. 1. Paris: Duménil, cxxv + 324 pp.

Last, H.R. 1961. 5. Family Staphylinidae. *In* M. Chûjô (editor), Coleoptera from Southeast Asia. Nature and Life in Southeast Asia, vol. 1: 305–309. Kyoto: Fauna and Flora Research Society.

Latreille, P.A. 1829. Crustacés, arachnides et partie des insectes. *In* G. Cuvier, Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Vol. 4. Paris: Déterville, xxvii + 1–584 pp.

Lea, A.M. 1904. Descriptions of new species of Australian Coleoptera. Part VII. The Proceedings of the Linnean Society of New South Wales 29 (1): 60–107.

Lea, A.M. 1923. On Australian Staphylinidae (Coleoptera). Transactions and Proceedings of the Royal Society of South Australia 47: 1–53.

LeConte, J.L. 1861. Classification of the Coleoptera of North America. Part. 1. Prepared for the Smithsonian Institution. Smithsonian Miscellaneous Collections 3: xxv + 1–214.

LeConte, J.L. 1863. List of the Coleoptera of North America. Prepared for the Smithsonian Institution. Smithsonian Miscellaneous Collections 6 (140): 1–56.

Lecoq, J.-C. 1984. Description d'une nouvelle espèce de *Palaminus* Erichson de Madagascar (Coleoptera, Staphylinidae, Paederinae). Revue Française d'Entomologie (n.s.) 6 (2): 79–80.

Lecoq, J.-C. 1986. Insectes Coléoptères Staphylinidae Paederinae, I. Pinophilini. *In* Faune de Madagascar 67: 1–183. Paris: Muséum national d'Histoire Naturelle.

Lecoq, J.-C. 1991. Sur quelques Pinophilini de Madagascar: nouvelles espèces, nouvelles captures (Col. Staphylinidae Paederinae). Bulletin de la Société Entomologique de France 95 (1990): 229–236.

Lecoq, J.-C. 1996. Les Staphylinidae (Coleoptera) du Musée royal de l'Afrique centrale récoltés aux Comores par R. Jocqué. Journal of African Zoology 110 (2): 129–155.

Leng, C.W. 1920. Catalogue of the Coleoptera of America, north of Mexico. Mt. Vernon, NY: J.D. Sherman, x + 470 pp.

Lucas, P.H. 1846. Histoire naturelle des animaux articulés. Deuxième partie. Insectes. *In* Exploration scientifique de l'Algérie. … Sciences

Physiques. Zoologie 2: 1–590. Paris: Gouvernement Nationale.

Lucas, R. 1920. Catalogus alphabeticus generum et subgenerum Coleopterorum orbis terrarum totius (famil., trib., subtr., sect. incl.). Archiv für Naturgeschichte (A) 84 (1918): 1–696.

Lundgren, R.W. 1998. Family Staphylinidae. The rove beetles. *In* S. Peck and M. Thomas (editors), A distributional checklist of the beetles (Coleoptera) of Florida, in *Arthropods of Florida and Neighboring Land Areas 16*: 37, 41–54.

Lynch Arribálzaga, F. 1884. Los estafilinos de Buenos Aires. Boletin de la Academia Nacional de Ciencias (Córdoba) 7: 5–392.

Machado, A., and P. Oromi. 2000. Elenco de los Coleópteros de las Islas Canarias. Catalogue of the Coleoptera of the Canary Islands. Madrid: Instituto de Estudios Canarios, 306 + 2 pp.

MacLeay, W. 1873. Notes on a collection of insects from Gayndah. Transactions of the Entomological Society of New South Wales 2: 79–205.

Matsuda, R. 1976. Morphology and Evolution of the Insect Abdomen, with special reference to developmental patterns and their bearings upon systematics. Oxford: Pergamon Press, viii + 534 pp.

Mickoleit, G. 1973. Über den Ovipositor der Neuropteroidea und Coleoptera und seine phylogenetische Bedeutung (Insecta, Holometabola). Zeitschrift für Morphologie der Tiere 74 (1): 37–64.

Moore, I., and E.F. Legner. 1974. Keys to the genera of the Staphylinidae of America north of Mexico exclusive of the Aleocharinae (Coleoptera: Staphylinidae). Hilgardia 42 (16): 548–563.

Moore, I., and E.F. Legner. 1975. A catalogue of the Staphylinidae of America North of Mexico (Coleoptera). University of California Division of Agricultural Sciences, Special Publication 3015: 1–514.

Moore, I., and E.F. Legner. 1979. An illustrated guide to the genera of the Staphylinidae of America North of Mexico exclusive of the Aleocharinae (Coleoptera). Division of Agricultural Sciences, University of California Publication 4093: 1–332.

Motschulsky, V. 1851. Lettre à Monsieur le Dr. Renard, Secrétaire de la Société Impériale des Naturalistes de Moscou. Bulletin de la Société Impériale des Naturalistes de Moscou 24 (2): 648–657.

Naomi, S.-I. 1988. Comparative morphology of the Staphylinidae and the allied groups (Coleoptera, Staphylinoidea). V. Cervix and prothorax. Kontyû 56 (3): 506–513.

Naomi, S.-I. 1989a. Comparative morphology of the Staphylinidae and the allied groups (Coleoptera, Staphylinoidea). IX. General structure, lateral plates, stigmata, and 1st to 7th segments of abdomen. Japanese Journal of Entomology 57 (3): 517–526.

Naomi, S.-I. 1989b. Comparative morphology of the Staphylinidae and the allied groups (Coleoptera, Staphylinoidea). X. Eighth to 10th segments of abdomen. Japanese Journal of Entomology 57 (4): 720–733.

Navarrete-Heredia, J.L., A.F. Newton, M.K. Thayer, J.S. Ashe, and D.S. Chandler. 2002. Guía ilustrada para los géneros de Staphylinidae (Coleoptera) de México. Guadalajara, Jalisco, México: Universidad de Guadalajara y CONABIO, xii + 401 pp.

Newton, A.F., and M.K. Thayer. 1992. Current classification and family-group names in Staphyliniformia (Coleoptera). Fieldiana: Zoology (New Series) 67: 1–92.

Newton, A.F., M.K. Thayer, J.S. Ashe, D.S. Chandler 2000. 22. Staphylinidae. *In* R.H. Arnett and M.C. Thomas, American beetles. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia. Vol. 1: 272–418. Boca Raton, FL: CRC Press.

Nixon, K.C. 1999–2002. Winclada. Version 1.00.08. Available at http://www.cladistics.com.

Normand, H. 1935. Contribution au catalogue des Coléoptères de Tunisie (4me fascicule). Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord 25 (9): 356–390.

Notman, H. 1929. New species of *Palaminus* from the West Indies, together with a synoptic review of the genus. American Museum Novitates 386: 1–17.

Outerelo, R. 1984. *Procirrus* (s.str.) *lefebvrei* Latreille, 1829, nuevo género y especies para la Península Ibérica (Col Staphylinidae, Paederinae). Miscellània Zoològica 8: 291–292.

Outerelo, R., and P. Gamarra. 1985. Las familias y géneros de los estafilínidos de la Península Ibérica. *In* Claves para la identificacion de la fauna Española 10: 1–139. Madrid: Universidad Complutense.

Porta, A. 1926. Fauna Coleopterorum italica. Vol. II. Staphylinoidea. Staphylinidae…. Piacenza: Stabilimento Tipografico Piacentino, 405 pp.

Redtenbacher, L. 1857. Fauna austriaca. Die Käfer. 2nd ed. Vienna: C. Gerold's Sohn, 129–976.

Redtenbacher, L. 1874. Fauna austriaca. Die Käfer. 3rd ed. Vol. 1. Vienna: C. Gerold's Sohn, cliii + 564 pp.

Reitter, E. 1906. Übersicht der mir bekannten, palaearktischen Arten der Coleopteren-Gattung

Oedichirus Er. Wiener Entomologische Zeitung 25: 263–264.

Rougemont, G.M. de. 2001. The staphylinid beetles of Hong Kong. Annotated check list, historical review, bionomics and faunistics. Memoirs of the Hong Kong Natural History Society 24: 1–146.

Sahlberg, R.F. 1847. Coleoptera diebus XV–XXVII Decembris anni MDCCCXXXIX ad Rio Janeiro lecta. Acta Societatis Scientiarum Fennicae 2 (2): 787–805.

Schaum, H. 1852. Catalogus Coleopterorum Europae. Herausgegeben vom Entomologischen Verein in Stettin. Vierte Auflage. Berlin: Schaum, v + 96 pp.

Schaum, H. 1859. Catalogus Coleopterorum Europae. Berlin: Nicolaische Verlagsbuchhandlung, iv + 121 pp.

Scheerpeltz, O. 1933. Staphylinidae VII. *In* S. Schenkling (editor), Coleopterorum Catalogus…. Vol. 6: Pars 129: 989–1500. Berlin: Junk.

Scheerpeltz, O. 1957. Staphylinidae (Col.) von Sumba und Flores. Verhandlungen der Naturforschenden Gesellschaft in Basel 68 (2): 217–357.

Scheerpeltz, O. 1961. Ergebnisse der Deutschen Afghanistan-Expedition 1956 der Landessammlungen für Naturkunde Karlsruhe. Staphylinidae (Coleoptera). Beiträge zur naturkundlichen Forschung in Südwestdeutschland 19 (3): 249–253.

Scheerpeltz, O. 1965. Wissenschaftliche Ergebnisse der Schwedischen Expedition 1934 nach Indien und Burma. Coleoptera Staphylinidae (except. Megalopsidiinae et Steninae). Arkiv för Zoologi (2) 17 (2): 93–371.

Scheerpeltz, O. 1974. Coleoptera aus Nordostafrika, Staphylinidae. Acta Entomologica Fennica 31: 3–49.

Seevers, C.H. 1971. Fossil Staphylinidae in Tertiary Mexican amber (Coleoptera). *In* Studies of fossiliferous amber arthropods of Chiapas, Mexico. Part II. University of California Publication in Entomology 63: 77–86.

Sharp, D. 1876. Contribution to an insect fauna of the Amazon Valley. Coleoptera-Staphylinidae. Transactions of the Entomological Society of London 1876: 27–424.

Sharp, D. 1886. Staphylinidae. *In* F.D. Godman and O. Salvin (editors), Biologia Centrali-Americana. Insecta. Coleoptera. Vol. 1 (2): 537–672. London: Taylor & Francis.

Sharp, D. 1889. The Staphylinidae of Japan. Annals and Magazine of Natural History (6) 3: 319–334.

Shibata, Y. 1973. Preliminary check list of the family Staphylinidae of Taiwan (Insecta: Coleoptera). Annual Bulletin of the Nichidai Sanko 16: 21–83.

Shibata, Y. 1977. Provisional check list of the family Staphylinidae of Japan. II. (Insecta: Coleoptera). Annual Bulletin of the Nichidai Sanko 20: 16–83.

Smetana, A. 1988. Revision of the tribes Quediini and Atanygnathini. Part II. The Himalayan region (Coleoptera: Staphylinidae). Quaestiones Entomologicae 24 (2): 163–464.

Smetana, A. 2004. Staphylinidae (*In* New Nomenclatural and Taxonomic Acts, and Comments), Omaliinae, Proteininae, Micropeplinae, Dasycerinae, Phloeocharinae, Olisthaerinae, Tachyporinae, Trichophyinae, Habrocerinae, Aleocharinae, Trigonurinae, Apaticinae, Piestinae, Osoriinae, Oxytelinae, Oxyporinae, Megalopsiinae, Steninae, Euaesthetinae, Leptotyphlinae, Pseudopsinae, Paederinae, Staphylininae. *In* I. Löbl and A. Smetana (editors), Catalog of Palaearctic Coleoptera. Vol. 2: 29–35; 237–272; 329–495; 504–698. Stenstrup: Apollo Books.

Smetana, A., and A. Davies. 2000. Reclassification of the north temperate taxa associated with *Staphylinus* sensu lato, including comments on relevant subtribes of Staphylinini (Coleoptera: Staphylinidae). American Museum Novitates 3287: 1–88.

Snodgrass, R.E. 1935. Principles of insect morphology. New York: McGraw-Hill, ix + 667 pp.

Solodovnikov, A. 2005. *Natalignathus*, gen. nov. and larvae of *Atanygnathus*: a missing phylogenetic link between subtribes Quediina and Tanygnathinina (Coleoptera: Staphylinidae: Staphylininae: Staphylinini). Invertebrate Systematics 19: 75–98.

Solodovnikov, A. 2006. Revision and phylogenetic assessment of *Afroquedius* gen. nov. from South Africa: toward new concepts of the genus *Quedius*, subtribe Quediina and reclassification of the tribe Staphylinini (Coleoptera: Staphylinidae: Staphylininae). Annals of the Entomological Society of America 99 (6): 1064–1084.

Spahr, U. 1981. Systematischer Katalog der Bernstein- und Kopal-Käfer (Coleoptera). Stuttgarter Beiträge zur Naturkunde (Serie B, Geologie und Paläontologie) 80: 1–107.

Tanner, V.M. 1927. A preliminary study of the genitalia of female Coleoptera. Transactions of the American Entomological Society 53: 5–50, pls. II–XV.

Thayer, M.K., and A.F. Newton. 1979. Revision of the south temperate genus *Glypholoma* Jeannel, with four new species (Coleoptera: Staphylinidae: Omaliinae). Psyche 85 (1) (1978): 25–63.

Tikhomirova, A.L. 1973. Morfoekologicheskie osobennosti i filogenez stafilinid (s katalogom fauny SSSR). Moskva: Izdatel'stvo Nauka. pp. 5–191.

Uhlig, M. 1989. Zur Morphologie der weiblichen Terminalia einiger Staphylinidenarten (Coleoptera). Verhandlungen XI. SIEEC Gotha 1986, Dresden 1989: 227–237.

Wendeler, H. 1956a. Neue Staphyliniden aus Brasilien (2. Teil). Dusenia 7 (1): 37–44.

Wendeler, H. 1956b. Neue Staphyliniden aus Brasilien (6. u. 7. Teil). Dusenia 7 (5): 261–276.

Winkler, A. 1925. Catalogus Coleopterorum Regionis Palaearcticae. Pars 1–3: 241–624. Wien: Winkler & Wagner.

Zheng, F.-k. 2001. Coleoptera: Staphylinidae. *In* H. Wu and C. Pan (editors), Insects of Tianmushan National Nature Reserve: 322–330. Beijing: Science Press. [in Chinese, English summary]

APPENDIX 1

List of Characters States

Character 0. Epistomal suture: 0 (Present); 1 (Absent). Uninformative.

The epistomal suture is absent in the Paederinae, but present in *Pseudopsis*.

Character 1. Head shape (including eyes): 0 (Rectangulate, elongate); 1 (Transverse; fig. 9); 2 (Elongate, strongly tapered posteriorly; figs. 6, 7); 3 (Hexagonal; fig. 2). CI/RI = 100/100.

The form of the head in the Paederinae varies and this list includes only a few of the many forms observed in the subfamily.

Character 2. Head, pedunculate base: 0 (Absent); 1 (Present; fig. 7). Uninformative.

The nuchal constriction or groove at the base of the head marks the anterior edge of the neck. For purposes of discussion and description the head extends anteriorly from this constriction and the neck extends posteriorly. The postocular portion of the head in the Procirrina is gradually tapered posteriorly in several genera, but in *Procirrus* is tapered then strongly narrowed then gradually tapered before reaching the edge of the neck and is referred to as pedunculate.

Character 3. Antennal form: 0 (Straight); 1 (Geniculate). Uninformative.

The first antennomere of geniculate antennae is notably elongate and commonly seen in the Cryptobiina.

Character 4. Antennomere 11, apical spiniform pencil of setae: 0 (Absent); 1 (Present; figs. 31, 32). Uninformative.

Character state 1 is unique in the subfamily.

Character 5. Antennomere 11, length: 0 (Shorter than 9 and 10 combined); 1 (longer than 9 and 10 combined). CI/RI = 100/100.

Elongation of antennomere 11 is uncommon in the subfamily.

Character 6. Maxillary palpus, palpomere 4, form: 0 (Parallel sided, slender); 1 (Nipple shaped); 2 (Fusiform, elongate; fig. 56); 3 (Securiform; figs. 71, 81). CI/RI = 75/80.

The nipple-shaped palpomere is wide basally with a subapical constriction then tapered to the apex; the fusiform palpomere is narrower basally and apically than medially; the securiform palpomere is large, blocky, and more or less rectangular to triangular.

Character 7. Maxillary palpus, palpomere 4, cross-section: 0 (Cylindrical); 1 (Compressed; fig. 30). CI/RI = 50/50.

Character 8. Maxillary palpus, palpomere 4, pubescence: 0 (Absent); 1 (Fine and dense; figs. 30, 71). CI/RI = 100/100.

The pubescence is fine and does not refer to thicker macrosetae, which are uncommon on palpomere 4 and sparse when present.

Character 9. Labrum, submedial anterior margin: 0 (Denticles and lobes absent; 1 (Denticles, one pair; fig. 97); 2 (Denticles, two pairs; fig. 57); 3 (Lobes, one pair; fig. 84). CI/RI = 50/40.

Character 10. Pronotum, length: 0 (Longer than wide; figs. 52, 66); 1 (Length and width subequal; fig. 5); 2 (Wider than long; fig. 89). CI/RI = 40/25.

Character 11. Postprocoxal lobe, punctation: 0 (Absent); 1 (Sparse); 2 (Dense; fig. 17). CI/RI = 50/71.

Character 12. Mesospiracular peritremes: 0 (Small); 1 (Enlarged; figs. 17, 93). CI/RI = 100/100.

For most species of the Paederinae the mesospiracular peritremes are narrow sclerites surrounding the mesothoracic spiracle. In the Procirrina these two sclerites are much enlarged, fused to each other medially (character 13), to the furcasternum anteriorly (character 15), and to the hypomeron laterally (character 14). The large sclerotized plate closes the procoxal cavities posteriorly (character 16) and the spiracles, no longer embedded in membrane, are immobile.

Character 13. Mesospiracular peritremes, median edge: 0 (Separated, medially); 1 (Fused, medially; fig. 17). CI/RI = 100/100.

Character 14. Mesospiracular peritremes, lateral margin: 0 (Separated from hypomeron); 1 (Fused to hypomeron; fig. 19). CI/RI = 100/100.

Character 15. Mesospiracular peritreme, anterior margin: 0 (Separated from furcasternum); 1 (Fused to furcasternum; fig. 17). CI/RI = 100/100.

Character 16. Procoxal cavity: 0 (Open); 1 (Closed by mesothoracic peritreme; fig. 19). CI/RI = 100/100.

Character 17. Elytra, apicolateral angle, macroseta: 0 (Absent; fig. 14); 1 (Present; fig. 11). Uninformative.

This seta is suberect, longer, and thicker than other elytral setae, posteromedially directed and found only in *Palaminus*.

Character 18. Elytra, contiguous, posterior margin: 0 (Broadly and evenly rounded); 1 (Sinuate, lobed laterally or lateromedially); 2 (Emarginate; figs. 1, 3, 5). CI/RI = 100/100.

This character is evident when the elytra are viewed in repose and the medial edges contiguous.

Character 19. Protibia, ctenidial depression: 0 (Absent; figs. 35, 41); 1 (Shallow); 2 (Deep). CI/RI = 50/50.

The protibial ctenidial depression of species of Procirrina, unlike that of most other species of the Paederinae, is shallow or lacking.

Character 20. Protarsomeres 1–4, form: 0 (Cylindrical or dorsoventrally flattened); 1 (1–3 bulbous; fig. 89); 2 (1–4 bulbous; fig. 44). CI/RI = 100/100.

Character 21. Protarsomere 5, ventral surface, pubescence: 0 (Absent or sparse); 1 (Dense; figs. 42, 45, 47). CI/RI = 100/100.

Dense pubescence on the ventral surface of the fifth tarsomere is uncommon, perhaps unique, in the subfamily.

Character 22. Metatibia, apical ctenidia: 0 (Present on both sides and separated, inner comb long and outer short and with few tines); 1 (Present on both sides and connected or nearly connected to each other; inner comb moderately shorter than outer and with numerous tines; fig. 39). CI/RI = 100/100.

This character refers to the length from the first to the last tine of each comb.

Character 23. Metatarsus, tarsomere 4, apical portion, length: 0 (Not or slightly extending beneath 5); 1 (Extending beneath 5; figs. 50, 51). CI/RI = 100/100.

Tarsomere 4 extends beneath 5 because the latter is inserted at the base (fig. 51, at arrow), rather than the apex, of the former.

Character 24. Abdominal segments III–VI, integument, imbricate macrosculpturing: 0 (Absent); 1 (Present; figs. 26–28). Uninformative.

The abdominal sculpturing of *Palaminus* is unique in the family.

Character 25. Abdominal segment III, paratergites: 0 (Two pairs); 1 (One pair); 2 (Paratergal carina present; figs. 23, 26). CI/RI = 66/80.

The paratergal carina is on the lateral side of III, extends posteriorly from the basal ridge, and is laterad or ventrad of the spiracle.

Character 26. Abdominal segments IV–VI, paratergites: 0 (One pair); 1 (Two pairs); 2 (Absent; fig. 26). CI/RI = 100/100.

Character 27. Abdominal segment VII, paratergites: 0 (Two pairs); 1 (One pair); 2 (Absent; fig. 33). CI/RI = 100/100.

Character 28. Abdominal intersegmental membrane, ''windows'': 0 (Absent); 1 (Present; figs. 24, 28). CI/RI = 100/100.

The ''window'' is oval, contiguous with anterior margin of the tergum or sternum; the membranous covering is pale and lacks the rectangular ''sclerites'' typical of the paederine intersegmental membrane.

Character 29. Abdominal terga and sterna IV to VI: 0 (Separated); 1 (Fused; fig. 26). CI/RI = 100/100.

Character 30. Abdominal tergum and sternum VII: 0 (Separated); 1 (Fused basally, with incision apically; figs. 33, 34); 2 (Fused, without incision). CI/RI = 100/100.

The incision is difficult to see, but it is marked by a notch at the middle of the lateral side of the posterior margin (fig. 33) and what appears, with a light microscope, to be a shallow groove extending anteriorly from the notch. In the enlarged view of the area (fig. 34) the groove is clearly an incision.

Character 31. Sternum III, posteriorly directed sublateral carina: 0 (Absent); 1 (Present; figs. 22, 27). CI/RI = 100/100.

Character 32. Tergum IX, lateroapical process: 0 (Attached to base of IX); 1 (Separated from base of IX; figs. 29, 99, 100). Uninformative.

Character 33. Tergum IX, lateroapical process, apex: 0 (Straight); 1 (Ventrally curved; fig. 104). CI/RI = 50/60.

Character 34. Tergum IX, lateroapical process, form: 0 (Curved, platelike lobe); 1 (Elongate and tapered prong; fig. 25). CI/RI = 33/0.

Character 35. Terga IX and X: 0 (Separated); 1 (Fused; fig. 87). Uninformative.

Character 36. Tergum X: 0 (Present); 1 (Absent). Uninformative.