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GENERA OF THE SUBTRIBE METALLICINA AND CLASSIFICATION,
RECONSTRUCTED PHYLOGENY AND GEOGRAPHICAL HISTORY OF THE SPECIES
OF *EUPROCTINUS* LENG AND MUTCHLER (COLEOPTERA: CARABIDAE: LEBIINI)

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ABSTRACT

The New World lebiine genus Euproctinus Leng & Mutchler (type-species - Euproctus fasciatus Solier) is removed from the subtribe Calleidina and placed in the subtribe Metallicina. A reconstructed phylogeny of this subtribe places the genera in the sequence, Parena-Metallica-Pachycallida-Euproctinus, with the ancestor of Euproctinus and that of the other three genera as sister groups. Adults of Euproctinus are readily distinguished by a ventral sensory pit on each of antennomeres 5-11. These pits also occur in the remaining metallicine genera, as well as the Old World genus Celaenephes Schmidt-Göbel, and some of the New World species of Coptodera Dejean. Keys distinguish the two subgenera and 16 of 17 species of Euproctinus, and each taxon is characterized in terms of structural features of adults, habitat, geographical distribution, chorological affinities, and phylogenetic relationships.

The geographical range of Euproctinus extends from central Chile to southern United States and Cuba. In México, species of Euproctinus live from sea level to moderately high elevation. However, only two (E. abjectus and E. ornatellus) of the seven species are known from low elevations, with E. abjectus ranging to more than 2000 meters. Mountain habitats include mesophytic montane and conifer-oak forest; the species are not known from high altitude conifer forest.

The monobasic subgenus Euproctinus includes the Chilean-Argentinian species E. fasciatus Solier. The species of the new subgenus Neoeuproctus (type-species - E. sigillatus Bates) are arranged in two groups, sequenced according to the reconstructed phylogeny: E. sigillatus group, including E. balli new species (type locality- México, Oaxaca, vic. Juchatengo), E. sigillatus (Bates), E. abjectus (Bates), E. subdeletus (Bates) and E. pallidus new species (type locality- México, Veracruz, Fortin de las Flores); and E. quadriplagiatus group, including E. trivittatus (LeConte), E. columbianus new species (type locality- Colombia, El Bergell), E. howdeni new species (type locality- Colombia, Valle de Cauca, 70 km. e. Buenaventura), E. putzeysi (Chaudoir), E. quadrivittis (Chaudoir), E. ornatellus (Bates), E. quadriplagiatus (Reiche), E. nigrotibialis new species (type locality- Panamá, Bocas del Toro, vic. Almirante), E. deliciolus (Bates), and E. panamensis new species (type locality- Panamá, Colon, Porto Bello). Seven synonymies are proposed with the senior synonym of each combination listed first: E. fasciatus (Solier)=E. kuscheli (Straneo); E. subdeletus (Bates)=E. montanus (Liebke); E. abjectus (Bates)=E. texanus (Wickham); and E. quadriplagiatus (Reiche)=E. fenestrellus (Bates)=E. metricus (Bates)=E. quadrinus (Bates)=E. xanthophaeus (Chaudoir).

A reconstructed phylogeny of the genera of the subtribe Metallicina, with the Calleidina + Gallerucidiina as out-group, indicates these relationships: Euproctinus as sister group of the ancestral stock of Parena + Metallica + Pachycallida; and Parena as the sister group of Metallica and Pachycallida. In the genus Euproctinus, subgenus Euproctinus and Neoeuproctus are sister groups, as are the species groups of Neoeuproctus: E. sigillatus and E. quadriplagiatus. Relationships in the E. sigillatus group are: E. balli - ([pallidus]) + ([sigillatus - (abjectus + subdeletus)]). In the E. quadriplagiatus group, relationships are: E. panamensis - and a trichotomy (branches 1, 2, and 3) plus a quadrichotomy (in branch 3) - (1. [E. trivittatus] + 2. ([columbianus - (howdeni - putzeysi)] + 3. [(quadrivittis) + (ornatellus) + (quadriplagiatus) + (nigrotibialis + deliciolus)]).

Metallicines are hypothesized to have arisen in tropical Gondwanaland in Mesozoic time, prior to development of the Atlantic Ocean. Differentiation of the genera was probably associated with the breakup of Gondwanaland, involving isolation of ancestral stocks both by separation of ranges by geological events ("vicariance"), and by dispersal of volant adults across barriers, such as open water. In South America, the metallicine isolate became Euproctinus, whose history of differentiation is related to events of the Tertiary Period: in South America, rise of the Andes Mountains, more extensive separation of South and Middle America in mid-Tertiary time, followed by connection of these two areas in the latter part of the Tertiary; isolation of Lower Central America from Nuclear Central America by sea barriers, and near isolation of Nuclear Central America from México north of the Isthmus of Tehuantepec, possibly by climatic and geological events. The Greater Antillean island of Cuba was probably populated by an oversea dispersal from Nuclear Central America. The three species of Euproctinus that have reached southern United States probably did so recently: the western E. balli and more eastern E. abjectus, by overland range extensions from the adjacent parts of México; and the Floridian E. trivittatus by oversea dispersal of volant adults, from Cuba.

RÉSUMÉ

Le lébini du genre Euproctinus Leng & Mutchler (espèce-type: Euproctus fasciatus Solier) du Nouveau-Monde est transféré de la sous-tribe Calleidina à la sous-tribe Metallicina. Une reconstitution phylogénique de cette sous-tribe situe les genres dans la séquence: Parena-Metallica-Pachycallida-Euproctinus avec Euproctinus comme ancêtre et les trois autres genres comme groupes sœurs. Les adultes d' Euproctinus sont aisément reconnus par la présence de puits sensoriels sur chacun des segments 5 à 11 de l'antenne. Ces puits sont aussi présents chez les genres métalliques restants, ainsi que dans le genre Celaenephes Schmidt-Göbel de l'Ancien-Monde, et quelques espèces de Coptodera Dejean du Nouveau-Monde. La répartition géographique d'Euproctinus s'étend de la région centrale du Chili aux états du sud des États-Unis, ainsi qu'à Cuba. Les clefs permettent de distinguer entre les deux sous-genres et 16 des 17 espèces. Chaque taxon est défini selon les caractères structuraux des adultes, l'habitat, la répartition géographique, les affinités chorologiques, et les relations phylogéniques. Au Mexique, on retrouve les espèces d'Euproctinus à partir du niveau de la mer jusqu'aux plateaux d'élévations modérées. Des sept espèces cependant, seulement deux (E. abjectus et E. ornatellus) sont connues pour habiter les régions de faibles altitudes, avec E. abjectus se répartissant à des altitudes dépassant 2000 mètres. Les espèces ne sont pas connues des forêts de conifères des haut-plateaux, ainsi que des habitats semi-humide de montagne (mesophytic montane) et les forêts de chênes et de conifères.

Le genre monobasique Euproctinus inclut les espèces E. fasciatus Solier du Chili et de l'Argentine. Les espèces du nouveau sous-genre Neoeuproctus (espèce-type: E. sigillatus Bates) sont distribuées dans deux groupes répartis selon la reconstitution phylogénique: le groupe E. sigillatus, incluant la nouvelle espèce E. balli (localité-type: México, Oaxaca, vic. Juchatengo), E. sigillatus (Bates), E. abjectus (Bates), E. subdeletus (Bates), et la nouvelle espèce E. pallidus (localité-type: México, Veracruz, Fortin de las Flores); et le groupe E. quadriplagiatus, incluant E. trivittatus (LeConte), la nouvelle espèce E. columbianus (localité-type: Colombia, El Bergell), la nouvelle espèce E. howdeni (localité-type: Colombia, Valle de Cauca, 70 km. e. Buenaventura), E. putzeysi (Chaudoir), E. quadrivittis (Chaudoir), E. ornatellus (Bates), E. quadriplagiatus (Reiche), la nouvelle espèce E. nigrotibialis (localité-type: Panamá, Bocas del Toro, vic. Almirante), E. deliciolus (Bates), et finalement la nouvelle espèce E. panamensis (localité-type: Panamá, Colon, Porto

Bello). Sept synonymies sont proposées, avec le dernier des synonymes décrits (*senior*) de chacune des combinaisons, énuméré le premier: *E. fasciatus* (Solier)=*E. kuscheli* (Straneo); *E. subdeletus* (Bates)=*E. montanus* (Liebke); *E. abjectus* (Bates)=*E. texanus* (Wickham); et *E. quadriplagiatus* (Reiche)=*E. fenestrellus* (Bates)=*E. metricus* (Bates)=*E. quadrinus* (Bates)=*E. xanthophaeus* (Chaudoir).

Une reconstitution phylogénique des genres de la sous-tribu des *Metallicina*, avec les *Calleidina* + *Gallerucidiina* comme groupe externe, indique les relations suivantes: *Euproctinus* comme groupe soeur du groupe ancestral de *Parena* + *Metallica* + *Pachycallida*; et *Parena* comme groupe soeur de *Metallica* et *Pachycallida*. Dans le genre *Euproctinus*, le sous-genre *Euproctinus* et *Neoeuproctus* sont groupes soeurs, comme le sont les groupes d'espèces *Neoeuproctus*: *E. sigillatus* et *E. quadriplagiatus*. Les relations à l'intérieur du groupe *E. sigillatus* sont: *E. balli* - ([*pallidus*] + [*sigillatus* - (*abjectus* + *subdeletus*)]). Dans le groupe *E. quadriplagiatus*, les relations sont: *E. panamensis* - et une trichotomie (lignée 1, 2, 3) ainsi qu'une quadrichotomie (dans la lignée 3) - (1. [*E. trivittatus*] + 2. [(*columbianus* - (*howdeni* - *putzeysi*)) + 3. [(*quadrivittis*) + (*ornatellus*) + (*quadriplagiatus*) + (*nigrotibialis* + *deciolus*)]).

On hypothe que les métallines sont apparues au Gondwanaland tropical durant le Mésozoic, antérieur au développement de l'océan Atlantique. La différenciation au niveau des genres, est probablement associée au démantèlement du Gondwanaland, impliquant l'isolation des souches ancestrales lors de la séparation des aires de répartition par de vastes événements géologiques ("vicariance"), et par dispersion des adultes ailés au-dessus des barrières naturelles, comme les vastes étendues d'eau. En Amérique du Sud, les métallines isolées sont devenues *Euproctinus*, dont l'histoire de la différenciation est reliée aux événements de la période Tertiaire: en Amérique Centrale, place d'origine des Andes, il se produit un accroissement de la séparation de l'Amérique du sud et centrale lors de la période mi-Tertiaire, suivie par la jonction des surfaces de ces dernières lors de la dernière partie du Tertiaire; isolation de la partie inférieure de l'Amérique Centrale du bloc de l'Amérique Centrale originelle par les barrières marines, et, isolation presque complète du bloc de l'Amérique Centrale originelle du secteur Mexicain, au nord d'Isthmus de Tehauntepec, possiblement par événements géologiques et climatiques. La colonisation de la grande île de Cuba est probablement le résultat d'une dispersion aérienne en provenance du bloc de l'Amérique Centrale originelle. Trois espèces d'*Euproctinus* ont probablement colonisé le sud des États-Unis que très récemment: à l'ouest *E. balli*, et plus à l'est *E. abjectus*, lors d'extinctions par voies terrestres à partir des secteurs Mexicains adjacents; et l'espèce de Floride *E. trivittatus* par dispersion aérienne à partir de Cuba.

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INTRODUCTION

The species of *Euproctinus* Leng & Mutchler have been difficult to identify because of their similar color patterns, and few available museum specimens of most species for comparisons.

The material I examined from 27 collections included all previously named species but one (listed as *incertae sedis*) and also included six new species. Prior to this study the subtribal affinities of *Euproctinus* were not resolved. Workers included the genus in the subtribe Calleidina. However, both Larson (1969: 23) and Erwin and Sims (1984: 399) suggested it should be placed in a separate subtribe of its own. Basilewsky (1984: 544) illustrated stylomere 2 of the ovipositor of the genera *Parena* Motschulsky, *Metallica* Chaudoir, and *Pachycallida* Jeannel, which he placed in the tribe Metallicini. My examination of specimens from these genera shows that *Euproctinus* belongs in this taxon, herein considered the subtribe Metallicina.

As a solution to the two above problems, I present a review of the genera of the subtribe Metallicina, and a revision of the species of one of its genera, namely, *Euproctinus*.

MATERIALS AND METHODS

Materials

This study is based on examination of 1156 adult *Euproctinus*, including types, 21 other metallicines, 15 calleidines, and 5 galleruciines. Some of the material was available in the Strickland Museum, University of Alberta (UASM). Additional material was borrowed from, or deposited in, the following institutions, noted in the text by the associated codens:

- BMNH Department of Entomology, British Museum (Natural History), Cromwell Road, London, England SW7 5BD
- CAS Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California, U.S.A. 94118
- CNC Canadian National Collection, Biosystematics Research Institute, Agriculture Canada, K. W. Neatby Building, Ottawa, Ontario, Canada K1A 0C6
- CSCA California State Collection of Arthropods, Division of Plant Industry, Department of Food and Agriculture, 1220 N. Street, Sacramento, California, U.S.A. 95814
- CUIC Department of Entomology, Comstock Hall, Cornell University, Ithaca, New York, U.S.A. 14850
- DAMA David R. Maddison collection, D. R. Maddison, MCZ, Harvard University, Cambridge, Massachusetts, U. S. A. 02138
- DEI Institut für Pflanzenschutzforschung Kleinmachnow, Stahnsdorfer Damm 81, Kleinmachnow, DDR-1532
- FSCA Department of Entomology, Florida State Collection of Arthropods, Gainesville, Florida, U.S.A. 32601
- GHNC G. H. Nelson collection, G.H. Nelson, Pomona, California, U.S.A. 91766-1889
- IZWP Instytut Zoologii, Polska Akademia Nauk, 00-679 Warszawa, Poland, ul. Wilcza 64
- JNEG Jacques Nègre collection, Jacques Nègre #9, Bd de Lesseps, Versailles 78,

- France.
- LACM Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California, U. S. A. 90007
- MCZ Department of Entomology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A. 02138
- MNHB Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität zu Berlin, 104 Berlin, Invalidenstrasse 43, D.D.R.
- MNHL Rijksmuseum van Natuurlijke Historie, Postbus 9517, 2300RA, Leiden, Nederland
- MNHP Entomologie, Museum National d'Histoire Naturelle, 45 Rue Buffon, Paris 75005, France.
- MRAC Musée Royal de l'Afrique Centrale, B-1980, Tervuren, Belgique.
- MZSP Museu de Zoologia, Universidade de São Paulo, Caixa Postal 7172, São Paulo, Brazil
- OUCO Department of Entomology, Ohio State University, Columbus, Ohio, U.S.A. 43210
- RTC Robert Turnbow collection, Robert Turnbow, Directorate of Engineering and Housing, Building 1404, Fort Rucker, Alabama, U.S.A. 36362
- SMC Scott McCleve collection, Scott McCleve, 2210-13th Street, Douglas, Arizona, U.S.A. 85607
- TAIK Department of Biology, Texas A&I University, Kingsville, Texas, U.S.A. 78363
- TAMU Department of Entomology, Texas A&M University, College Station, Texas, U.S.A. 77843
- UCBC Division of Entomology and Parasitology, University of California, Berkeley, Berkeley, California, U.S.A. 94720
- USNM Department of Entomology, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. 20560
- ZMKD Zoologisk Museum, Universitetsparken 15, DK 2100 Kobenhavn, Danmark
- ZSMG Zoologische Staatssammlung, Maria-Ward-Str. 1b, D-8000 München 19, West Germany

Methods

Taxonomic concepts, principles, criteria for ranking, and general working methods were the same as those described previously (Ball 1975, 1978; Allen and Ball, 1980).

Notes about species criteria.— Color pattern is the major feature for recognition of closely related species. The elytral color pattern was found to consist of a number of general forms. Some allopatric forms, described as species by previous authors, could not be separated except by color. These were judged to be conspecific. If they were sympatric, and could be separated on characters other than color pattern, they were treated as separate species.

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

Length of head (Hl) - linear distance from base of left mandible to posterior margin of left compound eye;

Width of head (Hw) - maximum distance across head, including compound eyes;

Length of pronotum (Pl) - linear distance from anterior to posterior margin, measured along the midline;

Maximum width of pronotum (Pmw) - greatest linear transverse distance;

Length of elytra (El) - linear distance from basal ridge to apex of longer elytron, measured along the suture.

Standardized Body Length (SBL), used as an index of overall size, is the sum of Hl, Pl, and El.

Preparation of material.— Dissections were made using standard techniques. Genitalia and other small structures were preserved in glycerine in microvials, pinned beneath the specimens from which they were removed. Larger structures and those that were gold-coated for study with the SEM were glued to cards pinned beneath the specimens from which they were removed.

Photographs of isolated structures were taken with a Cambridge S-150 "Stereoscan" Scanning Electron Microscope (SEM).

Notes about descriptions.— To avoid repetition, character states of lower-ranking taxa recorded in the descriptions of higher-ranking taxa are not repeated in the descriptions of the included lower-ranking taxa. Thus, the complete description of a species must be assembled from its taxonomic placement. Such a description can be obtained by reading the descriptions and diagnoses of the sequence of higher-ranking taxa in which the lower-ranking taxon is placed.

Species treatments.— Associated with the taxonomic treatment of each species are sections titled "Chorological affinities" and "Phylogenetic relationships". The section about chorological affinities offers information about range overlap of related species, which contributes evidence for ranking the taxa as separate species. Statements about phylogenetic relationships are based on the reconstructed phylogeny, which is presented following the taxonomic treatment.

STRUCTURES USED IN CLASSIFICATION

Notes about Terms

Most of the standard structural features used have been explained in recent publications (as in Ball and Shpeley, 1983: 746- 749).

Reproductive Tract of Selected Lebiini

The reproductive tract of several genera was examined for additional data on relationships. *Celaenephes* was previously illustrated (Shpeley *et al.*, 1985: 289), and the present study includes examination of the four metallicine genera, four calleidine genera, and *Gallerucidia*.

Terms are standard for associated parts. Near the base of the spermathecal gland duct, a "tubular sac" (Fig. 72, ts) of varying length is present in taxa of some genera.

The reproductive tract of the calleidines studied is similar to that of *Parena* (Fig. 72), but the tubular sac is markedly reduced or absent, and the spermatheca is as illustrated or somewhat longer, but not as elongate as in *Euproctinus* (Fig. 73). The reproductive tract of *Gallerucidia* has a smaller bursa copulatrix and a markedly longer spermathecal gland duct (Fig. 74).

Elytral Color Pattern

Abbreviations in Figs. 13, 21, 26, and 38 indicate the system of names required to describe the color pattern characteristics of adult *Euproctinus*.

Bicolored elytra are characteristic of most adults of most species, with the pale areas flavous to rufo-flavous, and dark areas more or less infuscated. The marginal groove is pale, except in *E. fasciatus* (Figs. 13 and 14). The central dark area is termed the median fascia (Figs. 21 and 26, mf). Extending anteriorly and posteriorly from the median fascia are the vittae: one sutural vitta (Fig. 26, sv) and one paralateral vitta (Fig. 26, pv). Basad of the median fascia on the elytral disc is the pale anterior discal spot (Figs. 21, 26, and 38, ads), and posteriorly, the posterior discal spot (Figs. 21, 26, and 38, pds). A discal setigerous puncture is located in each of these spots. Additional pale spots (Figs. 36-38) result from branching of the median fascia and the pre-basal parts of the vittae (Fig. 38, mfb and avb, respectively). A linear paralateral pale area (Fig. 38, ppa) characterizes a few taxa. A parahumeral spot occurs on the elytra of *E. balli* adults (Fig. 21, phs), and in adults of *E. fasciatus*; this spot extends to the humeral margin. Pale spots completely surrounded by dark marks are termed "closed". "Open" spots extend to at least one margin of an elytron. The basal and apical margins (Fig. 26, bm and am, respectively), humerus (Fig. 26, hu), and parascutellar areas (Fig. 26, psa) are pale or dark in color; these dark marks are more or less continuous with the adjacent vittae.

The discal spots in most specimens are more or less enclosed by the adjacent dark marks. These dark marks show considerable variation within some species. For example, some adults of *E. abjectus* have the markings extended to such an extent that the discal spots have nearly (Fig. 24) or completely (Fig. 25) disappeared. In adults of another species the dark markings have disappeared (Fig. 28) except for a broken, narrow median fascia. Still other adults are even more pale and lack dark marks (Fig. 66).

CLASSIFICATION

Authors once placed *Parena*, *Metallica*, *Pachycallida*, and *Euproctinus* in the subtribe Calleidina or tribe Calleidini. Basilewsky (1984: 542- 543) proposed a new tribe Metallicini to include the first three genera mentioned above. Synapotypic character states indicate that *Euproctinus* can be included in this group, but I rank it at the level of subtribe - Metallicina. This agrees with the ranking system used by most anglophone carabid specialists.

Ball & Hilchie (1983: 111- 112) presented a key to subtribes of Lebiini. The key had a footnote indicating that Larson (1969: 23) suggested *Euproctinus* belonged in its own subtribe. The key treated *Lebidia* Morawitz and *Gallerucidia* Chaudoir as galleruroid Calleidina. However, I believe that these two genera warrant their own subtribe, Gallerucidiina. This belief is based on the hypothesis that the group is monophyletic, related to the stem of the rest of the calleidine assemblage, and is structurally sufficiently distinct to warrant ranking at this level. As has been noted by other workers (recently, for example, by Ghiselin, 1985: 461), it is acceptable, even in a phylogenetically-based system, to use rank as an indication of relative amount of structural differentiation of a monophyletic group.

The couplets below are modified from the key of Ball & Hilchie *l. c.* to include the Gallerucidiina and the new subtribe Metallicina. (*Celaenephes* Schmidt-Göbel has been put into the subtribe Celaenephina after Habu [1982: 113-114].)

Modified Key to Subtribes of Lebiini to Include Metallicina and Gallerucidiina (Key from Ball & Hilchie [1983: 111- 112])

- A Sensory pit on ventral surface of antennomeres 4-11 or 5-11 B
 A' Sensory pit absent from ventral surface of antennomeres 5-11 2
 B (A) Antennomeres 4-11 ventrally each with sensory pit
 Subtribe Celaenephina
 B' Antennomeres 5-11 ventrally each with sensory pit 1
 1 (B') Tarsomere 4 of hind leg bilobed Subtribe Metallicina
 1' Tarsomere 4 of hind leg slightly emarginate
 Subtribe Pericalina (in part)
 2 (A') Head ventrally with at least one pair of suborbital setigerous punctures 3
 2' Head ventrally without suborbital setigerous punctures
 (see Ball & Hilchie, 1983, p. 111, couplet 4)
 3 (2) Labrum narrow, as long or longer than wide. Penultimate setigerous
 puncture of umbilical series of elytron displaced laterally
 Subtribe Pericalina (in part)
 3' Labrum normal, wider than long. Penultimate setigerous puncture of
 elytron not displaced laterally Subtribe Gallerucidiina

Subtribe Metallicina

Recognition.— Adults of this group have the following combination of characters: antennomeres 5-11 ventrally each with sensory pit; mentum edentate; glossal sclerite with four or more apical setae; paraglossae sclerotized; mandibles without anterior retinacular tooth; with ventral secretory groove; tarsomere 4 bilobed; and tarsomeres setose dorsally.

Apotypic features.— Head with suborbital setae (lost in some taxa); antennal pedicel with a carina (lost in some taxa); antennomeres 5 - 11 each with sensory area on ventral surface; stylothere 2 with basal lobe reduced or absent, if plesiotypically slender apically, without or with only two ensiform setae; if quadrate and broad, with more than four ensiform setae.

Included taxa.— This subtribe was erected by Basilwesky (1984: 542) for *Metallica*, *Pachycallida*, and *Parena* and includes also *Euproctinus*.

Geographical distribution (Map 1).— The range of *Parena* is the most extensive: from Africa, Madagascar, and India eastward throughout the Indo-Australian Archipelago to New Caledonia and Samoa; southward to the east central coastal region of Australia; and northward through the Philippines to Japan and China. *Metallica* is found throughout eastern Africa, and in Senegal in the west. *Pachycallida* has only been collected in Madagascar. The range of *Euproctinus* extends from southern California, Arizona, and Texas and Florida in the United States and Cuba, south throughout México and Central America southward to South America, central Chile and southern Brazil.

Key to the Genera of Metallicina

- 1 Sensory pits on dorsal and ventral surfaces of antennomeres 5-11 2
 1' Sensory pits on ventral surface only of antennomeres 5-11 3
 2 (1) Interval 9 of elytron less than half width of preceding interval; specimen

- from Africa, Madagascar, Oriental Asia, or Australia *Parena* Motschulsky, p. 269
- 2' Interval 9 of elytron as wide or wider than preceding interval; specimen from Africa *Metallica* Chaudoir, p. 273
- 3 (1') Interval 9 of elytron as wide or wider than preceding interval; specimen from Madagascar *Pachycallida* Jeannel, p. 276
- 3' Interval 9 of elytron less than half width of preceding interval; specimen from North, Central, or South America *Euproctinus* Leng & Mutchler, p. 276

Parena Motschulsky

Figs. 1, 4, 72; Map 1

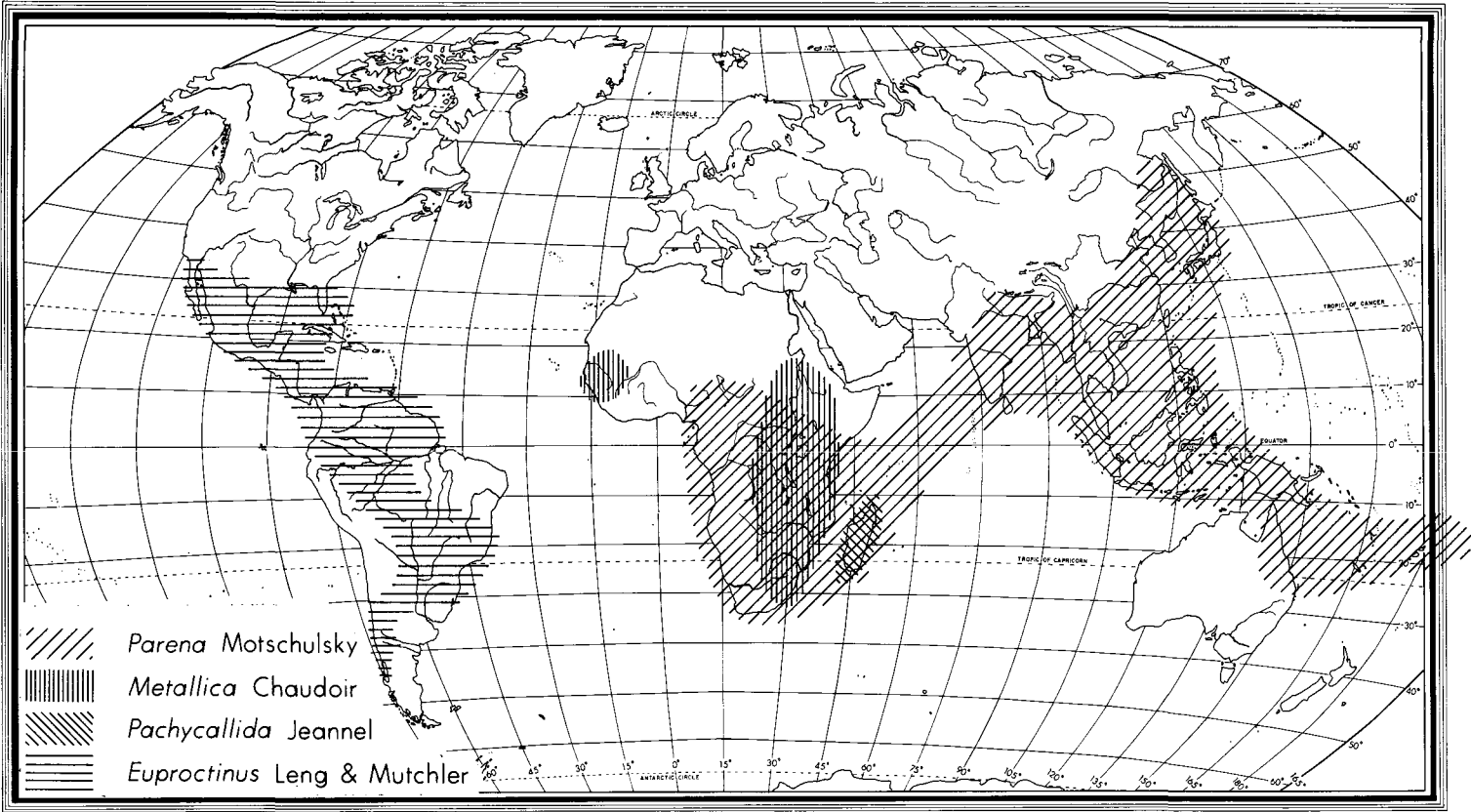
- Parena* Motschulsky, 1859: 31. TYPE-SPECIES: *Parena bicolor* Motschulsky, 1859: 32 (by monotypy).
Bothynoptera Schaum, 1863: 75 - 76. TYPE-SPECIES: *Bothynoptera dorsigera* Schaum, 1863: 76 (by monotypy).— Habu, 1967: 149.
Phloeodromius MacLeay, 1871: 85- 86. TYPE-SPECIES: *Phloeodromius piceus* MacLeay, 1871: 86 (by monotypy).— Csiki, 1932: 1455.
Crossoglossa Chaudoir, 1872: 177 - 178. TYPE-SPECIES: *Crossoglossa testacea* Chaudoir, 1872: 178 (subsequent designation).— Andrewes, 1919: 483.
Ceroglossa Chaudoir, 1878: 151. (Misspelling of *Crossoglossa* Chaudoir, 1872: 177 - 178).
Pazena Peringuey, 1896: 242. (Misspelling of *Parena* Motschulsky, 1859: 31).
Umgenia Peringuey, 1898: 324. TYPE-SPECIES: *Umgenia formidulosa* Peringuey, 1898: 324 (by monotypy).— Basilewsky, 1961: 213.
Prymira Fairmaire, 1899: 76. TYPE-SPECIES: *Prymira stigmatica* Fairmaire, 1899: 76 (by monotypy).— Csiki, 1932: 1455.
Euprymira Fairmaire, 1901: 122. (Incorrect usage by Fairmaire for *Prymira* Fairmaire, 1899: 76).

Diagnosis.— In addition to the characters of the subtribe, adults of this genus exhibit the following features. Color various, elytra partly metallic or not. Head with or without one pair of suborbital setae. Antennomeres 5- 11 each with sensory pit on dorsal surface. Mandibles (Fig. 1) with retinacular ridge of right mandible reduced (compared to *Euproctinus*) to retinacular tooth. Lacinia smooth on inner curved surface. Glossal sclerite with two or three pairs of setae medially, numerous pairs laterally. Mentum with or without one pair of setae. Submentum with two setae laterally each side. Three to four discal setae on each elytron. Males with biseriate adhesive vestiture on fore- and mid-tarsi. Interval 9 of elytron less than half width of interval 8. Internal sac of male genitalia with or without copulatory piece. Stylomere 2 of ovipositor (Fig. 4) with two or more dorsomedial and two or more dorsolateral ensiform setae; apex reduced (Habu, 1967: 167; Figs. 287 - 296). Reproductive tract as in Fig. 72, with markedly elongate tubular sac.

Checklist of Species of *Parena*¹

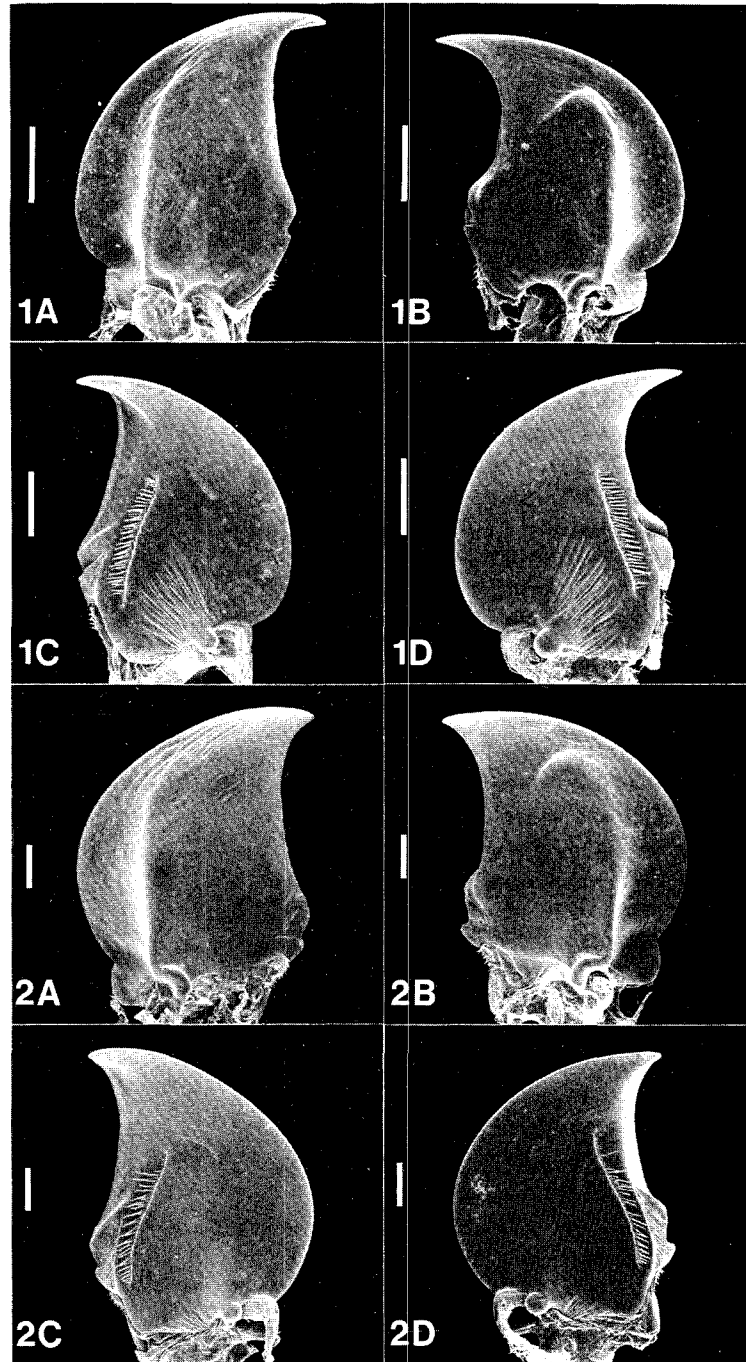
- africana Alluaud, 1917: 86. Cameroon, Kilimandjaro
albomaculata Habu, 1979: 55. Japan
alluaudi Jeannel, 1949: 973. Madagascar
amamiooshimensis Habu, 1964: 29 - 31. Japan
andrewesi Jedlička, 1934: 18. Luzon
bicolor Motschulsky, 1859: 32. Java

¹synonyms in italics



Map 1. Distribution ranges of Metallicina genera.

- cavipennis Bates, 1873: 316. China, Japan
 dorae Basilewsky, 1955: 129. Angola
 dorsigera Schaum, 1863: 76. British India, Tonkin
 esakii Habu, 1969: 115- 117. Taiwan
 fasciata Chaudoir, 1872: 179
 f. fasciata (*sensu stricto*). Borneo, Java, Celebes, Moluccas, New Britain,
 nor. Australia, Papua-New Guinea, Philippines
 plagiata MacLeay, 1876: 167 (*nec* Motschulsky)
 sloanei Csiki 1932: 1455
 f. unicolor Louwerens, 1949: 51. Java
 ferruginea Chaudoir, 1878: 151. French Congo, Zanzibar
 formosana Ohkura, 1978: 29. Taiwan
 hastata Heller, 1921: 528. Philippines
 kurosai Habu, 1967: 164. Japan
 laesipennis Bates, 1873: 317. Japan
 latecincta Bates, 1873: 315. Japan
 viridilineata Jedlička, 1939: 7
 levata Andrewes, 1931: 77. Sumatra
 madagascariensis Alluaud, 1917: 87. Madagascar
 malaisei Andrewes, 1947: 46. Burma
 mella Chaudoir, 1872: 179. Moluccas, Andonare
 monostigma Bates, 1873: 316. Japan
 japonica Jedlička, 1946: 10
 nigrolineata Chaudoir, 1852: 44
 n. nigrolineata (*sensu stricto*). British India, Ceylon, Burma, Tonkin,
 Japan, China, Krakatoa, Vietnam, Andaman Is.
 n. nipponensis Habu, 1964: 33- 34. Japan
 obscura Mateu, 1977: 161. Bhutan
 pendleburyi Andrewes, 1931: 484. North Borneo
 perforata Bates, 1873: 313. Japan
 picea MacLeay, 1871: 86. northern Australia
 piceola Chaudoir, 1877: 232. Amur (China)
 plagiata Motschulsky, 1864: 224. South Africa, Natal, West Africa,
 French Congo
 formidulosa Peringuey, 1898: 324
 scutata Alluaud, 1917: 87.
 politissima Chaudoir, 1883: 20. New Caledonia, Samoa
 quadrisignata Mateu, 1977: 164. Bhutan
 rubripicta Andrewes, 1928: 17. British India, Burma, Vietnam
 rufotestacea Jedlička, 1934: 17. China
 sellata Heller, 1921: 526. Philippines, Taiwan
 sellatoides Jedlička, 1940: 14.
 sticta Andrewes, 1947: 45. Burma
 stigmatica Fairmaire, 1899: 76. Madagascar
 tesari Jedlička, 1951: 60. Taiwan
 testacea Chaudoir, 1872: 178.



Figs. 1 and 2. SEM photographs of mandibles of *Metallicina*. A and C, left dorsal and ventral aspects, respectively, B and D, right dorsal and ventral aspects, respectively, of: 1, *Parena n. nipponensis* Habu; 2, *Metallica viridipennis* Chaudoir. Scale bars = 200 μm .

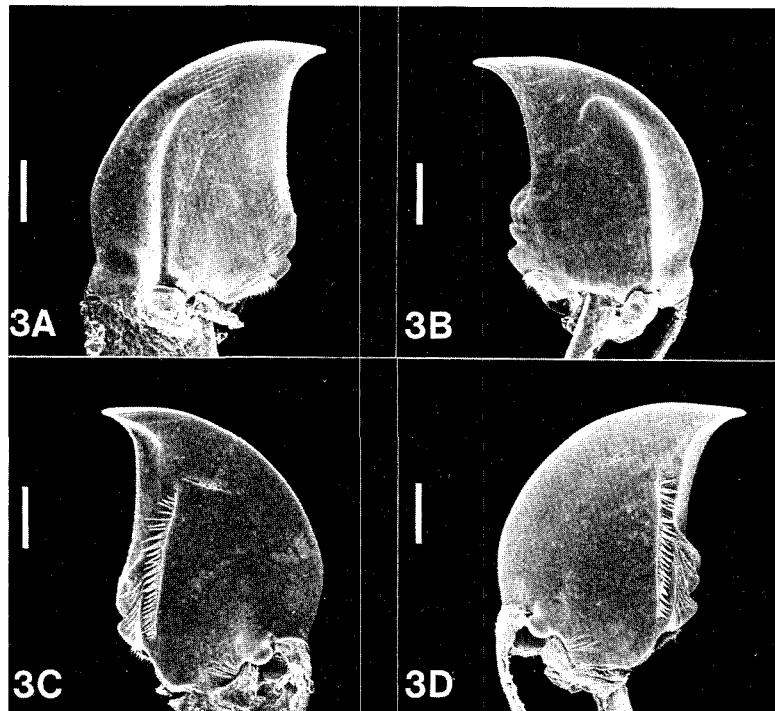


Fig. 3. SEM photographs of mandibles of *Metallicina*. A and C, left dorsal and ventral aspects, respectively, B and D, right dorsal and ventral aspects, respectively, of *Pachycallida rufoplagiata* Jeannel. Scale bars=200 μ m.

t. *testacea* (*sensu stricto*). British India, Sumatra

t. *cruralis* Andrewes, 1934: 286. Java

tripunctata Bates, 1873: 314. Japan

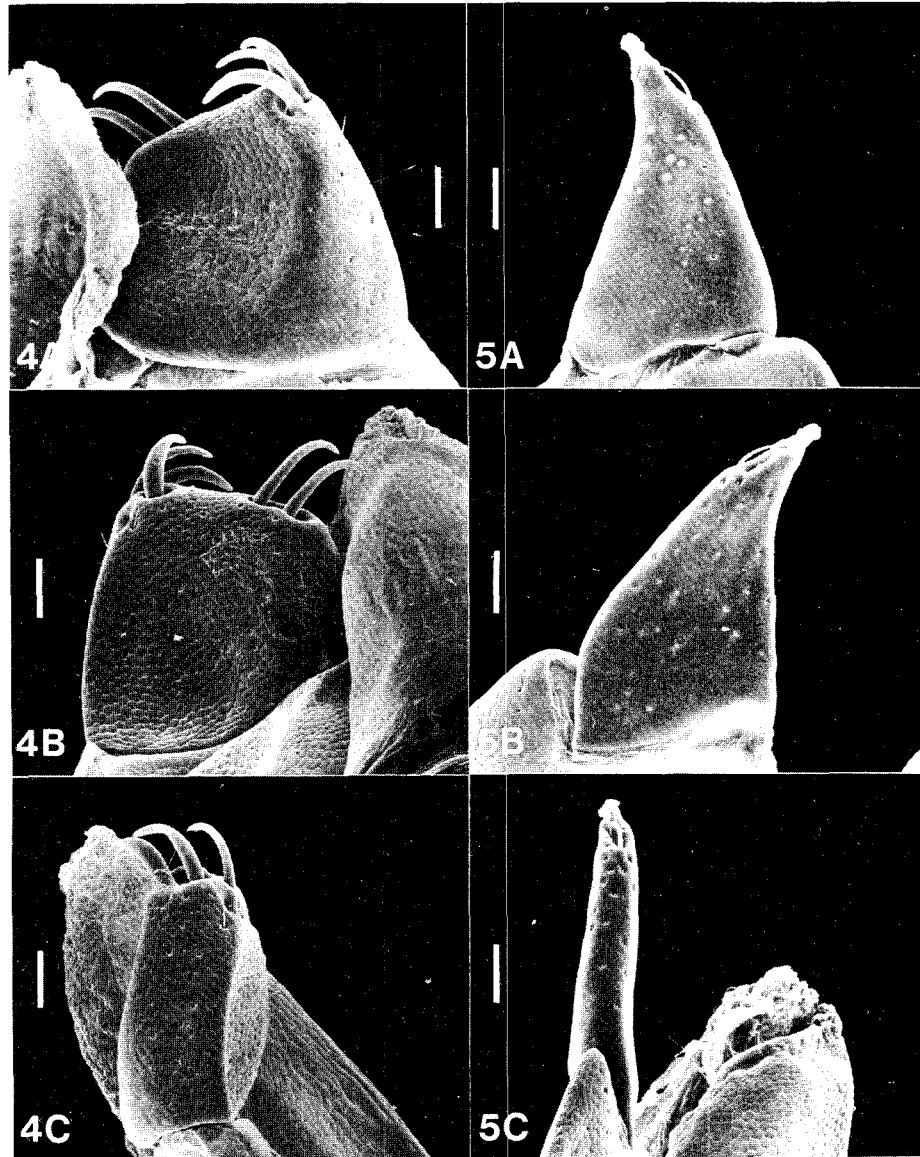
The names *Parena formosana* Jedlička and *Parena formosana* Ohkura are primary homonyms, even though the species described by Jedlička was removed from *Parena* and placed in the genus *Anchista* Nietner. A junior primary homonym is invalid as the name of a species, so a new name must be proposed for the species described by Ohkura. It is possible that *Parena* has more species described than actually exist. Rather than propose a replacement name at this time, I leave it to the subsequent revisor of the genus *Parena*.

Metallica Chaudoir

Figs. 2, 5; Map 1

Metallica Chaudoir, 1872: 175. TYPE-SPECIES: *Metallica viridipennis* Chaudoir, 1872: 177 (here designated).

Diagnosis.— In addition to the characters of the subtribe, adults of this genus exhibit the following features. Color various, elytra metallic or not. Head with one pair of suborbital setae. Antennomeres 5–11 each with sensory pit on dorsal surface. Mandibles (Fig. 2) with retinacular ridge of right mandible reduced (compared to *Euproctinus*) to retinacular tooth. Lacinia lobed on inner curved surface. Glossal sclerite with two pairs of setae medially. Mentum with one pair of setae. Submentum with two setae laterally each side. Three to four



Figs. 4 and 5. SEM photographs of ovipositors, right stylomeres, of *Metallicina*. A, medial aspect; B, lateral aspect; C, ventral aspect. Fig. 4. *Parana n. nipponensis* Habu. Fig. 5. *Metallica viridipennis* Chaudoir. Scale bars = 40 μ m.

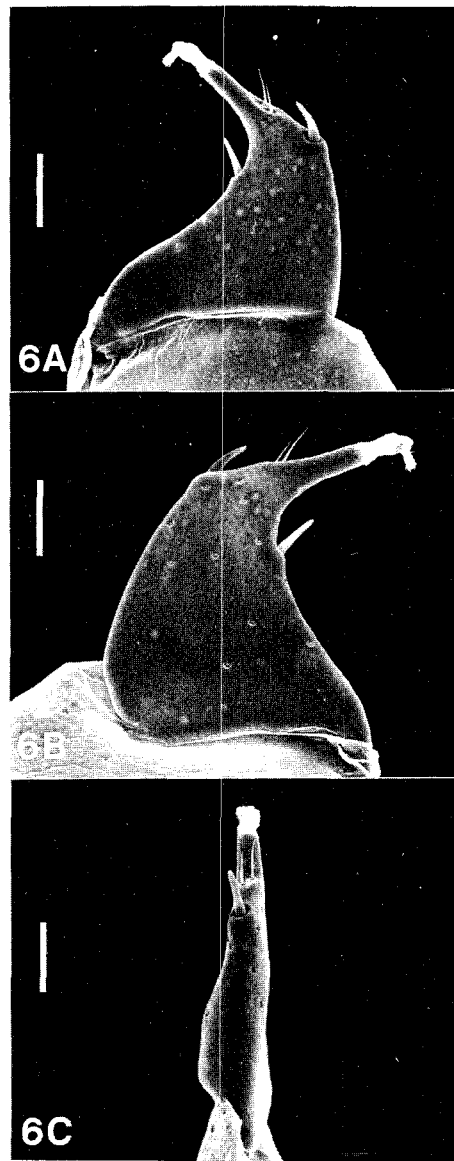


Fig. 6. SEM photographs of ovipositor, right stylomere of *Metallicina*. A, medial aspect; B, lateral aspect; C, ventral aspect of *Pachycallida rufoplagiata* Jeannel. Scale bars = 40 μ m.

discal setae on each elytron; interneur 6, 7, and/or 8 sparsely setose. Interval 9 as wide or wider than preceding interval. Males with biseriate adhesive vestiture on fore-tarsi; single row on mid-tarsi. Internal sac of male genitalia without copulatory piece. Stylocere 2 of ovipositor (Fig. 5) without ensiform setae; apex membranous. Reproductive tract similar to that of *Parena* (Fig. 72), but with extremely short tubular sac.

Checklist of Species of *Metallica*

aeneipennis Dejean 1831: 362. Senegal, Senegambia
capeneri Basilewsky, 1960: 73. Transvaal
mashunensis Peringuey, 1904: 180. South Rhodesia
purpuripennis Chaudoir, 1872: 176. Natal, Zanzibar
rufoplagiata Basilewsky, 1956: 146. Ruanda
viridipennis Chaudoir, 1872: 177. White Nile

Pachycallida Jeannel

Figs. 3, 6; Map 1

Pachycallida Jeannel, 1949: 968. TYPE-SPECIES: *Callida amplicollis* Fairmaire, 1899: 513 (original designation).

Diagnosis.— In addition to the characters of the subtribe, adults of this genus exhibit the following features. Bicolored, elytra completely or partly metallic. Head with one pair of suborbital setae. Mandibles (Fig. 3) with retinacular ridge of right mandible reduced (compared to *Euproctinus*) to retinacular tooth. Lacinia lobed on inner curved surface. Glossal sclerite with about five pairs of setae (medial pair longer than lateral pairs). Mentum with one pair of setae. Submentum with two setae laterally each side. Three discal setae on each elytron. Interval 9 as wide or wider than preceding interval. Males with biseriate adhesive vestiture on fore-tarsi; lacking from mid-tarsi. Internal sac of male genitalia without copulatory piece. Stylocere 2 of ovipositor (Fig. 6) with one dorsomedial and one dorsolateral ensiform seta; apex membranous. Reproductive tract as in *Metallica*, but tubular sac reduced to a small protuberance.

Checklist of Species of *Pachycallida*

amplicollis Fairmaire, 1899: 513.
 a. *amplicollis* (*sensu stricto*). Madagascar
 a. *diegana* Jeannel, 1949: 970. Madagascar
rufoplagiata Jeannel, 1949: 970- 971. Madagascar
sambiranensis Jeannel, 1949: 970. Madagascar

Euproctinus Leng & Mutchler

Euproctus Solier, 1849: 131 - 132 (*nec* Gené). TYPE-SPECIES: *Euproctus fasciatus* Solier, 1849: 132 (by monotypy).— Chaudoir, 1872: 182 - 186.— Horn, 1881: 156 & 158.— 1882: 138.— Bates, 1883: 194- 196.— Wickham, 1897: 109 - 110.— Cockerell, 1906: 240.— Maindron, 1906: 200.— Leng, 1920: 66.— Leng & Mutchler, 1927: 14.— Csiki, 1932: 1456.— Ball, 1960: 160.— Larson, 1969: 16.— Straneo, 1969: 970.— Erwin *et al.*, 1977: 4.60.— Reichardt, 1977: 442.— Erwin & Sims, 1984: 396, 399, 446.
Euproctinus Leng & Mutchler, 1927: 14 (replacement name for *Euproctus* Solier, 1849: 132).— Ball, 1960: 160.— Larson, 1969: 16, 23.— Erwin *et al.*, 1977: 4.60.— Reichardt, 1977: 441, 442.— Ball & Hölchle, 1983: 111.— Erwin & Sims, 1984: 396, 399, 446.

Andrewesella Csiki, 1932: 1456 (replacement name for *Euproctus* Solier, 1849: 132).— Darlington, 1934: 117.— Liebke, 1939: 106 - 107.— Blackwelder, 1944: 61.— Ball, 1960: 160.— Straneo, 1969: 970.— Erwin & Sims, 1984: 396, 399, 446.

Notes about synonymy.— Cockerell (1906: 240) listed *Euproctus* Solier as a preoccupied generic name, but did not propose a replacement name. Leng & Mutchler (1927) proposed *Euproctinus* to replace *Euproctus* Solier. Csiki, unaware of this, published *Andrewesella* as a replacement name in 1932. *Euproctinus* Leng & Mutchler has priority as the new name.

Diagnosis.— In addition to the characters of the subtribe, adults of this genus exhibit the following features. Color various, elytra not metallic. Head with or without one pair of suborbital setae. Retinacular ridge of right mandible prominent. Lacinia smooth on inner curved surface. Glossal sclerite with two pairs of setae medially, numerous pairs laterally. Mentum with one pair of setae. Submentum with one seta laterally each side. Two discal setae on each elytron. Males with biseriate adhesive vestiture on fore-tarsi; single row on mid-tarsi. Interval 9 of elytron less than half width of interval 8. Internal sac of male genitalia with flagellum-like copulatory piece. Stylocere 2 of ovipositor with one dorsomedial and one dorsolateral ensiform seta; apex pointed. Reproductive tract as in Fig. 73; spermatheca markedly elongate; tubular sac absent.

Description.— Body moderately elongate, somewhat deplanate. Standardized Body Length 3.48 to 6.60 mm. Dorsal surface glabrous except for fixed setae; dorsum of head with fine scattered punctures. Ventral surface with sparse fine setae.

Color. Body testaceous to brown; pale spots of elytra testaceous to rufo-testaceous; markings of elytra brown to piceous; antennae, mouthparts, and legs testaceous to rufo-piceous; tibiae testaceous to piceous.

Microsculpture. Microlines of various depth; sculpticells slightly convex to effaced. Mesh pattern on dorsal surface of head, pronotum, proepisternum, and lateral edges of abdominal sclerites isodiametric or slightly transverse, or microlines effaced; on elytra isodiametric, microlines nearly effaced in some species; mesosternum, metasternum, metepisternum, and medial area of abdominal sclerites slightly to markedly transverse, or microlines effaced; on ventral surface of head microlines effaced.

Luster. Shining, not iridescent.

Fixed setae. As in *Lebiini*. Head with or without one pair of suborbital setae. Glossal sclerite with four long setae apically. Penultimate labial palpomere bisetose; basal labial palpomere with single long or short seta. Umbilical series with about 16 setose punctures.

Head. Eyes large, subgena markedly reduced. Frons slightly convex, extended above dorsal margins of eyes. Longitudinal supraorbital carina between inner dorsal margin of eye and pair of adjacent supraorbital setae. Antennae moderately long, extended beyond base of pronotum. Antennomeres elongate except where noted. Scape of antenna with (Fig. 7A) or without depression on posterior surface. Antennomeres 5-11 each with sensory pit on ventral surface (Figs. 7B and 7C).

Mouthparts. Labrum rectangular, about twice as wide as long. Mandibles (Figs. 10 and 11) with laterally extended ventral margin of scrobe. Cutting edge of right and left mandibles formed by retinacular ridge. Premolar well developed or not. Ventral groove moderately long (Fig. 10C and 10D) or reduced (Fig. 11C and 11D). Ventral secretory groove on both mandibles. Maxillae typical for *Lebiini*; apical margin of maxillary palpomere 4 obliquely truncate. Labium: mentum transverse, apices of lateral lobes rounded; prementum with glossal sclerite and paraglossae fused basally, paraglossae membranous apico-medially. Glossal sclerite with four long setae apically; paraglossae with numerous setae apically (Figs. 8 and 9). Penultimate labial palpomere bisetose; basal labial palpomere with single long or short seta. Apical labial palpomere securiform, apex obliquely truncate.

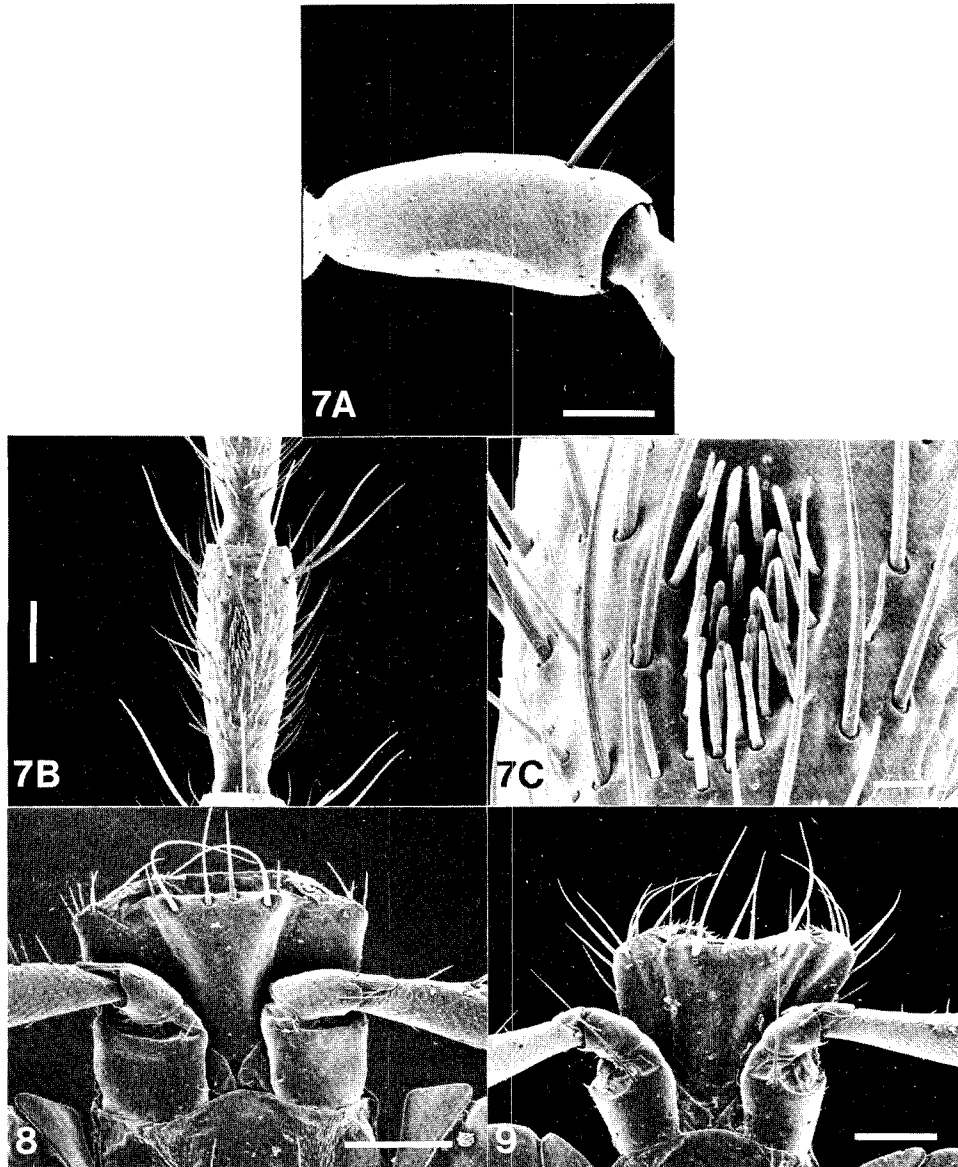
Prothorax. Pronotum moderately broad, subequal to width of head; width greater than length, widest in anterior half; anterior margin straight to slightly emarginate; lateral margin sinuate posteriorly; posterior margin nearly straight, produced anteriorly at hind angles; hind angles about right to obtuse; disc convex to nearly flat, median longitudinal depression linear; lateral grooves narrow to moderately wide; basal foveae shallow; posterior margin beaded or not. Propleura and prosterna average.

Pterothorax. Average, except mesepimeron strikingly narrowed in medial half; metepisternum longer than wide.

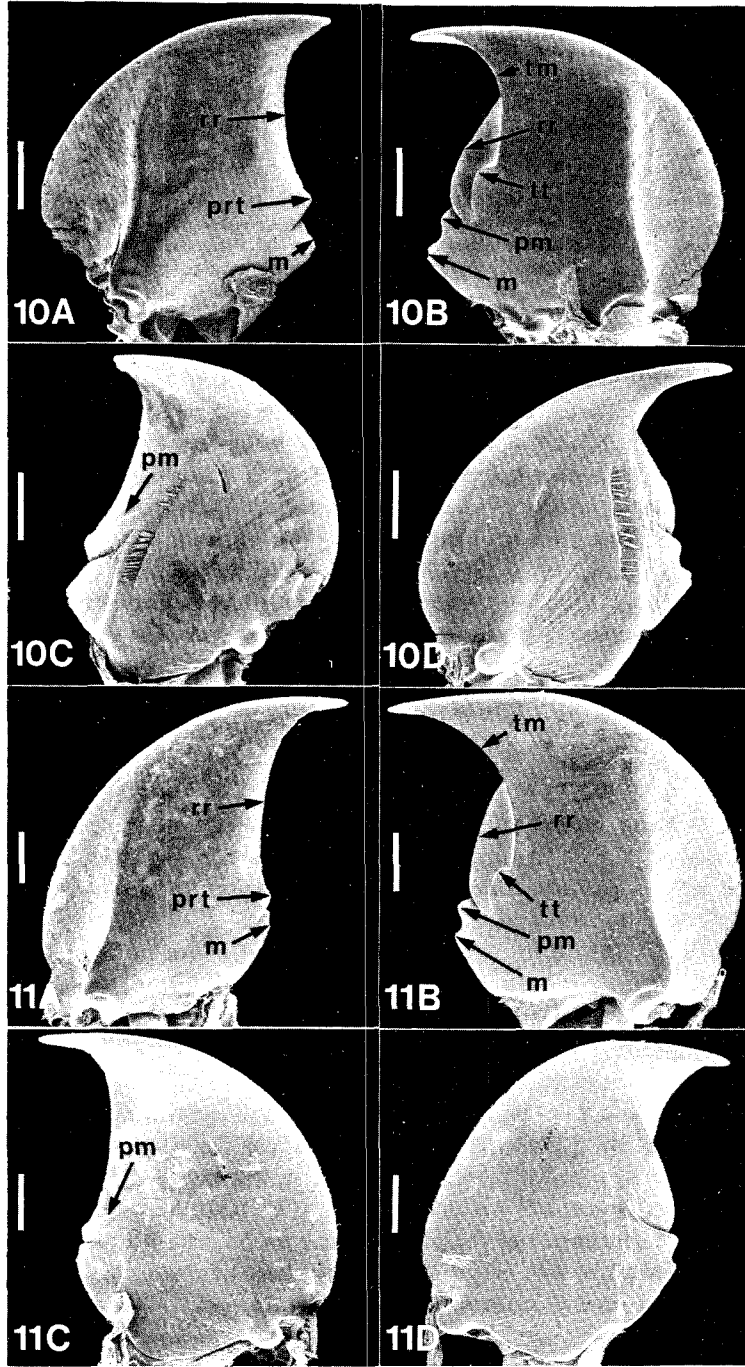
Elytra. Humerus rounded; apical margin subtruncate; sides nearly parallel to widened apically; laterally somewhat explanate or not. Basal ridge incomplete, extended to base of interneur 3. Interneurs shallow, each uniseriately punctate, punctures small, or interneurs represented by single row of small punctures. Intervals slightly convex to flat, each uniseriately punctate longitudinally, punctures fewer and finer than those of interneurs.

Hind wings. Fully developed, with large oblongum cell and wedge cell (Fig. 67).

Legs. Average, posterior tibia about 1.5 times length of posterior tarsus. Males with ventral surface of mid-tibia smooth, or with small blunt denticles. Fore-tibia with or without upper spur on inner surface. All femora antero-ventrally with two moderately long setae each; fore- and mid-trochanters ventrally with one long seta each; mid-coxae ventrally with



Figs. 7-9. SEM photographs of structures of *Euproctinus* species. Fig. 7: antennomeres, A, right scape, dorsal aspect, B, left antennomere 8, ventral aspect, C, left antennomere 7, ventral aspect, of *E. subdeletus*. Figs. 8 and 9, labium, ventral aspect: 8, *E. fasciatus* (Solier); 9, *E. subdeletus* (Bates). Scale bars: 7A, 7B, 8, 9 = 100 μ m, 7C = 10 μ m.



Figs. 10 and 11. SEM photographs of mandibles of *Euproctinus* species. A and C, left dorsal and ventral aspects, respectively, B and D, right dorsal and ventral aspects, respectively, of: 10, *E. fasciatus* (Solier); 11, *E. subdeletus* (Bates). Scale bars = 100 μ m. m, molar; pm, premolar; prt, posterior retinacular tooth; rr, retinacular ridge; tm, terebral margin; tt, terebral tooth.

one long seta and numerous shorter setae each. Tarsomeres with dorsal surfaces sparsely setose. Males with tarsomeres 1-3 of Fore-leg with biseriate adhesive vestiture, and tarsomeres 1 & 2 or 2 & 3 of mid-leg with single row of adhesive vestiture. Tarsal claws pectinate.

Abdominal sterna. Average for Lebiini. Sternum VI and VII with pubescence, several short to moderately long setae, or only one long seta laterally each side. (Long setae are as long or longer than anal setae; moderately long setae are about half length of anal setae; and short setae are longer than pubescence, about one quarter length of anal setae.) Sternum VII of males without medial apical notch.

Male genitalia. Median lobe expanded laterally, in dorsal view appearing rather oval; apical portion narrow with rounded apex. Apical orifice hemiopic; internal sac with distinct microtrichia. Long flagellum associated with internal sac; length of flagellum from one to three and a half times the length of median lobe. Parameres average, left larger than right.

Ovipositor. Stylomere 2 about falcate, one dorsomedial and one dorsolateral ensiform seta (Fig. 71).

Female genitalia. Bursa copulatrix with or without numerous short stout spines. Spermatheca markedly elongate; tubular sac absent (Fig. 73).

Classification.— Three ranks are used to indicate divergence and relationships in this genus, the formal subgenus, and informal species group and subgroup. Although one of the subgenera (*Euproctinus*, *sensu stricto*) is monobasic, the single species it contains (*E. fasciatus*), differs as much from its monophyletic sister taxon (the polybasic *Neoeuproctus*, new subgenus) as do taxa in other lebiine genera that are ranked as subgenera. As noted above (Ghiselin, *l. c.*), the use of ranking as an indicator of structural divergence is appropriate in a phylogenetic system, so long as the resulting groups are monophyletic.

Euproctinus baeri (Maindron) is listed as *incertae sedis* because its type was not located. This species is unplaced at the subgeneric level and may not even be a *Euproctinus*.

Geographical distribution.— The range of *Euproctinus* extends from southern California, Arizona, and Texas and Florida in the United States and Cuba, south throughout México and Central America to Chile, in southern South America.

Key to Subgenera of *Euproctinus*

- | | | |
|----|---|--|
| 1 | Head without suborbital setae; antennal pedicel evenly rounded posteriorly | <i>Euproctinus</i> Leng & Mutchler, p. 280 |
| 1' | Head with one pair of suborbital setae; antennal pedicel with depression on posterior surface, with dorso-posterior carina medially | <i>Neoeuproctus</i> , new subgenus, p. 284 |

Subgenus *Euproctinus* Leng & Mutchler

Type-species.— *Euproctus fasciatus* Solier, 1849: 132.

Recognition.— Adults of this subgenus are readily distinguished by the two characters given in the key. Additionally, the mandibles have a moderately long ventral groove; pronotum wider than head, hind angles obtuse, disc convex, lateral grooves moderately wide, posterior margin not beaded; upper spur present on inner surface of fore-tibia; males have adhesive vestiture on the second and third tarsomeres of the mid-leg; sternum VI and VII without long setae laterally; flagellum associated with the male genitalia is about 1.5 times length of median lobe; and in females the bursa copulatrix has numerous short stout spines.

Included taxa.— This subgenus includes only one species, *E. fasciatus* (Solier).

Geographical distribution.— This subgenus is found only in central Chile and bordering Argentina.

Euproctinus fasciatus (Solier)

Figs. 8, 10, 12–14; Map 2

Euproctus fasciatus Solier, 1849: 132. Type material: HOLOTYPE, labelled: MUSEUM PARIS, CHILI, CL. GAY 1845 [green paper]; green disc; TYPE [red paper]; *Euproctus fasciatus* G. et Sol Chili [handwritten] (MNHP). Type area: Chile.— Chaudoir, 1872: 182, 183.

Andrewesella fasciata; Csiki, 1932: 1456.— Blackwelder, 1944: 61.— Straneo, 1969: 970.

Andrewesella kuscheli Straneo, 1969: 970 - 971. NEW SYNONYMY. Type material: not seen. HOLOTYPE male, labelled: Chile, Aisen, Conhaique, 5-II-1956, KUSCHEL (Museum di Santiago). Type locality: Coyhaique, Aysen Province, Chile.

Note about synonymy.— I did not see the type of *Andrewesella kuscheli* Straneo. This species was distinguished from *E. fasciatus* by thicker antenna and broader elytral markings. A series of ten specimens from Epuyen, Argentina, shows not only the elytral patterns of *E. fasciatus* and *A. kuscheli*, but also intergrades. There were no differences in antennae. I believe the two forms are conspecific, with the broader elytral pattern occurring in the southern limit of the range of this species.

Recognition.— Absence of suborbital setae and details of the elytral color pattern (Figs. 13 and 14) readily distinguish adults of this species.

Description.— Character states of subgenus *Euproctinus* and the following. Average SBL 4.72 mm (males) and 4.84 mm (females).

Color. Body and appendages uniformly orange, with black elytral markings. Elytron as in Figs. 13 and 14, parahumeral spot extended to humeral margin, basal margin dark; median fascia transverse, broad, extended to lateral margin, lateral groove thus bicolored; anterior part of paralateral vitta developed or not; sutural and posterior part of paralateral vitta not developed; parascutellar area and apical margin pale; anterior and posterior discal spots open, posterior spot very short and broad.

Notes about variation.— The elytral color pattern varies from the typical northern form (Fig. 13) to the form found in the south, which has larger humeral and transverse fasciae, joined near the lateral margin (Fig. 14). There are no differences in pronota (Fig. 12). Of the 431 specimens seen, one did not have the humeral dark spot on either elytron.

Notes about habitat.— Specimens have been taken at elevations from near sea level to 1650 meters. The geographical range of this species includes four forest types - subtropical deciduous hardwood, beech, pine, and Valdivian rain forest. In correspondence, Luis Peña of Santiago states that specimens are often collected under bark and by beating. Adults are apparently not readily taken at light, in contrast to those of other species of *Euproctinus*.

Geographical distribution.— This species occurs in central Chile and bordering Argentina (Map 2).

Chorological affinities.— No other species of *Euproctinus* have been recorded from Chile, or the nearby localities for *E. fasciatus* in Argentina.

Material examined.— A total of 446 specimens, including types, were examined. Non-type material was seen from the following localities:

ARGENTINA Chubut. Epuye (BMNH); Pedrogoso Epuyen (BMNH) (for both the Chubut localities the labels read Chile, not Argentina as listed here); Neuquen. 59: Alumine, SE of Lago Alumine (ZMKD); 36: S.M. de los Andes, Cerro Chapelco (ZMKD); Rio Negro. San Carlos de Bariloche. Isla Victoria (LACM); 14: S.C. de Bariloche, Pampa del Toro (ZMKD).

CHILE (BMNH)(MCZ)(MNH); Aconagua. Cuesta el Melon (MCZ); 90 km s Illapel (Coquimbo)(MCZ); Piscicultura (MCZ); Rio Blanco (MCZ); Arauco. Alto Caicupil (MCZ); Butamalal (MCZ); Carmavida (MCZ); Contulmo (MNH); Pillim Pilli (MCZ); Pte. Trongol (USNM); Bio-Bio. El Abanico (CAS); Cautin. Cherquenco (MCZ); Temuco (CAS); 20 & 22 km e Temuco (CAS); Concepción. Concepción (CAS); Coquimbo. R. Los Molles (MCZ); 7 km e Los Molles (USNM); Curico. Buchen (MCZ); Cubillo, Cord. (MCZ); El Coigo, Cord. (MCZ); Linares. Fundo Malcho, Cord. Parral (MCZ); Las Cruces, Cord. Parral (MCZ); Villega, Cord. Parral (MCZ); Llanquihue. Puerto Montt (MNH); Malleco. Angol (USNM); 6 km w Angol (USNM); Pemehue (USNM); Rio Blanco (MCZ); Sierra de Nahuelbuta, w Angol (CAS); Sierra Nevada, Cord. Longuimay (MCZ); Maule. Pelluhue (MCZ); Tregualemu (MCZ); Ñuble. Atacalco (MCZ); Chovellen (MCZ); Las Truncas (UASM); Recinto (MCZ); 4 km se Recinto (CNC); 15 km nw Recinto

(USNM); 40 & 50 km e San Carlos (CAS); San Fabian de Alico (MCZ); **O'Higgins**. La Leonera (MCZ); Rengo, Thal (MNHB); **Santiago**. Curacavi (USNM); 8 & 9 km w Curacavi (USNM); El Canelo (CAS)(MCZ)(UASM); El Clarillo (MCZ); El Puemo (MCZ); Las Condes (MCZ); e Llay-Llay (USNM); 5-11 km s Melipella (USNM); Melcoton (MCZ); Penalolone (MCZ); Pirque (UASM); Quebrada de la Plata, nr Maipu (CAS); Rio Colorado (MCZ); Santiago (MNHB); **Valdivia**. Enco (MCZ); 13 km se Valdivia (USNM); **Valparaiso**. Quillota, Las Palmas (MCZ); Valparaiso (BMNH)(CAS). Collecting dates from August 7 to March 2.

Subgenus *Neoeuproctus*, new subgenus

Type-species.— *Euproctus sigillatus* Bates, 1883: 196 (here selected).

Derivation of name.— From “*neo*”, a Greek word for new, and “*Euproctus*”, the original name proposed for this genus.

Recognition.— Adults of this subgenus are readily distinguished by the two characters given in the key. Additionally, they have: mandibles with a reduced ventral groove; pronotum narrower than head except where noted, hind angles obtuse except where noted, lateral grooves moderately wide except where noted, posterior margin of pronotum beaded; adhesive vestiture on the first and second tarsomeres of the mid-legs of males; and bursa copulatrix of females without numerous short stout spines.

Included taxa.— This subgenus includes the remaining 15 species of the genus.

Geographical distribution.— The range of this subgenus extends from southern California, Arizona, and southeastern Texas and Florida in the United States and Cuba, south throughout México and Central America into northern South America, and southern Brazil.

Classification.— The species are arranged in two groups, the *sigillatus* group and the *quadriplagiatus* group.

Key to Species of Subgenus *Neoeuproctus*

Adults

- | | | |
|----|--|--|
| 1 | Upper spur on inner surface of fore-tibia present; sternum VII with two or more short to moderately long setae each side (Fig. 68) . . . <i>sigillatus</i> group | 2 |
| 1' | Upper spur on inner surface of fore-tibia absent; sternum VII with one long seta each side (Fig. 69) | 8 |
| 2 | (1) Integument uniformly brown OR elytron with two enclosed pale spots, apical pale spot of elytron short, inverted comma shaped, in intervals 2, 3, and 4 (Fig. 23) | <i>E. abjectus</i> (Bates) (in part), p. 291 |
| 2' | Integument testaceous to bicolored; elytron with one or two enclosed pale spots, or none | 3 |
| 3 | (2) Elytron with two enclosed pale spots, markings narrow to broad (Fig. 27) | <i>E. subdeletus</i> (Bates) (in part), p. 293 |
| 3' | Elytron with one enclosed pale spot, or none | 4 |
| 4 | (3) Elytron with one enclosed pale spot, faint or well developed | 5 |
| 4' | Elytron without an enclosed pale spot | 7 |
| 5 | (4) Elytron with enclosed pale spot basal | 6 |
| 5' | Elytron with enclosed pale spot apical (Fig. 26) | <i>E. subdeletus</i> (Bates) (in part), p. 293 |
| 6 | (5) Elytron with faint longitudinal spot in basal 0.5 (Fig. 24) | <i>E. abjectus</i> (Bates) (in part), p. 291 |
| 6' | Elytron with well developed oblong oval basal pale spot (Fig. 22); | |

	transverse medial marking	<i>E. sigillatus</i> (Bates), p. 291	
7	(4') Elytron with broad transverse medial marking; pale area at base and apex (Fig. 21)	<i>E. balli</i> , new species, p. 286	
7'	Elytron with diagonal medial marking restricted to interneurs; sutural and lateral markings absent (Fig. 28)	<i>E. pallidus</i> , new species, p. 295	
8	(1') Elytron with two enclosed pale spots		9
8'	Elytron with less than, or more than two enclosed pale spots		13
9	(8) Humeral pale area of elytron elongate; anterior pale spot nearly medial in position (Fig. 37)	<i>E. howdeni</i> , new species, p. 301	
9'	Humeral pale area of elytron reduced to absent; anterior pale spot nearly basal in position		10
10	(9') Tibiae black; specimen from Panamá		
	<i>E. nigrotibialis</i> , new species, p. 307	
10'	Tibiae testaceous to rufous		11
11	(10') Basal pale spot of elytron longitudinal, extended over most of interval 3, all of 4, and most of interval 5 (Fig. 39)		
	<i>E. quadrivittis</i> (Chaudoir), p. 302	
11'	Basal pale spot of elytron oblong oval, extended from interval 3 onto intervals 6, 7, or 8 (Figs. 40, 51-60)		12
12	(11') Sternum VI with one long seta each side		
	<i>E. quadriplagiatus</i> (Reiche), p. 303	
12'	Sternum VI without one long seta each side		
	<i>E. ornatellus</i> (Bates), p. 302	
13	(8') Elytron with three or more enclosed pale spots		14
13'	Elytron with one enclosed pale spot, or none		15
14	(13) Elytron with three enclosed pale spots (Fig. 36)		
	<i>E. columbianus</i> , new species, p. 300	
14'	Elytron with four enclosed pale spots (Fig. 38)		
	<i>E. putzeysi</i> (Chaudoir), p. 301	
15	(13') Elytron with one enclosed pale spot (Fig. 65)		
	<i>E. deliciolus</i> (Bates), p. 310	
15'	Elytron without an enclosed pale spot		16
16	(15') Elytron with pale vitta bordered by rufous band suturally, laterally, and apically (Fig. 35)	<i>E. trivittatus</i> (LeConte), p. 295	
16'	Integument uniformly flavous; specimen from Panamá		
	<i>E. panamensis</i> , new species, p. 312	

The *E. sigillatus* group

This group has five species which are characterized by the presence of an upper spur on the inner surface of the fore-tibia and two or more moderately long setae each side on sternum VII except where noted. Sternum VI has several short to moderately long setae each side except where noted. The geographical range of the *E. sigillatus* group extends from Costa Rica (Lower Central America) northward to southern United States, and is centered in Nuclear Middle America.

Euproctinus balli new species

Figs. 15, 21, 77; Map 3

Type Material.— HOLOTYPE male, labelled: MEXICO Oaxaca 21.8 mi n Juchatengo 7100' III.23.1966 in bromeliads; George E. Ball, D.R. Whitehead collectors; P163 [blue paper] (USNM). ALLOTYPE female, labelled: MEX. OAXACA 27.2 km s Miahuatlan oak-pine zone Alnus litter bromeliads 2440 m. June 14, 1979 79 - 34; MEXICAN EXP. 1979 J.S. Ashe, G.E. Ball, D. Shpeley collectors (USNM). Twelve additional PARATYPES, sex and label data as follows. Male: same as holotype (UASM). Male: 11 mi NE San Cristobal L.C., Chis. Mex. V.5.1969 H.F. Howden (UASM). Male: Carapan Michoacan Mex. VII-1-63 J. Doyen Collector (UCBC). Female: MEX. Chiapas 10.0 mi e San Cristobal 8300' 10.XII.65 in bromeliads George E. Ball, D.R. Whitehead collectors (UASM). Female: MEXICO Chiapas San Cristobal de las Casas 2250 m. 26 June 1973 Ginter Ekis (USNM). Female: 10 mi e Teopisca Chis. Mex. VI.2 1969 H. Howden (UASM). Female: 10 mi e Teopisca Chis. Mex. VII-12 1969 H.F. Howden (UASM). Female: 10 mi se Teopisca Rte 24 Chis. Mex. VI.3-5 1969 H. Howden (UASM). Female: ♀ winged, MEXICO Hidalgo 26.2 km N Zimapan Hwy 85 2562 meters 19 May 1973, u-v light T.L. and L.J. Erwin Collectors, T.L. and L.J. Erwin Collectors Expedition #5 in notebook #2 (USNM). Female: MEX. OAXACA 16.2 km n Las Animas Rte. 195 oak-Mimosa grove (dry) beating 2030 m. June 13, 1979 79-33; MEXICAN EXP. 1979 J.S. Ashe, G.E. Ball, D. Shpeley collectors (UASM). Female: MEX. Oaxaca Microondas Sta. 0.5 mi e jct Rtes 190 & 125 ca 8300' oak forest, August 23, 24, 1972, B.S. Heming, G.E. Ball Collectors (UASM). Female: MEX. Oaxaca 97.3 mi s Valle Nacional 7900' VIII.19.65 George E. Ball, D.R. Whitehead collectors (UASM).

The study material also included specimens from southern Arizona and northern Sonora, which are not included in the type series. I believe that they represent only one species, but because of the disjunct distribution and variation in coloration, decided to chose the southern area as the type locality, and specimens from nearby localities as the paratypes.

Type locality.— 21.8 miles north of Juchatengo and vicinity, state of Oaxaca, México.

Derivation of specific epithet.— Based on the surname of George E. Ball, who assisted in the collection of the type material, as well as specimens of most species of *Euproctinus*.

Recognition.— This species is readily distinguished by the form of the piceous markings of the elytra (Fig. 21).

Description.— Character states of the *sigillatus* group and the following. Average SBL 5.90 mm (males) and 6.03 mm (females).

Color. Pale areas of elytron, femora, mouthparts, and antennae testaceous; antennomeres 2- 4 darkened; markings of elytra, pronotum, head, tibiae, and tarsomeres rufous to piceous. Some specimens with basal half of elytron piceous, but apical margin pale, and paralaral vitta not developed; median fascia broad, only posterior margin slightly diagonal, predominantly transverse; discal spot in most specimens open.

Prothorax. Pronotum (Fig. 15) wider than head; lateral grooves wide.

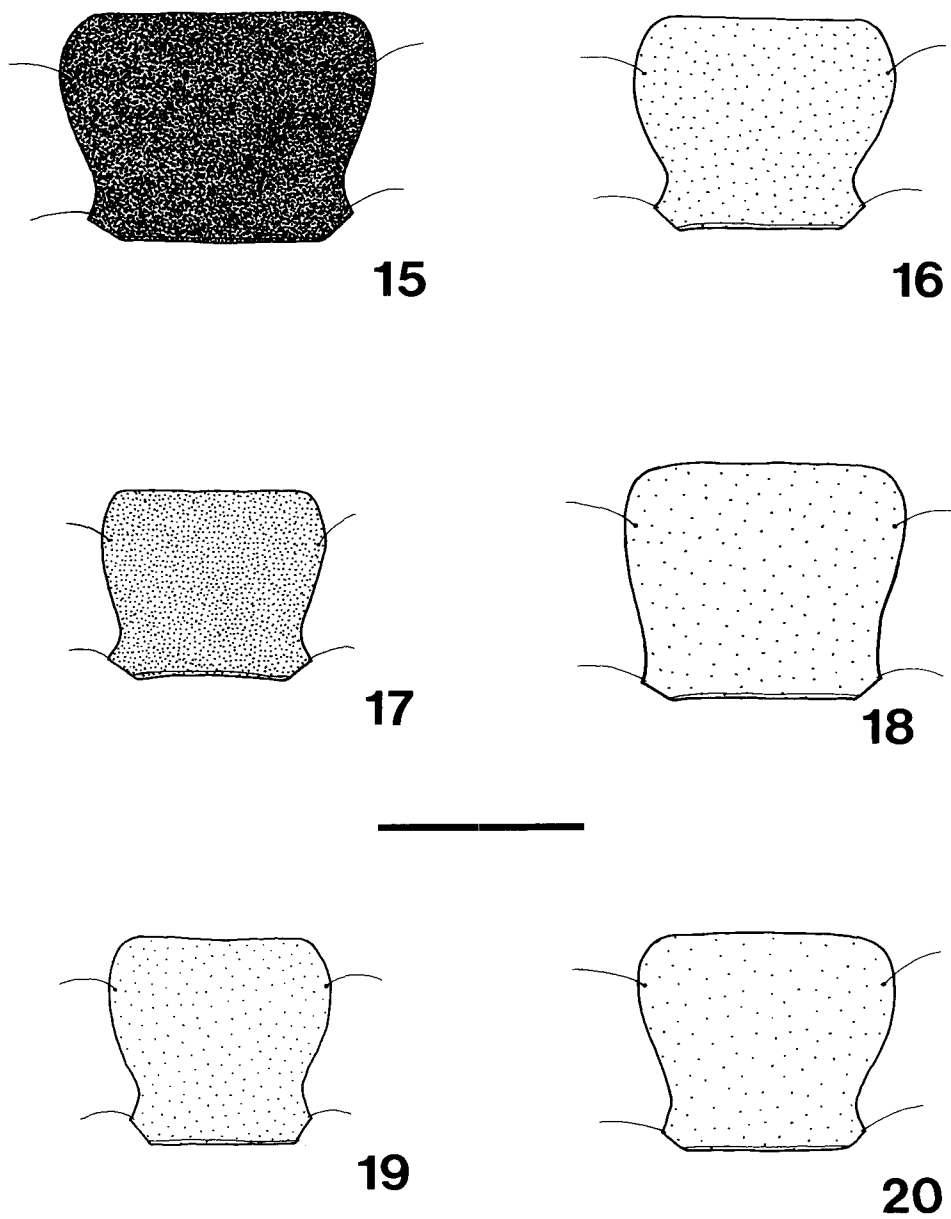
Male genitalia. Flagellum about 2.3 times length of median lobe.

Notes about variation.— Specimens from Arizona and Sonora have rufous pronota and heads, while those to the south are piceous. Also, some specimens from Oaxaca and Chiapas have the basal half of the elytron much darker than in Fig. 21, so that the only pale area is that of the apex.

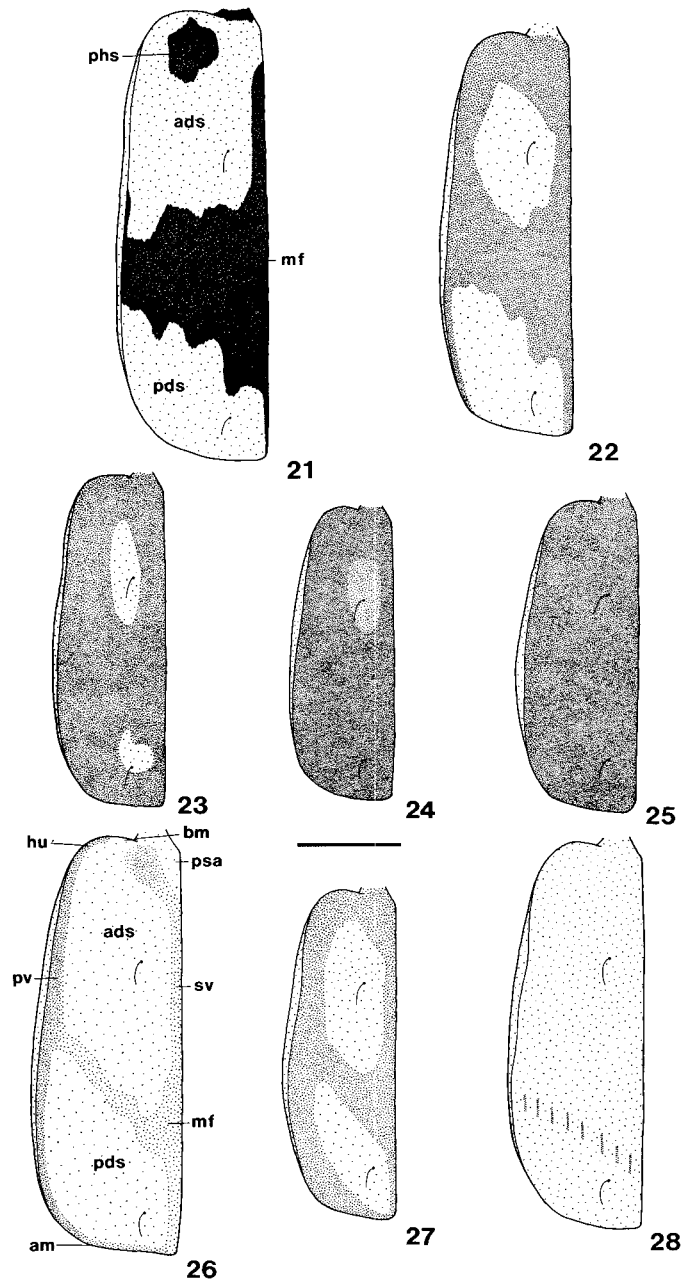
Notes about habitat.— In México, specimens were taken in oak, oak-mimosa, and oak-pine forest at elevations from 1950 to 2530 meters. Specimens were taken from bromeliads, by beating, and at u-v light. I collected teneral adults of this species on July 5 & 6, 1983 at u-v light in an oak-pine forest in Sonora, México. Adults of this species have been taken at elevations of 1340 and 1750 meters at the Arizona localities. The habitats in Arizona are primarily oak with either madroño and juniper or pine and juniper.

Geographical distribution.— This species is found in southern Arizona and northern Sonora, and in central and southern México, in the Pacific versant (Map 3).

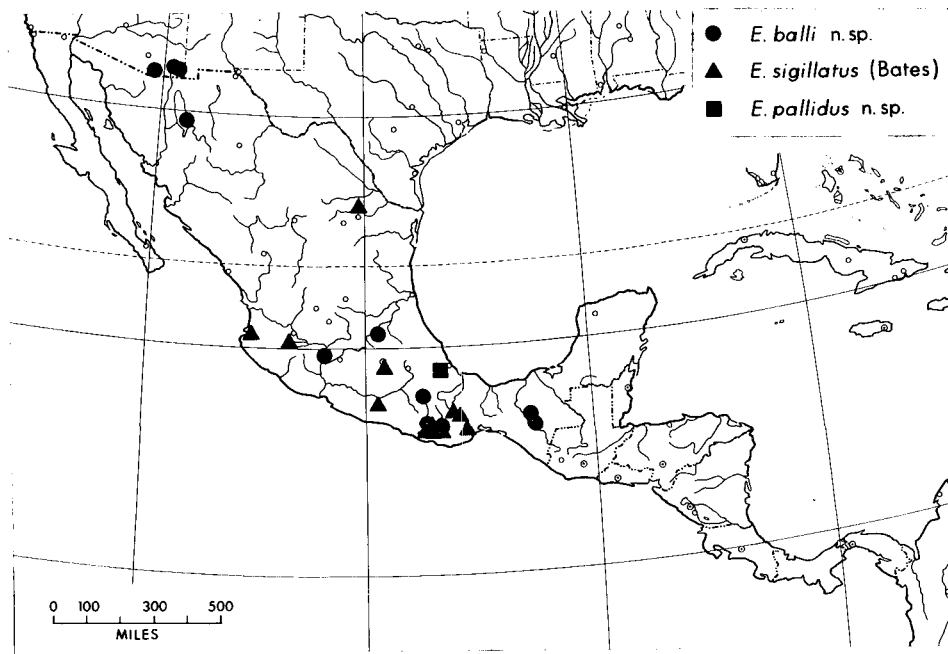
Chorological affinities.— The geographical range of this species overlaps those of *E. sigillatus*, *E. abjectus*, and *E. subdeletus*. Specimens of *E. balli* and *E. abjectus* have been collected at the same locality on the same day. Also, *E. balli* and *E. sigillatus* have been collected on the same day and at the same locality.



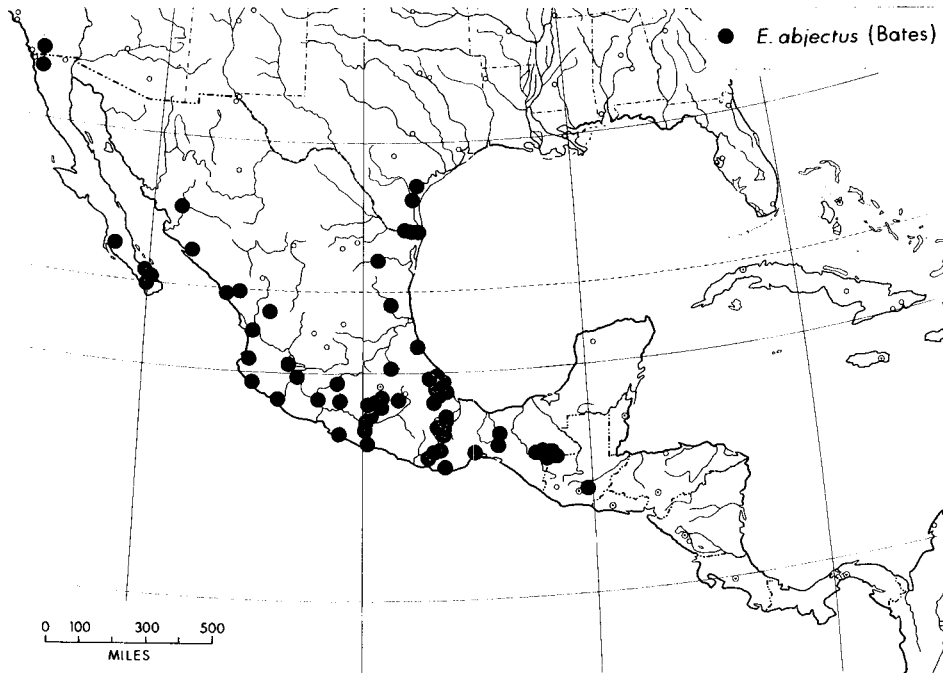
Figs. 15-20. Line drawings of pronota of *Euproctinus* species. Fig. 15. *E. balli* new species; Fig. 16. *E. sigillatus* (Bates); Fig. 17. *E. abjectus* (Bates); Figs. 18 and 19. *E. subdeletus* (Bates) (Fig. 18, specimen from Veracruz, Mexico; Fig. 19, specimen from S. Salvador, El Salvador); Fig. 20. *E. pallidus* new species.



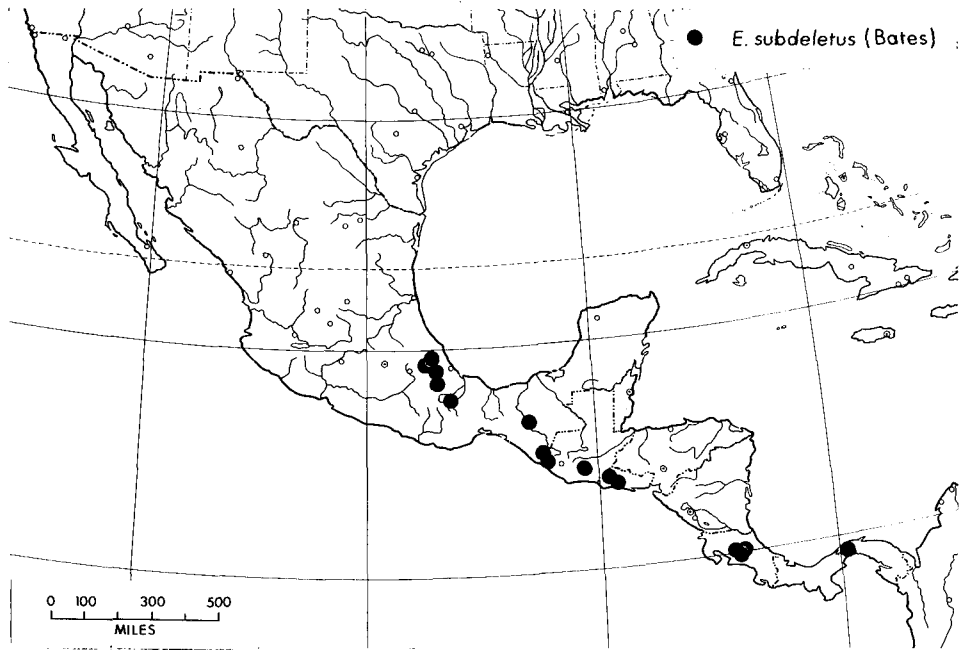
Figs. 21-28. Line drawings of left elytra of *Euproctinus* species. Fig. 21. *E. balli* new species; Fig. 22. *E. sigillatus* (Bates); Figs. 23-25 *E. abjectus* (Bates) (Fig. 23, specimen from Oaxaca, Mexico; Figs. 24 and 25, specimens from Texas, USA); Figs. 26 and 27. *E. subdeletus* (Bates) (Fig. 26, specimen from Veracruz, Mexico; Fig. 27, specimen from S. Salvador, El Salvador); Fig. 28. *E. pallidus* new species. Scale bar=1 mm. ads, anterior discal spot; am, apical margin; bm, basal margin; hu, humerus; median fascia; pds, posterior discal spot; pbs, parahumeral spot; psa, parascutellar area; pv, paralateral vitta; sv, sutural vitta.



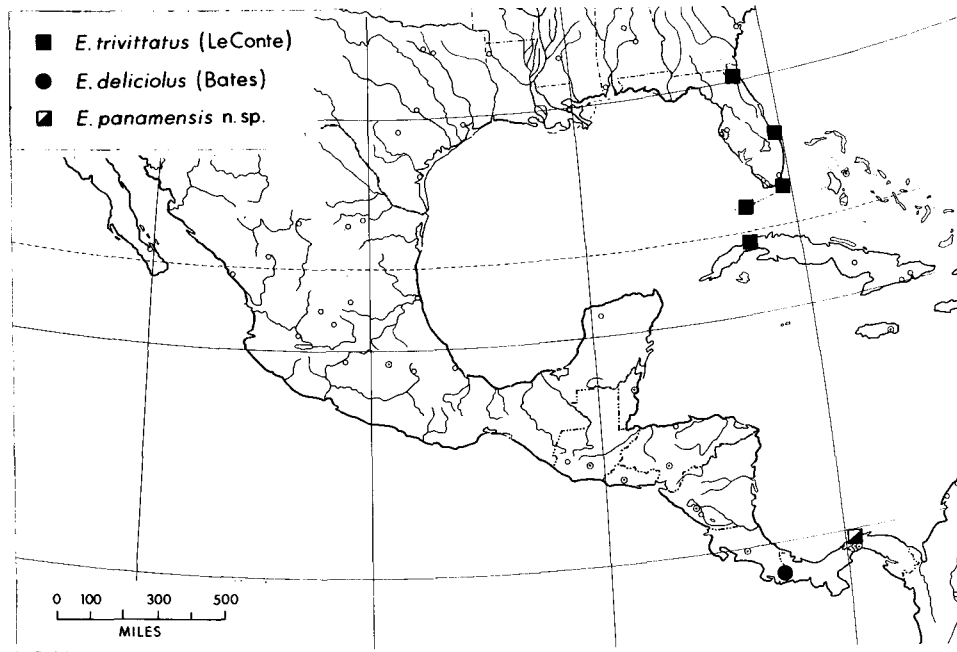
Map 3. Known distribution of *E. balli* new species, *E. sigillatus* (Bates), and *E. pallidus* new species.



Map 4. Known distribution of *E. abjectus* (Bates).



Map 5. Known distribution of *E. subdeletus* (Bates).



Map 6. Known distribution of *E. trivittatus* (LeConte), *E. deliciolus* (Bates), and *E. panamensis* new species.

Phylogenetic relationships.— Synapotypic features indicate that this species shared a common ancestry with the *E. sigillatus*-*E. pallidus* lineage (Fig. 77).

Material examined.— I examined 29 specimens, including types, and saw non-type material from the following localities:

MÉXICO (MNHB); **Sonora.** 2 & 4.5 km n Mesa de Tres Rios (UASM).

UNITED STATES Arizona. Cochise Co. Chiricahua M. (OUCO); Chiricahua Mts, Cave Cr. (CAS); Chir. Mts., w Turkey Crk. (SMC); Huachuca Mts., Copper Cn. (SMC). Collecting dates from March 23 to December 10.

Euproctinus sigillatus (Bates)

Figs. 16, 22, 77; Map 3

Euproctus sigillatus Bates, 1883: 196. Type material: LECTOTYPE (here selected) male, labelled: Type, H.T. [white disc ringed with red]; Juquila, Mexico, Hoege; B.C.A. Col. I.1., *Euproctus sigillatus*, Bates; *Euproctus sigillatus* Bates [handwritten (Bates)]; LECTOTYPE ♂, *Euproctinus sigillatus* Bts., By Erwin '76 (BMNH). Type locality: Juquila, state of Oaxaca, México.

Andrewesella sigillata; Csiki, 1932: 1456.— Blackwelder, 1944: 61.

Euproctinus sigillatus; Erwin *et al.*, 1977: 4.60.

Recognition.— Adults of this species are readily distinguished by the rufous to rufo-piceous markings of the elytra (Fig. 22).

Description.— Character states of the *sigillatus* group, and the following. Average SBL 5.95 mm (males) and 6.11 mm (females).

Color. Pale spots of elytron, legs, antennae, and mouthparts testaceous; pronotum and head rufous; markings of elytron rufous to rufo-piceous. Elytron (Fig. 22) with median fascia broad, diagonal; sutural and paralaral vitta broad, basal margin dark, apical margin pale; anterior and posterior discal spots of moderate size.

Prothorax. Pronotum (Fig. 16) with hind angles right.

Male genitalia. Flagellum about 2.6 times length of median lobe.

Notes about habitat.— A specimen was collected at one Mexican locality, at 1870 meters, at night, at u-v light, in a dry conifer-oak forest. Some adults of this species were taken from bromeliads and one at u-v and white light. Adults of this species were taken at elevations from near sea level (west coast of México) to 2160 meters.

Geographical distribution.— This species is known only from México (Map 3).

Chorological affinities.— The range of this species is overlapped by the ranges of *E. balli*, *E. abjectus*, and *E. subdeletus*.

Phylogenetic relationships.— Synapotypic features indicate that *E. sigillatus* is the sister-group of the *E. abjectus* and *E. subdeletus* lineages (Fig. 77).

Material examined.— I examined 23 specimens, including types, and saw non-type material from the following localities:

MÉXICO (MNHB); **Guerrero.** Chilapa (MNHB); **Jalisco.** Ajijic (UASM); Chapala, 6 mi w (UCBC); Puerto Vallarta (CNC); Mexico. 3 mi n Valle de Bravo (GHNC); **Morelos.** Cuernavaca (CUIC); Rte 115, nr Tejalpa (FSCA); **Nuevo Leon.** Chipinque Mesa, Monterrey (CNC); **Oaxaca.** 20 mi s Juchatengo (UASM); 21.8 mi n Juchatengo (UASM); Juquila (MNHB)(MNHP); 36.3 km n Oaxaca, Rte 190 (USNM); 115 mi s Oaxaca, Rte 131 (CNC); 10.5 km s San Pedro y San Pablo Ayutla (UASM); 56 mi nw Tehuantepec (UCBC); **Sinaloa.** 8 mi w El Palmito (UCBC). Collecting dates from March 23 to August 29.

Euproctinus abjectus (Bates)

Figs. 17, 23–25, 77; Map 4

Euproctus abjectus Bates, 1883: 196. Type material: LECTOTYPE (here selected) male, labelled: Type, H.T. [white disc ringed with red]; Almolonga, Mexico, Hoege; B.C.A. Col. I.1., *Euproctus abjectus*, Bates; *Euproctus abjectus* Bates [handwritten (Bates)]; LECTOTYPE ♂, *Euproctinus abjectus* Bts., By Erwin '76 (BMNH). Type locality: Almolonga, Veracruz, México.

Andrewesella abjecta; Csiki, 1932: 1456.— Blackwelder, 1944: 61.

Euproctinus abjectus; Erwin *et al.*, 1977: 4.60.

Euproctus texanus Wickham, 1897: 109, 110. NEW SYNONYMY. Type material: LECTOTYPE (here selected) female, labelled: Brownsville Texas Wickham; WICKHAM Collection 1933; *Euproctus texanus* type Wickh. [handwritten on label with red border] (USNM). Type locality: Brownsville, Texas, United States.— Leng, 1920: 66. *Andrewesella texana*; Csiki, 1932: 1456. *Euproctinus texanus*; Ball, 1960: 160.— Erwin *et al.*, 1977: 4.60.

Notes about type material.— Bates' description of *E. abjectus* listed several localities. The BMNH has four males and four females labelled the same as the lectotype (but without handwritten determination label), and are here selected as PARALECTOTYPES. The BMNH also has specimens from the following localities: Juquila (one male); Veracruz (one male); Soledad (one female); Cubilquitz (one male); and S. Geronimo (one female), and are here selected as PARALECTOTYPES. The latter three specimens bear handwritten determination labels (Bates'), and only the Soledad specimen is without a B.C.A. label.

The lectotype of *E. texanus* was collected by Wickham and bears a handwritten type label. Wickham did not give a locality or number of specimens seen. There are several other specimens with bear the same locality label. For these reasons, the specimen could not be designated as holotype. The USNM has four females labelled the same as the lectotype (months handwritten - one "VI", one "June", and two "July"), and are here selected as PARALECTOTYPES. The BMNH has one male labelled the same as the lectotype, with F.C. Bowditch Coll. label, and is here selected as PARALECTOTYPE. The MCZ has seven specimens, all labelled the same as the lectotype - two females with Roland Hayward Coll. label, two males and two females with Frederick Blanchard Collection label, and one female with F.C. Bowditch Coll. label, and are here selected as PARALECTOTYPES.

Note about synonymy.— The specimens described as *E. texanus* are the first and second forms as discussed in notes about variation. I believe them to be conspecific with *E. abjectus*.

Recognition.— Adults of this species are readily distinguished by their darker color and small to absent spots on the elytra (Figs. 23-25).

Description.— Character states of the *sigillatus* group and the following. Average SBL 4.51 mm (males) and 4.45 mm (females).

Color. Uniformly brown, with indistinct longitudinal spot on elytron, or with two testaceous spots on each elytron, (Figs. 23-25).

Prothorax. Pronotum (Fig. 17) with hind angles right; lateral grooves narrow.

Abdominal sterna. Sternum VI and VII each with several short setae laterally each side.

Male genitalia. Flagellum about 2.4 times length of median lobe.

Notes about habitat.— In México, collections were made between sea level and 2400 meters, in tropical deciduous forest at lower elevations, and in dry oak-mimosa forest at higher elevations. Specimens were collected at night, at u-v light; during the day, from bromeliads on oak trees; and during the day, from *Mimosa* shrubs, by beating. One specimen was taken in Baja California on *Nolina* (amaryllis). I collected this species in a dry valley in Oaxaca, México by beating *Mimosa*. In Texas, one specimen was taken on *Pithecolobium palens* (mimosa), and another on cotton.

Geographical distribution.— This species ranges from Guatemala north throughout México into southern California and Texas (Map 4).

Chorological affinities.— All of the species of *Neoeuproctus* found in México have been recorded from some of the states where this species is found.

Notes about variation.— This species is represented by three forms which differ from one another in color pattern: (1), unicolorous; (2), with an indistinct pale longitudinal spot in the basal half of the elytron; and (3), with two distinct pale spots on each elytron, the basal spot longitudinal, and the apical spot small, curved toward the suture. The third form is most distinctive, while the first two forms are nearly the same. A single specimen collected 3.5 miles

north of Ocosingo, Chiapas, México, has the posterior spot of each elytron extended anteriorly and slightly transversely so that the posterior and anterior spots nearly meet.

All three forms are represented in Bates' types. The specimen selected as lectotype is of the second form, while the specimen illustrated (Bates, 1883: pl. 7, Fig. 12) is of the third form. The third form is found only in the southern half of the range of this species. The first two forms appear to be equally distributed throughout the range of this species.

Phylogenetic relationships.— Synapotypic features indicate that this species and *E. subdeletus* are sister groups (Fig. 77).

Material examined.— I examined 365 specimens, including type material, and saw non-type material from the following localities:

GUATEMALA Cubilguitz (BMNH); S. Geronimo (BMNH).

MÉXICO (MNHB); **Baja California.** 2 mi e El Triunfo (UASM); 4 km e El Triunfo, Km 160 (CAS); 2 mi nw El Triunfo (UCBC); 1-2 km sw La Burrera (UASM); 3.7-5 km se La Huerta (UASM); 3.5 mi ne San Pedro (UCBC); 5.7 mi n San Pedro (UASM); 9.3 & 12.2 mi se San Perdido (CSCA); Santa Rosa (CAS); Santa Victoria (UASM); Sierra Laguna La Laguna, 17 air mi ene Todos Santos (UCBC); 14 mi n Todos Santos (CSCA); **Chiapas.** jctn Rtes 190 & 195 (CNC)(UASM); Chincultic, nr El Rincon (CNC); 14 mi sse Comitán (UCBC); 31 mi, se Comitán (TAMU); 32.5 mi e Comitán (UASM); El Chorreador, 5.5 mi e Chiapa de Corzo (UASM); El Rincon (UASM); 16.3 mi sw Las Cruces (UASM); Las Rosas (UCBC); Montebello (CNC); 3.5 mi n Ocosingo (UASM); 7 mi sw Ocozocuaula (UASM); **Colima.** Manzanillo (UASM); 15 mi nw Manzanillo (CSCA); **Guerrero.** Acapulco (BMNH); 2.5 mi ne Cacahuimilpa (TAMU); Iguala (UCBC); 8 mi n Iguala (CNC); 8 mi sw Iguala (TAMU); 10 & 19 mi n Mexcala (CNC); 5.3 km e Papanao, Rte. 200 (UASM); Petaquillas (UCBC); Rio Balsas (MCZ); **Hidalgo.** Pachuca (CAS); **Jalisco.** nr. Atenquique (TAMU); Est. Biol. Chamela (UCBC); Chapala (USNM); Chapala, 6 mi w (UCBC); Catalitlan (UASM); 3 mi ne Mazamitla (CSCA); Nevado de Colima road, 7 mi w hwy. jct. (TAMU); Puerto Vallarta (CAS); **México.** 4.3 mi ne Ixtapan (TAMU); Ixtapan de La Sal, Rte 55 (UASM); 3 mi n Valle de Bravo (GHNC); **Michoacan.** 5 mi e Apatzingan (UCBC); 9 mi s Cuartos Caminos (GHNC); 7 mi s Papazindan (OUCO); P.N. Morelos nr Morelia (USNM); **Morelos.** Cañon de Lobos, 9.1 mi e Cuernavaca (UASM); Cuernavaca (CAS); Tejalpa (FSCA)(UASM); Rte 115, nr Tejalpa (UASM); Tlaltizapan (MNHB); **Nayarit.** Jesus Maria (UCBC); La Mesa de Nayar (UCBC); 22 mi nw Tepic (UCBC); **Oaxaca.** El Camaron, 20 mi e Oaxaca (UCBC); 2.7 mi nw El Camaron (TAMU); 6 km e jct Rte 175 & Ixtepeji Rd (UASM); Juquila (BMNH)(MNHB); 16.2 km n Las Animas, Rte 195 (UASM); 14 mi s Matias Romero (TAMU); 8 mi s Miahuatlan (UASM); Oaxaca (CAS)(UASM); 10 km ne Oaxaca, Rte 175 (UASM); Rte 131, 70 km s Oaxaca, Rio de la Y, Km 20 w jct (CNC); Portillo del Rayo, Pochutla (CAS); 1 & 3 mi se Rio Hondo (TAMU); Tehuantepec (UCBC); 9 mi w Tehuantepec (TAMU); Valerio Trujano (CAS); Valle Nacional (MNHB); 32 mi s Valle Nacional (UASM); **Puebla.** Atlixco (CAS); **San Luis Potosi.** El Salto de Agua (CNC); **Sinaloa.** 6 mi s Culiacan (UCBC); La Guayanera, 32.9 mi ne Villa Union (CSCA); 2.5, 5, & 9 mi n Mazatlan (UCBC); 21 mi e Villa Union (CNC); **Sonora.** 7 mi w Alamos (UCBC); Tamaulipas. 17 mi s Linares, Nuevo Leon (TAMU); 1-2 mi e Nuevo Morelos (RTC); Rancho del Cielo, 8 mi w Gomez Farias (UASM); **Veracruz.** Almolonga (BMNH)(CAS)(MNHP); Cordoba (CAS)(USNM); 12 mi e Cordoba (GHNC); Cotaxtla Exp Sta, Cotaxtla (UCBC); Fortin de las Flores (FSCA)(UASM); Puente Nacional, 6 mi se Rinconada (UCBC); Rancho Clacotengo, ca 2-5 km n Fortin de las Flores (UASM); Soledad (BMNH); Tuxpan (CAS); Veracruz (BMNH); not mapped - Tepetlapa (MNHB).

UNITED STATES California. "So. Califa." (USNM); **Texas.** Burleson Co. Big Creek Park, Lake Somerville (TAMU); Cameron Co. (OUCO); Brownsville (BMNH)(CAS)(CNC)(CUIC) (GHNC)(MCZ)(USNM); 6 mi e Brownsville (TAMU); Esperanza Ranch, Brownsville (CAS)(USNM); La Paloma (USNM); Old Ft. Brown, Brownsville (CAS)(USNM); Sabal Palm Grove Sanct., nr Southmost (RTC)(UASM)(USNM); Hidalgo Co. (OUCO); Kleberg Co. Kingsville (TAIK); Velederos Creek (TAMU); San Patricio Co. Lake Corpus Christi State Park (GHNC); Welder Wildlife Refuge, 7 mi ne Sinton (UASM). Collecting dates from January 13 to December 21.

Euproctinus subdeletus (Bates)

Figs. 7, 9, 11, 18, 19, 26, 27, 67, 68, 70, 71, 73, 77; Map 5

Euproctus sudeletus Bates, 1883: 196. Type material: LECTOTYPE (here selected) male, labelled: Type, H.T. [white disc ringed with red]; Jalapa, Mexico, Hoege; B.C.A. Col. I.1., *Euproctus subdeletus*, Bates; *Euproctus subdeletus* Bates [handwritten (Bates')] (BMNH). Type locality: Jalapa, Veracruz, México.— Maindron, 1906: 200.

Andrewesella subdeleta; Csiki, 1932: 1456.— Liebke, 1939: 107.— Blackwelder, 1944: 61.

Euproctinus subdeletus; Erwin *et al.*, 1977: 4.60.

Andrewesella montana Liebke, 1939: 106, 107. NEW SYNONYMY. Type material: LECTOTYPE (here selected) female, labelled: San José de Costa Rica, Henry Schmidt leg. vend. 14.III.1911; Type [pink paper]; *Andrewesella montana* Lbk. Type, M. Liebke determ. [handwritten above type]; Mus. Zool. Polonicum, Warszawa 31/54; Inst.

Zool. P.A.N. Warszawa, Cotypus Nr. 1144 [red paper]; LECTOTYPE, *Andrewesella montana* LBK, By Erwin '76 (IZWP). Type locality: San José, Costa Rica.— Blackwelder, 1944: 61.
Euproctinus montana; Erwin *et al.*, 1977: 4.60.

Notes about type material.— Bates gave a second locality in his description of this species. The BMNH has one male labelled: Guatemala [handwritten]; Chinantla 4100 [handwritten]; B.C.A. Col. I.1., *Euproctus subdeletus*, Bates; and is here selected as PARALECTOTYPE.

Liebke stated he saw two specimens collected by H. Schmidt - one from La Caja, and a second from San José in Costa Rica. A second female specimen in IZWP bears a Liebke determination label with "Type" handwritten on it, as well as the red cotypus label (Nr. 1145) which the San José specimen has. However, this specimen was collected at San José by F. Nevermann. Therefore, this specimen cannot be included in the type series, even though it bears Liebke's determination label as described above.

Notes about synonymy.— I believe *A. montana* to be conspecific with *E. subdeletus*. The specimen described by Liebke does have broader elytral markings than do some of the specimens from México, but not broader than those with the broadest markings.

Recognition.— Specimens of this species are similar to those of *E. quadriplagiatus* in color pattern, but differ by lack of pronotal markings (Figs. 18-19).

Description.— Character states of the *sigillatus* group and the following. Average SBL 5.98 mm (males) and 6.24 mm (females).

Color. Dark testaceous, with rufo-testaceous head and pronotum, elytral markings (Figs. 26 and 27) rufo-testaceous to rufo-piceous (in some specimens the elytral markings are nearly absent). Elytron with median fascia diagonal, narrowed slightly (Fig. 27) to markedly (Fig. 26), sutural and paralateral vittae developed, parascutellar area and basal margin dark or pale, apical margin dark; discal spots closed, more (Fig. 26) or less (Fig. 27) extensively.

Male genitalia. Fig. 70. Flagellum about 2.6 times length of median lobe.

Notes about habitat.— In México, specimens were collected between 880 and 1520 meters. Specimens were collected from bromeliads in mesophytic montane forest, in eastern Veracruz. Others were taken at u-v light. In El Salvador, a single specimen was taken at 853 m. Six specimens were collected in Costa Rica on *Persea* (avocado).

Geographical distribution.— The range of this species extends from southern México to Panamá (Map 5).

Chorological affinities.— The range of this species is overlapped by the ranges of *E. balli*, *E. abjectus*, and *E. pallidus*. This species, *E. abjectus*, and *E. pallidus* have been taken at Fortin de las Flores, and nearby, in the state of Veracruz.

Notes about variation.— The narrow elytral pattern varies from rather "incomplete" (Fig. 26) to "complete" (Fig. 27) in México. Further south, the elytral markings are "complete", narrow to very broad.

Phylogenetic relationships.— See *E. abjectus*, above, and Fig. 77.

Material examined.— I examined 62 specimens, including types, and saw non-type material from the following localities:

COSTA RICA San Jose. 2 km s Colón (UASM); Irazu (USNM); San Jose (USNM); San Pedro de Montes de Oca (USNM).

EL SALVADOR San Salvador. S. Salvador (JNEG); Santa Ana. Santa Ana (USNM).

GUATEMALA Chianautla (BMNH).

MÉXICO (MNHB)(MNHP); **Chiapas**. 3.1 mi s Bochil, Rte 195 (UASM); 33.7 mi n Huixtla (UASM); 5.3 mi s Union Juarez (UASM); Volcan Tacana (UASM); **Durango**. (MNHB); Sierra de Durango (MNHP); **Oaxaca**. 92 mi s Oaxaca (CNC); **Queretaro**. 14 mi e Landa de Matamoros (TAMU); **Veracruz**. Almolonga (MNHP); Fortin de las Flores (UASM); 2 mi w Fortin de las Flores (UCBC); 10.4 mi sw Huatusco (UASM); Jalapa (BMNH)(MNHP); Rancho Clacotengo, 2-5 km n Fortin de las Flores (UASM); Texolo (CAS).

PANAMÁ ex C.Z., via Brownsville, Texas (USNM). Collecting dates from March 7 to December 21.

Note regarding localities.— The two Mexican localities from Durango are not mapped, as I believe this species is not found that far northwest in México. They may be from near México

City, as "Sierra de Durango" was previously used for localities near there.

Euproctinus pallidus new species

Figs. 20, 28, 77; Map 3

Type Material.— HOLOTYPE male, labelled: MEXICO: STATE OF, VERACRUZ, FORTIN DE LAS FLORES -, SUMIDERO: PLANTA DE LA CERVECERIA, ING, DANIEL RABAGO RES., ELEV.2500-3000 FT.; H. V. WEEMS, JR., COLL. AT LIGHT, 17-18 V 1965. (FSCA). ALLOTYPE female, labelled: MEXICO. Veracruz, Fortin de las Flores, 2900', 1.22.66, G.E. Ball family (USNM). Three additional PARATYPES, sex and label data as follows. Female: same as allotype (UASM). Female: MEX:Veracruz, Fortin de las Flores, VII-7 to 12-74, Elev.1010m; J.A.Chemsak, J.Powell, at lights (UCBC). Female: MEX. Veracruz Rte. 125 3.9 km ne Coscomatepec, acacias, in bromeliads, 1310 m. 78B-26 19.XII.78; MEXICAN EXP. 1978-1979, G.E. & K.E. Ball collectors (UASM).

Type locality.— Fortin de las Flores, in the state of Veracruz, México.

Recognition.— Adults of this species resemble general specimens of *E. subdeletus*, but can be readily distinguished by the characters given in the key.

Description.— Character states of the *sigillatus* group and the following. SBL 5.52 mm (male) and average SBL 5.40 mm (females).

Color. Elytra, legs, antennae and mouthparts testaceous; pronotum (Fig. 20) and head dark testaceous to rufo-testaceous. Elytron with only median fascia indicated as series of dark testaceous marks confined to interneurons, together in form of broken, narrow, diagonal line.

Abdominal sterna. Sternum VI with several short setae laterally each side; sternum VII with several shorter setae laterally each side.

Male genitalia. Flagellum about 2.4 times length of median lobe.

Notes about habitat.— In México, collections were made between 880 and 1310 meters. Specimens were collected in mesophytic montane forest zone, in eastern Veracruz, from bromeliads, and at light. One specimen was taken from a bromeliad growing on a large acacia tree, in a steep-sided, deep barranca.

Geographical distribution.— This species is known from the type locality and vicinity in the state of Veracruz, México (Map 3).

Chorological affinities.— The range of this species is overlapped by those of *E. abjectus* and *E. subdeletus*. Specimens of the latter two species have been collected at the type locality of *E. pallidus*.

Phylogenetic relationships.— Synapotypic features indicate that *E. pallidus* and the *E. sigillatus*-*E. subdeletus* lineage shared a common ancestry (Fig. 77).

Material examined.— I examined 5 specimens, including types.

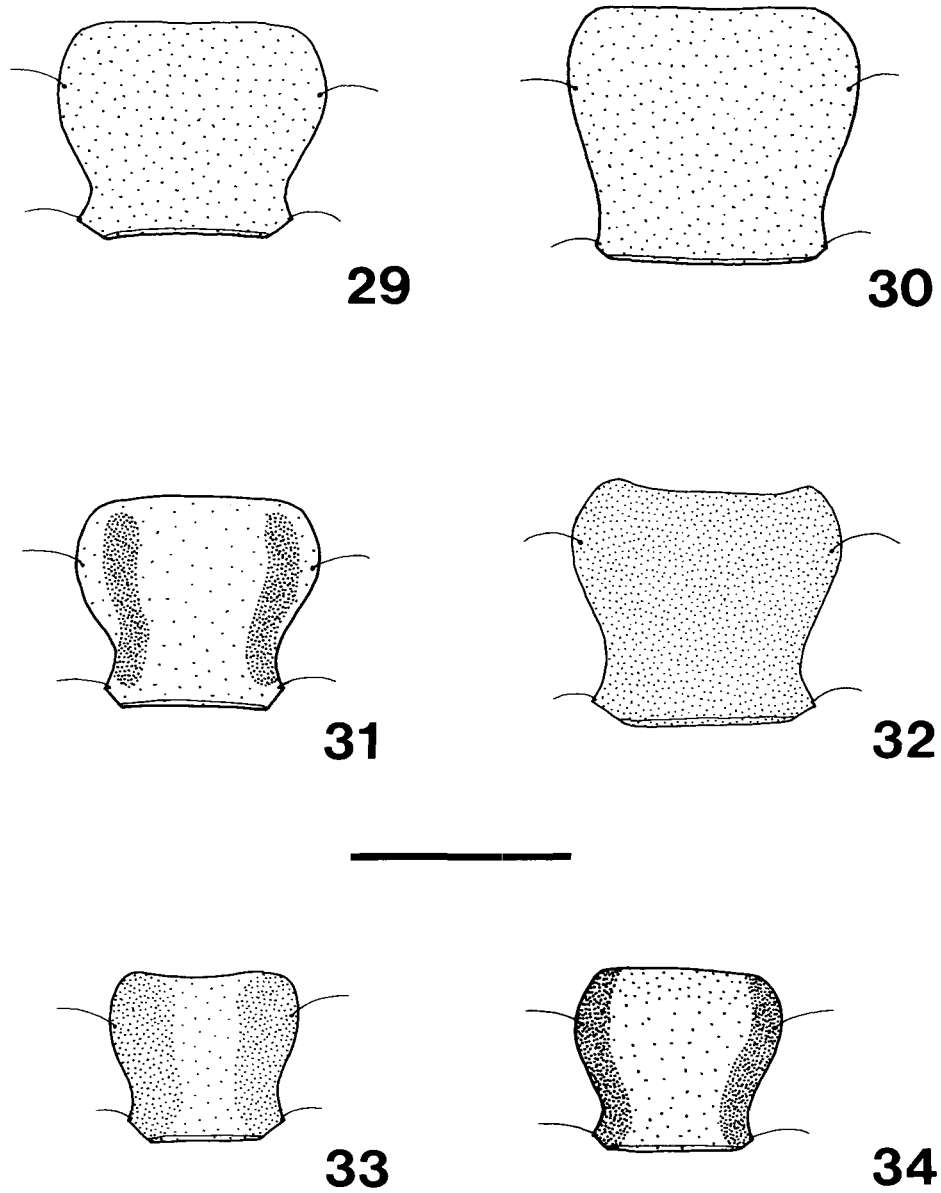
The *quadriplagiatus* group

This group has ten species which are characterized by the absence of an upper spur from the inner surface of the fore-tibia, one long seta each side on sternum VII, and sternum VI with one moderately long seta each side except where noted. The range of this group extends from Argentina to Florida and the Greater Antilles. Only two species, however, range as far north as México (Gulf versant, south of the Tropic of Cancer), and one species is isolated from the main range of the *quadriplagiatus* group, in Florida and Cuba.

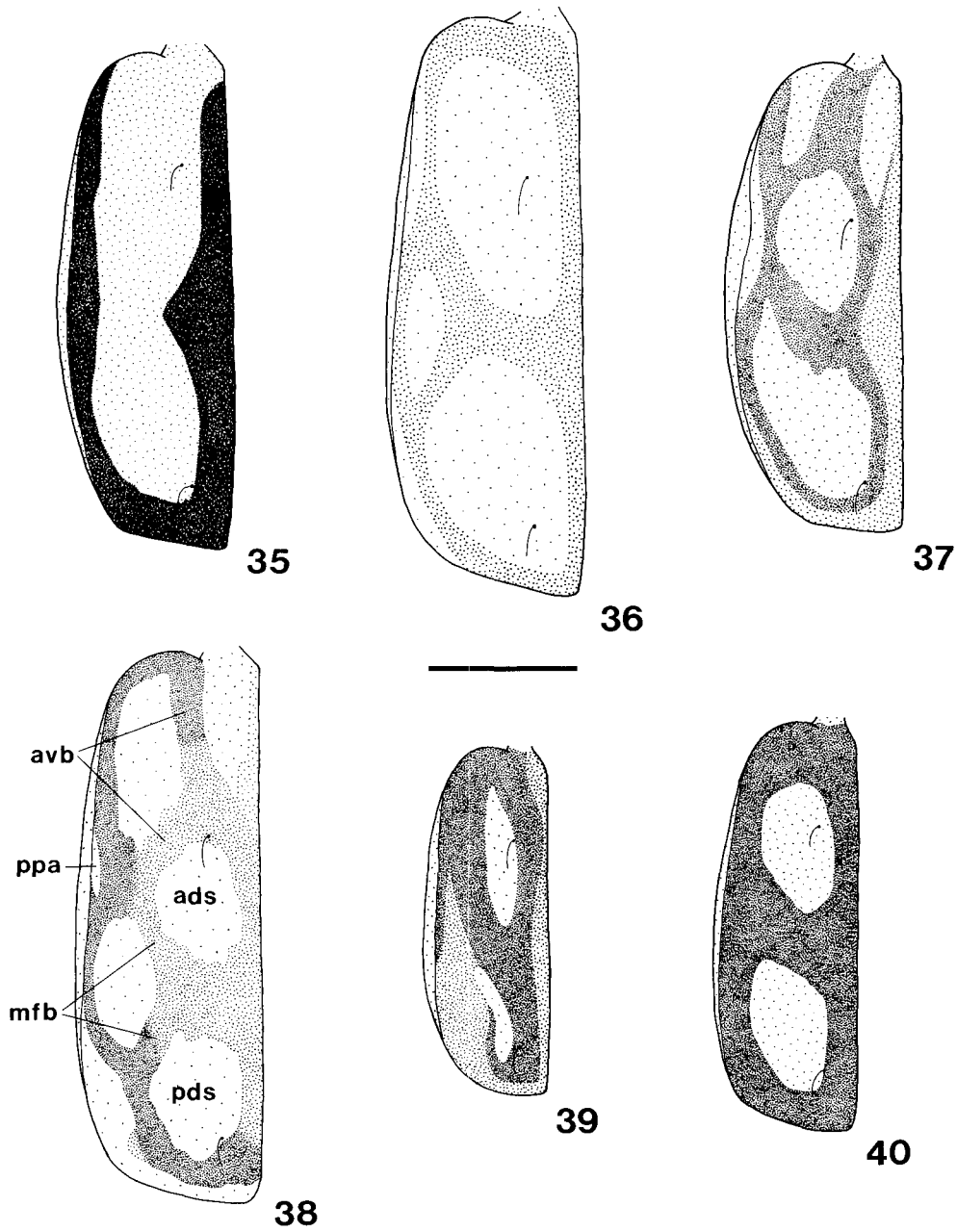
Euproctinus trivittatus (LeConte)

Figs. 29, 35, 77; Map 6

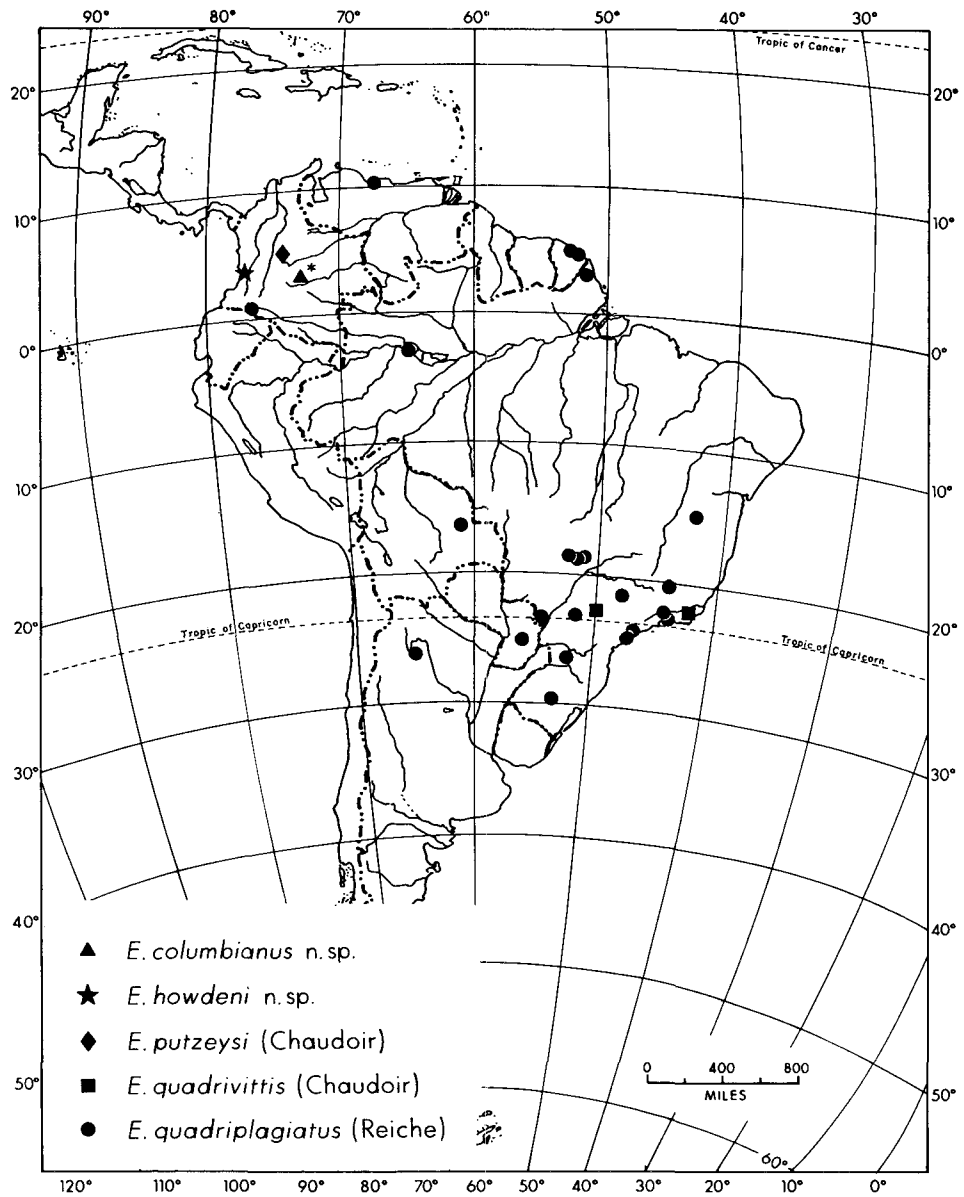
Onota trivittata LeConte, 1878: 373, 374. Type material: LECTOTYPE (here selected) female, labelled: Fla.; Type 5818 [red paper]; *Euproctus trivittatus* (LeC) [handwritten] (MCZ). Type locality: Ft. Capron, Florida, U.S.A.



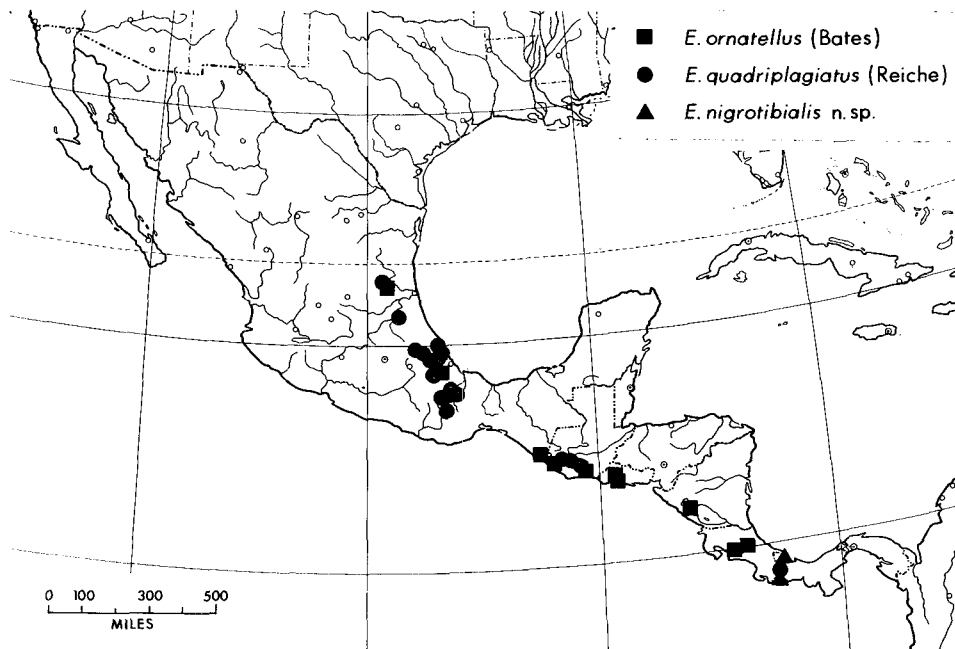
Figs. 29-34. Line drawings of pronota of *Euproctinus* species. Fig. 29. *E. trivittatus* (LeConte); Fig. 30. *E. columbianus* new species; Fig. 31. *E. howdeni* new species; Fig. 32. *E. putzeysi* (Chaudoir); Fig. 33. *E. quadrivittis* (Chaudoir); Fig. 34. *E. ornatellus* (Bates). Scale bar = 1 mm.



Figs. 35-40. Line drawings of left elytra of *Euproctinus* species. Fig. 35. *E. trivittatus* (LeConte); Fig. 36. *E. columbianus* new species; Fig. 37. *E. howdeni* new species; Fig. 38. *E. putzeysi* (Chaudoir); Fig. 39. *E. quadrivittis* (Chaudoir); Fig. 40. *E. ornatellus* (Bates). Scale bar = 1 mm. ads, anterior discal spot; avb, anterior vittal branches; mfb, median fascial branches; pds, posterior discal spot; ppa, pale paralateral area.



Map 7. Known distribution of *E. columbianus* new species, *E. howdeni* new species, *E. putzeysi* (Chaudoir), *E. quadrivittis* (Chaudoir), and *E. quadriplagiatus* (Reiche). (* Type locality of El Bergell, Colombia not located.)



Map 8. Known distribution of *E. ornatellus* (Bates), *E. quadriplagiatus* (Reiche), and *E. nigrotibialis* new species.

Euproctus trivittatus; Horn, 1891: 158.—1892: 138.—Wickham, 1897: 110.—Leng, 1920: 66.

Andrewesella trivittata; Csiki, 1932: 1456.—Darlington, 1934: 117.—Blackwelder, 1944: 61.

Euproctinus trivittatus; Ball, 1960: 160.—Larson, 1969: 80.—Erwin *et al.*, 1977: 4.60.—Erwin & Sims, 1984: 446.

Note about type material.—LeConte based his description of *Onota trivittata* on two specimens. His material is housed in the MCZ, and the first of two specimens bears an MCZ “type” label. This one has been selected as the lectotype, and the second, a male, labelled: Fla.; trivittatus 2 [handwritten] is here selected as **PARALECTOTYPE**.

Note about type locality.—Present-day Fort Pierce is approximately situated on the old locality of Fort Capron.

Recognition.—The trivittate elytral color pattern (Fig. 35) readily distinguishes adults of this species.

Description.—Character states of the *quadriplagiatus* group and the following. Average SBL 4.37 mm (males) and 4.58 mm (females).

Color. Rufo-testaceous with piceous elytral markings. Elytron with position of median fascia indicated by thickening of sutural vitta (Fig. 35), otherwise absent; sutural and paralaral vittae wide; parascutellar area and basal margin pale;

apical margin dark; discal spots connected, in form of broad, pale median vitta.

Prothorax. Pronotum (Fig. 29) with hind angles right; lateral grooves narrow.

Male genitalia. Flagellum about 1.8 times length of median lobe.

Notes about habitat.— The only available information is that most specimens were taken near sea level in coastal areas.

Geographical distribution.— This species is found throughout eastern Florida in the United States, and in Cuba (Map 6).

Chorological affinities.— No other species of *Euproctinus* have been recorded from Florida or Cuba.

Phylogenetic relationships.— This species forms a trichotomy with the ancestors of the *E. columbianus*-*E. putzeysi* and *E. quadrivittis*-*E. deliciolus* lineages (Fig. 77).

Material examined.— I examined 34 specimens, including types, and saw non-type material from the following localities:

CUBA Santa Maria del Mar ad Habana (IZWP); Santiago de las Vegas (MCZ).

UNITED STATES Florida. (MCZ); Duval Co. Jacksonville (USNM); Monroe Co. Key Largo (USNM); Key West (CAS)(USNM); St. Lucie Co. F. Capron (CAS)(MCZ)(USNM). Collecting dates from February 20 to May 31 in Florida, and July 1 to August 8 in Cuba.

Euproctinus columbianus new species

Figs. 30, 36, 77; Map 7

Type Material.— HOLOTYPE male, labelled: Columbien XI.96, El Bergell 1400m, Burger S. [on green paper]; Zool. Mus., Berlin (MNHB).

Type locality.— El Bergell, Colombia.

Note about type locality.— I could not locate the site of El Bergell on any maps. The type locality is probably an incorrect spelling of "El Vergel", which is used for numerous villages in Colombia.

Derivation of specific epithet.— Latinized name of the country in which this species is found.

Recognition.— This species is readily distinguished by the three pale spots on each elytron (Fig. 36).

Description.— Character states of the *quadriplagiatus* group and the following. SBL 6.04 mm (male).

Color. Pale spots of elytra testaceous; markings of elytra, dorsum of head and pronotum, legs, antennae and mouthparts rufous. Elytron (Fig. 36) with complex pattern: median fascia diagonal, forked laterally; sutural and paralaral vittae evident, basal and apical margins dark, parascutellar area narrowly pale; discal spots moderate in size, one secondary paralaral spot medially, and posterior paralaral pale area evident.

Prothorax. Pronotum (Fig. 30) narrower than head; hind angles obtuse; lateral grooves moderately wide.

Elytra. Interval 8 convex in apical one third.

Abdominal sterna. One pair of lateral setigerous punctures on sternum VI and VII. Setae absent, probably broken.

Male genitalia. Median lobe more elongate than typical for the subgenus; flagellum short, 0.75 length of median lobe (tip of flagellum blunt, not finely tapered as in males of other species of *Neoeuproctus*, probably broken).

Notes about habitat.— No information is available.

Geographical distribution.— This species is known only from the type locality in Colombia, indicated on Map 7 as a country record.

Chorological affinities.— This species, *E. howdeni* and *E. putzeysi* and *E. quadriplagiatus* are all recorded from different localities in Colombia.

Phylogenetic relationships.— Synapotypic features suggest that *E. columbianus* and the *E. howdeni*-*E. putzeysi* lineage shared a common ancestor (Fig. 77).

Material examined.— Holotype.

Euproctinus howdeni new species

Figs. 31, 37, 77; Map 7

Type Material.— HOLOTYPE female, labelled: 1200', Anchicaya Dam, 70 km.E.Buenaventura, Valle, Colombia, 11.20.1970.H.Howden. (USNM).

Type locality.— Anchicaya Dam and vicinity, 70 kilometers east of Buenaventura, Valle del Cauca department, Colombia.

Derivation of specific epithet.— This is based on the surname of Henry F. Howden, Dept. of Biology, Carleton University, Ottawa, Ontario, who collected the type specimen, as well as many other carabids that he has generously deposited in the Strickland Museum, University of Alberta.

Recognition.— This species is readily recognized by the numerous pale spots on each elytron (Fig. 37).

Description.— Character states of the *quadriplagiatus* group and the following. SBL 4.96 mm (female).

Color. Testaceous with brown pronotal (Fig. 31) and elytral markings. Elytron (Fig. 37) with complex pattern: vittae forked anteriorly, with dark line extended medially to basal margin; median fascia diagonal (posterior branch of fork probably lost); sutural and paralateral vittae irregular in outline; anterior discal spot rather small, posterior large, also two additional pale spots, one parascutellar, and one parahumeral; pale paralateral area evident; base mainly pale, apical margin dark.

Male genitalia. Unknown.

Notes about habitat.— The type locality, which has one of the highest rainfall records in South America, is largely primary rainforest (*pers. comm.* from H. Howden).

Geographical distribution.— This species is known only from the type locality in Colombia (Map 7).

Chorological affinities.— This species and its sister species *E. putzeysi*, as well as *E. columbianus* and *E. quadriplagiatus*, are all recorded from different localities in Colombia.

Phylogenetic relationships.— Synapotypic features suggest that *E. howdeni* and *E. putzeysi* are sister-groups (Fig. 77).

Material examined.— Holotype.

Euproctinus putzeysi (Chaudoir)

Figs. 32, 38, 77; Map 7

Euproctus putzeysi Chaudoir, 1872: 185, 186. Type material: HOLOTYPE male (beside handwritten box label from Chaudoir Coll. "Putzeysi, Chaud., Nouv. Grenada, Bogota, Putzeys"), labelled: TYPE [red paper]; Museum Paris, ex Coll. R. Oberthür [light green paper] (MNHP). Type locality: Santa Fe de Bogota, Colombia.

Andrewesella putzeysi; Csiki, 1932: 1456.— Blackwelder, 1944: 61.

Notes about type material.— The MNHP has a second male of this species with red "PARATYPE" and the light green collection labels. Chaudoir stated he had the sole specimen from Mr. Putzeys. Two specimens are labelled as belonging to the type series. Only one is valid. I accept the specimen with the "type" label as being the holotype.

Recognition.— Adults of this species are readily recognized by the elytral color pattern (Fig. 38).

Description.— Character states of the *quadriplagiatus* group and the following. SBL 5.56 mm (male).

Color. Pale spots of elytra testaceous; sutural spot, antennae, mouthparts, and legs dark testaceous; head and pronotum (Fig. 32) rufous; elytral markings rufous medially to rufo-piceous laterally. Elytron (Fig. 38) with complex pattern: vittae forked anteriorly, with two branches (avb), as in *E. howdeni* (*cf.* Fig. 37), and median fascia forked, as in *E. columbianus* (*cf.* Fig. 36); median fascia broad, slightly diagonal; sutural and paralateral vittae irregular; basal margin and parascutellar area dark, apical margin pale (probably secondarily so); discal spots reduced, two additional pale spots basad, one parahumeral (closed) and one parascutellar; additional paralateral spot medially; paralateral pale area small.

Abdominal sterna. Sternum VI with several moderately long setae laterally each side.

Male genitalia. Flagellum about 1.7 times length of median lobe.

Notes about habitat.— No information is available.

Geographical distribution.— This species is known only from the type locality, in Colombia (Map 7).

Chorological affinities.— See *E. howdeni* above.

Phylogenetic relationships.— See *E. howdeni* above and Fig. 77.

Material examined.— Holotype, and one specimen *ex* Oberthür Collection with no locality data (MNHP).

Euproctinus quadrivittis (Chaudoir)

Figs. 33, 39, 77; Map 7

Euproctus quadrivittis Chaudoir, 1872: 184, 185. Type material: HOLOTYPE male (beside handwritten box label from Chaudoir Coll. "quadrivittis Chaud, Bresil, Minas, Squires") labelled: TYPE [red paper]; Museum Paris, ex Coll R. Oberthür [light green paper] (MNHP). Type area: state of Rio de Janeiro, Brazil.

Andrewesella quadrivitta; Csiki, 1932: 1456.— Blackwelder, 1944: 61.

Recognition.— Adults of this species are readily distinguished by small size and elytral color pattern (Fig. 39).

Description.— Character states of the *quadriplagiatus* group and the following. SBL 3.68 mm (male) and 3.72 mm (female).

Color. Pale spots of elytron testaceous; antennae, mouthparts, and legs dark testaceous; head and pronotum (Fig. 33) brown to rufous, latter paler medially; elytral markings brown. Elytron (Fig. 39) with dark marks broad, including diagonal median fascia, sutural and paralaral vittae, basal and apical margins, and parascutellar area; discal spots narrow, elongate.

Male genitalia. Not studied.

Notes about habitat.— No information is available.

Geographical distribution.— This species is known only from the type locality and Orinhos in Brazil (Map 7).

Chorological affinities.— The range of this species is overlapped by that of *E. quadriplagiatus*.

Phylogenetic relationships.— This species forms a quadrichotomy with *E. ornatellus*, *E. quadriplagiatus*, and the ancestor of the *E. nigrotibialis*-*E. deliciolus* lineage (Fig. 77).

Material examined.— Holotype, and one specimen labelled:
BRAZIL São Paulo. FAZ D'ALHO ITU (MZSP). This locality is presently known as Ourinhos. Collecting date is January 22.

Euproctinus ornatellus (Bates)

Figs. 34, 40, 77; Map 8

Euproctus ornatellus Bates, 1883: 195. Type material: LECTOTYPE (here selected) female, labelled: Type, H.T. [white disc ringed with red]; Zapote, Guatemala, G.C. Champion; B.C.A. Col. I.I., *Euproctus ornatellus*, Bates; *Euproctus ornatellus* Bates [handwritten (Bates)]; LECTOTYPE ♀, *Euproctinus ornatellus* Bts., By Erwin '76 (BMNH). Type locality: Zapote, Guatemala.

Andrewesella ornatella; Csiki, 1932: 1456.— Blackwelder, 1944: 61.

Euproctinus ornatellus; Erwin *et al.*, 1977: 4.60.

Notes about type material.— The BMNH has the second specimen which Bates based his description of *E. ornatellus* on. This female specimen from El Reposo bears a handwritten (Bates') determination label as well as the B.C.A. Col. label, and is here selected as **PARALECTOTYPE**.

Recognition.— Adults of this species are readily recognized by the combination of small size and elytral pattern (Fig. 40).

Description.— Character states of the *quadriplagiatus* group and the following. Average SBL 4.53 mm (males) and 4.92 mm (females).

Color. Pale spots of elytron, legs, antennae, and mouthparts testaceous; pronotum and head testaceous to rufo-testaceous; markings of pronotum and elytra brown to rufo-piceous. Elytron (Fig. 40) with dark marks broad, including diagonal median fascia, sutural and paralateral vittae, basal and apical margins, and parascutellar area; discal spots closed, smaller than average.

Prothorax. Pronotum (Fig. 34) with hind angles right; lateral grooves narrow.

Abdominal sterna. Sternum VI without lateral setae (some pubescence only).

Male genitalia. Flagellum about 2.7 times the length of the median lobe.

Notes about habitat.— In México, collections were made at 365 to 915 meters. At the lowest elevation, one specimen was taken at night, at u-v light, in a palm forest. Adults of this species were collected in Guatemala at 240 meters and in El Salvador at 395 meters.

Geographical distribution.— The range of this species extends from east central México south to the western parts of Guatemala, El Salvador, Nicaragua, and Costa Rica (Map 8).

Chorological affinities.— This species and *E. quadriplagiatus* are recorded from Guatemala and San Luis Potosi and Veracruz in México.

Phylogenetic relationships.— See *E. quadrivittis* above and Fig. 77.

Material examined.— I examined 22 specimens, including types, and saw non-type material from the following localities:

COSTA RICA Alajuela. 6-8 km w Atenas (UASM); **San Jose**. La Caja, 8 km w San Jose (DEI); **Santa Clara**. Hamburg Farm (USNM).

EL SALVADOR La Libertad. Hidalgo Argentina (JNEG); 6 mi n La Libertad (USNM); Santa Tecla (USNM); **Morazan**. Perquin (JNEG); **San Salvador**. S. Salvador (JNEG).

GUATEMALA (MNHP); El Reposo (BMNH); Zapote (MNHP).

MÉXICO Chiapas. 20-25 mi n Huixtla (CNC); **San Luis Potosi**. 3.6 mi w El Naranjo (UASM); **Veracruz**. Fortin de las Flores (OUCO); Rio Metlec cyn., nw Fortin de las Flores (UCBC); **Yucatan**. Xcalacoop & 1 km s (RTC).

NICARAGUA Granada (USNM). Collecting dates from June 8 to October 1.

Euproctinus quadriplagiatus (Reiche)

Figs. 41–60, 77; Maps 7, 8

Dromius quadriplagiatus Reiche, 1842: 309, 310. Type material: HOLOTYPE (beside handwritten box label from Chaudoir Coll. “quadriplagiatus Reiche, Nouv Grenade, Coll Reiche”), labelled: TYPE [red paper]; *Dromius* [green paper]; *quadriplagiatus* Reiche, Rev. Cuv. 1842 309 [green paper]; Museum Paris, ex Coll R. Oberthür [green paper] (MNHP). Type area: Colombia.

Euproctus quadriplagiatus: Chaudoir, 1872: 183, 184.— Bates, 1883: 194.

Andrewesella quadriplagiata: Csiki, 1932: 1456.— Blackwelder, 1944: 61.

Euproctus xanthophaeus Chaudoir, 1872: 184. NEW SYNONYMY. Type material: HOLOTYPE (beside handwritten box label from Chaudoir Coll. “xanthophaea Chaud, Cayenne, Farnier”), labelled: TYPE [red paper]; Museum Paris, ex Coll R. Oberthür [light green paper] (MNHP). Type locality: Cayenne, French Guiana.

Andrewesella xanthophaea: Csiki, 1932: 1456.— Blackwelder, 1944: 61.

Euproctus fenestrellus Bates, 1883: 194, 195. NEW SYNONYMY. Type material, LECTOTYPE (here selected) male, labelled: Type, H.T. [white disc ringed with red]; Capetillo, Guatemala, G.C. Champion; B.C.A. Col. I.1., *Euproctus fenestrellus*, Bates; *Euproctus fenestrellus* Bates [handwritten (Bates)]; LECTOTYPE ♂, *Euproctinus fenestrellus* Bts., By Erwin '76 (BMNH). Type locality: Capetillo, Guatemala.

Andrewesella fenestrella: Csiki, 1932: 1456.— Blackwelder, 1944: 61.

Euproctinus fenestrellus: Erwin *et al.*, 1977: 4.60.

Euproctus metricus Bates, 1883: 196. NEW SYNONYMY. Type material: LECTOTYPE (here selected) male, labelled: Type, H.T. [white disc ringed with red]; Jalapa, Mexico, Hoegel; B.C.A. Col. I.1., *Euproctus metricus*, Bates; *Euproctus metricus* Bates [handwritten (Bates)]; LECTOTYPE ♂, *Euproctinus metricus* Bts., By Erwin '76 (BMNH). Type locality: Jalapa, Veracruz, México.

Andrewesella metrica: Csiki, 1932: 1456.— Blackwelder, 1944: 61.

Euproctinus metricus: Erwin *et al.*, 1977: 4.60.

Euproctus quadrinus Bates, 1883: 196. NEW SYNONYMY. Type material: HOLOTYPE female, labelled: Type, H.T.

[white disc ringed with red]; V. de Chiriqui, 2-3000 ft., Champion; B.C.A. Col. I.1., *Euproctus quadrinus*, Bates; No. 731, examined by Prof. Thaxter for, Laboulbeniaceae; *Euproctus quadrinus* Bates [handwritten (Bates')]; HOLOTYPE ♀, *Euproctinus quadrinus* Bts., By Erwin '76 (BMNH). Type locality: Volcan de Chiriqui, Panamá.
Andrewesella quadrina; Csiki, 1932: 1456.— Blackwelder, 1944: 61.
Euproctinus quadrinus; Erwin *et al.*, 1977: 4.60.

Notes about type material.— Bates gave several localities for *E. fenestrellus*. The BMNH has three female specimens as follows: one labelled Jalapa Mexico Hoege; B.C.A. Col. I.1., *Euproctus fenestrellus*, Bates; *Euproctus fenestrellus* var. [handwritten (Bates')]; one labelled Panajachel 5000 ft. Champion; B.C.A. Col. I.1., *Euproctus fenestrellus*, Bates; and one labelled Cerro Zunil 4-5000 ft. Champion; B.C.A. Col. I.1., *Euproctus fenestrellus*, Bates; ♀winged; ADP 22982; HOMOTYPE *Euproctinus fenestrellus* Bts.; all are here selected as PARALECTOTYPES. The specimen from Panajachel lacks its head and thorax.

As with his other descriptions, Bates also gave several localities for *E. metricus*. The BMNH has four males, one from Almolonga, and three from Jalapa. All bear the same B.C.A. Col. label as the lectotype. The second Jalapa specimen bears a third label - *Euproctus metricus* Bates [handwritten (Bates')]. The third Jalapa specimen has two other labels - ♂winged and HOMOTYPE *Euproctinus metricus* Bts. All four are here selected as PARALECTOTYPES. Also included in the type series from Jalapa, was a fourth specimen labelled same as the first, but is form A as discussed in notes about variation.

Notes about synonymy.— This species was the most difficult to diagnose due to the large number of separable forms. All of the forms previously associated with species names could be separated on the basis of elytral and pronotal color patterns. All forms have two enclosed pale spots on each elytron, and dark lateral margins of the pronotum. The spots vary in size and outline, as do the pronotal markings in length and width. I believe that this complex is one polymorphic species, and all these color forms are conspecific. The oldest available name is *E. quadriplagiatus* (Reiche), and all other names are junior synonyms.

Recognition.— Adults of this polymorphic species are similar to those of *E. ornatellus* where their ranges overlap, but are readily separated by the presence of a single long seta laterally on each side of sternum VI.

Description.— Character states of the *quadriplagiatus* group and the following. SBL 3.56-5.84 mm (males) and 3.92-5.96 mm (female).

Color. Pale spots of elytron, legs, antennae, and mouthparts testaceous to dark testaceous; pronotum and head testaceous to rufous; pronotal (Figs. 41-50) and elytral (Figs. 51-60) markings brown to piceous. Elytron with basic pattern as follows: median fascia of moderate width, diagonal; sutural and paralateral vittae developed; basal and apical margins and parascutellar area dark; discal spots closed, of moderate size.

Head. Antennomeres near quadrate to elongate.

Prothorax. Pronotum with hind angles right to obtuse; lateral grooves narrow to moderately wide.

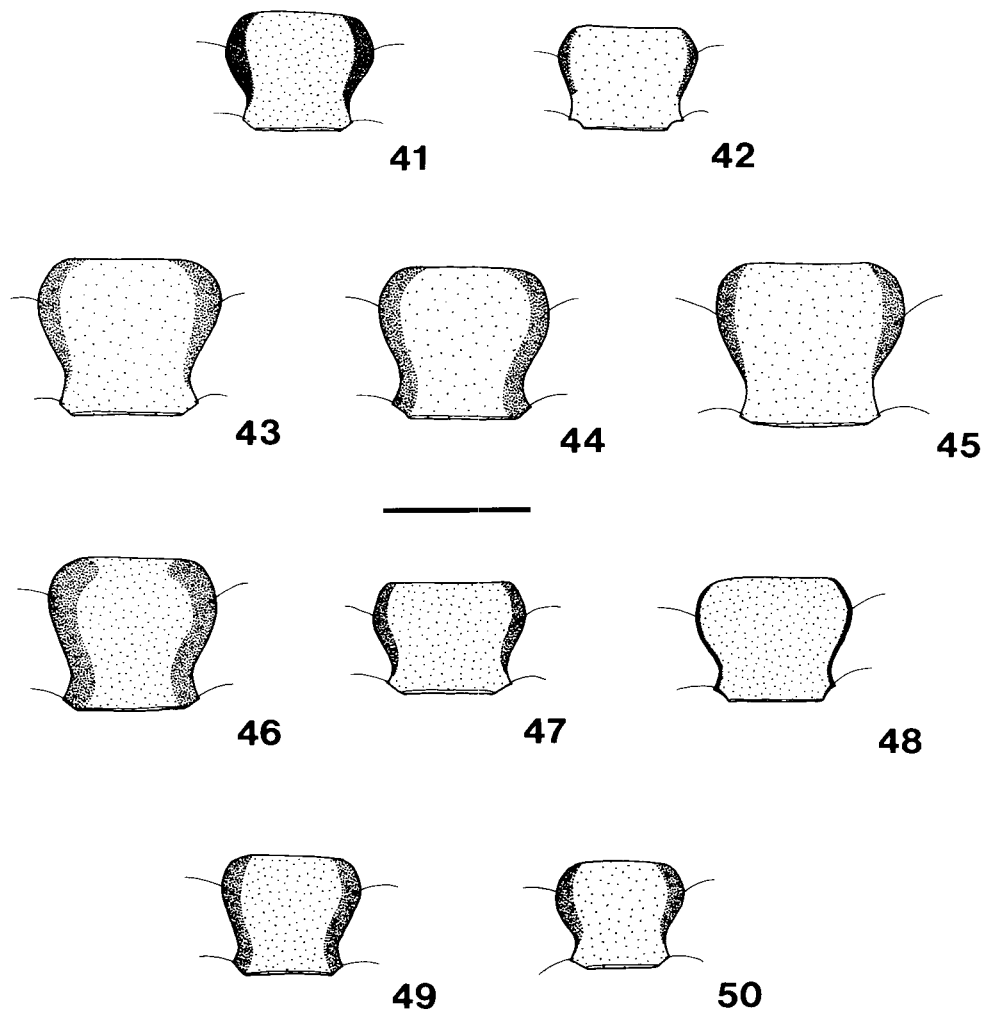
Male genitalia. Flagellum about 1.4 to 3.6 times the length of the median lobe (see notes about variation).

Notes about habitat.— One specimen was taken in Panamá by beating foliage. In México collections were made between 610 and 2240 meters, in mesophytic montane forest. One specimen was collected at u-v light, at night; and one in daylight, beaten from dead leaves on a standing tree. In Brazil and Venezuela specimens were taken at 700 and 1100 meters respectively.

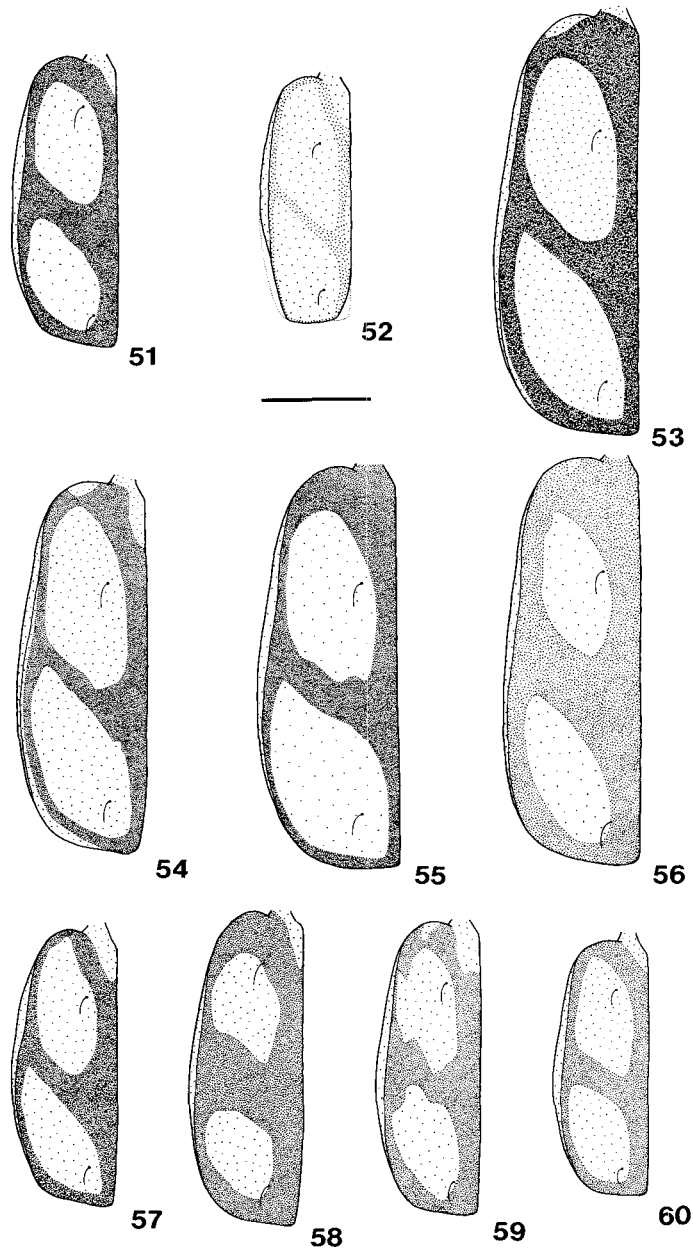
Geographical distribution.— The range of this species extends from northern Argentina and southern Brazil north to San Luis Potosi in México (Maps 7 and 8).

Chorological affinities.— The remaining species of the *quadriplagiatus* group, except for *E. trivittatus*, are found throughout the range of *E. quadriplagiatus* according to localities.

Notes about variation.— This highly variable species was separated into ten forms, based on elytral and pronotal color patterns, five of these previously described. The remaining five from the following localities will be referred to by letter: form A - México; form B - Colombia; form



Figs. 41-50. Line drawings of pronota of *E. quadriplagiatus* (Reiche). The following forms are discussed in the text under *E. quadriplagiatus* (Reiche). Fig. 41. *quadriplagiatus* form (specimen from Valle de Cauca, Colombia); Fig. 42. *xanthophaeus* form (specimen from Amapa, Brazil); Fig. 43. *fenestrellus* form (specimen from Veracruz, Mexico); Fig. 44. *metricus* form (specimen from Veracruz, Mexico); Fig. 45. *quadrinus* form (type of *Euproctus quadrinus* Bates, from Volcan de Chiriqui, Panamá); Fig. 46. form A (specimen from Oaxaca, Mexico); Fig. 47. form B (specimen from Santa Rosa, Colombia); Fig. 48. form C (specimen from Santa Catarina, Brazil); Fig. 49. form D (specimen from Santa Catarina, Brazil); Fig. 50. form E (specimen from unknown South American locality). Scale bar = 1 mm.



Figs. 51-60. Line drawings of left elytra of *E. quadriplagiatus* (Reiche). The following forms are discussed in the text under *E. quadriplagiatus* (Reiche). Fig. 51. *quadriplagiatus* form (specimen from Valle de Cauca, Colombia); Fig. 52. *xanthophaeus* form (specimen from Amapa, Brazil); Fig. 53. *fenestrellus* form (specimen from Veracruz, Mexico); Fig. 54. *metricus* form (specimen from Veracruz, Mexico); Fig. 55. *quadrinus* form (type of *Euproctus quadrinus* Bates, from Volcan de Chiriqui, Panamá); Fig. 56. form A (specimen from Oaxaca, Mexico); Fig. 57. form B (specimen from Santa Rosa, Colombia); Fig. 58. form C (specimen from Santa Catarina, Brazil); Fig. 59. form D (specimen from Santa Catarina, Brazil); Fig. 60. form E (specimen from unknown South American locality). Scale bar = 1 mm.

C - Brazil; form D - Brazil; and form E - unknown South American locality. The largest SBL is found in the *fenestrellus* form, and the smallest SBL in the *xanthophaeus* form. The broadest pronotal markings are found in the *metricus* form (Fig. 44) and form A (Fig. 46). The narrowest pronotal markings (confined to the lateral bead) are found in form C (Fig. 58). The broadest elytral markings are found in form A (Fig. 56) and form C (Fig. 58). The *xanthophaeus* form has the narrowest elytral markings (Fig. 52). Form D has an uneven border to the pale spots of the elytron (Fig. 59).

Also, some variation was noted in the length of the flagellum of the male genitalia. Forms are followed by the length of the flagellum compared to the length of the median lobe: *quadriplagiatus* (2.8X); *xanthophaeus* (none available); *fenestrellus* (1.9X); *metricus* (1.4X); *quadrinus* (2.3X); form A (2.1X); form B (male unknown); form C (2.7X); form D (3.6X); and form E (3.0X).

Specimens and population samples are too few to form the basis for a more detailed analysis of variation.

Phylogenetic relationships.— See *E. quadrivittis* above and Fig. 77.

Material examined.— I examined 165 specimens, including types, and saw non-type material from the following localities:

ARGENTINA Tucuman. Los Vasques (MNHP).

BOLIVIA Santa Cruz. Ñuño de Chavez (JNEG).

BRAZIL Amapa. Serro Lombard, Limao (USNM); Amazonas. Tefé (MNHP); Bahia. San Antonio da Barra (JNEG)(MNHP)(This locality is presently known as Condueba); San Antonio de Barra (MNHP); Goiás. Jatahy (MNHP); Mineiro (MNHP); Rio Verde(MNHP); Mato Grosso. (MNHP); R. Caraguata (MCZ); Minas Gerais. Caraca (MNHP); Parana. Londrina (MCZ); Serro do Mar (UASM); Rio de Janeiro. Itatiaya (BMNH); Petrop(MNHB); Rio Grande do Sul. (ZSMG); Santa Catarina. Nova Teutonia (CAS)(JNEG)(MCZ)(USNM)(ZSMG); São Paulo. Alto da Serra (MNHB); S. Paulo (USNM); Val. du Rio Pardo (MNHP).

COLOMBIA Santa Rosa (Kofan Indian Village) headwaters of Rio San Miquel, Int. Putomayo (UASM); Valle de Cauca. Valle Rio Jamundi, nr. Cali (CNC).

EL SALVADOR Santa Ana. Fripinio (JNEG).

FRENCH GUIANA Roches de Kourou (MNHP).

GUATEMALA (MNHP); Capetillo (BMNH); Cerro Zunil (MNHP); El Reposo (BMNH); Panajachel (BMNH); Zapote (MNHP).

MÉXICO Hidalgo. 3.2 km n Tlanchinol, Rte. 105 (UASM); Oaxaca. 24.5 km e Teotitlan, Puerto de Soledad (UASM); 15 & 32 mi s Valle Nacional (UASM); 32 mi s Valle Nacional (CNC); Puebla. 6 & 15 mi e Teziutlan (CNC); San Luis Potosí. 1 km e Las Abritas, Rte. 80 (DAMA); Veracruz. Almolonga (BMNH); Jalapa (BMNH)(MNHP); Jico (MNHB); 11 mi s Misantla (TA&M); 5 mi w Orizaba (CNC); Texelo (CAS).

PANAMÁ Chiriquí. 2 km s Hato de Volvan (USNM).

PARAGUAY (MNHP).

VENEZUELA Aragua. Rancho Grande (MNHL)(USNM). Collecting dates are March 21 to October 1 for the northern hemisphere, and June to March 28 for the southern hemisphere.

Euproctinus nigrotibialis new species

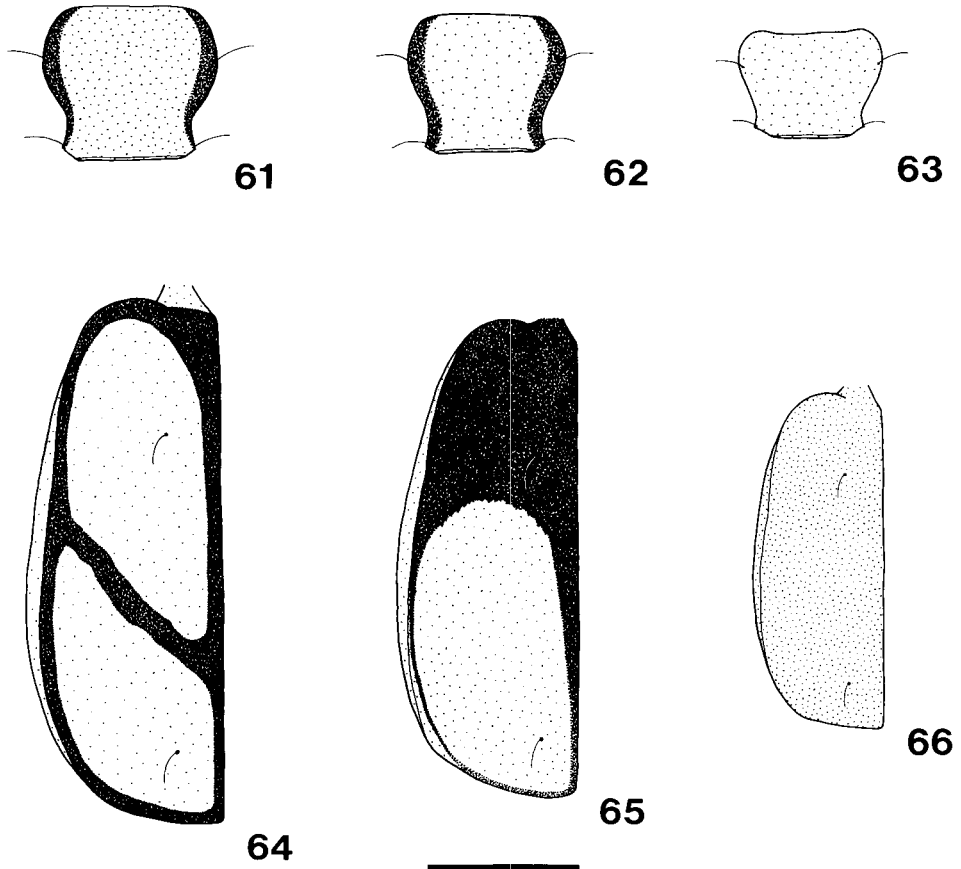
Figs. 61, 64, 77; Map 8

Type Material.— HOLOTYPE female, labelled: PANAMA. Bocas del Toro. 0.5- 1.0 km SW Almirante, 9°17'N-82°24'W, 04 July 1974; T.L.Erwin, D.R. Whitehead colls. beating, tree blossoms; ♀/wing; ADP 25707; Expedition #71, in notebook #3 (USNM). PARATYPE: one female labelled: Trinidad Riv, Pan., 8.VI.12, August Busck; *Euproctinus fenestrellus* Bates [handwritten]; ♀/wing, ADP 08665; eup 1 [yellow paper] (USNM).

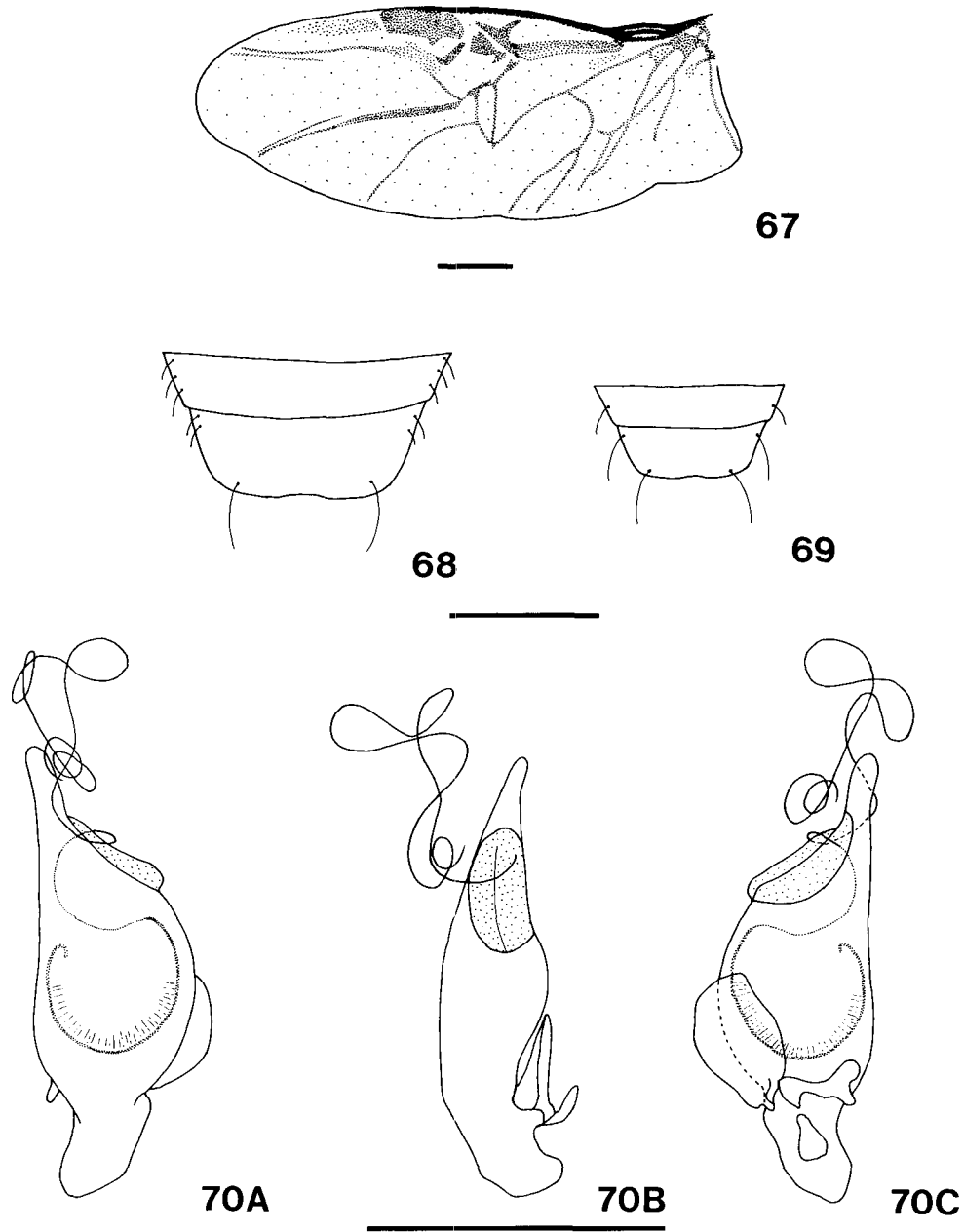
Type locality.— Vicinity of Almirante, Bocas del Toro province, Panamá.

Derivation of specific epithet.— From Latin, “*niger*”, and “*tibia*”, in allusion to the black tibiae which characterize this species.

Recognition.— The adults of this species are the only ones in *Euproctinus* which have black tibiae.



Figs. 61-66. Line drawings of pronota and left elytra of *Euproctinus* species. Figs. 61 and 64. *E. nigrotibialis* new species; Figs. 62 and 65. *E. deliciolus* (Bates); Figs. 63 and 66. *E. panamensis* new species. Scale bar = 1 mm.



Figs. 67-70. Line drawings of structures of *Euproctinus* species. Fig. 67. Left hind wing of *E. subdeletus* (Bates); Figs. 68 and 69. Sternum VI and VII of *E. subdeletus* (Bates) and *E. panamensis* new species, respectively; Fig. 70. Male genitalia of *E. subdeletus* (Bates), A, dorsal aspect, B, left lateral aspect, C, ventral aspect. Scale bar=1 mm.

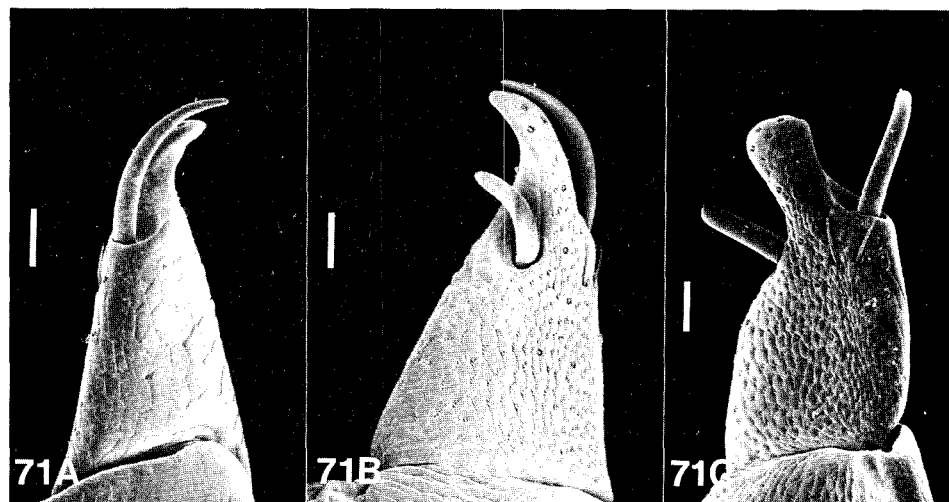


Fig. 71. SEM photographs of ovipositor, left stylomere of *E. subdeletus* (Bates). A, medial aspect; B, lateral aspect; C, ventral aspect. Scale bars = 20 μ m.

Description.— Character states of the *quadriplagiatus* group and the following. Average SBL 5.28 mm (females).

Color. Pale spots of elytron, femora, tarsomeres, antennae, and mouthparts testaceous; pronotum and head rufous; pronotal (Fig. 61) and elytral (Fig. 64) markings and tibiae black. Elytron (Fig. 64) with dark marks slender; median fascia diagonal; vittae evident, basal and apical margins and parascutellar area dark; discal spots closed, but extensive.

Male genitalia. Unknown.

Notes about habitat.— The holotype was taken by beating tree blossoms.

Geographical distribution.— This species is known only from Panamá (Map 8).

Chorological affinities.— This species and its sister species *E. deliciolus*, as well as *E. quadriplagiatus* and *E. panamensis*, are all recorded from Panamá.

Phylogenetic relationships.— Synapotypic features suggest that *E. nigrotibialis* and *E. deliciolus* are sister-groups (Fig. 77).

Material examined.— Holotype and paratype. Collecting dates are June 8 and July 4.

Euproctinus deliciolus (Bates)

Figs. 62, 65, 77; Map 6

Euproctus deliciolus Bates, 1883: 195, 196. Type material: HOLOTYPE female, labelled: Type, H.T. [white disc ringed with red]; V. de Chiriqui, 25-4000 ft., Champion; B.C.A. Col. I.1., *Euproctus deliciolus*, Bates; No. 730, examined by Prof. Thaxter for, Laboulbeniaceae; *Euproctus deliciolus* Bates [handwritten (Bates')]; HOLOTYPE δ , *Euproctinus deliciolus* Bts., By Erwin '76 (BMNH). Type locality: Volcan de Chiriqui, Panamá.

Andrewesella deliciola; Csiki, 1932: 1456.— Blackwelder, 1944: 61.

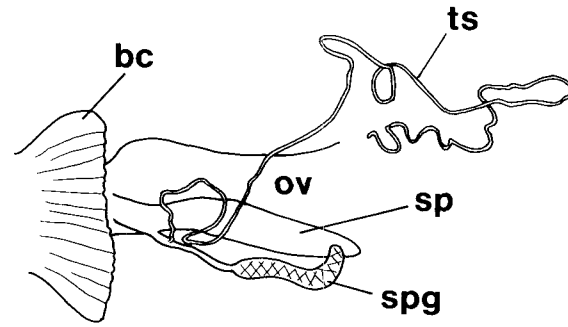
Euproctinus deliciolus; Erwin *et al.*, 1977: 4.60.

Recognition.— This species is readily distinguished by the large pale spot in the apical half of each elytron (Fig. 65).

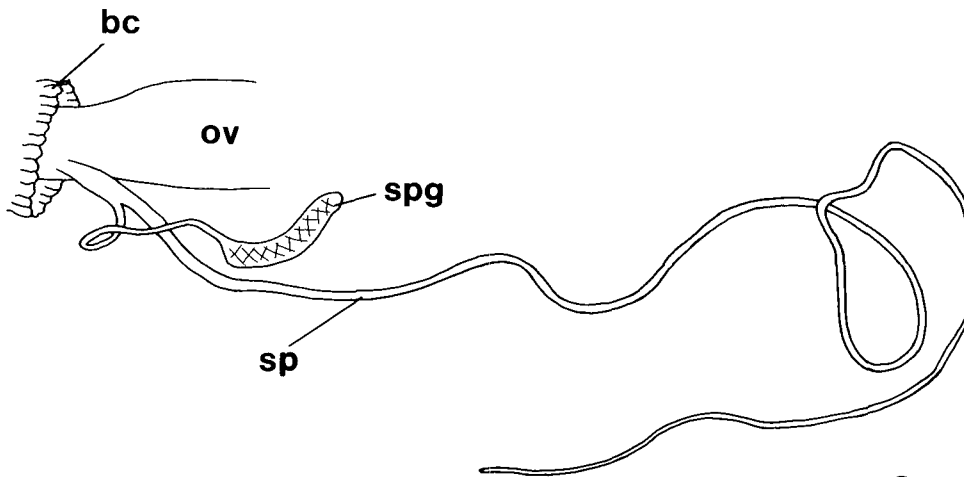
Description.— Character states of the *quadriplagiatus* group and the following. SBL 4.80 mm (female type).

Color. Testaceous with piceous pronotal (Fig. 62) and elytral markings. Elytron (Fig. 64) with basal area uniformly dark; without median fascia; sutural and parolateral vittae slender posteriorly; apical margin dark; pale area of disc probably comprised of extended posterior and reduced anterior spots.

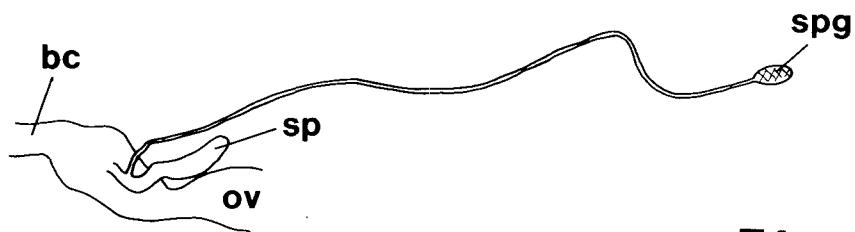
Abdominal sterna. Sternum VI without lateral setae (I was unable to determine if a lateral setigerous puncture was present or not, as the type is carded).



72



73



74

Figs. 72-74. Female reproductive tract of selected genera. Fig. 72. *Parena n. nipponensis* Habu; Fig. 73. *E. subdeletus* (Bates); Fig. 74. *Gallerucidia erotyloides* Bates. Scale bar = 1 mm. bc, bursa copulatrix; ov, oviduct; sp, spermatheca; spg, spermathecal gland; ts, tubular sac.

Male genitalia. Unknown.

Notes about habitat.— No information is available.

Geographical distribution.— This species is known only from the type locality in Panamá (Map 6).

Chorological affinities.— See *E. nigrotibialis* above.

Phylogenetic relationships.— See *E. nigrotibialis* above and Fig. 77.

Material examined.— Holotype.

Euproctinus panamensis new species

Figs. 63, 66, 69, 77; Map 6

Type Material.— HOLOTYPE, male, labelled: PortoBello, PanMar 14.11, AugustBusck; ♀/wing: ADP 08685, eup 6 [yellow paper] (USNM). ALLOTYPE female, labelled: PortoBello, PanMar 14.11 ♀/wing: ADP 08686 (USNM).

Type locality.— Porto Bello, Colon, Panamá.

Derivation of specific epithet.— Latinized name of the country in which this species is found.

Recognition.— This species is readily recognized by its flavous color, lack of elytral markings (Fig. 66), and near quadrate antennomeres.

Description.— Character states of the *quadriplagiatus* group and the following. SBL 3.48 mm (male) and 3.64 mm (female).

Color. Uniformly flavous.

Head. Antennomeres near quadrate.

Prothorax. Pronotum (Fig. 63) as wide or slightly wider than head.

Male genitalia. Flagellum about 2.6 times length of median lobe.

Notes about habitat.— No information is available.

Geographical distribution.— This species is known only from the type locality in Panamá (Map 6).

Chorological affinities.— See *E. nigrotibialis* above.

Phylogenetic relationships.— Synapotypic features indicate that this species shared a common ancestry with the *E. trivittatus*-*E. deliciolus* lineage (Fig. 77).

Material examined.— Holotype and allotype.

SPECIES INCERTAE SEDIS

Euproctinus baeri (Maindron)

Map 2

Euproctus baeri Maindron, 1906: 200. Type material: Type locality: Grau (Tumbez), Peru.

Andrewesella baeri; Csiki, 1932: 1456.— Blackwelder, 1944: 61.

Note regarding type.— The Maindron collection is in Paris. In the collection, a labelled space has been left for this species. There is neither a specimen nor a pinhole in the box bottom.

I believe that the type is not a *Euproctinus* even though the work of Maindron appears to have been reasonably accurate. Maindron states in his description that the specimen looks like one of *Calleida*, which is what I believe it is. Also, none of the *Euproctinus* species are metallic. Until the type can be located, this species will remain *incertae sedis*. Regardless, the type locality is indicated on Map 2.

Checklist of Species of *Euproctinus*²

- fasciatus Solier, 1848: 132. Argentina, Chile
kuscheli Straneo, 1969: 970, 971
balli, new species. Mexico, USA
sigillatus Bates, 1883: 196. Mexico
abjectus Bates, 1883: 196. Guatemala, Mexico, USA
texanus Wickham, 1897: 109, 110
subdeletus Bates, 1883: 196. Costa Rica, El Salvador, Guatemala, México,
Panamá
montanus Liebke, 1939: 106, 107
pallidus, new species. México
trivittatus LeConte, 1878: 373, 374. Cuba, USA
columbianus, new species. Colombia
howdeni, new species. Colombia
putzeysi Chaudoir, 1872: 185, 186. Colombia
quadrivittis Chaudoir, 1872: 184, 185. Brazil
ornatellus Bates, 1883: 195. Costa Rica, El Salvador, Guatemala, México,
Nicaragua
quadriplagiatus Reiche, 1842: 309, 310. El Salvador, Guatemala, México,
Panamá, South America
xanthophaeus Chaudoir, 1872: 184
fenestrellus Bates, 1883: 194, 195
metricus Bates, 1883: 196
quadrinus Bates, 1883: 196
nigrotibialis, new species. Panamá
deliciolus Bates, 1883: 195, 196. Panamá
panamensis, new species. Panamá

RECONSTRUCTED PHYLOGENY³

In this section, based on structural features, we offer a reconstructed phylogeny of the genera of the subtribe Metallicina and of the species of *Euproctinus*. Such inferences of relationships are used in conjunction with chorological data and zoogeographic theory to reconstruct the geographical history of the metallicine genera and the species of *Euproctinus*.

Phylogenetic Analysis of Structural Features – Genera of the Metallicina

Methods.— Characters used in the phylogenetic analysis were polarized on the basis of out-group comparison (Wiley, 1981: 139-146), using the ancestral lebiine Subtribe Celaenephina (Shpeley *et al.*, 1985) as out-group. Comparisons were also made with the subtribes Calleidina and Gallerucidiina, the other main groups included in the calleidine assemblage by previous authors (see Ball and Hilchie, 1983).

²Synonyms in italics

³This section was prepared jointly by George E. Ball and Danny Shpeley.

TABLE 1
 CHARACTERS AND PHYLOGENETIC DESIGNATION OF CHARACTER STATES FOR TAXA OF SUBTRIBES CELAENEPHINA,
 METALLICINA, CALLEIDINA, AND GALLERUCIDIINA

NO.	CHARACTER	CHARACTER STATES AND DESIGNATIONS	
		PLESIOTYPIC	APOTYPIC
01.	Left mand.: ant. ret. tooth	absent	present
02.	Ant. 5-11: sensory pits, ventral	absent	present
03.	Ovip.: stylomere 2, basal lobe	long	A. short B. absent (loss)
04.	Mand.: ventral groove	long	short
05.	Tergum VIII: extent sclerotization	sclerotized medially	A. lateral scl. area moderately extensive B. lateral scl. area reduced, medial memb. area more extensive
06.	Ovip: stylomere 2, no. ensiform setae	3 or more, (1 dorso-medial, 2 or more, dorso-lateral)	A. 2 (1 dorso-medial, 1 dorso-lateral) B. 5, or more (2 or more dorso-medial, 2 or more dorso-lat.) C. absent (loss)

(continued on next page)

Table 1 (continued)

NO.	CHARACTER	CHARACTER STATES AND DESIGNATIONS	
		PLESIOTYPIC	APOTYPIC
07.	Mid-leg: male tarsomeres, adhesive vestiture	absent	A. biseriate row B. single row C. absent (loss)
08.	Labium: paraglossa, extent sclerot.	unsc., membranous	sclerotized
09.	Labium: glossal sclerite, no. setae at apex	2	4 or more
10.	Tarsomere 4: form	apex slightly emarginate	A. bilobed B. apex only slightly emarg. (loss)
11.	Head: suborbital setae	absent	A. present B. absent (loss)
12.	Ant. pedicel, carina/depression	absent	A. present B. absent (loss)

(continued on next page)

Table 1 (continued)

NO.	CHARACTER	CHARACTER STATES AND DESIGNATIONS	
		PLESIOTYPIC	APOTYPIC
13.	Ovip.: stylomere 2, apex	rounded to pointed, w/o apical trichoid setae	A. broadly rounded, with apical trichoid setae B. membranous, aetose C. markedly reduced (loss)
14.	Ant. 5-11: sensory pits, dorsal	absent	A. present B. absent (loss)
15.	Right mand.: retinacular ridge	prominent	reduced
16.	Max.: lacinia, inner surface	smooth	lobed
17.	Mandible: ventral groove	long	short
18.	Male gen.: copulatory piece	absent	A. not flagellum-like B. flagellum-like
19.	Labium: palpiger, seta	absent	present
20.	Male gen.: flagellum length	short, less than length of median lobe	longer than length of median lobe

(continued on next page)

Table 1 (continued)

NO.	CHARACTER	CHARACTER STATES AND DESIGNATIONS	
		PLESIOTYPIC	APOTYPIC
21.	Spermatheca: length	short, ca. length of spermathecal gland w/duct	much longer than spermathecal gland w/duct
22.	Bursa copulatrix: armature	absent	present
23.	Fore tibia: upper spur	present	absent
24.	Pronotum: setae, laterally	two pairs	one pair

		Celaenephina				Metallicina		Calleidina		Galleruciina
		Celaenephes	Parena	Metallica	Pachycallida	Euproctrius	Neoeup			Gallerucida
24	pronotum, # lateral setae									
23	foretibia, upper spur									
22	bursa copulatrix armature									
21	spermatheca, length									
20	♂ genitalia, length flagellum	NA								NA
19	labium, seta, labial paliger									
18	♂ genitalia, copulatory piece		A			B	B		A	
17	mandibles, ventral groove					A	A			
16	lacinia, inner surface									
15	mandibles, retinacular ridge		A	A	A					
14	ant., sensory pits, dorsal		A	B	A					
13	stylomere 2, form of apex		C	B	B				A	A
12	ant. pedicel, carina, depression		A	A	A	B	A			
11	head, suborbital setae		A,B	A	A	B	A			A
10	tarsomere IV, form		A	A	A	A	A		A,B	A
9	labium, # setae, apex gloss. scler.									
8	labium, paraglossae, sclerotization									
7	middle leg, adhesive vestiture		A	B	C	B	B	A,B		A
6	stylomere 2, # ensiform setae		B	C	A	A	A	C		C
5	tergum VIII, ext. sclerotization		A	A	A	A	A	B		B
4	mandibles, ventral secretory groove									
3	stylomere 2, general form	B	B	B	A	B	B	B		B
2	ant., sensory pits, ventral									
1	left mand., ant. ret. tooth									

LEGEND

Character States : plesiotypic apotypic, single state apotypic, multiple state

Fig. 75. Phylogenetic classification and distribution of character states of Celaenephina, Metallicina, Calleidina, and Galleruciina.

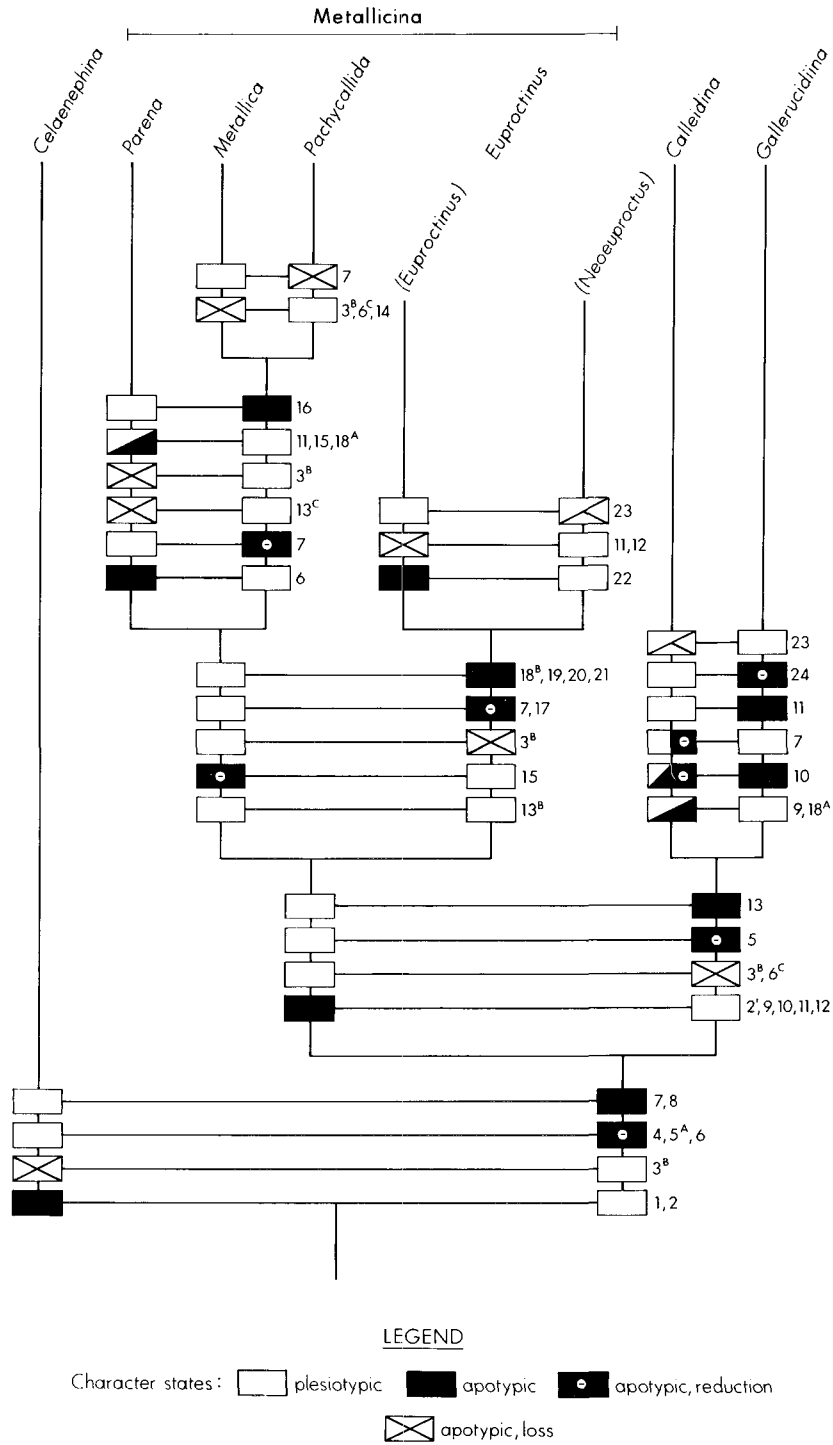


Fig. 76. Reconstructed phylogeny of Celaecephina, Metallicina, Calleidina, and Galleruciina.

Characters used (24, with 61 states) were those that experience has shown have diagnostic value in the Lebiini. We also included features of special importance in establishing the relationships of *Euproctinus*, because this genus is the central focus of this paper. Characters and their states are listed in Table 1. Distribution of states among the lebiine subtribes included is indicated in Fig. 75.

Taxa studied.— Representing the genera in Metallicina, other than *Euproctinus*, the following species were studied: *Parena n. nipponensis* Habu; *P. perforata* Bates; *P. tripunctata* Bates; *Metallica aeneipennis* Dejean; *M. capeneri* Basilwesky; *M. mashunensis* Peringuey; *M. viridipennis* Chaudoir; *Pachycallida a. amplicollis* Fairmaire; *P. a. diegana* Jeannel; and *P. rufoplagiatus* Jeannel.

Representing Calleidina, the following species were studied: *Calleida caerulea* Casey; *C. decora* Fabricius; *C. tropicalis* Bates; *Calleida* sp? (Ecuador); *Cylindronotum* sp? (Brazil); *Infernophilus castaneus* (Horn); *Onota angulicollis* Reiche; *Onota* sp? (Brazil); *Onota* sp? (Ecuador); *Otoglossa* sp? (Peru); *Plochionus formosus* Bates; *P. vittula* Csiki; *Plochionus* sp?-1 (Peru); *Plochionus* sp?-2 (Peru); and *Tecnophilus c. croceicollis* Ménétries.

Gallerucidia erotyloides Bates was the only species of Gallerucidiina studied.

Celaenephes parallelus Schmidt-Göbel and *C. linearis* (Walker) were studied as representatives of Celaenephina.

Notes about phylogenetic interpretation of characters.— Transformations of the following uni-directional characters are easily understood through out-group comparison: 01-05, 08, 09, 13, and 15-24. These are not discussed further, in the context of interpretation.

Character 06 (number of enciform setae on stylomere 2) exhibits a complex bi-directional transformation, involving an initial reduction (state A), then independent losses in two separate clades (state C; Calleidina + Gallerucidiina, and *Metallica*), and an increase in number from state A (state B; *Parena*). In spite of this inherent complexity, the general correlation of characters in the reconstructed phylogeny seems to adequately support our interpretation. In any event, a reversal from lower to higher numbers of setae does not seem to pose a difficult mechanical problem in developmental processes, for such changes have been inferred in numerous other groups.

Characters 07, 10-12, and 14 involve less complex transformations (*i.e.*, each a single loss). However, such transformations occur in features that are either more complex than stylomere setae or seem to be of greater taxonomic importance. Although suborbital setae (character 11) would not be expected to be developmentally more complex than setae of a stylomere, in fact their presence characterizes a major lebiine subtribe (the Pericalina; see Ball, 1975, and Ball and Shpeley, 1984), and might thus be expected to exhibit more stability. In fact, they are lost independently from members of two metallicine genera, *Parena* and *Euproctinus*.

Enlargement of tarsomere 4 (character 10) is an adaptation for arboreal life (Erwin, 1979: 552). The species of *Calleida* that have the simple tarsal form seem to be principally terrestrial rather than arboreal, and probably have reverted to a terrestrial existence. Thus the tarsal modification can be understood in a functional context, and as a result of a reversal.

Reversals in the other features (antennae, character 12 and 14; and male adhesive vestiture on the middle tarsi, character 07) are not so easily understood. Nonetheless, character correlation indicates that such reversals have occurred, rather than that these features are simply plesiotypic.

The reconstructed phylogeny.— This is indicated in Fig. 76. Most branching points seem well supported by characters states interpreted as synapotypic. The least well supported

TABLE 2
 NUMBER OF TIMES APOTYPIC CHARACTER STATES EVOLVED AMONG TAXA
 OF THE LEBIINE SUBTRIBES CELAENEPHINA, METALLICINA, CALLEIDINA,
 AND GALLERUCIDIINA

CHAR. STATE NO.	NUMBER OF TIMES CHARACTER STATES EVOLVED				
	1	2	3	5	
01	X				
02	X				
03A	X				
03B				X	
04	X				
05A	X				
05B	X				
06A	X				
06B	X				
06C		X			
07A	X				
07B			X		
07C	X				
08	X				
09		X			
10A			X		
10B		X			
11A		X			
11B		X			
12A	X				
12B	X				
13A	X				
13B	X				
13C	X				
14A	X				
14B		X			
15	X				
16	X				
17	X				
18A		X			
18B	X				
19	X				
20	X				
21	X				
22	X				
23		X			
24	X				
37	27	8	2	1	TOTALS

dichotomy is that for the basal split of the metallicines: there is only one synapotypy (character state 15- reduced retinacular ridge of the mandible) to hold together the Old World genera. Nonetheless, such a division (between Old World and New World tropical groups) fits in well with the geological event of the break-up of Gondwana in Cretaceous time. So, we feel reasonably confident that Old World and New World metallicines are sister groups.

Figure 76 also shows a sister group relationship between metallicines and Calleidina + Galleruciina. Relationships of these groups to one another had to be established because the metallicine and galleruciina genera were formerly a part of the Calleidina. The data seem to indicate that metallicines are related to the ancestry of the Calleidina (*sensu stricto*) and not directly to any of the genera presently included therein. The same is true of the Galleruciina.

Character evolution.— Of the 24 characters analyzed, reductions and losses are involved in the transformations of 13 (characters 03, 05-07, 10-15, 17, 23, and 24). Reduction in the ovipositor sclerites (characters 03, 06, and 13) is probably correlated with a change in the way that eggs are laid (see Ball and Hilchie, 1983, and Shpeley *et al.*, 1985 for a general discussion of evolution of the ovipositor in Lebiini).

Functional correlations of reduction in tarsomere 4 (character 10) were noted above. Reductions in mandibular features (characters 04, 15, and 17) possibly have functional correlations, though we cannot presently specify what they might be. Other reductions, such as setal loss (characters 11 and 24), spur loss (character 23), loss of more complex sense organs (character 14), reduction of adhesive vestiture on male mid-tarsi (character 07), reduction in extent of sclerotization of tergum VII (character 05), and modifications of form of the antennal pedicel (character 12) could have functional correlates as well, but we cannot suggest what they are.

Terminal states for the remaining 10 characters (01, 02, 08, 09, 16, and 18-22) represent increases or additions to the postulated plesiotypic conditions. Five characters (01, 08, 09, 16, and 19) involve mouthparts and have to do with food manipulation, or perhaps location (the setae on the glossal sclerite and on the palpi, characters 09 and 19). Four characters (18, and 20-22) are concerned with the reproductive organs, and probably represent important changes in sperm transfer and storage. Possibly, the correlation between increases in length of spermatheca (character 21) and length of the male flagellum (character 20) has a functional basis, such as Schincariol and Freitag (1986) reported for *Cicindela tranquebarica* Herbst.

One especially interesting feature for sensory physiologists is the sense organs on the ventral surfaces of antennomeres 5-11 (character 02) which apparently have evolved twice. Such organs have also appeared on the dorsal surfaces of these antennal articles (character 14), and as noted above, have been lost in the genus *Euproctinus*.

Table 2 summarizes data about homoplasy in the characters studied. Most apotypic states have evolved only once, but one seems to have made its appearance five times (state 03B). This is a reduction in the basal lobe of stylomere 2 of the ovipositor. Overall, less than a third of the apotypic states exhibit multiple origin, and most of these involve losses or reductions. These data illustrate the complexity of character evolution, and the need for caution in phylogenetically evaluating structural similarity.

Phylogenetic Analysis of Structural Features – Genus *Euproctinus*

Methods.— We used out-group comparison and correlation of characters. For characters 01-07 and 12, we used as out-group the Old World genera of Metallicina (see Fig. 75). These

TABLE 3
CHARACTERS AND PHYLOGENETIC DESIGNATION OF CHARACTER STATES FOR SPECIES OF THE GENUS *EUPROCTINUS*

NO.	CHARACTER	CHARACTER STATES AND DESIGNATIONS*	
		PLESIOTYPIC	APOTYPIC
01.	Suborbital setae	present	absent
02.	Antenna: pedicel, carina/depression	present	absent
03.	Pronotum: basal bead	present	absent
04.	Bursa copulatrix	unarmored	with spines
05.	Mid-leg: male tarsomeres, adhesive vestiture	on tarsomeres 1-4	1 ⁻ . on tarsomeres 2 and 3, only 2 ⁻ . on tarsomeres 1 and 2 only
06.	Mandibles: ventral groove	longer	shorter
07.	Male gen.: flagellum length	shorter (1.5X length of median lobe)	longer (more than 1.5X length of median lobe)
08.	Elytron: post. discal spot, form/size	very short, markedly transverse	A. longer, ca. .25 length of elytron B. ca. .5 length of elytron C. more than .5 length of elytron A ⁻ . less than .25 length of elytron B ⁻ . apical .5 elytron entirely dark

(continued on next page)

Table 3 (continued)

NO.	CHARACTER	CHARACTER STATES AND DESIGNATIONS*	
		PLESIOTYPIC	APOTYPIC
09.	Elytron: lateral groove, color	bicolored, dark & pale, with median fascia extended to margin of elytron	concolorous, pale, median fascia not extended to lateral margin
10.	Ab. Sternum VI: lateral setae	absent	1. several pairs, short 2. 1 pair, long 2 ⁻ . absent
11.	Ab. Sternum VII: lateral setae	absent	1. several pairs, short 2. 1 pair long
12.	Fore tibia: upper spur	present	absent
13.	Elytron: parahumeral dark spot	present, joined to humeral margin	A ⁻ . present, free of humeral margin B ⁻ . absent
14.	Elytron: median fascia	very broad toward suture, narrowed laterally, transverse	A. diagonal, continuous A ⁻ . diagonal, discontinuous
15.	Elytron: sutural vitta	absent	present

(continued on next page)

Table 3 (continued)

NO.	CHARACTER	CHARACTER STATES AND DESIGNATIONS*	
		PLESIOTYPIC	APOTYPIC
16.	Male anal setae: number	2	4
17.	Elytron: basal margin, color	dark	pale
18.	Pronotum: color	pale	1. uniformly infuscated 2. uniformly black 3. pale, w/ dark paralat. vittae 4. disc pale, margins dark
19.	Elytron: paralateral vitta	absent	present
20.	Elytron: anterior discal pale spot	moderately extensive, width & length subequal	1. markedly increased, med, fascia absent, or very narrow 2a. reduced, length more than width, fascia broad 2b. absent, surface compl. dark
21.	Elytron: apical margin, color	pale	a. dark a ⁻ . pale (loss)

(continued on next page)

Table 3 (continued)

NO.	CHARACTER	CHARACTER STATES AND DESIGNATIONS*	
		PLESIOTYPIC	APOTYPIC
22.	Elytron: median fascia, fork	not forked (<i>cf.</i> Fig. 40)	A. forked laterally (<i>cf.</i> Figs. 36 & 38) A ⁻ . post. branch of fork absent (<i>cf.</i> Fig. 37)
23.	Elytron: anterior paralateral pale mark	absent	present
24.	Elytron: anterior fork of vittae	absent	present (<i>cf.</i> Figs. 37 & 38)
25.	Tibia: color	pale	dark

* Symbols in table, for apotypic character states are as follows:

capital letters represent sequential change – A, B, C, enhancement of the original apotypic state; A⁻, B⁻, C⁻, progressive loss from the original apotypic state;

numbers (1, 2) represent different apotypic states, derived from the plesiotypic state; accompanying lower case letters (2a, 2b, *etc.*) represent transformation series for the character in question.

TABLE 4
CHARACTERS AND DISTRIBUTION OF PHYLOGENETICALLY DESIGNATED CHARACTER STATES AMONG THE SPECIES
OF *EUPROCTINUS*

CHAR. NO.	SPECIES AND CHARACTER STATES*															
	<i>fasc.</i>	<i>balli</i>	<i>sig.</i>	<i>abj.</i>	<i>subdel.</i>	<i>pallidus</i>	<i>trivitt.</i>	<i>columb.</i>	<i>howd.</i>	<i>putz.</i>	<i>quadri-vitt.</i>	<i>orn.</i>	<i>quadri-plag.</i>	<i>nigro.</i>	<i>del.</i>	<i>pan.</i>
01	a ⁻	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
02	a ⁻	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
03	a ⁻	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
04	a	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
05	1 ⁻	2 ⁻	2 ⁻	2 ⁻	2 ⁻	2 ⁻	2 ⁻	2 ⁻	?	2 ⁻	2 ⁻	2 ⁻	2 ⁻	?	?	2
06	-	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻
07	-	a	a	a	a	a	a	?	?	a	?	a	a	?	?	a
08	-	A	A	A ⁻ B ⁻	A	A	C	A	A	A	A ⁻	A ⁻	A	B	C	C
09	-	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻
10	-	1	1	1	1	1	2	2	2	1	2	2 ⁻	2	2	?	2
11	-	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2
12	-	-	-	-	-	-	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻	a ⁻
13	-	A ⁻	B ⁻	B ⁻	B ⁻	B ⁻	B ⁻	B ⁻	B ⁻	B ⁻	B ⁻	B ⁻	B ⁻	B ⁻	B ⁻	B ⁻
14	-	-	A	A	A	A ⁻	NA	A	A	A	A	A	A	A	NA	NA
15	-	a	a	a	a	-	a	a	a	a	a	a	a	a	a	-
16	-	a	-	-	-	-	-	-	?	-	-	-	-	?	?	-
17	-	a ⁻	-	-	(a ⁻)	a ⁻	a ⁻	-	a ⁻	-	-	-	-	-	-	a ⁻
18	-	2	-	1	-	-	-	-	3	-	-	4	4	4	4	-

(continued on next page)

Table 4 (continued)

CHAR. NO.	SPECIES AND CHARACTER STATES*															
	<i>fasc.</i>	<i>balli</i>	<i>sig.</i>	<i>abj.</i>	<i>subdel.</i>	<i>pallidus</i>	<i>trivitt.</i>	<i>columb.</i>	<i>howd.</i>	<i>putz.</i>	<i>quadri-vitt.</i>	<i>orn.</i>	<i>quadri-plag.</i>	<i>nigro.</i>	<i>del.</i>	<i>pan.</i>
19	-	-	a	a	a	-	a	a	a	a	a	a	a	a	a	-
20	-	-	2a ⁻	2a ⁻ b ⁻	1	1	1	-	-	-	2a ⁻	-	-	-	2b ⁻	1
21	-	-	-	a	a	-	a	a	a	a ⁻	a	a	a	a	a ⁻	a ⁻
22	-	-	-	-	-	-	-	a	a ⁻	a	-	-	-	-	NA	NA
23	-	-	-	-	-	-	-	a	a	a	-	-	-	-	-	-
24	NA	-	-	-	-	NA	-	-	a	a	-	-	-	-	NA	NA
25	-	(a)	-	-	-	-	-	-	-	-	-	-	-	a	-	-

*Symbols for character states are as follows:

a hyphen (-) represents a plesiotypic state;

for apotypic state, a minus sign indicates a loss, or reduction, from the apotypic state;

the lower case letter 'a', unaccompanied by a number, indicates the apotypic state for a two-state transformation series;

capital letters indicate states in a multi-state transformation series, with letters arranged sequentially to parallel the postulated steps in the series, *i.e.*, A, B, C; A⁻, B⁻, C⁻;

arabic numbers indicate independent transformations from the plesiotypic state (*i.e.*, 1, 2);

arabic numbers with lower case letters indicate sequential stages in a multi-state series, as indicated above;

parentheses around a letter or number, *i.e.*, (a⁻) indicate that the taxon exhibits both the plesiotypic and apotypic condition;

letters and numbers are used in accompanying Table 5 and in Fig. 77, as superscripts with their character numbers.

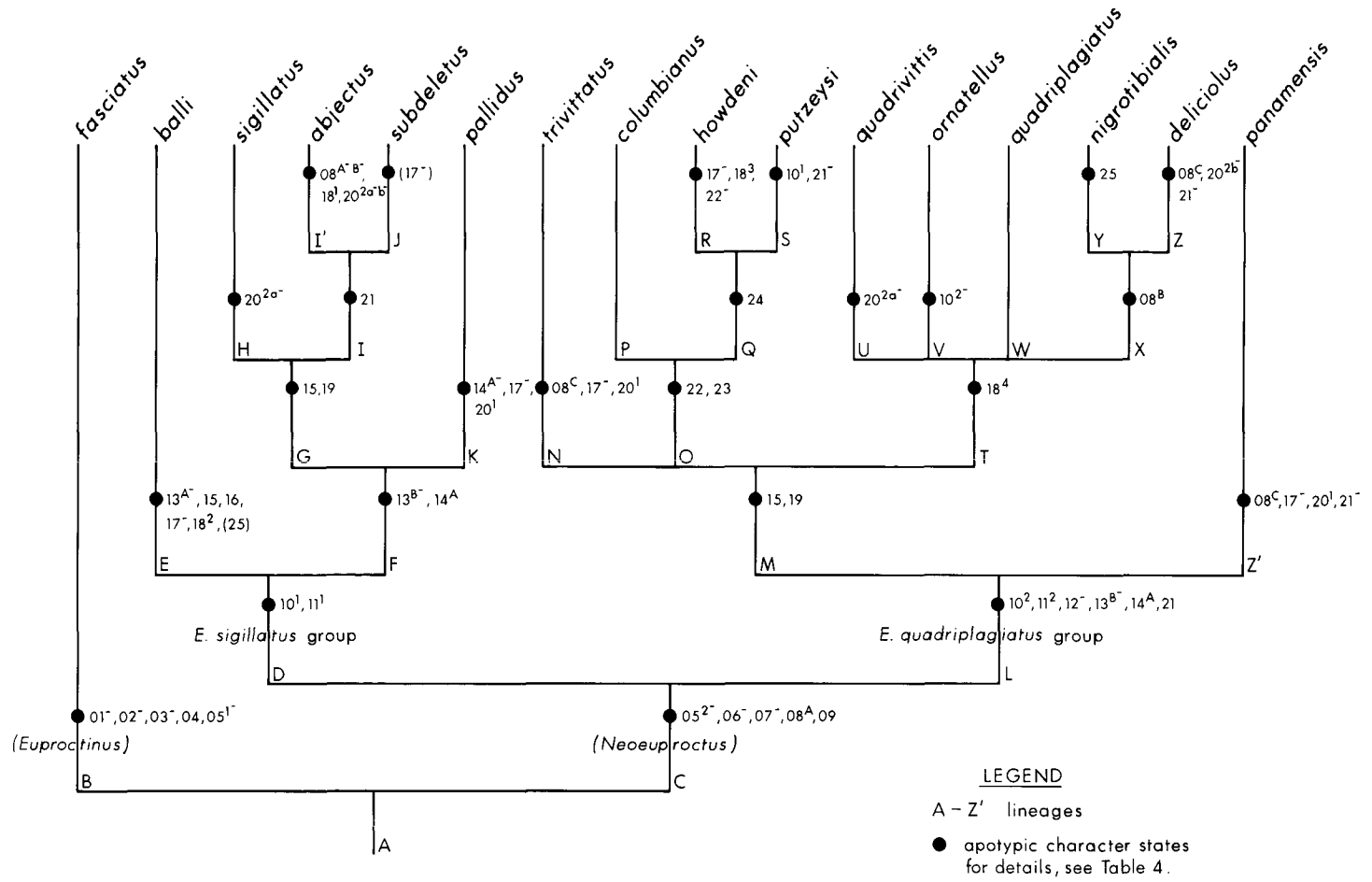


Fig. 77. Reconstructed phylogeny of the species of *Euproctinus* Leng & Mutchler.

characters were used in establishing the subgenera of *Euproctinus* as monophyletic sister groups. For the remaining characters, we used the subgenus *Euproctinus* as out-group for *Neoeuproctus*, accepting as the ancestral state of each character that which was shared by the two groups. Thus, the monobasic subgenus *Euproctinus* served as the “functional out-group” (Watrous and Wheeler, 1981) for evaluating character states of the polybasic subgenus *Neoeuproctus*.

Characters used are indicated in Tables 3 and 4. Each character is named and numbered in the sequence in which it appears in the phylogenetic diagram (Fig. 77), and where the numbers are used to indicate the position of each character transformation. Table 3 provides a phylogenetic designation for each character state, as plesiotypic or apotypic. Letters and numbers denote apotypies which appear as superscripts associated with their respective character numbers in Fig. 77. See the notes on Table 3 for details.

Of the characters used, color and color pattern, especially of the elytra, are prominent, not because we view such features as especially valuable, but rather because we have little else for analysis.

Notes about phylogenetic interpretation of character states.— Transformations of the following characters are easily understood through out-group comparison, and these are not discussed further in the context of designation: 01-05, 08-14, 16, 18-20, and 23-25.

Character 06 (mandibles, ventral grooves) concerns length of grooves. These are relatively short in members of both subgenera, relative to those of other metallicines. However, the grooves of *Neoeuproctus* mandibles are shorter than those of *Euproctinus*.

Character 07 (male genitalia, length of flagellum) has not been seen for all species, and hence in Table 4 the question marks in the row for this character. It is assumed that males not seen have long flagella, based on other features indicating membership in subgenus *Neoeuproctus*. We also note that one male of *E. quadriplagiatus* has a short flagellum (only 1.4 X length of median lobe). Since other males of this species have relatively long flagella, we assume that this short example represents an anomalous condition within the species.

For character 15 (elytron, sutural vitta), the basal part of the vitta cannot be seen in species characterized by a totally dark base of the elytron, nor can the vittae or median fascia be seen in taxa characterized by totally dark elytra. Presumably, however, parts of the darkening represent these marks that we hypothesize were identifiable in the ancestral stocks of such species.

For character 17 (elytron: basal margin, color), both plesiotypic and apotypic conditions are represented in *E. subdeletus*. We interpret this to mean that the apotypic condition was derived in this species independently of its derivation in other species. Of course, the opposite interpretation is also possible.

For character 21 (elytron: apical margin, color), adults of *E. putzeysi* and *E. deliciolus* are believed to have lost the dark color of the apical margin, and thus reverted to the ancestral condition. This is based on character correlation, leading us to believe that the ancestral stock of lineage M (Fig. 77) was characterized by a dark elytral apex.

For character 22 (elytron: median fascia, fork), character correlation was used to infer that *E. howdeni* adults had lost the posterior branch of the lateral fork, thus reverting to a more plesiotypic condition than that displayed by its close relatives, *E. columbianus* and *E. putzeysi*.

The reconstructed phylogeny (Fig. 77).— Monophyly of the subgenera (lineages B, *Euproctinus*, and C, *Neoeuproctus*) and species groups of *Neoeuproctus* (lineages D, *E. sigillatus* group; and L, *E. quadriplagiatus* group) is supported by two or more synapotypic

TABLE 5
 NUMBER OF TIMES APOTYPIC CHARACTER STATES EVOLVED AMONG
 SPECIES OF THE GENUS *EUPROCTINUS*

CHAR. STATE NO.	NUMBER OF TIMES CHARACTER STATES EVOLVED			
	1	2	3	6
01 ⁻	X			
02 ⁻	X			
03 ⁻	X			
04	X			
05 ¹⁻	X			
05 ²⁻	X			
06 ⁻	X			
07 ⁻	X			
08 ^A		X		
08 ^B	X			
08 ^C			X	
08 ^{A-}			X	
08 ^{B-}	X			
09 ⁻	X			
10 ¹		X		
10 ²	X			
10 ²⁻	X			
11 ¹	X			
11 ²	X			
12 ⁻	X			
13 ^{A-}	X			
13 ^{B-}		X		
14 ^A		X		
14 ^{A-}	X			
15		X		
16	X			
17 ⁻				X
18 ¹	X			
18 ²	X			
18 ³	X			
18 ⁴	X			
19		X		
20 ¹		X		
20 ^{2a-}			X	
20 ^{2b-}		X		
21		X		
21 ⁻			X	

(continued on next page)

Table 5 (continued)

CHAR. STATE NO.	NUMBER OF TIMES CHARACTER STATES EVOLVED				
	1	2	3	6	
22		X			
22 ⁻	X				
23	X				
24	X				
25		X			
42	27	11	4	1	TOTALS

character states. The *E. quadriplagiatus* group is not well resolved, including one trichotomy (lineage M) and one quadrichotomy (lineage T). Also, we are inclined to doubt that *E. panamensis* is phylogenetically as isolated as it seems to be, since it is characterized principally by lack of elytral color pattern. Similarly for the *E. sigillatus* group, *E. pallidus* is characterized principally by lack of color pattern. Thus, its seemingly isolated position might not reflect the reality of its relationships. To achieve a better resolution of relationships, additional characters are required, and particularly features more stable than color pattern.

Character evolution.— Table 5 shows the number of times each character state used in Fig. 77 is postulated to have evolved. Of 42 character states, two thirds have evolved only once. All but one of those postulated to have evolved more than once involve elytral color, and five of them (08^{A-}, 20^{A-}, 20^{2a-}, 20^{2b-}, and 21⁻) involve reduction of dark pigment.

Four character transformations involve reversals (08, 10, 21, and 22). Characters 08, 21, and 22 are parts of the elytral color pattern. The posterior discal spot (08) has been reduced three times, though not to the size as small as that of *E. fasciatus*. The apical margin (21) has reverted from dark to pale twice, and the posterior branch of the fork of the median fascia (22) has been lost once. Similarly, the lateral setae of sternum VI (character 10) have been lost once.

To obtain a better perspective about evolution of elytral color pattern, we provide a more generalized classification of color characters than used in the phylogenetic analysis. Table 6 lists eight color classes, arranged sequentially from darker to paler. The subgenus *Euproctinus* exhibits the putative ancestral pattern, with the species groups of *Neoeuproctus* exhibiting the derived pattern.

Although there is broad overlap in ranges of color classes by these two groups, the *E. sigillatus* group tends toward the darker end of the gradient, with the *E. quadriplagiatus* group tending toward the paler end. Both groups exhibit the bicolored condition, with vittae, fascia, and basal and apical margins dark, and the disc with two pale spots. Evidently, these combinations of similarities were evolved independently in each species group.

This same range of variation is seen (and exceeded!) in the genus *Lebia*, members of which have been taken at the same time and from the same place where specimens of *Euproctinus*

TABLE 6
GENERALIZED PATTERN OF TRANSFORMATION OF COLOR OF ELYTRA IN
EUPROCTINUS

SCORE	COLOR	TAXA		
		<i>Euproctinus</i>	<i>Neoeuproctus</i> <i>sigillatus</i> group	<i>quadriplagiatus</i> group
3+	concolorous, dark, no fascia; no vittae		X	
2+	bicolored; fascia & vittae thick & forked			X
1+	bicolored; fascia & vittae thick, not forked		X	X
0	bicolored; fascia, not vittae	X		
1-	bicolored; fascia & vittae thin		X	X
2-	bicolored; no fascia, vittae thin			X
3-	bicolored; fascia discontinuous, no vittae		X	
4-	concolorous, pale, no fascia; no vittae			X

have been collected. Perhaps these genera are parts of a complex based on mimicry, either Batesian or Müllerian.

GEOGRAPHICAL HISTORY

This section provides, in the form of hypotheses, a falsifiable explanation of the geographical distribution of the extant taxa of Metallicina, taking into account general theories about geological events that ought to have influenced the ranges of the biota through time. This presentation has two subsections, the first dealing with the geographical history of the genera, and the second dealing with the geographical history of the species of *Euproctinus*.

Chorological Aspects of Evolution—Genera of the Metallicina

Distribution pattern.— Of the four extant genera, one, *Euproctinus*, is confined to the New World, ranging from temperate South America northward through the tropics to subtropical

and warm temperate United States. The other three genera are in the Old World: *Pachycallida* occurs on the island of Madagascar; *Metallica* ranges widely in tropical Africa; and *Parena* ranges throughout the Old World Tropics, eastward to northern Australia, and northward in the tropical parts of the eastern Palaearctic Region to the Japanese Archipelago.

Geographical history.— The distribution pattern of these genera is essentially Gondwanian, and the history of the metallicines could be correlated with the geological history of that super-continent. The reconstructed phylogeny (Fig. 76) indicates that the ancestral stock of the Metallicina diverged first into the ancestor of the New World *Euproctinus* and of the Old World *Parena* + *Metallica* + *Pachycallida*. The second divergence removed the mainly Oriental *Parena* from the ancestor of the African *Metallica* + the Madagascan *Pachycallida*. The third divergence separated the ancestor of *Metallica* from that of *Pachycallida*.

This sequence of divergence might imply a similar sequence of the the break-up of Gondwanaland, with South America separating first, and Madagascar last. In fact, several sequences have been proposed, based on geological data (Wheeler, 1986: 197-199), none quite coinciding with the sequence required to explain divergence of the metallicine genera as the result of a series of vicariance events. As Wheeler points out, such lack of congruence of geological and distributional data requires hypothesizing dispersal to explain the observed distribution patterns, or a combination of dispersal and vicariance.

If the first divergence in the metallicine lineage was the result of separation of South America from Africa, some 90 million years before present (mybp) (Howarth (1981), then the second event (divergence of *Parena* from *Metallica* + *Pachycallida*) must have been due to dispersal, because the most likely way for the ancestor of *Parena* to have reached the Oriental Region would have been by way of the Indian sub-continent, which in the Cretaceous was an island, closer to the east African coast than it is presently. The divergence of the African *Metallica* from the Madagascan *Pachycallida* could have been the result of either vicariance or dispersal, with Madagascar separating from Africa about 75 mybp (Rabinowitz *et al.*, 1983). Following isolation on Madagascar, the ancestral stock of *Pachycallida* differentiated, and at the same time, the African metallicine stock evolved into the species of *Metallica*.

When India contacted the East Asian mainland, *Parena* became widespread, differentiating, with some lineages eventually reaching Africa in Tertiary time, probably when tropical forest was continuous between the Asian and African rain forests. Stocks of *Parena* also spread eastward into the Indo-Australian Archipelago, eventually reaching Australia.

More details of the evolution of this type of pattern are provided by Ball (1985: 310-315) in a reconstruction of the history of the galeritine genera, and by Noonan (1985: 11-16) in a reconstruction of the history of the selenophorine genera.

The hypothesis presented above, involving dispersal and vicariance, could be falsified by: 1. a reconstructed phylogeny of *Parena* that shows a different history from that suggested above; 2. discovery that the geographical ranges of the metallicine genera are substantially different from present understanding of what they are (*i.e.*, *Euproctinus* in the Old World, or Old World metallicines in the New World, or old endemic species of *Pachycallida* in Africa, or such of *Metallica* in Madagascar).

Chorological Aspects of Evolution— Genus *Euproctinus*

Reconstruction of the history of a primarily tropical taxon whose total range encompasses portions of both New World continents must take into account the extensive literature that treats the history of Middle America and its biota. This is summarized by Rosen (1975),

Whitehead (1976), Erwin (1979), Noonan (1979), and Savage (1982).

In this treatment, we summarize data about habitat and geographical distributions of the species of *Euproctinus*, offer an hypothesis to explain the patterns identified, and compare the patterns with those of other taxa. Major falsifiers of the hypothesis are also indicated, and predictions regarding future potential discoveries are made.

Areas.— The following discussion is based on 10 geographical areas, some of which are distinct zoogeographic sub-regions, others being distinguished as a convenience for this study. Each area contains a more or less distinctive assemblage of species of *Euproctinus*. They are listed in Table 7, and are delineated below, from south to north.

1. Southern trans-Andean South America: this area is co-extensive with most of the range of *E. fasciatus*, principally in temperate Chile, south of the Atacama desert, which developed in the Pleistocene (Duellman, 1979: 417). The range of this species extends into western Argentina, but we interpret this as the result of a recent range extension, eastward.

2. Southern cis-Andean South America: this area is east of the Andes and south of the Amazon Basin. Its southern limit is about 30° S. Lat.

3. Amazonian South America: the Amazon Basin.

4. Northern cis-Andean South America: this area is north of the Amazon Basin and east of the Andes. It includes the Guianas, and Venezuela.

5. Northern trans-Andean South America: an area north of the Amazon Basin in or west of the Andes, in Colombia, including the biotically rich Chocó region (Gentry, 1982).

6. Lower Central America: Costa Rica and Panamá, the area that, until the end of the Pleistocene, comprised a series of volcanic islands between the South American and North American continents. Whitehead (1976: 194) uses the term "southern Middle America" for this area. Howden and Young (1981) interpret a high degree of endemism in Scarabaeinae of Lower Central America as consistent with the geological evidence for emergent land here, since at least Miocene time.

7. Nuclear Central America: the area between the Isthmus of Tehuantepec and southern Nicaragua that has been dry land for the whole of the Tertiary (see Ball, 1975; Rosen, 1978; and Savage, 1982; and the geological references that they cite). Whitehead (*l.c.*) refers to this area as "Nuclear Middle America".

8. México north of the Isthmus of Tehuantepec: although this area and Nuclear Middle America have been connected by dry land throughout the Tertiary, it seems likely that, in the past, the connection has been markedly reduced by higher sea levels and with the shores supporting vegetation and habitats not suitable for terrestrial or fresh water organisms (see Ball, 1975).

9. Southwestern United States: included here are two disjunct locations: southern Gulf Coastal Texas, and southeastern Arizona.

10. Southeastern United States and the West Indies: included are peninsular Florida (and possibly adjacent mainland areas), and Cuba (possibly also other islands of the Greater Antilles).

The chorological pattern.— Of 16 species, five are known from South America; one is in both South and Middle America; and 10 are known from Middle America (México plus Central America). Of the last-named geographical assemblage, the ranges of two species extend into southwestern United States (Area 9). One species, *E. trivittatus*, occurs in the West Indies (Cuba) and in peninsular Florida (Area 10).

TABLE 7
GEOGRAPHICAL DISTRIBUTION OF THE SPECIES OF *EUPROCTINUS* IN TERMS OF SPECIFIED AREAS

AREA NO. NAME	SPECIES OF <i>EUPROCTINUS</i>															TOTAL SPECIES	
	<i>Euproc.</i>		<i>E. sigillatus</i> Group					<i>Neoeuproctus</i>					<i>E. quadriplagiatus</i> Group				
	<i>fasc.</i>	<i>balli</i>	<i>sig.</i>	<i>abj.</i>	<i>subdel.</i>	<i>pall.</i>	<i>triv.</i>	<i>columb.</i>	<i>howd.</i>	<i>putz.</i>	<i>quadri- vitt.</i>	<i>orn.</i>	<i>quadri- plag.</i>	<i>nigro.</i>	<i>delic.</i>	<i>pan.</i>	
10. Fla. + Cuba							X										1
9. S. W. U. S. A.		X		X													2
8. Mex. N. Tehuantepec		X	X	X	X	X						X	X				7
7. Nuclear Central America				X	X							X	X				4
6. Lower Central America						X						X	X	X	X	X	6
5. N. trans-Andean S. America								X	X	X			X				4
4. N. cis-Andean S. America													X				1
3. Amazonian S. America													X				1
2. S. cis-Andean S. America											X		X				2
1. S. trans-Andean S. America	X																1
Total No. Areas/Species	1	2	1	3	3	1	1	1	1	1	1	3	7	1	1	1	

In terms of species diversity, the overall pattern is one of subtraction from Middle America (Areas 6, 7, and 8) southward, northward, and eastward in the West Indies. In South America, the Amazon Basin (Area 3) is occupied by a single wide-ranging species of *Euproctinus*.

At a finer level of analysis, of the three South American species that occur south of the Amazon Basin, the range of one (*E. fasciatus*) is principally trans-Andean (Area 1), while the other two (*E. quadrivittis* and *E. quadriplagiatus*) are in the eastern part of the continent (Area 2). Of the four species in northern South America, three (*E. columbianus*, *E. howdeni*, and *E. putzeysi*) are known only from trans-Andean Colombia (Area 5), and one (*E. quadriplagiatus*) is known from the latter area and from farther east (Area 4).

At the northern end of the range, there are no species restricted to United States. At the southern end of the range, two species (*E. fasciatus* and *E. quadrivittis*) are endemic and possibly autochthonous in their respective areas.

The *Euproctinus* fauna of northern South America includes three endemics in Area 5 (*E. columbianus*, *E. howdeni*, and *E. putzeysi*) that are probably autochthonous there. In Middle America, there are seven apparently endemic species. These data, accepted at face value, indicate that Middle America has been a major center of diversification for *Euproctinus*, compared to South America. We believe, however, that the South American records are inadequate to provide an accurate impression of the diversity of its cis-Andean *Euproctinus* fauna. This belief affects our reconstruction of the geographical history of the genus (see below).

We regard *E. fasciatus* and *E. trivittatus* as relicts, *i.e.*, without living relatives that are close either geographically or phylogenetically. These two species are, respectively, at the known southwestern and northeastern geographical limits of *Euproctinus*.

Ecological aspects.— Locality data indicate that the species of *Euproctinus* inhabit collectively a wide range of forest types, from temperate Southern Hemisphere forest to tropical habitats such as palm savanna, deciduous forest and rain forest at low altitude, and to mesophytic temperate forest at higher altitudes in northern México. In altitude, the range of *Euproctinus* extends from sea level to 2600 m, with most species represented at elevations between 200 and 1500 m. The data, however, are too few to be interpreted in detail, for they do not show any simple, easily ordered pattern. The data are consistent, however, with the generally continental distribution pattern of the lowland species in Middle America. The ancestral habitat was probably lowland tropical forest, based on the fact that the Old World sister group of *Euproctinus* occurs in tropical arboreal habitats.

Speciation pattern.— Whitehead (1976: 191) distinguishes and characterizes continental as opposed to islandic patterns of speciation (see also Wheeler, 1979: 473). Characteristics of the continental pattern are (1), low altitude distributions, generally; (2), continuous (undifferentiated) populations in lowland forest, with wide geographic ranges; (3), not habitat restricted, thus ecological generalists. The species of *Euproctinus* meet criteria 1 and 2, and it seems likely that they meet criterion 3 as well, even though they are ecological specialists to the extent that adults are arboreal (Erwin, 1979 and 1985). Fully winged adults are probably quite vagile, at least over land, moving at night through the forests that they inhabit, an inference based on frequent occurrence of specimens at light. As Whitehead (1976: 192) explained, it seems likely that such species have escaped major pressures from Pleistocene climatic changes through avoiding restriction and thus isolation of populations, and they should be classified as demonstrating the continental speciation pattern. Certainly, sister species do not exhibit the clear-cut vicariance patterns that Savage (1982: Figs. 19-22) illustrates for various groups of

ectothermal vertebrates.

Phylogenetic and zoogeographic correlation.— The subgenera *Euproctinus* (*sensu stricto*) and *Neoeuproctus* are vicariant, with *Euproctinus* occupying southern trans-Andean South America, and *Neoeuproctus* occupying the rest of the range of the genus. The *E. (N.) sigillatus* group is known only from Middle America and southern United States. Within this group, ranges of most of the included species overlap broadly.

Of the four lineages in the *E. (N.) quadriplagiatus* group (N, O, T, and Z', Fig. 77), *E. panamensis* is known only from Lower Central America; *E. trivittatus*, a relict species, is known from the northeastern margin of the range of *Neoeuproctus*; the three species of the *E. putzeysi* lineage are confined to a restricted area in northern South America; and the species of lineage T range collectively from southern South America to northern Middle America, with one species (*E. quadriplagiatus*) covering the entire range of the lineage, one species (*E. quadrivittis*) confined to southern South America, and three species (*E. ornatellus*, *E. nigrotibialis*, and *E. deliciolus*) known only from Middle America, but probably not confined there.

In summary, only a general correlation has been identified between phylogenetic and zoogeographic patterns for the taxa of *Euproctinus*. However, the general correlation is sufficient to suggest that geographical factors have been important in differentiation of the extant taxa. More detailed correlations will have to await resolution of the quadrichotomy in the *E. quadriplagiatus* group, and discovery of the ecological information required to hypothesize the barriers and their locations that led to differentiation of the presently sympatric species and their immediate ancestors. For the present, it seems acceptable to assume that differentiation has been the result of geographic isolation of ancestral stocks, followed by dispersal of the vicars which resulted in the sympatric ranges of close relatives. The potential for dispersal in *Euproctinus* is indicated by the more widely ranging species, such as *E. abjectus* and especially *E. quadriplagiatus*.

History of differentiation of Euproctinus and its species.— In this section, we consider the processes that might have been involved in development of the distribution pattern described above. Savage (1982: 487-496) deals effectively with what he describes as “the central theoretical problem [of historical zoogeography]: dispersal versus vicariance”, showing that these terms represent alternating stages in development of biogeographic patterns.

Euproctinus is the New World counterpart of the pantropical subtribe *Metallicina*, and its ancestral stock is hypothesized to have been part of the Cretaceous age autochthonous Gondwanian fauna of South America. The ancestral habitat (*i.e.*, forest type) of the *Metallicina* cannot be specified in detail, but it was probably lowland tropical.

The ancestral stock of *Euproctinus* (*sensu lato*) probably became widespread, initially dispersing through the tropical part of the then-island continent, and later reaching the southern temperate areas. When the Andes developed, the ancestral range of the genus was probably interrupted, resulting in differentiation of the structurally less progressive subgenus *Euproctinus* and the more progressive *Neoeuproctus*, in trans-Andean and cis-Andean South America respectively. (Brooks *et al.*, 1981, propose a similar scenario for isolation in cis-Andean South America, of the freshwater sting-rays.) The *Euproctinus* stock eventually gave rise to *E. fasciatus*, which may be the only surviving representative of a species-level radiation in trans-Andean South America, or perhaps the only species of its subgenus to have evolved.

Central to our hypothesis for the geographical history of the subgenus *Neoeuproctus* is the more general hypotheses of the biotic and geological history of Middle America, as discussed by Savage (*l. c.*), and previously by Darlington (1957: 456-462) and Ross (1967). Briefly, Savage's account is as follows: First, prior to mid-Cretaceous, South America was isolated from the northern continents by a sea barrier. Second, during mid-Cretaceous-Palaeocene time, a more or less extensive connection joined northern South America and Nuclear Middle America, or at least partially bridged the gap that separated these areas. During this time, many stocks of the South American biota entered Middle America, forming the Generalized North American-Central American Track. Third, from the end of the Palaeocene to the end of the Miocene (or into the Pliocene), South America and Nuclear Central America were widely separated from one another. This separation provided the isolation required for differentiation of the highly distinctive Middle American biota. Fourth, in Pliocene time, an intercontinental connection (the Isthmus of Panamá) was reestablished, and this permitted as extensive biotic exchange, but principally there was movement from south to north.

While we agree with this sequence of events, we also agree with Hershkovitz (1966: 745) that there was as intermittent biotic exchange between South and Middle America throughout the Tertiary by stocks crossing the sea barriers that extended between the line of islands that constituted Lower Central America. (See also the following references as background for understanding current notions about history of some Middle American insect groups: Allen and Ball, 1980; Ball, 1975; 1978; and 1985; Clark, 1978; Erwin, 1979; and 1985; Goulet, 1974; Halffter, 1974; Howden and Young, 1981; Noonan, 1985; Wheeler, 1979; and Whitehead, 1976).

The question of the relationships of the West Indies to Middle America remains unresolved (Savage, *l. c.*), though we are not inclined to accept Rosen's (1975) hypothesis that the present Greater Antilles were once islands that bridged the Bolivar geosyncline between South and Middle America, acquiring then the older elements of the West Indian fauna that survived *in situ*. Rather, we believe that the Greater Antilles have been in their present positions since they were formed. Nonetheless, it was easier at some times in the past to reach the islands from the mainland than it is now. Lower sea levels would have reduced the size of the water gaps to be crossed, and volant animals, such as insects, would have found dispersal at such times relatively easy.

For the South American components of *Neoeuproctus*, both known and hypothesized, the sequence of antecedent events are less clear than for the Middle American components. We hypothesize three centers of differentiation: one, trans-Andean, Area 5 (above); a second, cis-Andean, south of the Amazon Basin, Area 2; and a third, cis-Andean, north of the Amazon Basin, probably including the Guianas and Venezuela, Area 4. We assume that in these areas, various stocks of *Neoeuproctus* were isolated from their adjacent vicars for more or less extended periods, though we are not in position to specify probable times or circumstances of isolation.

For the subgenus *Neoeuproctus*, then, we hypothesize the following sequence of events:

1. Vicariance of the ancestral stock of *Neoeuproctus*, as a result of over-water dispersal, probably in the Early Tertiary, resulting in differentiation of the South American stock into the *E. quadriplagiatus* group, and the Central American stock into the *E. sigillatus* group.

2. Differentiation of the *E. sigillatus* group in Central America and México, and eventual replacement of most of the representatives of this group from Lower Central America by later-arriving species of the *E. quadriplagiatus* group.

3. Differentiation of the *E. quadriplagiatus* group in South America, in the three centers noted above.

4. Spread into Central America, at various times, of stocks of the *E. quadriplagiatus* group represented by lineages N and T-Z'. The first to arrive was probably the ancestor of *E. trivittatus*, probably in pre-Pliocene time. Dispersing northward, it eventually reached Cuba, possibly at a time when water gaps between Middle America and the West Indies were narrower than now. From Cuba, adults of *E. trivittatus* dispersed to Florida, possibly during a Late Pleistocene glacial period, when, again, sea levels were depressed, and thus water gaps narrowed. This stock probably became extinct in mainland Middle America.

5. The other lineages of the *E. quadriplagiatus* group may have arrived sufficiently recently to have made the crossing on land, following the closure of the Bolivar geosyncline in late Pliocene time. Their South American populations ought to be sought in the refugia indicated by, for example, Prance (1982: 152, Fig. 11.9), in northeastern South America.

Potential falsifiers.— This zoogeographic hypothesis can be tested through discoveries in the future of additional character systems, new taxa, and range extensions of presently known species. Any character systems that indicate that groups hypothesized as monophyletic are in fact polyphyletic, would falsify portions of the zoogeographic hypothesis. Discoveries of new taxa that modify the ranges of the known species groups, or discoveries of populations of described species indicating ranges substantially different from those postulated could falsify portions of the zoogeographic hypothesis.

Predictions.— Based on the hypothesis presented here, we predict the following:

1. Additional species of *Euproctinus* that may be discovered will be in the New World (or in Australia), but not on other continents. (Discovery of Australian species of *Euproctinus* would show that the genus had extended its range rather more rapidly than we believe prior to Gondwanian breakup.)

2. Additional species of subgenus *Euproctinus* will be South American and trans-Andean in distribution.

3. Additional species of subgenus *Neoeuproctus* will be Middle American or from cis-Andean South America; or, if trans-Andean, they will be in the northern (*i.e.*, tropical) part of the continent. They will be members of the *E. quadriplagiatus* group, or of groups not yet discovered.

4. Species of the *E. quadriplagiatus* group presently known only from Lower Central America will be represented in northeastern South America by conspecific populations, or by specifically distinct vicars.

5. The range of *E. trivittatus*, if more extensive than present records indicate, will extend no further than the eastern shore of the Mississippi River, and will be close to the Gulf Coast; in México, only on the outer portion of the Yucatan Peninsula; and in the West Indies, only on islands of the Greater Antilles, additional to Cuba.

7. Southern South America and America north of México will continue to appear as marginal areas for this genus.

8. The trichotomy and quadrichotomy of the present reconstructed phylogeny will be resolved as dichotomies.

9. The relatively low diversity in Nuclear Central America exhibited by the species of *Neoeuproctus* will be shown to be an artifact of inadequate collecting in the area. Species endemic to the area will be found, and most will be members of the *E. sigillatus* group.

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